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No evidence for the 'rate-of-living' theory across the tetrapod tree of life

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Editor: Richard Field**Abstract**

Aim: The 'rate-of-living' theory predicts that life expectancy is a negative function of the rates at which organisms metabolize. According to this theory, factors that accelerate metabolic rates, such as high body temperature and active foraging, lead to organismic 'wear-out'. This process reduces life span through an accumulation of biochemical errors and the build-up of toxic metabolic by-products. Although the rate-of-living theory is a keystone underlying our understanding of life-history trade-offs, its validity has been recently questioned. The rate-of-living theory has never been tested on a global scale in a phylogenetic framework, or across both endotherms and ectotherms. Here, we test several of its fundamental predictions across the tetrapod tree of life.

Location: Global.

Time period: Present.

Major taxa studied: Land vertebrates.

Methods: Using a dataset spanning the life span data of 4,100 land vertebrate species (2,214 endotherms, 1,886 ectotherms), we performed the most comprehensive test to date of the fundamental predictions underlying the rate-of-living theory. We investigated how metabolic rates, and a range of factors generally perceived to be strongly associated with them, relate to longevity.

Results: Our findings did not support the predictions of the rate-of-living theory. Basal and field metabolic rates, seasonality, and activity times, as well as reptile body temperatures and foraging ecology, were found to be unrelated to longevity. In contrast, lower longevity across ectotherm species was associated with high environmental temperatures.

Main conclusions: We conclude that the rate-of-living theory does not hold true for terrestrial vertebrates, and suggest that life expectancy is driven by selection arising from extrinsic mortality factors. A simple link between metabolic rates, oxidative damage and life span is not supported. Importantly, our findings highlight the potential for rapid warming, resulting from the current increase in global temperatures, to drive accelerated rates of senescence in ectotherms.

KEYWORDS

basal metabolic rate, body size, body temperature, environmental temperature, field metabolic rate, longevity, the rate-of-living theory

1 | INTRODUCTION

The flame that burns twice as bright burns half as long.

The light that burns twice as bright burns half as long.

The quotes above, ascribed to Lau Tze (Laozi) and from 'Blade Runner', respectively, are thought to convey a universal truth: we have a semi-fixed capacity to do things, and we can either get through them intensively and quickly – or relaxedly but over a longer time. A fundamental principle of life history theory predicts that increased energy expenditure reduces life expectancy (Finkel & Holbrook, 2000; Furness & Speakman, 2008; Glazier, 2015; Hulbert, Pamplona, Buffenstein, & Buttemer, 2007; Magalhães, Costa, & Church, 2007; Pearl, 1928; Rubner, 1908; Van Voorhies, Khazaeli, & Curtsinger, 2003). The mechanistic explanation for this relationship stems from the assumption that higher metabolic rates increase the production of free radicals and other oxidants produced during aerobic respiration. These, in turn, trigger biomolecular damage that accelerates senescence (Barja, 2002; Beckman & Ames, 1998; Sohal, 2002). In line with these mechanisms, multiple studies have suggested that an organism's longevity is an inverse function of mass-specific metabolic rates (Atanasov, 2005; Kapahi et al., 2010; Ku, Brunk, & Sohal, 1993; Sohal, Svensson, Sohal, & Brunk, 1989; Wright et al., 2004). This trade-off is commonly referred to as the 'rate-of-living' theory (Pearl, 1928). According to this theory, degenerative processes lead to a failure of cellular constituents due to the accumulation of biochemical errors and the build-up of toxic metabolic by-products (Sohal, 1986). In support of this theory, comparative and experimental studies have shown that the increased expression of free radicals can shorten life span (Barja & Herrero, 1998; Melov et al., 2000; Orr & Sohal, 1994; Parkes et al., 1998; Sun & Tower, 1999).

Some alternative theories (Hamilton, 1966; Kirkwood, 1977; Kirkwood & Austad, 2000; Medawar, 1952; Réale et al., 2010) have been proposed to explain the variations in life span among animals. According to the evolutionary theories of senescence, species that are exposed to low intrinsic (e.g., replication errors and metabolic waste products and oxidation damage by reactive agents) and extrinsic (such as predation, food shortages or accidents) mortality rates will adapt by slowing down their 'pace of life' (Scharf et al., 2015). Accordingly, they will expand their reproductive potential by evolving longer life spans (Healy, Ezard, Jones, Salguero-Gómez, & Buckley, 2019; De Magalhães et al., 2007). In contrast, animals that are more likely to die due to extrinsic factors, rather than through senescence, benefit from investing in early reproduction at the expense of investment in long-term maintenance (Hamilton, 1966; Kirkwood, 1977; Kirkwood & Austad, 2000; Medawar, 1952).

