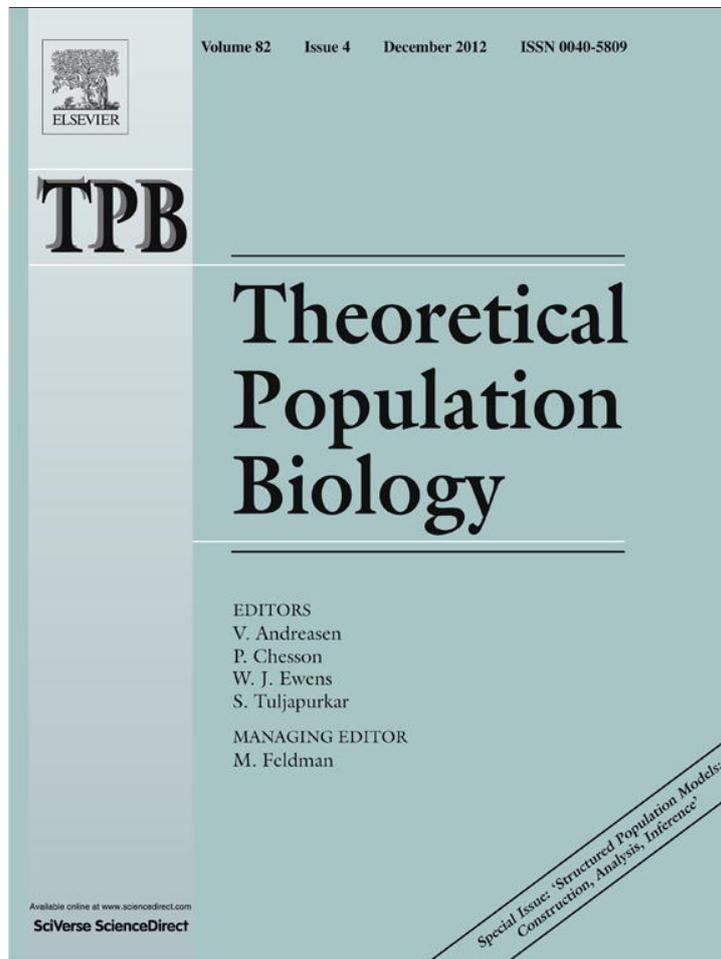


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Linking the population growth rate and the age-at-death distribution

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ABSTRACT

The population growth rate is linked to the distribution of age at death. We demonstrate that this link arises because both the birth and death rates depend on the variance of age-at-death. This bears the prospect to separate the influences of the age patterns of fertility and mortality on population growth rate. Here, we show how the age pattern of death affects population growth. Using this insight we derive a new approximation of the population growth rate that uses the first and second moments of the age-at-death distribution. We apply our new approximation to 46 mammalian life tables (including humans) and show that it is on par with the most prominent other approximations.

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1. Introduction

In age-structured populations with overlapping generations the population growth rate r is usually determined by the maternity function $l(x)m(x)$ which is the product of the age-specific survival rates $l(x)$ and fertility rates $m(x)$. The growth rate r describes the survival and fertility performance of all individuals and cohorts, in terms of the long-term population growth rate. The mean lifetime reproductive success R_0 is tightly linked to r and summarizes the survivorship and fertility performance of individuals within a cohort as they age. However, if a population of a long-lived species, like an elephant, and a population of a short-lived species, like a mouse, have identical values of R_0 , they will have very different values of r . This is because the average elephant produces its offspring over a much longer period than a mouse, and elephants reproduce at a far greater age (as measured by cohort generation time T_c). Lotka (1939) was the first to use this insight to develop an approximation of r from R_0 and generation time T_c . Many subsequent approximations use the same insight, (e.g. Coale, 1955; McCann, 1973). All of these start with Lotka's renewal equation

(Lotka, 1939) and focus on properties of the maternity function $l(x)m(x)$, such as R_0 , T_c or the variance of the normalized maternity function. Thus they use quantities that combine mortality and fertility figures.

In this paper we take a different approach: we focus on the age at death and its distribution. We start by considering population growth rate as the difference between birth and death rates. In a stable (increasing or decreasing) population, we show that both birth and death rates depend directly on the variance of age at death. We then focus on performance measures (lifetime reproduction, timing) conditional on age at death. The latter approach has been used by McGraw and Caswell (1996), Link et al. (2002) and Steiner and Tuljapurkar (2012) to explore “individual” fitness measures (see also Coulson et al., 2006). We show how some performance measures conditional on age at death can be averaged to determine population measures, but that the average of individual growth rates does not equal population growth rate.

Our results also yield a restatement of R_0 as an average of cumulative fertility over ages at death, and a similar restatement of T_c . These equations show that it is possible to separate the age patterns of death and of fertility in the way that they shape r , an approach we will exploit in later work. Finally, we derive a new approximation to r that identifies the contributions of the mean and variance in age at death. We use life tables of 46 mammalian species (including humans) to compare our approximation to those of Lotka (1939) and a widely used approximation (e.g., Tuljapurkar et al., 2009a) based on the reversion of series (Abramowitz and Stegun, 1972).

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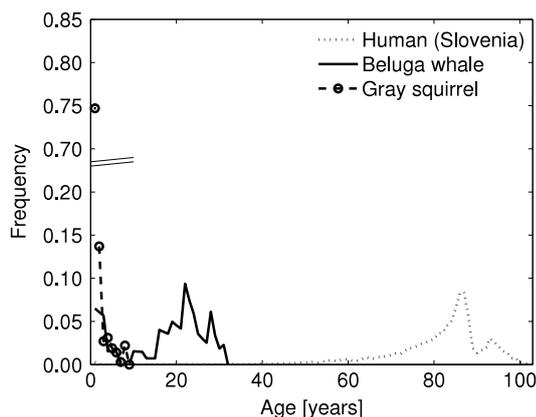


Fig. 1. Age-at-death distribution of three species: Gray squirrel (Barkalow et al., 1970), Beluga whale (Béland et al., 1988), and human (Human survival data for Slovenia, 2007; Human fertility data for Slovenia, 2006).

