

# Existence and Estimation of Negative Critical Allometry Model Parameter

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**Abstract-** In this paper, we provide an interval of existence of negative critical mortality rate parameters  $M_c$  and  $b$  in Allometry survival model, in the absence of age-specific mortality data by age.

**Index Terms-** Allometry, critical age, exponential growth, linear growth, mortality rate, negative critical age.

## I. INTRODUCTION

It has been recognized for more than 100 years that the rate of physiological processes is affected by body mass. Several theories have been put forth to explain the scaling of whole animal metabolic rate, ranging from single-cause explanations of supply system limitations (e.g., West et al. 2002)[1], to multi-cause assessments of the cellular pathways that determine the metabolic phenotype (e.g., Darveau et al. 2002)[2]. These model-oriented approaches address ultimate causes of scaling patterns across diverse models. An alternative approach to understanding metabolic scaling is to address more proximate relationships. Muscle, for example, shows the same patterns of scaling of oxidative enzymes. Regardless of the underlying basis for metabolic phenotype in whole animals, the molecular mechanism regulating the reciprocal change in muscle phenotype is still unknown. Muscles also exhibit phenotypic plasticity in bioenergetic enzymes as a result of differences between muscle fiber types, in response to ecological and behavioral changes and throughout ontogeny. It seems intuitive that within a species, individuals with larger bodies also have larger constituent parts. Larger humans tend to have longer legs, arms and torsos, bigger livers and larger hearts. This scaling relationship between the sizes of individual traits and the size of the whole body is called allometry[3]. Allometry describes how the characteristics of an organism scale with each other and with body size [4].

Accurately modelling the distribution of individual sizes at age is a fundamental problem, which must be addressed when modelling the dynamics of a population. Many important characteristics of a population, such as mortality rate, are size specific. For instance, fishing mortality rate is dependent on the size-specific selectivity of the fishing gear. In most cases, natural mortality is also size dependent. In addition, for some species that cannot be aged, size is the only available measurement that provides information about reproductive maturity [5].

A theory of population that fails to consider a major determinant of the characteristics of populations is not an adequate theory. Standard texts in population biology and ecology tend to ignore body size as a factor in population dynamics, although birth and death rates, survivorship and longevity, population density and home range size, cycle periods for population boom and crash, and the annual increment in mortality due to aging all show a strong correlation with body mass (Calder [6]). Julian Huxley and Georges Teissier coined the term allometry in 1936. In a joint paper, simultaneously published in English and French (Huxley and Teissier [7]), they agreed to use this term in order to avoid confusion in the field of relative growth. They also agreed on the symbols to be used in the algebraic formula of allometric growth:

$$Y = am^b$$

This makes body size a good choice for baseline analysis, using the scaling (heterogonic or allometric) equation of Huxley[8] and Kleiber[9]:

$$Y = am^b;$$

in which  $Y$  is a physiological, morphological, or ecological variable; the coefficient  $a$  is characteristic of a class or order of animals and the physical dimensional units (if any) being used in the measurement of  $Y$ ;  $m$  is body mass (kg); and the exponent  $b$  is the ratio of changes in orders of magnitude for  $Y$  compared to  $m$ , thus expressing the effect of body mass changes on  $Y$ .

The layout of this paper is as follows. First in section 2, we state the problem under consideration. This section is divided into two subsections, first in subsection 2.1 fully discussed with the linear growth allometry model problem, under this assumption, we derived the negative critical allometry parameter. Second in subsection 2.2 deals with the exponential growth allometry model problem, under this condition we derived the corresponding negative critical allometry parameter. Finally we give the conclusion about this paper in section 3.

## II. APPLICATIONS OF ALLOMETRIC SCALING LAW

### A. Linear Growth

Stocking is widely used in the management of freshwater and, to a lesser extent, coastal-marine fisheries (e.g., Heidinger[10]). A key problem in the management of stocked fisheries is the optimization of release size (e.g., Cowx[11]). The optimal release size depends on the contribution that fish of a particular size will make to the catch or shable stock and on the re-sources required to

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produce seed sh of that size. Of the data required to assess optimum size, the survival of seed sh of di erent sizes to the shable stock (and/or contribution to the catch) are the most di cult to obtain. Systematic assessments have been either entirely empirical (release - recapture of marked seed sh of di erent sizes) or based on detailed ecological studies(Wahl et al.[12]). However, the costs and e ort involved in both approaches restrict their use to a small number of sheries, and the results are not readily generalized. An alternative approach that implies a simple gen-eralization is the use of allometric mortality-size relationship (Lorenzen[13]). Provided that natural mortality in stocked sh is subject to a consistent al-lometry, then an estimate of mortality for a single reference size is su cient to predict survival for a range of different release sizes.

