

Methods in Ecology and Evolution

A pace and shape perspective on fertility

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Abstract

1. Aging is ubiquitous to all organisms, but aging does not always mean senescence. Counter to most evolutionary theories of aging, patterns of mortality and reproduction may remain unchanged or improve with age, as well as deteriorate. Describing this diversity presents a challenge to eco-evolutionary demography. The pace-shape framework of mortality tackled this challenge to qualify and quantify orthogonal components of aging patterns in mortality. Here we extend this framework to fertility.
2. Analogous to the logic of the mortality framework, we define a perspective, a framework and novel methods for the pace and shape of fertility. These distinguish between orthogonal components of time scale (pace) and distribution (shape) of reproduction over adult lifespan.
3. Our pace and shape framework mirrors that of mortality, through a shift of perspective from the mother giving birth, to the offspring being born. Our new measures overcome many problems associated with measuring natural fertility trajectories, have both a clear biological and mathematical interpretation, can be intuitively visualised, and satisfy and extend important conditions of the pace-shape paradigm.
4. A comprehensive framework of fertility pace-shape facilitates ecological and evolutionary research addressing interactions and trade-offs between components of birth and death patterns, across the whole tree of life. The burgeoning emergence of large comparative demographic data sources across wide environmental, geographical, temporal and phylogenetic ranges, combined with pace-shape measures, opens the door to comparative analyses of aging which were never possible before.

Keywords: *pace, shape, fertility, senescence, ageing, life history, demography, life tables*

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Introduction

People have questioned why we age since perhaps we began to reflect on our finitude. Evolutionary theories of aging offer general answers and conclude that senescence, which we define here to be increasing mortality and/or decreasing reproduction with age after maturity, is inevitable. According to these theories, the strength of natural selection diminishes following first reproduction (Hamilton, 1966) leading to concomitant physiological declines, due either to tradeoffs between early and late life (antagonistic pleiotropy theory; Medawar, 1952; Williams, 1957), or between somatic maintenance and reproductive investment (disposable soma theory; Kirkwood, 1977), or due to non-adaptive accumulation of deleterious germ-line mutations (mutation accumulation theory; Medawar, 1952). Results of theoretical models (Vaupel, Baudisch, Dölling, Roach, & Gampe, 2004; Baudisch, 2005, 2008; Baudisch & Vaupel 2012; Wensink, Caswell, & Baudisch, 2017) and empirical evidence (e.g. Garcia, Dahlgren, Ehrlén, & 2011; Jones *et al.*, 2014, Schaible *et al.*, 2015) eventually challenged this paradigm: aging is not in fact synonymous with senescence. As well as senescence, the diversity of aging patterns across the tree of life also includes *negligible senescence* (unchanging mortality and/or fertility with age) and *negative senescence* (decreasing mortality and/or increasing fertility with age). Aging, stripped of its deteriorative connotations, means simply to get older with time. From a comparative perspective, these findings should broaden our initial question to: everything ages, but why do only some things senesce?

Models suggest that aging patterns, whether senescence, negligible senescence or negative senescence, evolve independently of lifespan, whether this constitutes days, years, or centuries (Baudisch, 2008, Wensink, Wrycza, & Baudisch, 2014). That is, changes in parameters that affect the length of lifespan, and more generally the time scale of a life history, should not have any specific association with aging patterns. A clear view of the factors that determine aging patterns hence requires factoring out time. To that end, Baudisch (2011) developed the pace-shape perspective.

Pace and Shape of Mortality

In order to understand how and why - from an evolutionary perspective - an organism ages, we must understand the distribution of demographic events (survival, reproduction) over its life

course, otherwise termed *demographic trajectories*, or more specifically *survival/mortality trajectories* and *fertility trajectories*. To do so, it is paramount to correct for duration of life: a *rate* of aging depends on time and has a very different interpretation for longer- versus shorter-lived species. The original *pace-shape* framework approaches this problem by defining two dimensions for understanding aging patterns in mortality (Baudisch, 2011). The *pace* dimension captures time scale; it embraces all factors that describe a duration or rate of life. Life expectancy is a recommended pace measure (Wrycza & Baudisch, 2014), describing the expected (i.e. average) duration of life at a given age; usually at birth or age of maturity. The *shape* dimension includes all time-standardized measures capturing the distribution of death across an average life history. Lifespan equality measures, such as the Gini coefficient, Keyfitz's entropy¹, or the coefficient of variation describe the shape of mortality (Wrycza *et al.*, 2015) and quantify the degree to which organisms are likely to die at similar older ages (senescence), dissimilar ages (negligible senescence), or mostly similar younger ages (negative senescence). Taken together, pace and shape values allow description of aging as occupying some place in a two-dimensional pace-shape space.

The pace-shape perspective has proven useful in comparative aging studies (Baudisch *et al.*, 2013, Jones *et al.*, 2014, Colchero *et al.*, 2016, Archer *et al.*, 2016, Németh, 2017, Barks, Dempsey, Burg, & Laird, 2018, Overall & Faragher, 2019). Jones *et al.* (2014) find a remarkable diversity of aging patterns across 46 species. Organisms have life courses lasting from days to centuries, and show mortality patterns spanning extreme senescence through to extreme negative senescence with limited phylogenetic congruence. Distantly-related species may show similar mortality trajectories, whilst closely-related species may be surprisingly divergent. Relationships between pace and shape may tell us about how senescence evolves, or is constrained, within clades or environments. For example, Colchero *et al.* (2016) find an astoundingly tight linear pace-shape pattern for human populations across differing living conditions, and a similar weaker but significant relationship across heterospecific primate populations. Humans have generally developed increasing life-expectancy, along with a lock-step increase in lifespan equality. This suggests some evolutionary and/or mechanistic constraint on human senescence: the longer the life course, the

¹Originally, Demetrius derived the concept of entropy in biological populations as a dynamical analogue to the entropy of a physical system (Demetrius, 1974, 1975, 1976, 1978). The name Keyfitz' entropy emerged within the demographic literature as Keyfitz (1977) introduced the same concept and made it a central item in his book Applied Mathematical Demography.

more death is concentrated at the end of life. Baudisch *et al.* (2013) similarly detect a weaker dependence between pace and shape values in flowering plants: longer-lived plants have more equal, senescent, lifespans. Archer *et al.* (2018) find that dietary composition affects aging trajectories in *Drosophila melanogaster*: populations fed on high-carbohydrate, low-protein diets have shortened life expectancy, whilst carbohydrate alone lowered rate of senescence. Conversely for the common duckweed *Lemna turionifera*, Barks *et al.* (2018) find little conspecific variation in pace and shape of mortality among strains with divergent size and reproductive investment. These first studies open big questions about inter- and intra-species relationships of pace and shape of mortality, and dependences on phylogeny, physiology, functional traits and the environment.

