

1 Title: Bimodal breeding phenology in the parsley frog *Pelodytes punctatus* as a bet-hedging  
2 strategy in an unpredictable environment despite strong priority effects

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4 Running title: breeding in an unpredictable habitat

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20 ABSTRACT

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21 When environmental conditions are unpredictable, expressing alternative phenotypes spreads  
22 the risk of failure, a mixed strategy called bet-hedging. In the southern part of its range, the  
23 Parsley frog *Pelodytes punctatus* breeds ~~from both in~~ autumn ~~te~~and in spring. Our aim was to  
24 study the breeding phenology and reproductive success associated with the use of those two  
25 seasonal niches to understand how this breeding strategy can be maintained. Field surveys  
26 revealed that breeding phenology was typically bimodal with a higher breeding effort in  
27 autumn. More importantly, in spring, the survival rate of offspring was severely reduced by the  
28 presence of autumn tadpoles, indicating a clear priority effect. However, the autumn cohort  
29 often failed to survive over winter, in which case spring cohorts were often successful. Based  
30 on those results, we constructed a model in which females can allocate a variable portion of  
31 eggs to each season and added a priority effect. We conclude that the existence of the two  
32 breeding seasons may indeed constitute a bet-hedging strategy.

33

34 INTRODUCTION

35 Breeding phenology is one of the key components of adaptation to temporally variable  
36 environments. Temporal dynamics of both the biotic and abiotic environment impose selective  
37 constraints on parental development and physiological state (to be able to reproduce) as well as  
38 offspring survival (at the various developmental stages until they reach sexual maturity and  
39 start to reproduce) (Rand 1973). There is a vast amount of literature on intraspecific variation  
40 of breeding patterns in relation to environmental conditions, in particular latitude, altitude and  
41 climate. In the context of current climate change, many species in temperate regions have  
42 advanced their breeding time (e.g. Brown et al., 2016; Frederiksen et al., 2004; Møller, 2008),  
43 as a result of microevolutionary changes and/or of phenotypic plasticity (Charmantier &  
44 Gienapp 2014). Most of these studies concern species with a single reproductive peak in the  
45 year, which has to match as precisely as possible a seasonal peak of resource availability in  
46 order to maximise reproductive success (e.g. caterpillar availability for tits). The exact date of  
47 the resource peak may vary from year to year and species usually rely on cues to anticipate it  
48 and plastically delay or advance the onset of reproduction every year. However, in some cases  
49 reproductive success depends on even [more](#) irregular and/or unpredictable conditions. In such  
50 situations, species face the risk of complete reproductive failure at any given breeding attempt,  
51 a regime that favors [expressing the expression of](#) alternative phenotypes to spread the risk, ~~a~~  
52 ~~strategy known as bet-hedging~~ (Cohen 1970; Slatkin 1974; Philippi & Seger 1989; Leimar  
53 2005; Venable 2007).

54 Theory predicts that in stochastic environments, selection favors life history traits that reduce  
55 temporal fitness variation even if they result in lowered arithmetic mean fitness (Philippi &  
56 Seger 1989). ~~This risk-spreading strategy is called bet-hedging.~~ In temporally variable  
57 environments, [the](#) long-term fitness of a genotype is measured by the geometric mean of the  
58 fitness contribution over ~~successive years at the individual level or over~~ successive generations

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59 for a particular genotype (Lewontin & Cohen 1969; Olofsson *et al.* 2009; Simons 2011; Yasui  
60 & Yoshimura 2018). This geometric mean fitness is highly impacted by low values; hence,  
61 traits with lower fitness variation may have higher long-term fitness. In principle, lower  
62 variation in fitness can be achieved either using the same low-risk strategy (conservative bet-  
63 hedging), or displaying several strategies, either at once or over several instances (diversified  
64 bet-hedging). While there is an abundant theoretical literature on bet-hedging, empirical studies  
65 have provided limited evidence so far (Simons 2011), and the most comprehensive examples  
66 concern the timing of germination/diapause and the fraction of dormant seeds/diapausing  
67 eggs (Venable 2007; Gremer *et al.* 2016; García-Roger *et al.* 2017; Wang & Rogers 2018).  
68 Some studies even report experimental evolution of bet-hedging traits in response to  
69 unpredictable environment (Beaumont *et al.* 2009; Graham *et al.* 2014; Maxwell & Magwene  
70 2017; Tarazona *et al.* 2017).  
71 One of the best examples of stochastic, unpredictable environments are is provided by  
72 temporary ponds, alternating between inundation and drought where each breeding event is a  
73 bet as habitat desiccation can occur before the end of the breeding cycle. Several examples of  
74 bet-hedging occur in temporary ponds. Fairy shrimps (Anostraca) produce drought-resistant  
75 eggs showing asynchronous hatching at different hydroperiods (Saiah & Perrin 1990; Simovich  
76 & Hathaway 1997; Wang & Rogers 2018). Similarly, rotifers produce diapausing eggs to  
77 overpass unfavorable planktonic growing season and only a fraction of those eggs hatch when  
78 conditions are suitable (García-Roger *et al.* 2017; Tarazona *et al.* 2017).  
79 For amphibian species breeding in temporary ponds, drought can cause 100% mortality of eggs  
80 or larvae, resulting in complete failure of one breeding event. One way to reduce the risk of  
81 losing a breeding opportunity entirely is to spread this risk at a spatial scale, partitioning broods  
82 into various pools as done by the Neotropical poison frog *Allobates femoralis* (Erich *et al.*

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83 2015). Another bet-hedging strategy could be to split the breeding effort at a temporal scale and  
84 exploit all suitable temporal windows.

85 From an ecological point of view, such temporal niche partitioning is expected to reduce inter  
86 and intra-specific competition as well as resource depletion (Carothers & Jaksic 1984). For  
87 example, species may share the same habitat but have opposite activity patterns (nocturnal  
88 versus diurnal species), as is the case in Neotropical felid community or in grassland ants

89 (Albrecht & Gotelli 2001; Di Bitetti *et al.* 2010). The same type of temporal segregation at a  
90 daily scale is also observed within species: brown trout *Salmo trutta* reduces competition for a

91 limiting resource by sequential use of foraging areas (Alanärä *et al.* 2001). Voltinism in insects  
92 is another well-studied example of temporal partitioning at the annual scale which is an

93 adaptation to predictable seasonal cycles (Kivelä *et al.* 2013; Zeuss *et al.* 2017; Forrest *et al.*  
94 2019)

95 However, if successive seasonal cohorts overlap, fitness gains may be asymmetric, because  
96 progeny produced by late breeding may suffer from competition or even predation from earlier  
97 cohorts (Morin 1987; Ryan & Plague 2004; Eitam *et al.* 2005). Those priority effects are often

98 difficult to disentangle from seasonal effects due to environmental differences experienced by  
99 the temporal cohorts (Morin *et al.* 1990). If priority effects are strong, late breeders may select  
100 breeding sites in order to limit the competition by conspecifics (Halloy & Fiaño 2000; Halloy

101 2006; Sadeh *et al.* 2009) and this may restrict late breeders to poorer sites (Crump 1991).

102 In amphibians, this temporal partitioning of breeding activity is thought to regulate community  
103 dynamics through interspecific competition (Lawler & Morin 1993; Gottsberger & Gruber  
104 2004; Richter-Boix *et al.* 2006b, 2007c). Similarly, community composition may depend on

105 species arrival and priority effects whereby species arriving earlier monopolize available  
106 resources and gain a competitive advantage over late species (Morin *et al.* 1990; Blaustein &

107 Margalit 1996; Urban & De Meester 2009). In Mediterranean regions, climatic conditions are

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108 characterized by dry, hot summers and mild winters, with the maximum rainfalls in autumn and  
109 spring. This leads to large breeding asynchrony observed between and within amphibian species  
110 (Diaz-Paniagua 1988; Jakob, Poizat et al. 2003; Richter-Boix, Llorente et al. 2006; Vignoli,  
111 Bologna et al. 2007): whereas most species typically breed in spring, some species breed earlier  
112 at the end of winter, and some even breed in autumn in addition to spring.

113 The Parsley Frog *Pelodytes punctatus* is a small sized Anuran distributed in Spain and most of  
114 France (locally reaching neighboring countries). It has a broad ecological niche but has poor  
115 competitive abilities and is sensitive to fish predation (Morand & Pierre 1995; Crochet et al.  
116 2004; Richter-Boix et al. 2007b); it thus prefers seasonally flooded habitats to ~~than~~-large  
117 permanent water bodies (Guyétant et al. 1999; Salvidio et al. 2004; Richter-Boix et al. 2007a).

118 In Spain the parsley frog shows a bimodal breeding pattern with higher reproductive effort in  
119 spring than in autumn (Guyétant et al. 1999; Richter-Boix et al. 2006b). In France, in addition  
120 to spring breeding, autumnal breeding is also observed in Mediterranean regions and areas with  
121 mild oceanic climate (Guyétant et al. 1999; Jakob et al. 2003; Richter-Boix et al. 2006a;  
122 Cayuela et al. 2012) but the importance of autumn versus spring reproduction has not been  
123 quantified. In the rest of the range and at higher in-altitudes, only spring breeding occurs.

124 In the Mediterranean areas of southern France, the parsley frog uses temporary ponds that refill  
125 in September and October but may dry during autumn or later in late spring. Adults thus have  
126 ~~thus~~ to deal with very unpredictable environmental conditions for their future offspring. In  
127 addition to this unpredictable risk, tadpoles hatched in autumn or spring are exposed to very  
128 different environmental conditions, the most obvious being that the autumn tadpoles overwinter  
129 while the spring ones do not. This should result in drastically different developmental  
130 trajectories but also in different offspring survivals. Both seasonal cohorts may also interact,  
131 leading to a potential competitive advantage to the earlier cohort over the later, i.e. a priority  
132 effect. The relative success of each breeding period and the outcome of the interaction between

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133 cohorts are key parameters to understand the persistence of this two-peaks breeding strategy.  
134 In fact, several pieces of information are still lacking in order to understand the evolutionary  
135 basis of this seasonally variable breeding strategy. Do we have a single protracted breeding  
136 season or a really bimodal reproduction generated by the coexistence of alternative breeding  
137 timing (~~autumn or spring~~)? If so, what is the relative importance of autumn versus spring  
138 reproduction? What is the survival of offspring produced at the two breeding periods and how  
139 is it affected by the presence of conspecifics? Once this basic knowledge is obtained, it can be  
140 fed into theoretical models for the evolution of mixed breeding strategies.

141 In this paper, we characterize the breeding phenology (temporal dynamic, relative proportion  
142 of each breeding period) of parsley frog in a French Mediterranean area based on results from  
143 a 3-year field survey. We monitored the survival of offspring produced in each season to  
144 estimate the success of this breeding strategy. We also investigated the factors influencing  
145 breeding and tadpole survival, in particular whether there is a priority effects between seasonal  
146 cohorts. Finally, using an analytical model adapted from Cohen (Cohen 1966) we tested  
147 whether the coexistence of the two breeding periods can be interpreted as a bet-hedging  
148 strategy.

