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Breeding phenology of amphibians in a Mediterranean ephemeral stream (Ardèche, France)

Rémi DUGUET

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Subadult Western Spadefoot Toad *Pelobates cultripes* (Cuvier, 1829), Bourbouillet stream, 11th June 2021. Credit: Rémi Duguet. / Pélobate cultripède *Pelobates cultripes* (Cuvier, 1829) sub-adulte, ruisseau du Bourbouillet, 11 juin 2021. Crédit photo : Rémi Duguet.

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Breeding phenology of amphibians in a Mediterranean ephemeral stream (Ardèche, France)

Rémi DUGUET
Alcedo Faune et Flore,
85 impasse Baslaval, F-07110 Sanilhac (France)
rduguet@expertise-ecologique.fr

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ABSTRACT
We present the results of the monitoring of breeding phenology of an assemblage of eight species of amphibians in a Mediterranean ephemeral stream, located in the Ardèche department, France. For most species, during 11 consecutive years, phenology was rather constant from year to year, which is rather unusual in Mediterranean temporary ponds. The occurrence of summer breeding was not rare for three species: *Pelobates cultripes* (Cuvier, 1829), *Pelodytes punctatus* (Daudin, 1803) and *Hyla meridionalis* Böttger, 1874. Breeding occurrence is linked to rewetting events caused by active karst resurgences, fuelled by periods of intense rainfall episodes called “cévenol” episodes. We document for the first time a triannual breeding occurrence (spring, summer, and autumn), and an *in situ* record of a short tadpole development period, concerning particularly *P. cultripes*. The ecological factors which can explain this species richness and these unusual observations are outlined. In conclusion, we encourage the conservation and monitoring of amphibian communities in ephemeral streams, as the natural and scientific interests for this type of habitat are often underestimated.

KEY WORDS
Pools,
Mediterranean species assemblage,
triennial breeding flexibility,
shortening of larval development duration,
“cévenol” episode,
karst resurgence,
Pelobates cultripes.

RÉSUMÉ
Phénologie de la reproduction des amphibiens dans un ruisseau éphémère méditerranéen (Ardèche, France).
Les Amphibiens des milieux stagnants sont relativement bien étudiés dans le lit majeur des rivières et des ruisseaux, temporaires ou permanents. À l’inverse, les études concernant les peuplements d’Amphibiens dans les ruisseaux éphémères sont peu nombreuses. Cet article vise à contribuer à compenser ce manque d’études. Les ruisseaux éphémères se caractérisent par l’influence directe et majeure des précipitations, telles que des orages, sur leur alimentation en eau. Le ruisseau méditerranéen du Bourbouillet est situé dans l’éco-complexe de Païolive (sud du département de l’Ardèche, France). Un suivi de la reproduction des Amphibiens y a été réalisé pendant 11 ans. Un assemblage de huit espèces se reproduit dans trois fosses du ruisseau, alimentées par des résurgences karstiques entrant en activité à la suite de pluies intenses appelées épisodes « cévenols ». Nous avons constaté que certaines espèces, en particulier le Pélobate cultripède *Pelobates cultripes* (Cuvier, 1829), pouvaient se reproduire à une fréquence triennale, c’est-à-dire à la fois printanière, estivale et automnale, ce qui n’était pas documenté chez cette espèce. Nous avons aussi noté un record de brièveté du développement larvaire chez la même espèce. Cela illustre bien la flexibilité temporelle générale des Amphibiens en zone méditerranéenne. Nous présentons les facteurs écologiques qui peuvent rendre compte de la richesse de cet assemblage d’espèces. Entre autres, citons la relative régularité de la succession d’inondations et d’assecs, mais aussi les phénomènes de chasse, qui contribuent sans doute à limiter la prédation des larves d’amphibiens par les Insectes aquatiques et les Poissons éventuels. Pour conclure, cette étude atteste du fort enjeu que représente le ruisseau du Bourbouillet dans l’éco-complexe de Païolive – seul site d’Ardèche où se reproduisent huit espèces d’Amphibiens. Elle permet d’attirer l’attention des naturalistes, gestionnaires d’espaces naturels et aménageurs, sur l’intérêt souvent sous-estimé des ruisseaux éphémères.

MOTS CLÉS
Fosses,
cortège méditerranéen,
flexibilité triennale de la reproduction,
raccourcissement de la durée de développement larvaire,
épisode cévenol,
résurgence karstique,
Pelobates cultripes.

Fig. 1. — Flooding of the Bourbouillet stream in the section between the upstream pool and the intermediate pool, 20th December 2020. Credit: R. Duguet.

INTRODUCTION

Amphibians, including pond-dwelling species, are mostly common in natural, un- or poor-regulated rivers and streams, from the central channel to the farthest annexes (Morand & Joly 1995), and from headwater streams to large lowland rivers (Dalbeck *et al.* 2020). There, the highest richness is usually found in temporary, fishless water bodies that are protected from flooding episodes. Most of these species show temporal flexibility in reproduction (Morand & Joly 1995).

Most of the studies on the ecology of alluvial pond amphibians in Europe seem to have focused on permanent or intermittent river and stream environments, e.g., large alluvial valleys (Joly & Morand 1994; Morand & Joly 1995; Pintar 2001; Tester 2001), braided or gravel-bed rivers (Kuhn 2001; Landmann & Böhm 2001; Tockner *et al.* 2006) or foothill rivers (Cayuela *et al.* 2011). Amphibian communities in ephemeral streams are rarely studied, at least in Europe (but see Rodríguez Jiménez 1986, 1988; Duguet 2017). Ephemeral streams are characterised by a hydrological unpredictability due to rainfall (Datry *et al.* 2014; Stubbington *et al.* 2017).

The Bourbouillet stream is a Mediterranean ephemeral watercourse in the South of France, in the Ardèche department (Fig. 1). Three nearby remnant pools support a rather rich amphibian assemblage, with eight species present (Duguet 2017). Preliminary monitoring has revealed a triannual breeding phenology (i.e. over three successive seasons in a year) in *Pelobates cultripes* (Cuvier, 1829), whereas for most amphibian species in Europe, breeding occurs mostly once, sometimes twice, in a year (e.g., Nöllert & Nöllert 1993; Duguet & Melki 2003; Speybroeck *et al.* 2016).

We present new results from a longer sequence of monitoring, for 11 years, dealing with the breeding phenology of each species, and discussion about the ecological factors that may influence the existence of this species assemblage. In doing so, we wish to contribute to the improvement of knowledge about amphibian ecology in ephemeral watercourses, a subject that often lacks documentation.

