RESPONSES OF A POPULATION OF *AMBYSTOMA TIGRINUM* TO THERMAL AND OXYGEN GRADIENTS

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ABSTRACT: At water temperatures below 15 C, *Ambystoma tigrinum* moved in response to oxygen and thermal gradients, remaining in shallow water during the day and returning to deep water at night. Under these conditions, activity was reduced. In the absence of thermal and oxygen gradients at water temperatures below 15 C, movements were random. At water temperatures above 15 C, movement was random and activity increased. Temperature appeared to be the most important factor governing winter and spring activity and light seemed most important in governing summer activity.

THERE is considerable literature dealing with behavioral temperature regulation in reptiles, but little work has been done on temperature selection in amphibians. Brattstrom (1963) suggested that thermoregulation in amphibians is both behavioral and physiological. Prosser (1911) observed that *Ambystoma tigrinum* larvae moved to warm water near shore during the day and returned to deep water at the center of the lake which remained warmer than the shallow water at night. Lucas and Reynolds (1967) studied temperature selection in larval *Rana pipiens*, *Rana catesbeiana*, and *A. tigrinum*. They reported that *A. tigrinum* larvae exhibited a temperature preference of about 25 C. In later experiments the larvae did not aggregate at any one temperature, although they avoided temperatures below 14 C and above 33 C. We conducted the present study to determine the responses of adult *Ambystoma tigrinum* to oxygen and temperature gradients in a natural situation.

METHODS

The study was conducted at Taylor Well Pond on the Jornada Experimental Ranch, 27 miles NE Las Cruces, Dona Ana County, New Mexico. The pond was approximately 15 m $\times$ 40 m with a maximum depth of 3 m in January to 1 m in June prior to the summer rains. The pond had a uniformly sloping, silt-covered bottom.

Observations on movements of salamanders in the pond were made from January to July 1967 in order to obtain data from the coldest and hottest months. Direct observation of the movements of animals in the pond was impossible due to the concentration of suspended particles. A plastic float was sutured to an animal by a monofilament line through the tail. The line was of sufficient length to allow the salamanders to move along the bottom of the pond in the deepest part.

Movements of animals were recorded by following the movements of the numbered floats and recording the position of the

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floats on a grid map of the pond every 15 min. A total of 10–15 animals (half transformed, half neotenic) was followed for most of the day. Animals were released at various locations in the pond at different times of the day to check responses to thermal and oxygen gradients. Data on animals whose float lines fouled on submerged objects were not included in the analysis.

Measurements of deep and shallow water temperatures and dissolved oxygen were made on an hourly basis with YSI thermistor and telethermometer and Delta Model 75 portable oxygen analyzer respectively.

Since the movement of individuals was plotted on an hourly basis, it was possible to calculate an activity index for *Ambystoma tigrinum* (distance moved in feet per hour). The data were averaged for the marked population and summarized for the major time periods in the day.

Results

In the winter when water temperatures were higher in the shallow water during the day, the animals moved to the periphery and remained there (Fig. 1). As the shallow water temperature dropped in the early evening, the salamanders returned to the deep, warmer area in the middle of the pond where the dissolved oxygen levels remained above 3.0 ppm. Dissolved oxygen in the shallow water dropped as low as 1.5 ppm before sunrise. There was little evidence of surfacing to gulp air during the winter.

On 17 April, a strong wind during the day produced homogeneity of temperature and oxygen throughout the pond. In the absence of thermal and oxygen gradients, movements of the salamanders during the daylight hours were not confined to one area of the pond (Fig. 2), and the activity index was higher than on days when gradients were established (Table 1).

When the minimum water temperatures reached 15 C in early summer (mid-May through June) (Fig. 2), the salamanders did not select one portion of the pond as they had in the winter months, and they had a high activity index (Table 1). During this period there was little difference in temperature or oxygen concentrations between the deep and shallow water. Considerable surfacing activity was observed between 0300 and 0800 hr MST. During this period, the dissolved oxygen dropped below 1.5 ppm, and the salamanders were probably gulping air to supplement their oxygen supply from the water.

During the winter when salamanders were released in deep water, they quickly moved to the shallow water during the day, and night displaced animals moved to deep, warmer water. When salamanders were released at various points in the pond and thermal and oxygen gradients were absent, their movements were unori-

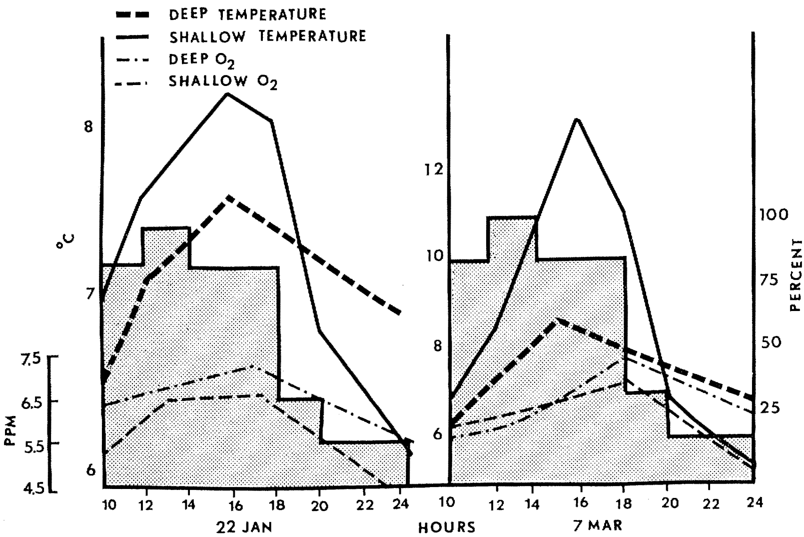

FIG. 1.—The per cent of tagged *Ambystoma tigrinum* (cross-hatched area) in shallow water at different times of the day as related to temperature and dissolved oxygen. The ppm scale refers to dissolved oxygen.

ented. Activity was limited at all periods in the day at water temperatures lower than 15 C, i.e., January through early April (Table 1). During this period, the animals increased activity, moving to the shallow inshore water by midmorning. After sunset and cooling of the shallow water, the salamanders moved to midpond and were relatively inactive.

