

The pace and shape of ageing

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Summary

1. Humans age, but how much more or less do we age compared with other species? Do humans age more than chimps, birds more than fish or sheep more than buffalos? In this article, I argue that current methods to compare patterns of ageing across species are limited because they confound two dimensions of age-specific change – the pace and the shape of ageing.
2. Based on the two axes of pace and shape, I introduce a new conceptual framework to classify how species age.
3. With this method, I rank species according to how strongly they age (shape) and how fast they age (pace). Depending on whether they are ranked by pace or by shape, species are ordered differently.
4. Alternative pace measures turn out to be highly correlated. Alternative shape measures are also highly correlated. The correlation between pace and shape ranking is negative but weak. Among the examples here, no species is long lived yet exhibits negligible ageing – contrary to the commonly held view that long-lived species are good candidates for negligible ageing.
5. Analysis of species in pace–shape space provides a tool to identify key determinants of the evolution of ageing for species across the tree of life.

Key-words: ageing, comparative, evolution, life-history biology, mortality, pace, senescence, shape

Introduction

Comparative research provides a necessary foundation for understanding how evolution has shaped the biology of ageing in different species. Across many animals and plants, researchers have compared the length of life and the rate of ageing to rank species according to how they age (Finch 1990). But how *much* or how *fast* they age, I argue, cannot be distinguished comparing ageing rates and longevity. Longevity and ageing rates depend on units of time, and the same unit of time for different species – say 1 month – encompasses different fractions of their life history. As illustrated later, this has important consequences for concluding how much or how little species age. Often one is tempted to believe that long-lived organisms show little or negligible ageing and short-lived organisms age rapidly (and thus strongly). I show that this view is misleading and perhaps even wrong.

Definitions of pace and shape of ageing

Below, following Medawar (1952), I use the term ageing to refer to the process of change in the risk of dying over adult ages without its colloquial connotation of deterioration and decay. Mortality could go up, down or remain constant. I reserve the

term senescence for increasing mortality with age and non-senescence for constant or decreasing mortality with age.

To compare ageing within and across different species, it is useful to distinguish two dimensions: the pace of ageing and the shape of ageing. The pace of ageing captures the time aspect of ageing; it is the time-scale on which mortality progresses. As such it is related to the tempo at which organisms survive and reproduce. The pace of ageing is fast for short-lived organisms and slow for long-lived ones. The shape of ageing, on the other hand, does not depend on time. It is captured by an adult age pattern of mortality (hazard of death) that is time standardized. Shape captures how sharply mortality increases (or decreases) with age.

To make a clear distinction between the concepts of the pace and the shape of ageing, language should be chosen carefully. Pace is described by words associated with time – e.g. rapid, fast or slow. Shape is described by words not associated with time but with magnitude or degree – e.g. flat, increasing or decreasing markedly or mildly.

Methods

MEASURES OF PACE AND SHAPE

Pace is measured by variables like life expectancy and longevity, which summarize the timing of death or age at maturity and

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generation time, which mark the timing of birth. Given the data available, in this article, I will mainly focus on the pace of death and will measure pace by life expectancy. Throughout the paper, age zero is defined to demarcate the onset of adulthood and thus 'life-expectancy' refers to 'life expectancy at maturity'.

To reveal the shape of ageing, time needs to be standardized. Standardized age is given by $x_s = x/L$, where x denotes age and L denotes life expectancy. Hence, standardized age one corresponds to 'one life-expectancy'. Standardized mortality, $\mu_s(x_s)$, equals nonstandardized mortality, $\mu(x)$, times life expectancy, i.e. $\mu_s(x_s) = \mu(x)L$ (see also example discussed in the following), because mortality depends inversely on units of time.

Other measures of pace could be used to standardize time, such as longevity, age at maturity or generation time. If pace is captured by generation time or some other measure, then mortality should be multiplied by that same measure to keep time comparably standardized on both axes, i.e. age and mortality.

