

Augmented discounting: interaction between ageing and time-preference behaviour

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Discounting occurs when an immediate benefit is systematically valued more highly than a delayed benefit of the same magnitude. It is manifested in physiological and behavioural strategies of organisms. This study brings together life-history theory and time-preference theory within a single modelling framework. We consider an animal encountering reproductive opportunities as a random process. Under an external hazard, optimal life-history strategy typically prioritizes immediate reproduction at the cost of declining fertility and increasing mortality with age. Given such ageing, an immediate reproductive reward should be preferred to a delayed reward because of both the risk of death and declining fertility. By this analysis, ageing is both a consequence of discounting by the body and a cause of behavioural discounting. A series of models is developed, making different assumptions about external hazards and biological ageing. With realistic ageing assumptions (increasing mortality and an accelerating rate of fertility decline) the time-preference rate increases in old age. Under an uncertain external hazard rate, young adults should also have relatively high time-preference rates because their (Bayesian) estimate of the external hazard is high. Middle-aged animals may therefore be the most long term in their outlook.

Keywords: discounting; time preference; reproduction; ageing

1. INTRODUCTION

'Discounting' describes a range of phenomena in which an immediate benefit is systematically valued more highly than a delayed benefit of the same magnitude (Logan 1965; Mazur 1987). Why should a person or animal discount a delayed reward? One possibility is a cost of waiting (Dasgupta & Maskin 2002). This may in certain circumstances take the form of an opportunity cost of forgoing other rewards while waiting for the delayed reward (Kacelnik 1997, 2003). A second possibility is the risk of not receiving a delayed reward. Thus, for reproductive rewards, the organism may die before the reward is realized (Iwasa *et al.* 1984; Houston & McNamara 1986). Even if an animal did not age, its expected reproductive output would decline into the future because of external causes of mortality such as predation. Natural selection therefore puts a premium on immediate reproduction. This is believed to be the ultimate evolutionary reason for ageing (Hamilton 1966).

Ageing involves a general deterioration in an animal's condition over time, with falling fertility and increasing mortality. Fertility here refers not just to physical ability to produce young, but also ability to nurture young if this is important (as is particularly the case for females of many species), and to find, win or attract a mate (as applies to males of most species). One influential theory of ageing, the antagonistic pleiotropy theory, posits that there may be selection for genes that have a positive effect early in life and a detrimental effect later (Williams 1957). At the level of the organism, fitness is maximized by adopting a

'disposable soma' strategy, with less investment in somatic maintenance than would be required to prevent any deterioration (Kirkwood 1977). Thus, ageing is the result of a trade-off between short-term and long-term fertility. Evidence from selection experiments and other sources lend weight to the existence of such a trade-off (Partridge & Gems 2002). Ageing, then, can be understood to be in large part a consequence of a life-history strategy that discounts the future.

Deterioration in an animal's condition through ageing results in the animal's being less able to benefit from a delayed reward (Trostel & Taylor 2001). In a study of the evolution of time preferences, Rogers (1994) considered how survival benefits—modelled as temporary reductions in mortality—should be valued after varying delays. This yielded two general conclusions. First, that the value of a survival benefit depends on the organism's reproductive value (expected remaining lifetime reproduction). Thus, time preferences should be high in young adults for which reproductive value typically declines rapidly. The second depends on allowing survival benefits to be transferred to relatives. Old individuals generally prefer to give such benefits to offspring, with a resulting time-preference rate equivalent to a discount factor of two per generation.

Here, we consider how delayed reproductive rewards should be valued. A general analysis is followed by a series of specific models making different assumptions about external hazards and biological ageing. Rather than taking rates of ageing as given, as did Rogers (1994), we use life-history theory to model ageing as an optimal response to an external hazard. In this way we combine life-history theory and time-preference theory within a single modelling framework.

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2. AN EVOLUTIONARY FRAMEWORK FOR TIME PREFERENCES

We treat an animal as a rational optimizer that takes decisions so as to maximize its Darwinian fitness. That is, we assume it has evolved optimal decision rules under natural selection. We suppose also that it may receive rewards that make a positive contribution to its fitness. Within this framework, we consider how the animal should value a delayed reward, relative to an immediate reward.

