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2 **Diversity of ageing across the tree of life**

3 Owen R. Jones^{1,2,*§}, Alexander Scheuerlein^{3,*}, Roberto Salguero-Gómez^{3,4}, Carlo
4 Giovanni Camarda⁵, Ralf Schaible³, Brenda B. Casper⁶, Johan P. Dahlgren^{1,2}, Johan
5 Ehrlén⁷, María B. García⁸, Eric Menges⁹, Pedro F. Quintana-Ascencio¹⁰, Hal
6 Caswell^{2,3,11,12}, Annette Baudisch³, James W. Vaupel^{1,3,13}

7 ¹ Max-Planck Odense Center on the Biodemography of Aging, Odense, Denmark

8 ² Department of Biology, University of Southern Denmark, Odense, Denmark

9 ³ Max Planck Institute for Demographic Research, Rostock, Germany

10 ⁴ University of Queensland, Brisbane, Australia

11 ⁵ Institut National d'Etudes Démographiques, Paris, France

12 ⁶ University of Pennsylvania, Philadelphia PA, USA

13 ⁷ Department of Ecology, Environment and Plant Sciences, Stockholm University,
14 Stockholm, Sweden

15 ⁸ Pyrenean Institute of Ecology (CSIC), Zaragoza, Spain

16 ⁹ Archbold Biological Station, Venus FL, USA

17 ¹⁰ University of Central Florida, Orlando FL, USA

18 ¹¹ Woods Hole Oceanographic Institution, Woods Hole MA, USA

19 ¹² Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam,
20 Amsterdam, The Netherlands

21 ¹³ Duke Population Research Institute, Duke University, Durham NC, USA

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25

26 *These authors contributed equally to the manuscript.

27 § Corresponding author. E-mail: jones@biology.sdu.dk; Tel: +4565502791

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1 **Evolution drives and is driven by demography. A genotype moulds its**
2 **phenotype's age-patterns of mortality and fertility in an environment; these two**
3 **patterns in turn determine the genotype's fitness in that environment. Hence, to**
4 **understand the evolution of ageing, age-patterns of mortality and reproduction**
5 **need to be compared for species across the tree of life. Yet few studies have done**
6 **so and only for a limited range of taxa. Here we contrast standardised age-**
7 **patterns for 11 mammals, 12 other vertebrates, 10 invertebrates, 12 vascular**
8 **plants, and a green alga. While it has been predicted that evolution should**
9 **inevitably lead to increasing mortality and declining fertility with age after**
10 **maturity, these species exhibit extraordinary variety, including increasing,**
11 **constant, decreasing, humped and bowed trajectories for both long and short-**
12 **lived species. This diversity challenges theoreticians to develop broader**
13 **perspectives on the evolution of ageing and empiricists to study the demography**
14 **of more species.**

15 To examine demographic age trajectories across the tree of life, we studied life tables¹
16 and population projection matrices² for multicellular species from a wide range of
17 taxonomic groups (Fig. 1; see Supplementary Methods for data sources and further
18 rationale). We strived to find species with reliable data and from diverse taxa. From
19 the data for each species we estimated smoothed trajectories of fertility, mortality, and
20 survivorship over age. Further research will undoubtedly refine the curves shown for
21 many of the species in Fig. 1 and reveal variation in different environments and for
22 different genotypes, but the general patterns are, we believe, serviceably accurate.

23 We standardised the demographic trajectories to facilitate comparison.
24 Specifically we standardised the age axis so that it starts at the mean age of
25 reproductive maturity and ends at a terminal age when only 5% of adults are still

1 alive. After this terminal age, sample sizes were usually small and determination of
2 age was often problematic. Fertility and mortality were mean-standardised by dividing
3 age-specific fertility and mortality by the respective weighted average levels of
4 fertility and mortality for all adults alive from maturity to the terminal age (See
5 Methods Summary). We refer to these standardised values as relative fertility and
6 relative mortality. From the highest level of relative mortality at the terminal age (top
7 left, Fig. 1) to the lowest level (bottom right, Fig. 1), species are ordered sequentially,
8 row-by-row and from left-to-right. For the 46 diverse species depicted here, the range
9 of variation in trajectories of fertility and mortality is unexpected. As an indication of
10 variability across species, in modern Japanese women (upper left of Fig. 1), mortality
11 at the terminal age (102 years) is more than 20 times higher than the average level of
12 adult mortality, while for white mangrove (*Avicennia marina*, lower right of Fig. 1)
13 the level of mortality at 123 years is less than half the average adult value.

