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1 **Population position along the fast-slow life-history continuum predicts**  
2 **intraspecific variation in actuarial senescence**

3

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16

17 Running title: **Intraspecific variation in senescence**

18 HC and BRS conceived the research questions. HC carried out the capture-recapture analyses and  
19 drafted the manuscript. JFL and BRS contributed to writing the manuscript. EB and JP collected  
20 field data. All authors gave final approval for publication.

21

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23

24 The data will be available on Dryad after paper acceptance.

49 **Introduction**

50

51 Most commonly accepted evolutionary theories of ageing posit that survival should decline with  
52 increasing age in any age-structured population (Hamilton 1966), a demographic process known as  
53 actuarial senescence. Medawar's (1952) mutation accumulation theory first stated that organisms  
54 age because the strength of natural selection weakens with age after first reproduction and therefore  
55 there is no purging of deleterious mutations that are only expressed late in life. In addition, actuarial  
56 senescence can emerge as a by-product of natural selection through antagonistic pleiotropy  
57 (Williams 1957). An allele may confer a benefit to the bearer early in life but may also be  
58 responsible for an impaired survival later in life. Finally, the disposable soma theory of aging  
59 postulates that actuarial senescence can result from a trade-off between allocation to reproduction  
60 in early life and somatic maintenance (Kirkwood 1977, Kirkwood & Austad 2000). In other words,  
61 individuals that preferentially allocate resources to growth and/or reproduction (e.g., gamete  
62 production and parental care) will have much less resources for somatic maintenance (e.g., enzyme-  
63 based repair mechanisms), which will ultimately lead to a decline in performance of fitness-related  
64 traits (e.g., survival) at advanced ages. So far, most studies focused on aging in the wild have been  
65 embedded within the two theoretical frameworks offered by both antagonistic pleiotropy and  
66 disposable soma theories of aging as these two theories share the similar prediction of a trade-off  
67 between reproductive effort and actuarial senescence (Gaillard & Lemaître 2017).

68 Although a few case studies on free-ranging populations failed to detect any increase in  
69 mortality rate with age (Jones et al. 2014, Cayuela et al. 2019c), most recent syntheses revealed  
70 two major facts. First, actuarial senescence is a nearly ubiquitous process in the living world  
71 (Nussey et al. 2013, Shefferson et al. 2017). Second, patterns of senescence can be highly variable  
72 among species (Jones et al. 2014, Tidière et al. 2016, Colchero et al. 2019). Comparative analyses  
73 have shown that senescence patterns across multi-cellular organisms can be predicted by ecological  
74 traits, lifestyles and covariation among life-history traits (Péron et al. 2010, Ricklefs 2010, Gaillard  
75 et al. 2016, Salguero-Gómez & Jones 2017). In particular, both age at the onset of senescence and  
76 rates of senescence appear to be linked to the position of a species along the fast-slow life-history  
77 continuum. Organisms that occupy the fast end of the continuum – short generation time, high  
78 annual fecundity, and low mean survival rates (Stearns 1983) – tend to experience earlier and faster  
79 actuarial senescence than organisms at the slow end of the continuum (Jones et al. 2008a, Salguero-  
80 Gómez & Jones 2017). Since life history variation does not only occur among, but also within  
81 species (Berven & Gill 1983, Cayuela et al. 2017), intraspecific variation in senescence patterns is  
82 expected and can be selected for (Stearns 2000, Stearns et al. 2000, Brommer et al. 2007, Holand

117 senescence and the speed and the shape of the relationship between mortality rate and age) differed  
118 between populations with slow and fast life histories. We focused our analyses on post-  
119 metamorphic survival as we did not expect senescence during larval development and assumed that  
120 senescence can begin once structural development is completed (i.e., metamorphosis). We expected  
121 that the pattern of intraspecific variation in actuarial senescence among populations would be  
122 similar to pattern in variation among species. Therefore, we tested the prediction that a fast pace-  
123 of-life should be associated with an earlier, faster actuarial senescence among populations of *B.*  
124 *variegata*.

