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Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction

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Animals exhibit an extraordinary diversity of life history strategies. These realized combinations of survival, development and reproduction are predicted to be constrained by physiological limitations and by trade-offs in resource allocation. However, our understanding of these patterns is restricted to a few taxonomic groups. Using demographic data from 121 species, ranging from humans to sponges, we test whether such trade-offs universally shape animal life history strategies. We show that, after accounting for body mass and phylogenetic relatedness, 71% of the variation in animal life history strategies can be explained by life history traits associated with the fast–slow continuum (pace of life) and with a second axis defined by the distribution of age-specific mortality hazards and the spread of reproduction. While we found that life history strategies are associated with metabolic rate and ecological modes of life, surprisingly similar life history strategies can be found across the phylogenetic and physiological diversity of animals.

The turquoise killifish, *Nothobranchius furzeri*, can complete its life cycle in 14 d (ref. [1]). In contrast, the Greenland shark only becomes sexually mature after 156 yr (ref. [2]). Despite their differences, the evolution of both these life histories is underpinned by the evolutionary principal of maximizing fitness through differing rates of survival, development and reproduction[3]. As these species demonstrate, different combinations of traits associated with fitness, known as life history traits[4], can successfully maintain viable populations over evolutionary time. The range of variation in life history traits and how they combine into life history strategies across the animal kingdom is vast. Hexactinellid sponges can live for millennia[5] while Gastrotrichs can complete their life cycle in days[6]. Pacific salmon (*Oncorhynchus tshawytscha*) release thousands of eggs in a single reproductive event[7], while Laysan albatross (*Phoebastria immutabilis*) are known to reproduce continuously for decades[8]. Understanding how variation in these traits combines into life history strategies, and in turn how these strategies relate to the range of forms, physiologies and ecologies found in the animal kingdom, is key to understanding issues ranging from the invasive potential of species[9] to the evolution of senescence[10].

Despite the diversity of life history strategies, not all strategies are possible. Darwinian demons, hypothetical organisms that live forever and reproduce at infinite rates, do not exist due to limitations in resources[11]. Life history strategies also reflects the environmental and physical constraints they evolve under. For example, to attain larger adult sizes individuals typically allocate resources towards development at the expense of reproductive output[4]. Many such trade-offs shape life history strategies[12]. The most well-understood of these is the fast–slow continuum[4,13] where the allocation of resources between survival, development and reproduction results in a continuum of strategies ranging from a combination of fast development, short lifespans and high reproductive rates, to combinations of slow development, longer lifespans and low reproductive rates[2]. Other axes of variation have also been described[13–16]. These typically relate to aspects of reproduction such as its annual intensity and duration, and its spread over the life course[14].

Identifying these axes of variation provides a framework that can aid in mapping how conservation management strategies[17], degrees of invasiveness[9] and diversity[18], relate to different life history strategies. However, current patterns of animal life history strategies are described on the basis of taxonomically restricted groups, typically Mammalia[11] and Aves[13,19], or do not account for the potential variation in life history traits that can be attributed to body size[16]. Hence our understanding of patterns in life history strategies effectively misses the wider variation in life history traits observed across the animal kingdom. Here, we use the recent rapid expansion in taxonomic coverage of animal demographic data[20] to incorporate age-related measures of mortality and reproduction[10], along with other life history traits (Fig. 1), into a test of the universality of life history patterns from the level of populations to the scale of the animal evolutionary tree (Fig. 2).

Results

The variation in life history traits observed amongst animals is shown across six life history traits (Figs. 2 and 3). Variation in traits ranged from generation times (T) of 2.4 to 53.2 yr in the eastern sand darter (*Ammocrypta pellucida*) and the black-browed albatross (*Thalassarche melanophris*) to low variation in distributions of mortality risks found

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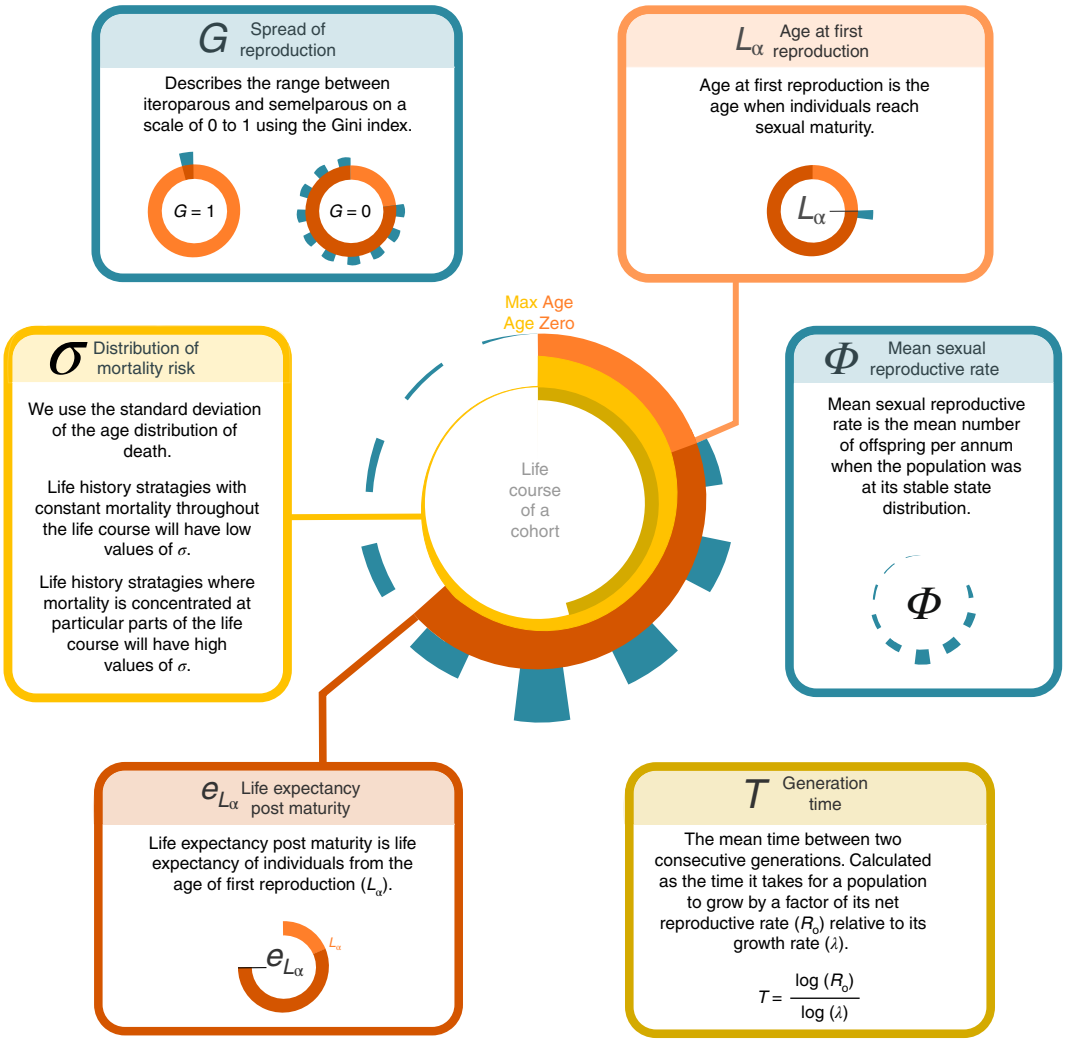