14 Such variability is not predicted by the standard evolutionary theories of
15 ageing^{1,3-6}. Such theories provide explanations solely for age patterns of increasing
16 mortality and decreasing fertility from maturity; the disposable soma theory⁶ does so
17 for species that segregate the germ line from the soma. Furthermore, for those species
18 that show a life-time increase in mortality, the canonical theory cannot account for the
19 different magnitudes of that increase, although the disposable soma theory points to
20 the crucial importance of trade-offs between the allocation of limited resources to
21 repair and maintenance vs. fertility and other imperatives.

22 The most striking pattern is the mortality trajectory for post-industrial humans,
23 exemplified by Japanese women in 2009. The steep rise in relative mortality for the
24 Japanese women is extreme even compared to historical populations such as the
25 Swedish cohort born in 1881 and to hunter-gatherers such as the Aché of Paraguay

1 whose mortality experience may be typical of humans over most of our existence^{1,2,7}.
2 The increased steepness of the rise of human mortality has largely occurred over the
3 past century, indicating that it was behavioural and environmental change (including
4 advances in health care) and not genetic change that moulded the current pattern^{2,7-9}.
5 Our close relatives, chimpanzees (*Pan troglodytes*) and baboons (*Papio*
6 *cynocephalus*) also show a rise in mortality with age but far less than that for hunter-
7 gatherers.

8 In several species mortality declines with age (Fig. 1, bottom row) and, in
9 some cases, notably for the desert tortoise (*Gopherus agassizii*), the decline persists
10 up to the terminal age. In other cases, an initial decline is followed by more or less
11 constant mortality (e.g. netleaf oak, *Quercus rugosa*). For species for which the
12 underlying data are based on stages, such as dwarf gorse (*Ulex minor*) or the red-
13 legged frog (*Rana aurora*), an asymptote is inevitable at older ages^{8,10}. To alert
14 readers to this, the mortality (and fertility and survival) curves derived from stage-
15 classified models are represented by dashed curves in Fig. 1 at ages beyond which a
16 cohort will have converged to within 5% of the quasi-stationary distribution (see
17 Methods description).

18 For most species in Fig. 1 the age-pattern of mortality is derived from data on
19 ages rather than stages. For some of these species, mortality levels off at advanced
20 ages (e.g., for the collared flycatcher, *Ficedula albicollis*, the great tit, *Parus major*,
21 the fruit fly, *Drosophila melanogaster*) and in others remains constant at all adult ages
22 (e.g., for *Hydra magnipapillata*). For hydra in the laboratory, this risk is so small that
23 we estimate 5% of adults would still be alive after 1400 years under those controlled
24 conditions.

1 The fertility trajectories show considerable variation. For humans the
2 trajectories are bell-shaped and concentrated at younger adult ages, but other shapes
3 are apparent in Fig. 1. The patterns for killer whales (*Orcinus orca*), chimpanzees,
4 chamois (*Rupicapra rupicapra*), and sparrowhawks (*Accipiter nisus*), are also
5 approximately bell-shaped but spread over more of the course of life. Other species
6 show trajectories of gradually increasing fertility (e.g. southern fulmars, and the
7 agave, *Agave marmorata*), asymptotic fertility (e.g. tundra voles, *Microtus*
8 *oeconomus*), or constant fertility (e.g. hydra). In addition to humans and killer whales,
9 bdelloid rotifers (*Macrotrachela* sp.), nematode worms (*Caenorhabditis elegans*), and
10 Bali mynah birds (*Leucopsar rothschildi*) have post-reproductive life spans, which
11 lends further support to the idea that this phenomenon may be widespread^{3-6,11}.

12 Although the demographic trajectories in Fig. 1 vary widely, most of the 46
13 species can be roughly classified along a continuum of senescence—running from
14 strong deterioration with age, to negligible deterioration, to negative senescence¹² and
15 improvement with age. There are, however, some deviations, e.g. for soay sheep (*Ovis*
16 *aries*) and dwarf gorse, which show mortality reductions with adult age followed by
17 deterioration. Fertility patterns show similar diversity.

