

Evolutionarily optimal age schedule of repair: Computer modelling of energy partition between current and future survival and reproduction

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Summary

The aim of this study was to clarify the relationships between environmental conditions and physiological constraints that persist during the evolution of a species on the one hand, and the strategies of energy investment used by an individual to repair on the other. We take as a basis for our study the evolutionary optimization approach and use as a criterion of optimality the individual's lifetime reproductive success. Using methods of mathematical theory of optimal control, we calculated some optimal strategies of energy partition between repair, current survival and reproduction for various levels of uncontrollable (external) mortality. The results are presented in the form of dependencies of mortality on age and dependencies of optimal energy partitioning on age and accumulated mortality risk. Three cases of energy partitioning were considered: that between reproduction and current survival, that between reproduction and repair, and that between current survival and repair. In the case of the trade-off between reproduction and current survival, we noted opposite influences of the levels of increase of uncontrollable and controllable sources of mortality on the strategy of energy partitioning, and the crucial role of the finiteness of maximum lifespan when age-independent sources of mortality only were present. In the case of the trade-off between reproduction and repair, we noted that controllable repair leads to the emergence of accelerated growth of mortality with age, which may be considered one possible cause of the accelerated ageing often observed in nature and expressed sometimes in the form of a Gompertz-Makeham equation. In the case of the trade-off between current survival and repair, we found that, in the case of increasing mortality, repair is sacrificed not only in favour of reproduction, but also in favour of current survival, so that accelerated ageing should be expected even when investment in reproduction does not increase with age. In general, we conclude that when mortality increases, the priority when expending energy is shifted primarily in favour of reproduction, then in favour of current survival, with repair having the lowest priority.

Keywords: energy allocation; evolution of ageing; optimal life histories; repair

Introduction

Preferential energy allocation of limited organismal resources to reproduction at the expense of individual survival seems to be the main cause of senescence, at least for higher animals (Medavar, 1952; Williams, 1957). In its most explicit form, this idea was expressed by Kirkwood (1981) as a need to divide energy and other resources of an individual between reproduction and repair in such a way as to optimize Darwinian fitness.

Within the framework of this general approach, some more specific questions arise which concern relationships between environmental conditions and physiological constraints in the course of species evolution on the one hand, and the optimal strategies of energy investment for repair on the other. Many of these questions were outlined by Kirkwood (1981). Here we try to answer some of them using a particular mathematical model which explicitly counterbalances the organism's investment in repair (i.e. future survival) with its investment in current survival (e.g.

safeguarding against hazards) and reproduction. We formulate the problem in terms of mathematical theory of optimal control and use two of the most concise and widespread forms of this theory: Pontryagin's maximum principle (Pontryagin *et al.*, 1962) and Bellman's dynamic programming (Bellman, 1957).

The maximum principle method allows one to explore the problem analytically but only in relatively simple cases. In more complex situations, numerical methods are necessary. Dynamic programming is a numerical procedure which does not allow an analytical solution but, compared with the maximum principle, does allow complex optimization problems to be formulated and solved (Mangel and Clark, 1988). Correspondingly, we use the maximum principle when the problem is simple, but use dynamic programming when it is more complex.

In some respects, the problems we pose and the methods we use are similar to those in Abrams and Ludwig (1995). The main difference in our approach is that it uses a more straightforward model of resource allocation and more explicit partition of causes of mortality into several conceptually different components. We believe this enables a better understanding of the peculiarities of an age schedule of repair. In addition, models of the type we use here match well the neural network approach to modelling the physiological processes of energy allocation in organisms (Mangel, 1990; Budilova *et al.*, 1995).

The model

We assume that in the evolution of a species, some criterion of fitness is maximized. For simplicity, take the lifetime reproductive success R_0 of the organism, defined by the integral:

$$R_0 = \int_0^T u(t)l(t) dt \quad (1)$$

where $u(t)$ is the fraction of energy allocated to reproduction, $l(t)$ is the survival function (i.e. the probability of survival to age t) and T is the maximum lifespan.

We agree that the Malthusian parameter, r , obtained by solving the Euler-Lotka equation

$$1 = \int_0^T e^{-rt}u(t)l(t) dt$$

could be a better measure of fitness, but believe that the complications introduced when using r instead of R_0 are not warranted here. It is known (Taylor *et al.*, 1974) that optimal r can be found by maximizing the right-hand side of the Euler-Lotka equation, keeping it equal to 1. Comparing the right-hand sides of Equation (1) and of the Euler-Lotka equation, we conclude that optimizing R_0 is equivalent to optimizing r when $r = 0$ (i.e. if the population size is stable). If $r \neq 0$, then optimizing r is equivalent to optimizing R_0 in the presence of an additional constant external mortality r , because the multiplier e^{-rt} may be formally considered part of survival. Acknowledging that we will usually consider a range of external mortalities, we believe that no essentially new feature would be introduced by changing R_0 for r as a criterion of optimality.

Another implicit simplification consists in equating the birth rate to the fraction of energy $u(t)$ allocated to reproduction in Equation (1). This means that we assume the rate of energy production to be constant (and equal to 1) independently of the individual's age. The maximum life span T is assumed to be finite. This is necessary for the maximum principle and dynamic programming methods of optimization to be applicable. In the case of semelparous species such an assumption is natural, whereas for iteroparous species it is somewhat artificial. We overcome this limitation, if necessary, simply by setting T to be very large.

Survival $l(t)$ is defined by the differential equation:

$$\frac{dl}{dt} = -\mu(t)l(t) \quad l(0) = 1 \quad (2)$$

where $\mu(t)$ is the mortality assumed to be composed of four components,

$$\mu(t) = a + bt + p(t) + q(t)$$

the first two of which are uncontrollable and the other two controllable by the individual. The first component, a , is the constant part of uncontrollable mortality (sometimes called ‘external’) and the second component, bt , is the part of mortality which increases uncontrollably with age at rate b (‘uncontrollable senescence’). In contrast to the first two components, the second and third components of $\mu(t)$ are assumed to be controllable by the individual, but in different ways. First, the individual can control its current level of mortality by allocating a fraction of energy $v(t)$ for this purpose, which we refer to as the fraction of energy allocated to current survival. Namely, we assume that the third component of mortality has the form:

$$p(t) = \frac{c}{v(t)}$$

where c is a non-negative constant. Secondly, the individual can control the rate of senescence – that is, the rate of irreversible increasing (‘accumulating’) mortality with age – by allocating a fraction of energy $w(t)$ for this purpose, which we refer to as the fraction of energy allocated to repair, or to future survival. Namely, we assume that the fourth component of mortality, $q(t)$, varies with age in accordance with the following differential equation:

$$\frac{dq}{dt} = \frac{d}{w(t)} \quad q(0) = 0 \quad (3)$$

where d is a non-negative constant.

