

Max-Planck-Institut für demografische Forschung
Max Planck Institute for Demographic Research
Konrad-Zuse-Strasse 1 · D-18057 Rostock · GERMANY
Tel +49 (0) 3 81 20 81 - 0; Fax +49 (0) 3 81 20 81 - 202;
<http://www.demogr.mpg.de>

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**Senescence vs. Sustenance:
Evolutionary-Demographic Models of
Aging**

Annette Baudisch (baudisch@demogr.mpg.de)
James W. Vaupel (jwv@demogr.mpg.de)

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**Senescence vs. Sustenance:
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by Annette Baudisch and James W. Vaupel

Humans, and many other species, suffer senescence: mortality increases and fertility declines 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.

Keywords: senescence, sustenance, aging, mortality, fertility, evolution, hydra, eusociality

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 all 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, pg. 398). And indeed, recently it has been found that sustenance is an optimal evolutionary strategy under some conditions (Baudisch 2008). Furthermore, field and laboratory studies have demonstrated that some organisms suffer negligible senescence over the course of life (Finch 1990, 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). 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 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 mortality-senescence and leave fertility-senescence to a later, more complex model. We assume that fertility is constant over age. This assumption might seem too drastically simplifying, but as a first step in studying senescence vs. sustenance, it is reasonable to focus on one process – mortality – instead of two. Senescence can simply be captured by an increase in mortality over adult ages and sustenance by a constant mortality pattern. Relaxing the constant-fertility assumption in models to be developed in the future will permit study of mortality and fertility senescence together.

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. 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, Darwinian fitness is given by the net reproductive rate

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

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 , where life expectancy at reproductive maturity is given by

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

and thus

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

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.

Note that for some species the amount of repair necessary to remove deterioration could be infeasible for the organism, even without having any relation to reproduction. In our model, we focus on species that potentially would be able to achieve sustenance if sufficient resources are diverted from reproduction to maintenance.

2.1 The Model

Assume individuals grow to their ultimate size and reach reproductive maturity at an age defined as age 0. Strategies following sustenance or senescence are denoted by o and * respectively.

Let m^o 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, $m^* > m^o$, because more resources are available for reproduction if the organism does not pay for costly maintenance.

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

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

The case of mortality-senescence is easily studied because the simple fitness measure given in (1) does not require an assumption about the shape of mortality, μ . 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 values of μ^* and the pace of deterioration, which determines how quickly mortality rises with age, senescing individuals have a life expectancy of e^* , which is shorter than e^o .

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

$$(2) \quad m^o / m^* = e^* / e^o.$$

The term on the left is a measure of how much reproduction is sacrificed to achieve sustenance; or equivalently how much reproduction is gained as a result of senescence. The term on the right is a measure of how much life expectancy is gained by achieving sustenance; or equivalently 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 equals the corresponding gain in life expectancy; senescence will be optimal if the required sacrifice of life expectancy equals the gain in reproduction.

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 to drastic” means in this context will become clear in the illustrative example 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. It 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 Illustrative Results for Gompertz-Makeham Mortality

Let the force of mortality at age x be described 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. The probability of surviving to age x is

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

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 if sustain relative to reproduction if senesce (*Condition 2* above), $p = \frac{c}{a+c}$, which captures the share of extrinsic mortality at age zero (and