18 A fast-slow continuum has been proposed to order species from those with
19 short lives and intense early reproduction to those with long lives and an extended
20 reproductive period¹³⁻¹⁶. Fig. 1 displays mortality and fertility over the adult lifespan;
21 pre-reproductive mortality trajectories are also of interest but beyond the scope of this
22 article. If distinguished by the length of life, then fast and slow life histories are
23 scattered irregularly across Fig. 1. Life spans range from the 1400 years for the hydra
24 to just 25 days for the nematode worms. Fast species such as water fleas (*Daphnia*
25 *longispina*) are followed in Fig. 1 by slow species such as the lion, while slow species

1 such as the chimpanzee occur adjacent to fast species such as the human louse
2 (*Pediculus humanus*) and the fruit fly. Furthermore, species with very different life
3 spans can display similar patterns of mortality, fertility and survivorship. For instance,
4 the water flea's trajectories are similar to the fulmar's, although water fleas reach
5 advanced old age at 48 days while the fulmars do so at 33 years.

6 If senescence is measured by how long it takes for death rates to rise from
7 some level to a higher level, then long-lived species senesce slowly. It is more
8 interesting to define senescence by the sharpness or abruptness rather than the speed
9 of the increase in mortality. Baudisch⁸ distinguishes the pace of life, i.e., whether
10 reproduction is fast and life spans are short or reproduction is slow and life spans are
11 long, from the shape of mortality and fertility trajectories, i.e., whether mortality rises
12 sharply with age and fertility falls sharply or whether mortality and fertility levels are
13 more constant. One measure of pace, the measure we use, is the terminal age to which
14 only 5% of adults survive; this measure is in days or years or some other unit of time.
15 One measure of shape, the one we use here, is the ratio of mortality at the terminal age
16 to the average level of adult mortality; this time-invariant measure does not change if
17 time is measured in days vs. years. More senescent species, with sharper increases in
18 mortality with age, have higher values of this measure of shape.

19 The measure can be used to further explore the surprising lack of association
20 between the length of life and the degree of senescence. Among the first 24 graphs,
21 those with the sharpest senescence, 11 species have relatively long life spans and 13
22 have relatively short life spans. Among the final 24 graphs, those with less
23 senescence, 13 species have relatively long life spans and 11 have relatively short life
24 spans. This weak negative association between the length of life and the degree of
25 senescence is reflected in a weak Spearman rank correlation of -0.13, which is not

1 significantly different from zero ($p = 0.362$). The Spearman correlations are also non-
2 significant when assessed for animals ($p = 0.414$) and for plants ($p = 0.07$) examined
3 separately. If the 12 plants in Fig. 1 are cross-tabulated as longer or shorter lived and
4 as more or less senescent, then three species fall into each of the four categories.
5 Hence the data support Baudisch's⁸ conjecture that pace and shape may be two
6 orthogonal axes of life histories.

7 A survivorship curve indicates the proportion of individuals that are still alive
8 at a given age. In Fig. 1, we plot survivorship from reproductive maturity on a
9 logarithmic scale. If mortality increases with age, the log-survivorship curve is
10 concave. If mortality is independent of age, log-survivorship is linear (e.g., roughly
11 from the hydra to the red abalone (*Haliotis rufesens*) in Fig. 1). For species with death
12 rates that decline with age, the curve is convex (e.g., from the red-legged frog to the
13 white mangrove at the bottom of Fig. 1). The classification of survivorship curves into
14 concave, linear and convex curves is known among biologists as Type I, II and III,
15 respectively^{17,18}, but normally the curves are plotted for lifespans starting at birth
16 rather than at maturity. When the evolutionary theory of ageing³⁻⁶ was being
17 developed, there was very little empirical evidence for Type III survivorship for adults
18 and scant evidence for Type II survivorship. The widespread recognition that
19 traditional theories of ageing predict adult senescence to be a universal trait led
20 researchers to strive to find evidence for senescence in, e.g., the mute swan (*Cygnus*
21 *olor*)¹⁹. For this species, fertility does decline and mortality does increase at the oldest
22 ages. The overall life course, however, is characterised by fertility that increases and
23 then slowly declines and by roughly constant mortality: the log-survivorship curve is
24 nearly straight. It is clear from our analyses that the full spectrum of Type I, II and III
25 survivorship curves are found for adults in nature.

1 Phylogenetic relatedness seems to play some role in the order of species in
2 Fig. 1, as shown by taxonomic clustering of mortality, fertility and survivorship
3 patterns. All mammals are clustered in the upper part of Fig. 1, while birds are
4 somewhat more scattered, from the Bali mynah in the first row to the great tit in the
5 7th row. Amphibians and reptiles are found in the lower half of the panel, with flat
6 mortality shapes and almost no overlap with mammals. In contrast, invertebrates are
7 scattered across the continuum of senescence, with bdelloid rotifers and water fleas
8 sharing the mammalian mortality pattern. The plants in our sample tend to occur
9 lower in our ordering, with the first being *Hypericum cumulicola*. Although some
10 angiosperm species appear to senesce²⁰⁻²², many angiosperm species appear not to²³,
11 perhaps as an artefact of the use of stage-based data¹⁰. The only alga in our data set,
12 oarweed (*Laminaria digitata*), falls in the last row.

