

1 **Variable rate of ageing within species: insights from the Darwin's frog**

2 Andrés Valenzuela-Sánchez^{1,2,3*}, Benedikt R. Schmidt^{4,5}, Claudio Azat³, Soledad Delgado¹,

3 Andrew A. Cunningham⁶, Jean-François Lemaître⁷, Jean-Michel Gaillard⁷, Hugo Cayuela⁸

4 ¹ONG Ranita de Darwin, Ruta T-340 s/n, Valdivia, Chile

5 ²Instituto de Conservación, Biodiversidad y Territorio, Facultad de Ciencias Forestales y

6 Recursos Naturales, Universidad Austral de Chile, Valdivia 5110566, Chile

7 ³Sustainability Research Centre & PhD in Conservation Medicine, Life Sciences Faculty,

8 Universidad Andres Bello, República 440, Santiago, Chile

9 ⁴Info fauna karch, Bâtiment G, Bellevaux 51, 2000 Neuchâtel, Switzerland

10 ⁵Institut für Evolutionsbiologie und Umweltwissenschaften, Universität Zürich,

11 Winterthurerstrasse 190, 8057 Zürich, Switzerland

12 ⁶Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY,

13 United Kingdom

14 ⁷Laboratoire de Biométrie et Biologie Evolutive, Université Lyon 1, CNRS, UMR 5558,

15 Villeurbanne F-769622, France

16 ⁸Department of Ecology and Evolution, Biophore, University of Lausanne, CH-1015

17 Lausanne, Switzerland

18 ***Corresponding author:** Andrés Valenzuela-Sánchez, Ruta T-340 s/n, Valdivia, Chile.

19 Email: andresvalenzuela.zoo@gmail.com

20

21 **Abstract**

22 Actuarial senescence, the increase in adult mortality risk with increasing age, is a
23 widespread phenomenon across the animal kingdom. The onset of senescence, as well as
24 the rate of increase in mortality as organisms age (i.e. ageing rate), varies markedly among
25 species. This variation has been associated with species' life history, body size, and
26 phylogeny. At the intraspecific level, occurrence of variation in ageing patterns remains
27 much more debatable. Here, we assess the level of within-species variation in ageing rates
28 of the southern Darwin's frog (*Rhinoderma darwinii*), a species endemic to the austral
29 temperate forest of South America. We quantified ageing rates in four *R. darwinii*
30 populations distributed in Chile across a latitudinal gradient of 700 km (38° to 45°S). Our
31 results reveal strong among-population variation in ageing rates, and these correlated with
32 population-specific generation time. Thus, a higher ageing rate occurred in populations
33 where individuals exhibited a faster pace of life. Our results, along with recent studies in
34 evolutionarily distant amphibian species, indicate that there can be substantial within-
35 species variation in the rate of ageing. These findings highlight amphibians as emerging
36 models to study the patterns and mechanisms of intraspecific variation in ageing rate in
37 natural populations.

38 **Keywords:** Amphibians; ageing rate; mortality; senescence

39

40

41 **Introduction**

42 Actuarial senescence, i.e., the increase in adult mortality risk with increasing age (hereafter
43 “ageing”), is a pervasive process across the animal kingdom (Nussey et al. 2013; Jones et
44 al. 2014). While ageing is widespread in the living world, both the onset and the rate of
45 increase in mortality risk with age (i.e. ageing rate) vary markedly across species (Jones et
46 al. 2014; Colchero et al. 2019). Studies on terrestrial vertebrates (mostly mammals and
47 birds) have shown that variation in ageing patterns across species are commonly associated
48 with body size (i.e., higher ageing rates in smaller species; Ricklefs 2000, 2010), pace of
49 life (i.e., earlier ageing and steeper ageing rates with faster life histories; Jones et al. 2008;
50 Lemaître & Gaillard 2013), and phylogeny (Ricklefs 2000; Lemaître et al. 2020).

51 Although between-species variation in ageing is now well documented, the
52 occurrence of variation in ageing patterns within a given species remains much more
53 debatable (Lemaître et al. 2013). Evidence from humans (Vaupel 2010) and some species
54 of non-human primates (Colchero et al. 2021), suggest that the rate of ageing can be
55 relatively constant within a species (i.e. the “invariant rate of ageing hypothesis” *sensu*
56 Colchero et al. 2021). On the contrary, comparisons of senescence patterns between free-
57 living and captive mammals have shown that, except for species with a very slow pace of
58 life, ageing rates are generally higher in the wild than in captivity (Lemaître et al. 2013,
59 Tidière et al. 2016). Natural selection can also lead to within-species variation in ageing,
60 both in the laboratory and in the wild (Stearns et al. 2000, Reznick et al. 2004).

61 Until now, our ability to quantify within-species variation in ageing rates has been
62 limited due to the scarcity of fine-scale demographic data across multiple wild populations
63 of a given species (Colchero et al. 2021). When available, long-term, individual-based

64 capture-recapture studies provide the gold standard to reliably assess variation in ageing
65 rates and to identify the eco-evolutionary drivers of such variation. For instance, recently
66 published studies in wild amphibian populations have shown that ageing rate can vary
67 within the same species along environmental gradients (Cayuela et al. 2020, 2021).

