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## DIEL PATTERN OF MOVEMENT AND AGGREGATION IN TADPOLES OF THE COMMON FROG, *RANA TEMPORARIA*

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### ABSTRACT

In a garden pond in London, tadpoles of the common frog, *Rana temporaria*, displayed a clear diel pattern of movement and aggregation. During the morning, tadpoles moved from the deeper area in the middle of the pond to the pond edges. The number of tadpoles around the edges peaked in the afternoon. At night tadpoles tended to disperse and move back to the deeper area. This cycle was closely related to the diel cycles of illumination and temperature. Tadpoles were not evenly distributed around the pond edges, and a stationary feeding aggregation was formed each day on the west to south-west edge. As there was no thermal gradients along the pond edges, the formation of this aggregation was probably due to factors other than temperature.

### INTRODUCTION

Anuran tadpoles are rarely evenly distributed in a pond and frequently form dense aggregations consisting of several hundred individuals. The structure and function of such aggregations has been studied by a number of authors, but the mechanisms which bring tadpoles together are complex (e.g. Bragg, 1954; Brattstrom, 1962; Wassersug and Hessler, 1971; Beiswenger, 1975). One classification system distinguishes between social aggregates which are formed by "biosocial mutual attraction" and simple (or asocial) aggregates formed by tactic responses to environmental stimuli such as light, temperature or food (Bragg, 1954; Wassersug, 1973). Under natural conditions, however, both social and asocial factors are probably operant in tadpole aggregations.

In comparison with studies of aggregation, diel activity in amphibian larvae has been little studied. Several species, however, have been shown to display diel movement patterns related to microhabitat selection (e.g. Mullally, 1953; Beiswenger, 1977; Heath, 1975; Dolmen, 1983; Holomuzki and Collins, 1983). In common with the vast majority of vertebrates, it is likely that such activity patterns are regulated primarily by daily fluctuations in illumination and temperature, possibly in conjunction with an endogenous time-keeping system.

Clearly then, illumination and temperature are involved in the modulation of both aggregative behaviour and diel movement patterns in larval amphibians. The present study set out to investigate diel movements and aggregations in relation to these environmental factors in tadpoles of the common frog

*Rana temporaria*. Aggregations of tadpoles of this species have been described by Savage (1952), and Ashby (1969) describes common frog tadpoles aggregating in patches of sunlight falling on a garden pond. There is, however, little other quantitative information relating to the behaviour of tadpoles of this species.

MATERIALS AND METHODS

The diel behaviour of common frog tadpoles was observed in a pond in the grounds of Westfield College, North London, in April 1982 (Fig. 1). The pond was constructed from concrete and had a surface area of about 4 sq. m. Apart from encrustations of algae, the pond edges were bare and shelved at an angle of about 45° to a flat bottom covered by a layer of leaf litter. Pond depth was about 20 cm. Submerged vegetation consisted mainly of filamentous algae. Smooth newts *Triturus vulgaris* were also found in the pond. A description of the surrounding habitat is provided by Griffiths (1984).

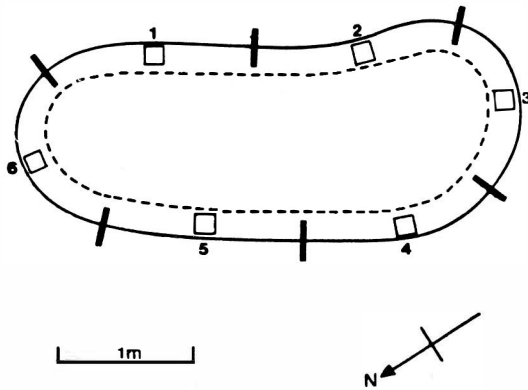


Fig. 1 The study pond. The shelving pond edge is the area between the outer solid line and the inner dotted line. A square indicates the position of each quadrat in each 1.5 m section of shoreline.

The total length of pond shoreline was 9 m, and this was divided into six 1.5 m sections. At least 8 hr before observations commenced, a 15 cm x 15 cm quadrat was placed in the middle of each 1.5 m section, such that it lay submerged on the shelving pond edge (Fig. 1). The position of each quadrat was secured with string tied to a stick on land. Observations commenced at 0500 hr and were repeated at intervals of 1-2 hr until 0200 hr the following day. During each observation period the number of frog tadpoles in each quadrat along the pond edge was counted. Water temperatures at the pond edges and in the pond centre at 15 cm depth were taken with a mercury thermometer graduated at intervals of 0.1°C, and illumination at the pond surface was measured with a EEL photoelectric photometer. At night observations were made using dim, red torchlight.

Observations of tadpole aggregations were made over 18-19th, 20-21st and 28-29th April 1982 (These dates will be subsequently referred to as days 1, 2 and 3). The tadpoles were all free-swimming, feeding independently, and had internal gills (Gosner (1960) stages 25-30).