MATERIALS AND METHODS

The study site (Fig. 2) is a 500 m section of the Bourbouillet stream (latitude 44.42°N, longitude 4.27°E, average elevation 120 m), belonging to the Païolive “ecocomplex” (Blandin *et al.* 2016) located on the edge of the Cévennes massif. Here, periods of intense rainfall, known as “cévenol” episodes, with a cumulative rainfall of at least 150 mm/day, occur most often from September to November (Boudevillain *et al.* 2009; Jaillet *et al.* 2012).

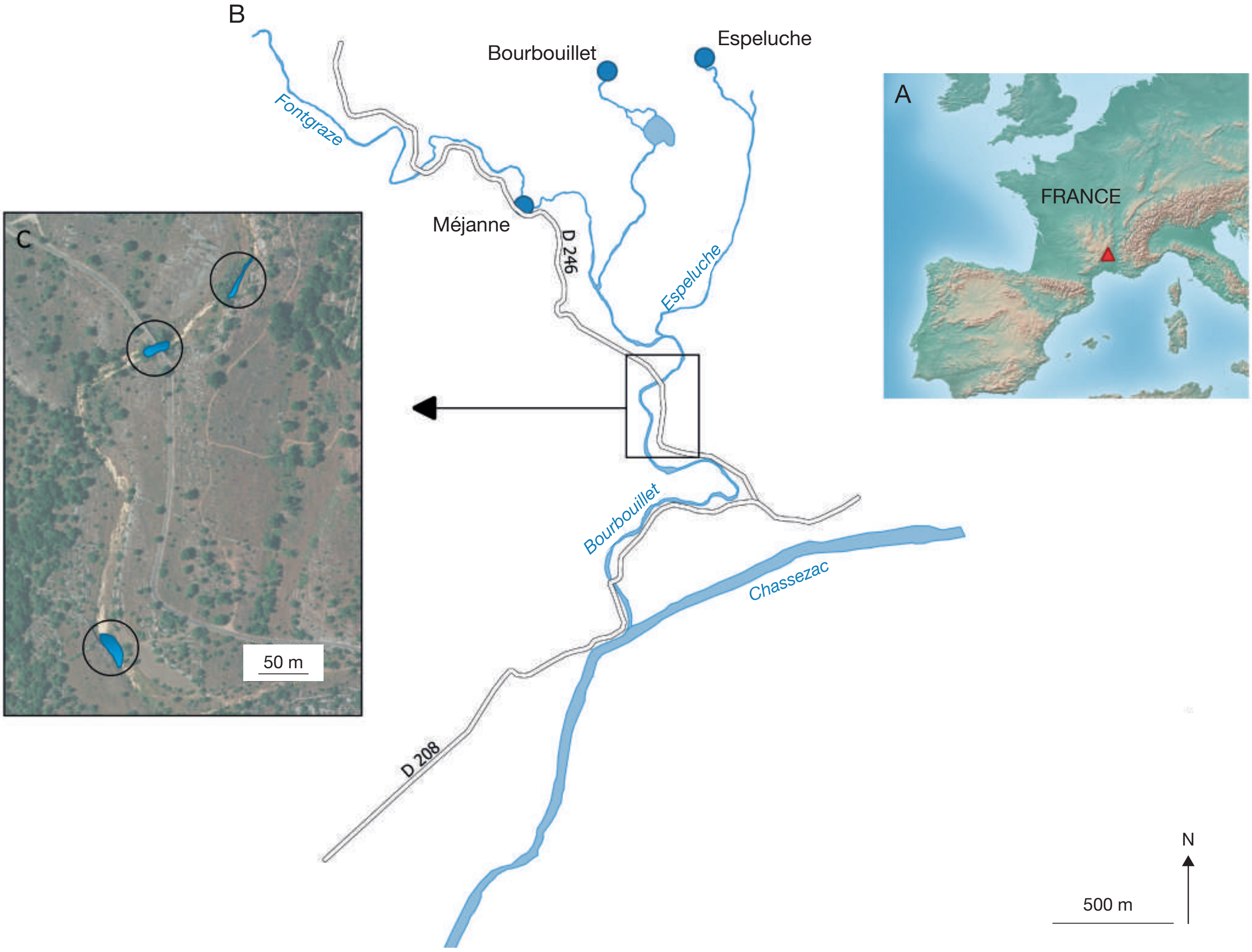

Fig. 2. — Red triangle indicates the locality of the study area (**A**), hydrographic network of the study area (**B**) and study site (**C**). Blue dots represent the main resurgences. Black open circles show remnant pools (in blue). White bands represent roads.

The stream is supplied by karstic resurgences, among others the "évent de Bourbouillet" and the "Espéluche 1 and 2" which have a maximum cumulative flow of 6300 l/sec (Anonyme 2014). Three main remnant pools (Fig. 3) support the reproduction of one urodela, *Lissotriton helveticus* (Razoumowsky, 1789) (Salamandridae) and seven anuran species: *Pelobates cultripes* (Cuvier, 1829) (Pelobatidae), *Pelodytes punctatus* (Daudin, 1803) (Pelodytidae), *Bufo spinosus* (Daudin, 1803) (Bufonidae), *Epidalea calamita* (Laurenti, 1768) (Bufonidae), *Hyla meridionalis* Böttger, 1874 (Hylidae), *Rana dalmatina* Fitzinger *in* Bonaparte, 1838 (Ranidae) and *Pelophylax ridibundus* (Pallas, 1771) *sensu lato* (Ranidae). All but one, *P. ridibundus*, are native in Ardèche (Duguet & Joly 2015).

The nearest breeding sites are within 600 m for *B. spinosus* and *P. ridibundus* (in the Chassezac river), and at least 1.2 km for the other species, except for *E. calamita*. Notably, no other breeding sites for *R. dalmatina* and *P. cultripes* are currently known in a radius of respectively 5 km and 20 km. Both are rare in Ardèche (e.g., Duguet 2020). *E. calamita*, which breeds mainly in ephemeral pools on the bedrock of the stream outside the study section, could therefore not be monitored with accuracy.

Approximately 207 visits were made between September 2010 and August 2021 (Table 1). The fieldwork was distributed rather randomly over the years, but with attention being paid to periods of rewetting or drying up of the streambed and pools.

