# HISTORIA NATURAL

## TADPOLE DIEL MIGRATIONS IN A PYRENEAN POPULATION OF *Rana temporaria*

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**Resumen:** Se estudiaron los fenómenos de migración en una población de renacuajos de *Rana temporaria* en un ibón situado a 2200 m de altitud en el Pirineo aragonés. A lo largo de un día, y a intervalos de una hora, se contó el número de renacuajos en tres cuadrados de control, situados a 0.1, 1.7 y 4.3 m de profundidad. Durante el día, se pudo registrar una migración importante hacia las zonas de menor profundidad en la orilla del ibón, y en dirección inversa al atardecer. Análisis de contenido intestinal indicaron que la agregación de las larvas en las orillas coincide con el período de mayor intensidad de su alimentación. No obstante, se concluye que las migraciones probablemente se deben más a factores de termorregulación que de alimentación.

### INTRODUCTION

The common frog, *Rana temporaria*, occurs in a vast area of Europe and tolerates a large range of ecological, climatic and altitudinal parameters (GROSSENBACHER, 1997).In Spain, it is known up to an altitude of 2950 m in the Pyrenean chain (ESTEBAN, 1997). At such high altitudes, one major challenge faced by the species is certainly the relatively shorter period in which open water is available for breeding and larval development.

AEBLI (1966), ANGELIER & ANGELIER (1968) and BRAND & GROSSENBACHER (1979) demonstrated in laboratory experiments that larvae of high altitude *R. temporaria* populations show a faster development as compared to larvae from lower altitudes. However, beside BALCELLS' (1956, 1975) observations on the onset of the breeding season relative to altitude, few field observations are available on the larval ecology and ethology of montane *R. temporaria* populations.

### MATERIAL AND METHODS

In the present paper we provide data which were gathered from 6.-29. July 1998 at the Ibón de las Ranas, a medium-sized glacial pond (water surface ca. 170 x 60 m; maximum depth 5 m), which is located at ca. 2200 m altitude in the Circo de Piedrafita, western Pyrenees, Aragón, Spain. The pond is located in an area without forest cover; the only higher vegetation are some *Rhododendron ferrugineum* shrubs at the edges. Thus, there are no shaded parts of the pond during the day. In the study period, it was populated by a large number of tadpoles in later developmental stages which were beginning to metamorphose on July, 29th. During the surveys of adult frogs around the pond, migrations of large numbers of tadpoles, mainly in the morning, were noted.

To describe this migration in a more systematic way, some standardized observations were carried out on July, 27th. Three control plots were defined by strings submerged on the pond bottom and fixed by stones as 1 x 1 m quadrats. Plot 1 was located at a water depth of 0.1 m, in an area were large tadpole aggregations had been observed before; plot 2 was at an intermediate depth of 1.7 m; and plot 3 was in the deepest part of the pond at 4.3 m. Roughly every hour, at each plot, temperature was measured at the pond bottom and the number of tadpoles recorded (tadpoles generally were close to the pond bottom and thus easy to count). At plots 2-3, tadpole counts were performed by diving; at plot 1, the marked quadrat was photographed and later counted the number of tadpoles on the photographs. During the study day, there were few clouds, and the pond was almost permanently exposed to the sun. During the night (darkness from 21:00 to 7:00 h) no regular counts and measurements could be performed due to the adverse climatic conditions (cold and windy).

A total of 90 tadpoles were collected from the shallow pond edge areas in the morning (9:00 h; 28 individuals), afternoon (16:00 h; 29 individuals), and evening (21:00 h; 33 individuals). These specimens were immediately sacrificed and preserved in 4% formalin. In the laboratory, their head and body length (HBL; from snout tip to cloaca) was measured, their intestine removed and dry weight of the intestine (DWI; mainly made up by its content) recorded. Considering the head and body of the tadpole as a sphere (with a diameter corresponding to HBL) and, in a more conservative approach, as cube, we calculated the tadpole's theoretical head and body volume, HBV1 (sphere) and HBV2 (cube), from the measured HBL values.

