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RESEARCH ARTICLE

Polyphenism predicts actuarial senescence and lifespan in tiger salamanders

Hugo Cayuela[1] | **Alycia C. R. Lackey**[2,3] | **Victor Ronget**[4] | **Benjamin Monod-Broca**[5] | **Howard H. Whiteman**[3,6]

[1]Laboratoire de Biométrie et Biologie Evolutive, Université Lyon 1, CNRS, UMR 5558, Villeurbanne, France; [2]Department of Biology, University of Louisville, Louisville, Kentucky, USA; [3]Department of Biological Sciences and Watershed Studies Institute, Murray State University, Murray, Kentucky, USA; [4]Institute of Organismic and Molecular Evolution, Johannes Gutenberg University, Mainz, Germany; [5]Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR5023 LEHNA, Villeurbanne, France and [6]Rocky Mountain Biological Laboratory, Gothic, Colorado, USA

Correspondence
Hugo Cayuela
Email: hugo.cayuela51@gmail.com

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Abstract

1. Actuarial senescence (called 'senescence' hereafter) often shows broad variation at the intraspecific level. Phenotypic plasticity likely plays a central role in among-individual heterogeneity in senescence rate (i.e. the rate of increase in mortality with age), although our knowledge on this subject is still very fragmentary. Polyphenism—the unique sub-type of phenotypic plasticity where several discrete phenotypes are produced by the same genotype—may provide excellent study systems to investigate if and how plasticity affects the rate of senescence in nature.
2. In this study, we investigated whether facultative paedomorphosis influences the rate of senescence in a salamander, *Ambystoma mavortium nebulosum*. Facultative paedomorphosis, a unique form of polyphenism found in dozens of urodele species worldwide, leads to the production of two discrete, environmentally induced phenotypes: metamorphic and paedomorphic individuals. We leveraged an extensive set of capture–recapture data (8948 individuals, 24 years of monitoring) that were analysed using multistate capture–recapture models and Bayesian age-dependent survival models.
3. Multistate models revealed that paedomorphosis was the most common developmental pathway used by salamanders in our study system. Bayesian age-dependent survival models then showed that paedomorphs have accelerated senescence in both sexes and shorter adult lifespan (in females only) compared to metamorphs. In paedomorphs, senescence rate and adult lifespan also varied among ponds and individuals. Females with good body condition and high lifetime reproductive success had slower senescence and longer lifespan. Late-breeding females also lived longer but showed a senescence rate similar to that of early-breeding females. Moreover, males with good condition had longer lifespan than males with poor body condition, although they had similar senescence rates. In

addition, late-breeding males lived longer but, unexpectedly, had higher senescence than early-breeding males.

4. Overall, our work provides one of the few empirical cases suggesting that environmentally cued polyphenism could affect the senescence of a vertebrate in nature, thus providing insights on the ecological and evolutionary consequences of developmental plasticity on ageing.

KEYWORDS
ageing, amphibian, paedomorphosis, phenotypic plasticity, polyphenism, survival

1 | INTRODUCTION

Identifying the factors shaping the astonishing diversity of mortality patterns observed in the wild is a major challenge for ecologists. Over the past two decades, studies have shown that the rate of actuarial senescence—that is the increase in mortality with age called 'senescence' thereafter—is highly variable at the interspecific level (Jones et al., 2014; Lemaître et al., 2020; Reinke et al., 2022). Among-species variation in senescence is partially explained by phylogeny (Lemaître et al., 2020), body size (Ricklefs, 2010) and the pace-of-life (Jones et al., 2008). Moreover, senescence strength varies broadly among populations of the same species. In some ectotherms, the amplitude of among-population changes of senescence rate—that is the rate of exponential increase in mortality with age—is almost as large as the variation range of this parameter observed across the whole mammalian phylogenetic group (Cayuela et al., 2021). Environmental factors such as temperature (Cayuela et al., 2021), anthropogenic disturbances (Cayuela et al., 2020) and predation (Reznick et al., 2004) widely explain population-specific variation in senescence rate in ectothermic vertebrates.

To date, the heterogeneity of senescence among individuals of the same population has been much less studied (e.g. Grunst et al., 2018; Rodríguez-Muñoz et al., 2019; Tully et al., 2020), except for the role of sex (Cayuela, Lemaître, et al., 2022; Lemaître et al., 2020; Marais et al., 2018). As predicted by the evolutionary theories of ageing (Hamilton, 1966; Medawar, 1952; Williams, 1957), among-individual variation in senescence is partially controlled by genetic factors (Austad & Hoffman, 2018; Flatt & Partridge, 2018) and studies have demonstrated the genetic inheritance of senescence patterns (Promislow et al., 1996; Snoke & Promislow, 2003). Nonetheless, phenotypic plasticity could also play an important role in the among-individual heterogeneity of senescence, although our knowledge on this subject is still very fragmentary. This knowledge gap is largely due to the difficulty of separating the relative effects of genetic background and those of phenotypic plasticity on the rate of senescence. In organisms such as cladocerans—in which it is possible to produce clonal cohorts—experimental studies have shown that perceived exposure to the threat of predation accelerates senescence (Pietrzak et al., 2015), likely due to an increase in early-life investment in reproduction performed at the expense of somatic maintenance. However, the influence of plasticity on senescence patterns is still unknown in most organisms, especially under natural conditions.

Polyphenism—the unique sub-type of phenotypic plasticity where several discrete phenotypes are produced by the same genotype (Mayr, 1963; Simpson et al., 2011; Yang & Pospisilik, 2019)—could provide excellent study cases to investigate if and how plasticity affects senescence rate (Flatt et al., 2013). Polyphenism may entail broad plastic variation in lifespan (Giraldo & Traniello, 2014; Guo et al., 2020; Heinze & Giehr, 2021). In eusocial Hymenoptera, for instance, breeding individuals of social ants and termites can live up to 30 years, whereas workers frequently have 10-fold shorter lifespans (Hölldobler & Wilson, 1990; Keller, 1998; Kramer & Schaible, 2013). Moreover, studies on various polyphenic invertebrates under laboratory conditions (e.g. ants, Kramer et al., 2016; flat worms, Tissenbaum, 2015) strongly suggest that developmental plasticity has carry-over effects on late-life survival performance, which could thus affect the senescence rate.

Urodeles (i.e. newts and salamanders) offer excellent insights to fill our knowledge gaps on the influence of polyphenism—and phenotypic plasticity more broadly—on senescence since (1) they have repeatedly and independently evolved polyphenism over their 200 million years of evolution (Bonett et al., 2022; Elinson & Del Pino, 2012); and (2) they are increasingly recognized as new model organisms for ecological and evolutionary studies of senescence (Reinke et al., 2022; Yun, 2021). Facultative paedomorphosis, a unique form of polyphenism found in dozens of urodele species worldwide (Denoël et al., 2005; Whiteman, 1994), leads to the production of two discrete, environmentally induced phenotypes: metamorphic and paedomorphic individuals. Metamorphs have a biphasic life cycle, with aquatic larval development followed by metamorphosis into a terrestrial adult. Paedomorphs show developmental heterochrony involving the retention of larval traits in adults under the control of neuroendocrine mechanisms (Boorse & Denver, 2002) and in response to environmental factors (e.g. water level of ponds, McMenamin & Hadly, 2010; Semlitsch, 1987; conspecific density, Semlitsch, 1987; Whiteman et al., 2012). Paedomorphic phenotypes may be the product of different ontogenetic processes, with progenesis as the most common. Progenesis consists of an acceleration of gonad development (Bonett et al., 2022; Denoël et al., 2005), which becomes functional at significantly younger ages than the usual onset of maturity in metamorphs, possibly at the cost of reduced adult survival (Lackey et al., 2019).