Species were detected mainly by nocturnal call and visual encounter surveys, i.e. without dipnetting, thanks to excellent observation conditions. These conditions included clear water (with the exception of short flooding episodes of 1-2 days with turbid waters), big parts of the bottom with no aquatic vegetation thanks to rocky slabs, and moderate depth (less than 1.5 m outside flooding episodes). The mating calls of *P. cultripes*, *P. punctatus* and *R. dalmatina*, sometimes inaudible from the surface, were detected with an Aquarian Audio H2a Hydrophone©. Observations at the three pools were combined to cope with imperfect detection rate (Petitot *et al.* 2014).

Thanks to relatively short development periods of most amphibian species larvae in the Mediterranean region, it was possible to clearly distinguish the larval cohorts of different reproductive events. Larval seasonal cohorts were therefore monitored without confusion, except for 2018, when *P. punctatus* summer and autumn cohorts were very close, and the

FIG. 3. — Upstream pool (**A**), intermediate pool (**C**), and downstream pool (**E**), a few days after a rewetting, 9th May 2021 (**A**, **C**, **E**) or dry, 17th June 2022 (**B**, **D**, **F**). Credits: R. Duguet.

P. cultripes late spring cohort mixed with the summer cohort. However, that did not influence the results.

The main difficulty was the monitoring of *B. spinosus* and *R. dalmatina* larval cohorts and, to a lesser extent, of *L. helveticus*, because of their low detection rates, related to the small adult population sizes. For example, the total number of *R. dalmatina* egg clutches per year was usually less than ten, and very often part of these dried out.

A "hydrological" year is usually defined as beginning on or about the 1st of September and ending on or about the 31st of August of the following year. In the South of Ardèche, the precise cut-off date coincides with a resumption of "céve-

Tableau 1. — Number of visits per year and monthly decade. Distinct breeding seasons are the "autumn", "spring" and "summer" . Abbreviations: **Apr.**, April; **Aug.**, August; **Dec.**, December; **Feb.**, February; **Jan.**, January; **Jul.**, July; **Jun.**, June; **Mar.**, March; **Nov.**, November; **Oct.**, October; **Sep.**, September.

	Autumn															**Spring**															**Summer**						
Year	**Sep.**			**Oct.**			**Nov.**			**Dec.**			**Jan.**			**Feb.**			**Mar.**			**Apr.**			**May**			**Jun.**			**Jul.**			**Aug.**			**Total**
2010-2011	1	–	–	–	–	1	1	1	–	1	–	–	–	1	–	1	2	1	1	2	1	1	–	–	–	–	1	1	–	–	1	1	1	–	–	–	20
2011-2012	1	1	–	1	1	1	1	1	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	1	–	1	–	1	–	–	1	–	–	–	1	1	17
2012-2013	1	1	1	–	1	–	1	–	–	–	1	–	–	–	–	–	1	2	1	2	1	–	1	–	–	–	–	–	–	–	–	–	1	1	1	1	18
2013-2014	1	–	1	–	1	1	–	–	–	–	–	–	–	1	1	–	1	2	–	1	–	–	–	–	–	–	–	–	1	1	1	1	1	–	–	–	15
2014-2015	1	1	1	1	–	1	1	1	1	–	1	–	–	–	1	–	–	1	2	1	–	–	1	1	–	–	–	–	1	–	–	1	–	1	–	1	20
2015-2016	1	1	1	1	1	–	–	1	–	1	1	1	–	–	–	1	1	2	1	2	–	1	1	–	2	1	1	–	–	1	1	1	–	–	1	–	26
2016-2017	–	1	–	1	–	1	–	–	–	2	1	–	–	–	1	1	1	1	1	1	1	1	1	1	–	–	1	–	–	1	1	1	–	–	–	1	21
2017-2018	–	–	1	–	1	1	1	1	–	–	–	–	1	1	1	–	–	–	–	2	2	1	–	–	–	1	1	–	–	1	–	1	–	3	–	1	21
2018-2019	1	–	1	1	–	1	–	–	–	–	1	–	–	–	–	1	–	–	2	1	1	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	13
2019-2020	–	–	–	–	1	–	–	–	–	1	–	–	–	1	–	–	–	–	1	1	–	1	–	–	1	–	1	–	–	1	–	1	–	2	–	–	2	14
2020-2021	–	1	1	–	2	–	1	1	–	1	1	–	1	–	–	–	–	1	2	–	1	–	–	–	–	1	–	–	–	1	–	1	1	1	2	1	1	22
Total	7	6	7	5	8	7	6	6	1	6	6	1	2	4	4	4	7	12	10	14	8	6	4	5	4	4	4	2	4	4	7	7	6	7	4	8	207

nol" episodes between August and October, as these intense periods of rainfall lead to a rewetting of the streams and the end of amphibian summer diapause ("estivation"). Indeed, a late summer breeding event of *P. punctatus* in the last decade of August 2020 is attached to the following autumn season, and therefore attributed to the hydrologic year 2020-2021.

According to field experience in Ardèche, a year is arbitrarily divided into three amphibian breeding seasons:

– "autumn", from September to January;

– "spring", from February to June;

– "summer", from July to August.

Thus, a year could present breeding episodes with an "annual", "biannual" or "triannual" occurrence, depending on whether a species breeds during one, two or three seasons in one hydrologic year.

Monitoring naturally ended in summer 2021, as there was no breeding that season and no larval cohorts from previous seasons to monitor, even if the pools were not dry that summer.

For each season and species, there are three types of reproduction status:

– "Attempt" means that calls or amplexus of anurans, or adult newts in the aquatic environment, were detected;

– "effective" means that we detected eggs or larvae;

– "success" means either larvae close to metamorphosis (e.g., tadpole with forelegs), or the presence of froglets, toadlets or efts.

As it is common in the Mediterranean region (e.g., Jakob *et al.* 1998 for *L. helveticus*), *P. ridibundus* calls and *L. helveticus* aquatic adults were detected in autumn, although these species clearly did not have any formal breeding activity, like mating, display, or egg laying. For this reason, the status "attempting to reproduce" was not applied to these special cases.

RESULTS

A total of 24 breeding episodes were considered: 11 in autumn, 11 in spring, and two in summer (Table 2; Fig. 4). All remaining seasons but one, were summers marked by a continuous drought - a very common phenomenon in numerous Mediterranean ponds.

During the study period, reproduction took place almost every year for all species but *E. calamita*. This species' breeding was occasional, with only three annual (spring or summer) episodes during the observation period. For information, this species probably breeds regularly in alternative breeding sites in the vicinity of the study pools.

