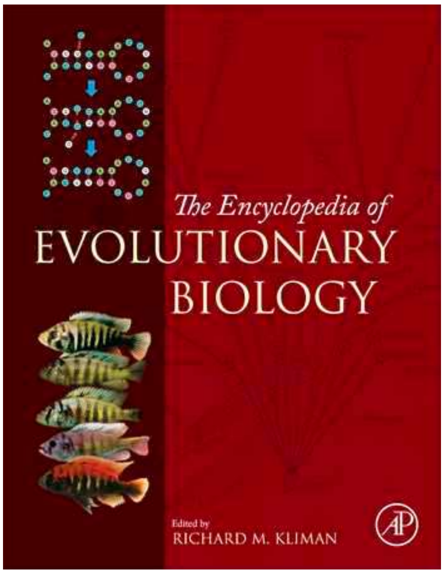

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Life Histories, Axes of Variation in

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Glossary

Allometric relationship A linear relationship on the log–log scale between a life history trait and body mass. Across species, this corresponds to evolutionary allometry. The intercept is the allometric coefficient and varies a lot across taxons and life styles. The slope of the relationship is the allometric exponent and varies little across taxons or life styles, being mostly dependent on the dimension of the trait.

Biological (or physiological) time A measure of perceived time by a given species in opposition to the absolute time unit. Biological time is scaled to body mass. A given absolute time period (say a month) is perceived as being much longer in small species than in large ones.

Dimensional analysis A standardized analysis of the relationships between different biological traits. The standardization is based on three fundamental dimensions (length, volume, and time) and their associated measurement units (e.g., centimeter, kilogram, and years). The dimensional analysis tracks the dimensions and the measurement units when performing calculations or comparisons among traits.

Lifestyle A description of the way of life characterizing a species. This mostly includes the type of diet, the mating tactic, and the habitat features individuals within a species share.

Pace of life A synonymous term for slow–fast continuum. Often used in a broader perspective including not only life history traits, but also physiological and behavioral traits.

Variability is an essential property of living organisms. Both Darwin (1859) and Fisher (1930) understood that evolution required variation. Biologists have been assessing the causes and the consequences of the variability they observe at all stages of biological organization, from the cell to the ecosystem, since the very first studies of life history. The diversity of life history traits, defined here as any phenotypic trait that influences the trajectory of a given individual from birth to death, is one of the most striking and intensively studied topics in evolutionary biology. Let us consider mammals as an example of the wide range of variation. This vertebrate class, which includes about 4600 extant species (Wilson and Reeder, 2005), displays tremendous variation in life history traits. While the gigantic blue whale (*Balaenoptera musculus*), the largest animal to have ever existed on earth, weighs 172 t, the tiny shrew (*Suncus etruscus*) only weighs 1 g. In addition to large variation in body mass (Silva and Downing, 1995), mammals display a tremendous variation of life histories. For example, the gestation time of the African elephant (*Loxodonta africana*) is 660 days, while in voles (*Microtus* sp.) it can be as short as 20 days (Hayssen *et al.*, 1993). Bats (Chiroptera, Rhinolophidae family) give birth to offspring weighing almost one-third of the mother's weight, while in polar bears (*Ursus maritimus*), offspring at birth are only about one-thousandth of their mother's body mass (Hayssen *et al.*, 1993). The chimpanzee (*Pan troglodytes*) gives birth to a single offspring every 4 or 5 years while the tenrec (*Tenrec ecaudatus*) can produce up to 32 embryos within a single litter (Hayssen *et al.*, 1993). Also, small marsupial mice belonging to the genus *Antechinus* reproduce only once during their lifetime (semelparity), while a long-lived species like roe deer (*Capreolus capreolus*) can reproduce up to 15 times (iteroparity). Finally, the European water vole (*Arvicola terrestris*) lives for less than 6 months in the wild, whereas some individuals of Bowhead whale (*Balaena mysticetus*) can survive for more than a century. This extreme variability is highly structured across species with some strong associations with life history traits. This covariation corresponds to life-history strategies (Stearns, 1976, 1980), which are organized along major axes of life history variation. For example, within the mammals, the African elephant has a long gestation time (in fact the longest ever reported), large size, long inter-birth intervals (by giving birth only every 4 years on average), produces a large single offspring at each reproductive attempt, has a delayed age at first breeding and a long life. In contrast, voles have a short gestation time, produce several litters each year each consisting of several offspring, have an early age at first parturition and a short life. This type of covariance defines an axis of life history variation that is frequently defined as the slow–fast continuum of life histories, by far the most intensively studied axis of life history variation, especially in vertebrates (but not only; see also Blackburn, 1991 on Hymenoptera and Franco and Silvertown, 1996 on plants). What is the origin of the slow–fast continuum concept? What is the current empirical evidence supporting the existence of this axis of life history variation in vertebrates? What are the structuring factors shaping the slow–fast continuum of life histories? What are the ecological and evolutionary consequences of this continuum? Are there other axes of life history variation than the slow–fast continuum? From a selected review of the literature published over the past

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50 years, we will try to provide answers to these questions. We will also identify gaps in our current understanding of life history variation.

A Brief History of the Origin of the Slow–Fast Continuum

Identifying the origin of a concept is difficult when several authors have contributed to our current understanding of it. This is exactly the case for the slow–fast continuum. The concept of the slow–fast continuum has no single, unique origin. As the main axis of life history variation, the slow–fast continuum is rooted in history of life history theory. In this respect, seminal work by Lack (1947) on clutch size in birds, Dobzhansky (1950) on latitudinal differences in the way natural selection operates in *Drosophila*, and Cole (1954) on the number of breeding attempts over the lifespan have all contributed to the emergence of the slow–fast continuum concept. However, the foundation of the slow–fast continuum is more precisely based on the concept of life history trade-offs and as such, is grounded in the principle of allocation proposed by Cody (1966) (itself partly inspired by Lack's works). This principle of allocation states that organisms have a limited amount of time or energy available for expenditure, so that allocating more to one biological function (e.g., growth, reproduction, or repair) should lead to the allocation of less energy to other functions. Thereby, the slow–fast continuum can be interpreted as the range of possible solutions to the trade-off between reproduction and survival.

In addition to these pillars of current life history theory, two important, but often overlooked papers, were published in 1962. First, Stahl (1962) called for more dimensional analyses (see **Box 1**) in biology when he stated "In order to define biological similarities in a meaningful way it is necessary to review the subject of dimensional analysis, which forms part of the basis for similarity theory" (p. 205). In particular, he identified that "two principles play a key role in biological analysis: conservation of volume and synchronism of times" (p. 209). Volume (like body mass or birth mass) and time (like age at first reproduction or lifespan) are the dimensions of traits most often included in empirical analyses of the slow–fast continuum. In the same year, MacArthur (1962) proposed a model extending Fisher's (1930) work to the density-dependent case, in which "the carrying capacity of the environment, K, replaces fitness as the agent controlling the action of natural selection" (p. 1897). This work set the basis for r-K selection (originally defined by MacArthur and Wilson (1967)) that led Pianka (1970) to launch his "r-K continuum" (p. 592). Pianka's r-K continuum provides the first axis of life-history variation with similarities and differences, to the slow–fast continuum (see below).