Life span represents trade-offs between reproduction and maintenance (e.g., the 'disposable soma theory'; Kirkwood, 2017). In taxa facing high extrinsic mortality rates, investing in maintenance is unlikely to pay off if an individual will be preyed upon before it has a chance to reproduce. According to this theory, this will lead to selection for earlier reproduction, and thus earlier senescence

and a shorter life span in taxa suffering high extrinsic mortality rates (Kirkwood & Austad, 2000). Under the disposable soma theory, early reproduction is thought to expose animals to a greater accumulation of age-specific mutations with pleiotropic effects (Gavrillova & Gavrillova, 2002). This has been associated with the 'antagonistic pleiotropy theory', which suggests that some genes encode phenotypes that offer benefits early on in life, while also encoding other traits that are harmful in advanced age (Hamilton, 1966; Kirkwood, 1977; Kirkwood & Austad, 2000; Medawar, 1952; Réale et al., 2010). Such harmful traits, expressed late in life, will be invisible to selection in animals that reproduce young, but will select strongly against animals that reproduce at older ages (Williams, Day, Fletcher, & Rowe, 2006).

The rate-of-living theory has been studied in insects, fish, birds and mammals (Austad & Fischer, 1991; Kelemen, Cao, Cao, Davidowitz, & Dornhaus, 2019; Lindstedt & Calder, 1976; Liu & Walford, 1975; Herreid, 1964). For example, Healy et al. (2014) found that metabolic rate was negatively associated with longevity in non-volant endotherms (supporting the rate-of-living theory). However, several limitations detract from the evidence supporting it. For example, some studies have ignored the influence of phylogenetic non-independence (Austad & Fischer, 1991; Hulbert et al., 2007; Lindstedt & Calder, 1976). Furthermore, some relatively recent studies (Furness & Speakman, 2008; Glazier, 2015; Magalhães et al., 2007; Speakman, 2005) contradict the expectations of the theory. For example, bats and birds have higher metabolic rates compared to, similar-sized, non-volant mammals (Brunet-Rossini & Austad, 2004; Kleiber, 1947; Réale et al., 2010; Wilkinson & Adams, 2019). Bats, nonetheless, are exceptionally long-lived (Lagunas-Rangel, 2019) and use twice as much energy over their lifetimes as do similar sized terrestrial mammals (Healy et al., 2014), indicating there is no fixed amount of energy consumption allocated to an organism's life span.

Magalhães et al. (2007) examined the effect of several factors, including metabolic rates, on the longevity of 1,456 vertebrate species. Their analyses revealed no relationship between metabolism and longevity in eutherians and birds, and a negative link in marsupials. That study, however, was almost entirely restricted to endotherms (94% of the species examined were mammals or birds) and thus could not provide a general explanation for the diversity of longevity across the vertebrate metabolic range. Other such studies (Austad & Fischer, 1991; Furness & Speakman, 2008; Healy et al., 2014; Herreid, 1964; Hulbert et al., 2007; Ku et al., 1993) have also focused almost exclusively on birds and mammals. Although selection from environmental factors (e.g., ambient temperature) may differ dramatically between endotherms and ectotherms, only a few comparative studies (Scharf et al., 2015; Stark & Meiri, 2018) have focused on ectotherm vertebrates, and these have generally ignored metabolic rates. A recent theory (Worm & Tittensor, 2018) suggests that ecological pressures shape evolutionary processes on small spatial and phylogenetic scales while environmental factors, particularly temperature, dominate on larger scales. Environmental effects are thus expected to strengthen when comparing ectotherms with

endotherms. A comprehensive empirical test of the rate-of-living theory across all land vertebrate groups could therefore be highly informative.

To fill this gap we assembled an unprecedented, global-scale, dataset for 4,100 species of terrestrial vertebrates (birds, mammals, reptiles and amphibians), and implemented a highly replicable, comparative test of the rate-of-living theory. We examined the relationship between longevity and a range of metabolically relevant factors, across mammals, birds, reptiles and amphibians. We tested the fundamental predictions that:

1. Slower metabolic rates are associated with prolonged longevity (Nunn & Barton, 2000; Sohal, 1986). This is a direct test of the rate-of-living theory. However, basal metabolic rates are problematic to define for ectotherms – and field metabolic rates for anything but endotherms are exceedingly rare (see below). We examined the relationship between longevity and a suite of additional proxies that are expected to be strongly correlated with metabolic rates.
2. Ectotherms (amphibians and reptiles) will live longer than similar-sized endotherms (mammals and birds) because their lower metabolic rates translate to lower mutation and oxidative damage rates (Hulbert et al., 2007; Sohal, 1986).
3. Nocturnal species (especially ectotherms) will live longer than diurnal ones. Nocturnality reduces exposure to solar radiation, and the lower night-time temperatures reduces ectotherm metabolic rates.
4. Reptiles that actively forage for food will have substantially higher metabolic rates than closely related 'sit-and-wait' foragers with otherwise similar ecologies – even in the same habitat (e.g., Anderson & Karasov, 1981; Nagy, Huey, & Bennett, 1984). Because high metabolic rates are expected to be linked to low longevities, we predict that 'sit-and-wait' foragers will live longer than 'actively-foraging' ones.
5. Body temperature will be negatively associated with ectotherm longevity because ectotherm metabolic rates increase with increasing temperature.
6. In seasonally cold regions many mammals and ectotherms hibernate or aestivate for extended periods (Turbill, Bieber, & Ruf, 2011), reducing metabolic rates, and are thus expected to live longer (Stark & Meiri, 2018; Stark, Tamar, Itescu, Feldman, & Meiri, 2018; Wilkinson & Adams, 2019). Furthermore, ectotherms inhabiting seasonally cold regions grow and metabolize slowly and thus present lower rates of metabolic by-product accumulation. We thus predicted that they will live longer than species living in warmer regions.

