

Reproductive Phenology and Temporal Patterns of Mate Access in Mediterranean Anurans

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Many temperate amphibians migrate annually to breeding ponds. The beginning and duration of the breeding period are influenced by meteorological factors, such as rainfall and temperature (Salthe and Mecham, 1974; Semlitsch, 1985), as well as biotic factors, such as interspecific competition (Wilbur, 1980; Crump, 1982) or factors influencing larval development (Wilbur, 1987). While much work has been directed at examining which males mate on a given night, little effort has been directed at determining how social conditions change throughout the breeding season.

In meridional areas of temperate regions (such as mediterranean areas in Europe), breeding periods are very short. Few studies have analyzed the reproductive phenology of mediterranean amphibians (Alvarez and Salvador, 1984; Díaz-Paniagua, 1986; Salvador et al., 1986; Rodríguez, 1988). In this report we examine the possible influence of environmental factors on the initiation of breeding and number of individuals participating in chorus activity during the breeding period in a temporary pond in northern Spain. We also examine how the sex ratio and average male and female body sizes vary throughout the breeding season.

In 1984 we studied a seasonal pool in Chozas de Arriba (42°31'N, 05°12'W; 830 m), León Province, Spain. The climate is continental Mediterranean, with cold winters (mean temperatures: January = 5.4 C, July = 24.6 C). The pool was part of a small lake complex which contained some permanent pools. The study pool was roughly 95 × 30 m with a maximum depth of 60 cm in late February; in August it dried completely. On three occasions we measured water depth at 44 regularly spaced points across the pool. The mean water depth was 14.3 cm on 31 March, 12.7 cm on 15 April and 11 cm on 30 April. The deepest part was densely covered in vegetation (among other plants *Juncus* sp., *Littorella uniflora*, *Ranunculus aquatilis*, and *Myriophyllum* sp.). The features of the area are described in more detail in Alvarez and Salvador (1984).

The pool was searched systematically an average of seven times each night for 84 consecutive nights, between sunset and 0200 h, from 15 February to 9 May. Each anuran was toe-clipped and its species, sex, and snout-vent length noted. Air and water temperatures were measured every night at 2200 h. In addition, relative humidity data at 1800 h and precipitation data from the nearest meteorological station (6 km) were collected. Phenology was analyzed after grouping the 84 nights into 12 one-week periods.

The significance of phenological differences (interspecific, and sexual within each species) was tested by means of chi-square comparisons applied to the proportion of individuals belonging to each species or sex that were encountered weekly (numbers were always counted over seven sampling nights). A stepwise multiple regression analysis was used to analyze the association between the daily number of amphibians and the environmental variables throughout the three weeks of highest abundance (21 days for each of the four species; Fig. 1). Parametric tests were performed on log-transformed data (Sokal and Rohlf, 1981).

Pelobates cultripes and *Bufo calamita* were the first two species to arrive at the pool (17 and 19 March, respectively). Two weeks later *Rana perezi* (31 March) and *Hyla arborea* (3 April) appeared. The length of the breeding period (calendar difference between the last and first days each species was observed) was 49 days for *B. calamita*, 41 days for *P. cultripes*, 40 days for *R. perezi*, and 36 for *H. arborea*. The phenology of the four species differed significantly (chi-square test performed with the number of individuals observed in 11 weeks grouped in eight periods: $\chi^2 = 783.3$, 21 df, $P < 0.001$). Two species pairs had synchronous phenological patterns: *B. calamita*-*P. cultripes* and *R. perezi*-*H. arborea*. There were no significant differences between sexes for *R. perezi* ($\chi^2 = 6.3$, 4 df, $P > 0.1$) and *H. arborea* ($\chi^2 = 4.7$, 4 df, $P > 0.1$). Females reached higher abundances before males (tests performed with the number of individuals observed in 11 weeks grouped in five periods: *P. cultripes*; $\chi^2 = 11.7$, 4 df, $P = 0.02$; *B. calamita*; $\chi^2 = 10.9$, 4 df, $P < 0.05$) (Fig. 1).