L. helveticus and *H. meridionalis* breeding occurrence was regular with eight and 12 episodes respectively, generally at an annual frequency, and mainly in spring, except for a 2014 spring-summer sequence for *H. meridionalis*. Note that *H. meridionalis* summer oviposition resumption has been observed as early as July, which seems very rare (e.g., Román & Ruiz 2003; Richter-Boix *et al.* 2006a).

B. spinosus and *R. dalmatina* breeding occurrence was regular, with ten episodes all in spring, but no breeding success was detected. Note that the lack of breeding in 2018 was correlated to very dry weather conditions in the Southern Ardèche, which are suspected to have had a negative impact on the pre-breeding migration of both species (Rose 2018).

P. ridibundus breeding occurrence was quite irregular, with seven episodes since 2014, usually annually, occurring mainly in spring, and in a few cases in summer.

Every year we noted breeding occurrences for *P. cultripes* and *P. punctatus*, with 20 and 23 episodes respectively. For *P. cultripes*, the frequency was annual, three times, biannual, seven times and triannual, one time in the 2013-2014 period. For *P. punctatus* the frequency was biannual ten times and triannual, one time in the 2017-2018 period. For both species, the biannual frequency occurred most often in an autumn-spring succession but once in 2018 in a spring-summer succession for *P. cultripes*. As for *H. meridionalis*, we notice *P. cultripes* summer oviposition in July, which is unusually early (e.g., Geniez & Cheylan 2012).

Autumn breeding success occurrence appeared to be relatively high for *P. punctatus* and low for *P. cultripes*.

Note that another amphibian, *Alytes obstetricans* (Laurenti, 1768) (Alytidae), could be heard sometimes on the study site, but it is considered anecdotal, since no tadpoles were ever found in these pools; these adults probably originate from the Chassezac surroundings.

TABLEAU 2. — Breeding status by successive breeding seasons of the species assemblage: *Bufo spinosus* (Daudin, 1803), *Epidalea calamita* (Laurenti, 1768), *Hyla meridionalis* Böttger, 1874, *Lissotriton helveticus* (Razoumowsky, 1789), *Pelobates cultripes* (Cuvier, 1829), *Pelodytes punctatus* (Daudin, 1803), *Pelophylax ridibundus* (Pallas, 1771), *Rana dalmatina* Fitzinger *in* Bonaparte, 1838. Abbreviations: **A**, attempt of reproduction; **Au.**, autumn; **E**, effective reproduction; **S**, reproductive success (see text for definitions); **Sp**. spring; **Su**. summer. Dashes indicate floodings pools with absence of breeding, and crossed-out boxes, dry streambed without possibility for breeding.

Hydrologic years	Breeding seasons	*E. calamita*	*L. helveticus*	*P. ridibundus*	*B. spinosus*	*H. meridionalis*	*R. dalmatina*	*P. cultripes*	*P. punctatus*
2010-2011	Au.	–	–	–	–	–	–	S	E
	Sp.	–	A	–	A	E	E	S	E
	Su.	X	X	X	X	X	X	X	X
2011-2012	Au.	–	–	–	–	–	–	E	S
	Sp.	–	A	–	E	A	A	E	S
	Su.	X	X	X	X	X	X	X	X
2012-2013	Au.	–	–	–	–	–	–	A	E
	Sp.	–	A	–	E	A	E	E	E
	Su.	X	X	X	X	X	X	X	X
2013-2014	Au.	–	–	–	–	–	–	E	E
	Sp.	–	–	E	E	S	E	E	E
	Su.	E	–	E	–	E	–	S	–
2014-2015	Au.	–	–	–	–	–	–	E	E
	Sp.	–	A	–	E	E	E	E	E
	Su.	X	X	X	X	X	X	X	X
2015-2016	Au.	–	–	–	–	–	–	–	S
	Sp.	–	E	A	E	S	E	S	S
	Su.	X	X	X	X	X	X	X	X
2016-2017	Au.	–	–	–	–	–	–	E	S
	Sp.	E	E	E	E	E	E	S	S
	Su.	X	X	X	X	X	X	X	X
2017-2018	Au.	–	–	–	–	–	–	–	A
	Sp.	–	–	S	–	E	–	S	E
	Su.	E	–	–	–	–	–	E	S
2018-2019	Au.	–	–	–	–	–	–	–	S
	Sp.	–	–	–	E	E	E	E	E
	Su.	X	X	X	X	X	X	X	X
2019-2020	Au.	–	–	–	–	–	–	–	S
	Sp.	–	E	S	A	E	E	S	E
	Su.	X	X	X	X	X	X	X	X
2020-2021	Au.	–	–	–	–	–	–	A	E
	Sp.	–	S	E	E	S	E	S	S
	Su.	–	–	–	–	–	–	–	–

DISCUSSION

The results look overall in line with the state of knowledge on the species breeding phenology in Europe. Biannual breeding occurrences, especially in spring and autumn, are already well documented for *P. punctatus* (Guyétant *et al.* 1999; Jakob *et al.* 2003; Salvidio *et al.* 2004; Richter-Boix *et al.* 2006a; Geniez & Cheylan 2012; Cayuela *et al.* 2012; Jourdan-Pineau *et al.* 2012; Escoriza 2017), *P. cultripes* (Salvidio & Quero 1987; Díaz-Paniagua 1988; Rodríguez Jiménez 1988; Salvador & Carrascal 1990; Díaz-Paniagua 1992; Lizana *et al.* 1994; Jakob *et al.* 2003; Thirion 2006; Geniez & Cheylan 2012; Martínez-Solano & García-París 2012; Recuero 2014; Priol 2015) and *H. meridionalis* (Richter-Boix *et al.* 2006a).

In addition, summer breeding occurrences are already documented for *P. punctatus*, *P. cultripes* (e.g., Geniez & Cheylan 2012) or *H. meridionalis* (Román & Ruiz 2003; Richter-Boix *et al.* 2006a), although the resumption of oviposition of *P. cultripes* and *H. meridionalis* as early as July is unpublished to our knowledge.

However, a *P. cultripes* triannual breeding occurrence in a single year is published here for the first time to our knowledge. It is possible that such an occurrence has not yet been published for any pond-dwelling amphibian species in Europe. Nevertheless we mention the possible exception of some Iberian *A. obstetricans* and/or *P. punctatus* populations, for whom the long potential breeding season can be interrupted by dry summers (Richter-Boix *et al.* 2006a; Montori *et al.* 2015; H. Uthleb, pers. comm.). We can hypothesise that the facultative triannual breeding mode observed here is linked to the summer occurrence of “cévenol” episodes in the surroundings of the stream; they increase atmospheric humidity, which can stop the amphibian estivation (personal observation) and activate karstic resurgences which fuel the stream, inducing its rewetting. Indeed, in summer 2021, even if the pools did not dry out, because water levels stayed high until the end of the preceding spring, no reproduction occurred in the absence of “cévenol” episodes.