Here and in other studies, using life expectancy might be preferable to other measures of pace, because multiplying mortality by life expectancy is mathematically equivalent to dividing mortality by its average level (see Appendix). Shape then is defined by the trajectory of age-specific mortality relative to average adult mortality. The trajectory falls above, at or below the level of one depending on whether late life mortality is larger, equal to or smaller than average mortality. The more the standardized mortality trajectory diverges from one, the more mortality has changed over the course of adult life, i.e. the steeper the shape of ageing (see e.g. right-hand panel of Fig. 2).

To rank species with respect to the shape of ageing, it is useful to capture shape by an index. Several indices can be devised. For example, if longevity is denoted by Ω and defined as the age when 99% of adults have died and only 1% are still alive, then shape can be measured by:

$$\frac{\Omega}{L} \text{ or } \frac{\mu(\Omega)}{\mu(0)} \text{ or } \frac{\mu(L)}{\mu(0)} \text{ or } \frac{\mu(\Omega)}{\bar{\mu}} \text{ or } \frac{\mu(L)}{\bar{\mu}},$$

where, as above, L denotes adult life expectancy, $\mu(0)$ denotes age-specific mortality at maturity and $\bar{\mu}$ denotes average adult mortality. The first index is simply the ratio of two pace measures. The second and third indices are based on initial adult mortality, $\mu(0)$, and are convenient if mortality changes monotonously over adult ages, e.g. for the Gompertz or Weibull model.

The two remaining indices are more general and capture shape also for nonmonotonous mortality functions. Note that none of these ratios depend on particular parametric forms.

The first ratio Ω/L will be the smaller, the steeper mortality increases with age. If all adults in a population would die at the same age, the ratio Ω/L equals one. The magnitude of the remaining ratios exceeds or falls below one if mortality increases or decreases with age. The more an index exceeds one, the stronger a species senesces; and the more an index falls below one, the better a species escapes senescence. If these indices equal one, then the species has sustained a constant level of adult mortality. For the second and third indices, this means that mortality has remained at its initial level; for the fourth and fifth indices, it means that mortality later in life is similar to the mortality an adult experiences on average at any other age.

DATA

To illustrate how the pace-shape distinction changes the comparative picture of species' ageing patterns, I extracted mortality parameters for the ten species listed in Fig. 3. I used different sources of published data based on different parametric mortality models (for specific models see Appendix). Finch (1990) provides estimates of Gompertz parameters for mortality starting at age at maturity for lake sturgeon (*Acipenser fulvescens*), herring gull (*Larus argentatus*), common swift (*Apus apus*), European robin (*Erithacus rubecula*) and Dall mountain sheep (*Ovis dallis*). Kaplan & Gurven (2007) fit the Siler model of mortality over total lifespan for hunter gatherers (*Homo sapiens*) and for wild and for captive chimps (*Pan troglodytes*). Parameter estimates for modern humans were derived by fitting life-table data for Swedish females in 2007 given in the Human Mortality Database (<http://www.mortality.org>) and for free ranging African buffalo (*Syncerus caffer*) by fitting data published by Sinclair (1977). Data for Swedish females and buffalo are well fit by the Gompertz law of mortality; the age-independent Makeham parameter was negligible for both data sets. Age at maturity for most of the species is taken for females from AnAge data base (<http://genomics.senescence.info/species/index.html>). Maturity for Swedish females was assumed to be 14 and for hunter gatherers to be 17. Wild chimps were assumed to mature at age 11 (Promislow 1991).

