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Breeding Phenology of an Amphibian Community in a Mediterranean Area

Here we studied the temporal breeding patterns and strategies of anuran assemblages in the Mediterranean region over five consecutive years. We collected monthly data on the number of clutches, tadpoles and metamorphic presence of six species in 98 ponds. The data showed a great seasonal temporal segregation of species. The breeding peak of those in permanent ponds was related to temperature whereas for temporary pond breeders rainfall pulses determined reproductive success. Many species showed a great plasticity of reproduction with two peaks: one in spring and the other in autumn. In spite of this temporal segregation, a large time overlap during the larval phase was observed among species. Three showed (*A. obstetricans*, *P. punctatus* and *R. perezi*) over-wintering tadpoles. Here we discuss temporal segregation, the differences in the breeding strategies among species, and variable conditions among years as factors that may favour the temporal coexistence of species in the Mediterranean region.

INTRODUCTION

Phenological patterns contribute to determining the temporal structure of communities because they represent physiological and morphological adaptations to resource use. In this context, these patterns may indicate that resources are used at different times of the year by distinct species. Coexistence of species can be attributed to the differential use of resources, both spatially and temporally (Ricklefs & Schluter 1993). Studies on amphibian communities in temperate regions agree that pond-breeding amphibian communities are organised along a wetland hydroperiod gradient, ranging from ephemeral ponds to large permanent lakes (Wellborn et al. 1996; Babbitt et al. 2003; Van Buskirk 2003).

In Mediterranean regions, temporary ponds are the main breeding habitats for several amphibian species (Blondel & Aronson 1999; Jakob et al. 2003). Many species often breed in the same pond, therefore, to avoid competition and predation pressure, amphibians often show temporal segregation in use of breeding ponds (Wilbur 1980, 1987; Paton & Crouch

2001); a phenomenon which has been documented in Mediterranean amphibian communities (Salvador & Carrascal 1990; Díaz-Paniagua 1992; Jakob et al. 2003). In these environments, the risk of reproductive failure depends on the length of the hydroperiod and the annual rainfall (Jakob et al. 2003). In dry years, lack of spring precipitations can cause substantial, if not complete, reproductive failure in some amphibians. Unpredictability characterises the ecosystems of the Mediterranean Basin. The climate in this region exhibits high spatio-temporal heterogeneity, from local to regional scales, which consequently results in high temporal and spatial unpredictability of environmental conditions (Blondel & Aronson 1999). In response to this unpredictability, many species show plastic strategies in the onset of breeding or select ponds with a hydroperiod that is adjusted to specific requirements for larval development (Diaz-Paniagua 1990; Morand & Joly 1995; Jakob et al. 2003). The documentation of species' phenology is an important first step to develop good management practices for the conservation of amphibian diversity (Paton & Crouch 2002), especially in Mediterranean regions, for which a link between diversity and environmental unpredictability has been described (Beja & Alcazar 2003; Jacob et al. 2003). This documentation is also crucial for the interpretation of the effects of climatic fluctuations (Stenseth et al. 2002) and changes on amphibian populations (Beebee 1995, 2002; Semlitsch et al. 1996; Blaustein et al. 2001, 2002).

Here we studied the breeding patterns of six anuran species that dominate a littoral Mediterranean region. We examined their breeding strategies over 5 years and studied the way in which phenology may have been determined by the highly variable climatic conditions over the study period.

