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

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 (Alanärä *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 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 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    $$W = \ (c \ s_1)^q \left((1 - c) \ s_2\right)^{1-q}$$

277   Or, equivalently

278    $$Log(W) = q \ Log(c \ s_1) + (1 - q) \ Log\left((1 - c) \ s_2\right)$$

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

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 (χ^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 (χ^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) χ^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 (χ^2_1=20.40, p-value= $6.3*10^{-6}$). The

321   spring spawning probability was not affected by the presence of autumn tadpoles (χ^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; χ^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, χ^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 χ^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   χ^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   χ^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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