Thermal conditions predict intraspecific variation in senescence rate in frogs and toads

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Variation in temperature is known to influence mortality patterns in ectotherms. Even though a few experimental studies on model organisms have reported a positive relationship between temperature and actuarial senescence (i.e., the increase in mortality risk with age), how variation in climate influences the senescence rate across the range of a species is still poorly understood in free-ranging animals. We filled this knowledge gap by investigating the relationships linking senescence rate, adult lifespan, and climatic conditions using long-term capture–recapture data from multiple amphibian populations. We considered two pairs of related anuran species from the Ranidae (*Rana luteiventris* and *Rana temporaria*) and Bufonidae (*Anaxyrus boreas* and *Bufo bufo*) families, which diverged more than 100 Mya and are broadly distributed in North America and Europe. Senescence rates were positively associated with mean annual temperature in all species. In addition, lifespan was negatively correlated with mean annual temperature in all species except *A. boreas*. In both *R. luteiventris* and *A. boreas*, mean annual precipitation and human environmental footprint both had negligible effects on senescence rates or lifespans. Overall, our findings demonstrate the critical influence of thermal conditions on mortality patterns across anuran species from temperate regions. In the current context of further global temperature increases predicted by Intergovernmental Panel on Climate Change scenarios, a widespread acceleration of aging in amphibians is expected to occur in the decades to come, which might threaten even more seriously the viability of populations and exacerbate global decline.

aging | amphibians | climate | ectotherms | temperature

Studies of age-specific changes in mortality have emphasized that actuarial senescence (i.e., the increase in mortality with age; called "senescence" hereafter) patterns are extremely diverse in the wild (1–3). To date, most studies have been conducted in birds and mammals and have demonstrated that the age at the onset of senescence (4, 5), the rate of senescence (1, 6), and the overall shape of mortality patterns (7, 8) all vary across species. Variation in senescence patterns across species is broadly explained by phylogeny (6), body size (1), and the pace of life (4). Although the genetic and physiological mechanisms modulating among-species variation in senescence are still poorly understood (9), empirical evidence accumulated so far shows that senescence is a ubiquitous phenomenon whose form and intensity vary considerably across the tree of life.

In contrast, much less research has focused on variation in senescence patterns across populations within a given species (3). This requires intensive long-term monitoring of multiple populations across a species' range, which is uncommon. Studies comparing captive and wild populations have shown that controlled environments in zoos slow down the senescence process in mammals (10), with deceleration more pronounced in short-lived than in long-lived species (11). Variation in age-dependent mortality patterns between populations of a given species has also been reported in the wild, suggesting that local environmental conditions (e.g., anthropogenic disturbance, habitat quality) may affect senescence patterns (12–14). However, the influence of environmental variation on the intensity of senescence is still poorly understood in most animal clades (3).

Climatic conditions might be a key factor driving intraspecific variation in senescence (15, 16), especially in ectotherms, because their metabolism, activity patterns, and lifespan all strongly depend on temperature (17, 18). Studies of both natural and experimental populations of invertebrates and ectothermic vertebrates have so far revealed that lifespan decreases with increasing ambient temperature (15, 16). In short-lived model organisms, the decrease in lifespan at high temperature is associated with accelerated senescence under laboratory conditions [*Caenorhabditis elegans* (19), *Drosophila melanogaster* (20), and *Nothobranchius furzeri* (21)]. However, lifespan is a

Significance

Using long-term demographic studies, we showed that warmer temperatures are associated with increased senescence rates and decreased lifespans in four amphibian species that are widely distributed across two continents (North America and Europe). Our study highlights the role of changing climatic conditions in the aging of ectotherms in the context of global warming.

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trait only partially correlated to senescence rate [e.g., $R^2 < 0.50$ in mammals (22)], which does not reliably reflect age-specific mortality patterns (9). To date, a link between senescence and climate has not been demonstrated in the wild, which limits our ability to assess the universality of this relationship and prevents reliable predictions about the influence of climate change on senescence.

Amphibians are excellent biological models to investigate the influence of climatic conditions on senescence patterns in nature. Previous studies have shown that as temperatures decrease along altitudinal and latitudinal gradients, the pace of life of amphibians slows down, involving delayed sexual maturity, less frequent egg deposition by females, and increased lifespan (23, 24); this slow pace of life is expected given the ecological effects of altitude in most taxa (25). At higher altitudes and latitudes, individuals maximize survival in cold conditions by reducing their activity period and placing themselves into an hypometabolic state that minimizes their energy expenditure (26, 27). At lower altitudes and latitudes, the activity period is longer (23); overall, metabolic activity increases, and warm conditions both diminish mitochondrial efficiency and accelerate the accumulation of oxidative damages (28), possibly leading to an earlier or faster senescence. This effect may be amplified by evaporative water loss that reduces the capacity of cutaneous respiration (29) and body temperature regulation (30) when individuals experience hot temperatures and low precipitation. These phenomena could have synergistic effects on age-dependent mortality, resulting in an acceleration of senescence with increasing temperature and decreasing precipitation.