We assume that all the needs of the organism, other than reproduction, current survival and repair, are almost constant and need not be included explicitly in the model. In particular, we neglect any allocation of energy to growth, which is equivalent to taking into consideration only the adult period of life history. That is, we assume:

$$u(t) + v(t) + w(t) = 1 \quad (4)$$

Thus the optimization problem we are to solve is the problem of searching, taking into account state equations (2) and (3) and constraint (4), for the functions $u(t)$, $v(t)$ and $w(t)$ that maximize the fitness criterion (1).

Below, we consider some particular cases of this optimization problem.

Trade-off between reproduction and current survival

Let us first disregard the fourth component $q(t)$ of total mortality $\mu(t)$, setting $q(t) \equiv 0$ and $w(t) \equiv 0$, and take into account only state equation (2) but not (3). Although our main objective is repair and the fourth component of mortality is responsible for it, let us study the behaviour of the model without this component, at least to form some point of reference.

The optimal solution can easily be found by the maximum principle method, writing the Hamiltonian for (1) and (2):

$$H(l, u, t) = u(t)l(t) - x(t)\mu(t)l(t)$$

or

$$H(l, u, t) = l(t) \left\{ u(t) - x(t) \left[a + bt + \frac{c}{1 - u(t)} \right] \right\}$$

where the co-state variable $x(t)$ is defined by the differential equation:

$$\frac{dx}{dt} = -\frac{\partial H}{\partial l} = -u(t) + x(t) \left[a + bt + \frac{c}{1 - u(t)} \right] \quad x(T) = 0 \tag{5}$$

and seeking the maximum of H in respect of u for each value of t .

To find this maximum, we calculate the partial derivative of H in respect of u and equate it to zero:

$$\frac{\partial H}{\partial u} = l(t) \left\{ 1 - x(t) \frac{c}{[1 - u(t)]^2} \right\} = 0$$

which gives:

$$u(t) = 1 - \sqrt{cx(t)} \tag{6}$$

Inserting (6) into (5), we obtain the following differential equation for $x(t)$:

$$\frac{dx}{dt} = 2\sqrt{cx(t)} + (a + bt)x(t) - 1 \quad x(T) = 0 \tag{7}$$

Solving numerically (7) for $x(t)$ and inserting the solution into (6), we find the optimal strategy $u(t)$ of energy partition between reproduction and current survival.

Below, we present examples of optimal strategies calculated for different values of the parameters a , b and c . We do not consider the case when c is zero, because any energy allocated to survival would have no effect and hence the optimal strategy should be to allocate, at any age, all energy to reproduction.

In Fig. 1, two cases when only the parameter c is not equal to zero – namely, $c = 0.015$ (upper curve) and $c = 0.030$ (lower curve) – are shown for $T = 100$. We see that for $c = 0.030$, the optimal value of u for all t distant enough from T is about 0.5. This is also the case for $c = 0.015$, but for t even still more distant from T .

Thus we may conclude that for finite T , the smaller is c the smaller should be the energy allocated to survival. This is not surprising, because for smaller c the effect of allocation of energy to survival is smaller than its effect on reproduction (which becomes 0 for $c = 0$). As regards dependence on age, we see that the fraction of energy allocated to survival decreases monotonically as t ap-

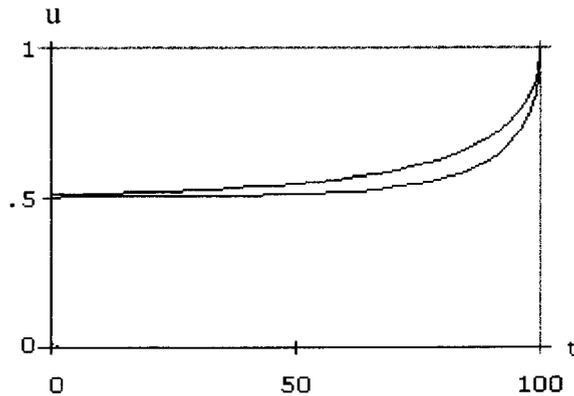


Figure 1. Dependence of u on t for $c = 0.015$ (upper curve) and $c = 0.030$ (lower curve) when $a = b = d = 0$ and $T = 100$.

proaches T . This is also intuitively acceptable, because to die at age t means not to be alive (and hence not to be able to reproduce) within the period from t to T , but certainly this loss is smaller when t is closer to the age of inevitable death T . At $t = T$, we must have $u(T) = 1$ for any c , as can be seen directly from (6) and (7).

For infinite T , the situation is quite different: independently of c the fraction of energy devoted to current survival at any age t is equal to 0.5. To make this intuitively more acceptable, let us try to minimize (1) directly for $T = \infty$ assuming that $u(t)$ is equal, for all t , to some constant, U . We have in this case:

$$R_0(U) = \int_0^{\infty} U e^{-\frac{c}{1-U}t} dt$$

Integrating gives:

$$R_0(U) = \frac{U(1-U)}{c}$$

Calculating the derivative of $R_0(U)$ with respect to U and equating it to 0 we obtain:

$$\frac{1-2U}{c} = 0$$

from which we find the optimal value $U = 1/2$, which indeed does not depend on c . (What, however, depends on c is optimal expected lifetime reproductive success of the individual, which is equal in this case to $R_0(1/2) = 1/4c$.)

Summarizing, when neither external mortality nor controllable or uncontrollable ageing are present, there is a striking distinction between the case of an unconstrained maximum lifespan (usually, iteroparous species) when the strategy of energy allocation does not depend on age, and the case of a fixed-in-advance maximum lifespan (usually, semelparous species) when it does. In fact, the limitation of the maximum lifespan may be considered simply as a kind of external uncontrollable mortality. The effect of this source of mortality consists in decreasing the fraction of energy spent on survival and hence increasing current controllable mortality $p(t)$ when t approaches T , which ends by allocating all energy to reproduction at $t = T$ (making mortality infinite at this point). This is illustrated in Fig. 2, which shows, for the same two cases in Fig. 1, the dependence of p (here a single component of the total mortality μ) on age t .