Theoretical and empirical studies Peterson and Wroblewski[14], Loren-zen [15]) point to the existence of an allometric relationship between natural mortality and body weight, of the form

$$M_w = M_u W^b \tag{1}$$

where  $M_w$  is natural mortality at weight  $W$  ;  $M_u$  is mortality at unit weight;  $b$  is the allometry exponent; and where there is an implied RHS coefficient of (unit weight)<sup>-b</sup>. Note that a mathematical structure of this form would also apply to a system transformed to corresponding dimensionless variables as mentioned in the Introduction.

B.Survival Model

The survival model follows that developed by Lorenzen [16] in which the allometric relationship between natural mortality and body length may be described by the equation<sub>1</sub>

$$M(l) = M_r \left(\frac{l}{l_r}\right)^b$$

where  $M(l)$  is the mortality rate at length  $l$ ,  $M_r$  is the instantaneous mortality rate at reference length  $l_r$  (e.g., 15 cm { as used by Lorenzen [16]),and  $b$  is the allometric exponent of the mortality-length relationship. This reference length,  $l_r$ , needs to be chosen as a parameter such that it is smaller than another parameter,  $l_0$ , the length at stocking.

If this equation accurately describes mortality in the stocked population, then the decline in population size of a stocked cohort (organisms of the same age and size) of original population size  $N_0$ , while su ciently large enough to be approximated as a continuous variable, is described by the differential equation.

$$\frac{dN(t)}{dt} = -N(t) M_r \left(\frac{l(t)}{l_r}\right)^b \tag{3}$$

where  $l(t)$  is length at time  $t$  and  $N(t)$  is the population size at time  $t$ . This differential equation may be solved explicitly if a linear growth model is substituted for  $l(t)$ . A linear length growth model is reasonably used in the empirical analysis, because time at large (i.e., the time interval between release at stocking and estimated survival age at

death or recapture) is short and the size of the sh is small relative to the reported maximum sizes in all stocking experiments analyzed in [16]. A model of the form

$$l(t) = l_0 + ut \tag{4}$$

is used where  $t$  is the time since stocking, and  $u$  is the linear length growth rate. Substitution of equation (4) into equation(3), integration, and division by  $N_0$  on both sides gives the following equation to predict survival,  $S(t)$  (proportion of stocked sh urviving), from the time of stocking to time  $t$ :

$$S(t) = \frac{N(t)}{N_0} = e^{-\frac{M_r(-l_0(\frac{l_0}{l_r})^b + (l_0+ut)(\frac{l_0+ut}{l_r})^b)}{(b+1)u}}, \tag{5}$$

: as was derived by Lorenzen [16] for the case where  $b \neq 1$ .

The two parameters  $M_r$  and  $b$  are of interest to many investigators in biogerontology and the evolutionary biology of aging [17 - 21]. Species com-parisons in mortality rates are aided by calculations of MRD (mortality rate doubling time) which changes in the same direction as lifespan and is given by

$$MRD = \frac{2^{\frac{1}{b}} l_r - l_0}{u} \tag{6}$$

In the presence of mortality data by age, the Allometric scaling param-eters  $M_r$  and  $b$  have been estimated by using various statistical methods like maximum likelihood, linear regression, and nonlinear regression[20-26]. Usually, an experimentalist knows the lifespan of each individual in a given population and can make use of standard techniques such as MLE or linear regression [22 & 23] to estimate the model parameters.

In the absence of age specific mortality data, in this paper we have de-veloped a method to estimate  $b$  from the instantaneous mortality rate at reference length, i.e.,  $M_r$ ; the original population size,  $N_0$ ; and the maximum lifespan,  $t_m$ .