To assess the relationship between age-specific mortality patterns and climatic conditions, we measured the influence of temperature and precipitation on among-population variation in senescence rate and adult lifespan in two pairs of frog and toad species from the Ranidae and Bufonidae families, which diverged more than 100 Mya (31). We focused on four species widely distributed in North America (Columbia spotted frog, *Rana luteiventris*, and Boreal toad, *Anaxyrus boreas*; Fig. 1) and Europe (common frog, *Rana temporaria*, and common toad, *Bufo*; Fig. 1). To perform these analyses, we took advantage of long-term capture–recapture (CR) data collected in 16 populations of *R. luteiventris* and *A. boreas* (eight per species) distributed along a broad climatic gradient in the western United States (Fig. 1 and *SI Appendix*, Table S1) and in four populations of *R. temporaria* and *B. bufo* (two per species) experiencing contrasted temperature conditions in Europe (Fig. 1 and *SI Appendix*, Table S1). More specifically, we tested whether warmer mean annual temperature was associated with higher senescence rate and shorter adult lifespan and, similarly, if higher mean annual precipitation was correlated with lower senescence rate and longer adult lifespan. As human activities may also influence local mortality patterns in amphibians (13, 32), we took into account the intensity of human footprint by including a quantitative, empirically based measure of ecological integrity in our models (33) (more details about this metric are given in *SI Appendix*, Supplementary analysis 1). Furthermore, as sexes may differ in terms of mortality patterns (6, 34) and physiological response to thermal stress, we tested whether the association among senescence, lifespan, and climatic conditions differed between males and females.

Results

Senescence Rate, Adult Lifespan, and Their Covariation. We performed Bayesian survival trajectory analyses and obtained estimates of sex-specific senescence rates from models that appropriately converged (see model estimates in *SI Appendix*, Tables S11–S27) for *R. luteiventris* (eight populations, Fig. 2*A*), *A. boreas* (eight populations, Fig. 2*B*), *R. temporaria* (two populations, Fig. 2*A*), and *B. bufo* (two populations, Fig. 2*B*). For populations LOTA and KETA of *A. boreas*, we removed sex as

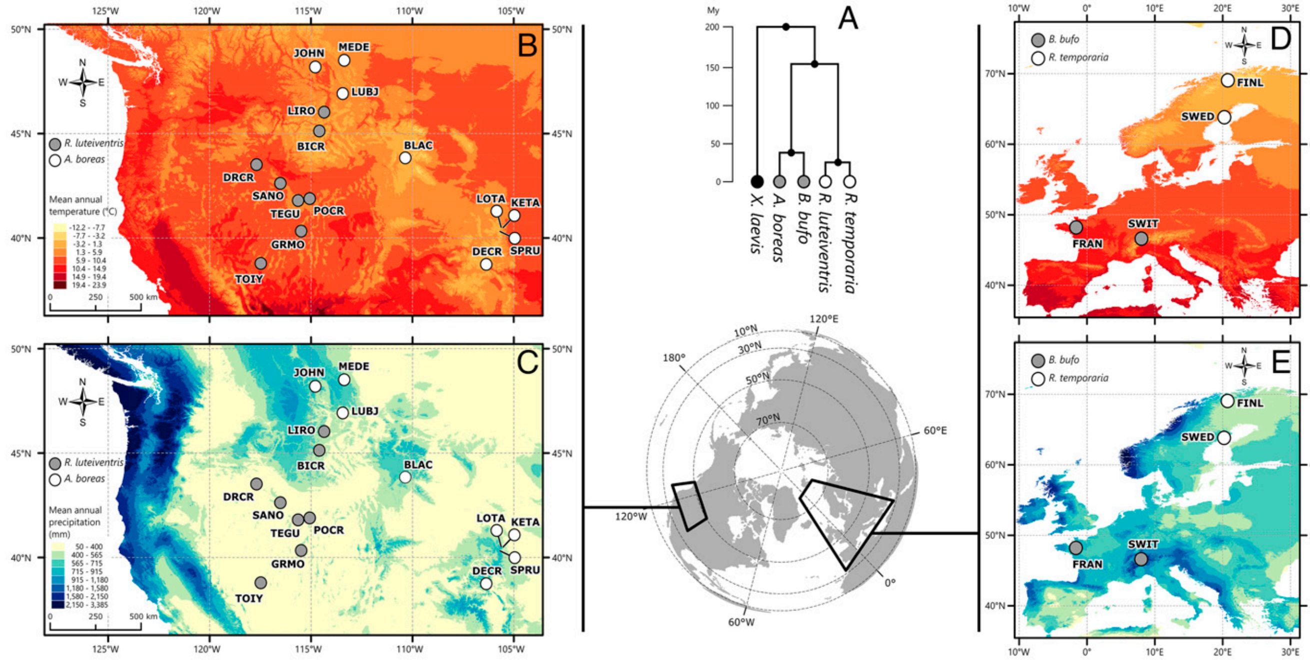

Fig. 1. Study system used to test the links among actuarial senescence rate, lifespan, and climatic conditions in four amphibian species from North America (Columbia spotted frog, *R. luteiventris*, and Boreal toad, *A. boreas*) and Europe (common frog, *R. temporaria*, and common toad, *B. bufo*). (*A*) Calibrated phylogenetic tree (retrieved from ref. 63, http://www.timetree.org/) presenting the phylogenetic relationships and divergence time among the four species; the African clawed frog (*Xenopus laevis*) was used as an outgroup. (*B* and *C*) Maps with background showing mean annual temperature (*A*) and mean annual precipitation (*B*) in the western United States (extracted from https://adaptwest.databasin.org). (*D* and *E*) Maps with background showing mean annual temperature (*D*) and mean annual precipitation (*E*) in Europe (extracted from https://www.worldclim.org/).

