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Pelodytes punctatus as a bet-hedging strategy in an
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5

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19

20 ABSTRACT

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 autumn to spring. Our aim was to study the
24 breeding phenology and reproductive success associated with the use of those two seasonal
25 niches to understand how this breeding strategy can be maintained. Field surveys revealed
26 that breeding phenology was typically bimodal with a higher breeding effort in autumn. More
27 importantly, in spring, the survival rate of offspring was severely reduced by the presence of
28 autumn tadpoles, indicating a clear priority effect. However, the autumn cohort often failed to
29 survive over winter, in which case spring cohorts were often successful. Based on those
30 results, we constructed a model in which females can allocate a variable portion of eggs to
31 each season and added a priority effect. We conclude that the existence of the two breeding
32 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
37 selective constraints on parental development and physiological state (to be able to reproduce)
38 as well as offspring survival (at the various developmental stages until they reach sexual
39 maturity and start to reproduce) (Rand 1973). There is a vast amount of literature on
40 intraspecific variation of breeding patterns in relation to environmental conditions, in
41 particular latitude, altitude and climate. In the context of current climate change, many species
42 in temperate regions have advanced their breeding time (e.g. Brown et al., 2016; Frederiksen
43 et al., 2004; Møller, 2008), as a result of microevolutionary changes and/or of phenotypic
44 plasticity (Charmantier & Gienapp 2014). Most of these studies concern species with a single
45 reproductive peak in the year, which has to match as precisely as possible a seasonal peak of
46 resource availability in order to maximise reproductive success (e.g. caterpillar availability for
47 tits). The exact date of the resource peak may vary from year to year and species usually rely
48 on cues to anticipate it and plastically delay or advance the onset of reproduction every year.
49 However, in some cases reproductive success depends on even irregular and/or unpredictable
50 conditions. In such situations, species face the risk of complete reproductive failure at any
51 given breeding attempt, a regime that favors expressing alternative phenotypes to spread the
52 risk, a strategy known as bet-hedging (Cohen 1970; Slatkin 1974; Philippi & Seger 1989;
53 Leimar 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). In temporally variable environments, long-term fitness of a genotype is
57 measured by the geometric mean of the fitness contribution over successive years at the
58 individual level or over successive generations for a particular genotypic (Lewontin & Cohen

59 1969; Olofsson *et al.* 2009; Simons 2011; Yasui & Yoshimura 2018). This geometric mean
60 fitness is highly impacted by low values; hence, traits with lower fitness variation may have
61 higher long-term fitness. In principle, lower variation in fitness can be achieved either using
62 the same low-risk strategy (conservative bet-hedging), or displaying several strategies, either
63 at once or over several instances (diversified bet-hedging). While there is an abundant
64 theoretical literature on bet-hedging, empirical studies have provided limited evidence so far
65 (Simons 2011), and the most comprehensive examples concern the timing of
66 germination/diapause and the fraction of dormancy seeds/diapausing eggs (Venable 2007;
67 Gremer *et al.* 2016; García-Roger *et al.* 2017; Wang & Rogers 2018). Some studies even
68 report experimental evolution of bet-hedging traits in response to unpredictable environment
69 (Beaumont *et al.* 2009; Maxwell & Magwene 2017; Tarazona *et al.* 2017).

70 One of the best examples of stochastic, unpredictable environments are temporary ponds,
71 alternating between inundation and drought where each breeding event is a bet as habitat
72 desiccation can occur before the end of the breeding cycle. Several examples of bet-hedging
73 occur in temporary ponds. Fairy shrimps (Anostraca) produce drought-resistant eggs showing
74 asynchronous hatching at different hydroperiods (Saiah & Perrin 1990; Simovich &
75 Hathaway 1997; Wang & Rogers 2018). Similarly, rotifers produce diapausing eggs to
76 overpass unfavorable planktonic growing season and only a fraction of those eggs hatch when
77 conditions are suitable (García-Roger *et al.* 2017; Tarazona *et al.* 2017).