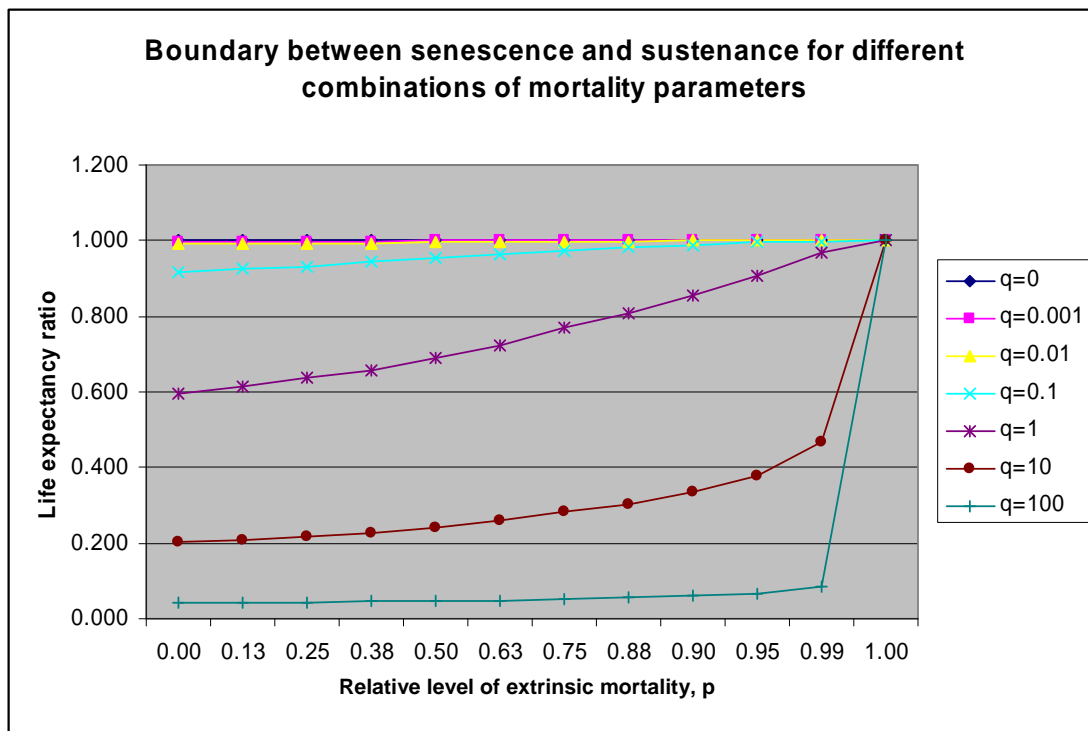
in sustenance), and $\rho = \frac{b}{a+c}$, which captures the magnitude of the rate of

deterioration relative to the level of mortality at maturity. The two ratios p and ρ account for the deterioration in *Condition 1* above and determine the ratio e^* / e^o .

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 $e^o = 1$, which implies that $a + c = 1$ and hence $c = p$, $a = 1 - p$, $b = \rho$ and

$$(3) \quad \frac{e^*}{e^o} = \int_0^{\infty} \exp\left\{-\frac{(1-p)}{\rho}(\exp(\rho x) - 1) - px\right\} dx.$$

This equation determines the boundary between sustenance and senescence, as illustrated in the Figure below. The ratio of e^* / e^o (which is equal to e^* since we have scaled time such that $e^o = 1$) is plotted for various combinations of the relative importance of extrinsic hazard, p , and the relative importance of the rate of deterioration to the overall level of mortality, ρ . Note that, at the boundary, it holds that $m^o / m^* = e^* / e^o$. Strategies below the line follow senescence; strategies above the line follow sustenance.



Since we assume that $e^* \leq e^o$ no value can exceed 1. Consider the case when $p = 0$, 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. Such queens might be able to boost their high fertility by investing less in maintenance—and suffering senescence. Suppose the rate of deterioration, b , which drives senescence, is comparable in magnitude to the low level of mortality at maturity, $a+c$, such that $\rho = 1$ (violet line). The value of 0.60 in the Figure implies that if sustenatant fertility exceeds three-fifths of senescent fertility, then sustenance is favored—because the gain in life expectancy outweighs the loss in reproduction. If ρ 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 sustenatant fertility were only a bit more than 4% of senescent fertility, sustenance would be favored.

Note the effect in the Figure of the relative level of extrinsic mortality, as captured by p . For any value of ρ , the higher the level of p , the closer sustenance fertility must be to senescent fertility for sustenance to be favored.

