

When Senescence Is Optimal and When It Is Not

Draft

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Abstract

A simple model is developed that captures the main features of life - reproduction, growth and maintenance. These features are determined by a single state variable, vitality. The resulting optimal life-history strategies are classified with respect to the course of their characteristic age-trajectory of mortality. It is shown that the range of optimal life histories is wide. The main factors that determine whether an optimal life-history follows a non-senescent strategy or a senescent strategy are the costs of growth and maintenance. Of almost equal importance are the costs of reproduction. Mortality conditions may have a strong influence on the boundary between non-senescence and senescence if the costs of maintenance and reproduction are relatively low. If the costs are too high, even reduction of intrinsic or extrinsic mortality to zero cannot shift a senescent strategy to a non-senescent one. Efficient systems of reproduction and growth and, to some extent, low mortality conditions lead to non-senescent life-history strategies.

1 Introduction

The goal of evolutionary demography is to understand how evolution shapes the age-trajectories of fertility, mortality, growth and transfers. This goal is the central concern of life-history theory (Roff, 2002; Stearns, 1992). What is the optimal age and size at maturity? What is the optimal number and size of offspring? What is the optimal frequency of reproductive events? What is the optimal length of life? Typically, in each case, trade-offs determine the optimal strategy since resources are limited.

An optimal life-history strategy maximizes an individual's fitness. Fitness captures the reproductive success of a genotype and can be measured by Lotka's intrinsic rate of population increase, r , implicitly defined by the Lotka equation,

$$1 = \int_0^{\infty} e^{-ra} l(a) m(a) da. \quad (1)$$

Another frequently used measure of fitness is the net reproductive rate, R , given by

$$R = \int_0^{\infty} l(a) m(a) da. \quad (2)$$

The survival function $l(a)$ indicates the probability of survival from birth (or conception) to age a and the maternity function $m(a)$ indicates age-specific reproduction.

Life-history optimization attempts to find an "evolutionary stable" strategy that cannot be invaded by any other strategy Smith (1982). A mutant which diverges from the optimal schedule would have slower population growth, ultimately resulting in its extinction. Therefore, the evolutionary stable strategy is given by the functions $l(a)$ and $m(a)$ that maximize r . Because no population can continue growing, in equilibrium this r_{max} must equal zero. Taylor et al. (1974) proved that maximizing life-time reproduction, R , is equivalent to maximizing the intrinsic rate of population increase, r , such that $r_{max} = 0$. Hence, in this paper, the functions $l(a)$ and $m(a)$ that maximize R correspond to the optimal strategy.

Are there evolutionary stable life history strategies that prevent mortality from rising with age? If senescence is defined as an increase in mortality with age, then non-senescence

corresponds to mortality trajectories that do not increase with age. Could non-senescent life-histories be optimal? Would a non-senescent strategy also involve increasing or constant fertility with age? What characteristics lead to senescent vs. non-senescent life-histories?

A previously developed model shows that non-senescence can be optimal (Vaupel et al., 2004). Size constitutes the central state variable in this framework. Mortality falls with increasing size and reproductive potential rises. The case of determinate growth, however, poses a challenge to this framework. Determinate growers, like humans, reach their final size at about the age of maturity. While, after the onset of reproduction, size remains constant, mortality steadily rises. This is incompatible with the strict size-dependence of mortality. A new model can be developed to address the deficiencies of the size-based model. To capture changing mortality at a constant size, the quality of size will be considered. The approach is rationalized in the following way. Even if size remains unchanged, all cells progressively accumulate damage over time and deteriorate. *Vitality*, defined as an individual's size adjusted for the functioning of body cells, can decline and therefore mortality can increase despite a constant body size.

Facing ubiquitous decay, life is sustained by processes of rejuvenation. The continuous creation of new, undamaged cells counterbalances deterioration. This balance determines whether or not vitality declines. The level of rejuvenation and repair will depend on the trade-offs between reproduction, on the one hand, and growth and maintenance, on the other. The optimal schedule of resource allocation then determines the optimal trajectory of vitality. Increasing vitality raises reproductive potential and lowers mortality. Reproduction results in offspring but entails slower growth or even decline in vitality. The trajectory of vitality over age determines the age-trajectories of fertility, mortality and growth. The following evolutionary-demographic model sheds light on the fundamental questions of life-history theory based on the single state variable vitality.

2 The Vitality Model

Survival depends on mortality. It seems natural to model mortality as an inverse function of vitality, denoted by ψ . A simple function for the force of mortality, μ , is

$$\mu(\psi) = \frac{b}{\psi} + c, \quad (3)$$

where b and c are constant parameters. The intrinsic parameter b captures all causes of death an individual can escape from by increasing its vitality, while the extrinsic parameter c captures the always prevalent, non-zero risk of death. Note that "extrinsic" and "intrinsic" refer to vitality-dependent vs. vitality-independent mortality.

Reproduction and growth depend on the level of available energy. In my model, available energy $\epsilon(\psi)$ depends on the difference between build-up and break-down processes at current vitality,

$$\epsilon(\psi) = k \psi^{0.75} - \kappa \psi, \quad (4)$$

where k and κ are constant parameters. Anabolic, build-up processes are directly linked to metabolic rate, which, based on the literature, is assumed to be proportional to vitality to the power 0.75 (Charnov, 1991; Lavigne, 1982; West et al., 2001). Catabolic, break-down processes are assumed to be proportional to vitality to the power one. Energy is maximum at vitality ψ_ϵ

$$\psi_\epsilon = \left(\frac{3k}{4\kappa} \right)^4. \quad (5)$$

A fraction $\pi(\psi)$ of $\epsilon(\psi)$ is allocated to growth and the remaining fraction $1 - \pi(\psi)$ to reproduction. Vitality ψ changes over time according to the difference between newly built cells and the unavoidable deterioration of functioning of current cells at a constant rate δ ,

$$\dot{\psi} = \pi(\psi)^{\eta_g} \epsilon(\psi) - \delta \psi. \quad (6)$$

Note that the constant parameter η_g (g for growth) has no effect if $\pi(\psi)$ equals either one or zero.

The level of $\pi(\psi)$ that corresponds to maintenance of current vitality is given by Eq. 6 when $\dot{\psi} = 0$,

$$\pi_0 = \left(\frac{\delta}{k\psi^{-0.25} - \kappa} \right)^{\frac{1}{\eta_g}}. \quad (7)$$

Vitality cannot increase indefinitely. An upper limit to ψ , denoted by Ψ , is reached at maximum investment $\pi(\psi) = 1$ and $\dot{\psi} = 0$,

$$\Psi \equiv \left(\frac{k}{\kappa + \delta} \right)^4. \quad (8)$$

Available energy must be nonnegative. This implies that

$$\psi \leq \left(\frac{k}{\kappa} \right)^4 \quad (9)$$

must hold. This is always true since ψ cannot exceed maximum attainable vitality Ψ .

Fertility is proportional to available energy $\epsilon(\psi)$ and determined by the fraction $1 - \pi(\psi)$ used for reproduction,

$$m(\psi) = \varphi [1 - \pi(\psi)]^{\eta_r} \frac{\epsilon(\psi)}{\psi^{\eta_j}}. \quad (10)$$

Available energy is divided by the initial vitality of offspring, ψ_0 . The constant parameter $\eta_j > 1$ (j for juvenile) captures the additional energy that is necessary to create one baby. The constant parameter η_r (r for reproduction) captures the costs of running a reproductive system parallel to a rejuvenation system. The constant φ is a scaling parameter set to the value that ensures that optimal lifetime reproduction is equal to one and, hence, $r_{max} = 0$.

2.1 The Parameters

2.1.1 k , κ and δ

Parameter k captures the speed of growth of vitality (Eqs. 4 and 6). Faster growth implies a quick fall in mortality (Eq. 3) and reduces the time of development. Furthermore, higher values of k decrease maintenance costs (Eq. 7) and increase maximum vitality (Eq. 8). Parameter κ is inversely related to maximum vitality. Elevating κ slows growth, increases

maintenance costs (Eq. 7) and decreases maximum vitality (Eq. 8). Parameter δ determines the speed of decline in vitality (Eq. 6). Higher δ increases maintenance costs (Eq. 7) and decreases maximum vitality (Eq. 8).

If all energy is allocated to reproduction, then δ determines the constant rate of increase in mortality (Eq. 3). A decline in vitality not only implies a reduction in survival but also a reduction in reproductive potential. Therefore, larger values of δ will tend to increase the investment of resources in growth in order to slow down the deterioration process.

Parameters k and κ determine the shape of the energy trajectory over vitality (Eq. 4). An increase in vitality beyond the threshold given in Eq. 5 leads to a decrease in energy and can only be optimal if the reduction in mortality offsets the loss in growth and reproductive potential. If $\kappa < 3\delta$ then energy is an increasing function of vitality because $\Psi < \psi_\epsilon$. Otherwise, the hump shape of energy with respect to vitality can lead to increasing fertility despite a fall in vitality.

Together, k , κ and δ determine the maximum level of vitality Ψ that is possibly attainable. The same maximum vitality can be reached by various combinations of these parameters taking into account their different effects on speed of growth and decay and available energy.

