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Research Article

**Senescence vs. sustenance:
Evolutionary-demographic models of aging**

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Senescence vs. sustenance: Evolutionary-demographic models of aging

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Abstract

Humans, and many other species, suffer senescence: mortality increases and fertility decreases with adult age. Some species, however, enjoy sustenance: mortality and fertility remain constant. Here we develop simple but general evolutionary-demographic models to explain the conditions that favor senescence vs. sustenance. The models illustrate how mathematical demography can deepen understanding of the evolution of aging.

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1. Introduction

Why do humans deteriorate with age? And why is this senescence common across many species—but not all species?

A brief answer is that we grow decrepit because we continually suffer damage and because some but not all of the damage is repaired. The cumulative imbalance between damage and repair produces senescence; with mortality rising and fertility falling with age (Kirkwood 1981; Baudisch 2008).

The more an organism invests in repair, the less the organism will degenerate with age. If repair is sufficient, then the organism can maintain itself. Such sustenance, however, is costly and requires resources the organism could otherwise invest in greater reproduction. Darwinian evolution optimizes this trade-off for each species—producing age-specific trajectories of mortality and fertility that depend on the species' bauplan and environment (Stearns 1992; Roff 2002). Kirkwood pioneered this important perspective on aging and developed it focusing on senescence (Kirkwood 1977). This article builds on Kirkwood's core idea and expands it to explain when sustenance is optimal.

Until recently it was generally thought that the evolutionary theory of aging implied that senescence is inevitable for multicellular iteroparous species (Medawar 1952; Williams 1957; Hamilton 1966). Many gerontologists assumed this was the case and the view is still widely held. As Williams observed, however, "*it is indeed remarkable that after a seemingly miraculous feat of morphogenesis a complex metazoan should be unable to perform the much simpler task of merely maintaining what is already formed*" (Williams 1957: 398). Over the last decades, field and laboratory studies have demonstrated that some organisms suffer negligible senescence over the course of life (Finch 1990; 2009; Vaupel et al. 2004). Notable examples are queens in eusocial species (Hölldobler and Wilson 1990; Keller and Genoud 1997; Keller 1998; Carey 2001) and hydra (Martinez 1998). And recently it has been found that sustenance can be an optimal evolutionary strategy under some conditions (Baudisch 2008). This article develops simple evolutionary-demographic models that yield general conditions for sustenance vs. senescence.

The models aim to capture the gist of why evolution favors either sustenance or senescence. We focus on species that potentially would be able to achieve sustenance if sufficient resources are diverted from reproduction to maintenance. We simplify the models as much as we can while retaining some minimal realism about the basic cornerstones of the life cycle of a species. In particular, we focus on age-invariant vs. increasing mortality over adult ages. We assume that fertility is constant over age. This assumption might seem too drastic, but as a first step in studying senescence vs. sustenance, it is reasonable to focus on one process – mortality – instead of two. Senescence can be captured by an increase in mortality over adult ages and sustenance by

an age-invariant mortality pattern. Relaxing the constant-fertility assumption in models to be developed in the future will permit study of mortality and fertility senescence together. In our models, age zero is defined as reproductive maturity.

2. A model with constant fertility and increasing mortality

Evolution favors sustenance over senescence if Darwinian fitness of the former strategy exceeds that of the latter. Thus, if a strategy of sustenance corresponds to a fitness of R^o and that of senescence to R^* , evolution favors sustenance over senescence if $R^o > R^*$. The models are based on the assumption of a stationary population closed to migration in a constant environment, where density dependence regulates population size via offspring survival. In such a population, as shown by Mylius and Diekmann (1995), Darwinian fitness is given by the net reproductive rate

$$R = \int_0^{\infty} l(x)m(x)dx, \quad (1)$$

where $l(x)$ denotes survival from age at maturity to age x , and $m(x)$ denotes age-specific reproduction. Age is scaled to equal zero at reproductive maturity and juvenile mortality is implicitly included in $m(x)$, which captures the so-called level of recruitment. If reproduction is constant over age, then $m(x) = m$ equals the production of progeny, per unit of time over the life course, that survive to reproductive maturity, and R equals the product of life expectancy at reproductive maturity, e_o , times reproduction, m , i.e.

