Variable rate of ageing within species: insights from Darwin's frogs

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Actuarial senescence, the increase in adult mortality risk with increasing age, is a widespread phenomenon across the animal kingdom. Although between-species variation in the rate of increase in mortality as organisms age (i.e. ageing rate) is now well documented, the occurrence of variation in ageing rate within a given species remains much more debatable. We evaluated the level of within-species variation in ageing rate in four populations of the southern Darwin's frog (*Rhinoderma darwinii*) from Chile. Our results revealed strong among-population variation in ageing rates, and these were correlated with the population-specific generation time. A higher ageing rate occurred in populations where individuals exhibited a faster pace of life. Our results, along with recent studies in evolutionarily distant amphibian species, indicate that there can be substantial within-species variation in the rate of ageing, highlighting amphibians as emerging models to study the patterns and mechanisms of intraspecific variation in ageing rate.

ADDITIONAL KEYWORDS: ageing rate – Amphibians – mortality – senescence.

INTRODUCTION

Actuarial senescence (i.e. the increase in adult mortality risk with increasing age; hereafter 'ageing') is a pervasive process across the animal kingdom (Nussey *et al.*, 2013; Jones *et al.*, 2014). Although ageing is widespread in the living world, both the onset and the rate of increase in mortality risk with age (i.e. ageing rate) vary markedly across species (Jones *et al.*, 2014; Colchero *et al.*, 2019). Studies on terrestrial vertebrates have shown that variations in ageing patterns across species are commonly associated with body size (i.e. higher ageing rates in smaller species; Ricklefs, 2000, 2010; Reinke *et al.*, 2022), pace of life (i.e. earlier ageing and steeper ageing rates with faster life histories; Jones *et al.*, 2008; Lemaître & Gaillard, 2013; Reinke *et al.*, 2022), phylogeny (Ricklefs, 2000; Lemaître *et al.*, 2020) and protective phenotypes (i.e. slower ageing rates in ectothermic tetrapods with physical or chemical protection; Reinke *et al.*, 2022).

Although between-species variation in ageing is now well documented, the occurrence of variation in

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ageing patterns within a given species remains much more debatable (Lemaître *et al.*, 2013). Evidence from humans (Vaupel, 2010) and some species of non-human primates (Colchero *et al.*, 2021) suggests that the rate of ageing can be relatively constant within a species (i.e. the 'invariant rate of ageing hypothesis' *sensu* Colchero *et al.*, 2021). On the contrary, comparisons of senescence patterns between free-living and captive mammals have shown that, except for species with a very slow pace of life, ageing rates are generally higher in the wild than in captivity (Lemaître *et al.*, 2013; Tidière *et al.*, 2016). Natural selection can also lead to within-species variation in ageing, both in the laboratory and in the wild (Stearns *et al.*, 2000; Reznick *et al.*, 2004).

Until now, our ability to quantify within-species variation in ageing rates has been limited owing to the scarcity of fine-scale demographic data across multiple wild populations of a given species (Colchero *et al.*, 2021). When available, long-term, individual-based capture–recapture studies provide the gold standard for reliable assessment of the variation in ageing rates and to identify the eco-evolutionary drivers of such variation. Here, using a 7-year capture–recapture study, we assess the level of within-species variation in ageing rates of the southern Darwin's frog (*Rhinoderma darwinii* Duméril and Bibron, 1841), a species endemic to the austral temperate forest of South America. We quantify ageing rates in four disparate *Rhinoderma darwinii* populations distributed in Chile across a latitudinal gradient of 700 km (38–45°S; Fig. 1A). We also explore associations between ageing rate and pace of life (measured by generation time; Gaillard *et al.*, 2005) and environmental factors [i.e. mean environmental temperature, environmental temperature seasonality and presence of the virulent pathogen *Batrachochytrium dendrobatidis* (Bd)]. These variables are known to influence among- and within-species variation in ageing rates in the wild. A faster pace of life has been associated with a steeper ageing rate at the interspecific (Jones *et al.*, 2008) and intraspecific (Cayuela *et al.*, 2020) levels. Cayuela *et al.* (2021) found that the ageing rate was positively associated with mean annual temperature in four amphibian species from North America and Europe. Temperature seasonality explains among-population variation in body size in *Rhinoderma darwinii* (i.e. a larger body size in more seasonal areas; Valenzuela-Sánchez *et al.*, 2015), and body size is positively associated with ageing rate at the interspecific scale (Jones *et al.*, 2008; Lemaître & Gaillard, 2013). Also, there is evidence that infection with *Mycobacterium bovis* can accelerate ageing in badgers (McDonald *et al.*, 2014; Hudson *et al.*, 2019). We end by discussing why among-population variation in ageing rates might

occur, and the available empirical evidence of within-species variation in ageing rates.