Why does the framework focus on mortality and neglect fertility? Mortality and fertility processes together constitute the driving forces of evolution and population dynamics. Results from theory (Baudisch, 2008) suggest separating pace from shape not only for mortality, but also for fertility.

Pace and Shape of Fertility

Every organism dies only once, and every organism must die. In contrast, organisms may produce many or few offspring, but not every organism will reproduce. Typical mortality patterns follow a monotonic trajectory, at least for ages following maturity, and existing shape methods (Wrycza, Missov, & Baudisch 2015) have required monotonicity to classify mortality into senescent, non-senescent and negative senescent patterns. Fertility trajectories, in contrast, are remarkably diverse, with increasing, decreasing, static, hump-shaped, periodic, semelparous and menopausal life cycles among many strategies found in nature. This poses a challenge to elegantly distinguish among senescent and non-senescent trajectories of fertility.

How can we overcome this challenge? Classic human demographic approaches capture hump-shaped fertility trajectories (e.g. Brass, 1975, Booth 1984), which is broadly representative for mammals (Gage, 2001), but not general enough for other organisms. Facing the issue of multiple births, human demographers study transition probabilities from zero children to one, one to two, and so on (e.g. Preston, Heuveline, & Guillot, 2001), but this 'parity' perspective does not make sense for species that give birth to more than one (or two) offspring at a time.

To loosen the mental knot, we suggest shifting perspective from the mother who gives birth, to the offspring that are born.² Every past, current or future individual has to be born, and each individual is only born once. From the perspective of all offspring ever born, one can imagine a "population" of unborn individuals waiting along a "survival curve" for the event of being born to a mother of a certain age. If children can expect on average to be born to a mother of younger age then fertility decreases on average with age, while if children can expect on average to be born to a mother of older age, fertility increases on average with age. The parallels of perspective with mortality are immediately clear. As the cumulative effect of uncertain mortality gives a survival curve, equally our perspective invites a cumulative fertility approach, which gives a monotonically increasing cumulative reproduction function.

If fertility does not change at all with age (negligible reproductive senescence), the cumulative reproduction function is linearly increasing, analagous to a type-II survival curve. A species with reproduction concentrated at the start of life and declining on average with age (reproductive senescence) has a concave-down cumulative reproduction function, analagous to a type-I survival curve. A species with reproduction concentrated toward the end of life and increasing on average with age (negative reproductive senescence) has a concave-up reproduction function, analagous to a type-III survival curve. Here we explain how to quantify the pace and shape of these functions, and how they are able to describe the diversity of reproductive strategies across the tree of life.

²Whilst we realise that among the diversity of Earth's species the terms "mother", "birth", "born" and even "individual" are subjective, ill-defined or perhaps not even applicable, we use them here for convenience and hope that they are generalisable enough for the method to be cogent in many scenarios.

Method

Let $m(x)$ denote the age-specific maternity function that captures the average number of offspring to a mother of age x , with first and last ages of reproduction denoted by α and β (note that for most organisms $\beta = \omega$, the maximum longevity). The function $B(x)$ defines cumulative reproduction up to age x as the total number of births to mothers up to age x :

$$B(x) = \int_{\alpha}^x m(t)dt. \quad (1)$$

Thus, $B(\alpha)$ is zero and $B(\beta)$ is the lifetime reproduction (which equals the total fertility rate, TFR , a quantity central to fertility studies in human demography (Preston, Heuveline, & Guil- lot, (2001)). For brevity, we denote $B = B(\beta)$ to capture total cumulative reproduction and $\tau = (\beta - \alpha)$ to capture reproductive lifespan. Based on these quantities, we suggest measures for the pace and shape of fertility. We present equations for the continuous case, which correspond to the continuous-time examples presented in the figures. The results generalise to discrete data, and we further discuss small adjustments to the method pertaining to discrete data in Appendix A1.

Shape of Fertility

Constant reproduction, defined as a perfectly even or equal spread of reproductive contributions $m(x)$ over age, represents a benchmark nil-senescence case. Graphically, this is depicted as a horizontal line in $m(x)$ (Fig.1a). The corresponding cumulative reproduction curve $B(x)$ rises linearly and forms a triangular shape in the x - $B(x)$ -space (Fig.1a) with an area given by half the product of its edges $\tau B/2$.

Organisms with reproductive senescence have reproduction concentrated towards the start of the life cycle (decreasing reproduction with age). These have concave-down $B(x)$ functions which for monotonic $m(x)$ schedules lie above the benchmark case (Fig.1f,g), or for non-monotonic reproductive schedules lie mostly above (Fig.1h). Conversely, organisms with negative senescence have reproduction concentrated towards the end of the life cycle (increasing reproduction with age). These have concave-up $B(x)$ functions which for monotonic $m(x)$ schedules lie below the benchmark case (Fig.1c,d), or for non-monotonic reproductive schedules lie mostly below

(Fig.1e). Organisms with nil (or negligible) senescence have reproduction which is either constant or otherwise evenly distributed across the life cycle. These have $B(x)$ functions that are approximately equal to or symmetrical about $\alpha + \tau/2$ (Fig.1a,b).

The difference between the benchmark area $\tau B/2$ and the area under the $B(x)$ curve indicates whether the actual fertility trajectory $m(x)$ follows a predominantly increasing or decreasing pattern with age. It is related to the Gini coefficient, a shape measure for mortality (Wrycza, Missov and Baudisch 2015), yet differs in important aspects (see Appendix A3). To facilitate comparisons across species, the difference is standardised by both fertility and reproductive lifespan. It follows that

$$S = \frac{1}{\tau B} \left(\int_{\alpha}^{\beta} B(x) dx - \frac{\tau B}{2} \right). \quad (2)$$

Within the parentheses, the integral is the area under the cumulative reproduction curve and the quotient is the area of the triangular space under the diagonal benchmark line of constant reproduction. The entire term describes the difference between the two areas. Different lifespans and reproductive outputs mean that between species, these areas may differ considerably in magnitude. Compare for example a conifer tree with a lifespan of hundreds of years and thousands of seedlings per year to a bear living less than two decades and birthing only one or two cubs per year. Therefore, the factor $1/\tau B$ standardises the difference between the two terms.