RESULTS

Frog tadpoles displayed a clear diel pattern of movement and aggregation. During the morning tadpoles moved shoreward from the centre of the pond, and numbers of tadpoles around the pond edges peaked in the afternoon (Fig. 2). During this period, tadpoles were observed grazing on the algae at the pond edges. At night the tadpoles tended to disperse from the edges and move back into deeper water. On day 1 this diel distribution pattern closely followed the illumination cycle. On days 2 and 3, however, the

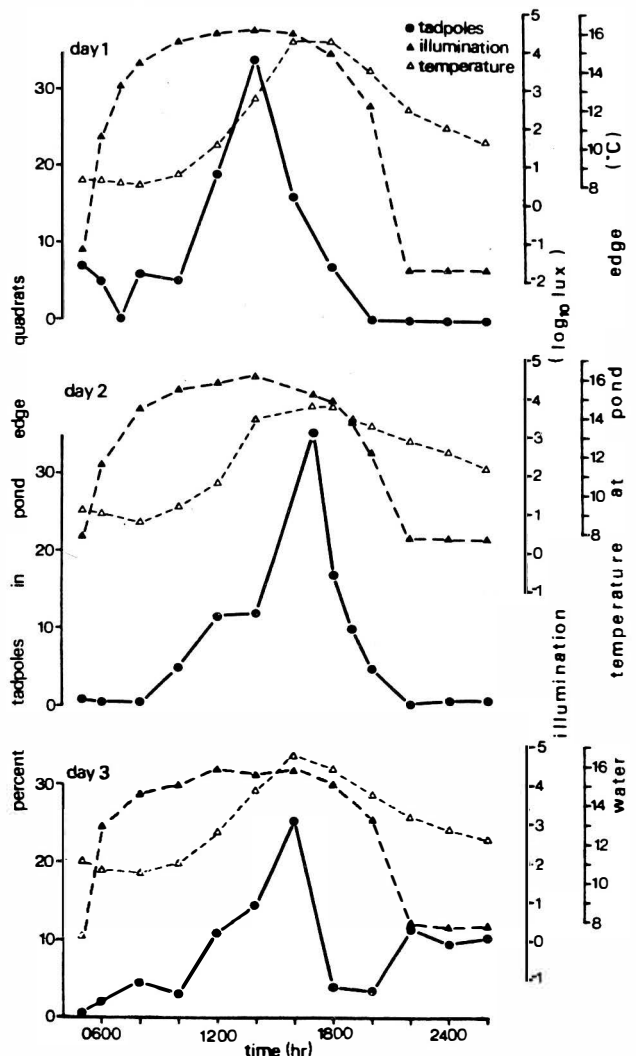


Fig. 2 Diel movement of common frog tadpoles in relation to illumination and pond edge water temperature. Tadpole numbers are expressed as percentages (no. counted/total counted on that day x 100) for easier comparison of results.

numbers of tadpoles around the pond edges showed a closer correspondence with temperature than illumination. During the daytime (i.e. 0600-1800 hr) the pond edges were significantly warmer than deeper water in the middle of the pond (Wilcoxon matched-pairs signed-ranks test (one-tailed):  $N = 15$ ,  $T = 25.5$ ,  $P < 0.05$ ). At night (i.e. 0200-0500 hr) this relationship was reversed and the deep water was warmest ( $N = 11$ ,  $T = 11$ ,  $P = 0.025$ ). However, the temperature difference between the pond edges and the deeper water never exceeded  $1.5^{\circ}\text{C}$ .

During the daytime tadpoles were not evenly distributed around the pond edge (Fig. 3). As tadpoles moved shoreward in the morning, numbers became more closely aggregated towards one end of the pond, and were densest in area 4. The densest aggregation was observed at 1700 hr on day 2, when 75 tadpoles were counted in quadrat 4. Overall, over 40 per cent of all tadpoles counted were observed in quadrat 4. Moreover, this aggregation was stationary and did not change in position over the diel cycle. To assess whether this non-uniform distribution of tadpoles was related to a temperature gradient along the pond edges, on day 1 the water temperature was taken in each quadrat during each observation period from 0500-1800 hr. However, pond edge temperatures did not differ significantly between the six areas (Friedman two-way analysis of variance,  $\chi^2 r = 10.3$ ,  $P > 0.05$ ). Although inactive and unaggregated tadpoles frequently oriented perpendicularly to the shoreline, with the head pointing away from the pond, tadpole aggregations were unpolarized.