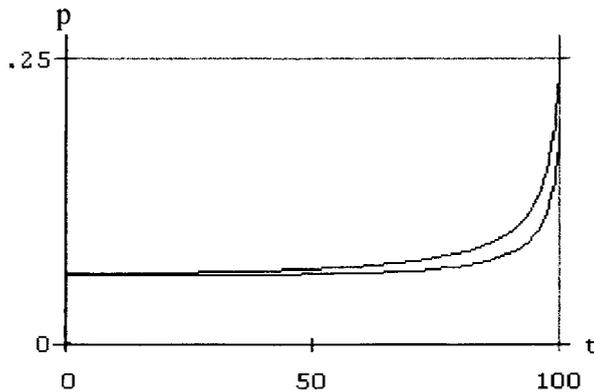


Figure 2. Dependence of current controlled mortality p on t for $c = 0.015$ (upper curve) and $c = 0.030$ (lower curve) when $a = b = d = 0$ and $T = 100$.

That the fraction of energy allocated to current survival decreases when t approaches T implies that statistically we observe an increase in mortality with age from $q(0) = c/v(0)$ at $t = 0$ up to infinity at $t = T$. This illustrates once again that a standard definition of ageing as an increase in mortality with age is not adequate. Indeed, in the above situation, when only c differs from 0, there is no accumulation of mortality (which we intuitively associate with ageing), since, in principle, the individual could at any age reduce mortality down to its minimum possible value of c simply by allocating all available energy to current survival.

Let us now look at the influence of the level of external mortality, associated with the parameter a , on the optimal energy partition between reproduction and current survival. In Fig. 3, two optimal strategies of energy allocation for $a = 0.075$ (upper curve) and $a = 0.015$ (lower curve), both for $c = 0.03$, are shown. We can see that, as with $a = 0$, the optimal value of $u(t)$ tends to some constant U , confined between 0.5 and 1, when t is sufficiently distant from T . But this constant is now no longer 0.5 and is determined by the values of a and c , the effects of which on U are in the opposite direction: U is larger for larger values of a and for smaller values of c . The first effect is widely known (Stearns, 1992): more severe external conditions alter an individual's priorities in favour of reproduction. The inverse effect of increasing c was explained above: for larger values of c , the benefits of allocating additional energy to current survival also increase. What we wish to emphasize, particularly in this connection, is that the opposite effect of increasing a and c is due to the distinction between the uncontrollability and controllability of these two sources of mortality.

It is interesting to note that the effect of the dependence of U (i.e. the fraction of energy allocated to reproduction in the case of infinite T) on c , which was absent in the case of $a = 0$, is present now when $a > 0$. In fact, U depends only on the ratio of c to a , $k = c/a$. To demonstrate this, let us again directly maximize (1) assuming that $u(t) = U$ and $T = \infty$.

We have:

$$R_0(U) = \int_0^{\infty} U e^{-(a + \frac{c}{1-U})t} dt$$

which, after integrating, gives:

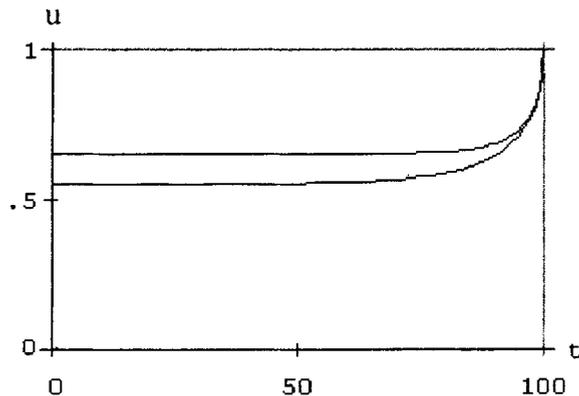


Figure 3. Dependence of u on t for $a = 0.075$ (upper curve) and $a = 0.015$ (lower curve) when $c = 0.030$, $b = d = 0$, and $T = 100$.

$$R_0(U) = \frac{U(1-U)}{a(1-U)+c}$$

Calculating the derivative of $R_0(U)$ with respect to U and equating it to 0, we obtain a quadratic equation:

$$aU^2 - 2U(a+c) + (a+c) = 0$$

from which we find the optimal solution:

$$U = (1 + c/a) \left(1 - \sqrt{\frac{c/a}{1 + c/a}} \right)$$

The dependence of U on $k = c/a$ is illustrated in Fig. 4 for $k = 0-10$. We see that U decreases monotonically with k . But k is directly proportional to c and inversely proportional to a . Hence U , the fraction of energy allocated to reproduction, is a decreasing function of c for fixed a and an increasing function of a for fixed c .

Until now we have assumed parameter b to be zero. In Fig. 5, we present two curves obtained with $b = 0.01$ (upper curve) and $b = 0.001$ (lower curve) for $c = 0.03$ and $a = 0$. The effect of the rate of uncontrollable growth of mortality associated with b may be interpreted as follows: it is similar to the effect of constant external mortality associated with a , but increases with age. Namely, it is expressed as an age-related steady increase in the fraction of energy allocated to reproduction, $u(t)$, and hence as a decrease in the fraction of energy allocated to current survival, and the greater is b the faster is this increase in $u(t)$. Note, however, that this effect is quite different from the similar increase in $u(t)$ with age we observed in Fig. 1. There it was caused by the finiteness of T , whereas here the cause is an age-related linear growth in mortality, bt . Of course, the increase in $u(t)$ due to the finiteness of T is also observed in Fig. 5, but we consider this simply to be an end effect, which manifests itself only when t is very close to T , which, in turn, is so large that the behaviour of the strategy near T has no real importance.

