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

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1 **Abstract:**

2 Comparative studies of mortality in the wild are necessary to understand the evolution of
3 aging, yet ectothermic tetrapods are under-represented in this comparative landscape despite
4 their suitability for testing evolutionary hypotheses. We present a study of aging rates and
5 longevity across wild tetrapod ectotherms, utilizing data from 107 populations (77 species) of
6 reptiles and amphibians. We test hypotheses of how thermoregulatory mode, temperature,
7 protective phenotypes, and pace of life-history contribute to aging. Controlling for phylogeny
8 and body size, ectotherms display a higher diversity of aging rates than endotherms, and include
9 phylogenetically-widespread evidence of negligible aging. Protective phenotypes and life-history
10 strategies further explain macroevolutionary patterns of aging. By adding ectothermic tetrapods,
11 our comparative analyses enhance our understanding of the evolution of aging.

12 **One-Sentence Summary:** Aging rates are highly variable among ectothermic tetrapods in the
13 wild, ranging from negligible aging to fast aging rates, and aging rates decrease in species with
14 protective phenotypes (e.g., armor, venom) and slow-paced life histories.

15 **Main Text:** Comparative studies of animal aging rates in the wild are critical for assessing the
16 potential limits of longevity and understanding ecological and evolutionary factors shaping
17 variation in aging strategies (1–3). Demographic indicators of aging include adult longevity and
18 whether, and at what rate, age-specific mortality accelerates with advancing adult age. Previous
19 comparative studies have provided important insights regarding the evolution of demographic
20 aging in the endothermic tetrapods (birds and mammals; e.g., 2–6). However, ectotherms hold
21 most of the records for animal longevity, and comprise 26 of the 30 known records for vertebrate
22 species with maximum longevity estimated to be over 100 years (8–11) (tetrapod examples
23 include Galapagos tortoises, eastern box turtles, European pond turtles, and *Proteus*

24 salamanders). Additionally, some ectothermic tetrapods may exhibit low or even negligible
25 (sensu 12) mortality and reproductive aging (1, 13–18). Understanding whether, and how, natural
26 selection has shaped mortality trajectories and longevity requires phylogenetically-controlled
27 tests to determine whether these species-specific results are anomalies that evolved in specific
28 lineages of ectotherms, or if they are common and repeated evolutionary outcomes. Recent
29 advances in contrasting endotherm and ectotherm longevity have contributed to a phylogenetic
30 perspective on lifespan (10, 11), but often use maximum longevity as their metric, which is not
31 based on the age-specific mortality trajectory and is strongly influenced by sample size, so can
32 lead to inaccurate conclusions (19, 20). Additionally, the lack of comparative analyses of aging
33 rates in ectothermic tetrapods is a major gap in our knowledge(21). A comprehensive analysis of
34 aging across ectothermic tetrapods requires decades of field-based population-level research,
35 international collaborations, and powerful quantitative tools. Integrating these efforts across
36 studies and taxa allows for using data from ectotherms to test evolutionary hypotheses of aging
37 (21), and for a phylogenetic understanding of the evolution of aging across tetrapods.

38 The evolutionary genetics of aging result from age-specific mutation-selection balance
39 trajectories where mutations have age-specific effects that may be strictly deleterious in later
40 adult stages or ages, and/or beneficial earlier (i.e., antagonistically pleiotropic, 22). Hypotheses
41 for how natural selection and the environment interact to shape this balance were first formulated
42 by Medawar (23), and further developed by Hamilton (24) and others (25–27). In ectotherms,
43 body temperature varies with the environment and, because metabolism responds to temperature,
44 ectothermic metabolism and cellular processes downregulate in cold temperatures, allowing for
45 extended periods of brumation and aestivation. In addition, after controlling for body size,
46 ectotherms have lower resting metabolic rates than endotherms (28). Accordingly, the

47 Thermoregulatory Mode Hypothesis predicts that ectothermic lineages have evolved lower aging
48 rates and greater longevities than their similarly-sized endothermic counterparts (29, 30).
49 Layered on top of metabolic mode, environmental temperature itself is expected to be a strong
50 driver of mortality in ectotherms, impacting both the evolution and the plasticity of aging
51 through metabolic mechanisms (10, 31, 32, but see 33). Within many endothermic species,
52 individuals with lower body temperatures have been found to live longer and age slower than
53 those with higher body temperatures (29, 34), but across species, this pattern is less clear (35).
54 Similarly, ectotherms in cooler climates may also exhibit longer lifespans compared to those in
55 warmer climates (10, 11; Temperature Hypothesis, hereafter).