A value of ρ of 100 might seem, at first thought, to be very large—the rate of deterioration is 100 times larger than the level of mortality at maturity. Large values of ρ , however, characterize humans. At maturity the level of human mortality today in long-lived populations is about 1 in 10,000 and even in prehistoric populations it may have been 1 in 100 (Gurven and Kaplan 2007). Because the rate of deterioration for humans is about 0.1, this implies values of ρ of roughly 1000 today and 10 in the distant past.

In the extreme cases, when ρ is 0 or p is 1, we see that the ratio e^*/e^o equals one. This case is trivial since $\rho = 0$ or $p = 1$ imply that mortality is constant and thus sustenance is given in any case. Figure 1 also helps to better define what “significant deterioration” means in Condition 1 above. No deterioration and thus no senescence pertains to the trivial case of $\rho = 0$. Negligible deterioration pertains to magnitudes of ρ up to 0.01. Since the lines in the Figure are close to horizontal at the level of 1, it is not worth to sacrifice a significant fraction of reproduction to achieve true sustenance, since negligible senescence is close enough to no senescence.

Significant deterioration is found at values of ρ of the magnitude above 0.1. In this case, sustenance could increase lifespan significantly compared to the case of senescence. The larger the rate of deterioration, the faster mortality increases relative to its age independent level, the more likely sustenance can bring significant benefits in terms of longer lifespan compared to senescence.

Deterioration is strong at magnitudes of ρ around 10 and very strong at 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.

In sum, whether senescence or sustenance is the better strategy does not depend on the absolute level of either deterioration or the extrinsic hazard of death but on the relative magnitude of deterioration to the level of sustenance-mortality. If deterioration is of a larger or the same magnitude or even one magnitude lower than the sustenance level of the hazard of death, then sustenance entails significant survival benefits.

3. A Model of Protected Niches

In the Figure, the area above the boundary line, where sustenance is favored, is larger for small values of p , i.e. for individuals with small relative extrinsic mortality c . In the following, we will explore an alternative scenario focusing on the effect of protection on senescence vs. sustenance.

Consider a stationary population of individuals that are randomly distributed over their environment with all individuals forced to follow the same strategy. Either the species chooses sustenance, or the species chooses senescence. What would happen if the environment harbored a few rare protected niches that, by chance, could be occupied by a fraction of individual of the population? Each individual in the population is equally likely to end up in a safe place or not. Thus, some individuals are protected and others are not. 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 safe life?

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 such 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

$$(3) \quad \pi > \frac{R_-^* - R_-^o}{(R_+^o - R_+^*) + (R_-^* - R_-^o)}.$$

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. 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 0.001 to favor the evolution of sustenance for all individuals in the population.

Hydra vulgaris appear to suffer high extrinsic mortality from predation in the wild: individuals reproduce several times per week in the laboratory and may 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 data). It had been predicted that high extrinsic mortality should lead to rapid senescence (Williams 1957), which has been refuted (Arbams 1993, Caswell 2007). If there are uncommon, protected crevices in the wild that a few hydra can occupy, the model outlined above corroborates the result that high extrinsic mortality does not determine whether species senesce or sustain.

4. Perspectives

Our purpose is to elucidate why some species senesce and others sustain. We showed 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, but this remains to be shown.

The conditions for senescence vs. sustenance depend on dimensionless quantities: m^o / m^* , e^* / e^o , p , ρ 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/tempo of life and the path/quantum of aging. Senescent species can be short or long lived—and sustenance species can be short or long lived (Baudisch 2007, Baudisch 2008). Charnov's research demonstrates the importance of dimensionless numbers in understanding life histories for different species (e.g. Charnov 2002, Charnov 2005, Charnov et al. 2007)).

Many species' life histories will be either sustenance 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 such species—most conveniently, short-lived ones—would deepen understanding of how sustenance and senescence evolved.

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