2.1.2 b and c

Parameters b and c determine the overall level of mortality (Eq. 3). Higher levels of mortality discount future reproduction. Therefore it seems reasonable that low levels of mortality should be associated with non-senescent strategies and high levels of mortality should be associated with senescent strategies. This hypothesis is investigated below.

Parameter b captures the state-dependent component of mortality, i.e. b determines how important it is to attain and maintain a high vitality. High b determines the minimum level of state-dependent mortality, b/Ψ , which also depends on maximum vitality Ψ . Since b/ψ_0 determines infant mortality, the magnitude of b also influences the optimal vitality at birth. Parameter c captures the state-independent mortality component. The overall level of infant mortality is given by $b/\psi_0 + c$ and the minimum mortality that can be attained is given by $b/\Psi + c$.

2.1.3 η_r and η_g

Parameter η_r determines how energy is translated into reproduction (Eq. 10) and hence it determines the propensity to share resources between reproduction and growth. Values below one favor parallel investment in growth and reproduction.

Parameter η_g determines the maintenance costs of a certain vitality (Eq. 7). Large η_g implies higher maintenance costs at each level of vitality. Therefore, low values of η_g favor non-senescence strategies. During periods of parallel growth and reproduction, higher η_g implies a reduced speed of growth.

Both parameters η_r and η_g capture efficiencies and determine how advantageous it is to specialize in growth and reproduction, i.e. how costly it is to run a growth and reproduction system in parallel.

3 Solution

An optimal investment trajectory $\pi^*(\psi)$ (the star indicates “optimal”) is found by maximizing life time reproduction (Eq. 2). I did this by applying a dynamic programming approach, following a backward procedure and assuming stepwise constant vitality (Bellman, 1965). Vitality ψ can be normalized through division by some reasonable base unit of ψ and is therefore dimensionless. Consequently, initial vitality (for the algorithm) can be set equal to one. The path of $\pi^*(\psi)$ determines the optimal vitality trajectory and the time τ it takes to reach the subsequent level of vitality. Summing over τ gives the corresponding age-trajectory.

Since the single state approach only allows for monotonic state trajectories, a second artificial state is given by an ”up” and ”down” mode of vitality. Any state path starts off in up mode, with the option of switching to down mode. Switching back to up mode is not possible. The backward procedure begins at vitality $\psi = 1$ in down mode and successively proceeds backward to maximum vitality $\psi = \Psi$. At each level of vitality in down mode the optimal decision is whether to maintain or decrease current vitality. At maximum vitality, up mode is assumed and vitality is followed backward down to $\psi = 1$ again. At each level of vitality in up mode the optimal decision is whether to increase or maintain vitality or switch

into down mode.

Note that once $\pi = 0$ is optimal π has to remain zero. Since the creation of new cells requires perfect originals, all current cells will have accumulated some damage if the steady process of creation is interrupted.

Vitality at birth, ψ_0 , does not influence the optimal investment path. As a constant it can be taken outside the integral in Eq. 2. Therefore, in a dynamic optimization procedure $\pi^*(\psi)$ is found without taking into account ψ_0 in the maternity function in (10). Afterwards, optimal vitality at birth is simply calculated by solving

$$\psi_0 = \max_{\psi} \frac{R^*(\psi)}{(\psi)^{\eta_j}}, \quad (11)$$

where $R^*(\psi)$ captures optimal remaining reproduction at vitality ψ .

4 Size

Size itself does not enter the model. It is, however, a variable closely linked to vitality that can be measured. One measure of size is the accumulated number of body cells. The change in size ξ is given by the difference between newly created tissue at current vitality ψ and the amount of old body parts shed at a rate δ_{ξ}

$$\dot{\xi} = \pi(\psi)^{\eta_g} \epsilon(\psi) - \delta_{\xi} \xi. \quad (12)$$

Thus, having linked size and vitality the model can be rooted in reality. So far, vitality has been dimensionless and the time units arbitrary. Initial vitality (for the algorithm) was normalized to $\psi = 1$, dividing by some reasonable base unit. Now, this "reasonable base unit" ψ_{base} can be established via

$$\xi_0/\psi_0 = \psi_{base} \quad (13)$$

where ξ_0 is obtained from empirical data. Also the unit of time can be established. The time it takes for size to change from in ξ_0 to ξ_1 in the model should be equal to the time that it takes

Table 1: Linking the Dynamics of Size, ξ , and Vitality, ψ .

	$\dot{\xi} = 0$	$\dot{\psi} = 0$
$\delta_{\xi} < \delta_{\psi}$	$\dot{\psi} < 0$	$\dot{\xi} > 0$
$\delta_{\xi} = \delta_{\psi}$	$\dot{\psi} = 0$	$\dot{\xi} = 0$
$\delta_{\xi} > \delta_{\psi}$	$\dot{\psi} > 0$	$\dot{\xi} < 0$

in reality for this change in size. For this connection, knowledge about δ_{ξ} is indispensable.

Table 1 summarizes the different dynamics in vitality and size depending on the rate of deterioration in functioning of cells $\delta_{\psi}(= \delta)$ and the rate of loss in old body cells δ_{ξ} . Note that a constant size could correspond to any mortality trajectory, depending on the relation of δ_{ξ} to δ_{ψ} . Without knowledge about the relation between δ_{ξ} and δ_{ψ} patterns of growth cannot be linked directly to patterns of mortality.

5 The Eight Varieties of Life Histories

Eight different types of optimal strategies can be found to result from this model, classified with respect to the specific trajectory of π . From birth to maturity $\pi(\psi) = 1$ and vitality increases. After maturity $\pi(\psi)$ drops below one. Vitality might be maintained, increase or decrease. Once maintenance of vitality is optimal, it will be optimal at all subsequent ages in this one state model. The eight strategies are described below. Each description of a strategy begins at maturity. Note that the function $\pi(\psi)$ captures the trajectory of actual investment over vitality whereas the function $\pi_0(\psi)$ determines the level of investment that would be necessary to maintain the current level of vitality ψ .

5.1 Strategies with Senescence

5.1.1 Senescence

Senescence corresponds to a strategy of $\pi = 0$. Vitality decreases exponentially at a rate δ .

Senescence captures the familiar case of Gompertzian mortality, with mortality and fertility patterns similar to those of many mammals, birds, and other species. Reproduction is initiated and mortality rises exponentially when investment switches from one to zero. Note that both reproduction and maintenance are costly. An example is illustrated in Fig. 1 with the parameter combination

$$\eta_r = 2, \eta_g = 2, b = 0.3, c = 0.01, k = 3, \kappa = 0.8, \delta = 0.1. \quad (14)$$

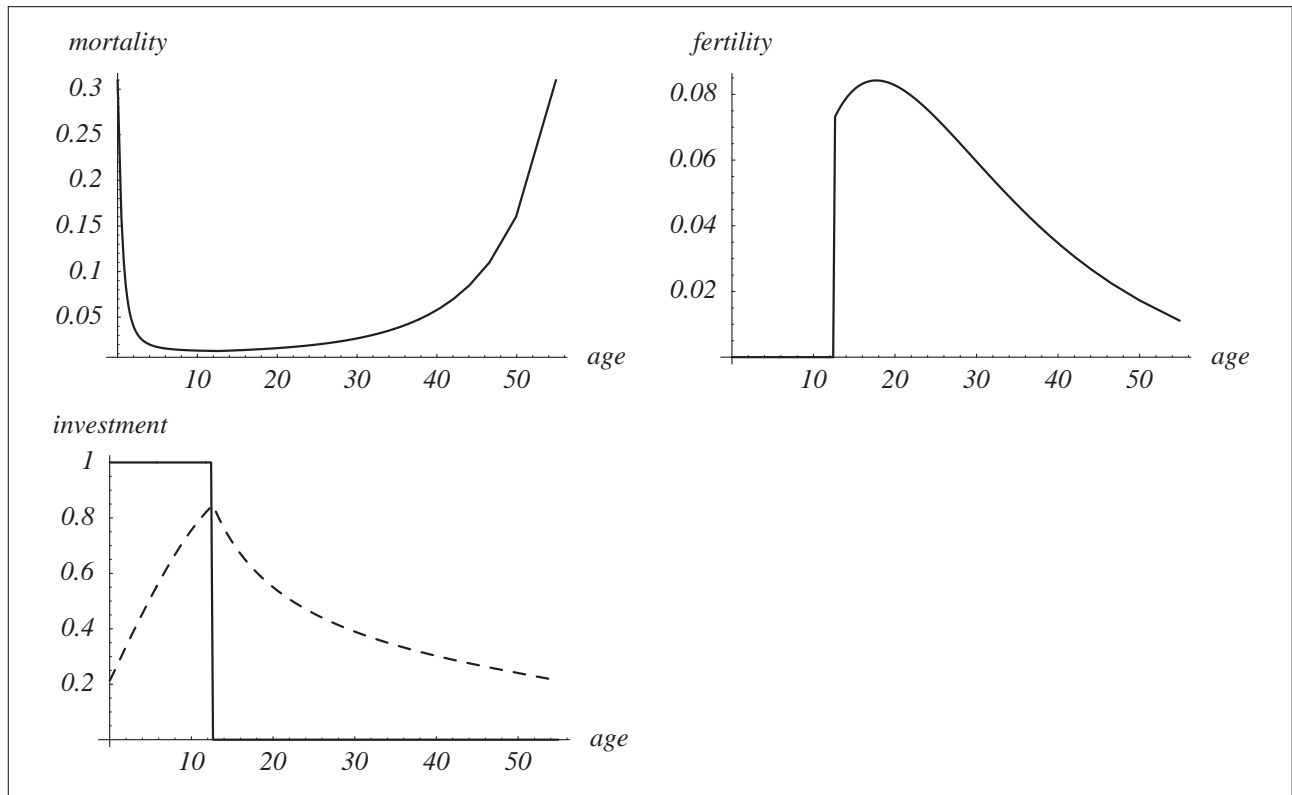


Figure 1: Example of Senescence. (Dashed line: π_0 , level of investment required for maintenance)