149

## 150 MATERIAL AND METHODS

### 151 **Field survey**

152 The field study was carried out from September 2007 to August 2010 in 19 ponds situated  
153 around Montpellier, southern France (Annex 1). Those ponds are man-made environments,  
154 often dug out to provide drinking water for livestock (sheep and cows) or for game. The ponds  
155 surveyed included temporary and permanent sites. We define here the autumn breeding season  
156 as the period spanning from September to December and the spring breeding season from

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157 January to April. We surveyed each pond twice each month. During each visit, we recorded the  
158 depth of the pond.

159

### 160 **Sampling methods**

161 At every visit (mostly diurnal), we looked for newly deposited egg masses throughout the entire  
162 water body and classified the egg masses as small, medium and large, corresponding to an  
163 average of 75, 150 and 250 eggs per mass, respectively (Salvador & Paris 2001), and personal  
164 observation). The parsley frog's embryonic period ranges from 5 days at 15°C to 15 days at  
165 10°C (Toxopeus *et al.* 1993). Moreover, embryos stay attached to the jelly for several additional  
166 days (Guyétant *et al.* 1999). Thus, with an interval of 15 days between two successive visits,  
167 we may have missed a few masses but we have avoided double-counting masses since 15-day  
168 old masses can readily be distinguished from new ones based on the developmental stages of  
169 the embryos. In only 2% of the larval cohorts produced, ~~were~~ small larvae ~~were~~ observed in  
170 ponds where we did not notice the presence of egg masses before. ~~Note that~~ The probability of  
171 detection of an egg mass, even if not perfect, was similar in autumn and in spring.

172 We estimated the number of amphibian larvae and invertebrates present in the ponds using 5  
173 to 10 dipnet sweeps (depending on the pond size). The anuran community of the area consists  
174 of 7 species: *Pelodytes punctatus*, *Pelobates cultripipes*, *Alytes obstetricans*, *Bufo bufo*, *Epidalea*  
175 *calamita*, *Hyla meridionalis*, and *Pelophylax sp.*, (*P. ridibundus* and/or *P. perezi* & *P. kl. grafi*,  
176 depending on the sites). Potential predators of tadpoles are urodeles and aquatic invertebrates.  
177 Two urodele species (*Lissotriton helveticus* and *Triturus marmoratus*) were recorded in the  
178 ponds but due to the rare occurrence of *Triturus marmoratus*, only *Lissotriton helveticus* was  
179 included in subsequent analyses (as adults as well as larvae).

180 We also surveyed dragonfly larvae (Anisoptera) and backswimmers (Heteroptera,  
181 Notonectidae) that are potential predators of tadpoles (Richter-Boix *et al.* 2007a) except during

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182 the first year. Diving beetles (Coleoptera, Dytiscidae) are also known to prey on tadpoles but  
183 were very rare in the studied ponds and thus not considered for this study.

184 We divided the total counts for each amphibian larvae and invertebrate predators captured in  
185 each pond by the number of dipnet sweeps taken in each pond. This procedure yielded a crude  
186 proxy for density on the basis of catch per unit effort and could therefore be compared across  
187 localities.

188

### 189 **Reproductive effort and offspring survival**

190 Reproductive strategy of parsley frog was described by two measures: the ~~probability presence~~  
191 ~~of spawning-egg masses (binary variable: whether some eggs were laid or not when we visited~~  
192 ~~a pond finding a least one egg mass in one visited pond)~~ and the ~~breeding effort number of egg~~  
193 ~~masses (integer, non-zero; applies only to cases where egg masses are present when there was~~  
194 ~~at least one egg mass).~~ Spawning probability indicates if any new egg mass was observed  
195 during a visit. Breeding effort measures the quantity of eggs produced when there was at least  
196 one egg mass. We normalized the number of egg masses by their size (e.g. a small egg mass  
197 equals ½ medium egg mass).

198 For each breeding event, we estimated the ~~hatching rate~~ as the ratio of the number of small  
199 tadpoles (Gosner stage 26, free swimming tadpole) to the number of eggs spawned. Similarly,

200 we quantified the ~~survival rate from egg to metamorph~~ as the ratio of the number of metamorphs  
201 (Gosner stage 42-43) to the number of eggs spawned. ~~Finally, we calculated the survival rate~~

202 ~~during larval stage as the ratio of the number of metamorphs over the number of small tadpoles.~~  
203 ~~This index could only be estimated in about one third of the breeding events. When hatching~~  
204 ~~was successful (i.e. the number of small tadpoles was not null) in about one third of the breeding~~  
205 ~~event), we could calculate the survival during larval stage as the product of the two former~~  
206 ~~ratios.~~

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207 The number of tadpoles in a pond was estimated using the mean number of tadpoles caught per  
208 dipnet sweep scaled to a sampling surface of 1 m<sup>2</sup> (we estimated that one dipnet sweep sampled  
209 a surface of 0.5 m<sup>2</sup>, taking the dipnet size and the length of the haul into account) and then  
210 multiplied by the surface of the pond. This should not be taken as an attempt to estimate  
211 precisely the number of tadpoles present in a pond at a given time but as an index of abundance  
212 that can be compared between ponds and between breeding events. It was sometimes impossible  
213 to follow the larval development and metamorphosis of offspring from a particular breeding  
214 event. Indeed, parsley frogs may breed three to four times during each seasonal breeding event.

215 In these cases, the successive sub-cohorts produced are indistinguishable after a few weeks,  
216 and we summed the eggs counted in two or three successive visits to evaluate survival from a  
217 combination of breeding events within a given season (and within a site). Survival measures  
218 should be viewed as an index to assess the differences of reproductive success between seasons  
219 as there is no reason to expect any seasonal bias in this index.

220

#### 221 **Explanatory variables**

222 Explanatory variables for the breeding probability and breeding effort are the season, depth of  
223 the pond as well as the presence of conspecific and inter-specific competitors (larvae of anuran  
224 species) and predators (invertebrates and adult newts) in the pond. ~~The two~~ Except for the depth  
225 of the pond, - all those explanatory variables - last categories of variables - were also applied to  
226 explain the success (offspring survival) of breeding events. We summed the density of  
227 competitors and similarly the density of predators despite the differences in competitive  
228 performance and predation pressure of the various species toward parsley frog tadpoles.

229 To assess the potential impact of predation and competition on survival rates, we evaluated the  
230 mean density of predators and competitors encountered by parsley frog tadpoles during their  
231 larval development. More precisely, data from literature indicates that only small tadpoles (<12

232 mm snout-vent length) have lower survival due to predation by aquatic invertebrates (Tejedo  
233 1993). Above this size, the predators will only injure them or even fail to catch them. Larvae  
234 laid in autumn reached this limit size in about 3 months, whereas only 1.5 month is necessary  
235 for larvae laid in spring (personal observation). Thus, we used the mean density of predators  
236 and competitors over a period of 3 months after spawning date for autumn tadpoles and 1.5  
237 months for spring tadpoles.

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### 239 **Statistical analyses**

240 All statistical analyses were performed on R 3.4.1 (R Core Team 2018). To assess if pond  
241 characteristics differed between seasons, we applied a linear model for the depth of the pond  
242 and generalized linear models with a quasi-poisson family for all other variables to account for

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243 overdispersion. ~~Breeding probability~~ *The presence of egg masses* and ~~breeding effort~~ *the number*  
244 *of egg masses* were analysed using a generalized mixed model with site as random effect, with  
245 a binomial family or a negative binomial family (to account for overdispersion), respectively.

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246 The ~~survival-hatching rates~~ *and survival rates from egg to metamorph* were often zero hence  
247 we decided to analyse them as binary variables using a generalized mixed model with site as

248 random effect and a binomial family. Those *derived binary* -variables, called *hatching success*  
249 *and the metamorphosis, success* ~~breeding success and hatching success~~, are the probability of  
250 ~~producing~~ *observing* at least one *hatchling or one metamorph in a pond where egg masses were*  
251 ~~observed or one hatchling~~. The significance of fixed effects were tested using Chi<sup>2</sup> tests to  
252 compare nested models (Zuur *et al.* 2009).

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### 255 **Bet-hedging model**

256 Finally, we wondered if the coexistence of two breeding periods could result from a bet-hedging  
257 strategy, with the optimal strategy being to split the breeding effort between the two favourable  
258 seasons to spread the risk of complete failure (Seger & Brockman 1987). The following model  
259 is [an ESS model](#) derived from Saiah and Perrin (Saiah & Perrin 1990) on the hatching  
260 probability of fairy shrimp seasonal cohorts. This ~~scir~~ model was primarily inspired by Cohen  
261 (~~Cohen 1966~~), ~~reviewed by (Seger, J. and Brockman 1987)~~ on the optimal reproduction strategy  
262 of an annual plant whose seeds can either germinate or remain dormant. In our case, there are  
263 two strategies: autumn breeding with initial success (i.e. the ability of offspring to persist until  
264 spring) depending on the environmental conditions, and spring breeding with success  
265 depending mainly on the presence of autumn tadpoles, hence on the initial success of autumn  
266 breeding (as suggested by the results on success of autumn and spring breeding events, see  
267 below).

268 Let  $c$  be the proportion of eggs laid in autumn (thus  $1-c$  in spring) – we assume, in agreement  
269 with our data (see results), that  $c$  represents a fixed strategy, i.e. the frogs cannot predict failure  
270 in advance to avoid laying in autumn, nor can they avoid laying eggs in spring when an autumn  
271 cohort is present. As mentioned above, the autumn cohort is assumed to succeed or fail, at  
272 random, with probability  $q$  and  $1-q$  respectively. When it succeeds, a fraction  $s_1$  of the offspring  
273 survive to reproductive age. The spring cohort completely fails whenever the autumn cohort  
274 has survived in a pond (a reasonable simplification based on our survival rates estimates, see  
275 below–), otherwise a proportion  $s_2$  of spring tadpoles survive. Overall, the ~~mean expected~~  
276 number of ~~individuals offspring reaching sexual maturity produced per female~~ is  $c s_1$  when  
277 the autumn cohort doesn't fail and  $(1 - c) s_2$  when it does.

278 If each frog reproduced only during one year, the optimal strategy would maximize the  
279 geometric mean of the annual reproductive outcome (Dempster 1955) which is

$$280 \quad W = (c s_1)^q ((1 - c) s_2)^{1-q}$$

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281 Or, equivalently

$$282 \quad \text{Log}(W) = q \text{Log}(c s_1) + (1 - q) \text{Log}((1 - c) s_2)$$

283 However, reproductive life lasts more than one year in frogs (say,  $n$  years), which in itself is a  
284 way to spread the risk of failure among successive cohorts of offspring – an uncertainty remains  
285 however, for each frog, on how many ( $k$ ) of the  $n$  breeding years will not allow the autumn  
286 cohort to survive. For each individual,  $k$  is distributed binomially with probability  $1-q$  so that

$$287 \quad \text{Log}(W) = \sum_{k=0}^n \binom{n}{k} (1 - q)^k q^{n-k} \text{Log}(c s_1 (n - k) + (1 - c) k s_2)$$

288 where  $\binom{n}{k}$  represents the number of possible repartitions of the  $k$  years with autumn failure  
289 among the total number of breeding years  $n$ .