$S > 0$ is positive reproductive senescence,

$S = 0$ is nil reproductive senescence, and

$S < 0$ is negative reproductive senescence.

This is because increasing reproduction with age gives a cumulative function which necessarily lies underneath the constant equivalent (therefore has a smaller area). Decreasing reproduction with age gives a cumulative function which necessarily lies above the constant equivalent (therefore has a larger area). As standardisation means the smallest (theoretical) area under the cumulative reproduction curve is zero and the largest (theoretical) area is 1, whilst the area under the constant equivalent is always 0.5, all shape values are constrained to fall within the interval $-0.5 < S < 0.5$. Shape values at the extremes can be defined theoretically, as we lay out in the discussion, but are very unlikely to be observed in nature.

Standardisation may also be achieved by directly scaling x and $B(x)$ in the appropriate manner before calculating S . Using \hat{x} and $\hat{B}(x)$ to represent standardised age and standardised cumulative reproduction:

$$\hat{x} = \frac{x - \alpha}{\tau} \quad (3)$$

and

$$\hat{B}(x) = \frac{B(x)}{B}. \quad (4)$$

These quantities equal zero at maturity, $\hat{x}(\alpha) = \hat{B}(\alpha) = 0$, and one at the last age of reproduction, $\hat{x}(\beta) = \hat{B}(\beta) = 1$. Therefore \hat{x} captures the proportion of reproductive lifespan and \hat{B} captures the proportion of total lifetime offspring. Based on standardised quantities the shape of fertility can then be found using

$$S = \int_0^1 \hat{B}(\hat{x}) d\hat{x} - 0.5. \quad (5)$$

Standardising prior to calculating S is a useful approach for both full and partial fertility functions. A partial fertility function can be defined in $x(a)$ to $x(b)$, where $\alpha \leq a$, $a < b$ and $b \leq \beta$. These partial fertility functions may not start with $a = \alpha$, i.e. $B(a) = 0$, and/or may not end with $b = \beta$, i.e. $B(b) = B$. For a partial fertility curve therefore, the benchmark constant reproduction case is not defined as linear from $B(\alpha)$ to $B(\beta)$ (in any case α and β may be unknown), but as constant linear reproduction from $\hat{B}(a) = 0$ to $\hat{B}(b) = 1$.

Pace of Fertility

Similar to the logic of mortality, we can construct a survivorship concept for birth. Instead of a population of living individuals awaiting their uncertain age at death, we consider a population of unborn children awaiting their event of being born to a mother of uncertain age. Survival is the delay of mortality, so we term this *birth-delay*, and define the *birth-delay function* as the percentage of unborn babies to mothers of age x :

$$b(x) = 1 - \frac{B(x)}{B}. \quad (6)$$

Using this concept, we can construct a measure for the *pace of fertility* calculated as the expected waiting time until birth for a child, given by

$$P = \int_{\alpha}^{\beta} 1 - \frac{B(x)}{B} dx = (\beta - \alpha) - \frac{1}{B} \int_{\alpha}^{\beta} B(x) dx. \quad (7)$$

Pace of fertility can be interpreted as the age of the mother (minus α) at the birth of an average child. This is the reproductive equivalent to life expectancy, the average age at death. Equation 7 simplifies given the definition of shape in equation 2 and that of reproductive lifespan τ and reveals how pace relates to shape:

$$P = \tau - (S\tau + \frac{\tau}{2}) = \tau(0.5 - S). \quad (8)$$

Pace P can take any value of a fraction of total reproductive lifespan τ , because shape values range between -0.5 and 0.5 . For constant birth patterns, S equals zero and P is exactly half of the length of total reproductive lifespan τ . If shape is positive, then pace will be shortened. If shape is negative, then pace will be prolonged. In principle, pace and shape constitute two independent dimensions. Only relative to the total reproductive lifespan τ does S determine whether the majority of offspring are born earlier or later in life. The fact that S is a constituent part of the formula for P has no effect on the actual value of reproductive lifespan, be it months or centuries, since S need not have any relationship with τ ; it merely scales it when finding P .

Examples

Shapes of fertility curves may take almost any conceivable form, given the vast diversity of approaches to types of reproduction (sexual, asexual), timings of reproduction (aseasonal vs seasonal, semelparous vs iteroparous, annual vs multiannual) and influencing factors (sex determination, sex ratio, resource availability, environmental conditions). Reproductive lifespan may last from hours to days, centuries or even millennia. We could never hope to fully represent such diversity here, but have chosen several common shapes of reproductive output, illustrated in Figure 1 with corresponding shape values in Table 1. These are matched to a number of real fertility trajectories representing a broad range of clades, life forms, reproductive lifespans and environments, illustrated in Figure 2 with corresponding shape, pace, age at maturity and maximum longevity values also in Table 1.

Figs. 1a and 2a (*Rhododendron maximum*; McGraw, 1989) show constant reproduction. Rate of reproduction does not change with age, and cumulative reproduction is close to the baseline case, giving a shape value close to zero (Table 1). Figs. 1b and 2b (*Rupicapra rupicapra*; Caughley, 1970) shows a hump-shaped reproductive curve. Although reproduction changes with age, the overall balance remains even and shape is still close to zero (Table 1). Figs. 1c-e and 2c-e show varying extremities of negative senescence for concave-down (Fig.1c; Fig.2c: freshwater crocodile *Crocodylus johnsoni*, Tucker, 1997), concave-up (Fig.1d; Fig.2d St. John's Wort *Hypericum cumulicola*, Quintana-Ascencio, Menges & Weekley, 2003) and hump-shaped (Fig.1e; Fig.2e Mute swan *Cygnus olor*, Jones *et al.*, 2008) curves, giving shape values of corresponding negative magnitude (Table 1). Figs. 1f-h and 2f-h show varying extremities of senescence for concave-down (Fig.1f; Fig.2f Mediterranean fruit fly *Ceratitis capitata*, Carey *et al.*, 1998;), concave-up (Fig.1g; Fig.2g nematode worm *Caenorhabditis elegans*, Chen *et al.*, 2007) and hump-shaped (Fig.1h; Fig.2h guppy *Poecilia reticulata*, Reznick, Bryant & Holmes, 2006) curves giving shape values of corresponding positive magnitude (Table 1). It is easy to see how for the real organisms, mature longevity is adjusted by shape to yield the correct pace (Table 1).