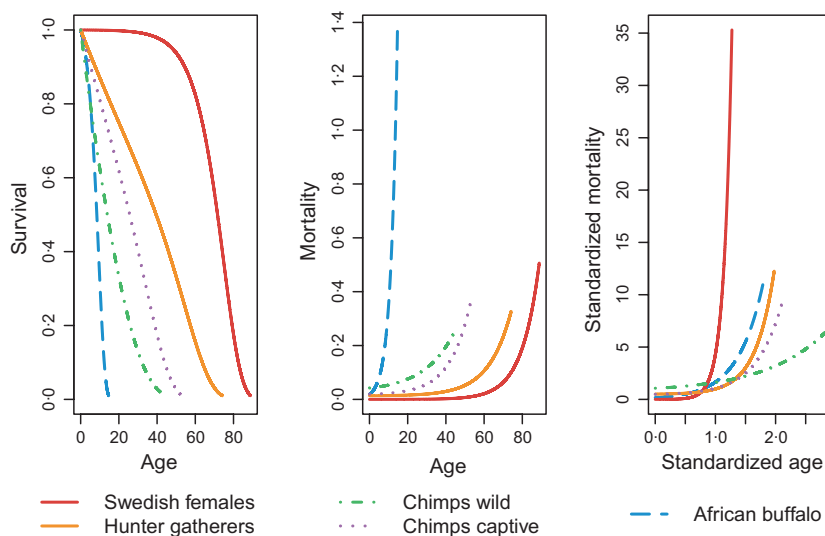
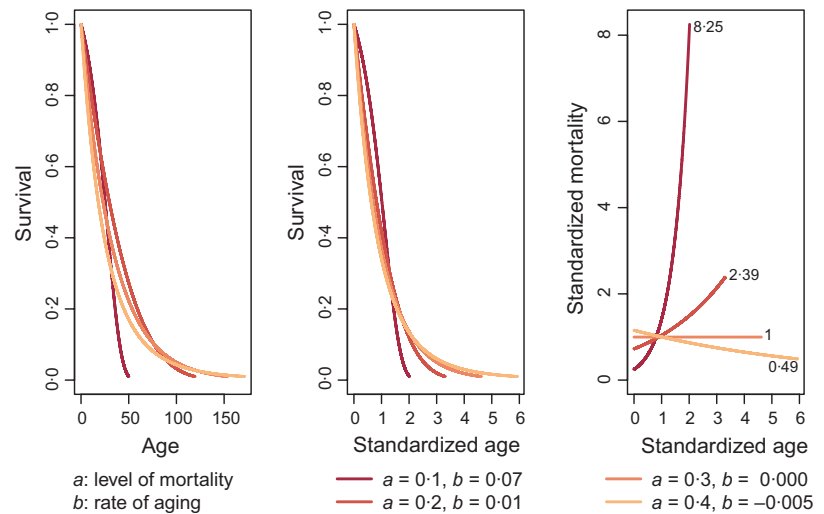


Fig. 1. Survival curves (left) and age patterns of mortality (the hazard of death) in standard view (middle) vs. shape view of ageing (right) for free ranging buffalo, modern Swedes, hunter gatherers, as well as wild and captive chimpanzees. In both panels, trajectories are plotted until the age when 99% of adults are expected to be dead. Age zero corresponds to reproductive maturity. Note that the middle panel depicts age-specific mortality rate rather than probability of death (see Appendix), so mortality can exceed the level of one.

Fig. 2. The panels display survival curves over age, survival curves over standardized age, as suggested by Pearl & Miner (1935), and, as in the right-hand panel of Fig. 1, pace-standardized mortality curves. The figure is based on simulated data for four hypothetical species assuming Gompertz mortality with parameters given in the legend. In the right-hand panel, the numbers labelling the curves capture the strength of ageing, measured by the shape index $\mu(\Omega)/\bar{\mu}$. The boundary between senescence and non-senescence can only be detected in the third panel. It is demarcated by the species that exhibits constant mortality with shape index equal to one.



Given the specific parameter estimates and age-specific mortality function for each species, I calculated life-expectancy, L , the age when 99% of adults are dead, Ω , and the various indices of shape.

Results

Fig. 1 illustrates the consequences of shifting perspectives from a standard view of ageing to a new pace-standardized view that reveals the shape of ageing. From a standard perspective of senescence (middle panel), mortality increases earliest and most markedly for buffalo (Gompertz $b = 0.294$) and latest and less markedly for Swedish females ($b = 0.117$). One might

conclude that buffalos show stronger senescence than Swedes. Similarly, for captive chimps, the increase in mortality starts earlier and is more pronounced than for hunter gatherers. Free ranging chimps show the highest mortality, yet the increase is less steep. The standard view, however, is confounded by pace.