The direct consequence of reducing the fraction of energy allocated to current survival with age is an increase in the corresponding component of mortality $p(t) = c/v(t)$, which is added to uncontrollable linear growth bt . Again, as in Fig. 1, this additional increase in mortality may be interpreted as ageing by an external observer, although it is, in principle, completely reversible at

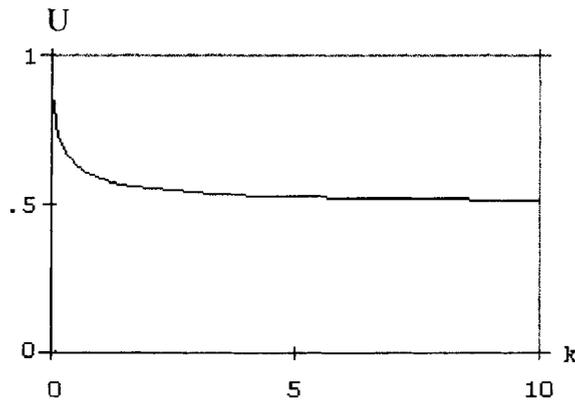


Figure 4. Dependence of U , the fraction of energy allocated to reproduction in the case of infinite T , on $k = c/a$ when $b = d = 0$.

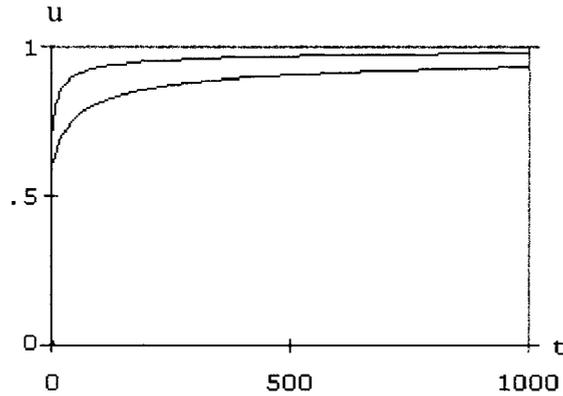


Figure 5. Dependence of u on t for $b = 0.01$ (upper curve) and $b = 0.001$ (lower curve) when $c = 0.030$, $a = d = 0$, and $T = 1000$.

any age. The dependence of $p(t)$ on t for the two strategies of energy allocation presented in Fig. 5 is shown in Fig. 6. We see that the growth of $p(t)$ slows with age during the initial part of the life history, then becomes nearly stable so that $p(t)$ grows almost linearly. The resulting behaviour of the total mortality $\mu(t) = bt + p(t)$ will be the same: growth, slow at the beginning, then becomes linear (though having a rate exceeding b). In the next section, this result will be compared with the behaviour of the mortality curve when mortality is accumulated.

Trade-off between reproduction and repair

Now we disregard the components of the model relating to $p(t)$ by setting $p(t) \equiv 0$ and $v(t) \equiv 0$. This does not necessarily mean that no energy is spent on survival but rather that this proportion of energy is roughly constant and therefore can be omitted from the optimization procedure.

Thus, we focus on the partition of energy between reproduction and the prevention of an irreversible age-dependent increase in mortality. To solve the problem, the optimality criterion (1) should be maximized with respect to $u(t)$, taking into account both state equations (2) and (3). One way to do this is to apply the maximum principle.

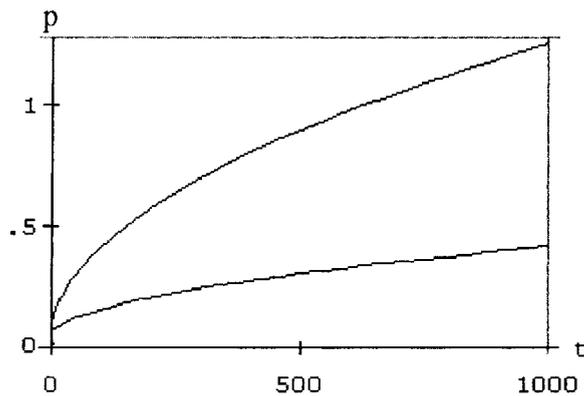


Figure 6. Dependence of current controlled mortality p on t for $b = 0.01$ (upper curve) and $b = 0.001$ (lower curve) when $c = 0.030$, $a = d = 0$, and $T = 1000$.

The Hamiltonian in this case has the form:

$$H(l, q, u, t) = u(t)l(t) - x(t)u(t)l(t) + y(t) \frac{d}{1 - u(t)}$$

or

$$H(l, q, u, t) = l(t)\{u(t) - x(t)[a + bt + q(t)]\} + y(t) \frac{d}{1 - u(t)}$$

where the co-state variables $x(t)$ and $y(t)$ are defined by the differential equations:

$$\frac{dx}{dt} = -\frac{\partial H}{\partial l} = -u(t) + x(t)[a + bt + q(t)] \quad x(T) = 0 \tag{8}$$

and

$$\frac{dy}{dt} = -\frac{\partial H}{\partial q} = l(t)x(t) \quad y(T) = 0 \tag{9}$$

The maximum principle also gives the condition that permits us to express $u(t)$ as a function of $l(t)$, $y(t)$ and t :

$$u(t) = 1 - \sqrt{\frac{-y(t)d}{l(t)}} \tag{10}$$

Replacing $u(t)$ in (2), (3), (8) and (9) by (10), we obtain a system of four differential equations for two state and two co-state variables, $l(t)$, $q(t)$, $x(t)$ and $y(t)$. Finding the solution to this system and replacing $l(t)$ and $y(t)$ in (10) by their solutions, we will obtain the optimal strategy of energy partition $u(t)$.

The above system of differential equations can be solved only using numerical methods; that is, by discretizing the problem at this stage. Another approach is to discretize the problem at the beginning and apply dynamic programming. In some respects, this approach is preferable for problems like those considered here. Both the building of models and the finding of solutions are more explicit and intuitively comprehensible. In addition, survival, $l(t)$, is not included in dynamic programming as a state variable, which reduces the dimensionality of the problem.

In the present case, the method of dynamic programming proceeds as follows. Lifetime from 0 to maximum life span T and the range in variation of the component of mortality q from 0 to some maximum Q are divided into small steps Δt and Δq , and a gain function $F(t, q)$ is defined as the maximum expected reproductive success which can be attained in the interval from t to T if the cumulative component of mortality is equal to q at t . The function $F(t, q)$ can be calculated by iterating backwards from T to 0 starting from some known values of this function, $F(T, q)$ at $t = T$. In particular, in our case it is natural to set $F(T, q) = 0$ for all q , assuming that no offspring are produced at $t = T$. In parallel with $F(t, q)$, the optimal fraction of energy $u(t, q)$ is also calculated.

