AGING

Diverse aging rates in ectothermic tetrapods provide insights for the evolution of aging and longevity

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Comparative studies of mortality in the wild are necessary to understand the evolution of aging; yet, ectothermic tetrapods are underrepresented in this comparative landscape, despite their suitability for testing evolutionary hypotheses. We present a study of aging rates and longevity across wild tetrapod ectotherms, using data from 107 populations (77 species) of nonavian reptiles and amphibians. We test hypotheses of how thermoregulatory mode, environmental temperature, protective phenotypes, and pace of life history contribute to demographic aging. Controlling for phylogeny and body size, ectotherms display a higher diversity of aging rates compared with endotherms and include phylogenetically widespread evidence of negligible aging. Protective phenotypes and life-history strategies further explain macroevolutionary patterns of aging. Analyzing ectothermic tetrapods in a comparative context enhances our understanding of the evolution of aging.

Comparative studies of animal aging rates in the wild are critical for assessing the potential limits of longevity and for understanding ecological and evolutionary factors shaping variation in aging strategies (*1*–*3*). Demographic indicators of aging include adult longevity and measures that capture whether, and at what rate, age-specific mortality accelerates with advancing adult age. Previous comparative studies have provided important insights regarding the evolution of demographic aging in endothermic tetrapods [birds and mammals; e.g., (*2*–*7*)]. However, ectotherms hold most of the records for animal longevity and make up 26 of the 30 known records for vertebrate species with maximum longevity estimated to be >100 years (*8*–*11*) (tetrapod examples include Galápagos tortoises, eastern box turtles, European pond turtles, and *Proteus* salamanders). Additionally, some ectothermic tetrapods may exhibit low or even negligible [sensu (*12*)] mortality and reproductive aging (*1*, *13*–*18*). Understanding whether and how natural selection has shaped mortality trajectories and longevity requires phylogenetically controlled tests to determine whether these species-specific results are anomalies that evolved in specific lineages of ectotherms or if they are common and recurrent evolutionary outcomes. Recent advances in contrasting endotherm and ectotherm longevity have contributed to a phylogenetic perspective on lifespan (*10*, *11*) but often use maximum longevity as their metric. This metric is not based on the age-specific mortality trajectory and is influenced by sample size, so it can lead to inaccurate conclusions (*19*, *20*). Additionally, the lack of comparative analyses of mortality trajectories in ectothermic tetrapods—and the aging metrics that derive from them—is a major knowledge gap (*21*). A comprehensive analysis of demographic aging across ectothermic tetrapods requires decades of field-based population-level research, international collaborations, and powerful quantitative tools. Integrating these efforts across studies and taxa allows for testing evolutionary hypotheses of aging (*21*) and for a phylogenetic understanding of the evolution of aging across tetrapods.

The evolutionary genetics of aging result from age-specific mutation-selection balance trajectories, where mutations have age-specific effects that may be strictly deleterious in later adult stages or ages and/or beneficial earlier (i.e., antagonistically pleiotropic) (*22*). Hypotheses for how natural selection and the environment interact to shape this balance were first formulated by Medawar (*23*) and further developed by Hamilton (*24*) and others (*25*–*27*). In ectotherms, body temperature varies with the ambient environment and, because metabolism responds to temperature, ectothermic metabolism and cellular processes down-regulate in cold temperatures, which allows for extended periods of brumation. Additionally, after controlling for body size, ectotherms have lower resting metabolic rates than endotherms (*28*). Accordingly, the thermoregulatory mode hypothesis predicts that ectothermic lineages have evolved lower aging rates and greater longevities than their similarly sized endothermic counterparts (*29*, *30*). Layered on top of metabolic mode, environmental temperature itself is expected to be a strong driver of mortality in ectotherms, affecting both the evolution and the plasticity of aging through metabolic mechanisms [(*10*, *31*, *32*), but see (*33*)]. Within many endothermic species, individuals with lower body temperatures live longer and age slower than those with higher body temperatures (*29*, *34*), but across species, this pattern is less clear (*35*). Similarly, ectotherms in cooler climates may also exhibit longer lifespans compared with those in warmer climates [(*10*, *11*); referred to as the temperature hypothesis hereafter].

Phenotypes that alter age-specific mutation-selection trajectories would be expected to result in the evolution of altered rates of aging (*24*), provided genetic variation exists (*27*, *36*). For example, species with phenotypes that reduce mortality risk are expected to have lower rates of aging than those without [(*21*); the protective phenotypes hypothesis]. Previous work has shown that ectothermic tetrapods, such as amphibians, with chemical protection mechanisms can live longer than those without; however, how this trait (and any associated behavior) affects the rate of aging remains unknown (*11*, *37*, *38*). Tetrapod ectotherms are well suited for enabling direct comparisons of the rates of aging among species with and without phenotypes that have such physical or chemical protections. Within reptiles, diverse traits may confer protection from predation and/or environmental stressors, including

turtle shells, crocodilian armor, and snake venom [even if such traits are exaptations sensu (*39*)]. Similarly, in amphibians, many species produce toxic or unpalatable secretions (*40*). Despite these characteristics, the protective phenotypes hypothesis has not been tested across ectothermic tetrapods using robust aging metrics [but see (*10*, *11*, *37*) for analyses using maximum longevities].

