

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 m² (we estimated that one dipnet sweep sampled
209 a surface of 0.5 m², 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 Chi² 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 = 2.2×10^{-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= 6.3×10^{-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, $\chi^2=10.60$, p -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 $\chi^2=4.63$, p -
368 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 ($\gamma^2=2.75$, p -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 the quasi-
377 exclusion between the two cohorts: there were only 4 cases in total (out of 47 observations)

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Commenté [PD1]: Donner l'unité : est-ce des % ???

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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
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569

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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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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

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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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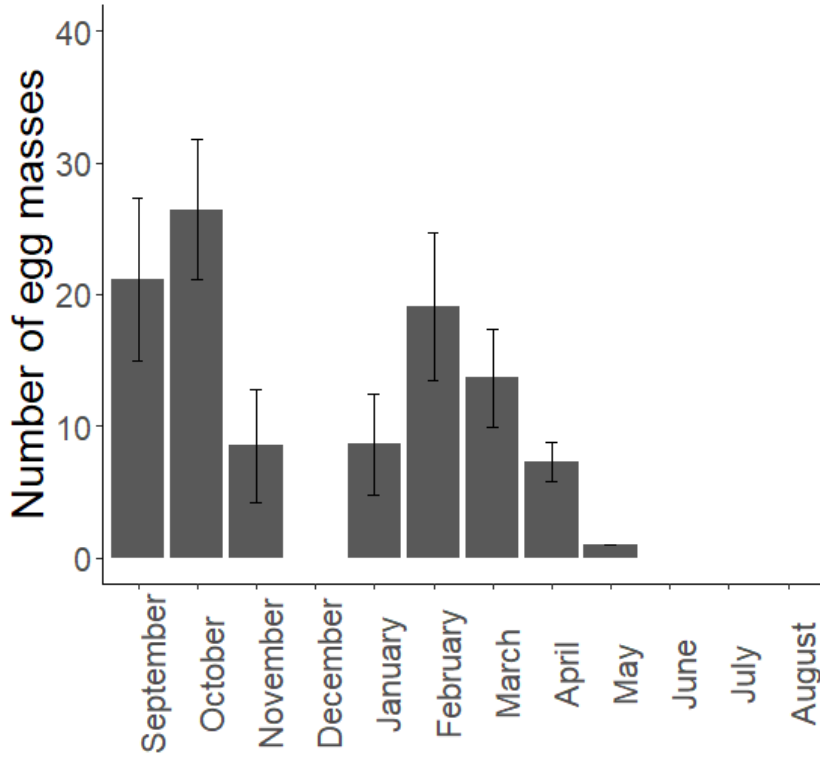
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<u>Variable</u>	<u>Tested effect</u>	<u>χ^2 value</u>	<u>p-value</u>
<u>Presence of egg masses</u>	<u>Season</u>	<u>2.3101</u>	<u>0.1284</u>
	<u>Depth</u>	<u>20.398</u>	<u>6.289e-06</u>
	<u>Density of invertebrates</u>	<u>0.1869</u>	<u>0.6655</u>
	<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>	<u>9.25</u>	<u>0.0023</u>
<u>Hatching success</u>	<u>Season</u>	<u>11.119</u>	<u>0.00085</u>
	<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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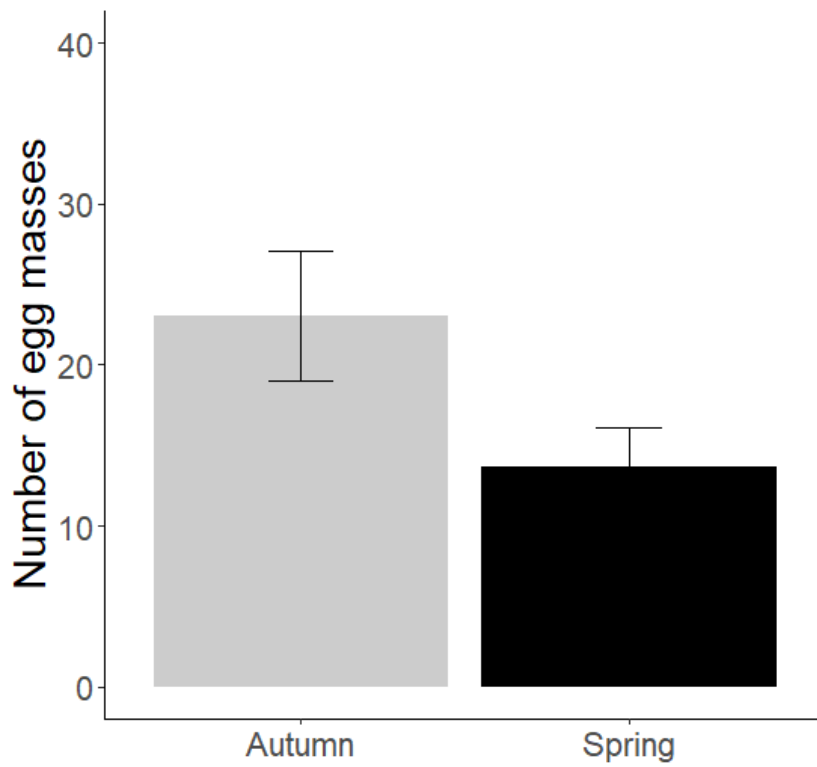
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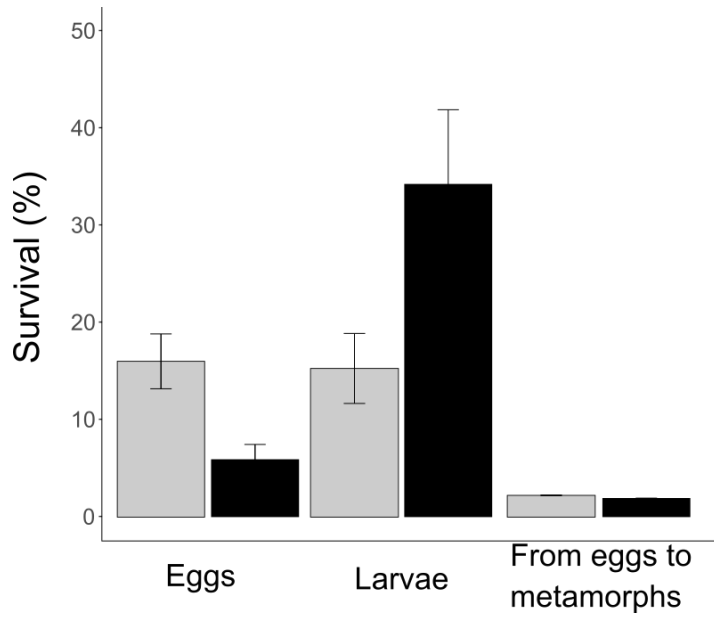
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Figure 1: Mean monthly ~~reproductive effort~~ number of egg masses produced by the parsley frog for each recorded breeding event of the parsley frog (in number of egg masses produced for each recorded breeding event). Error bars are standard errors 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.