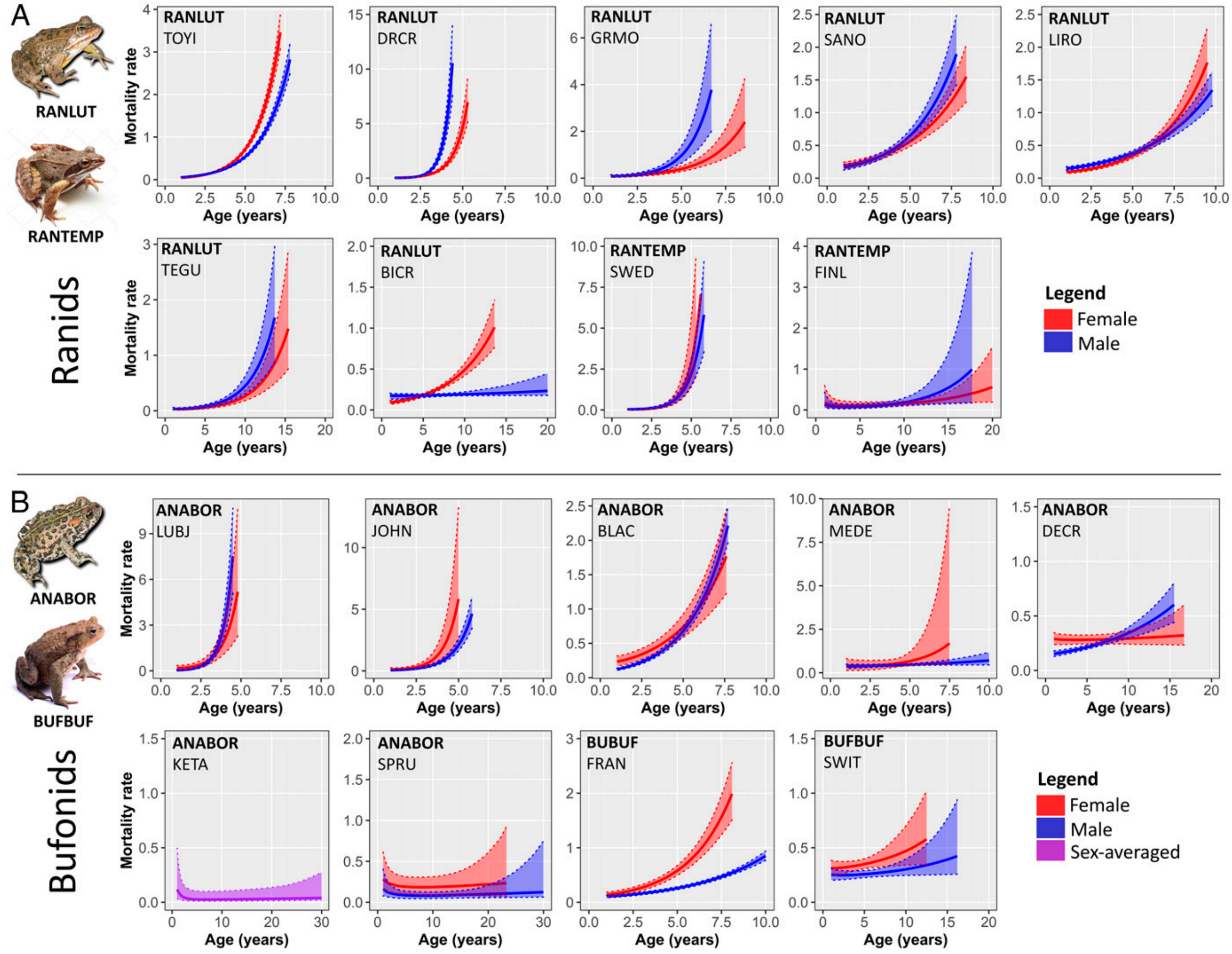

Fig. 2. Mortality curves for males (blue) and females (red) of 18 ranid (*A*) and bufonid (*B*) populations from North America and Europe. Two ranid species, *R. luteiventris* (RANLUT) and *R. temporaria* (RANTEMP), and two bufonid species, *A. boreas* (ANABOR) and *B. bufo* (BUFBUF), were considered. The parameters a_0 and a_1 extracted from the Siler model did not converge for one population of *R. luteiventris* (POCR); furthermore, for one population of *A. boreas* (LOTA), credible intervals of mortality rate early in life were very large. Senescence patterns are thus not displayed for these two populations, but parameter estimates are available in *SI Appendix*, Tables S16 and S23. Age presented on the *x*-axis of mortality curves corresponds to the age from onset of adulthood.

a variable from the model to reach model convergence and therefore obtained a senescence rate estimate for the sexes combined.

Senescence rates varied widely among populations within the same species. In *R. luteiventris*, senescence rates ranged from 0.05 (95% CRI: 0.01 to 0.12; population BICR) to 2.09 (95% CRI: 1.87 to 2.31; population DRCR) in males and from 0.07 (95% CRI: 0.004 to 0.21; population POCR) to 1.34 (95% CRI: 1.21 to 1.49; population DRCR) in females. In *A. boreas*, senescence rates ranged from 0.05 (95% CRI: 0.001 to 0.15; population SPRU) to 1.66 (95% CRI: 1.44 to 1.88; population LUBJ) in males and from 0.06 (95% CRI: 0.002 to 0.19; population SPRU) to 1.27 (95% CRI: 0.88 to 1.69; population JOHN) in females. Although the number of populations studied was smaller in *R. temporaria* and *B. bufo*, senescence rates displayed a relatively similar range of variation in these species (Fig. 3 *A* and *B*), suggesting that senescence rates are highly variable within species among ranid and bufonid populations on both continents.