2. Preliminaries

2.1. Ages at death

Suppose that the mortality rate is $\mu(x)$ at age x so that survivorship to age x is

$$l(x) = e^{-\int_0^x \mu(a) da}. \quad (1)$$

Each individual of course has just one age at death, call it T , and this is random in the sense that the distribution of age at death is determined by how mortality changes with age. The probability that an individual dies between ages x and $(x + dx)$, for tiny dx , is $\mu(x) l(x) dx$, and we write $\phi(x) = l(x) \mu(x)$. An individual's life expectancy is an average (expectation) over the distribution of ages at death,

$$\mathbb{E} T = \int_0^\infty x \phi(x) dx = \int_0^\infty l(x) dx = e_0, \quad (2)$$

where the (known) second equality also reflects a general property of averages over T that is proved in the Appendix A (Eq. (A.20) with $f(a) = 1$). The variance in age at death is

$$\sigma_D^2 = \mathbb{E} (T^2) - e_0^2 = \int_0^\infty (x - e_0)^2 \phi(x) dx. \quad (3)$$

A high variance in age at death means that deaths can occur over a wide range of ages and are not sharply concentrated at a particular age. Examples include some birds in which adult death rates change only slowly with age, some plants in which death rates may actually decline with age as size increases, early humans and several animal species (Jones et al., 2008). Small variances in age at death are expected in species (mostly semelparous) that have sharply defined ages at reproduction followed rapidly by death (such as Pacific salmon), or populations with low early mortality followed by a rapid increase in senescent mortality, for example modern humans (Tuljapurkar et al., 2009b). In Fig. 1 we plot examples of the distribution of age-at-death for a short-living, a long-living species, and one of intermediate longevity.

2.2. The renewal equation

The standard approach to finding r uses the renewal equation. Writing age-specific fertility as $m(x)$, the famous Euler–Lotka renewal equation states that r is the largest real solution of

$$1 = \int_0^\infty e^{-ra} l(a) m(a) da. \quad (4)$$

In words, this equation says an individual's expected reproduction at each age, discounted at rate r , must add up to 1. This restatement allows us to write a renewal equation for any self-renewing population, a fact that we exploit later. We note also Lotka's approximation

$$r \approx \frac{\log R_0}{T_c}, \quad (5)$$

with mean lifetime reproductive success $R_0 = \int_0^\infty l(a) m(a) da$ and generation time $T_c = \frac{1}{R_0} \int_0^\infty a l(a) m(a) da$.

The renewal equation (4) focuses attention on the reproductive ages at which $m(x) > 0$, indeed it is commonly said that only the reproductive ages matter to fitness. But deaths occur at all ages, reproductive or not, so the renewal equation yields little direct insight about death rates or the difference between birth and death rates. To get at these we must analyze the balance between birth and death.

3. Birth, death and population growth

3.1. Per-capita rates determine r

Consider the difference between births and deaths in a stable population whose growth rate is r . Writing $N(t)$ for the total population number, $B(t)$ and $D(t)$ for the birth and death rates at time t , define the per-capita birth rate $b(t) = B(t)/N(t)$ and the per-capita death rate $d(t) = D(t)/N(t)$. The stable growth rate r is given exactly (see Appendix A Eq. (A.8)) by the difference in per-capita birth and death rates,

$$r = \frac{B(t)}{N(t)} - \frac{D(t)}{N(t)} = b(t) - d(t) \quad (6)$$

These per-capita rates can be written explicitly in terms of r , $l(x)$, $m(x)$ (see Appendix A Eqs. (A.15) and (A.17)).

Does this tell us anything that the renewal equation doesn't? Yes, in a stationary population in which growth rate $r = 0$. Here the per-capita birth rate (see Appendix A Eq. (A.15) with $r = 0$) is exactly

$$b(t) = \frac{B(t)}{N(t)} = \frac{1}{e_0}, \quad (7)$$

where e_0 is the life expectancy: $e_0 := \int l(a) da$. Of course per-capita death rate exactly equals the per-capita birth rate and so contains no additional information. So when $r = 0$, the average length of life e_0 determines the birth rate needed to maintain a population of a given total population. It is perhaps not widely appreciated that Eq. (7) applies to a density-dependent population at a steady equilibrium, however complex the density regulation. In the field or in the laboratory, it is often possible to estimate $N(t)$ and life expectancy, so if the population is stationary we can infer the birth rate $B(t)$. But of course many populations are not stationary—is there a generalization of Eq. (7)?

3.2. Variance in age at death matters in stable populations

In a growing population per-capita births must exceed per-capita deaths (cf. Eq. (6)). How do these rates compare to those in a stationary population of the same size? For small r we find (see Appendix A Eqs. (A.24) and (A.27)) that

$$b(t) = \frac{1}{e_0} + \frac{r}{2} + r \frac{\sigma_D^2}{2e_0^2}, \quad \text{and} \quad d(t) = \frac{1}{e_0} - \frac{r}{2} + r \frac{\sigma_D^2}{2e_0^2}, \quad (8)$$

where $\sigma_D^2 = \int (a - e_0)^2 \mu(a) l(a) da$ is the variance (standard deviation) of the age at death.

This new result reveals that, relative to a stationary population, a growing population has a higher per-capita birth rate (not surprising) and the increase in birth rate depends (surprisingly) on the variance in age at death σ_D^2 . A growing population will also have a lower per-capita death rate (whenever $\sigma_D < e_0$ which is typical). Why is there a contribution to both birth and death rates that is proportional to the variance in age at death? The intuitive reason is that a growing population's age composition is always skewed towards younger ages (because age structure contains the factor e^{-ra} , see Appendix A Eq. (A.9)). Hence any variance in age at death around e_0 produces a positive change in both rates when $r > 0$; the opposite hold in a declining population (when $r < 0$). To maintain growth in a population of current size $N(t)$, the birth rate must exceed the stationary level by an amount that increases with the variance in age at death.

But the above result contains growth rate r as a separate object. How do ages at death affect r per se?

4. Individuals, death and reproduction

In longitudinal observations of a population we record the age T of each individual death. Suppose that we are interested in individuals rather than the population. Then it makes sense to ask: how do we describe the reproductive performance of individuals who die at a given age? McGraw and Caswell (1996) examined such individual "fitness" and they, as well as (Link et al., 2002), explored the question: what is the relationship between these individual measures and population fitness, as given by r ? Here we show that the analysis of the distribution of age at death sheds new light on both individual performance and the determinants of r .