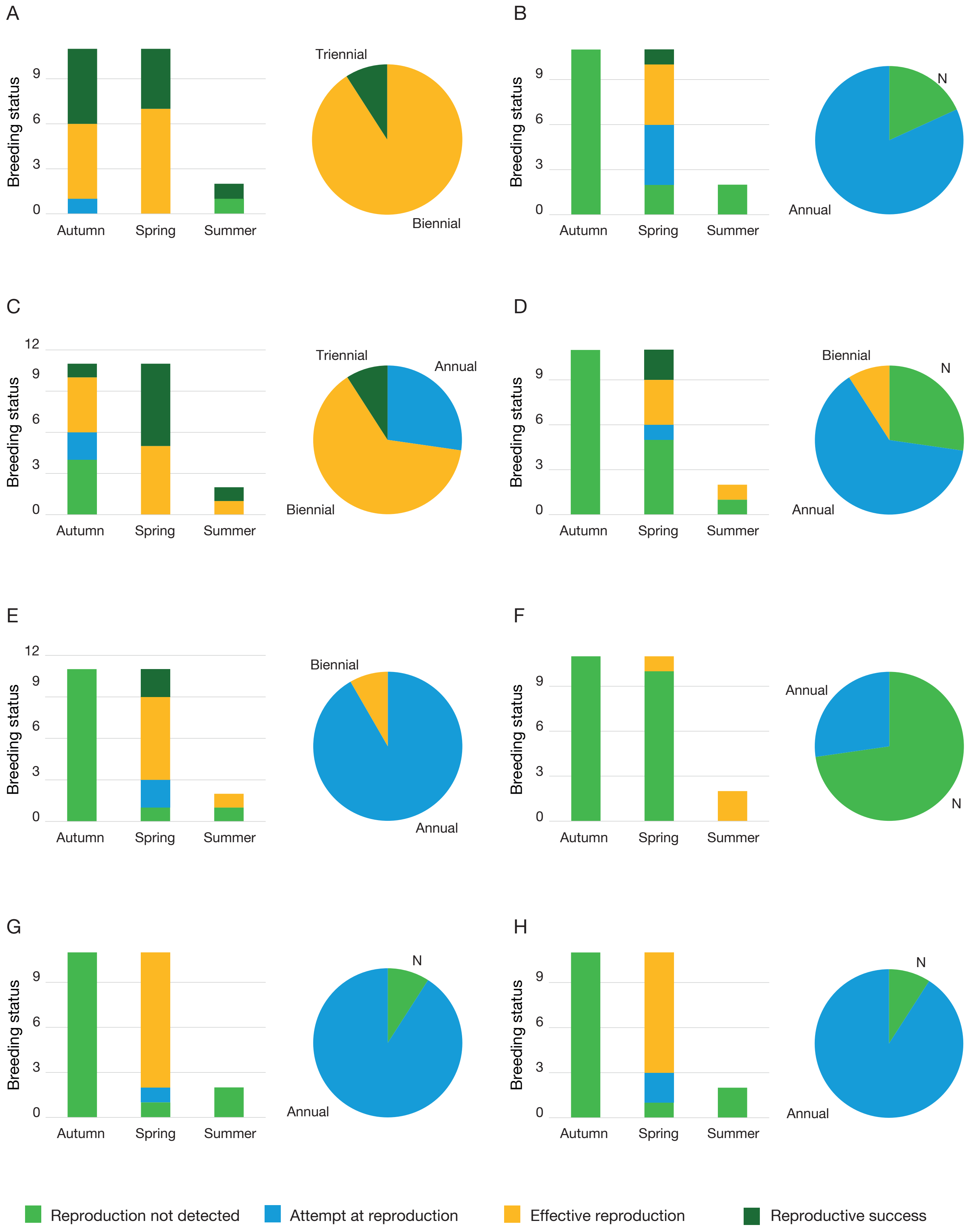

Fig. 4. — Breeding status by season (left) and occurrence per year (right) of the species assemblage. **A**, *Pelodytes punctatus* (Daudin, 1803); **B**, *Lissotriton helveticus* (Razoumowsky, 1789); **C**, *Pelobates cultripes* (Cuvier, 1829); **D**, *Pelophylax ridibundus* (Pallas, 1771); **E**, *Hyla meridionalis* Böttger, 1874; **F**, *Epidalea calamita* (Laurenti, 1768) ; **G**, *Rana dalmatina* Fitzinger *in* Bonaparte, 1838; **H**, *Bufo spinosus* (Daudin, 1803). Abbreviation: **N**, reproduction non detected.

Interestingly, an extremely short duration of *P. cultripes* full tadpole development, i.e. about 70 days, was noticed in summer 2014 (Duguet 2017), probably due to the high temperatures of summer, or the progressively drying out of pools; it could also be the consequence of local adaptation of the *P. cultripes* population to the unpredictable flow regime. This finding was previously unpublished to our knowledge for *in situ* conditions, as the minimum known tadpole development period in the wild was around three months (e.g., Alvárez *et al.* 1990; Martínez-Solano & García-París 2012). But such a record, i.e. 74-84 days at 28 °C, was already noticed in experimental conditions (Talavera & Sanchiz 1987), and it was then only a matter of time before it was observed in the wild. However, Gómez-Mestre *et al.* (2013), by experimentally lowering water levels, could only induce a shortening of the *P. cultripes* larval development to 86 days.

We can notice that this observation is in line with the general assumption that tendency towards short larval period and synchronisation of oviposition with hydrology, are common adaptations to both alluvial environments (Morand *et al.* 1997; Tockner *et al.* 2006) and Mediterranean environments (Richter-Boix *et al.* 2006b), as temporal unpredictability of the aquatic habitat and niche breadth, is a major ecological factor faced by amphibians.