In [29] we have derived the following result for linear growth

$$t_m^* \approx t_m = \frac{1}{u} \left[ (l_r)^{\frac{b}{b+1}} \left( \frac{(b+1)u \ln N_0}{M_r} \right) + l_0 \left(\frac{l_0}{l_r}\right)^b \right]^{\frac{1}{b+1}} - l_0 \tag{7}$$

The average mortality rate of steady state population subject to age specific mortality rates of equation (2) is [20 & 21]

$$A_{av} = \frac{1}{\int_0^{t_m} S(t) dt} \tag{8}$$

Equation (7) gives,

$$\frac{M_r}{(b+1)u} = \frac{\ln N_0}{-l_0 \frac{l_0}{l_r}^b + (l_0+ut) \left(\frac{l_0+ut}{l_r}\right)^b} \tag{9}$$



And from equation (8), we get

$$b+1 = A_{av} e^x \int_x^\infty \left(\frac{(b+1)l_r}{u^b}\right)^{\frac{1}{b+1}} \frac{e^{-z}}{z^{b+1}} dz, \quad (10)$$

$$\approx A_{av} \frac{l_r}{u} e^x \int_x^\infty \frac{e^{-z}}{z} dz, \quad \text{see [29]}$$

$$\text{Where } x = \frac{M_r l_0 \left(\frac{l_0}{l_r}\right)^b}{(b+1)u} = \frac{\ln N_0}{\left(\frac{l_0+ut_m}{l_0}\right)^{b+1}-1}$$

### C. Existence of negative critical parameter

Recall that the age at which the mortality rate,  $M_r \left(\frac{l}{l_r}\right)^b$  of initial population  $N_0$  has ceased increasing or, equivalently, it tends to a constant, is called a critical age,  $t_c$  [30]. The remaining population left from an original population size  $N_0$  surviving at this critical age is called critical population,  $N_c$ , and the corresponding Allometry parameter in  $M_r \left(\frac{l}{l_r}\right)^b$  is called critical Allometry  $l_r$  parameter,  $b_c$ . Since the partials of  $b$  with respect to  $N_0$  and  $t_m$  become zero at  $M_r = \frac{A_{av} t_m b + 1}{l_0^b}$

and using (9), we get,

$$\frac{A_{av} t_m}{\ln N_0} = \frac{(b+1)ut_m}{l_0 \left[\left(\frac{l_0+ut_m}{l_0}\right)^{b+1}-1\right]} \quad (11)$$

From (11) it follows that

$$\frac{A_{av} t_m}{\ln N_0} = \begin{cases} < 1 \text{ if } b > 0, \\ = 1 \text{ if } b = 0, \\ > 1 \text{ if } b < 0. \end{cases} \quad (12)$$

The point  $c$  at which  $b$  changes sign is said to be the critical point of  $b$ .

From our earlier work [30], we know that, for a given  $A_{av}$ ,  $t_m$ ; and  $N_0$

With  $\frac{A_{av} t_m}{\ln N_0} < 1$ .

$$t_c = t_m \text{ and } N_c = e^{A_{av} t_c}. \quad (13)$$

On the contrary, when  $\frac{A_{av} t_m}{\ln N_0} > 1$ ,

$$t_c = \frac{\ln N_0}{A_{av}}, N_c = e^{A_{av} t_c} \text{ and } t_c \neq t_m \quad (14)$$

Note that  $t_c$   $t_m$  for any given  $A_{av}$ ;  $t_m$  and  $N_0$ . We also know that [31], the asymptotic solution  $b$  of (10) is a continuous function in the variables  $A_{av}$ ;  $t_m$  and  $N_0$  from puberty through critical life span (or,  $N_0$   $N_c$ ). What happens to solution  $b$  when  $N_0$   $N_c$  (below the critical population). As we have already equated  $t_m$  with  $t_c$  when  $\frac{A_{av} t_m}{\ln N_0} < 1$ , what is then actual (species) maximum life span,  $t_m$ ? Such  $t_m > t_m$  exists, since the critical population  $N_c$  has not yet diminished to one survivor. How to determine this  $t_m$ ? This in turn, leads us to consider negative allometry parameter, since  $\frac{A_{av} t_m}{\ln N_0} > 1$

for  $N_0 = N_c$ .