78 For amphibian species breeding in temporary ponds, drought can cause 100% mortality of
79 eggs or larvae, resulting in complete failure of one breeding event. One way to reduce the risk
80 of losing a breeding opportunity entirely is to spread this risk at a spatial scale, partitioning
81 brood into various pools as done by the Neotropical poison frog *Allobates femoralis* (Erich *et*
82 *al.* 2015). Another bet-hedging strategy could be to split the breeding effort at a temporal
83 scale and exploit all suitable temporal windows.

84 From an ecological point of view, such temporal niche partitioning is expected to reduce inter
85 and intra-specific competition as well as resource depletion (Carothers & Jaksić 1984). For
86 example, species may share the same habitat but have opposite activity patterns (nocturnal
87 versus diurnal species), as is the case in Neotropical felid community or in grassland ants
88 (Albrecht & Gotelli 2001; Di Bitetti *et al.* 2010). The same type of temporal segregation at a
89 daily scale is also observed within species: brown trout *Salmo trutta* reduces competition for a
90 limiting resource by sequential use of foraging areas (Alanära *et al.* 2001). Voltinism in insect
91 is another well-studied example of temporal partitioning at the annual scale which is an
92 adaptation to predictable seasonal cycles (Kivelä *et al.* 2013; Zeuss *et al.* 2017; Forrest *et al.*
93 2019)

94 However, if successive seasonal cohorts overlap, fitness gains may be asymmetric, because
95 progeny produced by late breeding may suffer from competition or even predation from
96 earlier cohorts (Morin 1987; Ryan & Plague 2004; Eitam *et al.* 2005). Those priority effects
97 are often difficult to disentangle from seasonal effects due to environmental differences
98 experienced by the temporal cohorts (Morin *et al.* 1990). If priority effects are strong, late
99 breeders may select breeding sites in order to limit the competition by conspecifics (Halloy &
100 Fiaño 2000; Halloy 2006; Sadeh *et al.* 2009) and this may restrict late breeders to poorer sites
101 (Crump 1991).

102 In amphibians, this temporal partitioning of breeding activity is thought to regulate
103 community dynamics through interspecific competition (Lawler & Morin 1993; Gottsberger
104 & Gruber 2004; Richter-Boix *et al.* 2006b, 2007c). Similarly, community composition may
105 depend on species arrival and priority effects whereby species arriving earlier monopolize
106 available resources and gain a competitive advantage over late species (Morin *et al.* 1990;
107 Blaustein & Margalit 1996; Urban & De Meester 2009). In Mediterranean regions, climatic
108 conditions are characterized by dry, hot summers and mild winters, with the maximum

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

114 The Parsley Frog *Pelodytes punctatus* is a small sized Anuran distributed in Spain and most
115 of France (locally reaching neighboring countries). It has a broad ecological niche but has
116 poor competitive abilities and is sensible to fish predation (Morand & Pierre 1995; Crochet *et*
117 *al.* 2004; Richter-Boix *et al.* 2007b); it thus prefers seasonally flooded habitats to than large
118 permanent water bodies (Guyétant *et al.* 1999; Salvidio *et al.* 2004; Richter-Boix *et al.*
119 2007a). In Spain the parsley frog shows a bimodal breeding pattern with higher reproductive
120 effort in spring than in autumn (Guyétant *et al.* 1999; Richter-Boix *et al.* 2006b). In France, in
121 addition to spring breeding, autumnal breeding is also observed in Mediterranean regions and
122 areas with mild oceanic climate (Guyétant *et al.* 1999; Jakob *et al.* 2003; Richter-Boix *et al.*
123 2006a; Cayuela *et al.* 2012) but the importance of autumn versus spring reproduction has not
124 been quantified. In the rest of the range and in altitude, only spring breeding occurs.

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

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

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

151

152 MATERIAL AND METHODS

153 **Field survey**

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

159 from January to April. We surveyed each pond twice each month. During each visit, we
160 recorded the depth of the pond.

161

162 **Sampling methods**

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

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

183 We also surveyed dragonfly larvae (Anisoptera) and backswimmers (Heteroptera,
184 Notonectidae) that are potential predators of tadpoles (Richter-Boix *et al.* 2007a) except
185 during the first year. Diving beetles (Coleoptera, Dytiscidae) are also known to prey on
186 tadpoles but were very rare in the studied ponds and thus not considered for this study.