From a shape perspective (right panel), the image is reversed and leads to opposite conclusions. Although buffalos initially senesce more strongly than Swedish females, at the age that corresponds to about 80% of adult life-expectancy mortality trajectories crossover. Thereafter, human senescence progresses much more steeply than that of buffalo. Relative to its average level, human mortality increases 35-fold compared to

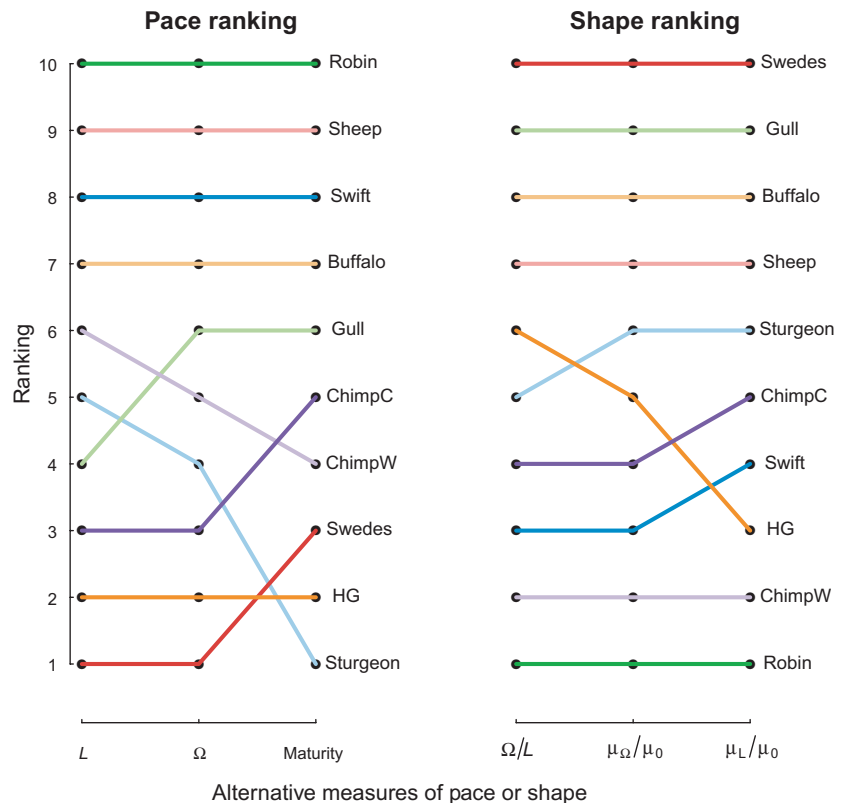


Fig. 3. Species ranking with respect to pace and shape of ageing. High rank orders correspond, respectively, to fast pace and steep shape. Low ranks correspond to slow pace and shallow shape. Straight horizontal lines indicate that alternative measures rank species in similar order. Notation: L , life-expectancy; Ω , longevity; μ_{Ω} , μ_L , μ_0 , mortality at the age of longevity, life expectancy and maturity, respectively.

only an 11-fold increase for buffalos. Swedish females do not reach ages that exceed their expected length of life by more than 30% whereas buffalos reach ages that correspond to almost twice their life expectancy. Similarly, hunter gatherers reveal a steeper shape of senescence than captive chimps. Wild chimps experience the weakest increase in mortality and live comparatively longest.

As in many medical and biological applications, data on death are often presented in terms of survival curves rather than age-specific mortality, the left-hand panel of Fig. 1 displays the survival curves that correspond to the data in the other two panels.

Fig. 2 demonstrates that similar survival curves can correspond to opposite shapes of senescence. The lightest curve with falling mortality and shape index $\mu(\Omega)/\bar{\mu} < 1$ shows negative senescence. The species with constant mortality and $\mu(\Omega)/\bar{\mu} = 1$ shows ‘sustenance’ – it demarcates the boundary between senescence and nonsenescence. The two species with increasing mortality and $\mu(\Omega)/\bar{\mu} > 1$ show senescence. Fig. 2 illustrates that pace-standardized mortality patterns and corresponding indices of shape can capture both the boundary between senescence and nonsenescence as well as the strength of ageing (right-hand panel). These important aspects of ageing remain hidden when data about death are presented in the usual way as survival curves (left-hand panel), or, as suggested by Pearl & Miner (1935), as survival curves over standardized age (middle panel).