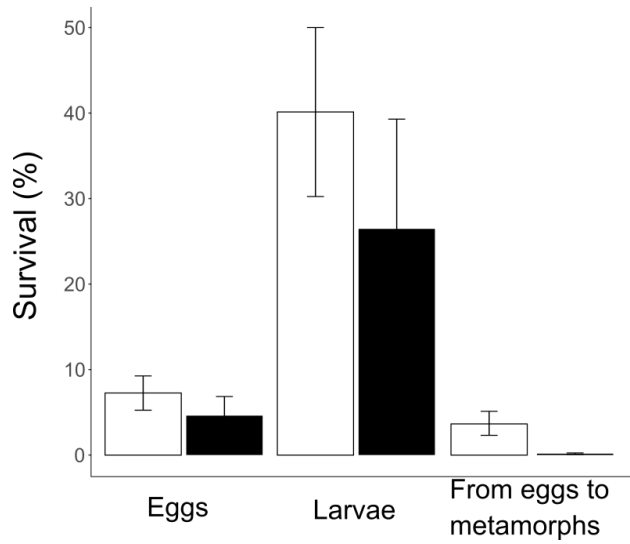
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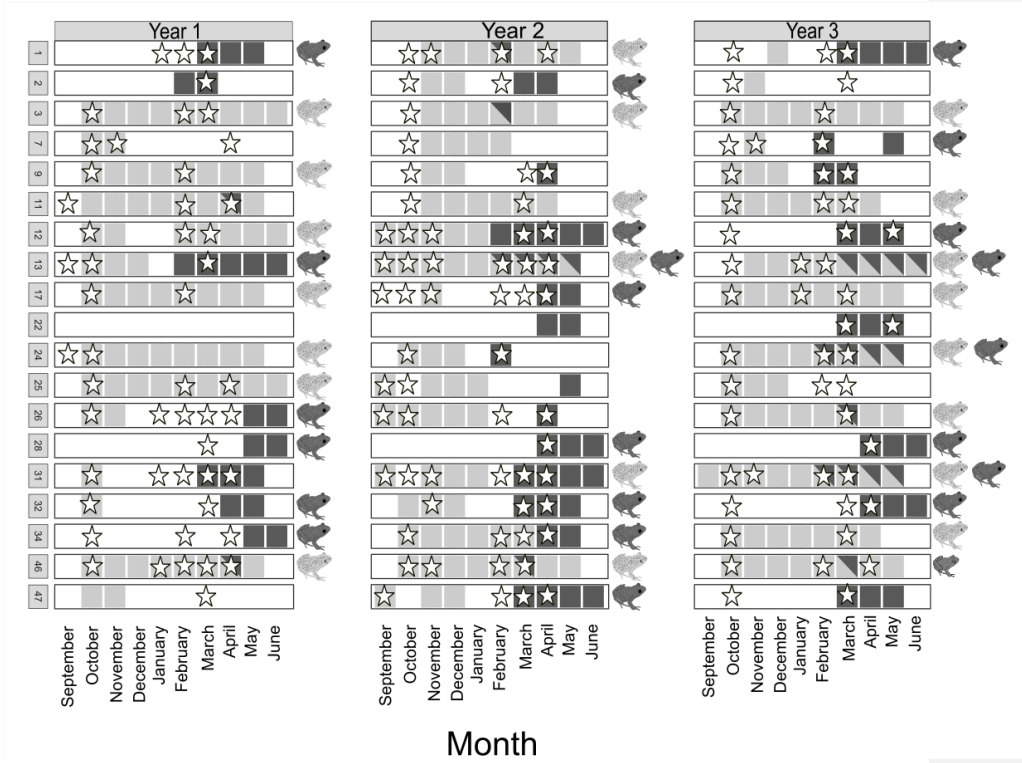
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804 Figure 3: Mean survival rates during embryonic stages (hatching rate, n=159), larval stages
 805 (n=79) and from eggs to metamorphs (n=163). Error bars are standard errors, among sites,
 806 among year. Autumn in grey and spring in black.