We can assume that the regularity of yearly breeding occurrences for most species observed here contrasts with the usual alternation of "favourable" and "unfavourable" years observed in in Mediterranean temporary ponds (Jakob *et al.* 2003; Richter-Boix *et al.* 2006a, 2007; Gómez-Rodríguez *et al.* 2010b; Cayuela *et al.* 2012). This could be especially evident in such a small number of pools like on the study site (Gómez-Rodríguez *et al.* 2010a). These general patterns are interpreted as an avoidance of predation and competition within the community, as these strong ecological factors depend on the variable interannual rainfall patterns of the Mediterranean area. Then, we can make the hypothesis that pools of an ephemeral stream like the Bourbouillet, which are regularly flooded every year because of powerful karstic resurgences, offer at least as good ecological conditions for a rich amphibian community, as other types of Mediterranean watercourses or ponds. This is also supported by Rodríguez Jiménez's (1988) similar considerations on the breeding conditions of the amphibian community in another ephemeral stream in the South of Spain. Common parameters for communities of both sites exist, including alternation of pool drying and flushing. Flushing effects push predators like insects or fish, and sediments, downstream from the pools, thus limiting predation on amphibian larvae and eggs as well as landfill of the pools by organic matter. Moreover, stream rewetting events limit the risk of larvae desiccation, e.g., in late spring and summer, and, by supplying water in the pools, reduce intensity of competition between amphibian larvae as well as limiting the density of predators. Second, occasional dryings of the pools in both locations also reduce predator density, while improving remineralisation of organic matter deposits. Moreover, summer drying may limit the size of local *P. ridibundus* populations, a very competitive species, as its late breeding period exposes its larvae to a high desiccation risk.

Nevertheless, population sizes of *B. spinosus* and *R. dalmatina*, and even *L. helveticus*, are relatively low. This probably reveals some poorly known ecological "constraints" at the site, as for example the predation of spring eggs or larvae by overwintering *P. punctatus* and sometimes *P. cultripes* tadpoles (e.g., Jourdan-Pineau *et al.* 2012).

A drawback of hydrological "favourable" conditions at the Bourbouillet is predation of amphibian larvae by fish *Squalius cephalus* (Linnaeus, 1758), who when returning to pools after a period of stream flow resumption find themselves confined and starving.

Another drawback is the risk of desiccation of larvae due to downstream drift. This risk can probably be significant in autumn when "cévenol" episodes are more intense, and can lead to longer and more powerful flooding, as for example in 2014. This may explain some autumn breeding failure for *P. punctatus*, as happened in 2014, even if some tadpoles of this species, much more numerous in autumn than in spring, can escape by chance from drifting. We assume that drift may be one reason why the *P. cultripes* breeding success is low in autumn: indeed, the reproductive effort, e.g. the calling activity, is weaker in autumn than in spring, so the tadpoles are fewer and globally more exposed to the risk of drifting.

We also noticed in one pool that almost every year, part of *R. dalmatina* egg clutches were drying out because of a quick drop of water levels after the flow stops. One can also assume that absence of *A. obstetricans* breeding occurrence at the Bourbouillet, although present in the nearby Chassezac, may be linked to the short hydroperiod of pools (Richter-Boix *et al.* 2008, but see also Montori *et al.* 2015), as the development of *A. obstetricans* tadpoles is rather slow.

CONCLUSIONS

These considerations show the ecological originality of the Bourbouillet area and the importance of ensuring its conservation and monitoring, especially as global climate change is predicted to influence the intensity and pattern of "cévenol" episodes. Additionally it is probably the only location in Ardèche where eight amphibian species currently breed.

We recommend that amphibian surveys, among other taxa, should be encouraged in ephemeral streams. These streams are ecosystems of high natural heritage value which are often underestimated in field surveys and conservation plans, as well as in public policies for sites and species protection.

These results also show that it is possible to discover or highlight natural history facts about "well studied" amphibians without invasive means, i.e. by visual and acoustic encounter survey methods, provided that engagement is frequent, regular and long-term.

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REFERENCES

Anonyme 2014. — *Fiche de caractérisation des masses d'eau souterraine V2, FRDG118, Calcaires jurassiques de la bordure des Cévennes. État des connaissances 2014*. Agence de l'Eau RMC & BRGM, Lyon, Orléans, 10 p.

Alvárez J., Salvador A., Martin J. & Gutierrez A. 1990. — Desarrollo larvario del sapo de espuelas (*Pelobates cultripes*) en charcas temporales del NW de la Península Ibérica (Anura: Pelobatidae). *Revista española de herpetología* 4: 9-15.

Blandin P., Aberlenc H.-P., Bauvet C., Bianchin N., Cocklebetian A., Coute A., Deso G., Duguet R., Gaymard M., Holtof J.-F., Hugonnot V., Ladet A., Lagarde F., Lhermenier W., Lhomme M., Morin D., Perrette C., Richard F. & Schwaab F. 2016. — L'écocomplexe de Païolive en Ardèche méridionale (France): un pic de biodiversité du Hotspot méditerranéen. *Ecologia mediterranea* 42 (2): 51-95. https://doi.org/10.3406/ecmed.2016.1991

Boudevillain B., Sebastien A., Claud C., Ducrocq V., Joly B., Joly A., Lambert D., Nuissier O., Plu M., Ricard D., Arbogast P., Berne A., Chaboureau J.-P., Chapon B., Crepin F., Delrieu G., Doerflinger E., Funatsu B.M., Kirstetter P.-E., Masson F., Maynard K., Richard E., Sanchez E., Terray L. & Walpersdorf A. 2009. — Projet Cyprim, partie I. Cyclogenèses et précipitations intenses en région méditerranéenne: origines et caractéristiques. *La Météorologie* 66: 18-28. https://doi.org/10.4267/2042/28828

Cayuela H., Cheylan M. & Joly P. 2011. — The best of a harsh lot in a specialized species: breeding habitat use by the yellow- bellied toad (*Bombina variegata*) on rocky riverbanks. *Amphibia-Reptilia* 32 (4): 533-539. https://doi.org/10.1163/156853811x614461

Cayuela H., Besnard A., Bechet A., Devictor V. & Olivier A. 2012. — Reproductive dynamics of three amphibian species in Mediterranean wetlands: The role of local precipitation and hydrological regimes. *Freshwater Biology* 57 (12): 2629-2640. https://doi.org/10.1111/fwb.12034

Dalbeck L., Hachtel M. & Campbell-Palmer R. 2020. — A review of the influence of beaver *Castor fiber* on amphibian assemblages in the floodplains of European streams and rivers. *Herpetological Journal* 30 (2): 135-146. https://doi.org/10.33256/hj30.3.135146

Datry T., Larned S. T. & Tockner K. 2014. — Intermittent rivers: a challenge for freshwater ecology. *Bioscience* 64 (3): 229-235. https://doi.org/10.1093/biosci/bit027

Díaz-Paniagua C. 1988. — Temporal segregation in larval amphibian communities in temporary ponds at a locality in SW Spain. *Amphibia-Reptilia* 9 (1): 15-26. https://doi.org/10.1163/156853888x00161

Díaz-Paniagua C. 1992. — Variability in timing of larval season in an amphibian community in SW Spain. *Ecography* 15 (3): 267-272. https://doi.org/10.1111/j.1600-0587.1992.tb00034.x

Duguet R. 2017. — Fréquence et succès de la reproduction du Pélobate cultripède *Pelobates cultripes* (Cuvier, 1829) (Anura: Pelobatidae) dans un cours d'eau intermittent méditerranéen en Ardèche (France). *Bulletin de la Société herpétologique de France* 163: 1-14.