Fig. 2 is based on simulated species with increasing, constant and decreasing mortality patterns, because published mortality parameters for species with nonsenescence based on large enough sample sizes are not available yet. Note, however, that the darkest curve resembles the pattern of hunter gatherers; it has the highest shape index of 8.25, indicating the strongest senescence. The parameters chosen for the remaining species have high levels of mortality relative to rates of ageing; this is characteristic for many species in the wild (as indicated in the left-hand panel of Fig. 1).

Fig. 3 shows how species rank along the pace and shape axes of ageing, applying alternative measures for pace and shape. Table 1 gives the Spearman's rank correlation coefficients. Both Fig. 3 and Table 1 corroborate that (1) alternative pace measures are highly correlated; (2) alternative shape measures are also highly correlated; and (3) the correlation between pace and shape ranking is negative but weak.

Depending on whether ranking is performed with respect to pace or to shape, species rank differently. Fig. 3 shows that various combinations of pace and shape, fast–weak (robin), fast–strong (buffalo, sheep) and slow–strong (Swedes) can be found. Some species remain on similar ranks for both pace and shape (captive chimps remain between ranks 3 and 5, sturgeon between 4 and 6). The only pattern that is not observed among this list of species is slow–weak, i.e. long lived and negligible senescence. This may come as a surprise because species with extreme lifespan are often viewed as those that have managed to escape senescence. Instead, I find that modern humans, the longest lived among this sample of species, show the strongest senescence.

Table 1. Spearman's rank correlation coefficients between alternative measures of pace, alternative measures of shape and between measures of pace and shape for the ten species listed in Fig. 3

Pace measures	Longevity	Life expectancy	Maturity
Life expectancy, L	1.000	0.964	0.806
Longevity, Ω	0.964	1.000	0.890
Maturity (age 0)	0.806	0.890	1.000
Shape measures	Ω/L	$\mu(\Omega)/\mu(0)$	$\mu(L)/\mu(0)$
Ω/L	1.000	0.988	0.927
$\mu(\Omega)/\mu(0)$	0.988	1.000	0.964
$\mu(L)/\mu(0)$	0.927	0.964	1.000
Shape measures			
Pace measures	Ω/L	$\mu(\Omega)/\mu(0)$	$\mu(L)/\mu(0)$
Life expectancy L	−0.515	−0.479	−0.394
Longevity Ω	−0.382	−0.358	−0.273
Maturity (age 0)	−0.248	−0.261	−0.151

Given the data available, here I confine the analysis to mortality. Ageing is captured not only by the change in mortality with age but also by the change in fertility with age. All definitions and analyses can be replicated for reproduction.

Discussion

LINK TO GOMPERTZ AND WEIBULL MODEL

Usually, the functional form of mortality and its corresponding ageing rate are assumed to describe the shape of ageing. For example, if mortality follows an exponential pattern, it is modelled by the Gompertz law, $\mu(x) = a e^{bx}$, where the parameter $a \equiv \mu(0)$ captures the initial level of adult mortality and the parameter b captures the rate of ageing, i.e. the relative change in mortality with age x (Gompertz 1825; Finch 1990). Both parameters are given in units $1/\text{time}$. Therefore, the level of mortality and the rate of ageing do not reflect the true *shape* of ageing – they are measures of *pace*. This is generally true also for other mortality models such as the Gompertz–Makeham or the Weibull model (see Appendix). To reveal the true shape of ageing, the parameters need to be time standardized. For the Gompertz model, standardized mortality, i.e. shape, is given by

$$\mu_s(x_s) = a_s e^{b_s x_s},$$

with parameters $a_s = a L$ and $b_s = b L$. Because $x_s = x/L$, the product $b_s x_s$ equals bx , and thus

$$\mu_s(x_s) = a_s e^{b_s x_s} = a L e^{bx} = \mu(x) L.$$

If mortality is well fit by a particular functional form, one might consider measuring shape by time-standardized mortality parameters, like a_s or b_s . But measuring shape by a single mortality parameter does not account for all components of shape. Focusing on the ageing rate ignores the corresponding level of mortality; focusing on the level ignores the rate; both

are important aspects of the shape of ageing. Ricklefs (1998) constructed the parameter ω as a measure of the ageing rate for the Weibull model. But ω is a function of two parameters (see Appendix). This implies that theoretically, an infinite number of different combinations of these parameters can lead to the same ageing rate, i.e. there is a risk that species with different shapes of ageing might falsely be assigned to the same ageing type. I suggest that the shape indices derived earlier offer a better way of comparing shapes than using time-standardized ageing rates.