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

191

192 **Reproductive effort and offspring survival**

193 Reproductive strategy of parsley frog was described by two measures: the probability of
194 spawning and the breeding effort. Spawning probability indicates if any new egg mass was
195 observed during a visit. Breeding effort measures the quantity of eggs produced when there
196 was at least one egg mass. We normalized the number of egg masses by their size (e.g. a
197 small egg mass equals $\frac{1}{2}$ 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 from egg to metamorph as the ratio of the number of metamorphs
201 (Gosner stage 42-43) to the number of eggs spawned. When hatching was successful (i.e. in
202 about one third of the breeding event), we could calculate the survival during larval stage as
203 the product of the two former ratios.

204 The number of tadpoles in a pond was estimated using the mean number of tadpoles caught
205 per dipnet sweep scaled to a sampling surface of 1 m² (we estimated that one dipnet sweep
206 sampled a surface of 0.5 m², taking the dipnet size and the length of the haul into account) and
207 then multiplied by the surface of the pond. This should not be taken as an attempt to estimate

208 precisely the number of tadpoles present in a pond at a given time but as an index of
209 abundance that can be compared between ponds and between breeding events. It was
210 sometimes impossible to follow the larval development and metamorphosis of offspring from
211 a particular breeding event. Indeed, parsley frogs may breed three to four times during each
212 seasonal breeding event. In these cases, the successive sub-cohorts produced are
213 undistinguishable after a few weeks, and we summed the eggs counted in two or three
214 successive visits to evaluate survival from a combination of breeding events within a given
215 season (and within a site). Survival measures should be viewed as an index to assess the
216 differences of reproductive success between seasons as there is no reason to expect any
217 seasonal bias in this index.

218

219 **Explanatory variables**

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

227 To assess the potential impact of predation and competition on survival rates, we evaluated
228 the mean density of predators and competitors encountered by parsley frog tadpoles during
229 their larval development. More precisely, data from literature indicates that only small
230 tadpoles (<12 mm snout-vent length) have lower survival due to predation by aquatic
231 invertebrates (Tejedo 1993). Above this size, the predators will only injure them or even fail
232 to catch them. Larvae laid in autumn reached this limit size in about 3 months, whereas only

233 1.5 month is necessary for larvae laid in spring (personal observation). Thus, we used the
234 mean density of predators and competitors over a period of 3 months after spawning date for
235 autumn tadpoles and 1.5 months for spring tadpoles.

236

237 **Statistical analyses**

238 All statistical analyses were performed on R 3.4.1 (R Core Team 2018). To assess if pond
239 characteristics differed between seasons, we apply a linear model for the depth of the pond
240 and generalized linear models with a quasi-poisson family for all other variables to account
241 for overdispersion. Breeding probability and breeding effort were analysed using a
242 generalized mixed model with site as random effect, with a binomial family or a negative
243 binomial family (to account for overdispersion), respectively. The survival rates were often
244 zero hence we decided to analyse them as binary variables using a generalized mixed model
245 with site as random effect and a binomial family. Those variables, called breeding success and
246 hatching success, are the probability of producing at least one metamorph or one hatchling.
247 The significance of fixed effects were tested using Chi² tests to compare nested models (Zuur
248 *et al.* 2009).

249

250

251 **Bet-hedging model**

252 Finally, we wondered if the coexistence of two breeding periods could result from a bet-
253 hedging strategy, with the optimal strategy being to split the breeding effort between the two
254 favourable seasons to spread the risk of complete failure (Seger, J. and Brockman 1987). The
255 following model is derived from Saiah and Perrin (Saiah & Perrin 1990) on the hatching
256 probability of fairy shrimp seasonal cohorts. This model was primarily inspired by Cohen
257 (Cohen 1966), reviewed by (Seger, J. and Brockman 1987) on the optimal reproduction

258 strategy of an annual plant whose seeds can either germinate or remain dormant. In our case,
259 there are two strategies: autumn breeding with initial success (i.e. the ability of offspring to
260 persist until spring) depending on the environmental conditions and spring breeding with
261 success depending mainly on the presence of autumn tadpoles, hence on the initial success of
262 autumn breeding (as suggested by the results on success of autumn and spring breeding
263 events, see below).