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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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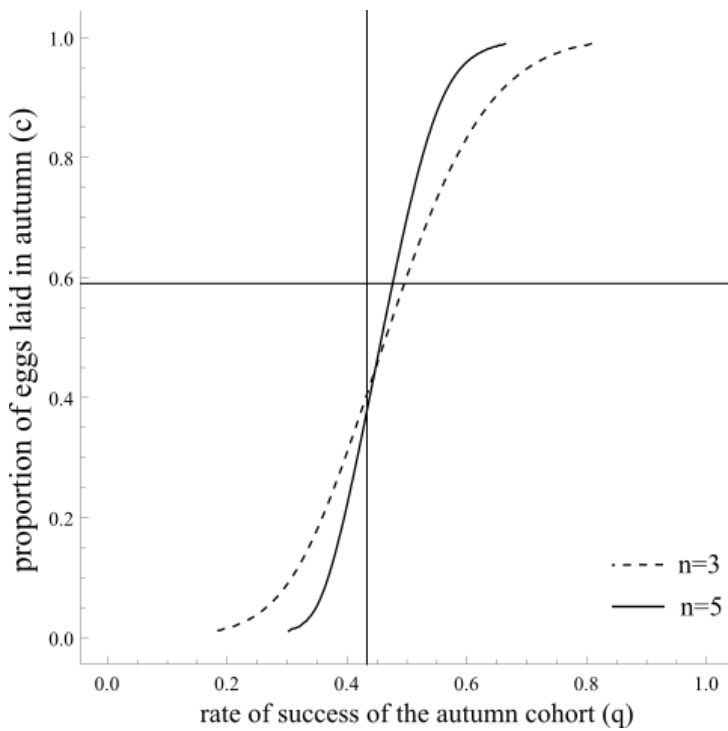
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Figure 5: Summary of breeding strategy of the Parsley frog in the 19 studied sites (vertical lines) in the three successive years: presence of egg masses (stars), presence of tadpoles (squares) and success of the breeding event (presence of metamorphosis, 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