4.1. Individual reproduction: amount, timing, and growth rate

One component of an individual's "fitness" is its lifetime reproduction (Clutton-Brock, 1988). Any individual who dies at age T has a lifetime reproduction of

$$M(T) = \int_0^T m(a) da. \tag{9}$$

A second component of fitness is timing, the average age at which an individual's offspring are produced. This is the ratio of (i) a weighted sum of ages until death, in which we weight each age by the number of offspring produced at that age, to (ii) the lifetime number of offspring $M(T)$. For an individual who dies at age T , the weighted sum is

$$K(T) = \int_0^T a m(a) da \tag{10}$$

Hence the mean age of reproduction for such an individual is

$$A(T) = \frac{K(T)}{M(T)}. \tag{11}$$

And a final (if complicated) measure of individual fitness: what would be the stable growth rate of a hypothetical population made up of only those individuals who die at a particular age T ? Let's call this growth rate $\rho(T)$; to keep notation simple we leave out the argument when it is safe to do so. Applying the logic of Eq. (4) here, the sum of all reproduction, when discounted at rate ρ , must equal 1, so we have

$$H(T, \rho) = \int_0^T e^{-\rho a} m(a) da = 1. \tag{12}$$

To understand this growth rate, we apply Lotka's approximation to find

$$\rho(T) \approx \frac{\log M(T)}{A(T)} = \frac{\log M(T)}{K(T)/M(T)}. \tag{13}$$

All these individual measures depend on the age-pattern of fertility: the age of maturity (first reproduction), how fast fertility increases with age, whether and when it peaks with increasing age, and the speed of senescent decline in fertility. With these results, it is easy to translate any given pattern of $m(x)$ to predict how individual performance changes with age at death.

4.2. From individuals to population

Ages at death are in fact distributed according to the density ϕ that reflects age-specific mortality. Are population measures—net reproductive rate R_0 , generation time T_c , growth rate r —averages over individual measures?

For a population, the average lifetime reproduction must be the average of individual lifetime reproduction $M(T)$ over the distribution of T . And indeed (see Appendix A Eq. (A.20) with F, f replaced by M, m)

$$\mathbb{E} M(T) = \int_0^\infty \phi(a) M(a) da = R_0. \tag{14}$$

What about the average age of reproduction? The population's reproductive timing T_c is defined in (13). But does this equal the average over ages at death of the individual timing $A(T) = K(T)/M(T)$ defined in Eq. (11)? We find that the population timing can be expressed (see Appendix A Eq. (A.20) with $F(x)$ replaced by $K(T)$) as

$$T_c = \frac{1}{R_0} \mathbb{E} K(T) = \frac{\mathbb{E} K(T)}{\mathbb{E} M(T)}. \tag{15}$$

But the average of individual timing is

$$\bar{T} = \mathbb{E} \left(\frac{K(T)}{M(T)} \right) = \int_0^\infty \phi(a) \frac{K(a)}{M(a)} da. \tag{16}$$

So the answer to our question is no: the expectation of a ratio (Eq. (16)) is not equal to the ratio of expectations (Eq. (15)).

What about growth rate: is r the average of the "individual" rates $\rho(T)$? In the individual renewal equation (12), the discount rate $\rho(T)$ changes when we consider individuals with different ages at death. But in the population there is only one discount rate r for all individuals regardless of age at death. Using the notation in the individual renewal equation (12), we can rewrite the population renewal equation (see Appendix A Eq. (A.20) with $F(x)$ replaced by $H(T, r)$) as

$$\mathbb{E} H(T, r) = \int_0^\infty \phi(a) H(a, r) da = 1. \tag{17}$$

Given that the renewal equation involves a nonlinear function of growth rate, it should be clear that $r \neq \mathbb{E} \rho(T)$, except perhaps in rather special cases.

For added perspective on the difference between individuals and populations, compare Lotka's approximation to $\rho(T)$ in (13) to Lotka's approximation to r in (5); the average of the former over ages at death certainly will not equal r . Clearly one reason for the inequality is the difference noted earlier between the population mean age of reproduction and the average of individual reproductive timing.

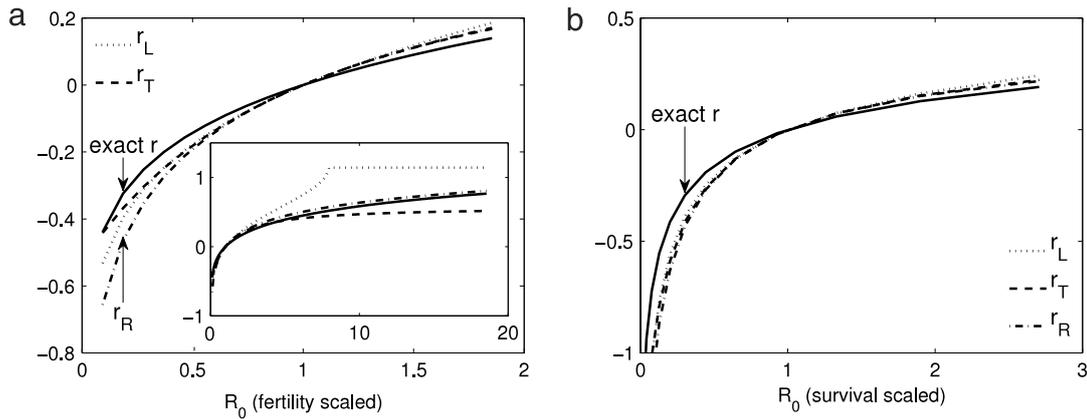


Fig. 2. The intrinsic growth rate r and its approximation by Eqs. (19)–(21) for the life table of the Uinta ground squirrel *Spermophilus armatus* (Slade and Balph, 1974). (a) Different R_0 -values are obtained by scaling the vector of age-dependent fertility rates \mathbf{m}_x with a factor ranging from 0.1 to 2. The inset shows the same plot for large R_0 -values, the scaling factor ranges here from 0.1 to 20. The Lotka-Approximation r_L has complex values for large R_0 , which is seen by the straight dotted line in the inset, because just the real part of r_L is plotted. (b) The R_0 -values are obtained by scaling the age-dependent survival rates \mathbf{p}_x with a factor ranging from 0.1 to $1/p$ where p is the maximal entry of the \mathbf{p}_x -vector: $p = \max_x p_x$.

