

AN ANALYSIS OF THE EVOLUTION OF LIFE HISTORY TRAITS

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ABSTRACT

The evolution and relationship between life-history traits has been a popular research topic over the past several decades. Previous research has generally focused on a single or small number of species, or a single trait. I utilized multiple trait-based datasets to create a collection of 777 *Mammalia* species across five taxonomic orders (*Artiodactyla*, *Carnivora*, *Chiroptera*, *Primates*, *Rodentia*) to examine the relationships between size, longevity, maturity age, and number of offspring, both within the taxonomic orders and across the *Mammalia* clade. I found that although the general pattern followed classic “fast-slow continuum”, there were some exceptions to this pattern, specifically body size in *Chiroptera* and litter size in *Artiodactyla* and *Primates*. This suggests that although a correlation between certain life-history traits exist, “slow” traits (large size, long life, few offspring) do evolve in species with “fast” traits when limited by other factors, such as the size requirements for flight.

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TABLE OF CONTENTS

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
CHAPTER	
I. INTRODUCTION.....	1
II. METHODS.....	8
Dataset Collection And Preparation.....	9
Statistical Analysis.....	10
Hierarchical Clustering.....	11
III. RESULTS.....	12
Statistical Analyses: How Do Life-History Traits Covary?.....	12
Body Mass In Relation To Lifespan, Sexual Maturity Age, And Litter Size.....	12
Litter Size In Relation To Lifespan And Sexual Maturity Age.....	14
Sexual Maturity Age In Relation To Lifespan.....	16
Hierarchical Clustering Analysis.....	18
IV. DISCUSSION.....	19

REFERENCES.....	23
VITA.....	29

LIST OF TABLES

1 Number of species included in each phylogenetic order in the dataset.....	10
2 Total number of taxonomic classifications within <i>Mammalia</i> represented in the dataset.....	10
3 The r and r^2 values across all phylogenetic orders.....	17

LIST OF FIGURES

1 Regression of lifespan to body mass in each phylogenetic order.....	13
2 Regression of body mass to sexual maturity age in each phylogenetic order.....	13
3 Regression of average litter size to body mass in each phylogenetic order.....	14
4 Regression of average litter size to lifespan in each phylogenetic order.....	15
5 Regression of average litter size to sexual maturity age in each phylogenetic order.....	15
6 Regression of sexual maturity age to lifespan in each phylogenetic order.....	16
7 Phylogenetic Tree of Subclasses Euarchontogires and Laurasiatheria from Springer et al. (2004).....	21

CHAPTER I

INTRODUCTION

As technology has begun to be more integrated into scientific research, data archiving, cultivation, and access are becoming more important throughout all fields of science. Biology, particularly genomics, has fully embraced the use of large archived datasets. Researchers in evolution and ecology have been slower to embrace the use of large data collections, a topic that has been addressed before (Fabian & Flatt, 2012; Hampton et al., 2013). While the use of large datasets in evolution and ecological studies has increased in recent years, most big data examinations are focused on climate change and genomic research. Hampton et al. (2013) proposed that this issue is due to the fact that while ecologists produce large amounts of data, there is a lack of culture of data curation, archival, and sharing, so that specific ecological data is often difficult to locate and/or access (Fabian & Flatt, 2012; Hampton et al., 2013). This could also be due to accessibility and the wide variety of data collected in evolution and ecological studies. Climate data for example, has free public datasets available from the National Oceanic and Atmospheric Administration, with average temperatures and rainfall, along with hourly temperatures and rainfall since the 1960s (see: <https://www.ncdc.noaa.gov/cdo-web/datasets>). These basic variables and measurements are fairly standard across most climate studies. This is often not possible in many evolution and ecological studies, as research can cover topics such as

distributions, behaviors, interactions and life histories of species, populations, and communities, making a “catch all” dataset difficult to cultivate and quantify. Even basic information, such as body measurements, are normally collected based on the taxonomic classification. Size measurements can include wingspan, shell size, or nose-to-tail length, which makes data standardization a difficult process due to the extremely large number of possible variables. Despite the challenges with large trait-based datasets, some organizations have begun to cultivate data, making their archives free and available to the public. Amniote (Myhrvold et al., 2015), PanTHERIA (Jones et al., 2009), and COMADRE (Salguero-Gomez et al., 2016) provide free, trait-based datasets, while Traitbank (Parr et al., 2016) is a repository for ecologists to upload their data, which is then aggregated and managed for public access. These datasets provide researchers with large amounts of easily accessible and verified data. Such datasets make it possible to address broad ecological and evolutionary questions within and across phylogenetic classifications.

Life history theory explores how natural selection and other evolutionary forces optimize an organism’s fitness with respect to their traits at various stages of development. Stearns (1992) identified the principle life history traits as: 1) size at birth, 2) growth pattern, 3) age at maturity, 4) size at maturity, 5) number/size/sex ratio of offspring, 6) age and size specific reproductive investments, 7) age and size specific mortality schedules 8) length of life. These traits and their connection to constraining relationships, or trade-offs, shape and optimize an organism’s phenotype. Understanding life-history traits is critical for understanding how natural selection shapes an organism’s fitness in response to ecological challenges, as life-history traits are the principal components of fitness (Stearns, 1992). Stearns (1992) describes importance of life

history theory as the key to understanding natural selection, genetic variation, and population dynamics of interacting species (Stearns, 1992).

There are still many unknowns surrounding the evolution of life histories. One reason for this is due to the convergent evolution of life history traits throughout the phylogenetic tree. For example, large body size and long lifespans have evolved independently, numerous times across a wide variety of species, throughout the history of life. For example, the common mammal ancestor is predicted to have been a short lived, small, mouse-like insectivore (O’Leary et al., 2013), meaning that large bodies and greater longevity have evolved multiple times even when focusing exclusively on the *Mammalia* clade. Indeed, local adaptations are common and can generally be attributed to a specific response to a specific environmental condition or competition. Lineage specific traits and the relationship between these traits can be more difficult to examine without a specific ecological driver. Recent research has begun to work backwards, focused on the molecular mechanisms, that can be attributed to a single life history trait. These approaches analyze cellular characteristics between species at opposite ends of that trait (e.g. small mammal/large mammal) (Croco et al., 2017) to find molecular similarities that influence the same factors. Researchers have found that the convergent mechanisms for the evolution of large body size has been attributed to: the high replicative potential of normal cells (Lorenzini, 2005), having an efficient spindle assembly check point (Lorenzini, 2011), accurate erythropoiesis (Croco, 2016), decreased telomerase activity (Gomes, 2011; Seluanov, 2007), and the increase expression of oncosuppressors (Sulak, 2016). Similarly, the suggested mechanisms for the evolution of increased longevity in species include: improved Ku recognition of DNA double strand breaks (Lorenzini, 2009), more efficient 53BP1/γH2AX DNA damage foci formation (Croco, 2017; Fink, 2011), and decreased telomere length (Gomes, 2011). In primates,

