DIEL PATTERNS OF ACTIVITY AND VERTICAL MIGRATION IN TADPOLES OF THE COMMON TOAD, *BUFO BUFO*

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ABSTRACT

The diel pattern of activity and vertical migration of common toad tadpoles, *Bufo bufo*, was studied at Llysdinam pond in mid-Wales in 1985 and 1986. Toad tadpoles were predominantly day-active with peaks mainly occurring between 1400 h and 2000 h. The diel activity pattern corresponded with daily cycles of illumination and temperature, but no consistent relationship with the activity of predatory dytiscid beetles was observed. Differences between 1985 and 1986 in the pattern of vertical migration within the water column could be related to the distribution of submerged plants in the pond. In both years, however, tadpoles occurred mainly in the middle of the water column during the day.

INTRODUCTION

Although it is well-known that anuran tadpoles may form aggregations around the edges of ponds during the day, and disperse into deeper water by night (Mullally, 1953; Beiswenger, 1977; Beebee, 1985; Griffiths, 1985a) other aspects of their daily activity patterns have been little studied. As well as horizontal movements from shoreline to deep water within a pond, amphibian larvae may display vertical movements within the water column, as demonstrated by a number of urodele larvae (Anderson & Graham, 1967; Anderson & Williamson, 1974; Branch & Altig, 1981; Holomuzki & Collins, 1983). Daily cycles of illumination and temperature are certainly important in regulating tadpole activity patterns (Beiswenger, 1977; Griffiths, 1985a), but also of importance are the activity cycles of potential predators. The larvae of tiger salamanders (Ambystoma tigrinum), for example, alter their activity patterns in the presence of dytiscid beetles and this may minimise the risk of predation (Holomuzki, 1986).

At Llysdinam pond in mid-Wales common toad (*Bufo bufo*) tadpoles suffer heavy predation from both larval and adult great diving beetles (*Dytiscus marginalis*), and in some years the tadpole population may be eliminated completely (Harrison, 1985). Preliminary qualitative observations revealed that during the daytime tadpoles could be seen actively swimming in the pond. At night, however, this swimming activity became much less evident, with tadpoles remaining immobile or swimming short distances only. This suggested that catches of tadpoles in funnel traps might reflect activity.

In this paper we (1) examine the diel activity patterns of common toad tadpoles in relation to microhabitat, illumination, temperature, and great diving beetle activity and (2) describe the stratification of tadpoles within the water column.

MATERIALS AND METHODS

Llysdinam Pond, Newbridge-on-Wye, is situated about 200m above sea level, has a surface area of just under 900m², and had a maximum depth of 0.7m at the time of the study. Open water occupies about 300m² of the total surface area of the pond, the remaining 600m² consisting of *Glyceria maxima* swamp. The pond is completely surrounded by a plastic barrier and pitfall trap system and the breeding migrations of amphibians at the pond have been monitored annually since 1981 (Harrison, *et al.*, 1983; Gittins, 1983; Griffiths *et al.*, 1986).

The study sites within the pond were (1) the shoreline of the open water, which was about 30m in length and lined with *Glyceria maxima*, and (2) the deep, central area of the pond which was about 0.7m deep. In 1985 the water column in the deep area of the pond was free of vegetation. This was a result of the drought during the previous year, which eliminated a large proportion of the submerged plants. By 1986, however, the vegetation had recovered and the water column was occupied by a dense growth of submerged plants (mainly *Ceratophyllum demersum*).

The funnel traps described by Griffiths (1985b) were used for monitoring tadpole behaviour in each of the two study areas. In the shoreline area, ten traps were submerged close to the edge of the pond in about 0.15m of water. The traps were spaced out at 3m intervals and were positioned so that they faced towards the pond centre. In the deep water area tadpoles were captured at different depths using sets of three traps strung together vertically. Each vertical set consisted of one trap positioned just below the water surface, the second at about 0.35m depth, and the third resting on the pond bottom at 0.7m. Four sets of traps were suspended about 3m apart from a 0.2m wide wooden bridge which spanned the open water area of the pond. To reduce shading effects, the traps were suspended from the ends of 0.5m long rods placed at right-angles to the bridge. A further four sets of traps were placed along the edge of the *Glyceria* swamp where it bordered the open water area. Here the traps were attached to canes driven into the pond bottom with access being gained by a dingy. This trapping regime therefore covered all the microhabitats available to tadpoles in the open water areas of the pond.