The daily abundance of *P. cultripes* was positively correlated with water temperature ($r = 0.43$, $N = 21$, $P < 0.05$) and amount of rainfall on the preceding day ($r = 0.46$, $N = 21$, $P < 0.05$). These two variables accounted for 27.4% of the observed variance. For *B. calamita*, the daily variation in number of individuals was marginally correlated with air temperature ($r^2 = 17.1\%$, $N = 21$, $P = 0.06$). The abundance of *R. perezi*

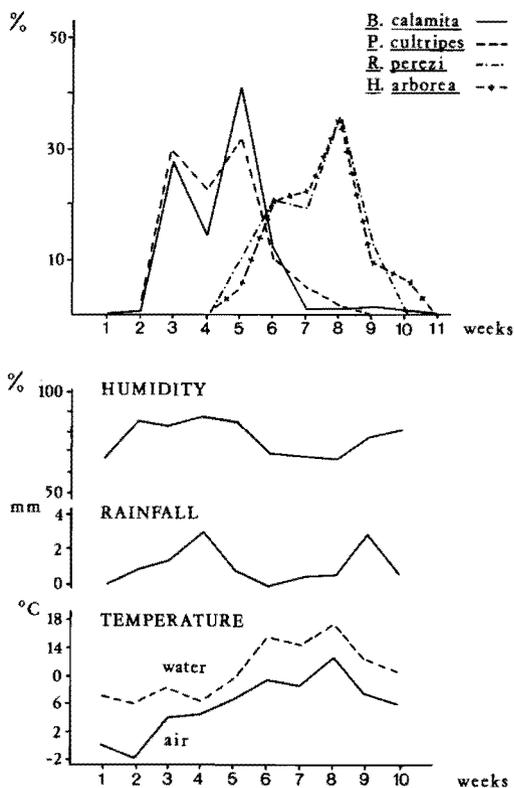


FIG. 1. Weekly variation in the percentage of individuals observed in breeding activity, and of the meteorological variables (week 1 = 3-9 March).

was significantly correlated with air temperature ($r^2 = 35\%$, $N = 21$, $P < 0.01$). Finally, for *H. arborea* the number of individuals observed each day was correlated with water temperature ($r^2 = 43.4\%$, $N = 21$, $P < 0.01$).

Length of breeding period of the four species was inversely correlated with the variance explained by the meteorological variables ($r = -0.97$, $N = 4$, $P < 0.05$). This indicates that the species least dependent on the meteorological variables have the most prolonged breeding periods.

The percentage of males observed for the entire season was higher than the percentage of females for all four species (*B. calamita*, 68%, $N = 94$; *P. cultripes*, 62%, $N = 101$; *R. perezi*, 70%, $N = 194$; *H. arborea*, 84%, $N = 175$; these percentages differ significantly [$P < 0.05$] from 50%). The mean nightly sex ratio (male:female) for *P. cultripes* was 2.4:1; comparable values were 3.7:1 for *B. calamita*, 2.6:1 for *R. perezi*, and 26.2:1 for *H. arborea*.

The frequency of nights of capture per individual differed significantly among the four species ($\chi^2 = 122.7$, 6 df, $P < 0.001$). Males of *H. arborea* on average stayed a greater number of nights than did those of other species (5.2 nights; $P < 0.001$ and 2 df for all three pairwise comparisons with the remaining species: *R. perezi*, $\chi^2 = 95.1$; *B. calamita*, $\chi^2 = 31.8$; and *P. cultripes*, $\chi^2 = 42.5$). The males of the other three species stayed an average of 1.4-2.2 nights; male *B. cal-*

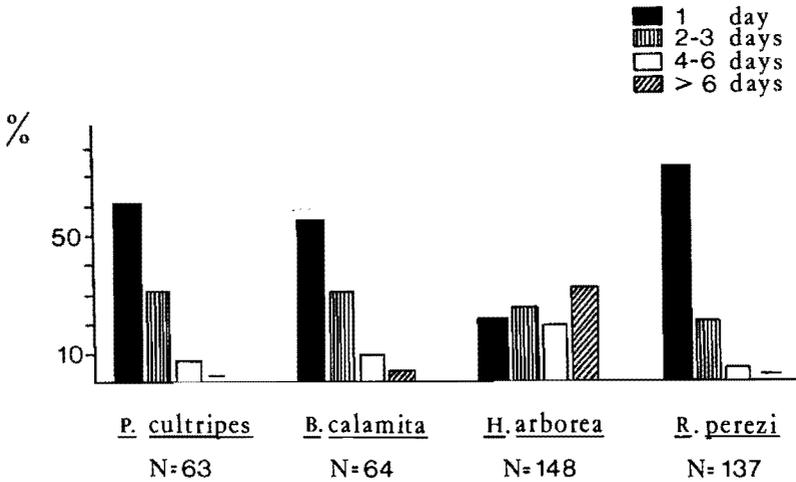


FIG. 2. Percentage of capture-recapture nights for the males of the four anuran species.

amita were present longer than *R. perezi* ($\chi^2 = 8.5$, $P < 0.05$).