56 Phenotypes that alter age-specific mutation-selection trajectories would be expected to
57 result in the evolution of altered rates of aging (24), provided genetic variation exists (27, 36).
58 For example, species with phenotypes that reduce mortality risk are expected to have lower rates
59 of aging than those without (21) (the so-called Protective Phenotypes Hypothesis). Previous
60 work shows that ectothermic tetrapods, such as amphibians, with chemical protection
61 mechanisms can live longer than those without, though how this trait (and any associated
62 behavior) affects the rate of aging remains unknown (11, 37, 38). Tetrapod ectotherms are well-
63 suited for enabling direct comparisons of the rates of aging among species with and without
64 phenotypes that have such physical or chemical protections. Within reptiles, diverse traits may
65 confer protection from predation and/or environmental stressors, including turtle shells,
66 crocodylian armor, and snake venom (even if such traits are exaptations sensu 39). Similarly, in
67 amphibians, many species produce toxic or unpalatable secretions (40). Despite these
68 characteristics, the Protective Phenotypes Hypothesis has not been tested across ectothermic
69 tetrapods using robust aging metrics (but see 10, 11, 37 for analyses using maximum longevities)

70 Aging and longevity may co-evolve through direct or indirect selection on life-history
71 traits that are genetically correlated (3). Under antagonistic pleiotropy, genes that confer higher
72 fitness in early life relative to late life will increase in frequency in populations that are skewed
73 toward younger age classes (24). Because many ectothermic tetrapods have indeterminate
74 growth and fecundity (41, 42), life-history theory predicts that such species should have stronger
75 selection against deleterious late-age mutations relative to species with determinate growth and
76 fecundity (21). Indeed, any species in which individuals from older age classes contribute more
77 to population growth (e.g., fecundity, behavior) relative to other species should have concomitant
78 slower aging. Thus, the aging rate may evolve from genetic covariation among life-history traits,
79 such as annual fecundity, age of first reproduction, and annual survival. This results in a slow-
80 fast continuum of life histories (43–46) that should match slow vs. fast aging rates (the Slow-Fast
81 Continuum Hypothesis). For example, fast aging, expected to be correlated with a short
82 reproductive lifespan, should evolve in a correlated manner with fast pace of life, and vice versa
83 (43, 47). Therefore, the existence of a strong positive covariation among life-history traits (e.g.,
84 48) predicts that the aging rate should covary with age of first reproduction (negatively) and with
85 annual fecundity (positively) such that species that mature relatively early or that allocate
86 relatively more energy to reproduction early in life display faster aging and shorter longevity
87 (45, 49, 50).

88 We applied comparative phylogenetic methods to tetrapod mark-recapture data to
89 analyze variation within ectotherm demographic aging and longevity in the wild, to compare
90 aging and longevity to endotherms, and to address the following four distinct but not mutually-
91 exclusive hypotheses: i) Thermoregulatory Mode, ii) Temperature, iii) Protective Phenotypes,
92 and iv) Slow-Fast Continuum. We analyzed long-term capture-recapture data collected in the

93 wild from 107 populations of 77 species, with study length averaging 17 years (ranging from 4 to
94 60 years), to assess macroevolutionary patterns of aging rate and longevity in free-living
95 amphibians and non-avian reptiles. We present the first comprehensive comparative analysis of
96 patterns of aging across these ectotherms and estimate both the rate of aging (computed as the
97 slope of the relative rate of increasing age-specific mortality derived from the Gompertz model-
98 β_1) and longevity (computed as the number of years after the age of first reproduction until 95%
99 of adults in a given cohort have died, as opposed to the age of the longest-lived individual).
100 Specifically, we test: i) whether ectotherms consistently age more slowly and live longer than
101 endotherms, ii) whether annual mean, minimum, or maximum environmental temperature
102 experienced by a population covaries with rate of aging and longevity, iii) whether species with
103 protective phenotypes (either physical or chemical) age slower and live longer than those without
104 physical or chemical protections, and iv) whether the rate of aging and longevity strongly covary
105 with other biological traits such as age at first reproduction and annual fecundity.

106 **Aging in ectothermic tetrapods**

107 All orders represented by the 77 reptile and amphibian species for which age-specific
108 estimates of mortality could be estimated had at least one species with negligible aging ($\beta_1 \sim 0$;
109 Fig 1, Data S1). Notably, turtles had slow rates of aging (mean $\beta_1 \pm SE = 0.04 \pm 0.01$), with a
110 narrow range relative to the number of species represented (-0.013 – 0.225 for 14 species; Fig 2,
111 Table S1). When corrected for body size and phylogeny (Table S2), crocodylians, tuatara, and
112 salamanders were similarly slow in aging (crocodylians: mean $\beta_1 = 0.14 \pm 0.06$, tuatara: 0.005,
113 and salamanders: 0.18 ± 0.05) in comparison to squamates (mean $\beta_1 = 0.55 \pm 0.14$) and frogs
114 (mean $\beta_1 \pm SE = 0.41 \pm 0.06$; Fig 2, Data S1). Turtles and tuatara exhibited greater longevity
115 (95% of adult lifespan) than most other ectothermic tetrapods, with mean longevitys of 39 ($\pm SE$

116 6) and 137 years, respectively, compared to crocodylians (21 years \pm 5), squamates (12 years \pm
117 2), frogs (8 years \pm 0.6), and salamanders (10 years \pm 1; Table S1-S2, Data S1), again when
118 corrected for the potential confounding effects of body size and phylogeny.