MATERIAL AND METHODS

STUDY DESIGN

From 2014 to 2020, we carried out a capture–recapture study of four *Rhinoderma darwinii* populations in Chile (Fig. 1A): Monumento Natural Contulmo (CON); Reserva Biológica Huilo Huilo (HUI); Parque Tantauco (TAN); and Reserva Natural Melimoyu (MER). The populations are within native old-growth forests sharing similar characteristics, such as the absence of anthropogenic stressors besides the emerging chytrid fungus, Bd (Valenzuela-Sánchez *et al.*, 2022). The elevation is ~500 m a.s.l. at CON and HUI and ~10 m a.s.l. at TAN and MER. Each year, we carried out surveys during one period in early summer at the peak of the reproductive season (January–February; see Valenzuela-Sánchez *et al.*, 2014). Briefly, all captured frogs were measured [snout-to-vent length (SVL)] and photographed for individual recognition (for further details, see Valenzuela-Sánchez *et al.*, 2014, 2017, 2022).

ASSESSMENT OF AGEING PATTERNS

We used the Bayesian survival trajectory analysis (BaSTA) package in R (Colchero *et al.*, 2012) to assess interpopulation variation in trajectories of age-specific mortality during adulthood. This model allows the estimation of apparent mortality rate at a given age, while accounting for imperfect detection, left-truncated (i.e. unknown birth date) and right-censored (i.e. unknown death date), from capture–recapture data. Birth dates were estimated for a variable proportion of adult frogs that were first captured as juveniles (Supporting Information, Table S1), and death dates were unknown for all adults (and estimated as a latent variable using BaSTA). Specifically, the year of birth of each adult frog that was first captured as a juvenile was derived using the population-specific SVL of recently metamorphosed frogs (i.e. size at birth; CON = 9.30 mm, HUI = 10.12 mm, TAN = 8.19 mm and MER = 8.88 mm) and regression coefficients (slope and intercept) of a population-specific growth model describing the change in SVL in juveniles from year t to year $t + 1$. Given that we previously detected time variation in recapture probability across primary capture periods (Valenzuela-Sánchez *et al.*, 2017, 2022), we allowed this parameter to vary among primary capture periods. In BaSTA, we fitted a Siler model on age-specific mortality data (Siler, 1979) to obtain comparable metrics for each population (for a
