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A pace and shape perspective on fertility

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Abstract

1. Ageing is ubiquitous to all organisms, but ageing does not always mean senescence. Counter to most evolutionary theories of ageing, the 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 ageing 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 life span.

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 visualized 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 ageing which were never possible before.

KEYWORDS
ageing, demography, fertility, life history, life tables, pace, senescence, shape

1 | INTRODUCTION

People have questioned why we age since perhaps we began to reflect on our finitude. Evolutionary theories of ageing 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 trade-offs 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 (Baudisch, 2005, 2008; Baudisch & Vaupel, 2012; Vaupel, Baudisch, Dölling, Roach,

& Gampe, 2004; 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: ageing is not in fact synonymous with senescence. As well as senescence, the diversity of ageing 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). Ageing, 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 ageing patterns, whether senescence, negligible senescence or negative senescence, evolve independently of life span, whether this constitutes days, years or centuries (Baudisch, 2008; Wensink, Wrycza, & Baudisch, 2014). That is, changes in parameters that affect the length of life span, and more generally the time-scale of a life history, should not have any specific association with ageing patterns. A clear view of the factors that determine ageing patterns hence requires factoring out time. To that end, Baudisch (2011) developed the pace–shape perspective.

1.1 | 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 ageing 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 ageing 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' entropy (Originally, 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) or the coefficient of variation describe the shape of mortality (Wrycza, Missov, & Baudisch, 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 ageing as occupying some place in a two-dimensional pace–shape space.

The pace–shape perspective has proven useful in comparative ageing studies (Baudisch et al., 2013; Jones et al., 2014; Colchero et al., 2016; Archer et al., 2018; Németh, 2017; Barks, Dempsey, Burg,

& Laird, 2018; Overall & Faragher, 2019). Jones et al. (2014) find a remarkable diversity of ageing 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 life span equality. This suggests some evolutionary and/or mechanistic constraint on human senescence: the longer the life course, the 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, life spans. Archer et al. (2018) find that dietary composition affects ageing 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.

1.2 | 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 et al., 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. Booth, 1984; Brass, 1975), which are 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. (Whilst 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 generalizable enough for the method to be cogent in many scenarios.) 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, whilst 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, analogous 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, analogous to a type-I survival curve. A species with reproduction concentrated towards the end of life and increasing on average with age (negative reproductive senescence) has a concave-up reproduction function, analogous 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.

2 | METHODS AND METHODS

Let $m(x)$ denotes 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:

$$B(x) = \int_{\alpha}^{x} m(t)\mathrm{d}t. \tag{1}$$

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 et al., 2001]). For brevity, we denote $B = B(\beta)$ to capture total cumulative reproduction and $\tau = (\beta - \alpha)$ to capture reproductive life span. 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 generalize to discrete data, and we further discuss small adjustments to the method pertaining to discrete data in Appendix A1.

2.1 | 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 $m(x)$ (Figure 1a). The corresponding cumulative reproduction curve $B(x)$ rises linearly and forms a triangular shape in the x–$B(x)$-space (Figure 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 (Figure 1f,g), or for non-monotonic reproductive schedules lie mostly above (Figure 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 (Figure 1c,d), or for non-monotonic reproductive schedules lie mostly below (Figure 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 $\alpha + \tau/2$ (Figure 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 et al., 2015), yet differs in important aspects (see Appendix A3). To facilitate comparisons across species, the difference is standardized by both fertility and reproductive life span. It follows that

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

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 life spans and reproductive outputs mean that between species, these areas may differ considerably in magnitude. Compare for example a conifer tree with a life span 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 $1/\tau B$ standardizes the difference between the two terms.