Discussion

Population dynamics and life history evolution hinge on both survival *and* reproduction. The focus *only* on mortality of the original pace-shape framework and comparative analyses that use it (Promislow, 1991; Abrams, 1993; Reznick, Bryant & Holmes 2005; Gorbunova, Bozzella & Seluanov 2008; Monaghan, Charmantier, Nussey, & Ricklefs 2008; Nussey, Froy, Lemaitre, Gail- lard, & Austad 2013; Jones & Vaupel 2017), is a story half-told: both are important to the evolution of senescence.

Interpreting our method

Our shift of perspective from the mother to the baby means the problem of defining pace and shape of reproduction becomes more tractable and comparable, in some senses, to survival curves but with different interpretation.

Our pace and shape measures satisfy a key property of survival pace-shape measures, which is that pace and shape are orthogonal to one another. It seems immediately intuitive that pace and shape of fertility are related, given the latter (eq. 2) appears in the equation for the former (eq. 8). *Within* a single fertility curve, shape determines pace relative to the maximum reproductive longevity τ : they are linked. However *between* different fertility curves, pace and shape are not analytically related: any τ may be combined with any S , therefore any P may result from any S .

Our measure of the shape of reproductive aging fits most properties previously defined as important for the shape of mortality (Wrycza, Missov, Baudisch 2015). First, shape measures should be dimensionless. Standardisation of *both* time and total offspring produced means that our measure is dimensionless: standardised time and standardised offspring number are unitless, and range from 0 to 1 for every fertility trajectory. Second, the same shape value should result from any two fertility trajectories with different pace but the same distribution of reproduction over age. Since we standardise each fertility function in the same ways, this is the case. Third, the threshold between senescence and negative senescence should show a clear boundary value, intuitively chosen to be zero, above which senescence is observed and below which negative senescence is observed. Under our definition here that senescence and negative senescence are a relative balance of more reproduction at younger and older ages respectively, our measure

satisfies this third condition. We recognise however that for non-monotonous trajectories this could include elements of both senescence and negative senescence at different ages, and we discuss below how to tease these different processes apart. Fourth, shape values for patterns at the upper and lower extremes should approach respectively the maximum and the minimum shape value. Since $B(x)$ must start at 0 and increase monotonically to B , shape can approach but never reach the limits of 0.5 and -0.5, which would require $B(x)$ to start at B or end at 0, respectively. A biological interpretation of $S = 0.5$ would be a life cycle where all mothers mature at exactly the same age and all offspring are born exactly upon reaching maturity, and $S = -0.5$ would mean a life cycle where all mothers die at the exact same age and all offspring are born exactly at death. One can see then from both a biological and mathematical perspective, why these extremes are theoretical. Extreme senescence of $S = 0.5$ is unlikely: there is little evolutionary benefit to surviving once lifetime reproduction is achieved. This is evident in the scarcity of species with post-reproductive lifespans. Extreme negative senescence is often seen in nature in the form of semelparity: at the population level, few individuals may reproduce at young ages whilst most individuals reproduce at similar older ages, which gives a sharp concave-up $B(x)$ function. Incidentally, our measure is different from survival shape measures in actually defining a bound on this negative senescence: $S = -0.5$.

Our equations uncover a possible third dimension of aging that should be incorporated into the pace-shape fertility framework. Whilst the total 'amount' of survival is always the same, starting with 100% alive and ending with 100% dead, the total 'amount' of reproduction B varies between individuals, populations and species. Ecologists and evolutionary biologists have long been using lifetime reproduction to understand aging and evolutionary trade-offs (e.g. Wheelwright & Logan 2004; Ricklefs & Cadena 2007; Berger *et al.* 2015). It is recommended to analyse survival and reproduction trajectories only after onset of maturity, given evolutionary theories of senescence only kick in upon maturity. This approach ignores juvenile mortality, which is a measure of offspring quality and is often inversely related to number of offspring produced. Because of this, number of offspring is not necessarily a good measure of reproductive investment between species. On the one hand, our measures may help in this case by normalising by the number of offspring. On the other hand, we may be remiss in normalising total offspring number, if number and quality of offspring are expected to be a good measure of reproductive investment, especially within species. The nature of demographic data is also important: fer-

tility may be measured at the level of the individual or the population and it would not be pertinent for example to compare total population offspring (i.e. the sum of $m(x)$) between populations with different numbers of individuals. In such a case, average number of offspring per individual should be calculated. Data collection is important: if censuses are performed immediately prior to reproductive events, data include juvenile mortality therefore B is not equal to offspring number but could reflect reproductive investment better if lower-quality offspring are more likely to die in early life. In such cases, different interpretations and conclusions may need to be drawn when compared to post-breeding census data, especially if juvenile mortality is dependent on the age of the parent(s).

Comparisons to methods for pace and shape of survival

Given parallels between pace-shape of reproduction and of survival, existing pace-shape methods for survival are naturally related to pace-shape of fertility, but different perspectives and interpretations mean they may not be so easily applicable.

Some existing methods concerning pace of survival are directly applicable to reproduction. Our pace of reproduction measure is equivalent to life expectancy if we understand that 'survival' is remaining in the pool of offspring yet to be born, and 'death' is being born. 'Longevity' is maximum time to wait to be born, i.e. reproductive longevity.

Existing survival shape methods could perhaps be used for reproduction. Rearranging eq. 8 we find:

$$S = 0.5 - \frac{P}{\tau} \quad (9)$$

This structure contrasts the ratio between expected time to birth (P) and potential maximum time to birth (τ) with the same ratio for constant reproduction (0.5). The same structure is predominant in several survival shape measures evaluated by Wrycza, Missov, & Baudisch (2015), contrasting the constant case with the actual case, such as the ratio of remaining life expectancy at some age against life expectancy (their Measure 4), the ratio of remaining life expectancy lost due to death against life expectancy (their Measure 5, based on Keyfitz's Entropy), or the ratio of standard deviation against life expectancy (their Measure 6).