13 Such clustering within broad taxonomic levels of kingdom (plants, animals),
14 or class (mammals, birds), suggests that primitive traits related to the *bauplan* of
15 species may play a pivotal role in determining patterns of ageing. In fact, the
16 evolutionary conservatism of mechanistic determinants of ageing has been highlighted
17 by genetic studies²⁴ and it has been suggested that asexual reproduction²⁵,
18 modularity²⁶, lack of germ line sequestration from the soma^{27,28}, the importance of
19 protected niches²⁹, regenerative capacity, and the paucity of diverse cell types³⁰ may
20 facilitate the escape from senescence in some clades. Many of the species in the lower
21 half of Fig. 1—the reptiles, vascular plants, alga, and coral—continue to grow after
22 reproductive maturity to sizes much larger than those at maturity. For these
23 indeterminate growers, mortality is approximately constant or decreases somewhat
24 with age, while fertility is more or less constant or increases somewhat. Species with

1 indeterminate growth may exhibit patterns of senescence that are fundamentally
2 different from those of species with determinant growth^{12,31-33}.

3 Roughly constant mortality and fertility are experienced by vertebrates such as
4 collared flycatchers and red-legged frogs, invertebrates such as hermit crabs (*Pagurus*
5 *longicarpus*) and red abalone, and vascular plants such as great rhododendron
6 (*Rhododendron maximum*) and armed saltbush (*Atriplex acanthocarpa*), with the age
7 at 5% survivorship ranging from five years for the collared flycatcher to the 14
8 centuries for hydra. It remains to be seen whether the similarity of patterns of
9 mortality, fertility and survivorship among disparate groups of species is a
10 coincidence or represents convergent solutions to similar evolutionary challenges.

11 Although hundreds of theories have been proposed to explain the proximate
12 mechanisms of ageing^{34,35}, theories to explain the ultimate evolutionary causes of the
13 varieties of ageing, illustrated by the diverse range of trajectories in Fig. 1, are in their
14 infancy. Scattered studies, however, suggest profitable directions for research. It is
15 only recently that researchers have extended their analyses beyond the traditional age-
16 structured framework³⁶; more complex demographic models show that selection
17 gradients in clonal or stage-structured organisms can be non-monotonic³⁷⁻⁴⁰. As
18 recognised in the disposable soma theory⁶, differences in life history constraints
19 among species, and the resulting differences in optimal resource allocation among
20 vital processes provide a promising direction for explaining empirical observations
21 about diverse fertility^{32,37-39,41-43} and mortality^{32,41,43} trajectories. Current theoretical
22 approaches, however, do not yet explain in detail why senescence has evolved in
23 some species and not in others. Datasets that are currently available for research on
24 ageing are taxonomically biased: high-quality data on hundreds of mammal and bird
25 species exist but data on other vertebrate taxa and on invertebrates are sparse. There is

1 very limited knowledge of the age-patterns of mortality and fertility in species of
2 algae, fungi and bacteria^{32,43,44}.

3 The mortality and fertility trajectories of any species depend on the
4 environment in which they are measured. Most human experience is bounded by the
5 trajectories of modern Japanese and the hunter-gatherers in Fig. 1. Although
6 population ecologists have long studied the responses of mortality and fertility to
7 environmental factors, few studies have focused on the shape of the age trajectories.
8 Environmental and genotypic variation has been documented in laboratory studies of
9 nematode worms, medflies, *Drosophila* and other model species⁴⁵ and in a field study
10 of *Plantago*²⁰. Available evidence suggests that variation can be considerable for a
11 species but that the qualitative shapes of mortality and fertility trajectories are similar,
12 as illustrated by humans in Fig. 1 (see also our Supplementary Note and Extended
13 Data Figure 1 highlighting intraspecific variation in the mortality trajectories of
14 laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*)). In addition to the
15 dearth of data for most species, and for variation within a species, little information is
16 available on mortality at advanced ages beyond the age cut-off in Fig. 1. In the species
17 for which such data are available, mortality approaches a plateau at the oldest ages
18 (e.g., for humans, *Drosophila* and nematode worms) or declines (for Medflies)⁴⁵⁻⁴⁷.
19 The deceleration of mortality at high ages is more apparent if death rates are plotted
20 on a log scale rather than the linear scale used in Fig. 1⁴⁵.