$S > 0$ is positive reproductive senescence,

$S = 0$ is nil reproductive senescence and

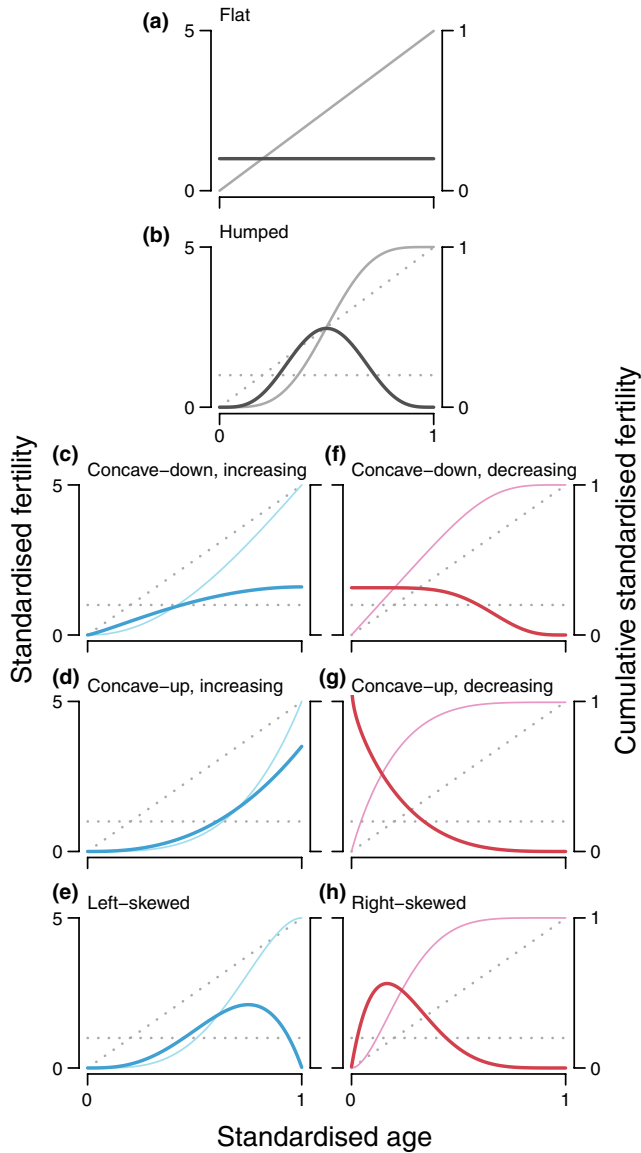$S < 0$ is negative reproductive senescence.

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 (standardized 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 standardized 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)

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 standardization 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.

Standardization 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 standardized age and standardized cumulative reproduction:

$$\hat{x} = \frac{x - \alpha}{\tau} \tag{3}$$

and

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

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 life span and $\hat{B}$ captures the proportion of total lifetime offspring. Based on standardized quantities, the shape of fertility can then be found using

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

Standardizing 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 $\alpha \le a$, $a < b$, and $b \le \beta$. These partial fertility functions may not start with $a = \alpha$, that is, $B(a) = 0$, and/or may not end with $b = \beta$, that is, $B(b) = B$. 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 $\hat{B}(b) = 1$.

2.2 | 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:

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

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

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

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 life span τ and reveals how pace relates to shape:

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

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 three 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

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, *Rhododendron maximum*	4.774 y	−0.030	5 y	14 y
2b	Chamois, *Rupicapra rupicapra*	4.047 y	−0.007	1 y	9 y
2c	Freshwater crocodile, *Crocodylus johnsoni*	17.329 y	−0.126	12 y	40 y
2d	St. John's Wort, *Hypericum cumulicola*	3.632 y	−0.317	0 y	4 y
2e	Mute swan, *Cygnus olor*	7.730 y	−0.068	2 y	16 y
2f	Mediterranean fruit fly, *Ceratitis capitata*	23.499 d	0.110	3 d	63 d
2g	Nematode worm, *Caenorhabditis elegans*	2.171 d	0.394	4 d	25 d
2h	Guppy, *Poecilia reticulata*	14.530 m	0.092	2 m	38 m

Abbreviations: y, years; m, months; d, days.

Pace *P* can take any value of a fraction of total reproductive life span 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 life span 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. Shape *S* determines whether the majority of offspring are born earlier or later in life only relative to the total reproductive life span τ. The fact that *S* is a constituent part of the formula for *P* has no effect on the actual value of reproductive life span, be it months or centuries, since *S* need not have any relationship with τ; it merely scales it when finding *P*.