METHODS

Study site and period

The study was carried out in protected natural areas surrounding Barcelona (NE Iberian Peninsula), including the Natural Park of Garraf and the Metropolitan Park of Collserola. At an altitude of 70-100 m and 2-10 km wide, the coastal plateau runs North-South for about 50 km. It is bordered by a chain of small mountains (maximum 600 m altitude) called the Prelitoral Sierra and holds the Llobregat delta in the middle of the area. The climate in this zone is

Mediterranean, with hot, dry summers, mild winters and two rain periods, one in spring and the other in autumn. The amount of precipitation varies considerably between years in this region (Fig. 1). The hydroperiods of the ponds monitored ranged from ephemeral and temporary ponds to permanent water bodies. Ephemeral pools (ponds contained surface water for a maximum of two months) refilled after each rainfall period. Temporary ponds were flooded by spring and autumn rainfall. The shallowest temporary ponds often dried out in winter, whereas the deepest temporary ponds held water until the end of spring or early summer. It is important to consider that a pond's position on the gradient of hydroperiod could be dynamic, and that especially some temporary ponds change position along this gradient annually in function of climatic conditions (Semlitsch et al. 1996). Some of the deepest ponds remained "permanent" all summer during some years while others dried up from June to August in drought years.

The mean monthly air temperature, precipitation and number of rainfall days were recorded at the "Observatori Fabra" meteorological station, located in the study area. The amphibian community in this zone comprises seven anuran species (*Alytes obstetricans*, *Pelobates cultripes*, *Pelodytes punctatus*, *Bufo calamita*, *Bufo bufo*, *Hyla meridionalis* and *Rana perezi*) and *Salamandra salamandra*, with an introduced and isolated population of *Triturus marmoratus* and *Triturus helveticus* in one locality. We focused our study on the anuran community but excluded *Pelobates* because it is a rare species in the area and few data are available to produce a good description of its phenology.

Sampling methods

To determine reproductive success of species, we counted clutches. Amphibian clutches were sampled monthly in several ponds over five consecutive years (1999-2003). The first year we sampled 42 ponds and increased the number sampled in successive years. During 2001, 2002 and 2003 a total of 98 ponds were sampled. During all years, ponds were systematically searched 2-3 times per month (depending on rainfall) for newly deposited eggs. At smaller sites with little or no vegetation, we conducted an exhaustive sample of the site while at larger deeper sites we sampled the littoral and submerged vegetation zone. We regularly spent up to 30 minutes sampling these ponds until we were satisfied that we had

searched all the main zones of egg deposition for each species. Clutches were identified to species level, marked with a natural signal in order to avoid their inclusion in future visits, and then released. We also deep-netted each pond for tadpoles, sampling banks and all bottom types to detect larvae and metamorphs. Immediately after sampling and identification, these were released back to their ponds of origin. Metamorphs were considered as individuals with forelimbs captured during larvae sampling. The larva sampling effort differed from year to year and from pond to pond, so abundance values are not presented here, but the sampling effort each month was sufficient to document larvae and metamorph phenology for each species and year. These data were finally coded as larval and metamorph presence/absence in a given month and year.

Data analysis

To compare the reproductive effort of each species during the study period, the number of clutches found each month was divided by the sampling effort (number of ponds visited during month and time searching for clutches) to make reproductive effort comparable between years. Sampling effort was not constant during the five years, mainly because of the increase in ponds sampled during the last three.

In contrast to other phenological studies, we did not use the first clutches found of a particular species. We estimated the timing of the seasonal peak throughout the entire breeding season (the central tendency, *T*) using the month co-ordinate of the centre of gravity of the area below graphs of monthly means:

$$T = \frac{\sum_{i=1}^{12} M \cdot x_m}{\sum_{i=1}^{12} x_m}$$

where x_m is the breeding effort in month *M* (January = 1,…December = 12). This is an index that is sensitive to changes in the timing of the seasonal cycle (Edwards & Richardson 2004). The average seasonal cycle over the five-year period for each species was used to determine whether species were unimodal or bimodal breeders. A fundamental difference between temperate regions and many Mediterranean zones is that there is just one breeding period peak in the former but usually two in the latter: one in spring and the other in autumn. At

	R^2	$F_{1, 56}$	p	temperature	precipitation	days of precipitation
Pelodytes punctatus	0.0541	1.0762	0.3666	-0.18	-0.17	0.11
Bufo calamita	0.3567	10.3537	0.00001	**0.231***	**0.342***	**0.305***
Bufo bufo	0.0969	2.0033	0.1239	**-0.28***	-0.08	-0.12
Hyla meridionalis	0.1685	3.7854	0.0152	0.215	**-0.32***	**0.511***
Rana perezi	0.1334	2.8741	0.4418	**0.368***	-0.07	0.180

Multiple regression results. Significant betas are bolded at alpha = 0.05.