## DISCUSSION

The diel cycle of shoreward movement in tadpoles of *Rana temporaria* follows closely the pattern observed in two species of toad tadpoles (Mullally, 1953; Beiswenger, 1977). Moreover, similar diel movement patterns have been observed in salamander larvae (e.g. Heath, 1975; Holomuzki and Collins, 1983). Beiswenger (1977) observed that the increase in American toad (*Bufo americanus*) tadpole activity in the morning was more closely related to light than temperature, and suggested that this allows tadpoles to anticipate the heating of the shallow areas and to move into them accordingly. Certainly, behavioural thermoregulation is well-developed in larval amphibians (e.g. Lucas and Reynolds, 1967; de Vlaming and Bury, 1970) and even in the shallow Westfield pond there was a slight (but significant) temperature difference between the pond edges and the deeper water during both the day and the night. Although the diel movements of frog tadpoles were therefore probably thermoregulatory in function, responses to changes in illumination may assist in the orientation to warmer waters.

Although there existed a slight thermal stratification in the Westfield pond, there did not appear to be any thermal gradients along the pond shoreline. The daily aggregation of frog tadpoles on the west to south-west edge was therefore probably due to factors other than temperature. Daytime aggregations of frog tadpoles

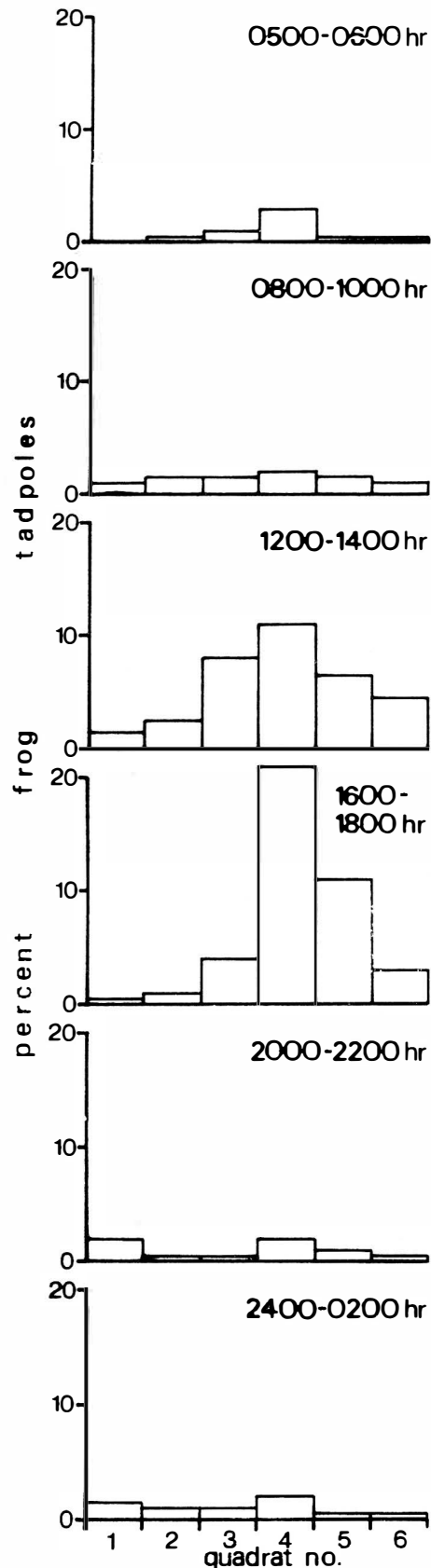


Fig. 3. Diel pattern of aggregation of tadpoles along the pond edge. Tadpole numbers are expressed as percentages (no. counted/total counted  $\times 100$ ) using data from all three days of observations.

along the same shoreline were also observed in 1981 (unpublished observation). The growth of algae along this edge may have been more luxuriant than in other areas (although this was not visually apparent). Alternatively, the tadpoles may have had an innate directional preference for this area. Beiswenger (1977) also reports of two aggregations of *Bufo americanus* tadpoles which were observed to form in the same places each day. The reasons for such behaviour, however, remain unclear.

Beiswenger (1975) classifies the aggregations formed by *Bufo americanus* tadpoles into stationary and moving types. Stationary aggregations are sub-divided into necrophagous groups, feeding groups and metamorphic groups. The aggregations of *Rana temporaria* tadpoles reported here correspond to Beiswenger's feeding groups. These groups are usually confined to shallow areas with little or no vegetation, and are characterized by tadpoles which are primarily engaged in feeding behaviour. Feeding is interspersed by short swims, during which tadpoles may "butt" each other. Such aggregations constantly stir the substrate and thus make the food supply more readily available. No moving aggregations were observed in *Rana temporaria*, but this may have been related to the small size of the pond.

As Beiswenger (1977) points out, it is more meaningful to interpret the formation of tadpole aggregations in terms of a complex of several variables (both social and asocial) operating simultaneously or sequentially, rather than in terms of a single environmental variable. As a result of the close relationship between the daily cycle of light and temperature it is often tenuous to attempt to distinguish between a phototactic and a thermotactic response under field conditions. Moreover, factors such as light and temperature should not be assumed to be directly causative in the regulation of diel behaviour patterns when their role as synchronizers of endogenous biological clocks has not been fully evaluated.

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