3 | 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 life span 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 life spans and environments, illustrated in Figure 2 with corresponding shape, pace, age at maturity and maximum longevity values also in Table 1.

Figures 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). Figures 1b and 2b (*Rupicapra rupicapra*; Caughley, 1970) show a hump-shaped reproductive curve. Although reproduction changes with age, the overall balance remains even and shape is still close to zero (Table 1). Figures 1c–e and 1,2c–e show varying extremities of negative senescence for concave-down (Figures 1c and 2c: freshwater crocodile *Crocodylus johnsoni*, Tucker, 1997), concave-up (Figures 1d and 2d; St. John's Wort *Hypericum cumulicola*, Quintana-Ascencio, Menges, & Weekley, 2003) and hump-shaped (Figures 1e and 2e; Mute swan *Cygnus olor*, Jones et al., 2008) curves, giving shape values of corresponding negative magnitude (Table 1). Figures 1f–h and 1,2f–h show varying extremities of senescence for concave-down (Figures 1f and 2f; Mediterranean fruit fly *Ceratitis capitata*, Carey, Liedo, Müller, Wang, & Chiou, 1998), concave-up (Figures 1g and 2g; nematode worm *Caenorhabditis elegans*, Chen et al., 2007) and hump-shaped (Figures 1h and 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).
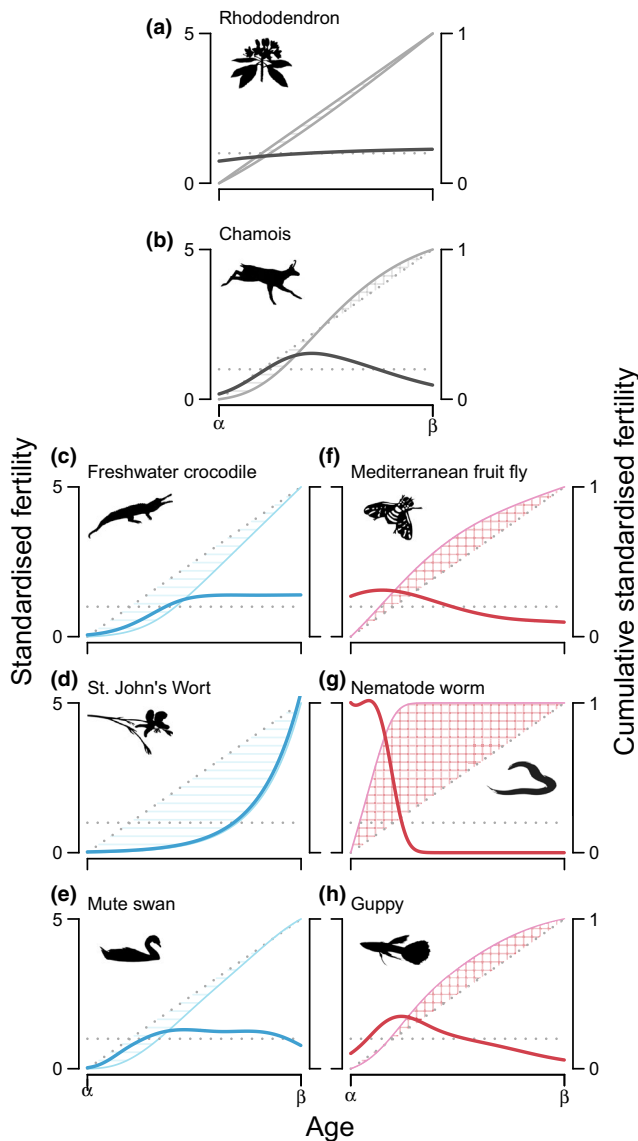
FIGURE 2 Empirical examples of diverse reproductive strategies in nature, corresponding loosely to the theoretical examples of Figure 1. Thick lines represent $m(x)$ functions and thin lines represent $B(x)$ functions. Dotted lines represent benchmark cases of constant reproduction (standardized fertility = 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)

4 | 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 (Abrams, 1993; Gorbunova, Bozzella, & Seluanov, 2008; Jones &

Vaupel, 2017; Monaghan, Charmantier, Nussey, & Ricklefs, 2008; Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013; Promislow, 1991; Reznick, Bryant, & Holmes, 2006), is a story half-told: both are important to the evolution of senescence.