Consider a reward i . Let $u_i(\tau)$ be its expected contribution to fitness if it is due after a delay τ . This is assumed normally to be a decreasing function of τ . The instantaneous *time-preference rate* θ is defined as the proportional reduction in value (i.e. fitness benefit) of the reward per unit delay for small delays:

$$\theta = \lim_{d\tau \rightarrow 0} \left[\frac{u_i(0) - u_i(d\tau)}{u_i(0) \times d\tau} \right] = -\frac{\dot{u}_i(0)}{u_i(0)}, \quad (2.1)$$

where \dot{u}_i denotes the derivative of u_i with respect to delay. This definition is essentially the same as that given by Rogers (1994).

We now restrict consideration to reproductive rewards. Such a reward may be a direct mating opportunity, or a resource that may with a certain probability be translated into a mating opportunity. The contribution to reproductive output of a specific reward is modelled as a product of the animal's current fertility and the reward magnitude. The question we analyse below is: what should the time-preference rate be for such reproductive rewards under a trade-off between the present and the future?

3. MODELLING A SIMPLE ANIMAL

We consider a simple animal with a life-history strategy and a behavioural strategy. The life-history strategy is concerned with maximizing the expected value of a stream of future reproductive output. The relevant strategy variable determines the extent to which the animal maintains itself against deterioration at the cost of a loss of immediate reproductive output. The behavioural strategy is defined by a time-preference rate θ which specifies the rate at which an animal will value an immediate reward more highly than a delayed reward in a real-time binary choice. An animal is not assumed to forgo other activities while waiting for a delayed reward.

For what follows, two temporal variables are employed: t denotes an animal's age, usually measured from adulthood, and τ denotes delay in receipt of a reward.

Maximizing fitness will be taken to be equivalent to maximizing the expected number of offspring. This amounts to assuming that the viability of offspring is not dependent on parental age, and that population size is approximately stable. *Fitness* is then given by

$$w = \int_0^{\infty} m(t)s(t)dt, \quad (3.1)$$

where $m(t)$ is the expected rate of reproductive output at age t if the animal survives to that age, and $s(t)$ is the probability of surviving to age t .

In what follows we assume that the modelled animal

has a marginal cost of reproduction of zero: that is, its condition and reserves after a reproductive act are the same as before. The animal can be conceptualized as an idealized male, which makes no contribution to care of its offspring, and for which the act of mating is costless. It encounters reproductive opportunities at a constant mean rate ρ . The animal's fertility as a function of age is $F(t)$, and describes its ability to convert reproductive opportunities into offspring. The rate of reproductive output is therefore given by $m(t) = \rho F(t)$. Substituting this into equation (3.1) gives

$$w = \rho \int_0^{\infty} F(t)s(t)dt. \quad (3.2)$$

Natural selection will tend to favour a life-history strategy that maximizes this expression.

4. ANALYSIS

We consider an animal of age t for which a reproductive reward of magnitude δh is due after a delay τ . We denote the expected contribution of this reward to fitness by $u(\tau)$. If the reward is immediate, there is no risk of the animal dying before it is received. The fitness contribution is thus

$$u(0) = \delta h F(t). \quad (4.1)$$

If the reward is delayed by a small amount $d\tau$, the chance of the animal still being alive after the delay, given that it was alive at age t , is $s(t + d\tau)/s(t)$. Its fertility after the delay is $F(t + d\tau)$. The expected fitness contribution is therefore

$$u(d\tau) = \delta h F(t + d\tau) \frac{s(t + d\tau)}{s(t)}. \quad (4.2)$$

Using equations (4.1) and (4.2) to evaluate the limit as $d\tau \rightarrow 0$ of $(u(d\tau) - u(0))/u(0) \times d\tau$, and referring back to equation (2.1), gives

$$\theta = -\frac{\dot{u}(0)}{u(0)} = \mu(t) - \frac{\dot{F}(t)}{F(t)}, \quad (4.3)$$

where $\mu(t)$ is *mortality rate* at age t :

$$\mu(t) = -\frac{\dot{s}(t)}{s(t)}, \quad (4.4)$$

and \dot{F} , \dot{s} are the derivatives of F , s with respect to age.