68 Here, we assess the level of within-species variation in ageing rates of the southern
69 Darwin's frog (*Rhinoderma darwinii*), a species endemic to the austral temperate forest of
70 South America. We quantified ageing rates in four disparate *R. darwinii* populations
71 distributed in Chile across a latitudinal gradient of 700 km (38° to 45°S) (Fig. 1A). We also
72 explore associations between ageing rate and pace of life (measured by generation time,
73 Gaillard et al. 2005) and environmental factors (i.e. mean environmental temperature,
74 environmental temperature seasonality, and presence of the virulent pathogen
75 *Batrachochytrium dendrobatidis* [Bd]). These variables are known to influence among- and
76 within-species variation in ageing rates in the wild. A faster pace of life has been associated
77 with a steeper ageing rate at the interspecific (Jones et al. 2008) and intraspecific (Cayuela
78 et al. 2020) levels. Cayuela et al. (2021) found that ageing rate was positively associated
79 with mean annual temperature in four amphibian species from North America and Europe.
80 Temperature seasonality explains among-population variation in body size in *R. darwinii*
81 (i.e. a larger body size in more seasonal areas; Valenzuela-Sánchez et al. 2015) and body
82 size is positively associated with ageing rate at the interspecific scale (Jones et al. 2008,
83 Lemaître & Gaillard 2013). Also, there is evidence that infection with *Mycobacterium bovis*
84 can accelerate ageing in badgers (McDonald et al., 2014; Hudson et al., 2019). We end by
85 discussing why among-population variation in ageing rates might occur, and the available
86 empirical evidence of within-species variation in ageing rates.

87

88 **Methods**

89 **Study design**

90 From 2014 to 2020, we carried out a capture-recapture study of four *R. darwinii*
91 populations in Chile (Fig. 1A): Monumento Natural Contulmo ('CON'), Reserva Biológica
92 Huilo Huilo ('HUI'), Parque Tantauco ('TAN') and Reserva Natural Melimoyu ('MER').
93 The populations are within native old-growth forests sharing similar characteristics, such as
94 the absence of anthropogenic stressors besides the emerging chytrid fungus Bd
95 (Valenzuela-Sánchez et al. 2022). Each year, we carried out one survey period in early
96 summer during the peak of the reproductive season (January-February; see Valenzuela-
97 Sánchez et al. 2014). Briefly, all captured frogs were measured (snout-to-vent length, SVL)
98 and photographed for individual recognition (see Valenzuela-Sánchez et al. 2014, 2017,
99 2022 for further details).

100

101 **Assessing ageing patterns**

102 We used the "Bayesian survival trajectory analysis" (BaSTA) package in R (Colchero et al.
103 2012) to assess interpopulation variation in trajectories of age-specific mortality during
104 adulthood. This model allows to estimate the apparent mortality rate at a given age, while
105 accounting for imperfect detection, left-truncated (i.e., unknown birth date) and for right-
106 censored (i.e., unknown death date) from capture-recapture data. Birth dates were estimated
107 for a variable proportion of adult frogs that were first captured as juveniles (Table S1) while
108 death dates were unknown for all adults (and estimated as a latent variable using BaSTA).

109 Since we previously detected time variation in recapture probability across primary capture
110 periods (Valenzuela-Sánchez et al. 2017, 2022), we allowed this parameter to vary among
111 primary capture periods. In BaSTA, we fitted a Siler model on age-specific mortality data
112 (Siler 1979) to obtain comparable metrics for each population (for a justification of the use
113 of this model, see Lemaître et al. [2020]). The Siler model is given by:

$$114 \quad \mu(x) = a_0 \exp(-a_1 x) + c + b_0 \exp(b_1 x)$$

115 where a_0 , a_1 , b_0 , b_1 and c are the parameters of the mortality function, x the age in years,
116 and $\mu(x)$ the age-specific rate of mortality. The exponential function with parameters a
117 describes the changes in mortality in the early adult stage, whereas c gives the lower limit
118 of mortality during the adult stage. The exponential function with b parameters corresponds
119 to the mortality increase during the senescent stage. The parameter b_1 measures the
120 exponential increase in mortality rate with increasing age during the senescent stage and
121 corresponds to the ageing rate in vertebrates (Lemaître et al. 2020). We ran four MCMC
122 chains with 40,000 iterations, a burn-in of 10,000, and no thinning. Chain convergence was
123 evaluated using the potential scale reduction factor (Colchero et al. 2012).

124 We conducted a pairwise comparison to evaluate differences in ageing rate between
125 populations. For each pair of populations, we evaluated the proportion of the posterior
126 distributions of b_1 that did not overlap using the R package “overlapping” (Pastore 2018).
127 This value can range from 0 to 1, where zero indicates perfect overlap between the two
128 distributions and a value of 1 indicates the total absence of overlap. Therefore, this value
129 can be interpreted as the probability that the ageing rate differs between a given pair of
130 populations.

