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Gompertz mortality, natural selection, and the 'shape of ageing'

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ABSTRACT

Question: Proposals for measuring the *shape of ageing* are dimensionless comparisons of early adult mortality (Z_0) with aggregate mortality over the adult lifespan. What do the *shape parameters* actually measure? And how do they relate to the optimal age/size at maturity?

Methods: Dimensional analysis is applied to an adult Gompertz mortality function, $Z_x = Z_0 e^{c \cdot x}$. R_0, fitness in non-growing populations, is maximized with respect to the age at maturity, α.

Conclusions: A constant value for *any* 'shape of ageing' number among a collection of species implies that they also have the same value for the ratio of the two Gompertz parameters, c/Z_0 (if mortality is Gompertz). Z_0 appears in both the shape measure(s) and the formula for the optimal α; this provides a link between the rate of ageing and the criterion for the initiation of reproductive maturation. This ESS result suggests that (perhaps) Z_0, external mortality rate early in adulthood, and not any mass-specific physiological rate, should determine the ageing rate.

Keywords: rate of living, maturation, fish, senescence, mortality rate

Six *main problems* have dominated the study of life histories in an evolutionary context: (1) What is lifetime fitness [*r*/*k* selection, density-dependent fitness (R_0), stochastic environment fitness, etc.]? (2) What determines the size/age at maturity? (3) What sets the schedule/amount of reproductive allocation throughout adulthood? (4) What is the optimal investment per offspring (size of a kid)? (5) How do we conceptualize/calculate male fitness [sexual selection, alternative life histories (e.g. sneaker males)]? (6) Ageing (e.g. increase in mortality with adult age).

Of these six main problems, ageing has received the least attention, probably because it seems remote from, or minor compared with, the other key problems, and because its proper study requires detailed field life tables. Ageing is of major concern to human gerontologists (who sometimes study non-human 'model animal systems', usually in the

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laboratory) but not to most evolutionary ecologists; even to merely show ageing in field populations is a tough job.

Ageing is the 'decline' of performance *usually* seen over the adult lifespan in reproduction (fecundity), survival rate (increase in mortality rate), and *many other* physiological performance criteria studied by gerontologists. I say *usually* because fecundity increases with adult size (= increasing age) in indeterminate growers (most fish, most invertebrates except insects), and mortality may decrease with increasing body size, even into adulthood (e.g. Charnov *et al.*, 2013). *Demographic ageing* is the increase in mortality rate over the adult lifespan, and is usually parameterized by forms like the Gompertz function (exponential increase in the rate of death as adulthood progresses). Clearly, many physiological performance attributes feed into the death rate, and its increase has often been considered as simply ageing (e.g. Baudisch, 2011). [For general reviews/overviews of the evolutionary theories of ageing/senescence, see Stearns (1992), Kirkwood (1977), and Kirkwood and Austad (2000).]

This paper is about demographic ageing, and has two aims. The first is to discuss how we may measure a 'quantity of ageing'. There are many proposed numbers to measure demographic ageing, and Baudisch (2011), who reviews many proposals in her paper, has distinguished between 'shape' measures and 'pace' measures. Maximum lifespan is often used as a 'pace' measure. What is the pace of life? Answer: 1/maximum-lifespan is the pace of adult life. The main problem with this measure of ageing is that it really does not capture the *increase* in mortality as adulthood progresses, in that constant exponential death is what most people mean by no/zero demographic ageing – and this, of course, also yields a maximum lifespan. In 1993, I suggested that the main problem in measuring ageing was to find a measure that can in principle reveal that two species have similar ageing rates *even when they have different lifespans*. How might we conclude that mice and elephants have similar ageing rates and are different from, say, indeterminate growing fish? My proposed measure (Charnov, 1993, p. 130), discussed below, was originally motivated by G.C. Williams' evolutionary theory of ageing, which suggested that mice and elephants, being determinate growing endothermic mammals, *ought to be similar in ageing*, *and different from fish*. I can now suggest a more intuitive interpretation for the *shape* measure. The second aim of this paper is to develop a fundamental connection between *shape* measures of ageing and the life-history question of the optimal size/age at maturity. This will provide an additional meaning for the quantitative measure developed.