In this study, we quantified how facultative paedomorphosis (progenesis) is associated with senescence rate and adult lifespan in the Arizona Tiger Salamander (*Ambystoma mavortium nebulosum*). We used a massive set of capture–recapture data (8948 individuals, 24 years of monitoring, 1990–2013) collected from a metapopulation of *A. m. nebulosum* located in western Colorado. We first modelled the developmental pathways of salamanders using multistate capture–recapture models that especially quantify transitions (i.e. paedomorphosis and metamorphosis) between larval and adult stages. We estimated annual rates of paedomorphosis and metamorphosis, along with recapture and stage-specific survival probabilities. This analysis provided basic information on the life cycle of the studied salamanders and the properties of our capture–recapture data (e.g. pond-specific and morph-specific recapture probabilities). Then, taking advantage of these first results, we performed Bayesian age-specific mortality analyses focused on the adult stage only to examine associations between morphs (paedomorphs vs. metamorphs), senescence rate and adult lifespan. We tested the hypothesis that paedomorphs of both sexes show a higher senescence rate and shorter lifespan than metamorphs since paedomorphs are expected to have lower body condition (Lackey et al., 2019), favour early-life investment in reproduction at the expense of survival (Bonett et al., 2022), and may experience stressful environmental conditions in ponds during the winter (Whiteman et al., 2012). Lastly, we examined whether senescence rates and lifespan were associated with among-individual variation in body condition and reproductive traits (age at first reproduction, lifetime egg production) in paedomorphs. We tested the hypotheses that paedomorphs with higher lifetime-averaged body condition would have slower senescence and longer lifespan; that paedomorphs with early first reproduction would experience faster senescence and shorter lifespan due to a trade-off between early reproductive performance and adult survival, especially late in life (Kirkwood & Rose, 1991; Williams, 1957); and that high lifetime egg production, due to high body condition (Lackey et al., 2019), is associated with low senescence and long lifespan in females.

2 | MATERIALS AND METHODS

2.1 | Study organism, study area and data collection

Tiger salamanders are found throughout North America (Petranka, 1998). The Arizona Tiger Salamander (*A. m. nebulosum*, formerly *Ambystoma tigrinum nebulosum*; Irschick & Shaffer, 1997; Shaffer & McKnight, 1996) is often facultatively paedomorphic (Figure 1; Collins, 1981; Whiteman et al., 2012) and occurs in a variety of aquatic habitats from western Colorado and Utah to south-central New Mexico and central Arizona.

Our study site is located in western Colorado at the Mexican Cut Nature Preserve (3640 m a.s.l.; 39.027 N, 107.067 W). At this subalpine site, salamanders breed, develop and forage in an array of 24 ponds, with strongly limited dispersal in or out of this watershed as these ponds are isolated from other ponds by at least 1 km (Whiteman et al., 1996; Wissinger et al., 2003). Salamanders in this population are facultatively paedomorphic. Larvae can metamorphose and disperse into terrestrial environments as metamorphs or mature into paedomorphs that retain their larval aquatic characteristics as sexually mature adults (Denoël et al., 2005; Whiteman, 1994). Four large permanent ponds (L01, L03, L05 and L12) provide suitable habitat for paedomorphs (Lackey et al., 2019). Most other ponds are temporary, which occasionally produce metamorphs.

In this study, we analysed data collected between 1990 and 2013 from salamanders with partially known cohorts. Larval salamander age classes were assigned based on distinct size distributions and the development of gills, limbs and toes (Whiteman et al., 2012). Larval development may last from 1 to 5 years. The survey design is described in detail in Lackey et al. (2019). In brief, larval and adult salamanders were individually marked with passive integrated transponder (PIT) tags or toe clips. Each year during the ice-free summer months (usually June–September; Wissinger & Whiteman, 1992; Whiteman & Wissinger, 2005), larval, paedomorphic and metamorphic salamanders were captured with dip nets. We recorded body length and mass, maturity, sex, evidence of breeding condition, capture date and pond. Both breeding and non-breeding metamorphs return to the ponds each summer to mate and/or forage (Wissinger & Whiteman, 1992; Whiteman, 1994; Whiteman et al., 1996). Every year, captures are conducted 5–6 days a week during the summer, with relatively equal sampling effort in each pond based on volume. Given previous mark–recapture estimates, over 95% of adult salamanders in this population have been recorded in these surveys (Whiteman, 1997). Summary statistics about the number of individuals captured annually and their stage, sex and morph are provided in Tables S1 and S2. The research was approved by both the MSU IACUC and the RMBL Animal Welfare Committee. The Colorado Parks and Wildlife collecting permit number is HP0339.

2.2 | Modelling developmental pathways using multistate capture–recapture models

We modelled the developmental pathways of salamanders using multistate capture–recapture models (Lebreton et al., 2009). We estimated annual demographic parameters: larval survival, adult survival as well as paedomorphosis and metamorphosis probabilities. The model is based on 15 states (Figure S1) describing the life stage (larvae vs. adult), the adult morph (paedomorph vs. metamorph) and sex (male vs. female) as well as the pond occupied by larvae and paedomorphs (L01, L03, L05 and L12). In metamorphs, we did not consider pond-specific parameters since individuals may use multiple ponds for foraging or mating during the summer and spend the rest of the year on land, contrary to larvae and