Fig. 1 | Life history traits used in our analysis to describe the life history strategies of a given animal population. The circle represents the life course of a cohort from birth (0 yr) clockwise to death, with each different coloured concentric band describing the sequence and timing of life history events, quantified using the metrics described in the boxes. For more information on how these were calculated see Supplementary Methods.

in humans (σ=0.01) to the more highly variable mortality risks found across the life course of the smooth Australian abalone (*Haliotis laevigata*) (σ=0.07, Fig. 2). Reproductive traits varied from mean reproductive rates of 0.02 offspring a year in humans to 225,595 a year in northern pike (*Esox lucius*), with the distribution of reproduction ranging from semelparous species such as the Chinook salmon (G=0.83) to iteroparous species such as the Murray River turtle (*Emydura macquarii*, G=0.18).

While life history traits vary greatly, the combinations of these traits into life history strategies is reportedly relatively constrai ned[4,13,15,19,21–25]. Here, we find that, after controlling for body size and phylogenetic relatedness (Fig. 4, Supplementary Table 1 and Supplementary Fig. 1), animal life history strategies vary across two axes of variation defined by: (1) traits associated with the fast–slow continuum and (2) the distribution of age-specific mortality hazards and of reproduction (Figs. 3 and 4). This general pattern of two axes was also found across taxonomic subgroupings and in our robustness analysis (Supplementary Tables 2 and 3). The presence of these patterns across disparate animal groups highlights the fundamental nature of the drivers of life history strategies. Moreover, while different measures of life history traits were used, this pattern is broadly similar to those found in plants, which also show two axes of variation in life history strategies[14].

As predicted by the fast–slow continuum, generation time, age at first reproduction (L_α) and life expectancy post-maturity (e_{L_α}) are all positively correlated (Fig. 3). These three traits define one of the axes of variation in life history strategies, which accounts for 46% of the variation in the full analysis of the 121 species in our dataset (Fig. 3). Along this axis, species range from short-lived early reproducers, such as the Uinta ground squirrel (*Urocitellus armatus*) and the greater prairie chicken (*Tympanuchus cupido*), to long-lived, slow-maturing animals, such as the northern fulmar (*Fulmarus glacialis*) and the violescent sea-whip (*Paramuricea clavata*). The association of these life history traits follows previous expectations, particularly in the case of L_α and T, which have been suggested as proxies of the fast–slow continuum[21]. An axis relating to these traits is found in all of our additional analyses of taxonomic groups (Mammalia, Aves, endotherm and ectotherm) and in the case where T is removed from the analysis (Supplementary Tables 2 and 3).

Contrary to predictions from the fast–slow continuum[13], mean reproductive rate (Φ) is not negatively associated with the other fast–slow continuum traits, with a negative association (loaded to the fast end) only found in the analyses of endotherms and Mammalia (Supplementary Table 2 and Supplementary Fig. 2). Instead, mean reproductive rate was found to be more regularly associated with the second axis (Supplementary Table 2 and