2 | METHODS

2.1 | Data collection

We assembled a global dataset on the maximum life span of 4,100 terrestrial vertebrate species (538 amphibians, 1,153 birds, 1,061

mammals and 1,348 reptiles) from the literature (mainly from De Magalhaes & Costa, 2009; Stark & Meiri, 2018; and Stark et al., 2018; see Appendix for a full list of sources). We corrected for the potential bias in which larger samples increase the chance of finding a higher maximum (Stark & Meiri, 2018; Stark et al., 2018) by using sample size as a predictor. We recorded sample sizes from the original publications reporting longevity. Much of our data (especially for endotherms) were taken from the AnAge database (De Magalhaes & Costa, 2009). In AnAge sample sizes are classified as 'small' (up to 10 specimens), 'medium' (11–100), 'high' (101–1,000 individuals) and 'Questionable' for missing data on sample size. We opted to be conservative and classified AnAge 'small' samples as relying on data from one individual; medium samples as relying on data from 11, and large samples as based on data on 101 sampled individuals. Species with no sample sizes were classified as questionable. Analyses in which we used the midpoint of the size estimates from AnAge (i.e., 5, 55 and 555 specimens for 'small', 'medium' and 'large' samples, respectively) yielded qualitatively similar results (not shown).

We performed a sensitivity analysis incorporating only the 2,140 species for which maximum longevity was estimated from 30 or more individuals (i.e., based on numerical data from the primary literature indicating at least 30 specimens were studied, and only on the 'high' category of AnAge). We accounted for the fact that longevity of captive individuals is often higher than that of wild ones (Scharf et al., 2015; Stark & Meiri, 2018) by treating data origin as another predictor. Data on the predictor variables (see Supporting Information Appendix S1) were gathered from the sources used to estimate longevity, and, if not reported there, from the primary literature (see Appendix for a full list of sources). We accounted for body size in our analysis by using body mass (in grams) as a predictor. We collected data on mean body mass for each species using data from AnAge (De Magalhaes & Costa, 2009) for birds and mammals, from Slavenko, Tallowin, Itescu, Raia, and Meiri (2016) for reptiles and from Stark and Meiri (2018) for amphibians. To account for differences between the sexes we averaged the mean body size of females and males if those were reported separately. For endotherms, mass data are routinely reported. For amphibians and reptiles body size data are almost always reported as lengths (Meiri, 2010; Pincheira-Donoso & Hodgson, 2018; Santini, Benítez-lópez, Ficetola, & Huijbregts, 2018). To enable a comparison of all taxa we converted body length to mass using the clade and measurement-specific allometric equations (Feldman & Meiri, 2013; Feldman, Sabath, Pyron, Mayrose, & Meiri, 2016; Santini et al., 2018).

We classified species as diurnal, nocturnal, crepuscular or cathemeral (the latter two were expected to have intermediate longevities). We defined 706 reptiles for which data were available as either 'sit-and-wait' or 'active foragers' (Meiri, 2018).

Distribution data are from Roll et al. (2017) for reptiles, the International Union for Conservation of Nature (IUCN; <https://www.iucnredlist.org/resources/spatial-data-download>) for amphibians and mammals, and BirdLife (<http://datazone.birdlife.org>) for birds. Climatic data were obtained by intersecting range maps with mean annual temperature and temperature seasonality (from CHELSA; Karger et al., 2017) at 30 arc seconds (high resolution).

Field metabolic rates (FMR, in kJ/day) were obtained from the primary literature (e.g., Green & Christian, 2007; Kingsbury, 1995; Murray et al., 2014; Murray et al., 2015; Nagy, 2005; Smith, Christian, & Green, 2008). Basal metabolic rates (ml O₂/hr) were obtained from the literature (Bushuev, Tolstenkov, Zubkova, Solovyeva, & Kerimov, 2017; Lovegrove, 2003; McKechnie & Wolf, 2004; Naya, Naya, & White, 2018; Sieg et al., 2009; Uyeda, Pennell, Miller, Maia, & McClain, 2017; White, Frappell, & Chown, 2012; White, Phillips, & Seymour, 2006; White & Seymour, 2003; Žagar, Simčič, Carretero, & Vrezec, 2015; Zhang, Guo, Zhang, Lin, & Ji, 2018). Metabolic rate data were available for 820 species in our database.