5. Death as a determinant of r

5.1. A new look at r , R_0 and T_c

Our analysis provides a new perspective on how the distribution of death shapes r . We have rewritten the Euler–Lotka equation as an average over age at death in Eq. (17). More explicitly,

$$1 = \int_0^\infty \phi(a) \left(\int_0^a e^{-rx} m(x) dx \right) da. \tag{18}$$

This equation separates the age-pattern of fertility, in brackets, from mortality, which is the outer average over ages at death. So we have a method for studying the separate contributions of mortality and fertility to r . For one possibility, given a parametrization of $m(x)$ we can explore the shape of the integral in brackets, and then examine the average over death. For another possibility, we could treat the right-hand side as the expectation in (17), and then expand the random value T around its mean e_0 using the delta method.

Yet another approach is via Lotka's approximation. Recall that $M(x)$ is the cumulative reproduction up to age x , and that Eq. (14) shows that R_0 is the average

$$R_0 = \int_0^\infty \phi(a)M(a) da.$$

Thus R_0 is determined by the concordance of the age-patterns of death and of cumulative reproduction. In a similar way T_c is determined by the average of cumulative age-weighted reproduction as shown in Eq. (15). These relationships should allow us to disentangle the effect on r of mortality—especially the mean and variance of age at death—and of fertility—the speed at which fertility rises with age, whether it reaches a peak, and how fast it then declines. We believe such an approach would yield useful insights into mortality senescence and reproductive senescence. We do not pursue this here, but turn to a different question.

5.2. A new approximation to r

In Eq. (6) we show that r is the difference between per-capita birth and death rates. We have also shown that the variance of age at death matters to both rates. Using per-capita rates we obtain (see Appendix A.4) a new approximation r_T to the stable growth rate:

$$r_T = \frac{R_0 - 1}{R_0 T_c - \frac{R_0 - 1}{2} \frac{\mu_D}{e_0}}, \tag{19}$$

where we define $\mu_D = e_0^2 + \sigma_D^2$ as the second moment of the age-at-death distribution. The novelty and main virtue of this approximation is that it explicitly shows how changes in the mean age at death, e_0 , and the variance in age at death, σ_D^2 , affect growth rate.

We consider two other approximations. Lotka's approximation r_L is the smallest of the two roots of $f(r) = \ln \mathbb{E}(e^{-rx})$ where $f(r)$ is developed as a Taylor-series at $r = 0$ (see Appendix A.5 for further details). This yields (Lotka, 1939, p. 121, Eq. (167))

$$r_L = \frac{T_c}{\sigma^2} - \frac{\sqrt{T_c^2 - 2\sigma^2 \ln R_0}}{\sigma^2} \tag{20}$$

where $\sigma^2 = \int (x - T_c)^2 m(x) l(x) dx / R_0$ is the variance of the normalized net maternity function or the demographic dispersion (Tuljapurkar et al., 2009a).

The third approximation r_R has been known in demography and ecology (e.g., Tuljapurkar et al., 2009a) and is derived by the reversion of series (Wachter (unpublished manuscript), Abramowitz and Stegun (1972, p. 16), Pollard (1970), Le Bras (1969, pp. 877–879), Appendix A.6)

$$r_R = \frac{\ln R_0}{T_c} + \frac{\sigma^2 (\ln R_0)^2}{2 T_c^3}. \tag{21}$$

In Fig. 2, we plot our approximation r_T together with r_L , r_R , and the exact $r = \ln(\lambda)$. The approximation values are obtained from modified life tables from the Uinta ground squirrel. We see that for small R_0 - and small r -values all approximations are good estimates of r and that they depart from r in the same direction. For bigger values of R_0 and r (see inset in Fig. 2) the approximations r_L and r_T do worse with r_L being a poor estimator and r_T underestimating r whereas r_R being the best estimator but exceeding r .

Further approximations of r exist (e.g. Coale, 1955; McCann, 1973) as do iteration methods (e.g. Keyfitz (1968, p. 111); Keyfitz and Caswell (2005, p. 130)) but we concentrate on r_L and r_R , because they are the most commonly used in literature.

6. Methods and results

6.1. Quality of the approximations

In this section we compare the quality of the approximations given in Eqs. (19)–(21) by applying them to the life tables of 46 species. The absolute errors are very small so we plot only the relative difference of r_L , r_R , and r_T to $r = \ln \lambda$ in Fig. 3. The absolute

