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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 wild, ranging from negligible aging to fast aging rates, and aging rates decrease in species with 13 14 protective phenotypes (e.g., armor, venom) and slow-paced life histories. Main Text: Comparative studies of animal aging rates in the wild are critical for assessing the 15 potential limits of longevity and understanding ecological and evolutionary factors shaping 16 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 most of the records for animal longevity, and comprise 26 of the 30 known records for vertebrate 21 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

salamanders). Additionally, some ectothermic tetrapods may exhibit low or even negligible 24 (sensu 12) mortality and reproductive aging (1, 13-18). Understanding whether, and how, natural 25 selection has shaped mortality trajectories and longevity requires phylogenetically-controlled 26 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 rates in ectothermic tetrapods is a major gap in our knowledge(21). A comprehensive analysis of 33 34 aging across ectothermic tetrapods requires decades of field-based population-level research, international collaborations, and powerful quantitative tools. Integrating these efforts across 35 studies and taxa allows for using data from ectotherms to test evolutionary hypotheses of aging 36 37 (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 38 trajectories where mutations have age-specific effects that may be strictly deleterious in later 39 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	crocodilian 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 traits that are genetically correlated (3). Under antagonistic pleiotropy, genes that confer higher 71 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., 48) predicts that the aging rate should covary with age of first reproduction (negatively) and with 84 annual fecundity (positively) such that species that mature relatively early or that allocate 85 86 relatively more energy to reproduction early in life display faster aging and shorter longevities (45, 49, 50). 87

We applied comparative phylogenetic methods to tetrapod mark-recapture data to
analyze variation within ectotherm demographic aging and longevity in the wild, to compare
aging and longevity to endotherms, and to address the following four distinct but not mutuallyexclusive hypotheses: i) Thermoregulatory Mode, ii) Temperature, iii) Protective Phenotypes,
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 amphibians and non-avian reptiles. We present the first comprehensive comparative analysis of 95 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- β_1) and longevity (computed as the number of years after the age of first reproduction until 95% 98 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 with other biological traits such as age at first reproduction and annual fecundity. 105

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), crocodilians, tuatara, and 112 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 to squamates (mean $\beta_1 = 0.55 \pm 0.14$) and frogs 113 114 (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 longevities of 39 (\pm SE 116 6) and 137 years, respectively, compared to crocodilians (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

expected, there was a negative relationship between aging rate and longevity in both groups, with 128

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 $\beta_1 \pm SE$; physical: 0.05 \pm 0.01, chemical:0.29 \pm 0.06,

142 neither: 0.47 ± 0.07). Species with physical protection lived longer than those with no protection

and those with chemical protection (mean years \pm SD; physical: 36 ± 5 , neither: 10 ± 3 ,

144 chemical:11 \pm 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 crocodilians, 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 years. For comparison, primate aging rates are between 0.04 - 0.50 (longevity: 4 - 84 years), 176 177 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 longevities 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 longevities. 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).

Lastly, we document that the slow-fast continuum of life histories is strongly involved in shaping aging. 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, Fig 4). A similar pattern has been documented in birds and mammals, where an earlier age at first reproduction 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 (64, 65), this positive relationship between age at first reproduction and adult longevity is thus 234 235 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.

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249 References and Notes

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456	Supplementary Materials							
457	Materials and Methods							
458	Supplementary Text							
459	Figs. S1 to S7							

460Tables S1 to S8

461 References (67-89)

462 Data S1



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 number of years from the age of 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. Shading represents taxonomic orders. The number next to
the bar represents the number of populations included in this study. Figure was made with iTOL
(*89*) and silhouettes are available on phylopic.org.





Fig. 2. Measures of rates of aging and longevity across ectotherms. Letters denote statistical
significance (p < 0.05) across orders after correcting for body mass and phylogeny (Table S2).
Bars show +/- 1 SE. Points are uncorrected values for visualization. The rate of aging here is the
mortality slope derived from a Gompertz model. Longevity is the number of years from the age
of first reproduction at which 95% of the individuals in a population have died. Green denotes
reptiles and purple denotes amphibians.



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.



Fig 4. Slow-fast Continuum Hypothesis. Solid lines show the estimated statistically significant (p < 0.05) relationships between variables and are derived from 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).