125

## 126 **Material and methods**

127

### 128 *Study system*

129

130 *Bombina variegata* populations occur in different types of habitats where the spatiotemporal pattern  
131 of breeding resource availability differs widely. In riverine environments, the patches of rock pools  
132 used by toads to reproduce are constantly available in space and time, making breeding resources  
133 highly predictable at the scale of the lifetime of an individual. By contrast, rut patches resulting  
134 from logging operations appear and disappear stochastically in forests, making breeding resource  
135 availability unpredictable. The annual probability of patch appearance varies from 0.20 to 0.50  
136 while the rate disappearance ranges from 0.05 to 0.20, depending on the year and the population  
137 (Cayuela et al. 2016a).

138 Previous studies showed that the populations from these two types of environment have  
139 different life history strategies. Fast populations from forest environment have accelerated life  
140 histories, with lower postmetamorphic survival and higher fecundity than in riverine habitats.  
141 Moreover, the fast life history is associated with higher dispersal (i.e., dispersal syndrome) caused  
142 by the high patch turn-over resulting from logging operations (Cayuela et al. 2016c, 2019b).  
143 Dispersal is facilitated by a phenotypic specialization that is transgenerationally transmitted:  
144 individuals from fast forest populations reared in common garden have a higher boldness and  
145 exploration propensity than those from riverine slow populations (Cayuela et al. 2019b). The  
146 association between high dispersal maintained throughout lifespan, pre-natally determined  
147 behavior, and accelerated life history (i.e., life history syndrome; Réale et al. 2010) is likely  
148 determined by polygenic bases and gene with pleiotropic effects (Saastamoinen et al. 2018).  
149 Furthermore, changes in dispersal regime within spatially structured populations of *B. variegata*  
150 lead to strong variation in neutral genetic structure. Fast forest populations have a higher genetic

185 pattern used to identify individuals is not fixed before that age. Yet, this method permits to survey  
186 the toads for the rest of their lives in a non-invasive way. Only individuals can be aged which are  
187 one or two years old at first capture (Cayuela et al. 2016b), leading to partially known birth date;  
188 this incomplete knowledge of age of individuals is handled using Bayesian survival trajectory  
189 analyses (see the section *Capture-recapture modeling*). Sex cannot be assessed with certainty  
190 before sexual maturity (2-3 years old) due to the lack of nuptial pads in immature males. For this  
191 reason, we did not include an effect of sex in the analyses. Yet, we expect that excluding sex from  
192 our analyses should not alter our conclusions since previous studies in these populations did not  
193 detect sex-specific effects on survival (Cayuela et al. 2016a, 2016c). Details about the number of  
194 survey years, individual age and sampling effort are provided in Appendix 1 (Table 2). A more  
195 complete description about the capture-recapture survey, the individual recognition method and  
196 population description can be found in Cayuela et al. (2016a, 2016c).

197

#### 198 *Capture-recapture modeling*

199

200 We investigated actuarial senescence patterns using Bayesian survival trajectory analyses  
201 implemented in the R package BaSTA (Colchero et al. 2012a, 2012b). BaSTA allowed us to  
202 account for imperfect detection, left-truncated (i.e., unknown birth date (age)) and right-censored  
203 (i.e., unknown death date) capture-recapture data in our analysis. Our analyses focus on the post-  
204 metamorphic stage at which senescence is expected to occur (as in Colchero et al. 2019). BaSTA  
205 allows estimation of two parameters: age-dependent survival and the proportion of individuals  
206 dying at a given age (i.e. age-dependent mortality rate). Given the results of previous analyses  
207 (Cayuela et al. 2016a, 2016b), we allowed recapture probabilities to vary among years. As the study  
208 period and number of survey years differ among populations (Appendix 1), the four populations  
209 were analyzed separately. We used deviance information criterion (DIC) to select models that fitted  
210 the data best (Colchero et al. 2019) and we compared the outputs of the best-supported model of  
211 the four populations by inspecting mean estimates and 95% credible intervals (CRI) (Anderson et  
212 al. 2001, Amrhein et al. 2019). This allowed us to investigate population-specific variation in the  
213 shape of the age-specific mortality patterns. We considered the four mortality functions  
214 implemented in BaSTA: exponential, Gompertz, Weibull and logistic. For the three last functions,  
215 we considered three potential shapes: *simple* that only uses the basic functions described above;  
216 *Makeham* (Pletcher 1999); and *bathhtub* (Silver 1979). As individuals which are less than one year  
217 old cannot be individually recognized, we conditioned the analyses at a minimum age of one. Four  
218 MCMC chains were run with 50000 iterations and a burn-in of 5000. Chains were thinned by a

253 after individuals are 2-3 years old and reached an asymptote at an age of 3 to 4 years. This suggests  
254 an early, fast senescence with a short reproductive lifespan.

