

## SUMMER MICROHABITAT USE AND DIEL ACTIVITY CYCLES IN A HIGH ALTITUDE PYRENEAN POPULATION OF *RANA TEMPORARIA*

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Habitat use and activity was studied in a common frog (*Rana temporaria*) population at an altitude of 2200 m in the Circo de Piedrafita, Spain, was studied during July 1998. Adult and juvenile frogs clearly selected moist microhabitats, and avoided dry substrates such as pasture and rocks. Marshes and puddles were the preferred microhabitat of both adults and juveniles; the shore and the water body itself of a larger pond were selected by adults but much less so by juveniles. Regular surveys over seven days indicated that adults showed both diurnal and nocturnal activity, whereas juveniles were more strictly diurnal. The percentage of adults observed at night in the pond was negatively correlated with the minimum air temperature. The rather aquatic habits and diurnal activity patterns appear to differ from low-altitude populations of *R. temporaria*. They are discussed as adaptations to the lack of humid substrates (forest leaf litter) at high altitudes, and to the extreme and unpredictable climatic conditions (low nocturnal temperatures, and sudden rapid temperature decreases at night) in montane environments.

*Key words:* frog, Spain, Pyrenees, alpine environments, activity, microhabitat

### INTRODUCTION

The ecology and biology of the common frog, *Rana temporaria*, has been well-studied in Europe. The wide array of available literature (see Grossenbacher *et al.*, 1988) permits geographical, altitudinal and temporal comparisons of common frog ecology (Miaud *et al.*, 1999). The species can thus be considered as a good model organism to survey the impact of human activities, landscape transformations and other factors on amphibian populations, especially considering the recently discussed trends of global amphibian declines (e.g. Wake, 1991; Blaustein & Wake, 1995).

Publications on common frog ecology mostly concern populations and their dynamics during the breeding season (e.g., Haapanen, 1970; Cooke, 1975; Grossenbacher, 1980; Pascual & Montori, 1981; Hintermann, 1984; Ryser, 1986; Kneitz, 1998), and phenology (Balcels, 1957; 1975; Haapanen, 1982; Bea *et al.*, 1986; Beattie, 1987). Few papers have analysed the ecology of the species in its summer habitat, and the published studies (e.g. Loman, 1978; 1980; 1984; Strijbosch, 1980; Pasanen *et al.*, 1993; Kneitz, 1998) generally refer to low-altitude populations in partly forested areas. Populations of *R. temporaria* in alpine environments, such as at the northern edge of its range or high mountain areas, have been studied in the context of shifts of their breeding season (Balcels, 1957; 1975), larval and breeding adaptations (Aebli, 1966;

Combes, 1967; Angelier & Angelier, 1968; Brand & Grossenbacher, 1979), adaptations to wintering under extremely cold conditions (Pasanen & Karhapää, 1997; Laitinen & Pasanen, 1998; Pasanen *et al.*, 1998), age structure (Ryser, 1996), and time allocation during breeding (Elmberg & Lundberg, 1991).

Many of the recently detected amphibian declines seem to affect montane populations of amphibians, such as *Rana cascadae* in North America (Blaustein & Wake, 1995) or the genus *Atelopus* in South America (Lötters, 1997). This may be partly due to increasing ultraviolet radiation, which has been demonstrated to be a contributory factor in the deaths of eggs and embryos of several species (e.g. Blaustein *et al.*, 1994; Pedraza & Lizana, 1997). Knowledge of the natural adaptations of high-mountain amphibian populations may therefore be important in developing adequate measures for the prevention of future declines. In the present paper, we analyse microhabitat choice and diel activity cycles in a population of *Rana temporaria* at an altitude of 2200 m in the Pyrenean mountain range.

### MATERIALS AND METHODS

#### STUDY AREA

Studies were centred around the Ibón de las Ranas, a medium-sized glacial pond (water surface ca. 170 x 60 m; maximum depth 5 m), which is situated at ca. 2200 m altitude in the Circo de Piedrafita, western Pyrenees, Aragón, Spain (42°49'N, 0°17'W). All observations were carried out in July, 1998. During this period, in the pond, a large number of tadpoles were present which began to metamorphose on 29 July. *Rana temporaria*

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were common in and around the pond, and could clearly be classified into two size/age classes: juveniles (snout-vent length 15–26 mm) and adults (snout-vent length >50 mm); only very few intermediate, subadult specimens were seen (Vences *et al.*, 1999).