290 The selection gradient on  $c$  is the derivative of the function  $\text{Log}(W)$  , which indicates whether  
291 selection favors an increase in  $c$  (if positive) or a decrease (if negative):

$$292 \quad G[c] = \sum_{k=0}^n \binom{n}{k} (1 - q)^k q^{n-k} \frac{(s_1 + s_2) k - n s_1}{c(k (s_1 + s_2) - n s_1) - k s_2}$$

293 If some value of  $c$  within the authorized interval  $[0,1]$  results in  $G[c]=0$  then it is considered an  
294 evolutionary stable strategy (ESS) provided the second derivative is negative (i. e.  $G[c]$  is  
295 positive below the ESS and negative above).

296 We explored numerically ~~traced the fitness curves and~~ the selection gradients in order to find  
297 potential ESS using Mathematica (Wolfram Research Inc. 2018) based on the following

298 parameter combinations. We set survival probabilities based on our estimates of survival from  
299 egg to metamorphose:  $s_1 = 0.047$  (estimated among breeding events producing offspring that  
300 survived until spring) and  $s_2 = 0.038$  (in the absence of autumn tadpoles). We assumed that  
301 survival and fecundity were equal for both seasonal cohorts for the rest of the life cycle. We set  
302 the number of reproductive years  $n = 3$  to  $5$ , according to a study of age structure of a breeding

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303 population in Spain (Esteban *et al.* 2004). Note that this model applies at the individual level  
304 (as developed above) as well as at the genotype level.

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## 306 RESULTS

### 307 Characteristics of temporal niches

308 Pond depth was not significantly different between the autumn (here from September to  
309 December) and spring (here from January to April) breeding seasons (Table 1). The densities  
310 of amphibian larvae (other than parsley frog) were not significantly different. In autumn,  
311 extreme densities of *Epidalea calamita* tadpoles were recorded in some small ponds whereas  
312 the well-known spring breeding-species (*Hyla meridionalis*, *Pelophylax sp.*, *Triturus*  
313 *marmoratus*, *Lissotriton helveticus*) reproduce later than the parsley frog, hence their larvae are  
314 only present from April onwards. The density of potential invertebrate predators was higher in  
315 autumn than in spring ( $\chi^2_1 = 37.17$ , p-value = 0.005) with the lowest density being from  
316 December to March. On the contrary, the number of adult newts (potential predators of parsley  
317 frog tadpoles) was higher in spring than in autumn ( $\chi^2_1 = 369.36$ , p-value =  $2.2 \cdot 10^{-16}$ ).

318

### 319 Breeding phenology

320 We registered 184 breeding events, 79 in autumn and 105 in spring. Note that in two sites, one  
321 breeding event was recorded in May. The ~~number of egg masses breeding effort recorded in~~  
322 ~~one pond~~ showed a bimodal pattern with a peak in October and another in February (Figure 1).

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323 ~~Note that in two sites, one breeding event was recorded in May.~~

324 The ~~presence of egg masses spawning probability~~ (finding at least one egg mass when visiting  
325 a pond) was not significantly different between the two seasons ( $0.18 \pm (0.02)$ , mean ~~( $\pm$ S.E)~~ per  
326 visit in autumn and  $0.22 \pm (0.02)$  per visit in spring, (over 429 and 470 visits, respectively)  
327  $\chi^2_1 = 2.31$ , p-value = 0.128, see also [Annex-Table 2](#)). This ~~spawning probability variable~~ was not

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328 affected by the presence of anurans from other species (larvae), nor by the presence of predators  
329 (invertebrates or adult newts). It was positively related to the depth of the pond ( $\chi^2_1=20.40$ , p-  
330 value=  $6.3 \times 10^{-6}$ ). The ~~presence of egg masses observed in spring spawning probability~~ was not  
331 affected by the presence of autumn tadpoles ( $\chi^2_1=0.03$ , p-value= 0.875).

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332 The ~~breeding effort~~ *number of egg masses* was higher in autumn than in spring ( $23.0 \pm (4.0)$  egg  
333 masses per breeding event in autumn and  $13.7 \pm (2.4)$  in spring;  $\chi^2_1=9.25$ , p-value=0.002, Fig.  
334 2, [Table 2](#) and Annex [23](#)). As a result, autumn breeding contributed slightly more than spring  
335 breeding to the production of egg masses (57% versus 42.9%).

336

### 337 **Breeding success**

338 *Hatching success* (i.e. the percentage of breeding events producing at least one larvae) was  
339 higher in autumn than in spring (68.4% and 43.8% respectively,  $\chi^2_1=11.12$ , p-value= 0.001,  
340 [Table 2](#)). *Metamorphosis success* (i.e. the percentage of breeding events producing at least one  
341 metamorph) was not significantly different between the two seasons (34.2% in autumn and  
342 29.8% in spring  $\chi^2_1= 0.39$ , p= 0.531).

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343 ~~Drought-en~~ (pond totally dried up) caused the total failure of 7 breeding events (~~9% of the~~  
344 ~~breeding events~~) in autumn and of 5 breeding events in spring (~~4.8%~~) over the 3 year-survey  
345 and the 19 sites (~~representing 9% and 4.8% of the breeding events, those percentages are not~~  
346 ~~significantly different,  $\chi^2_1= 0.66$ , p= 0.42~~). Drought caused mortality of offspring at different  
347 developmental stages (mostly eggs for autumn cohort and tadpoles for spring cohort). ~~As a~~  
348 ~~consequence, breeding success~~ (i.e. the percentage of breeding events producing at least one  
349 metamorph) was not significantly different between the two seasons (34.2% in autumn and  
350 29.8% in spring  $\chi^2_1= 0.39$ , p= 0.531).

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351 ~~Neither *breeding-hatching success nor metamorphosis success, nor hatching success* were~~  
352 explained by interspecific competition (the density of other amphibian larvae) or by predation  
353 (density of potential invertebrate predators or number of adult newts, *see Table 2*).

354 Survival rates are represented in Figure 3 and Annex 34. The *survival rates from egg to*  
355 *metamorph* were similarly low (autumn: 2.24 %  ~~$\pm(-0.61)$~~  and spring: 1.97 %  ~~$\pm(0.73)$~~ , *Table*  
356 *2*), resulting in a higher contribution (74.6%) of autumn breeding in the overall production of  
357 metamorphs per site and per year (due to the higher breeding effort in autumn, see above).

358 The autumn cohort persisted until spring in 34/79 breeding events (43%,  
359 corresponding to the rate of initial success,  $q$ , see bet-hedging model). In  
360 those cases, tadpoles laid in spring coexisted in their pond with tadpoles  
361 from the autumn cohort. ~~From the point of view of spring breeders, in 28/57~~  
362 ~~cases, they found autumn tadpoles in the pond.~~ The presence of an autumn  
363 cohort of parsley frog tadpoles significantly reduced the *metamorphosis*  
364 *success of spring cohorts breeding event* to 18.4% in presence of autumn tadpoles,  
365 versus 40.0% in absence of autumn tadpoles,  $\chi^2_1=10.60$ ,  $p\text{-value}=0.005$ ). This  
366 reduction effect was not significant for the *hatching success* (32.6% in presence  
367 of autumn tadpoles, versus 53.6% in absence of autumn tadpoles  $\chi^2_1=4.63$ ,  $p\text{-}$   
368  $\text{value}=0.099$ ). Accordingly, all *three* survival rates were reduced in the  
369 presence of autumn tadpoles and this effect was most pronounced for the  
370 *survival from egg to metamorphs* (3.77%  ~~$\pm(+1.4)$~~  versus 0.16%  ~~$\pm(+0.08)$~~  in absence  
371 versus presence of autumn tadpoles, Figure 4 and Annex 45).

372 ~~We also tested if the *metamorphosis success* of autumn tadpoles might be affected by the~~  
373 ~~presence of spring tadpoles, but this was not the case ( $\gamma^2_1=2.75$ ,  $p\text{-value}=0.097$ ).~~

374 Finally, ~~the~~ figure 5 summarizes the breeding strategy of parsley frog showing the presence of  
375 egg masses, tadpoles and the ~~outcome-metamorphs of the breeding event (production of~~  
376 ~~metamorphs)~~ in each studied site, over the three years of survey. It illustrates ~~ed~~ the quasi-  
377 exclusion between the two cohorts: ~~there were only 4 cases in total (out of 47 observations)~~

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378 where metamorphs from the two seasonal cohorts emerged in spring in the same pond during  
379 the same year.

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### 381 Maintenance of spring breeding

382 Selection gradients based on our bet-hedging model predict that a mixed strategy is maintained  
383 when the rate of initial success of the autumn cohort ( $q$ ) is between 0.2 and 0.8 for a number of  
384 reproductive years  $n = 3$ . In this condition, a pure autumn strategy is predicted above 0.8, and  
385 a pure spring strategy below 0.2. (Figure 64). The maintenance of this strategy is less probable  
386 if the number of reproductive years increases ( $n = 5$  years of breeding), with a reduced range of  
387  $q$  leading to a stable mixed strategy.

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## 389 DISCUSSION

### 390 Cost and benefits of a bimodal breeding phenology

391 We used field surveys to describe the breeding phenology of the parsley frog in the French  
392 Mediterranean region but also to quantify the relative contribution and success of each seasonal  
393 reproduction (autumn and spring reproduction). This quantification, rarely achieved in the wild  
394 (but see Licht 1974; Banks & Beebee 1988; Gascon 1992; Wheeler *et al.* 2015), is essential to  
395 understand the evolution of this bimodal breeding strategy. We confirmed the existence of two  
396 distinct seasonal peaks in breeding activity, probably mediated by cold temperature in  
397 December and January as adult parsley frogs tend to breed in mild and rainy periods as was  
398 previously observed (Toxopeus *et al.* 1993; Guyétant *et al.* 1999; Jakob *et al.* 2003). However  
399 breeding episodes occurred even in the absence of rainfall as long as ponds were filled with  
400 water (personal observations and Richter-Boix *et al.* 2006b).

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401 The ~~breeding effort~~ number of egg masses in our population was higher in autumn than in spring.

402 This is in apparent contradiction with Richter-Boix *et al.* (2006b) who found that a four-fold

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403 ~~higher spring~~ breeding effort ~~in spring was four fold higher~~ than ~~in~~ autumn ~~breeding effort~~ in  
404 the northeast of the Iberian Peninsula. While we don't have a definitive explanation for this  
405 difference, we suggest it could be related to higher competition among anuran larvae in autumn  
406 in north-east Spain compared to France. In our study area in southern France, larvae of  
407 *Pelodytes punctatus* are typically the only anuran larvae found after the summer drought in the  
408 ponds in autumn. In contrast, four other species of Anura (*Hyla meridionalis*, *Epidalea*  
409 *calamita*, *Alytes obstetricans* and *Pelophylax perezi*) have tadpoles in autumn and three of them  
410 (i.e. all except *E. calamita*) can have overwintering tadpoles in Spanish ponds (Richter-Boix *et*  
411 *al.* 2006b). These authors also showed that *Pelodytes punctatus* tadpoles suffer from interaction  
412 with *Hyla meridionalis* (Richter-Boix *et al.* 2007b). It is thus possible that increased  
413 competition for *Pelodytes punctatus* larvae in autumn and winter ~~compared to our study area~~  
414 makes the autumn niche less favourable in northeastern Spain compared to ~~our study area in~~  
415 southern France and reduce parsley frog investment in autumn breeding there.