Aging and longevity may coevolve through direct or indirect selection on life-history traits that are genetically correlated (*3*). Under antagonistic pleiotropy, genes that confer higher fitness in early life relative to late life will increase in frequency in populations that are skewed toward younger age classes (*24*). Because many ectothermic tetrapods have indeterminate growth and fecundity (*41*, *42*), life-history theory predicts that such species should have stronger selection against mutations with deleterious late-age effects (be they antagonistically pleiotropic or not) relative to species with determinate growth and fecundity (*21*). Any species in which individuals from older age classes contribute more to population growth (e.g., through fecundity or behavior) relative to other species should have concomitant slower aging. Thus, the aging rate may evolve from genetic covariation among life-history traits, such as annual fecundity, age at first reproduction, and annual survival. This results in a slow-fast continuum of life histories (*43*–*46*) that should match slow-to-fast aging rates (the slow-fast continuum hypothesis). For example, fast aging, expected to be correlated with a short reproductive lifespan, should evolve in a correlated manner with fast pace of life, and vice versa (*43*, *47*). Therefore, the existence of a strong positive covariation among life-history traits (*48*) predicts that the aging rate should covary with age at first reproduction (negatively) and with annual fecundity (positively) such that species that mature relatively early or those that allocate relatively more energy to reproduction early in life display faster aging and shorter longevities (*45*, *49*, *50*).

We applied comparative phylogenetic methods to mark-recapture data from tetrapods to analyze variation in ectotherm demographic aging and longevity in the wild, to compare aging and longevity (using a mortality trajectory–derived metric) with endotherms, and to address the following four distinct but not mutually exclusive hypotheses: (i) thermoregulatory mode, (ii) temperature, (iii) protective phenotypes, and (iv) slow-fast continuum. We analyzed long-term capture-recapture data collected in the wild from 107 populations of 77 species, with study length averaging 17 years (ranging from 4 to 60 years), to assess macroevolutionary patterns of aging rate and longevity in amphibians and nonavian reptiles (hereafter referred to as reptiles in contrast with the endothermic avian reptiles, hereafter referred to as birds). We present the first comprehensive comparative analysis of patterns of aging across these ectotherms and estimate both the rate of aging (computed as the slope of the relative rate of age-specific mortality derived from the Gompertz model, β_1) and longevity (computed as the number of years after the age at first reproduction until 95% of adults in a given cohort have died, as opposed to the age of the longest-lived individual). Specifically, we test the following: (i) whether ectotherms consistently age more slowly and live longer

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than endotherms; (ii) whether annual mean, minimum, or maximum environmental temperature experienced by a population covaries with rate of aging and longevity; (iii) whether species with protective phenotypes (either physical or chemical) age slower and live longer than those without physical or chemical protection; and (iv) whether rate of aging and longevity strongly covary with other biological traits, such as age at first reproduction and annual fecundity.

Aging in ectothermic tetrapods

All orders represented by the 77 reptile and amphibian species for which age-specific estimates of mortality were estimated had at least one species with negligible aging (β_1 ~ 0; Fig. 1 and data S1). Notably, turtles had slow rates of aging (mean $\beta_1 \pm$ SE = 0.04 ± 0.01), with a narrow range relative to the number of species represented (−0.01 to 0.23 for 14 species; Fig. 2 and table S1). When corrected for body