Comparing metabolic rates between endotherms and ectotherms is problematic. Endotherm metabolic rates are lowest at intermediate temperatures, their thermoneutral zone (TNZ, e.g., Hill, Wyse, & Anderson, 2012; usually around 25°C). Thus, endotherm basal metabolic rates are easy to define, standardize and measure. Ectotherm metabolic rates, however, generally increase monotonically with body temperature, at least within the range of temperatures used to study their standard metabolic rates (Andrews & Pough, 1985; White et al., 2006). Furthermore, ectotherm tetrapod performance increases with temperature until an 'optimum' maximal rate is reached, and then decreases sharply (e.g., Huey & Kingsolver, 1989). Ectotherm metabolic rates and performances are thus usually examined at several experimental temperatures. We opted to compare the metabolic rates that result in maximized potential performance. We consider these temperatures to be at the TNZ of endotherms – but at the optimal temperatures for ectotherms. At these temperatures endotherms do not need to expend extra energy for thermoregulation – while ectotherms operate most efficiently. Therefore, we used basal metabolic rate (BMR) data for endotherms. For ectotherms, when data from more than one temperature were available for a given species, we selected the metabolic rate data that were measured at the operative temperature closest to the class or order mean. Thus, for reptiles we selected data measured at temperatures as close as possible to 31°C, which is the average body temperature of active squamates (across 1,089 species; Meiri, 2020). In amphibians we selected data measured as close as possible to 30°C for anurans, and to 25°C for urodeles, based on experimental analyses of their temperature preferences (Anderson & Beitinger, 1979; Araujo et al., 2013; Bachmann, 1969; Ballinger & McKinney, 1966; Bider & Morrison, 1981; Bohlin & Beitinger, 1979; Bradford, 1984; Brattstrom, 1963; Brattstrom, 1968; Brattstrom, 1970; Brown, 1975; Catenazzi, Lehr, & Vredenburg, 2014; Darlington, 1957; Frishkoff, Hadly, & Daily, 2015; Katz & Gil, 1997; Luddecke & Sanchez, 2002; Richter-Boix et al., 2015; Stuart, 1951; Wells, 2007; Wygoda & Williams, 1991). A sensitivity analysis in which resting metabolic rates were those measured at temperatures as close as possible to 25°C yielded qualitatively identical results. We refer to these rates collectively as resting metabolic rates (RMR, comprising BMR for mammals and birds and resting metabolic rates for amphibians and reptiles as defined above).

We compared longevity of endotherms and ectotherms to determine whether this fundamental difference in metabolic rates influences longevity (Gillooly, Gomez, & Mavrodiev, 2017). We also

analysed mammals, birds, reptiles and amphibians separately, to determine whether these fundamental divisions of the vertebrate tree of life result in specific metabolism/longevity relationships. Our aim was to examine this relationship on different parts of the tree, rather than merely treat them as nuisance variables to be corrected for using phylogenetic regression.

We log₁₀ transformed data on body size, maximum longevity, basal and field metabolic rates and sample size, to normalize residuals and reduce heteroscedasticity. All statistical tests were performed using R 3.6.1 (R Core Team, 2019).

We combined the most up-to-date, complete phylogenetic trees for each class (Faurby & Svenning, 2015; Jetz & Pyron, 2018; Prum et al., 2015; Stark et al., 2018), and estimated the phylogenetic signal in longevity data using phylogenetic generalized least squares regression (PGLS; Freckleton, Harvey, & Pagel, 2002), implemented in the R package 'caper' (and its dependencies: 'ape', 'phytools', 'plyr', 'car', 'fmsb' and 'FSA'). We combined the trees using the methods and scripts outlined in Roquet, Lavergne, and Thuiller (2014). We accounted for shared ancestry using PGLS (Freckleton et al., 2002; Orme, Freckleton, Thomas, & Petzoldt, 2013) with the maximum likelihood value of Pagel's λ . A λ of 0 indicates that no phylogenetic signal exists (i.e., that the trait has evolved independently of phylogeny). A λ close to 1 indicates a strong phylogenetic signal, in agreement with a Brownian motion model of evolution (Freckleton et al., 2002).

To tease apart the potential effects of body size and metabolic rates on longevity, we compared Akaike information criterion (AIC) scores of models containing FMRs or RMRs alone, FMRs or BMRs and body size, and body size alone, as predictors. If the full model presented a higher AIC than a partial model nested in it, we interpreted this as a sign that the additional predictors have little effect following Arnold (2010). We verified this by comparing the significance of the body size and metabolic rate terms in the full models.

We possessed FMR data for c. 5% (209 species) and RMR data for c. 20% (820 species) of our species. For other variables we possessed data for > 80% (often > 95%) of species. Thus, we ran models with three different combinations of predictors for all land vertebrates and for each class separately (all corrected for body size, data origin, sample size and phylogeny): (a) with FMRs; (b) with RMRs; (c) with mean annual temperature, temperature seasonality, and activity time together. For reptiles, we fitted two additional models: with foraging mode and with body temperature (all corrected for body size, data origin, sample size and phylogeny).

