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Thermal Control of Aggregation Behavior in Tadpoles

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Allee (1931), Bragg (1946, 1948, 1954, 1961), Richmond (1947), Carpenter (1953), Brattstrom and Warren (1955), and Stuart (1961) have discussed aggregation behavior in tadpoles. Bragg (1954) recognized feeding and metamorphic aggregations, the data for which are extensive. Others (*supra cit.*) have noted that cannibalism and protection against leeches are also stimuli for aggregation behavior. Aggregation behavior in tadpoles where no demonstratble external stimuli are apparent has been termed "social aggregation" by Bragg. Neither extensive nor microclimatic water temperatures were recorded by Bragg.

The purpose of this paper is to document several cases of tadpole aggregations that are related to temperature and to discuss the advantages of such aggregations.

THERMAL CONTROL OF AGGREGATIONS

Hyla regilla.—A description of a "social aggregation" of tadpoles of the Pacific Treefrog, Hyla regilla, given by Brattstrom and Warren (1955) showed that: 1. The stimuli mentioned in the literature (food, cannibalism, etc.) for aggregations were not present. 2. The tadpoles were in the warmest part of a shallow pool. 3. Orientation of the tadpoles was such that the tails of about three-fourths of them pointed to the position of the sun, thus presumedly exposing the maximum amount of dorsal surface area of the tadpole to the sun's rays, providing for the greatest amount of heat absorption from the sun. 4. By absorbing radiant energy, the large mass of black bodies would be expected to warm their immediate environment more effectively than would many isolated bodies.

Hyla crucifer.—On May 4, 1957, at Coram, Long Island, New York, tadpoles of the Spring Peeper were found in an aggregation three feet in diameter at 6:30 p.m. in a small pond (water depth: 4 inches). Tadpoles were in water with a temperature of 16.2° C. Six inches away there were no tadpoles and the water varied from 15.8° to 14.2° C. The surface water temperature above the aggregation was 15.8° C. (Fig. 1c).

On May 5, 1957, at 1:30 p.m., several *H. crucifer* tadpole aggregations were noted at Lake Panamoka, Long Island, New York. One aggregation (Fig. 1A) consisting of approximately 75 individuals was in water having a temperature of 24.8°C. There was none in nearby water of 21°, 22°, or 27°C. In another area (Fig. 1B) a group was at a temperature of 28°C. Nearby temperatures dropped to 25.8°C. and rose to 29.7°C. near shore.

Rana boylei.—The following observations on tadpoles of the California Yellow-Legged Frog, made on the Smith River, Smith River State Park, Del Norte County, California, June 28-29, 1954, provide additional evidence for the thermal control of certain tadpole aggregations.



FIC. 1A-C.—Sectional diagrams of ponds containing tadpole aggregations of *Hyla crucifer*. A and B, Lake Panamoka, Long Island, N.Y.; C, Coram, Long Island, N. Y.

At one place on the swift river a small cove was formed by the river-carried boulders that formed a small spit or barrier parallel to the side of the river. At the time of these observations, this cove, 30 feet wide and 40 feet long, had a bottom of fine sand. The river current had only a slight influence on the movement and temperature of the water within this cove. An aggregation of *Rana boylei* tadpoles (approximately 1 to 2 cm. long) numbering about 1,000 individuals was in the cove. No food or other obvious stimuli could account for the aggregation. Water temperatures were taken at many points, and the positions of the tadpoles were mapped at various times.

When first observed, at 9:00 p.m., June 28, the tadpoles were aggregated in a mass (Fig. 2A) at the bottom of the pool. About 80 per cent of the individuals were in an area one foot in diameter; the remainder was scattered within an area three feet wide and 10 feet long. The water within which the tadpoles were congregated was 15° C. Both surface and shallow water temperatures were 14° C. There was little or no movement of the individuals within the aggregation.

The following morning the pond was checked at 9:00 a.m. before the sun had reached the pool. At this time the individuals in the aggregation were more dispersed (Fig. 2B), most of them were within an area 20 feet in diameter. There were more random movements of individuals at this time. Bottom water temperatures within the 20-foot circles occupied by the tadpoles were all 15.6° C. The surface water temperature (1 inch) was 14.0° C. and the water four inches deep was 15.2° C. The shallow water at the edge of the pond was 14.2° C.