#### MICROHABITAT CHOICE

A study area of 250 m x 150 m (3.75 ha), with the pond at its centre, was divided into 60 plots of 25 m x 25 m. Four of the plots were located in the centre of the pond (100% plot surface made up by water). These plots could not be surveyed and were therefore excluded from further analysis. For each of the remaining 56 plots we estimated the percentage of surface covered by a certain microhabitat (type of substrate or vegetation). Microhabitats were classified as follows: (1) pastures on granitic stony soils (dominated by *Festuca eskia* and *Nardus stricta*, with *Trifolium alpinum*, *Conopodium majus*, *Armeria pubinervis*, *Hieracium pilosella*, *Jasione laevis* and other plants); (2) scree (smaller loose rocks and stones, covering the surface, mainly on some slopes within the study area; with scattered specimens of *Silene rupestris*, *Cardamine resedifolia*, and *Leucanthemopsis alpina* in places); (3) pond (surface of the Ibón de las Ranas); (4) rock surface (parts of the surface made up of pure rock, generally at the same level as the surrounding substrate and not in the form of loose boulders); (5) boulders (large, loose rocks, some of more than 2 m diameter, covering the surface, mainly on some of the slopes within the study area); (6) subalpine shrubs (almost exclusively low (< 1m) bushes of *Rhododendron ferrugineum*, with some specimens of *Vaccinium myrtillus*); (7) pond shore (shore of the Ibón de las Ranas, with a vegetation similar to that of the brook edges; generally, due to wind effects, the water scoured deep recesses under the shoreline which were used as refugia by amphibians and other animals); (8) dry brooks (very small brooks in which, during the study period, no water was present except after rain); (9) scattered pines (single specimens or small groups of *Pinus uncinata*); (10) rocky pond shore (the pond shore consisted of large boulders and scree in places, without any vegetation); (11) brooks (very small and shallow brooks running to and from the pond, generally of less than 1.5 m width; vegetation at the edges largely similar to that recorded for the marsh areas, except for the lower incidence of mosses); (12) marsh, including some small puddles (characterized by the presence of different mosses, e.g. *Cratoneuron commutatum*, and other plants adapted to humidity such as *Carex fusca*, *Carex frigida*, *Juncus articulatus*, *Catabrosa aquatica*, *Saxifraga stellaris*, *Leontodon pyrenaicus*, *Epilobium alsinifolium*, *Dactylorhiza maculata*).

We carried out four surveys of the entire study area on 18 July (1200–1400 hrs), 22 July (1900–2100 hrs), 27 July (2300–0100 hrs) and 28 July (0700–0900 hrs). Plots were surveyed in a random order; each plot was intensively surveyed for 5 min by two researchers (but without looking under stones or into similar refuges).

We recorded every frog encountered (distinguishing between adult and juvenile/subadult frogs) and the plot and microhabitat in which it was first observed. Observed frogs were considered as active because (1) we regularly saw feeding activity during the day and night, and (2) it is unlikely that specimens would expose themselves to the risk of predators and climatic changes if not to actively feed, thermoregulate or migrate. Due to the absence of forest and dense vegetation in the study area, visibility of frogs was similar in most microhabitat types. In fact it is likely that frogs were only overlooked in boulder habitat during the day, due to the large number of holes and crevices into which they could escape before being recorded. However, during the nocturnal surveys (when frogs were generally easier to approach) no individuals were found in amongst boulders. This suggests that the daytime numbers may not have been strongly under-recorded in this microhabitat.

The percentages of area covered by different microhabitat types in the whole study area were compared statistically to the number of individuals recorded in each microhabitat type. We calculated the expected numbers of individuals for each microhabitat type (assuming that the number of individuals should be proportionally equivalent to the surface covered by the microhabitat type under a null hypothesis of no habitat selection), and compared them with the observed numbers using Chi-square tests (e.g. Castilla & Bauwens, 1992; Galán, 1994). To determine microhabitat preference, we calculated Ivlev's electivity index (Ivlev, 1961; see also Cock, 1978; Krebs, 1989).