131 Finally, we conducted an exploratory visual analysis to identify factors that might
132 explain among-population variation in ageing rate. We plotted ageing rate estimated for
133 each of the four studied populations against population-specific generation time (extracted
134 from Valenzuela-Sánchez et al. 2022), mean annual temperature (extracted from
135 Valenzuela-Sánchez et al. 2015), temperature seasonality (extracted from Valenzuela-
136 Sánchez et al. 2015), and Bd infection presence (extracted from Valenzuela-Sánchez et al.
137 2022) at these populations.

138

139 **Results**

140 The number of captures, adults found, and percentage of adults with known birth date are
141 presented as Table S1.

142 We found two different patterns of ageing, which did not follow a latitudinal cline
143 (Fig. 1B, C). Ageing rates were higher (more than a twofold difference) in CON ($b_1 =$
144 1.010 , 95% Bayesian credible interval [CRI]= $0.654 - 1.366$) and TAN ($b_1 = 0.998$, 95%
145 CRI = $0.793 - 1.207$) than in HUI ($b_1 = 0.423$, 95% CRI = $0.253 - 0.649$) or MER ($b_1 =$
146 0.481 , 95% CRI = $0.097 - 0.820$). The pairwise analysis of overlap between the posterior
147 distributions of ageing rates provided strong evidence of a difference between populations
148 with fast and slow ageing (i.e. the probability that b_1 was different between a pair of
149 populations with high vs. low ageing rate was consistently higher than 0.9) (Fig. 1C).

150 A negative association occurred between ageing rate and generation time: the two
151 populations with higher ageing rates had a shorter generation time (i.e. 2.7 and 3.2 years in
152 CON and TAN, respectively) than the two population with the lower ageing rates (4.8 and

153 3.7 years in HUI and MER, respectively; Fig. 1D). None of the environmental factors we
154 analysed accounted for population differences in ageing rate (Fig. 1D), although small
155 sample size might have prevented a proper quantitative assessment of these putative
156 associations.

157

158 **Discussion**

159 Our findings in *R. darwinii* provide clear evidence of large among-population variation in
160 ageing rates within this species (Fig. 1).

161 Among-population variation in ageing rate are expected to occur due to at least through
162 two intertwined mechanisms. (1) As ageing rate increases in organisms with fast life-
163 history strategies (Jones et al. 2008), population-specific variation in biological times, such
164 as generation time, are expected to be associated with variation in ageing rate. Our results
165 support the existence of a positive association between ageing rate and pace of life among
166 populations of *R. darwinii*: the two populations with the highest ageing rates were the two
167 with the shortest generation times (Fig. 1D). These results are similar to those reported for
168 the amphibian, *Bombina variegata* (Cayuela et al. 2020). (2) As ageing rate increases with
169 increasing mean mortality rate during adulthood (i.e., Williams' (1957) second prediction
170 of ageing evolution, reviewed in Gaillard & Lemaître 2017), population-specific patterns of
171 environmentally driven adult mortality are expected to cause variation in ageing rate. This
172 could explain the acceleration in ageing rate observed in badgers infected with
173 *Mycobacterium bovis* (McDonald et al. 2014, Hudson et al. 2019). Due to lethal effect of
174 Bd infection, adults from CON have the highest mortality rate among the four studied *R.*

175 *darwinii* populations (see Valenzuela-Sánchez et al. 2017, 2022). In agreement with
176 William's second prediction, this population also exhibited the highest ageing rate. The
177 HUI and TAN populations, however, had dissimilar ageing patterns despite having similar
178 mean mortality rates (Fig. S1).

179 Among-population variation in ageing rates in amphibians and other organisms has been
180 attributed to local environmental conditions such as environmental temperature (Ganetzky
181 and Flanagan 1978, Valenzano et al. 2006, Lee and Kenyon 2009, Cayuela et al. 2020,
182 2021). For example, Cayuela et al. (2021) found that among-population variation in ageing
183 rate was positively associated with mean annual temperature across four amphibian species.
184 We did not find any clear association between ageing rate and environmental temperature
185 in our study system. The link between ageing rate and environmental temperature could be
186 caused by several behavioural, physiological, and genetic mechanisms. For instance,
187 Cayuela et al. (2021) argued that metabolic depression during hibernation could slowdown
188 the ageing process leading to the slow ageing rate they observed in populations of *R.*
189 *luteiventris*, *A. boreas*, and *R. temporaria* inhabiting cold areas. In *R. darwinii*, hibernation
190 duration is most likely driven by temperature seasonality as more seasonal areas exhibit
191 colder and longer winters (Valenzuela-Sánchez et al. 2015). In addition, as seasonality is
192 positively associated with body size in *R. darwinii* (Valenzuela-Sánchez et al. 2015),
193 allometric constraints on ageing rate (Ricklefs 2000, 2010) could lead to a faster ageing in
194 populations within less seasonal areas. In our study, TAN and HUI populations inhabit,
195 respectively, the least and most seasonal areas known for populations of this species
196 (Valenzuela-Sánchez et al. 2015). Among these populations the observed pattern of ageing
197 was as expected, with TAN exhibiting a faster ageing than HUI (Fig. 1D). Individuals from

198 CON and MER, however, experience a moderate and similar seasonality but contrasting
199 ageing patterns (Fig. 1D). Altogether, our results from this small set of populations suggest
200 that ageing patterns in *R. darwinii* are unlikely to be driven by a single major structuring
201 factor. Instead, ageing rate might be determined by the interactions of multiple factors, such
202 as seasonality and Bd infection.