5.1.2 Delayed senescence

Delayed senescence corresponds to a strategy of $\pi > \pi_0$ followed by $\pi = 0$. Vitality first increases and then decreases exponentially at a rate δ . At younger ages reproduction increases while mortality decreases. Only after reproduction sharply rises mortality increases exponentially. Delayed senescence can be optimal if the propensity to share resources between reproduction and growth is strong ($\eta_r < 1$) but maintenance is costly ($\eta_g > 1$). Since extrinsic mortality is high, early reproduction is favored. Still, a larger reproductive potential is striven for and established. Then, in a second reproductive peak this potential is finally harvested at the cost of total deterioration of the individual. Fertility can fall while mortality also falls. An example is illustrated in Fig. 2 with the parameter combination

$$\eta_r = 0.5, \eta_g = 2, b = 0.2, c = 0.1, k = 3, \kappa = 0.8, \delta = 0.1. \quad (15)$$

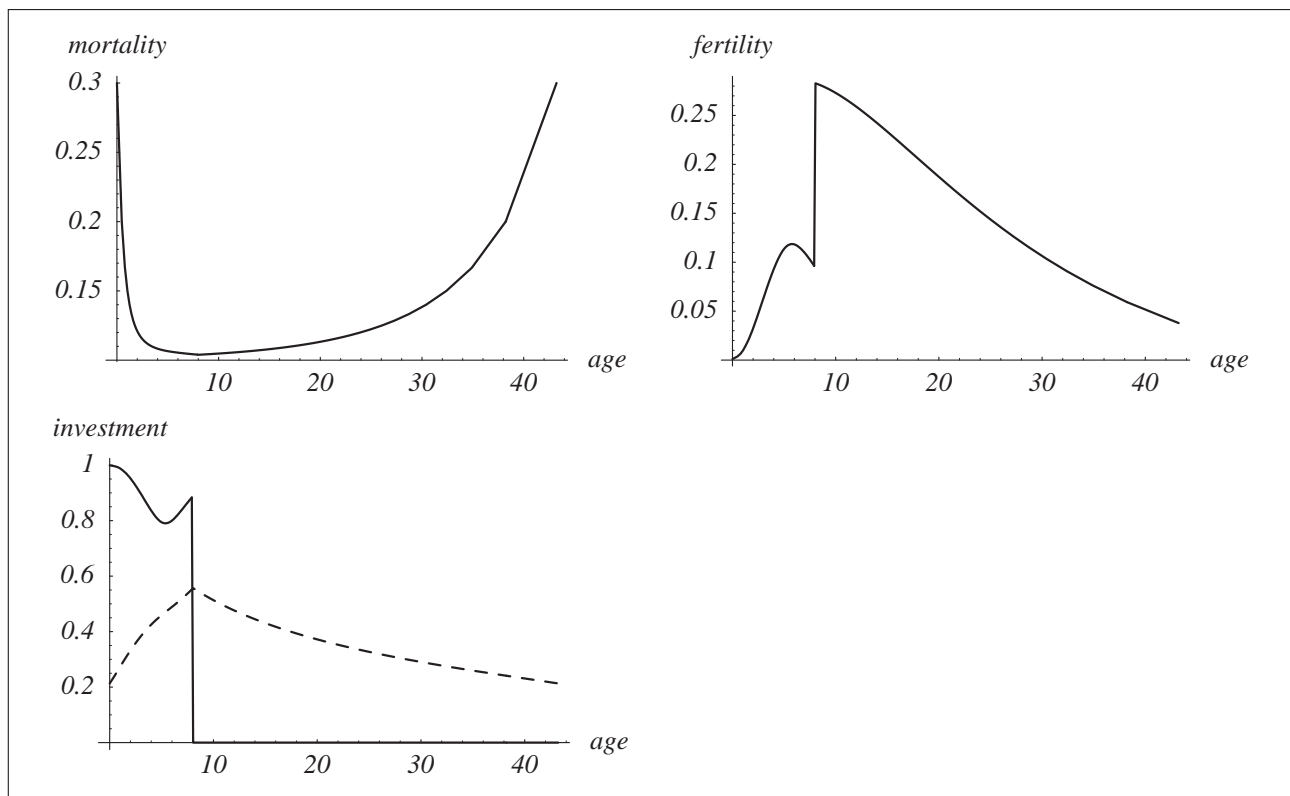


Figure 2: Example of Delayed Senescence. (Dashed line: π_0 , level of investment required for maintenance)

5.1.3 Subsistence

Subsistence corresponds to a strategy of $0 < \pi < \pi_0$, where $\pi \approx \pi_0$. Vitality slowly decreases.

Investment after maturity falls just slightly below maintenance level which is indicated by the dashed line. The missing fraction of energy that would be necessary to truly maintain vitality is used to increase reproductive output. If maintenance is cheap ($\eta_g < 1$) the increase in mortality can be retarded in such a way that, virtually, the individual maintains its state. An example is illustrated in Fig. 3. Life-expectancy at birth is only 13 and about 31 at maturity $\alpha = 8$. The high intrinsic and low extrinsic mortality favor the investment in growth. The example pertains to the parameter combination

$$\eta_r = 2, \eta_g = 0.5, b = 1, c = 0.001, k = 3, \kappa = 0.8, \delta = 0.1. \quad (16)$$

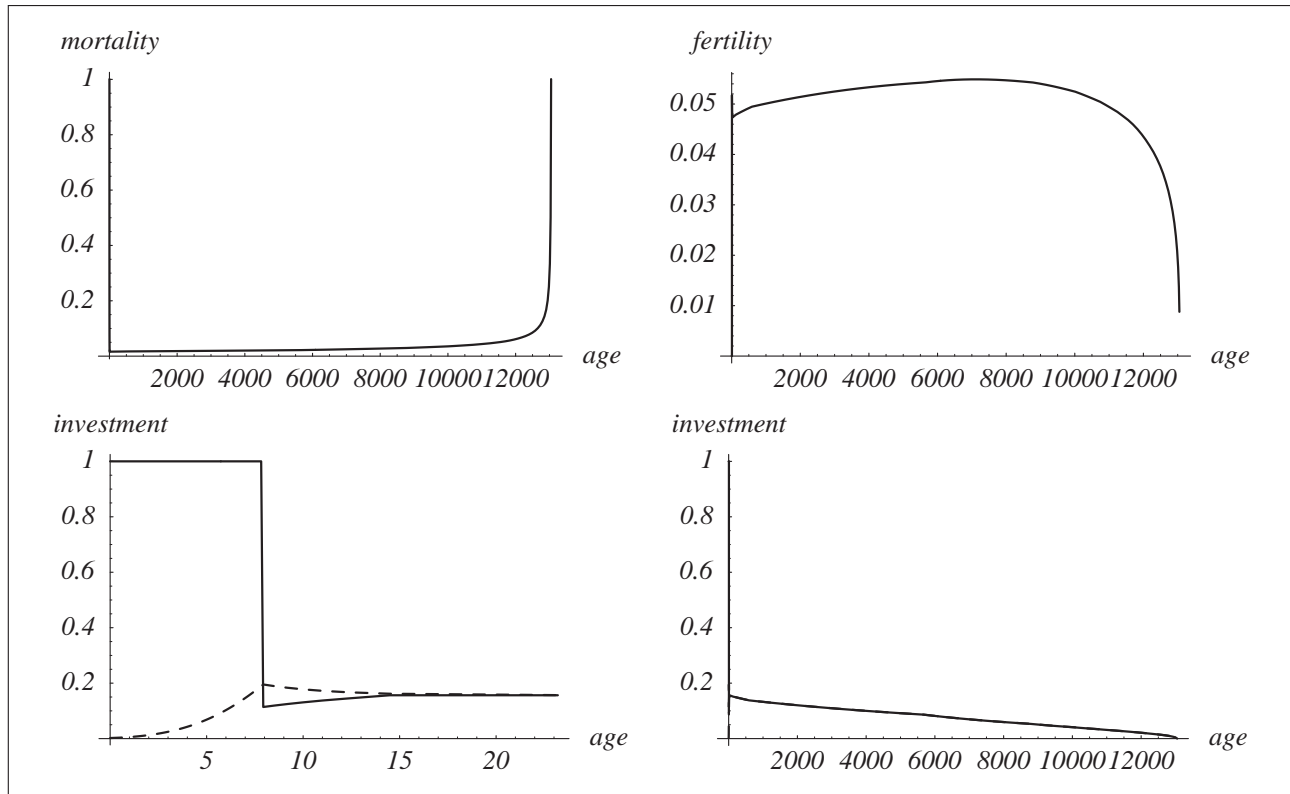


Figure 3: Example of Subsistence. (Dashed line: π_0 , level of investment required for maintenance) Note that in the lower right picture the trajectories of π and π_0 overlap, because π falls just slightly below π_0 .