#### ACTIVITY

To record frog diel activity, we surveyed the numbers of adult and juvenile specimens along the pond shore over seven days (18, 19, 22, 23, 24, 26, 28 July) at three-hour intervals (eight surveys per day). We distinguished between frogs sitting (1) in the water, (2) on the shore (< 1 m from the water; generally frogs which needed only one jump to reach the water), and (3) frogs sitting 1–3 m from the water. Water temperature ( $\pm 0.1^\circ\text{C}$ ) was measured at one shallow plot (water depth ca. 10 cm) of the Ibón de las Ranas at the end of each survey using a digital thermometer. Minimum and maximum air temperatures were obtained from the Respomuso meteorological station. Each 24 hr interval was completed by the same researcher or team of researchers (generally two people). Data are therefore comparable within each 24 hr period, but comparison of numbers among the seven days must be done more cautiously as different workers had different abilities to detect frogs.

#### RESULTS

##### MICROHABITAT CHOICE

In the four surveys, a total of 2537 observations were made (677 adults, 1860 juveniles). *Rana temporaria* used all microhabitats available in the study

TABLE 1. Absolute and relative (as percentages) numbers of adult (Ad.) and juvenile (Juv.) *Rana temporaria* observed during four surveys at (1) 1200-1400 hrs; (2) 1900-2100 hrs; (3) 2300-0100 hrs; and (4) 0700-0900 hrs in the study area, separately for 12 microhabitat classes as defined in Materials and Methods.

| microhabitat type | % microhabitat | Ad. 1   | Ad. 2   | Ad. 3   | Ad. 4    | Ad. 1-4  | Juv. 1   | Juv. 2   | Juv. 3  | Juv. 4 | Juv. 1-4 | Total (Ad. + Juv.) |
|-------------------|----------------|---------|---------|---------|----------|----------|----------|----------|---------|--------|----------|--------------------|
| pasture           | 39.6%          | 16(9%)  | 12(8%)  | 19(11%) | 2(1%)    | 49(7%)   | 126(13%) | 13(16%)  | 7(11%)  | 6(75%) | 270(15%) | 319(13%)           |
| scree             | 17.9%          | 1(<1%)  | 0(0%)   | 0(0%)   | 0(0%)    | 1(<1%)   | 0(0%)    | 0(0%)    | 0(0%)   | 0(0%)  | 0(0%)    | 1(<1%)             |
| pond surface      | 15.3%          | 25(14%) | 21(14%) | 77(45%) | 171(96%) | 294(43%) | 1(<1%)   | 1(<1%)   | 8(13%)  | 2(25%) | 12(1%)   | 306(12%)           |
| rock surface      | 12.0%          | 1(<1%)  | 1(1%)   | 0(0%)   | 0(0%)    | 2(<1%)   | 0(0%)    | 4(1%)    | 0(0%)   | 0(0%)  | 4(<1%)   | 6(<1%)             |
| boulders          | 5.0%           | 0(0%)   | 2(1%)   | 0(0%)   | 0(0%)    | 2(<1%)   | 0(0%)    | 0(0%)    | 0(0%)   | 0(0%)  | 0(0%)    | 2(<1%)             |
| subalpine shrubs  | 4.0%           | 5(3%)   | 2(1%)   | 2(1%)   | 0(0%)    | 9(1%)    | 0(0%)    | 1(<1%)   | 0(0%)   | 0(0%)  | 1(<1%)   | 10(<1%)            |
| pond shore        | 2.4%           | 91(52%) | 56(37%) | 44(26%) | 2(1%)    | 193(29%) | 192(19%) | 66(8%)   | 11(18%) | 0(0%)  | 269(15%) | 462(18%)           |
| dry brooks        | 1.1%           | 3(2%)   | 1(1%)   | 1(1%)   | 1(1%)    | 6(1%)    | 104(11%) | 42(5%)   | 1(2%)   | 0(0%)  | 147(8%)  | 153(6%)            |
| scattered pines   | 0.8%           | 0(0%)   | 0(0%)   | 0(0%)   | 0(0%)    | 0(0%)    | 0(0%)    | 0(0%)    | 0(0%)   | 0(0%)  | 0(0%)    | 0(0%)              |
| rocky pond shore  | 0.8%           | 19(11%) | 31(20%) | 0(0%)   | 0(0%)    | 50(7%)   | 8(1%)    | 2(<1%)   | 0(0%)   | 0(0%)  | 10(1%)   | 60(2%)             |
| brooks            | 0.7%           | 6(3%)   | 4(3%)   | 12(7%)  | 2(1%)    | 24(4%)   | 331(34%) | 102(13%) | 7(11%)  | 0(0%)  | 440(24%) | 464(18%)           |
| marsh/puddles     | 0.4%           | 9(5%)   | 22(15%) | 16(9%)  | 0(0%)    | 47(7%)   | 22(23%)  | 456(57%) | 27(44%) | 0(0%)  | 707(38%) | 754(30%)           |
| Total             | 100%           | 176     | 152     | 171     | 178      | 677      | 986      | 805      | 61      | 8      | 1860     | 2537               |