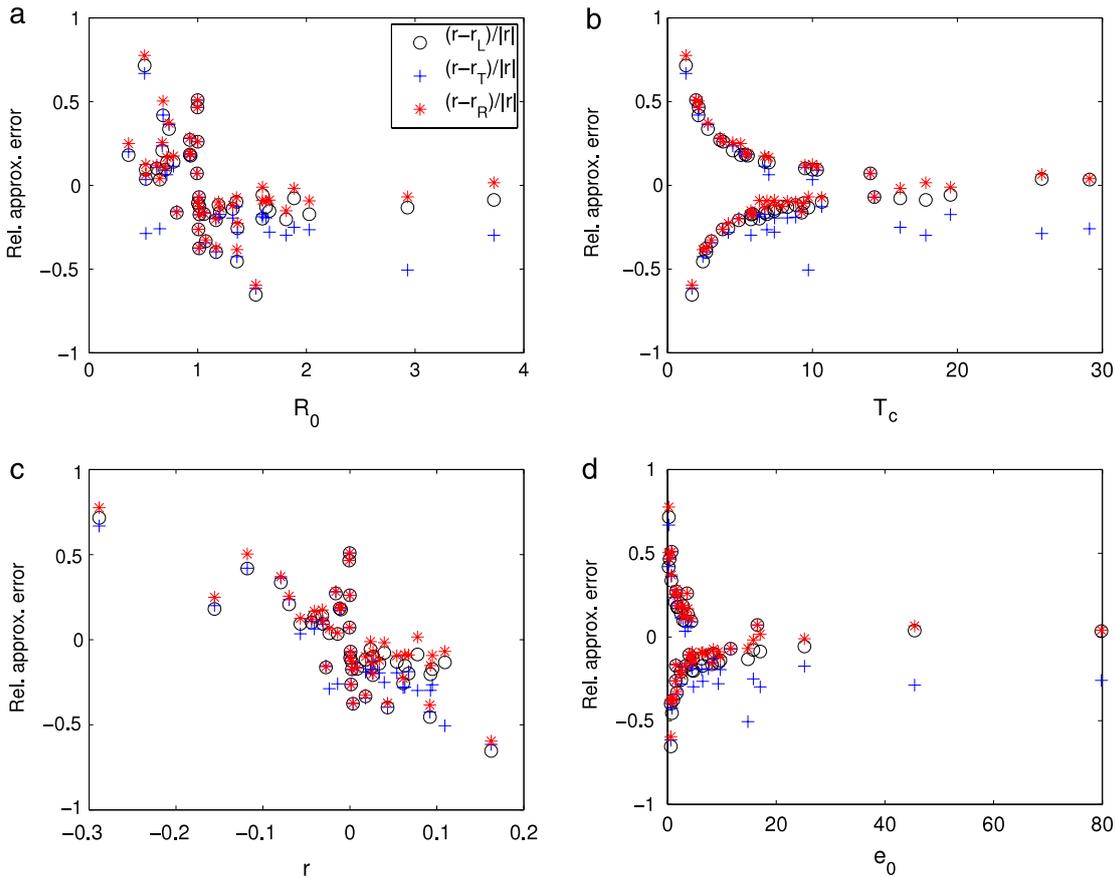


Fig. 3. The relative approximation errors plotted against (a) R_0 , (b) T_c , (c) exact r , (d) e_0 . Circles correspond to the error of Lotka's approximation, crosses to the error of our approximation, and stars to the error of the approximation r_R . We obtain the relative error by dividing the absolute error by the absolute value of the exact r . Data points correspond to 46 mammalian species (including human). See Table B.2 in the Appendix B for references and life history characteristics of all the species.

differences are $r - r_L$, $r - r_R$, $r - r_T$; and the relative differences are calculated by dividing the absolute differences by the absolute value of r , namely $|r|$. We extracted 46 life tables of mammals (including humans) from the literature. These life tables cover a large range of life histories and the approximation errors are plotted against R_0 (Fig. 3(a)), T_c (Fig. 3(b)), r (Fig. 3(c)), and e_0 (Fig. 3(d)). The plots in Fig. 3 show the following properties and trends:

1. The relative errors are the same in magnitude and sign for nearly all approximations. The quality of our approximation r_T is comparable to both other approximations r_L and r_R . See also Table B.1 in the Appendix B which shows the high correlation coefficients of the three approximations.
2. The growth rate tends to be underestimated by all approximations when $R_0 < 1$ (and $r < 0$), and it tends to be overestimated when $R_0 > 1$ (and $r > 0$, see Fig. 3(a) and (c), but also Fig. 2).
3. The smaller T_c is, the bigger the relative approximation errors (see Fig. 3(b)). The bigger T_c is, the less well our approximation r_T performs compared to the others, which can be seen by the crosses lying further away from the circles and stars for a specific T_c -values (species).
4. The relative approximation error of all approximations is biggest for small e_0 (see Fig. 3(d)).

6.2. Quantities that enter r_T

Our new approximation r_T given in Eq. (19) uses four quantities of the life table and the age-at-death distribution. They are the mean lifetime reproductive success R_0 , the generation time T_c and

the first two moments of the age-at-death distribution e_0 and μ_D . The approximation r_T depends on R_0 and T_c in known relation:

$$\frac{\partial r_T}{\partial R_0} = \frac{T_c}{\left(R_0 T_c - \frac{R_0 - 1}{2} \frac{\mu_D}{e_0}\right)^2} > 0 \tag{22}$$

$$\begin{aligned} \frac{\partial r_T}{\partial T_c} &= \frac{R_0(1 - R_0)}{\left(R_0 T_c - \frac{R_0 - 1}{2} \frac{\mu_D}{e_0}\right)^2} \\ &= \begin{cases} < 0 & \text{if } R_0 > 1, \text{ i.e. } r > 0 \\ \geq 0 & \text{if } R_0 \leq 1, \text{ i.e. } r \leq 0. \end{cases} \end{aligned} \tag{23}$$

The first equation reflects the relation of r to R_0 , namely $\partial r / \partial R_0 = 1 / (R_0(T_c - r\sigma^2)) > 0$ (Keyfitz and Caswell, 2005, p. 136). The second Eq. (23) reflects another known relation given below in Eq. (26). The derivatives of r_T in respect to e_0 and μ_D are:

$$\frac{\partial r_T}{\partial e_0} = \frac{-\frac{(R_0 - 1)^2}{2} \frac{\mu_D}{e_0^2}}{\left(R_0 T_c - \frac{R_0 - 1}{2} \frac{\mu_D}{e_0}\right)^2} < 0 \tag{24}$$

$$\frac{\partial r_T}{\partial \mu_D} = \frac{\frac{(R_0 - 1)^2}{2} \frac{1}{e_0}}{\left(R_0 T_c - \frac{R_0 - 1}{2} \frac{\mu_D}{e_0}\right)^2} > 0 \tag{25}$$

and we see that r_T decreases with e_0 and that r_T increases with μ_D ; a result that parallels $\partial r / \partial \sigma^2 = r^2 / (2(T_c - r\sigma^2)) > 0$ from Keyfitz and Caswell (2005, p. 135).

7. Discussion

We have examined how the growth of a stable population is shaped by the age-distribution of death. We showed that both birth and death rates in a stable population depend on the variance of age at death, unless the population is stationary. We then showed that population growth can be analyzed in terms of the distribution of age at death. We started by considering individuals who die at some given age T , and found exact expressions for their lifetime reproductive success and mean timing of reproduction. We used these to provide an exact renewal equation for a hypothetical population of individuals who die at a given age. Next we showed how the performance of such individuals is averaged over the distribution of death ages to find the growth rate of the population. We show that these results shed useful light on the difference between “individual” measures of fitness and population growth (first pointed out by McGraw and Caswell, 1996).

Finally, we derived a new approximation of r , which links r not only to R_0 , T_c but additionally to the moments of the age-at-death distribution. We compared our approximation to two other approximations, namely those of Lotka and one based on the reversion of series, by applying all three to the life tables of 46 species. We found that the inclusion of the age-at-death provides a reasonable approximation of r .