Note that in the normal case of fertility declining with age ($\dot{F} < 0$), both terms in equation (4.3) make a positive contribution to the time-preference rate. This has a straightforward interpretation. With both mortality risk and declining fertility, a delayed reward is of lower value than an immediate reward for two reasons. First, the animal may die before the delayed reward is received. Second, even if the animal does not die it will have reduced fertility when the delayed reward is received. The time-preference rate is equal to the sum of these two effects. Thus, the time-preference rate will normally be greater than the external hazard rate because of the effect of declining fertility and increasing mortality due to ageing. The effect of ageing is therefore to augment the time-preference rate implied by a purely behavioural response to the extrinsic hazard in the absence of ageing.

We now explore the consequences of this analysis by considering specific models.

5. TIME PREFERENCES WITH NO AGEING UNDER A KNOWN HAZARD RATE

(a) Model one: no ageing and a constant, known hazard rate

In this model the animal suffers no age-related deterioration, and there is a constant environmental hazard rate λ . This may be regarded as a 'known' hazard rate. This is not to imply that the animal has any mental conception of the hazard rate, but simply that it is evolutionarily adapted to the environment characterized by this hazard.

Substituting into equation (4.3) yields the simple result

$$\theta = \lambda, \quad (5.1)$$

i.e. the time-preference rate is independent of age and has a constant value equal to the extrinsic hazard rate.

6. AGEING

(a) Model two: simple ageing (steady fertility decline)

We now allow for ageing. We consider a simple model of ageing in which fertility declines steadily, but age has no effect on mortality. The animal makes a single life-history decision concerning the level of resources to invest in maintenance against declining fertility, with remaining resources invested in immediate reproduction. The decision is specified by a variable y with $0 \leq y \leq 1$. A larger value of y means that fertility declines more slowly, but at the cost of fewer resources going into immediate reproduction.

The animal's age t is measured from when it reaches sexual maturity. At this point its fertility is

$$F(0) = F_M(1 - y),$$

where F_M denotes the maximum possible fertility, achievable at $t = 0$ if it invests $y = 0$ in maintenance. Fertility is modelled as declining according to

$$F(t) = F_M(1 - y)\exp(-g(y)t), \quad (6.1)$$

where $g(y)$ is a decreasing function of y . As with model one, we assume a constant hazard rate λ and no age-related mortality. Hence the probability of being alive after time t is

$$s(t) = \exp(-\lambda t). \quad (6.2)$$

Substituting from equations (6.1) and (6.2) into equation (3.2) gives fitness:

$$\begin{aligned} w(y) &= \rho F_M(1 - y) \int_0^{\infty} \exp\{-(g(y) + \lambda)t\} dt \\ &= \frac{\rho F_M(1 - y)}{g(y) + \lambda}. \end{aligned} \quad (6.3)$$

An optimal value of y is one that maximizes this expression.

For example, take

$$g(y) = \begin{cases} b(y_0 - y)^2/y & \text{for } y < y_0, \\ 0 & \text{for } y \geq y_0. \end{cases}$$

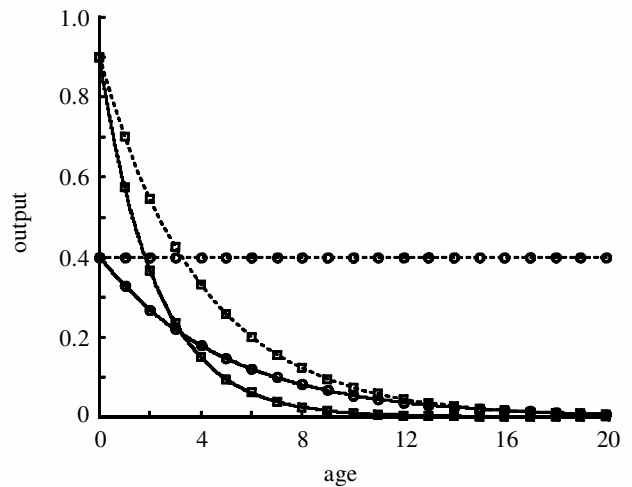


Figure 1. Model two: simple ageing. The figure shows reproductive output against age for two different values of the maintenance parameter y . In each case, dashed lines show reproductive output in the absence of extrinsic mortality, and solid lines show expected reproductive output allowing for an extrinsic mortality of $\lambda = 0.2$. The area under the solid curve represents expected future reproductive output. Squares, $y = 0.1$; circles, $y = 0.6$ giving no ageing.