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

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

$$276 \quad W = (c s_1)^q ((1 - c) s_2)^{1-q}$$

277 Or, equivalently

$$278 \quad \text{Log}(W) = q \text{Log}(c s_1) + (1 - q) \text{Log}((1 - c) s_2)$$

279 However, reproductive life lasts more than one year in frogs (say, n years), which in itself is a
280 way to spread the risk of failure among successive cohorts of offspring – an uncertainty
281 remains however, for each frog, on how many (k) of the n breeding years will not allow the

282 autumn cohort to survive. For each individual, k is distributed binomially with probability $1-q$
 283 so that

$$284 \quad \text{Log}(W) = \sum_{k=0}^n \binom{n}{k} (1-q)^k q^{n-k} \text{Log}(c s_1 (n-k) + (1-c) k s_2)$$

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

287 The selection gradient is

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

288 We traced the fitness curves and the selection gradients using Mathematica (Wolfram
 289 Research Inc. 2018) based on the following parameter combinations. We set survival
 290 probabilities based on our estimates of survival from egg to metamorphose: $s_1 = 0.047$
 291 (estimated among breeding events producing offspring that survived until spring) and $s_2 =$
 292 0.038 (in the absence of autumn tadpoles). We assumed that survival and fecundity were
 293 equal for both seasonal cohorts for the rest of the life cycle. We set the number of
 294 reproductive years $n = 3$ to 5 , according to a study of age structure of a breeding population in
 295 Spain (Esteban *et al.* 2004). Note that this model applies at the individual level (as developed
 296 above) as well as at the genotype level.

297

298 RESULTS

299 **Characteristics of temporal niches**

300 Pond depth was not significantly different between the autumn (here from September to
 301 December) and spring (here from January to April) breeding seasons (Table 1). The densities
 302 of amphibian larvae (other than parsley frog) were not significantly different. In autumn,
 303 extreme densities of *Epidalea calamita* tadpoles were recorded in some small ponds whereas

304 the well-known spring breeding-species (*Hyla meridionalis*, *Pelophylax sp.*, *Triturus*
305 *marmoratus*, *Lissotriton helveticus*) reproduce later than the parsley frog, hence their larvae
306 are only present from April onwards. The density of potential invertebrate predators was
307 higher in autumn than in spring ($\chi^2_1= 37.17$, p-value = 0.005) with the lowest density being
308 from December to March. On the contrary, the number of adult newts (potential predators of
309 parsley frog tadpoles) was higher in spring than in autumn ($\chi^2_1= 369.36$, p-value = $2.2*10^{-16}$).

310

311 **Breeding phenology**

312 We registered 184 breeding events, 79 in autumn and 105 in spring. The breeding effort
313 showed a bimodal pattern with a peak in October and another in February (Figure 1). Note
314 that in two sites, one breeding event was recorded in May.

315 The spawning probability (finding at least one egg mass when visiting a pond) was not
316 significantly different between the two seasons (0.18 (0.02), mean (S.E) per visit in autumn
317 and 0.22 (0.02) per visit in spring, (over 429 and 470 visits, respectively) $\chi^2_1=2.31$, p-value=
318 0.128, see also Annex 2). This spawning probability was not affected by the presence of
319 anurans from other species (larvae), nor by the presence of predators (invertebrates or adult
320 newts). It was positively related to the depth of the pond ($\chi^2_1=20.40$, p-value= $6.3*10^{-6}$). The
321 spring spawning probability was not affected by the presence of autumn tadpoles ($\chi^2_1=0.03$, p-
322 value= 0.875).

323 The breeding effort was higher in autumn than in spring (23.0 (4.0) egg masses per breeding
324 event in autumn and 13.7 (2.4) in spring; $\chi^2_1=9.25$, p-value=0.002, Fig. 2 and Annex 3). As a
325 result, autumn breeding contributed slightly more than spring breeding to the production of
326 egg masses (57% versus 42.9%).