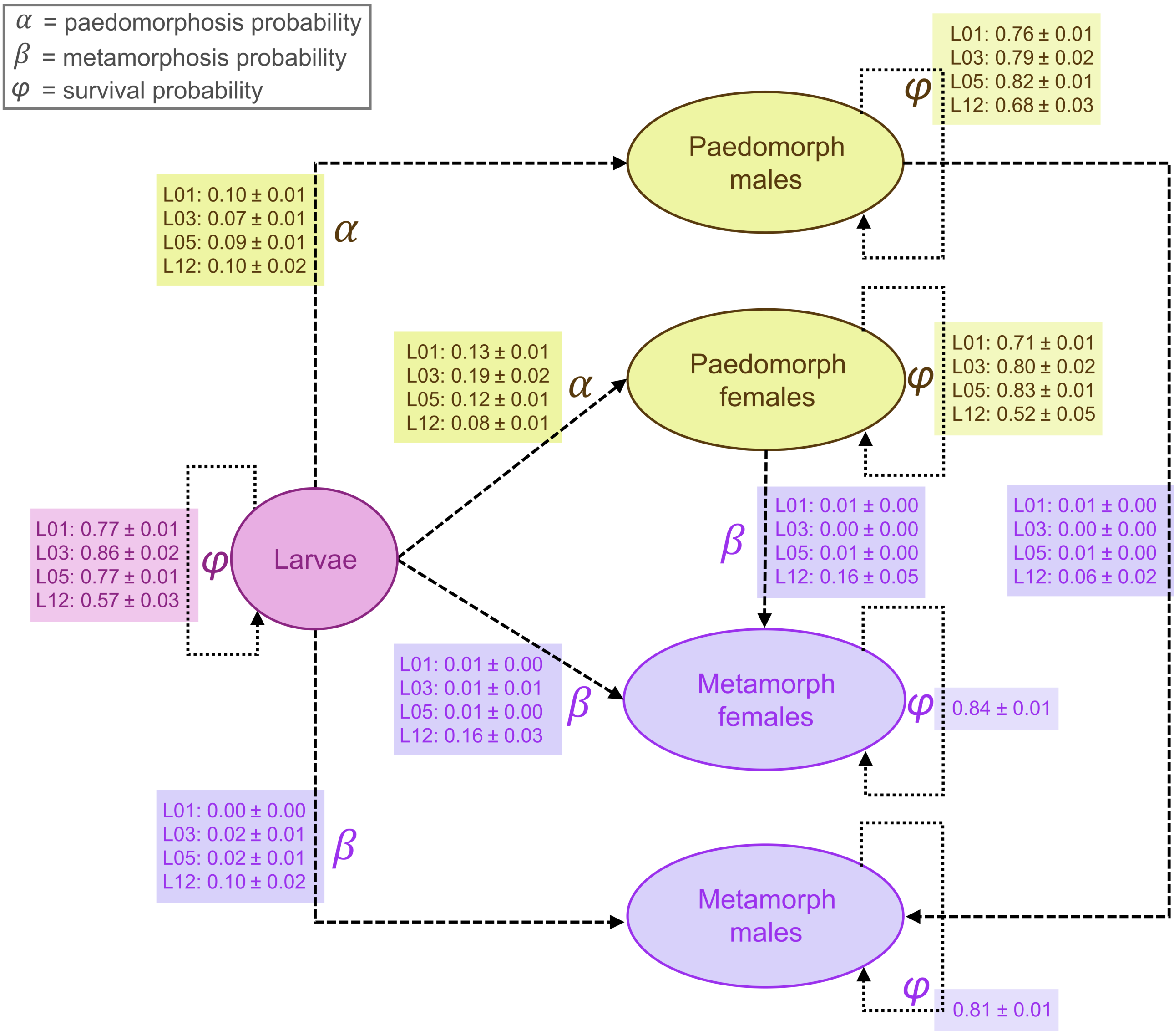

FIGURE 1 Life cycle and associated demographic rates (mean and standard error) in a polyphenic salamander, *Ambystoma mavortium nebulosum*. Inferences were produced from multistate capture–recapture models (the 95% confidence intervals are provided in Table S4). Larvae and paedomorphs occupy four ponds (L01, L03, L05 and L12). Metamorphs can move among ponds; their demographic rates are therefore averaged across ponds. Transition probabilities between larvae and morphs (α and β) are shown with broken lines. Survival probabilities (φ) are shown in dashed lines.

paedomorphs that are fully aquatic and remain in the same pond throughout the year. The model, implemented in the program E-SURGE (Choquet et al., 2009), and related analyses are described in Supplementary Material.

2.3 | Estimating morph-, sex- and pond-specific senescence rate and adult lifespan

Senescence rate and adult lifespan were estimated using Bayesian survival trajectory analyses implemented in the R package BaSTA (Colchero et al., 2012; Colchero & Clark, 2012). We used adult observations only to focus on the mortality that occurs after the age of first reproduction since senescence is expected to begin at this stage (Hamilton, 1966; Williams, 1957). In this subset, we retained 5359 individuals (for more details, see Table S2) with 46% of known birth year (53% and 29% in metamorphs and paedomorphs, respectively).

Simulations by Colchero and Clark (2012) showed that BaSTA models are highly efficient to investigate age-dependent mortality even when a substantial proportion of dates of birth and death are unknown and the recapture probability is less than 1. BaSTA, therefore, allowed us to account for imperfect detection, left-truncated (i.e. unknown birth date) and right-censored (i.e. unknown death date) capture–recapture data in our analysis. We used non-informative priors using the BaSTA default values of the initial parameters. Four MCMC chains were run with 50,000 iterations and a burn-in of 5000. Chains were thinned by a factor of 50. These

MCMC settings result in posteriors of $n=900$. Model convergence was evaluated using the diagnostic analyses implemented in BaSTA, which calculate the potential scale reduction for each parameter to assess convergence (Gelman et al., 2013).

We analysed the morphs, sexes and ponds separately to identify the models best describing mortality patterns for each group of individuals. This approach also allowed us to consider variation in recapture probability between morphs, sexes and ponds; our multistate model showed that recapture probability varies among these individual groups (Table S5). Since individuals were monitored from the larval stage, their developmental strategy was known with certainty. We considered as metamorphs and paedomorphs the individuals having kept the same morph throughout their adult lifetime. By contrast, we excluded individuals with a mixed developmental strategy (i.e. paedomorphs that have metamorphosed) from the analyses because of their rarity in our dataset; as shown by our multistate model, the annual probability that a paedomorph metamorphoses is generally less than or equal to 0.01 in the ponds hosting the most salamanders (Figure 1). Furthermore, like in the multistate model, we did not examine the pond-specific senescence rate in metamorphs since individuals may disperse among ponds, use them for reproduction or foraging during a short period and spend the rest of the year on land. Moreover, as the multistate model revealed broad annual variation in recapture probability (Table S5), we specified year-dependent recapture probabilities (Table S6) using the command ‘recaptTrans’.

For each group of individuals (morph, sex and pond), we considered four different models (Gompertz, Weibull, logistic and exponential) with three distinct functions (simple, Makeham and bathtub), except for the exponential model. The deviance information criterion (DIC) was used to rank the models. The Gompertz model (simple or bathtub functions) was the most appropriate model for all morphs and ponds in both sexes (Tables S6 and S7), except for metamorphic males, for which the Weibull model was the best-supported model. Nevertheless, the 95% CRI of mortality curves drawn from Gompertz and Weibull models broadly overlapped (Figure S2); hence, we kept the Gompertz model (simple) for metamorphic males to facilitate the comparison of model parameters among sexes, morphs and ponds. Morph-, sex- and pond-specific differences in senescence rates were evaluated by examining the distribution of posterior probabilities (mean and 95% credible intervals; noted thereafter 95% CRIs) of b_1 parameters. Furthermore, we also calculated Kullback–Leibler divergence between the demographic parameters of metamorphs and paedomorphs (Table S18).

Following the approach and terminology used in previous studies (Cayuela, Monod-Broca, et al., 2022; Lemaître et al., 2020; Reinke et al., 2022), we estimated morph-, sex- and pond-specific adult lifespan using three metrics: ‘lifespan 50%’ and ‘lifespan 80%’, defined as the age at which 50% and 80% of the individuals alive at the onset of adulthood are dead, respectively; and ‘life expectancy’ from the onset of adulthood, defined as the average adult age at death. Lifespan metrics were calculated by numerically solving the lx (survivorship) equation for the best-supported survival model, which was either simple Gompertz (Equation 1) or bathtub Gompertz (Equation 2).

$$l(x) = e^{\frac{b0}{b1}(1-e^{b1x})} \tag{1}$$

$$l(x) = e^{\frac{a0}{a1}(-e^{a1x}-1)-cx+\frac{b0}{b1}(1-e^{b1x})} \tag{2}$$

Adult life expectancy was computed numerically using the following formula $\int_0^{+\infty} lxdx$. All measurements were calculated using the posterior distributions of parameters from the best-supported survival model, which allowed us to get the posterior distribution of each lifespan metric.

2.4 | Assessing associations between senescence rates, adult lifespan and reproductive traits in paedomorphs

We investigated how body condition and reproductive traits influenced senescence rate and lifespan in paedomorphs; metamorphs were excluded due to the small sample size. For these analyses, we used the Gompertz model (simple), which on average best described the mortality curves of both sexes (Tables S6 and S7). We used the dataset of individual traits published by Lackey et al. (2019) and considered three variables: average lifetime body condition index (available in both sexes), age at first reproduction (in both sexes) and predicted lifetime egg production (in females only). We calculated the average lifetime body condition index by dividing snout–vent length by mass and averaging across all adult captures. Age at first reproduction was determined as the first adult capture in breeding condition (swollen cloaca). For each female, predicted lifetime egg production was calculated using the regression-predicted number of eggs a female would produce given a female's body condition index multiplied by the number of years a female was captured in breeding condition. Additional details on these measures are provided in Lackey et al. (2019).