119 **Thermoregulatory Mode Hypothesis**

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

133 **Temperature Hypothesis**

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

137 **Protective Phenotypes Hypothesis**

138 We considered three categories of protection: physical (armor and shells), chemical
139 (venom and skin toxins), and neither physical nor chemical (Fig S4). Within ectothermic
140 tetrapods, species with physical or chemical protection aged slower than species with neither
141 physical nor chemical protection (mean $\beta_1 \pm \text{SE}$; physical: 0.05 ± 0.01 , chemical: 0.29 ± 0.06 ,
142 neither: 0.47 ± 0.07). Species with physical protection lived longer than those with no protection
143 and those with chemical protection (mean years $\pm \text{SD}$; physical: 36 ± 5 , neither: 10 ± 3 ,
144 chemical: 11 ± 1 , Table S5, Data S1).

145 **Slow-fast Continuum Hypothesis**

146 We examined relationships between both the age of first reproduction and annual
147 fecundity and rate of aging and longevity. As expected under the slow-fast continuum
148 hypothesis, the rate of aging was negatively associated with the log age of first reproduction, and
149 positively associated with the log annual fecundity (Table 2). However, because class (i.e.,
150 reptile or amphibian) influenced these relationships, we further investigated these associations
151 within class. This analysis revealed a class-dependent structure of the slow-fast continuum
152 results. A decreasing rate of aging with increasing age of first reproduction structured the life
153 history variation in reptiles, whereas an increasing rate of aging with increasing annual fecundity
154 structured the life history variation in amphibians (Table S6, Fig 4A-4B). In both amphibians and
155 reptiles, longevity was positively associated with the age of first reproduction, as expected under
156 the slow-fast continuum hypothesis (Table 2, Fig. 4C). However, longevity was not related to
157 annual fecundity in either class (Table S6, Fig 4D). Importantly, all of these results were still true
158 when we restricted the analyses to the best quality datasets (i.e., >25% of known-age individuals
159 monitored and study length equal to or longer than the median longevity), demonstrating that
160 variable data quality among populations has no detectable influence (Table S8).

161 Discussion

162 We found greater variation in aging rates and longevities across wild ectothermic
163 tetrapods than in birds and mammals. Our study thus demonstrates that the parameter space for
164 aging rates and longevities is much larger in ectotherms than previously thought. Turtles,
165 crocodylians, and salamanders have remarkably low aging rates and extended longevities for
166 their size. Most turtles have physical protection (bony shells), as well as a relatively slow pace of
167 life, which both contribute to the negligible aging and exceptional longevity. Future work that
168 focuses on turtles with soft shells (versus rigid, as in this study) may help disentangle causes of
169 slow turtle aging. While turtle aging rates are low overall, they are surprisingly variable. For
170 example, in *Chrysemys picta*, age at maturity, longevity, and aging rates vary significantly
171 among populations (8, 11, 12, this study). Our analyses thus provide clear evidence that
172 ectotherms have a remarkable diversity of aging rates and longevities and add to the growing
173 literature on ectotherm longevity (e.g., 10, 11). Within ectotherms, rates of aging ranged from -
174 0.013 to 2.0, corresponding to a continuum from negligible aging to fast aging. Ectotherm
175 longevity (measured here as the age when 95% of adults have died) ranged from 1 year to 137
176 years. For comparison, primate aging rates are between 0.04 – 0.50 (longevity: 4 – 84 years),
177 with a human aging rate of about 0.1(longevity:100 years; 2). The overall mammalian rates of
178 aging ranged from 0.03 to 1.2, with a single high value observed in eastern moles (*Scalopus*
179 *aquaticus*) representing an outlier (Fig S1). Although negligible aging was not observed in the
180 mammals included in our sample, it has been identified in naked mole-rats (51). One notable
181 group of vertebrates missing from our comparisons is fishes, which themselves have highly
182 variable aging rates and longevities and contain species of great interest to aging biology (e.g.,
183 rock fish, bigmouth buffalo, and short-lived poeciliids) (52–55).