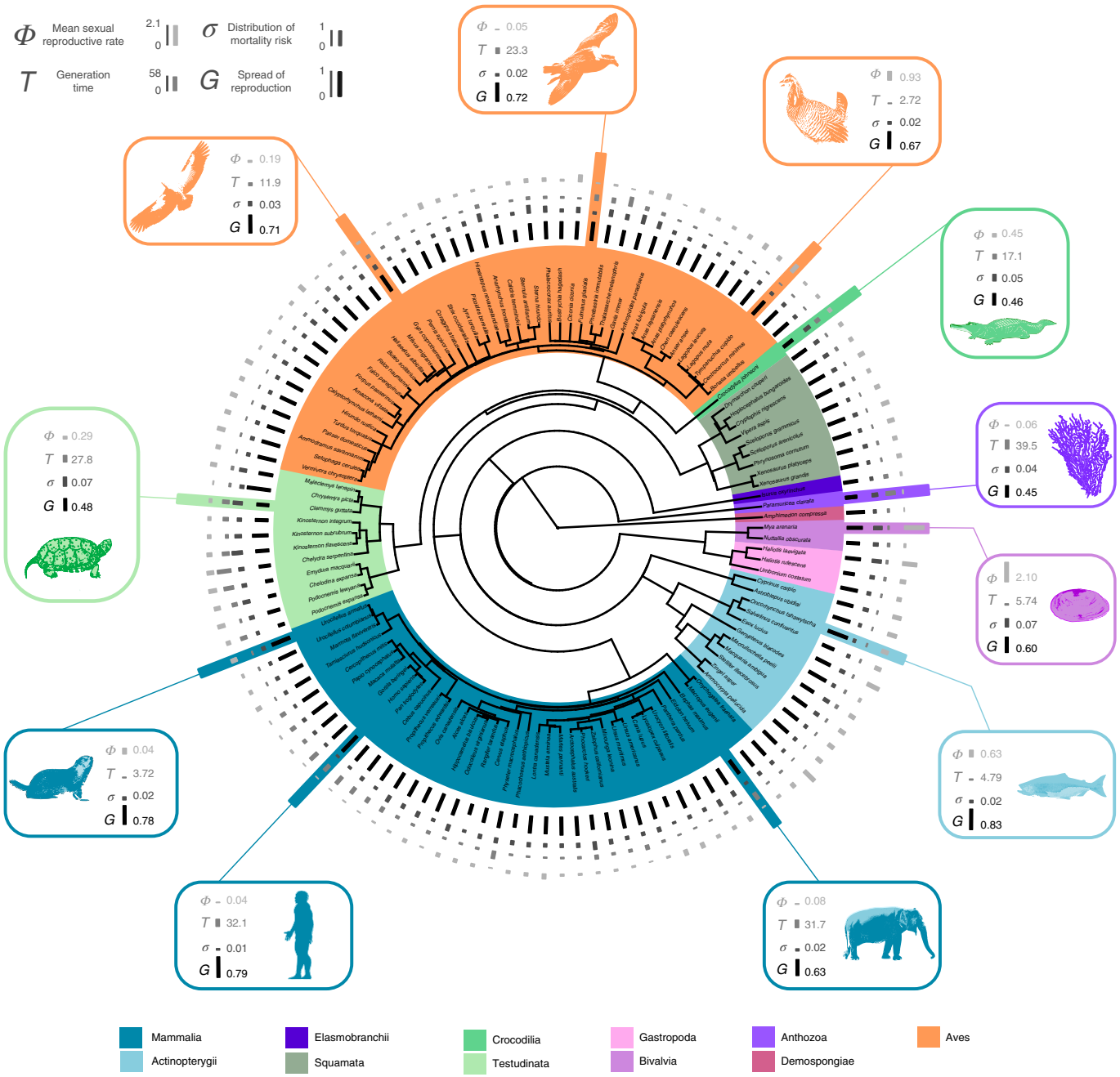

Fig. 2 | Variation in life history traits across 121 species of vertebrate and invertebrate animals. A phylogeny of the species, coloured by clade, is shown with bar plots representing the mean sexual reproductive rate, generation time, distribution of mortality risk and the spread of reproduction of each species; see Fig. 1. A range of different life histories across clades are highlighted, clockwise from the top right: *Tympanuchus cupido* (greater prairie chicken), *Crocodylus johnsoni* (freshwater crocodile), *Paramuricea clavata* (violescent sea-whip), *Mya arenaria* (soft-shell clam), *Oncorhynchus tshawytscha* (Chinook salmon), *Elephas maximus* (Asian elephant), *Homo sapiens* (human), *Urocitellus armatus* (Uinta ground squirrel), *Clemmys guttata* (spotted turtle), *Gyps coprotheres* (Cape vulture) and *Fulmarus glacialis* (northern fulmar).

Supplementary Fig. 2). This weaker association may reflect that trade-offs involving reproduction do not always result in changes in numbers of offspring. For example, Stearns[4] seminal study of life history strategies in mammals found that the developmental level of offspring, as ranked from precocial to altricial, was a major component of a secondary axis of variation. While mean reproductive rate was not consistently associated with a fast–slow continuum, we find that mass-specific reproductive output, a measure of reproduction more closely related to reproductive productivity[26], was correlated with the axis of variation associated with T, L_a and e_{L_a}, with fast-living species associated with higher reproductive productivities (Supplementary Table 4). This highlights that potential trade-offs between survival and reproduction are likely to be determined by how resources are allocated across several facets of reproduction, including maternal and paternal allocation in terms of both the number and quality of offspring.

Along with mean reproductive rate we find that the distribution of mortality risk and, for the overall analysis as well as the endotherm and the Aves subsets, the spread of reproduction over the life course (G) describes a second axis of variation in life history