Because age at first reproduction (315 males, 211 females) and lifetime reproductive success (205 females) are known for a smaller number of individuals than average lifetime body condition (407 males, 577 females), the three variables were tested separately. In addition, because body condition and age at first reproduction differ between sexes (Lackey et al., 2019) and lifetime egg production is calculated for females only, we built models for each sex separately. Moreover, to quantify their effect on senescence rate and lifespan, the three variables were discretized using the median as a threshold to define two categories (e.g. low vs. high lifetime egg production). Although BaSTA allows including continuous variables, their effects are applied to the mortality rate (or survival probability, depending on the optional structure used) and not to the different model parameters (e.g. the senescence rate b_1). Therefore, we used categorical variables to examine the effect of average lifetime body condition, age at first reproduction and lifetime egg production on senescence rate specifically.

3 | RESULTS

3.1 | Descriptive statistics of capture–recapture monitoring

We captured 8948 individuals during the 24 years of monitoring. The total number of individuals captured in ponds ranged from 388 (L03) to 3316 (L01) at the larval stage, from 290 (L03) to 2938 (L01) in paedomorphic males, from 166 (L12) to 2712 (L01) in paedomorphic females and were 1453 and 1851 for metamorphic males and females, respectively. Annual statistics of captures are presented in Table S1.

3.2 | Developmental pathways and associated vital rates

The full model was the best supported by the data; see the model selection procedure in Table S3 and the complete set of model estimates in Tables S4 and S5. Survival differed among life stages (larvae vs. adults), morphs (paedomorphs vs. metamorphs), sexes and ponds (Figure 1). Mean adult survival was on average higher in metamorphs than in paedomorphs in both sexes (Figure 1). We also found that pond was an important driver of the annual survival of larvae and paedomorphs (Figure 1). Survival of larvae and paedomorphs of both sexes was consistently lower in pond L12 than in the other ponds (Figure 1).

The model revealed that paedomorphosis was the most common developmental pathway used by salamanders in three of the four ponds studied (L01, L03 and L05). In females, the yearly probability that larvae turned into a paedomorph was between 12 (pond L05) and 19 times (L03) higher than the probability that they would metamorphose (Figure 1); a similar pattern was found in males. Furthermore, the yearly probability that a paedomorph turned into metamorph was very low (≤0.01) in ponds L01, L03 and L05, regardless of sex. Nevertheless, our analyses showed that the pond of origin strongly affects individual developmental strategies. In pond L12, the lower survival at both larval and adult stages was associated with contrasted shifts in paedomorphosis and metamorphosis probabilities compared to the other ponds. The probability that larvae turned into a metamorphic female was two times higher than the probability that it became paedomorphic female (Figure 1). In males, the transition probability was similar for both morphs. Furthermore, the yearly probability that a paedomorph turned into metamorph was on average 16 times (0.16) and 6 times (0.06) higher in pond L12 than in other ponds for females and males, respectively.

Recapture probability varied among life stages, morphs, sexes and ponds. It was the lowest in larvae (from 0.03 in 1995 to 0.42 in 2010) and lower in metamorphs (e.g. males: from 0.14 to 0.61) than in paedomorphs, in particular in pond L12 (e.g. males: from 0.51 to 0.92; Table S5). Recapture probability also differed between sexes in a pond-specific way (Table S5).

3.3 | Morph-, sex- and pond-specific differences in senescence rates and adult lifespan

Our analyses showed that mortality rate increased with age in both morphs and sexes (Figures 2 and 3 and Figure S3), indicating that salamanders experienced actuarial senescence. The complete model outputs produced for each sex, morph and pond are presented in Tables S8–S17. Senescence rates varied from 0.06 to 0.30 in males (Figure 3) and from 0.12 to 0.30 in females (Figure 2), depending on morphs and ponds. Senescence rates of paedomorphs were consistently higher than in metamorphs (Figures 2 and 3); the 95% CRIs of paedomorph senescence rates did not overlap those of metamorphs in both sexes, except for pond L05 in females. The amplitude of morph-specific differences in senescence depended on the pond occupied by paedomorphs: the 95% CRIs of paedomorph senescence rates broadly overlapped for ponds L01, L03 and L12, while they did not for pond L05, where the senescence rate was the lowest among paedomorphs. The senescence of paedomorphic males was five times higher in ponds L12 ($b_1=0.30$), L03 ($b_1=0.29$) and L01 ($b_1=0.29$), and three times higher in pond L05 ($b_1=0.18$) than in metamorphic males ($b_1=0.06$). Although the differences between morphs were less marked, a similar pattern was found in females: the senescence rate of paedomorphs was two times higher in ponds L03 ($b_1=0.30$), L12 ($b_1=0.29$) and L01 ($b_1=0.27$), and 1.5 times higher in pond L05 ($b_1=0.18$) than in metamorphic females ($b_1=0.12$).

In females, the increase in senescence was associated with a substantial decrease in adult lifespan and life expectancy (Figure 2a,b). The lifespan 50%, 80% and life expectancy were shorter in paedomorphs (median across ponds: 9.87, 13.81 and 9.72 years, respectively) than in metamorphs (12.07, 17.97 and 12.12 years, respectively). This pattern was exacerbated in pond L12, where paedomorph lifespan 50% and 80% and life expectancy were 5.73, 8.26 and 5.69 years respectively. By contrast, in males, lifespan 50% and 80% and the life expectancy of paedomorphs were higher (median across ponds: 9.79, 12.80 and 9.52 years, respectively) than that of metamorphs (5.14, 10.09 and 6.20 years, respectively; Figure 3b), due to lower mortality in young paedomorphic adults. The basal mortality rate (parameter *b*0 in the Gompertz model) was higher in paedomorphs than in metamorphs (Figure 3a; Tables S13–S17). As in females, lifespan 50% and 80% and the life expectancy of paedomorphic males were consistently the shortest in pond L12 (6.71, 9.46 and 6.53 years, respectively; Figure 3).

3.4 | Associations between senescence rates, adult lifespan and individual traits in paedomorphs

Paedomorph mortality depended on individual condition and reproductive traits, often in sex-specific way. First, our findings revealed that adult lifespan was positively associated with average body condition over paedomorph lifetime (Figure 4). Females and males with good body condition had longer lifespan and life