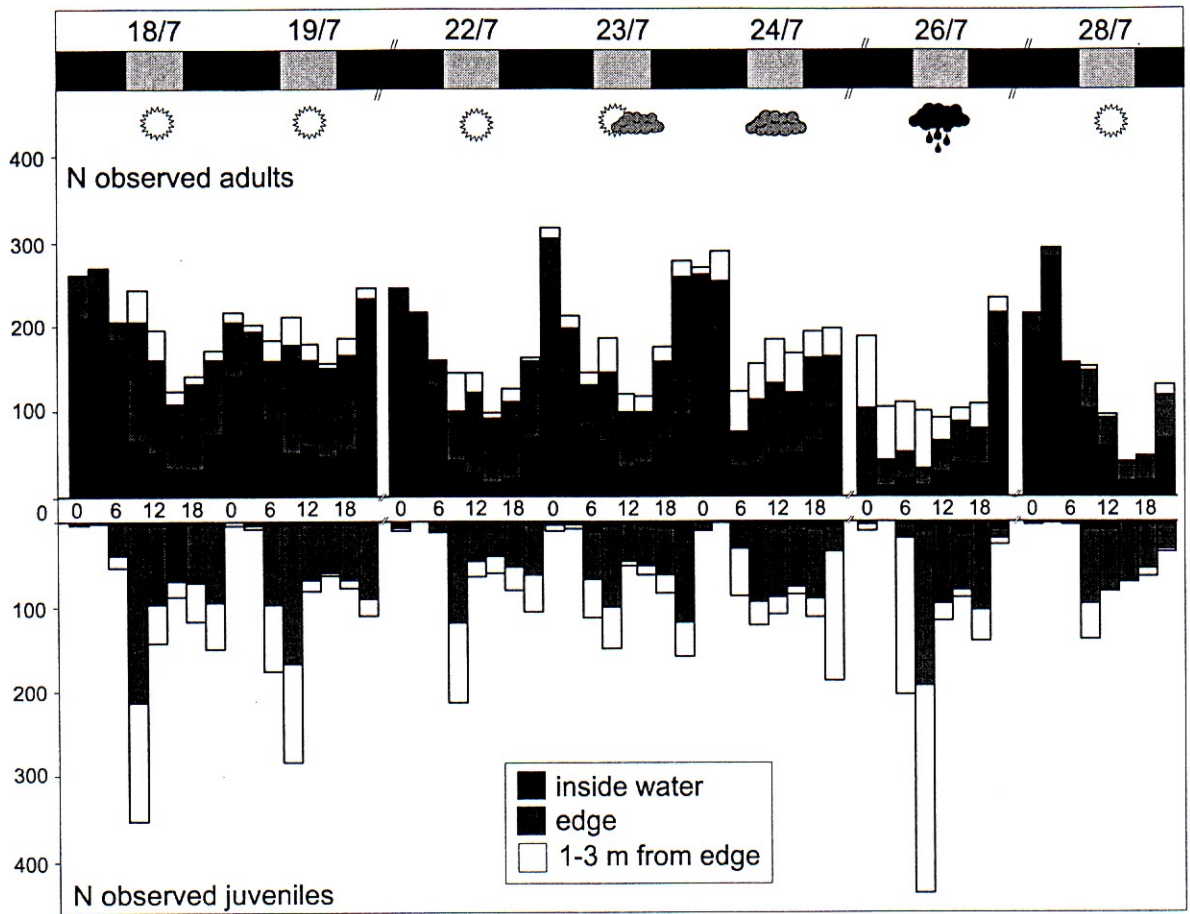


FIG. 1. Activity (total number of observed frogs, separately for adults and juveniles) of *Rana temporaria* as recorded during 3hr-interval surveys on 7 days and nights around the Ibón de las Ranas pond. The upper bar gives approximate timing of light, dusk/dawn and darkness, and general meteorological conditions.