Table 1. – Summary of the multiple regression results of the Reproductive effort with the climatic factors considered: monthly air temperature, monthly cumulative precipitation and monthly days of precipitation.

the end of summer and early autumn, the environment reverts back to spring-like conditions with mild temperatures and another peak of precipitation. Consequently, many species display bimodal breeding seasonality. For unimodal species, the timing of the seasonal peak was calculated over the entire year, whereas for bimodal species it was calculated separately for the first six months and the last six months of the year, as in previous studies on other bimodal organisms (Edwards & Richardson 2004). For species with two breeding periods, we compared reproductive effort between both periods with an analysis of variance of the five-year period.

To explore the relationship between the breeding period and climatic fluctuations between years, we correlated the reproductive effort for each species with the climatic data: mean monthly temperature, monthly precipitation and monthly number of rainy days. Standard linear multiple regression was considered appropriate because there was minimal autocorrelation in the phenological time series.

RESULTS

Clutches of all species of Anura were well localised and counted, except *A. obstetricans*. The reproductive behaviour of this species makes it difficult to establish when eggs were laid on water because they hatch in a few hours. Therefore, no data on reproductive effort (number of clutches per unit effort) is available for this species. We documented the presence of small tadpoles in early Gosner stage as an indication of a recent reproductive event but did not
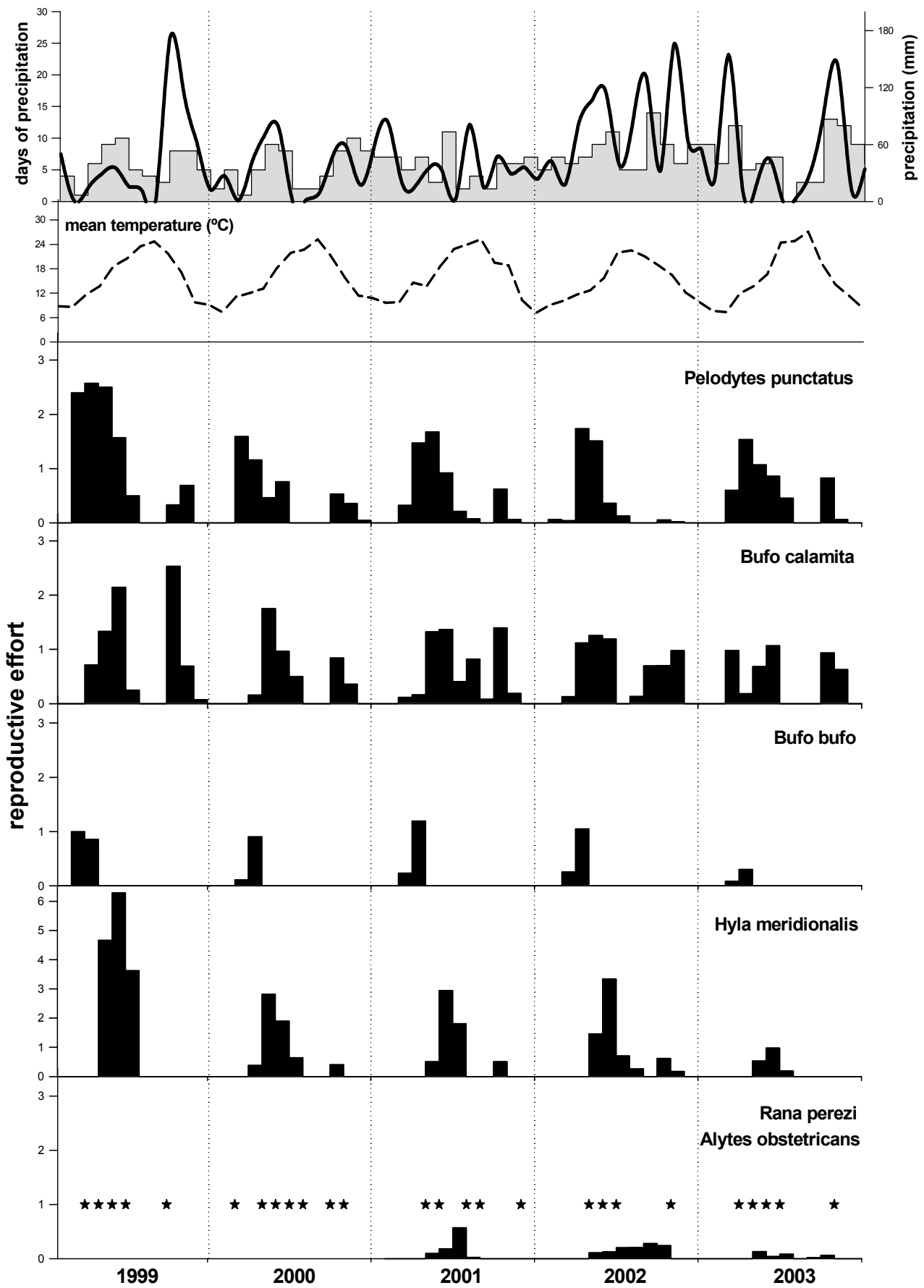
Fig. 1. – Diagram showing the monthly climatic conditions during the five years, and the reproductive effort for each species with the exception of *Alytes obstetricans*. Stars in the top-down figure indicate the observation of *Alytes* tadpoles with early Gosner stages as an indication of recent reproduction event.

