

Correlation between body size and longevity: New analysis and data covering six taxonomic classes of vertebrates

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ABSTRACT

Large bodied species are known to live longer than small bodied species. However, it is less clear whether the positive correlation varies across taxa. In this short communication, we combine data entries from literature and databases on body mass and maximum life span for 3722 species covering taxonomic Classes *Chondrichthyes*, *Teleostei*, *Amphibia*, *Reptilia*, *Aves*, and *Mammalia*. We then analyse the $\log(\text{maximum life span}) - \log(\text{body mass})$ relationship using generalized linear model with nested random intercepts and slopes for Class/Order/Family. Our analyses generally demonstrate the positive longevity – body mass relationship but also reveal that slopes and intercepts differ slightly among all Classes except *Reptilia* and *Amphibia*. Highest slopes can be found in Classes *Aves* and *Chondrichthyes*. Differences between the smallest and largest Family-level slopes was more than threefold. While these preliminary analyses provide a brief overview of body size – longevity relationships across taxa, the dataset collated in the present study could serve as a start point for in-depth phylogenetic analyses to uncover complex pathways through which body size and its correlates might have evolved.

1. Introduction

Body size is a well-known correlate for many life-history traits, such as the age at maturity and metabolism (Peters 1983; Charnov 1993). In general, large bodied species live longer than small bodied species, such that there is a clear positive correlation between body mass and longevity, i.e., the maximum life span (Hutchings 2021). However, while the positive association between these two variables is qualitatively well established, the magnitude of the correlation varies and some species largely deviate in their maximum life span from that expected based on the body mass alone. For example, in their meta-analyses of 1368 bird and mammal species, Healy et al. (2014) found that the correlation between body mass and longevity differed between volant and non-volant species, generally volant species living longer. Such differences in the body mass - longevity relationship suggest that species might respond differently to declining body masses, which is a projected consequence of climate change (reviewed by Gardner et al., 2011) and

other anthropogenic pressures such as harvesting (reviewed by Kuparinen and Festa-Bianche 2017). A steep change in longevity due to body mass reduction can erode population growth rate and, hence, affect species resilience, recovery ability and the risk of extinction (Dulvy et al., 2004; Mace et al., 2008).

In the present short communication, we combine data on body masses and maximum life spans from the taxonomic Classes *Amphibia*, *Aves*, *Chondrichthyes*, *Mammalia*, *Reptilia*, and *Teleostei*. We analyse, across 3722 species, the variation in the relationship between body mass and maximum life span using linear mixed models, with particular focus on investigating potential differences among Classes and on estimating how much variation is further associated with the taxonomic Order and Family. As the end product of our meta-analyses, we provide intercepts and slopes for the $\log(\text{longevity}) - \log(\text{body mass})$ relationship for 420 Families in 99 Orders and 6 Classes as well as new collated data covering longevity and body size for 3722 species across six Classes.