To estimate whether we had sufficient statistical power to reject a null hypothesis we conducted power analyses (using an online power calculator: <https://www.danielsoper.com/statcalc/calculator.aspx?xml:id=9>) for the regressions of resting metabolic rate (RMR), FMR, temperature seasonality and mean annual temperature analyses. Because body size was a factor in all these analyses, we set the number of predictors to two. Because our null models were always either strongly rejected ($p < .005$), or clearly not rejected ($p \geq .1$, see the Results section and tables), we used two alpha values: the 'traditional' .05 (Fisher, 1925) and a more stringent .005 (Johnson, 2013; Benjamin

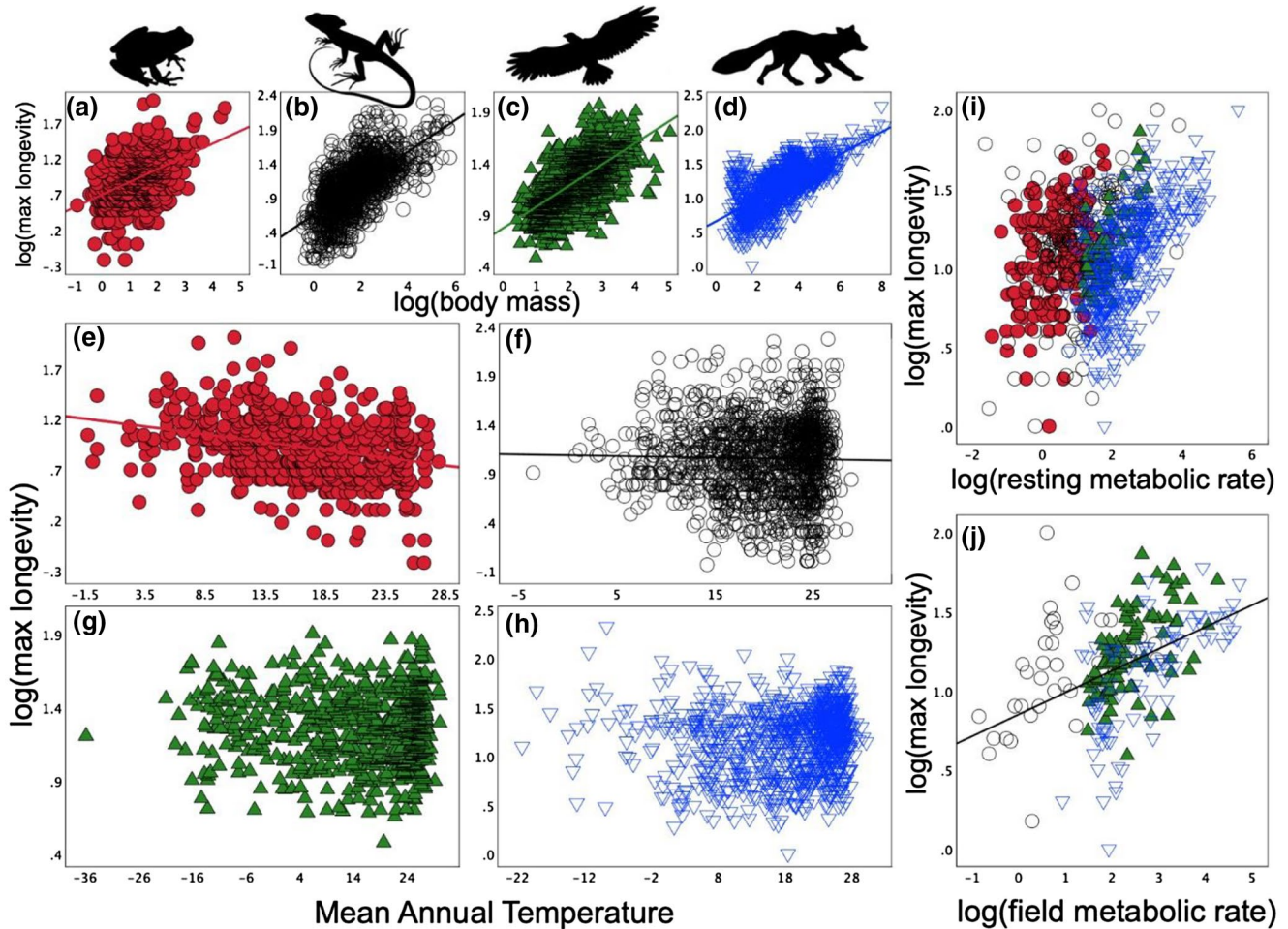


FIGURE 1 The relationship between longevity (y axis of all panels, \log_{10} transformed) and (a–d) body mass (in g, \log_{10} transformed) of amphibians (red circles), reptiles (black circles), birds (green triangles) and mammals (inverted blue triangles). (e–h) Mean annual temperature (regression lines only shown for amphibians and reptiles for which the relationship is significant), (i) basal metabolic rate (in ml O_2 /hr, \log_{10} transformed), according to the colour codes depicted in the top plots and (j) field metabolic rate (kJ/day, \log_{10} transformed) [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2018) to calculate power. Sample sizes were those for the relevant clades and analyses. We estimated power for two hypothetical relationships: a weak pattern ($R^2 = .15$) and a medium one ($R^2 = .4$). Analyses were conducted for each class separately. The power analyses we used do not take into account the phylogenetic correction, and may thus overestimate the power associated with PGLS models to some extent (due to the lower degrees of freedom associated with the non-independence of phylogenetically structured data). While it is difficult to estimate exactly how this will affect power, PGLS retains much of the power of non-phylogenetic analyses, and hence we believe that the power we estimate is at least close to the actual power of our tests. We found most of our analyses had high power to reject a null hypothesis, for all taxa. Exceptions were restricted to low power ($\beta = .21$ for alpha of .005 and $\beta = .56$ for alpha of .05) for the FMR analysis of reptiles with a weak effect size. All other analyses had power $> .8$, mostly $> .9$ (see Supporting Information Appendix S2.1 for full power analyses results).