327

328 **Breeding success**

329 Hatching success (i.e. the percentage of breeding events producing at least one larvae) was
330 higher in autumn than in spring (68.4% and 43.8% respectively, $\chi^2_1=11.12$, p-value= 0.001).
331 Drought (pond totally dried up) caused the total failure of 7 breeding events (9% of the
332 breeding events) in autumn and of 5 breeding events in spring (4.8%) over the 3 year-survey
333 and the 19 sites. Drought caused mortality of offspring at different developmental stages
334 (mostly eggs for autumn cohort and tadpoles for spring cohort). As a consequence, breeding
335 success (i.e. the percentage of breeding events producing at least one metamorph) was not
336 significantly different between the two seasons (34.2% in autumn and 29.8% in spring $\chi^2_1=$
337 0.39, p= 0.531).

338 Neither breeding success nor hatching success were explained by interspecific competition
339 (the density of other amphibian larvae) or by predation (density of potential invertebrate
340 predators or number of adult newts).

341 Survival rates are represented in Figure 3 and Annex 4. The survival rates from egg to
342 metamorph were similarly low (autumn: 2.24 % (0.61) and spring: 1.97 % (0.73)), resulting in
343 a higher contribution (74.6%) of autumn breeding in the overall production of metamorphs
344 per site and per year (due to the higher breeding effort in autumn, see above).

345 The autumn cohort persisted until spring in 34/79 breeding events (43%, corresponding to the
346 rate of initial success, q , see bet-hedging model). In those cases, tadpoles laid in spring
347 coexisted in their pond with tadpoles from the autumn cohort. From the point of view of
348 spring breeders, in 28/57 cases, they found autumn tadpoles in the pond. The presence of an
349 autumn cohort of parsley frog tadpoles significantly reduced the success of spring breeding
350 event to 18.4% in presence of autumn tadpoles, versus 40.0% in absence of autumn tadpoles,
351 $\chi^2_1=10.60$, p-value= 0.005). This reduction effect was not significant for the hatching success
352 (32.6% in presence of autumn tadpoles, versus 53.6% in absence of autumn tadpoles
353 $\chi^2_1=4.63$, p-value=0.099). Accordingly, all survival rates were reduced in the presence of

354 autumn tadpoles and this effect was most pronounced for the survival from egg to
355 metamorphs (3.77 (1.4) versus 0.16 (0.08) in absence versus presence of autumn tadpoles,
356 Figure 4 and Annex 5).

357 Finally, the figure 5 summarize the breeding strategy of parsley frog showing the presence of
358 egg masses, tadpoles and the outcome of the breeding event (production of metamorphs) in
359 each studied site, over the three years of survey. It illustrated the quasi-exclusion between the
360 two cohorts.

361

362 **Maintenance of spring breeding**

363 Selection gradients based on our bet-hedging model predict that a mixed strategy is
364 maintained when the rate of initial success of the autumn cohort (q) is between 0.2 and 0.8 for
365 a number of reproductive years $n = 3$. In this condition, a pure autumn strategy is predicted
366 above 0.8, and a pure spring strategy below 0.2. (Figure 4). The maintenance of this strategy
367 is less probable if the number of reproductive years increases ($n = 5$ years of breeding), with a
368 reduced range of q leading to a stable mixed strategy.

369

370 DISCUSSION

371 **Cost and benefits of a bimodal breeding phenology**

372 We used field surveys to describe the breeding phenology of the parsley frog in the French
373 Mediterranean region but also to quantify the relative contribution and success of each
374 seasonal reproduction (autumn and spring reproduction). This quantification, rarely achieved
375 in the wild (but see (Licht 1974; Banks & Beebee 1988; Gascon 1992; Wheeler *et al.* 2015),
376 is essential to understand the evolution of this bimodal breeding strategy. We confirmed the
377 existence of two distinct seasonal peaks in breeding activity, probably mediated by cold
378 temperature in December and January as adult parsley frogs tend to breed in mild and rainy

379 periods as was previously observed (Toxopeus *et al.* 1993; Guyétant *et al.* 1999; Jakob *et al.*
380 2003). However breeding episodes occurred even in the absence of rainfall as long as ponds
381 were filled with water (personal observations and Richter-Boix *et al.* 2006b)).