count them. Reproductive activities ranged from species with a highly synchronised period (like *B. bufo*) to others that breed during a long period and produce several larval cohorts (e.g. *B. calamita, H. meridionalis, A. obstetricans*)(Fig. 1). Two species showed a date of reproduction in function of temperature. *B. bufo* bred at the end of winter just after year minimums and before temperature increase during spring, thereby showing a negative relationship with temperature. In contrast, *R. perezi* was positively correlated with temperature and its reproductive period extended throughout the summer when temperatures were maximal (Table 1). *B. bufo* showed little variation in the reproductive peak between years, whereas that of *R. perezi* varied. Other species, like *P. punctatus, B. calamita* and *H. meridionalis*, were more plastic in reproductive success, depending on the date of precipitation (Table 1). These species showed higher variation of reproductive peaks between years in function of precipitation peak or the number of rainy days (Fig. 2). However, they showed distinct sensitivities to temperature. For example *P. punctatus* reproduced earlier in spring than the
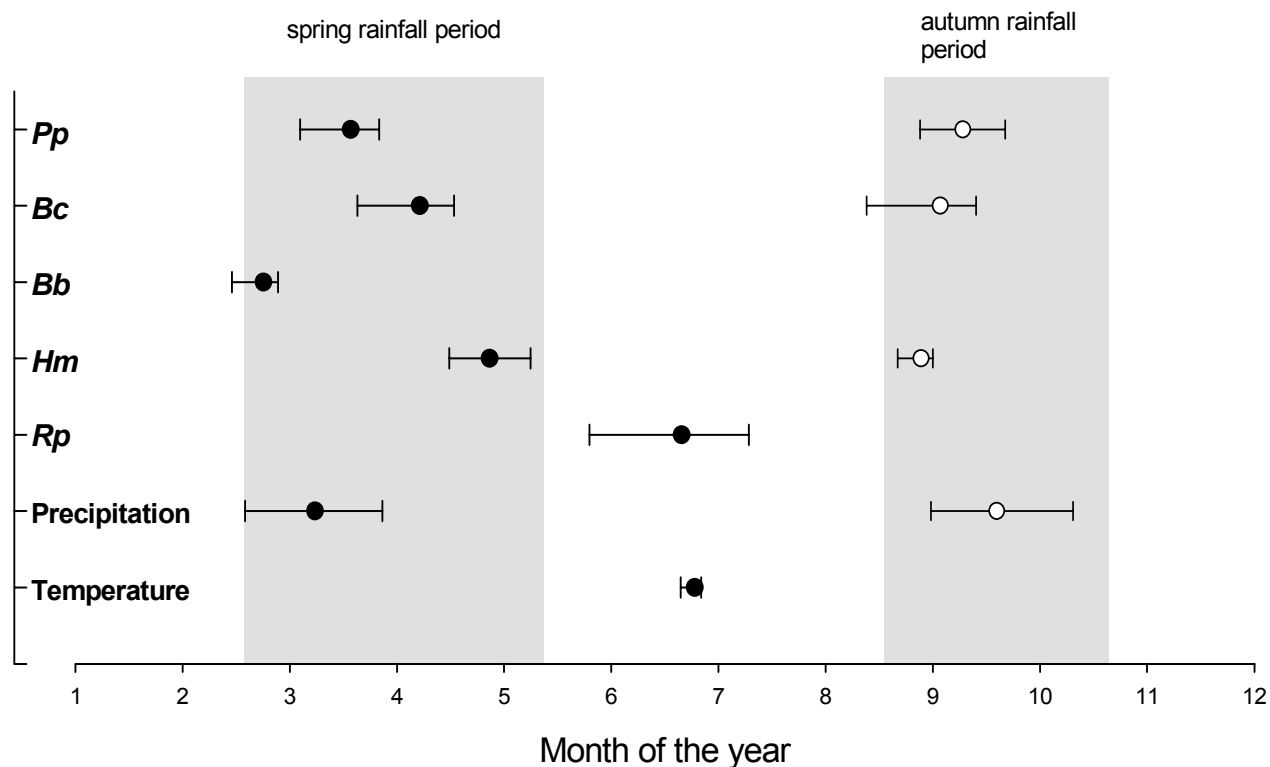