Non-monotonous mortality trajectories posed a challenge to previous survival shape measures (Wrycza, Missov, Baudisch 2015), because e.g. u-shaped mortality patterns could lead to shape

values that indicated negative senescence and falsely classified declining and u-shaped patterns in the same category. Our measures outline a solution: though our method will yield the same shape values for many different reproduction patterns (Fig.1a,b; 2a,b), it is possible to explore and evaluate the shape of these different patterns by looking at partial reproduction curves³, such as up until versus after age at maximum fertility. Truly flat fertility patterns should retain their partial shape values close to zero, while hump or u-shaped patterns should show values different from zero over part of their range. When $S \approx 0$, inferences about senescence cannot really be made unless multiple partial values covering the whole fertility function are considered: increases or decreases for any single part mean little in the absence of knowledge of preceding or anteceding levels of reproduction.

Comparative demographic analyses

Our method opens the door for 1) comparative research on fertility senescence, and 2) comparative research on ecological and evolutionary dynamics capturing interactions between both birth and death patterns, across populations or species.

Existing comparative research has often focussed on individual components of reproduction such as age at maturity, iteroparity or clutch/litter size (e.g. Promislov & Harvey 1990), which constitute elements of pace-shape trajectories. Our measurements are in a sense functions of these elements: pace is governed by age at maturity and maximum longevity, and modulated by shape which is influenced both by iteroparity and seed number, clutch size or litter size, among other elements.

At the other end of the scale are comparative analyses using mathematical means to combine demographic elements into single measurements describing the whole life cycle. Generation time measures the pace of renewal in a population, hinging on both survival and reproduction and is generally considered a proxy for organisms' position on the fast-slow continuum (Gaillard *et al.* 2005). The pace and shape measures we suggest aim to separate survival from reproduction and to separate orthogonal components of both, to the extent that is possible. This decomposition hopefully facilitates a clearer view on trade offs within and between survival and reproduction, and complements mathematical approaches to combining them.

³Gini coefficient as measure of survival shape can also be calculated over partial age ranges (Shkolnikov, Andreev, Begun 2003), but has not been applied to classify non-monotonous survival shape up to now.

Statistical decomposition of multiple demographic measures, which define emergent orthogonal axes of life history, are becoming increasingly common in comparative demographic analysis. This takes an informatics-based approach, informed by many correlated demographic quantities (e.g. life expectancy, generation time, reproductive value, population growth rates), combined with statistical methods such as principal component analysis (Salguero-Gomez 2016; Paniw, Ozgul & Salguero-Gómez 2017) or factor analysis (Bielby *et al.* 2007), to give emergent life-history properties. Resulting measures are inherently combinations of survival and fertility (provided of course both were included in the initial data), and often indicate a primary axis describing some sort of fast-slow continuum, and a secondary axis describing iteroparity. The degree to which these axes explain the data depends on the organisms: less variance is explained in plants (Salguero-Gómez 2017) compared to mammals (Bielby *et al.* 2007). Our aims are similar in seeking to find orthogonal components of life history traits, but the approach and applications differ. For pace-shape, we aim to measure specific, identified properties of single demographic trajectories which can be calculated for single populations. Statistical decomposition methods on the other hand measure holistic and emergent information from whole life histories and can only be calculated using data from many populations.

Pace and shape of fertility describe properties of the whole reproductive age trajectory in a way that others cannot; yet they are orthogonal measurements, which means that they can be used to explore patterns, relationships and trade-offs between the duration and spread of reproductive effort. This orthogonality means that observed patterns must be a result of constraints imposed by, or relationships to, heritage or the environment. Relationships between pace and shape could differ in their mean and variance between different clades, or at different phylogenetic levels, such as the tight relationships observed in humans (Colchero *et al.*, 2016) versus the looser relationships observed in angiosperms (Baudisch, 2013). Fig.3 shows empirical support, in the case of a few examples, for the theoretical assertion that pace and shape of fertility are orthogonal across diverse multicellular species. Combining pace and shape of survival with pace and shape of fertility opens new avenues of research. There is no mathematical reason for relationships between the pace and shape of fertility, and the pace and shape of survival. All four measurements together may be used to understand patterns, relationships and trade-offs between the duration of life and reproductive life, and the spread of mortality and fertility across the life course.

Statistical rigour should be observed when conducting comparative analysis of our pace and shape measures. Across species, our pace measure is likely to follow a log-normal distribution as it is real and bounded at 0 and ∞ ; it is probably pertinent to log-transform pace prior to analysis, or if pace is the response variable, to use gamma regression. Our shape measure is bounded at -0.5 and 0.5, which presents a unique analysis problem as fitted parameters and residual error should not estimate values outside this range. The best solution is perhaps to add 0.5 to all values so that shape is bounded at 0 and 1, then it is appropriate to logit-transform shape so it is described on a more continuous scale, or when shape is the response variable, to use beta regression.

Application of our method

Demographic knowledge is fragmented across the tree of life, and application of our method will differ among species. Recent research analysing a metadatabase of 22 published demographic databases (Conde, Staerk, Colchero, da Silva, Schöley, *et al.*, 2019) showed that amongst the tetrapods, fertility data is more freely available for birds and reptiles, whilst among the mammals we generally know more about survival. That said, the few tetrapod fertility schedules there are (for just 1.3% of tetrapod species) were always found in combination with survival schedules, so it appears that for existing data our methods will mainly be useful for supplementing analyses of survival. Naturally, the wealth of survival and fertility schedules available for humans (www.humanfertility.org) means that our methods can be used to extend knowledge of human demographic aging beyond survival.

Similar assessment of plant demographic information has not yet been attempted, but certainly given their sessile nature, a great deal more full demographic models of plants exist (Salguero-Gómez *et al.* 2015) than for animals (Salguero-Gómez *et al.* 2016). Given some plants (trees) live so long, period fertility data may be easier to collect than survival data: in this case, our methods may be useful for analysing demographic aging in species where it would otherwise not be possible.

A distinct advantage in studying the shape of fertility is that shape can in principle not only be calculated for populations, but also over the life course of an individual. Every individual (mother, at least) has their own lifetime reproductive trajectory; in contrast to survival, where

every individual only dies once. Using our methods it may be possible to compare reproductive aging between individuals and explore patterns of heterogeneity contributing to average aging trajectories and their variance within populations. This is a unique approach: measures of aging usually hinge on population-level data and so understanding variation in aging requires comparing between populations.

Variation in survivorship and fertility schedules is perhaps something that is not addressed often enough, and this certainly could affect calculation of pace and shape values. Given confidence limits on $m(x)$, or indeed $l(x)$, it would be possible to calculate resulting variation in pace and shape. For example, smaller sample sizes at older age mean that variance in reproductive schedules is likely to increase with age. This problem could affect reproductive pace and shape: negatively senescent life histories are likely to be more susceptible as high levels of reproduction occur later in life, whereas for senescent life histories most reproduction has happened before old age.