We then examined whether senescence rate was associated with lifespan in *R. luteiventris* and *A. boreas*, the two species for which the number of populations monitored was large enough to address this question. Linear models indicated that senescence rate was negatively related to lifespan in both *R. luteiventris* (slope of −0.26 ± 0.06; likelihood ratio test [LR] test: χ^2 = 9.78, P = 0.002) and *A. boreas* (slope of −0.39 ± 0.14; LR test: χ^2 = 7.53, P = 0.001), but variation in adult lifespan only accounted for a limited proportion of the variation in senescence rate (R^2= 0.52 and 0.36 in *R. luteiventris* and *A. boreas*, respectively).

Relationships among Senescence Rates, Adult Lifespan, and Climatic Conditions. Temperature was a strong predictor of variation in senescence rate in the four species studied (Fig. 4 *C* and *D* for *R. luteiventris* and *A. boreas*, respectively, and Fig. 3 *A* and *B* for *R. temporaria* and *B. bufo*, respectively). The regression model [log(b_1) ∼ Temp_30yrMean + Precip_30yrMean + Human_footprint + Species + Sex] built for *R. luteiventris* and *A. boreas* (model adjusted R^2 = 0.43) indicated that senescence rate increased with mean annual temperature (slope of 0.92 ± 0.29; LR test: χ^2 = 10.35, P = 0.001), whereas mean annual precipitation and human footprint did not influence

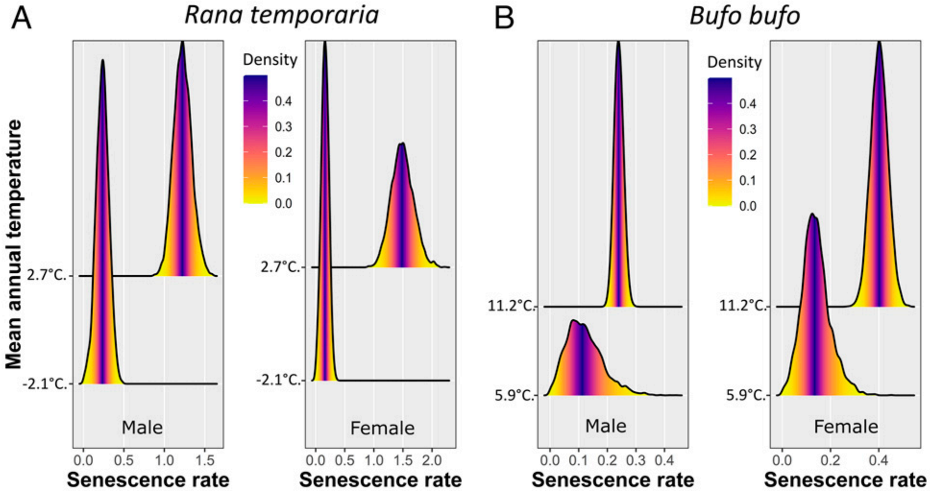

Fig. 3. Senescence rates in males and females in four *R. temporaria* and *B. bufo* populations exposed to contrasting mean annual temperatures (averaged for a 30-y period, 1970 to 2000) in Europe. We present posterior distribution of senescence rates (parameter b_1) from Siler models built for each population of *R. temporaria* (*A*) and *B. bufo* (*B*).

senescence rate (*SI Appendix*, Table S4). Commonality analysis, which decomposes regression R^2 into its unique (i.e., variance accounted by a single predictor) and common (i.e., variance accounted by a set of predictors) contributions, also supported this interpretation (Table 1). Mean annual temperature had a unique contribution of 0.18 (corresponding to 40.5% of the total variance explained by the model; *SI Appendix*, Table S5), whereas the unique contributions of mean annual precipitation and human footprint were close to zero. Mean annual temperature also had a common contribution of 0.25 (i.e., 57.3% of the total variance explained by the model) with the two other environmental predictors; by contrast, mean annual precipitation and human footprint had a negligible common contribution (0.003; *SI Appendix*, Table S5). Regression models performed on the two species separately (Fig. 3 *C* and *D* and *SI Appendix*, Table S7) and models including a synthetic variable obtained from a principal component analysis (PCA) (*SI Appendix*, Supplementary analysis 2) also showed that senescence rate increases with mean annual temperature.

Our analyses also suggest that mean annual temperature may predict adult lifespan, although with an effect much less marked than for senescence rate. The regression model [log(lifespan) ~ Temp_30yrMean + Precip_30yrMean + Human_footprint + Species + Sex] (model adjusted $R^2 = 0.15$) indicated that mean annual temperature tended to have a weak negative effect (slope of -0.24 ± 0.16; LR test: $\chi^2 = 2.65$, $P = 0.10$) on adult lifespan when both *R. luteiventris* and *A. boreas* were included in the same model; by contrast, mean annual precipitation and human footprint did not influence lifespan (*SI Appendix*, Table S4). The effect of mean annual temperature was statistically significant (slope of -0.27 ± 0.12; LR test: $\chi^2 = 4.25$, $P = 0.04$) when mean annual precipitation was removed from the model, which was likely due to collinearity issues. A commonality analysis showed that the unique contributions of mean annual temperature and mean annual precipitation were 0.04 (47% of the total variance explained by the model) and 0.004 (5.5%), respectively, and that their common contribution was 0.03 (44%; Table 1 and *SI Appendix*, Table S6). Importantly, regression analyses performed on the two species separately showed that the signal detected in the general model was driven mainly by *R. luteiventris*. Adult lifespan decreased with increasing mean annual temperature in *R. luteiventris* (slope of -0.28 ± 0.06; LR test: $\chi^2 = 17.46$, $P = 2.939\text{e-}05$) but not in *A. boreas* (*SI Appendix*, Table S7). Overall, our analyses showed that adult lifespan decreases with increasing mean annual temperature with different intensity across species.