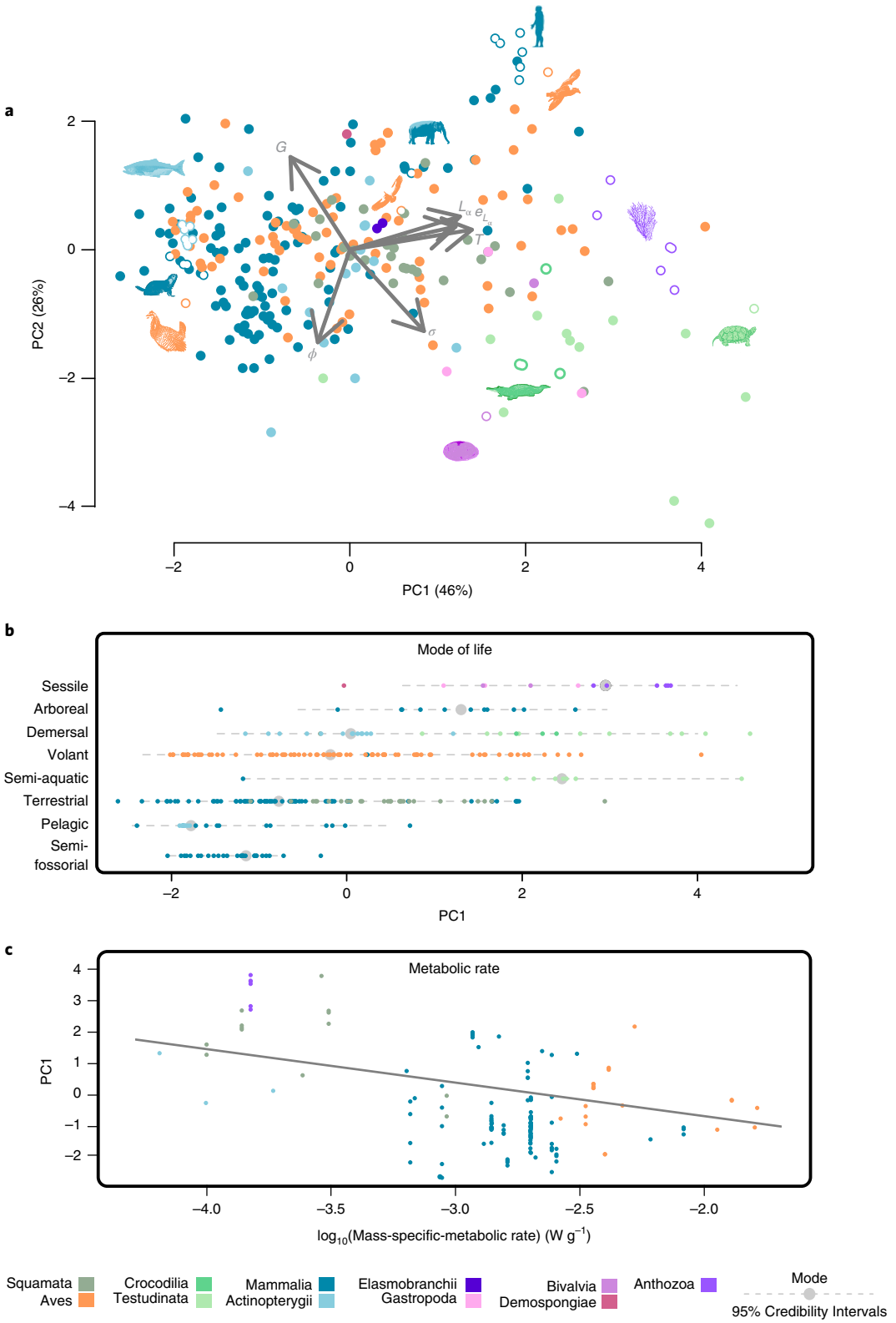

Fig. 3 | Principal component analysis and the influence of mode of life and metabolic rate on the position of populations along the first principal component axis (PC1). a, Principal component analysis of the full dataset of 285 populations from 121 animal species showing two axes of variation explaining 71% of the variation (PC1 and PC2). **b**, PC1 is associated with mode of life; sessile (populations = 12, species = 7) and demersal (populations = 28, species = 19) modes of life are associated with a slower pace of life in comparison to pelagic species (populations = 21, species = 7). **c**, Mass-specific metabolic rate is lower for species associated with a slower pace of life for 42 species across 137 populations (intercept = −2.71, lower 95% credibility interval (CI) = −7.80, higher 95% CI = 2.04; slope = −1.11, lower 95% CI = −2.01, higher 95% CI = −0.22; Supplementary Table 4). The life history traits are: distribution of mortality risk, age at first sexual reproduction, mean life expectancy post-maturity, generation time, mean sexual reproductive rate and the spread of reproduction across the life course. Populations of highlighted species are represented with open circles and are shown from left to right (with number of populations in brackets): *Urocitellus armatus* (4), *Oncorhynchus tshawytscha* (2), *Tympanuchus cupido* (1), *Gyps coprotheres* (1), *Mya arenaria* (1), *Elephas maximus* (1), *Crocodylus johnsoni* (3), *Homo sapiens* (6), *Fulmarus glacialis* (1), *Paramuricea clavata* (6) and *Clemmys guttata* (1).

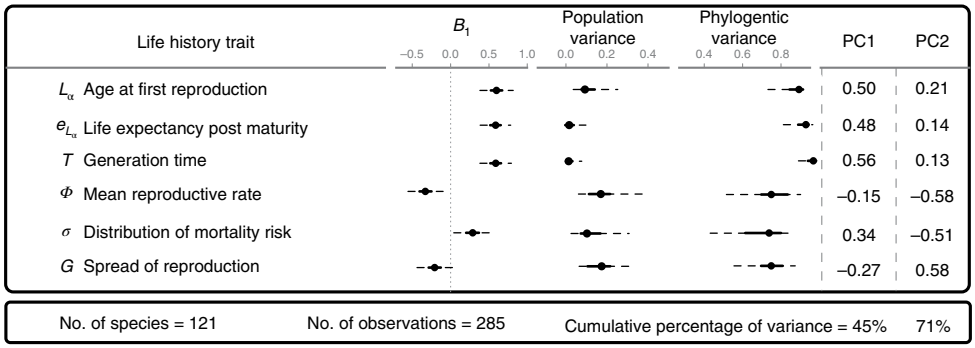

Fig. 4 | Posterior distributions, modes and 95% CI for the effect of $\log_{10}$ body mass on the $\log_{10}$ of each of the life history traits, variance at the population and phylogenetic scales and the principal component loadings of phylogeny- and body mass-corrected life history traits. Scores with loading greater than 0.4 or less than −0.4 are highlighted in bold. The slope of $\log_{10}$ body mass regressed on each life history trait is given by B_1. The variance terms are given as the proportion of variance attributed to population- and phylogenetic-level variance in each body mass model. All data in the $\log_{10}$ body mass models are *z*-scored. PC1 and PC2 describe the loadings for the first two principal components.

strategies (Figs. 3 and 4; Supplementary Tables 2 and 3). This second axis of variation closely resembles previous observations of the dichotomy between traits associated with biological times, referred to as pace of life traits[27,28], and traits associated with how life events are distributed across the life course, referred to as shape of life traits[27,28] (Fig. 3). These 'shape' traits, along with mean reproductive rates, in general correlate such that species with more iteroparous reproductive strategies, higher mean reproductive rates and more variable mortality risks over the life course, such as the Australian freshwater crocodile (*Crocodylus johnsoni*) and the soft-shell clam (*Mya arenaria*), are at one end of the continuum with the other extreme being occupied by species such as the Chinook salmon (*Oncorhynchus tshawytscha*) and humans (*Homo sapiens*).

The association between the distribution of mortality risk and the spread of reproduction across the life course found here reflects the expected trade-off between allocating resources towards current reproduction at the expense of future survival. Reproductive strategies with high degrees of iteroparity are expected to be associated with lower juvenile survival rates[29,30]. Here, we find that higher degrees of iteroparity (low G) are associated with higher variability in mortality risk across the life course, with such species also found to have lower juvenile survival rates in our analysis (Figs. 3 and 4; Supplementary Table 4). Interestingly we don't find this association in the subsets of mammals and ectotherms (Supplementary Table 2 and Supplementary Fig. 2). In the case of the Mammalia subset, high degrees of semelparity are associated with the slow end of the fast–slow continuum. This is probably linked to the narrower reproductive window in long-lived mammalian species due to both late ages of sexual maturity and reproductive senescence, which are common amongst mammals[31,32]. This is particularly evident in species with post- reproductive lifespans in our analysis[33], such as humans (*Homo sapiens*) and Asian elephants (*Elephas maximus*), which have narrow reproductive windows due to long juvenile phases and continued survival after reproductive age. In contrast, in ectotherms the slow end of the fast–slow continuum is associated with high degrees of iteroparity. This is probably due to the low degrees of reproductive senescence reported in ectotherm groups with asymptotic growth[10,34–37], where species, such as *Crocodylus johnsoni* and *Clemmys guttata* continue to reproduce across their entire life course after maturity.