longevity-associated gene categories have been identified and examined (Jobson et al., 2010), as well as the biological processes that modulate lifespan (Muntané et al., 2018). While this has provided insight into what drives these traits at a molecular level, this research still does not address any of the ecological and environmental factors, or relationships between these traits that have been observed in numerous studies. This approach indicates that body size and longevity are driven by different molecular mechanisms, yet the pattern of large species generally having longer lifespans than smaller species, specifically in mammals, has been shown in numerous studies (Bielby et al., 2007; Fisher et al., 2001; Harvey & Promislow, 1990; Myhrvold et al., 2015; Oli, 2004; Ricklefs, 2000). If these life history traits are driven by different molecular mechanisms, what relationships exist between these traits and how closely are they related?

The relationship between life history traits can be difficult to properly examine, but previous research suggests that life-history traits are constrained evolutionarily by trade-offs (Stearns, 1992). In the absence of such trade-offs we would expect the evolution of a ‘Darwinian demon’, a species with infinite energy that can exist never making energy trade-offs between size, reproduction investments, growth, development, and longevity. However, because individuals have limited energy, trade-offs among life-history traits constrain the evolution of such traits. To address these energy requirements that constrain the evolution of life-history traits, previous research often used models built on r/K selection theory. This classified species as r-selected, meaning generally smaller, producing a high number of offspring, exhibiting low energy investment in offspring, type 3 survivorship pattern, or K-selected, which is associated with generally larger individuals, a low number of offspring, high energy investment in offspring, and type 1 or 2 survivorship pattern. While this theory has been criticized due to its ambiguity (Getz, 1993; Stearns, 1988; Wilbur et al., 1974), the general ideas behind this theory

provide the framework for the models of life history that are often used today. The classic fast-slow continuum, defined by Reynolds (2003) as: “fast life” meaning small adult size/offspring, mature early, short generation time, high fecundity, short lifespan and “slow life” being the opposite of those traits. Many studies have examined and supported the fast-slow continuum (Bennett & Owens, 2002; Bielby et al., 2007; Elgar, 1990; Fisher et al., 2001; Franco & Silvertown, 1996; Harvey & Promislow, 1990; Loehle, 1988; Myhrvold et al., 2015; Oli, 2004; Ricklefs, 2000; Saether, 1987). This model of life-history evolution does have some underlying problems however and can be controversial due to the lack of specifics in traits, consistency in methods, and external ecological/biological factors (Jeschke & Kokko, 2009). There are also general inconsistencies with certain species that repeatedly defy the fast-slow continuum. For example, birds are extremely long lived in relation to their body mass when compared to mammals (Finch, 1994; Austad & Holmes, 1995), which is also seen in bats (Fenton & Kunz, 2005; Foley et al., 2018; Jones & MacLarnon, 2001; South & Wilkinson, 2002), and mammals that hibernate (Blanco & Zehr, 2015; Lyman et al., 1981; Turbill et al., 2011; Zehr et al., 2014). Despite these issues, the fast-slow continuum can generally be applied to mammalian life histories (Bielby et al., 2007; Fisher et al., 2001; Harvey & Promislow, 1990; Myhrvold et al., 2015; Oli, 2004; Ricklefs, 2000) and served as a predictor in my examination of life-history relationships. While Bergmann’s Rule has generally been supported (Ashton et al., 2000; Ashton, 2002; Dayan & Meirl, 2003), suggesting that species body size increases with its distance from the equator, my goal for this research was focused more on the relationships between the traits and across taxonomic groups.

Previous research examining the evolution of life history traits has often focused on a limited number of species and limited number of traits. Few studies, in contrast, have used large

datasets to focus on multiple traits across a large scale of taxonomic classes. In the present study, I utilized large ecological and evolutionary datasets to explore broad-scale relationships between life history traits, both within and across taxonomic groups. Specifically, I examined relationships between adult size, sexual maturity age, lifespan, and clutch/litter size in 777 species across five taxonomic orders in Mammalia (*Artiodactyla*, *Carnivora*, *Chiroptera*, *Primates*, *Rodentia*). I selected these life history traits and species for specific reasons. Previous studies (Stearns, 1980; Stearns, 1992) have suggested that higher-taxonomic level examinations could provide a better representation of lineage-specific trait divergence, in life history evolution focused studies, as the species have shared ancestry (phylogeny). The genetic similarities from shared ancestors can provide an expected covariance between species, which can help when differentiating between lineage-specific effects and local adaptive effects (Whitehead, 2012). I focused on these specific life-history traits, as they are key life-history traits that are present in a range of taxonomic groups, and as such, they allow for comparisons across a large proportion of animals. By using data that represents each of the life history categories and that are consistent across all taxonomic groups being analyzed, we can gain insight on the correlations between life history traits across multiple taxonomic groups, thus providing more information on the evolution of these traits at a broad scale.

Many of the past examinations of these life-history traits suggests general patterns may exist within the lineage specific traits of species. For example, based on the fast-slow continuum hypothesis, larger mammals generally have longer lifespans, reach sexual maturity at a higher age, and have smaller clutch/litter sizes (Bennett & Owens, 2002; Bielby et al., 2007; Elgar, 1990; Fisher et al., 2001; Franco & Silvertown, 1996; Harvey & Promislow, 1990; Loehle, 1988; Myhrvold et al., 2015; Ricklefs, 2000; Saether, 1987). As a result, I expected adult body size to

have an inverse relationship with clutch/litter size and a direct, positive relationship with lifespan and sexual maturity age. I also expected lifespan and sexual maturity age to have an inverse relationship with clutch/litter size, but a direct, positive relationship with each other. I expected the exception to this prediction to be the order *Chiroptera*, due to previous research (Fenton & Kunz, 2005; Foley et al., 2018; Jones & MacLarnon, 2001; South & Wilkinson, 2002) suggesting that bat body mass has little relationship with other traits, possibly due to the size restrictions needed for flight.