However, perhaps the easiest way to identify the origin of the slow–fast continuum is to simply identify the first use of this term. It was coined for the first time by Stearns (1983) in his pioneering comparative analysis of mammalian life histories when he wrote "This suggests that both size and phylogeny have significant independent effects on patterns of covariation in life-history traits, and that both effects contribute to the ordering of mammal species onto a "slow-fast" continuum" (p. 186). Regardless of when the term was born, or the historical contributions that led to our development of life history theory, empirical analyses of slow–fast continuum have accumulated over the last three decades.

Box 1 What is dimensional analysis?

Dimensional analysis was devised by physicists, but can be defined in an evolutionary biology context as a standardized analysis of the relationships between different biological traits. The standardization is based on three fundamental dimensions (length, volume, and time) and their associated measurement units (e.g., centimeters, kilograms, and years). The dimensional analysis tracks the dimensions and the measurement units when performing calculations or comparisons among traits. The problem of converting metrics from one dimensional unit to another is thus a main objective of dimensional analyses.

All life history traits can be related to a fundamental dimension, or derived units. For instance, gestation and incubation periods, weaning or hatchling periods, age at first reproduction, and lifespan are all measured in units of times (i.e., days, weeks, months, or years), antler size of deer is measured in units of length (centimeters or meters), and body mass has a dimension of volume measured in units of mass. Such an heterogeneity in dimension has obvious practical consequences. For instance, the dimensional analysis implies an allometric exponent to one-third (not 1) when regressing antler size against body mass (on a log–log scale) to assess the type of allometry (i.e., positive, negative, or isometry). Indeed, physical constraints lead us to expect isometric relationships among traits sharing the same dimension. The dimensional analysis thus provides the theoretical background for constructing dimensionless numbers (e.g., ratio between age at first reproduction and lifespan) that are expected to be size-independent (see Charnov, 1993).

Empirical Analyses of Life History Variation in Vertebrates

We will now review the evidence in support of this slow–fast continuum, the way the continuum is identified, and its biological meaning. We conducted a literature search in ISI Web of Knowledge using first the topic keywords 'slow–fast or fast–slow' and then 'pace of life' and, in both cases, refined the research domains to 'Zoology' and 'Evolutionary Biology.' We added the term 'pace of life' because it has become a general term for measuring the speed of a life cycle in ecological (e.g., Wiersma *et al.*, 2007) and physiological (Hille and Cooper, 2015) contexts. We identified 253 and 96 papers respectively and screened the summaries to select 29 studies of vertebrates in which at least one covariation among life history traits was tested (**Table 1**). We also identified 12 studies reporting analyses of a measure of species-specific positions on the slow–fast continuum in relation to other biological processes (**Table 2**). It is noteworthy that we did not identify any analysis in amphibians and that most studies focused on only one vertebrate class (only Herrando-Pérez *et al.*'s (2012) study encompassed a wide range of species including mammals, birds, reptiles, and fishes).

Table 1 Review of comparative analyses in which the slow–fast continuum of life histories across species has been investigated using only traits measuring biological times (‘Time metrics’) or both time metrics and traits measuring other dimensions (‘Non-time metrics’). The taxonomic group analyzed (with its associated sample size in brackets), the method used to assess the slow–fast continuum, the support for the existence of a slow–fast continuum, and the reference, are provided. As traits measured as counts per unit of time (like annual fecundity) have the dimension of time, they are included as time metrics (see Allainé *et al.*, 1987 for further details). Corrections for allometric and/or phylogenetic constraints are displayed in italics. The studies are sorted in chronological order of publication

Time metrics	*Non-time metrics*	*Taxon/method*	*References*
Gestation time Age at eye opening Duration of lactation Inter-birth interval Number of litters per year Age at first reproduction Longevity	Offspring mass Number of offspring *Adult mass*	Mammals ($N=65$) PCA PC1 accounting for 68.1% of life history variation *Corrected for allometric constraints* *Replicated at different taxonomic levels* **Support**	Stearns (1983)
Gestation time Age at first reproduction Number of offspring per season	Neonatal mass Neonatal mass/Adult mass Litter size Litter size × Neonatal mass/ Adult mass *Adult mass*	Lagomorphs ($N=22$) PCA PC2 accounting for 36.1% of life history variation **Support**	Swihart (1984)
Gestation time Age at weaning Estrous cycle length Age at first reproduction Age at maturity (both sexes) Lifespan Inter-birth interval	Adult mass (males) Neonatal mass Neonatal brain mass Adult brain mass *Adult mass*	Primates ($N=135$) Bivariate linear regressions (log–log scale) *Corrected for allometric constraints* *Analyzed at the taxonomic level of subfamily* **Support**	Harvey and Clutton-Brock (1985)
Gestation time Age at weaning Age at independence Lifespan Age at first reproduction Inter-birth interval	Litter size Birth mass Litter mass *Adult mass*	Carnivores ($N=112$) Bivariate linear regressions (log–log scale) *Corrected for allometric constraints* *Replicated at different taxonomic levels* **Support**	Gittleman (1986)
Incubation time (per egg) Time to fledging Age at first reproduction	Clutch size Egg mass *Adult mass*	European birds ($N=191$ genera) Bivariate linear regressions (log–log scale) *Corrected for allometric constraints* *Analyzed at the taxonomic level of genus* **Support**	Saether (1987)
Gestation time Inter-birth interval Age at first reproduction Lifespan r-max	Neonatal mass Litter size *Adult mass*	Primates ($N=58$) Bivariate linear regressions (log–log scale) *Corrected for allometric constraints* **Support**	Ross (1988)
Adult survival Age at first reproduction	Clutch size	European birds ($N=107$) Bivariate linear regressions (log–log scale) *Corrected for allometric constraints* *Replicated at different taxonomic levels* **Support**	Saether (1988)
Gestation time Age at weaning Period of maternal care	Adult brain mass Litter size Neonatal mass Neonatal brain mass	Mammals ($N=712$) Bivariate linear regressions (log–log scale) *Corrected for allometric constraints* *Replicated at different taxonomic levels*	Read and Harvey (1989)

(*Continued*)

Table 1 Continued

Time metrics	*Non-time metrics*	*Taxon/method*	*References*
Age at first reproduction Period as independent juvenile Inter-birth interval Lifespan Reproductive lifespan Annual fecundity	Litter mass Basal metabolic rate Litter body growth rate Litter brain growth rate Annual biomass production *Adult mass*	**Support**	
Annual fecundity Age at first reproduction Adult life expectancy		Mammals ($N=80$) Birds ($N=114$) PCA PC1 accounting for 74% (mammals) and 85% (birds) of life history variation *Corrected for allometric constraints* **Support**	Gaillard *et al.* (1989)
Juvenile mortality Gestation time Lactation time Period of maternal care Inter-birth interval Period of adolescence Age at first reproduction Lifespan Reproductive lifespan Annual fecundity	Litter size Neonatal mass Litter mass Body growth rate Annual litter mass Lifetime output (number of offspring) Lifetime output (total litter mass)	Bivariate linear regressions (log–log scale) Mammals ($N=48$) *Corrected for allometric constraints* *Replicated at different taxonomic levels* **Support**	Promislow and Harvey (1990)
Age at first reproduction Annual survival	Body growth rate	Reptiles ($N=16$ snakes and 20 lizards) Bivariate linear regressions (log–log scale) *Corrected for phylogenetic inertia* **Support**	Shine and Charnov (1992)
Adult length Hatchling length Clutch frequency Age at first reproduction	Hatchling mass Length at maturity Clutch size	Lacertids ($N=16$) PCA PC1 accounting for 73.7% of life history variation *Corrected for allometric constraints* *Corrected for phylogenetic inertia* **No Support**	Bauwens and Uriarte-Diaz (1997)
Brood frequency Age at first reproduction Annual mortality	Clutch size *Adult length*	Lizards ($N=90$) PCA PC1 accounting for 52.5% of life history variation *Corrected for allometric constraints* *Corrected for phylogenetic inertia* **Support**	Clobert *et al.* (1998)
Gestation time Age at weaning Period of maternal care Age at first reproduction Period as independent juvenile Lifespan Reproductive lifespan Litter frequency Annual fecundity	Brain mass Litter size Neonatal mass Litter mass Resting metabolic rate *Adult mass*	Insectivores ($N=63$) Bivariate linear regressions (log–log scale) *Corrected for phylogenetic inertia* **Partial Support**	Symonds (1999)
Incubation time Age at first reproduction	Clutch size Egg mass Nestling growth rate	Birds ($N=34$) PCA PC1 accounting for 71% of life history variation	Ricklefs (2000)