203 Among-population variation in ageing rate is available for a range of amphibian species
204 (Fig. 2). These studies show that ample variation in ageing rates can exist within species of
205 amphibians. For example, the magnitude of variation in ageing rates across populations of
206 *Rana luteiventris* and *Anaxyrus boreas* was larger than the overall variation estimated
207 across 101 mammalian species (Lemaître et al. 2020, Cayuela et al. 2021). These findings,
208 along with those in the current study, highlight amphibians as emerging models to study the
209 patterns and mechanisms of intraspecific variation in ageing rates in natural populations.
210 We encourage researchers to take advantage of the increasing number of long-term,
211 individually based studies in amphibians and other poorly studied taxonomic groups in
212 terms of ageing patterns to conduct comparative analyses to explore within-species
213 variation in ageing. Such analyses are likely to provide important insights into the forces
214 driving the evolution, maintenance, and variation of ageing across natural populations.

215

216

217 **Data availability statement**

218 Data and code will be available at Zenodo.

219

220 **References**

- 221 Cayuela, H., Arsovski, D., Thirion, J. M., Bonnaire, E., Pichenot, J., Boitaud, S., ... &
222 Besnard, A. (2016). Contrasting patterns of environmental fluctuation contribute to
223 divergent life histories among amphibian populations. *Ecology*, 97(4), 980-991.
- 224 Cayuela, H., Olgun, K., Angelini, C., Üzümlü, N., Peyronel, O., Miaud, C., ... & Schmidt, B.
225 R. (2019). Slow life-history strategies are associated with negligible actuarial senescence
226 in western Palaearctic salamanders. *Proceedings of the Royal Society B*, 286, 20191498.
- 227 Cayuela, H., Lemaître, J. F., Bonnaire, E., Pichenot, J., & Schmidt, B. R. (2020). Population
228 position along the fast–slow life-history continuum predicts intraspecific variation in
229 actuarial senescence. *Journal of Animal Ecology*, 89(4), 1069-1079.
- 230 Cayuela, H., Lemaître, J. F., Muths, E., McCaffery, R. M., Frétey, T., Le Garff, B., ... &
231 Pilliod, D. S. (2021). Thermal conditions predict intraspecific variation in senescence rate
232 in frogs and toads. *Proceedings of the National Academy of Sciences of the USA*, 118(49),
233 e2112235118.
- 234 Cayuela, H., Dorant, Y., Forester, B. R., Jeffries, D. L., Mccaffery, R. M., Eby, L. A., ... &
235 Funk, W. C. (2022). Genomic signatures of thermal adaptation are associated with clinal
236 shifts of life history in a broadly distributed frog. *Journal of Animal Ecology*, in press.
237 <https://doi.org/10.1111/1365-2656.13545>
- 238 Colchero, F., Jones, O. R., & Rebke, M. (2012). BaSTA: an R package for Bayesian
239 estimation of age-specific survival from incomplete mark–recapture/recovery data with
240 covariates. *Methods in Ecology and Evolution*, 3(3), 466-470.

241 Colchero, F., Jones, O. R., Conde, D. A., Hodgson, D., Zajitschek, F., Schmidt, B. R., ... &
242 Gaillard, J. M. (2019). The diversity of population responses to environmental change.
243 Ecology Letters, 22(2), 342-353.

244 Colchero, F., Aburto, J. M., Archie, E. A., Boesch, C., Breuer, T., Campos, F. A., ... &
245 Alberts, S. C. (2021). The long lives of primates and the 'invariant rate of ageing'
246 hypothesis. Nature Communications, 12(1), 3666.

247 Gaillard, J. M., Yoccoz, N. G., Lebreton, J. D., Bonenfant, C., Devillard, S., Loison, A., ...
248 & Allaine, D. (2005). Generation time: a reliable metric to measure life-history variation
249 among mammalian populations. The American Naturalist, 166(1), 119-123.

250 Gaillard, J., Lemaître, J., Berger, V., Bonenfant, C., Devillard, S., Douhard, M., Gamelon,
251 M., Plard, F. & Lebreton, J.-D. (2016). Life histories, axes of variation. In: Encyclopedia
252 of Evolutionary Biology (ed Kliman, R.M.) Academic Press, Oxford, pp. 312–323

253 Gaillard, J. M., & Lemaître, J. F. (2017). The Williams' legacy: A critical reappraisal of his
254 nine predictions about the evolution of senescence. Evolution, 71(12), 2768-2785.

255 Gaillard, J. M., & Lemaître, J. F. (2020). An integrative view of senescence in nature.
256 Functional Ecology, 34(1), 4-16.