CHAPTER II

METHODS

Fabian and Flatt describe life history evolution by categorizing relevant traits into five categories: size, development, offspring number, lifespan, and survival (Fabian & Flatt, 2012). In the present study, I focused on size, number of offspring, development, and longevity, as variation and a lack of standardization among ecological datasets make survival rates difficult to accurately measure and compare across a broad range of species. Adult body mass, average lifespan, sexual maturity age, and average litter size represent my selected traits of size, longevity, number of offspring, and development, as they provided the largest and most diverse data available. As the number of organisms and variety of species in this examination covers such a wide range of values, I was cautious in both my approach to analysis and in interpreting the results. Previous studies have used a variety of different analyses to examine trait-based comparisons to remove factors such as behavior, environment, and other ecological factors that could possibly influence the results. Since my examination is looking at groups of organisms in a very large-scale analysis, I used the “rules of thumb for comparative analysis” as described by Stearns (1992). Traits were examined and compared across each of the 5 taxonomic orders and overall (taxonomic class). Previous studies (Stearns, 1980; Stearns, 1992) have suggested that in studies of life history evolution, higher-taxonomic level examinations can provide a better

representation of lineage-specific trait divergence, as the species have shared ancestry (phylogeny). The genetic similarities of the species provides an expected covariance between them, as species with the most recent shared ancestry would be expected to share similar traits. These expected covariances can help differentiate between lineage-specific effects and local adaptive effects (Whitehead, 2012). At the present time, my aim was to provide a first exploration of the relationships between life-history traits at broad phylogenetic scales; as such, I didn't utilize phylogenetic comparative analysis methods, although this will be a critical next step in this line of research.

Dataset Collection And Preparation

I downloaded full datasets of all life-history traits listed above from the *Amniote Life History* (Myhrvold et al., 2015), *PanTHERIA* ((Jones et al., 2009), and *AnAge* (Magalhães et al., 2009). All analyses described below were performed in R (version 3.5.2). I first removed any data that did not contain a reference and removed all species not in the taxonomic class Mammalia. I next compared different variables for each of the life history traits being examined (size, development, offspring produced, and longevity) to determine which traits had the largest amount of information available and were measured in the same manner (or could easily be converted to the same measurement). The specific life-history variables selected for this study were the following: average adult body mass (kg), average lifespan (years), average age of sexual maturity (years), and average litter size. I then removed any species with missing data. All species with multiple entries were aggregated and averaged. The remaining data was comprised of 1038 different species, across 26 different phylogenetic orders. The majority of these species were classified in 5 different orders, which I chose to analyze as they provided a similar number

of species in each. The final collection of mammals represented approximately 14% of all 5,416 *Mammalia* species (Reeder & Wilson, 2005) with a total of 777 species.

Table 1 Number of species included in each phylogenetic order in the dataset

Taxonomic Order	Species
Artiodactyla	159
Carnivora	152
Chiroptera	152
Primate	127
Rodentia	187

Table 2 Total number of taxonomic classifications within *Mammalia* represented in the dataset

Classification	Total Number
Order	5
Family	75
Genus	356
Species	777

Statistical Analysis

I approached this study as an examination of the relationships between these 4 life history traits. All statistical analysis regression models examined each phylogenetic order individually, comparatively, and combined. Specifically, I used linear regression to examine the pair-wise relationships between body size, lifespan, sexual maturity age, and average litter size, for the all-species group and each individual order. Body mass was log-transformed to condense the range

in values, not for distribution purposes. This approach is recommended to reduce error, while maintaining similar relationships between data (Smith, 1984). The range in values in the other 3 traits were not large enough to require a *log* transformation.

Hierarchical Clustering

Hierarchical clustering analysis (Johnson, 1967) is a form of statistical analysis that constructs a hierarchy of like groups (clusters) and is commonly used in genomic research due to its ability to discover similarities between objects within large amounts of data. The goal of this analysis was to identify which traits appear to be most strongly correlated or related, regardless of ancestry. To examine the similarities in correlations of life history traits between these species, I used the *pvclust package* (Suzuki & Shimodaira, 2006) as the clustering method, which clusters using two types of *p*-values: approximately unbiased (AU) and a bootstrap probability value (BP). Correlations are computed between each trait. These values are then examined with each life history trait belonging to its own cluster. In every iteration the distance between any two clusters *A* and *B* is taken to be the mean of all distances $d(x, y)$ between pairs of objects *x* in *A* and *y* in *B*, that is, the mean distance between elements of each cluster. Each iteration updates the distance between existing cluster connections and a new cluster *X* is given based on the proportional averaging of the distances of $d_{A, X}$ and $d_{B, X}$. Standard bootstrap resampling is used to determine BP, while multiscale bootstrap resampling is used to calculate AU. These two bootstrap methods are alternative ways to generate *p*-values, meaning that clusters with: AU \geq 95% and/or BP \geq 95%, are considered to be strongly correlated (Shimodaira & Suzuki, 2006).

CHAPTER 3

RESULTS

Statistical Analyses: How Do Life-History Traits Covary?

Body Mass In Relation To Lifespan, Sexual Maturity Age, And Litter Size

Body mass was significantly and positively correlated with both lifespan and sexual maturity age in all of the five individual orders (Figure 1; Figure 2; Table 3). The r^2 values ranged from 0.19 to 0.69 for sexual maturity age (overall $r^2 = 0.4214$) and 0.1 to 0.56 for lifespan (overall $r^2 = 0.3259$) (Table 3), suggesting that variation in body mass is correlated with a substantial amount of the variation in both sexual maturity age and lifespan in all taxonomic groups.