(*Continued*)

Table 1 Continued

Time metrics	*Non-time metrics*	*Taxon/method*	*References*
Survival to maturity Annual fecundity Annual adult mortality	*Adult mass*	*Corrected for allometric constraints* **Support**	
Age at first reproduction Lifespan	Slope of the fecundity-length relationship Egg volume Fecundity at maturity	Fishes (*N*=84 populations/49 species) PCA PC1 accounting for 51.8% of life history variation *Corrected for allometric constraints* *Corrected for phylogenetic inertia* **Support**	Rochet *et al.* (2000)
Lifespan Age at weaning Gestation time Annual fecundity	Neonatal mass Mass at permanent exit from the pouch Mass at weaning Litter size *Adult mass*	Metatherians (*N*=161) Bivariate linear regressions (log–log scale) *Corrected for allometric constraints* *Corrected for phylogenetic inertia* **Support (but for gestation time)**	Fisher *et al.* (2001)
Gestation time Inter-birth interval Age at weaning Age at first reproduction	Litter mass Neonatal mass *Adult mass*	Mammals (*N*=267) Factor analysis PC1 accounting for 40% of life history variation *Corrected for allometric constraints* *Corrected for phylogenetic inertia* **Support**	Bielby *et al.* (2007)
Age at first reproduction Age at last reproduction Juvenile survival Annual adult survival Annual fecundity		Rodents (*N*=43 populations/29 species) PCA PC1 accounting for 84% of life history variation **Support**	Dobson and Oli (2007a)
Age at first reproduction Age at last reproduction Juvenile survival Annual adult survival Annual fecundity		Mammals (*N*=143) PCA PC1 accounting for 81.7% of life history variation *Corrected for allometric constraints* *Replicated at different taxonomic levels* **Support**	Dobson and Oli (2007b)
Age at first reproduction Inter-birth interval Lifespan	Fecundity (number of offspring per clutch/litter) Offspring mass *Adult mass*	Fishes (*N*=46) Mammals (*N*=100) Birds (N=302) PCA PC1 accounting for 66% (fishes), 78% (mammals), and 60% (birds) of life history variation *Corrected for allometric constraints* *Corrected for phylogenetic inertia* **Support**	Jeschke and Kokko (2009)
Annual fecundity Nursing care period Lifespan	Clutch size Number of broods Egg mass Laying date *Adult mass*	Passerines (*N*=68) PCA PC1 accounting for 34.8% of life history variation *Corrected for phylogenetic inertia* **Support**	Reif *et al.* (2010)
Gestation time Age at weaning Inter-birth interval	Brain size *Adult mass*	Lemur (*N*=24) PCA PC1 accounting for 67.8% of life history variation *Corrected for phylogenetic inertia* **Support**	Catlett *et al.* (2010)
Gestation time Lactation time	Litter size Birth mass	Carnivores (*N*=85) Bivariate linear regressions (log–log scale)	Paemelaere and Dobson (2011)

(*Continued*)

Table 1 Continued

Time metrics	*Non-time metrics*	*Taxon/method*	*References*
Period of maternal care Age at first reproduction Age at independence Inter-birth interval Lifespan	Litter mass *Adult mass*	*Corrected for allometric constraints* *Corrected for phylogenetic inertia* **Support when uncorrected for body size but No support when corrected**	
Age at first reproduction Annual fecundity Lifespan	*Adult mass*	Mammals ($N=152$) Birds ($N=225$) Reptiles ($N=37$) Fishes ($N=115$) PCA PC1 accounting for 65.4% of life history variation *Corrected for phylogenetic inertia* **Support**	Herrando-Pérez *et al.* (2012)
Lifespan Age at 50% maturity Spawning interval Spawning duration	Growth coefficient Length at 50% maturity Fecundity at maturity Slope of fecundity-length relationship Relative fecundity (number of oocytes per gram) *Adult length*	Scombrids ($N=42$) PCA PC2 accounting for 23% of life history variation **Support**	Juan-Jorda *et al.* (2013)
Age at first reproduction Gestation time Lactation time Lifespan	Neonatal mass Litter size *Adult mass*	Mammals ($N=41$) PCA PC1 accounting for 66.5% of life history variation *Corrected for phylogenetic inertia* **Support**	Swanson and Dantzer (2014)
Nestling period	Clutch size Egg size relative to adult mass Body growth rate Absolute latitude	Birds ($N=9$) PCA **Support**	Stager *et al.* (2014)
Lifespan Age at first reproduction Annual fecundity	Length at maturity Maximum body size Offspring size	Barents Sea Fishes ($N=76$) PCA and RDA PC1 (PCA) and PC2 (RDA) accounting for 64.2% and 13.3% of life history variation, respectively *Corrected for allometric constraints* (RDA) *Corrected for phylogenetic inertia* **Support**	Wiedmann *et al.* (2014)

To assess covariation among life-history traits, multivariate analyses are a reliable method. However, although the first analysis performed by Stearns (1983) relied on a Principal Component Analysis (PCA), subsequent works in the 1980s and 1990s typically used a series of bivariate linear regressions. The justification for not using multivariate analyses was generally based on two main arguments (see e.g., Harvey and Clutton-Brock, 1985): the necessity of having complete information for all traits in each species in the analysis, and the difficulty of interpreting a statistical combination of traits. Accumulation of life history data over the last 20 years has reduced the problem of missing data, as has the development of new methods for dealing with missing data in multivariate analyses (Josse and Husson, 2011). Problems of interpreting principal components of PCA in a biological context only occur when a heterogeneous set of traits in terms of dimension are included in analyses. These issues can easily be dealt with by accounting for the dimensionality of traits (see below). In recent years, as revealed by an examination of **Table 1**, PCA has become the rule when analyzing axes of life history variation, with all but two studies published since 2000 based on multivariate analyses. The move to PCA can even be detected within the work of the same group of researchers (e.g., Oli, 2004 vs. Dobson and Oli, 2007a,b, 2008).