257 Ganetzky, B., & Flanagan, J. R. (1978). On the relationship between senescence and age-
258 related changes in two wild-type strains of *Drosophila melanogaster*. Experimental
259 Gerontology, 13(3-4), 189-196.

260 Haddow-Brown, N. (2019). Spatio-temporal, climatic and individual-level variation in the
261 infection probability and intensity with *Batrachochytrium dendrobatidis* in syntopic

262 amphibians from the temperate forest of Chile. Thesis Master of Science in Wild Animal
263 Health, University of London.

264 Healy, K., Ezard, T.H., Jones, O.R., Salguero-Gomez, R. & Buckley, Y.M. (2019). Animal
265 life history is shaped by the pace of life and the distribution of age-specific mortality and
266 reproduction. *Nat. Ecol. Evol.*, 3, 1217–1224.

267 Hudson, D. W., Delahay, R., McDonald, R. A., McKinley, T. J., & Hodgson, D. J. (2019).
268 Analysis of Lifetime Mortality Trajectories in Wildlife Disease Research: BaSTA and
269 Beyond. *Diversity*, 11(10), 182.

270 Jones, O. R., Gaillard, J. M., Tuljapurkar, S., Alho, J. S., Armitage, K. B., Becker, P. H., ...
271 & Coulson, T. (2008). Senescence rates are determined by ranking on the fast–slow life-
272 history continuum. *Ecology Letters*, 11(7), 664-673.

273 Jones, O. R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C. G., Schaible, R., Casper, B.
274 B., ... & Vaupel, J. W. (2014). Diversity of ageing across the tree of life. *Nature*,
275 505(7482), 169-173.

276 Kirkwood, T. B., & Holliday, R. (1979). The evolution of ageing and longevity. *Proceedings*
277 *of the Royal Society of London Series B: Biological Sciences*, 205(1161), 531-546.

278 Kirkwood, T. B., & Rose, M. R. (1991). Evolution of senescence: late survival sacrificed for
279 reproduction. *Philosophical Transactions of the Royal Society of London. Series B:*
280 *Biological Sciences*, 332(1262), 15-24.

281 Laurila, A., Karttunen, S., & Merilä, J. (2002). Adaptive phenotypic plasticity and genetics
282 of larval life histories in two *Rana temporaria* populations. *Evolution*, 56 (3), 617-627.

283 Lee, S. J., & Kenyon, C. (2009). Regulation of the longevity response to temperature by
284 thermosensory neurons in *Caenorhabditis elegans*. *Current Biology*, 19(9), 715-722.

285 Lemaître, J. F., & Gaillard, J. M. (2013). Polyandry has no detectable mortality cost in female
286 mammals. *PLoS One*, 8(6), e66670.

287 Lemaître, J. F., Gaillard, J. M., Lackey, L. B., Clauss, M., & Müller, D. W. (2013).
288 Comparing free-ranging and captive populations reveals intra-specific variation in aging
289 rates in large herbivores. *Experimental Gerontology*, 48(2), 162-167.

290 Lemaître, J. F., Ronget, V., Tidière, M., Allainé, D., Berger, V., Cohas, A., ... & Gaillard, J.
291 M. (2020). Sex differences in adult lifespan and aging rates of mortality across wild
292 mammals. *Proceedings of the National Academy of Sciences of the USA*, 117(15), 8546-
293 8553.

294 McDonald, J. L., Smith, G. C., McDonald, R. A., Delahay, R. J., & Hodgson, D. (2014).
295 Mortality trajectory analysis reveals the drivers of sex-specific epidemiology in natural
296 wildlife–disease interactions. *Proceedings of the Royal Society B: Biological Sciences*,
297 281(1790), 20140526.

298 Nussey, D. H., Froy, H., Lemaître, J. F., Gaillard, J. M., & Austad, S. N. (2013). Senescence
299 in natural populations of animals: widespread evidence and its implications for bio-
300 gerontology. *Ageing research reviews*, 12(1), 214-225.

301 Pastore, M. (2018). Overlapping: a R package for Estimating Overlapping in Empirical
302 Distributions. *The Journal of Open Source Software*, 3 (32), 1023.

303 Reznick, D. N., Bryant, M. J., Roff, D., Ghalambor, C. K., & Ghalambor, D. E. (2004). Effect
304 of extrinsic mortality on the evolution of senescence in guppies. *Nature*, 431(7012), 1095-
305 1099.

306 Ricklefs, R. E. (2000). Intrinsic aging-related mortality in birds. *Journal of Avian Biology*,
307 31(2), 103-111.

308 Ricklefs, R. E. (2010). Life-history connections to rates of aging in terrestrial vertebrates.
309 *Proceedings of the National Academy of Sciences of the USA*, 107(22), 10314-10319.

310 Stearns, S. C., Ackermann, M., Doebeli, M., & Kaiser, M. (2000). Experimental evolution
311 of aging, growth, and reproduction in fruitflies. *Proceedings of the National Academy of*
312 *Sciences of the USA*, 97(7), 3309-3313.

