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2 HABITAT PREDICTABILITY AND LIFE HISTORY TACTICS

3 Title:

4 Contrasting patterns of environmental fluctuation contribute to divergent life histories among
5 amphibian populations

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21

22 *Abstract.* Because it modulates the fitness returns of possible options of energy expenditure at
 23 each ontogenetic stage, environmental stochasticity is usually considered a selective force in
 24 driving or constraining possible life histories. Divergent regimes of environmental fluctuation
 25 experienced by populations are expected to generate differences in the resource allocation
 26 schedule between survival and reproductive effort and outputs. To our knowledge, no study
 27 has previously examined how different regimes of stochastic variation in environmental
 28 conditions could result in changes in both the temporal variation and mean of demographic
 29 parameters, which could then lead to intra-specific variation along the slow–fast continuum of
 30 life history tactics. To investigate these issue, we used capture–recapture data collected on
 31 five populations of a long-lived amphibian (*Bombina variegata*) experiencing two distinct
 32 levels of stochastic environmental variation: (i) constant availability of breeding sites in space
 33 and time (‘predictable environment’), and (ii) variable spatio-temporal availability of breeding
 34 sites (‘unpredictable environment’). We found that female breeding propensity varied more
 35 from year to year in unpredictable than in predictable environments. Although females in
 36 unpredictable environments produced on average more viable offspring per year, offspring
 37 production was more variable between years. Survival at each ontogenetic stage was slightly
 38 lower and varied significantly more from year to year in unpredictable environments. Taken
 39 together, these results confirm that increased environmental stochasticity can modify the
 40 resource allocation schedule between survival and reproductive effort and outputs and may
 41 lead to intra-specific variation along the slow–fast continuum of life history tactics.

42

43 *Key words:* life history; slow–fast continuum; environmental predictability; demography;
 44 *multievent capture-recapture models; amphibian; Bombina variegata*

45 INTRODUCTION

46 Identifying the rules that shape life history evolution is a crucial challenge for evolutionary
 47 biology. According to life history theory, ontogenesis involves a sequence of developmental
 48 events that are ordered to optimize survival and reproductive outputs (Stearns 1992). Over a
 49 lifetime, energy and trophic resources are allocated between growth, somatic maintenance and
 50 reproductive effort (Pianka 1976). Growth and somatic maintenance include investments that
 51 contribute to longevity, whereas reproductive effort includes investments in offspring
 52 production and assistance that contribute to fecundity. Because it modulates the fitness returns
 53 of possible options of energy expenditure at each ontogenetic stage, stochastic environmental
 54 variation is usually considered a selective force in driving or constraining possible life
 55 histories (Levins 1968, Schaffer 1974, Tuljapurkar et al. 2009).

56 When environmental fluctuation generates strong variation in adult mortality, natural
 57 selection favors a short lifespan, early maturity and large reproductive outputs (characteristics
 58 of ‘fast’ life histories along a ‘slow–fast continuum’; e.g. Kraus et al. 2005). In contrast, when
 59 environmental fluctuation affects birth rate and juvenile mortality, it contributes to the
 60 selection for a longer lifespan, later maturity and smaller reproductive outputs (characteristics
 61 of ‘slow’ life histories; e.g. Morris et al. 2008). For species with long lifespans, selective
 62 forces drive the evolution of traits that favor a canalization process (sensu Gaillard and
 63 Yoccoz 2003) of adult survival since this demographic parameter has the highest impact on
 64 fitness. Such a reduction of variation in adult survival may initially be achieved by trade-offs
 65 between vital rates (Stearns 1992, Shaw and Levin 2011). In particular, adults may modulate
 66 their yearly breeding investment or may temporarily cease to breed at any age to increase
 67 longevity (Warner 1998, Rideout et al. 2005, Ruf et al. 2006). Reduced variation in adult
 68 survival may also result from behavioral or physiological processes that buffer the impact of
 69 environmental fluctuation. For instance, this can be seen in adaptive behavioral mechanisms

70 such as the wing-fanning and shade-seeking of endotherms that allow individuals to maintain
 71 their body temperature in increasing ambient temperatures, which may drastically reduce
 72 adult survival variation due to temperature fluctuation (Welbergen et al. 2008).

73 By constraining the availability and quality of resources that could be used by an
 74 iteroparous organism over its lifetime, environmental fluctuation also regulates the spread of
 75 reproductive effort over time (Tuljapurkar et al. 2009). An organism's ability to reproduce
 76 strongly depends on a combination of environmental and physiological factors (McNamara
 77 and Houston 1996), which include its fat reserves, foraging skills, parasite load and the
 78 responsiveness of its immune system. Given these constraints, at each breeding opportunity
 79 an iteroparous organism has to make a decision whether or not to breed, and if it does breed, it
 80 must modulate its breeding investment in accordance with its lifetime fitness gain (Reznick
 81 and Yang 1993, Muths et al. 2010, Souchay et al. 2014). Variation in food availability due to
 82 environmental fluctuation (e.g. yearly weather variation) may lead to insufficient energy
 83 accumulation for initiating oocyte development in females, which therefore skip reproduction
 84 (Jenouvrier et al. 2003). Moreover, environmental fluctuation also regulates the availability
 85 and quality of resources required by offspring during their development, which may lead
 86 organisms to modulate breeding investment accordingly. Breeding females may respond to
 87 fluctuation in food availability by delaying oocyte production, which increases their fitness as
 88 this produces offspring with higher fat content, which can better survive and grow in low-food
 89 environments (Reznick and Yang 1993).

90 As is predicted at inter-specific level (Stearns 1992), at intra-specific level, divergent
 91 regimes of environmental conditions experienced among populations are expected to generate
 92 differences in the resource allocation schedule between survival and reproductive effort and
 93 outputs (Van Tienderen 2000). For instance, a population of *Capreolus capreolus* submitted
 94 to the harsh environmental conditions generated by the co-occurrence of high hunting

95 pressure and predation by lynx exhibited a slower life history cycle than that of a population
 96 in less harsh conditions (Nielsen et al. 2009). Conversely, an acceleration of the life history
 97 cycle has been reported in *Sarcophilus harrisi*; the population responded to increased adult
 98 mortality due to a pathogen by increasing reproductive effort at an earlier age, implying an
 99 abrupt transition from iteroparity to semelparity (Jones et al. 2008). These studies provide an
 100 interesting overview on how contrasting environmental conditions can impact – sometimes
 101 very quickly – the trade-off between mean survival and reproductive effort and outputs, and in
 102 turn affect the speed of the life history cycle at intra-specific level. However, no previous
 103 study has yet examined how different regimes of stochastic variation in environmental
 104 conditions could result in changes in both the temporal variation and mean of demographic
 105 parameters, which could then lead to intra-specific variation along the slow–fast continuum of
 106 life history tactics.

107 The aim of this study was to test if contrasting levels of environmental fluctuation
 108 contribute to divergent life histories among free-ranging populations of a long-lived
 109 amphibian, the yellow-bellied toad (*Bombina variegata*). We conducted a study on five
 110 populations of *B. variegata* including two levels of stochastic environmental variation: (i)
 111 constant availability of breeding sites in space and time (called hereafter ‘predictable
 112 environments’ as breeding site availability was predictable from one year to another) and (ii)
 113 stochastic spatio-temporal availability of breeding sites, which were randomly created or
 114 destroyed each year by human activity (called hereafter ‘unpredictable environments’ as
 115 breeding site availability was not predictable from year to year). In each population studied,
 116 we considered the following key parameters: (i) age-dependent survival, (ii) female breeding
 117 propensity, (iii) offspring productivity per female per year (a proxy for female fitness) and
 118 (iv) temporal variation of these vital rates. Using capture–recapture data collected in both
 119 predictable and unpredictable environments, we specifically tested the hypothesis that

120 survival would be lower on average and more variable from year to year in unpredictable
 121 environments, whatever the ontogenetic stage considered (juvenile, subadult or adult);
 122 increased mortality was expected to result from human activity (e.g. through pollution or
 123 habitat alteration) (Mann et al. 2009, Semlitsch et al. 2009) and/or from the cost induced by
 124 moving from an aging rut network to a more recent one (Bonte et al. 2012). We also tested the
 125 hypothesis that a female could modify its schedule of resource allocation to reproduction
 126 according to the degree of environmental fluctuation. In particular, we predicted that breeding
 127 propensity would be more variable from year to year in unpredictable environments. In
 128 parallel, we hypothesized that offspring productivity would also be more variable from year to
 129 year, but would be higher on average in unpredictable environments. Accordingly, we
 130 expected that enhanced environmental stochasticity could result in an accelerated life history
 131 cycle.

132
 133 METHODS

134 *Biological model*

135
 136 *Bombina variegata* is a long-lived anuran. The life expectancy ranges from 4 to 10 years in
 137 natural conditions given the estimated survival rate of 0.7–0.9 (Beshkov and Jameson 1980,
 138 Cayuela et al. 2014, 2015b and the present study); some individuals reach an age of more than
 139 20 years in the wild and almost 30 years in captivity (Smirina 1994). This species breeds in
 140 small water bodies characterized by stochastic water level variation. Its long lifespan and
 141 iteroparity are assumed to be a response to habitat uncertainty (Joly and Morand 1994,
 142 Morand and Joly 1995, Cayuela et al. 2014). Furthermore, females display risk-spreading
 143 tactics such as egg clutch fractionation over space and time (Buschmann 2002). The

144 flexibility of the ovarian functioning of bombinatorids allows the continuous production or
 145 resorption of oocytes over the course of the breeding season (Guarino et al. 1998).