area except for ‘scattered pines’. In ‘scree’ and ‘boulders’, only one or two individuals were observed (Table 1). Total numbers of observations (adults + juveniles) in the different microhabitats were not directly related to the area covered by each microhabitat type. This result is highly supported by the statistical analysis ( $\chi^2=70691.5$ ,  $df=10$ ,  $P<0.0001$ ; microhabitat type ‘scattered pines’ excluded from analysis). Considering adults and juveniles together, many more specimens than expected by chance alone were observed in the microhabitats ‘pond shore’, ‘rocky pond shore’, ‘marsh/puddles’, ‘brooks’ and ‘dry brooks’. On the contrary, fewer individuals than expected were seen in the microhabitats ‘pastures’, ‘subalpine shrubs’, ‘boulders’, ‘scree’ and ‘rock surface’. Highly significant differences were found when comparing the numbers of adults and juveniles found in each microhabitat type ( $\chi^2=21250.1$ ,  $df=8$ ,  $P<0.0001$ ; microhabitat types ‘scattered pines’, ‘boulders’ and ‘scree’ excluded from analysis). Most adults were observed in the ‘pond’ microhabitat (43% of the observations) which harboured almost no juveniles (1%). On the other hand, juveniles were mainly observed in the ‘marsh/puddles’ (38%) and ‘brooks’ (24%) microhabitats which were used only by a few adults (7% and 4%, respectively).

Ivlev’s electivity indices are summarized in Table 2. They indicate the degree to which the number of frogs observed in a certain microhabitat differs from the number expected from the area covered by this

microhabitat when assuming a random distribution of frogs. In adult *R. temporaria* the highest values were those of the microhabitats ‘marsh/puddles’, followed by ‘pond shore’, ‘rocky pond shore’, ‘brooks’ and ‘pond surface’. The remaining microhabitat types were used less frequently than expected (Ivlev’s indices  $<0$ ). In juveniles, ‘marsh/puddles’ and ‘brooks’ had the highest indices, followed by ‘dry brooks’ and ‘pond shore’; all other microhabitat types had negative indices. The main differences between adults and juveniles were the negative values of ‘pond surface’ and ‘rocky pond shore’ in juveniles (positive values in adults) and the negative value of ‘dry brooks’ in adults (positive value in juveniles).

ACTIVITY

During the seven survey days, we made a total of 14755 observations (9695 adults, 5060 juveniles). The recorded absolute numbers of adult and juvenile frogs in each time interval are shown in Fig. 1. The percentages of adults (Fig. 2) and juveniles (Fig. 3) active in water, at the pond edge, and at 1-3 m distance from the pond edge is given separately for the six days without rainfall and for the single 24 hr period in which precipitation was recorded. Adults were active at night as well as during the day, with the highest numbers recorded during the night and early morning (before dawn). The number of adult frogs seen at night (sum of numbers at 2100 hr, 0000 hr, 0300 hr, 0600 hr: 5752 specimens)

TABLE 2. Ivlev's electivity index (Ivlev 1961) of microhabitat types, calculated for adult and juvenile *Rana temporaria* in the study area (from total numbers of adults and juveniles in Table 1).

| microhabitat     | adults | juveniles |
|------------------|--------|-----------|
| pastures         | - 0.69 | - 0.46    |
| scree            | - 0.98 | -         |
| pond surface     | + 0.48 | - 0.92    |
| rock surface     | - 0.95 | - 0.96    |
| boulders         | - 0.89 | -         |
| subalpine shrubs | - 0.50 | - 0.98    |
| pond shore       | + 0.84 | + 0.72    |
| dry brooks       | - 0.11 | + 0.76    |
| scattered pines  | -      | -         |
| rocky pond shore | + 0.80 | - 0.19    |
| brooks           | + 0.67 | + 0.94    |
| marsh/puddles    | + 0.89 | + 0.98    |

was significantly higher ( $\chi^2=337.5$ ,  $df=1$ ,  $P<0.0001$ ) than that observed during the day (sum of numbers at 0900 hr, 1200 hr, 1500 hr, 1800 hr: 3943 specimens). At night, a higher percentage of frogs was seen in the water (3739 out of 5752 individuals; 65%) than during the day (1192 out of 3943; 30%); the difference was highly significant ( $\chi^2=2095.8$ ,  $df=1$ ,  $P<0.0001$ ).

The water temperature of the pond was rather stable in the study period, with recorded temperatures in shallow areas near the shore between 15.8 and 22.5°C. According to the data in Table 3, the difference between minimum and maximum water temperatures in the seven study days (mean=4.37°C, SD=1.37°C, range=1.8-5.0°C) was much smaller than the difference

between minimum and maximum air temperatures (mean=8.94°C, SD=3.08°C, range=5.8-13.8°C) as recorded by the Respomuso meteorological station (Mann-Whitney *U*-test,  $P<0.01$ ). Minimum air temperatures were always lower than minimum water temperatures (mean difference=6.5°C, SD=2.39°C, range=4.2-9.6°C). Water and air temperatures generally reached their minimum values in the early morning (0600 hr) according to our personal observations. The percentage of adult frogs observed in the water at that time (Table 3) was negatively correlated with the minimum air temperature ( $r=-0.87$ ;  $P<0.05$ ; Fig. 4).