The pool was checked again at 10:00 a.m. Sunlight had reached various parts of the pool as it penetrated through the surrounding foliage. About 80 per cent of the tadpoles now occupied the shallow parts of the pool where the temperature was 17.0° C. Surface and bottom water temperatures at the center of the pond were 15.0°C. The tadpoles in the shallow water were beginning to feed. The remaining 20 per cent of the tadpoles occurred in a tight aggregation in the center of the pond. As the sunlight passed between the leaves of the trees, the aggregation followed the sunlight as it moved about the pond in small patches. From time to time individuals would leave the aggregation and move into the shallow water (Fig. 2C).

Unfortunately it was necessary to stop observations at this time. The subsequent daily behavior of these tadpoles can be inferred from the casual observations made on this and other ponds in the area the previous day (Figs. 2D-G).

Bufo boreas.—Observations on several aggregations during the morning of August 4, 1955, at Rabbit Ears Pass, Routt National Forest, Colorado, showed that the tadpoles of the Western Toad not only chose the warmest strata, but also frequented the warmest peripheral areas within the ponds (Fig. 3).

Bufo canorus.—Mullally (1953) has shown that tadpoles of this toad are sensitive to small differences in water temperature. They often desert areas which are $1-2^{\circ}$ C. cooler than the preferred



FIG. 2A-G.—Vertical and sectional diagrams of a pond showing aggregation behavior in tadpoles (dots) of *Rana boylei* associated with temperatures at different times of the day.

water. Mid-day surface temperatures of the lower Gaylor and Tioga Pass Lakes were 20-23 °C., while the shallow margins $\frac{1}{2}$ -2 inches deep were 27-33 °C. Every observation in the daytime revealed the tadpoles crowded into the warmest, to 33 °C., and the shallowest water available. After sundown they dispersed into

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deeper water. Diurnal warmth probably attracts the tadpoles to the shallow marginal areas and the coolness of deeper water may prevent normal growth (Mullally, 1953).

Adaptive Value of Tadpole Aggregations

Such tadpole aggregations as have been cited above would seem to have survival value. By following a thermal gradient to warm areas, the animal gains a higher body temperature and hence more rapid metabolism. A higher metabolic rate would result in a faster rate of development and shorten the period before metamorphosis (Volpe, 1953, 1957). Early metamorphosis would be of survival value in those areas where ponds dry up rapidly or where predation is high.



FIG. 3.—Vertical and sectional diagrams of three ponds at Rabbit Ears Pass, Colorado, showing aggregations of tadpoles (dots) of *Bufo boreas* associated with the warmest water temperatures available in a given pond. Aggregation on line E-F includes the metamorphosing individuals on land.

A tadpole reaching metamorphosis rapidly would also escape other perils. Rose (1958), for example, has noted that water in which tadpoles or fish have grown inhibits growth of others of their own kind. Larger animals may completely suppress the growth of smaller ones and may eventually kill them by this waterborn inhibition. Under natural conditions of over production only the more rapidly growing would be expected to survive. This may be a relationship favoring rather rapid evolutionary advances in aquatic organisms. (Also see Richards, 1958). It is interesting in this regard to recall the discussion by Cowles (1949) concerning the transition of aquatic to land vertebrates, to note that some amphibian larvae have been reported as tolerating a wider range in temperture than the adult (Schechtman and Olson, 1941; Brattstrom and Warren, 1955), and to note that on some occasions a metamorphosing aggregation may leave the water against a thermal gradient (*Bufo w. fowleri*, pond on Moriches Road, Long Island, New York, July 17, 1958, 9:30 a.m. The water temperature dropped from 25.9° C. 12 inches from shore to 25.3° , 23.0° , 22.8° to 21.4° C. (interval distance = 3 inches) as one approached the shore.)

Reed and Marx (1959) have illustrated cases of floods destroying tadpoles. A more rapid growth rate would be expected to decrease the chance of being destroyed by floods.