The accuracy of all approximations studied here depends on T_c . The larger T_c , the better r_L and r_R approximate the growth rate r (see Fig. 3(b)). This can be explained by looking at the first-order term of the Taylor series which gives the approximation $r \approx (\ln R_0)/T_c$ (see also Charnov, 1993, p. 118, and references therein). This means that for fixed R_0 the bigger T_c is, the closer r tends to zero. Or in other words, the bigger T_c is, the smaller the absolute value of r . As most approximations assume that r is close to zero the approximations consequently do worse for large absolute values of r . This relation between T_c and r is supported by empirical evidence (e.g. Sinclair, 1996, where longer T_c dampens fluctuations of population size). And this statement can be also proven with the help of calculus as found in Keyfitz and Caswell (2005, p. 136):

$$\frac{dr}{dT_c} = \frac{-r}{T_c - r\sigma^2} \quad (26)$$

which is negative if $r > 0$ and positive if $r < 0$, because $r\sigma^2$ is relatively small compared to T_c . Also see Pollard (1970, Eq. (24)) where the derivatives are obtained from the Taylor-series of r and are also negative.

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Appendix A

All integrals in this appendix are from 0 to ∞ unless otherwise stated.

A.1. Standard theory revisited

Please see Keyfitz and Caswell (2005) for recent a review. In general age-structured demography, the population density is $n(x, t)$ meaning that at time t there are $n(x, t)dx$ individuals between ages x and $x+dx$. The density satisfies (e.g. Kot, 2001, p. 351)

$$\frac{\partial n}{\partial x} + \frac{\partial n}{\partial t} = -\mu(x)n(x, t), \quad (A.1)$$

with boundary condition

$$n(0, t) = \int m(a)n(a, t) da. \quad (A.2)$$

Total birth rate $B(t)$ is

$$B(t) = n(0, t), \quad (A.3)$$

and total death rate $D(t)$ is

$$D(t) = \int \mu(a)n(a, t) da. \quad (A.4)$$

Integrate the partial differential equation (A.1) with respect to age x and get

$$\left[n(x, t) \right]_0^\infty + \frac{\partial}{\partial t} \int n(x, t) dx \stackrel{(A.4)}{=} -D(t) \quad (A.5)$$

$$\text{thus } \frac{dN(t)}{dt} \stackrel{(A.3)}{=} B(t) - D(t), \quad (A.6)$$

with $N(t) = \int n(a, t) da$ being the total population size at time t . Stability means

$$\frac{dN(t)}{dt} = rN(t), \quad (A.7)$$

so we get the text equation (6)

$$r = \frac{B(t)}{N(t)} - \frac{D(t)}{N(t)} =: b(t) - d(t). \quad (A.8)$$

In a stable population growing at rate r the population number density at age x and time t is

$$n(x, t) = e^{rt} u(x) = e^{rt} e^{-rx} l(x) u(0), \quad (A.9)$$

for the stable age distribution $u(x)$ and some constant $u(0)$. The birth rate $B(t)$ (total births per unit time) is just $n(0, t) = e^{rt} u(0)$ but this must equal the total rate at which offspring are produced,

$$B(t) \stackrel{(A.2)-(A.3)}{=} \int m(a) n(a, t) da \quad (A.10)$$

$$\stackrel{(A.9)}{=} e^{rt} u(0) \int e^{-ra} l(a) m(a) da \equiv e^{rt} u(0). \quad (A.11)$$

The line above yields the renewal equation,

$$\int e^{-ra} l(a) m(a) da = 1. \quad (A.12)$$

Using the above for a stable population, we see that

$$b(t) = \frac{B(t)}{N(t)} \stackrel{(A.2)}{=} \frac{\int m(a) n(a, t) d}{\int n(a, t) da} \quad (A.13)$$

$$\stackrel{(A.9)}{=} \frac{e^{rt} u(0) \int e^{-ra} m(a) l(a) da}{e^{rt} u(0) \int e^{-ra} l(a) da} \quad (A.14)$$

$$\stackrel{(A.12)}{=} \frac{1}{\int e^{-ra} l(a) da}, \quad (A.15)$$

whereas

$$d(t) = \frac{D(t)}{N(t)} \stackrel{(A.4)}{=} \frac{\int \mu(a) n(a, t) da}{\int n(a, t) da} \quad (A.16)$$

$$\stackrel{(A.9)}{=} \frac{\int e^{-ra} \mu(a) l(a) da}{\int e^{-ra} l(a) da}, \quad (A.17)$$

and both equal $1/e_0$ for $r = 0$.

A.2. A general equality

Note that (e.g. Fisher, 1930, p. 23)

$$\phi(x) = \mu(x) l(x) = -\frac{dl(x)}{dx}, \quad (A.18)$$

and that $l(0) = 1$ and $l(x)$ goes to zero as $x \rightarrow \infty$ so that

$$\int \phi(x) dx = [-l(x)]_0^\infty = 1. \tag{A.19}$$

We assume that density of age at death $\phi(x)$ has finite moments. Let $f(x)$ be an integrable function of age x and $F(x) = \int_0^x f(a) da$. Then see that

$$\begin{aligned} \int f(a) l(a) da &= [F(x) l(x)]_0^\infty + \int \phi(a) F(a) da \\ &= \int \phi(a) F(a) da \end{aligned} \tag{A.20}$$

where we use integration by parts on the second expression.

A.3. New results

To get text equation (8), first use General Result (A.20) above with $f(a) = a$ to see that

$$\int a l(a) da = \int \phi(a) \frac{a^2}{2} da = \frac{1}{2} \mu_D = \frac{1}{2} (e_0^2 + \sigma_D^2). \tag{A.21}$$

The last equality is obtained from the standard variance equation $\sigma_D^2 = \mathbb{E}(T^2) - (\mathbb{E}T)^2$ see text equation (3). Then expand $b(t)$ and $d(t)$ from Eqs. (A.15) and (A.17) in r near $r = 0$:

$$b(t) \approx \frac{1}{e_0} + r \frac{\int a l(a) da}{(\int l(a) da)^2} \tag{A.22}$$

$$\stackrel{(A.21)}{=} \frac{1}{e_0} + r \frac{\mu_D}{2 e_0^2} \tag{A.23}$$

$$= \frac{1}{e_0} + \frac{r}{2} + r \frac{\sigma_D^2}{2 e_0^2}, \tag{A.24}$$

and

$$d(t) \approx \frac{1}{e_0} + r \frac{[-\int a \mu(a) l(a) da][\int l(a) da] + [\int a l(a) da][\int \mu(a) l(a) da]}{[\int l(a) da]^2} \tag{A.25}$$

$$\stackrel{(A.21)}{=} \frac{1}{e_0} + r \frac{-e_0^2 + \frac{\mu_D}{2}}{e_0^2} \tag{A.26}$$