255 Age-dependent survival patterns were relatively similar between the populations with the  
256 same life history strategies but differed markedly between strategies (Fig. 3). In slow populations  
257 (Fig. 3A and 3B), the cumulative probability of surviving until a given age decreased slowly over  
258 a toad's lifetime: it was 0.78 until age three, 0.43 until age six, 0.17 until age nine, and finally 0.00  
259 until age 12 (Appendix 1, Table 2-3). In fast populations (Fig. 3C and 3D), cumulative survival  
260 probability decreased rapidly after two years: it was 0.58 until age three, 0.07 until age six, and  
261 0.00 until age nine (Appendix 1, Table 4-5).

262

## 263 **Discussion**

264

265 We provide the first clear evidence for actuarial senescence in a wild amphibian that is associated  
266 with an intraspecific slow-fast life history difference. The onset of actuarial senescence was earlier  
267 in individuals from fast populations and individuals show a faster rate of actuarial senescence than  
268 individuals in slow populations.

269

### 270 *Population viability, elasticity of demographic parameters, and potential confounding factors*

271

272 Population matrix models showed that the four populations had population growth rates higher than  
273 1 and can therefore be considered to be viable. Moreover, we highlighted changes in the elasticity  
274 of demographic rates: slow population have higher elasticities for adult survival and lower  
275 elasticities for pre-breeding survival and fecundity than fast populations. Taken together, our results  
276 suggest that life history acceleration in forest populations is not caused by an ongoing demographic  
277 decline or transient dynamics. By contrast, variation in life history speed seems to rely on stable  
278 demographic strategies covarying with behavioral syndromes that likely have genetic bases  
279 (Cayuela et al. 2019b).

280 Although the habitat type (forest vs riverine) is confounded with latitude in our study  
281 system, it is unlikely that the difference in latitude has an effect on demographic traits and actuarial  
282 senescence. First, a previous study showed that climate has idiosyncratic effects on population  
283 dynamics and there was no evidence for an influence of latitude on demographic rates in *B.*  
284 *variegata* (Cayuela et al. 2016b). Second, populations with slow life history strategies occurring in  
285 quarry habitats can be found in the northern part of the study area (Cayuela et al. 2019a), which  
286 suggests that latitude is not an important predictor of demographic rates. Third, life history variation

320 precise quantification of this onset) and had a faster rate of actuarial senescence than individuals  
321 from slow populations.

322         In our study system, individuals from fast populations occurring in forest environment face  
323 higher level of environmentally-driven mortality (associated with the unpredictability of breeding  
324 patches) than individuals from the slow populations. In fast *B. variegata* populations, logging  
325 management frequently lead to the destruction of breeding patches, which decreases adult survival  
326 via direct mortality during harvesting operations (Cayuela et al. 2018). In addition, as the natural  
327 silting of ruts decreases local breeding success over time, individuals frequently disperse to  
328 colonize new patches and likely incur energy and mortality costs related to the different stages of  
329 the dispersal process (i.e., emigration, transience, and immigration; Boualit et al. 2019, Cayuela et  
330 al. 2019b). By contrast, slow populations occur in non-managed habitats with very limited human  
331 activity where dispersal is virtually absent, which likely decrease environmentally-driven mortality  
332 (Cayuela et al. 2019b). Since Williams (1957) pioneering contribution on this topic, the relationship  
333 between environmentally-driven mortality and actuarial senescence has been heavily discussed (see  
334 Gaillard & Lemaître 2017 and Ronget et al. 2017 for reviews). According to Williams (1957), high  
335 level of adult mortality should lead to a much stronger rate of actuarial senescence, a prediction  
336 which was validated by simulations (Gaillard & Lemaître 2017), at least in absence of density-  
337 dependent or condition-dependent mortality over the entire life course (Abrams 1993, Williams &  
338 Day 2003; see also Moorad et al. 2019 for a recent review). For instance, if mortality during the  
339 juvenile period is strongly condition-dependent, only the most robust individuals will reach  
340 adulthood which can postpone and/or decrease actuarial senescence rates (Ronget et al. 2017). Such  
341 information is currently lacking in *B. variegata* but would provide important insights on how  
342 environmentally-driven mortality modulate the selective forces acting against actuarial senescence.