Table 1. Results for model two. As the extrinsic hazard rate λ increases, optimal investment y^* in maintenance against deteriorating fertility falls. The rate of fertility decline $g(y^*)$ therefore increases. The time preference rate θ is greater than λ , and any change in λ results in an amplified change in θ because of the change in investment in maintenance.

λ	y^*	$g(y^*)$	$\theta = \lambda + g(y^*)$
0.5	0.209	0.073	0.573
0.2	0.290	0.033	0.233
0.1	0.358	0.016	0.116
0.05	0.425	0.007	0.057

Thus there is no ageing when the maintenance level y is at or above y_0 . Below this level, fertility declines with age. The rate of decline is small with y just below y_0 , but increases as y is further reduced. Taking $b = 0.1$ and $y_0 = 0.6$, figure 1 shows reproductive output conditional on still being alive, $m(t) = \rho F(t)$ (dashed curve), and expected rate of future reproductive output allowing for mortality, $m(t)s(t)$ (solid curve), for two values of y .

There is a unique optimal value $0 < y^* < y_0$ that maximizes fitness in equation (6.3). (This can easily be shown.) Table 1 gives the optimal value y^* , and the corresponding rate of fertility decline $g(y^*)$ for different values of the extrinsic hazard rate λ . Note that a higher hazard rate results in a lower y^* , and hence a higher rate of fertility decline. Also shown is the instantaneous time-preference rate θ . This is independent of age because both μ and (\dot{F}/F) do not change with age in this model. The table illustrates the previously discussed result that the time-preference rate is greater than the extrinsic hazard rate, because of declining fertility.

Under the trade-off theory of ageing, an increase in the external hazard rate will normally select for a life-history strategy with an increased rate of ageing. In this model

this is manifested as an increased rate of fertility decline. Conversely, a fall in the external hazard rate selects for a decreased rate of fertility decline. The consequence is that when the organism reaches its new evolutionary optimum, the change in its time-preference rate is greater than the original change in λ : that is, the effect of a change in λ is amplified in θ . This is apparent in table 1.

(b) Model three: realistic ageing

In model two, mortality was independent of age, and fertility declined at a constant proportional rate (i.e. exponentially). We now make more realistic assumptions, with advancing age resulting in mortality increasing at an increasing rate and fertility falling off at an increasing rate. A pattern of mortality rates increasing sharply in old age is observed in people and in a wide range of animal species in captivity (Finch 1990), whereas data for various human populations show that age-specific paternity rates typically tend to peak in early adulthood and then fall off at an increasing rate (Rogers 1994). Such an acceleration in the rate of deterioration with age may be explained in general terms as follows: one of the physiological functions that suffers age-related damage is the capability to repair further age-related damage. Positive feedback processes of this type have been modelled at a cellular level (Kowald & Kirkwood 1996).

Our model is similar to that proposed by Kirkwood & Rose (1991). As before, the animal is assumed to make a single life-history decision characterized by an investment y of resources into maintenance against age-related deterioration at the cost of declining immediate reproduction. Again, if $y \geq y_0$ there is no deterioration with age.

Mortality at age t after reaching adulthood is given by
$$\mu(t) = \lambda + \alpha[\exp(\beta t) - 1], \tag{6.4}$$

where $\alpha[\exp(\beta t) - 1]$ represents intrinsic (i.e. age-dependent) mortality, and λ represents extrinsic mortality. This gives a survival function:

$$s(t) = \exp\{-\lambda t + \alpha t - \alpha(\exp(\beta t) - 1)/\beta\}. \tag{6.5}$$

Fertility declines according to

$$F(t) = F_M(1 - y)\exp\{\alpha t - \alpha(\exp(\beta t) - 1)/\beta\}. \tag{6.6}$$

In the limit of $\beta \rightarrow 0$, equation (6.6) yields $F(t) = F_M(1 - y)$. We assume that this applies at $\beta = 0$.