313 Tidière, M., Gaillard, J. M., Berger, V., Müller, D. W., Lackey, L. B., Gimenez, O., ... &
314 Lemaître, J. F. (2016). Comparative analyses of longevity and senescence reveal variable
315 survival benefits of living in zoos across mammals. *Scientific Reports*, 6(1), 36361.

316 Valenzano, D. R., Terzibasi, E., Cattaneo, A., Domenici, L., & Cellerino, A. (2006).
317 Temperature affects longevity and age-related locomotor and cognitive decay in the short-
318 lived fish *Nothobranchius furzeri*. *Aging cell*, 5(3), 275-278.

319 Valenzuela-Sánchez, A., Harding, G., Cunningham, A. A., Chirgwin, C., & Soto-Azat, C.
320 (2014). Home range and social analyses in a mouth brooding frog: testing the coexistence
321 of paternal care and male territoriality. *Journal of Zoology*, 294(4), 215-223.

322 Valenzuela-Sánchez, A., Cunningham, A. A., & Soto-Azat, C. (2015). Geographic body size
323 variation in ectotherms: effects of seasonality on an anuran from the southern temperate
324 forest. *Frontiers in Zoology*, 12: 37.

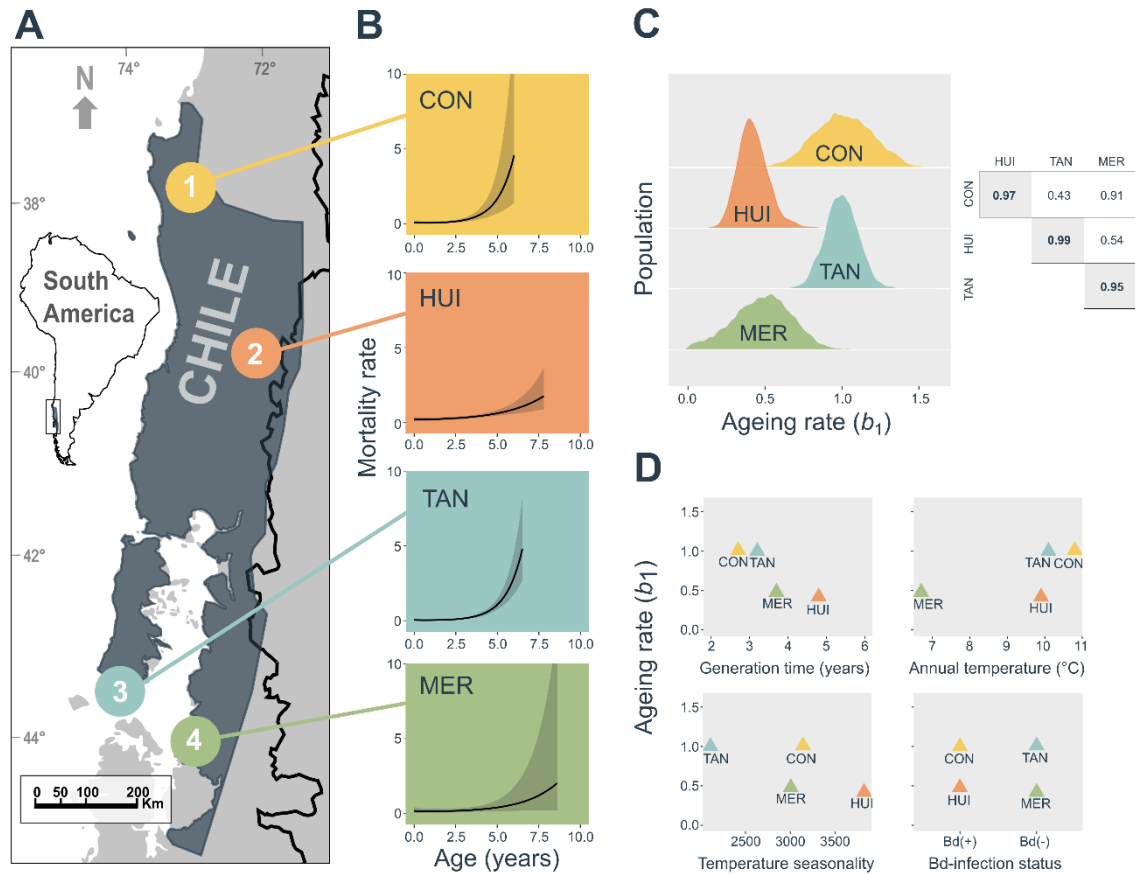
325 Valenzuela-Sánchez, A., Schmidt, B. R., Uribe-Rivera, D. E., Costas, F., Cunningham, A.
326 A., & Soto-Azat, C. (2017). Cryptic disease-induced mortality may cause host extinction
327 in an apparently stable host–parasite system. *Proceedings of the Royal Society B:*
328 *Biological Sciences*, 284(1863), 20171176.