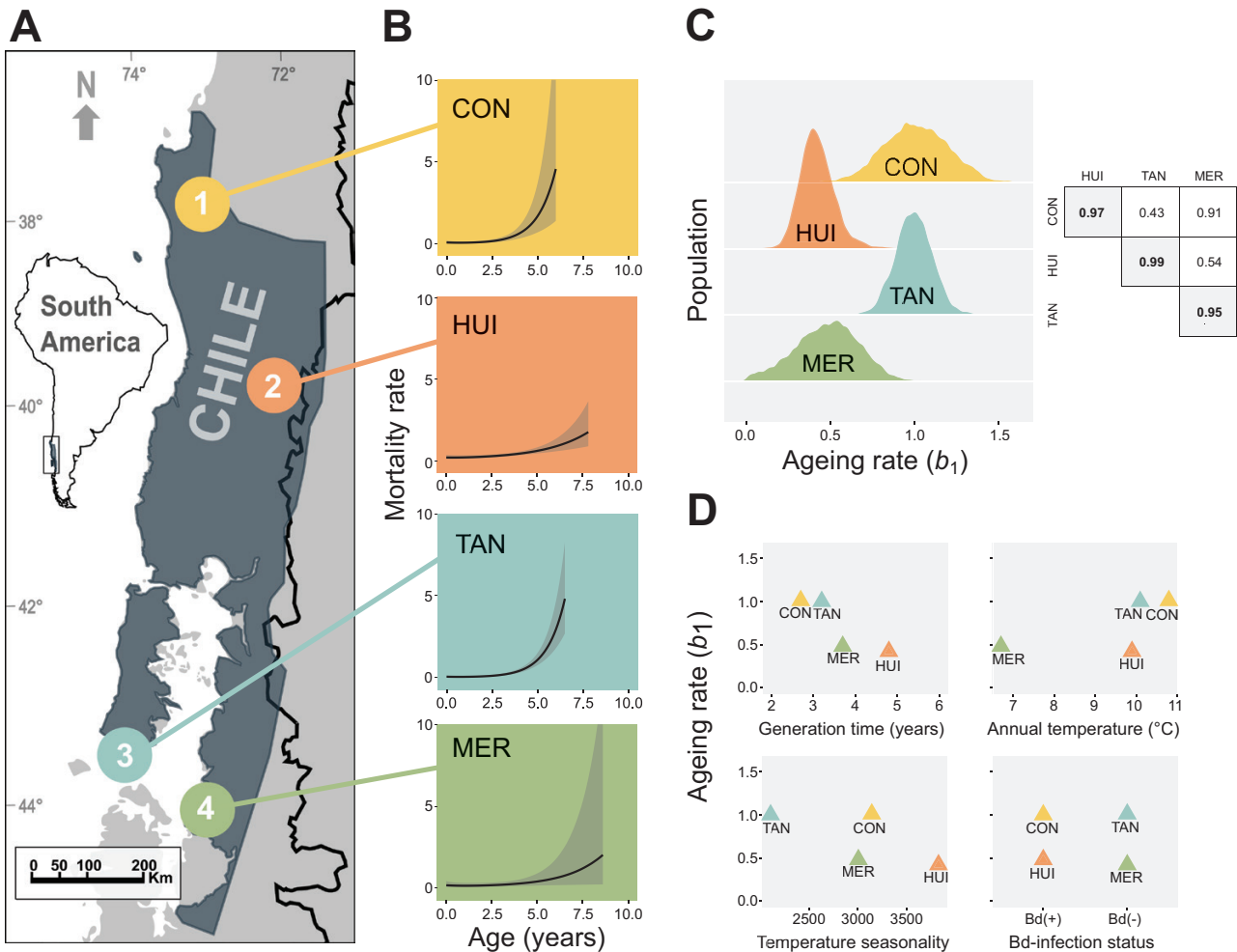
Figure 1. Actuarial senescence patterns in adults from four southern Darwin's frog (*Rhinoderma darwinii*) populations located in Southern Chile. A, study area showing the studied populations: 1 = Contulmo (CON); 2 = Reserva Biológica Huilo Huilo (HUI); 3 = Parque Tantauco (TAN); and 4 = Reserva Elemental Melimoyu (MER). B, age-specific mortality rate for each population. Note that this is a hazard rate, not a probability (i.e. it is not one minus survival). The shaded areas represent the Bayesian 95% credible intervals. C, density plots for the posterior distributions of the ageing rate parameter, b_1, from the Siler model. This parameter represents the magnitude of the exponential increase in mortality rate with age during the ageing stage. D, relationship between ageing rate and generation time (extracted from the study by Valenzuela-Sánchez *et al.*, 2022), mean annual temperature (extracted from the study by Valenzuela-Sánchez *et al.*, 2015), temperature seasonality (extracted from the study by Valenzuela-Sánchez *et al.*, 2015) and presence of *Batrachochytrium dendrobatidis* (Bd) infection (extracted from the study by Valenzuela-Sánchez *et al.*, 2022) in each population.

justification of the use of this model, see Lemaître *et al.*, 2020). The Siler model is given by:

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

where a_0, a_1, b_0, b_1 and c are the parameters of the mortality function, x the age in years, and $\mu(x)$ the age-specific rate of mortality. The exponential function with a parameters describes the changes in mortality in the early adult stage, whereas c gives the lower limit of mortality during the adult stage. The exponential function with b parameters corresponds to the increase in mortality during the senescent

stage. The parameter b_1 measures the exponential increase in mortality rate with increasing age during the senescent stage and corresponds to the ageing rate in vertebrates (Lemaître *et al.*, 2020). We ran four Markov chain Monte Carlo chains with 40 000 iterations, a burn-in of 10 000 and no thinning. Chain convergence was evaluated using the potential scale reduction factor (Colchero *et al.*, 2012).