Fig. 2. – Mean of the seasonal peak during the five years of study for each species and for cumulative precipitation and air temperature. Errors bars indicate maximum and minimum values. Black circles indicate spring season, and open circles autumn season. The two grey areas indicate the range of the two rainfall periods in the area of study.

other two species, but later in autumn. *H. meridionalis* was the most thermophile species, breeding later in spring and earlier in autumn than *P. punctatus* and *B. calamita* (Fig. 2). These three species showed a bimodal strategy with a second breeding period in early autumn, which coincided with the precipitation peak at the end of summer. The reproductive effort of *P. punctatus* and *H. meridionalis* differed between the two breeding periods ($F_{1,58}$ = 24.5416; $p < 0.001$ and $F_{1,58}$ = 15.8515; $p = 0.0011$ respectively), with a higher reproductive effort in spring than in autumn. In contrast, the effort observed for *B. calamita* did not differ between periods ($F_{1,58}$ = 0.7578; $p = 0.1523$)(Fig. 3). Based on the detection of larvae in early Gosner stages in ponds, *A. obstetricans* seems to be a continuous breeder during all year with a short pause during the winter. A intensive local study during one year showed a peak of reproduction for *A. obstetricans* in March, but with continuous reproductive events from February to November (unpublished data). Over-wintering tadpoles were observed in successive years for three species: *A. obstetricans*, *P. punctatus* and *R. perezi*, with early metamorphs in spring (Fig. 4). This overlapping of larval cohorts results in an extensive period of metamorph emergence in practically all species, except *B. bufo*, which showed a higher synchronisation of reproduction and metamorph success (Fig. 4).