$$R = m \int_0^{\infty} l(x)dx = me_o,$$

where life expectancy at reproductive maturity is given by

$$e_o = \int_0^{\infty} l(x)dx.$$

The trade-off in resource allocation between survival and reproduction implies that as the level of reproduction m increases, life expectancy e_o decreases. Thereby, even though m is assumed to be constant, basic insights about how the trade off between survival and reproduction determines senescence vs. sustenance can be gained without specifying the age-dependence of fertility.

2.1 The basic model

Assume individuals grow to their ultimate size and reach reproductive maturity at an age defined as age 0. Strategies over adult ages implying sustenance or senescence are denoted by $^{\circ}$ and * respectively.

Let m° be the level of reproduction per unit time if an individual enjoys sustenance after maturity. Let m^* be the level if the individual suffers senescence after maturity. In general, $m^* > m^{\circ}$, because more resources are available for reproduction if the organism does not pay for costly maintenance.

Let μ° be the force of mortality given sustenance; then life expectancy e° is simply the inverse of μ° , because

$$e^{\circ} = \int_0^{\infty} l(x) dx = \int_0^{\infty} e^{-\mu^{\circ} x} dx = \frac{1}{\mu^{\circ}}.$$

In case of senescence, mortality increases with age, reflecting the deterioration of the organism. Let μ^* be the initial force of mortality at maturity if the individual deteriorates. Depending on the value of μ^* and the pace of deterioration, which determines how quickly mortality rises with age, senescing individuals have a life expectancy of e^* . We assume that $e^* > e^{\circ}$, i.e., that senescence reduces life expectancy.

The expected reproductive output of an individual is $R^{\circ} = m^{\circ} e^{\circ}$ given sustenance and $R^* = m^* e^*$ given senescence. Sustenance and senescence are equally desirable if and only if these two quantities are equal. Rearranging terms leads to the condition:

$$\frac{m^{\circ}}{m^*} = \frac{e^*}{e^{\circ}}. \quad (2)$$

The term on the left captures the relative amount of reproduction an organism could achieve if it maintains its body compared to the reproductive output it could have if it would senesce. This ratio is always smaller than or equal to one; the smaller the ratio the more reproduction is lost to the organism when it attempts to maintain its body. Thus, this term is a measure of how much reproduction is sacrificed to achieve sustenance.

The term on the right captures how much shorter an organism would live if it would senesce compared to the lifespan it could achieve if it paid enough for maintenance. This ratio is also always smaller than or equal to one; the smaller the ratio the more survival is gained by maintaining the organism. Thus, this term is a measure of how much life expectancy is gained by achieving sustenance.

Equivalently, one could say that the term on the left measures how much reproduction is gained as a result of senescence, and the term on the right measures how much life expectancy is sacrificed as a result of senescence.

Sustenance and senescence will be equally optimal if costs equal benefits. Sustenance will be optimal if the required sacrifice of reproduction is less than the corresponding gain in life expectancy; senescence will be optimal if the required sacrifice of life expectancy is less than the gain in reproduction.

Note that sustenance can be optimal even if the necessary sacrifice in reproduction is large, as long as the gain in life expectancy is big enough. To put this differently, sustenance is optimal:

Condition 1

if the gain in life expectancy is high due to either (a) a reduced level of mortality at maturity, $\mu^o < \mu^*$, or (b) avoidance of significant deterioration,

Condition 2

provided that the relative reduction in reproduction m^o/m^* due to diversion of resources towards maintenance is not too drastic.

What “significant deterioration” and “not too drastic” means in this context will become clear in the illustrative examples below.

These general conditions are in agreement with the conditions for sustenance in previous models (Vaupel et al. 2004; Baudisch 2008); the earlier models are more complex, including juvenile periods, indeterminate growth, and the possibility of inverse senescence over adult ages. The advantage of the simple approach taken above is that it reveals the core trade off between reproduction and survival. The basic model can be used as the starting point for more complex models. We will explore one possibility in the following, but many other model variants can be developed.