416 ~~The survival rate~~ ~~Offspring survival~~ (from egg to metamorph) was low in both seasons. The  
417 combination of ~~numbers of egg masses~~ ~~breeding effort~~ and survival rates eventually resulted in  
418 a higher contribution of autumn breeding to the overall production of metamorphs. The overall  
419 low survival rates of offspring that we found is in line with previous field studies in anurans  
420 (e.g. Licht 1974; Banks & Beebee 1988) and can be caused by pond desiccation, predation,  
421 inter and intra-specific competition for food and parasitism or pathogen infections. Our study  
422 revealed no obvious effect of variation in predation on tadpole survival even if the predation  
423 pressure encountered by tadpoles at the beginning of their development varies from site to site  
424 (but not between seasons). This may seem surprising since many studies experimentally  
425 demonstrated that predation cause substantial mortality to tadpole populations (e.g. ~~Tejedo~~  
426 1993; Van Buskirk & Arioli 2005). This may be due to the lack of information about predation  
427 during the first year of survey which reduced our statistical power or to the fact that causative

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428 factors are numerous and more complex to identify in the field. However, other studies reported  
429 no effect of predation on tadpole survival (Hartel *et al.* 2007) or even a positive effect (Barandun  
430 & Reyer 1997), probably due to predator-induced phenotypic plasticity. Nevertheless, our  
431 results suggest that the predation pressure is probably not a stronger constraint in one season  
432 than in the other.

433 Spring tadpoles should be exposed to more competitors during their development than autumn  
434 tadpoles since the majority of amphibian species in the local community breed in March and  
435 April. Nevertheless, we found no effect of interspecific competition on survival for any of the  
436 two seasonal tadpole cohorts. This seems surprising since parsley frog is a poor competitor as  
437 a tadpole compared to most species of the anuran community, in particular *Hyla meridionalis*  
438 and *Rana perezi*, ~~perezi~~ present in spring in permanent ponds (Richter-Boix *et al.* 2007b). On  
439 the contrary, in small temporary ponds and during autumn and winter season, Parsley frog  
440 tadpoles encounter mostly *Bufo bufo* and *Epidalea calamita* with even lower competitive  
441 abilities (Richter-Boix *et al.* 2007b). We hypothesized that interspecific competition effect was  
442 not detected in our study due to numerous uncontrolled sources of variation.

443

#### 444 **Priority effects**

445 We revealed a striking negative effect of the presence of conspecific autumn tadpoles on the  
446 survival of spring tadpoles in the Parsley Frog. Previous studies have demonstrated the  
447 occurrence of such intraspecific priority effect in amphibians in experimental settings (Morin  
448 *et al.* 1990; Eitam *et al.* 2005; Murillo-Rincón *et al.* 2017) but as far as we know, our study is  
449 the first evidence for intraspecific, inter-cohort competition in amphibians in nature. In the field,  
450 we observed in several occasions that large autumn tadpoles were eating freshly laid eggs of  
451 their own species, which could partly explain the lower hatching rate of spring eggs in presence  
452 of autumn tadpoles. Moreover, (Tejedo 1991) previously described how parsley frog tadpoles

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453 ~~preys on~~ ~~depredates~~ *Epidalea calamita* eggs. In this latter study, ~~predatory~~ ~~eeous~~ tadpoles were  
454 exclusively old tadpoles and they could cause a loss of 50 to 100% of the eggs. Oophagy has  
455 also been demonstrated to be responsible for interspecific priority effects between *Scaphiosus*  
456 *couchii* and *Bufo speciosus* (Dayton & Fitzgerald 2005). Intraspecific oophagy has been  
457 described ~~on~~ ~~in~~ some anuran species (Summers 1999; Dayton & Wapo 2002) and has been  
458 proposed as an energetic opportunistic response in food shortage in temporary ponds.

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459 However, the presence of autumn tadpoles also affects the larval survival (post-hatching) of  
460 spring tadpoles. This may reflect competition for resources between large autumn and small  
461 spring tadpoles as shown in *Rana arvalis* (Murillo-Rincón *et al.* 2017). Interference competition  
462 mediated by microorganisms may also play a role: smaller tadpoles could display coprophagy  
463 instead of feeding on higher quality resources (Beebee & Wong 1992; Baker & Beebee 2000).

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464 This large priority effect between the two seasonal tadpole cohorts of parsley frog has a great  
465 impact on the overall efficiency of breeding: in most ponds, there could be only one successful  
466 breeding period, autumn or spring. Nonetheless, we found no indication that spring breeders  
467 select their oviposition site to avoid conspecifics, as other amphibian species sometimes do  
468 (Sadeh *et al.* 2009). Accordingly, the ~~spawning probability~~ ~~presence of egg masses~~ was also  
469 unaffected by the presence of potential competitors or predators.

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#### 471 **Seasonal partitioning of breeding: a bet-hedging strategy?**

472 The temporal partitioning of breeding activity could reflect several evolutionary processes: 1)  
473 the existence of two specialized phenotypes either genetically determined (in which case we  
474 would expect temporal genetic differentiation between cohorts) or set by early environmental  
475 cues (phenotypic plasticity); 2) a use of alternative strategies by some or all individuals (bet-  
476 hedging). We previously demonstrated that the two temporal cohorts do not reflect two  
477 genetically distinct temporal populations (Jourdan-Pineau *et al.* 2012) but breeding phenology

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478 may still be set once for good for each individual. In this case, breeding in autumn or in spring  
479 could be determined by the physiological state (and sexual maturity) of the breeder and  
480 maintained year after year, by physiological constraints (typically the case for a capital breeder  
481 species which stores energy for future reproduction (e.g. ~~Lardner & Loman 2003~~). In a  
482 diversified bet-hedging strategy, individual breeding activities could vary from year to year  
483 (each year, individuals would “choose” one breeding season) or individuals could split their  
484 breeding effort between the two seasons in some or most years. There is no individual data  
485 available for this species and our only attempt to mark adults with visible implant alpha tags was  
486 not successful. Preliminary results based on genotyping of eggs, spawned in the same pond at  
487 different periods, suggests that females could breed several times in one year but this has to be  
488 confirmed (unpublished data). Clearly, this is a line of research to develop in the future if we  
489 want to fully understand the evolution of reproduction in this system.

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490 Based on our field survey, it appears that the bimodal breeding phenology of parsley frog is a  
491 typical diversified bet-hedging strategy. The large priority effect between the two seasonal  
492 cohorts, combined with high unpredictability of conditions that result in failure or success of  
493 entire cohorts, results in frequency dependent-selection and favour risk-spreading strategies:  
494 the best option is to develop in ponds with the smaller number of conspecific competitors. These  
495 conditions are found partly in autumn, when the habitat becomes favourable after the dry  
496 summer period, or in spring, as some of the autumn cohorts have died in the winter, leaving the  
497 habitat free. Poethke et al. (~~Poethke et al.~~ 2016) developed a theoretical model in which they  
498 outlined this impact of competition on the evolution of bet-hedging strategy. Using a model for  
499 optimal germination fraction, based on field data on desert plants, Gremer and Venable (~~Gremer  
500 & Venable 2014~~) also showed that density-dependence could explain the observed bet-hedging  
501 strategy of germination spread in time (i.e. not all seeds at once). Density-dependence was not

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502 included in our model and we do not have field data to assess its effect in our populations. This  
503 would be a fruitful line of research to improve our understanding of this breeding system.

504 In the parsley frog, our model shows that the observed mixed breeding strategy ( $0 < c < 1$ ) is  
505 maintained if the rate of initial success of the autumn cohort ( $q$ ) is between 0.2 and 0.8 (if  
506 females have on average 3 years of breeding in their lifetime) or between 0.35 and 0.65 (for 5  
507 years of breeding). Those conditions are fulfilled according to our field estimates ( $q=0.43$ ). We  
508 estimated the proportion of eggs laid in autumn by all breeders ( $c=0.57$ ) but could not estimate  
509 this proportion at the individual level. Survival rates set in the model were based on our field  
510 estimates of survival from egg to metamorphosis; hence, we assumed similar survival after  
511 metamorphosis of the two cohorts. Unfortunately, we have no information about survival of  
512 parsley frog during its adult terrestrial life. However, the adult survival is an important  
513 parameter in our model since it determines the number of reproductive years. The mixed  
514 breeding strategy is less stable when the number of breeding opportunities per lifetime increases  
515 – as the risk is now spread over several successive years. Indeed, experiencing variation in  
516 reproductive success among those opportunities is less harmful when it is possible to try again  
517 the next year. A skeletochronology study conducted in a upland population in Spain indicated  
518 that the mean age of sampled parsley frog females was 5.01 years (with a standard deviation of  
519 1.99) (Esteban *et al.* 2004). Assuming a minimal age at first reproduction of 1 year (as done by  
520 Esteban *et al.* 2004), this translates into an average number of reproductive years or females of  
521  $n = 4$ . Our evaluation of the bet-hedging strategy with  $n = 5$  is thus probably conservative.

522 We previously showed that the parsley frog successfully exploits two temporal niches in the  
523 Mediterranean region thanks to a high phenotypic plasticity of tadpole development to face  
524 very different seasonal environments (Jourdan-Pineau *et al.* 2012). Recently, the combination  
525 of phenotypic plasticity and bet-hedging has been theoretically investigated, suggesting that  
526 phenotypic plasticity could further minimize fitness variances caused by mismatches between

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527 phenotype and environment (Rádai 2020; Haaland *et al.* 2021). Interestingly, in the wolf spider,  
528 temperature and day length leads to alternative developmental types within broods. This cohort  
529 splitting is both probabilistic and sensitive to environment, a phenomenon proposed as being a  
530 plastic bet-hedging strategy by Rádai (Rádai 2020). In this case, the various plastic phenotypes,  
531 triggered by environmental variations, constitute a bet-hedging response to grassland habitats  
532 with substantial and unpredictable year-to-year variation.