146 In Western Europe, *Bombina variegata* populations occupy both natural (Cayuela et
 147 al. 2011, 2013) and artificial environments (Cayuela et al. 2014, 2015a). In natural
 148 environments such as riverbanks (usually considered as ancestral habitats), these toads breed
 149 in rocky pools and natural depressions filled by floodwater or rainwater. The availability of
 150 natural breeding sites depends on long-term spatio-temporal changes in waterbed
 151 morphology; on the scale of a toad's lifetime, natural breeding site availability is therefore
 152 highly predictable ('predictable environment'). In contrast, *B. variegata* individuals that
 153 occupy artificial environments, such as woodlands exploited for logging or agricultural areas,
 154 breed in artificial water bodies such as ruts, ditches and residual puddles created by skidders
 155 or farming equipment. Thus the inter-annual predictability of potential breeding sites depends
 156 on short-term spatio-temporal variation driven by logging or farming operations. In exploited
 157 woodlands, for instance, rut networks are created during logging operations (Cayuela et al.
 158 2015a) and are filled in at the end of the exploitation of the forest patch or in the following
 159 two years; on the scale of an individual's lifespan, the availability of breeding sites is
 160 therefore highly stochastic in artificial environments ('unpredictable environment').

161

162 | *Surveyed populations and fieldwork*

163

164 As in most studies that compare intraspecific and interspecific life history strategies (e.g.
 165 Gaillard and Yoccoz 2003, Nilsen et al. 2009, Miller et al. 2011, but also see Lawson et al.
 166 2015 and Barraquand and Yoccoz 2013), we indirectly assessed environmental stochasticity
 167 through variations in demographic rates. No specific measures of environmental predictability
 168 (e.g. pond duration) were available for the studied populations. The study was conducted on

169 five *B. variegata* populations in France (TABLE 1, see also in Appendix A for a map and
 170 details concerning environmental characteristics): three in unpredictable environments and
 171 two in predictable environments. The three ‘unpredictable environment’ populations
 172 (hereafter POP1, POP2 and POP3) were located in the Ardennes, Meuse and Charente
 173 departments respectively. In these areas the species reproduces in networks of water bodies
 174 resulting from logging and farming operations (e.g. ruts, ditches and residual puddles); these
 175 are distributed in a landscape matrix consisting of managed woodlands and agricultural areas
 176 (Cayuela et al. 2015a). The two ‘predictable environment’ populations were located in two
 177 distinct watersheds in the Ardèche department. Here, the species breeds in networks of rocky
 178 pools and natural depressions filled by floodwater or rainwater in the vicinity of river
 179 channels (Cayuela et al. 2011, 2013). In these areas, the surrounding landscape mainly
 180 consists of non-managed woodlands.

181 The five populations were monitored using capture–recapture methods during survey
 182 periods varying from 5 to 10 years between 2000 and 2014 (see TABLE 1). The capture–
 183 recapture (CR) survey design has previously been described in published studies (POP1,
 184 Pichenot 2008; POP2, Cayuela et al. 2014); a similar design was used for POP3, POP4 and
 185 POP5 (details concerning the survey design are provided in Appendix A, TABLE A1 - A6). It
 186 consisted of capturing the toads by hand or with a dip net during daylight hours (09:00–
 187 19:00). Capture sessions were carried out during the breeding season from late May to July.
 188 The entire study area was carefully checked every year in order to census all available water
 189 bodies. The yellow-bellied toads were captured in all distinct water-body networks (ranging
 190 from 3 networks in POP5 to 80 networks in POP2), which were made up of between 2 water
 191 bodies (POP2, POP4 and POP5) to more than 100 water bodies (e.g. in POP4 and POP5). At
 192 each capture session, we sampled all water bodies in all networks. The time required to
 193 sample the entire study area in a single session varied from 1 (POP3) to 15 days (POP2). We

194 considered three age classes: juveniles (captured after their first overwintering), subadults
 195 (captured after their second overwintering) and sexually mature adults (captured after at least
 196 three overwinterings). Although one study has considered that individuals can be sexually
 197 mature at the age of 2 (Barandun et al. 1997), four others consider the sexual maturity of this
 198 species to be the age of 3 (Kapfberger 1982, 1984, Rafinska 1991, Plytycz and Bigaj 1993). In
 199 any case, even if gonads may already be producing viable gametes at the age of 2, we
 200 assumed that individuals would be only marginally involved in breeding before the age of 3
 201 because male reproductive success and female fecundity often increases with size/age in
 202 amphibians (Wells 1977, Arak 1983, Woolbright 1983, Wells 2010). Therefore, we have
 203 assumed that yellow-bellied toads become sexually mature at the age of 3. The size (snout–
 204 vent length) of juveniles ranged from 22–29 mm, the size of subadults ranged from 30–34 m
 205 and individuals become sexually mature with a mean body length of 35 mm in males and 36
 206 mm in females. We identified gender on the basis of forearm size and the presence of nuptial
 207 pads in males (Kyriakopoulou-Sklavounou et al. 2012). We identified each individual by the
 208 specific pattern of black and yellow mottles on its belly, which were recorded by photographs.
 209 To minimize misidentification errors, multiple comparisons of individual patterns were
 210 performed using the pattern-matching software Extract Compare (Hiby and Lovell 1990).

211

212 | *Multievent model design*

213

214 The CR data was modeled using a re-parameterized version of the robust design proposed by
 215 Cayuela et al. (2014). The model follows the typical structure of ‘standard’ robust design
 216 (Nichols et al. 1994, Kendall et al. 1997, 2012), i.e. made up of two nested levels of capture
 217 occasions. ‘Secondary sessions’ encompass several field sessions performed over the same
 218 year. Sampling sessions were also conducted over successive years: ‘primary periods’

219 correspond to yearly sessions. During a primary period (i.e. between secondary sessions), we
 220 assumed that the state of an individual was fixed and transitions between states were thus
 221 allowed between primary periods only.

222 The model was conditional on the occasion of first capture and an ‘unborn individual’
 223 state was included, which allowed us to model the probability of being recruited as a juvenile
 224 between two primary periods. After being recruited, individuals could successively transition
 225 between three ontogenetic stages, i.e. juvenile, subadult and adult, given they survived. As is
 226 typical in a capture–recapture framework, survival estimates include both death and
 227 permanent emigration, i.e. apparent survival: see Schmidt et al. (2007) for a discussion on this
 228 point in amphibians. We assumed that sexually mature *Bombina variegata* individuals could
 229 breed or skip breeding each year (see Cayuela et al. 2014). Since individuals were captured in
 230 aquatic breeding sites only, non-breeding toads were considered as not available for capture
 231 (Church et al. 2007, Muths et al. 2010). Skipping breeding in a given year was thus equivalent
 232 to becoming a temporary emigrant and shifting to an unobservable state (Kendall and Nichols
 233 2002). In the model, transitions between breeding/non-breeding states were assumed to obey a
 234 Markov chain process.

235 We specified our states as conditional on the occasion of first capture (TABLE 2).
 236 Because gender is not identifiable in juveniles or subadults, we used a multi-event CR
 237 approach (Pradel 2005) to model uncertainty in gender assignment; gender was thus coded as
 238 a state instead of as a group as is usual in CR data modeling. Individuals could occupy one of
 239 the eleven distinct states: (*UM*) unborn male, (*UF*) unborn female, (*JM*) alive juvenile male,
 240 (*JF*) alive juvenile female, (*SM*) alive subadult male, (*SF*) alive subadult female, (*BM*)
 241 breeding male, (*BF*) breeding female, (*NBM*) non-breeding adult male, (*NBF*) non-breeding
 242 adult female, (†) dead individual. Ten state transitions were possible for the recruitment and
 243 age transition probabilities between two primary periods (FIG.1, matrix A). Given that we

244 examined recruitment without accounting for gender-dependency, α^{JM}/α^{JF} were constrained
 245 to be equal (the parameter is hereafter quoted α). Moreover, age transition probabilities
 246 $\beta^{JM}/\beta^{JF}/\beta^{SM}/\beta^{SF}$ were fixed at 1 between secondary sessions and at 0 between primary
 247 periods. For the survival probability between two primary periods, ten state transitions were
 248 possible (FIG.1, matrix Φ). Given that the parameters ϕ^{BNM} and ϕ^{BNF} were not identifiable,
 249 ϕ^{BM}/ϕ^{BNM} and ϕ^{BF}/ϕ^{BNF} were constrained to be equal in the model. Survival transition
 250 probabilities were fixed at 1 between secondary sessions. For breeder/non-breeder transitions
 251 between two primary periods, four state transitions were possible (FIG.1, matrix Y). The
 252 transition probabilities γ^{BM}/γ^{BF} and $\gamma^{NBM}/\gamma^{NBF}$ were fixed at 1 between secondary sessions.
 253 Concerning field observation, i.e. events *sensu* multi-event modeling formulation, six
 254 observation probabilities were considered (FIG.1, matrix P). Note that as non-breeding
 255 individuals were not available for recapture, their recapture probability was fixed at 0.