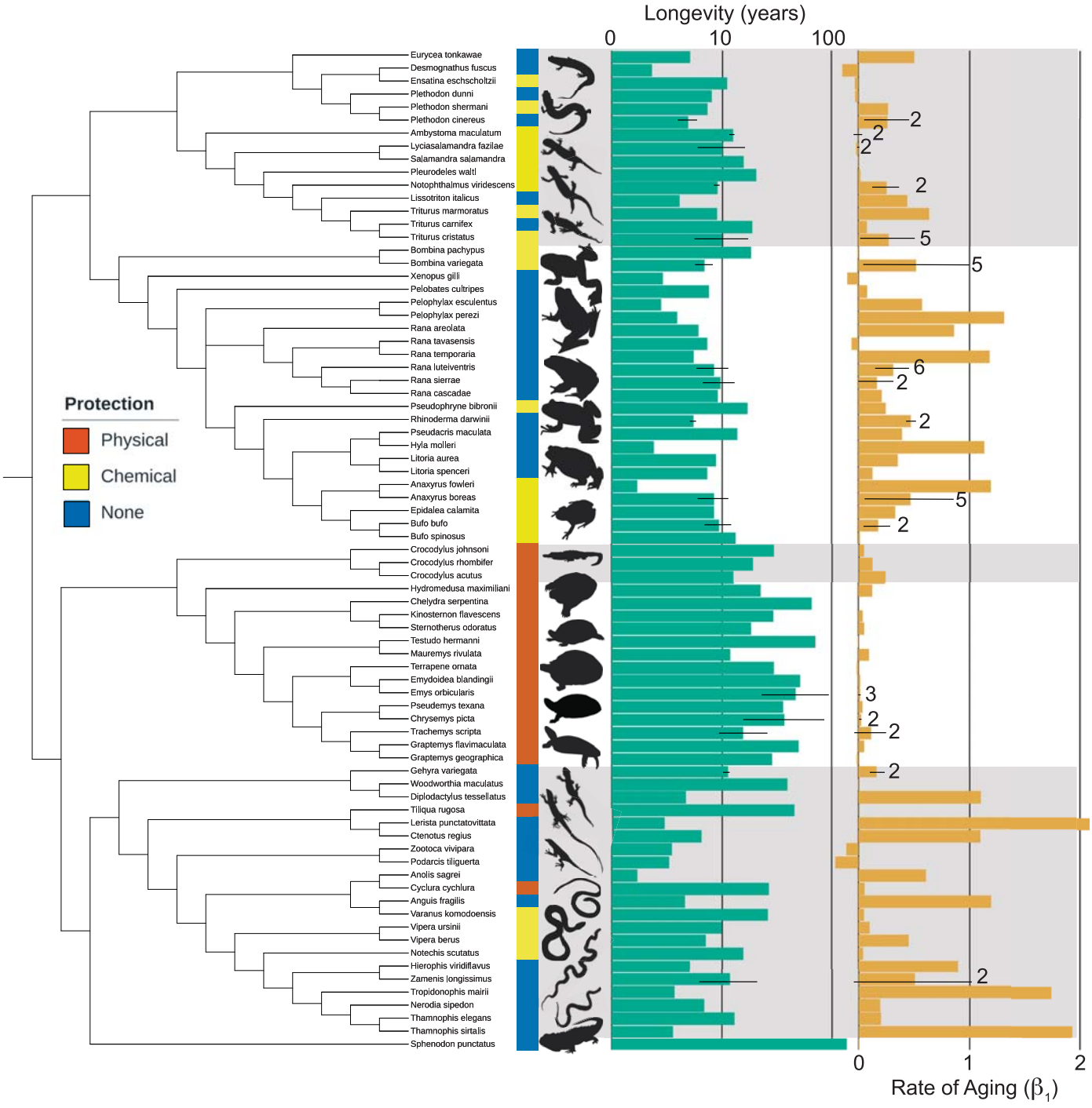

Fig. 1. Tetrapod ectotherms and their measures of aging. The rate of aging is the Gompertz slope parameter indicating how mortality risk increases with age (in number of years since first reproduction). Longevity is the estimated number of years from the age at first reproduction at which 95% of the individuals in a population have died. Error bars show ±1 SD for species for which multiple populations were analyzed. The number next to the bar represents the number of populations included in this study. Shading represents taxonomic orders. Figure was made with iTOL (*67*), and silhouettes are available on phylopic.org.

Table 1. Statistical output for PGLSs and phylogenetic analyses of covariance (ANCOVAs) comparing ectotherms and endotherms for the thermoregulatory mode hypothesis. Group is a factor with two levels: ectotherms versus endotherms. Dashes indicate not applicable. Df, degrees of freedom; Sum sq, sum of squares; Mean sq, mean of the sum of squares; Est, estimate; Adj R^2, adjusted coefficient of determination.

Model	Df	Sum sq	Mean sq	F value	Est	*P* value
Ectotherms versus endotherms						
Rate of aging (Adj R^2 = 0.05)						
Group	1	0.01	0.01	0.001	−0.38	0.77
Log mass	1	126.84	126.84	14.20	−0.08	<0.001
Log mass × group	1	15.64	15.64	1.75	0.04	0.19
Residuals	222	1982.80	8.93	–	–	–
Log longevity (Adj R^2 = 0.20)						
Group	1	2.00	1.96	0.08	−0.31	0.89
Log mass	1	1496.7	1496.7	59.10	0.22	<0.001
Log mass × group	1	6.50	6.50	0.26	−0.03	0.61
Residuals	222	5621.90	25.32	–	–	–
Log longevity (Adj R^2 = 0.38)						
Rate of aging	1	1787.63	1787.63	90.30	−0.87	<0.001
Group	1	2.23	2.23	0.11	−0.63	0.74
Log mass	1	855.15	855.15	43.14	0.17	<0.001
Rate of aging × group	1	108.01	108.01	5.46	0.56	0.02
Residuals	221	4374.00	19.79	–	–	–