We conducted a pairwise comparison to evaluate differences in ageing rate between populations. For each pair of populations, we evaluated the proportion of the posterior distributions of b_1 that did not overlap

using the R package 'overlapping' (Pastore, 2018). This value can range from zero to one, where value of zero indicates perfect overlap between the two distributions and a value of one indicates the total absence of overlap. Therefore, this value can be interpreted as the probability that the ageing rate differs between a given pair of populations.

Finally, we conducted an exploratory visual analysis to identify factors that might explain among-population variation in ageing rate. We plotted ageing rate estimated for each of the four studied populations against population-specific generation time, mean annual temperature (extracted from the study by Valenzuela-Sánchez *et al.*, 2015), temperature seasonality (extracted from the study by Valenzuela-Sánchez *et al.*, 2015) and the presence of Bd infection (extracted from the study by Valenzuela-Sánchez *et al.*, 2022) in these populations. Generation time was calculated as the inverse of the elasticity of the population growth rate to changes in fecundity (Bienvenu & Legendre, 2015). This parameter was calculated using the R package POPBIO v.2.7 (Stubben & Milligan, 2007) on a prebreeding census, age-structured matrix population model parameterized with population-specific vital rates (for further details, see Valenzuela-Sánchez *et al.*, 2022).

RESULTS

The total number of captures, number of adults found, and the percentage of adults with known birth date are presented in the Supporting Information (Table S1).

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

A negative association occurred between ageing rate and generation time: the two populations with higher ageing rates had a shorter generation time (i.e. 2.7 and 3.2 years in CON and TAN, respectively) than the two population with the lower ageing rates (4.8 and 3.7 years in HUI and MER, respectively; Fig. 1D). None of the environmental factors we analysed accounted for population differences in ageing rate (Fig. 1D),

although small sample size might have prevented a proper quantitative assessment of these putative associations.

DISCUSSION

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

Among-population variations in ageing rate are expected to occur by at least two intertwined mechanisms. First, as ageing rate increases in organisms with fast life-history strategies (Jones *et al.*, 2008), population-specific variation in biological times, such as generation time, are expected to be associated with variation in ageing rate. Our results support the existence of a positive association between ageing rate and pace of life among populations of *Rhinoderma darwinii*: the two populations with the highest ageing rates were the two with the shortest generation times (Fig. 1D). These results are similar to those reported for the amphibian *Bombina variegata* (Cayuela *et al.*, 2020). Second, as ageing rate increases with increasing mean mortality rate during adulthood [i.e. Williams' (1957) second prediction of ageing evolution, reviewed by Gaillard & Lemaître, 2017], population-specific patterns of environmentally driven adult mortality are expected to cause variation in ageing rate. This could explain the acceleration in ageing rate observed in badgers infected with *M. bovis* (McDonald *et al.*, 2014; Hudson *et al.*, 2019). Owing to the lethal effect of Bd infection, adults from CON have the highest mortality rate among the four studied *Rhinoderma darwinii* populations (see Valenzuela-Sánchez *et al.*, 2017, 2022). In agreement with William's second prediction, this population also exhibited the highest ageing rate. The HUI and TAN populations, however, had dissimilar ageing patterns despite having similar mean mortality rates (Supporting Information, Fig. S1).