LINK TO PREVIOUS APPROACHES OF TIME STANDARDIZATION

Pearl & Miner (1935) proposed that age should be standardized by life expectancy to compare how different species age. Eakin (1994) demonstrated how this scaling of age opens the door for dimensionless analysis in a mathematical framework. Pearl and Miner compare species' survival curves, i.e. trajectories that decrease monotonously from 1 at time zero to 0 when the last individual of the population dies. Their approach is illustrated in the middle panel of Fig. 2. The authors distinguish among three basic types of survival curves (rectangular, intermediate, diagonal) that classify species according to different types of ageing. But survival curves, plotted over age or over standardized age, are determined by the age pattern of mortality in a highly nonlinear and cumulative way (see Appendix). Following Pearl and Miner, all four survival curves in the middle panel of Fig. 2 might be classified as diagonal because of the high level of mortality, but the right panel of Fig. 2 shows that the curves imply qualitatively different mortality patterns. Compared with survival curves, the age pattern of mortality contains much more information about the shape of ageing, especially information that can be used to distinguish between senescent and nonsenescent species and that can be used to determine the steepness of shape. As illustrated by Figs 1 and 2, survival curves hide these important aspects of shape. Therefore, the pace–shape approach is based on mortality patterns rather than survival curves.

Also based on mortality patterns, the statistical field of survival analysis (Cox & Oakes 1984) compares mortality among different subpopulations, often of the same species under different treatments, e.g. dietary restriction or medical interventions. In survival analysis, subpopulations are assumed to share a similar baseline mortality curve and to differ either by a proportionality factor that raises or lowers the curve (proportional hazard model) or by a factor that scales age by accelerating or decelerating time (accelerated failure time model). Time in this framework is not dimensionless but given in units of the baseline group. Caswell *et al.* (1998) used such an approach in an ecological framework, adapting time for different species to the time scale of a baseline species (the Harbor Porpoise). The age of each species was scaled by the ratio of its age at maturity to the age at maturity of the Harbor porpoise.

In contrast to such models, the pace–shape approach does not scale age to any particular baseline species, nor does it assume that the mortality curve for a species is related by some

function to a baseline mortality curve. Age patterns of mortality vary so much across species that the differences cannot in general be captured by a proportionality factor or a factor that slows or speeds up time. The pace–shape approach provides a flexible way to compare ageing across species.

The approach suggested here goes beyond scaling of time. It provides a framework to systematically rank and classify species with respect to how fast they age and how strongly they age, revealing the boundary between senescence and nonsenescence.

Discussion of results

LINK TO PREVIOUS FINDINGS

Commonly, long-lived species are taken as good candidates for negligible senescence. But Table 1 and Fig. 3 show evidence that supports the contrary view. This evidence, however, does not rule out the existence of long-lived species that show negligible or negative senescence. Ten species constitute too small a sample to draw conclusions about the relationship between pace and shape. Using empirical data from Promislow (1991) for 56 species of mammals in the wild I found no significant correlation between the pace of ageing measured by life expectancy and the shape of ageing measured by the proportional increase in mortality between the maturity and the expected age at death. Because the data set has known problems (Gaillard *et al.* 1994), this finding needs to be verified when a larger, more reliable data set is compiled.