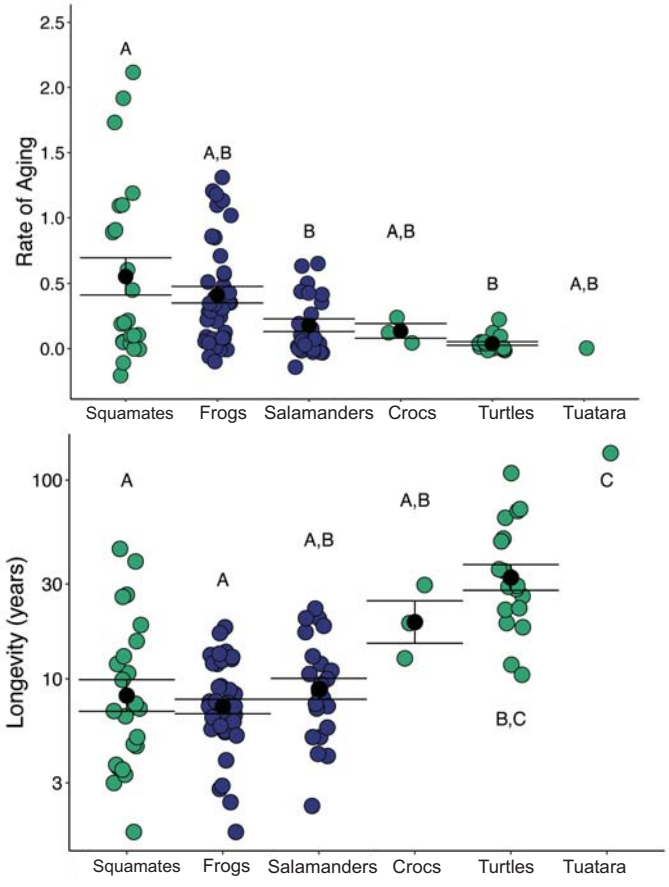

Fig. 2. Measures of rates of aging and longevity across ectotherms. Groups that share letters are not significantly different ($P > 0.05$) after correcting for body mass and phylogeny (table S2). Bars show ±1 SE. Points are uncorrected values for visualization. The rate of aging is the mortality slope derived from a Gompertz model. Longevity is the number of years from the age at first reproduction at which 95% of the individuals in a population have died. Green denotes reptiles, and purple denotes amphibians.

size and phylogeny (table S2), crocodilians, tuatara, and salamanders were similarly slow in aging (crocodilians: mean $\beta_1 = 0.14 \pm 0.06$; tuatara: 0.005; and salamanders: 0.18 ± 0.05) in comparison with squamates (mean $\beta_1 = 0.55 \pm 0.14$) and frogs (mean $\beta_1 = 0.41 \pm 0.06$) (Fig. 2 and data S1). Turtles and tuatara exhibited greater longevity than most other ectothermic tetrapods, with mean longevities of 39 (SE, ±6 years) and 137 years, respectively, compared with crocodilians (21 ± 5 years), squamates (12 ± 2 years), frogs (8 ± 0.6 years), and salamanders (10 ± 1 years) (tables S1 and S2 and data S1), again when corrected for the potential confounding effects of body size and phylogeny.

Thermoregulatory mode hypothesis

Controlling for phylogeny and body size across tetrapods, aging rate and longevity did not differ between ectotherms and endotherms (Table 1 and Fig. 3; see fig. S1 for raw values by taxonomic class). Ectotherms ranged well above and below the known aging rates for endotherms ($C_v = 1.40$ for ectotherms and 1.15 for endotherms, where C_v is the coefficient of variation) and had the greatest longevities ($C_v = 0.37$ for ectotherms and 0.32 for endotherms) (fig. S1). The aging patterns of ectotherms were thus more diverse rather than slower than those reported in endotherms. The ectotherm variance in aging rate was significantly greater than the endotherm variance ($F_{106/118} = 5.49$, where $F_{106/118}$ is the F statistic on 106 and 118 degrees of freedom; $P < 0.001$), although the variance in longevities was not statistically different ($F_{106/118} = 1.31$; $P = 0.16$). As expected, there was a negative relationship between aging rate and longevity in both groups, with faster aging rates corresponding to shorter longevity, but the slope of the relationship was more negative in ectotherms than in endotherms (Table 1 and Fig. 3C). The negative association between rate of aging and longevity varied considerably among mammals, birds, reptiles, and amphibians when considered by taxonomic class (fig. S2 and table S3).

Temperature hypothesis

Within ectotherms, the rate of aging increased with mean environmental temperature in reptiles but decreased with mean temperature in amphibians (Table 2 and fig. S3). Models using minimum and maximum temperatures instead of mean temperature showed the same patterns (table S4).

Protective phenotypes hypothesis

We considered three categories of protection: physical (armor and shells), chemical (venom and skin toxins), and neither physical nor chemical (fig. S4). Within ectothermic tetrapods, species with physical or chemical protection aged slower than species with neither physical nor chemical protection (mean $\beta_1 \pm$ SE:

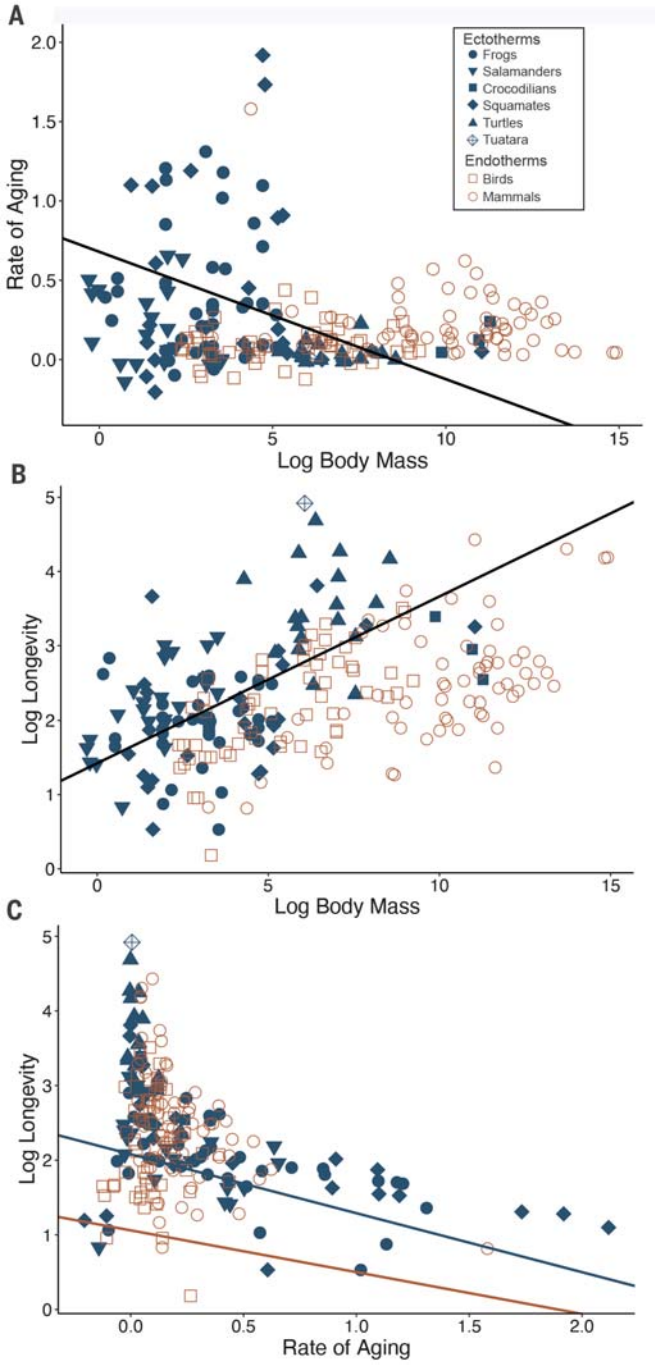

Fig. 3. Comparison between ectothermic and endothermic tetrapods for rates of aging, longevity, and the relationship between aging rate and longevity. (**A**) Comparison for rates of aging. (**B**) Comparison for longevity. (**C**) Comparison for relationship between aging rate and longevity. Trend lines indicate the estimated slopes of each relationship, representing the terms of interest for each model (predicted values not shown). Orange denotes endotherms, and blue denotes ectotherms. Black lines in (A) and (B) show the conditional effect where the interaction term equals zero (i.e., no difference between endotherms and ectotherms). See Table 1 for *P* values of these interactions.

physical, 0.05 ± 0.01; chemical, 0.28 ± 0.06; neither, 0.47 ± 0.07). Species with physical protection lived longer than those with no protection and those with chemical protection (mean years ± SE: physical, 36 ± 5; neither, 11 ± 3; chemical, 11 ± 1) (table S5 and data S1).

Slow-fast continuum hypothesis

We examined relationships between both the age at first reproduction and annual fecundity and rate of aging and longevity. As expected under the slow-fast continuum hypothesis, the rate of aging was negatively associated with the log-transformed age at first reproduction and positively associated with the log-transformed annual fecundity (Table 2). However, because reptiles and amphibians differed in these relationships, we further investigated these associations within each class. This analysis revealed a class-dependent structure of the slow-fast continuum results. Across reptiles, slower rates of aging corresponded to later ages at first reproduction (table S6 and Fig. 4, A and B). Across amphibians, faster rates of aging were associated with larger annual fecundities (table S6 and Fig. 4, A and B). In both amphibians and reptiles, longer 95% longevity was positively associated with later ages at first reproduction, as expected under the slow-fast continuum hypothesis (Table 2 and Fig. 4C). However, longevity was not related to annual fecundity in either class (table S6 and Fig. 4D).

Robustness of findings

Notably, none of these results changed when we restricted the analyses to the best-quality datasets (i.e., >25% of known-age individuals monitored and study length equal to or longer than the median longevity). This demonstrates that variable data quality among populations has no detectable influence (table S8).