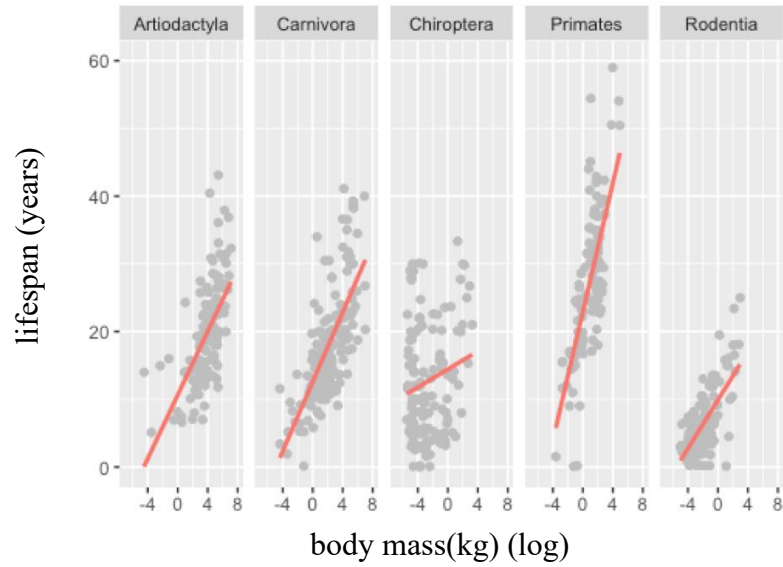


Figure 1 Regression of lifespan to body mass in each phylogenetic order

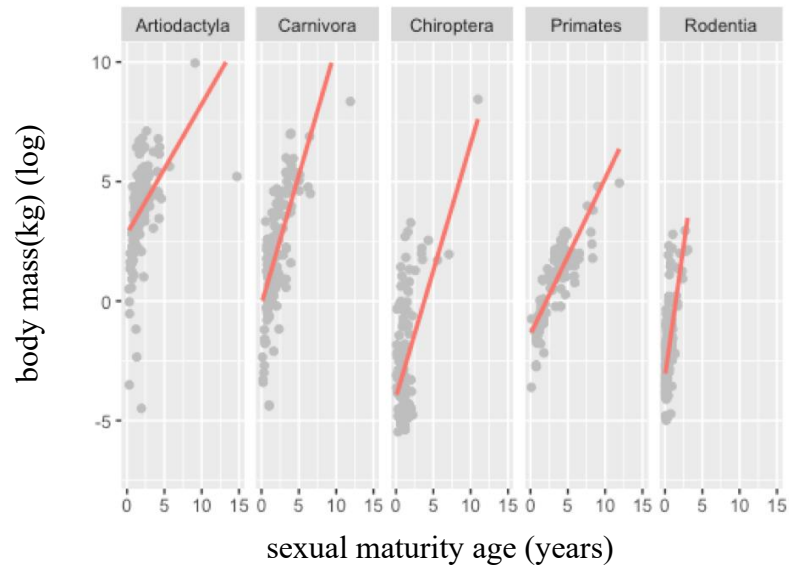


Figure 2 Regression of body mass to sexual maturity age in each phylogenetic order

The litter size relationship appears slightly weaker. I found the relationship between body mass and litter size to be significantly and negatively correlated across the all-species group and

in four of the five orders, with r^2 values ranging from 0.0313 to 0.1948 (Figure 3; Table 3). There was no significant relationship between body mass and litter size in *Chiroptera* (Table 3).

Together, these results suggest that in general species with larger body sizes also tend to have longer lifespans, mature later in life, and have fewer offspring in their litters.

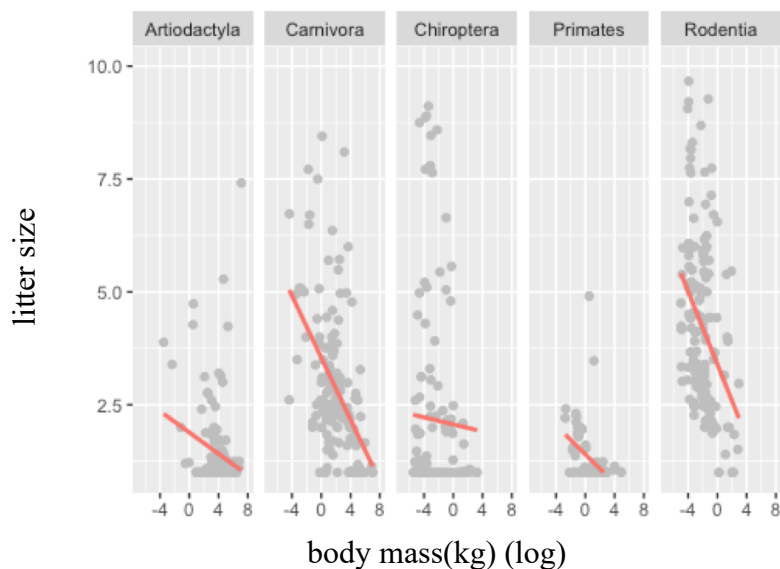


Figure 3 Regression of average litter size to body mass in each phylogenetic order

Litter Size In Relation To Lifespan And Sexual Maturity Age

Litter size was negatively correlated with lifespan in the all species grouping and in four of the five orders (Figure 4; Table 3). There was no significant relationship between litter size and lifespan in *Artiodactyla* (Table 3). Likewise, sexual maturity age and litter size were significantly and negatively correlated in *Carnivora* and *Primates* (Figure 5; Table 3).

There was no significant relationship between sexual maturity age and litter size in the *all-species* grouping, *Artiodactyla*, *Chiroptera*, or *Rodentia*.

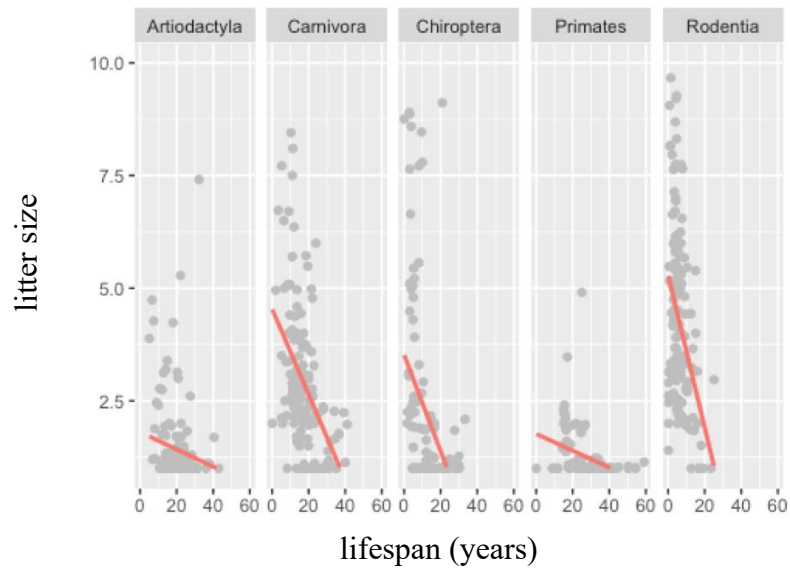


Figure 4 Regression of average litter size to lifespan in each phylogenetic order