5.1.4 Delayed subsistence

Delayed subsistence corresponds to a strategy of $\pi > \pi_0$ followed by $0 < \pi < \pi_0$, where $\pi \approx \pi_0$. Vitality first increases and then decreases at a very slow pace.

The cheap costs of maintenance favor investment in growth. The level of extrinsic morality together with reasonable costs of reproduction promote an early age of maturity. An example is illustrated in Fig. 4 with the parameter combination

$$\eta_r = 1, \eta_g = 0.5, b = 0.1, c = 0.02, k = 3, \kappa = 0.7, \delta = 0.2. \quad (17)$$

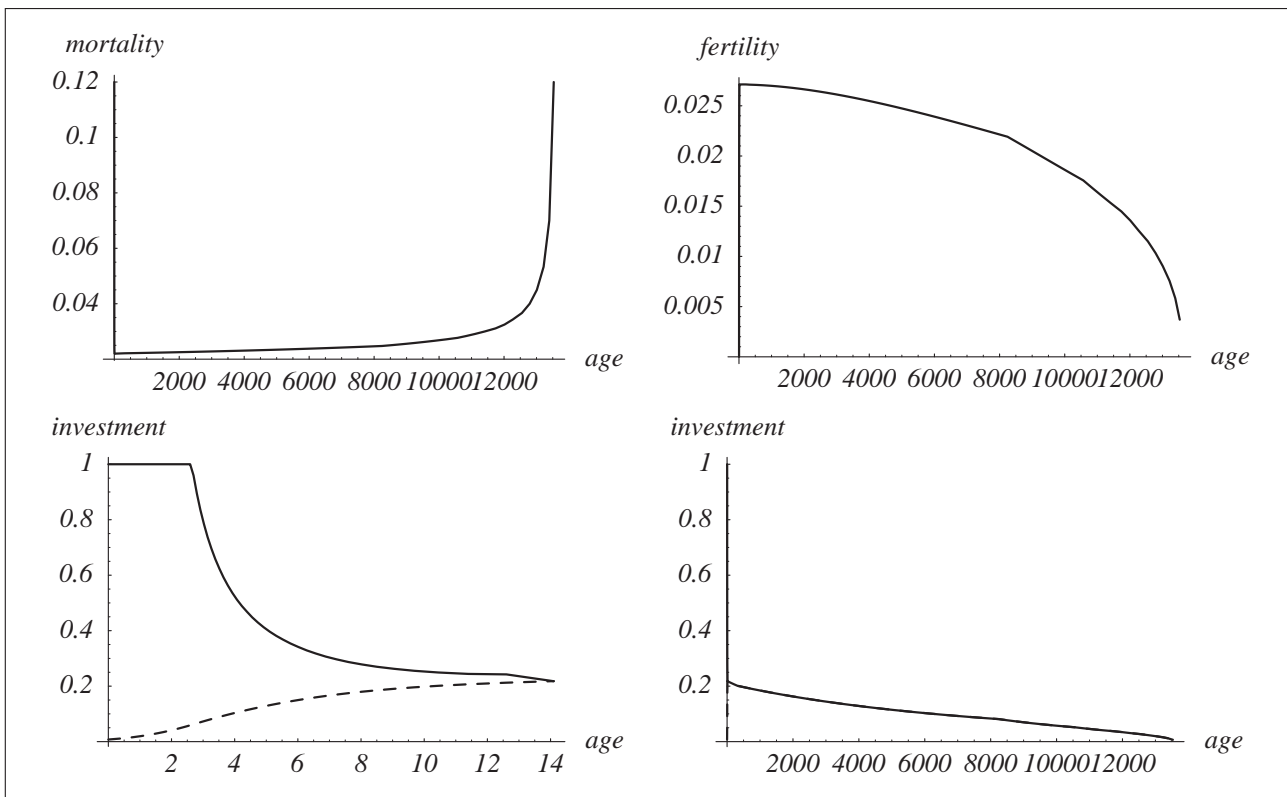


Figure 4: Example of Delayed Subsistence. (Dashed line: π_0 , level of investment required for maintenance) Note that in the lower right picture the trajectories of π and π_0 overlap, because π falls just slightly below π_0 .

5.2 Strategies with Sustenance

5.2.1 Sustenance

Sustenance corresponds to a strategy of $\pi = \pi_0$ immediately after the period of development. Vitality is maintained.

The case of sustenance is illustrated in Fig. 5. At the age of maturity investment steps down to maintenance level. Reproduction starts and both mortality and fertility remain at non-zero, constant levels. Costly reproduction and maintenance ($\eta_r > 1$, $\eta_g > 1$) but low mortality as compared to the example in Fig. 1 characterize this example with the parameter combination

$$\eta_r = 2, \eta_g = 2, b = 0.2, c = 0.001, k = 3, \kappa = 0.8, \delta = 0.1. \quad (18)$$

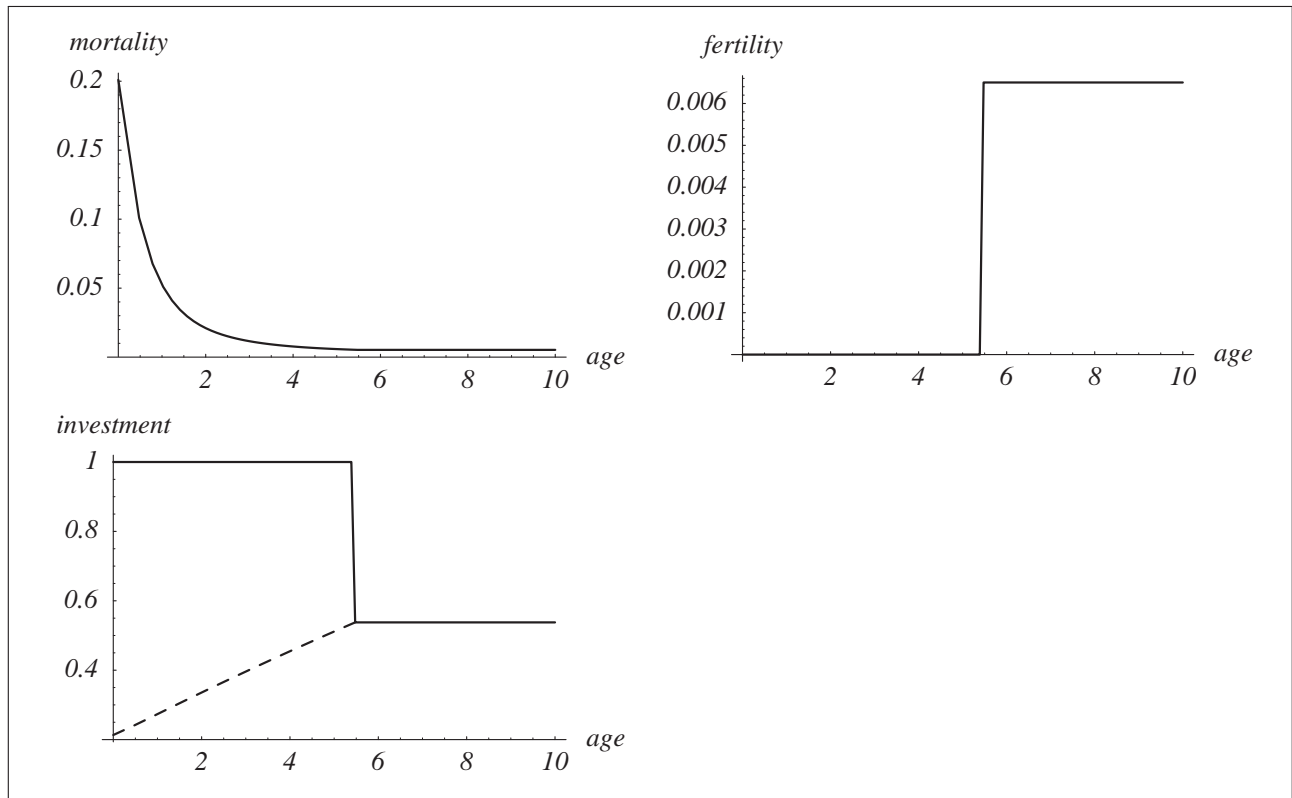


Figure 5: Example of Sustenance. (Dashed line: π_0 , level of investment required for maintenance)

5.2.2 Supersustenance

Supersustenance corresponds to a strategy of $\pi > \pi_0$ followed by $\pi = \pi_0$. Vitality first increases and then is maintained.