The analyses performed on the four populations of *R. temporaria* and *B. bufo* in Europe supported our findings from North American species. Senescence rates were higher in the population experiencing warmer temperatures than in the one experiencing colder temperatures in both *R. temporaria* (Fig. 3*A*) and *B. bufo* (Fig. 3*B*). In addition, adult lifespan was also influenced by thermal conditions: In R. temporaria, lifespan was 80% longer in the population experiencing colder temperatures (FINL: 12 and 12.5 y in females and males, respectively) than that experiencing warmer temperatures (SWED: 4 y in both females and males). Similarly, in the population of *B. bufo* experiencing colder temperatures (SWIT: 6 and 7 y in females and males, respectively), lifespan was longer than in the population experiencing warmer conditions (FRAN: 4.5 and 5.5 y in females and males, respectively).

Associations among Sex-Related Differences in Senescence Rate and Adult Lifespan and Temperature. We investigated sex-related differences in senescence rate and adult lifespan responses to thermal conditions in two ways. First, we examined the relationships between these two mortality metrics and mean annual temperature by quantifying the interactive effect of temperature and sex. We did not detect any interactive effect in either mortality metric (*SI Appendix*, Table S8). Then, we examined whether the magnitude of sex bias in senescence rate (measured as the [female senescence rate/male senescence rate] ratio) and adult lifespan ([female lifespan/male lifespan] ratio) was influenced by thermal conditions. The magnitude of sex bias in senescence rate was associated with mean annual temperature in *R. luteiventris* (slope of -0.21 ± 0.07; LR test: $\chi^2 = 8.10$, $P = 0.004$; $R^2 = 0.60$) but not in *A. boreas* (*SI Appendix*, Table S9). Selected models indicated that *R. luteiventris* males experienced a higher senescence rate than females at high temperature (Fig. 4*C*). In contrast, females experienced higher senescence rates than males at low temperature. Furthermore, the magnitude of the sex bias in adult lifespan was not influenced by mean annual temperature in either of the two species (*SI Appendix*, Table S9).

Discussion

We used a unique set of long-term CR studies of four amphibian species from two divergent clades occurring on two