Duguet R. 2020. — Découverte d'une nouvelle localité du Pélobate cultripède *Pelobates cultripes* (Cuvier, 1829) le long de la rivière Ardèche. *Bulletin de la Société herpétologique de France* 173: 53-56.

Duguet R. & Joly P. 2015. — Les Grenouilles « vertes » (*Pelophylax* sp.) en Rhône-Alpes, *in* Grossi J.-L. & Fonters R. (eds), *Les Amphibiens et Reptiles de Rhône-Alpes.* LPO coordination Rhône-Alpes, Lyon: 258-269.

Duguet R. & Melki F. (eds) 2003. — *Les Amphibiens de France, Belgique et Luxembourg.* Biotope, Mèze, 480 p.

Escoriza D. 2017. — Sapillo moteado septentrional – *Pelodytes punctatus*, *in* Salvador A. & Martínez-Solano I. (eds), *Enciclopedia Virtual de los Vertebrados Españoles.* Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org, dernière consultation le 31 décembre 2021.

Geniez P. & Cheylan M. 2012. — *Les Amphibiens et Reptiles du Languedoc-Roussillon et régions limitrophes*. Atlas biogéographique. Biotope , Mèze/ Muséum national d'Histoire naturelle, Paris, 448 p.

Gómez-Rodríguez C., Díaz-Paniagua C., Bustamante J., Portheault A. & Florencio M. 2010a. — Inter-annual variability in amphibian assemblages: implications for diversity assessment and conservation. *Aquatic Conservation: Marine Freshwater Ecosystems* 20 (6): 668-677. https://doi.org/10.1002/aqc.1134

Gómez-Rodríguez C., Diaz-Paniagua C., Bustamante J., Serrano L. & Portheault A. 2010b. — Relative importance of dynamic and static environmental variables as predictors of amphibian diversity patterns. *Acta Oecologica* 36 (6): 650-658. https://doi.org/10.1016/j.actao.2010.10.002

Guyétant R., Temmermans W. & Avrillier J. N. 1999. — Phénologie de la reproduction chez *Pelodytes punctatus* Daudin, 1802 (Amphibia, Anura). *Amphibia-Reptilia* 20 (2): 149-160. https://doi.org/10.1163/156853899x00169

Jaillet S., Cailhol D., Arnaud J., Astrade L., Belingard C., Boche E., Cornillon T., Couchoud I., Duguet R., Franck N., Gauchon C., Hellstrom J., Le Roux P. Monteil P., Peyronel O., Pons-Branchu E., Sadier B. & Thomas M. 2012. — Les crues du système karstique de Foussoubie (Ardèche, France). Une analyse géomorphologique et hydrodynamique des circulations dans la zone épinoyée du karst. *Collection EDYTEM, Cahiers de géographie* 13: 115-138. https://doi.org/10.3406/edyte.2012.1209

Jakob C., Veith M., Seitz A. & Crivelli A. J. 1998. — Données préliminaires sur la communauté d'amphibiens de la Réserve Naturelle de Roque-Haute dans le sud de la France. *Ecologia Mediterranea* 24 (2): 235-240. https://doi.org/10.3406/ecmed.1998.1867

Jakob, C. Poizat G., Veith M., Seitz A. & Crivelli A. J. 2003. — Breeding phenology and larval distribution of amphibians in a Mediterranean pond network with unpredictable hydrology. *Hydrobiologia* 499: 51-61. https://doi.org/10.1023/A:1026343618150

Joly P. & Morand A. 1994. — Theoretical habitat templets, species traits, and species richness: amphibians in the Upper Rhône River and its floodplain. *Freshwater Biology* 31 (3): 455-468. https://doi.org/10.1111/j.1365-2427.1994.tb01752.x

Kuhn J. 2001. — Biologie der Erdkröte (*Bufo bufo*) in einer Wildflusslandschaft (obere Isar, Bayern), *in* Kuhn J., Laufer H. & Pintar M. (eds), Amphibien in Auen. *Zeitschrift für Feldherpetologie* 8: 31-42.

Landmann A. & Böhm C. 2001. — Amphibien in Gebirgsauen: Artenbestand, Laichplatzangebot und Laichplatznutzung durch Grasfrosch (*Rana temporaria*) und Erdkröte (*Bufo bufo*) in den Auen des Tiroles Lech, *in* Kuhn J., Laufer H. & Pintar M. (eds): Amphibien in Auen. *Zeitschrift für Feldherpetologie* 8: 57-70.

Lizana M., Márquez R. & Martín-Sanchez R. 1994. — Reproductive biology of *Pelobates cultripes* in Central Spain. *Journal of Herpetology* 28 (1): 19-27. https://doi.org/10.2307/1564675

Martínez-Solano M. & García-París I. 2012. — *Pelobates cultripes* Cuvier, 1829 – Messerfuß, *in* Grossenbacher K. (ed.), *Handbuch der Reptilien und Amphibien Europas*. Aula-Verlag, Wiebeisheim: 441-463.

Montori A., Gomez D. & Del Amo R. 2015. — Fenologia i corologia de la comunitat d'amfibis del Parc del Garraf i d'Olèrdola. *Butlletí de la Societat Catalana d'Herpetologia* 22: 7-23.

Morand A. & Joly P. 1995. — Habitat variability and space utilization by the amphibian communities of the French Uper-Rhone floodplain. *Hydrobiologia* 300-301: 249-257. https://doi.org/10.1007/BF00024465

Morand A., Joly P. & Grolet O. 1997. — Phenotypic variation in metamorphosis in five anuran species along a gradient of stream influence. *Comptes Rendus de l'Académie des Sciences* 320 (8): 645-652. https://doi.org/10.1016/s0764-4469(97)85698-3

Nöllert A. & Nöllert C. 1993. — *Die Amphibien Europas.* Kosmos Verlags-GmbH, Stuttgart, 382 p.