256

257 | *Building biological scenarios*

258

259 The parameterization was implemented in the E-SURGE program (Choquet et al. 2009),
 260 which provides robust tools of advanced numerical convergence and refines parameter
 261 estimates by detecting redundant mathematical parameters.

262 The datasets from the five populations differ markedly in terms of the number of study
 263 years and capture sessions per year (Appendix A, TABLE A2–A6) and we did not expect any
 264 identical parameters in the different populations. Thus, the expected benefit in terms of
 265 precision or statistical power of simultaneously analyzing the five datasets would be rather
 266 small or null, while the cost in terms of computation would be high. As a result, we separately
 267 analyzed the five datasets and then compared the mean and variance of vital rates provided by
 268 the best-fitted model for each population.

269 For each population, competing models were ranked through a model-selection
 270 procedure using Akaike information criteria adjusted for a small sample size (AICc) and AICc
 271 relative weights (Burnham and Anderson 2002). We tested our hypotheses concerning
 272 recapture and state transition probabilities from the general model [$\alpha(\text{YEAR})$, $\phi(\text{YEAR} \times$
 273 $\text{AGE})$, $\gamma(\text{YEAR} \times \text{SEX})$, $p(\text{YEAR} + \text{AGE} + \text{SEX})$]. Variation in survival between ontogenetic
 274 stages (AGE) was tested by specifying state transition differences between the three stages
 275 coded as states in the model. Since we were interested in investigating female breeding
 276 investment, we accounted for gender-dependent variation (SEX) in breeding probability by
 277 considering state transition differences between genders coded as states in the model. Initial
 278 state probability was held to be different between ontogenetic stages and gender. Furthermore,
 279 recruitment probability α was held to be different among years (YEAR).

280 From the general model, we successively modeled field observation, breeding
 281 probability and survival probability. We used a downward testing procedure by removing the
 282 effects one by one and retained the best linear combination at each step. First, we tested
 283 whether recapture probability p varied between years (YEAR), as well as between ontogenetic
 284 stages (AGE) and gender in sexually mature adults (SEX). For the last hypothesis, p^{JM}/p^{JF} ,
 285 p^{SM}/p^{SF} and p^{BM}/p^{BF} were held to be different. Since we aimed at investigating the yearly
 286 breeding propensity of females, we then considered gender-specific differences in breeding
 287 probability and tested whether breeder/non-breeder transitions γ varied between years
 288 (YEAR). For this last hypothesis, the pair of transitions was held to be different γ^{BM}/γ^{BF} and
 289 $\gamma^{NBM}/\gamma^{NBF}$. We then tested whether survival probability ϕ differed (1) between years
 290 (YEAR) and (2) between ontogenetic stages (AGE). For the third hypothesis, ϕ^{JM}/ϕ^{JF} ,
 291 ϕ^{SM}/ϕ^{SF} and ϕ^{BM}/ϕ^{BF} were constrained to be equal.

292 Because the violation of the closure assumption may bias survival estimates in robust
 293 design models (Kendall 1999), we assessed the robustness of our analysis by removing

294 secondary sessions in which only a few individuals were encountered. Within a primary
 295 period, the secondary session resulting in the maximum number of encountered toads has
 296 been retained as the reference session for this year. For each primary period, we removed all
 297 secondary sessions in which the number of captured toads was less than 50% of the number of
 298 toads encountered during this reference session. This led to the exclusion of between 5 and 10
 299 sessions (detailed in Appendix B, TABLE B1) depending on the population and the year
 300 (mainly early or late secondary sessions during the breeding season). Then we fitted to these
 301 reduced datasets the best-supported model from our model selection procedure for each
 302 population. The comparisons of mean and temporal survival variance with and without the
 303 removal of these secondary sessions are provided in the appendix (Appendix B, FIG. B1 and
 304 FIG. B2). Only marginal discrepancies were detected, so the potential violation of the closure
 305 assumption is not an issue in our analysis. Moreover, unlike many other amphibians (Ranids,
 306 Bufonids and Hylids), the yellow-bellied toad has a lateral line as well as complete interdigital
 307 webs (Seidel et al. 2001), which are adaptations for an extended aquatic breeding period.
 308 Prolonged spermiation and the presence of post-vitellogenic follicles (Guarino 1998)
 309 throughout the period of breeding activity allow this species of toad to reproduce from April
 310 to August (Di Cerbo and Biancardi 2004), which makes individuals available for capture
 311 during this relatively long period. Taken together, these factors suggest that the closure
 312 assumption may hold in our study

313

314 *Quantifying temporal variation in survival and breeding propensity*

315

316 We built models with yearly variation in survival and breeding transition for all five
 317 populations [$\alpha(\text{YEAR})$, $\square(\text{AGE} \times \text{YEAR})$, $\gamma(\text{AGE} \times \text{YEAR})$, $p(\text{CST})$] in order to obtain
 318 annual estimates of survival rates along with their estimated variance and covariance. Using

319 the methods proposed in Gould and Nichols (1998), we estimated the temporal variance in
 320 survival of all age classes by removing the effects of sampling variance from the estimated
 321 total variance in survival. We used these calculated standard deviations resulting from the
 322 yearly variation in survival probability as indicators of variation in survival of a certain age
 323 class over time, which was in turn a proxy for estimating the presence of canalization of the
 324 given trait. We then used the method proposed by Gaillard and Yoccoz (2003) to compare the
 325 temporal variation variance of survival rates between ontogenetic stages and populations. This
 326 method compares the maximum variance of survival we can expect (from the observed mean
 327 survival rate) with the observed variance in juvenile, subadult and adult survival. This
 328 maximum variance is $s \times (1 - s)$, where s is the mean survival rate. Between the observed
 329 variance and the maximum variance, we then obtained the ratio of possible variation (called
 330 ‘temporal variation ratio’ hereafter, following the terminology used by Gaillard and Yoccoz,
 331 2003) and compared this between ontogenetic stages and populations. In order to provide
 332 uncertainty measures of the temporal variation ratio of survival (and breeding) rates, we
 333 bootstrapped in the individual capture–recapture histories. Because E-surge does not provide
 334 an automatic procedure for bootstrapping CMR-histories, we had to perform this manually.
 335 We thus limited our approach to 50 bootstraps per population. For each bootstrap of each
 336 population, we fitted the best model we obtained from the model selection procedure and
 337 applied the Gould and Nichols (1998) method. This allowed us to obtain a variance for the 50
 338 bootstraps, from which we derived the 95% CI of the temporal variation ratio of survival rate.
 339 We then used the overlap of the 95% CIs to discuss the statistical differences between the
 340 variation estimates. Temporal variation ratios of breeding propensity were calculated using
 341 the same procedure.

342

343 *Quantifying annual offspring production and its temporal variance*

344

345 From the same model, annual offspring production was estimated as the number of newly
 346 recruited juvenile females at t per number of breeding females at $t - 1$. The number of
 347 recruited juvenile females at time t (NRJ) and the number of annual breeding females at $t - 1$
 348 (NBF) were derived (i) from the number of juveniles captured at t and breeding females
 349 captured at $t - 1$, (ii) from their capture probability estimates at a given secondary session
 350 (CPJ : the capture probability of juveniles at a secondary session of year t ; $CPBF$: the capture
 351 probability of breeding females at a secondary session of year $t - 1$), (iii) from the best
 352 supported model, and (iv) from the number of secondary sessions at t (K) and $t - 1$ (L).
 353 Annual offspring production was thus expressed as: $(NRJ / (1 - (1 - CP)^K)) / (NBF / (1 - (1 -$
 354 $CPBF)^L))$. The variance and covariance of annual fecundity was estimated using the methods
 355 as described for survival probability.

356

357 RESULTS

358

359 The model selection procedure and best-supported model for each population are provided in
 360 TABLE 3. We did not detect differences in the average breeding propensity of females
 361 (breeding vs. skipping reproduction during two consecutive years) between unpredictable and
 362 predictable environments (FIG. 2). However, small overlaps in the 95% CI of the temporal
 363 variation ratios (FIG. 2) indicated that breeding propensity was more variable over time in
 364 unpredictable than in predictable environments. Furthermore, although breeding females in
 365 unpredictable environments annually produced more offspring on average, offspring
 366 production was more variable over time (small overlaps in the 95% CI, see FIG. 3).

367

368

In the five populations, survival differed between ontogenetic stages (juvenile,
 subadult and adult) and increased with age (FIG. 4). At the three ontogenetic stages, survival

369 was lower in unpredictable environments. Small overlaps in the 95% CI of the temporal
 370 variation ratios indicated that the survival of juveniles and subadults was more variable in
 371 unpredictable environments, while large overlaps in the 95% CI suggested that temporal
 372 variability of adult survival was similar in both environments (FIG. 4).