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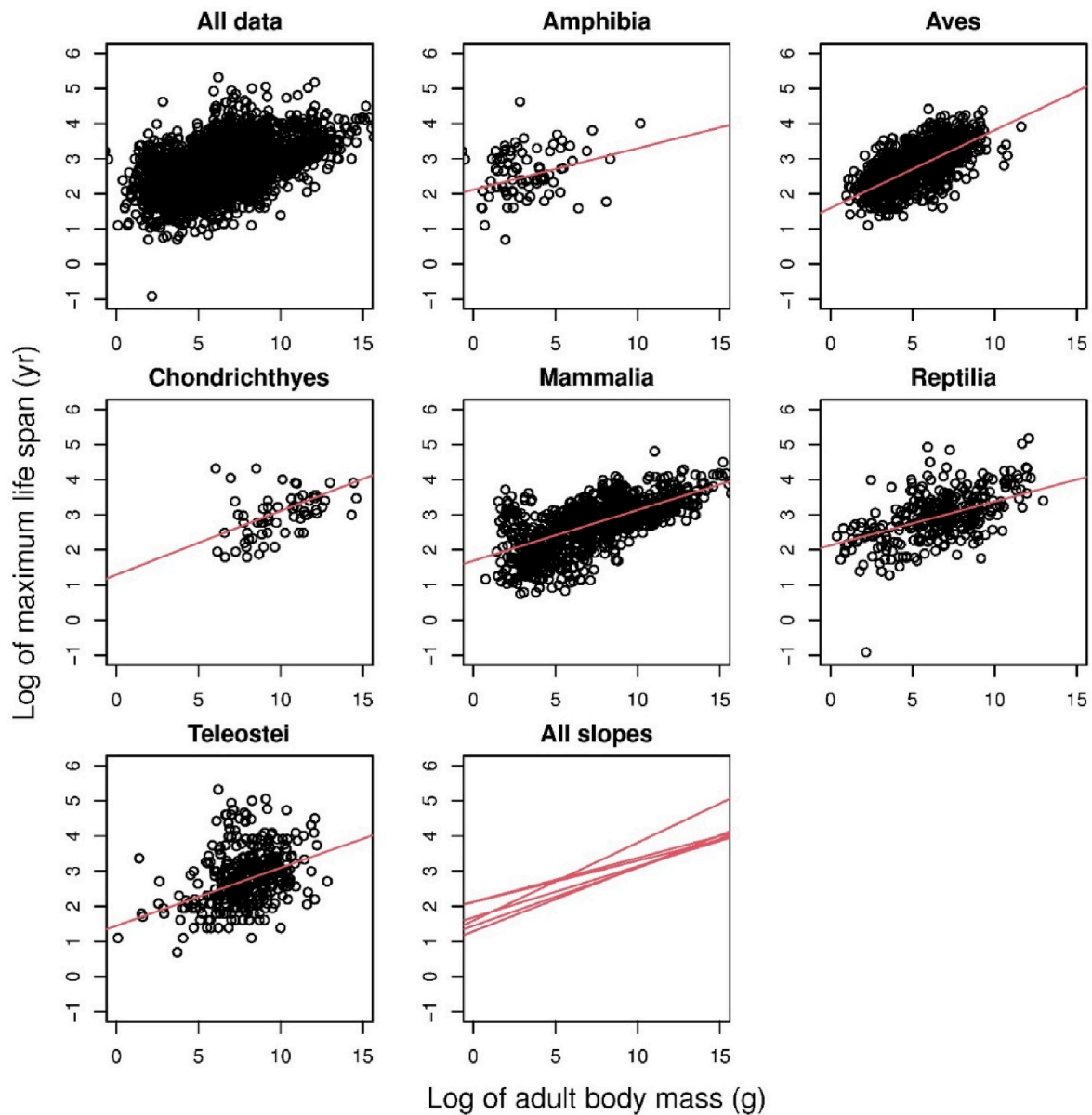


Fig. 1. Logarithms of species-specific average adult body mass and maximum lifespan plotted jointly and for each taxonomic class separately. Red lines describe linear mixed model fits averaged for each Class. The mixed model includes nested random effects for Class/Order/Family for the intercept and Class/Order for the slope.

2. Materials and methods

2.1. Data collection

Maximum lifespan and body mass data were extracted from the AnAge vertebrate database (de Magalhães and Costa, 2009), with additional mass entries supplemented from Mull et al. (2019), from the Fish Base (Froese and Pauly, 2022), Amniote (Myrkvold et al., 2015) and AmphibiO (Oliviera et al., 2017) databases, respectively (data additional to AnAge is listed in Table S1). AnAge is a comprehensive database of animal longevity and other life history metrics (de Magalhães and Costa, 2009). It is a compilation of values from the literature and several datasets that currently features entries for over 4000 species across all vertebrate classes, particularly mammals and birds. AnAge also features a measure of quality of each data entry: ‘low’, ‘questionable’, ‘acceptable’, and ‘high’. Only data entries of ‘acceptable’ and ‘high’ quality were included in our analysis. Data from FishBase was used to supplement body mass entries for teleost fishes. FishBase is a global data

system on fishes, including taxonomy, biology, trophic ecology, and life history information in excess of 33,000 species of fish compiled from over 52,000 references (Froese and Pauly, 2022). Additional mass data for amphibians was accessed from the AmphibiO database of amphibian ecological traits, a compilation of more than 6500 species from over 1500 pieces of primary literature (Oliviera et al., 2017). Similarly, reptilian body mass records were compiled from the Amniote database of life history traits of birds, mammals and reptiles (Myrkvold et al., 2015). The entire dataset can be accessed through Dryad and it contains observations for 3722 species from 420 Families, from 99 Order and from 6 Classes (see Data availability statement below).