2.2 Results for Gompertz-Makeham mortality

Let the force of mortality at age x be given by $\mu(x) = ae^{bx} + c$. Note that b determines the rate of deterioration and that c captures age-independent “extrinsic” mortality. In this model, at maturity, when $x = 0$, $\mu^o = \mu^* = a + c$. If b is zero (i.e., given sustenance), then the force of mortality remains constant at this level and the probability of surviving to age x is $l(x) = \exp\{-(a+c)x\}$. If b exceeds zero (i.e., given senescence), then the force of mortality increases with age and survival is given by

$$l(x) = \exp\left\{-\left(\frac{a}{b}\right)(\exp(bx) - 1) - cx\right\}.$$

As above, let reproduction per unit time given sustenance be denoted by m^o , and let reproduction per unit time given senescence be constant and equal to m^* , with $m^* > m^o$.

The model can be described by three ratios that are dimensionless: m^o/m^* ,

which measures reproduction given sustenance relative to reproduction given senescence (*Condition 2* above), $C = c/(a+c)$, which captures the share of extrinsic mortality at age zero (and in sustenance), and $B = b/(a+c)$, which captures the magnitude of the rate of deterioration relative to the level of mortality at maturity.

Equation (2) implies that the ratio of life expectancies, e^*/e^o determines the boundary between conditions that favor senescence vs. conditions that favor sustenance. Because e^*/e^o is dimensionless, any unit of time can be used to calculate the numerator and denominator. Therefore, the unit can be chosen such that $e^o = 1$. Since $e^o = 1/\mu^o$ this implies that $a+c = 1$ and hence $c = C$, $a = 1-C$ and $b = B$. If survival $l(x)$ is expressed in terms of these dimensionless numbers, the ratio e^*/e^o becomes,

$$\frac{e^*}{e^o} = \int_0^{\infty} \exp \left\{ -\frac{1-C}{B} (\exp(Bx) - 1) - Cx \right\} dx, \quad (3)$$

since life expectancy is given by the integral of survival $l(x)$ over all ages.

The value of Equation (3) demarcates the boundary between sustenance and senescence. Equation (2) implies that if the ratio m^o/m^* exceeds this value, then sustenance is the optimal strategy; if the ratio falls short of this level, senescence is optimal. Since life expectancy given senescence is always shorter than life expectancy given sustenance, $e^* \leq e^o$, no value can exceed 1. Figure 1 illustrates how the boundary between senescence and sustenance depends on the relative importance of the extrinsic risk of death (C) and deterioration (B).

Consider the trivial case when B is 0, i.e. the deterioration parameter b is 0. Since there is no deterioration, there is no need for repair. Since sustenance and senescence in this scenario are equivalent strategies, the ratio plotted on the graph, the ratio of e^*/e^o , is 1.

In the non-trivial case of positive deterioration one can distinguish between negligible and significant deterioration. If B is of magnitude about 0.01 or smaller, deterioration happens so slowly that the loss in life expectancy due to senescence can be neglected. It is worth little to sacrifice reproduction to achieve true sustenance since a negligible senescent strategy yields a life expectancy that is virtually the same as the life expectancy of a strategy of true sustenance.

Significant deterioration is found at values of B of the magnitude 0.1 and above. In this case, sustenance could increase lifespan significantly compared to the case of senescence. Strong deterioration can be associated with magnitudes of B around 10 and very strong deterioration with magnitudes of around 100. In the latter case, the benefits of repair are so large that huge cuts in reproduction can be accepted in order to pay for maintenance.

Note the effect in the Figure of the relative level of extrinsic mortality, as captured by C . For any value of B , the higher the level of C , the closer sustenance fertility must be

to senescent fertility for sustenance to be favored. Thus, riskier environments leave less room for sustenance to evolve.