The pace–shape distinction puts a new perspective on other findings. Kaplan & Gurven (2007) concluded that chimps age much faster than humans and die earlier—their result pertains to the pace of ageing. Figs. 1 and 3 show that with regard to the shape of ageing, humans rank higher and thus show stronger senescence than chimps. The comparative study by Jones *et al.* (2008) also focuses on the pace of ageing. Using individual-level long-term data and different measures of ageing, the authors found that the fast–slow life-history continuum (Stearns 1992; Roff 2002) also holds for senescence—long-lived organisms senesce slowly; short-lived organisms senesce rapidly. Their finding supports the result presented here that pace measures are highly correlated.

LINK TO THE EXTRINSIC, AGE-INDEPENDENT RISK OF DEATH

Fig 1 compares the shape of mortality for species with exponentially increasing adult mortality. As some species are free ranging and others are protected, a main difference between them is the level of age-independent mortality. As hypothesized by Williams (1957), a high age-independent hazard of death should favour the evolution of senescence. Williams' hypothesis has spurred research efforts for several decades. The pace–shape distinction clarifies that the level of the age-independent hazard mainly sets the timeframe of life. The rank order of the length of life for the four primate species is consistent with Williams' hypothesis. The African buffalo, however, shows a much faster pace of ageing than primates, even though

its age-independent mortality was estimated to be negligible. This suggests that the age-independent hazard is not the only variable determining the pace of ageing. Other variables such as social system, brain size, ability to survive with single vs. multiple disorders, and probably many more also have to be considered as important determinants of pace and similarly as determinants of shape.

To draw conclusions about how the shape of ageing is affected by the age-independent hazard of death, more refined hypotheses are needed (Caswell 2007). Baudisch & Vaupel (2010) hypothesize that the shape of ageing (i.e. how strongly senescence is favored) is determined not by the absolute age-independent hazard of death but by two relative quantities: the ratio of age-independent mortality to mortality at maturity and the ratio of the intrinsic rate of deterioration to mortality at maturity. In the Gompertz–Makeham case, these ratios pertain to $c/(a + c)$ and $b/(a + c)$ (see Appendix for notation).

FUTURE DIRECTIONS

Much is known about the pace of ageing (Finch 1990; Carey & Judge 2000; Carey 2003), but knowledge about the shape of ageing is limited. It is well established that mortality for humans in countries with high life expectancies is well captured by a Gompertz curve – exponentially increasing mortality, from about age 35 to age 90 or so (Thatcher, Kannisto, & Vaupel 1998; Thatcher 1999) and also that a Gompertz curve provides a serviceable fit to observed patterns of adult mortality in other species (as discussed in Finch (1990) and Promislow (1991)). The Gompertz curve, however, is only one model and it is not a good fit for all species, especially not for those that show a decline in death rates with age (Vaupel *et al.* 1998). Although specific parametric mortality functions were used to produce the results presented earlier, pace and shape measures do not hinge on any particular functional form: they can be directly measured from life-table data if available. The functional form of mortality is only one aspect of shape: there seems to be much more to be discovered. A systematic comparison of time-standardized indices of senescence across species has been, up until now, lacking.

Virtually, nothing is known about the relationship between the pace of ageing and the shape of time-standardized mortality. Understanding the relationship between pace and shape requires understanding of their physiological and environmental determinants in different species. It is known that the pace of life is linked to the metabolic rate of an organism; this rate scales with body size and depends on temperature (Gillooly *et al.* 2001; Savage *et al.* 2004; Speakman 2005). Also it seems clear that the shape of mortality patterns should depend on an organism's capacity for repair and regeneration, growth and learning (Kirkwood 1977; Vaupel *et al.* 2004; Baudisch 2008; Finch 2009). Research is needed to reveal the determinants of pace and shape for different species across the tree of life.

Researchers have pointed out that species with negligible senescence can have a shorter or a longer lifespan (Finch 1990) and that a long lifespan says nothing about whether a species shows senescence or not (Roach 1993). Thus, species with

extreme life spans should not rashly be cited as species that have managed to escape senescence – they only live at a very slow pace. Whether they escape senescence is a different question. Theoretical results from evolutionary demographic models (Vaupel *et al.* 2004; Baudisch 2008) suggest that the pace and shape of ageing are two distinct dimensions that can vary independently. We found that both short-lived species and long-lived species can exhibit the same shape of mortality over adult life, increasing, constant or decreasing, more or less pronounced. Future research should carefully examine the relationship between pace and shape, not only for mammals but also for species across the tree of life.