3 | RESULTS

The relationships between BMRs/RMRs and FMRs and longevity were not significant across all the land vertebrates or within any class, except for reptilian FMRs (Figure 1a,c; Table 1), when accounting for body size, phylogeny, sampling intensity and data origin (wild/captive individuals) (Supporting Information Appendix S3). The results remained similar (also for reptile FMR) when we analysed only species for which longevity estimates were based on large sample sizes ($n \geq 30$; Supporting Information Appendix S2.2). Most of our statistical models strongly favoured models with body size over models with metabolic rates, or models with a combination of size and metabolic rates (see Supporting Information Appendix S2.3).

Contrary to the predictions of the rate-of-living theory, activity times were uncorrelated with vertebrate longevity, nor were they associated with longevity within any class, with the exception of cathemeral tetrapods, which live 11.1% longer ($n = 538$, $\lambda = .634$,

TABLE 1 Phylogenetic generalized least squares regression (PGLS) model for the relationship between metabolic rates and longevity among and within land vertebrates

Metabolic rate (MR)	Group	n	Slope ± SE	R ²	λ	p
Resting/Basal MR	Tetrapods	662	-0.028 ± 0.024	.19	.913	.24
	Amphibia	123	0.089 ± 0.053	.14	.494	.09
	Reptilia	165	-0.004 ± 0.037	.12	.849	.91
	Mammalia	405	-0.050 ± 0.042	.23	.831	.23
	Aves	94	0.035 ± 0.091	.31	.650	.70
Field MR	Tetrapods	183	-0.039 ± 0.074	.19	.820	.59
	Reptilia ^a	25	-0.338 ± 0.084	.79	.000	.0007
	Mammalia	74	0.021 ± 0.096	.22	.962	.82
	Aves	84	0.096 ± 0.145	.19	.400	.50

Note: Slopes are for metabolic rates, lambda and R² values are for the full model [with sample size, body size and data origin (captive/wild) as predictors]. Tetrapods = all land vertebrates.

^aNo data on amphibian field metabolic rates were available.

TABLE 2 Full phylogenetic generalized least squares regression (PGLS) model for land vertebrates

Factor	Estimate ± 1 SE	t	R
Intercept	0.758 ± 0.177	4.2	< .0001
Body mass (log ₁₀ grams)	0.132 ± 0.008	16.4	< .0001
Origin of data (wild) ^a	-0.065 ± 0.012	-5.1	< .0001
Sample size (log ₁₀)	0.085 ± 0.006	13.6	< .0001
Mean annual temperature (°C)	-0.001 ± 0.006	-2.0	.04
Temperature seasonality (standard deviation ^a 100)	0.001 ± 0.001	0.8	.40
Activity time (cathemeral) ^b	0.042 ± 0.018	2.3	.02
Activity time (crepuscular) ^b	0.020 ± 0.022	0.8	.37
Activity time (nocturnal) ^b	0.005 ± 0.016	0.3	.75

Note: Model R² = .20, n = 3,050 species, λ = .920, p < .0001.

^aThis is the difference between the intercept for species for which longevity is estimated from individuals in nature and for those for which it is known from captive individuals.

^bValues for activity times are intercepts and are compared to the intercept (0.758 ± 0.177) for diurnal species.

R² = .15, p < .0001; Table 2) and nocturnal amphibians, which live 13.5% longer (n = 538, λ = .588, R² = .24, p < .0001) than diurnal species. Likewise, temperature seasonality was uncorrelated with vertebrate longevity either across or within classes (Table 2).

Mean annual temperature emerged as the only climatic predictor significantly (and negatively) associated with tetrapod longevity (slope = -0.001 ± 0.006 log years/°C; p = .04; Figure 1b; Table 2). Life spans were longer in colder climates. Interestingly, considered individually, the longevity of endotherm classes (Mammalia: slope = -0.004 ± 0.006, p = .53; Aves: slope = -0.001 ± 0.009, p = .17) were not associated with temperature, whereas amphibian and reptilian longevity were higher in colder regions (Amphibia: n = 404, λ = .580, slope = -0.009 ± 0.002, p < .0001; Reptilia: n = 953, λ = .801, slope = -0.006 ± 0.002, p = .005). Models based only on well-sampled species gave mostly qualitatively similar results (Supporting Information Appendix S2.2). Reptile body temperature (n = 453, λ = .794, slope = -0.001 ± 0.002; p = .49) was not associated with

longevity. Moreover, foraging mode (active versus sit-and-wait foraging: intercept = 0.977 ± 0.190, p = .65, n = 496, λ = .838) was not associated with reptilian longevity (see Supporting Information Appendix S2.2 for well-sampled models).