Among-population variation in ageing rates in amphibians and other organisms has been attributed to local environmental conditions such as environmental temperature (Ganetzky & Flanagan, 1978; Valenzano *et al.*, 2006; Lee & Kenyon, 2009; Cayuela *et al.*, 2020, 2021). For example, Cayuela *et al.* (2021) found that the among-population variation in ageing rate was positively associated with mean annual temperature across four amphibian species. We did not find any clear association between ageing rate and environmental temperature in our study system. A link between ageing rate and environmental temperature could be caused by several behavioural, physiological and genetic mechanisms. For instance, Cayuela *et al.* (2021) argued that metabolic depression during hibernation
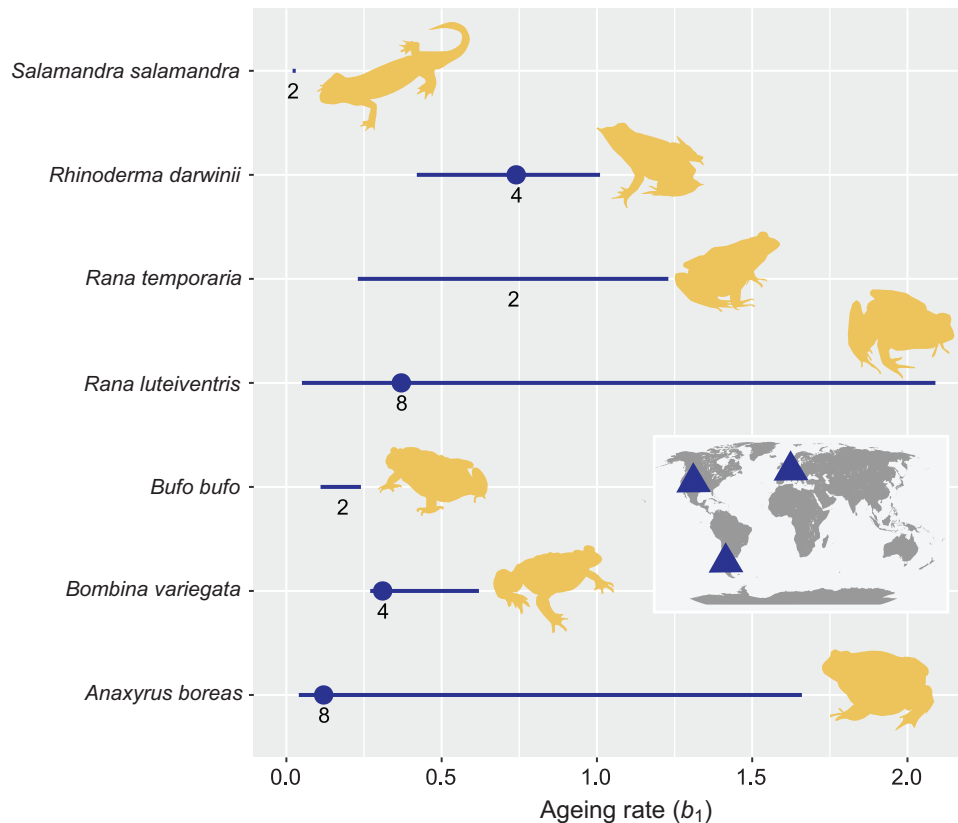
Figure 2. Among-population variation in ageing rate (i.e. b_1 parameter from the Siler model) in amphibians. The range of minimum and maximum values (lines), the median (dots; only for species with more than two studied populations) and the number of populations studied (numbers) are displayed. In the inset, we show the geographical location of the studied populations. Data were obtained as follows: *Anaxyrus boreas* (Cayuela *et al.*, 2021), *Bombina variegata* (Cayuela *et al.*, 2020), *Bufo bufo* (Cayuela *et al.*, 2021), *Rana luteiventris* (Cayuela *et al.*, 2021), *Rana temporaria* (Cayuela *et al.*, 2021), *Rhinoderma darwinii* (this study) and *Salamandra salamandra* (Cayuela *et al.*, 2019).

could slow down the ageing process, leading to the slow ageing rate they observed in populations of *Rana luteiventris*, *Anaxyrus boreas* and *Rana temporaria* inhabiting cold areas. In *Rhinoderma darwinii*, the duration of hibernation is most likely to be driven by temperature seasonality, because more seasonal areas exhibit colder and longer winters (Valenzuela-Sánchez *et al.*, 2015). In addition, given that seasonality is positively associated with body size in *Rhinoderma darwinii* (Valenzuela-Sánchez *et al.*, 2015), allometric constraints on ageing rate (Ricklefs, 2000, 2010) could lead to faster ageing in populations within less seasonal areas. In our study, TAN and HUI populations inhabit, respectively, the least and most seasonal areas known for populations of this species (Valenzuela-Sánchez *et al.*, 2015). Among these populations, the observed pattern of ageing is as expected, with TAN exhibiting a faster ageing than HUI (Fig. 1D). Individuals from CON and MER, however, experience a moderate and similar seasonality but contrasting ageing patterns (Fig. 1D). Altogether, our results from this small

set of populations suggest that ageing patterns in *Rhinoderma darwinii* are unlikely to be driven by a single major structuring factor. Instead, the ageing rate might be determined by the interactions of multiple factors, such as seasonality and Bd infection.