Most of the available studies reported statistically significant covariation among life history traits and thereby supported the existence of a slow–fast continuum, providing clear evidence that it corresponds to the primary main axis of life history variation across species in mammals, birds, reptiles, and fishes (**Table 1**). The position of a species on the slow–fast continuum ranges from species with high adult survival and low reproductive output (the slow end of the continuum

Table 2 Studies reporting analyses of a measure of species-specific positions on the slow–fast continuum in relation to other biological processes. The metric used to assess the position of a given species on the continuum, the taxonomic group studied, the biological process analyzed, and the reference are all listed in the table. The studies are ordered chronologically. All metrics used but one (in italics) had a dimension of time

Metric	*Taxon*	*Biological process*	*References*
Dental development	Hominin	Evolution	Dean *et al.* (2001)
F/α ratio (annual fecundity/age at first reproduction)	*Mammals*	*Demography*	Oli (2004)
Generation time	Mammals and birds	Senescence	Jones *et al.* (2008)
Age at first reproduction	Muroid rodents	Exploratory behavior	Careau *et al.* (2009)
Nonlinear combination of annual fecundity, age at first reproduction, and annual adult survival	Mammals and birds	Senescence	Péron *et al.* (2010)
Age at sexual maturity	Mammals, birds, amphibians, and reptiles	Senescence	Ricklefs (2010)
Generation time	Marine fishes	Temporal variation in demography	Bjorkvoll *et al.* (2012)
Annual fecundity	Birds	Perception of predation risk	Hua *et al.* (2013)
Generation time	Mammals	Placentation type	Garratt *et al.* (2013)
Generation time	Mammals and birds	Age-specific contributions to fitness	Saether *et al.* (2013)
Age at which cumulative loop elasticity reaches 50% of total elasticity	Carnivores	Management strategies	Van de Kerk *et al.* (2013)
Generation time	Mammals	Transient dynamics	Gamelon *et al.* (2014)

illustrated by Primates in mammals) to species with low adult survival and high reproductive output (the fast end of the continuum illustrated by lagomorphs in mammals). This axis of life history variation associates with principle of resource allocation (i.e., the Cody (1966) Principle of Allocation) supporting the hypothesis that a trade-off between survival and reproduction does shape the diversity of life histories across species within classes, and even orders, of vertebrates. In this narrow sense, it suggests that there is a universal slow–fast continuum of life history variation across vertebrates. Remarkably, in the most detailed analysis of the slow–fast continuum in vertebrates published to date ($N=46$ fish, 100 mammal, and 302 bird species), Jeschke and Kokko (2009) came to the opposite conclusion, writing "In other words, there is no universal fast-slow continuum" (p. 872). So, how can we reconcile what appears to be the contrasting conclusions of Jeschke and Kokko (2009) with our conclusions from a more up-to-date review of the literature? A likely explanation involves the variation among empirical studies in the approaches they use and subtle differences in the questions asked between early and current analyses. Different empirical analyses have corrected for different confounding factors and have worked with different life history traits, and these differences need to be taken into account before a clear take-home message of the existence of a slow–fast continuum within vertebrate lineages emerges.

Problems of Dimensionality When Assessing a Slow–Fast Continuum

Studies correcting for body mass and phylogeny have revealed allometric and evolutionary constraints, but even after having corrected for these processes, a slow–fast continuum of life histories still persists (**Table 1**). Body mass obviously has a major influence on all biological processes (Peters, 1983; Calder, 1984) and accounts for most of the variation observed in life history traits across species. Interestingly, while the slow–fast continuum shows up at both absolute and mass-dependent scales, the relative contribution of traits and the ranking of a given species along this continuum generally differ quite markedly. For instance, cetaceans obviously live in the slow line by displaying late age at first reproduction, low fecundity and long lifespan. However, for a given size, cetaceans rank among the fastest species in relation to the very large size they can reach in their marine habitat (Gaillard *et al.*, 1989). On the other hand, within a given lineage, the relative ranking of species on the continuum remains rather constant independent whether allometry is accounted for or not. The effects of phylogeny are also quite obvious, but often strongly covary with ecological factors. For instance, all bats belong to the order Chiroptera and share strong similarities including a remarkably long lifespan for their mass and their ability to fly. The phylogenetic inertia, which generates statistical problems of nonindependence among data points, has been increasingly accounted for (**Table 1**). However, the empirical evidence so far accumulated indicates that the phylogenetic inertia does not markedly influence the detection and the strength of the slow–fast continuum. The question of accounting for (or not) variation in body mass and phylogeny prior to analyse life history variation has focused most of the attention of evolutionary biologists (see, e.g., Jeschke and Kokko, 2009). However, the problem of dimensionality (**Box 1**) has been overlooked, even though it is likely a more crucial issue for interpreting life history variation from comparative analyses of life history traits.

Broadly speaking, Pianka's (1970) r-K continuum was the first formally proposed axis of life history variation. In addition to the trade-off between survival and reproduction, this continuum also includes in the covariation body mass, population size, climate, and intra- and interspecific competitions. In its original form it was a rather poor example of an axis of biological covariation in terms of dimensionality! Among other flaws not detailed here (see Stearns, 1977; Boyce, 1984 for further details), the r-K continuum of Pianka confuses the underlying pattern of life history variation with density-dependence, a process potentially involved to explain the pattern. Stearns (1976) was the first to start to separate the underlying pattern from the density-dependent component when he opposed the 'r-selection label' to the 'K-selection label,' which provides *sensu stricto*, the first slow–fast continuum. In the early 1980s, use of the concept of physiological time (that because "metabolic rate and longevity change with body size, time itself may be scaled", Lindstedt and Calder, 1976 (p. 91)) to life history analysis led some biologists to the view that observed covariation among traits measured in time units is an allometric consequence rather than a direct product of natural selection (Lindstedt and Calder, 1981; Calder, 1984). This explains why evolutionary biologists, starting with Stearns (1983), then searched for the existence of a slow–fast continuum of life histories after correcting for allometric constraints, providing unambiguous support for it (e.g., Harvey and Clutton-Brock, 1985; Gittleman, 1986; Saether, 1987; Gaillard *et al.*, 1989; Read and Harvey, 1989). A lively debate about whether allometric constraints or natural selection processes determine most of the observed life history covariation then took place in the late eighties (see, e.g., Read and Harvey, 1989). As allometric variation is itself under natural selection processes, such a separation between allometry and adaptation is highly disputable. Nowadays, it is widely accepted that both allometry and natural selection are acting to determine observed variation in life history. Thus, studying the slow–fast continuum requires consideration of the crucial problem of dimensionality (**Box 1**).

In all but three studies (Gaillard *et al.*, 1989; Dobson and Oli, 2007a,b), a mixture of traits with different dimensions were analyzed, leading researchers to question the interpretation of a slow–fast continuum, because common sense tells us that the slow–fast continuum is obviously based on the concept of time. As recognized in other research areas, including paleontology (see, e.g., Robson and Wood, 2008), life history traits can be classified into two broad categories: traits that describe the timing of life history events like age at first reproduction, gestation time, or longevity (corresponding to physiological times) and traits like mass, or growth rates, that are not biological times, but are correlated with biological times (as notably observed by Stahl (1962)). While the concept of biological similarity (Stahl, 1962) relies upon the use of time (e.g., gestation time, age at maturity, longevity) and time frequencies (e.g., heart beats/minute, annual fecundity, annual survival) to measure a time scale, it does not permit the inclusion of volume traits (like body, birth, or brain mass), nonstandardized number (like litter size or clutch size), or changes of volume over time (like growth rate). So far, most studies of the slow–fast continuum have included litter size or clutch size (**Table 1**) although these traits do not have the dimension of time. It was well established that litter size varies non-monotonously across mammalian species before any empirical analysis of slow–fast continuum was performed (Tuomi, 1980). The right metric for measuring the reproductive output in the context of a time scale is the fecundity per time unit (e.g., annual fecundity, Allainé *et al.*, 1987) because some small species produce several litters per reproductive season and some large species only reproduce every second, third, or fourth year. The use of clutch/litter size instead of annual fecundity in Jeschke and Kokko (2009) is likely to account for most of the differences they reported between analyses accounting for body mass or not. Moreover, among the common pitfalls, lots of analyses of the slow–fast continuum include redundancy in life history traits. Such nonindependence between traits is likely to alter both the assessment of relationships in bivariate analyses (as nicely pointed out almost 30 years ago by Sutherland *et al.*, 1986) and the relative contribution of life history traits to the slow–fast continuum by deviating the first major axis of the PCA towards redundant variables. Our literature survey thus points out that problems of dimensionality occur in most empirical studies (see **Table 1**), which likely explain differences of interpretation among studies and prevent a reliable understanding of the slow–fast continuum.