While trade-offs play a fundamental role in shaping life history patterns, how species interact with their environment is expected to be an important driver of interspecific variation in life history strategies within the constraints of these trade-offs. Classical life history theory predicts that species subject to high mortality risks will have a quicker onset of senescence and have life history strategies associated with the fast end of the fast–slow continuum[38]. Support for this includes the increased lifespans found in species with ecological modes of life associated with reduced environmentally driven mortality[39]. Here, we find that both demersal and sessile species are more associated with the slow end of the T, L_a and e_{L_a} continuum when compared to pelagic species (Fig. 3, Supplementary Fig. 3 and Supplementary Tables 4 and 5). Similar associations between pelagic and demersal lifestyles have been previously found with the fast–slow continuum[40]. Fast life history traits have also been found to be associated with the increased activity and risk-taking behaviour associated with pelagic modes of life[41]. The finding that both benthic and sessile species are associated with slower life histories also suggests the broader importance of motility in determining life history strategies. The rate at which species interact within their ecological communities, both with regards to obtaining resources and with avoiding predators, is likely to be a fundamental determinant of the optimal allocation of resources within life history space.

Metabolic rate has long been associated with life history traits[42] and is likely to be an important determinant of a species position within life history space. The rate at which an organism expends and uses energy is intrinsically linked to the rate at which it can grow, or produce reproductive mass[42]. High metabolic rates are predicted to be associated with faster life history strategies and have been previously linked to rapid development and early sexual maturity[43]. We find such an association in our analysis with higher mass-specific metabolic rates found in species positioned on the fast end of the fast–slow continuum (Fig. 3 and Supplementary Table 4). This pattern largely reflects the position of ectotherms and endotherms along the first axis of variation in life history space, with ectotherms such as turtles (Testudinata), crocodiles (Crocodilia) and corals (Anthozoa) found at the slow end of the fast–slow continuum, while endothermic Mammalia and Aves species were found to be typically associated with the fast end of the continuum (Fig. 3 and Supplementary Fig. 3). However, while there are cases of species with high metabolic rates and slow life histories, such as humans (*Homo sapiens*) and fulmars (*Fulmarus glacialis*), our analysis finds that between major taxonomic groups species follow the classic predictions of metabolic theory with regards to life history traits[42].

Intraspecific variation in life history space, as represented by population-level variation, is likely to reflect the lability of species' life histories to abiotic and biotic drivers. This variability, however, is not equally distributed across the various life history traits. The life history traits T, L_a and e_{L_a} (Fig. 4) are strongly associated with species mean body mass and phylogenetic ancestry ($h^2 = 0.89$–0.97; Fig. 4). This finding contrasts with the lack of a phylogenetic signal observed in similar traits among plants[14,44], indicating potentially

fundamental differences between animals and plants regarding constraints on life history evolution. In contrast, the distributions of mortality risk and reproduction over the life course show weaker associations with body mass and have lower phylogenetic signals (Fig. 4). Instead, these traits, together with mean sexual reproduction, have higher intraspecific variation (Fig. 4). This is well demonstrated in humans, where populations are broadly distributed across the second axis of variation (Fig. 3) due to population differences in the distribution of both mortality risk and reproduction, a pattern that is in agreement with recent findings by Colchero et al.[27]. This highlights that changes in life history strategies in response to perturbations may be mediated along this second axis of variation; with changes in where mortality and reproduction occur in the life course being more flexible than other life history traits.

Discussion

Here we show that, while animal life history traits vary greatly, 71% of the variation associated with life history strategies can be explained by two axes of variation after correcting for mass and phylogeny. These results extend frameworks of life history strategies, which aim to link aspects of evolution[45,46], ecology[14] and behaviour[47] to life history strategies, across the range of taxonomic groups in our analysis. Our results also highlight the importance of extending such frameworks to include measures of life history traits related to the second axis of variation. In particular, we find that population variation in life history traits is associated with the second axis which may indicate that changes in population dynamics are particularly associated with this axis, as was recently found with changes to degree of iteroparity in carnivorous marsupials[48]. However, while extending life history frameworks may improve our understanding of the drivers of population dynamics, our analysis also finds that species at different levels of conservation risk are found across the full range of life history space (Supplementary Fig. 3 and Supplementary Table 4). This suggests that, while understanding life history strategies is an important component of conservation management[17], across broad phylogenetic and physiological groupings, no particular life history strategy seems to be exempt from contemporary Anthropocene risks[49].

Our results also support the conclusion that, despite the diversity of animal forms in our analysis, which range from sponges to humans, life history strategies are universally defined by trade-offs across the animal kingdom. Such universal patterns have also been found across the diversity of plant forms[14] suggesting that trade-offs associated with the fast–slow continuum, mortality risks and degree of iteroparity may be the main drivers of life history variation across the tree of life[10]. While these trade-offs shape life history strategy space, we find that metabolic rates and particular ecological modes of life, such as being demersal or sessile, are associated with certain regions of life history strategy space. These associations support previous findings that the position of a species within life history strategy space is driven by traits related to the rate at which an organism can both acquire and process resources from the environment[8]. However, other fundamental biological traits, such as the ability to reproduce clonally, are associated with many sessile species and are also likely to be important drivers of various aspects of life history, such as senescence[50]. Expanding demographic measures of life history traits to animal groups, which share such fundamental traits with other major taxonomic groups such as plants, will allow for a deeper understanding of the fundamental drivers of life history strategies.

Methods

Data collection. *Animal life history components.* To calculate a series of animal life history traits relating to development, survival and reproduction we used matrix population models from the COMADRE Animal Matrix Database[20]. This database contains demographic data compiled as age-, size- or developmental stage-structured matrix population models. For each population, we used the mean and pooled matrix population models available in the COMADRE database[20]. Only matrix population models that were parameterized from non-captive populations in non-manipulated conditions, and which could be divided into separate sexual and clonal reproduction matrices, were used (Supplementary Methods). To ensure that each matrix population model represented a complete life cycle, we only included those that were irreducible, primitive and hence ergodic, as tested using the popdemo package[51]. This reduced the initial number of 2,207 populations representing 455 species down to 279 populations representing 120 species. To include human populations into our analysis, we used life tables of human populations from Keyfitz & Flieger[52–54], giving an overall of 285 populations representing 121 species in our analysis.