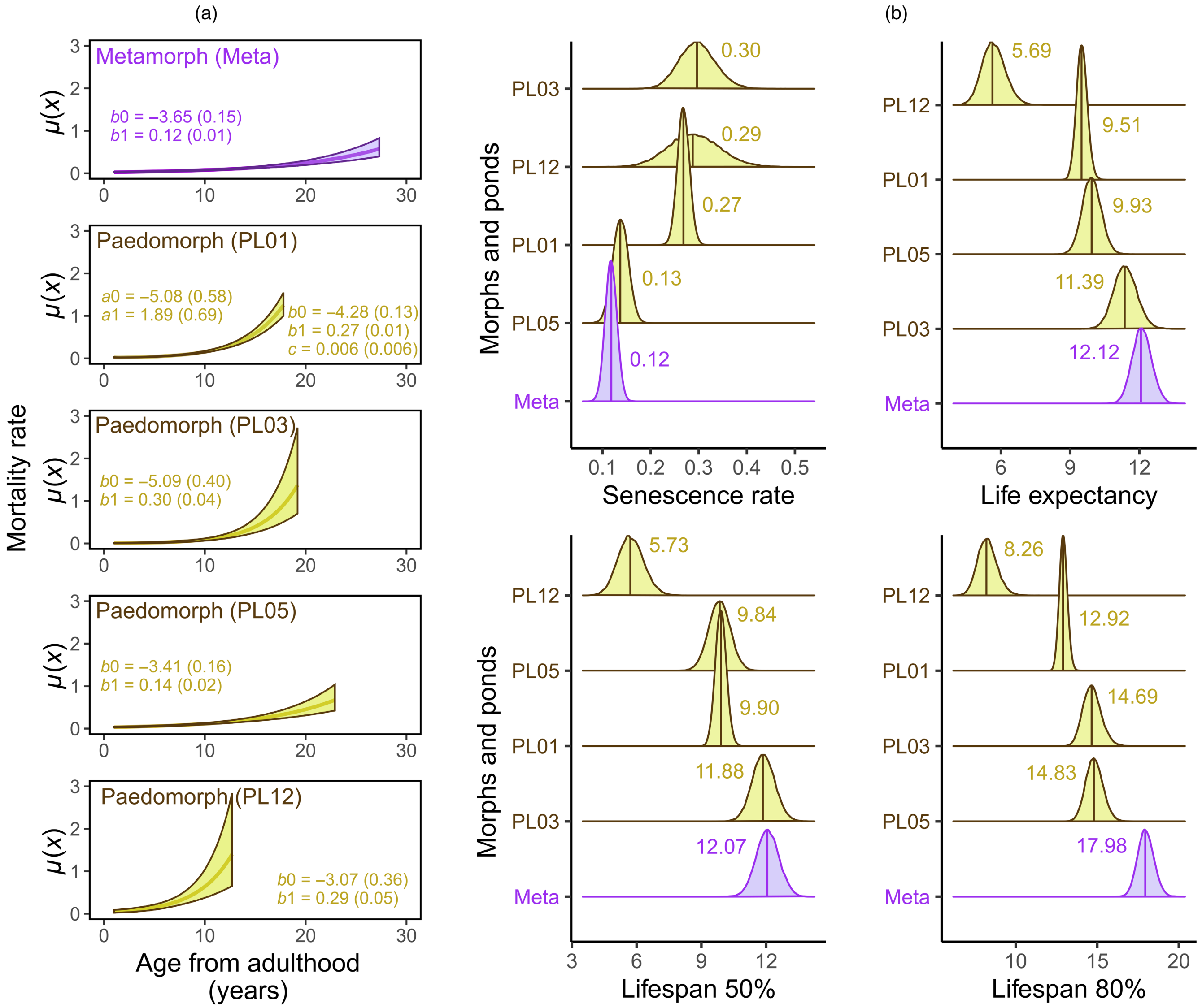

FIGURE 2 Polyphenism, senescence and lifespan in females of *Ambystoma mavortium nebulosum*. On the left (a), we show age-dependent mortality curves (mean and 95% credible intervals) drawn for metamorphs and paedomorphs occupying four ponds (L01, L03, L05 and L12). The age mortality curves are from Gompertz models (with simple or bathtub functions), whose estimates are provided in Tables S8–S12. In 'simple' Gompertz model, the parameters *b*0 and *b*1 correspond to basal mortality and senescence rates, respectively (and their standard error in bracket). The Gompertz model with bathtub function (i.e. Siler model) includes two exponential functions describing young adult mortality (*a*0 and *a*1) and late-life mortality (*b*0 and *b*1) and a parameter for constant mortality (*c*). On the right (b), we show posterior distributions of sex-specific senescence rate (i.e. *b*1), life expectancy and lifespan (50% and 80%) of paedomorphs and metamorphs. The average value of each parameter is provided alongside the distribution.

expectancy than those with poor condition. Moreover, senescence rate was negatively associated with body condition in females (Figure 4). Females with good condition had slower senescence (b_1 = 0.22) than those with poor condition (b_1 = 0.31). By contrast, senescence rate was similar (around 0.30; Figure 4) in males with good and poor conditions.

Our analyses also showed that adult lifespan and life expectancy were positively associated with age at first reproduction. Late-breeding males and females have longer lifespan and life expectancy than early-breeding individuals (Figure 5). Furthermore, our analyses revealed that senescence rate was positively associated with age at first reproduction in males (Figure 5). Early-breeding males experienced slower senescence (b_1 = 0.24) than late-breeding males (b_1 = 0.35; Figure 5, Table S11). By contrast, senescence rate was similar (around 0.26, Figure 5, Table S12) in late- and early-breeding females.

Lastly, our findings revealed that females with high lifetime egg production—which increases with average body condition (Lackey et al., 2019)—had a longer lifespan (15.10 and 19.02 years for lifespan 50% and 80%, respectively) and life expectancy (14.49 years) than those with low lifetime egg production (10.61, 13.39 and 10.18 years for lifespan 50%, lifespan 80% and life expectancy, respectively). In addition, senescence rate tended to be lower (95% CRIs partially overlapped; Table S23) in females with high lifetime egg production (b_1 = 0.21) than in females with low lifetime egg production (b_1 = 0.30).