329 Valenzuela-Sánchez, A., Azat, C., Cunningham, A. A., Delgado, S., Bacigalupe, L. D.,
330 Beltrand, J., ... & Cayuela, H. (2022). Interpopulation differences in male reproductive
331 effort drive the population dynamics of a host exposed to an emerging fungal pathogen.
332 *Journal of Animal Ecology*, in press. <https://doi.org/10.1111/1365-2656.13603>

333 Vaupel, J. W. (2010). Biodemography of human ageing. *Nature*, 464(7288), 536-542.

334 Williams, G. C. (1957). Pleiotropy, natural-selection, and the evolution of senescence.
335 *Evolution* 11:398–411.

336

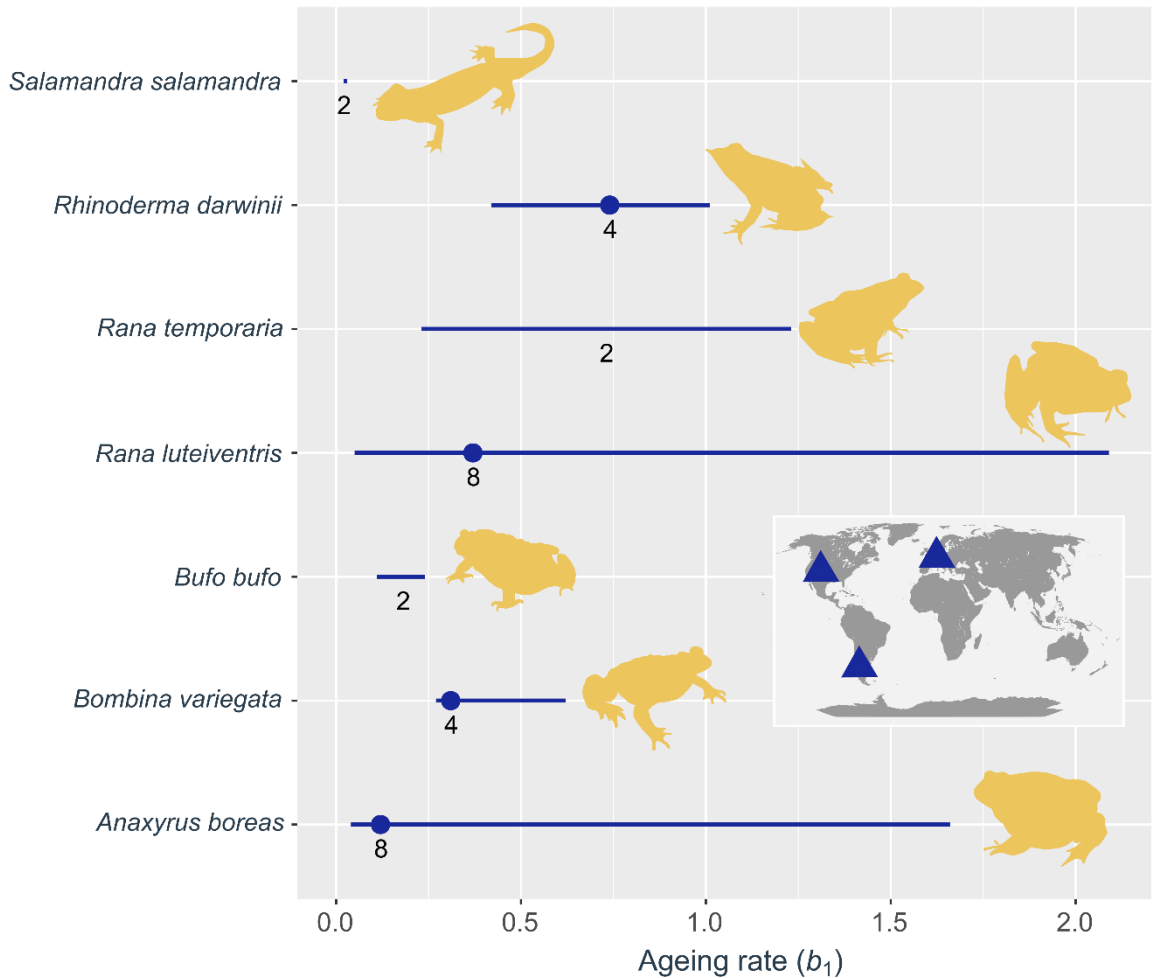


337

338 **Figure 1.** Actuarial senescence patterns in adults from four Southern Darwin's frog
 339 (*Rhinoderma darwinii*) populations located in Southern Chile. (A) Study area showing the
 340 studied populations: 1= Contulmo ('CON'), 2= Reserva Biológica Huilo Huilo ('HUI'), 3=
 341 Parque Tantauco ('TAN'), 4=Reserva Elemental Melimoyu ('MER'). (B) Age-specific
 342 mortality rate at each population. Note that this is a hazard rate, not a probability (i.e., it is
 343 not $1 - \text{survival}$). The shaded areas represent the Bayesian 95% credible intervals. (C)
 344 Density plots for the posterior distributions of the ageing rate parameter, b_1 , from the Siler
 345 model. This parameter represents the magnitude of the exponential increase in mortality
 346 rate with age during the ageing stage. (D) Relationship between ageing rate and generation
 347 time (extracted from Valenzuela-Sánchez et al. [2022]), mean annual temperature
 348 (extracted from Valenzuela-Sánchez et al. [2015]), temperature seasonality (extracted from

349 Valenzuela-Sánchez et al. [2015]), and *Batrachochytrium dendrobatidis* (Bd) infection
350 presence (extracted from Valenzuela-Sánchez et al. [2022]) at each population.