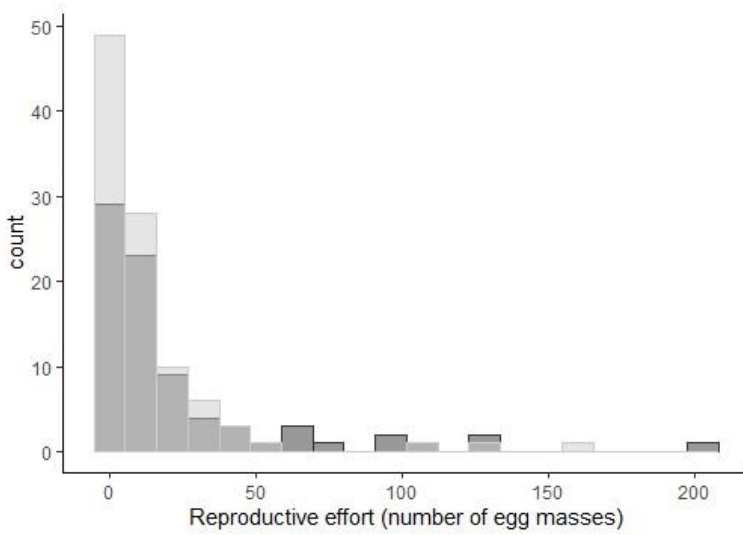
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837 ~~Annex 2: Results of the statistical analyses performed to explain the variation of breeding~~
838 ~~probability, breeding effort, breeding success and hatching probability. Bold letters indicate a~~
839 ~~significant test (p-value < 0.05).~~
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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.