Thus β determines the rate at which physiological condition deteriorates with age. We assume a functional relationship between y and β :

$$\beta = \begin{cases} \beta_0(y_0/y - 1) & \text{if } y < y_0, \\ \beta = 0 & \text{if } y \geq y_0. \end{cases}$$

Increasing y reduces β , and therefore causes physiological deterioration to proceed more slowly, up to $y = y_0$ where physiological deterioration does not occur. However, increasing y reduces initial fertility. Thus there is a trade-off between short-term and long-term reproductive output.

The parameters y_0 , α and β_0 are treated as exogenously determined for the purposes of this model. We have retained the value $y_0 = 0.8$ used by Kirkwood & Rose (1991). For illustrative purposes we take $\alpha = 0.002$,

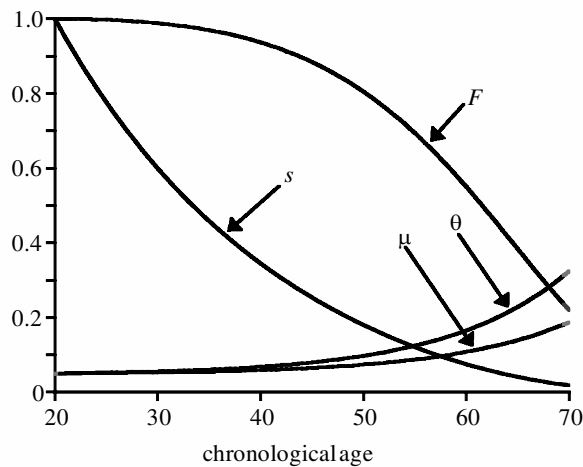


Figure 2. Model three: realistic ageing under a known hazard rate. s , dependence of survival from adulthood; F , fertility; μ , mortality; θ , time-preference rate on chronological age, taking adulthood to occur at age 20. $\alpha = 0.002$, $\beta_0 = 0.05$, $y_0 = 0.8$, $\lambda = 0.05$. Investment in maintenance is given by $y^* = 0.297$.

$\beta_0 = 0.05$ and $\lambda = 0.05$, to give an ageing profile similar to that for humans at the optimum value of y . These parameters result in an optimal value $y^* = 0.297$. Figure 2 shows the results, with adulthood taken to occur at a chronological age of 20. We see that the time-preference rate increases with advancing age. This is a simple consequence of both mortality and the rate of fertility decline increasing with age.

7. THE EFFECT OF AN UNCERTAIN HAZARD RATE

So far it has been assumed that extrinsic hazards occur at a known, constant rate. This would apply if successive generations always found themselves in exactly the same environment. It seems more likely in general that there will be variability across potential environments, with animals not being certain of the extrinsic hazard rate of the environment into which they are born. Even if overlapping generations of parents and offspring tend to occupy the same environment, as long as a small proportion of offspring disperse some time between birth and adulthood, evolution would have to condition preferences on the statistical distribution of environmental hazard rates as we assume here.

Discounting under an uncertain hazard rate was considered by Sozou (1998) and Azfar (1999). We briefly review the main result. A determinate constant hazard rate λ implies an exponential survival function. However, if the hazard rate is uncertain this is no longer the case. Instead, if there is some prior distribution for the hazard rate, the survival function is a weighted superposition of exponential functions corresponding to hazard rates. Let the probability of an underlying hazard rate λ_i be p_i for $i = 1, 2, \dots, n$. The probability of survival to at least time t is then

$$s(t) = p_1 \exp(-\lambda_1 t) + p_2 \exp(-\lambda_2 t) + \dots + p_n \exp(-\lambda_n t). \tag{7.1}$$

The instantaneous expectation of extrinsic mortality, given by substituting from equation (7.1) into equation (4.4), is a decreasing function of t . This result has a Bayes-