21 Deeper understanding of the evolutionary demography of ageing depends on
22 the compilation of demographic data on diverse species investigated in the wild as
23 well as in laboratories and zoos⁸ and on the development of more inclusive theories
24 that can account for negligible and negative senescence^{42,48} as well as for the
25 steepness of deterioration with age in senescent species. In such empirical and

- 1 theoretical studies, researchers should guard against anthropocentric intuition about
- 2 ageing: humans, especially modern humans, are extreme outliers in Fig. 1.
- 3

1 **Figure Legend:**

2 Figure 1: Demographic trajectories. Relative mortality (red) and fertility (blue)
3 as functions of age, from maturity to the age when only 5% of the adult
4 population is still alive; mortality and fertility are scaled relative to their means.
5 Subplots are arranged in order of decreasing relative mortality at the terminal
6 age. Survivorship (on a log scale) from maturity is depicted by the shaded
7 areas. Broken lines, for trajectories derived from projection matrices, start at
8 the age when cohorts have converged to within 5% of their quasistationary
9 distribution. See Supplementary Methods.

10

1 **METHODS SUMMARY**

2 **Selection of examples**

3 We aimed to examine demographic trajectories for organisms across the tree of life.
4 We therefore chose representative datasets compiled from the published literature for
5 the major groups of organisms including vertebrate and invertebrate animals, plants,
6 and algae. Within the vertebrates we included exemplars of every major clade
7 including primates and other mammals, birds, reptiles, amphibians and fish.
8 Representatives for the invertebrates included insects, molluscs, cnidarians and a
9 crustacean. In the plant group we included both gymnosperms and angiosperms and,
10 finally, we included a green alga. We favoured datasets that covered longer time
11 periods, with larger sample sizes and, when possible, we preferred datasets that
12 included information on realised reproduction and recruitment to those that simply
13 recorded reproductive output. In addition, for dioecious species, we favoured datasets
14 for females. See Supplementary Methods 1 and 2 for details.

15

16 **Calculation of standardised trajectories**

17 We classified the studies as: (1) cohort studies; (2) period studies with number at risk
18 and numbers dying within a period; (3) period studies depicting an age structure at a
19 single point in time; or (4) stage-structured population projection matrices (see
20 Supplementary Methods 2 for details). We considered mortality and fertility
21 trajectories from the age at maturity to the age at which 5% survivorship from
22 maturity occurs. The trajectories of all data types, except the projection matrix data,
23 were smoothed using P-splines⁴⁹. We then calculated the force of mortality (μ_x) and

1 fertility rate (m_x) before standardising them by dividing them by the respective
2 averages, weighted by survivorship from maturity (l_x).

3

4 **Author Contributions**

5 This research project was initiated by JWV. AS wrote the first draft; ORJ with help
6 from AS, RSG, HC, AB and JWV wrote subsequent drafts; JWV and ORJ completed
7 the final draft. The Figure was produced by ORJ with suggestions from JWV, AS, AB
8 and HC. AB suggested the method of standardisation and the distinction between
9 shape and pace. CGC developed methods to smooth mortality and fertility trajectories.
10 HC and RSG contributed to the analysis of stage-classified species. AS, RSG, ORJ
11 and HC each provided data, derived from the literature, for several species. RS
12 contributed unpublished data for hydra; JE, JD, and MBG for *Borderea*; RSG and
13 BBC for *Cryptantha*; and EM and PQ-A for *Hypericum*. AS, ORJ, RSG and HC
14 screened the species for data quality.

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1 **Extended Data Figure 1 | Standardized mortality trajectories for**
2 **laboratory rats, a, and mice, b.** Each line represents a different
3 strain/sex/population. See Supplementary Methods for sources. We
4 standardised the age axis to consider the trajectories from age at maturity
5 to the age at which 5% survivorship from maturity occurs. The
6 trajectories were smoothed using P-splines. We then calculated the force
7 of mortality ($\mu(x)$) and standardised it by dividing by the average value,
8 weighted by survivorship from maturity (l_x). Note that the sample sizes in
9 most cases were small (c. 50-60 individuals) and thus random
10 fluctuations may lead to erratic curves in some cases.

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