Finally, we observed that ectotherms (amphibians and reptiles together) demonstrate similar longevity to similar-sized endotherms (birds and mammals together), despite an order of magnitude difference in BMRs (Supporting Information Appendix S2.4). Accounting for body size and phylogeny alone, birds live longer than amphibians and reptiles, which, in turn, live longer than mammals (Supporting Information Appendix S2.4).

4 | DISCUSSION

The rate-of-living theory (Finkel & Holbrook, 2000; Lints, 1989; Pearl, 1928; Speakman, 2005) underpins key predictions of life

history and ageing theories (Jin, 2010). Despite using the most comprehensive world-wide vertebrate dataset created to date, we failed to find support for the predictions of this theory. We implemented both direct and indirect measurements of metabolic rates. Very few measurements gave any indication that fast metabolic rates are associated with longevity within vertebrate classes, across the fundamental divide in the metabolic range of 'fast-living' endotherms versus 'slow-living' ectotherms, or across all tetrapods. RMRs and FMRs were uncorrelated with longevity (except for reptile FMR, which varies with longevity according to the rate-of-living predictions, but with $n = 25$). Furthermore, proxies for metabolic rates, such as activity times, seasonality and body temperatures, did not reveal a relationship with longevity across the tetrapod tree of life. Animals grow faster in warmer regions (Kingsolver & Huey, 2008), and ectothermic vertebrates are no exception. This can lead to small adult size ('the temperature-size rule'; Atkinson, 1994; Stillwell, 2010; Van Rijn, Buba, DeLong, Kiflawi, & Belmaker, 2018) and shorter life span. In our study, we found a similar and significant role for high environmental temperatures in driving shorter life span (although the temperature-size rule is unlikely to be the driver, as amphibians and reptiles show no size-temperature clines either within or between species; Adams & Church, 2008; Slavenko et al., 2019; Slavenko & Meiri, 2015). Our findings align with recent predictions emerging from the mathematical integration between neutral, metabolic and niche theories (Worm & Tittensor, 2018) that evolutionary processes on a global scale are dominated by environmental temperatures.

4.1 | The drivers of ageing in tetrapods

The paucity of direct estimates of metabolic rate led us to examine indirect proxies for which much more data were available. Ectotherm metabolic rates vary positively with activity body-temperature across most of the temperature range (Gillooly, Brown, West, Savage, & Charnov, 2001). We had thus predicted that shorter life span should be associated with higher energy expenditure (via high activity), diurnal activity and high body temperature. These predictions were not supported by our data. The major differences in body temperatures, and both RMRs and FMRs, between ectotherms and endotherms (White et al., 2006) do not translate into differences in life spans. We did find that the variation in reptilian longevity is related to their FMR. However, the small sample size (25 species, 19 if considering only those for which data on the sample size were used to determine longevity) and weak power (Tversky & Kahneman, 1971) make this link tenuous. However, even with additional predictors (such as sample size or body size) in our power analysis, most of our models maintained high power ($> .8$).

A caveat is required. Our data on FMRs and RMRs of reptiles are poorly correlated with our indirect indices of reptile metabolic rates: neither are related to activity times (although just one species for which we have FMR data is nocturnal), foraging mode nor mean annual temperature. Body temperature was (positively) correlated with standard metabolic rates ($n = 173$) but not with FMRs ($n = 25$; mass

was used as a covariate in all these analyses). Thus, it may be that the factors we examined are not good proxies for metabolic rates (see results for the relationship between RMR and FMR in Supporting Information Appendix S2.4). Alternatively, metabolic rates, being measured at rest for all species, regardless of factors such as foraging mode, may not capture the actual underlying rates during activity. Data on FMRs may well be much more useful but, again, are hard to come by. The null findings for endotherms in our study might also be due to the potential association between flight and increased life span (Healy et al., 2014; Holmes & Austad, 1994; Munshi-South & Wilkinson, 2010; Wilkinson & South, 2002).

Nocturnal ectotherms have lower body temperatures, and thus lower FMRs, than diurnal ones. Furthermore, diurnal animals are exposed to solar radiation, which may subject them to harmful mutations. Nocturnality, however, was only (positively) associated with longevity in amphibians (as also shown in Stark & Meiri, 2018), whereas the other groups demonstrated no such relationship. We postulate that the effects of solar radiation may be mitigated through the possession of more resistant skin. That reptiles, unlike amphibians, do not show an effect of activity time on longevity, suggests that it is radiation that probably causes the differences in longevity between diurnal and nocturnal amphibians. Diel differences in temperatures and the resulting difference in metabolic rates, however, do not affect longevity (otherwise, we would expect these also to affect reptiles). It may be that the effect of activity time on longevity operates via differential predation pressures on different parts of the diel cycle. For example, Healy et al. (2014) found that crepuscular flying endotherms have shorter life spans (compared to nocturnal or diurnal species), perhaps because they are exposed to both diurnal and nocturnal predators, resulting in higher extrinsic mortality.