373

374 DISCUSSION

375

376 Comparing the population dynamics in unpredictable environments (variable spatio-temporal
 377 availability of breeding sites created by human activity) and predictable environments
 378 (persistent availability of natural breeding sites) reveals divergent life history tactics in *B.*
 379 *variegata*. While on average female breeding propensity did not differ between environments,
 380 our results demonstrated that it was more variable from year to year in unpredictable than in
 381 predictable environments. In addition, although females produced on average more viable
 382 offspring per year in unpredictable environments, offspring production was more variable
 383 from year to year. Survival at the three ontogenetic stages was slightly lower and more
 384 variable (except in adults) from year to year in unpredictable environments. Taken together,
 385 the differences recorded in vital rates indicate that populations in unpredictable environments
 386 respond to increased overall mortality by increasing offspring production, leading to an
 387 acceleration of the life history cycle.

388

389 *Alternative hypothesis*

390

391 It is possible that alternative mechanisms – for example, differences in weather, predation or
 392 competition regimes – may have caused the observed pattern in demographic rate mean and
 393 variation. Weather is often considered the most important environmental driver of amphibian

394 vital rates (reviewed in Walls et al. 2013). Yet in our studied populations, the strongest yearly
 395 weather variations were recorded for populations in which the spatial configuration of ponds
 396 was most stable over time and in which vital rates were the least variable (Appendix A,
 397 TABLE A1). This suggests that the differences of mean and variance in vital rates in our
 398 findings did not result from local differences in weather variability. Another possible factor
 399 could be local differences in the occurrence of predators. However, this seems rather unlikely
 400 because predation has been found to have a small effect on tadpole survival of *B. variegata*
 401 compared to drought risks (Morand 1997). In addition, after metamorphosis, *B. variegata*
 402 displays anti-predator strategies (described in Bajger 1980) involving numerous venom glands
 403 that produce a noxious secretion (König and Bininda-Emonds 2011) as well as behavioral
 404 responses such as defensive postures (the ‘unken reflex’, see Toledo et al. 2011) in which
 405 toads exhibit their aposematic coloration. A third possible factor could be local differences in
 406 the presence of competitors. However, *B. variegata* breeds in highly temporary water bodies
 407 that are avoided by most other amphibians (Morand and Joly 1995, Morand 1997), so local
 408 differences in the amphibian community are not likely to have an impact on the demographic
 409 rate of *B. variegata*.

410

411 *Contrasting patterns of environmental fluctuation influence female breeding propensity and*
 412 *offspring productivity*

413

414 Our results indicate that female breeding propensity was on average similar in the two
 415 environments, but was more variable from year to year in unpredictable environments. In *B.*
 416 *variegata*, the decision to reproduce depends on a variety of external factors (e.g. water
 417 deficit) and the physiological state of the female during the current breeding opportunity
 418 (Cayuela et al. 2014), in line with the concept of ‘state-based life history’ (McNamara and

419 Houston 1996). In females, the energetic costs of breeding are usually related to three factors:
 420 the storage of lipids in body fat ('capital breeder tactic'; Fitzpatrick 1976, Bonnet et al. 1998),
 421 internal sexual mechanisms (especially oogenesis dynamics), and escaping unwanted sexual
 422 attention and possible injury inflicted by males during attempts at amplexus (Wells 2010).
 423 These costs are likely to be enhanced by spatio-temporal unpredictability of breeding sites. In
 424 managed woodlands in particular, breeding sites are created by logging operations that leave
 425 deep ruts that fill with rainwater (Cayuela et al. 2015a) and typically remain attractive for
 426 toads for two years. This type of water body creation generates strong local stochasticity of
 427 available breeding sites. As a result, the inter-annual fidelity of females to breeding sites is
 428 lower and more variable in unpredictable than in predictable environments (Pichenot 2008,
 429 Cayuela et al. *in prep*). Breeding propensity that is more variable over time in unpredictable
 430 environments could thus be a result of the costs induced by moving from an aging rut network
 431 to a more recent one. These costs could be indirect, due to lost metabolic energy in
 432 movement, or direct, due to the time invested in movement (Bonte et al. 2012) that may
 433 prevent a female from breeding during a reproduction opportunity.

434 Differences in annual offspring productivity between the two types of environment
 435 indicate contrasting lifetime schedules of resource allocation to breeding. Risk-spreading
 436 tactics, including bet-hedging and adaptive coin-flipping (see Philippi and Seger 1989, Wilbur
 437 and Rudolf 2006), have been highlighted in various organisms (Veening et al. 2008, Childs et
 438 al. 2010, Nevoux et al. 2010, Gamelon et al. 2013). In *B. variegata*, risk-spreading tactics
 439 (e.g. egg clutch fractionation over space and time) usually allow females to cope with
 440 reproductive success uncertainty caused by high desiccation risk in oviposition sites
 441 (Buschmann 2002). In predictable environments, our results indicate that the inter-annual
 442 predictability of breeding site availability allows females to more consistently spread their
 443 breeding effort over multiple reproduction opportunities in a year. Since female breeding

444 investment in a given reproduction period depends on past breeding status (Cayuela et al.
 445 2014), subsequent fitness gains (number of offspring) are therefore annually lower, but more
 446 constant over time in predictable environments. In contrast, in unpredictable environments,
 447 the inter-annual unpredictability of breeding site availability and localization constrains the
 448 allocation of breeding investment over time. Since egg resorption allows females to recover
 449 energetic resources that can be reinvested later, yearly fitness gains are higher on average, but
 450 less constant from year to year. Our results show that contrasting patterns of environmental
 451 fluctuation could regulate risk-spreading tactics among populations by shaping the trade-off
 452 between mean and variance of breeding investment and subsequent fitness gains.

453

454 *Contrasting patterns of environmental fluctuation influence survival across ontogenetic*
 455 *stages*

456

457 Our results show that mean survival increases with age while temporal variation decreases,
 458 which is in line with the environmental canalization paradigm of ‘slow species’ (Yoccoz and
 459 Gaillard 2003). The survival estimates of adults in our study are congruent with those found
 460 in previous studies ($\square = 0.80$ in Plytycz and Bigaj 1993, $\square = 0.74$ in Cayuela et al. 2014). In
 461 amphibians, post-metamorphosis survival is positively correlated with age and size (Altwegg
 462 and Reyer 2003, Garner et al. 2011, Schmidt et al. 2012). Compared to most anurans,
 463 recorded *B. variegata* survival rates and longevity (Smirina 1994) are high when corrected for
 464 allometry (see the HAGR website: <http://genomics.senescence.info>). This is likely due to anti-
 465 predator and anti-microbial strategies – specific and unique families of antimicrobial peptides
 466 in bombinatorid skin secretions protect them against invasion by pathogenic microorganisms
 467 and also play a role in protecting the animal from ingestion by predators (Conlon 2011, König
 468 and Bininda-Emonds 2011).

469 At each ontogenetic stage, survival was slightly lower and more variable in
 470 unpredictable environments. In these environments, the inter-annual unpredictability of
 471 breeding sites may result in high dispersal propensity, thus reducing apparent survival (in
 472 amphibians, see Perret et al. 2003, Schmidt et al. 2007); in capture–recapture approaches,
 473 apparent survival estimates include both death and permanent emigration (Nichols et al. 1994,
 474 Kendall et al. 1997). The lower survival rate may also be the result of dispersal costs in
 475 unpredictable environments. For example, increased mortality may result from logging if
 476 operations are carried out in the spring. Logging activities near breeding ponds may also
 477 negatively impact survival due to changes in the surface temperature of the soil and loss of
 478 moisture (Semlitsch et al. 2009). Moreover, rut filling resulting from path restoration during
 479 reproduction activity could lead to catastrophic mortality in breeding adults. Finally, in
 480 agricultural areas, prolonged exposure to pesticides can alter growth before and after
 481 metamorphosis by inhibiting normal thyroid activity and/or increase susceptibility to disease
 482 through the suppression of the humoral response (Mann et al. 2009).

483

484 *Conclusion*

485

486 Taken together, the differences recorded in *B. variegata* vital rates in unpredictable and
 487 predictable environments demonstrate that different regimes of stochastic variation in
 488 environmental conditions may contribute to intraspecific variation of life history tactics along
 489 the ‘slow–fast’ continuum. An increase in offspring productivity as well as increased variation
 490 in adult survival (leading to a decrease in average annual adult survival) results in an
 491 acceleration of the life history cycle in populations in unpredictable artificial environments.
 492 Habitat anthropization modifies the spatio-temporal availability of breeding sites and
 493 contributes to divergent selection gradients at intra-specific scales. Because of this new

494 selective pressure, *B. variegata* colonization of human-impacted habitats may lead to local
 495 adaptations that could minimize to some extent the fitness costs induced by changes in the
 496 regime of environmental fluctuation. Understanding the processes of this adaptation
 497 (plasticity vs. selection) requires further investigation based on experimental and/or
 498 translocation approaches.

499

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501

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514

515 LITERATURE CITED

516

517 Altwegg, R., and H. U. Reyer. 2003. Patterns of natural selection on size at metamorphosis in
 518 water frogs. *Evolution* 57:872–882.