The case of Supersustenance is illustrated in Fig. 6. Investment falls smoothly from one down to maintenance level. Mortality decreases while fertility increases until the trajectories reach a constant level. Both reproduction and maintenance are cheap in this example ($\eta_r < 1$, $\eta_g < 1$) and mortality is low as can be seen from the parameter combination

$$\eta_r = 0.5, \eta_g = 0.5, b = 0.2, c = 0.004, k = 3, \kappa = 0.8, \delta = 0.1. \quad (19)$$

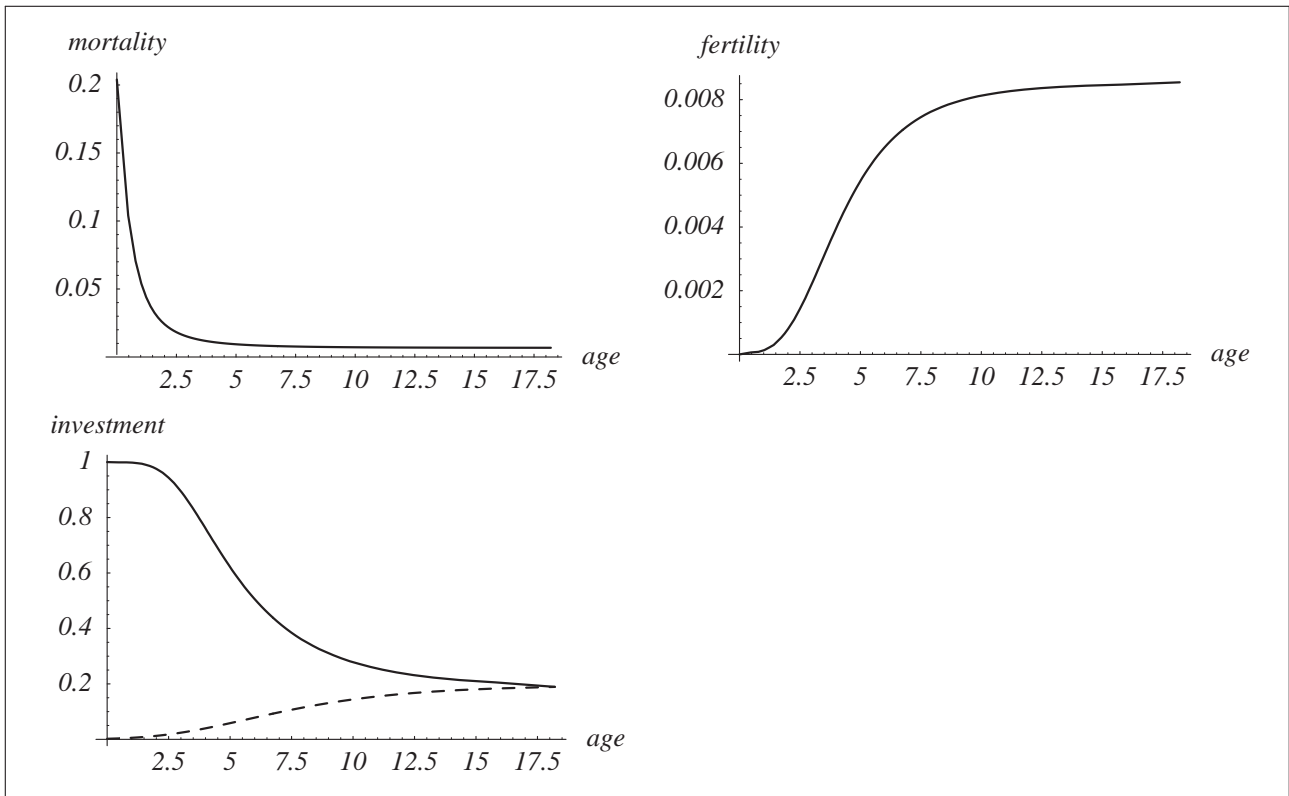


Figure 6: Example of Supersustenance. (Dashed line: π_0 , level of investment required for maintenance)

5.3 Strategies with Both Senescence and Sustenance

5.3.1 Partial senescence

Partial senescence corresponds to a strategy of $\pi < \pi_0$ followed by $\pi = \pi_0$. Vitality decreases and then is maintained.

The case of partial senescence is very interesting. The propensity to share resources between reproduction and growth is small ($\eta_r = 2$) and therefore exclusive investment is desirable. A high reproductive potential is build up during development and then harvested at the cost of falling vitality until a level of vitality is reached that still keeps mortality at a sufficiently low level, maintained at low costs ($\eta_g = 0.5$). An example is illustrated in Fig. 7 with the parameter combination

$$\eta_r = 2, \eta_g = 0.5, b = 0.2, c = 0.004, k = 3, \kappa = 0.7, \delta = 0.2. \quad (20)$$

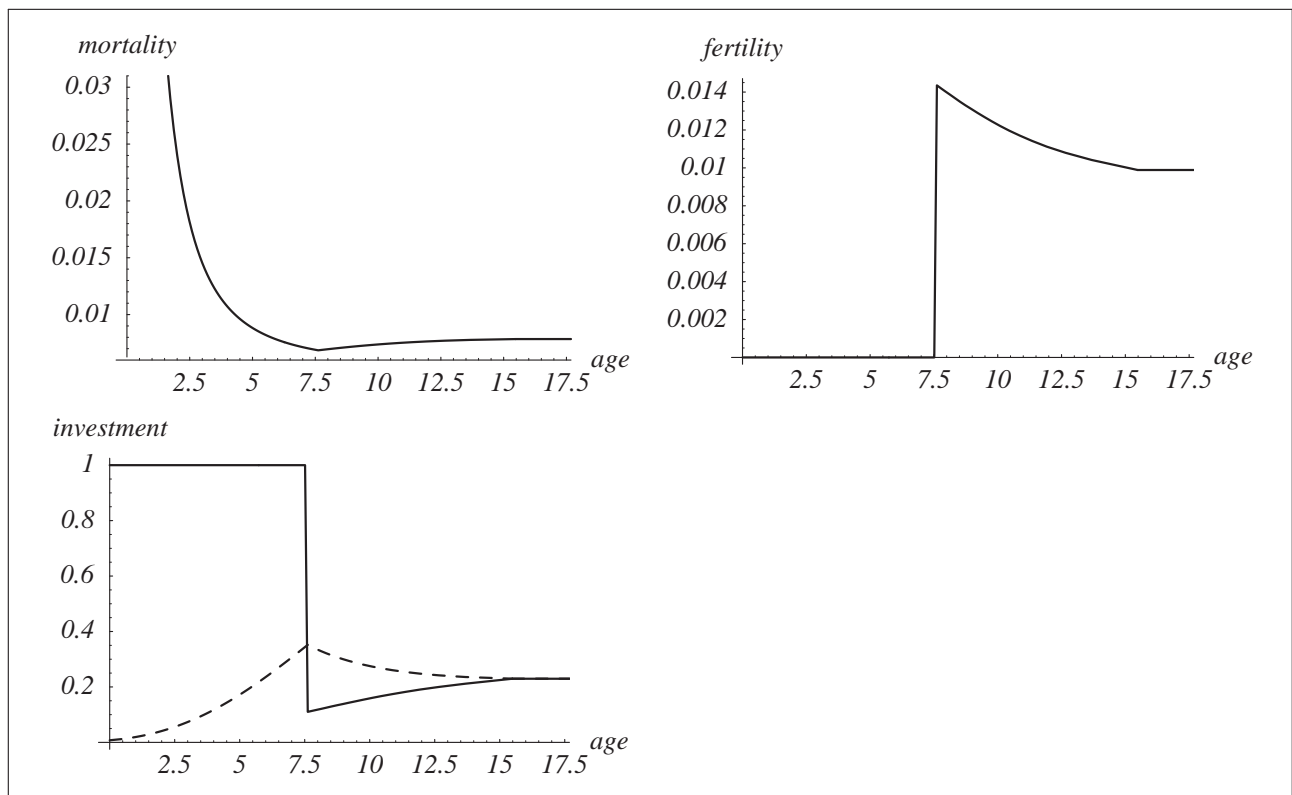


Figure 7: Example of Partial Senescence. (Dashed line: π_0 , level of investment required for maintenance)

5.3.2 Delayed partial senescence

Delayed partial senescence corresponds to a strategy of $\pi > \pi_0$, followed by $0 < \pi < \pi_0$, followed by $\pi = \pi_0$. Vitality first increases, then decreases and then is maintained.

