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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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Summary paragraph

Animals exhibit an extraordinary diversity of life history strategies. These realised combinations of survival, development, and reproduction are predicted to be constrained by physiological limitations and 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 both the fast-slow continuum and by a separate 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 lifecycle in just 14 days1. In contrast, the Greenland shark only becomes sexual mature after 156 years2. Despite their differences, the evolution of both these life histories is underpinned by the same evolutionary principal of maximising fitness through differing rates of survival, development, and reproduction3. As these species demonstrate, different combinations of traits associated with fitness, known as life history traits4, 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 millennia5 while Gastrotrichs can complete their life cycle within days6. Pacific salmon (*Oncorhynchus tshawytscha*) release thousands of eggs in a single reproductive event7, while Laysan albatross (*Phoebastria immutabilis*) individuals are known to reproduce continuously for decades8. 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 our understanding of questions ranging from the invasive potential of species9 to the evolution of senescence10.

Despite the diversity of life history strategies, not all are possible. Darwinian demons, hypothetical organisms which live forever and reproduce at infinite rates, do not exist due to limitations in resources11. The structure of 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 output4. There are many such trade-offs that shape life history strategies12. The most well-understood of these results is the fast-slow continuum4,13 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 rates2. Additional axes of variation beyond the fast-slow continuum have also been described13-16. These typically relate to various moments of reproduction such as its annual intensity, duration, and its spread across the life course14.

Identifying these major axes of variation provides a framework which can aid in mapping how conservation management strategies17, degrees of invasiveness9 and diversity18 relate to different life history strategies. However, current patterns of animal life history strategies are either based on taxonomically restricted groups, typically Mammalia11 and Aves13,19, or do not account for the potential variation in life history traits that can be attributed to body size16. Hence our current understanding of patterns in life history strategies effectively misses the wider variation in life history traits observed across the animal kingdom. Here, we exploit the recent rapid expansion in taxonomic coverage of animal demographic data20 to incorporate age related measures of mortality and reproduction10, along with other life history traits (Figure 1), into a test of the universality of life history patterns from the level of populations to the scale of the animal evolutionary tree (Figure 2).

**Results**

The variation in life history traits observed amongst animals is shown across six life history traits (Figures 2,3). Variation in traits ranged from generation times (*T*) of 2.4 to 53.2 years in the Eastern sand darter (*Ammocrypta pellucida*) and the Black-browed Albatross (*Thalassarche melanophris*) to low variation in distributions of mortality risks found in humans ( = 0.01) to the more highly variable mortality risks found across the life course of the smooth Australian abalone (*Haliotis laevigata*) ( = 0.07, Figure 2). Reproductive traits varied from mean reproductive rates of 0.02 offspring per annum in humans to 225,595 per annum 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 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 constrained4,13,15,19,21-25. Here, we find that, after controlling for body size and phylogenetic relatedness (Figure 4, Supplementary Table 1; Supplementary Figure 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 (Figure 3, Figure 4). This general pattern of two axes was also found across taxonomic sub groupings and in our robustness analysis (Supplementary Tables 2-3). The presence of these patterns across such 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 strategies14.

As predicted by the fast-slow continuum, generation time (*T*), age at first reproduction (*La*), and life expectancy post maturity are all positively correlated (Figure 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 (Figure 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 *La* and *T*, which have been suggested as proxies of the fast-slow continuum21. An axis relating to these traits is found in all of our additional analyses of taxonomic groups (Mammalia, Aves, Endothermic, Ectothermic) and in the case where *T* is removed from the analysis (Supplementary Table 2-3).

Contrary to predictions from the fast-slow continuum13, 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, Supplementary Figure 2). Instead mean reproductive rate (*Φ*) was found to be more regularly associated with the second axis (Supplementary Table 2, Supplementary Figure 2). This weaker association may reflect that trade-offs involving reproduction may 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 productivity26, was correlated with the axis of variation associated with *T*, *La* and , 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 (*Φ*) 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 strategies (Figure 3-4, Supplementary Table 2-3). This second axis of variation closely resembles previous observations of the dichotomy between traits associated with biological times, referred to as pace of life traits27,28, and traits associated with how life events are distributed across the life course, referred to as shape of life traits27,28 (Figure 3). These “shape” traits along with mean reproductive rates 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 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 (G) 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 rates29,30. 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 (Figure 4; Figure 3; Supplementary Table 4). Interestingly we don’t find this association in the subsets of mammals and ectotherms (Supplementary Table 2, Supplementary Figure 2). In the case of the mammal subset high degrees of semelparity are associated with the slow end of the fast-slow continuum. This is likely linked to the narrower reproductive window in long lived mammals species due to both late ages of sexual maturity and reproductive senescence which is common amongst mammals31,32. This is particularly evident in species with post reproductive lifespans in our analysis33, Humans (*Homo sapiens*) and Asian Elephants (*Elephas maximus*), which have narrow reproductive windows due to long juvenile phases and continued survival post reproductive age. In contrast, in ectotherms the slow end of the fast-slow continuum is associated with high degrees of iteroparity. This is likely due to the low degrees of reproductive senescence reported in ectotherm groups with asymptotic growth10,34-37, where species, such as *Crocodylus johnsoni* and *Clemmys guttata* continue to reproduce across their entire life course post 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 continuum38. Support for this includes the increased lifespans found in species with ecological modes of life associated with reduced environmentally driven mortality39. Here we find that both demersal and sessile species are more associated with the slow end of the *T*, *La* and continuum when compared to pelagic species (Figure 3; Supplementary Figure 3; Supplementary Table 4-5). Similar associations between pelagic and demersal lifestyles have been previously found with the fast slow continuum40, with fast life history traits also found to be associated with the increased activity and risk taking behaviour associated with pelagic modes of life41. 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 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 traits42 and is likely to be an important determinant of a species position within life history space. The rate at which an organism expends and utilises energy is intrinsically linked with the rate at which it can grow, or produce reproductive mass42. High metabolic rates are predicted to be associated with faster life history strategies and have been previously linked to rapid development and early sexual maturity43. 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-slowcontinuum (Figure 3, 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), 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 (Figure 3, Supplementary Figure 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 traits42.