184 In addition to expanding the domain for aging research and gaining insights into
185 ectotherm aging, we used novel data to test four hypotheses on the evolution of aging in a
186 comparative framework. Our test of the Thermoregulatory Mode Hypothesis revealed that,
187 contrary to the expectation, ectotherms did not have slower rates of aging (Adjusted $R^2=0.05$,
188 $p=0.26$) or longer lifespans (Adjusted $R^2=0.20$, $p=0.64$) than similar-sized endotherms.
189 However, thermoregulatory mode does appear to modulate the relationship between aging rate
190 and longevity (when phylogenetically and body-mass controlled: Adjusted $R^2=0.38$, Fig 3C).

191 We found mixed support for the Temperature Hypothesis as it relates to rate of aging (in
192 agreement with Stark and colleagues' work on maximum longevity; *10, 11*); mean
193 environmental temperature interacted with class such that the rate of aging increased with
194 temperature in reptiles, but decreased with temperature in amphibians (Fig S3, Table 2).
195 Moreover, this interaction corresponded to the same directionalities when we tested for a
196 relationship with minimum or maximum environmental temperature (Table S4). We found no
197 association between longevity and mean, minimum, or maximum environmental temperature.
198 Because temperature is a proximate mediator of cellular and biochemical processes, it is also
199 likely a driver of local adaptation among populations – and plasticity within individuals – for
200 phenotypes related to aging and longevity (*31*, reviewed in *56*). Temperature increases ectotherm
201 metabolic rate (or at least the length of the active season) and putatively hastens accumulation of
202 molecular damage via multiple processes such as free radical production, telomere attrition,
203 secretion of cytokines from senescent cells, and DNA damage (*56*). For example, in garter
204 snakes and at least one frog species, thermal differences among populations have been
205 hypothesized to be an agent of selection for life-history divergence, including aging (*33, 57*).
206 Laboratory experiments that raise ectotherms under different thermal regimes can directly test

207 for the proximate effect of temperature on aging (e.g., 58), and are necessary to tease apart how
208 temperature might influence the evolution of aging. Whether and how global warming will
209 impact the evolution of aging rates remains unknown, but will become especially important to
210 understand for making management and conservation decisions to avoid species extinctions.

211 Our analyses also support the Protective Phenotypes Hypothesis within ectothermic
212 tetrapods. Species with physically protective phenotypes, such as armor, spines, or shells, aged
213 more slowly and lived much longer for their size than those without protective phenotypes
214 (Table S5). Though species with chemical protection have greater maximum longevity than
215 those without (38, 59), we provide here the first evidence that metrics describing the adult
216 mortality trajectory are linked to these protective phenotypes. This result may explain uniquely
217 slow rates of aging in turtles, coupled with extended longevity. Salamanders also aged slowly
218 relative to other tetrapod ectotherms. We were unable to include behaviors such as fossorial
219 lifestyles or seasonal activity, that may function as behavioral protections by reducing predation
220 risk, with a consequence of low mortality rates (3, though see 11 which found that microhabitat
221 preference, including fossorial behavior, did not influence maximum longevity). Moreover,
222 many salamanders have regenerative capabilities that could contribute to slowing aging through
223 greater damage repair efficiency (15, 60, 61).

224 Lastly, we document that the slow-fast continuum of life histories is strongly involved in
225 shaping aging. Both rates of aging and longevity were associated with other biological traits
226 (e.g., age at first reproduction and annual fecundity) in reptiles and amphibians. Earlier age at
227 first reproduction in reptiles was correlated with faster aging rates (Table 2, Fig 4). A similar
228 pattern has been documented in birds and mammals, where an earlier age at first reproduction
229 corresponded to an earlier age at the onset of senescence (62, 63). Amphibian species with

230 higher annual fecundities, and therefore greater annual reproductive allocation, had faster rates of
231 aging, which has also been found in birds and mammals, and supports Hamilton's original
232 prediction (24). Earlier age of first reproduction was also associated with shorter longevity in
233 both amphibians and reptiles (Fig 4). Heralded as a key component of the life-history portfolio
234 (64, 65), this positive relationship between age at first reproduction and adult longevity is thus
235 robust across tetrapod ectotherms as well. These results are congruent with patterns detected in
236 endothermic vertebrates (4) and fit into an existing evolutionary framework of genetic
237 correlations underlying relationships among life-history traits, including aging and longevity.
238 Further work on the quantitative genetic and genomic bases of aging and longevity are necessary
239 to test broadly whether the phenotypic associations are underlain by genetic correlations.

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

248

249 **References and Notes**

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444 Data Collection: All authors

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446 Visualization: BAR, HC

447 Funding Acquisition: AMB, FJJ, DAWM

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450 Writing—review & editing: AMB, FJJ, JFL, JMG, AML

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452 **Competing interests:** Authors declare that they have no competing interests.

453 **Data and materials availability:** Data and code used for these analyses are available in Dryad
454 (#TBD). Individual mark-recapture datasets can be obtained by contacting specific dataset
455 owners (see Data S1).