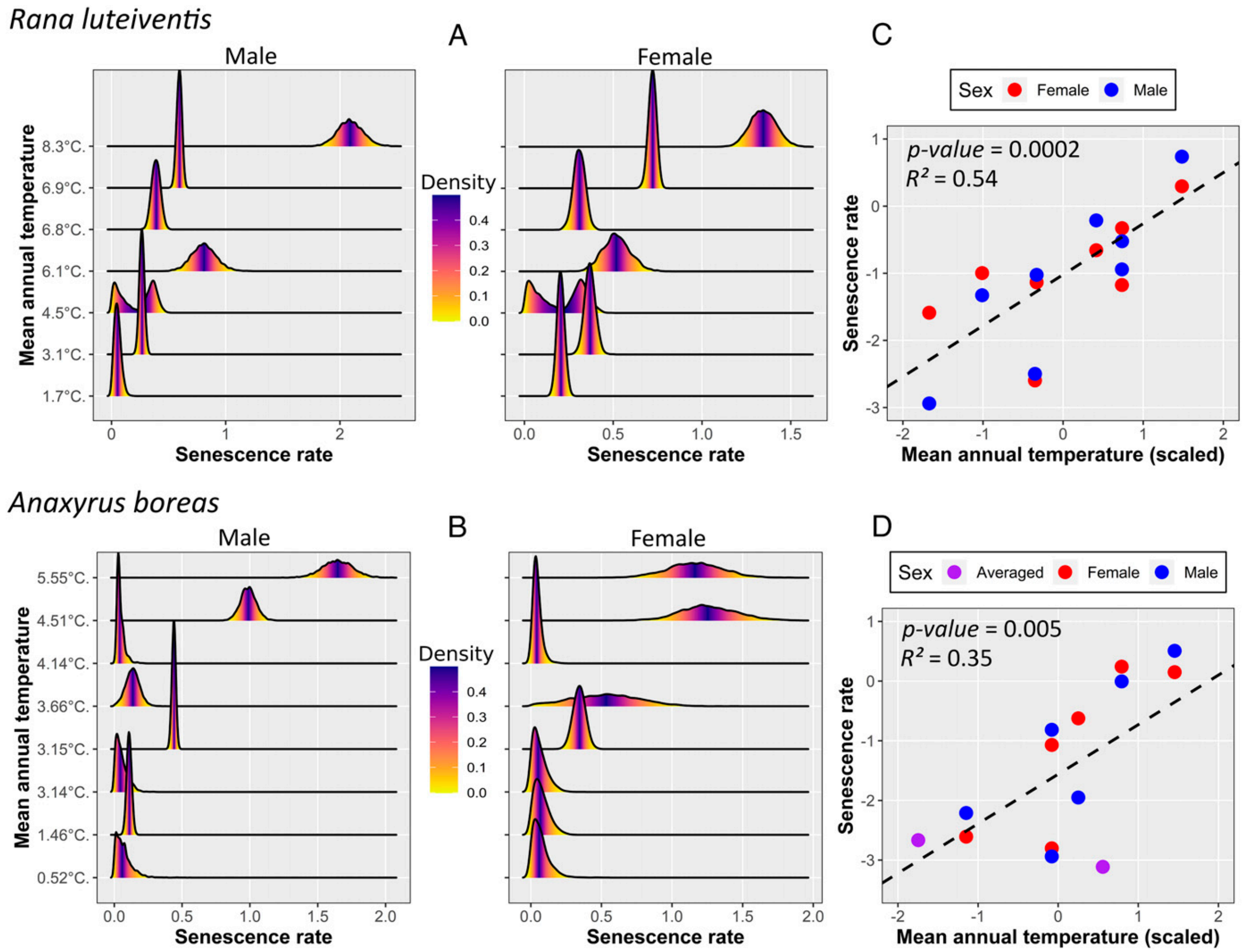

Fig. 4. Senescence rates in males and females in 16 *R. luteiventris* and *A. boreas* populations exposed to a range of mean annual temperatures (averaged for a 30-y period, 1990 to 2019) in North America. (*A* and *B*) Posterior distribution of senescence rates (parameter b_1) from Siler models built for each population. (*C* and *D*) Senescence rates [i.e., $\log(b_1)$] as a function of mean annual temperature (centered and reduced) in *R. luteiventris* (*C*) and *A. boreas* (*D*). The dashed line is extracted from the regression model [$\log(b_1) \sim$ temperature] from which sex was removed because of its negligible effect on senescence rate (*SI Appendix*, Tables S7 and S8).

continents to test whether population-specific mortality patterns were associated with temperature and precipitation along broad bioclimatic gradients. The four species exhibited wide among-population variation in senescence rates. In both *R. luteiventris* and *A. boreas*, we found climate-dependent clinal variation in senescence. The rate of senescence increased with mean annual temperature, whereas the influence of mean annual precipitation was negligible. In *R. luteiventris*, senescence acceleration led to a reduced lifespan in warmer environments. We found similar patterns in Europe by considering populations exposed to contrasting thermal conditions: populations of *B. bufo* and *R. temporaria* from warmer environments had higher rates of senescence and shorter lifespan than populations exposed to colder conditions.

Table 1. Commonality analysis for senescence rate and adult lifespan in *A. boreas* and *R. luteiventris*

Predictors	Unique	Common	Total
Senescence rate			
Temp_30yrMean	0.18	0.25	0.44
Precip_30yrMean	0.01	0.26	0.27
Human_footprint	0.00	0.13	0.13
Adult lifespan			
Temp_30yrMean	0.04	0.01	0.04
Precip_30yrMean	0.004	0.008	0.01
Human_footprint	0.03	−0.03	0.003

Unique contributions measure the part of variance that is uniquely accounted for by a single predictor (i.e., mean annual temperature, Temp_30yrMean; mean annual precipitation, Precip_30yrMean; and human footprint index, Human_footprint); by contrast, common contributions measure how much variance is common to a predictor set.

Large Among-Population Variation in Senescence Rate Occurs in Anurans. Using a multispecies, multipopulation set of long-term CR data from ectothermic vertebrates, our study revealed large among-population variation in senescence rate. In both *R. luteiventris* and *A. boreas*, the magnitude of intraspecific variation in senescence rate was larger than that estimated using the same modeling approach across 140 mammalian populations (0.01 to 1.17) (6). Our results support the conclusion of a previous analysis on the yellow-bellied toad (*Bombina variegata*), a widely distributed temperate anuran in Europe, which showed that senescence patterns strongly differ among populations in response to local environmental conditions (13). Overall, the large among-population variation in senescence rate we report here suggests a small contribution of phylogeny on this mortality trait across anurans.

Senescence Rate Is Strongly Associated with Temperature in Anurans. Climatic conditions could be a primary driver of aging in ectotherms in nature. Senescence rates were positively associated with temperature in *R. luteiventris* and *A. boreas.* This pattern was consistent with those observed in the two European species, *R. temporaria* and *B. bufo*, in which senescence rates were higher in warmer conditions. Accelerated senescence was associated with shorter lifespan in warmer environments in all species except *A. boreas*. Overall, the consistent patterns we report from two continents and from two families (i.e., Ranidae and Bufonidae), which diverged more than 100 Mya (31), indicate that senescence invariably accelerates with increasing temperature among anuran lineages. Although our approach is correlative, temperature is likely a key causative agent of senescence variation in the four studied species, in line with what has been proposed from experimental studies of ectothermic model organisms [*C. elegans* (19), *D. melanogaster* (20), and *N. furzeri* (21)].

Decelerated senescence with lower temperatures is likely caused by several behavioral, physiological, and genetic mechanisms. Long annual seasons of low temperatures force amphibians to lengthen their annual overwintering period (up to 8 to 9 mo in the four studied species). Temperatures in overwintering sites are typically low, ranging from 0 to −5.2 °C (35, 36) in the terrestrial sites of *A. boreas* and from 1 to 3.7 °C in the aquatic sites of *R. luteiventris* (27, 37). Such cold conditions drive individuals into a hypometabolic state (27), which likely causes an interruption of the overall aging process [like in insects and worms (38, 39)]. This probably leads to the negligible senescence rate ($b_1 < 0.05$) observed in *R. luteiventris*, *A. boreas*, and *R. temporaria* populations experiencing a mean annual temperature lower than 4 °C (Figs. 3 and 4). Moreover, temperature-dependent senescence may not only be a byproduct of general thermodynamic changes but could also have a genetic basis. A study of three Asian bufonid and ranid species identified molecular signals of adaptation to altitude in a series of orthologous genes involved in the regulation of lifespan and lipid metabolism (40), the main source of energy during anuran overwintering (27).