The high extrinsic mortality favors an early onset of reproduction. Cheap maintenance together with a high level of deterioration increase the tendency to invest in growth and maintenance over some period of life. An example is illustrated in Fig. 8. Note that investment is plotted over the life-course to clarify the strategy. Each step corresponds to a one unit change in vitality. Vitality increases after the age of maturity $\alpha = 4$ until it reaches a peak of about 60 at age 14. Then vitality starts to fall. The period of decline in vitality is slowed down to an extent that the corresponding changes in mortality and fertility are negligible over the main part of life ($e^0(\alpha) = 22$). The example pertains to the parameter combination

$$\eta_r = 1, \eta_g = 0.5, b = 0.3, c = 0.01, k = 3, \kappa = 0.7, \delta = 0.2. \quad (21)$$

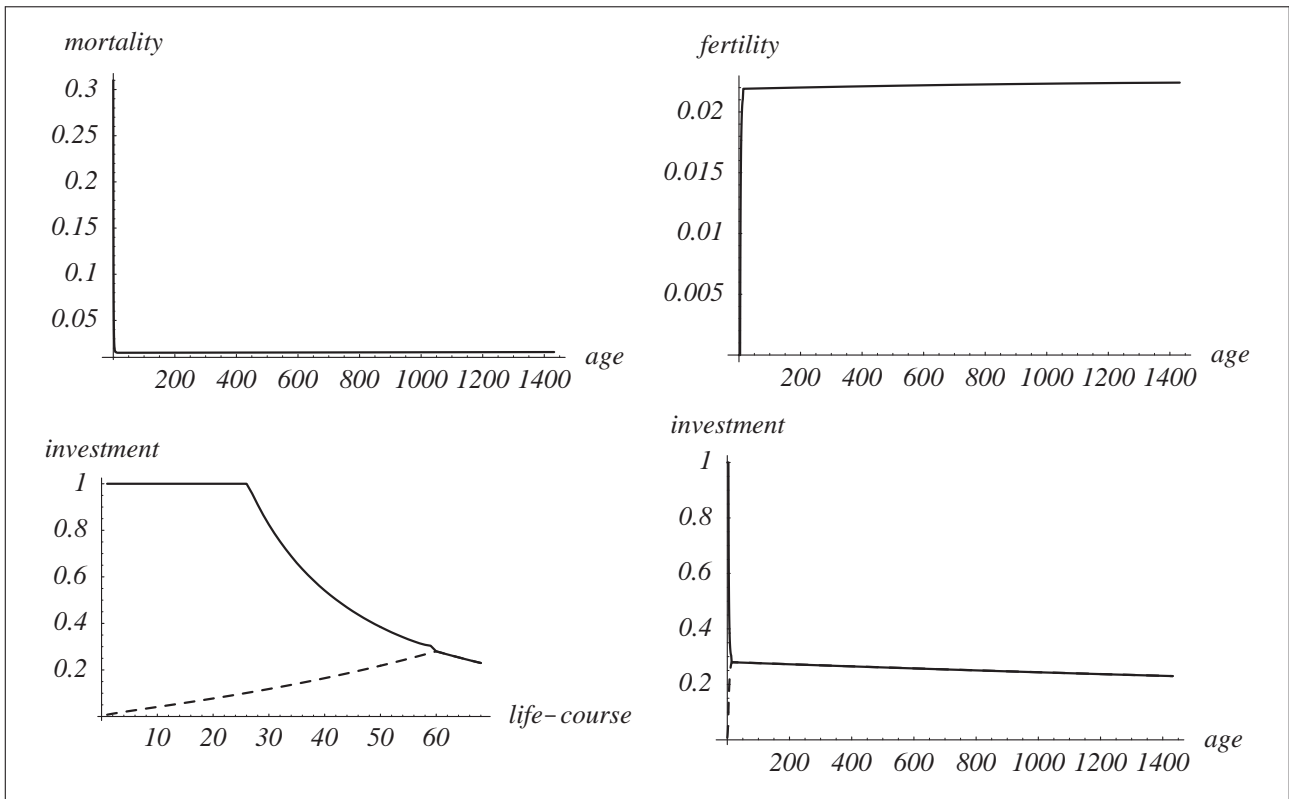


Figure 8: Example of Delayed Partial Senescence. (Dashed line: π_0 , level of investment required for maintenance. Life-course: measures the number of one unit changes in vitality) Note that in the lower right picture the trajectories of π and π_0 overlap, because π falls just slightly below π_0 .

6 Senescence Surfaces

The model sheds light on the characteristics that determine whether senescent or non-senescent life-histories are optimal. Whether a particular life-history is classified as senescent or non-senescent can be determined by the proportion of lifetime reproduction that is realized at ages when mortality rises, i.e. $\pi < \pi_0$. This indicator of senescence, S , is given by

$$S = \frac{\sum_{x=0}^{\infty} J_x l_x m_x}{\sum_{x=0}^{\infty} l_x m_x}, \quad (22)$$

where $J_x = 1$ if $\pi(\psi(x)) < \pi_0(\psi(x))$ and $J_x = 0$ otherwise. If $S = 1$ the strategy is fully senescent and if $S = 0$ then the strategy is fully non-senescent. All values in between describe mixed strategies. For the eight strategies discussed above, the "senescence" and "subsustenance" strategies are fully senescent, the "sustenance" and "supersustenance" strategies are fully non-senescent, and the other strategies are mixed.

Figure 9 illustrates the degrees of senescence indicated by S for combinations of η_r and η_g given the specific parameter combination $k = 3, \kappa = 0.8$ and $\delta = 0.1$. Surfaces span over different mortality conditions determined by b and c .

Three main features are noteworthy. First, low costs of reproduction ($\eta_r = 0.5$) correspond to non-senescent strategies over a broad range of intrinsic and extrinsic mortality while expensive reproduction ($\eta_r = 2$) mainly results in senescent life-histories. Second, low costs of reproduction promote mixed strategies whereas expensive reproduction favors exclusive strategies. Third, the left and right column appear to be roughly mirrored. High extrinsic mortality c only corresponds to senescent areas when maintenance costs are high ($\eta_g = 2$), whereas the opposite is true for low costs of maintenance ($\eta_g = 0.5$). This is striking. Low extrinsic risk of death favors senescence and high extrinsic risk favors non-senescence if maintenance is cheap.

Further points can be noted. Increasing intrinsic mortality b broadens the range of extrinsic hazards where mixed strategies are optimal if reproduction is cheap. If reproduction and maintenance are expensive, then non-senescence is only optimal at very low levels of mortality. If only reproduction is costly but maintenance is reasonable then very low mortality corresponds to mixed strategies.

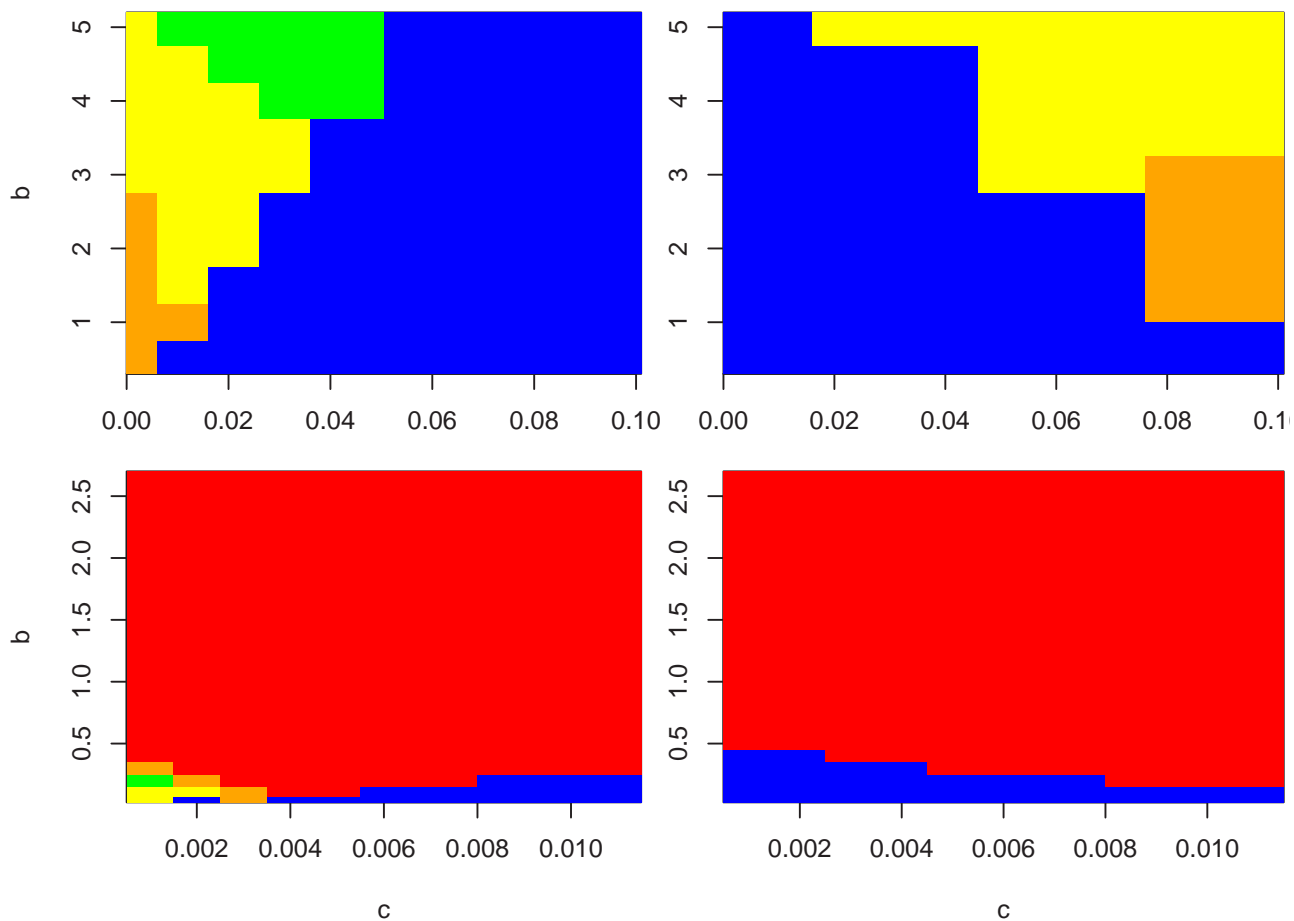


Figure 9: Senescence surfaces: *Red*=Senescence ($S=1$), *Blue*=Non-senescence ($S=0$), *Green*=Mixed ($0 < S < 0.35$), *Yellow*=Mixed ($0.35 < S < 0.65$), *Orange*=Mixed ($0.65 < S < 1$). Rows: $\eta_r = 0.5, \eta_r = 2$, Columns: $\eta_g = 0.5, \eta_g = 2$. In all cases $k = 3, \kappa = 0.8, \delta = 0.1$.