382 The breeding effort in our population was higher in autumn than in spring. This is in apparent
383 contradiction with Richter-Boix *et al.* (2006b) who found that spring breeding effort was four-
384 fold higher than autumn breeding effort in the northeast of the Iberian Peninsula. While we
385 don't have a definitive explanation for this difference, we suggest it could be related to higher
386 competition among anuran larvae in autumn in north-east Spain compared to France. In our
387 study area in southern France, larvae of *Pelodytes punctatus* are typically the only anuran
388 larvae found after the summer drought in the ponds in autumn. In contrast, four other species
389 of Anura (*Hyla meridionalis*, *Epidalea calamita*, *Alytes obstetricans* and *Pelophylax perezi*)
390 have tadpoles in autumn and three of them (i.e. all except *E. calamita*) can have overwintering
391 tadpoles in Spanish ponds (Richter-Boix *et al.* 2006b). These authors also showed that
392 *Pelodytes punctatus* tadpoles suffer from interaction with *Hyla meridionalis* (Richter-Boix *et*
393 *al.* 2007b). It is thus possible that increased competition for *Pelodytes punctatus* larvae in
394 autumn and winter compared to our study area make the autumn niche less favourable in
395 northeastern Spain compared to southern France and reduce parsley frog investment in
396 autumn breeding there.

397 Offspring survival (from egg to metamorph) was low in both seasons. The combination of
398 breeding effort and survival rates eventually resulted in a higher contribution of autumn
399 breeding to the overall production of metamorphs. The overall low survival rates of offspring
400 that we found is in line with previous field studies in anurans (e.g. Licht 1974; Banks &
401 Beebee 1988) and can be caused by pond desiccation, predation, inter and intra-specific
402 competition for food and parasitism or pathogen infections. Our study revealed no obvious
403 effect of variation in predation on tadpole survival even if the predation pressure encountered

404 by tadpoles at the beginning of their development varies from site to site (but not between
405 seasons). This may seem surprising since many studies experimentally demonstrated that
406 predation cause substantial mortality to tadpole populations (e.g. (Tejedo 1993; Van Buskirk
407 & Arioli 2005)). This may be due to the lack of information about predation during the first
408 year of survey which reduced our statistical power or to the fact that causative factors are
409 numerous and more complex to identify in the field. However, other studies reported no effect
410 of predation on tadpole survival (Hartel *et al.* 2007) or even a positive effect (Barandun &
411 Reyer 1997) probably due to predator-induced phenotypic plasticity. Nevertheless, our results
412 suggest that the predation pressure is probably not a stronger constraint in one season than in
413 the other.

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

424

425 **Priority effects**

426 We revealed a striking negative effect of the presence of conspecific autumn tadpoles on the
427 survival of spring tadpoles in the Parsley Frog. Previous studies have demonstrated the
428 occurrence of such intraspecific priority effect in amphibians in experimental settings (Morin

429 *et al.* 1990; Eitam *et al.* 2005; Murillo-Rincón *et al.* 2017) but as far as we know, our study is
430 the first evidence for intraspecific, inter-cohort competition in amphibians in nature. In the
431 field, we observed in several occasions that large autumn tadpoles were eating freshly laid
432 eggs of their own species, which could partly explain the lower hatching rate of spring eggs in
433 presence of autumn tadpoles. Moreover, (Tejedo 1991) previously described how parsley frog
434 tadpoles predates *Epidalea calamita* eggs. In this latter study, predaceous tadpoles were
435 exclusively old tadpoles and they could cause a loss of 50 to 100% of the eggs. Oophagy has
436 also been demonstrated to be responsible for interspecific priority effect between *Scaphiosus*
437 *couchii* and *Bufo speciosus* (Dayton & Fitzgerald 2005). Intraspecific oophagy has been
438 described on some anuran species (Summers 1999; Dayton & Wapo 2002) and has been
439 proposed as an energetic opportunistic response in food shortage in temporary ponds.

440 However, the presence of autumn tadpoles also affect the larval survival (post-hatching) of
441 spring tadpoles. This may reflect competition for resources between large autumn and small
442 spring tadpoles as shown in *Rana arvalis* (Murillo-Rincón *et al.* 2017). Interference
443 competition mediated by microorganism may also play a role: smaller tadpoles could display
444 coprophagy instead of feeding on higher quality resources (Beebee & Wong 1992; Baker &
445 Beebee 2000). This large priority effect between the two seasonal tadpole cohorts of parsley
446 frog has a great impact on the overall efficiency of breeding: in most ponds, there could be
447 only one successful breeding period, autumn or spring. Nonetheless, we found no indication
448 that spring breeders select their oviposition site to avoid conspecifics, as other amphibian
449 species sometimes do (Sadeh *et al.* 2009). Accordingly, the spawning probability was also
450 unaffected by the presence of potential competitors or predators.