343         In our study system, actuarial senescence likely evolves from an adjustment of resource  
344 allocation strategies in response to environmentally-driven mortality (Kirkwood & Rose 1991;  
345 Stearns 2000, Baudisch & Vaupel 2012). In others words, individuals from the fast populations  
346 might be able to cope with higher level of environmentally-driven mortality by allocating more  
347 resources to reproduction at the expense of somatic maintenance (see Cayuela et al. 2016a, 2016b  
348 for an in-depth discussion). This might ultimately lead to a faster decline in survival probabilities  
349 of individuals with age, as expected under the disposable soma theory of ageing (Kirkwood &  
350 Austad 2000). In contrast, environmentally-driven mortality is lower in riverine environment where  
351 the predictability of breeding patches is high and human activity is virtually inexistent.  
352 Accordingly, individuals may allocate fewer resources to reproduction – females produce a lower  
353 number of juveniles per year (Cayuela et al. 2016a) – and more to somatic maintenance, resulting

388 2017), then phylogenetic constraints would be a weak explanation for senescence patterns across  
389 the tree of life (Antonovics & van Tienderen 1991). Second, if there is intraspecific variation in  
390 senescence, this variation could explain the weakness of the phylogenetic signals in actuarial  
391 senescence patterns in several taxa (Salguero-Gómez & Jones 2017). It may well be that  
392 phylogenetic signals could become more apparent once intraspecific variation is taken into account.  
393 Such a combination of microevolutionary and macroevolutionary patterns of senescence would  
394 lead to a deeper understanding of the evolutionary biology of senescence.

395

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405

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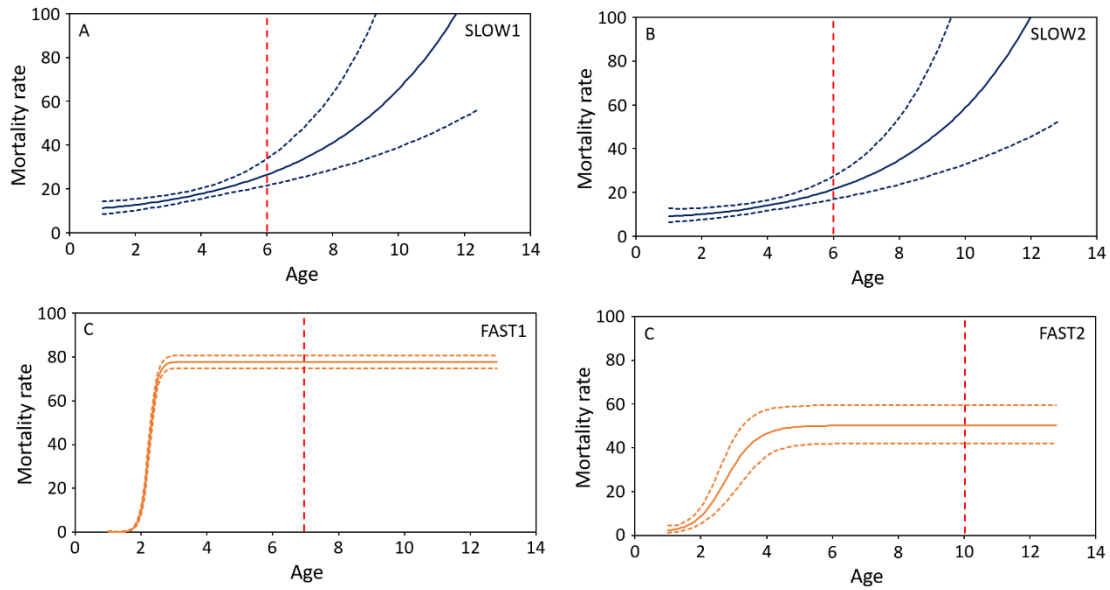
611