4.1 | 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 (Equation 2) appears in the equation for the former (Equation 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 ageing fits most properties previously defined as important for the shape of mortality (Wrycza et al., 2015). First, shape measures should be dimensionless. Standardization of *both* time and total offspring produced means that our measure is dimensionless: standardized time and standardized 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 standardize 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. However, we recognize 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 life spans. 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 ageing 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 ageing and evolutionary trade-offs (e.g. Berger, Lemaître, Gaillard, & Cohas, 2015; Ricklefs & Cadena, 2007; Wheelwright & Logan, 2004). 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 normalizing by the number of offspring. On the other hand, we may be remiss in normalizing 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: fertility 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).

4.2 | 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, that is, reproductive longevity.

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

$$S = 0.5 - \frac{P}{\tau}. \tag{9}$$

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 et al. (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' 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 et al., 2015), because, for example, 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 (Figures 1a,b and 2a,b), it is possible to explore and evaluate the shape of these different patterns by looking at partial reproduction curves, (Gini 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.) such as up until versus after age at maximum fertility. Truly flat fertility patterns should retain their partial shape values close to zero, whilst 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.

4.3 | Comparative demographic analyses

Our method opens the door for (a) comparative research on fertility senescence, and (b) 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. Promislow & 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.

Statistical decomposition of multiple demographic measures, which define emergent orthogonal axes of life history, is 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-Gómez et al., 2015; 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 et al. 2016) 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 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, heritance 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). Figure 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
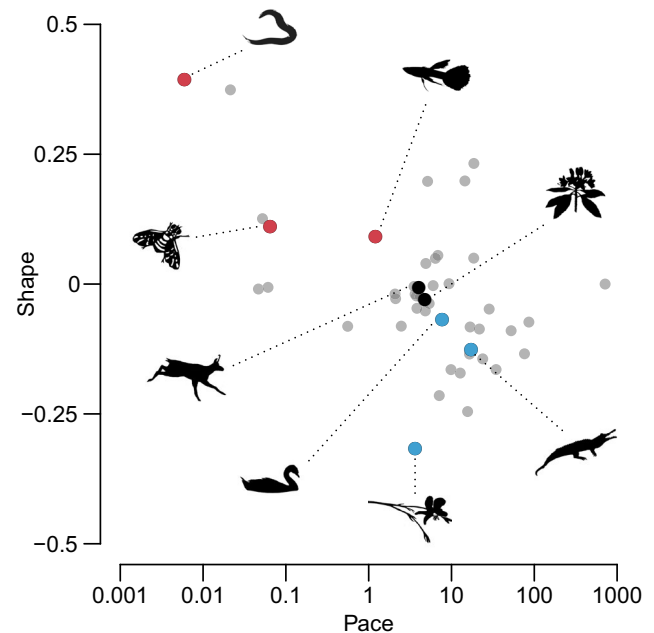

FIGURE 3 Fertility pace–shape space for 46 multicellular species featuring in Jones et al. (2014). Example species from Figure 2 are shown with large points and labelled using the corresponding silhouette. Pace is shown on a log scale

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.

4.4 | 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 et al., 2019) showed that among the tetrapods, fertility data are 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.humanferti

lity.org) mean that our methods can be used to extend knowledge of human demographic ageing 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, Jones, Archer, et al., 2016; Salguero-Gómez, Jones, Jongejans, 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 ageing 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 ageing between individuals and explore patterns of heterogeneity contributing to average ageing trajectories and their variance within populations. This is a unique approach: measures of ageing usually hinge on population-level data and so understanding variation in ageing 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.

4.5 | Use of the methods with survival and other proxies of ageing

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 ageing (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 ageing. 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 ageing 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 ageing across the tree of life.

4.6 | 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 ageing 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 ageing, and why? How do survival and reproduction link within and across populations or species? As ageing seems to root in trade-offs between survival and reproduction (Baudisch & 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.

AUTHORS' CONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

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

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