451

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

453 The temporal partitioning of breeding activity could reflect several evolutionary processes: 1)
454 the existence of two specialized phenotypes either genetically determined (in which case we
455 would expect temporal genetic differentiation between cohorts) or set by early environmental
456 cues (phenotypic plasticity); 2) a use of alternative strategies by some or all individuals (bet-
457 hedging). We previously demonstrated that the two temporal cohorts do not reflect two
458 genetically distinct temporal populations (Jourdan-Pineau *et al.* 2012) but breeding phenology
459 may still be set once for good for each individual. In this case, breeding in autumn or in spring
460 could be determined by the physiological state (and sexual maturity) of the breeder and
461 maintained year after year, by physiological constraints (typically the case for a capital
462 breeder species which stores energy for future reproduction *e.g.* (Lardner & Loman 2003)). In
463 a diversified bet-hedging strategy, individual breeding activities could vary from year to year
464 (each year, individuals would “choose” one breeding season) or individuals could split their
465 breeding effort between the two seasons in some or most years.

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

478 In the parsley frog, our model shows that the observed mixed breeding strategy is maintained
479 if the rate of initial success of the autumn cohort (q) is between 0.2 and 0.8 (if females have
480 on average 3 years of breeding in their lifetime) or between 0.35 and 0.65 (for 5 years of
481 breeding). Those conditions are fulfilled according to our field estimates (0.43). We estimated
482 the proportion of eggs laid in autumn by all breeders (0.57) but could not estimate this
483 proportion at the individual level. Survival rates set in the model were based on our field
484 estimates of survival from egg to metamorphosis; hence, we assumed similar survival after
485 metamorphosis of the two cohorts. Unfortunately, we have no information about survival of
486 parsley frog during its adult terrestrial life. However, the adult survival is an important
487 parameter in our model since it determines the number of reproductive years. The mixed
488 breeding strategy is less stable when the number of breeding opportunities per lifetime
489 increases – as the risk is now spread over several successive years. Indeed, experiencing
490 variation in reproductive success among those opportunities is less harmful when it is possible
491 to try again the next year. A skeletochronology study conducted in a upland population in
492 Spain indicated that the mean age of sampled parsley frog females was 5.01 years (with a
493 standard deviation of 1.99) (Esteban *et al.* 2004). Assuming a minimal age at first
494 reproduction of 1 year (as done by Esteban *et al.* 2004), this translates into an average number
495 of reproductive years or females of $n = 4$. Our evaluation of the bet-hedging strategy with $n =$
496 5 is thus probably conservative.

497 We previously showed that the parsley frog successfully exploits two temporal niches in the
498 Mediterranean region thanks to a high phenotypic plasticity of tadpole development to face
499 very different seasonal environments (Jourdan-Pineau *et al.* 2012). Recently, the combination
500 of phenotypic plasticity and bet-hedging has been theoretically investigated, suggesting that
501 phenotypic plasticity could further minimize fitness variances caused by mismatches between
502 phenotype and environment (Haaland *et al.* 2020; Rádai 2020). Interestingly, in the wolf

503 spider, temperature and day length leads to alternative developmental types within broods.
504 This cohort splitting is both probabilistic and sensitive to environment , a phenomenon
505 proposed as being a plastic bet-hedging strategy by Rádai (Rádai 2020). In this case, the
506 various plastic phenotypes, triggered by environmental variations, constitute a bet-hedging
507 response to grassland habitats with substantial and unpredictable year-to-year variation.
508 The breeding strategy of parsley frog seems to constitute an original example of bet-hedging
509 strategy driven by high environmental stochasticity and large inter-cohort priority effect.
510 Characterizing adult survival and individual breeding pattern (using mark-recapture and
511 parentage assignment of egg masses) would allow further refining our model and seeing how
512 it can apply to other anuran species.

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518

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