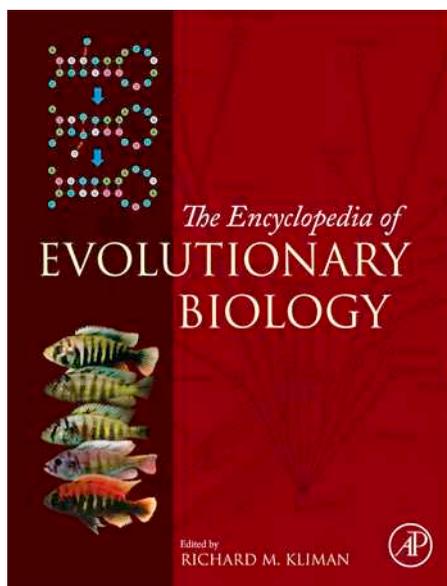


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Life Histories, Axes of Variation in

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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

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”

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 hatching 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](#)).

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.

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

| <i>Time metrics</i> | <i>Non-time metrics</i> | <i>Taxon/method</i> | <i>References</i> |
|---|--|--|---------------------------------|
| 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 <i>Adult mass</i> | Mammals ($N=65$) PCA PC1 accounting for 68.1% of life history variation <i>Corrected for allometric constraints</i> <i>Replicated at different taxonomic levels</i> Support | Stearns (1983) |
| Gestation time Age at first reproduction Number of offspring per season | Neonatal mass Neonatal mass/Adult mass Litter size Litter size \times Neonatal mass/ Adult mass <i>Adult mass</i> | 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 <i>Adult mass</i> | Primates ($N=135$) Bivariate linear regressions (log–log scale) <i>Corrected for allometric constraints</i> <i>Analyzed at the taxonomic level of subfamily</i> 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 <i>Adult mass</i> | Carnivores ($N=112$) Bivariate linear regressions (log–log scale) <i>Corrected for allometric constraints</i> <i>Replicated at different taxonomic levels</i> Support | Gittleman (1986) |
| Incubation time (per egg) Time to fledging Age at first reproduction | Clutch size Egg mass <i>Adult mass</i> | European birds ($N=191$ genera) Bivariate linear regressions (log–log scale) <i>Corrected for allometric constraints</i> <i>Analyzed at the taxonomic level of genus</i> Support | Saether (1987) |
| Gestation time Inter-birth interval Age at first reproduction Lifespan r-max | Neonatal mass Litter size <i>Adult mass</i> | Primates ($N=58$) Bivariate linear regressions (log–log scale) <i>Corrected for allometric constraints</i> Support | Ross (1988) |
| Adult survival Age at first reproduction | Clutch size | European birds ($N=107$) Bivariate linear regressions (log–log scale) <i>Corrected for allometric constraints</i> <i>Replicated at different taxonomic levels</i> 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) <i>Corrected for allometric constraints</i> <i>Replicated at different taxonomic levels</i> | Read and Harvey (1989) |

(Continued)

Table 1 Continued

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

(Continued)

Table 1 Continued

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

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

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

| <i>Metric</i> | <i>Taxon</i> | <i>Biological process</i> | <i>References</i> |
|---|--|---------------------------------------|----------------------------------|
| Dental development | Hominin | Evolution | Dean <i>et al.</i> (2001) |
| <i>F/α ratio (annual fecundity/age at first reproduction)</i> | Mammals | Demography | Oli (2004) |
| Generation time | Mammals and birds | Senescence | Jones <i>et al.</i> (2008) |
| Age at first reproduction | Muroid rodents | Exploratory behavior | Careau <i>et al.</i> (2009) |
| Nonlinear combination of annual fecundity, age at first reproduction, and annual adult survival | Mammals and birds | Senescence | Péron <i>et al.</i> (2010) |
| Age at sexual maturity | Mammals, birds, amphibians, and reptiles | Senescence | Ricklefs (2010) |
| Generation time | Marine fishes | Temporal variation in demography | Bjorkvoll <i>et al.</i> (2012) |
| Annual fecundity | Birds | Perception of predation risk | Hua <i>et al.</i> (2013) |
| Generation time | Mammals | Placentation type | Garratt <i>et al.</i> (2013) |
| Generation time | Mammals and birds | Age-specific contributions to fitness | Saether <i>et al.</i> (2013) |
| Age at which cumulative loop elasticity reaches 50% of total elasticity | Carnivores | Management strategies | Van de Kerk <i>et al.</i> (2013) |
| Generation time | Mammals | Transient dynamics | Gamelon <i>et al.</i> (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 <i>et al.</i> (1998) |
| 0.26 | | | 0.84 | 0.78 | Bielby <i>et al.</i> (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 <i>et al.</i> (2010) |
| 0.58 | −0.20 | | −0.39 | −0.28 | Juan-Jorda <i>et al.</i> (2013) |
| −0.86 | −0.86 | | −0.81 | −0.73 | Swanson and Dantzer (2014) |

^aPresented 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 placental 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

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