$$= \frac{1}{e_0} - \frac{r}{2} + r \frac{\sigma_D^2}{2 e_0^2}. \tag{A.27}$$

A.4. Derivation of our approximation

Our aim is to derive an approximation of r that includes the moments of the age-at-death distribution. The time-dependent factor of $K = Qe^{rt}$ is a solution of the linear, homogeneous Lotka integral equation and accounts for population growth or shrinkage. For stationary populations the following equations hold (Kot, 2001, pp. 354, 357)

$$B = K = K \int e^{-ra} m(a) l(a) da \tag{A.28}$$

$$N = K \int e^{-ra} l(a) da. \tag{A.29}$$

The number of deaths in stationary populations can be calculated by

$$D = K \int e^{-ra} \mu(a) l(a) dx. \tag{A.30}$$

Using again a first order Taylor expansion of e^{-ra} around $r = 0$ for Eqs. (A.28)–(A.30) we obtain the approximations

$$B \approx K \left(\int l(a) m(a) da - r \int a l(a) m(a) da \right) \tag{A.31}$$

$$D \approx K \left(\int \mu(a) l(a) da - r \int a \mu(a) l(a) da \right) \tag{A.32}$$

$$N \approx K \left(\int l(a) da - r \int a l(a) da \right). \tag{A.33}$$

Using the definitions of e_0, R_0, T_c and Eq. (A.21), Eqs. (A.31)–(A.33) can be rewritten as

$$B \approx KR_0 (1 - r T_c) \tag{A.34}$$

$$D \approx K (1 - r e_0) \tag{A.35}$$

$$N \approx K \left(e_0 - \frac{r}{2} \mu_D \right). \tag{A.36}$$

Dividing Eqs. (A.34) and (A.35) by Eq. (A.36) we yield the per-capita birth and death rates

$$\frac{B}{N} \approx \frac{R_0 (1 - r T_c)}{e_0 - \frac{r}{2} \mu_D} \tag{A.37}$$

$$\frac{D}{N} \approx \frac{1 - r e_0}{e_0 - \frac{r}{2} \mu_D} \tag{A.38}$$

and we can approximate these rates by their Taylor-Series in the vicinity of $r = 0$ by truncating the series after the second term:

$$\frac{B}{N} \approx \frac{R_0}{e_0} \left(1 - r T_c + \frac{r}{2} \frac{\mu_D}{e_0} \right) \tag{A.39}$$

$$\frac{D}{N} \approx \frac{1}{e_0} \left(1 - r e_0 + \frac{r}{2} \frac{\mu_D}{e_0} \right). \tag{A.40}$$

Rewriting Eq. (A.8) by substituting Eqs. (A.39) and (A.40), yields

$$r \approx \frac{1}{e_0} \left(R_0 - 1 - r(R_0 T_c - 1) + r \frac{R_0 - 1}{2} \frac{\mu_D}{e_0} \right) \tag{A.41}$$

and solving Eq. (A.41) for r leads to our new approximation r_T

$$r_T = \frac{R_0 - 1}{R_0 T_c - \frac{R_0 - 1}{2} \frac{\mu_D}{e_0}}. \tag{A.42}$$

A.5. Notes on Lotka's approximation

Lotka's approximation r_L is the smallest of the two roots of $f(r) = \ln \mathbb{E}(e^{-rx})$ where $f(r)$ is developed as a Taylor-series at $r = 0$. The term $\mathbb{E}(e^{-rx})$ is the expectation of e^{-rx} with respect to the normalized net maternity function $l(x) m(x)/R_0$ of the focal population. Equivalently, $\mathbb{E}(e^{-rx})$ is the moment generating function of the normalized net maternity function, and $\ln \mathbb{E}(e^{-rx})$ is the cumulant generating function of the normalized net maternity function. Both generating functions can be written as power series

$$\mathbb{E}(e^{-rx}) = \sum_{n=0}^{\infty} \mu_n \frac{(-r)^n}{n!} \tag{A.43}$$

$$\ln \mathbb{E}(e^{-rx}) = \sum_{n=0}^{\infty} \kappa_n \frac{(-r)^n}{n!} \tag{A.44}$$

where μ_n and κ_n denote the n -th moment and the n -th cumulant. To obtain r that solves Eq. (1), one can solve either

$$\mathbb{E}(e^{-rx}) = \frac{1}{R_0} \tag{A.45}$$

Table B.1

The Pearson correlation matrix of the three approximations r_T , r_L , and r_R obtained for the 46 mammalian life tables. As the matrix is symmetrical, we omit the lower triangular entries.

	r_L	r_R	r_T
r_L	1.0000000	0.9994254	0.9977825
r_R		1.0000000	0.9963749
r_T			1.0000000

or, by taking the logarithm of Eq. (A.45),

$$\ln \mathbb{E}(e^{-rx}) = -\ln R_0. \tag{A.46}$$

Lotka calculated r_L as the smallest root of the quadratic polynomial obtained by truncating Eq. (A.44) after the second-order term (Dublin and Lotka, 1925; Lotka, 1939).

A.6. Reversion of series

We quote from Abramowitz and Stegun (1972, p. 16) to outline the derivation of r_R :

Table B.2

Life history characteristics and references for the 46 mammalian species used in Fig. 2.