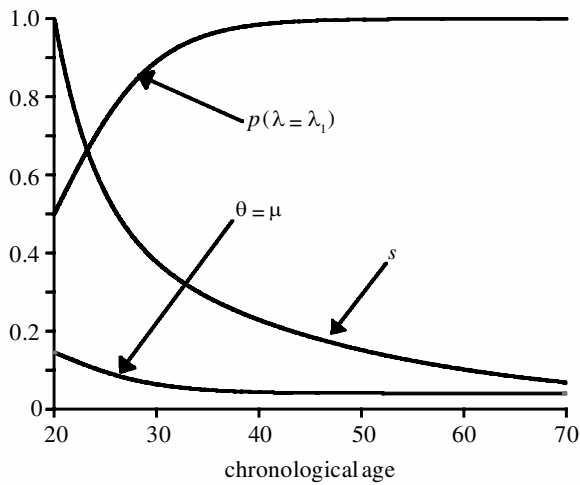


Figure 3. Model four: unknown hazard rate which can take one of two values, and no age-related physiological decline. Curves shown are: the probability that the true hazard rate is the lower value of λ_1 as a function of age since adulthood; s , the survival function; and θ , the time-preference rate, equal to μ , expected mortality. Adulthood is taken to occur at chronological age 20. $p_1 = 0.5$, $\lambda_1 = 0.04$, $\lambda_2 = 0.25$.

ian interpretation: at age t from reaching maturity the animal's estimate for the distribution of the hazard rate should be conditioned on its having survived to that age. As age increases, larger values of the hazard rate become progressively less likely.

For the present study a simple prior distribution will be considered, with the hazard rate taking one of two discrete values. In this case, the posterior probability of the hazard rate λ_1 , conditional on having survived to age t , is

$$p(\lambda = \lambda_1 | t) = \frac{p_1 \exp(-\lambda_1 t)}{p_1 \exp(-\lambda_1 t) + (1 - p_1) \exp(-\lambda_2 t)}. \quad (7.2)$$

Similarly $p(\lambda = \lambda_2 | t) = 1 - p(\lambda = \lambda_1 | t)$.

Model four below considers time preferences under an uncertain hazard rate, but without ageing. This enables the uncertain hazard to be understood in isolation from the effects of ageing. Model five considers the effect of an uncertain hazard rate with realistic ageing.

(a) Model four: no ageing and an uncertain extrinsic hazard rate

From equations (7.1) and (4.4), the expected mortality allowing for the uncertainty in λ is

$$\mu = \frac{p_1 \lambda_1 \exp(-\lambda_1 t) + (1 - p_1) \lambda_2 \exp(-\lambda_2 t)}{p_1 \exp(-\lambda_1 t) + (1 - p_1) \exp(-\lambda_2 t)}. \quad (7.3)$$

Putting $p_1 = 0.5$, $\lambda_1 = 0.04$ and $\lambda_2 = 0.25$, figure 3 shows the posterior probability equation (7.2) as a function of the animal's age. Also shown is the instantaneous time-preference rate θ . Physiological condition does not deteriorate with age, so that $\theta = \mu$ (see equation (4.3)). As the animal's survival time increases, it becomes progressively more likely that the true hazard rate is the lower value λ_1 . Thus, the expected chance of dying per unit time falls off with t , and therefore θ declines with age.

Model four shows that the presence of an uncertain hazard rate with no age-related deterioration results in an instantaneous time-preference rate that falls off with age.