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533 ~~In conclusion, The breeding strategy of parsley frog seems to constitute an original example~~  
534 ~~of bet hedging strategy driven by high environmental stochasticity and large inter cohort~~  
535 ~~priority effect. Characterizing adult survival and individual breeding pattern (using mark-~~  
536 ~~recapture and parentage assignment of egg masses) would allow further refining our model and~~  
537 ~~seeing how it can apply to other anuran species. In the Parsley Frog, priority effect is not the~~  
538 ~~only factor influencing the relative success of the spring and autumn strategies in terms of future~~  
539 ~~recruitment: autumn tadpoles metamorphose earlier and at a much larger size than spring~~  
540 ~~tadpoles (Jourdan-Pineau *et al.* 2012, unpublished data), which should confer to them a~~  
541 ~~significant advantage in terms of survival to adulthood (Smith 1987; Altwegg & Reyer 2003;~~  
542 ~~Székely *et al.* 2020) (REF) even if we don't know of size and date of metamorphosis affects~~  
543 ~~survival and ultimately fitness in our model. In addition, there is no significant difference in~~  
544 ~~cohort survival (the probability to produce at least one metamorph) between spring and autumn,~~  
545 ~~in spite of a slightly higher risk of drought (and hence complete dye-off of the cohort) in~~  
546 ~~autumn. Density-dependence (on which we have no information) might partly explain why~~  
547 ~~autumn cohorts do as well as spring cohorts in spite of higher drought risk. Last, our measures~~  
548 ~~of breeding success are very rough because counting precisely the number of larvae from each~~  
549 ~~cohorts in the ponds over the course of the season is extremely difficult. There is thus still much~~  
550 ~~to learn to fully understand the advantages and disadvantages of autumn and spring strategies~~  
551 ~~in this species.~~

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552 Last, as explained above, we still don't know if individual females usually breed once a year  
553 (either spring or autumn) or several times a year (potentially spring and autumn of the same  
554 year). Capture-mark-recapture of adults and larvae would alleviate some of these limitations  
555 but would be highly challenging. -However, our results remain valid for a large range of  
556 parameters these uncertainties should not affect our conclusion that the breeding strategy of  
557 parsley frog constitute an original example of bet-hedging strategy driven by high  
558 environmental stochasticity and large inter-cohort priority effect.

559

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565

566 CONFLICT OF INTEREST DISCLOSURE

567 The authors of this article declare that they have no financial conflict of interest with the content  
568 of this article. HJ-P is one of the PCIEvolBiol recommenders.

569

570 REFERENCES

- 571 Alanärä, A., Burns, M.D. & Metcalfe, N.B. (2001). Intraspecific resource partitioning in  
572 brown trout: The temporal distribution of foraging is determined by social rank. *J. Anim.*  
573 *Ecol.*, 70, 980–986.
- 574 Albrecht, M. & Gotelli, N.J.J. (2001). Spatial and temporal niche partitioning in grassland  
575 ants. *Oecologia*, 126, 134–141.
- 576 Altwegg, R. & Reyer, H.-U.U. (2003). Patterns of natural selection on size at metamorphosis  
577 in water frogs. *Evolution (N. Y.)*, 57, 872–882.
- 578 Baker, G.C. & Beebee, T.J.C. (2000). Evidence for the induction of interference competition  
579 between anuran larvae in plastic pond cages. *Amphib. Reptil.*, 21, 25–37.
- 580 Banks, B. & Beebee, T. (1988). Reproductive success of natterjack toads *Bufo calamita* in  
581 two contrasting habitats. *J. Anim. Ecol.*, 57, 475–492.
- 582 Barandun, J. & Reyer, H. (1997). Reproductive ecology of *Bombina variegata*: development  
583 of eggs and larvae. *J. Herpetol.*, 31, 107–110.

Code de champ modifié

584 Beaumont, H.J.E., Gallie, J., Kost, C., Ferguson, G.C. & Rainey, P.B. (2009). Experimental  
585 evolution of bet hedging. *Nature*, 462, 90–93.

586 Beebee, T.J.C. & Wong, A.L.C. (1992). Prototheca-mediated interference competition  
587 between anuran larvae operates by resource diversion. *Physiol. Zool.*, 65, 815–831.

588 Di Bitetti, M.S., De Angelo, C.D., Di Blanco, Y.E. & Paviolo, A. (2010). Niche partitioning  
589 and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, 36, 403–  
590 412.

591 Blaustein, L. & Margalit, J. (1996). Priority effects in temporary pools: nature and outcome of  
592 mosquito larva-toad tadpole interactions depend on order of entrance. *J. Anim. Ecol.*, 65,  
593 77–84.

594 Brown, C.J., O'Connor, M.I., Poloczanska, E.S., Schoeman, D.S., Buckley, L.B., Burrows,  
595 M.T., *et al.* (2016). Ecological and methodological drivers of species' distribution and  
596 phenology responses to climate change. *Glob. Chang. Biol.*, 22, 1548–1560.

597 Van Buskirk, J. & Arioli, M. (2005). Habitat specialization and adaptive phenotypic  
598 divergence of anuran populations. *J. Evol. Biol.*, 18, 596–608.

599 Carothers, J.H. & Jaksic, F.M. (1984). Time as a Niche Difference : The Role of Interference  
600 Competition. *Oikos*, 42, 403–406.

601 Cayuela, H., Besnard, A., Béchet, A., Devictor, V. & Olivier, A. (2012). Reproductive  
602 dynamics of three amphibian species in Mediterranean wetlands: The role of local  
603 precipitation and hydrological regimes. *Freshw. Biol.*, 57, 2629–2640.

604 Charmantier, A. & Gienapp, P. (2014). Climate change and timing of avian breeding and  
605 migration: Evolutionary versus plastic changes. *Evol. Appl.*, 7, 15–28.

606 Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *J. Theor.*  
607 *Biol.*, 12, 119–129.

608 Cohen, D. (1970). A Theoretical Model for the Optimal Timing of Diapause. *Am. Nat.*, 104,

609 389–400.

610 Crochet, P.A., Chaline, O., Cheylan, M. & Guillaume, C.P. (2004). No evidence of general  
611 decline in an amphibian community of Southern France. *Biol. Conserv.*, 119, 297–304.

612 Crump, M.L. (1991). Choice of Oviposition Site and Egg Load Assessment by a Treefrog.  
613 *Herpetologica*, 47, 308–315.

614 Dayton, G.H. & Fitzgerald, L.A. (2005). Priority effects and desert anuran communities. *Can.*  
615 *J. Zool.*, 83, 1112–1116.

616 Dayton, G.H. & Wapo, S.D. (2002). Cannibalistic Behavior in *Scaphiopus couchii*: More  
617 Evidence for Larval Anuran Oophagy. *J. Herpetol.*, 36, 531–532.

618 Dempster, E.R. (1955). Maintenance of genetic heterogeneity. In: *Cold Spring Harbor*  
619 *Symposia on Quantitative Biology*. pp. 25–31.

620 Eitam, A., Blaustein, L. & Mangel, M. (2005). Density and intercohort priority effects on  
621 larval *Salamandra salamandra* in temporary pools. *Oecologia*, 146, 36–42.

622 Erich, M., Ringler, M., Hödl, W. & Ringler, E. (2015). Brood-partitioning behaviour in  
623 unpredictable environments: hedging the bets? *Behav. Ecol. Sociobiol.*, 69, 1011–1017.

624 Esteban, M., Sanchez-Herraiz, M.J., Barbadillo, L.J. & Castanet, J. (2004). Age structure and  
625 growth in an isolated population of *Pelodytes punctatus* in northern Spain. *J. Nat. Hist.*,  
626 38, 2789–2801.

627 Forrest, J.R.K., Cross, R. & Caradonna, P.J. (2019). Two-year bee, or not two-year bee? How  
628 voltinism is affected by temperature and season length in a high-elevation solitary bee.  
629 *Am. Nat.*, 193.

630 Frederiksen, M., Harris, M.P., Daunt, F., Rothery, P. & Wanless, S. (2004). Scale-dependent  
631 climate signals drive breeding phenology of three seabird species. *Glob. Chang. Biol.*,  
632 10, 1214–1221.

633 García-Roger, E.M., Carmona, M.J. & Serra, M. (2017). Modes, mechanisms and evidence of

634 bet hedging in rotifer diapause traits. *Hydrobiologia*, 796, 223–233.

635 Gascon, C. (1992). Aquatic predators and tadpole prey in central Amazonia: field data and  
636 experimental manipulations. *Ecology*, 73, 971–980.

637 Gottsberger, B. & Gruber, E. (2004). Temporal partitioning of reproductive activity in a  
638 neotropical anuran community. *J. Trop. Ecol.*, 20, 271–280.

639 Graham, J.K., Smith, M.L. & Simons, A.M. (2014). Experimental evolution of bet hedging  
640 under manipulated environmental uncertainty in *Neurospora Crassa*. *Proc. R. Soc. B*  
641 *Biol. Sci.*, 281.

642 Gremer, J.R., Kimball, S. & Venable, D.L. (2016). Within-and among-year germination in  
643 Sonoran Desert winter annuals: bet hedging and predictive germination in a variable  
644 environment. *Ecol. Lett.*, 19, 1209–1218.

645 Gremer, J.R. & Venable, D.L. (2014). Bet hedging in desert winter annual plants: Optimal  
646 germination strategies in a variable environment. *Ecol. Lett.*, 17, 380–387.

647 Guyétant, R., Temmermans, W. & Avriillier, J.N. (1999). Phénologie de la reproduction chez  
648 *Pelodytes punctatus* Daudin, 1802 (Amphibia, Anura). *Amphibia-Reptilia*, 20, 149–160.

649 Haaland, T.R., Wright, J. & Ratikainen, I.I. (2021). Individual reversible plasticity as a  
650 genotype-level bet-hedging strategy. *J. Evol. Biol.*, 34, 1022–1033.

651 Halloy, M. (2006). Choice of oviposition site in *Pleurodema borellii* (Leptodactylidae):  
652 importance of conspecific tadpole size. *South Am. J. Herpetol.*, 1, 72–78.

653 Halloy, M. & Fiaño, J.M. (2000). Oviposition Site Selection in *Pleurodema borellii* (Anura:  
654 Leptodactylidae) May Be Influenced by Tadpole Presence. *Copeia*, 2000, 606–609.

655 Hartel, T., Nemes, S. & Mara, G. (2007). Breeding phenology and spatio-temporal dynamics  
656 of pond use by the yellow-bellied toad (*Bombina variegata*) population: The importance  
657 of pond availability and duration. *Acta Zool. Litu.*, 17, 56–63.

658 Jakob, C., Poizat, G., Veith, M., Seitz, A. & Crivelli, A.J. (2003). Breeding phenology and

659 larval distribution of amphibians in a Mediterranean pond network with unpredictable  
660 hydrology. *Hydrobiologia*, 499, 51–61.

661 Jourdan-Pineau, H., David, P. & Crochet, P.-A. (2012). Phenotypic plasticity allows the  
662 Mediterranean parsley frog *Pelodytes punctatus* to exploit two temporal niches under  
663 continuous gene flow. *Mol. Ecol.*, 21, 876–86.

664 Kivelä, S.M., Välimäki, P. & Gotthard, K. (2013). Seasonality maintains alternative life-  
665 history phenotypes. *Evolution*, 67, 3145–60.

666 Lardner, B. & Loman, J. (2003). Growth or reproduction? Resource allocation by female  
667 frogs *Rana temporaria*. *Oecologia*, 137, 541–546.

668 Lawler, S.P. & Morin, P.J. (1993). Temporal Overlap, Competition, and Priority Effects in  
669 Larval Anurans. *Ecology*, 74, 174–182.

670 Leimar, O. (2005). The evolution of phenotypic polymorphism: randomized strategies versus  
671 evolutionary branching. *Am. Nat.*, 165, 669–681.