Gómez-Mestre I., Kulkarni S. & Buchholz D. R. 2013. — Mechanisms and consequences of developmental acceleration in tadpoles responding to pond drying. *PLOS ONE* 8 (12): e84266. https://doi.org/10.1371/journal.pone.0084266

Jourdan-Pineau H., David P. & Crochet P.-A. 2012. — Phenotypic plasticity allows the Mediterranean parsley frog *Pelodytes punctatus* to exploit two temporal niches under continuous gene flow. *Molecular Ecology* 21 (4): 876-886. https://doi.org/10.1111/j.1365-294x.2011.05420.x

Petitot M., Manceau N., Geniez P. & Besnard A. 2014. — Optimizing occupancy surveys by maximizing detection probability: application to amphibian monitoring in the Mediterranean region. *Ecology and Evolution* 4 (18): 3538-3549. https://doi.org/10.1002/ece3.1207

Pintar M. 2001. — Langzeitbeobachtung an Amphibienlaichplätzen in einem Auenwald westlich von Wien, *in* Kuhn J., Laufer H. & Pintar M. (eds), Amphibien in Auen. *Zeitschrift für Feldherpetologie* 8: 157-167.

Priol P. 2015. — *Suivi d'une espèce rare en vue de sa conservation: dynamique spatiale et temporelle de populations de Pélobate cultripède (*Pelobates cultripes*) en Aquitaine.* MSc thesis, École pratique des hautes Études, Montpellier, 92 p.

Recuero E. 2014. — Sapo de espuelas – *Pelobates cultripes*, *in* Salvador A. & Martínez-Solano I. (eds), *Enciclopedia Virtual de los Vertebrados Españoles*. Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/anfibios/pelcul.html, dernière consultation le 31 décembre 2021.

Richter-Boix A., Llorente G. A. & Montori A. 2006a. — Breeding phenology of an amphibian community in a Mediterranean area. *Amphibia-Reptilia* 27 (4): 549-559. https://doi.org/10.1163/156853806778877149

Richter-Boix A., Llorente G. A. & Montori A. 2006b. — A comparative analysis of the adaptive developmental plasticity hypothesis in six Mediterranean anuran species along a pond permanency gradient. *Evolutionary Ecology Research* 8 (6): 1139-1154.

Richter-Boix A., Llorente G. A. & Montori A. 2007. — Structure and dynamics of an amphibian metacommunity in two regions. *Journal of Animal Ecology* 76 (3): 607-618. https://doi.org/10.1111/j.1365-2656.2007.01232.x

Richter-Boix A., Llorente G. A. & Montori A. 2008. — Estructura y dinámica de la comunidad de anfibios anuros en El Garraf, *in* Diputació de Barcelona (ed.), *V Trobada d'estudiosos del garraf: comunicacions presentades el dia 16 de novembre de 2006 a castelldefels.* Diputació de Barcelona, Barcelona: 41-49.

Rodríguez Jiménez A. J. 1986. — Notas sobre la fenologia y ecologia de *Hyla meridionalis* (Boettger, 1874) durante su desarrollo larvario y metamorfosis en cursos fluviales temporales. *Miscellania Zoologica* 10: 247-252.

Rodríguez Jiménez A. J. 1988. — Fenologia de una comunidad de anfibios asociada a cursos fluviales temporales. *Doñana, Acta Vertebrata* 15 (1): 29-43.

Román J. & Ruiz G. 2003. — Reproducción estival de *Hyla meridionalis* en la comarca de Doñana. *Boletín de la Asociación Herpetológica Española* 14: 54.

Rose C. 2018. — *Étude des routes migratoires des amphibiens au niveau d'un point de conflit dans la vallée de l'Ibie.* Mémoire de stage, Master 2 Écologie, Gestion et Diagnostic des Écosystèmes, Université Bourgogne Franche-Comté, Besançon, 30 p.

Salvador A. & Carrascal L. 1990. — Reproductive phenology and temporal patterns of mate access in Mediterranean anurans. *Journal of Herpetology* 24 (4): 438-441. https://doi.org/10.2307/1565070

Salvidio S. & Quero J.-Y. 1987. — Observations sur l'activité de *Pelobates cultripes* (Anura, Pelobatidae), *Bufo calamita* et *Bufo bufo* (Anura, Bufonidae) dans la mare du Grand Travers (Hérault). *Bulletin de la Société herpétologique de France* 41: 1-7.

Salvidio S., Lamagni L., Bombi P. & Bologna M. A. 2004. — Distribution, ecology and conservation of the parsley frog (*Pelodytes punctatus*) in Italy (Amphibia, Pelodytidae). *Italian Journal of Zoology* 71: 73-81. https://doi.org/10.1080/11250003.2004.9525540

Speybroeck J., Beukema W., Bok B., Van der Voort J. & Velikov I. 2016. — *Field Guide to the Amphibians and Reptiles of Britain and Europe*. Bloomsbury Natural History, Londres, 432 p.

Stubbington R., Chadd R., Cid N., Csabai Z., Miliša M., Morais M., Munné A., Pařil P., Pešić V., Tziortzis I., Verdonschot R. C. M. & Datry T. 2017. — Biomonitoring of intermittent rivers and ephemeral streams in Europe: current practice and priorities to enhance ecological status assessments. *Science of The Total Environment* 618: 1096-1113. https://doi.org/10.1016/j.scitotenv.2017.09.137

Talavera R. R. & Sanchiz B. 1987. — Temperature dependence of larval development in *Pelobates cultripes* (preliminary experiments), *in* van Gelder J. J., Strijbosch H. & Bergers P. J. M. (eds), *Proceedings of the 4th Ordinary General Meeting of the Societas Europaea Herpetologica.* Faculty of Sciences, Nijmegen.

TESTER U. 2001. — Relations between the habitat requirements of the European tree frog (*Hyla a. arborea*) and dynamic floodplains, *in* KUHN J., LAUFER H. & PINTAR M. (eds), Amphibien in Auen. *Zeitschrift für Feldherpetologie* 8: 15-20.

THIRION J.-M. 2006. — *Le Pélobate cultripède* Pelobates cultripes *(Cuvier, 1829) sur la façade atlantique française: chorologie, écologie et conservation*. MSc thesis, École pratique des hautes Études, Montpellier, 229 p.

TOCKNER K., KLAUS I, BAUMGARTNER C. & WARD J. V. 2006. — Amphibian diversity and nestedness in a dynamicfloodplain river (Tagliamento, NE-Italy). *Hydrobiologia* 565: 121-133. https://doi.org/10.1007/s10750-005-1909-3

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