Among-population variation in ageing rate is now available for a range of amphibian species (Fig. 2). These studies show that ample variation in ageing rates can exist within species in this taxonomic group. For example, the magnitude of variation in ageing rates across populations of *Rana luteiventris* and *A. boreas* was larger than the overall variation estimated across 101 mammalian species (Lemaître *et al.*, 2020; Cayuela *et al.*, 2021). These findings, along with those of the present study, highlight amphibians as emerging models to study the patterns and mechanisms of intraspecific variation in ageing rates in natural populations. We encourage researchers to take advantage of the increasing number of long-term, individually based studies in amphibians and other poorly studied taxonomic groups in terms of ageing

patterns to conduct comparative analyses to explore within-species variation in ageing. Such analyses are likely to provide important insights into the forces driving the evolution, maintenance and variation of ageing across natural populations.

DATA AVAILABILITY

Data are available at https://doi.org/10.5281/zenodo.7072271.

REFERENCES

Bienvenu F, **Legendre S. 2015**. A new approach to the generation time in matrix population models. *The American Naturalist* **185**: 834–843.

Cayuela H, **Olgun K**, **Angelini C**, **Üzüm N**, **Peyronel O**, **Miaud C**, **Avcı A**, **Lemaitre JF**, **Schmidt BR. 2019**. Slow life-history strategies are associated with negligible actuarial senescence in western Palaearctic salamanders. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20191498.

Colchero F, **Aburto JM**, **Archie EA**, **Boesch C**, **Breuer T**, **Campos FA**, **Collins A**, **Conde DA**, **Cords M**, **Crockford C**, **Thompson ME**, **Fedigan LM**, **Fichtel C**, **Groenenberg M**, **Hobaiter C**, **Kappeler PM**, **Lawler RR**, **Lewis RJ**, **Machanda ZP**, **Manguette ML**, **Muller MN**, **Packer C**, **Parnell RJ**, **Perry S**, **Pusey AE**, **Robbins MM**, **Seyfarth RM**, **Silk JB**, **Staerk J**, **Stoinski TS**, **Stokes EJ**, **Strier KB**, **Strum SC**, **Tung J**, **Villavicencio F**, **Wittig RM**, **Wrangham RW**, **Zuberbühler K**, **Vaupel JW**, **Alberts SC. 2021**. The long lives of primates and the 'invariant rate of ageing' hypothesis. *Nature Communications* **12**: 3666.

Colchero F, **Jones OR**, **Conde DA**, **Hodgson D**, **Zajitschek F**, **Schmidt BR**, **Malo AF**, **Alberts SC**, **Becker PH**, **Bouwhuis S**, **Bronikowski AM**, **De Vleeschouwer KM**, **Delahay RJ**, **Dummermuth S**, **Fernández-Duque E**, **Frisenvaenge J**, **Hesselsøe M**, **Larson S**, **Lemaître JF**, **McDonald J**, **Miller DAW**, **O'Donnell C**, **Packer C**, **Raboy BE**, **Reading CJ**, **Wapstra E**, **Weimerskirch H**, **While GM**, **Baudisch A**, **Flatt T**, **Coulson T**, **Gaillard JM. 2019**. The diversity of population responses to environmental change. *Ecology Letters* **22**: 342–353.

Colchero F, **Jones OR**, **Rebke M. 2012**. BaSTA: an R package for Bayesian estimation of age-specific survival from incomplete mark–recapture/recovery data with covariates. *Methods in Ecology and Evolution* **3**: 466–470.

Gaillard JM, **Lemaître JF. 2017**. The Williams' legacy: a critical reappraisal of his nine predictions about the evolution of senescence. *Evolution* **71**: 2768–2785.

Gaillard JM, **Yoccoz NG**, **Lebreton JD**, **Bonenfant C**, **Devillard S**, **Loison A**, **Pontier D**, **Allaine D. 2005**. Generation time: a reliable metric to measure life-history variation among mammalian populations. *The American Naturalist* **166**: 119–123.

Ganetzky B, **Flanagan JR. 1978**. On the relationship between senescence and age-related changes in two wild-type strains of *Drosophila melanogaster*. *Experimental Gerontology* **13**: 189–196.