672 Lewontin, R.C. & Cohen, D. (1969). On population growth in a randomly varying  
673 environment. *Proc. Natl. Acad. Sci. U. S. A.*, 62, 1056–1060.

674 Licht, L.E. (1974). Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora*  
675 and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Can. J. Zool.*,  
676 52, 613–627.

677 Maxwell, C.S. & Magwene, P.M. (2017). When sensing is gambling: An experimental system  
678 reveals how plasticity can generate tunable bet-hedging strategies. *Evolution (N. Y.)*, 71,  
679 859–871.

680 Møller, A.P. (2008). Climate change and micro-geographic variation in laying date.  
681 *Oecologia*, 155, 845–857.

682 Morand, A. & Pierre, J. (1995). Habitat variability and space utilization by the amphibian  
683 communities of the French upper-rhone floodplain. *Hydrobiologia*, 300–301, 249–257.

684 Morin, P. (1987). Predation, breeding asynchrony, and the outcome of competition among  
685 treefrog tadpoles. *Ecology*, 68, 675–683.

686 Morin, P.J., Lawler, S.P. & Johnson, E.A. (1990). Ecology and Breeding Phenology of Larval  
687 *Hyla-Andersonii* - the Disadvantages of Breeding Late. *Ecology*, 71, 1590–1598.

688 Murillo-Rincón, A.P., Kolter, N.A., Laurila, A. & Orizaola, G. (2017). Intraspecific priority  
689 effects modify compensatory responses to changes in hatching phenology in an  
690 amphibian. *J. Anim. Ecol.*, 86, 128–135.

691 Olofsson, H., Ripa, J. & Jonzén, N. (2009). Bet-hedging as an evolutionary game: the trade-  
692 off between egg size and number. *Proc. Biol. Sci.*, 276, 2963–9.

693 Philippi, T. & Seger, J. (1989). Hedging one's evolutionary bets, revisited. *Trends Ecol.*  
694 *Evol.*, 4, 41–44.

695 Poethke, H.J., Hovestadt, T. & Mitesser, O. (2016). The evolution of optimal emergence  
696 times: bet hedging and the quest for an ideal free temporal distribution of individuals.  
697 *Oikos*, 125, 1647–1656.

698 R Core Team. (2018). R: A Language and Environment for Statistical Computing.

699 Rádai, Z. (2020). Cohort splitting from plastic bet-hedging: insights from empirical and  
700 theoretical investigations in a wolf spider. *Theor. Ecol.*

701 Rand, W.M. (1973). A Stochastic Model of the Temporal Aspect of Breeding Strategies. *J.*  
702 *theor. Biol.*, 40, 337–351.

703 Richter-Boix, A., Llorente, G.A. & Montori, A. (2006a). A comparative analysis of the  
704 adaptive developmental plasticity hypothesis in six Mediterranean anuran species along a  
705 pond permanency gradient. *Evol. Ecol. Res.*, 8, 1139–1154.

706 Richter-Boix, A., Llorente, G.A. & Montori, A. (2006b). Breeding phenology of an  
707 amphibian community in a Mediterranean area. *Amphibia-Reptilia*, 27, 549–559.

708 Richter-Boix, A., Llorente, G.A. & Montori, A. (2007a). A comparative study of predator-

709 induced phenotype in tadpoles across a pond permanency gradient. *Hydrobiologia*, 583,  
710 43–56.

711 Richter-Boix, A., Llorente, G.A. & Montori, A. (2007b). Hierarchical competition in pond-  
712 breeding anuran larvae in a Mediterranean area. *Amphibia-Reptilia*, 28, 247–261.

713 Richter-Boix, A., Llorente, G.A. & Montori, A. (2007c). Structure and dynamics of an  
714 amphibian metacommunity in two regions. *J. Anim. Ecol.*, 76, 607–618.

715 Ryan, T.J. & Plague, G.R. (2004). Hatching asynchrony, survival, and the fitness of  
716 alternative adult morphs in *Ambystoma talpoideum*. *Oecologia*, 140, 46–51.

717 Sadeh, A., Mangel, M. & Blaustein, L. (2009). Context-dependent reproductive habitat  
718 selection: the interactive roles of structural complexity and cannibalistic conspecifics.  
719 *Ecol. Lett.*, 12, 1158–64.

720 Saiah, H. & Perrin, N. (1990). Autumnal vs spring hatching in the fairy shrimp  
721 *Siphonophanes grubii* (Dybowski)(Crustacea, Anostraca): diversified bet-hedging  
722 strategy? *Funct. Ecol.*, 4, 769–775.

723 Sakai, S. & Harada, Y. (2005). Production of offspring using current income and reserves:  
724 size-number trade-off and optimal offspring, size. *J. Theor. Biol.*, 233, 65–73.

725 Salvador, A. & Paris, M.G. (2001). *Anfibios Espanoles*.

726 Salvidio, S., Lamagni, L., Bombi, P. & Bologna, M.A. (2004). Distribution, ecology and  
727 conservation of the parsley frog ( *Pelodytes punctatus* ) in Italy (Amphibia,  
728 Pelodytidae) . *Ital. J. Zool.*, 71, 73–81.

729 Seger, J. & Brockman, H.J. (1987). What is bet-hedging? *Oxford Surv. Evol. Biol.*, 4, 182–  
730 211.

731 Simons, A.M. (2011). Modes of response to environmental change and the elusive empirical  
732 evidence for bet hedging. *Proc. R. Soc. B Biol. Sci.*, 278, 1601–1609.

733 Simovich, M. & Hathaway, S. (1997). Diversified bet-hedging as a reproductive strategy of

734 some ephemeral pool anostracans (Branchiopoda). *J. Crustac. Biol.*, 17, 38–44.

735 Slatkin, M. (1974). Hedging one's evolutionary bets. *Nature*, 250, 704–705.

736 Smith, D.C. (1987). Adult Recruitment in Chorus Frogs : Effects of Size and Date at  
737 Metamorphosis Author ( s ): David C . Smith Published by : Ecological Society of  
738 America Stable URL : <http://www.jstor.org/stable/1939265> ADULT RECRUITMENT  
739 IN CHORUS FROGS : EFFECTS OF SIZE A. *Ecol. Soc. Am.*, 68, 344–350.

740 Summers, K. (1999). The effects of cannibalism on Amazonian poison frog egg and tadpole  
741 deposition and survivorship in *Heliconia axil* pools. *Oecologia*, 119, 557–564.

742 Székely, D., Cogălniceanu, D., Székely, P., Armijos-Ojeda, D., Espinosa-Mogrovejo, V. &  
743 Denoël, M. (2020). How to recover from a bad start: Size at metamorphosis affects  
744 growth and survival in a tropical amphibian. *BMC Ecol.*, 20, 1–8.

745 Tarazona, E., García-Roger, E.M. & Carmona, M.J. (2017). Experimental evolution of bet  
746 hedging in rotifer diapause traits as a response to environmental unpredictability. *Oikos*,  
747 126, 1162–1172.

748 Tejedo, M. (1991). Effect of Predation by 2 Species of Sympatric Tadpoles on Embryo  
749 Survival in Natterjack Toads (*Bufo-Calamita*). *Herpetologica*, 47, 322–327.

750 Tejedo, M. (1993). Size-dependent vulnerability and behavioral responses of tadpoles of two  
751 anuran species to beetle larvae predators. *Herpetologica*, 49, 287–294.

752 Toxopeus, A., Ohm, M. & Amtzen, J. (1993). Reproductive biology of the parsley frog,  
753 *Pelodytes punctatus*, at the northernmost part of its range. *Amphibia-reptilia*, 14, 131–  
754 147.

755 Urban, M.C. & De Meester, L. (2009). Community monopolization: Local adaptation  
756 enhances priority effects in an evolving metacommunity. *Proc. R. Soc. B Biol. Sci.*, 276,  
757 4129–4138.

758 Venable, D.L. (2007). Bet hedging in a guild of desert annuals. *Ecology*, 88, 1086–1090.

759 Wang, C.-C. & Rogers, D.C. (2018). Bet hedging in stochastic habitats: an approach through  
760 large branchiopods in a temporary wetland. *Oecologia*, 188, 1081–1093.

761 Wheeler, C.A., Bettaso, J.B., Ashton, D.T. & Welsh, J. (2015). Effects of water temperature  
762 on breeding phenology, growth, and metamorphosis of foothill yellow-legged frogs  
763 (*Rana boylei*): a case study of the regulated mainstem and unregulated tributaries of  
764 California's Trinity River. *River Res. Appl.*, 31, 132-1276–1286.

765 Wolfram Research Inc. (2018). Mathematica, Version 11.3.

766 Yasui, Y. & Yoshimura, J. (2018). Bet-hedging against male-caused reproductive failures  
767 may explain ubiquitous cuckoldry in female birds. *J. Theor. Biol.*, 437, 214–221.

768 Zeuss, D., Brunzel, S. & Brandl, R. (2017). Environmental drivers of voltinism and body size  
769 in insect assemblages across Europe. *Glob. Ecol. Biogeogr.*, 26, 154–165.

770 Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects*  
771 *models and extensions in ecology with R*. Springer Science & Business Media.

772  
773 Table 1: Description of the seasonal niches regarding adult breeding (upper part) and larval  
774 development (lower part) of the parsley frog. Mean and standard error (se) of the explanatory  
775 variables depending on the season (autumn and spring). N: sample size. *P.p* is *Pelodytes*  
776 *punctatus*. Depth are in centimeters. Density of amphibian larvae or invertebrate predators is  
777 the mean number of individuals sampled in one dipnet sweep. Parsley frog is excluded from  
778 calculations indicating “amphibian larvae” or “anuran adults”. \* denotes significant difference  
779 between season for the considered variable.

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781

Variable	Autumn			Spring		
	N	mean	se	N	mean	se
<i>Adult breeding</i>						
Depth	416	58.03	2.16	459	62.86	2.17
Density of amphibian larvae	429	3.25	1.40	470	1.17	0.54
Density of invertebrate predators*	279	0.81	0.13	275	0.41	0.08
Number of adult newts*	429	0.13	0.03	464	1.08	0.12
<i>Tadpole development</i>						
Density of amphibian larvae during development	52	0.67	0.26	54	3.97	1.93
Density of invertebrates predators during development	39	0.66	0.15	46	0.79	0.17
Number of adult newts during development	52	0.34	0.15	54	0.49	0.13

782

783 Table 2: Results of the statistical analyses performed to explain the variation of presence of egg  
784 masses, number of egg masses, hatching success and metamorphosis success. Bold letters  
785 indicate a significant test (p-value < 0.05).