DISCUSSION

Here we report on the temporal segregation of breeding periods and the reproductive strategies of six anuran species. Two species showed a relatively fixed reproduction date: *B. bufo* and *R. perezi*. All subpopulations of the former were observed to be highly synchronised in time at the end of winter, when the increase in air and water temperatures appear important for initiating reproductive activities, as previously reported (Reading 1998), whereas the reproductive period for *R. perezi* was linked to high temperatures but was extensive during the hottest months, which were more constant between years than rainfall periods or temperatures of winter. This fixed strategy is suitable for species that use permanent or predictable habitats for breeding, as in the case of *B. bufo* and *R. perezi* (Morand & Joly 1995; Duguet & Melki 2003; García-París 2004). For species that use temporary ponds, and therefore unpredictable habitats between years in the Mediterranean region, a plastic
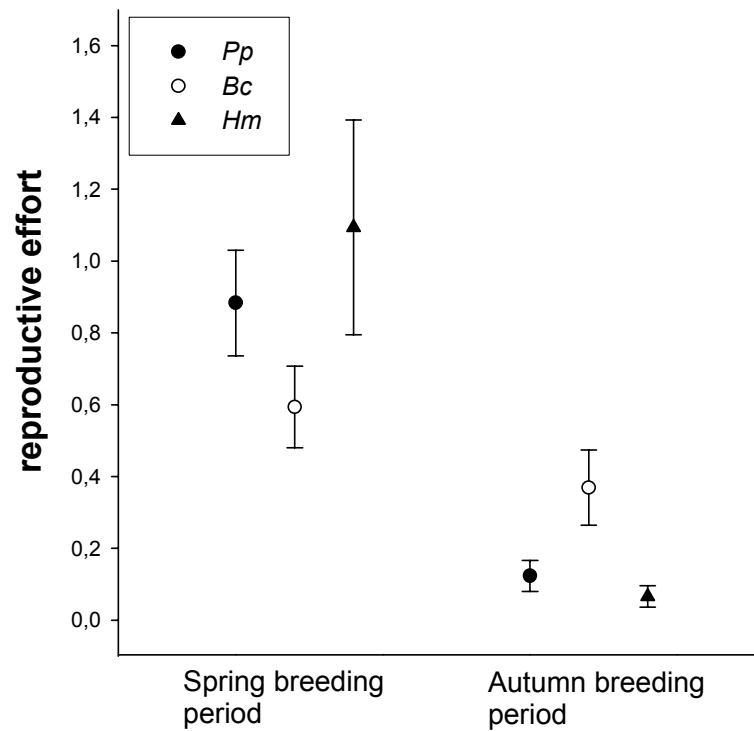
Fig. 3. – Seasonal reproductive effort (mean and standard error) for species with two reproductive peaks, before and after summer.

reproductive strategy allows populations to adjust their breeding period to rainfall episodes (Salvador & Carrascal 1990; Guyétant, et al. 1999; Jakob et al. 2003; Joly 2003).

Several researchers have reported on the influence of rainfall and temperature on anuran breeding (e.g. Salvador & Carrascal 1990; Donnelly & Guyer 1994; Bertoluci & Rodrigues 2002; Oseen & Wassersug 2002), and have proposed that species differ in their responses to these exogenous factors depending on whether they are spring versus summer breeders or whether they are explosive versus prolonged breeders (Oseen & Wassersug 2002). For spring- and summer-breeders, reproduction was not constrained by temperature as in winter species, but differences in timing between species indicates a preference for given temperature ranges in the adult and larval stages.