Body size, metabolic rate, mass-specific reproductive output, IUCN status and mode-of-life data. We collated data for adult body mass from a variety of sources including Myhrvold et al.[55] and Fishbase[56] and used geometric reconstructions to calculate sizes for groups such as corals to facilitate comparative analysis (see Supplementary Methods and Supplementary Data). For mass-specific reproductive output, we collated data on offspring mass and mean number of offspring per annum from sources including Myhrvold et al.[55] and Fishbase[56], and divided the annual reproductive mass produced by adult body mass (see Supplementary Methods). For metabolic rate, we collated data on mass-specific basal metabolic rate for mammals and birds and mass-specific standard metabolic rate for ectotherms from various sources[57–63] (see Supplementary Methods and Supplementary Data). We collated conservation status of species using the International Union for Conservation of Nature (IUCN) Red List[64]. The mode of life for each species was defined as one of the following: sessile, demersal, pelagic, semiaquatic, terrestrial, arboreal or volant using the criteria from Fishbase[56] and Healy et al.[39] (Supplementary Data).

Phylogeny. To incorporate the inherent non-independent relationships among species due to phylogenetic relatedness and to include the error associated with building such phylogenetic relationships, we constructed a distribution of 100 supertrees using available phylogenies and the open tree of life as a backbone[65] (Supplementary Methods).

Analysis. *Life history traits.* From each matrix population model, we calculated six life history traits: age at first sexual reproduction, life expectancy post maturity, generation time, distribution of mortality risk, mean sexual reproductive rate and the spread of reproduction. Mean reproductive rate is the annual mean fecundity of a population weighted by its stable stage distribution. Generation time is the mean number of years necessary for a cohort to replace itself. The distribution of mortality risk is measured as the standard deviation of the distribution of mortality across the life course. A high value would indicate that mortality is unevenly distributed across the life course, while a low value indicates mortality is more evenly distributed. For the spread of reproduction, which was measured using the Gini index on the life table decomposition of the matrix population model: $G=1$ describes populations that are fully semelparous, with all individuals reproducing at the same age; $G\approx 0$ represents the most extreme iteroparous case or equal reproduction across all ages in a population. For full details of the calculation of each metric see Supplementary Methods.

Body size analysis. To quantify associations between life history traits and body mass, we used a series of Bayesian phylogenetic mixed models. The animal term in the MCMCglmm package was used to correct for phylogeny and an additional variance term was used to account for several populations per species[66]. Body mass and all life history traits were $\log_{10}$ transformed, mean centred, and expressed in units of standard deviation, before performing the regressions. To incorporate the error associated with building phylogenies, each life history trait versus body mass model was re-run for 100 constructed phylogenies using the mulTree package[67,68]. Matrix dimension was included as a covariate to control for potential confounding effects related to life history traits[69].

Axes of life history. To determine the main axes of life history variation in animals, we performed a principal component analysis. To simultaneously correct for the effect of both body size and phylogeny, we used the residuals of each life history metric calculated from the body size Bayesian phylogenetic mixed models and the mode of the posterior distribution for each model parameter. We determined the number of axes retained in the principle component analysis through Horn's parallel analysis using the paran package[70]. To illustrate the life history space filled by the major taxonomic, mode of life and thermoregulatory groups we fitted ellipses defined by the 95% bivariate credibility intervals relating to the principle component scores for each group. The pairwise overlap between each group was calculated using a Bayesian inference approach to sample 100 fitted ellipses, using the functionality of the SIBER package[71] for each group to incorporate the error associated with fitting such ellipses.

Mode of life, mass-specific metabolic rate and mass-specific reproductive output analysis. To further explore the relationship between ecological mode of life, mass-specific metabolic rate, mass-specific reproductive output and life history strategies, we ran a series of Bayesian phylogenetic mixed models with the values

along the first principle component analysis axis against each of these traits, with population and phylogeny controlled as random effects as described above.

Taxonomic subgroup analysis. To explore the consistency of the pattern of life history strategies across major taxonomic and thermoregulatory groups, we ran analyses on subsets of the full dataset including: (1) only endotherms, (2) only ectotherms, (3) only Aves and (4) only Mammalia (Supplementary Methods). Limited sample size precluded the analysis of other major groups (for example, Crocodilia and Testudinata).

Robustness analysis. To test the robustness of our analysis we also conducted a series of additional analyses including where we: (1) did not correct each life history trait for body mass, (2) used a metric of mean sexual reproduction rate that was not weighted by the stable state distribution, (3) used the standard deviation of the *lxmx* curve instead of using the Gini index as a measure of reproductive spread and (4) conducted the main analysis without the inclusion of generation time.

Reporting Summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All demography data are available from the COMADRE database (http://www.compadre-db.org). Additional data are available in Supplementary Data.

Code availability

The code used to generate the analysis can be accessed on Github: https://github.com/healyke/Healy_et_al_2019_Animal_Life_History.