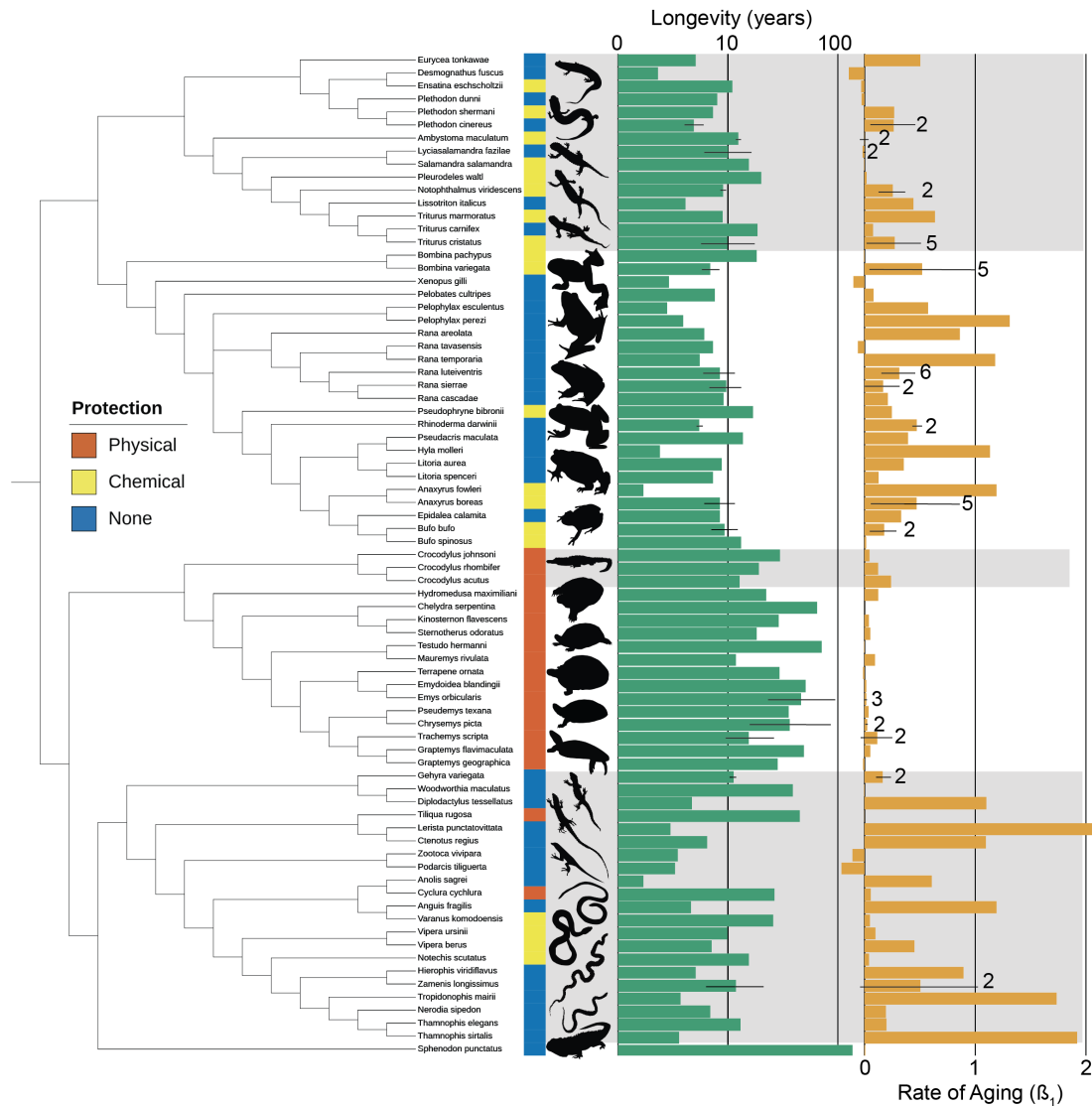
456 **Supplementary Materials**

457 Materials and Methods

458 Supplementary Text

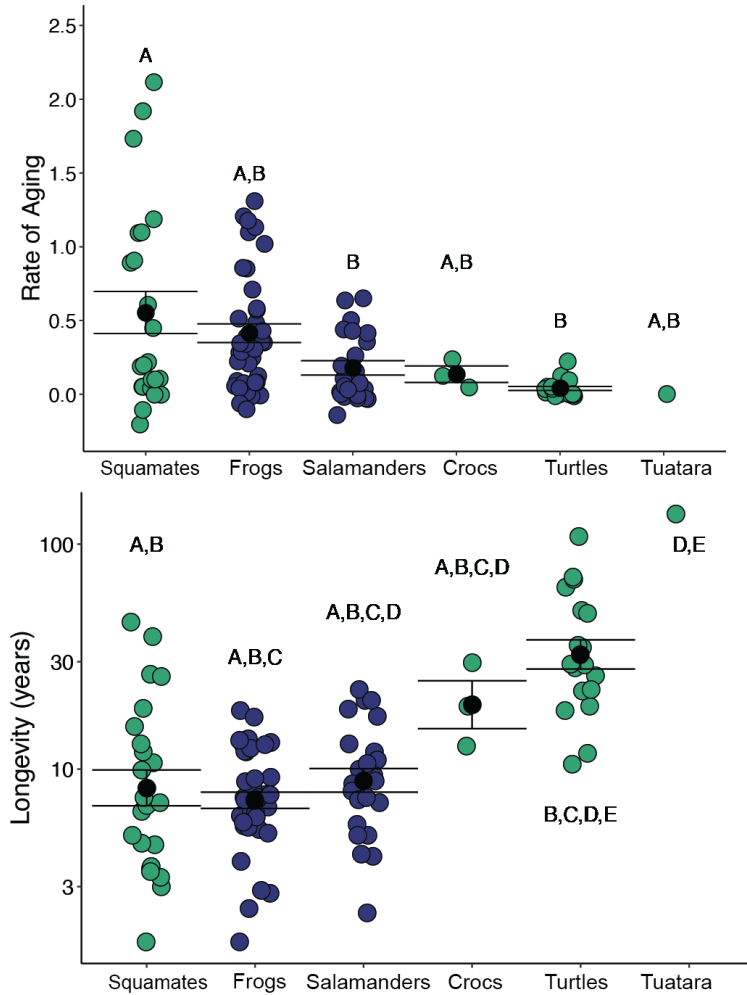
459 Figs. S1 to S7

460	Tables S1 to S8
461	References (67-89)
462	Data S1



463

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



471

472 **Fig. 2. Measures of rates of aging and longevity across ectotherms.** Letters denote statistical
 473 significance ($p < 0.05$) across orders after correcting for body mass and phylogeny (Table S2).

474 Bars show ± 1 SE. Points are uncorrected values for visualization. The rate of aging here is the
 475 mortality slope derived from a Gompertz model. Longevity is the number of years from the age
 476 of first reproduction at which 95% of the individuals in a population have died. Green denotes
 477 reptiles and purple denotes amphibians.