Our analyses revealed that the amount of variation in senescence rate explained by mean annual precipitation alone (i.e., its unique contribution) was negligible, whereas its common contribution with mean annual temperature was substantial (29% of the total variance explained by the model; *SI Appendix*, Table S5). Although this pattern may be due to collinearity issues, higher mean annual temperature and frequent precipitation deficits at warmer sites might have a synergistic effect on the acceleration of senescence. Dehydration caused by summer drought leads to decreased capacity of anurans to increase their aerobic metabolism (41, 42), contract their muscles (43), and thermoregulate (44, 45). In *R. luteiventris*, periods of extended drought have also been associated with decreased adult survival in semiarid environments (46).

Temperature May Affect Sex-Related Variation in Senescence Rate. Temperature modulated between-sex differences in senescence rate in *R. luteiventris*. Females senesced faster than males at lower temperatures, whereas the opposite pattern occurred in populations exposed to warmer temperatures. Because of the XY sex chromosome system of the North American ranids (47), heterogametic males (i.e., XY) might experience faster senescence than homogametic females (i.e., XX) (48). In *R. luteiventris*, male-biased senescence rates occurred when mean annual temperature was at or above 6 °C (Fig. 4*C*). In contrast, females senesced faster than males at a temperature lower than 3 °C. This sex difference might be due to a shift in energy allocation in females toward reproduction at the expense of somatic maintenance in populations experiencing long hibernation periods (in ranids, see ref. 49). In *R. luteiventris*, reproduction takes place shortly after the end of overwintering, often when snow is still present, which limits the ability of females to forage before spawning and may reinforce the evolutionary tradeoff between reproduction and actuarial senescence (50).

In contrast, we did not find evidence that climatic conditions influenced between-sex variation in senescence rates of *A. boreas*. This contrasting result between species (that often cooccur in breeding wetlands) could be due to interspecific variation in traits that affect the magnitude of sex difference in aging rate, such as the sex determination system (XY in *R. luteiventris* and likely ZW in *A. boreas* like many bufonids), mating behavior (51), and female breeding frequency (52). Overall, our study highlights that the environmental impact on sex-specific variation in senescence differs among species experiencing relatively similar climatic conditions.

Conclusions

Improving our understanding of the influence of climatic conditions on lifespan and actuarial senescence patterns is critical to predicting how climate change will impact population dynamics of ectotherms in the next decades. For many years, knowledge about the effect of climate-related variables (e.g., temperature) on senescence was restricted to laboratory studies performed on model organisms (19–21). Our study provides the evidence of a tight link between temperature and actuarial senescence in free-ranging populations of ectothermic vertebrates (anurans) living in boreal and temperate environments. Although senescence rates varied broadly among populations within a species' range, they consistently accelerated in response to higher ambient temperature. Furthermore, this relationship was consistent among lineages that diverged millions of years ago. Taken together, our correlative study of amphibian populations in the wild and previous experiments based on laboratory models indicate that temperature-dependent acceleration of senescence is likely to be pervasive in ectotherms. Alas, further global temperature increase predicted by updated Intergovernmental Panel on Climate Change scenarios (2021) might lead to a widespread acceleration of aging in ectotherms in the decades to come. The resulting increase in mortality, especially late in life when female reproductive output is often the highest, might exacerbate the decline of many ectotherm populations that already face multiple environmental stressors.

Material and Methods

Data Collection.

Ranid and bufonid populations in North America. We collected CR data from 16 populations or metapopulations (*lato sensu*) across a large part of the distribution range of *R. luteiventris* and *A. boreas* in the western United States (Fig. 1). The duration of the monitoring varied among populations, ranging from 15 to 19 y and from 11 to 29 y for *R. luteiventris* and *A. boreas,* respectively (see detailed information in *SI Appendix*, Table S10). The studied populations were generally spread over multiple waterbodies used for breeding, were large enough to conduct CR studies, and were typically conveniently located for researchers and workers.

We focused on adult frogs (more than 45-mm snout–vent length) and toads (more than 50 mm) captured during annual visual encounter surveys at the study sites. We conducted surveys usually between June and early August for *R. luteiventris* and between May and June for *A. boreas.* At each site, one to eight workers searched for animals along the shoreline of deeper water bodies or the entire surface area of wadable water bodies. Most sites were surveyed two to four times a year to increase capture rates. Toads were surveyed at night using headlamps, whereas frogs were surveyed during the day when air temperatures were above 10 °C. Surveys ended either when the entire area was thoroughly searched or about 30 min after the last individual was captured.

All captured individuals were checked for a mark. Unmarked individuals were injected with a passive integrated transponder (PIT) tag into the dorsal subcutaneous tissue (or marked with a unique toe clip pattern, LIRO only through 2012). We recorded the PIT tag number of all newly marked animals as well as all recaptured individuals. After handling, frogs and toads were released close to the location where they were captured or at least within the same water body.

Climatic data were compiled from the 800-m Parameter–Elevation Relationships on Independent Slopes Model Climate Group (53). For the 30-y period of 1990 to 2019, we calculated the mean annual temperature and mean annual cumulative precipitation at each site. Because sites often represented complexes of multiple water bodies spread over sometimes large areas (e.g., lakes within mountain basins or several kilometers of stream), we used the coordinates of the area of highest individual abundance for our modeled climatic data. Furthermore, for each population, we extracted a quantitative, empirically based measure of human footprint (i.e., ecological integrity index) suitable for landscape-level assessments in the United States (33); for details about the method used, see *SI Appendix*, Supplementary analysis 1.