Table 1. Statistical output for PGLSs and phylogenetic ANCOVAs comparing ectotherms

and endotherms for the Thermoregulatory Mode Hypothesis. Group is a factor with two

- levels: ectotherms vs. endotherms. Interaction (bold) terms denote group differences after
- correcting for body mass plotted in Fig 3. These were not statistically significant for rate of aging
- or longevity (see Fig 3).

Model		Sum Sa	Maan Sa	F	Est	Р-
		sum sq	Mean Sq	value		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		107.47	107.47	5.43	0.56	0.02
Residuals	221	4378.00	19.81			

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.

I Christ Note:DidSqSqvalueEstvalueTemperature HypothesisRate of aging (Adj $R^2 = 0.06, \lambda = 0.0$)Class10.010.010.05-0.280.18Mean temp10.0030.0030.002-0.0020.08Class × mean temp11.051.055.560.0040.02Log mass1010.011.015.39-0.070.003Residuals10218.540.20Log longevity (Adj $R^2 = 0.15, \lambda = 0.67$)Class10.720.720.660.420.71Mean temp11.231.231.12-0.0010.56Log mass10.180.180.17-0.0010.66Log mass11.02109.441.07Protective Phenotypes HypothesisRate of aging (Adj $R^2 = 0.11, \lambda = 0.13$ 0)22.791.407.85None: 0.20 Physical: -0.32 Chemical: 0.22.Log mass10.130.130.750.020.39Residuals10318.340.18Log mass10.130.130.750.020.39Residuals10318.340.18Log mass11.25	PGLS Model		Sum	Mean	F	Fet	Р-
Temperature Hypothesis Rate of aging (Adj $R^2 = 0.06$, $\lambda = 0.0$ Image: Relation of a structure interval interv			Sq	Sq	value	LSt	value
Rate of aging (Adj $R^2 = 0.06$, $\lambda =$ 0) I 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 1.55 5.66 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 $R^2 = 0.15$, $\lambda =$ - - </td <td>Temperature Hypothesis</td> <td></td> <td>-</td> <td></td> <td>-</td> <td></td> <td></td>	Temperature Hypothesis		-		-		
0) I 0.01 0.01 0.05 -0.28 0.18 Class mean temp 1 0.003 0.002 -0.002 0.08 Class × mean temp 1 1.05 1.05 5.56 0.004 0.02 Log mass 102 18.54 0.20	Rate of aging (Adj $R^2 = 0.06$, $\lambda =$						
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	0)						
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Class × mean temp11.051.055.560.0040.02Log mass11.011.015.39-0.070.003Residuals10218.540.20Log longevity (Adj $R^2 = 0.15$, $\lambda = 0.67$)Class10.720.720.660.420.71Mean temp11.231.231.12-0.0010.51Class × mean temp10.180.180.17-0.0010.66Log mass122.3422.3420.410.18<0.001	Mean temp	1	0.003	0.003	0.002	-0.002	0.08
Log mass11.011.015.39-0.070.003Residuals10218.540.20 </td <td>Class \times mean temp</td> <td>1</td> <td>1.05</td> <td>1.05</td> <td>5.56</td> <td>0.004</td> <td>0.02</td>	Class \times mean temp	1	1.05	1.05	5.56	0.004	0.02
Residuals10218.540.20Image: constraint of the second s	Log mass	1	1.01	1.01	5.39	-0.07	0.003
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Residuals	102	18.54	0.20			
0.67)0.670.710.720.720.660.420.71Mean temp11.231.231.12-0.0010.51Class × mean temp10.180.180.17-0.0010.66Log mass122.3422.3420.410.18<0.001	Log longevity (Adj $R^2 = 0.15$, $\lambda =$						
Class10.720.720.660.420.71Mean temp11.231.231.12-0.0010.51Class × mean temp10.180.180.17-0.0010.66Log mass122.3422.3420.410.18<0.001	0.67)						
Mean temp11.231.231.12-0.0010.51Class × mean temp10.180.180.17-0.0010.66Log mass122.3422.3420.410.18<0.001	Class	1	0.72	0.72	0.66	0.42	0.71
Class × mean temp10.180.180.17-0.0010.66Log mass122.3422.3420.410.18<0.001	Mean temp	1	1.23	1.23	1.12	-0.001	0.51