- 519 Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. Pages 181–210
 520 in P. Bateson, editor. Mate choice. Cambridge University Press, Cambridge, UK.
- 521 Bajger, J. 1980. Diversity of defensive responses in populations of fire toads (*Bombina*
 522 *bombina* and *Bombina variegata*). *Herpetologica* 36:133–137.
- 523 Barraquand, F., and N. G. Yoccoz. 2013. When can environmental variability benefit
 524 population growth? Counterintuitive effects of nonlinearities in vital rates. *Theoretical*
 525 *Population Biology* 89:1–11.
- 526 Beshkov, V. A., and D. L. Jameson. 1980. Movement and abundance of the yellow-bellied
 527 toad *Bombina variegata*. *Herpetologica* 36:365–370.
- 528 Bonnet, X., D. Bradshaw, and R. Shine. 1998. Capital versus income breeding: an ectothermic
 529 perspective. *Oikos* 83:333–342.
- 530 Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E.
 531 Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S.
 532 Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C.
 533 Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. Travis. 2012.
 534 Costs of dispersal. *Biological Reviews* 87:290–312.
- 535 Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a
 536 practical information-theoretic approach. Springer Verlag, New York, New York, USA.
- 537 Buschmann, H. 2002. Fecundity of yellow-bellied toads *Bombina variegata* under free-range
 538 conditions: an indication of risk-spreading strategy. *Amphibia-Reptilia* 23:362–369.
- 539 Cayuela, H., M. Cheylan, and P. Joly. 2011. The best of a harsh lot in a specialized species:
 540 breeding habitat use by the yellow-bellied toad (*Bombina variegata*) on rocky riverbanks.
 541 *Amphibia-Reptilia*, 32:533–539.

- 542 Cayuela, H., A. Besnard, and P. Joly. 2013. Multi-event models reveal the absence of
 543 interaction between an invasive frog and a native endangered amphibian. *Biological*
 544 *Invasions* 15:2001–2012.
- 545 Cayuela, H., A. Besnard, E. Bonnaire, H. Perret, J. Rivoalen, C. Miaud, and P. Joly. 2014. To
 546 breed or not to breed: past reproductive status and environmental cues drive current
 547 breeding decisions in a long-lived amphibian. *Oecologia* 176:107–116.
- 548 Cayuela, H., J. Lambrey, J. P. Vacher, and C. Miaud. 2015a. Highlighting the effects of land-
 549 use change on a threatened amphibian in a human-dominated landscape. *Population*
 550 *Ecology* 57:433–443.
- 551 Cayuela, H., D. Arsovski, S. Boitaud, E. Bonnaire, L. Boualit, C. Miaud, P. Joly, and A.
 552 Besnard. 2015b. Slow life history and rapid extreme flood: demographic mechanisms and
 553 their consequences on population viability in a threatened amphibian. *Freshwater Biology*
 554 60:2349–2361.
- 555 Childs, D. Z., C. J. E. Metcalf, and M. Rees. 2010. Evolutionary bet-hedging in the real
 556 world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal*
 557 *Society B: Biological Sciences* 277:3055–3064.
- 558 Choquet, R., L. Rouan, and R. Pradel. 2009. Program E-SURGE: a software application for
 559 fitting multievent models. Pages 845–865 in D. L. Thomson, E. G. Cooch, and M. J.
 560 Conroy, editors. *Modeling demographic processes in marked populations*. Springer
 561 Verlag, New York, New York, USA.
- 562 Church, D. R., L. L. Bailey, H. M. Wilbur, W. L. Kendall, and J. E. Hines. 2007. Iteroparity
 563 in the variable environment of the salamander *Ambystoma tigrinum*. *Ecology* 88:891–
 564 903.
- 565 Conlon, J. M. 2011. Structural diversity and species distribution of host-defense peptides in
 566 frog skin secretions. *Cellular and Molecular Life Sciences* 68:2303–2315.

- 567 Fitzpatrick, L. C. 1976. Life history patterns of storage and utilization of lipids for energy in
 568 amphibians. *American Zoologist* 16:725–732.
- 569 Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case
 570 of environmental canalization? *Ecology* 84:3294–3306.
- 571 Gamelon, M., J. M. Gaillard, E. Baubet, S. Devillard, L. Say, S. Brandt, and O. Gimenez.
 572 2013. The relationship between phenotypic variation among offspring and mother body
 573 mass in wild boar: evidence of coin-flipping? *Journal of Animal Ecology* 82:937–945.
- 574 Garner, T. W., J. Rowcliffe, and M. C. Fisher. 2011. Climate change, chytridiomycosis or
 575 condition: an experimental test of amphibian survival. *Global Change Biology* 17:667–
 576 675.
- 577 Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in
 578 animal populations. *Ecology* 79:2531–2538.
- 579 Guarino, F. M., L. Bellini, G. Mazzarella, and F. Angelini. 1998. Reproductive activity of
 580 *Bombina pachypus* from southern Italy. *Italian Journal of Zoology* 65:335–342.
- 581 Hiby, L., and P. Lovell. 1990. Computer aided matching of natural markings: a prototype
 582 system for grey seals. Pages 57–61 in P. S. Hammond, S. A. Mizroch and G. P. Donovan,
 583 editors. The proceedings of the symposium and workshop on individual recognition and
 584 the estimation of cetacean populations parameters, Reports of the International Whaling
 585 Commission. The Red House, Cambridge, UK.
- 586 Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on the
 587 temporal population dynamics of southern fulmars. *Journal of Animal Ecology* 72:576–
 588 587.
- 589 Joly, P., and A. Morand. 1994. Theoretical habitat templates, species traits, and species
 590 richness: amphibian in the Upper Rhône and its floodplain. *Freshwater Biology* 31:455–
 591 468.

- 592 Jones, M. E., A. Cockburn, R. Hamede, C. Hawkins, H. Hesterman, S. Lachish, D. Mann, H.
 593 McCallum, and D. Pemberton. 2008. Life-history change in disease-ravaged Tasmanian
 594 devil populations. *Proceedings of the National Academy of Sciences* 105:10023–10027.
- 595 Kapfberger, D. 1982. Untersuchungen zur Ökologie der Gelbbauchunke, *Bombina variegata*
 596 *variegata* L. 1758 (Amphibia, Anura). Doctoral dissertation, University of Erlangen-
 597 Nürnberg, Germany.
- 598 Kapfberger, D. 1984. Untersuchungen zu Populationsaufbau, Wachstum und Ortsbeziehungen
 599 der Gelbbauchunke, *Bombina variegata variegata* (Linnaeus, 1758). *Zoologischer*
 600 *Anzeiger* 212:105–116.
- 601 Kendall, W. L., and J. D. Nichols. 2002. Estimating state-transition probabilities for
 602 unobservable states using capture-recapture/resighting data. *Ecology* 83:3276–3284.
- 603 Kendall, W. L., J. D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using
 604 capture-recapture data with Pollock's robust design. *Ecology* 78:563–578.
- 605 Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of the
 606 closure assumption. *Ecology* 80:2517–2525.
- 607 Kendall, W. L., G. C. White, J. E. Hines, C. A. Langtimm, and J. Yoshizaki. 2012. Estimating
 608 parameters of hidden Markov models based on marked individuals: use of robust design
 609 data. *Ecology* 93:913–920.
- 610 König, E., and O. R. Bininda-Emonds. 2011. Evidence for convergent evolution in the
 611 antimicrobial peptide system in anuran amphibians. *Peptides* 32:20–25.
- 612 Kraus, C., D. L. Thomson, J. Kuenkele, and F. Trillmich. 2005. Living slow and dying
 613 young? life-history strategy and age-specific survival rates in a precocial small mammal.
 614 *Journal of Animal Ecology* 74:171–180.

- 615 Kyriakopoulou-Sklavounou, P., E. Papaevangelou, and N. Kladisios. 2012. A scanning
 616 electron microscopic study of the surface morphology of nuptial pads in male amphibians
 617 (Genus: *Bombina*, *Pelophylax*, *Rana*). *Acta Herpetologica* 7:81–90.
- 618 Lawson, C. R., Y. Vindenes, L. Bailey, and M. Pol. 2015. Environmental variation and
 619 population responses to global change. *Ecology letters* 18:724–736.
- 620 Levins, R. 1968. *Evolution in changing environments: some theoretical explorations*.
 621 Princeton University Press, New Jersey, USA.
- 622 Mann, R. M., R. V. Hyne, C. B. Choung, and S. P. Wilson. 2009. Amphibians and
 623 agricultural chemicals: review of the risks in a complex environment. *Environmental*
 624 *Pollution* 157:2903–2927.
- 625 McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. *Nature* 380:215–
 626 221.
- 627 Miller, D. A., W. R. Clark, S. J. Arnold, and A. M. Bronikowski. 2011. Stochastic population
 628 dynamics in populations of western terrestrial garter snakes with divergent life histories.
 629 *Ecology* 92:1658–1671.
- 630 Morand, A., and P. Joly. 1995. Habitat variability and space utilization by the amphibian
 631 communities of the French Upper-Rhone floodplain. *Hydrobiologia* 301:249–257.
- 632 Morand, A. 1997. Stabilité relative des habitats de développement larvaire et de reproduction
 633 de *Bombina variegata* et *Bufo calamita*: l'insuffisance des Modèles rK et rKA. *Geobios*
 634 30:23–36.
- 635 Morris, W. F., C. A. Pfister, S. Tuljapurkar, C. V. Haridas, C. L. Boggs, M. S. Boyce, E. M.
 636 Bruna, D. R. Church, T. Coulson, D. F. Doak, S. Forsyth, J. M. Gaillard, C. C. Horvitz,
 637 S. Kalisz, B. E. Kendall, T. M. Knight, C. T. Lee, and E. S. Menges. 2008. Longevity can
 638 buffer plant and animal populations against changing climatic variability. *Ecology* 89:19–
 639 25.