Table 2: Strategies for Cheap vs Costly Reproduction and Maintenance for Low and High intrinsic and extrinsic hazard of Death.

	$\eta_g = 0.5$				$\eta_g = 2$			
$\eta_r = 0.5$	4.2	<i>del sub</i>	<i>del sub</i>	<i>super</i>	4.2	<i>super</i>	<i>del sen</i>	<i>del sen</i>
	<i>b</i> 2.2	<i>del sub</i>	<i>super</i>	<i>super</i>	<i>b</i> 2.2	<i>super</i>	<i>super</i>	<i>del sen</i>
	0.2	<i>super</i>	<i>super</i>	<i>super</i>	0.2	<i>super</i>	<i>super</i>	<i>super</i>
	<hr/>	<i>c</i> 0.001	0.041	0.081	<hr/>	<i>c</i> 0.001	0.041	0.081
$\eta_r = 2$	2.2	<i>sub</i>	<i>sub</i>	<i>sub</i>	2.2	<i>sen</i>	<i>sen</i>	<i>sen</i>
	<i>b</i> 1.2	<i>sub</i>	<i>sub</i>	<i>sub</i>	<i>b</i> 1.2	<i>sen</i>	<i>sen</i>	<i>sen</i>
	0.2	<i>part</i>	<i>sub</i>	<i>del sub</i>	0.2	<i>sust</i>	<i>sust</i>	<i>sen</i>
	0.1	<i>part</i>	<i>del part</i>	<i>sust</i>				
	<hr/>	<i>c</i> 0.001	0.005	0.009	<hr/>	<i>c</i> 0.001	0.005	0.009

sen: senescence, del sen: delayed senescence, sub: subsustenance, del sub: delayed subsustenance, sust: sustenance, super: supersustenance, part: partial senescence, del part: delayed partial senescence

6.1 Costs and Risks

The values of the indicator of senescence S are determined by the underlying life-history strategies. Table 2 shows the interplay between cheap and costly reproduction and growth for low and high intrinsic and extrinsic hazards of death, with parameter values corresponding to those in Figure 9.

Values of $\eta_r < 1$ pertain to cases when reproduction is cheap (row one). The propensity for parallel investment in reproduction and growth is high. Therefore, efficient reproduction is associated with supersustenance strategies.

Values of $\eta_g < 1$ pertain to cases when growth is cheap (column one). Any decay is easily retarded to such a slow pace that the decline in vitality is virtually equivalent to maintenance but with the benefits that more energy can be used for reproduction. Therefore, efficient maintenance is associated with subsustenance strategies.

If the extrinsic hazard of death is high, early maturity is favored. This reduces the time of development and hence vitality at maturity. Vitality, however, determines the level of energy available and therefore the potential to reproduce. This potential might be small if

reproduction starts very early and should therefore be maintained if affordable. An increase in the extrinsic hazard of death shifts the strategy from subsustenance to sustenance. The shift from senescence to non-senescence indicated by S therefore reflects a shift from virtual maintenance to real maintenance of vitality. This explains the observation that higher levels of extrinsic mortality can favor non-senescence rather than senescence if maintenance is cheap, which, at first sight, seems counter-intuitive.

If maintenance is costly, $\eta_g > 1$, then increasing c promotes senescence. Any attempt to retard deterioration is expensive. Instead, reproductive potential is build up and subsequently harvested using all energy available and no energy is allocated to maintenance. In this case, the decay for organisms is assumed here to be exponential. Generally, for high maintenance costs, low levels of mortality favor non-senescence.

Supersustenance is a strategy that simultaneously allows for an early age of maturity but also for a further build up of reproductive potential. As long as reproduction and/or maintenance is cheap it can be optimal to precede any period of decay by a period of parallel investment in growth and reproduction. Since high levels of extrinsic mortality favor an early onset of reproduction, such combined strategies can be optimal when c becomes larger.

If both reproduction and growth are costly, $\eta_r > 1$ and $\eta_g > 1$, then exclusive allocation, i.e. senescence is optimal. Sustenance is favored only if total mortality is very low, because a low level of vitality requires little maintenance costs.

6.2 When Costs are Low

When costs of reproduction are low then supersustenance is favored. An especially efficient and cheap way of reproduction is vegetative propagation. If a newly grown unit of biomass could equally well remain a part of the individual or become a new individual itself, then any investment in growth is equivalently an investment in reproduction.

Candidate species for low costs of growth and maintenance are modular organisms. Body parts are easily replaced. Species with low costs of maintenance are expected to follow strategies of subsustenance. This may be indistinguishable from a non-senescence strategy in nature.

Complicated reproductive strategies could indicate high costs of reproduction. Highly

differentiated organisms with non-replaceable body parts might have higher maintenance costs.

7 The Humanesque Case

The example in Figure 1 corresponds to a senescence strategy ($S = 1$) and captures the general features of human life history. Mortality falls until the age of maturity of $\alpha \approx 13$. Mortality rises at a constant rate $\delta = 0.1$ from maturity onwards. Reproduction follows a hump-shaped curve. Note that the simple model does not capture menopause. Life-expectancy at birth as well as life-expectancy at maturity equal 25. If time units would correspond to years this setting of parameters might capture the main features of ancient human life-history. However, vitality in humans is only partly determined by the functioning of body cells. What makes humans a special case is the large brain with the capacity to learn and to acquire human capital (Kaplan and Robson, 2002). Still, the "humanesque" case can be used to understand what parameter crucially affects the boundary between senescence and non-senescence. Results are shown in Tables 3 and 4.

7.1 Changes in Efficiencies

The effects of deviations of the efficiency parameters from the humanesque case are shown in Table 3. Increasing η_g from 0.4 to 2 shifts the strategy between five different categories, ranging from supersustenance to senescence. This is a striking finding. Increasing η_r from 0.4 to 2 shifts the strategy between three different categories, ranging from supersustenance to senescence.

The costs of maintenance, η_g , are the crucial determinant of life-history strategies as classified above. The costs of reproduction, η_r , are of almost equal importance to the optimal life-history.

7.2 Changes in Mortality

Reduction in the mortality parameters b (to 0.1) or c (to 0.004) can change the strategy from senescent to non-senescent. Remarkably, however, their impact is constraint by the efficiencies

Table 3: Changes in Efficiencies

η_r	η_g	S	Strategy
2	0.4	0	Supersustenance
2	0.45	0.87	Delayed subsustenance
2	0.6	1	Subsustenance
2	1.0	0	Sustenance
2	2	1	Senescence
0.4	2	0	Supersustenance
1.0	2	0	Sustenance
2	2	1	Senescence

$k = 3$, $\kappa = 0.8$, $\delta = 0.1$, $b = 0.3$, and $c = 0.01$

Table 4: Interaction Between Efficiencies and Mortality

η_r	η_g	b	c	S
2	2	0.3	0.004	0
2	2	0.1	0.01	0
3	2	0.3	0	1
3	2	0	0.01	1
2	3	0.3	0	1
2	3	0	0.01	1

$k = 3$, $\kappa = 0.8$, and $\delta = 0.1$

as shown in Table 4. Higher costs of reproduction ($\eta_r = 3$) or maintenance ($\eta_g = 3$) preclude non-senescence even for zero levels of intrinsic or extrinsic mortality. The efficiencies of the growth and reproductive systems restrict life histories in their adaption to changing mortality conditions. For $\eta_r = \eta_g = 2$, the effects of changes in mortality on age and vitality at maturity, life-expectancy and the indicator of senescence can be seen in Figures 10 and 11.