Name	Reference	R_0	T_c	r	e_0	μ_D
Spectacled flying fox (<i>Pteropus conspicillatus</i>)	Fox et al. (2008)	0.364	5.05	-0.156	1.83	9.01
Gray fox (<i>Urocyon cinereoargenteus</i>)	Michod and Anderson (1980)	0.511	1.27	-0.288	0.24	0.36
Lemur (<i>Propithecus diadema edwardsi</i>)	Pochron et al. (2004)	0.522	10.00	-0.057	3.26	39.51
Killer whale (<i>Orcinus orca</i>)	Olesiuk et al. (1990)	0.522	25.82	-0.024	45.47	2841.58
Black bear (<i>Ursus americanus</i>)	Yodzis and Kolenosky (1986)	0.624	9.49	-0.044	2.86	27.42
Human (Slovenia) (<i>Homo sapiens</i>)	Human survival data for Slovenia (2007), Human fertility data for Slovenia (2006)	0.651	29.12	-0.014	79.83	6537.65
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Schwartz et al. (1998)	0.673	4.50	-0.070	1.38	6.35
Raccoon dogs (<i>Nyctereutes procynoides</i>)	Helle and Kauhala (1993)	0.681	2.14	-0.118	0.21	0.59
Grizzly bear (<i>Ursus arctos horribilis</i>)	Knight and Eberhardt (1985)	0.699	10.32	-0.031	4.39	49.89
Sea otter (<i>Enhydra lutris</i>)	Monson et al. (2000)	0.716	6.99	-0.041	3.73	40.11
Daurian ground squirrel (<i>Spermophilus dauricus</i>)	Luo and Fox (1990)	0.736	2.79	-0.079	0.70	2.10
Blue Wildebeest (<i>Connochaetes taurinus taurinus</i>)	Attwell (1982)	0.777	6.70	-0.032	2.46	23.59
Panamanian spiny pocket mouse (<i>Liomys adspersus</i>)	Fleming (1971)	0.807	9.25	-0.028	8.17	69.19
Himalayan Tahr, stat. population (<i>Hemitragus jemlahicus</i>)	Caughley (1970a)	0.927	5.37	-0.012	2.85	21.36
Uinta ground squirrel (<i>Spermophilus armatus</i>)	Slade and Balph (1974)	0.927	3.62	-0.016	1.59	6.02
Beaver (<i>Castor canadensis</i>)	Payne (1984)	0.935	5.55	-0.010	1.80	10.44
Beluga whale (<i>Delphinapterus leucas</i>)	Béland et al. (1988)	0.993	14.00	-0.000	16.54	359.54
Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	Bronson (1979)	0.998	2.15	-0.001	0.39	1.10
Western jumping mouse (<i>Zapus princeps</i>)	Falk and Millar (1987)	0.999	1.96	-0.000	0.75	2.02
Chamois (<i>Rupicapra rupicapra</i>)	Caughley (1970b)	1.000	3.83	-0.000	3.59	18.34
Northern Fur Seal (<i>Callorhinus ursinus</i>)	Barlow and Boveng (1991)	1.003	9.39	0.000	4.00	54.01
Columbian ground squirrel (<i>Spermophilus columbianus</i>)	Zammuto (1987)	1.007	3.80	0.001	1.52	5.52
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Stolen and Barlow (2003)	1.012	14.27	0.001	11.60	243.86
Bobcat (<i>Lynx rufus</i>)	Rolley (1985)	1.013	2.67	0.004	1.07	3.80
Dall sheep (<i>Ovis dalli</i>)	Simmons et al. (1984)	1.016	5.76	0.002	3.31	28.65
Spiny rat (<i>Proechimys semispinosus</i>)	Fleming (1971)	1.016	7.93	0.002	4.67	44.41
Mongoose (<i>Helogale parvula</i>)	Waser et al. (1995)	1.059	5.88	0.008	1.54	8.29
Black-tailed prairie dog (<i>Cynomys ludovicianus</i>)	Hoogland (1995)	1.075	3.03	0.018	1.72	7.10
Large-headed rice rat (<i>Oryzomys capito</i>)	Fleming (1971)	1.167	4.91	0.026	2.40	12.65
Gray squirrel (<i>Sciurus carolinensis</i>)	Barkalow et al. (1970)	1.170	2.67	0.043	0.60	2.36
Southern Pig-tailed Macaque (<i>Macaca nemestrina</i>)	Ha et al. (2000)	1.191	8.85	0.018	7.53	128.00
South American Fur Seal (<i>Arctocephalus australis</i>)	Lima and Pàez (1997)	1.204	6.71	0.025	4.27	44.58
Gelada baboon (<i>Theropithecus gelada</i>)	Dunbar (1980)	1.323	7.38	0.034	9.71	107.34
Yellow baboon (<i>Papio cynocephalus</i>)	Storz et al. (2002)	1.356	10.64	0.027	8.44	122.54
Belding's ground squirrel (<i>Spermophilus beldingi</i>)	Sherman and Morton (1984)	1.361	2.44	0.092	0.80	2.53
Roe deer (<i>Caprolus capreolus</i>)	Johnson (1982)	1.365	4.19	0.061	2.53	14.87
Townsend's ground squirrel (<i>Spermophilus townsendii</i>)	Smith and Johnson (1985)	1.534	1.69	0.163	0.61	1.27
Eastern White-bearded Wildebeest (<i>Connochaetes taurinus albojubatus</i>)	Watson (1970)	1.595	6.34	0.068	4.54	41.08
Indian rhinoceros (<i>Rhinoceros unicornis</i>)	Dinerstein and Price (1991)	1.596	19.52	0.024	25.20	822.30
African buffalo (<i>Syncerus caffer</i>)	Sinclair (1977)	1.629	8.27	0.054	6.28	74.34
Red deer (<i>Cervus elaphus</i>)	Benton et al. (1995)	1.660	7.37	0.063	9.34	115.48
Himalayan Tahr, increasing pop. (<i>Hemitragus jemlahicus</i>)	Caughley (1970a)	1.813	5.75	0.093	4.77	42.98
Weeping capuchin, small groups (<i>Cebus olivaceus</i>)	Robinson and O'Brien (1991)	1.885	16.05	0.040	15.78	441.87
Caribou (<i>Rangifer tarandus</i>)	Messier et al. (1988)	2.026	6.86	0.095	6.47	67.37
Horse (<i>Equus caballus</i>)	Garrott and Taylor (1990)	2.930	9.72	0.109	14.78	256.64
Weeping capuchin, large groups (<i>Cebus olivaceus</i>)	Robinson and O'Brien (1991)	3.725	17.82	0.078	17.06	493.07

Given

$$y = ax + bx^2 + cx^3 + dx^4 + ex^5 + fx^6 + gx^7 + \dots \tag{A.47}$$

then

$$x = Ay + By^2 + Cy^3 + Dy^4 + Ey^5 + Fy^6 + Gx^7 + \dots \tag{A.48}$$

where

$$aA = 1, \quad a^3B = -b, \quad a^5C = 2b^2 - ac, \tag{A.49}$$

$$a^7D = 5abc - a^2d - 5b^2$$

$$a^9E = 6a^2bd + 3a^2c^2 + 14b^4 - a^3e - 21ab^2c \tag{A.50}$$

⋮

We yield r_R when equating (A.44) with (A.46), applying (A.48), that is $x = r$ and $y = -\log R_0$, and truncating the expression for r after the quadratic term.

Appendix B

See Tables B.1 and B.2.

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