- 640 Muths, E., R. D. Scherer, and B. A. Lambert. 2010. Unbiased survival estimates and evidence
 641 for skipped breeding opportunities in females. *Methods in Ecology and Evolution* 1:123–
 642 130.
- 643 Nevoux, M., J. Forcada, C. Barbraud, J. Croxall, and H. Weimerskirch. 2010. Bet-hedging
 644 response to environmental variability, an intraspecific comparison. *Ecology* 91:2416–
 645 2427.
- 646 Nichols, J. D., J. E. Hines, K. H. Pollock, R. L. Hinz, and W. A. Link. 1994. Estimating
 647 breeding proportions and testing hypotheses about costs of reproduction with capture-
 648 recapture data. *Ecology* 75:2052–2065.
- 649 Nilsen, E. B., J. M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. Van Laere, and J. D.
 650 Linnell. 2009. A slow life in hell or a fast life in heaven: demographic analyses of
 651 contrasting roe deer populations. *Journal of Animal Ecology* 78:585–594.
- 652 Perret, N., R. Pradel, C. Miaud, O. Grolet, and P. Joly. 2003. Transience, dispersal and
 653 survival rates in newt patchy populations. *Journal of Animal Ecology* 72:567–575.
- 654 Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. *American Zoologist*
 655 16:775–784.
- 656 Pichenot, J. 2008. Contribution à la Biologie du Sonneur à ventre jaune (*Bombina variegata*,
 657 L.), Ecologie spatiale et approche multi-échelle de la sélection de l'habitat en limite
 658 septentrionale de son aire de répartition. Doctoral dissertation, University of Champagne-
 659 Ardennes, France.
- 660 Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. *Trends in Ecology*
 661 and *Evolution* 4:41–44.
- 662 Plytycz, B., and J. Bigaj. 1993. Studies on the growth and longevity of the yellow-bellied
 663 toad, *Bombina variegata*, in natural environments. *Amphibia-Reptilia* 14:35–44.

- 664 Pradel, R. 2005. Multievent: an extension of multistate capture–recapture models to uncertain
 665 states. *Biometrics* 61:442–447.
- 666 Rafinska, A. 1991. Reproductive biology of the fire-bellied toads, *Bombina bombina* and *B.*
 667 *variegata* (Anura: Discoglossidae): egg size, clutch size and larval period length
 668 differences. *Biological Journal of the Linnean Society* 43:197–210.
- 669 Reznick, D., and A. P. Yang. 1993. The influence of fluctuating resources on life history:
 670 patterns of allocation and plasticity in female guppies. *Ecology* 74:2011–2019.
- 671 Rideout, R. M., G. A. Rose, and M. P. Burton. 2005. Skipped spawning in female iteroparous
 672 fishes. *Fish and Fisheries* 6:50–72.
- 673 Ruf, T., J. Fietz, W. Schlund, and C. Bieber. 2006. High survival in poor years: life history
 674 tactics adapted to mast seeding in the edible dormouse. *Ecology* 87:372–381.
- 675 Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. *The*
 676 *American Naturalist* 108:783–790.
- 677 Semlitsch, R. D., B. D. Todd, S. M. Blomquist, A. J. Calhoun, J. W. Gibbons, J. P. Gibbs, G.
 678 J. Graeter, E. B. Harper, D. J. Hocking, M. L. Hunter, D. A. Patrick, T. A. G.
 679 Rittenhouse, and B. B. Rothermel. 2009. Effects of timber harvest on amphibian
 680 populations: understanding mechanisms from forest experiments. *Bioscience* 59:853–
 681 862.
- 682 Shaw, A. K., and S. A. Levin. 2011. To breed or not to breed: a model of partial migration.
 683 *Oikos* 120:1871–1879.
- 684 Schmidt, B. R., M. Schaub, and S. Steinfartz. 2007. Apparent survival of the salamander
 685 *Salamandra salamandra* is low because of high migratory activity. *Frontiers in Zoology*
 686 4:1–7.

- 687 Schmidt, B. R., W. Hödl, and M. Schaub. 2012. From metamorphosis to maturity in complex
 688 life cycles: equal performance of different juvenile life history pathways. *Ecology* 93:657–
 689 667.
- 690 Smirina, E. M. 1994. Age determination and longevity in amphibians. *Gerontology* 40:133–
 691 146.
- 692 Souchay, G., G. Gauthier, and R. Pradel. 2014. To breed or not: a novel approach to estimate
 693 breeding propensity and potential trade-offs in an Arctic-nesting species. *Ecology*
 694 95:2745–2756.
- 695 Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- 696 Toledo, L. F., I. Sazima, and C. F. Haddad. 2011. Behavioural defences of anurans: an
 697 overview. *Ethology Ecology and Evolution* 23:1–25.
- 698 Tuljapurkar, S., J. M. Gaillard, and T. Coulson. 2009. From stochastic environments to life
 699 histories and back. *Philosophical Transactions of the Royal Society B-Biological*
 700 *Sciences* 364:1499–1509.
- 701 Van Tienderen, P. H. 2000. Elasticities and the link between demographic and evolutionary
 702 dynamics. *Ecology* 81:666–679.
- 703 Veening, J. W., W. K. Smits, and O. P. Kuipers. 2008. Bistability, epigenetics, and bet-
 704 hedging in bacteria. *Annual Review of Microbiology* 62:193–210.
- 705 Walls, S. C., W. J. Barichivich, and M. E. Brown. 2013. Drought, deluge and declines: the
 706 impact of precipitation extremes on amphibians in a changing climate. *Biology* 2:399–
 707 418.
- 708 Warner, R. R. 1998. The role of extreme iteroparity and risk avoidance in the evolution of
 709 mating systems. *Journal of Fish Biology* 53:82–93.

710 Welbergen, J. A., S. M Klose, N. Markus and P. Eby. 2008. Climate change and the effects of
711 temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B:*
712 *Biological Sciences* 275:419–425.

713 Wells, K. D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour* 25:666–
714 693.

715 Wells, K. D. 2010. *The ecology and behavior of amphibians*. University of Chicago Press,
716 Chicago, Illinois, USA.

717 Wilbur, H. M., and V. H. Rudolf. 2006. Life-history evolution in uncertain environments: bet
718 hedging in time. *American Naturalist* 168:398–411.

719 Woolbright, L. L. 1983. Sexual selection and size dimorphism in anuran amphibia. *American*
720 *Naturalist* 121:110–119.

721

722

SUPPLEMENTAL MATERIAL

723

Appendix A

724 Survey design and Environmental characteristics of the five studied populations of *Bombina*
725 *variegata*.

726

Appendix B

727 Assessing a potential bias of vital rates resulting from the violation of the population closure
728 assumption

729

730 TABLE 1. Survey design characteristics for the five populations investigated in the study:
 731 study period, survey duration, number of capture sessions performed during the survey period,
 732 total number of captures, and number of individuals identified during the survey.

	Study period	Survey duration	Capture sessions	Number of captures	Number of individuals
POP1	2000–2008	8 years	45	953	581
POP2	2008–2014	7 years	23	12300	9418
POP3	2005–2014	10 years	111	1053	456
POP4	2010–2014	5 years	40	3053	1154
POP5	2010–2014	5 years	37	2086	758

733

734

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735 TABLE 2. Definition of parameters estimated in the capture–recapture multi-event model.