2.2. Analyses

To linearize and normalize the data, both the adult body mass (g) and the maximum life span (yr) were log transformed. In the absence of a unified phylogenetic tree available for all of the species included in our dataset, we adopted a simplified approach and investigated the data

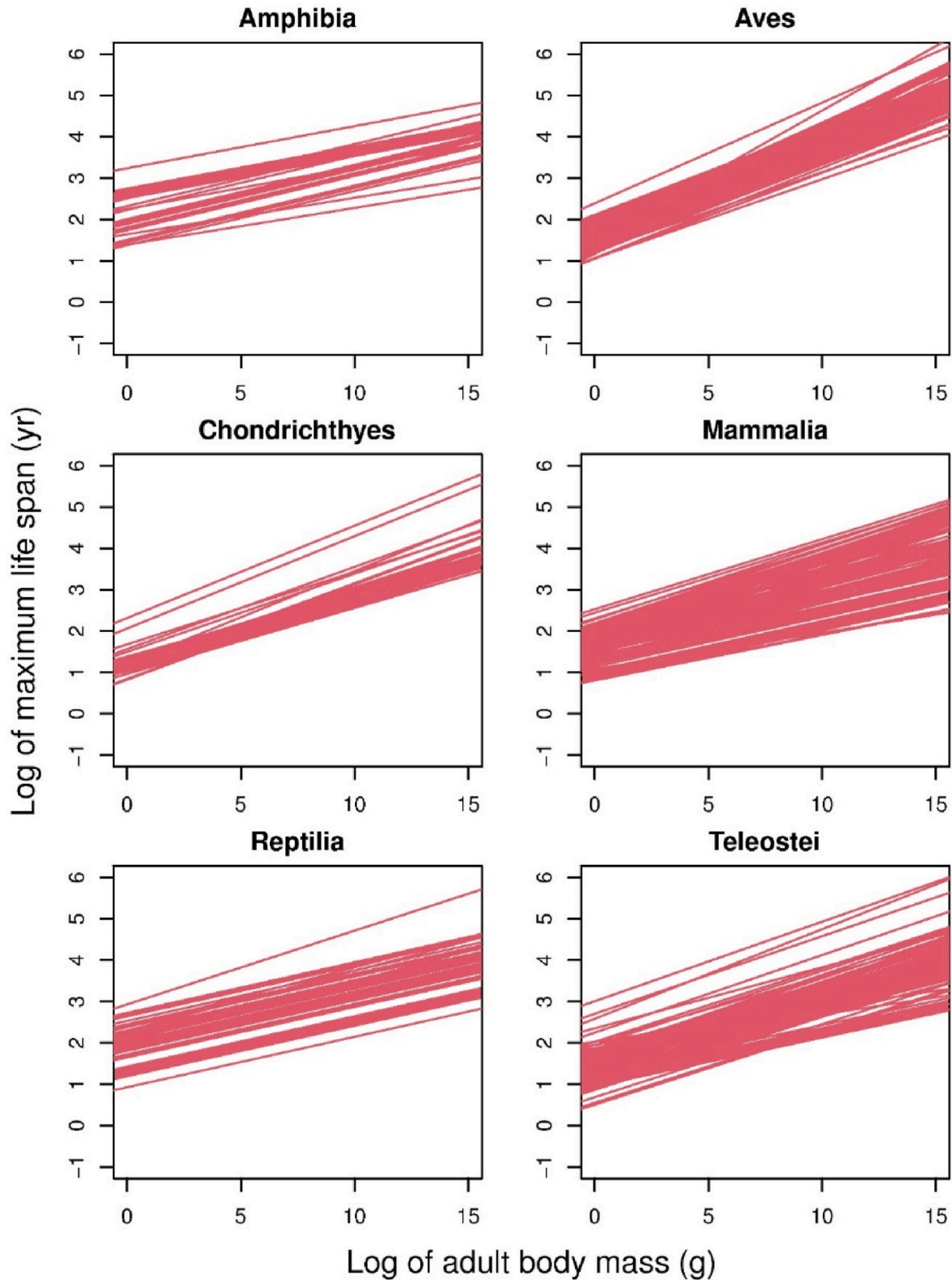


Fig. 2. Individual regression fits for each of the analyzed 420 Families: *Amphibia* (N = 24), *Aves* (N = 114), *Chondrichthyes* (N = 24), *Mammalia* (N = 122), *Reptilia* (N = 48), *Teleostei* (N = 88).