Toad tadpole behaviour was studied during May and June of 1985 and 1986 by checking the traps every 2h over several 24h periods. In 1985 these were 27-28 May and 31 May-1 June (i.e. two 24h periods), whilst in 1986 the dates were 27-28, 29-30 May, 1-2, 5-6, 11-12 and 17-18 June (six 24h periods). Trapping sessions conducted after these dates revealed very few tadpoles. The toad tadpoles captured in each trap were counted and then released. It was assumed that the number of tadpoles captured per 2h interval reflected tadpole activity over that period. All tadpoles were at Gosner (1960) stages 26-30 and were between 15 and 20mm in length.

Over the last three days of the study in 1986 the number of adult and larval stage great diving beetles, *Dytiscus marginalis*, captured in the traps was also recorded. Measurements of water temperature at the top and bottom of the water column were taken using a mercury thermometer, and illumination at the pond surface was recorded using a portable illuminometer.

RESULTS

In 1985 the total number of tadpoles captured was 1429 on day 1 and 379 on day 3. This dramatic drop in numbers over a few days was also observed in 1986. On days 1 to 5 in this year the number of tadpoles captured ranged from 1366 (day 2) to 3162 (day 5) and then fell



Fig. 1 Diel patterns of activity of toad tadpoles in different regions of Llysdinam pond in 1985 and 1986. Percentage activity every 2h was averaged over 2 days (1985) and 6 days (1986).

to only 38 on day 6. In total, 11,643 tadpoles were captured over the six days in 1986.



Fig. 2 The diel activity pattern of toad tadpoles on days 4, 5 and 6 1986, displayed in relation to illumination, temperature (mean of measurements taken at the top and bottom of water column) and dytiscid beetle activity.



Fig. 3 Diel patterns of toad tadpole stratification in the water column in 1985 and 1986. The percentage captured at each level was averaged over 2 days (1985) and 5 days (1986). Data from day 6 in 1986 were omitted from the analysis as few tadpoles were captured in the deep water area on this day.

Toad tadpoles were mainly day-active with most captures being made in the afternoon and early evening (Fig. 1). With the exception of the shoreline in 1985, tadpole activity peaked between 1400h-2000h. The overall diel activity pattern appeared to be related to both illumination and water temperature (Fig. 2). The activity of dytiscid beetles varied from day to day and was neither clearly nocturnal or diurnal. No clear relationship between tadpole activity and dytiscid beetle activity was evident. However, on all three days beetle captures were high from 2400h-0400h, a period when there was little tadpole activity.

In the deep water areas most tadpoles were captured in the middle of the water column in both years (Fig. 3). However, there were clear differences between the two years in the pattern of vertical migration. In 1985 the majority of tadpoles spent the night on the bottom of the pond. During the morning there appeared to be a steady migration into the middle of the water column where most tadpoles stayed until nightfall. This was followed by a return to the pond bottom. The following year, however, tadpoles were captured in midwater throughout the diel cycle and a clear pattern of vertical migration was much less evident. Rather more tadpoles were captured at the top of the water column in 1986 than in 1985 although this surface-dwelling behaviour was largely confined to the afternoon hours.

Over days 4-6 in 1986 the percentage of tadpoles captured in deep water ranged from 32 to 91 per cent, whilst that of beetles was 48-69 per cent. Thus the distribution of both tadpoles and beetles between shoreline and deep water varied from day to day and no consistent relationship between the two could be established. The number of beetles captured was too low to obtain a meaningful picture of their diel vertical distribution pattern. However, pooling data over days 4-6 suggested that beetles preferred the upper layers of the water column both by day and by night (Table 1), although statistical analyses of these data showed that this trend was not significant.

	N	Тор	Middle	Bottom	
DAY (0600-2000h)	45	36%	36%	29%	
(2200-0400h)	19	63%	21%	16%	

TABLE 1: The distribution of *Dytiscus marginalis* (larval and adult beetles pooled) within the water column during daytime and night-time. Differences between the three regions were not significant (Friedman two-way analyses of variance: day, $\lambda^2 r = 1.31$, P < 0.05; night, $\lambda^2 r = 4.87$, P < 0.05).