The values of k , κ , and δ are of no direct importance to the boundary between non-senescence and senescence. Their influence on the strategy by changing the level of maximum vitality Ψ can be offset by changes in intrinsic mortality b . The parameters k , κ , and δ set the speed

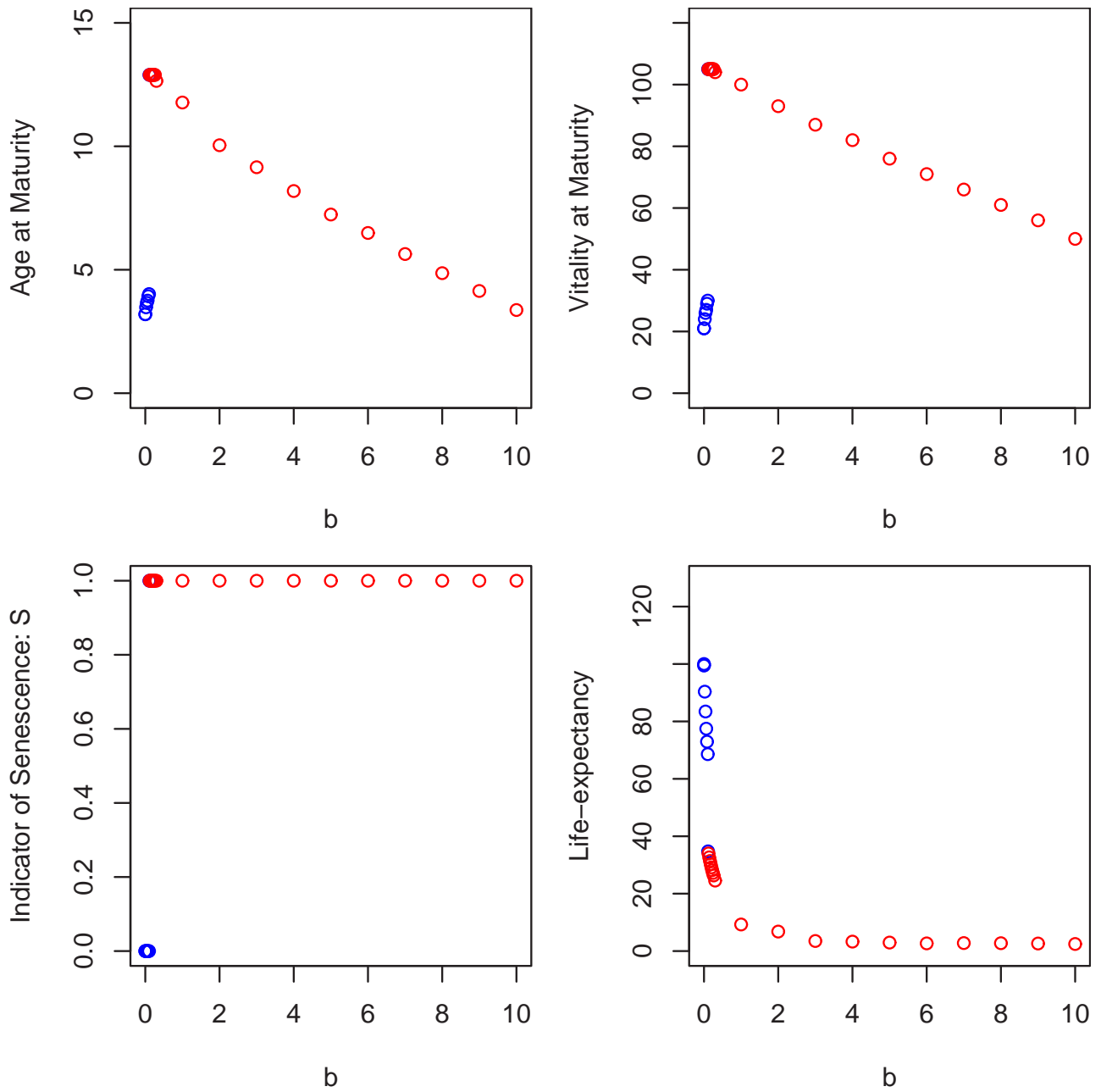


Figure 10: Changes in vitality-dependent mortality component b . (red=senescence, blue=sustenance)

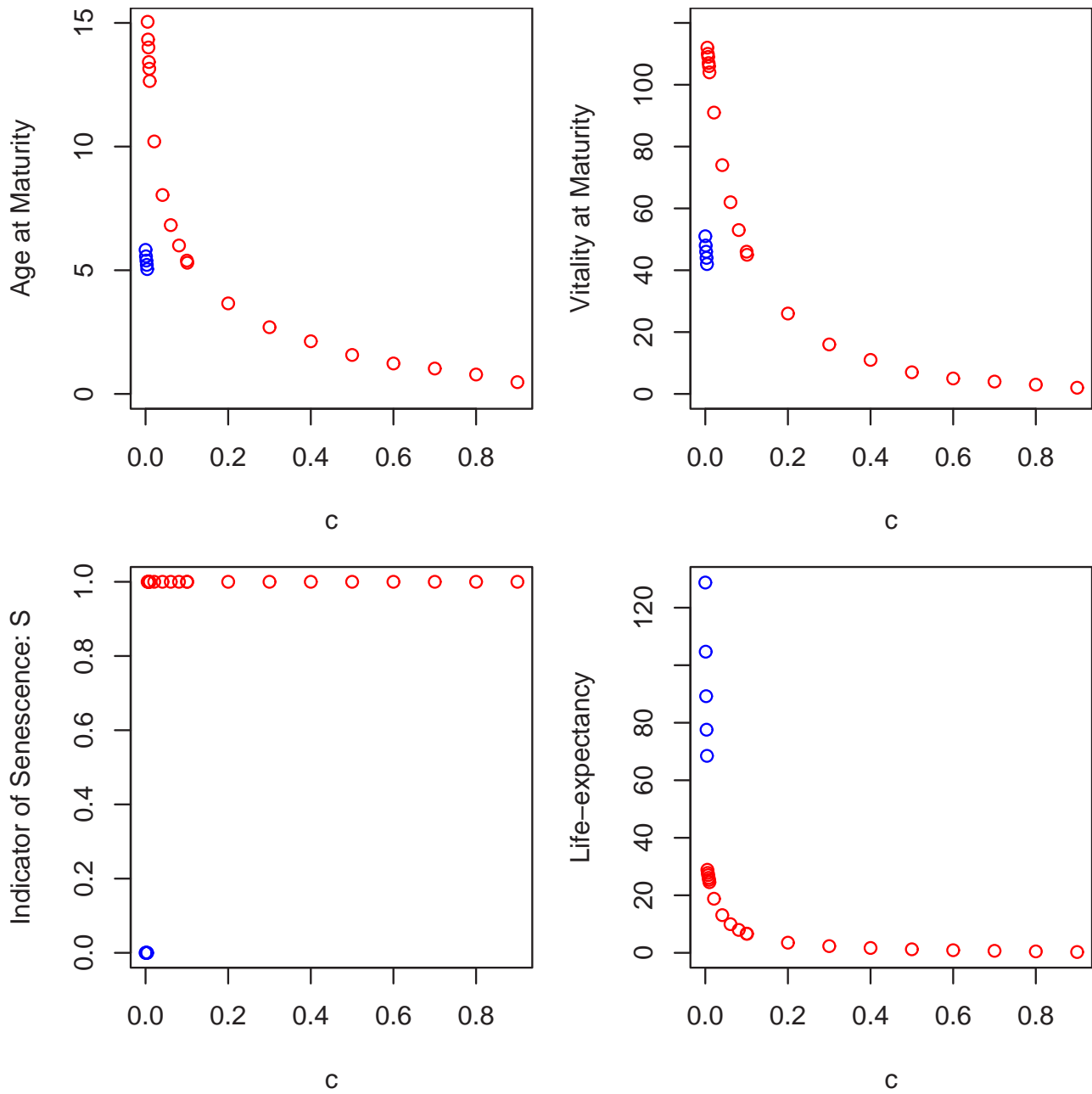


Figure 11: Changes in vitality-independent mortality component c . (red=senescence, blue=sustenance)

of growth and decay and therefore can be used to determine the time and size scale of the strategy.

8 Summary

The simple model developed above captures the main features of life - reproduction, growth and maintenance. The results show that the range of optimal life histories is wide.

The costs of growth and maintenance fundamentally determine whether an optimal life-history follows a non-senescent strategy or a senescent strategy. Of almost equal importance are the costs of reproduction. Mortality conditions may have a strong influence on the boundary between non-senescence and senescence if the costs of maintenance and reproduction are relatively low. If the costs are too high, even reduction of intrinsic or extrinsic mortality to zero cannot shift a senescent strategy to a non-senescent one.

High intrinsic mortality b increases the importance of high vitality. How important it is to attain and maintain this high vitality depends on the level of the extrinsic hazard c . The mortality parameters mainly influence details of a life-history, i.e. optimal age and vitality at maturity as well as life-expectancy.

Gompertzian senescence, i.e. exponential increasing mortality, is the prevalent optimal strategy only if both reproduction and maintenance are costly. If maintenance is cheap, then Gompertzian senescence is never optimal. If maintenance is costly but reproduction is cheap then Gompertzian senescence is only optimal at high levels of mortality.

Efficient maintenance and growth systems favor maintenance strategies while efficient reproductive systems favor strategies of parallel growth and reproduction.

Research is needed to pin-point the kind of species that follow different kinds of life-histories. The possibly broad ranging categories should be determined by the efficiencies of growth and reproductive systems. Modularity, vegetative reproduction, simple reproduction and growth as well as protected environments are characteristics that may lead to non-senescent strategies.

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