### RESULTS

The study results are presented in Figure 1. At plot 1, an important variation of temperature was observed; temperature rised from 16 °C at 9:00 h to 23.5 °C at 18:00 h. Few tadpoles (8 indiv./m$^2$) were observed at 9:00 h; the number rised quickly to values between 76 indiv./m$^2$ and 390 indiv./m$^2$ in the morning, until a steep increase ocurred, with up to 3500 indiv./m$^2$ recorded at 16:00 and 18:00 h. During this interval, tadpoles were observed in enormous densities at certain shallow parts of the pond,

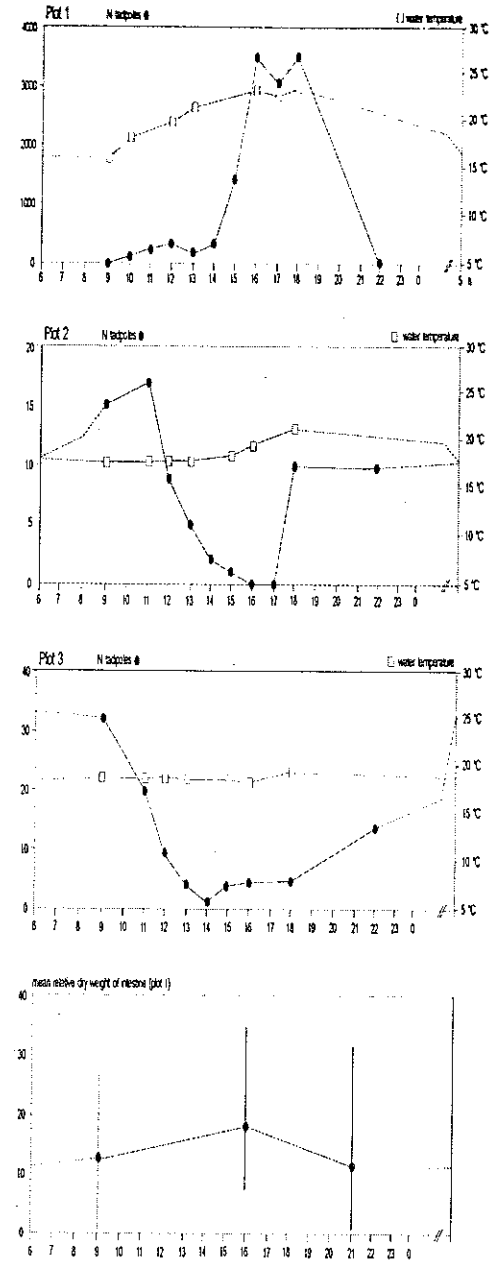


**Figure 1.** Diel variation in number of *R. temporaria* tadpoles and water temperature at three control plots in the Ibón de las ranas, and mean relative dry weight of intestine of tadpoles (DWI/HBV1*10$^6$) captured near plot 1. Dashed lines indicate the assumed values in time intervals in which no observations were made.

generally at the very pond edges and partly in shore areas in which they were not completely covered by water. After sunset, at 22:00 h, no tadpoles at all were present. At plot 2, a slight increase in tadpole number was observed from 9:00 h to 11:00 h (from 15 to 17 indiv./$m^2$), followed by a steep decrease; tadpole numbers dropped to 0 indiv./$m^2$ at 16 and 17 h. The numbers increased again at 18 h and had similar values at 22:00 h. Temperatures, at plot 2, slightly increased during the day (from 17.7°C at 9:00 h to 21.3°C at 18:00 h). At plot 3, the maximum number of tadpoles (35 indiv./$m^2$) was observed at 9:00 h; numbers decreased to a minimum of 1 indiv./$m^2$ at 14:00 h, and then slightly began to increase again; at 22:00 h, a number of 15 indiv./$m^2$ was recorded. Temperatures at plot 3 were largely invariable; from 9:00 h to 18:00 h, an increase of only 0.6 °C was observed (from 18.9 to 19.5 °C).