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References

1. Vrtílek, M., Žák, J., Pšenička, M. & Reichard, M. Extremely rapid maturation of a wild African annual fish. *Curr. Biol.* **28**, R822–R824 (2018).
2. Nielsen, J. et al. Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*). *Science* **353**, 702–704 (2016).
3. Stearns, S. C. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* **87**, 476–486 (2000).
4. Stearns, S. C. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* **41**, 173–187 (1983).
5. De Magalhaes, J. & Costa, J. A database of vertebrate longevity records and their relation to other life-history traits. *J. Evol. Biol.* **22**, 1770–1774 (2009).
6. Brusca, R., Moore, W. & Shuster, S. *Invertebrates* 3rd edn (Sinauer Associates, 2016).
7. Gross, M. R. Disruptive selection for alternative life histories in salmon. *Nature* **313**, 47 (1985).
8. Hughes, P. W. Between semelparity and iteroparity: empirical evidence for a continuum of modes of parity. *Ecol. Evol.* **7**, 8232–8261 (2017).
9. Capellini, I., Baker, J., Allen, W. L., Street, S. E. & Venditti, C. The role of life history traits in mammalian invasion success. *Ecol. Lett.* **18**, 1099–1107 (2015).
10. Jones, O. R. et al. Diversity of ageing across the tree of life. *Nature* **505**, 169–173 (2014).
11. Law, R. Optimal life histories under age-specific predation. *Am. Nat.* **114**, 399–417 (1979).
12. Stearns, S. C. *The Evolution of Life Histories* (Oxford Univ. Press, 1992)
13. Bielby, J. et al. The fast–slow continuum in mammalian life history: an empirical reevaluation. *Am. Nat.* **169**, 748–757 (2007).
14. Salguero-Gómez, R. et al. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proc. Natl Acad. Sci. USA* **113**, 230–235 (2016).
15. Bauwens, D. & Diaz-Uriarte, R. Covariation of life-history traits in lacertid lizards: a comparative study. *Am. Nat.* **149**, 91–111 (1997).
16. Paniw, M., Ozgul, A. & Salguero-Gómez Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. *Ecol. Lett.* **21**, 275–286 (2017).
17. Bischof, R. et al. Regulated hunting re-shapes the life history of brown bears. *Nat. Ecol. Evol.* **2**, 116 (2018).
18. Winemiller, K. O., Fitzgerald, D. B., Bower, L. M. & Pianka, E. R. Functional traits, convergent evolution, and periodic tables of niches. *Ecol. Lett.* **18**, 737–751 (2015).
19. Gaillard, J.-M. et al. An analysis of demographic tactics in birds and mammals. *Oikos* **56**, 59–76 (1989).
20. Salguero-Gómez, R. et al. COMADRE: a global data base of animal demography. *J. Anim. Ecol.* **85**, 371–384 (2016).
21. Gaillard, J.-M. et al. Generation time: a reliable metric to measure life-history variation among mammalian populations. *Am. Nat.* **166**, 119–123 (2005).
22. Oli, M. K. The fast–slow continuum and mammalian life-history patterns: an empirical evaluation. *Basic Appl. Ecol.* **5**, 449–463 (2004).
23. Dobson, F. S. & Oli, M. K. Fast and slow life histories of mammals. *Ecoscience* **14**, 292–297 (2007).
24. Read, A. F. & Harvey, P. H. Life history differences among the eutherian radiations. *J. Zool.* **219**, 329–353 (1989).
25. Ricklefs, R. E. Life-history connections to rates of aging in terrestrial vertebrates. *Proc. Natl Acad. Sci. USA* **107**, 10314–10319 (2010).
26. Brown, J. H., Hall, C. A. S. & Sibly, R. M. Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nat. Ecol. Evol.* **2**, 262–268 (2018).
27. Colchero, F. et al. The emergence of longevous populations. *Proc. Natl Acad. Sci. USA* **113**, E7681–E7690 (2016).
28. Wrycza, T. F., Missov, T. I. & Baudisch, A. Quantifying the shape of aging. *PLoS ONE* **10**, e0119163 (2015).
29. Cole, L. C. The population consequences of life history phenomena. *Q. Rev. Biol.* **29**, 103–137 (1954).
30. Charnov, E. L. & Schaffer, W. M. Life-history consequences of natural selection: Cole's result revisited. *Am. Nat.* **107**, 791–793 (1973).
31. Martin, J. G. & Festa-Bianchet, M. Age-independent and age-dependent decreases in reproduction of females. *Ecol. Lett.* **14**, 576–581 (2011).
32. Huber, S. & Fieder, M. Evidence for a maximum 'shelf-life' of oocytes in mammals suggests that human menopause may be an implication of meiotic arrest. *Sci. Rep.* **8**, 14099 (2018).
33. Lahdenperä, M., Mar, K. U. & Lummaa, V. Reproductive cessation and post-reproductive lifespan in Asian elephants and pre-industrial humans. *Front. Zool.* **11**, 54 (2014).
34. Congdon, J. D. et al. Testing hypotheses of aging in long-lived painted turtles (*Chrysemys picta*). *Exp. Gerontol.* **38**, 765–772 (2003).
35. Congdon, J., Nagle, R., Kinney, O. & van Loben Sels, R. Hypotheses of aging in a long-lived vertebrate, Blanding's turtle (*Emydoidea blandingii*). *Exp. Gerontol.* **36**, 813–827 (2001).
36. Vaupel, J. W., Baudisch, A., Dölling, M., Roach, D. A. & Gampe, J. The case for negative senescence. *Theor. Popul. Biol.* **65**, 339–351 (2004).
37. Barneche, D. R., Robertson, D. R., White, C. R. & Marshall, D. J. Fish reproductive-energy output increases disproportionately with body size. *Science* **360**, 642–645 (2018).
38. Williams, G. C. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**, 398–411 (1957).
39. Healy, K. et al. Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. Lond. B* **281**, 20140298 (2014).
40. Bjørkvoll, E. et al. Stochastic population dynamics and life-history variation in marine fish species. *Am. Nat.* **180**, 372–387 (2012).
41. Nakayama, S., Rapp, T. & Arlinghaus, R. Fast–slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *J. Anim. Ecol.* **86**, 192–201 (2017).
42. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).
43. Reznick, D. N., Bryant, M. J., Roff, D., Ghalambor, C. K. & Ghalambor, D. E. Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* **431**, 1095–1099 (2004).
44. Burns, J. H. et al. Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. *J. Ecol.* **98**, 334–344 (2010).
45. Auer, S. K., Dick, C. A., Metcalfe, N. B. & Reznick, D. N. Metabolic rate evolves rapidly and in parallel with the pace of life history. *Nat. Commun.* **9**, 14 (2018).
46. Baker, T. R. et al. Fast demographic traits promote high diversification rates of Amazonian trees. *Ecol. Lett.* **17**, 527–536 (2014).
47. Sepp, T., McGraw, K. J., Kaasik, A. & Giraudeau, M. A review of urban impacts on avian life-history evolution: does city living lead to slower pace of life? *Glob. Change Biol.* **24**, 1452–1469 (2018).
48. Collett, R. A., Baker, A. M. & Fisher, D. O. Prey productivity and predictability drive different axes of life-history variation in carnivorous marsupials. *Proc. R. Soc. Lond. B* **285**, https://doi.org/10.1098/rspb.2018.1291 (2018).
49. Allen, W. L., Street, S. E. & Capellini, I. Fast life history traits promote invasion success in amphibians and reptiles. *Ecol. Lett.* **20**, 222–230 (2017).
50. Salguero-Gómez, R. Implications of clonality for ageing research. *Evol. Ecol.* **32**, 9–28 (2018).
51. Stott, I., Hodgson, D. J. & Townley, S. popdemo: an R package for population demography using projection matrix analysis. *Methods Ecol. Evol.* **3**, 797–802 (2012).
52. Keyfitz, K. & Flieger, W. *World Population: An Analysis of Vital Data* (Univ. of Chicago Press, 1968).