using linear mixed effect models with nested random effects. The initial model fitted to data had the following structure:

$$\log(\text{Lifespan}) \sim \alpha(\text{Class/Order/Family}) + \beta(\text{Class/Order/Family}) \times \log(\text{Bodymass}) + \varepsilon \quad (\text{eqn 1})$$

Where α and β describe the intercept and the slope, respectively, whereas ε is the residual term. Both the regression parameters α and β had a fixed effect and the nested random effects. Family was the lowest taxonomic level included in the analyses as many genera had only one observation (one species). The model was then reduced stepwise and the

Table 1

Comparison of slopes of the body size effect on the maximum life span by classes across the data. Slopes include the fixed effect part as well as the random slopes at the level of Class and Order, extracted from the initial regression model. The slopes differ among classes in all but one pairwise comparisons (marked with yellow).

Regression fit			Pairwise differences				
Class	Average slope	Standard error	Aves	Chondrichthyes	Mammalia	Reptilia	Teleostei
Amphibia	0.118	0.004	t=27.46, df=36.10, p<0.01	t=-11.11, df=41.67, p<0.01	t=-6.96, df=42.05, p<0.01	t=-1.89, df=31.03, p=0.068	t=-11.20, df=52.46, p<0.01
Aves	0.222	0.002		t=7.90, df=29.47, p<0.01	t=28.57, df=229,68, p<0.01	t=43.85, df=152.66, p<0.01	t=18.344, df=158.85, p<0.01
Chondrichthyes	0.182	0.004			t=-7.18, df=32.32, p<0.01	t=-11.70, df=27.08, p<0.01	t=-3.16, df=37.68, p<0.01
Mammalia	0.145	0.002				t=8.31, df=167.0, p<0.01	t=6.09, df=181.03, p<0.01
Reptilia	0.125	0.003					t=-13.93, df=125.68, p<0.01
Teleostei	0.165	0.002					

Table 2

Comparison of intercepts of the body size effect on the maximum life span by classes across the data. Intercepts include the fixed effect part as well as the random intercepts at the level of Class, Order and Family, extracted from the initial regression model. Intercepts differ in all but two pairwise comparisons (marked with yellow).

Regression fit			Pairwise differences				
Class	Average intercept	Standard error	Aves	Chondrichthyes	Mammalia	Reptilia	Teleostei
Amphibia	2.117	0.071	t=-5.04, df=25.31, p<0.01	t=6.70, df=41.08, p<0.01	t=4.10, df=26.84, p<0.01	t=-0.080, df=35.65, p=0.9367	t=6.03, df=33.07, p<0.01
Aves	1.593	0.032		t=4.11, df=27.85, p<0.01	t=-2.53, df=224.29, p=0.012	t=-9.35, df=65.09, p<0.01	t=2.88, df=128.06, p<0.01
Chondrichthyes	1.288	0.071			t=5.20, df=31.13, p<0.01	t=9.52, df=48.06, p<0.01	t=1.86, df=44.49, p=0.0688
Mammalia	1.686	0.031				t=-7.37, df=77.1, p<0.01	t=4.42, df=151.95, p<0.01
Reptilia	2.126	0.050					t=9.76, df=111.64, p<0.01
Teleostei	1.445	0.037					

intercepts and slopes (comprising of fixed and random effects) were extracted for each Family. Next, we investigated whether intercepts and slopes significantly differed and at which taxonomic levels. All the Analyses were made with R (R Core Team 2021).