Species like *R. perezi* or *H. meridionalis,* which inhabit permanent ponds, were also prolonged breeders. Conversely, species that used temporary or ephemeral ponds, like *B. calamita* or *P. punctatus*, were explosive breeders whose reproductive effort was more associated with rain during spring-like seasons. However, reproductive activity for these two
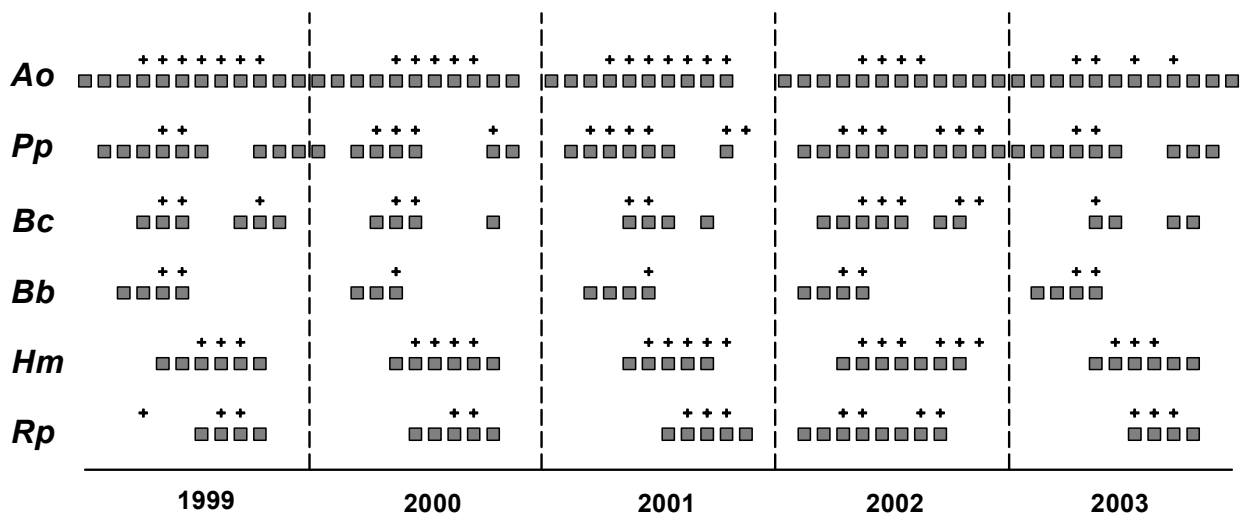
Fig. 4. – Diagram showing the presence or absence of tadpoles (grey boxes) and presence of metamorphs (crosses) for each species.

species was detected in wet summers, although it was delayed in dry summers until the arrival of the autumn rains.

The role of temporal segregation in species coexistence

The differences in the onset and duration of the breeding season determine temporal segregation in adult and larval communities and could reduce interspecific interactions (Bertoluci & Rodrigues 2002; Jacob et al. 2003). Temporal segregation during spring and summer reflects adult physiological response to abiotic factors or to reduce competition for calling and reproductive success (Duellman & Trueb 1994). Water and air temperature are crucial factors for adult calling behaviour (Oseen & Wassersug 2002) and for the larval development of several species (Morand et al. 1997); although species have distinct physiologically preferred ranges for these variables. Species that breed in early spring are physiologically adapted to cold water (John-Alder et al. 1988). Generally, these species breed in permanent ponds with lower water temperature fluctuations during the day than temporary ponds. This may explain why temporary pond breeders reproduce later in spring when air temperature warms shallow waters more quickly and contributes to rapid larval development.

The effects of strong competition have been reported between asynchronously breeding anurans in predator-free ponds, which questions the notion of weak interspecific competition between temporally separated species (Morin 1987; Morin et al. 1990; Sredl & Collins 1991;

Lawler & Morin 1993). However, predation greatly reduces the intensity of competitive interactions between asynchronously breeding species (Morin 1983, 1987). Species differences in habitat use for reproductive purposes (e.g. Donelly & Guyer 1994; Morand & Joly 1995), distinct predation pressure across the hydroperiod habitat gradient (e.g. Woodward 1983; Gunzburger & Travis 2004) and asynchronously reproductive activity (e.g. Díaz-Paniagua 1988; Salvador & Carrascal 1990; Jacob et al. 2003) may jointly favour a dynamic coexistence of several species between years during spring when all species show larval overlap.