Use of the methods with survival and other proxies of aging

The methods presented here can be 'ported' almost directly across to analyses of survival, and we present derivations for this in Appendix A2. But demographic measures of aging (mortality and fertility) are not the only proxies of change in organismal "performance". Life history variables at the individual level including anatomy (e.g. body mass), physiology (e.g. metabolic rate), behaviour (e.g. mating attempts), or ontogeny (e.g. growth rate) could be considered proxies of aging. Our framework of comparing actual age patterns in a variable with benchmark "null" trajectories could in theory be used to underpin methods describing pace and shape for any aging proxy, provided reasonable benchmark and boundary conditions can be described, and solid interpretation of the outcomes exist.

Applying the pace-shape framework to both survival and fertility opens new doors into understanding interactions, covariation and trade-offs between the four dimensions of pace and shape of both survival and fertility. This, and the potential development of pace-shape methods for other life history measures, could help uncover new understanding in patterns and processes of aging across the tree of life.

Conclusions

Comparative biology, life history biology and evolutionary theories of senescence offer many insights about general patterns and relationships between survival and reproduction, yet much remains to be explained. For example, a typology of aging is missing: why do humans age like humans, birds like birds, and fish like fish? What type of physiology or environment relates to what kind of aging, and why? How do survival and reproduction link within and across populations or species? As aging seems to root in tradeoffs between survival and reproduction (Baudisch and Vaupel 2012), much could be gained from a combined pace shape mortality fertility approach in comparative studies: the methods presented here facilitate just such an approach.

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Authors' Contributions

AB and IS conceived the ideas; AB developed the methodology and further revised it with IS; IS prepared the examples, code and figures; AB wrote the initial draft; AB and IS wrote the manuscript. All authors contributed critically and gave final approval for publication.

Data Availability

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.cs5786r>

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Table 1: Pace-Shape parameters for curves shown in Figures 1 and 2. Pace is the measure described in equation 8, shape is the measure described in equation 5, and both are accurate to 3 decimal places. α is the age at maturity and β is the maximum age, which for all species is the same as ω the maximum longevity, all accurate to the nearest unit. Abbreviations: y, years; m, months; d, days.

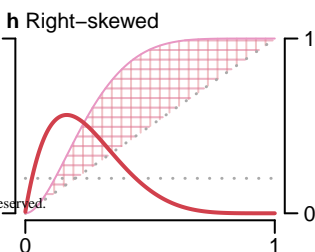
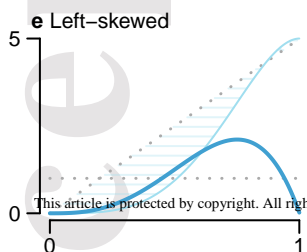
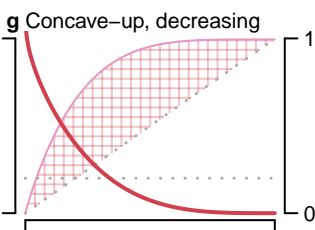
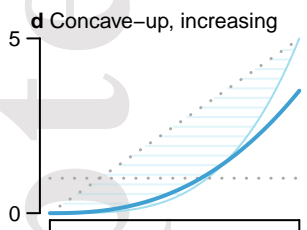
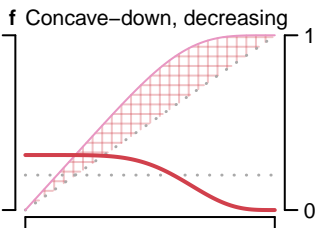
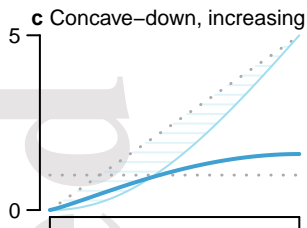
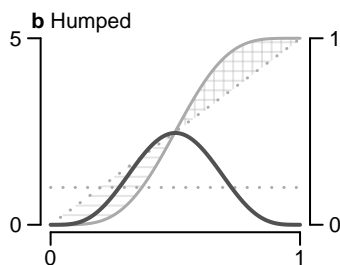
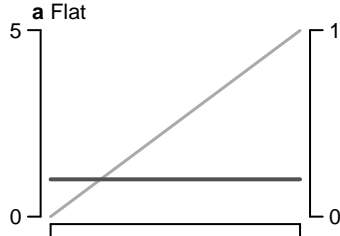
Figure	Species	Pace	Shape	α	β
1a	Flat	0.500	0.000	0	1
1b	Humped	0.500	0.000	0	1
1c	Concave-down, increasing	0.643	-0.143	0	1
1d	Concave-up, increasing	0.778	-0.278	0	1
1e	Left-skewed	0.667	-0.167	0	1
1f	Concave-down, decreasing	0.334	0.167	0	1
1g	Concave-up, decreasing	0.175	0.325	0	1
1h	Right-skewed	0.250	0.250	0	1
2a	Rhododendron, <i>Rhododendron maximum</i>	4.774y	-0.030	5y	14y
2b	Chamois, <i>Rupicapra rupicapra</i>	4.047y	-0.007	1y	9y
2c	Freshwater crocodile, <i>Crocodylus johnsoni</i>	17.329y	-0.126	12y	40y
2d	St. John's Wort, <i>Hypericum cumulicola</i>	3.632y	-0.317	0y	4y
2e	Mute swan, <i>Cygnus olor</i>	7.730y	-0.068	2y	16y
2f	Mediterranean fruit fly, <i>Ceratitis capitata</i>	23.499d	0.110	3d	63d
2g	Nematode worm, <i>Caenorhabditis elegans</i>	2.171d	0.394	4d	25d
2h	Guppy, <i>Poecilia reticulata</i>	14.530m	0.092	2m	38m