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479

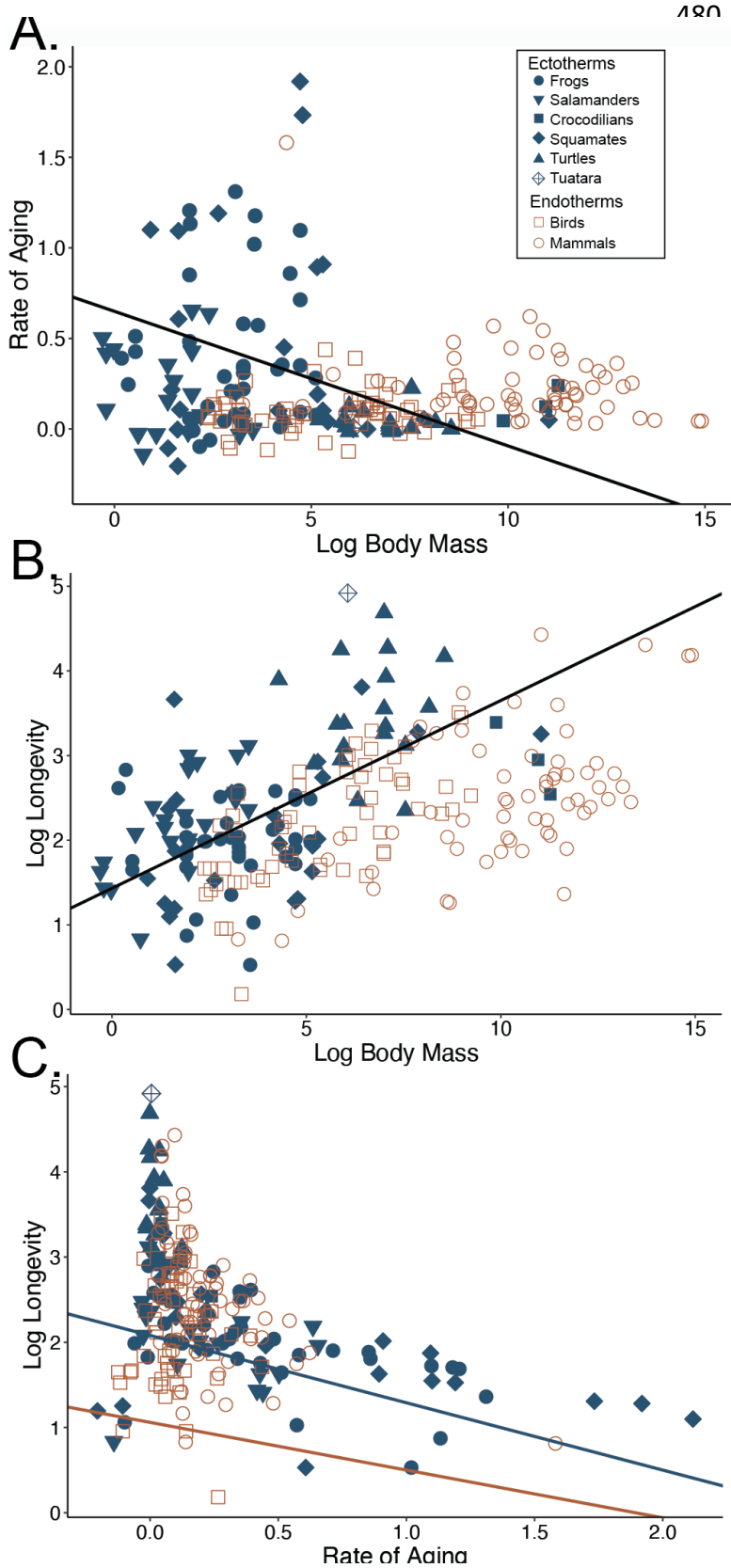
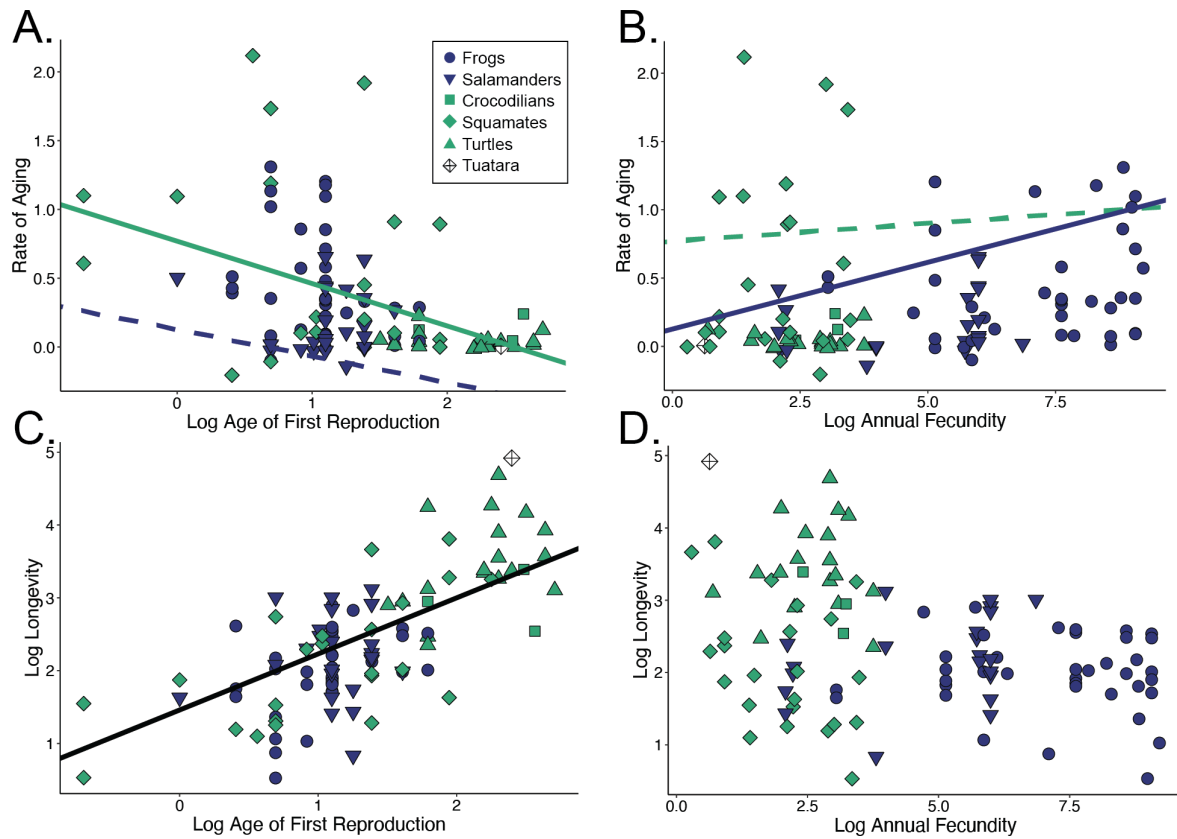


Fig. 3. Comparison between ectothermic and endothermic tetrapods for (A) rates of aging, (B) longevity, and (C) the relationship between aging rate and longevity. Trend lines indicate the estimated slopes of each relationship, representing the terms of interest for each model (predicted values not shown).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



501

502 **Fig 4. Slow-fast Continuum Hypothesis.** Solid lines show the estimated statistically significant
 503 ($p < 0.05$) relationships between variables and are derived from PGLSs from Table 2. Dashed
 504 lines are included for visualizing the contrasting class. Predicted values are not shown. Green
 505 denotes reptiles and purple denotes amphibians. The black line in C denotes the overall effect (no
 506 difference between reptiles and amphibians). Age at first reproduction and annual fecundity
 507 themselves did not differ by class (when controlling for phylogeny and body mass; Table S7).