Based on good life-table data, and preferably long-term individual-level data, e.g. from capture–recapture studies, one could ask: Does the pace–shape relationship vary among taxa? Cohort data on age-specific mortality, fertility and growth could help to disentangle environmental from physiological determinants of pace and shape (Roach, Ridley, & Dudycha 2009). Similarly, comparing data for the same species in the wild vs. in captivity or in a colder vs. warmer habitat would be helpful. Data on age-specific as well as size-specific mortality and fertility could help disentangle changes in mortality because of learning, change in body size or changes in other physiological characteristics.

PACE–SHAPE SPACE AS A TOOL TO REVEAL PATTERNS

Using the pace–shape (PS) distinction, the ageing patterns of species can be sorted along two clearly defined axes that span the pace–shape space, as illustrated in Fig 4. With only ten data points, the PS space provides insights similar to those from Table 1 and Fig 3: species can be found in all areas of the diagram except for the combination slow–weak, represented

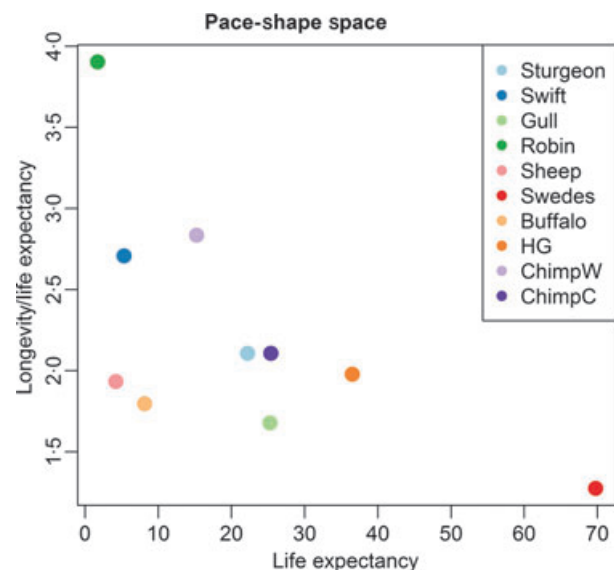


Fig. 4. Example of a Pace–Shape Space. Pace is measured by life expectancy, and shape is measured by the ratio of longevity to life expectancy, the ‘tail of longevity’; the longer the tail, the weaker senescence. Data are the same as in Fig 3.

by the upper right corner. But when a larger number of species can be included in the analysis, certain species will form clusters in different corners of the PS space. The presentation of data in PS space will become a valuable tool in revealing patterns. Patterns observed in PS space will spur hypothesis about why species cluster together – do they share a common physiology, or a common ecology or a common phylogenetic history? The variables that are common to all species in a cluster will represent key candidates for being important determinants of ageing.

PS spaces can be spanned by different indices of pace and shape. The list of indices suggested in this article can be extended to reveal more details of the shape of a life history, e.g. the life-history invariants suggested by Charnov (2002, 2005) and Charnov, Warne, & Moses (2007). More elaborate measures can be developed based on the mathematical framework provided by the field of formal demography (Lotka 1934, 1956; Keyfitz 1968, 1985; Vaupel 2010), but more sophisticated measures require more detailed data.

Indices that allow a clear distinction between increasing, constant and decreasing mortality will be especially valuable in distinguishing between senescence, negligible senescence and negative senescence. I speculate that viewing species in PS space could identify new model species that are short-lived yet show little or no senescence, potentially permitting study of species in the laboratory that successfully avoid senescence.

Conclusion

Understanding the phylogenetic, ecological and physiological determinants of ageing is a large and exciting project for research in evolutionary biodemography and life-history biology. The distinction between the pace and the shape of ageing offers a new conceptual framework for these future endeavours. Complementing current knowledge on the pace of ageing, theory and hypotheses are needed that shed light on the shape of ageing, the relationship between the pace and the shape of ageing and the determinants of pace and shape for different species across the tree of life.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Parametric Models of Mortality.

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