The dry weight of the intestine (DWI) of specimens captured near the pond edge (mean ± standard deviation, minimum-maximum in parentheses) increased from 21 ± 13 mg (1-48 mg) at 9 h to 40 ± 13 mg (12-61 mg) at 16 h, and decreased to 23 ± 18 mg (1-83 mg) at 21:00 h. The variation in DWI was correlated with variation in HBL among the three samples (mean HBL 14.8 mm at 9:00 h, 16.1 mm at 16:00 h, 15.6 mm at 21:00 h) but these low size differences did not fully account for the observed DWI differences. In pairwise ANCOVA comparisons of DWI, using either HBV1 or HBV2 as covariates, significant differences ($p<0.01$) were found between the data of 9:00 h and 16:00 h, and between the data of 16:00 h and 21:00 h. Similarly, significant differences ($p<0.005$) were found in Mann-Whitney U-tests comparing the ratios DWI/HBV1 and DWI/HBV2 between 9:00 and 16:00 h, and 16:00 and 21:00 h, respectively.

## Discussion

Results demonstrate a distinct migratory behaviour in *Rana temporaria* tadpoles in the Ibón de las Ranas. During the morning, larvae began migrating from the deepest parts of the pond towards the pond edges, and finally gathered in very large numbers and densities at the shallow pond edges. In the evening, a migration in the opposite direction was observed. As we could ascertain by diving, during the night the tadpoles were evenly distributed on the bottom of the pond, without forming aggregations, and with higher densities in the deepest parts of the pond.

Feeding and digestion of the tadpoles obviously took place mainly during the day; weight and volume of the intestine content of the studied specimens were rather low in the morning, higher in the afternoon, and again low in the evening. This indicates that the tadpoles may migrate towards feeding grounds at the pond edges. However, most of the pond bottom was covered by a similar vegetationless mud layer, and there were no indications that more or different food was present at the shallow pond edges. We also do not believe that the observed migrations were a case of predator avoidance (during the daily aggregations, the tadpoles were certainly very exposed to attacks by different predators). We consider it as more probable that the migrations constituted a thermoregulatory behaviour. The water temperature at the shallow pond edges showed an important decrease during the night, whereas the water at 4.3 m depth (plot 3) remained constantly warm. During the day, however, the highest temperatures were reached in the shallow areas, coinciding with the largest tadpole aggregations. Additionally, the dark brown tadpoles probably absorbed additional thermal energy from direct solar radiation to which they were exposed in the shallow water.

Our results are in accordance with published data on migratory behaviour in *R. temporaria* tadpoles. Griffiths & Mylotte (1986) observed that tadpoles of *R. temporaria* stay close to the spawning site until external gills and a mouth are developed; dispersal of tadpoles was completed ca. 30 days after hatching. Augert & Joly (1994) observed how tadpoles dispersed after hatching from the spawning site and aggregated in the shallowest parts of a pond; as their observations were probably all done during the day, a migration to the deeper parts in the evening is possible. Griffiths (1985) reported a migratory tadpole behaviour which exactly corresponds to our observations. During the morning, tadpoles dispersed from the deeper areas in the middle of the pond to the pond edges, with a peak in tadpole number around the edges at afternoon. Griffiths (1985) also observed tadpole aggregations which were formed at certain spots of the edges, and which could not be explained by temperature gradients. The highest density of tadpoles recorded in these aggregations was 75 tadpoles in one sample quadrat of 15x15 cm (3300 indiv./$m^2$). These comparative data show that migration towards the pond edges during the day, which is also known in urodelan larvae (Heath, 1975; Holomuzki & Collins, 1983), appears to be a widespread pattern in *Rana temporaria* and may be one of the behavioural conditions which enable the species to successfully reproduce in relatively cold high mountain ponds.

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