Most ectotherms and many mammals reduce their metabolism in highly seasonal regions by means of hibernation, aestivation or torpor (Storey & Storey, 1990; Turbill et al., 2011). During this time they may also be less exposed to predation (Turbill et al., 2011). Seasonality, however, was not associated with longevity.

Large species demonstrate slower mass-specific metabolic rates (Clarke, Rothery, & Isaac, 2010; Kleiber, 1947; Nagy, 2005; White, Blackburn, & Seymour, 2009), and this has been linked to longer life spans (Kirkwood, 1977; Sohal, 1986). However, our findings suggest that the relationship between size and longevity does not stem from metabolic rates, but from other size-related intrinsic and extrinsic factors. Larger animals may be less vulnerable to predation (e.g., they can be preyed upon by fewer species), starvation and extreme environmental conditions, such as drought (Peterson & Wroblewski, 1984; Sogard, 1997), which could affect mortality rate independently of metabolic rate. Moreover, reduced extrinsic mortality, as a consequence of larger size, may alter the optimum for investment in somatic maintenance: lower predation risk could lead to investment in somatic maintenance and repair becoming more profitable. Longer lives could allow organisms to achieve a larger size, which in turn enables greater reproduction success. This is because larger mothers often have larger offspring, which may be more likely to survive (Kirkwood & Holliday, 1979). In ectotherms, larger

size also allows more offspring to be produced. We thus view size as a factor that affects longevity through mechanisms (such as its relationship with time to maturity, and predation rates) not directly related to metabolic rates or affected by them. In other words, the relationship between metabolic rate and longevity is spurious and only arises because both are correlated with body size.

4.2 | Ageing and climate change: the 'burning quickly' hypothesis

Importantly, we found that high environmental temperature is associated with low ectotherm longevity. This observation may reflect an effect of mortality rates. First, in colder environments animals are usually active for shorter periods during the year (Johnston & Dunn, 1987), thereby reducing their exposure to predation risk and food shortages (Turbill et al., 2011). Moreover, hotter, more tropical, regions probably host a greater diversity of species. Consequently, more predator and parasite species are likely to inhabit such regions. If higher predator and parasite species diversity (rather than their abundance, specificity and lethality) results in high extrinsic mortality risk, this may select for shorter life span. This observation suggests an unexpected link between the vulnerability of a species (especially ectotherms) and the unprecedented global warming that the planet is currently experiencing (IPCC, 2013). Indeed, if increasing ambient temperatures reduce longevity, then multiple life-history characteristics that evolve in coordination with a species' life span (e.g., reduced lifetime reproductive success, skewed sex ratios etc.) could be affected (Bókony, Milne, Pipoly, Székely, & Liker, 2019; Cunningham, While, & Wapstra, 2017; Huey et al., 2012; Seebacher, White, & Franklin, 2015). This may increase extinction risk across a wide range of taxa. Importantly, therefore, our findings add a previously overlooked layer to the range of factors that are commonly used to develop predictions regarding the threat of extinction to species in the Anthropocene.

The use of maximum longevity in comparative studies is not ideal. Maxima may be unrepresentative of the species as a whole (Carey, 2003). Furthermore, longevity estimates based on unequal numbers of individuals for different species would result in higher maxima reported for species associated with larger samples, biasing the analyses (Scharf et al., 2015). Unfortunately, much more data exist on maxima than on actuarial ageing (Healy et al., 2014; Scharf et al., 2015), which would be a better indicator for testing the 'rate-of-living' theory. However, maxima are the commonest metric of longevity in comparative studies (Healy et al., 2014; Magalhães et al., 2007; Scharf et al., 2015; Wilkinson & Adams, 2019), and are likely to be tightly associated with means. Additionally, we accounted here for the uneven sampling in our analyses.

The rate-of-living theory has been proposed as an explanation for the variation in longevity across the animal tree of life (Atanasov, 2005; Healy et al., 2019; Hulbert et al., 2007; Kapahi et al., 2010; Ku et al., 1993; Sohal, Svensson, Sohal, & Brunk, 1989; Wright et al., 2004). Despite the high power of our statistical models, our analysis

lends it no support. We thus conclude that the evidence supporting the theory is at best idiosyncratic. Recently, some smaller-scale experimental and meta-analytical studies (Glazier, 2015; Hou & Amunugama, 2015; Hulbert et al., 2007; Vaanholt, Daan, Garland, & Visser, 2010; Van Voorhies et al., 2003;) revealed no effects of metabolism on longevity, challenging the validity of the theory. Our global-scale phylogenetic comparative analyses provide the first body of robust evidence that the rate-of-living theory does not hold across a broad spectrum of life-history and ecological traits from across the vertebrate tree of life. Our study resets our fundamental understanding of the role of metabolic rates on the trajectories of adaptive evolution, and raises serious questions about many of the current assumptions and predictions, for which we found no support or validation in our study.

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DATA AVAILABILITY STATEMENT

All data used in the analyses and the associated metadata are available in Supporting Information Appendix S1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX

LONGEVITY DATA SOURCES

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