3. Three illustrative examples

The following section considers application of the model to (1) eusocial species, (2) hydra and (3) humans.

3.1 Queens and workers

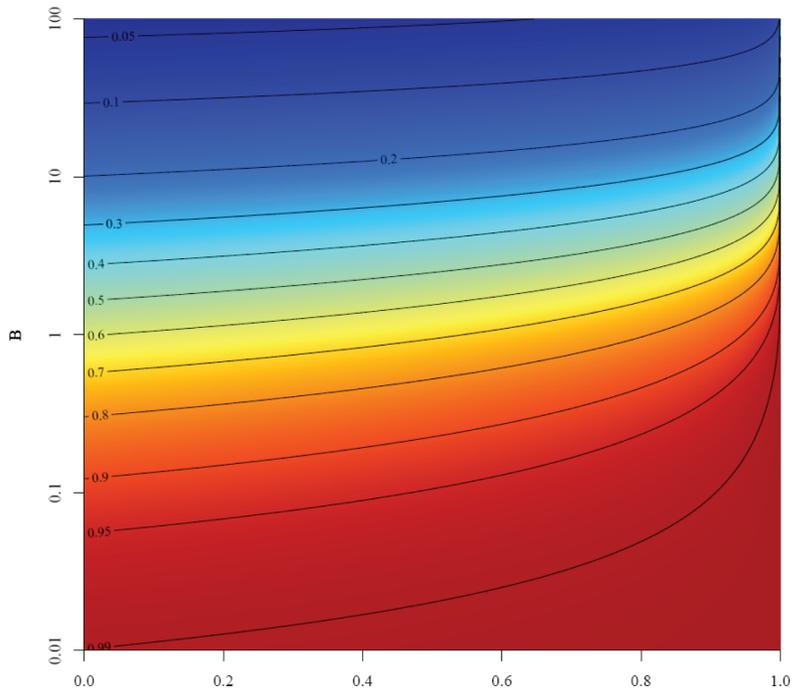
Consider the case when $C = 0$, i.e., when extrinsic mortality c is negligible. This might be the case for the highly protected queens in eusocial species like bees, ants and termites. In principle such queens might be able to boost their high fertility by investing less in maintenance—and suffering senescence, but in practice this may not be optimal. Suppose the rate of deterioration, b , is comparable in magnitude to the low level of mortality at maturity, $a + c$, such that $B = 1$. The value of 0.60 in the Figure implies that if sustenent fertility exceeds three-fifths of senescent fertility, then sustenance is favored—because the gain in life expectancy outweighs the loss in reproduction. If B is 100, then the value is 0.04 and highlights the large loss in life expectancy when the rate of deterioration is high: even if sustenent fertility were only a bit more than 4% of senescent fertility, sustenance would be favored.

Workers in eusocial species do not reproduce but they do contribute to the reproductive output of the queen and hence of the colony. If workers invest less in maintenance of themselves, then they can contribute more resources to the production of new workers. Let m^* and m^o be the number of new workers that can be produced per unit time by the average worker if workers senesce or sustain, with $m^* > m^o$ and with m^* and m^o being measures of the senescent vs. sustenent— fertility— of workers. For workers, the value of c is much higher than for queens and a may also be higher. Hence the value of B may be considerably less than one. If, for instance, B were 0.1 and if C were 0.9, then the Figure indicates that senescence would be favored even if sustenent fertility was nearly 99% as high as senescent fertility.

3.2 Hydra

Hydra vulgaris appear to suffer high extrinsic mortality from predation in the wild. Individuals reproduce several times per week in the laboratory and probably also produce progeny frequently in the wild, but the world is not covered by hydra, so they must suffer a correspondingly high death rate. Hydra, however, enjoy sustenance at a very low death rate under laboratory conditions (Martinez 1998: MPIDR hydra lab unpublished

Figure 1: Contour plot of senescent life expectancy as a fraction of sustenent life expectancy for various values of the standardized extrinsic mortality rate C and the standardized rate of deterioration with age B