To calculate $F(t, q)$ and $u(t, q)$ for any t , given the values of $F(t + \Delta t, q)$ for all q , the following equation, the basic equation of dynamic programming (Mangel and Clark, 1988), is used:

$$F(t, q) = \max_u \left\{ \left[F\left(t + \Delta t, q + \frac{d}{1 - u} \Delta t\right) + u \right] \exp[(-a - bt - q)\Delta t] \right\}$$

The optimal value $u(t, q)$ is that value of u that furnishes the maximum value for the right-hand side of this equation. Below, several examples of optimal strategies for different values of the parameters a , b and d are given.

In Fig. 7, only the parameter d is non-zero; that is, no uncontrollable mortality is present and the rate of age-related mortality accumulation depends on the fraction of energy allocated to repair,

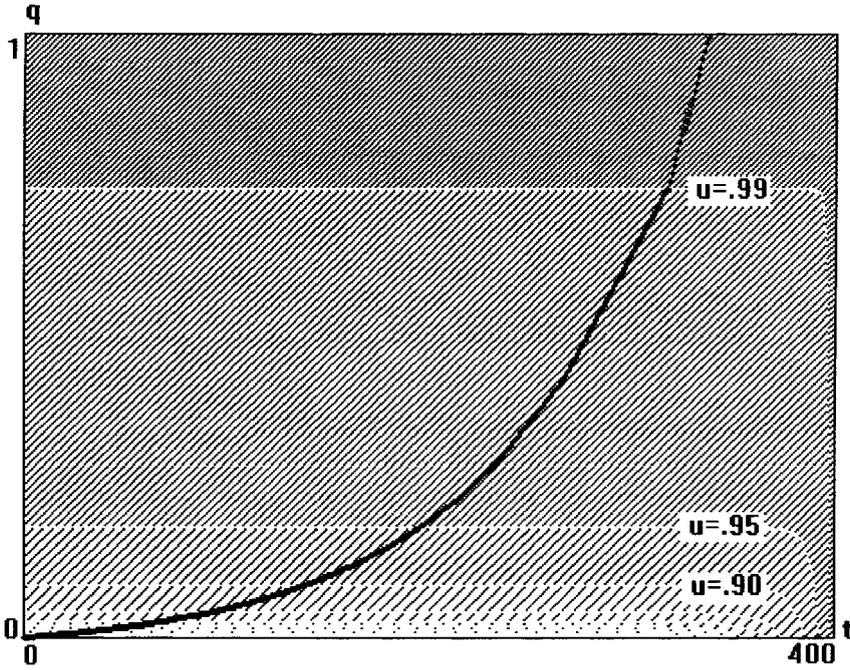


Figure 7. Dependence of u on t and q (shown by density of hatching) and dependence of q on t (bold curve) for $d = 0.000125$, $a = b = c = 0$, and $T = 400$.

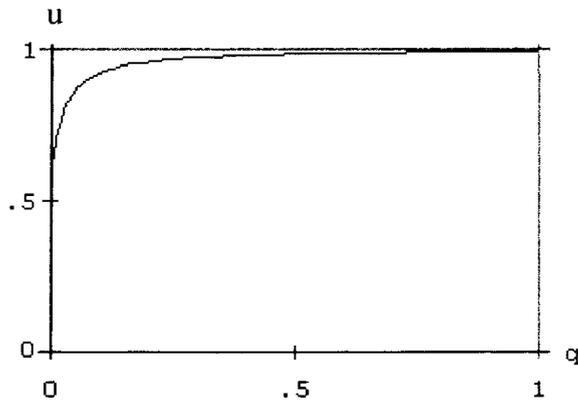


Figure 8. Dependence of u on accumulated mortality q at $t = T/2$ for $d = 0.000125$, $a = b = c = 0$, and $T = 400$.

$w = 1 - u$. As a result, for all t not very close to T , the optimal energy partition does not depend on t but clearly depends on q , the level of mortality attained at this age. The form of dependence of u on q for $d = 0.000125$ is shown in more detail in Fig. 8 for $t = T/2$. Because the optimal fraction of energy allocated to repair decreases with increasing mortality, it is intuitively acceptable: it does not make sense to spend energy on future survival when there is a high probability of death in the near future. This effect is similar to that of external uncontrollable mortality (associated with the parameter a in the expression for $\mu(t)$ and illustrated by Fig. 2): accumulated mortality would

become uncontrollable and influence the optimal energy partition in the corresponding way. This conclusion contrasts with the effect of augmentation of the level of current controllable mortality associated with the parameter c . This was illustrated in Fig. 1, where the optimal fraction of energy allocated to current survival increases for higher c . We see that when q , the accumulated mortality, increases from 0 to infinity, the optimal value of u increases up to a value of 1 and, correspondingly, the fraction of energy allocated to repair, w , decreases to 0.

Although the strategy of optimal energy partition does not depend explicitly on age t (for t sufficiently distant from T), decisions on energy allocation do depend on age because of increasing q with t for any individual life history. This is shown in Fig. 7, where the bold curve shows the dynamics of accumulating mortality by an individual with age: the accumulated mortality, q , grows and correspondingly the fraction w of energy allocated to repair decreases. In turn, decreasing w with age increases the rate of accumulating mortality, d/w . This leads to the form of dependence of q on t that we see in Fig. 7: mortality is accumulated at an increasing rate with age, although this accumulation would be linear if the fraction of energy allocated to repair was constant. Note that in the case of uncontrollably increased mortality presented in Fig. 6, we did not observe such an acceleration, although the fraction of energy allocated to survival did decrease.

The observed acceleration correlates well, at least qualitatively, with the widely observed real dependence of mortality on age. The most well known of such approximations is the Gompertz-Makeham equation (Gompertz, 1825; Makeham, 1860):

$$\mu(t) = \alpha e^{\beta t} + \gamma$$

(α , β and γ are non-negative constants), which clearly demonstrates an accelerated growth in mortality with age. Our results argue for an explanation of this effect in terms of some kind of autocatalytic process. Indeed, because d (i.e. the minimum rate of accumulated mortality attainable when all energy is allocated to repair) is greater than 0, some increase in mortality occurs for any t (including $t = 0$). But this increase in mortality causes a reduction in the fraction of energy allocated to repair, w , which, in turn, augments the rate of increase in mortality, d/w , which, as a consequence, results in a still greater reduction in the amount of energy allocated to repair, and so on.