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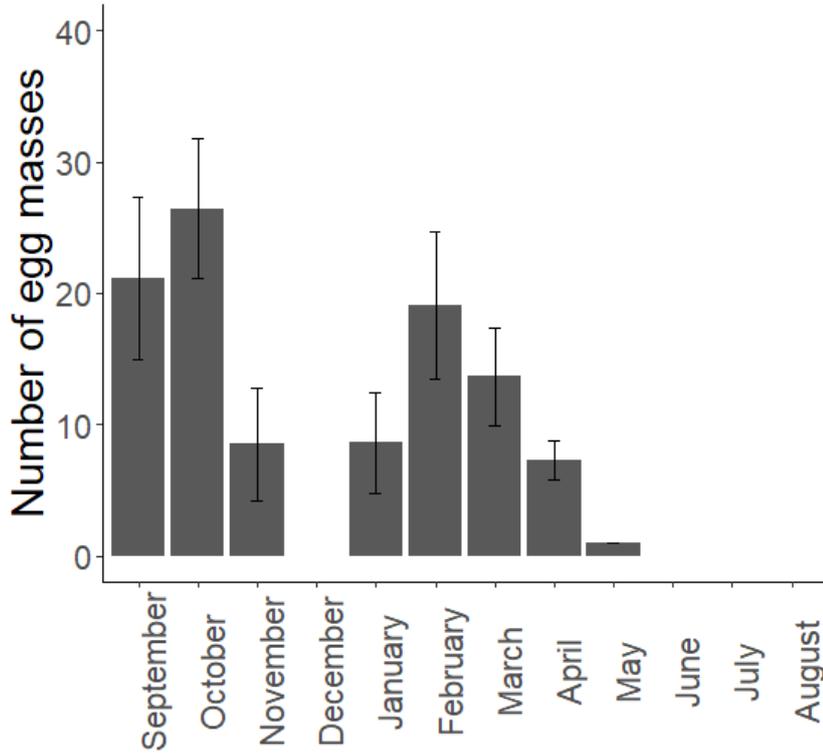
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<u>Variable</u>	<u>Tested effect</u>	<u><math>\chi^2</math> value</u>	<u>p-value</u>
<u>Presence of egg masses</u>	<u>Season</u>	<u>2.3101</u>	<u>0.1284</u>
	<b><u>Depth</u></b>	<b><u>20.398</u></b>	<b><u>6.289e-06</u></b>
	<u>Density of invertebrates</u>	<u>0.1869</u>	<u>0.6655</u>
	<u>Number of adult newts</u>	<u>0.2419</u>	<u>0.6229</u>
	<u>Density of amphibian larvae</u>	<u>0.1292</u>	<u>0.7192</u>
	<u>Number of adult anurans</u>	<u>0.3972</u>	<u>0.5286</u>
<u>Number of egg masses</u>	<u>Season</u>	<b><u>9.25</u></b>	<b><u>0.0023</u></b>
<u>Hatching success</u>	<u>Season</u>	<b><u>11.119</u></b>	<b><u>0.00085</u></b>
	<u>Density of invertebrates</u>	<u>0.1549</u>	<u>0.6939</u>
	<u>Number of adult newts</u>	<u>0.8315</u>	<u>0.3618</u>
	<u>Density of amphibian larvae</u>	<u>0.1501</u>	<u>0.6984</u>
<u>Metamorphosis success</u>	<u>Season</u>	<u>0.3932</u>	<u>0.5306</u>
	<u>Density of invertebrates</u>	<u>0.6914</u>	<u>0.4057</u>
	<u>Number of adult newts</u>	<u>0.4911</u>	<u>0.4835</u>
	<u>Density of amphibian larvae</u>	<u>1.8085</u>	<u>0.1787</u>

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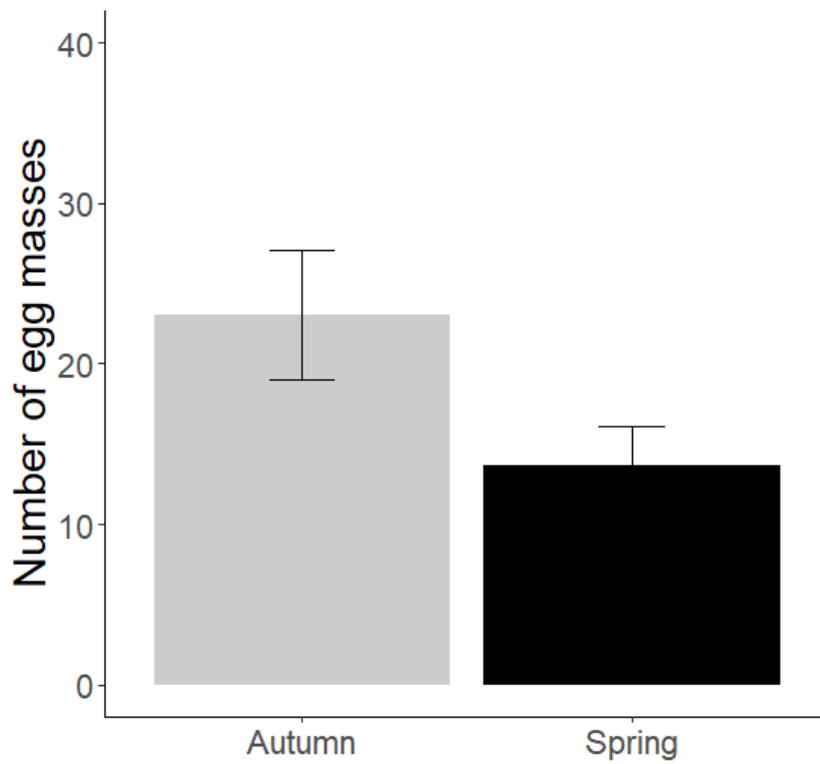
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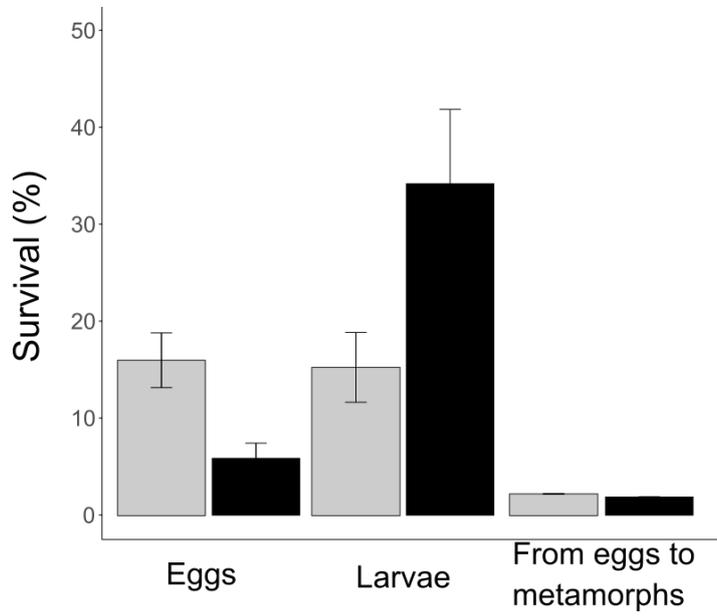
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Figure 1: Mean monthly ~~reproductive effort~~ number of egg masses produced by the parsley frog for each recorded breeding event of the parsley frog (in number of egg masses produced for each recorded breeding event). Error bars are standard errors among sites among years.



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798 Fig 2: Mean number of egg masses produced per season by the parsley frog for each recorded  
799 breeding event~~reproductive effort per season (in number of egg masses produced for each~~  
800 ~~recorded breeding event)~~. Error bars are standard errors, among sites, among year. Autumn in  
801 grey and spring in black.

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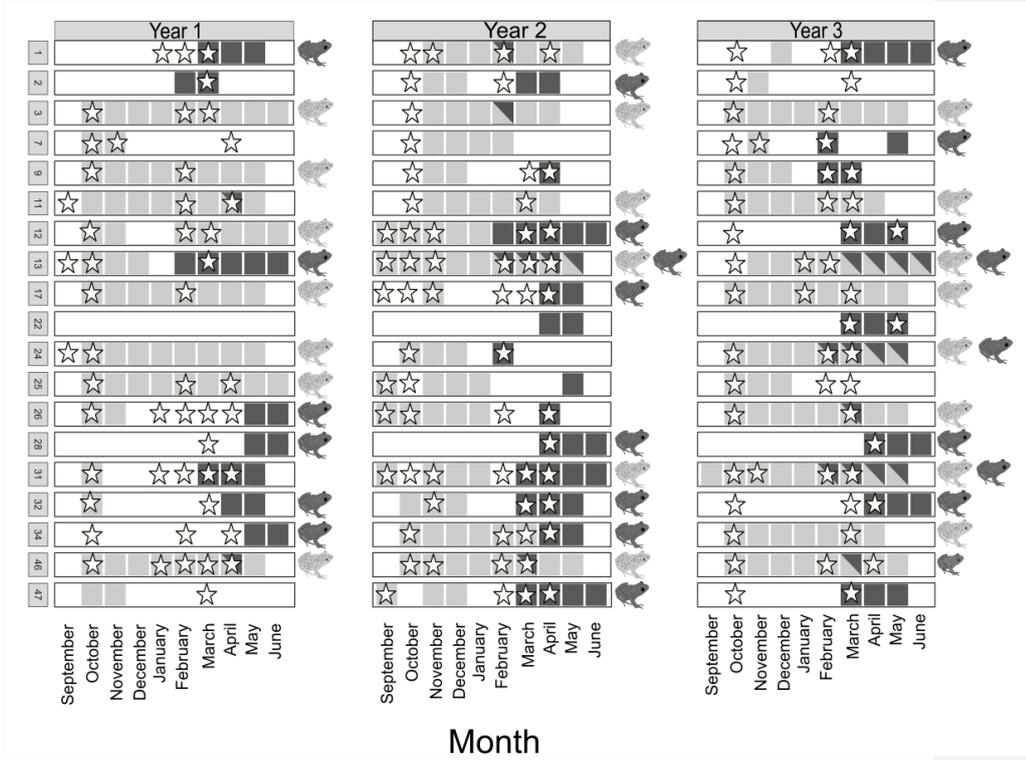
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804 Figure 3: Mean survival rates during embryonic stages (hatching rate, n=159), larval stages  
 805 (n=79) and from eggs to metamorphs (n=163). Error bars are standard errors, among sites,  
 806 among year. Autumn in grey and spring in black.