High winds resulted in uniform temperatures throughout the pond during at least 50% of the days in April and May. Under these conditions the salamanders were active at all hours.

The activity pattern of *A. tigrinum* was reversed in June when midday water temperatures approached 25 C, and movements were random. Activity was greatest from early evening until approximately one hour after sunrise but greatly reduced at midday.

Discussion

Prosser (1911) observed the movement of *Ambystoma tigrinum* larvae from the middle of the lake to the warm water near shore during the day and back to the deep water which remained warmer at night. That pattern is similar to that observed in this study at water temperatures below 15 C. Lucas and Reynolds (1967) reported that *A. tigrinum* larvae exhibited a thermal preference at 25 C the day following collection. In subsequent laboratory studies the salamanders did not aggregate at any one temperature but did avoid

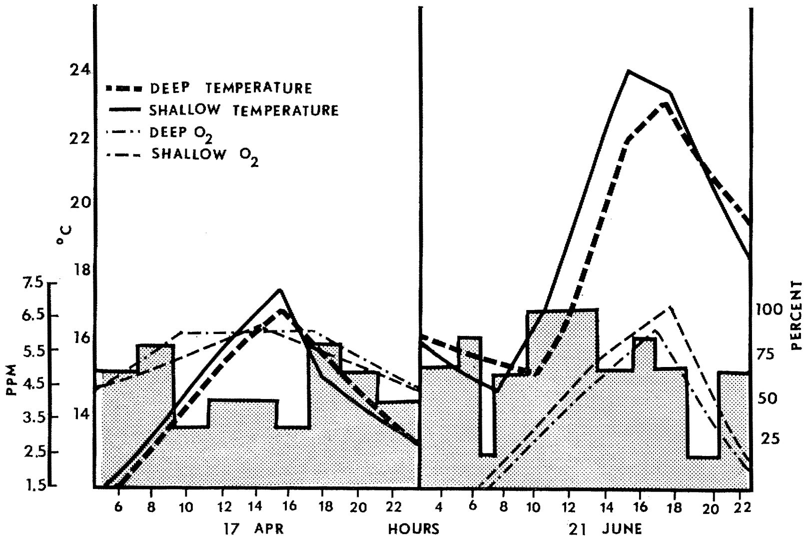

FIG. 2.—The per cent of tagged *Ambystoma tigrinum* in shallow water at different times of the day as related to temperature and dissolved oxygen. Method of presentation as in Fig. 1.

temperatures below 14 C and above 33 C. The behavior of *A. tigrinum* in our study confirms the laboratory studies of Lucas and Reynolds to the extent that, under natural conditions, *A. tigrinum* became more active and did not select an area of high or low temperature in the pond at temperatures above 15 C.

The increase in activity of a natural population of *A. tigrinum* at temperatures above 15 C partially supports the contention of Whitford and Sherman (1968) that 15 C may represent an optimum activity temperature for temperate zone amphibians. The present study indicates that 15 C is a critical temperature affecting both thermal environment selection and activity level in *A. tigrinum.* However, there was no indication that 15 C was an optimum temperature for activity, since the mean activity index was similar at environmental temperatures of 15 C and above.

Surfacing activity was minimal at oxygen levels above 1.5 ppm, and the salamanders did not aggregate in the shallow water to take advantage of rapid oxygen diffusion when dissolved oxygen fell below 1.5 ppm. Also, the salamanders remained in the warmer shallow water during the winter months, although the daytime oxygen concentration was slightly higher in the deep water in the middle of the pond. Consequently, we suggest that temperature is more important than oxygen as a factor influencing the activity and behavior of *A. tigrinum.* In the warm months when activity was not

TABLE 1.—Variation in the diel activity index of tagged *Ambystoma tigrinum* in relation to season and temperature gradients. The activity index is the average distance in feet moved per hour between points of sighting.

Date	Time of day	Mean Activity Index (ft/hr)	Mean temperature difference °C between deep and shallow water
22 Jan.	midday	4.1	1.0
	sunset	3.8	1.2
	night	2.0	2.5
7 March	sunrise	1.4	0.2
	midday	2.5	1.0
	sunset	3.0	10.0
	night	2.8	2.0
17 April	sunrise	11.2	0.0
	midday	10.1	0.0
	sunset	10.0	0.0
	night	8.0	1.0
7 June	sunrise	8.8	0.0
	midday	4.1	2.0
	sunset	8.9	0.0
	night	9.0	1.0

limited by temperature, light became an important factor affecting the activity period with the high activity in reduced light at night, dawn and dusk. Therefore we conclude that *A. tigrinum* responds to thermal gradients at water temperatures below 15 C and that diel activity is regulated by both temperature and light. The intensity of activity appears to be directly related to temperature, reaching a maximum at temperatures greater than 15 C.

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