Intraspecific variation within 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*, *La*, and (Figure 4) are strongly associated with species mean body mass and phylogenetic ancestry (h2 = 0.89-0.97, Figure 4). This finding contrasts with the lack of a phylogenetic signal observed in similar traits among plants14,44, indicating potentially fundamental differences between animals and plants regarding constraints on life history evolution. In contrast, the distribution of mortality risk () and reproduction over the life course (*G*) show weaker associations with body mass and have lower phylogenetic signals (Figure 4). Instead, these traits, together with mean sexual reproduction (*Φ),* have higher intra-specific variation (Figure 4). This is well demonstrated in humans, where populations are broadly distributed across the second axis of variation (Figure 3) due to population differences in the distribution of both mortality risk and reproduction, a pattern which is in agreement with recent findings by Colchero *et al*27. This finding 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 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 evolution45,46, ecology14 and behaviour47 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 are associated with the second axis which may indicate that changes in population dynamics may be particularly associated with this axis, such as recently found with changes to degree of iteroparity in carnivorous marsupials48. 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 Figure 3; Supplementary Table 4). This suggests that, while understanding life history strategies is an important component of conservation management17, across broad phylogenetic and physiological groupings no particular life history strategy seems to be exempt from contemporary Anthropocene risks49.

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 forms14 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 life10. 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 environment8. However, other fundamental biological traits, such as the ability to reproduce clonally, are also associated with many sessile species and are also likely to be important drivers various aspects of life history, such as senescence50. Expanding demographic measures of life history traits to animal groups, which share such fundamental traits with other major metazoan 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 Database20. This database contains demographic data compiled as age, size- or developmental stage-structured matrix population models (MPMs). For each population, we used the mean and pooled MPMs available in the COMADRE database20. Only MPMs that were parameterised from non-captive populations in un-manipulated conditions, and which could be divided into separate sexual and clonal reproduction matrices were used (Supplementary methods). To ensure that each MPM represented a complete life cycle, we only included those that were irreducible, primitive and hence ergodic, as tested using the popdemo package51. This reduced the initial number of 2207 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 196852, 197153 and 199054, 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 Fishbase56 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 Fishbase56 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 IUCN red list64. The mode-of-life for each species was defined as either sessile, demersal; pelagic; semiaquatic; terrestrial; arboreal or volant using the criteria from Fishbase56 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 backbone65 (Supplementary methods).

**Analysis**

*Life history traits*: From each MPM, we calculated six life history traits: age at sexual reproduction (*Lα*), life expectancy post maturity (*eLα*); generation time (*T*); distribution of mortality risk ; mean sexual reproductive rate (*Φ*); and the spread of reproduction as measured using the Gini index (*G*). 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 MPM, G = 1 describes populations that are fully semelparous, with all individuals reproducing at the same age, with G ~ 0 representing the most extreme iteroparous case or equal reproduction across all ages in a population. For full details on 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 (BPMM) using the animal term in the MCMCglmm package to correct for phylogeny and an additional variance term to account for multiple populations per species66. Body mass and all life history traits were log10 transformed, mean centred and expressed in units of standard deviation prior to 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 package67, 68. Matrix dimension was included as a co-variate to control for potential confounding effects relating to life history traits69.

*Axes of life history*: To determine the main axes of life history variation in animals, we performed a principal component analysis (PCA). 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 BPMMs using the mode of the posterior distribution for each model parameter. We determined the number of axes retained in the PCA using Horn’s parallel analysis using the paran package70. To illustrate the life-history space filled by the major taxonomic, mode-of-life and thermoregulatory groups we fit ellipses defined by the 95% bivariate confidence interval relating to the PC 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 package71, 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 BPMMs with the values along the first PCA 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 (e.g. Crocodilia, 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 traits 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.

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**Author Contributions**

KH 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. YMB & RS-G designed the research and all authors contributed to analysis, design, discussion and interpretation of the results, and writing of the manuscript.

**Data Availability**

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

**Code Availability**

Code used to run the analysis is available on Github <https://github.com/healyke/Healy_et_al_2019_Animal_Life_History>.

**Competing Interests Statement**

We report no competing interests.

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**Figure legends**

**Figure 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 years) 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 1.

**Figure 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 (Φ), generation time (*T*), distribution of mortality risk and the spread of reproduction (*G*) of each species; See Figure 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), *Fulmarus glacialis* (northern fulmar).

**Figure 3. Principal Component Analysis (PCA) and the influence of mode-of-life and metabolic rate on the position of populations along the first principal component axis (PC1). (A)** PCA of the full dataset of 285 populations from 121 animal species show two axes of variation explaining 71% of the variation. **(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% 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 (Lα); mean life expectancy post maturity ; generation time (T); mean sexual reproductive rate (Φ) and the spread of reproduction across the life course (G). 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).

**Figure 4. Posterior distributions, modes and 95% credibility intervals for the effect of log10 body mass on the log10 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 log10 body mass regressed on each life history trait is given by *B1*. 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 log10 body mass models are z-scored. PC1 and PC2 describe the loadings for the first two principal components.