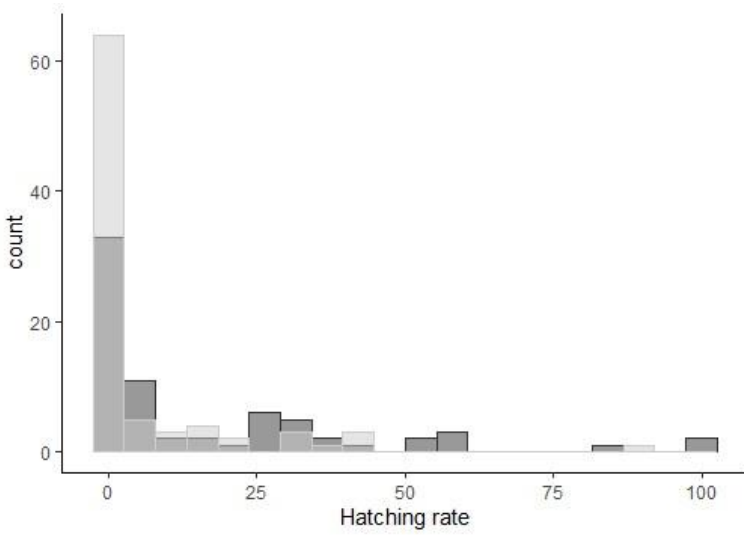


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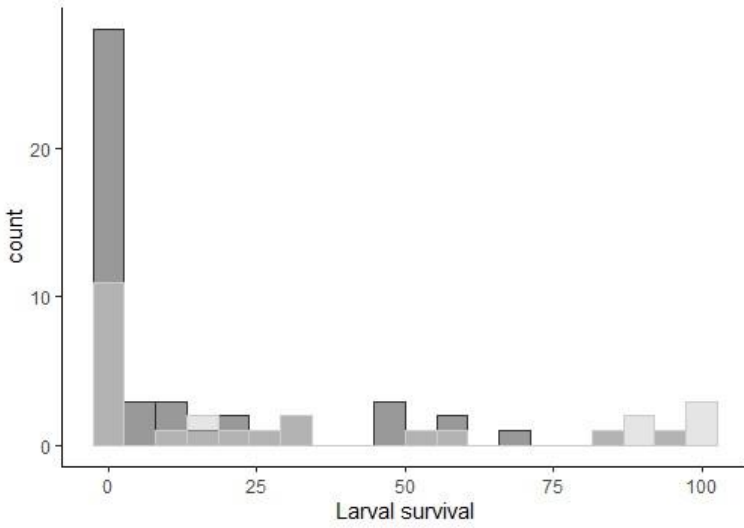
849 Annex 34: Distribution of ~~survival~~ *hatching rate, survival rate during larval stage and survival*
 850 *rate during embryonic stages (hatching rate), larval stages and from eggs to metamorphs.*
 851 Autumn in dark grey and spring in light grey.