Brattstrom and Warren (1955) noted that in a tadpole aggregation of *Hyla regilla* most of the tadpoles were oriented with their tails pointed to the sun. They also noted that this would probably expose the greatest dorsal surface to the sun's rays and suggested further that an additional advantage to aggregations was that a group of tadpoles might be able to absorb more heat as a mass than as isolated individuals. This hypothesis was tested by the following experiment (I wish to thank Miss Julie Cajiao for her assistance).





FIG. 4.—Rate of heat gain of two pans of water, one (dots) containing tadpoles; one (crosses) without tadpoles, both exposed to an infra-red lamp 13 inches over the water surface.

Two white porcelain pans of equal size and with the same amount of pond water were placed under two separate infra-red sun lamps. Sixteen *Rana catesbeiana* tadpoles (average length 3 inches) were placed in one pan. No tadpoles were placed in the other. (This situation does not strictly test the hypothesis—aggregated vs. non-aggregated tadpoles, but in small pans it is not possible to induce a natural aggregation with the large tadpoles used. In a similar experiment carried out under natural conditions, in sunlight, where one pan contained tadpoles artificially concentrated in the center and the other pan contained dispersed tadpoles, the results were the same. In the experiment being discussed it is obvious from the results that putting additional tadpoles into the control pan would do nothing but reduce the gap between the lines on Figs. 4 and 5. It is also obvious that the experiment could be conducted using inanimate black objects, and I suspect the results would be the same). The temperatures in the two pans were allowed to equalize; the lamps were turned on; and the change in water temperature was noted (thermometer immersed in water) The experiments were conducted in a room which maintained a fairly constant temperature $(23.0\pm1^{\circ}C.)$.

In the first experiment the lamps were placed 15 inches over the table (13 inches over the water). The experiment was started



FIG. 5.—Rate of heat gain of two pans of water, one (dots) with tadpoles, the other (crosses) without, both exposed to an infra-red lamp 7 inches over the water surface.

at a temperature of 22° C. and stopped 90 minutes later. The results are shown in Figure 4. In the second experiment the lamps were placed 9 inches over the table (7 inches over the water) and the experiment was started at 5°C. (This was accomplished by precooling pans, water, and tadpoles with ice). The results of this experiment is shown in Figure 5.

It is apparent from Figures 4 and 5 that the water temperature in the pan with the tadpoles rises at a faster rate than the control and maintains a temperature higher than the control. That this rise in temperature is due directly to the heat absorbed by the tadpoles and dispersed to the water (and is not due to any "metabolic heat" produced by the tadpoles) is obvious because before and after each experiment both pans returned to room temperature (or a little below due to evaporative cooling) and maintained the same temperature in spite of the activity of the tadpoles in one pan. Whether small tadpoles can absorb enough heat to raise their body temperature or can thermally alter their environment is unknown. Studies on the behavior of tadpoles in thermal gradients and the effect of acclimation on this behavior are in progress.

DISCUSSION

The effect of temperature on metabolic rate in ectotherms is well known (Bullock, 1955; Fry, 1947; Volpe, 1953, 1957). It is also known that the rate of metamorphosis is dependent upon the rate of metabolism, hence the importance of temperature. Temperature is thus probably responsible for the differences in the number of seasons needed for certain tadpoles to metamorphose. For example, it is commonly noted (*e.g.* Wright and Wright, 1949:446) that it takes *Rana catesbeiana* two years to metamorphose in eastern United States. Bleakney (1952) has shown that *R. catesbeiana* needs three years to metamorphose in Nova Scotia, and others have shown that in the south and midwest bullfrogs may metamorphose in one year (Moore, 1949). Recently Cohen and Howard (1958) have shown that on the San Joaquin Experimental Range, California, bullfrogs may metamorphose in six months.

CONCLUSIONS

When other stimuli (food, metamorphism, parasites, etc.) are absent (the so-called "social" aggregation of Bragg, 1954), aggregation behavior in some tadpoles appears to be thermally controlled. Aggregation is apparently the result of individual tadpoles responding to microclimatic thermal gradients. Tadpoles in aggregations absorb more radiant heat and disperse more heat to the surrounding water than do isolated tadpoles (or empty pans of equal water volume). The survival value of temperature-controlled aggregations in tadpoles appears to be related to an increase in body temperature. This results in an increase in metabolism and thus decreases the time needed before metamorphosis.

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