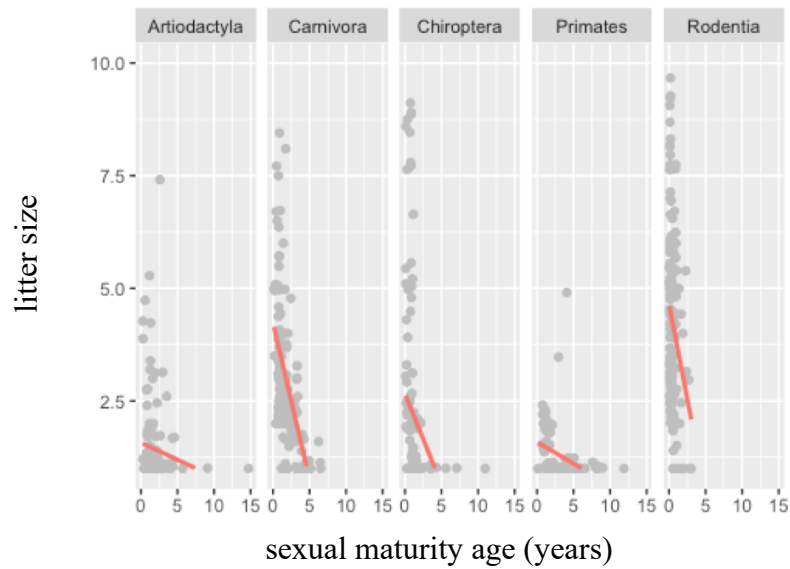


Figure 5 Regression of average litter size to sexual maturity age in each phylogenetic order

Sexual Maturity Age In Relation To Lifespan

Sexual maturity age was strongly and positively correlated with lifespan in the all species grouping and in all five individual orders (Figure 6; Table 3). The r^2 values ranged from 0.2336 to 0.6325, suggesting that variation in sexual maturity age is strongly correlated with lifespan across taxonomic groups (Table 3).

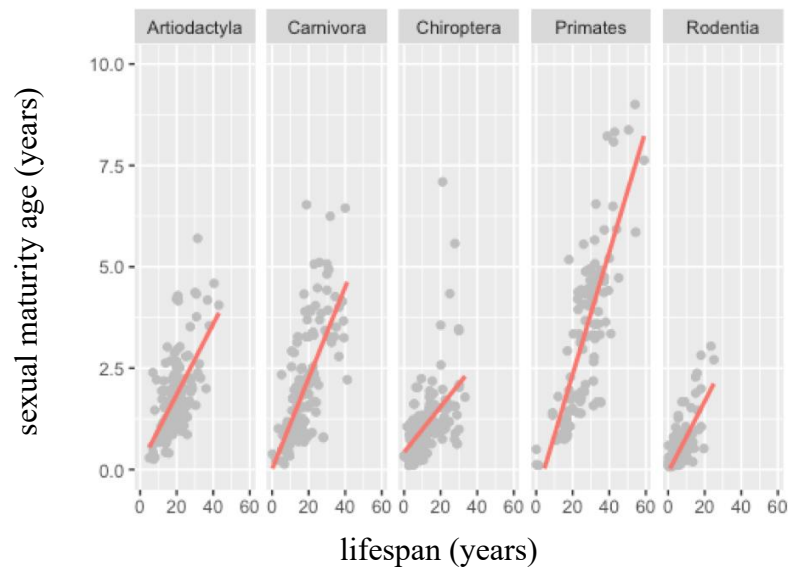


Figure 6 Regression of sexual maturity age to lifespan in each phylogenetic order

Table 3 – The r and r² values across all phylogenetic orders.

All	Trait	lit size			lifespan			s.m.age		
		r	r ²	p	r	r ²	p	r	r ²	p
	a.b.mass	-0.3774	0.1424	***	0.6262	0.1424	***	0.5709	0.3259	***
	lit size				-0.4858	0.236	***	-0.4049	0.1439	
	lifespan							0.7873	0.6199	***
Artiodactyla										
	a.b.mass	-0.1769	0.0313	**	0.6505	0.4231	***	0.4411	0.1946	*
	lit size				-0.1275	0.0163		-0.1131	0.0128	
	lifespan							0.4834	0.2336	***
Carnivora										
	a.b.mass	-0.4413	0.1948	***	0.3225	0.5012	***	0.7205	0.5192	***
	lit size				-0.4647	0.2159	***	-0.2244	0.2898	***
	lifespan							0.7619	0.5804	***
Chiroptera										
	a.b.mass	-0.0284	0.0008		0.3225	0.104	***	0.5387	0.2902	***
	lit size				-0.2884	0.0832	***	-0.2244	0.0503	
	lifespan							0.6434	0.4139	***
Primates										
	a.b.mass	-0.4462	0.1991	***	0.7449	0.5549	***	0.8325	0.6931	***
	lit size				-0.3485	0.1214	***	-0.2941	0.0865	*
	lifespan							0.7953	0.6325	***
Rodentia										
	a.b.mass	-0.3359	0.1128	***	0.6992	0.4889	***	0.6843	0.4683	***
	lit size				-0.3283	0.1078	***	-0.2123	0.0451	
	lifespan							0.7176	0.5149	***

Note. p-values are represented by significance levels: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). All blank cells have a p-value > 0.05

Hierarchical Clustering Analysis

Body mass, lifespan and sexual maturity age were strongly correlated with one another, with AU and BP values both greater than 0.95 for all the relationships (meaning estimated computed $p < 0.05$) between these three traits. Litter size AU/BP values indicated an insignificant relationship with body mass (AU = 0.36, BP = 0.38) and an even weaker relationship with lifespan and sexual maturity age. While these values indicate that litter size could be influenced by the three other traits, the correlation between litter size with body mass, lifespan, and sexual maturity age is much weaker. These results support the statistical analysis which suggest a stronger correlation between body mass, lifespan, and sexual maturity age, which implies that larger species tend to have greater longevity and mature later in life.