The highest numbers of frogs 1-3 m from the shore was observed in the morning at 0900 hr on four out of the five cloudless days (Figs. 1-2). On the single rainy day, the activity of the adult frogs changed markedly, with an overall higher percentage of active frogs out of the water, and less difference in observed numbers between day and night (Fig. 2).

Juveniles showed a distinct difference in activity between day and night. Numbers of juveniles observed during the six sunny days decreased by 94% from 2100 hr to 0000 hr (748 observed specimens at 2100 hr; 46 observed specimens at 0000 hr). The number of juveniles seen at night (sum of numbers at 2100 hr, 0000 hr, 0300 hr, 0600 hr: 1507 specimens) was significantly lower ( $\chi^2=989$ ,  $df=1$ ,  $P<0.0001$ ) than during the day (sum of numbers at 0900 hr, 1200 hr, 1500 hr, 1800 hr: 3553 specimens). Observed number of juveniles was highest on the single rainy day (Fig. 1), but the reduction in activity at night was similarly drastic. No relevant differences were observed in percentages of juveniles in the water, at the shore or 1-3 m from the

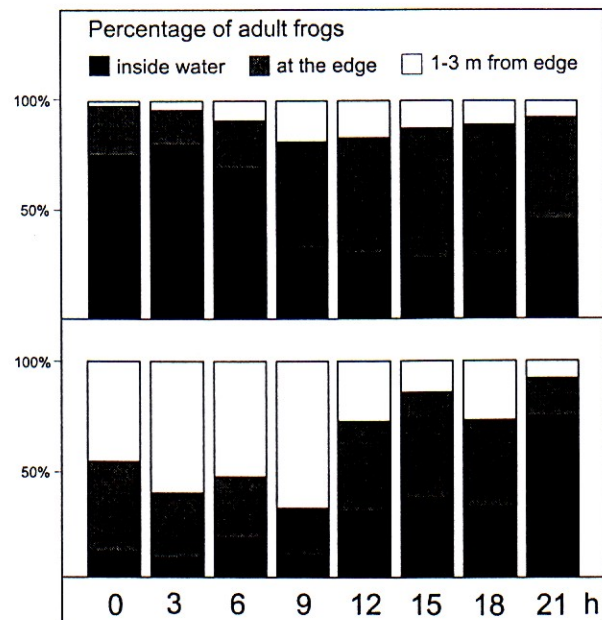


FIG. 2. Percentage of adult *Rana temporaria* in water (black), at the pond edge (grey) and 1-3 m from pond edge (white) recorded in each 3h-interval survey around the Ibón de las Ranas pond. The upper bars indicate the percentages summarized for the six cloudless days and nights (18, 19, 22, 23, 24 and 28 July) and the lower bars indicate the percentages on one rainy day and night (26 July).

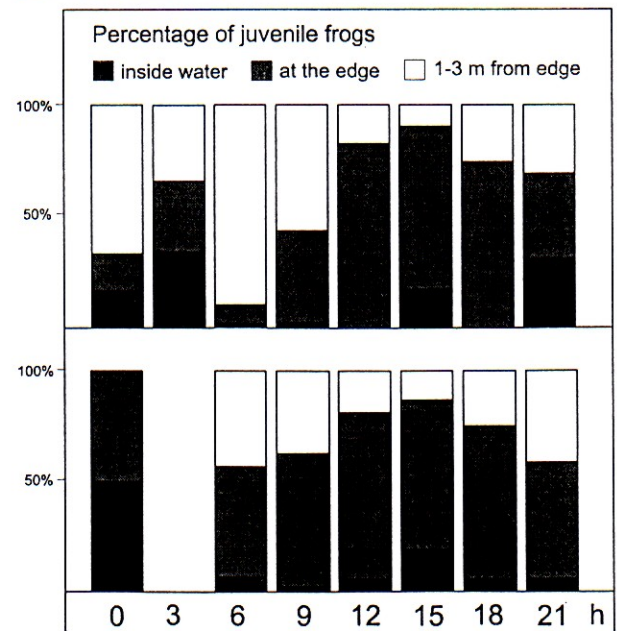


FIG. 3. Percentage of juvenile *Rana temporaria* in water (black), at the pond edge (grey) and 1-3 m from pond edge (white) recorded in each 3h-interval survey around the Ibón de las Ranas pond. The upper bars indicate the percentages summarized for the six cloudless days and nights (18, 19, 22, 23, 24 and 28 July) and the lower bars indicate the percentages on one rainy day and night (26 July). No juveniles were found during the 0300 survey on 26 July.