53. Keyfitz, N. & Flieger, W. *Population: Facts and Methods of Demography* (W. H. Freeman, 1971).
54. Keyfitz, N. & Flieger, W. *World Population Growth and Aging: Demographic Trends in the Late Twentieth Century* (Univ. of Chicago Press, 1990).
55. Myhrvold, N. P. et al. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109–3109 (2015).
56. Froese, R. & Pauly, D. (eds) *FishBase* (World wide web electronic publication, accessed 13 June 2016); http://www.fishbase.org.
57. White, C. R. & Seymour, R. S. Mammalian basal metabolic rate is proportional to body mass2/3. *Proc. Natl Acad. Sci. USA* **100**, 4046–4049 (2003).
58. White, C. R., Phillips, N. F. & Seymour, R. S. The scaling and temperature dependence of vertebrate metabolism. *Biol. Lett.* **2**, 125–127 (2006).
59. McNab, B. K. Ecological factors affect the level and scaling of avian BMR. *Comp. Biochem. Physiol. A* **152**, 22–45 (2009).
60. Killen, S. S. et al. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *Am. Nat.* **187**, 592–606 (2016).
61. Genoud, M., Isler, K. & Martin, R. D. Comparative analyses of basal rate of metabolism in mammals: data selection does matter. *Biol. Rev.* **93**, 404–438 (2018).
62. Ultsch, G. R. Metabolic scaling in turtles. *Comp. Biochem. Physiol. A* **164**, 590–597 (2013).
63. Fristoe, T. S. et al. Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals. *Proc. Natl Acad. Sci. USA* **112**, 15934–15939 (2015).
64. *The IUCN Red List of Threatened Species* (IUCN, 2019); http://www.iucnredlist.org.
65. Hinchliff, C. E. et al. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl Acad. Sci. USA* **112**, 12764–12769 (2015).
66. Hadfield, J. D. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22 (2010).
67. Guillerme, T. & Healy, K. *mulTree: A Package for Running MCMCglmm Analysis on Multiple Trees* (Zenodo, 2014); https://doi.org/10.5281/zenodo.12902
68. Healy, K. Eusociality but not fossoriality drives longevity in small mammals. *Proc. R. Soc. Lond. B* **282**, 20142917 (2015).
69. Salguero-Gomez, R. & Plotkin, J. B. Matrix dimensions bias demographic inferences: implications for comparative plant demography. *Am. Nat.* **176**, 710–722 (2010).
70. Dinno, A. *paran: Horn's Test of Principal Components/Factors* R package v.1.5.2 (CRAN, 2012); https://cran.r-project.org/web/packages/paran/index.html.
71. Jackson, A. L., Inger, R., Parnell, A. C. & Bearhop, S. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* **80**, 595–602 (2011).

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Author contributions

K.H. designed and conducted the analysis, collated body size, mode of life, metabolic rate and phylogenetic data and wrote the manuscript. T.H.G.E contributed additional human demography data. O.R.J. provided additional code used in the analysis. Y.M.B. and R.S.-G. designed the research. All authors contributed to analysis, design, discussion and interpretation of the results and writing of the manuscript.

Competing interests

The authors declare no competing interests.

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Software and code

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Data collection	No software was used to collect data.
Data analysis	R: Language and Environment for Statistical Computing. version 3.4.0. All Code used within the analysis is available at https://github.com/healyke/Healy_et_al_2019_Animal_Life_History

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All demography data will be made available from the COMADRE database (http://www.compadre-db.org). Additional data are available in Supplementary Data.

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Study description	Comparative analysis of animal life history traits calculated from population projection models. Analysis include controls for body mass, matrix dimension and for pseudo-replication arising from the shared ancestry of species. Additional analysis includes correlating axes of life history variation against mass specific metabolic rate, reproductive productivity and species mode-of-life. Detailed description of all data and the analysis carried out are outlined in the supplementary files (S1).
Research sample	We used population projection models from the COMADRE database which represented 285 populations of 121 animal species. Taxonomic groups represented within the sample include Mammalia, Aves, Actinopterygii, Demospongiae, Reptilia, Gastropoda, Elasmobranchii, Bivalvia, Anthozoa as outlined in the supplementary files (S1) and in Supplementary Data. This represents the currently available demographic data, in the form of population projection models, for the Animal Kingdom and will be made available on publication.
Sampling strategy	Sample sizes were determined by the number of population projection models from the COMADRE database which meet the criterion outlined in the supplementary files (S1).
Data collection	The COMADRE database was used for demography data. Addition data was collated by the lead author (KH) from the literature and existing databases as described in detail in the supplementary files (S1)
Timing and spatial scale	Data from the COMADRE database are collected from the literature and covers a global scale. A full description of how the data is collected in COMADRE is outlined in Salguero-Gómez, R. , Jones, O. R., Archer, C. R., Bein, C. , Buhr, H. , Farack, C. , Gottschalk, F. , Hartmann, A. , Henning, A. , Hoppe, G. , Römer, G. , Ruoff, T. , Sommer, V. , Wille, J. , Voigt, J. , Zeh, S. , Vieregg, D. , Buckley, Y. M., Che-Castaldo, J. , Hodgson, D. , Scheuerlein, A. , Caswell, H. , Vaupel, J. W. and Coulson, T. (2016), COMADRE: a global data base of animal demography. J Anim Ecol, 85: 371-384. doi:10.1111/1365-2656.12482
Data exclusions	From the initial COMADRE dataset, which contains over 400 species, population projection models which did not meet the criterion outlined in the supplementary files (S1) were excluded from the study. This resulted in a dataset of 285 population projection models representing 121 species.
Reproducibility	There was no experimental element to this study. The results of this study can be reproduced as outlined in detail in the supplementary files (S1).
Randomization	As this was a comparative analysis of the available data of animal species demography randomization of the data was not relevant to this study. Covariates including, body mass, matrix dimension were controlled as described in the Methods section and in the supplementary files (S1).
Blinding	As this study used an existing dataset of population projection models blinding was not relevant.

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