Hudson DW, **Delahay R**, **McDonald RA**, **McKinley TJ**, **Hodgson DJ. 2019**. Analysis of lifetime mortality trajectories in wildlife disease research: BaSTA and beyond. *Diversity* **11**: 182.

Jones OR, **Gaillard JM**, **Tuljapurkar S**, **Alho JS**, **Armitage KB**, **Becker PH**, **Bize P**, **Brommer J**, **Charmantier A**, **Charpentier M**, **Clutton-Brock T**, **Dobson FS**, **Festa-Bianchet M**, **Gustafsson L**, **Jensen H**, **Jones CG**, **Lillandt BG**, **McCleery R**, **Merilä J**, **Neuhaus P**, **Nicoll MA**, **Norris K**, **Oli MK**, **Pemberton J**, **Pietiäinen H**, **Ringsby TH**, **Roulin A**, **Saether BE**, **Setchell JM**, **Sheldon BC**, **Thompson PM**, **Weimerskirch H**, **Jean Wickings E**, **Coulson T. 2008**. Senescence rates are determined by ranking on the fast–slow life-history continuum. *Ecology Letters* **11**: 664–673.

Jones OR, **Scheuerlein A**, **Salguero-Gómez R**, **Camarda CG**, **Schaible R**, **Casper BB**, **Dahlgren JP**, **Ehrlén J**, **García MB**, **Menges ES**, **Quintana-Ascencio PF**, **Caswell H**, **Baudisch A**, **Vaupel JW. 2014**. Diversity of ageing across the tree of life. *Nature* **505**: 169–173.

Lee SJ, **Kenyon C. 2009**. Regulation of the longevity response to temperature by thermosensory neurons in *Caenorhabditis elegans*. *Current Biology* **19**: 715–722.

Lemaître JF, **Gaillard JM. 2013**. Polyandry has no detectable mortality cost in female mammals. *PLoS One* **8**: e66670.

Lemaître JF, **Gaillard JM**, **Lackey LB**, **Clauss M**, **Müller DW. 2013**. Comparing free-ranging and captive populations reveals intra-specific variation in ageing rates in large herbivores. *Experimental Gerontology* **48**: 162–167.

Lemaître JF, **Ronget V**, **Tidière M**, **Allainé D**, **Berger V**, **Cohas A**, **Colchero F**, **Conde DA**, **Garratt M**, **Liker A**, **Marais GAB**, **Scheuerlein A**, **Székely T**, **Gaillard JM. 2020**. Sex differences in adult lifespan and ageing rates of mortality across wild mammals. *Proceedings of the National Academy of Sciences of the United States of America* **117**: 8546–8553.

McDonald JL, **Smith GC**, **McDonald RA**, **Delahay RJ**, **Hodgson D. 2014**. Mortality trajectory analysis reveals the drivers of sex-specific epidemiology in natural wildlife–disease interactions. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20140526.

Nussey DH, **Froy H**, **Lemaître JF**, **Gaillard JM**, **Austad SN. 2013**. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews* **12**: 214–225.

Pastore M. 2018. Overlapping: a R package for estimating overlapping in empirical distributions. *The Journal of Open Source Software* **3**: 1023.