The effect of augmentation of the parameter d on optimal energy partition can be seen in Fig. 9, which demonstrates that, for $d = 0.00019$, as compared with $d = 0.000125$ in Fig. 7, the optimal value of u for the same q is lower – that is, the optimal value of w is higher. That means that for bigger d it is optimal to spend more energy on repair at the same level of accumulated mortality. This correlates with a similar conclusion above in relation to augmentation of the parameter c and makes common sense: for bigger d the investment in repair becomes relatively more profitable (or rather less unprofitable!).

As regards individual life history, we see from comparing Fig. 9 with Fig. 7 that, despite the fact that more energy is spent on repair for $d = 0.00019$, higher values of q are attained for younger ages compared with $d = 0.000125$. That means, in particular, that the expected lifespan is less for $d = 0.00019$.

The next example, presented in Fig. 10, illustrates the influence of an additional uncontrollable source of mortality given by $a = 0.1$. We see, by comparing Fig. 10 with Fig. 7, that an additional mortality of this kind accelerates u towards 1 with increasing q . Roughly speaking, Fig. 10 may be likened to Fig. 7 shifted down by 0.1. That is, an additional external mortality decreases the amount of energy invested in repair.

The situation presented in Fig. 11 differs from that in Fig. 10 due to the dependence of uncontrollable mortality on age that is the result of an explicit dependence of the optimal decision on age t . Namely, for the same level of q , older organisms should devote a larger proportion of energy

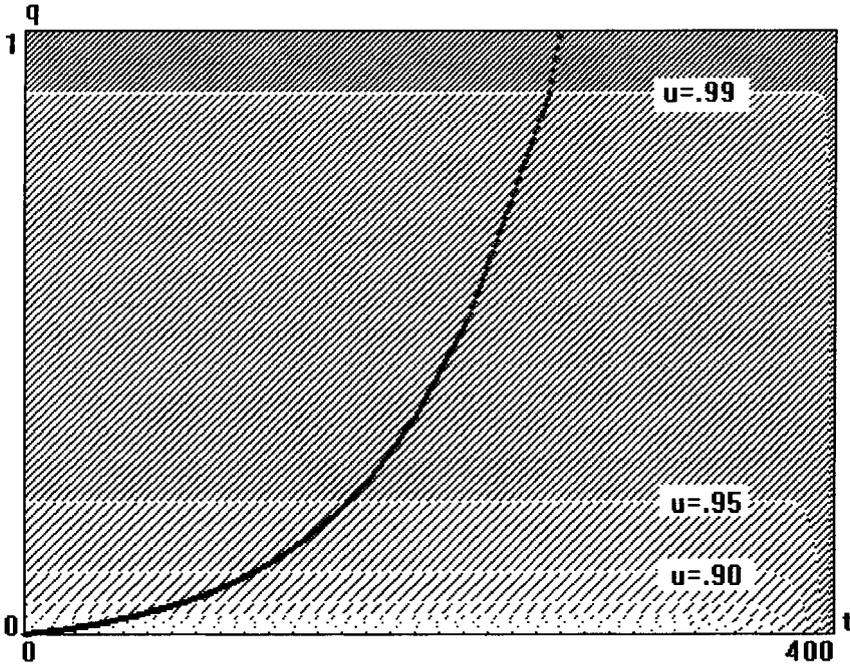


Figure 9. Dependence of u on t and q (shown by density of hatching) and dependence of q on t (bold curve) for $d = 0.00019$, $a = b = c = 0$, and $T = 400$.

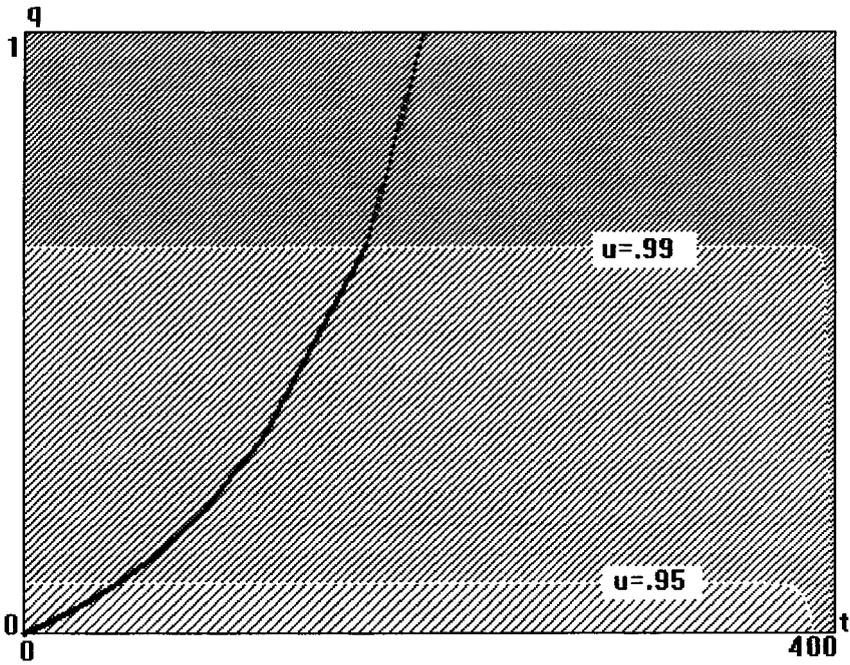


Figure 10. Dependence of u on t and q (shown by density of hatching) and dependence of q on t (bold curve) for $a = 0.1$, $d = 0.000125$, $b = c = 0$, and $T = 400$.