However, for species with two peaks of reproduction, seasonal breeding activity could be a strategy that reduces multi-specific tadpole overcrowding, especially in temporary and ephemeral ponds, by means of temporal partitioning of the habitat. In a previous study on competition among tadpole species, we observed that the two species with highest reproductive effort in the second period (*P. punctatus* and *B. calamita*) were the least competitive species of the community (unpublished data). For temporary pond species, the autumn breeding period may provide a new opportunity in recently refilled ponds which are free of interspecific competition from early breeders like *B. bufo* or ower-winter species like *A. obstetricans* or *R. perezi*. Thus, autumn breeding may reduce the intraspecific overlapping of cohorts, which occurs in late spring-breeders. Summer pond drying eliminates tadpoles produced in early bouts of breeding, reduces competition and predation from insects, and regenerates nutrients locked up in dead aquatic organisms (Morin et al. 1990). If temporary autumn ponds retain water long enough for a second reproductive effort to complete development, individuals that breed in autumn might even produce the same number of offspring as early breeders. The larval period of many of the species studied is negatively correlated with water temperatures; these species show shorter larval periods at higher temperature (e.g. Morand et al. 1997). This observation may explain that, in many cases, autumn clutches develop more slowly than late spring cohorts and show relatively poor reproductive success.

In contrast, species that reproduce later in summer or autumn in temporary or permanent ponds which persist during the winter can over-winter and then be much more competitive than early spring cohorts. It remains to be elucidated whether this bimodal reproductive strategy

is a result of the production of multiple clutches per female or by the presence of two temporal subpopulations with an early- and a late-breeding group. More information about reproductive effort within and between years and demographic population structure is required to explain the presence of distinct reproductive strategies in seasonal environments and how these strategies and climatic fluctuations allows the coexistence of species (Morand et al. 1997; Stenseth et al. 2002).

The responses of species to the varying environment of the Mediterranean region reflect and generate opportunities for coexistence mediated by environmental variation. Species respond directly to their environment, changing patterns of such physiological processes as resource uptake, growth and reproduction; and they also affect the environment, most notably during larvae phase through their consumption of resources, which alters the patterns of resource availability for other species. Environmental variation resulted in striking changes in the relative abundances of species in temporary ponds (Semlitsch et al. 1996). These communities cannot be viewed as being in equilibrium; nevertheless, species interactions and density dependence play a significant role (Semlitsch et al. 1996; Crochet et al. 2004). Differences between species in their phenology of activities, or in their relatively non-linear responses to and effects on resources, can maintain diversity (Chesson et al. 2004). Spatial differences along hydroperiod gradient at regional level and local temporal uncertainty resource availability offers many opportunities for such differentiation in species' responses and their coexistence.

Conservation implications

Regulations designed to protect pond-breeding amphibians will have to be developed at regional scale and not at local scale. The lost of breeding habitats is one of the major menaces of amphibian communities in our area of study. In Spain, it is estimated that more than 60% of wetlands have disappeared in the last 50 years (Gallego-Fernández et al. 1999). These processes of wetland disappearance have usually been associated with changes in the structure of the landscape, which in turn, are related to changes in social and economic factors, however in the last year land-use regulators created new man-made ponds to flora and fauna conservation. The problem is that normally these new man-made ponds are

permanent ponds which favour some amphibian species but are unfavourable for others. We think that the best strategy is the creation and preservation of multiple small ponds than to a single large pond (Jacob et al. 2003). Land- use regulators and the administrations should consider the conservation of a whole pond mosaic with varying hydroperiods and minimal nearest-neighbour distances among ponds to favour the connection of highly instable sub-populations and the maintenance of the metapopulation (Paton et al. 2002; Jacob et al. 2003), which is thought to apply to many populations of pond-breeding amphibians (Marsh & Trenham 2001) but not all are seems to be structured as metapopulations (Smith & Green 2005).

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