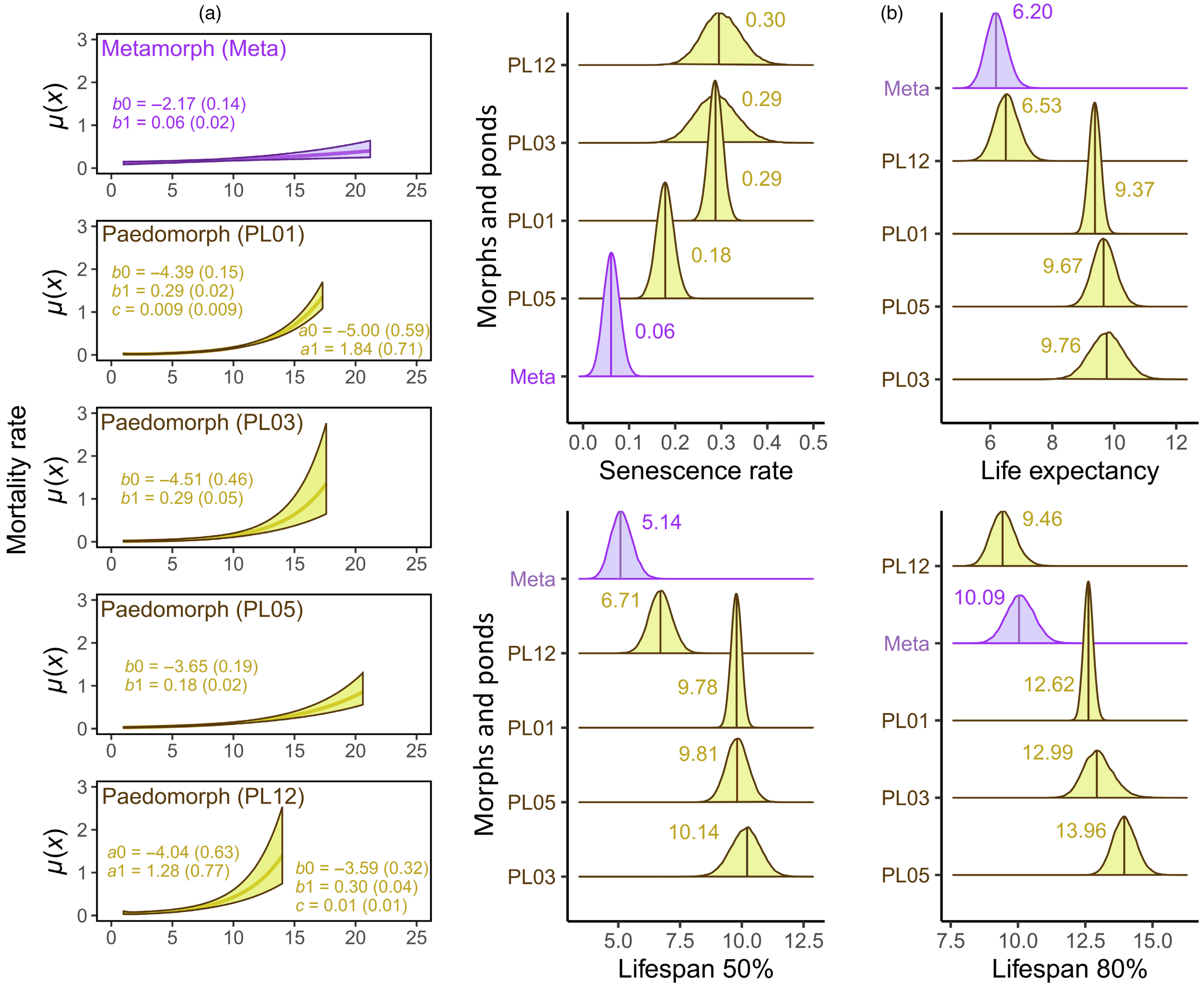

FIGURE 3 Polyphenism, senescence and lifespan in males of *Ambystoma mavortium nebulosum*. On the left (a), we show age-dependent mortality curves (mean and 95% credible intervals) drawn for metamorphs and paedomorphs occupying four ponds (L01, L03, L05 and L12). The age mortality curves are from models, whose estimates are provided in Tables S13–S17. The parameters *b*0 and *b*1 correspond to basal mortality and senescence rates, respectively (and their standard error in bracket) in the Gompertz model. The Gompertz model with bathtub function (i.e. Siler model) includes two exponential functions describing young adult mortality (*a*0 and *a*1) and late-life mortality (*b*0 and *b*1) and a parameter for constant mortality (*c*). On the right (b), we show posterior distributions of sex-specific senescence rate (i.e. *b*1), life expectancy and adult lifespan (50% and 80%) of paedomorphs and metamorphs. Adult lifespan at 50% and 80% correspond to the age (in years) at which 50% and 80% of the individuals alive at the onset of adulthood are dead, respectively. The average value of parameters is provided alongside the distribution.

4 | DISCUSSION

Our study provides one of the few empirical cases highlighting the role of polyphenism and developmental plasticity on the senescence of a vertebrate in nature by leveraging data from 24 years of monitoring. We used an original study system where genetically similar individuals (brothers and sisters from the same clutch) become different morphs and experience completely different life histories and ecologies through their life. We showed that paedomorphic salamanders have accelerated senescence (in both sexes) and shorter adult lifespan (in females only) compared to metamorphs. In paedomorphs, senescence rate and adult lifespan also varied among ponds and were associated with body condition, breeding timing and reproductive output. Overall, our work provides insights into the ecological and evolutionary consequences of environmentally cued polyphenism on senescence in a vertebrate.

4.1 | Plastic ontogenetic pathways

Our multistate capture–recapture models provided a fine-grained modelling of the demography of a Urodele population with facultative paedomorphosis. We have shown that paedomorphosis is the most commonly used ontogenetic pathway: in ponds L01, L03 and L05, the annual rate of transformation of larvae into paedomorphs

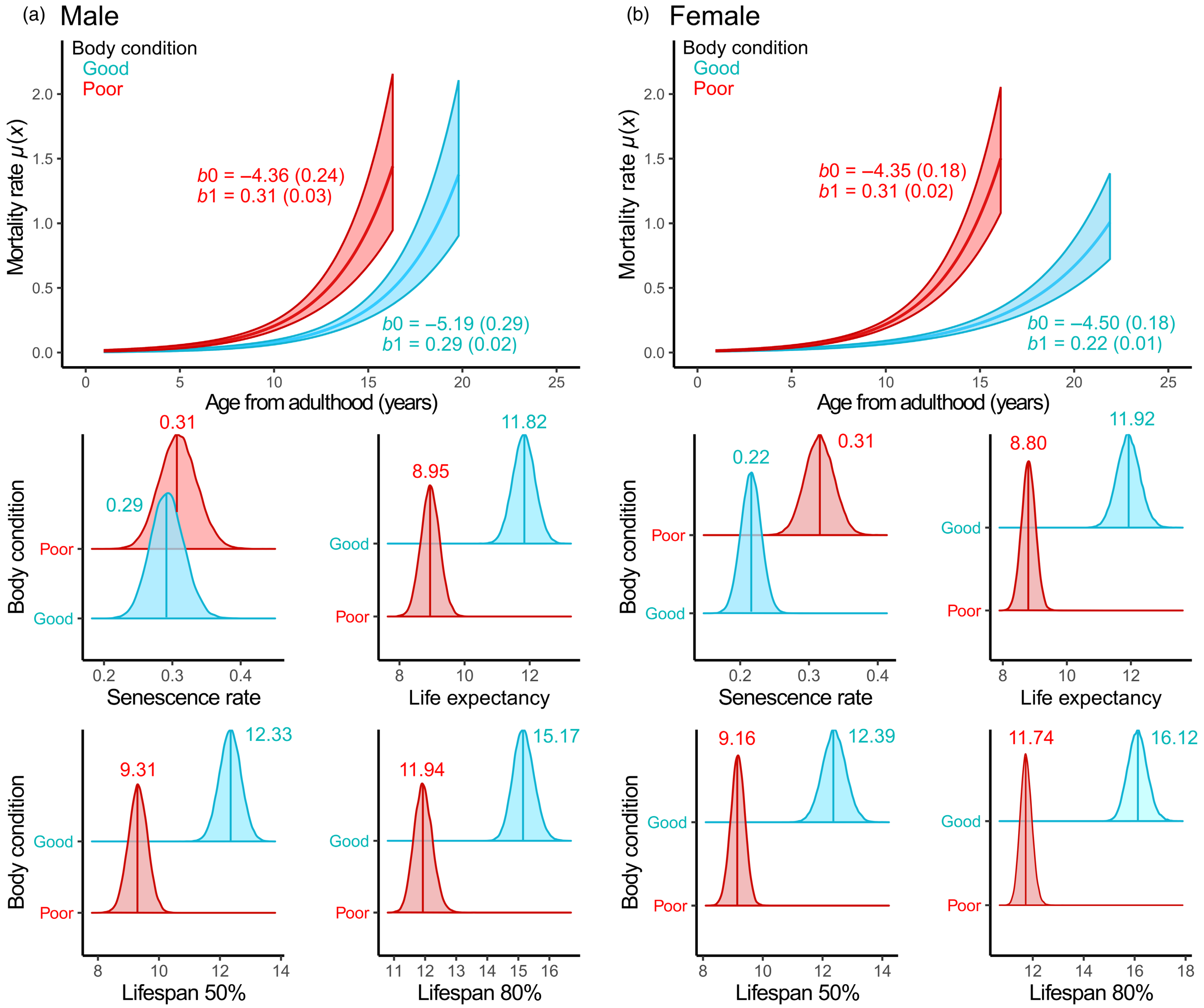

FIGURE 4 Senescence rate, lifespan and average body condition in paedomorphic males (a) and females (b) of *Ambystoma mavortium nebulosum*. We show age-dependent mortality curves (mean and 95% credible intervals) drawn for individuals with poor and good body condition, using the median of body condition (males: 0.22, females: 0.23) as a threshold to delineate the two classes. The age mortality curves are from Gompertz models, whose estimates are provided in Tables S21 and S22. The parameters *b*0 and *b*1 correspond to basal mortality and senescence rates, respectively (and their standard error in bracket). Moreover, we show the posterior distribution of sex-specific senescence rates (parameter *b*1), adult lifespan (50% and 80%) and life expectancy calculated for individuals with poor and good body conditions. Adult lifespan at 50% and 80% correspond to the age (in years) at which 50% and 80% of the individuals alive at the onset of adulthood are dead, respectively. The average value of parameters is provided alongside the distribution.

was seven to 19 times higher (both sexes combined) than the rate of transformation into metamorphs. Moreover, in these three ponds, the change of morph after sexual maturity seems to be relatively rare. The annual rates of paedomorph transformation into metamorphs were equal to or less than 1%. In this population of *A. m. nebulosum*, paedomorphosis often arises as a default ('best of a bad lot') strategy when the growing conditions are so poor that most larvae cannot reach the minimum critical size for metamorphosis (Whiteman, 1994; Whiteman et al., 2012). Larvae that do reach the critical size threshold metamorphose into terrestrial adults, while slower-growing larvae can achieve more fitness by maturing into reproductive paedomorphic adults than by delaying development or attempting metamorphosis.