TABLE 3. Number and percentage of adult frogs observed in the water at 0600 hr (relative to total number of frogs observed at that time) over the seven study days. Minimum and maximum temperatures of water (own measurements in a shallow area near the shore of the Ibón de las Ranas) and air (Respomuso meteorological station) are given for the preceding 24 hours.

|                                    | 18 July | 19 July | 22 July | 23 July | 24 July | 26 July | 28 July |
|------------------------------------|---------|---------|---------|---------|---------|---------|---------|
| $T_{\max}$ (water)                 | 20.9°C  | 21.9°C  | 21.4°C  | 20.5°C  | 19.5°C  | 22.5°C  | 20.5°C  |
| $T_{\max}$ (air)                   | 19.0°C  | 19.6°C  | 20.0°C  | 17.0°C  | 19.6°C  | 20.0°C  | 20.0°C  |
| $T_{\min}$ (water)                 | 15.9°C  | 17.1°C  | 16.9°C  | 16.9°C  | 17.8°C  | 16.3°C  | 15.8°C  |
| $T_{\min}$ (air)                   | 10.0°C  | 12.0°C  | 7.6°C   | 11.2°C  | 13.6°C  | 12.0°C  | 6.2°C   |
| Total no. observed frogs (0600 hr) | 204     | 181     | 159     | 144     | 121     | 108     | 155     |
| Percent frogs in water (0600 hr)   | 88.7%   | 48.6%   | 79.9%   | 56.3%   | 27.3%   | 18.5%   | 99.4%   |

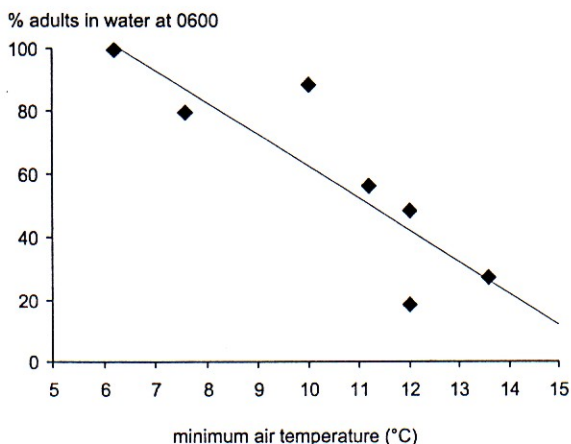


FIG. 4. Scatterplot of the percentage of adult *Rana temporaria* observed in water at 0600 hr vs. minimum air temperature as recorded by the Respomuso meteorological station on the corresponding night (regression analysis:  $y = 10.21x + 165.7$ ;  $r^2 = 0.76$ ,  $df = 1, 6$ ;  $F = 15.84$ ,  $P < 0.05$ ).

shore between the six cloudless days and the single rainy day (Fig. 3).

Some of these activity patterns of adults (higher percentage of specimens in the pond at night) and juveniles (almost exclusively diurnal activity) were also evident among the four surveys done for the microhabitat preference analysis (see Table 1).

## DISCUSSION

In the study area and period, adult and juvenile *Rana temporaria* were largely dependent on aquatic or moist microhabitat types. The poorly used microhabitats (see Table 2) were in a very dry condition in July 1998. A temporary reduction in activity, or aestivation, may not be advantageous in the Circo de Piedrafita area considering the shortness of the activity period in montane areas (see Elmberg & Lundberg, 1991). The frogs were therefore probably forced to remain active in the brook and dry brook areas, marshes, puddles, and in and around the pond. The adults especially used the pond as summer habitat, and showed more aquatic habits during the night than during the day. According to the mark-recapture data of Vences *et al.* (1999), about 770 adults were present in and around the pond during the study period, of which by far the majority (93%) were males.