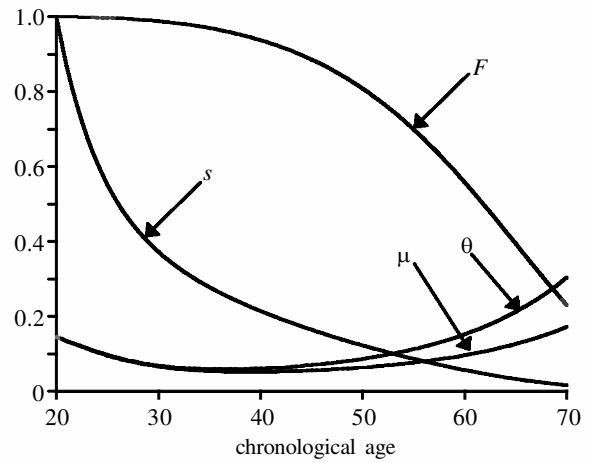


Figure 4. Model five: realistic ageing under an unknown hazard rate. s , dependence of survival from adulthood; F , fertility; μ , mortality; θ , time-preference rate on chronological age, taking adulthood to occur at age 20. $\alpha = 0.002$, $\beta_0 = 0.05$, $y_0 = 0.8$, $p_1 = 0.5$, $\lambda_1 = 0.04$, $\lambda_2 = 0.25$. Investment in maintenance is given by $y^* = 0.298$.

However, model three has shown that realistic ageing with no uncertainty in the hazard rate results in an instantaneous time-preference rate that increases with age. What then is the effect of an uncertain hazard rate combined with realistic ageing? This is explored below.

(b) Model five: realistic ageing and an uncertain extrinsic hazard rate

We now consider an animal that exhibits realistic ageing, using the ageing model of model three, but which is subject to an uncertain hazard rate as in model four. This condition changes with age according to the decision variable y exactly as in model three, and fertility is described again by equation (6.6). The expression for mortality changes from equation (6.4) to

$$\mu = \frac{p_1 \lambda_1 \exp(-\lambda_1 t) + (1 - p_1) \lambda_2 \exp(-\lambda_2 t)}{p_1 \exp(-\lambda_1 t) + (1 - p_1) \exp(-\lambda_2 t)} + \alpha [\exp(\beta t) - 1]. \quad (7.4)$$

Keeping the same parameters y_0 , α , β_0 used in figure 2 for the dependence of fertility and intrinsic mortality on age, and the same parameters p_1 , λ_1 , λ_2 used in figure 3, the behaviour of model five is shown in figure 4. Optimal investment in maintenance is given by $y^* = 0.298$. This is very close to that of model three, shown in figure 2, and thus fertility declines according to the same pattern. However, overall expected mortality initially decreases with age, before eventually increasing as physiological decline kicks in. The overall effect is that the instantaneous time-preference rate is higher in early adulthood than middle age, and higher also in old age than middle age.

This result is a consequence of the characteristic pattern of biological ageing. The time preference rate in equation (4.3) can be written as the sum of two effects: first, extrinsic mortality, the expected value of which must decline with age under an uncertain hazard rate; and second, the effect of ageing. A key feature of the ageing process is that it proceeds slowly in early adulthood, but accelerates dramatically at later ages. Hence, the effect of declining expected extrinsic mortality will be greater than the effects

of ageing in early adulthood for a reasonable degree of uncertainty in the hazard rate, so that the time-preference rate decreases during early adulthood. In old age, however, the effect of ageing dominates, with increasing mortality and an increasing rate of fertility decline resulting in an increasing time-preference function.

We have also evaluated the effect of replacing the discrete prior distribution for the hazard rate considered above with an exponential distribution. In the absence of age-dependent mortality this results in a hyperbolic survival function of the form $s(t) = k/(1 + kt)$ (Sozou 1998). When this form of uncertainty in the hazard rate is combined with realistic ageing, the U-shaped time-preference function of model five is again observed, with this result holding for a wide range of values of k .

8. DISCUSSION

Biological ageing can be understood as a consequence of adaptation to external pressure, particularly mortality, which causes a given amount of delayed reproduction to make a smaller expected contribution to fitness than the same amount of immediate reproduction. That is, declining physiological condition with age is a *consequence* of discounting the future in life-history strategy. But physiological ageing should itself be a *cause* of preferring immediate over delayed reproductive rewards: declining physiological condition means that an organism is able to derive less fitness benefit from a delayed reward. The overall effect is that, at the evolutionary optimum, the time-preference rate will be greater than the extrinsic mortality rate. A change in extrinsic mortality should be expected to result in an amplified change in the time-preference rate, after a new life-history optimum has been reached.