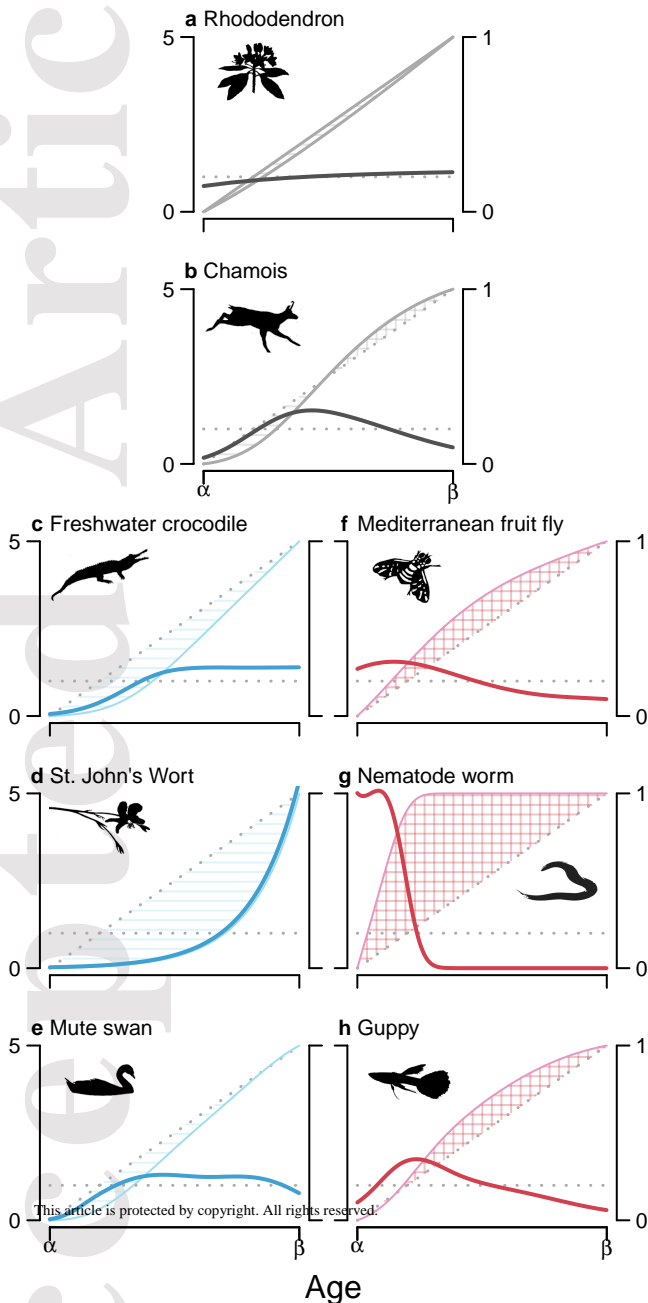
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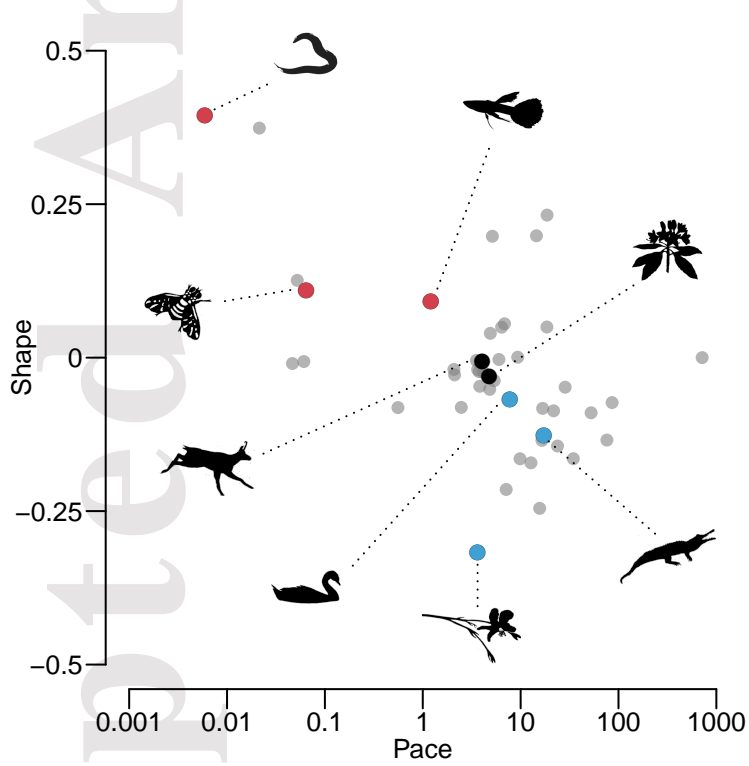
Figure 1 Theoretical examples of eight possible fertility functions. Corresponding shape and pace values for each panel are shown in Table 1. Thick lines represent $m(x)$ functions and thin lines represent $B(x)$ functions. Dotted lines represent benchmark cases of constant reproduction (standardised fertility = 1) and its cumulative counterpart. Shading represents shape value, with positive areas above the $B(x)$ curve and negative areas below. Distributions which are symmetrical about $\tau/2$ (panels a, b), which is equal to 0.5 in the case of standardised fertility, have shape close to zero (negligible senescence). Reproduction loaded towards later life results in negative shape, which indicates negative senescence (in blue; panels c, d, e). Reproduction loaded towards earlier life results in positive shape, which indicates senescence (in red; panels f, g, h).

Figure 2 Empirical examples of diverse reproductive strategies in nature, corresponding loosely to the theoretical examples of Figure 1. Thick lines represent $m(x)$ functions and thin lines represent $B(x)$ functions. Dotted lines represent benchmark cases of constant reproduction (standardised fertility = 1) and its cumulative counterpart. Shading represents shape value, with positive areas above the $B(x)$ curve and negative areas below. **a** *Rhododendron maximum*; **b** *Rupicapra rupicapra*; **c** *Crocodylus johnsoni*; **d** *Hypericum cumulicola*; **e** *Cygnus olor*; **f** *Ceratitis capitata*; **g** *Caenorhabditis elegans*; **h** *Poecilia reticulata*. Corresponding shape, pace, α and β values for each species are shown in Table 1. Reproductive strategies range from negative senescence (panels c, d, e) through negligible senescence (panels a, b) to senescence (panels f, g, h).

Figure 3 Fertility pace-shape space for 46 multicellular species featuring in Jones *et al.* 2014. Example species from Figure 2 are shown with large points and labeled using the corresponding silhouette. Pace is shown on a log scale.







Appendix

A1. Adjustments to accommodate discrete data

We presented our method and examples in continuous time, but demographic data is usually collected on a discrete-time basis, forming 'life tables'. Lifetable functions can be defined either *within* an age interval, such as age-specific mortality, probability of surviving or dying during an age class, or *up to* exact age x , such as survivorship up to age x . In our fertility scenario, the *within* and *up to* types of function are respectively represented by age-specific fertility $m(x)$, which happens during the age interval x to $x + n$, where n denotes the length of an age class, and by cumulative reproduction $B(x)$, which happens up to exact age x . This implies for both mortality and fertility that we need k age classes, but $k + 1$ exact ages in order to define an age-range that is closed at both ends.