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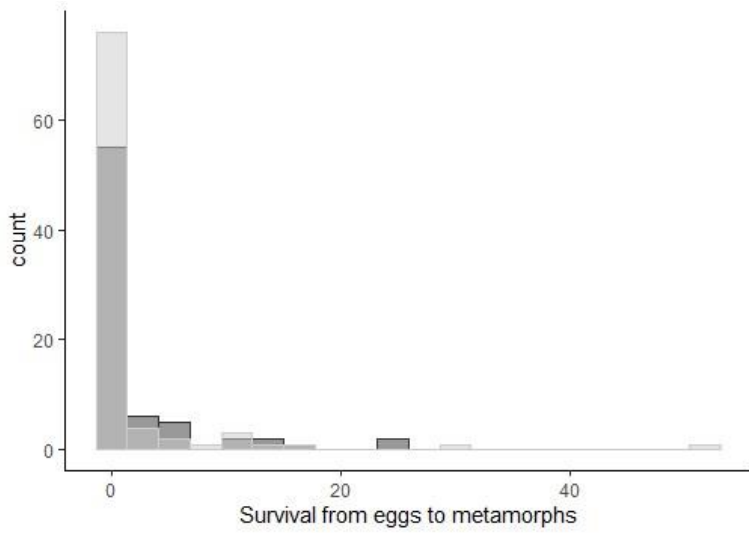
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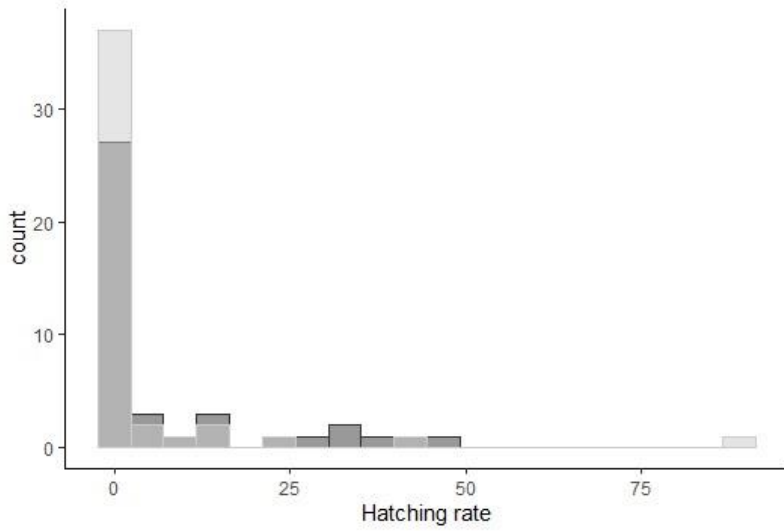
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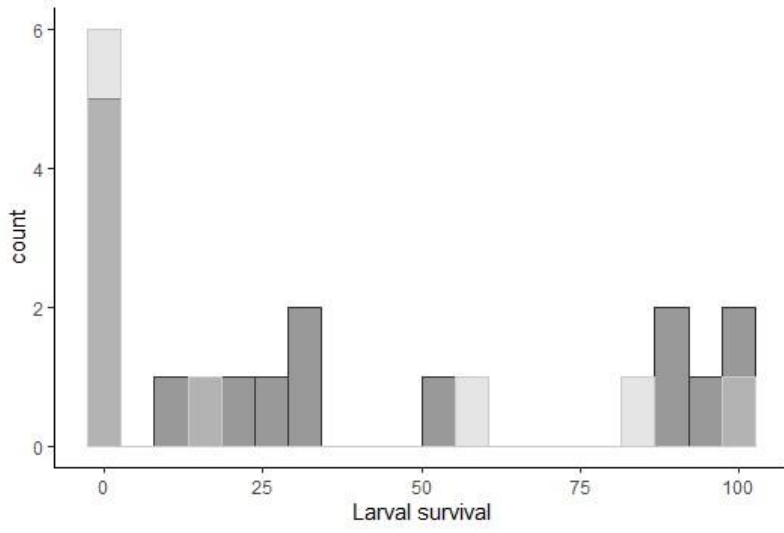
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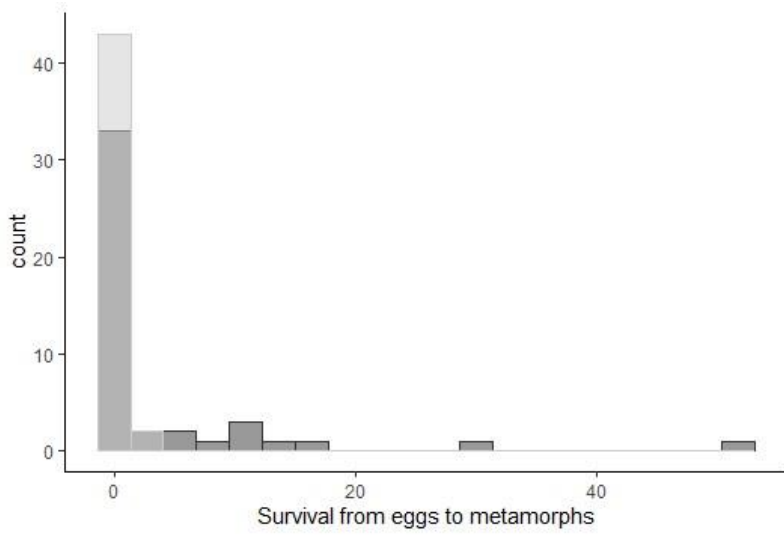
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 858 Annex 45: ~~Distribution of~~ Distribution of *hatching rate, survival rate during larval stage and*
 859 *survival rate from eggs to metamorphosis survival during embryonic stages (hatching rate), larval*
 860 ~~stages and from eggs to juveniles~~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



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