Importantly, when the dimensionality of all traits is restricted to physiological times and any trivial redundancy among traits is avoided or accounted for by using multivariate analyses, traits equally contribute to the slow–fast continuum, which supports the concept of biological similarities (Gaillard *et al.*, 1989; Dobson and Oli, 2007b). Only considering physiological times included in PCA performed so far also provides remarkable support for this remark (**Table 3**). Therefore, to answer clearly the question raised by Jeschke and Kokko (2009), body mass should not be included when assessing the slow–fast continuum of life history. We thus share their suggestion 'to reserve the term ''fast–slow continuum' to the raw data,' but only when traits with a dimension of time are considered (p. 876).

What Shapes the Slow–Fast Continuum of Life Histories?

Three main factors have been identified that shape the slow–fast continuum: body mass, phylogeny, and ecology. Western (1979) was the first to recognize that life history variation can be partitioned into an allometric component, and one or several non-allometric components. All analyses have identified a major role of allometric relationships in generating variation in life history traits across species (e.g., Peters, 1983; McMahon and Bonner, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Brown and West, 2000 for reviews). As a rule of thumb, about 50% of life history variation observed across species can be statistically explained by variation in body mass, as long as the range of body sizes included in analyses spans several orders of magnitude. The trade-off between reproduction and survival persists when body mass effects are accounted for in analyses, indicating that the diversity of life history strategy is not solely due to differences in size (Stearns (1983), Gaillard *et al.* (1989), and Read and Harvey (1989) on mammals,

Table 3 Loadings of the traits with a dimension of time on the axis of life history variation interpreted as a slow–fast continuum in a set of empirical PCA studies reporting the loadings of each trait on the slow–fast continuum. In virtually all instances (exceptions in bold), all traits positively covary (same sign for physiological times and opposite sign for time frequencies) and the loadings are remarkably similar, providing a clear support for the concept of biological similarities

Trait 1	*Trait 2*	*Trait 3*	*Trait 4*	*Trait 5*	*References*
0.91	0.90	– 0.86	0.77	0.89	Stearns (1983)
0.74	0.96	– 0.88			Swihart (1984)
	0.82	– 0.79	0.79[a]		Clobert *et al.* (1998)
0.26			0.84	0.78	Bielby *et al.* (2007)
	0.90		0.94	0.67	Jeschke and Kokko (2009) – Fish raw
	0.89		0.86	0.15	Jeschke and Kokko (2009) – Fish corrected
	0.90		0.87	0.73	Jeschke and Kokko (2009) – Mammals raw
	0.83		0.47	0.73	Jeschke and Kokko (2009) – Mammals corrected
	0.90		0.81	0.52	Jeschke and Kokko (2009) – Birds raw
	0.62		0.39	– **0.42**	Jeschke and Kokko (2009) – Birds corrected
0.40			0.41	0.43	Catlett *et al.* (2010)
0.58	– 0.20		– 0.39	– 0.28	Juan-Jorda *et al.* (2013)
– 0.86	– 0.86		– 0.81	– 0.73	Swanson and Dantzer (2014)

[a] Presented as – 0.79 for annual mortality in the original paper.

Trait 1: Gestation (Stearns, 1983; Swihart, 1984; Bielby *et al.*, 2007; Catlett *et al.*, 2010; Swanson and Dantzer, 2014); Spawning duration (Juan-Jorda *et al.*, 2013).

Trait 2: Age at first reproduction (Stearns, 1983; Swihart, 1984; Clobert *et al.*, 1998; Jeschke and Kokko, 2009; Swanson and Dantzer, 2014); Age at 50% maturity (Juan-Jorda *et al.*, 2013).

Trait 3: Annual fecundity (Swihart, 1984; Clobert *et al.*, 1998); Number of litters per year (Stearns, 1983).

Trait 4: Annual survival (Clobert *et al.*, 1998); Age at weaning (Bielby *et al.*, 2007; Catlett *et al.*, 2010); Lifespan (Stearns, 1983; Jeschke and Kokko, 2009; Juan-Jorda *et al.*, 2013; Swanson and Dantzer, 2014).

Trait 5: Inter-birth interval (Stearns, 1983; Bielby *et al.*, 2007; Jeschke and Kokko, 2009; Catlett *et al.*, 2010; Juan-Jorda *et al.*, 2013; Lactation time (Swanson and Dantzer, 2014).

Swihart (1984) on lagomorphs, Harvey and Clutton-Brock (1985) on primates, Gittleman (1986) on carnivores, Saether (1987) on European birds, Saether and Gordon (1994) on ungulates).

Phylogeny also has an influence on the ranking of species on the slow–fast continuum. For instance, bats and primates in mammals, and Procellariiformes in birds, have much slower life histories than predicted by their size. While early studies accounted for the possible confounding effects of phylogeny by replicating the analyses at different taxonomic levels (e.g., Stearns, 1983) or performing analyses at a higher taxonomic level (like genera, e.g., Saether, 1987), methodological advances in phylogenetic methods have allowed phylogenetic inertia to be appropriately corrected for in life history analyses (Freckleton *et al.*, 2002), including PCA (e.g., Phylogenetic PCA, Revell, 2009, 2010).

The ecological factors shaping variation on the slow–fast continuum have not yet been clearly identified, which looks a bit paradoxical given that the original Pianka (1970) r-K continuum explicitly associated covariation among life history traits with ecological factors. According to Fisher *et al.* (2001), "most studies have failed to find robust ecological correlates of life history diversity in birds, mammals, and other taxa" (p. 3538). Some studies have identified habitat type (i.e., aerial, terrestrial, and marine, Gaillard *et al.*, 1989; Pontier *et al.*, 1990) or diet (Saether and Gordon, 1994; Fisher *et al.*, 2001) as structuring factors. Recently, stronger evidence that the lifestyle influences the pace of life of a species has been proposed. For example, evidence is accumulating that tropical birds have a slower life history than their temperate counterparts, likely as a function of lower basal metabolic rates (Wiersma *et al.*, 2007; Jimenez *et al.*, 2014) and smaller organ size (Wiersma *et al.*, 2012). For a given size, arboreal mammals live longer than those that live on the ground (Shattuck and Williams, 2010), and flying mammals outlive their nonflying relatives (Healy *et al.*, 2014). In addition, energy-saving strategies have been reported to shape species-specific pace of life. Thus, hibernation slows the pace of life in mammals (Turbill *et al.*, 2011). However, the current lack of evidence for strong structuring effects of ecological correlates might be explained by the simplicity of the metrics used to assess ecological correlates.