Parameter	Definition
α	probability that a newly metamorphosed individual is recruited (FIG.1, matrix A)
β	probability that an individual does not reach the next ontogenetic stage (FIG.1, matrix A)
ϕ	probability that an individual survives (FIG.1, matrix Φ)
γ^B	probability that a sexually individual bred at time t , given it has bred at $t - 1$ (FIG.1, matrix Y)
γ^{NB}	probability that a sexually mature individual skipped a breeding opportunity at time t , given it skipped breeding at $t - 1$ (FIG.1, matrix Y)
p	probability that an individual was recaptured during a secondary session (FIG.1, matrix P)

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737 TABLE 3. Model selection procedure showing the competing models run for each population:
 738 r = model rank, k = number of parameters, $Dev.$ = residual deviance, $AICc$ = Akaike
 739 information criteria adjusted for a small sample size and their derivate quantities, $w = AICc$
 740 relative weight.

r	Model definition				k	$Dev.$	$AICc$	w
	Survival	Breeding	Recruitment	Recapture				
POP1 (Unpredictable)								
1	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	59	11,942.87	12,064.39	1.00
2	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	50	11,973.54	12,076.38	0.00
3	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	75	11,929.29	12,085.74	0.00
4	AGE × YEAR	SEX × YEAR	YEAR	YEAR	72	11,954.25	12,104.19	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	64	12,006.38	12,139.06	0.00
6	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	61	12,100.12	12,226.37	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	67	12,556.51	12,705.64	0.00
POP2 (Unpredictable)								
1	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	61	127,315.07	127,437.49	0.92
2	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	49	127,331.91	127,430.19	0.08
3	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	44	127,364.50	127,452.73	0.00
4	AGE × YEAR	SEX × YEAR	YEAR	YEAR	58	127,603.53	127,719.91	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	50	128,088.70	128,188.98	0.00
6	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	47	128,126.73	128,220.98	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	55	128,228.80	128,339.15	0.00
POP3 (Unpredictable)								
1	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	67	19,925.58	20,062.09	0.58
2	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	85	19,888.94	20,062.98	0.42
3	AGE × YEAR	SEX × YEAR	YEAR	YEAR	83	19,908.03	20,077.88	0.00
4	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	70	19,946.22	20,088.96	0.00
5	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	64	19,986.76	20,117.05	0.00
6	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	56	20,010.99	20,124.74	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	76	20,730.38	20,885.61	0.00
POP4 (Predictable)								

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1	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	34	40,734.24	40,802.44	1.00
2	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	35	41,777.84	41,848.05	0.00
3	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	35	42,156.09	42,226.3	0.00
4	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	43	42,149.91	42,236.23	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	36	42,183.84	42,256.06	0.00
6	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	39	42,323.67	42,401.93	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	YEAR	40	42,412.86	42,493.13	0.00
POP5 (Predictable)								
1	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	34	25,874.07	25,942.37	1.00
2	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	34	26,963.43	27,031.73	0.00
3	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	43	26,995.75	27,082.23	0.00
4	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	35	27,019.16	27,089.48	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	36	27,049.63	27,121.97	0.00
6	AGE × YEAR	SEX × YEAR	YEAR	YEAR	49	27,199.63	27,298.25	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	38	27,255.67	27,332.05	0.00

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743 FIG.1. Elementary matrices for state–state and events transitions: UM = unborn male, UF =
 744 unborn female, JM = juvenile male, JF = juvenile female, SM = subadult male, SF = subadult
 745 female, BM = breeding male, BF = breeding female, NBM = non-breeding male, NBF = non-
 746 breeding female, \dagger = dead, NS = not seen, J = seen juvenile, S = seen subadult, M = seen
 747 sexually mature male, F = seen sexually mature female.

748 FIG. 2. Conditional breeding probability (breeding or skipping breeding during two
 749 consecutive years) and temporal variation ratio of breeding propensity of *B. variegata* females
 750 studied in France over the 2000–2014 period. The 95% CI is shown using error bars.

751 FIG. 3. Annual offspring productivity (number of recruited females per female per year) and
 752 temporal variation (standard deviation) in five populations of *B. variegata* studied in France
 753 over the 2000–2014 period. The 95% CI is shown using error bars.

754 FIG. 4. Mean annual survival at three ontogenetic stages (juvenile, subadult and adult) and
 755 temporal variation ratios in five populations of *B. variegata* studied in France over the 2000–
 756 2014 period. The 95% CI is shown using error bars.

matrix A (recruitment and age transition)

$$\begin{array}{c}
UM \\
UF \\
JM \\
JF \\
SM \\
SF \\
BM \\
BF \\
NBM \\
NBF \\
\dagger
\end{array}
\begin{pmatrix}
1 - \alpha^{JM} & 0 & \alpha^{JM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 - \alpha^{JF} & 0 & \alpha^{JF} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \beta^{JM} & 0 & 1 - \beta^{JM} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \beta^{JF} & 0 & 1 - \beta^{JF} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \beta^{SM} & 0 & 1 - \beta^{SM} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \beta^{SF} & 0 & 1 - \beta^{SF} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}$$

matrix Φ (survival transition)

$$\begin{array}{c}
UM \\
UF \\
JM \\
JF \\
SM \\
SF \\
BM \\
BF \\
NBM \\
NBF \\
\dagger
\end{array}
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \phi^{JM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 - \phi^{JM} \\
0 & 0 & 0 & \phi^{JF} & 0 & 0 & 0 & 0 & 0 & 0 & 1 - \phi^{JF} \\
0 & 0 & 0 & 0 & \phi^{SM} & 0 & 0 & 0 & 0 & 0 & 1 - \phi^{SM} \\
0 & 0 & 0 & 0 & 0 & \phi^{SF} & 0 & 0 & 0 & 0 & 1 - \phi^{SF} \\
0 & 0 & 0 & 0 & 0 & 0 & \phi^{BM} & 0 & 0 & 0 & 1 - \phi^{BM} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{BF} & 0 & 0 & 1 - \phi^{BF} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{NBM} & 0 & 1 - \phi^{NBM} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{NBF} & 1 - \phi^{NBF} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}$$

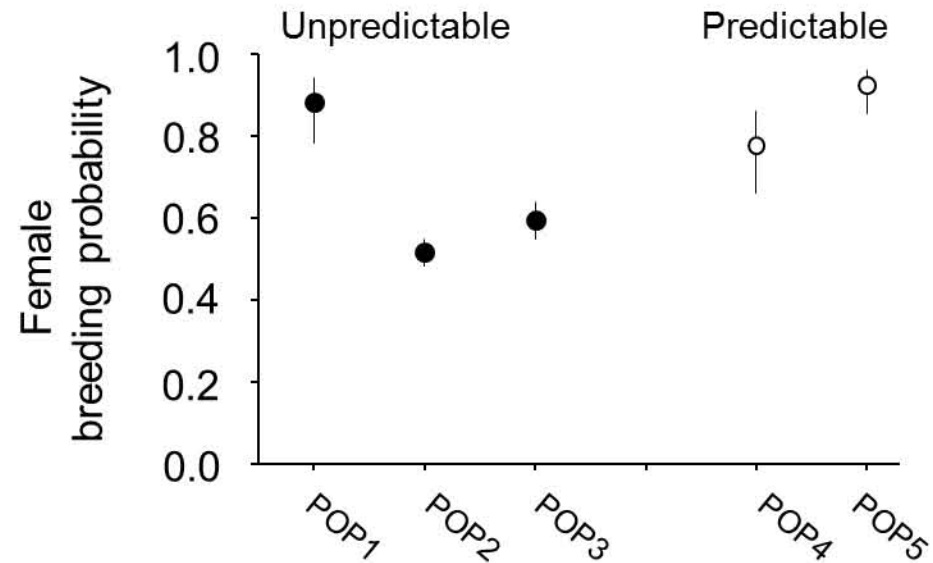
matrix Y (breeder/non-breeder transition)

$$\begin{array}{c}
UM \\
UF \\
JM \\
JF \\
SM \\
SF \\
BM \\
BF \\
NBM \\
NBF \\
\dagger
\end{array}
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BM} & 0 & 1 - \gamma^{BM} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BF} & 0 & 1 - \gamma^{BF} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 - \gamma^{NBM} & 0 & \gamma^{NBM} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 - \gamma^{NBF} & 0 & \gamma^{NBF} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}$$

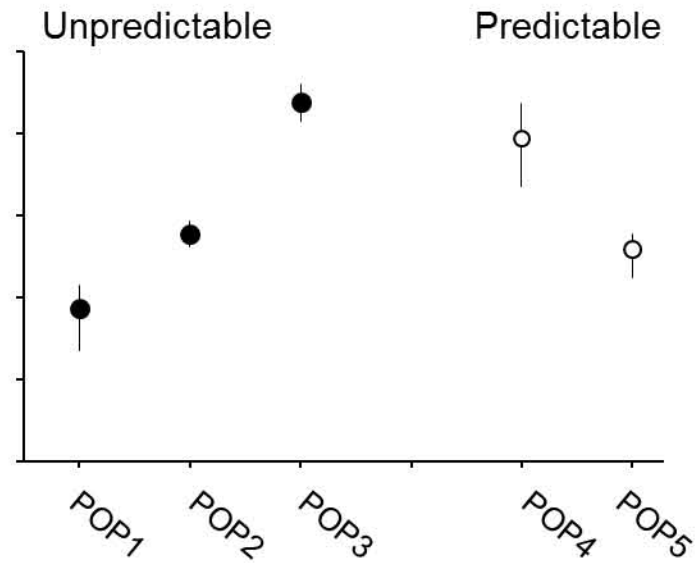
matrix P (recapture)

$$\begin{array}{c}
UM \\
UF \\
JM \\
JF \\
SM \\
SF \\
BM \\
BF \\
NBM \\
NBF \\
\dagger
\end{array}
\begin{pmatrix}
NS & J & S & M & F \\
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 \\
1 - p^{JM} & p^{JM} & 0 & 0 & 0 \\
1 - p^{JF} & p^{JF} & 0 & 0 & 0 \\
1 - p^{SM} & 0 & p^{SM} & 0 & 0 \\
1 - p^{SF} & 0 & p^{SF} & 0 & 0 \\
1 - p^{BM} & 0 & 0 & p^{BM} & 0 \\
1 - p^{BF} & 0 & 0 & 0 & p^{BF} \\
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0
\end{pmatrix}$$