Log mass122.3422.3420.410.18<0.01Residuals102109.441.07 \cdot \cdot \cdot \cdot Protective Phenotypes HypothesisRate of aging (Adj R ² = 0.11, λ = 0) \cdot	Class × mean temp	1	0.18	0.18	0.17	-0.001	0.66
Residuals102109.441.07IIIProtective Phenotypes HypothesisRate of aging (Adj $\mathbb{R}^2 = 0.11, \lambda = 0$)II <td< td=""><td>Log mass</td><td>1</td><td>22.34</td><td>22.34</td><td>20.41</td><td>0.18</td><td>< 0.001</td></td<>	Log mass	1	22.34	22.34	20.41	0.18	< 0.001
Protective Phenotypes Hypothesis Rate of aging (Adj $R^2 = 0.11, \lambda = 0$) Image: Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4">Colspan="4"Colspan="4">Colspan="4"Co	Residuals	102	109.44	1.07			
Protective Phenotypes Hypothesis Rate of aging (Adj $\mathbb{R}^2 = 0.11, \lambda = 0$) Image: Colspan=10 and							
Rate of aging (Adj $\mathbb{R}^2 = 0.11, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.11, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.11, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$)Image: Constraint of aging (Adj $\mathbb{R}^2 = 0.44, \lambda = 0$) <td>Protective Phenotypes Hypothesi</td> <td>S</td> <td></td> <td></td> <td></td> <td></td> <td></td>	Protective Phenotypes Hypothesi	S					
0)11 <t< td=""><td>Rate of aging (Adj $R^2 = 0.11$, $\lambda =$</td><td></td><td></td><td></td><td></td><td></td><td></td></t<>	Rate of aging (Adj $R^2 = 0.11$, $\lambda =$						
Protection22.791.407.85None: 0.20 <0.001 Physical: -0.32 Chemical: 0.2210.130.130.750.020.39Log mass10.130.130.750.020.39Residuals10318.340.18Log longevity (Adj $\mathbb{R}^2 = 0.44, \lambda$ = 0)235.2517.6242.15None: -0.32 Physical: 0.89 Chemical: 2.08 <0.001 Protection235.2517.6242.15None: -0.32 Physical: 0.89 Chemical: 2.08 <0.001 Log mass11.251.253.000.060.09Residuals10343.060.42 <0.001	0)						
Log mass10.130.130.75Physical: -0.32 Chemical: 0.22Log mass10.130.130.750.020.39Residuals10318.340.18Log longevity (Adj $R^2 = 0.44, \lambda$ = 0)Protection235.2517.6242.15None: -0.32 Physical: 0.89 Chemical: 2.08<0.001	Protection	2	2.79	1.40	7.85	None: 0.20	< 0.001
Log mass10.130.130.75Chemical: 0.22Log mass10.130.130.750.020.39Residuals10318.340.18Log longevity (Adj $R^2 = 0.44, \lambda$ = 0)Protection235.2517.6242.15None: -0.32 Physical: 0.89 Chemical: 2.08<0.001						Physical: -0.32	
Log mass10.130.130.750.020.39Residuals10318.340.18Log longevity (Adj $\mathbb{R}^2 = 0.44, \lambda$ = 0)Protection235.2517.6242.15None: -0.32 Physical: 0.89 Chemical: 2.08<0.001						Chemical: 0.22	
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Log mass	1	0.13	0.13	0.75	0.02	0.39
Log longevity (Adj $\mathbb{R}^2 = 0.44$, λ = 0)Image: Constraint of the second system o	Residuals	103	18.34	0.18			
= 0) 2 35.25 17.62 42.15 None: -0.32 <0.001	Log longevity (Adj R ² = 0.44, λ						
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	=0)						
Log mass 1 1.25 1.25 3.00 0.06 0.09 Residuals 103 43.06 0.42	Protection	2	35.25	17.62	42.15	None: -0.32	< 0.001
Log mass 1 1.25 1.25 3.00 0.06 0.09 Residuals 103 43.06 0.42						Physical: 0.89	
Log mass 1 1.25 1.25 3.00 0.06 0.09 Residuals 103 43.06 0.42						Chemical: 2.08	
Residuals 103 43.06 0.42	Log mass	1	1.25	1.25	3.00	0.06	0.09
	Residuals	103	43.06	0.42			

Slow-fast Continuum Hypothesis						
Rate of aging (Adj $R^2 = 0.18$, $\lambda = 0$)						
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			