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808  
 809 Figure 4: Mean survival rates during embryonic stages (hatching rate n=86), larval stages  
 810 (n=27) and from eggs to juveniles (n=90) of spring cohorts, in presence (black) or absence  
 811 (white) of older tadpoles laid in autumn. Error bars are standard errors, among sites, among  
 812 year.  
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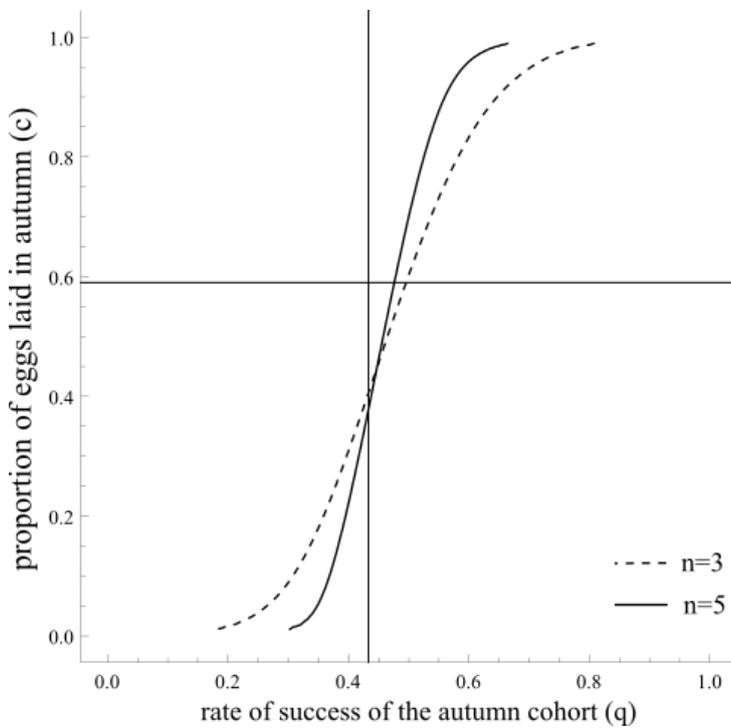
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Figure 5: Summary of breeding strategy of the Parsley frog in the 19 studied sites (vertical lines) in the three successive years: presence of egg masses (stars), presence of tadpoles (squares) and success of the breeding event (presence of metamorphosis, frogs). Grey is indicative of autumn events and black is indicative of spring events.

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824 Figure 6: Evolutionary stable strategy (~~solid~~ black lines), based on a bet-hedging model,  
825 predicting the proportion of eggs laid in autumn (c, x-axis) in relation to the rate of success of  
826 the autumn cohort (q, y-axis), depending on the number of breeding years (n). We set the  
827 survival ~~probability rate~~ of autumn tadpoles ~~to 4.7%~~ (estimated among breeding events  
828 ~~producing offspring that survived until spring~~) and the survival rate of spring tapdoles ~~to 3.8%~~,  
829 (estimated in absence of autumn cohort) ~~to 4.7% and 3.8%, respectively~~. The horizontal and  
830 vertical lines indicates the field estimates of c and q.

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832 Annex 1: Surveyed ponds (n°, names and area) and their geographic localization (in decimal  
833 degrees, WGS84).

N°	Pond name	Area	Latitude	Longitude
S01	Pataris	Cournonterral	43.5694	3.6951
S02	Fertalière	Cournonterral	43.569	3.6812
S03	Logis du Bois	Notre-Dame de Londres	43.8406	3.7462
S07	Jasses	Notre-Dame de Londres	43.8657	3.7828
S09	SEGA	Notre-Dame de Londres	43.8147	3.7817
S11	Fesq	Notre-Dame de Londres	43.8028	3.7919
S12	Bouillés Ouest	Cournonterral	43.5694	3.6951
S13	Bergerie	Cournonterral	43.5803	3.7019
S17	Combe l'Escure	Cournonterral	43.5733	3.6994
S22	Pioch noir	Gardiole	43.4947	3.7544
S24	GMP	Cazevieille	43.7708	3.7945
S25	PMP	Cazevieille	43.7708	3.7950
S26	Seuilles	Cazevieille	43.7597	3.7772
S28	Anduze	Gardiole	43.4787	3.7318
S31	Farlet	Gardiole	43.4908	3.7415
S32	Pierre Tintante	Gardiole	43.4826	3.7341
S34	Roubiac	Cazevieille	43.7597	3.7879
S46	Boissière	Notre-Dame de Londres	43.8337	3.7461
S47	Mège	Gardiole	43.4936	3.7544

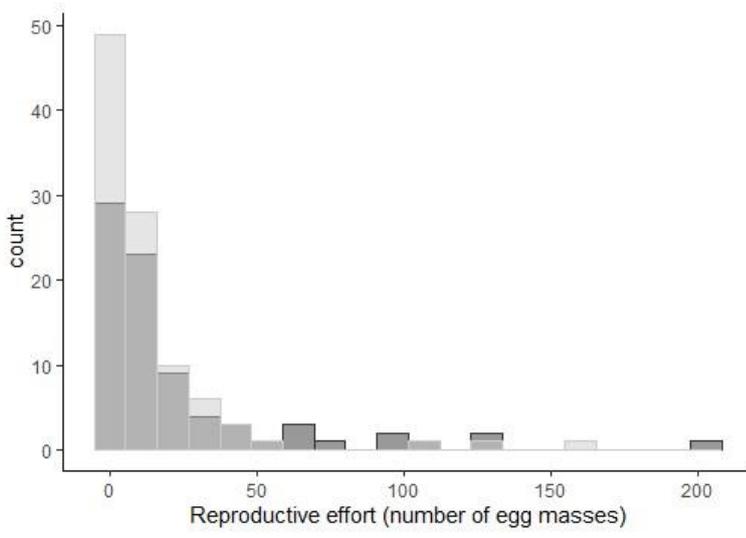
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837 ~~Annex 2: Results of the statistical analyses performed to explain the variation of breeding~~  
838 ~~probability, breeding effort, breeding success and hatching probability. Bold letters indicate a~~  
839 ~~significant test (p-value < 0.05).~~  
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844 Annex 23: Distribution of the ~~reproductive effort~~ number of egg masses produced at each  
845 breeding event per season (~~in number of egg masses produced for each breeding event~~). Autumn  
846 in dark grey and spring in light grey.

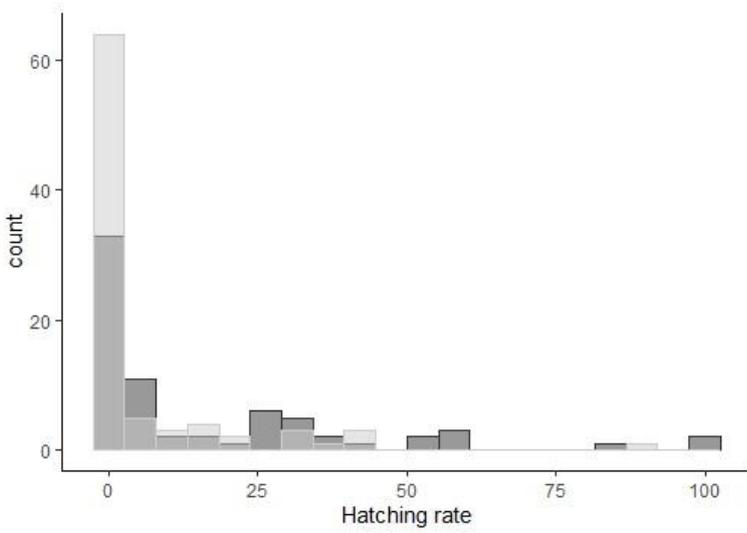


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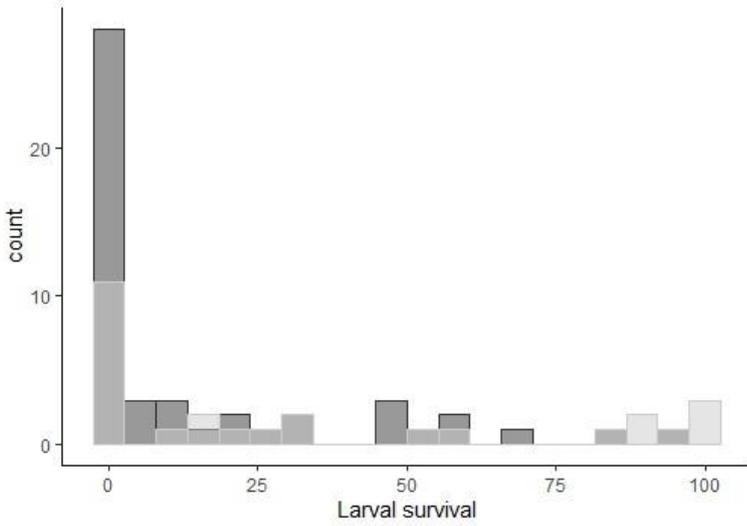
849 Annex 34: Distribution of ~~survival~~ *hatching rate, survival rate during larval stage and survival*  
 850 *rate during embryonic stages (hatching rate), larval stages and* ~~from eggs to metamorphs.~~  
 851 Autumn in dark grey and spring in light grey.

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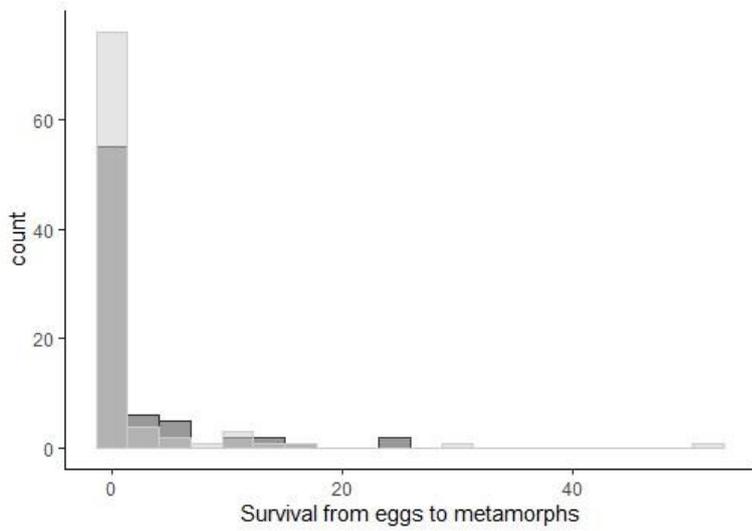
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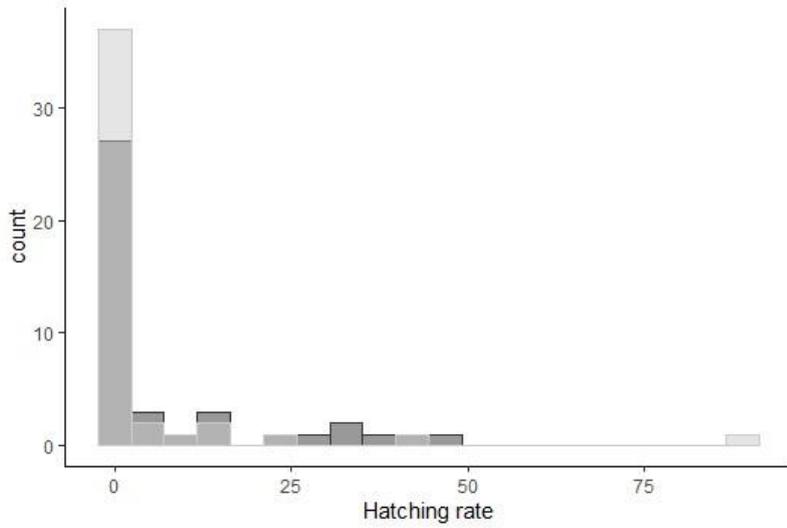
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 858 Annex 45: ~~Distribution of~~ Distribution of *hatching rate, survival rate during larval stage and*  
 859 *survival rate from eggs to metamorphosis survival during embryonic stages (hatching rate), larval*  
 860 ~~stages and from eggs to juveniles~~ of spring cohorts, in presence (dark grey) or absence (light  
 861 grey) of older tadpoles laid in autumn.



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