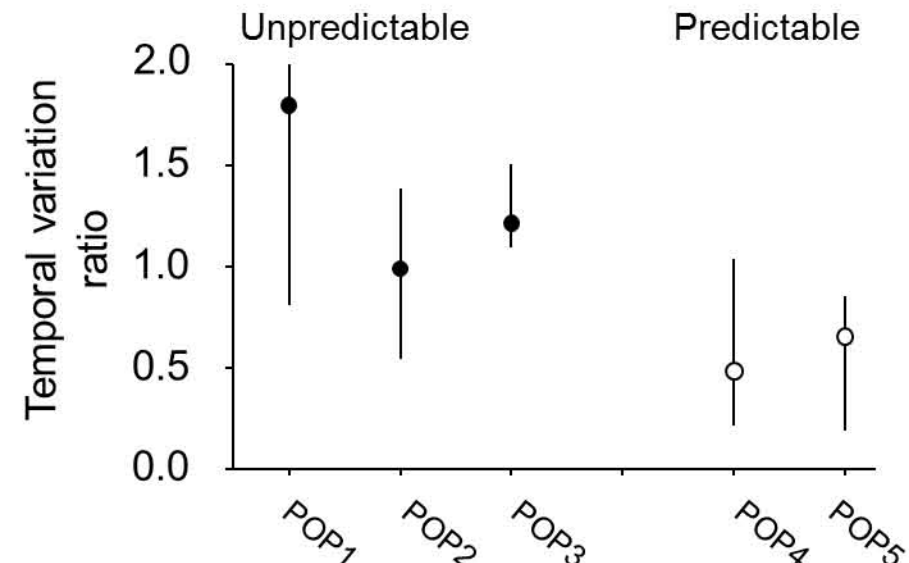
**Breeding
two consecutive years**



**Skipping breeding
two consecutive years**

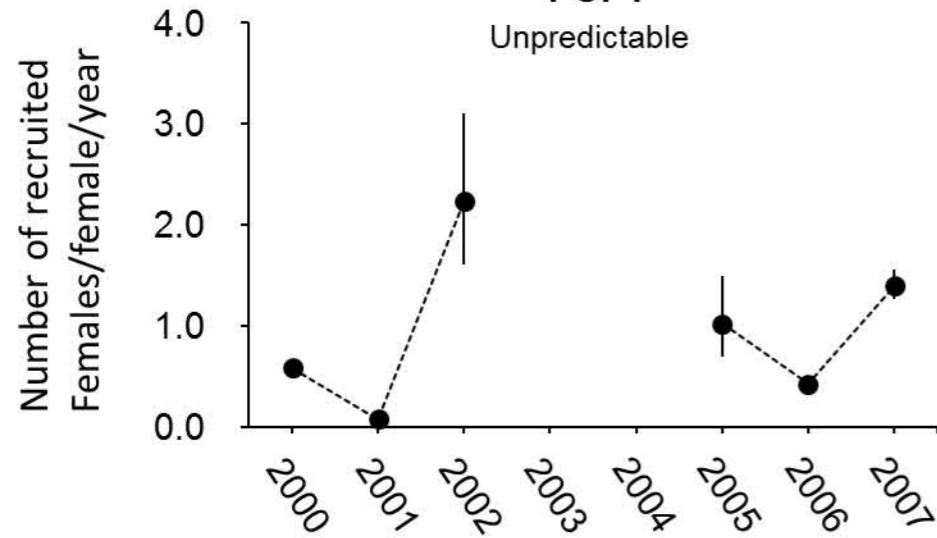


**Breeding
probability**

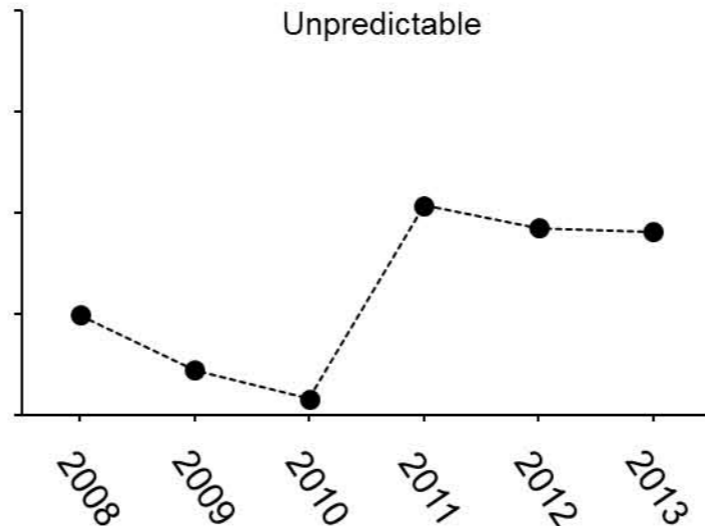


POP1

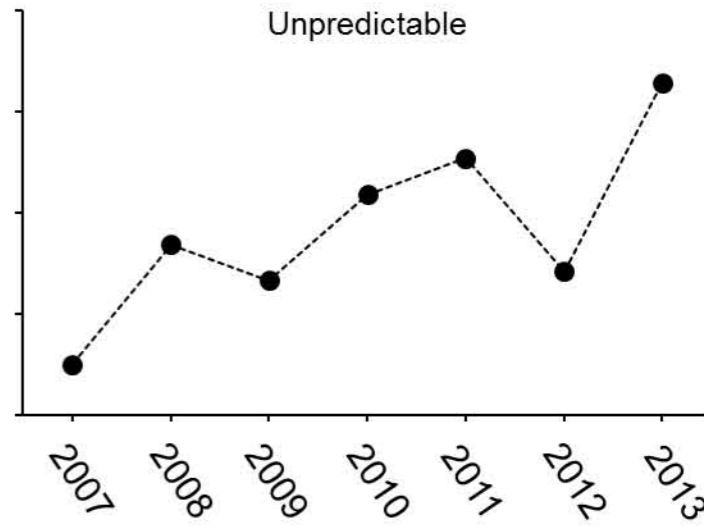
Unpredictable

**POP2**

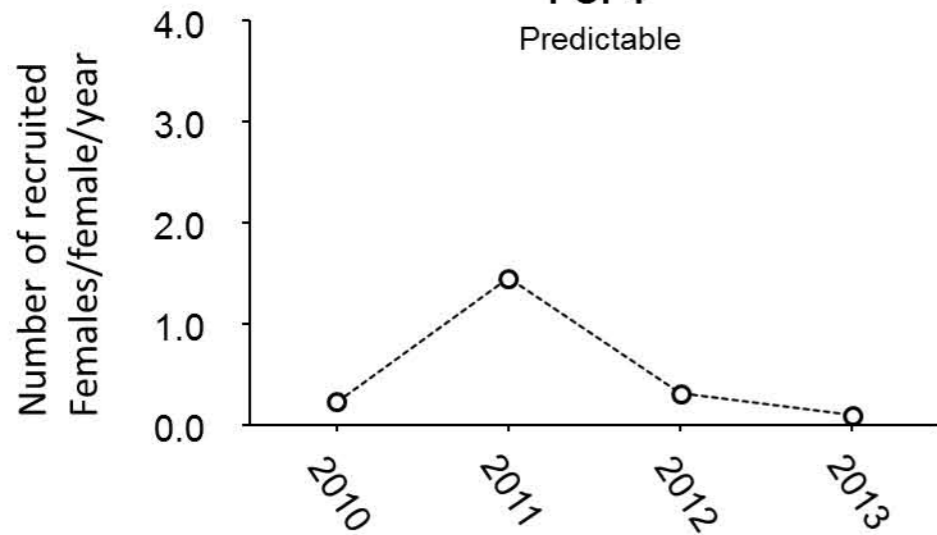
Unpredictable

**POP3**

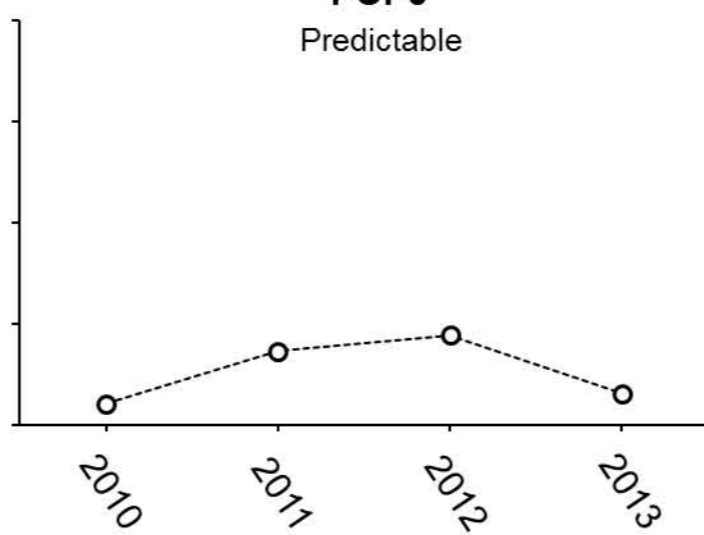
Unpredictable

**POP4**

Predictable

**POP5**

Predictable

Temporal variation
of recruitment (std deviation)