The aquatic environment seems to play an important role in the selection of the ontogenetic pathways taken by salamanders. In pond L12, the rate of transformation of larvae into metamorphs is five times higher in males and 16 times higher in females compared to other ponds. This particularly high metamorphosis rate is likely related to the rapid growth and large body size of the larvae in this pond (Whiteman et al., 2012). Such growth advantage could result from low larval density caused by high winter mortality (26% reduction in larval survival in pond L12 compared to the other ponds), potentially induced by a lack of dissolved oxygen (Whiteman, unpublished data). At the same time, the annual rate of paedomorph transformation into metamorphs in pond L12 is six times higher in males and 16 times higher in females

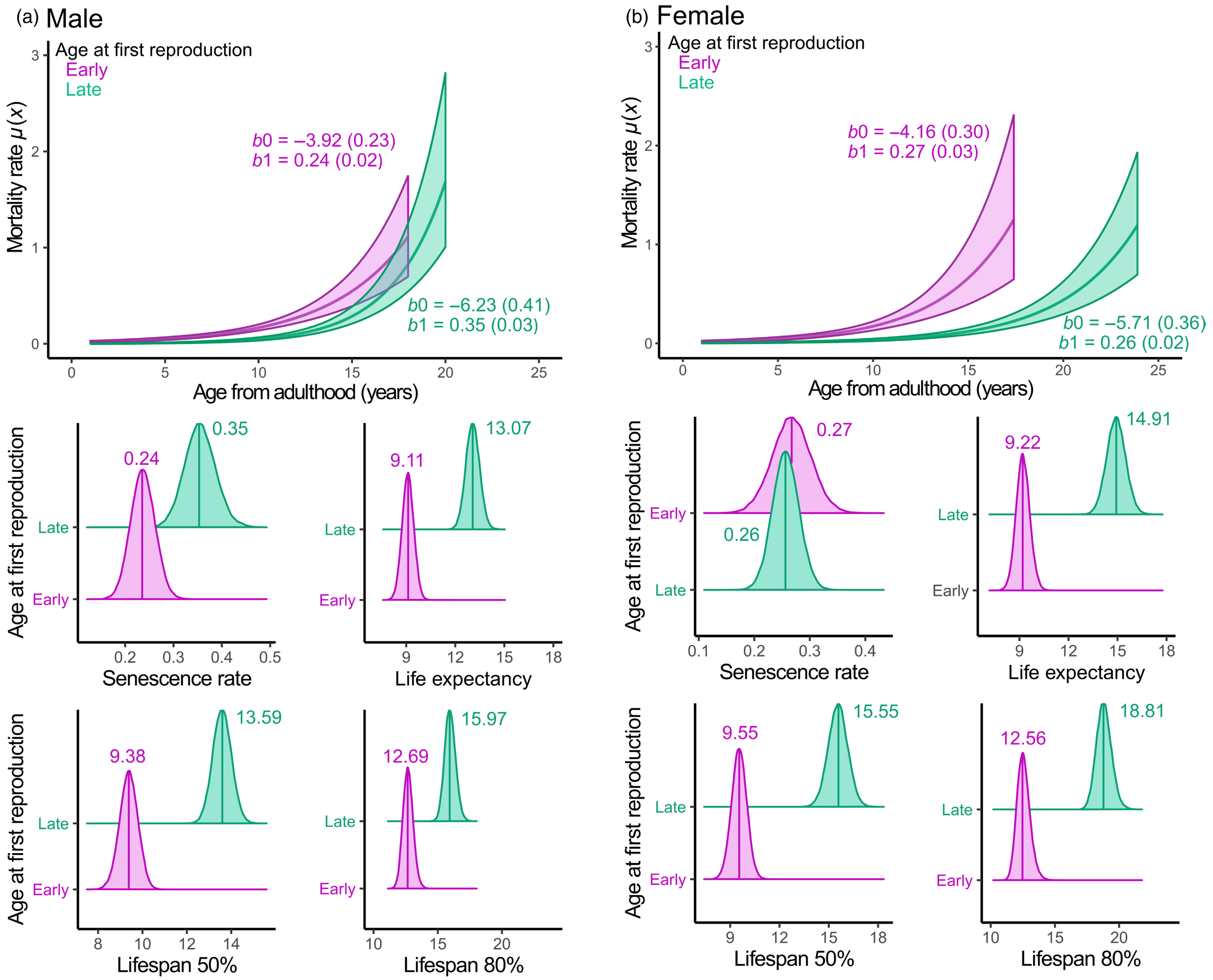

FIGURE 5 Senescence rate, lifespan and age at first reproduction in paedomorphic males (a) and females (b) of *Ambystoma mavortium nebulosum*. We show age-dependent mortality curves (mean and 95% credible intervals) drawn for early-breeding and late-breeding individuals, using the median of age at first reproduction (males: 7 years, females: 9 years) as a threshold to delineate the two classes. The age mortality curves are from Gompertz models, whose estimates are provided in Tables S19 and S20. The parameters *b*0 and *b*1 correspond to basal mortality and senescence rates, respectively (and their standard error in bracket). Furthermore, we show the posterior distribution of sex-specific senescence rates (parameter *b*1), adult lifespan (50% and 80%) and life expectancy calculated for early-breeding and late-breeding individuals. Adult lifespan at 50% and 80% correspond to the age (in years) at which 50% and 80% of the individuals alive at the onset of adulthood are dead, respectively. The average value of parameters is provided alongside the distribution.

than that observed in the other ponds. These relatively high rates of annual morph change (6% in males, 16% in females) could result from an adaptive strategy to reduce the risk of winter mortality, with paedomorph survival dropping by 35% and 13% in females and males, respectively, compared to other ponds.

4.2 | Associations between facultative paedomorphosis, senescence and adult lifespan

Bayesian age-dependent mortality analyses provided evidence of a tight link between facultative paedomorphosis and the rate of senescence. Metamorphs had a senescence rate 1.5 to 5 times lower than that of paedomorphs, depending on the pond occupied and sex. Although the factors (e.g. conspecific density, freezing) causing pond-specific variation in mortality remain poorly understood, our results support the idea that local environmental changes can affect senescence rate as previously demonstrated in other vertebrates (birds, Holand et al., 2016; squamates, Tully et al., 2020; anurans, Cayuela, Monod-Broca, et al., 2022). Overall, the senescence rate of metamorphs was relatively low (~0.08, average in both sexes) and slightly lower than the average rate of senescence (0.18 ± 0.05) calculated for Urodele species in a recent large-scale comparative study (Reinke et al., 2022). By contrast, the senescence rate of paedomorphs was often higher (from 0.18 to 0.30, depending on the ponds) than the average rate reported in Reinke's work, suggesting that facultative paedomorphosis might be an important driver for the evolution of senescence among newts and salamanders.