Discussion

We found greater variation in aging rates and longevities across wild ectothermic tetrapods than in birds and mammals. Turtles, crocodilians, and salamanders have notably low aging rates and extended longevities for their size. Most turtles have physical protection (bony shells) as well as a relatively slow pace of life, both of which contribute to their negligible aging and exceptional longevity. Future work that focuses on turtles with soft shells (versus rigid, as in this study) may help disentangle causes of slow turtle aging. Although turtle aging rates are low overall, they are surprisingly variable. For example, within *Chrysemys picta*, age at maturity, longevity, and aging rates vary greatly even among populations (*13*, *16*, *17*). Moreover, in this issue, da Silva *et al.* (*51*) show that turtles in captivity demonstrate slow-to-negligible aging rates, similar to our findings in wild species. Our analyses thus provide clear evidence that ectotherms have a great diversity of aging rates and longevities and add to the growing literature on ectotherm aging (*10*, *11*). Within ectotherms, rates of aging ranged from −0.013 to 2.1, corresponding to a continuum from negligible aging to very fast aging. Ectotherm longevity (estimated as the number of years after first reproduction when 95% of adults have died) ranged from 1 to 137 years. For comparison, primate aging rates are between 0.04 and 0.50 (longevity: 4 to 84 years), with a human aging rate of ~0.1 [longevity:100 years (*2*)]. The overall mammalian rates of aging ranged from 0.03 to 0.63, with a single high value of 1.6 observed in eastern moles (*Scalopus aquaticus*), representing an outlier (fig. S1). Although negligible aging was not observed in any mammals included in our analyses, it has been identified in naked mole rats (*52*). One notable group of vertebrates missing from our comparisons is fishes, which have highly variable aging rates

and longevities and contain species of great interest to aging biology (e.g., rock fish, bigmouth buffalo, and short-lived poeciliids) (*53*–*56*).

In addition to expanding the domain for aging research and gaining insights into ectotherm aging, we used newly collected data to test four hypotheses on the evolution of aging in a phylogenetic comparative framework. Our test of the thermoregulatory mode hypothesis revealed that, contrary to expectations, ectotherms did not have slower rates of aging or longer lifespans compared with similar-sized endotherms. However, thermoregulatory mode does appear to modulate the relationship between aging rate and longevity (when phylogenetically and body-mass controlled: Fig. 3C).

We found mixed support for the temperature hypothesis as it relates to rate of aging [in agreement with Stark and colleagues' work on maximum longevity (*10*, *11*)]; mean environmental temperature interacted with class such that the rate of aging increased with temperature in reptiles but decreased with temperature in amphibians (fig. S3 and Table 2). Moreover, this interaction corresponded to the same directionalities when we tested for a relationship with minimum or maximum environmental temperature (table S4). We found no association between longevity and mean, minimum, or maximum environmental temperature. Because temperature is a proximate mediator of cellular and biochemical processes, it is also likely an agent of selection for local adaptation among populations—and plasticity within individuals—for phenotypes related to aging and longevity [(*31*), reviewed in (*57*)]. By definition, increasing environmental temperature increases ectotherm metabolic rate (barring offsetting thermoregulatory behavior) and putatively hastens accumulation of molecular damage through multiple processes, such as free radical production, telomere attrition, secretion of cytokines from senescent cells, and DNA damage (*57*). For example, in garter snakes and the Columbia spotted frog, thermal differences among populations have been hypothesized to be an agent of selection for life-history divergence, including aging (*33*, *58*). Laboratory experiments that raise ectotherms under different thermal regimes can directly test for the proximate effect of temperature on aging (*59*) and are necessary to tease apart how temperature might influence the evolution of aging. Whether and how global warming will affect the evolution of aging rates remains unknown but will become especially important to understand for making management and conservation decisions that prevent species extinctions.

Our analyses also support the protective phenotypes hypothesis within ectothermic tetrapods. Species with physically protective phenotypes, such as armor, spines, or shells, aged more slowly and lived much longer for their size than those without protective phenotypes (table S5). Although species with chemical protection have greater maximum longevities than those without (*37*, *38*), we provide evidence that metrics describing the adult mortality trajectory are linked to these protective phenotypes. This result may explain uniquely slow rates of aging in turtles coupled with extended longevities. Salamanders also aged slowly relative to other tetrapod ectotherms. We were unable to include behaviors, such as fossorial lifestyles, aquatic versus terrestrial behavior, or seasonal activity, that may function as behavioral protections by reducing predation risk and lowering mortality rates [(*3*) though see (*11*), which found that microhabitat preference, including fossorial behavior, did not influence maximum longevity]. Moreover, many salamanders have regenerative capabilities that could contribute to slowing

Table 2. Statistical output for ectotherm PGLSs showing output of all predictor variables for the temperature, protective phenotypes, and slow-fast continuum hypotheses. Protection is a factor with three levels: none, chemical, and physical. Class is a factor with two levels: reptile and amphibian. Dashes indicate not applicable. λ, Pagel's λ.