Females of the four species stayed on average only one night in the pool (the percentages of females present for one night were: 95% for *P. cultripes*; 77% for *B. calamita*; 82% for *R. perezi*; and 82% for *H. arborea*). For three of the species, females spent significantly less time at the pool than did males (*P. cultripes*, $\chi^2 = 12.6$, $P < 0.001$; *B. calamita*, $\chi^2 = 4.2$, $P < 0.05$; *H. arborea*, $\chi^2 = 35.6$, $P < 0.001$). For *R. perezi* the difference was not significant ($\chi^2 = 1.2$, $P > 0.1$) (Fig. 2).

The mean size of individuals of each species varied daily throughout the breeding season, when considering the size of individuals on their first night of capture. In *P. cultripes* and *H. arborea* male size decreased as the breeding period advanced (correlations of snout-vent length with day order since 3 March: $r = -0.48$, $N = 61$, $P < 0.001$, and $r = -0.27$, $N = 147$, $P < 0.01$, respectively). For *B. calamita* and *R. perezi* these correlations were not significant ($r = 0.02$, $N = 64$, $P > 0.1$, and $r = -0.03$, $N = 137$, $P > 0.1$, respectively). For three of the species, female size decreased significantly as the breeding season progressed (*P. cultripes*, $r = -0.43$, $N = 35$, $P < 0.001$; *B. calamita*, $r = -0.62$, $N = 28$, $P < 0.01$; *H. arborea*, $r = -0.59$, $N = 27$, $P < 0.01$). However, for *R. perezi*, it increased significantly ($r = 0.50$, $N = 56$, $P < 0.001$).

The temporal pattern of breeding in these species agrees with that described in the southwestern Iberian Peninsula (Díaz-Paniagua, 1986; Rodríguez, 1988). However, in the northwestern Iberian Peninsula (our study area) the dates of the onset of breeding are later than in the southwest. Moreover, the duration of the breeding season of these species shows a marked decrease with latitude. These differences suggest that as latitude decreases and temperature increases, the breeding period begins earlier and lengthens (Baldauf, 1952; Douglas, 1979). The influence of temperature in the daily abundance of species in our study area was probably due to low values in winter, in contrast to the southwestern Iberian Peninsula (av-

erage temperature above 10 C). A similar result has been reported for populations of amphibians in the southern United States (Semlitsch, 1981, 1983; Semlitsch and McMillan, 1980).

The analysis of daily fluctuations in individual numbers demonstrates that weather conditions play an important role in determining the abundance of these four species in the pool during the breeding season. However, meteorological variables only explain a limited amount of the variance (Semlitsch, 1985). The mean nightly sex ratio was positively correlated across species with the mean number of nights in which males were caught ($r = 0.99$, $N = 4$, $P = 0.01$). Males may stay longer to compensate for a high degree of competition for mates as the number of females decreases (see Kluge, 1981, and Godwin and Roble, 1983 for similar results).

The reduction in size of males as the season progresses may be related to competition between males for mates (Davies and Halliday, 1977; see Arak, 1983 for a review). Smaller males may arrive later to reduce competition for mates with other larger males, or because small males mature later. A similar pattern of decrease in size of the females can be explained if the females prefer an optimum-sized male to increase fertilization success (Davies and Halliday, 1977). Thus, larger females may arrive earlier to find males of similar size (Arak, 1983). The positive correlation between size and dates for female *R. perezi* cannot be explained by such arguments. Our data show that the proportion of females in the first half of the breeding period of *R. perezi* (23%) is significantly less than in the second half of the breeding season (34%; $\chi^2 = 3.8$, $P = 0.05$).

Though our results point out the importance of reproductive phenology to intrasexual competition and mate access in these anuran species, additional work is needed to document the significance of male-biased sex ratios for the action of sexual selection in this and similar systems. Elucidation of the factors responsible for seasonal variation in the sizes of in-

dividuals participating in breeding activity (e.g., investigation of growth and maturation rates) also awaits study.

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