351



352
 353
 354
 355
 356
 357
 358
 359
 360
 361
 362

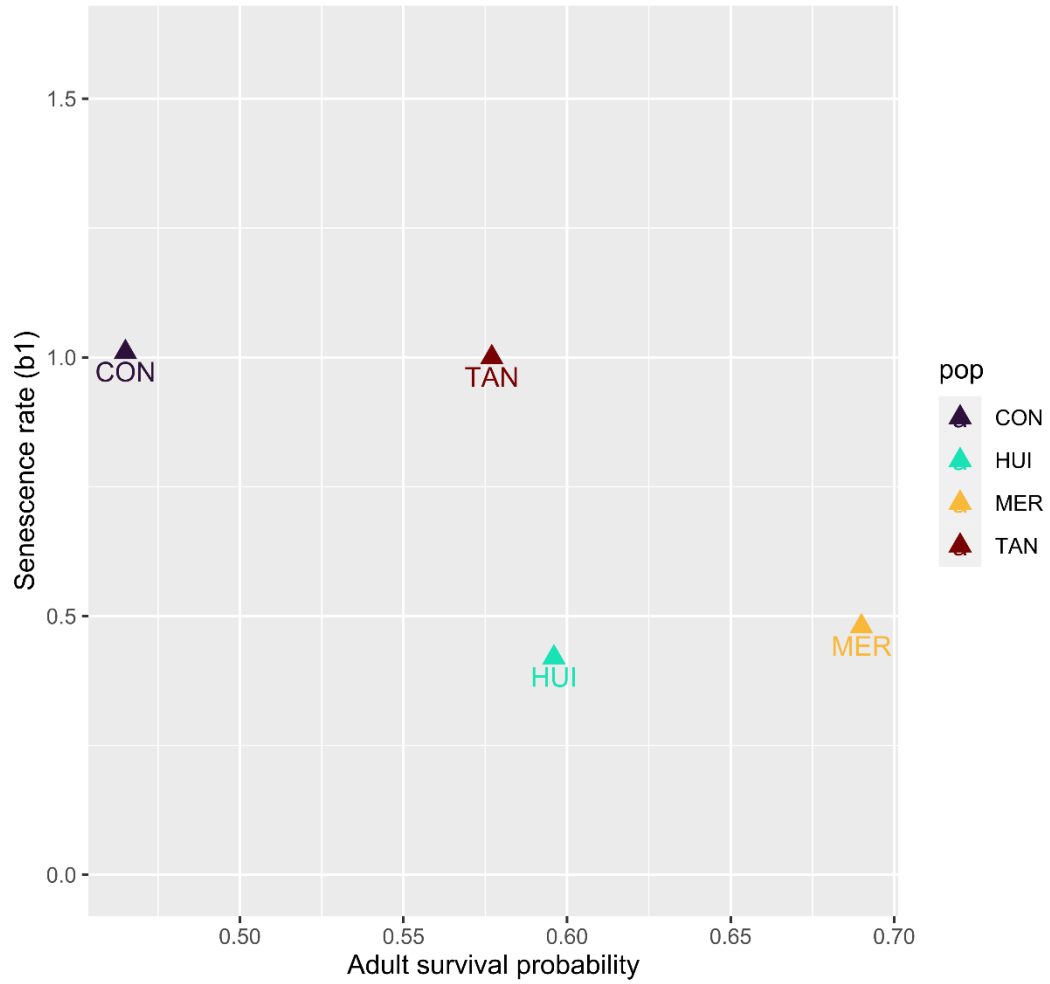
Figure 2. Among-population variation in ageing rate (i.e., b_1 parameter from Siler model) in amphibians. The range of minimum and maximum values (line), median (dot; only species with more than two studied populations), and number of populations studied (numbers) are displayed. In the inset we show the geographical location of the studied populations. Data obtained from: *Anaxyrus boreas* (Cayuella et al. 2021), *Bombina variegata* (Cayuella et al. 2020), *Bufo bufo* (Cayuella et al. 2021), *Rana luteiventris* (Cayuella et al. 2021), *Rana temporaria* (Cayuella et al. 2021), *Rhinoderma darwinii* (this study), *Salamandra salamandra* (Cayuella et al. 2019).

363 **Table S1.** Details of the 7-year capture-recapture study (2014-2020) at four populations of
364 the Southern Darwin's frog (*Rhinoderma darwinii*) in southern Chile.

Site	CON	HUI	TAN	MER
No. frogs	77	228	306	23
No. captures	101	352	426	38
Percentage of frogs with known birth date	36.4	21.5	29.7	73.9

365

366



367

368 **Figure S1.** Relationship between ageing rate and annual adult survival probability

369 (extracted from Valenzuela-Sánchez et al. [2022]) in four populations of the Southern

370 Darwin's frog (*Rhinoderma darwini*) in southern Chile.

371