Note: Each contour on the graph represents some level between the limits of zero and one of the ratio of e^*/e^o (which is equal to e^* since time is scaled such that $e^o = 1$). The colors provide an alternative description of the value of this ratio, with the red tones representing values close to one and the blue tones representing values close to zero. Sustenance is favored over senescence if the ratio of fertility rates m^o/m^* , which also varies between zero and one, is higher than the e^*/e^o ratio plotted in the graph. There are many values of the fertility ratio that satisfy this condition when the life-expectancy ratio is low, so sustenance has more opportunity to evolve for species in the upper left portion of the graph. In contrast, senescence tends to be favored in the lower right portion of the graph. As emphasized in the main text, however, this rough rule of thumb only provides a starting point for more careful, detailed analysis. There are blue species that suffer senescence and red species that enjoy sustenance.

data). Williams (1957) hypothesized that high extrinsic mortality should lead to rapid senescence. Abrams (1993), Caswell (2007) and Baudisch “The pace and shape of ageing”³ provide a more nuanced analysis. In our model, as summarized in the Figure, it is not c but C , the ratio of c to $a+c$, that is the critical variable. The Figure indicates that high values of C tend to favor senescent mortality, especially if B is low. Higher values of extrinsic mortality c will, for any specific values of a and b , lead to higher values of C and lower values of B ; thus hydra are probably located near the right edge of the Figure and toward the bottom, favoring senescence. Yet hydra do not senesce.

Seymour and Doncaster (2007) address this puzzle, for bristlecone pines and other species as well as hydra, using a model in which entrenched adults “crowd out” juveniles, depriving almost all juveniles of a place to occupy. Building on this basic idea, we can take our simple model one step further. Consider a stationary population of individuals that are distributed over their environment with all individuals following the same strategy determined by their common genome. Suppose each individual in the population has an equal, small, non-heritable chance of ending up in a safe place, a protected niche. Even though all individuals in the population follow the same strategy (of either senescence or sustenance), mortality is low for individuals that occupy these favorable spots relative to the high mortality suffered by individuals that do not, simply due to the different extrinsic hazards. Could it be advantageous for the whole population to choose sustenance, if in this way the few lucky individuals occupying the protected niches would have the prospect of a long life?

The fitness of the population is given by the sum of the reproductive success of the protected and the unprotected individuals. Let π be the proportion of individuals in protected niches. Let the superscript o vs. * denote sustenance vs. senescence and the subscript $_+$ vs. $_-$ denote protected vs. unprotected. If the species chooses sustenance, let R_+^o be total expected reproduction of the individuals that occupy protected niches and let R_-^o be the value for those that do not. Similarly let R_+^* and R_-^* be the corresponding values if the species chooses senescence. The reproductive output of all individual, protected and unprotected, constitute the next generation. Thus, sustenance will be favored if

$$\pi R_+^o + (1 - \pi)R_-^o > \pi R_+^* + (1 - \pi)R_-^*$$

Rearranging terms yields the alternative requirement

$$\pi > \frac{R_-^* - R_-^o}{(R_+^o - R_+^*) + (R_-^* - R_-^o)} \tag{4}$$

The minimum proportion of individuals of the population who need to find a safe spot

³Manuscript is available from the author on request.

in order for sustenance to evolve depends on the differential reproductive success between protected and unprotected places under different aging strategies. Each of the two terms in the numerator will be small since mortality is high in a hazardous environment, and the difference, although positive, may be close to zero. In contrast, the first difference in the denominator may be large if the reproductive output of the protected, long-lived individuals is not too small. Suppose the numerator is 0.1 and the first difference in the denominator is 100. Then the proportion of favorable niches would only have to exceed the value 0.001 to favor the evolution of sustenance for all individuals in the population.

3.3 Humans

At maturity the chance of death for humans in long-lived populations today is about 1 in 10,000 per year. Because the rate of deterioration for humans is about 0.1 per year, this implies values of B of roughly 1000. This value would put humans beyond the upper left corner of Figure 1, deep into the realm favoring sustenance. Yet humans senesce. This appears to pose a severe challenge to our model.