Reinke BA, **Cayuela H**, **Janzen FJ**, **Lemaître JF**, **Gaillard JM**, **Lawing AM**, **Iverson JB**, **Christiansen DG**, **Martínez-Solano I**, **Sánchez-Montes G**, **Gutiérrez-Rodríguez J**, **Rose FL**, **Nelson N**, **Keall S**, **Crivelli AJ**, **Nazirides T**, **Grimm-Seyfarth A**, **Henle K**, **Mori E**, **Guiller G**, **Homan R**, **Olivier A**, **Muths E**, **Hossack BR**, **Bonnet X**, **Pilliod DS**, **Lettink M**, **Whitaker T**, **Schmidt BR**, **Gardner MG**, **Cheylan M**, **Poitevin F**, **Golubović A**, **Tomović L**, **Arsovski D**, **Griffiths RA**, **Arntzen JW**, **Baron JP**, **Le Galliard JF**, **Tully T**, **Luiselli L**, **Capula M**, **Rugiero L**, **McCaffery R**, **Eby LA**, **Briggs-Gonzalez V**, **Mazzotti F**, **Pearson D**, **Lambert BA**, **Green DM**, **Jreidini N**, **Angelini C**, **Pyke G**, **Thirion JM**, **Joly P**, **Léna JP**, **Tucker AD**, **Limpus C**, **Priol P**, **Besnard A**, **Bernard P**, **Stanford K**, **King R**, **Garwood J**, **Bosch J**, **Souza FL**, **Bertoluci J**, **Famelli S**, **Grossenbacher K**, **Lenzi O**, **Matthews K**, **Boitaud S**, **Olson DH**, **Jessop TS**, **Gillespie GR**, **Clobert J**, **Richard M**, **Valenzuela-Sánchez A**, **Fellers GM**, **Kleeman PM**, **Halstead BJ**, **Grant EHC**, **Byrne PG**, **Frétey T**, **Le Garff B**, **Levionnois P**, **Maerz JC**, **Pichenot J**, **Olgun K**, **Üzüm N**, **Avcı A**, **Miaud C**, **Elmberg J**, **Brown GP**, **Shine R**, **Bendik NF**, **O'Donnell L**, **Davis CL**, **Lannoo MJ**, **Stiles RM**, **Cox RM**, **Reedy AM**, **Warner DA**, **Bonnaire E**, **Grayson K**, **Ramos-Targarona R**, **Baskale E**, **Muñoz D**, **Measey J**, **de Villiers FA**, **Selman W**, **Ronget V**, **Bronikowski AM**, **Miller DA. 2022**. Diverse aging rates in ectothermic tetrapods provide insights for the evolution of aging and longevity. *Science* **376**: 1459–1466.

Reznick DN, **Bryant MJ**, **Roff D**, **Ghalambor CK**, **Ghalambor DE. 2004**. Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* **431**: 1095–1099.

Ricklefs RE. 2000. Intrinsic ageing-related mortality in birds. *Journal of Avian Biology* **31**: 103–111.

Ricklefs RE. 2010. Life-history connections to rates of ageing in terrestrial vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 10314–10319.

Siler W. 1979. A competing-risk model for animal mortality. *Ecology* **70**: 750–757.

Stearns SC, **Ackermann M**, **Doebeli M**, **Kaiser M. 2000**. Experimental evolution of ageing, growth, and reproduction in fruitflies. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 3309–3313.

Stubben C, **Milligan B. 2007**. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* **22**: 1–23.

Tidière M, **Gaillard JM**, **Berger V**, **Müller DW**, **Lackey LB**, **Gimenez O**, **Clauss M**, **Lemaître JF. 2016**. Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. *Scientific Reports* **6**: 36361.

Valenzano DR, **Terzibasi E**, **Cattaneo A**, **Domenici L**, **Cellerino A. 2006**. Temperature affects longevity and age-related locomotor and cognitive decay in the short-lived fish *Nothobranchius furzeri*. *Ageing Cell* **5**: 275–278.

Valenzuela-Sánchez A, **Azat C**, **Cunningham AA**, **Delgado S**, **Bacigalupe LD**, **Beltrand J**, **Serrano JM**, **Sentenac H**, **Haddow N**, **Toledo V**, **Schmidt BR**, **Cayuela H. 2022**. Interpopulation differences in male reproductive effort drive the population dynamics of a host exposed to an emerging fungal pathogen. *Journal of Animal Ecology* **91**: 308–319.

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

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

Valenzuela-Sánchez A, **Schmidt BR**, **Uribe-Rivera DE**, **Costas F**, **Cunningham AA**, **Soto-Azat C. 2017**. Cryptic disease-induced mortality may cause host extinction in an apparently stable host–parasite system. *Proceedings of the Royal Society B: Biological Sciences* **284**: 20171176.

Vaupel JW. 2010. Biodemography of human ageing. *Nature* **464**: 536–542.

Williams GC. 1957. Pleiotropy, natural-selection, and the evolution of senescence. *Evolution* **11**: 398–411.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

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

Figure S1. Relationship between ageing rate and annual adult survival probability (extracted from the study by Valenzuela-Sánchez *et al.*, 2022) in four populations of the southern Darwin's frog (*Rhinoderma darwinii*) in southern Chile.