CHAPTER IV

DISCUSSION

Here, I have illustrated the relationships between several life-history traits across a broad range of species in the *Mammalia* class. As predicted, adult body mass had a strong, positive correlation with lifespan and sexual maturity age and a negative correlation with litter size. This suggests that larger species tend to live longer, mature later, and have fewer offspring. This pattern has been seen in multiple studies in plants (Franco & Silvertown, 1996; Loehle, 1988), fish (Elgar, 1990), reptiles (Myhrvold et al., 2015), birds (Bennett & Owens, 2002; Myhrvold et al., 2015; Ricklefs, 2000; Saether, 1987), and mammals (Bielby et al., 2007; Fisher et al., 2001; Harvey & Promislow, 1990; Myhrvold et al., 2015; Oli, 2004; Ricklefs, 2000). Lifespan and sexual maturity age specifically show a very strong relationship ($r^2 = 0.6199$, $p < 0.001$), which has previously been described as a proportional constant (Berrigan & Charnov, 1990). and could explain the strong relationship between these traits. The relationships between body mass and lifespan ($r^2 = 0.3921$, $p < 0.001$) and between body mass and sexual maturity age ($r^2 = 0.3259$, $p < 0.001$) are also notable (Table 3). Cluster analysis further supported the regression models, indicating the strongest relationship as cluster 1 (lifespan and sexual maturity age), followed by cluster 2 (cluster 1 + adult body mass). The p -values for litter size generated during cluster analysis were above the threshold ($p < 0.05$) to be considered as having a significant relationship with the remaining traits (Table 7). These patterns align with the general patterns seen in my regression models as well.

Examining *Artiodactyla*, *Carnivora*, *Chiroptera*, *Primates*, and *Rodentia* from a phylogenetic evolutionary scale might help illustrate patterns in the emergence of these four life history traits. For example, using a genome based, phylogenetic tree (Springer et al., 2004), the five *Mammalia* orders (*Artiodactyla*, *Carnivora*, *Chiroptera*, *Primates*, and *Rodentia*) fall into two subclasses, Euarchontoglires and Laurasiatheria (Figure 8) (Springer et al., 2004). Primates and Rodentia are both found in Euarchontoglires, but are on different sides of an evolutionary fork (Figure 8). The differences in evolution between Primates and Rodentia are classic examples of the fast-slow continuum. This could help explain why although Rodentia and Primates have the same general patterns in their life history traits, Primates, in general, are larger, live longer, mature later, and have fewer offspring (slow), while Rodentia are the opposite (fast). The possible evolutionary relationship of lineage-specific traits might be more apparent when examining the phylogenetic orders of *Chiroptera*, *Artiodactyla*, and *Carnivora*. These three orders are all members of subclass Laurasiatheria, which has been suggested could a more recent common ancestor (Springer et al., 2004) (Figure 8). Many of the relationships between life history traits in these three orders share very similar patterns, with a few exceptions, specifically body mass and litter size. Body mass and litter size seem to have almost no relationship in *Chiroptera*, which was predicted, as previous work has suggested that body mass is largely independent from other life history traits in bats (Fenton & Kunz, 2005; Foley et al., 2018; Jones & MacLarnon, 2001; South & Wilkinson, 2002). *Artiodactyla*, the order of the even-hooved land-dwelling mammals, litter size appears to have no significant relationship with lifespan or maturity age and has an $r^2 = 0.031$ with adult body mass.

This could be due to the wide range of trait values in *Artiodactyla* (body mass = 5.12kg to 1814.36kg, lifespan = 5 years to 75 years, maturity age = 0.25 years to 15 years), but having an average litter size of 1.38 (with a max value of 7), suggesting that despite having a large range in body mass, longevity, and maturity age, the number of offspring doesn't seem to change proportionally with these traits (Table 3).

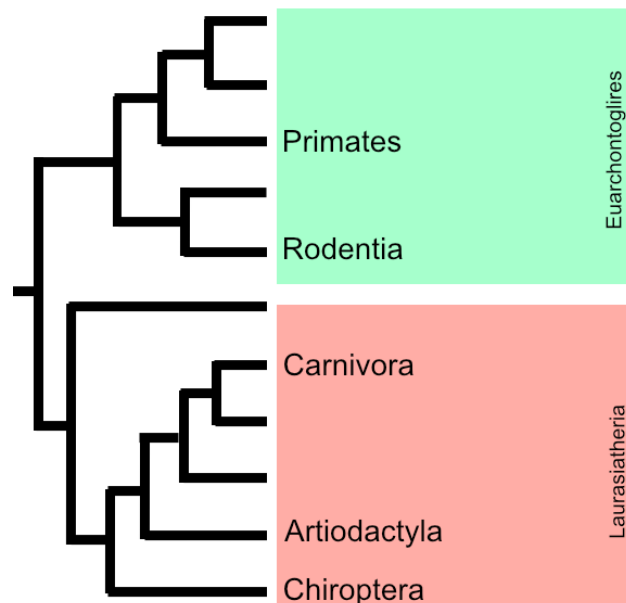


Figure 7 Phylogenetic Tree of Subclasses Euarchontoglires and Laurasiatheria from Springer et al. (2004)

The patterns observed in this analysis still generally follow the traditional fast-slow continuum. I would suggest that future life-history research take advantage of big data from multiple disciplines. For example, analyzing the genomes, climates, energy requirements, and life history traits of all life simultaneously, could provide more insight on the ecological factors that have caused these patterns to appear numerous times throughout the history of life. As the

research community continues the trend of standardizing, cultivating, and archiving free access datasets, future research may have enough data resources to attempt life history analysis at that cross-discipline scale. A better understanding of why these life-history traits evolve and the relationship between lineage specific traits could help provide a blueprint for conservation efforts. Knowing the ecological drivers behind traits such as size, longevity, and reproductive success could help identify and predict species more sensitive to climate change, habitat loss, or other environmental factors.