In lifetables, the initial age group starts from zero, and initial survivorship is defined as 100% at exact age zero. The last age group is also defined by its lower bound, but is left open to the top. The remaining death counts within that open interval are included in the cumulative death counts by assuming an average remaining lifetime common to those individuals.

For fertility, we require for cumulative reproduction that $B(\alpha) = 0$, and $B = B(\beta)$. Since reproduction happens within age classes, first age-specific reproduction $m(\alpha)$ happens within the initial adult age class α to $\alpha + n$, and last reproduction $m(\beta - n)$ happens within the age-interval $\beta - n$ to β . Therefore

$$B(x) = \begin{cases} 0 & \text{if } x = \alpha \\ \sum_{t=\alpha}^{x-n} m(t) & \text{otherwise.} \end{cases} \quad (1)$$

For $x = \beta$, the sum includes all reproduction until age $\beta - n$. In the data it has to be ensured then that indeed $m(\beta - n)$ corresponds to the final age class where reproduction exceeds zero.

This note of caution is important because, typically, data end at the age of last non-zero reproduction, as most species do not have a postreproductive lifespan. Here problems arise because the age range includes only k instead of $k + 1$ age groups. Then a pseudo age-group has to be added to properly define β as the age when all reproduction has been completed. Otherwise, reproduction in the last age class is not counted.

Again, analagous to closing the lifetable for the final survivors that die within the last open-

ended age-interval, we must make assumptions about how to close the cumulative birth function for offspring experiencing the event of birth during the final age interval.

If passed any $m(x)$ data with a final value other than NA, our R functions thus assume that (for k age classes) the age of reproductive cessation equals the age at last reproduction plus the difference between the final two reproductive ages, $\beta = x(k) + x(k) - x(k - 1)$.

Once we have defined β and calculated $B(x)$, we find for shape that

$$S = \frac{1}{\tau B} \left(\sum_{x=\alpha}^{\beta} B(x) - \frac{\tau B}{2} \right). \quad (2)$$

and for pace that

$$P = \tau (0.5 - S). \quad (3)$$

As an example, given an age vector of $x = [1,2,3,4,5]$ and an associated age-specific reproduction schedule of $m(x) [0,1,3,4,2]$, we define age of maturity $\alpha = 2$ and consequently $B(2) = 0$, $B(3) = 1$, ..., $B(5) = 8$. $B(5) \neq B$, as $m(5) > 0$. The last two offspring are born at age $5 < x < \beta$. We may assume that the life table has not been fully completed and that $\beta = 6$, or we may know that is the case. Then, x becomes $[1,2,3,4,5,6]$ and $m(x)$ becomes $[0,1,3,4,2,NA]$. Thus we can complete $B(x)$: $[0,0,1,4,8,10]$.

A2. Extension of the method to mortality trajectories

Let $\mu(x)$ denote the age-specific mortality function that captures the average hazard of death of an individual at age x . Function $H(x)$ defines the cumulative hazard up to age x as

$$H(x) = \int_{\alpha}^x \mu(t) dt. \quad (4)$$

In line with the framework presented in this paper, we consider the hazard over reproductive ages, that is beginning at age α . Note that $H(x)$ corresponds to the logarithmic transformation of the survivorship function, i.e. $H(x) = -\ln l(x)$, where $l(x)$ captures the fraction of individuals that survive from initial age (here defined as α) up to age x .

Constant age-specific mortality represents the benchmark case and corresponds to a linearly increasing cumulative hazard function $H(x)$. Analogous to fertility, it forms a triangular shape in the x - $H(x)$ -space with an area calculated as the halfened product of its edges: adult lifespan

($\tau \equiv \omega - \alpha$) times maximum cumulative hazard at the final age, $H \equiv H(\omega)$, divided by two, which gives $\tau H/2$. Here, ω denotes maximum age, which can be defined as the age until which less than a small fraction (e.g. 1%) of adults will survive.

Analog to the fertility case, the difference of the area under the $H(x)$ curve to the benchmark area $\tau H/2$ indicates, whether the actual mortality pattern follows a predominantly increasing or decreasing pattern over age. Standardising for adult lifespan, the *shape of mortality* is given by an equivalent expression as

$$S = \frac{1}{\tau} \left(\frac{\tau H}{2} - \int_{\alpha}^{\omega} H(x) dx \right). \quad (5)$$

Compared to the shape of fertility, we reversed the order of terms in the shape expression for mortality to remain consistence with the logic of positive/negative senescence being associated with positive/negative shape values: positive senescence is associated with worsening and corresponds to a decrease in fertility, but an increase in mortality; negative senescence is associated with improvement and corresponds to an increase in fertility, but a decrease in mortality.

$S > 0$ Positive (mortality) senescence,

$S = 0$ Nil (mortality) senescence,

$S < 0$ Negative (mortality) senescence.

As for fertility, shape values of mortality here range within the interval $-0.5 < S < 0.5$.

A3. Comparison to the Gini coefficient

How different is this new shape measure of mortality to the Gini coefficient, a main candidate for measuring survival shape? Even though the logic of a diagonal benchmark reminds of the Gini coefficient, the shape measure suggested here differs in important aspects. First, the Gini coefficient for survival is calculated based on a population that is rank-ordered by increasing lifespan (Shkolnikov, Andreev, Begun, 2003), similar to the original Gini coefficient being calculated based on a rank-ordered population of increasing income (Gini, 1921). Consequently, the cumulative lifespan/income curves of the Gini coefficient always fall below the benchmark, which in economics is known as the Lorentz curve (Lorenz, 1905). In contrast, our measures depict cumulative curves of reproduction (or mortality) over age, and age-specific cumulative

curves may cross the benchmark at any point. This allows for an intuitive understanding of positive and negative areas of senescence balancing each other over the life cycle. Second, Gini is calculated based on a ratio of the difference between the benchmark and the cumulative curve to the total area of the triangle. Our measure simply calculates the difference between the benchmark and the cumulative curve. Still, our measure will be closely linked to Gini as well as other measures of mortality shape.

The main advantage of suggesting this new shape measure of mortality here is its direct comparability to the shape measure of fertility, which allows measuring the processes of birth and death with similar tools.

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