We have modelled the time-preference function for reproductive rewards under various assumptions concerning environmental hazards and biological ageing. Where ageing occurs, the rate is determined endogenously as an optimal life-history strategy. Under an uncertain environmental hazard rate, and the most realistic ageing assumptions (i.e. an accelerating decline of fertility and increasing intrinsic mortality with age), the model suggests that time preferences will be lowest in middle age. The explanation can be simply stated as follows.

- (i) The young adult acts as if there may be no tomorrow, i.e. the environmental hazard rate may be high. Hence its time-preference rate is high.
- (ii) The middle-aged adult knows that the environmental hazard rate is low. At the same time, its rate of physiological decline is still fairly modest. Thus, it can take a long-term view and its time-preference rate is low.
- (iii) The old adult knows that the environmental hazard rate is low, but its physiological state is deteriorating rapidly, with declining fertility and increasing intrinsic mortality. It therefore knows that there is no tomorrow.

Our approach is directly applicable to male life-history strategy and behaviour in species where males make no contribution to their offspring after mating. The result is that time-preference rates become very large when fertility

is declining rapidly and mortality is high. There are also some similarities with the situation faced by females during periods when they are potentially reproductively active but not contributing resources to current offspring. Mate choice involves a trade-off between quality and time: a choosier female may find a better mate, but at the cost of waiting longer before breeding. Experimental results suggest that, in some species at least, females become less choosy as they age, corresponding to a higher time-preference rate (Kodric-Brown & Nicoletto 2001; Moore & Moore 2001); physiological ageing may be part of the reason.

Rogers (1994) has also modelled the dependence of short-term time preferences on age for humans, taking fertility and mortality curves as given. Rewards constitute short-term survival benefits in Rogers's model, but reproductive benefits in ours. Even so, both models suggest that time-preference rates should fall from early adulthood to middle age. One apparently surprising finding of Rogers is that changes in mortality have little effect on time-preference rates. The explanation appears to be that in Rogers's model mortality is 'factored out': that is, a sacrifice of a present benefit for a future benefit is conditional on survival. In our model, by contrast, mortality is 'factored in': a sacrifice of a reproductive benefit now for one in the future carries the risk that the benefit will be lost altogether if death intervenes. For the reproductive rewards we consider, our formulation is closer to those used in other biological models of ageing (Kirkwood & Rose 1991; Shanley & Kirkwood 2000).

Rogers (1994) also allows (costless) transfers of rewards from one individual to another. This results in time-preference rates tending towards a value equivalent to a discount factor of two per generation. The existence of such transfers also leads to a possible trade-off between number of offspring and wealth per offspring (Rogers 1990). Not all forms of reward, however, can readily be transferred in this way.

One apparent difficulty with applying evolutionary analysis to human behaviour is that people are not obvious fitness maximizers. In the developed world in particular, a great deal of consumption does not contribute to reproduction, survival or helping relatives. This is presumably because people have evolved preferences for certain outcomes (status, stimulation, etc.) which corresponded well to fitness in the ancestral environment, but not in the modern environment. Evolutionary models can therefore be used to understand preferences for forms of consumption which, in the modern environment, are proxies for activities that enhanced fitness in the ancestral environment. We believe that not only rewards which involve sexual enjoyment, but also other forms of 'visceral' pleasure—eating, drinking, partying, etc.—are proxies for reproduction, and should be subject to broadly similar forms of time-preference function. That is, declining physiological condition results in a preference for immediate consumption over future consumption (Trostel & Taylor 2001).

Bringing these ideas together suggests that people may have different time preferences for different kinds of reward. Where transfers to relatives are not feasible, declining physiological condition provides a strong reason for preferring immediate consumption to delayed consumption. By contrast, in situations where resources can

be transferred to relatives, Rogers's (1994) analysis suggests that a declining ability to benefit personally from a resource is less relevant. Thus, for humans, time-preference rates may be higher for non-fungible than for fungible rewards.

P.D.S. is supported by a research fellowship at the LSE. R.M.S. is supported by the ESRC-funded Centre for Economic Learning and Social Evolution (ELSE) at UCL. We are grateful to two referees for helpful comments on this paper.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.