REFERENCES

- Ashton, K. G. (2002). Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, *11*(6), 505-523. doi:10.1046/j.1466-822X.2002.00313.x
- Ashton, K. G., Tracy, M. C., & de Queiroz, A. (2000). Is Bergmann's rule valid for mammals? *American Naturalist*, *156*(4), 390-415. doi:10.1086/303400
- Bennet, P., & Owens, P. (2002). *Evolutionary ecology of birds: Life histories, mating systems, and extinction*. Oxford University Press, Oxford, United Kingdom.
- Bielby, J., Mace, G. M., Bininda-Emonds, O. R. P., Cardillo, M., Gittleman, J. L., Jones, K. E., . . . Purvis, A. (2007). The fast-slow continuum in mammalian life history: An empirical reevaluation. *American Naturalist*, *169*(6), 748-757. doi:10.1086/516847
- Blanco, M. B., & Zehr, S. M. (2015). Striking longevity in a hibernating lemur. *Journal of Zoology*, *296*(3), 177-188. doi:10.1111/jzo.12230
- Charnov, E. L., & Berrigan, D. (1990). Dimensionless numbers and life history evolution: Age of maturity versus the adult lifespan. *Evolutionary Ecology*, *4*(3), 273-275. doi:10.1007/BF02214335
- Croco, E., Marchionni, S., & Lorenzini, A. (2016). Genetic instability and aging under the scrutiny of comparative biology: A meta-analysis of spontaneous micronuclei frequency. *Mechanisms of Ageing and Development*, *156*, 34-41. doi:10.1016/j.mad.2016.04.004
- Croco, E., Marchionni, S., Storci, G., Bonafe, M., Franceschi, C., Stamato, T. D., . . . Lorenzini, A. (2017). Convergent adaptation of cellular machineries in the evolution of large body masses and long life spans. *Biogerontology*, *18*(4), 485-497. doi:10.1007/s10522-017-9713-9
- de Magalhaes, J. P., & Costa, J. (2009). A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology*, *22*(8), 1770-1774. doi:10.1111/j.1420-9101.2009.01783.x
- Elgar, M. A. (1990). Evolutionary compromise between a few large and many small eggs - comparative evidence in teleost fish. *Oikos*, *59*(2), 283-287. doi:10.2307/3545546

- Fabian, D., & Flatt, T. (2012). Life history evolution. *Nature Education Knowledge*, 3.
- Finch, C. E. (1994). *Longevity, senescence, and the genome*: University of Chicago Press.
- Fink, L. S., Roell, M., Caiazza, E., Lerner, C., Stamato, T., Hrelia, S., . . . Sell, C. (2011). 53BP1 contributes to a robust genomic stability in human fibroblasts. *Aging-Us*, 3(9), 836-845. doi:10.18632/aging.100381
- Fisher, D. O., Owens, I. P. F., & Johnson, C. N. (2001). The ecological basis of life history variation in marsupials. *Ecology*, 82(12), 3531-3540. doi:10.1890/0012-9658(2001)082[3531:tebolh]2.0.co;2
- Foley, N. M., Hughes, G. M., Huang, Z. X., Clarke, M., Jebb, D., Whelan, C. V., . . . Teeling, E. C. (2018). Growing old, yet staying young: The role of telomeres in bats' exceptional longevity. *Science Advances*, 4(2), 12. doi:10.1126/sciadv.aao0926
- Franco, M., & Silvertown, J. (1996). Life history variation in plants: An exploration of the fast-slow continuum hypothesis. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 351(1345), 1341-1348. doi:10.1098/rstb.1996.0117
- Getz, W. M. (1993). Metaphysiological and evolutionary dynamics of populations exploiting constant and interactive resources - r-k selection revisited. *Evolutionary Ecology*, 7(3), 287-305. doi:10.1007/bf01237746
- Gomes, N. M. V., Ryder, O. A., Houck, M. L., Charter, S. J., Walker, W., Forsyth, N. R., . . . Wright, W. E. (2011). Comparative biology of mammalian telomeres: Hypotheses on ancestral states and the roles of telomeres in longevity determination. *Aging Cell*, 10(5), 761-768. doi:10.1111/j.1474-9726.2011.00718.x
- Hampton, S. E., Strasser, C. A., Tewksbury, J. J., Gram, W. K., Budden, A. E., Batcheller, A. L., . . . Porter, J. H. (2013). Big data and the future of ecology. *Frontiers in Ecology and the Environment*, 11(3), 156-162. doi:10.1890/120103
- Holmes, D. J., & Austad, S. N. (1995). The evolution of avian senescence patterns: implications for understanding primary aging processes. *American Zoologist*, 35(4), 307-317.
- Jeschke, J. M., & Kokko, H. (2009). The roles of body size and phylogeny in fast and slow life histories. *Evolutionary Ecology*, 23(6), 867-878. doi:10.1007/s10682-008-9276-y
- Jobson, R. W., Nabholz, B., & Galtier, N. (2010). An Evolutionary Genome Scan for Longevity-Related Natural Selection in Mammals. *Molecular Biology and Evolution*, 27(4), 840-847. doi:10.1093/molbev/msp293

- Johnson, S. C. (1967). Hierarchical clustering schemes. *Psychometrika*, 32(3), 241-254.
doi:10.1007/bf02289588
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., . . . Carbone, C. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology*, 90(9), 2648-2648.
- Jones, K. E., & MacLarnon, A. (2001). Bat life histories: Testing models of mammalian life-history evolution. *Evolutionary Ecology Research*, 3(4), 487-505.
- Kunz, T. H., & Fenton, M. B. (2005). *Bat ecology*. University of Chicago Press.
- Loehle, C. (1988). Tree life-history strategies - the role of defenses. *Canadian Journal of Forest Research*, 18(2), 209-222. doi:10.1139/x88-032
- Lorenzini, A., Fink, L. S., Stamato, T., Torres, C., & Sell, C. (2011). Relationship of spindle assembly checkpoint fidelity to species body mass, lifespan, and developmental rate. *Aging-Us*, 3(12), 1206-1212. doi:10.18632/aging.100416
- Lorenzini, A., Johnson, F. B., Oliver, A., Tresini, M., Smith, J. S., Hdeib, M., . . . Stamato, T. D. (2009). Significant correlation of species longevity with DNA double strand break recognition but not with telomere length. *Mechanisms of Ageing and Development*, 130(11-12), 784-792.
- Lorenzini, A., Tresini, M., Austad, S. N., & Cristofalo, V. J. (2005). Cellular replicative capacity correlates primarily with species body mass not longevity. *Mechanisms of Ageing and Development*, 126(10), 1130-1133.
- Lyman, C. P., O'Brien, R. C., Greene, G. C., & Papafrangos, E. D. (1981). Hibernation and longevity in the turkish hamster *mesocricetus-brandti*. *Science*, 212(4495), 668-670.
doi:10.1126/science.7221552
- Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, 30(3), 331-351. doi:10.1046/j.1365-2699.2003.00837.x
- Muntané, G., Farré, X., Rodríguez, J. A., Pegueroles, C., Hughes, D. A., de Magalhaes, J. P., . . . Navarro, A. (2018). Biological processes modulating longevity across primates: a phylogenetic genome-phenome analysis. *Molecular Biology and Evolution*, 35(8), 1990-2004.
- Myhrvold, N. P., Baldrige, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, S. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles: Ecological Archives E096-269. *Ecology*, 96(11), 3109-3109.