PGLS model	Df	Sum sq	Mean sq	F value	Est	*P* value
Temperature hypothesis						
Rate of aging (Adj R^2 = 0.06, λ = 0)						
Class	1	0.01	0.01	0.05	−0.28	0.17
Mean temp	1	0.0003	0.0003	0.002	−0.002	0.09*
Class × mean temp	1	1.02	1.02	5.41	0.004	0.02
Log mass	1	0.96	0.96	5.09	−0.06	0.004
Residuals	102	19.27	0.19	–	–	–
Log longevity (Adj R^2 = 0.14, λ = 0.68)						
Class	1	0.71	0.71	0.63	0.42	0.71
Mean temp	1	1.26	1.26	1.12	−0.001	0.50*
Class × mean temp	1	0.15	0.15	0.13	−0.001	0.72
Log mass	1	22.34	22.34	19.83	0.18	<0.001
Residuals	102	114.90	1.13	–	–	–
Protective phenotypes hypothesis						
Rate of aging (Adj R^2 = 0.12, λ = 0)						
Protection	2	2.96	1.48	8.41	None: 0.22 Physical: −0.31 Chemical: 0.21	<0.001*
Log mass	1	0.15	0.15	0.88	0.02	0.35
Residuals	103	18.14	0.18	–	–	–
Log longevity (Adj R^2 = 0.44, λ = 0)						
Protection	2	35.42	17.71	42.38	None: −0.33 Physical: 0.91 Chemical: 2.09	<0.001*
Log mass	1	1.10	1.10	2.64	0.06	0.11
Residuals	103	43.04	0.42	–	–	–
Slow-fast continuum hypothesis						
Rate of aging (Adj R^2 = 0.17, λ = 0)						
Log age at reproduction	1	1.09	1.09	6.44	−0.26	0.01*
Log annual fecundity	1	0.36	0.36	2.11	0.07	0.04*
Class	1	0.25	0.25	1.49	0.45	0.03
Log mass	1	2.63	2.63	15.74	−0.03	0.41
Residuals	99	16.64	0.17	–	–	–
Log longevity (Adj R^2 = 0.50, λ = 0)						
Log age at reproduction	1	9.08	9.08	23.50	0.75	<0.001*
Log annual fecundity	1	8.70	8.70	22.54	−0.06	0.19*
Class	1	4.36	4.36	11.28	−0.08	0.79
Log mass	1	18.52	18.52	47.96	0.06	0.25
Residuals	99	38.22	0.39	–	–	–

**P* values correspond to tests of the specific hypothesis in question.

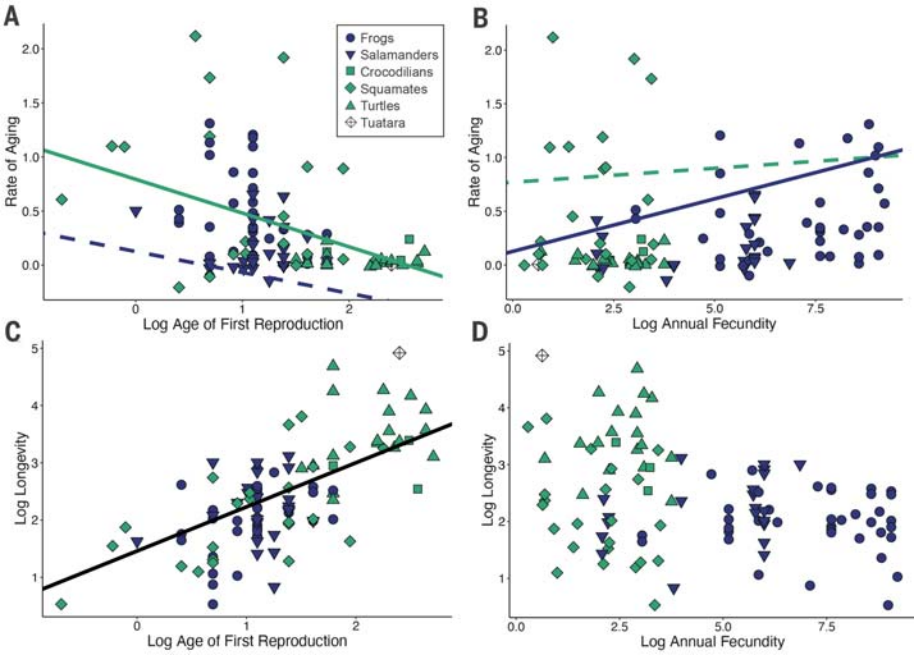

Fig. 4. Slow-fast continuum hypothesis. (**A** to **D**) Solid lines show the estimated statistically significant ($P < 0.05$) relationships between variables and are derived from phylogenetic generalized least squares regressions (PGLSs) from Table 2. Dashed lines are included for visualizing the contrasting class. Predicted values are not shown. Green denotes reptiles, and purple denotes amphibians. The black line in (C) denotes the overall effect (no difference between reptiles and amphibians). Age at first reproduction and annual fecundity themselves did not differ by class (when controlling for phylogeny and body mass; table S7).

aging through greater damage repair efficiency (*15*, *60*, *61*).