DISCUSSION

There is some evidence to suggest that toad tadpoles may display changes in microhabitat selection during development (Beebee, 1985). Unfortunately, it was not possible to monitor ontogenetic changes in behaviour during the present study as no tadpoles beyond Gosner (1960) stage 30 were captured in the pond in either year. This was a result of the dramatic drop in tadpole numbers observed in June of both years. A possible explanation for this decline is that tadpoles move into the swamp area of the pond at this stage of development and are consequently no longer captured around the shoreline and in deep water. However, traps placed in the swamp after the decline captured very few tadpoles. A much more likely cause of the drop in numbers is predation by invertebrates, especially by larvae and adults of the beetle *Dytiscus marginalis*. These have been shown to be responsible for heavy predation of toad tadpoles in the pond over short periods of time (Harrison, 1985).

Occasionally, certain traps captured exceptionally large numbers of tadpoles which may have reflected social aggregations. As these aggregations would have resulted in fewer tadpoles available for capture at other trap sites it seems unlikely that the daytime peaks in trap catches were a reflection of aggregation rather than general swimming activity. Indeed, the diel pattern of trap catches corresponds with direct observations of tadpole activity during the day and the night.

Unlike salamander larvae (Holomuzki, 1986), the activity pattern of toad tadpoles was not clearly related to that of great diving beetles. Although the present study was based on fairly low captures of beetles, and larval and adult beetles were pooled in the analysis, the clear-cut nocturnal/littoral habits observed in other species of *Dytiscus* (Aiken, 1986: Holomuzki, 1986) were not apparent in *D. marginalis* at Llysdinam pond.

Wassersug (1973) describes two modes of schooling tadpoles. The 'Xenopus' mode consists of in aggregations of polarised tadpoles in midwater, and contrasts with the 'Bufo' mode, in which tadpoles form up in shallows or on the pond bottom. These two modes of schooling can be related to the morphology, palatability and ecology of tadpoles, and whereas Xenopus are well-adapted for filter-feeding in midwater, Bufo tadpoles are better adapted for a scavenging existence on the pond bottom (Wassersug, 1973). It was not clear whether the toad tadpoles observed in midwater in Llysdinam pond were in polarised schools, but in other respects their daytime behaviour conformed more closely to the Xenopus mode. Interestingly, these results are consistent with those obtained on Bufo americanus by Heyer (1976), who netted most tadpoles in the middle of the water column during the day.

The clear difference between 1985 and 1986 in the diel pattern of vertical migration of tadpoles can be related to the growth of submerged plants over the two years. In 1985, when the water column was devoid of vegetation, toad tadpoles could rest at night only amongst deadvegetation on the bottom of the pond. In 1986, however, inactive tadpoles could rest amongst the vegetation which filled the water column, and thus maintain their midwater position throughout the diel cycle (even during this 'resting' period, however, tadpoles are not completely inactive and may intersperse long periods of immobility with short swims).

Why tadpoles should congregate at all in midwater is less clear. Salamander larvae have been observed to stratify at the pond surface and on the pond bottom at different phases of the diel cycle (Holomuzki & Collins, 1983). Movement into warm water at the surface or in shallows during the daytime may be a result of behavioural thermoregulation, whilst stratification at the surface at night may be associated with feeding activity (Anderson & Graham, 1967; Heath, 1975; Branch & Altig, 1981). If behavioural thermoregulation was taking place in Llysdinam pond, toad tadpoles would be expected to congregate at the highest temperatures (i.e. shoreline and pond surface) during the day, but this was not the case. Most toad tadpole activity is probably concerned with filterfeeding and vertical migrations may follow those of the plankton upon which the tadpoles feed. Indeed, the midwater congregation observed at Llysdinam pond is consistent with a study of toad tadpole gut contents from the same site, which has shown that the diet contains a high proportion of motile plankton but little detritus (Harrison, 1985). Alternatively, as Bufo bufo tadpoles are lungless until just before metamorphosis (Savage, 1961), variations in oxygen concentration within the water column may influence activity.

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