As indicated in *Condition 1*, B is high if either b is high or $a+c$ is low. For humans, b , the rate of deterioration with age, is low compared with many other species and the value of $a+c$ is very low. Hence B is high because of the very low level of mortality at maturity.

Over time, mortality at maturity, $a+c$, has fallen dramatically. In hunter-gatherer populations it is about 1 death in 100 (Gurven and Kaplan 2007) and may have been this high or even higher over most of the long course of human evolution. For b about 0.1 this implies values of B of 10, a value much lower than 1000 but still in the blue region of Figure 1. Although Gurven and Kaplan estimated the rate of deterioration to be nearly 0.1, they observed that mortality “appears to be characterized by two stages. Mortality remains stable and fairly low at around 1 percent per year from the age of maturity until around age 40.” After that age, mortality increases exponentially. Recent paleodemographic research findings are consistent with this conclusion (Svenja Weise, personal communication). Most of lifetime reproduction occurs before age 40, especially when death rates are high such that many people fail to survive past 40. There is some reproduction after age 40 and people above 40 help take care of and hence enhance the survival chances of young relatives. To a first approximation, however, the integral in eq. (3) might be taken from maturity to 40 for humans in populations with low life expectancies. If mortality from maturity to 40 “remains stable and fairly low”, then e^*/e^o in eq. (3) evaluated from maturity to 40 is close to one. We therefore hypothesize that, over the course of the evolution of human life histories, reducing the rate of deterioration b over the main reproductive period, thereby achieving true sustenance, would not have brought significant fitness benefits.

To the extent that reproduction occurs—or could occur in less senescent humans—

after age 40 and to the extent that older people help younger relatives survive, reducing b would increase fitness. Cutting b in half would roughly double remaining life expectancy at age 40; reducing b to zero would multiply human life expectancy by a factor of 100 or more in populations today with low mortality at maturity, leading to lifespans of around 10,000 years. We hypothesize that the life expectancy gains are so large that the cost—in reduced lifetime fertility—of lowering b after age 40 must be substantial. Some tentative evidence suggests that the value of b is almost the same for all humans alive today and has been the same for all humans in the past (Vaupel 2010): b is roughly the same for hunter-gatherer populations and modern Swedes. On the other hand, a and c vary considerably across individuals and populations and have been greatly reduced over time. The rate of deterioration may be an invariant that is so critical for evolution that the rate is tightly specified and is very difficult to alter.

4. Perspectives

In this article we seek to shed light on why some species senesce and others sustain. We show that if senescence is captured by an increase in mortality over adult ages, then in a simple model evolution favors sustenance over senescence if the sacrifice in reproduction to achieve sustenance is smaller than the sacrifice in life expectancy resulting from senescence. We believe that this result will also hold for more complex models.

The conditions for senescence vs. sustenance depend on dimensionless quantities:

$$m^o/m^*, e^*/e^o, B, C \text{ and } \frac{R_-^* - R_-^o}{(R_+^o - R_+^*) + (R_-^* - R_-^o)}.$$

Because these quantities are independent of the unit of time, species that senesce can live weeks, month or centuries; and species that do not can also live weeks, month or centuries. This finding supports the importance of the distinction between the pace of aging and the shape of aging. Senescent species can be short or long lived—and sustenat species can be short or long lived (Baudisch “The pace and shape of ageing”⁴; Baudisch 2007). Charnov’s research demonstrates the importance of dimensionless numbers in understanding life histories for different species (e.g., Charnov 2002; 2005; Charnov, Warne, and Moses 2007).

Many species’ life histories will be either sustenat or senescent. There are, however, some species with individuals that can elect sustenance or senescence depending on environmental cues: queens vs. workers in eusocial species are an example. For other species it may be possible to nudge successive generations from sustenance toward senescence or visa-versa by environmental manipulations. Identifying and studying

⁴Manuscript is available from the author on request.

such species—most conveniently, short-lived ones—would deepen understanding of how sustenance and senescence evolved.

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