3. Results

As expected, the log of body mass was a significant correlate of the log of maximum adult life span (fixed slope: 0.163, $t = 7.87$, $df = 4.61$, $p < 0.01$). In the random slope, the family level random effect could be reduced (Chisq = 0.043, $df = 1$, $p = 0.837$) but order could not (Chisq = 17.87, $df = 1$, $p < 0.01$). In the random intercept, family level random effect could not be reduced (Chisq = 415.37, $df = 1$, $p < 0.01$). Thus, the final model included Class/Order/Family nested random effect structure

in the intercept and Class/Order nested random effect structure in the slope. Variance components for Class, Order and Family were 28.6%, 20.4%, and 22.5%, respectively, and 28.5% of variation remained residual, i.e. this amount of variation was present among species within Family. Final intercepts and slopes including both the fixed and random effects (420 intercepts according to the number of Families and 99 slopes according to the number of Orders in the data) were extracted from the final model and Class level average fits were plotted together with the raw data in Fig. 1. As can be seen, positive association between the log of body mass and the log of adult maximum life span is evident, but at the Class level the average fits show slight differences both in the intercepts and slopes (Fig. 1). Family-specific fits within each Class are shown Fig. 2. Pairwise t-tests reveal that the intercepts differ among all Classes except between *Reptilia* and *Amphibia* and *Chondrichthyes* and

Teleosts, whereas slopes differ among all Classes except *Reptilia* and *Amphibia* (Tables 1 and 2 and supplementary materials).

4. Discussion

While we confirmed the universal positive association between the body mass and longevity (Fig. 1), our pairwise comparison also detected significant, albeit small, differences in the linearized relationships among the studied Classes, except for the slope and the intercept between *Amphibia* and *Reptilia* and for the intercept between *Chondrichthyes* and *Teleostei* (Tables 1 and 2). While the differences in intercepts mainly reflect differences in body sizes among the studied Classes, the slope mirror the strength of the correlation between body size and longevity. On average, the slope of the relationship was highest in *Aves* and lowest in *Amphibia*, with the slope of *Aves* being about double of the slope of *Amphibia*. Over 70% of variation in body mass - maximum life span slope was explained by taxonomy, whereas less than 30% of variation remained among species within Families. Jointly, these findings suggest that taxonomic differences in the body mass - longevity relationship exist, but also confirm the positive correlation across the studied taxa. None of the family level slopes was negative (Fig. 2) and the slopes ranged between 0.082 and 0.312, thus, the difference between extremes was threefold.

If the body mass - longevity relationships can be considered constant, then potential changes in body size owing to anthropogenic impacts or changing climate would have varied effects on the longevity of different species. For example, Birds (*Aves*) and bony fish (*Chondrichthyes*) have the steepest slopes (Table 1) and therefore reductions in body size would lead to greatest losses in life span, which might affect their population growth rates and reduce their resilience to disturbances and environmental changes. Interestingly, the global conservation status of bony fishes has rapidly declined, such that over the past seven years the proportion of species classified by International Union of Conservation of Nature (IUCN) as threatened, has increased from 25% to 32.6–37.5% (Dulvy et al., 2021). This pattern is largely driven by overfishing (Dulvy et al., 2021). Similarly, birds are experiencing a biodiversity decline, deteriorating conservation status, and a general decrease in body size worldwide for over three decades (Lees et al., 2022).

In the present short communication we present a new, open access dataset that collates body size -longevity relationships for 3722 species within six taxonomic Classes. Our preliminary linear mixed-model analyses on one hand confirm the positive association between body size and longevity but on the other hand suggest that there might be taxonomic differences in the slope and the intercept of the log-transformed relationship. To better understand these differences, full phylogenetic analyses are warranted and we hope that the new dataset provides a solid starting point for such analyses. Nonetheless, as a preliminary scratch, we provide intercept and slope estimates for the body mass - longevity relationship for 420 Families in 99 Orders and 6 Classes. While the present study focuses only on one correlation among two life-history traits at the level of Family, more generally it highlights the importance of meta-analyses to detect universal correlation patterns. Not only do these help to better understand biome functioning but can also serve as useful rules of thumb for rapid but informed status assessments and management decisions.

Author contribution statement

JAH and EY initiated the study, EY collected the data, AK analyzed the data. EY and AK wrote the manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data and analyses codes will be open access through Dryad

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We dedicate this study to our co-author Jeffrey Hutchings who we suddenly lost during the course of the study. We thank Tiina Sävilammi for her advice during the analyses.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2023.103917> and raw data, analyses codes, and estimated intercepts and slopes can be found online in Dryad at <https://doi.org/10.5061/dryad.kwh70rz72>.

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