508 **Table 1. Statistical output for PGLSs and phylogenetic ANCOVAs comparing ectotherms**
 509 **and endotherms for the Thermoregulatory Mode Hypothesis.** Group is a factor with two
 510 levels: ectotherms vs. endotherms. Interaction (bold) terms denote group differences after
 511 correcting for body mass plotted in Fig 3. These were not statistically significant for rate of aging
 512 or longevity (see Fig 3).

Model	Df	Sum Sq	Mean Sq	F value	Est	P-value
Ectotherms vs Endotherms						
Rate of aging (Adj R ² =0.06)						
Group	1	0.01	0.01	0.001	-0.39	0.76
Log mass	1	129.00	129.00	14.46	-0.08	<0.001
Log mass × group	1	16.44	16.44	1.84	0.04	0.18
Residuals	222	1979.85	8.92			
Log longevity (Adj R ² =0.20)						
Group	1	1.96	1.96	0.08	-0.30	0.89
Log mass	1	1479.83	1479.83	59.16	0.22	<0.001
Log mass × group	1	6.83	6.83	0.27	-0.03	0.60
Residuals	222	5620.40	25.32			
Log longevity (Adj R ² =0.37)						
Rate of aging	1	1787.63	1787.63	90.24	-0.87	<0.001
Group	1	2.23	2.23	0.11	-0.63	0.74
Log mass	1	851.72	851.72	42.99	0.17	<0.001
Rate of aging × group	1	107.47	107.47	5.43	0.56	0.02
Residuals	221	4378.00	19.81			

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522 **Table 2. Statistical output for ectotherm PGLSs showing output of all predictor variables**
523 **for the Temperature, Protective Phenotypes, and Slow-fast Continuum Hypotheses.**
524 Protection is a factor with three levels: none, chemical, and physical. Class is a factor with two
525 levels: reptile and amphibian. Bold P-values correspond to tests of the specific hypothesis in
526 question.

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	0.18
Mean temp	1	0.003	0.003	0.002	-0.002	0.08
Class × mean temp	1	1.05	1.05	5.56	0.004	0.02
Log mass	1	1.01	1.01	5.39	-0.07	0.003
Residuals	102	18.54	0.20			
Log longevity (Adj R ² = 0.15, λ = 0.67)						
Class	1	0.72	0.72	0.66	0.42	0.71
Mean temp	1	1.23	1.23	1.12	-0.001	0.51
Class × mean temp	1	0.18	0.18	0.17	-0.001	0.66
Log mass	1	22.34	22.34	20.41	0.18	<0.001
Residuals	102	109.44	1.07			
Protective Phenotypes Hypothesis						
Rate of aging (Adj R ² = 0.11, λ = 0)						
Protection	2	2.79	1.40	7.85	None: 0.20 Physical: -0.32 Chemical: 0.22	<0.001
Log mass	1	0.13	0.13	0.75	0.02	0.39
Residuals	103	18.34	0.18			
Log longevity (Adj R ² = 0.44, λ = 0)						
Protection	2	35.25	17.62	42.15	None: -0.32 Physical: 0.89 Chemical: 2.08	<0.001
Log mass	1	1.25	1.25	3.00	0.06	0.09
Residuals	103	43.06	0.42			

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Slow-fast Continuum Hypothesis						
Rate of aging (Adj R ² = 0.18, λ = 0)						
Log age at repro	1	1.08	1.08	6.48	-0.26	0.01
Log annual fecundity	1	0.39	0.39	2.34	0.07	0.04
Class	1	0.28	0.28	1.71	0.46	0.02
Log mass	1	2.78	2.78	16.73	-0.03	0.41
Residuals	99	16.44	0.17			
Log longevity (Adj R ² = 0.52, λ = 0)						
Log age at repro	1	9.75	9.75	26.34	0.77	<0.001
Log annual fecundity	1	8.89	8.89	24.00	-0.06	0.22
Class	1	4.20	4.20	11.34	-0.06	0.85
Log mass	1	19.38	19.38	52.32	0.05	0.32
Residuals	99	36.66	0.37			

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