Despite the rather low sample size (data only available for seven days), our results indicated that the

percentage of adult frogs active in the pond at night increased as air temperature decreased. Water temperature was less variable than air temperature, and minimum air temperature values were clearly lower than minimum water temperatures. In the Circo de Piedrafita, night-time temperatures may drop to values around 0°C even in summer. The Respomuso meteorological station recorded 3.0°C on 2 July 1998. It can therefore be concluded that the adult frogs appear to use the pond at least partly as a refuge from the cold. Also, the rather high degree of diurnal activity of adults at the Ibón de las Ranas (not found by Loman, 1980, in a low altitude population) may be explained by the relatively low temperatures at night.

The juveniles differed both in microhabitat choice and activity from the adults. The pond was used very little by juveniles, and their activity was almost exclusively diurnal. This corresponds partly with the observations of Loman (1980) who also found largely diurnal activity in juvenile *R. temporaria*. There are several possible reasons underlying this niche segregation of adults and juveniles. (1) Adults and juveniles of the same frog species may differ in prey preference. Since we did not study prey availability in the different microhabitat types, no statements are currently possible concerning this factor. (2) Predator avoidance may also influence juvenile activity cycles. The niche segregation may even be related to cannibalism; in several analysed stomach contents of adult *R. temporaria* from the Ibón de las Ranas, we found juvenile frogs (D. R. Vieites & S. Nieto, pers. obs. in 1998). Considering the high population density of adults, they may constitute one of the most important predators of the juvenile frogs. (3) It also may be important that *R. temporaria* tadpoles are largely day-active (Griffiths, 1985; Piqué *et al.*, in press), as with many pond dwelling anuran larvae which generally show a positive phototaxis (Duellman & Trueb, 1986). The possibility therefore cannot be excluded that frogs may only change later in development to a more nocturnal activity pattern. (4) Most probably, the activity patterns of juveniles are heavily influenced by climatic factors. Juvenile frogs are clearly more sensitive to rapid air temperature decreases with the risk of freezing (Pasanen & Karhapää, 1997). Also, they are less mobile than adult frogs, and may thus not be able to reach soon enough larger, warm water bodies when temperatures begin to decrease

quickly. It may therefore be an advantage for juveniles to shelter soon after dusk to avoid the danger of freezing.

Some information is available on the fact that high-mountain populations of *R. temporaria* can be aquatic all-year-round (Combes, 1967; Nöllert & Nöllert, 1992; Serra-Cobo *et al.*, 1998). However, often the pattern observed in lowland areas (spring and occasional autumn migration to the breeding site; terrestrial summer habitat; see Loman, 1978; Strijbosch, 1980; Verrell & Halliday, 1985; Hintermann, 1984; Ryser, 1986; Kneitz, 1998) is believed to be typical for the species (e.g. Esteban, 1997). Many of the habitat types generally used by the common frog in lowlands, such as meadows and forest (Loman, 1978), forest, coppice strips, pastures and meadows (Strijbosch, 1980), gardens, chalk, greensands, deciduous woods (Beebee, 1985), meadows and leaf litter (Galán, 1989) and coniferous forest (Pasanen *et al.*, 1993) are not found or are less common in alpine environments.

As a conclusion from the results presented here, literature data, and our own, informal observations on many additional populations, adult common frogs at high altitudes tend to have rather aquatic habits during summer, and to show a high degree of daytime activity. These patterns may be a response to (1) increased aridity of the terrestrial environments at high altitudes where no forest cover with associated leaf litter layer is present, and (2) the low nocturnal air temperatures and the danger of a sudden drop in temperature in an unpredictable environment.

The differences between montane and lowland populations of *Rana temporaria*, however, do not only extend to microhabitat choice and activity of adults. Montane populations show an accelerated larval development at certain temperatures (Aebli, 1966; Angelier & Angelier, 1968; Brand & Grossenbacher, 1979) which probably leads to differences in tadpole morphology (Vences *et al.*, 1998), differences in colour pattern (increased number and size of black spots: Nöllert & Nöllert, 1992), shorter hindlimbs (e.g. Vences *et al.*, 1998), modified time allocation during the breeding period (Elmberg & Lundberg, 1991), and older age at maturity (Miaud *et al.*, 1999). This variation, at least in the Pyrenees, does not appear to be correlated with relevant genetic differentiation (unpublished allozyme data of M. Veith and M. Vences). Detailed long-term comparative studies on neighbouring high- and low-altitude populations of *Rana temporaria* will therefore probably allow the identification of further morphological, ecological and ethological adaptational responses of anurans to the selective pressures of alpine environmental conditions.

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