Evolutionary Consequences of the Slow–Fast Continuum

As rightly noted by Ricklefs (2000), analyses of life history variation have, for many years, contributed to "divorcing life-history from its environmental context" (p. 13). While the search for more refined ecological factors that likely shape the ranking of species on the slow–fast continuum has still to be performed, evidence is mounting concerning the evolutionary consequences of a given position on the slow–fast continuum. Indeed, several studies have assessed the effect of the species-specific position along the continuum on different biological processes like demography (Saether *et al.*, 2013), senescence (Jones *et al.*, 2008), or parent–offspring conflicts via placentation types (Garratt *et al.*, 2013). They clearly showed that slow- and fast-living species should markedly differ in demographic responses to human disturbance or climate change. Most of these studies ranked species on the continuum with an appropriate measure of time, with generation time, the weighted mean age of mothers in a stable population, being the most frequently used metric. In addition to closely matching a species position on the slow–fast continuum identified through the use of the first component of a PCA conducted on time-related traits (correlation coefficients of 0.903 in mammals, Gaillard *et al.*, 2005), generation time is functionally the most relevant metric at the population level. Generation time proportionally decreases with increasing r-max (i.e., the maximum population growth rate a given species can reach in absence of any resource limitation, Caughley, 1977) across species, leading the product between r-max and generation time (i.e., the per-generation growth rate) to be a dimensionless number (*sensu* Charnov, 1993). Thus, within a lineage and in absence of specific adaptations, the per-generation growth rate is expected to be a constant independent of body mass. Moreover, generation time defines the scale at which genes pass from parents to offspring. It consequently obviously correlates with how quickly a lineage can evolve (Okie *et al.*, 2013) with species at the slow end of the continuum evolving at a slower rate than those at the fast end (Martin and Palumbi, 1993; Galtier *et al.*, 2009; Bromham, 2011). We could thus expect slow-living species to be more resistant to environmental perturbations but to be less able to respond to such perturbations (either by demographic or evolutionary changes) than fast-living species (Morris *et al.*, 2008; Gamelon *et al.*, 2014). Therefore, the position of the species along the slow–fast continuum of life history variation has important consequences from both ecological and evolutionary viewpoints.

Are There Other Axes of Life History Variation Than the Slow–Fast Continuum?

The slow–fast continuum identified from multivariate analyses only accounts for approximately half of the variation observed in life history traits, meaning that, for a given position on the slow–fast continuum, species are organized according to some other sources of covariation. This was recognized since Stearns (1983) identified a precociality–altriciality continuum after accounting for the slow–fast continuum. Subsequent analyses provided similar findings by identifying other axes of life history variation, involving covariations among some reproductive traits. For example, a gradient of allocation of reproductive effort over the lifetime going from semelparity to marked iteroparity accounted for about 10% of the demographic variation observed among mammalian species, once the effects of allometry and of the pace of life were accounted for (Gaillard *et al.*, 1989). On the other hand, Bielby *et al.* (2007) pointed out the existence of an offspring size–offspring number trade-off in mammals after accounting for the slow–fast continuum. These authors questioned the general relevance of the slow–fast continuum based on the argument that (1) there is more than one axis of variation in life histories across species, so that species can be fast or slow in different ways (Bielby *et al.*, 2007), and (2) strongly correlated traits in some taxonomic groups are poorly correlated in others. For example, the loadings of weaning age on the slow–fast continuum in Artiodactyls was only half those reported in other mammalian groups. While it is evident that the slow–fast continuum only corresponds to one axis of life history variation as demonstrated by our literature review (**Table 1**), the conclusion that the covariation of traits shaping the slow–fast continuum differs among groups does not hold. The detailed life history analysis performed by Bielby *et al.* (2007) involved traits with different dimension (e.g., time, volume, non-standardized number), and this heterogeneity in dimension among traits shaping the axes of life history variation prevents interpretation of axes of variation as corresponding to slow–fast continuums. As reported in the **Table 3**, when restricted to physiological times and frequencies, the slow–fast continuum is remarkably constant across taxonomic groups. Again, instead of mixing traits with different dimensions, we recommend looking for a series of axes of life history variation based on comparable traits (i.e., meeting the concept of biological similarity), which will be easy to interpret. For instance, performing a comparative analysis including a wide range of physiological times including developmental and demographic traits would offer a powerful way to assess the full complexity of life history variation.

Perspectives: Beyond Interspecific Analyses and Toward an Integrated Pace of Life Syndrome

The study of the axes of life history variation has primarily been performed at the interspecific level. However, these axes cannot account for all the variability of life history traits. For a given species, for a given ecological type, and for a given taxonomic position, variation in life history is still important. It is nowadays widely recognized that considerable variation in life history occurs among populations within a given species, and also among individuals within a population. Until now, whether the fundamental trade-off between survival and reproduction shapes a slow–fast continuum at these lower levels of biological organization has yet to be investigated. In roe deer, it has been shown that declining populations live at a slower pace of life than colonizing ones (Nilsen *et al.*, 2009). Similarly, heavily hunted wild boar (*Sus scrofa*) populations exhibited fastest life-history speed than lightly hunted ones (Servanty *et al.*, 2011). However, a recent comparative demographic analysis among eight contrasted populations of a lizard species (*Sceloporus grammicus*) did not find any evidence for a slow–fast continuum (Pérez-Mendoza *et al.*, 2013). Further work is clearly required to understand such patterns of variation.

While available analyses of life history variation have mostly been performed in an ecological context, a more holistic view is required, and this has started to emerge. For instance, a recent study aiming at understanding the life history differences between tropical and temperate birds, has suggested that a physiological slow–fast continuum is also existing (Hille and Cooper, 2015). In addition, the increasing popularity of personality analysis in ecology allows identification of behavioral syndromes (Sih *et al.*, 2004) that can be related to individual life history variation. The works of Careau *et al.* (2009) and Hua *et al.* (2013) relating the pace of life with exploratory behaviors of muroids and the perception of predation risk, respectively, and by Patrick and Weimerskirch (2014) on the links between personality and senescence rates among individuals provide insightful examples of what can be done in the next future. Finally, while available analyses of life history variation have mostly been performed in an ecological context, a more global view is required and has started to emerge. The search for a better understanding of life history differences between tropical and temperate birds has led researchers to include physiological traits, suggesting that a physiological slow–fast continuum may also exist (Hille and Cooper, 2015). Therefore, we envisage a fully integrated view of life history variation including a covariation of axes of variation defined not only by times, volumes, and physiology as currently understood in the concept of pace of life syndrome (Hille and Cooper, 2015), but also by behavior and molecular evolution.

See also: Life History: Pike. Life History, What is?. *r*- and *K*-Selection in Fluctuating Environments, Theory of

References

Allainé, D., Pontier, D., Gaillard, J.M., *et al.*, 1987. The relationship between fecundity and adult body weight in homeotherms. Oecologia 73, 478–480.

Bauwens, D., Uriarte-Diaz, R., 1997. Covariation of life-history traits in lacertid lizards: A comparative study. American Naturalist 149, 91–111.

Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., *et al.*, 2007. The fast–slow continuum in mammalian life history: An empirical reevaluation. American Naturalist 169, 748–757.