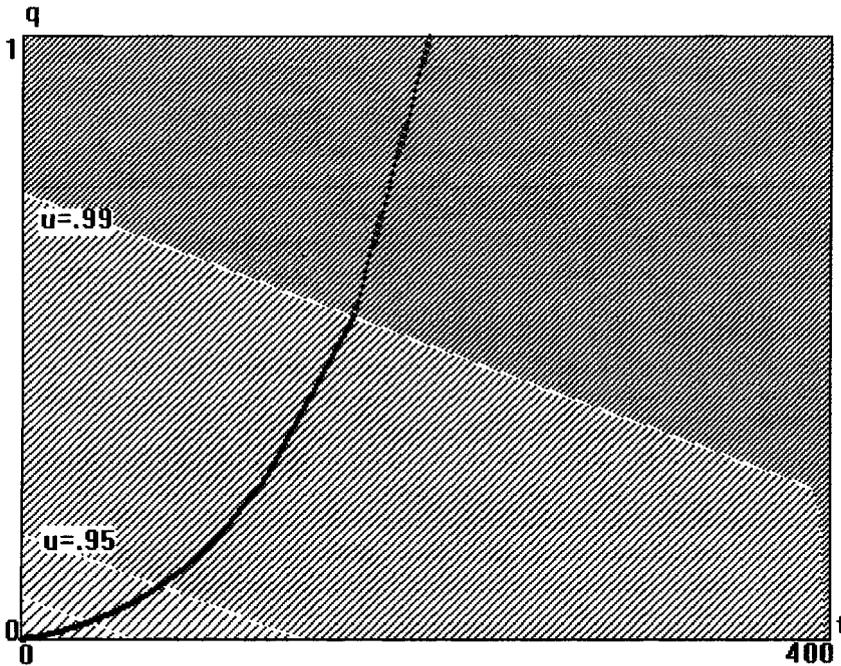


Figure 11. Dependence of u on t and q (shown by density of hatching) and dependence of q on t (bold curve) for $b = 0.005$, $d = 0.000125$, $a = c = 0$, and $T = 400$.

to reproduction compared with younger ones. However, this distinction is not fundamental, at least for t distant enough from T , and simply reflects the increase in overall mortality with age. Indeed, if we replace the state variable q by the sum $q + bt$, we obtain (Fig. 12) a picture similar to that in Fig. 7, where there is no dependence of the optimal energy partition strategy on t for t not very close to T .

Nevertheless, the difference between Figs 11 and 12 may be important from the point of view of modelling the structure of the neuroendocrine network that controls optimal energy partition control (Budilova *et al.*, 1995) because the organism should have two sensors in the first case, one for age t and the other for accumulated mortality q , and only one sensor, for $q + bt$, in the second.

Trade-off between current survival and repair

Let us now calculate some optimal energy partitions between current survival and repair assuming that the reproduction rate is constant at 1 (which amounts to maximizing the mean expected lifespan of the individual). The following basic dynamic programming equation may be used for this purpose:

$$F(t, q) = \max_v \left\{ \left[F\left(t + \Delta t, q + \frac{d}{1-v} \Delta t\right) + 1 \right] \exp\left[\left(-\frac{c}{v} - q\right) \Delta t\right] \right\}$$

where v is the fraction of energy allocated to survival. For $c = 0.05$ and $d = 0.0025$, the optimal solution is presented in Fig. 13. We see that the optimal energy partition is shifted in favour of survival at the expense of repair as accumulated mortality q grows. Because, as seen in Fig. 13,

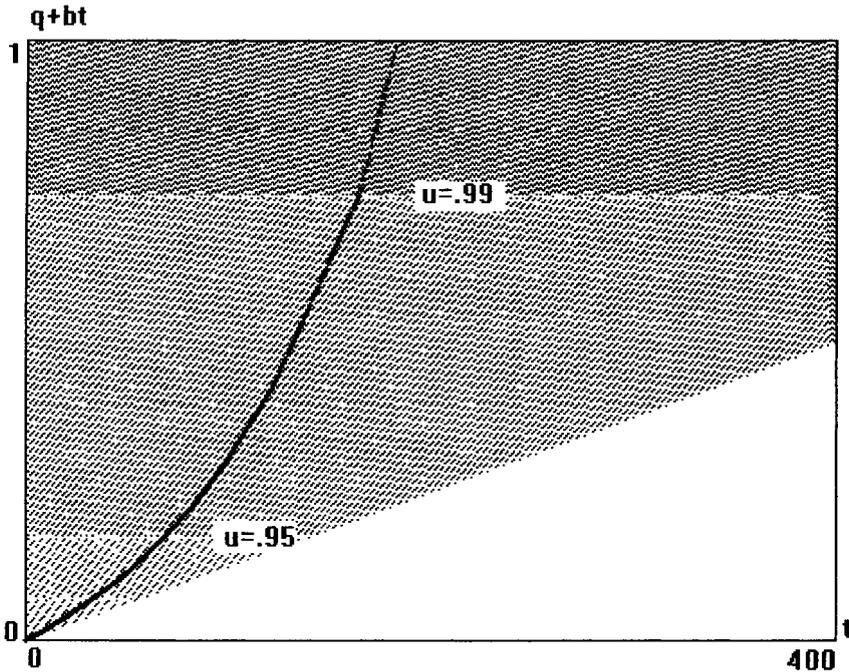


Figure 12. The same as in Fig. 11, but with the axis q replaced by $q + bt$.

accumulated mortality increases during an individual's life history, we will observe a constant shift in energy in favour of current survival as the individual ages.

The effect of decreasing the parameter c , associated with current survival, from 0.05 to 0.001, may be seen in Fig. 14. The result is rather natural: for the same accumulated mortality, energy investment is shifted in Fig. 14, compared with Fig. 13, in favour of repair at the expense of current survival. But the same general tendency persists: more and more energy should be devoted to current survival as mortality accumulates.

Note, also, that in the same way as with the trade-off between reproduction and repair, we again observe the phenomenon of accelerated (faster than simple linear) growth in mortality during an individual's life history caused by a decrease in energy investment to repair with age. Thus, we may expect manifestations of this phenomenon even when reproductive effort does not increase with age.

Discussion

The main objectives of this study were to determine evolutionarily optimal strategies for allocating energy to current and future survival and to determine the resulting individual patterns of increasing mortality with age. Three cases of energy partitioning were considered: that between reproduction and current survival (maintenance), that between reproduction and repair (future survival), and that between current and future survival.