Morph differences in senescence could result from three non-mutually exclusive mechanisms: first, the increased senescence of paedomorphs could be due to trade-off in energy allocation between reproduction and somatic maintenance. Progenesis leads to the acceleration of gonadal development, thus allowing earlier reproduction (Bonett et al., 2022; Denoël et al., 2005; Whiteman, 1994); in the studied population, paedomorphic males and females breed for the first time 1.1 years and 0.3 years earlier on average, respectively, than metamorphs (Lackey et al., 2019). This increase in early-life investment in reproduction could be achieved at the expense of somatic maintenance, leading to accelerated senescence as expected by the classical theories of senescence (Hamilton, 1966; Kirkwood & Rose, 1991; Williams, 1957). Second, the increased senescence of paedomorphs might be caused by an increase in average adult mortality in ponds during the winter, a period during which metamorphs are absent from the aquatic environment and protected from harsh conditions (e.g. freezing) in terrestrial overwintering shelters. This explanation is consistent with Williams' theoretical prediction No. 2 (Gaillard & Lemaître, 2017; Williams, 1957) establishing that the rate of senescence increases when the average adult mortality increases under the action of environmental factors. Third, increased senescence could be a by-product of the 'best of a bad lot' strategy of paedomorphs. Paedomorphic males and females have, on average, a poorer body condition than their metamorphic counterparts (Lackey et al., 2019). As we showed that senescence rate is higher in paedomorphs with poor body condition than in those with high body condition (at least in females), depleted physiological condition might be the cause of the accelerated senescence of paedomorphs. Whatever the mechanism involved, our study suggests that increased senescence could be a delayed cost of adaptive plasticity, which improves early-life performance in constraining environments at the expense of survival late in life.

The variation in senescence between paedomorphs and metamorphs was associated with changes in lifespan and life expectancy, which differed between sexes. In females, the lifespan (both 50% and 80%) and life expectancy were longer in metamorphs than in paedomorphs from all ponds, with the notable exception of those from pond L03, where low basal mortality allows lifespan 50% and life expectancy similar to that of metamorphs. By contrast, metamorphic males displayed the shortest lifespan (both 50% and 80%), although they have the lowest senescence rate in the study population. This short lifespan was due to the lower survival of young adults, metamorphic males having the highest basal mortality rate regardless of morph, sex and pond considered. These results indicate a partial decoupling between the rate of senescence and lifespan metrics, as previously demonstrated at the intra- and interspecific levels in amphibians (Cayuela et al., 2021; Cayuela, Lemaître, et al., 2022; Reinke et al., 2022).

4.3 | Associations between individual traits, senescence and lifespan in paedomorphs

Our analyses showed that the mortality of paedomorphs was condition-dependent. Females with good average body condition have a rate of senescence 1.5 times lower and a lifespan (80%) 1.4 times longer (leading to a gain of 4 years of life) than those with poor body condition. In males, senescence rate was little influenced by body condition, but the lifespan of individuals with good body condition was still 1.3 times (three additional years of life) than that of those with poor body condition. These patterns of condition-dependent mortality probably result from delayed (carry-over) effects of larval development on adult performance, affecting the basal mortality rate in both sexes. In the population studied, extrinsic factors such as the high density of conspecifics deplete the body condition of larvae in some ponds and during certain years (Whiteman et al., 2012). These larvae produce paedomorphs that also suffer from poor body condition (Lackey et al., 2019), which leads to reduced survival, including late in life in females (i.e. higher senescence rate). Our results provide one of the few empirical cases suggesting the existence of a silver-spoon effect on actuarial senescence; such effects seem more pronounced on reproductive senescence (see the meta-analysis of Cooper & Kruuk, 2018).

Our analyses also revealed associations between mortality metrics and reproductive traits. The age at first reproduction was associated with the adult lifespan of females. The lifespan (50% and 80%) of late breeders was 1.5 higher (leading to a gain of 6 years of life) than that of early breeders. In males, the lifespan extension of late breeders was less marked due to an acceleration of mortality late in life (see next paragraph). Overall, these patterns are consistent with life-history theory, which predicts a negative association between longevity and age at first reproduction due to evolutionary trade-offs (Roff, 1993; Stearns, 1992). They are also congruent with the observations made at the interspecific level in ectothermic tetrapods (77 species of amphibians and reptiles), in which lifespan was positively correlated with the age at first reproduction (Reinke et al., 2022).

Our work also highlighted relationships between the rate of senescence and reproductive traits. In males, the senescence rate is 1.5 times lower in early-breeding individuals than in late-breeding individuals. This result supports the idea that males delaying their first reproduction—for instance, due to poor body condition (Lackey et al., 2019)—also suffer from late-life decrease in survival. By contrast, the senescence rate of early- and late-breeding females was similar, indicating sex-specific differences between senescence-reproduction associations. Furthermore, our analyses have shown that females with a high lifetime egg production—associated with good body condition in the studied population (Lackey et al., 2019)—tend to show slower senescence compared to females with low lifetime egg production. Taken together, these results do not indicate the existence of a trade-off between reproduction and late-life survival, as expected by ageing theories (Hamilton, 1966; Kirkwood & Rose, 1991; Williams, 1957) and evidenced at the interspecific level (Jones et al., 2008; Reinke et al., 2022). Instead, our results suggest that individuals experiencing suitable larval environment benefit at the paedomorph stage from good body condition, which allows maximization of reproductive capacity (early reproduction, high lifetime egg production) without substantial cost of adult survival, including late in life. Overall, our results are congruent with those of recent studies showing that the generalization of associations (negative or positive) between life-history traits across different levels of biological organization (species, populations, individuals) is challenging, potentially because the processes determining trait–trait relationships (e.g. resource allocation or acquisition) differ at each level (Haave-Audet et al., 2022; Van de Walle et al., 2023).

5 | CONCLUSIONS

We showed that significant among-individual variation in the rate of senescence can exist within the same population. Our results are in agreement with previous studies showing that senescence patterns can vary between morphs (e.g. in birds, Grunst et al., 2018) or according to local environmental variation within spatially structured populations. (e.g. in snakes, Tully et al., 2020). Our analyses specifically indicate that increased senescence could be a delayed cost of adaptive plasticity, paedomorphosis improving early-life performance in constraining environments at the expense of survival later in life. In addition, our results revealed that senescence rate differs among ponds in paedomorphs. These findings are consistent with those of previous studies on reproductive senescence showing that conditions prevailing in the natal environment (e.g. population density, weather) can influence both early development and breeding performance late in life (e.g. in mammals and birds, Cooper & Kruuk, 2018). Taken together, our work and a few others (e.g. in arthropods, Pietrzak et al., 2015; Tully, 2023) underline the role potentially played by adaptive plasticity in the variability of senescence trajectories within the animal kingdom.

AUTHOR CONTRIBUTIONS

HC, ACRL, VR and HHW conceived the ideas and designed the methodology; ACRL, HHW and BM-B collected and/or curated the capture–recapture data; HC and VR analysed the data; and HC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.sxksn0394 (Cayuela et al., 2024).

ORCID

Hugo Cayuela https://orcid.org/0000-0002-3529-0736
Alycia C. R. Lackey https://orcid.org/0000-0001-8279-6417
Victor Ronget https://orcid.org/0000-0001-9991-0482
Benjamin Monod-Broca https://orcid.org/0000-0002-9133-5548

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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