Bjorkvoll, E., Grotan, V., Aanes, S., *et al.*, 2012. Stochastic population dynamics and life-history variation in marine fish species. American Naturalist 180, 372–387.

Blackburn, T.M., 1991. Evidence for a "fast–slow" continuum of life-history traits among parasitoid Hymenoptera. Functional Ecology 5, 65–74.

Boyce, M.S., 1984. Restitution of r- and K-selection as a model of density-dependent natural selection. Annual Review of Ecology and Systematics 15, 427–447.

Bromham, L., 2011. The genome as a life-history character: Why rate of molecular evolution varies between mammal species. Philosophical Transactions of the Royal Society of London B 366, 2503–2513.

Brown, J.H., West, G.B., 2000. Scaling in Biology. Oxford: Oxford University Press.

Calder, W.A., 1984. Size, Function, and Life History. Cambridge: Harvard University Press.

Careau, V., Bininda-Emonds, O.R.P., Thomas, D.W., Réale, D., Humphries, M.M., 2009. Exploration strategies map along fast–slow metabolic and life-history continua in muroid rodents. Functional Ecology 23, 150–156.

Catlett, K.K., Schwartz, G.T., Godfrey, L.R., Jungers, W.L., 2010. "Life history space": A multivariate analysis of life history variation in extant and extinct malagasy lemurs. American. Journal of Physical Anthropology 142, 391–404.

Caughley, G., 1977. Analysis of Vertebrate Populations. Chichester: Wiley & Sons.

Charnov, E.L., 1993. Life History Invariants. Some Explorations of Symmetry in Evolutionary Ecology. Oxford: Oxford University press.

Clobert, J., Garland, T., Barbault, R., 1998. The evolution of demographic tactics in lizards: A test of some hypotheses concerning life history evolution. Journal of Evolutionary Biology 11, 329–364.

Cody, M.L., 1996. A general theory of clutch size. Evolution 20, 174–184.

Cole, L.C., 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29, 103–137.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection. London: J Murray.

Dean, C., Leakey, M.G., Reid, D., *et al.*, 2001. Growth processes in teeth distinguish humans from *Homo erectus* and earlier hominins. Nature 414, 628–631.

Dobson, F.S., Oli, M.K., 2007a. Fast and slow life histories of rodents. In: Wolff, J. O., Sherman, P.W. (Eds.), Rodent Societies: An Ecological & Evolutionary Perspective. Chicago, IL: University of Chicago Press, pp. 99–105.

Dobson, F.S., Oli, M.K., 2007b. Fast and slow life histories of mammals. Ecoscience 14, 292–299.

Dobson, F.S., Oli, M.K., 2008. The life histories of orders of mammals: Fast and slow breeding. Current Science 95, 862–865.

Dobzhansky, T., 1950. Evolution in the tropics. American Scientist 38, 208–221.

Fisher, D.O., Owens, I.P.F., Johnson, C.N., 2001. The ecological basis of life history variation in marsupials. Ecology 82, 3531–3540.

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. New York, NY: Dover.

Franco, M., Silvertown, J., 1996. Life history variation in plants: An exploration of the fast–slow continuum hypothesis. Philosophical Transactions of the Royal Society of London B 351, 1341–1348.

Freckleton, R.P., Harvey, P.H., Pagel, M., 2002. Phylogenetic analysis and comparative data: A test and review of evidence. American Naturalist 160, 712–726.

Gaillard, J.M., Pontier, D., Allainé, D., *et al.*, 1989. An analysis of demographic tactics in birds and mammals. Oikos 56, 59–76.

Gaillard, J.M., Yoccoz, N.G., Lebreton, J.D., *et al.*, 2005. Generation time: A reliable metric to measure life history variation among mammalian populations. American Naturalist 166, 119–123.

Galtier, N., Blier, P.U., Nabholz, B., 2009. Inverse relationship between longevity and evolutionary rate of mitochondrial proteins in mammals and birds. Mitochondrion 9, 51–57.

Gamelon, M., Gimenez, O., Baubet, E., *et al.*, 2014. Influence of life-history tactics on transient dynamics: A comparative analysis across mammalian populations. American Naturalist 184, 673–683.

Garratt, M., Gaillard, J.M., Brooks, R.C., Lemaître, J.F., 2013. Diversification of the eutherian placenta is associated with changes in the pace of life. Proceedings of the National Academy of Science of the United States of America 110, 7760–7765.

Gittleman, J.L., 1986. Carnivore life history patterns: Allometric, phylogenetic, and ecological associations. American Naturalist 127, 744–771.

Harvey, P.H., Clutton-Brock, T.H., 1985. Life history variation in Primates. Evolution 39, 559–581.

Hayssen, V.D., van Tienhoven, A., van Tienhoven, A., 1993. Asdell's Patterns of Mammalian Reproduction: A compendium of Species-Specific Data. Ithaca, NY: Cornell University Press.

Healy, K., Guillerme, T., Finlay, S., *et al.*, 2014. Ecology and mode-of-life explain lifespan variation in birds and mammals. Proceedings of the Royal Society of London B 281, 20140298.

Herrando-Pérez, S., Delean, S., Brook, B.W., Bradshaw, C.J.A., 2012. Strength of density feedback in census data increases from slow to fast life histories. Ecology and Evolution 2, 1922–1934.

Hille, S.M., Cooper, C.B., 2015. Elevational trends in life histories: Revising the pace of life framework. Biological Reviews 90, 204–213.

Hua, F., Fletcher Jr., R.J., Sieving, K.E., Dorazio, R.M., 2013. Too risky to settle: Avian community structure changes in response to perceived predation risk on adults and offspring. Proceedings of the Royal Society of London B 280, 20130762.

Jeschke, J.M., Kokko, H., 2009. The roles of body size and phylogeny in fast and slow life histories. Evolutionary Ecology 23, 867–878.

Jimenez, A.G., Cooper-Mullin, C., Calhoon, E.A., Williams, J.B., 2014. Physiological underpinnings associated with differences in pace of life and metabolic rate in north temperate and neotropical birds. Journal of Comparative Physiology B 184, 545–561.

Jones, O.R., Gaillard, J.M., Tuljapurkar, S., *et al.*, 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. Ecology Letters 11, 664–673.

Josse, J., Husson, F., 2011. Multiple imputation in principal component analysis. Advances in Data Analysis and Classification 5, 231–246.

Juan-Jorda, M.J., Mosqueira, I., Freire, J., Dulvy, N.K., 2013. Life in 3-D: Life history strategies in tunas, mackerels and bonitos. Reviews in Fish Biology and Fisheries 23, 135–155.

Lack, D., 1947. The significance of clutch size. Ibis 89, 302–352.

Lindstedt, S.L., Calder, W.A., 1976. Body size and longevity in birds. Condor 78, 91–94.

Lindstedt, S.L., Calder, W.A., 1981. Body size, physiological time, and longevity of homeothermic animals. Quarterly Review of Biology 56, 1–16.

MacArthur, R.H., 1962. Some generalized theorems of natural selection. Proceedings of the National Academy of Science of the United States of America 48, 1893–1897.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton, NJ: Princeton University Press.

Martin, A.P., Palumbi, S.R., 1993. Body size, metabolic rate, generation time, and the molecular clock. Proceedings of the National Academy of Science of the United States of America 90, 4087–4091.

McMahon, T.A., Bonner, J.T., 1983. On Size and Life. New York, NY: Scientific American Library.