The most interesting thing that we noted when considering the case of the trade-off between reproduction and current survival was the opposite influences of the levels of increase of uncontrollable and controllable sources of mortality on the strategy of energy partitioning. While in-

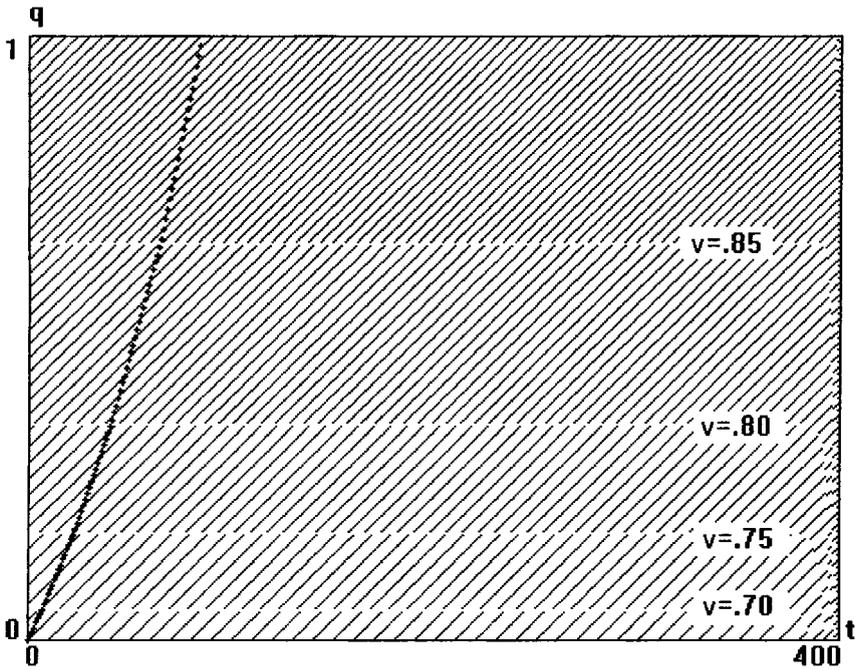


Figure 13. Dependence of v on t and q (shown by density of hatching) and dependence of q on t (bold curve) for $c = 0.05$, $d = 0.0025$, $a = b = 0$, and $T = 400$.

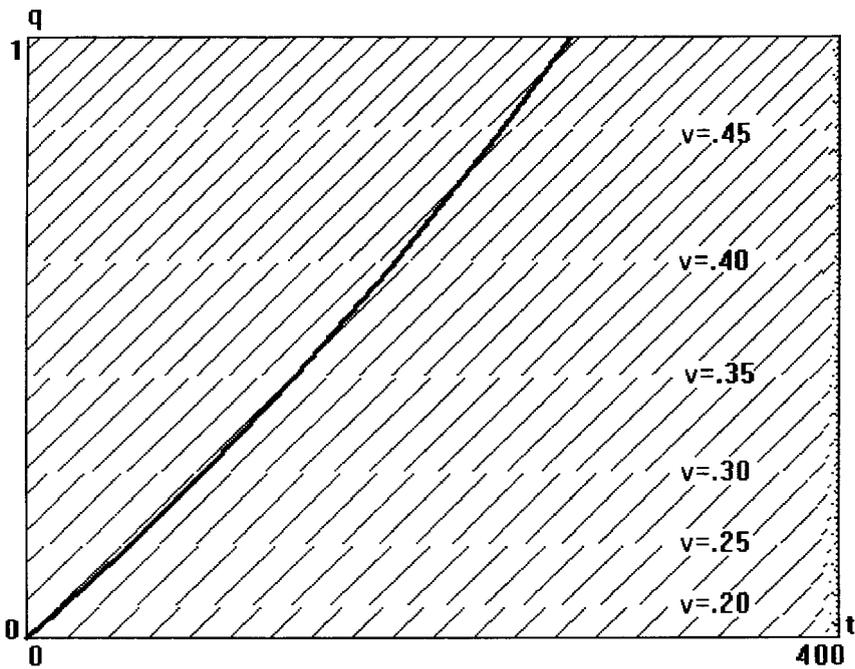


Figure 14. Dependence of v on t and q (shown by density of hatching) and dependence of q on t (bold curve) for $c = 0.001$, $d = 0.0025$, $a = b = 0$, and $T = 400$.

creasing uncontrollable external mortality shifts the investment in energy in favour of reproduction at the expense of individual survival, intensifying the source of currently controllable mortality forces the organism to devote more energy to its own survival (simply because the relative effectiveness of investing in survival increases).

We also noted the crucial role of the finiteness of maximum lifespan when age-independent sources of mortality only were present. The constraint imposed on the maximum lifespan influences the strategy, making it age-dependent. The effect of this constraint on the optimal decision is the more pronounced the closer the organism is to the age of maximum lifespan (when all energy should be allocated to reproduction). But limiting the maximum lifespan becomes less important if there is an increase in mortality with age, whether uncontrollable or controllable, or both (though the end effect of the need to allocate more and more energy to reproduction persists).

The control of increased mortality (i.e. controllable repair) consists of the emergence of accelerated growth of mortality with age. The age-dependent increase in mortality reduces the proportion of energy devoted to repair, which, in turn, augments the rate of increase in mortality, which further reduces the amount of energy allocated to repair, and so on. That is, the accumulation of mortality is inherently autocatalytic. In a sense, this may be considered one possible explanation of the accelerated ageing often observed in nature and expressed sometimes in the form of a Gompertz-Makeham equation.

It was also shown that when mortality is increased, repair is sacrificed not only in favour of reproduction but in favour of current survival too, so that accelerated ageing should be expected even when the investment in reproduction does not increase with age. In general, we may conclude that when mortality increases, the priority when expending energy is shifted primarily in favour of reproduction, then in favour of current survival, with repair having lowest priority.

Some problems remain. In particular, to simplify the calculations and interpretation of the results, we did not take into account energy invested in growth. Based on natural physiological assumptions and a non-seasonal environment, it is optimal to switch abruptly from growth to reproduction (Ziolko and Kozlowski, 1983). But what would be the effect of this switch on the allocation of energy to repair? In a seasonal environment, it is often optimal to switch from growth to reproduction at some moment during the reproductive part of the year and to resume reproduction at the beginning of the reproductive period the following year (Kozlowski and Uchmanski, 1987). Should we also expect some kind of repeated rejuvenation (increased investment in repair) in this case? It is important to use insight into the problems of energy partition, gained here using an evolutionary optimization approach, to clarify the principal physiological mechanisms of realizing optimal strategies (Budilova *et al.*, 1995).

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