Ranid and bufonid populations in Europe. We took advantage of CR data collected in four populations of *R. temporaria* (SWED and FINL) and *B. bufo* (FRAN and SWIT) with contrasting mean annual temperature to examine whether temperature had a similar effect on senescence rates in other ranid and bufonid species in another continent. Mean annual temperature differed greatly between the four study sites: *R. temporaria*, SWED: 2.7 °C., FINL: −2.1 °C.; *B. bufo*, FRAN: 11.2 °C., and SWIT: 5.9 °C. (Fig. 1 and *SI Appendix*, Table S10). Additional information about study duration, period, and sample size is available in *SI Appendix*, Table S10. The CR method used to monitor the four populations has been described in detail in previous studies [FRAN (54), SWED (55), FINL (56), and SWIT (57)]. Climate data for the four study sites were extracted from the *worldclim* database (https://worldclim.org).

Estimation of Senescence Rate and Adult Lifespan. Senescence rate (i.e., the exponential rate of increase of mortality risk with increasing age from the age of first reproduction and onwards) and adult lifespan (i.e., the age at which 80% of the individuals alive at the species-specific age of first reproduction were projected to be dead, see ref. 6) were estimated using Bayesian survival trajectory analyses implemented in the R package BaSTA (58, 59). Simulations by Colchero and Clark (58) showed that BaSTA models are robust to uncertainty in birth and death dates when estimating mortality rate (defined as the probability of an individual of age x to die before reaching age x+1) or hazard rate (defined as the risk of death for an individual of a given age). BaSTA allowed us to account for imperfect detection, left-truncated (i.e., unknown birth date [age]), and right-censored (i.e., unknown death date) CR data in our analysis. We specified a year-dependent recapture probability for all populations. We ran four Markov chains chains with 50,000 iterations and a burn-in period of 5,000. Chains were thinned by a factor of 50. Model convergence was evaluated using the diagnostic analyses implemented in BaSTA, which calculates the potential scale reduction for each parameter to assess convergence.

Following Lemaître et al. (6), we fitted a Siler model (60) to model age-specific mortality in every population of each species and obtain comparable metrics. Sex was introduced in each population-specific model as an explanatory variable. The five-parameter Siler model is given by

$$\mu(x) = a_0\exp\left(-a_1x\right) + c + b_0\exp(b_1x),$$

where a_0, a_1, b_0, b_1, and $c \geq 0$ are the parameters of the mortality function, μ the mortality rate, and x the age in years. The first exponential function with parameters a describes mortality in the early adult stage, whereas c gives the lower limit of mortality during the adult stage. The second exponential function with b parameters corresponds to the mortality increase during the senescent stage. The parameter b_1 of the Siler model measures the exponential increase in mortality rate with age during the senescence stage, and it is therefore commonly used to measure senescence rate in vertebrates (6). Furthermore, we used the life tables produced in BaSTA to estimate sex-specific adult lifespans (in years).

Assessing the Associations among Senescence Rate, Adult Lifespan, and Climatic Conditions. In *R. luteiventris* and *A. boreas*, we assessed the associations among senescence rates and mean annual temperature, mean annual precipitation, and human footprint index using multiple regression models. We first performed a general analysis in which we evaluated these associations by including them in the same model. Mean annual temperature, mean annual precipitation, and human footprint were not strongly correlated across the 16 study sites (*SI Appendix*, Table S3); Pearson's correlation coefficient was lower than 0.7, the threshold value recommended by Dormann et al. (61) to avoid multicollinearity issues. Hence, the three variables (centered and reduced) were included in the following model: [log(b_1) ∼ Temp_30yrMean + Precip_30yrMean + Human_footprint + Species + Sex] in which the additive effects of species and sex were also incorporated. We used likelihood-ratio tests to examine whether the effect of the predictors on senescence rates was statistically significant ($P < 0.05$); a similar approach was used in all regression analyses. Then, we performed a commonality analysis, a robust approach to examine multicollinearity among predictors (62), and measured unique (i.e., the part of variance uniquely accounted for by a single predictor) and common (i.e., the part of variance accounted for by set of predictors) contributions of the three environmental variables to senescence rate variation. Furthermore, an additional modeling approach including a synthetic variable from a PCA was used to support the inferences obtained through multiple regression and commonality analyses (*SI Appendix*, Supplementary analysis 2). Next, we performed partial regression models in which *R. luteiventris* and *A. boreas* were examined separately to assess the contribution of the two species to the senescence–temperature relationship detected in the general analysis. As the unique contribution of Precip_30yrMean and Human_footprint was negligible (Table 1), these two variables were removed, leading to the retained model [log(b_1) ∼ Temp_30yrMean + Sex]. We conducted similar analyses to evaluate the influence of Temp_30yrMean, Precip_30yrMean, and Human_footprint on adult lifespan of *R. luteiventris* and *A. boreas*. Furthermore, in *R. temporaria* and *B. bufo*, in which a limited number of populations was available, we compared posterior distributions of the b_1 parameter to evaluate whether senescence rate differed between pairs of populations experiencing warm and cold temperatures, respectively.

Examining Sex-Related Differences in Senescence Rate Response to Temperature. We investigated sex-related differences in senescence response to temperature in two ways. First, we evaluated whether the relationship between senescence rate (or lifespan) and mean annual temperature differed between sexes using the model [log(b_1) ∼ Temp_30yrMean × Sex]. Second, we examined how the magnitude of the sex bias in senescence rate (or lifespan) was influenced by thermal conditions. We built a linear model in which the [female senescence rate/male senescence rate] ratio, a common metric of sex bias magnitude (6), was included as the response variable and mean annual temperature as the explanatory variable.

Data Availability. All data are included in the article and/or supporting information.

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