To begin, how shall we quantify ageing, particularly demographic ageing? I will answer this through reference to the most widely used model for demographic ageing, the Gompertz function. Charnov (1993, ch. 7) and Baudisch (2011) introduced dimensionless numbers to characterize how mortality changes – it increases and rarely decreases – over the adult lifespan. Their goal was to provide an index with which to compare species that otherwise had very different mortality rates (very different adult lifespans). Charnov's index (and one of Baudisch's) was the ratio of the maximum adult lifespan to 1/(instantaneous mortality rate in early adulthood). I argued that this number ought to be larger for indeterminate growers (fish) than determinate growers (mammals), because fish should delay death so as to benefit from the increasing fecundity that comes with the larger body size of later adulthood. A comparison of mammals versus fish supported this hypothesis. Baudisch called this measure, and others like it, the *shape of ageing*. She developed several interrelated measures that effectively removed absolute time from the adult life history, and applied the measures to a collection of species. The various measures were highly inter-correlated, so it did not matter which measure was used (more on this later). All of

the shape measures were dimensionless comparisons of early adult mortality to aggregate mortality for adulthood.

This section asks a simple question: *What does the shape parameter actually measure?* I will use the assumption of Gompertz mortality to answer this question; the exact answer will be for the Gompertz function, but the general concept will apply more widely.

Let Z_0 be the instantaneous mortality rate at the onset of adulthood. Let T_m be the oldest adult age that is defined, for example, as the age when only 1% of an adult cohort is still alive (any small percentage will work here; age zero is the onset of adulthood). Then, a dimensionless number that compares early adult mortality to the maximum lifespan is the 'shape of ageing', or

$$T_m \Big/ \frac{1}{Z_0} = Z_0 \cdot T_m$$

Our goal is to ask what a collection of species that share the same $Z_0 \cdot T_m$ number *have in common*. Our hunch/claim is that they 'age in similar ways', and we want to know what that actually means.

Suppose mortality at adult age x is Z_x, where $x = 0$ is the onset of adulthood. Suppose further that mortality increases (decreases) with x according to the Gompertz function, i.e. $Z_x = Z_0 \cdot e^{c \cdot x}$, a simple exponential. (Indeed, a great many adult Z_x schedules fit this equation.)

It is straightforward to turn the Z_x schedule into a cumulative survival curve (L_x curve) because $L_x = e^{-\int_a^x z(y)dy}$, and then to set $L_x = 0.01$ and solve for the appropriate age ($=T_m$):

$$0.01 = \exp\left[-\int_0^{T_m} Z(y)\, dy\right]$$

Note that our final answer will be of the form $T_m = G(Z_0, c)$, since we have integrated out actual time x. Thus, our 'shape of ageing' parameter

$$T_m \Big/ \frac{1}{Z_0}$$

will be $Z_0 \cdot G(Z_0, c)$. We need not write down the G function to analyse the measure; note that it is solely a function of Z_0 and c (and our 0.01, of course).

Now we can answer our question: If we have a collection of species that each display the same value for the 'shape of ageing', $Z_0 \cdot G$, what do the species really have in common? As $Z_0 \cdot G$ is a dimensionless number, it can only be a function of other dimensionless numbers; but there is only *one* dimensionless number associated with the two parameters of the Gompertz curve used to calculate T_m ($=G$). That number is, of course, c/Z_0, since both c and Z_0 have units of 1/time. Thus the answer to our question is simple: with Gompertz mortality, all species with the same $Z_0 \cdot T_m$ number also have *the same* c/Z_0 *number*. [I note in passing that the other candidates for a 'shape of ageing' parameter discussed by Baudisch (2011) have exactly the same property: a constant value for each implies a constant value for c/Z_0.]

$c/Z_0 =$ *constant* means that the rate of increase in mortality with age (c) is proportional to the initial mortality rate (Z_0); the higher the proportionality *constant*, the *faster* the

demographic ageing. Of course, c/Z_0 itself has an advantage as a *shape* measure in that constant adult mortality (which is what we mean by zero-ageing) is when $c = 0$, and thus the c/Z_0 *shape* is zero. Likewise, negative ageing would yield $c < 0$, and thus a negative *shape* measure. In the parlance of dimensional analysis, we choose to measure the rate of ageing in units of the initial mortality, Z_0. In those time^{-1} units, species are alike if they have the same c/Z_0 value.

As we will often not have the full L_x schedule for field populations, the $Z_0 \times T_m$ number will often be more useful, provided T_m is estimated in comparable ways for the various species. Fishery scientists have studied a version of this 'shape of ageing' parameter for over 50 years because they use its numeric value to estimate Z_0 using T_m. [Their T_m is slightly different from the one used here in that it is total maximum age, whereas ours is maximum adult age; see Charnov (1993, p. 131) for discussion of the two.] The latest fish data set has Z_0^{-1} and their T_m proportional with the constant ~5 [$r^2 = 0.89$, $N = 226$ spp.; see Then *et al.* (2015) for a detailed discussion and earlier literature].