Morris, W.F., Pfister, C.A., Tuljapurkar, S., *et al.*, 2008. Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89, 19–25.

Nilsen, E.B., Gaillard, J.M., Andersen, R., *et al.*, 2009. A slow life in hell or a fast life in heaven: Demographic analyses of contrasting roe deer populations. Journal of Animal Ecology 78, 585–594.

Okie, J.G., Boyer, A.G., Brown, J.H., *et al.*, 2013. Effects of allometry, productivity and lifestyles on rates and limits of body size evolution. Proceedings of the Royal Society of London B 280, 20131007.

Oli, M.K., 2004. The fast–slow continuum and mammalian life-history patterns: An empirical evaluation. Basic and Applied Ecology 5, 449–463.

Paemelaere, E., Dobson, F.S., 2011. Fast and slow life histories of carnivores. Canadian Journal of Zoology 89, 692–704.

Patrick, S.C., Weimerskirch, H., 2014. Senescence rates and late adulthood reproductive success are strongly influenced by personality in a long-lived seabird. Proceedings of the Royal Society of London B 280, 20141649.

Pérez-Mendoza, H.A., Zuniga-Vega, J.J., Zurita-Gutierrez, Y.H., *et al.*, 2013. Demographic importance of the life-cycle components in *Sceloporus grammicus*. Herpetologica 69, 411–435.

Péron, G., Gimenez, O., Charmantier, A., Gaillard, J.M., Crochet, P.A., 2010. Age at the onset of senescence in birds and mammals is predicted by early-life performance. Proceedings of the Royal Society of London B 277, 2849–2856.

Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge: Cambridge University Press.

Pianka, E.R., 1970. On r- and K-selection. American Naturalist 104, 592–597.

Pontier, D., Allainé, D., Trouvilliez, J., *et al.*, 1990. Are demographic patterns of birds related to biological and environmental parameters? In: Maynard-Smith, J., Vida, G. (Eds.), Organizational Constraints of the Dynamics of Evolution. Manchester: Manchester University Press, pp. 311–320.

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.

Read, A.F., Harvey, P.H., 1989. Life history differences among the eutherian radiations. Journal of Zoology 219, 329–353.

Reif, J., Vermouzek, Z., Vorizek, P., *et al.*, 2010. Population changes in Czech passerines are predicted by their life-history and ecological traits. Ibis 152, 610–621.

Revell, L., 2009. Size-correction and principal components for interspecific comparative studies. Evolution 63, 3258–3268.

Revell, L.J., 2010. Phylogenetic signal and linear regression on species data. Methods in Ecology and Evolution 1, 319–329.

Ricklefs, R.E., 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor 102, 9–22.

Ricklefs, R.E., 2010. Life history connections to rates of aging in terrestrial vertebrates. Proceedings of the National Academy of Science of the United States of America 107, 10314–10319.

Robson, S.L., Wood, B., 2008. Hominin life history: Reconstruction and evolution. Journal of Anatomy 212, 394–425.

Rochet, M.J., Cornillon, P.A., Sabatier, R., Pontier, D., 2000. Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. Oikos 91, 255–270.

Ross, C., 1988. The intrinsic rate of natural increase and reproductive effort in primates. Journal of Zoology 214, 199–219.

Saether, B.E., 1987. The influence of body weight on the covariation between reproductive traits in European birds. Oikos 48, 79–88.

Saether, B.E., 1988. Pattern of covariation between life-history traits of European birds. Nature 331, 616–617.

Saether, B.E., Coulson, T., Grotan, V., *et al.*, 2013. How life history influences population dynamics in fluctuating environments? American Naturalist 182, 743–759.

Saether, B.E., Gordon, I.J., 1994. The adaptive significance of reproductive strategies in ungulates. Proceedings of the Royal Society of London B 256, 263–268.

Schmidt-Nielsen, K., 1984. Why is Animal Size So Important? Cambridge: Cambridge University Press.

Servanty, S., Gaillard, J.M., Ronchi, F., *et al.*, 2011. Influence of harvesting pressure on demographic tactics: Implications for wildlife management. Journal of Applied Ecology 48, 835–843.

Shattuck, M.R., Williams, S.A., 2010. Arboreality has allowed for the evolution of increased longevity in mammals. Proceedings of the National Academy of Science of the United States of America 107, 4635–4639.

Shine, R., Charnov, E.L., 1992. Patterns of survival, growth, and maturation in snakes and lizards. American Naturalist 139, 1257–1269.

Sih, A., Bell, A.M., Johnson, J.C., Ziemba, R.E., 2004. Behavioral syndromes: An integrative overview. Quarterly Review of Biology 79, 241–277.

Silva, M., Downing, J.A., 1995. CRC Handbook of Mammalian Body Masses. Boca Raton, FL: CRC Press Inc.

Stager, M., Cerasale, D.J., Dor, R., Winckler, D.W., Cheviron, Z.A., 2014. Signatures of natural selection in the mitochondrial genomes of *Tachycineta swallows* and their implications for latitudinal patterns of the "pace of life". Gene 546, 104–111.

Stahl, W.R., 1962. Similarity and dimensional methods in biology. Science 137, 205–212.

Stearns, S.C., 1976. Life-history tactics – Review of ideas. Quarterly Review of Biology 51, 3–47.

Stearns, S.C., 1977. Evolution of life-history traits – Critique of theory and a review of data. Annual Review of Ecology and Systematics 8, 145–171.

Stearns, S.C., 1980. A new view of life-history evolution. Oikos 35, 266–281.

Stearns, S.C., 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos 41, 173–187.

Sutherland, W.J., Grafen, A., Harvey, P.H., 1986. Life history correlations and demography. Nature 320, 88.

Swanson, E.M., Dantzer, B., 2014. Insulin-like growth factor-1 is associated with life-history variation across Mammalia. Proceedings of the Royal Society of London B 281, 20132458.

Swihart, R.K., 1984. Body size, breeding season length, and life history tactics of lagomorphs. Oikos 43, 282–290.

Symonds, M.R.E., 1999. Life histories of the Insectivora: The role of phylogeny, metabolism and sex differences. Journal of Zoology 249, 315–337.

Tuomi, J., 1980. Mammalian reproductive strategies: A generalized relation of litter size to body size. Oecologia 45, 39–44.

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 of London B 280, 20130762.

Van de Kerk, M., de Kroon, H., Conde, D.A., Jongejans, E., 2013. Carnivora population dynamics are as slow and as fast as those of other mammals: Implications for their conservation. PLoS ONE 8, e70354.

Western, D., 1979. Size, life history and ecology in mammals. African Journal of Ecology 17, 185–204.

Wiedmann, M.A., Primicerio, R., Dolgov, A., Ottesen, C.A.M., Aschan, M., 2014. Life history variation in Barents Sea fish: Implications for sensitivity to fishing in a changing environment. Ecology and Evolution 4, 3596–3611.

Wiersma, P., Munoz-Garcia, A., Walker, A., Williams, J.B., 2007. Tropical birds have a slow pace of life. Proceedings of the National Academy of Science of the United States of America 104, 9340–9345.

Wiersma, P., Nowak, B., Williams, J.B., 2012. Small organ size contributes to the slow pace of life in tropical birds. Journal of Experimental Biology 215, 1662–1669.

Wilson, D.E., Reeder, D.A.M., 2005. Mammal Species of the World: A Taxonomic and Geographic Reference, third ed. Baltimore, MD: The John Hopkins University Press.