Lastly, we document that the slow-fast continuum of life histories is correlated with aging patterns. Both rates of aging and longevities were associated with other biological traits (e.g., age at first reproduction and annual fecundity) in reptiles and amphibians. Earlier age at first reproduction in reptiles was correlated with faster aging rates (Table 2 and Fig. 4). A similar pattern has been documented in birds and mammals, where an earlier age at first reproduction corresponded to an earlier age of onset of senescence (*62*, *63*). Amphibian species with higher annual fecundities, and therefore greater annual reproductive allocation, had faster rates of aging, which has also been found in birds and mammals and supports Hamilton's original prediction (*24*). Earlier age at first reproduction was also associated with shorter longevity in both amphibians and reptiles (Fig. 4). Heralded as a key component of the life-history portfolio (*64*, *65*), this positive relationship between age at first reproduction and adult longevity is thus robust across tetrapod ectotherms as well. These results are congruent with patterns detected in endothermic vertebrates (*4*) and fit into an existing evolutionary framework of genetic correlations underlying relationships among life-history traits, including aging and longevity. Further work on the quantitative genetic and genomic bases of aging and longevity is necessary to broadly test whether genetic correlations underlie these phenotypic associations.

The evolution of aging rates and longevity has seemingly multiple determinants, from life-history traits to morphological adaptations, yielding complex aging patterns across free-ranging tetrapods (*1*). Long-term studies of species from wild populations were necessary for understanding such complexity in the natural context in which aging evolved (*66*) and enabled the use of more-accurate aging metrics. Our compilation of long-term field studies clarifies patterns underlying the evolution of aging rate in tetrapod vertebrates, highlighting links among protective phenotypes, life-history tactics, and aging variation in the wild.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abm0151
Materials and Methods
Supplementary Text
Figs. S1 to S7
Tables S1 to S8
References (*69*–*90*)
MDAR Reproducibility Checklist
Data S1

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REPORTS

AGING

Slow and negligible senescence among testudines challenges evolutionary theories of senescence

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Is senescence inevitable and universal for all living organisms, as evolutionary theories predict? Although evidence generally supports this hypothesis, it has been proposed that certain species, such as turtles and tortoises, may exhibit slow or even negligible senescence—i.e., avoiding the increasing risk of death from gradual deterioration with age. In an extensive comparative study of turtles and tortoises living in zoos and aquariums, we show that ~75% of 52 species exhibit slow or negligible senescence. For ~80% of species, aging rates are lower than those in modern humans. We find that body weight positively relates to adult life expectancy in both sexes, and sexual size dimorphism explains sex differences in longevity. Unlike humans and other species, we show that turtles and tortoises may reduce senescence in response to improvements in environmental conditions.

How much can aging be altered, slowed, or brought to a halt altogether? In the past century, we have witnessed unprecedented increases in human longevity (*1*). Yet, research on humans and nonhuman primates shows that these improvements have resulted from averting early deaths and age-independent sources of mortality, not from reducing the rate of aging (*2*, *3*). The rate of aging is a measure of the speed at which the risk of mortality increases with age. It is the direct result of senescence, a gradual deterioration of bodily functions that manifests as an increase in mortality risk with age after sexual maturity (*4*). Current evolutionary theories of senescence state that, among all organisms with a clear separation between somatic and germline cell lineages, senescence is inevitable (*4*, *5*). Paradoxically, empirical evidence (*6*, *7*) and evolutionary demographic models (*8*, *9*) have proposed that evolution may permit some species to reduce or even avoid the effects of senescence (i.e., negligible senescence).

Species that continue growing after reproductive maturity (e.g., turtles and tortoises) (*8*) are the prime candidates for escaping senescence. These indeterminately growing species may gain survival advantages and larger reproductive potential with age, which allows them to invest more in somatic maintenance and potentially slowing senescence. To date, only a handful of studies have investigated senescence in animal species with indeterminate growth, such as turtles and tortoises (*10*–*13*), where different populations of the same species can show evidence of both senescence and negligible senescence (*12*–*15*). Thus, the question remains: Can some species slow or even avoid growing old? And if so, under what circumstances?

In this work, we carried out an extensive study of age- and sex-specific mortality and growth patterns in turtles and tortoises (order Testudines). Using the Species360 Zoological Information Management System (ZIMS) (*16*), we obtained husbandry records for 52 species spanning a diversity of life-history strategies, body weights, and longevities (table S1). Using Bayesian survival trajectory analysis (*17*, *18*), we estimated for females (47 species) and males (39 species) adult age-specific mortality, remaining adult life expectancy, and aging rates. From the best-fitting models, we calculated 95% credible intervals (CIs) of aging rates at the age when the survival function reached 0.2 (i.e., when 80% of adults are expected to have died) (*19*). We considered this age to be sufficiently advanced to occur after the onset of senescence but not so late as to greatly increase the uncertainty in the estimated aging rates.

CIs of aging rates included zero for 74.5% of species (35 species) for females and 79.5% (31 species) for males (Fig. 1). CIs of some species were either negative [i.e., *Testudo graeca* and *Siebenrockiella crassicollis*, 4.2% (2 species) for females and 2.6% (1 species) for males] or spanned narrowly around zero (e.g., females of *Aldabrachelys gigantea* and males of *Gopherus berlandieri*), which may suggest the existence of negligible senescence among these species. CIs

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