- National Centers for Environmental Information, N. Climate Data Online: Dataset Discovery. Retrieved from <https://www.ncdc.noaa.gov/cdo-web/datasets>
- O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P., . . . Cirranello, A. L. (2013). The Placental Mammal Ancestor and the Post-K-Pg Radiation of Placentals. *Science*, 339(6120), 662-667. doi:10.1126/science.1229237
- Oli, M. K. (2004). The fast-slow continuum and mammalian life-history patterns: an empirical evaluation. *Basic and Applied Ecology*, 5(5), 449-463. doi:10.1016/j.baae.2004.06.002
- Parr, C. S., Schulz, K. S., Hammock, J., Wilson, N., Leary, P., Rice, J., & Corrigan, R. J. (2016). TraitBank: Practical semantics for organism attribute data. *Semantic Web*, 7(6), 577-588. doi:10.3233/sw-150190
- Promislow, D. E. L., & Harvey, P. H. (1990). Living fast and dying young - a comparative-analysis of life-history variation among mammals. *Journal of Zoology*, 220, 417-437. doi:10.1111/j.1469-7998.1990.tb04316.x
- Reynolds, J. D. (2003). Life histories and extinction risk. *Macroecology*. Blackwell Publishing, Oxford, UK, 195-217.
- Ricklefs, R. E. (2000). Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor*, 102(1), 9-22. doi:10.1650/0010-5422(2000)102[0009:ddeoat]2.0.co;2
- Saether, B. E. (1987). The influence of body-weight on the covariation between reproductive traits in european birds. *Oikos*, 48(1), 79-88. doi:10.2307/3565691
- Salguero-Gomez, R., Jones, O. R., Archer, C. R., Bein, C., de Buhr, H., Farack, C., . . . Vaupel, J. W. (2016). COMADRE: A global data base of animal demography. *Journal of Animal Ecology*, 85(2), 371-384. doi:10.1111/1365-2656.12482
- Seluanov, A., Chen, Z. X., Hine, C., Sasahara, T. H. C., Ribeiro, A., Catania, K. C., . . . Gorbunova, V. (2007). Telomerase activity coevolves with body mass not lifespan. *Aging Cell*, 6(1), 45-52. doi:10.1111/j.1474-9726.2006.00262.x
- Smith, R. J. (1984). Allometric scaling in comparative biology - problems of concept and method. *American Journal of Physiology*, 246(2), R152-R160.
- Sorlie, T., Perou, C. M., Tibshirani, R., Aas, T., Geisler, S., Johnsen, H., . . . Borresen-Dale, A. L. (2001). Gene expression patterns of breast carcinomas distinguish tumor subclasses with clinical implications. *Proceedings of the National Academy of Sciences of the United States of America*, 98(19), 10869-10874. doi:10.1073/pnas.191367098

- Sorlie, T., Tibshirani, R., Parker, J., Hastie, T., Marron, J. S., Nobel, A., . . . Botstein, D. (2003). Repeated observation of breast tumor subtypes in independent gene expression data sets. *Proceedings of the National Academy of Sciences of the United States of America*, 100(14), 8418-8423. doi:10.1073/pnas.0932692100
- Springer, M. S., Stanhope, M. J., Madsen, O., & de Jong, W. W. (2004). Molecules consolidate the placental mammal tree. *Trends in Ecology & Evolution*, 19(8), 430-438. doi:10.1016/j.tree.2004.05.006
- Stearns, S. C. (1980). A new view of life-history evolution. *Oikos*, 35(2), 266-281. doi:10.2307/3544434
- Stearns, S. C. (1988). The evolution of life-history traits - a critique of the theory and a review of the data. *Current Contents/Agriculture Biology & Environmental Sciences*(29), 14-14.
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.
- Sulak, M., Fong, L., Mika, K., Chigurupati, S., Yon, L., Mongan, N. P., . . . Lynch, V. J. (2016). TP53 copy number expansion is associated with the evolution of increased body size and an enhanced DNA damage response in elephants. *Elife*, 5, 30. doi:10.7554/eLife.11994
- Suzuki, R., & Shimodaira, H. (2006). Pvcust: An R package for assessing the uncertainty in hierarchical clustering. *Bioinformatics*, 22(12), 1540-1542. doi:10.1093/bioinformatics/btl117
- Turbill, C., Bieber, C., & Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B-Biological Sciences*, 278(1723), 3355-3363. doi:10.1098/rspb.2011.0190
- van Noordwijk, A. J. (2002). Evolutionary ecology of birds: Life histories, mating systems and extinction. *Nature*, 418(6898), 588-589. doi:10.1038/418588a
- Whitehead, A. (2012). Comparative genomics in ecological physiology: Toward a more nuanced understanding of acclimation and adaptation. *Journal of Experimental Biology*, 215(6), 884-891. doi:10.1242/jeb.058735
- Wilbur, H. M., Tinkle, D. W., & Collins, J. P. (1974). Environmental certainty, trophic level, and resource availability in life-history evolution. *American Naturalist*, 108(964), 805-817. doi:10.1086/282956
- Wilkinson, G. S., & South, J. M. (2002). Life history, ecology and longevity in bats. *Aging Cell*, 1(2), 124-131. doi:10.1046/j.1474-9728.2002.00020.x
- Wilson, D. E., & Reeder, D. M. (2005). *Mammal species of the world: A taxonomic and geographic reference* (Vol. 1): JHU Press.

Zehr, S. M., Roach, R. G., Haring, D., Taylor, J., Cameron, F. H., & Yoder, A. D. (2014). Life history profiles for 27 strepsirrhine primate taxa generated using captive data from the Duke Lemur Center. *Scientific Data*, 1, 11. doi:10.1038/sdata.2014.19

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