It is of great interest that demographic ageing is often well described using the increase in mortality *from a beginning rate of* Z_0, and the useful descriptors are how fast *this* rate increases over the adult lifespan. This is because optimal life-history theory *also assigns a special role to* Z_0. To see this, consider a population unchanging in size where the appropriate fitness measure is the net reproductive rate, R_0. For any age-structured population, R_0 can be written in a very compact form (Charnov, 1997): $R_0 = S \times b \times E$, where S is survival to maturity, b is per unit time birth rate, and E is average length of the adult lifespan. We call $b \times E$ the reproductive value at adulthood, label it V, and express R_0 as $R_0 = S \times V$; S goes down as maturity is delayed, whereas V goes up. We can solve for the optimal age at maturity (first reproduction, age α) by setting $d(\log R_0)/d\alpha = 0$. The general answer, derived in Charnov (1993, pp. 15–16) is very simple: $Z_0 = d(\log V)/d\alpha$. The Z_0 is the external mortality rate at the very end of the juvenile period, which will be the adult Gompertz Z_0 provided there is no great discontinuity in mortality due to maturation. Because all species with the same 'shape of ageing' have the same c/Z_0 number (call it B^{-1}), we have $d(\log V)/d\alpha = B \times c$.

The *shape of ageing B is thus the proportionality constant* that links the rate of gain in reproductive ability (through delay in maturity) to the rate of increase in mortality (c) throughout adulthood. Note that I have not predicted a c value through some optimal repair allocation scheme for V; this rule is for that part of the allocation that involves the initiation of reproduction itself. My purpose is simply to give an optimal life-history interpretation for the B number. Note also that I could use T_m^{-1} instead of c, in which case the proportionality constant would be in terms of the original 'shape of ageing' number, $Z_0 \times T_m$.

Because the $d(\log V)/d\alpha$ will often look a lot like a mass-specific growth allometry [an approximately –0.25 power function with associated height parameter (Charnov, 1993, ch. 5)], this logic also establishes a connection/correlation between dimensional ageing parameters [T_m^{-1}, c; called by Baudisch (2011) *pace of ageing* measures] and the power function that describes mass-specific growth. Physiological rates that underlie relative mass production at the onset of maturity are thus correlated with ageing; many of these show an approximately –0.25 power function behaviour with body mass (see below for what this means).

Finally, it is possible that the Z_0 from the life-history optimization (the late larval Z that controls the time of transition to adulthood) is not the same as the early adult mortality. Suppose we have an insect with a crawling larval stage followed by a flying adult stage; such a *highly discontinuous* life history may have almost no relation between the mortality at the

end of the larval period and the mortality at the beginning of adulthood. Ageing for such life histories would follow a time schedule set by the adult early Z, and not the larval Z.

In closing, let me repeat/amplify one important message: The previous two paragraphs suggest a novel perspective on the relationship between ageing and various (per unit mass) physiological rates (those associated with growth/mass production), particularly those that show approximately –0.25 power function behaviour with adult body mass. We have known for over a century that bigger bodied mammals have longer maximum lifespans *and* lower mass-specific physiological rates (metabolic and many other rates), and this has led to much research into whether one or more of these physiological rates acts as a *main cause* of ageing (resulting in many 'rate of living' hypotheses, all of which feature 'wear and tear mechanisms', with/without consideration of repair investments and/or energy trade-offs). Simply put: Is the larger T_m for larger mammals *caused* by any of the lower mass-specific physiological rates? The optimal size/age at maturity model, however, merely *associates* the rates related to relative growth rate with Z_0, at least for life histories where late larval mortality becomes early adult mortality. This is because the $d(\log V)/d\alpha$ involved in the maturation decision will so often look like an approximately –0.25 power function with maturation body size; offspring production is, after all, the reallocation of personal growth potential to instead produce offspring. This suggests that the association of the mass-specific physiological rates with ageing may not be causal at all; the apparent correlation arises merely because of the association of the rates with Z_0: *Perhaps it is Z_0 alone that sets the time-scale for ageing for determinate growers*. This would explain why ageing patterns in nature sometimes seem related to the adult mortality rate/risk independent of underlying physiological rates (e.g. altricial birds demonstrate slow ageing and high metabolic rates). We can test this: the discontinuous life histories (larvae crawl/adults fly; also altricial birds) must often break/alter the typical (–0.25 power function) connection between physiological rates, body size, and the adult Z, particularly the early adult Z. I predict that ageing will follow adult Z_0, not the rates. Or perhaps the mass-specific physiological rates set the time course for cellular/tissue damage, and the Z_0 sets the time course for repair processes, the value of investment in repair that delays ageing. In either case, the connection between physiological rates (particularly mass production rates) and Z_0, set by the maturation decision itself, is of key importance.

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