617 **Table 2.** Model selection results. Deviance information criterion (DIC) for each of the mortality  
618 function considered in the four studied populations of *Bombina variegata*. We considered the four  
619 mortality functions implemented in BaSTA program: exponential (EXP), Gompertz (GOM),  
620 Weibull (WEI) and logistic (LOG). For the three last functions, we considered three potential  
621 shapes: simple that only uses the basic functions described above (“simple”); Makeham (“make”);  
622 and bathtub (“bath”).

Function	SLOW1	SLOW2	FAST1	FAST2
LOG_simple	13883.1	9770.011	6539.856	79770.16
LOG_bath	13408.63	9511.085	<b>6164.568</b>	<b>76039.06</b>
LOG_make	13878.78	9706.06	6559.085	79669.19
EXP	16151.69	11085.02	8179.035	120984.4
GOM_simple	13515.9	9104.43	6859.955	91054.45
GOM_bath	<b>13210.67</b>	<b>8855.467</b>	6797.639	89020.97
GOM_make	13534.36	9065.034	6888.318	91053.47
WEI_simple	13793.82	9451.142	6811.184	87726.47
WEI_bath	13406.18	9230.966	6653.47	85057.55
WEI_make	13790.13	9464.459	6805.522	87757.15

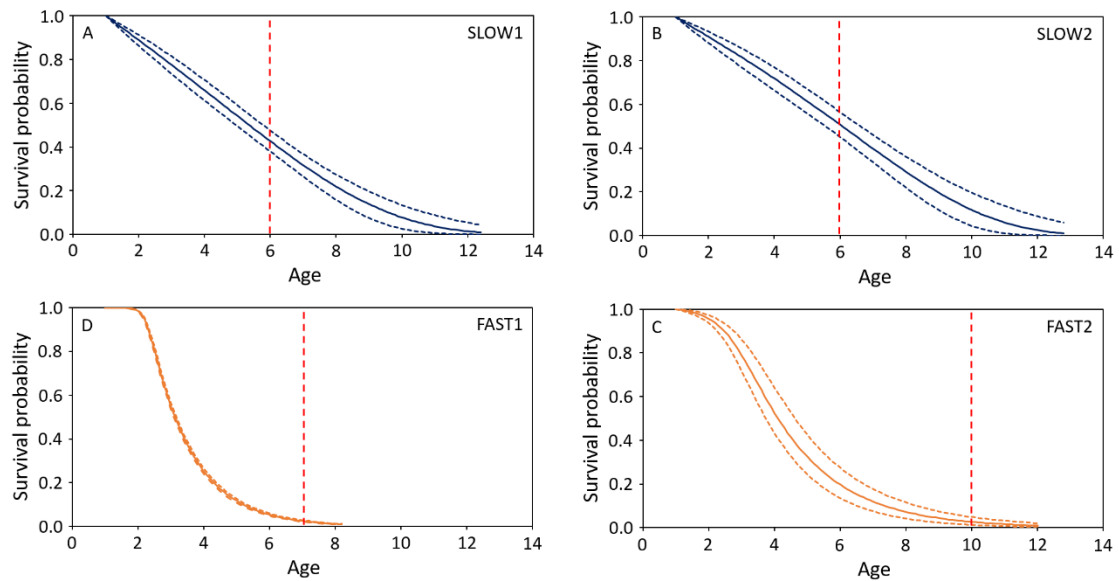
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632 **Fig. 2.** Mortality rate (i.e., proportion of individuals dying at a given age) in two fast (FAST1 and  
 633 FAST2) and slow (SLOW1 and SLOW2) populations of *Bombina variegata*. The predictions on the left of the vertical dashed line correspond to observed ages while those on the right are model  
 634 projections.  
 635



636

637 **Fig. 3.** Survival probability until a given age in two fast (FAST1 and FAST2) and slow (SLOW1  
 638 and SLOW2) populations of *Bombina variegata*. The predictions on the left of the vertical dashed  
 639 line correspond to observed ages while those on the right are model projections.

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