To determine the negative allometry parameter consider (13)

with  $N_0$

$N_c$  and (14) with  $t_c = \frac{\ln N_0}{A_{av}}$ . Upon substitution  $N^0 = N_c$  into (10), we get

$$b_c + 1 = A_{av} e^{\xi} \int_{\xi}^{\infty} \frac{e^{-z}}{z} dz, \quad (15)$$

With

$$\xi = \frac{\ln N_c}{\left(\frac{l_0+ut_c}{l_0}\right)^{b_c+1}-1}, \text{ where } t_c = t_m \text{ when } \frac{A_{av} t_m}{\ln N_0} < 1.$$

And  $t_c = \frac{\ln N_0}{A_{av}}$  when  $\frac{A_{av} t_m}{\ln N_0} > 1$ .

Eq. (15) gives

$$b_c + 1 \leq \frac{A_{av} t_c}{\ln N_c} l_0 \left[\left(\frac{l_0+ut_c}{l_0}\right)^{b_c+1}-1\right].$$

The above inequality ensures the existence of solution  $\alpha_c$ , provided  $\frac{A_{av} t_c}{\ln N_c} = 1$ . As a consequence, we get

$$b_c + 1 \leq l_0 \left[\left(\frac{l_0+ut_c}{l_0}\right)^{b_c+1}-1\right]. \quad (16)$$

A close observation of the inequality (16) reveals that any  $b \leq 0$  also satisfies it. This result, in fact, motivates us to consider the negative critical allometry parameter. On the other hand, in the neighbourhood of the critical point

$\frac{A_{av} t_c}{\ln N_c} = 1$ , it is necessary that  $\frac{A_{av} t_c}{\ln N_c} > 1$  if  $b < 0$  from (12).

Hence

$$(-b_c + 1)ut_c \leq l_0 \left[\left(\frac{l_0+ut_c}{l_0}\right)^{b_c+1}-1\right]. \quad (17)$$

Invalid for  $N_0 = N_c$ . provided  $\frac{A_{av} t_c}{\ln N_c} > 1$ . Clearly  $\frac{A_{av} t_c}{\ln N_c} > 1$

holds when  $t_c > \frac{\ln N_0}{A_{av}}$  in (14). In case of (13),  $\frac{A_{av} t_c}{\ln N_c} > 1$  if

$N_0 < N_c$  and this gives  $t_c > \frac{\ln N_0}{A_{av}} = t_c \frac{\ln N_c}{\ln N_0}$ . We designate

$t_m^* = t_c \frac{\ln N_c}{\ln N_0}$  as the actual maximum life span.

Since  $t_m^*$  becomes very large numerically as  $N_0 \rightarrow 1$  [30], we can choose any finite value greater than  $t_c$  and  $t_m^*$ . Fortunately, we shall not use the numerical value of  $t_m$  in our sequel.

Numerical experiments show that the transition from  $b_c$  to  $b$  is extremely slow. The graphical illustration should enhance the understanding of this idea [19]. Further, it follows from (9) that as  $b \rightarrow 0$  at  $N_0 = N_c$ ,  $M_r \rightarrow A_{av}$ , since

$$M_r = \frac{\ln N_c}{t_c} = A_{av}.$$

As  $b_c$  changes sign, from (9) we obtain

$$\frac{M_r}{(-b_c+1)u} = \frac{\ln N_c}{-l_0 \frac{l_r}{l_r} b_c + (l_0+ut_c) \left(\frac{l_0+ut_c}{l_r}\right)^{-b_c}} \quad (18)$$

Which gives

$$M_r = \frac{\ln N_c}{t_c} \frac{(-b_c+1)ut_c}{-l_0 \frac{l_r}{l_r} b_c + (l_0+ut_c) \left(\frac{l_0+ut_c}{l_r}\right)^{-b_c}} \geq \frac{\ln N_c}{t_c}$$

Thus

$$M_r \geq \frac{\ln N_c}{t_c}.$$

C.Linear Allometry Survival function

In the neighbourhood of the critical point,  $\frac{A_{av} t_c}{\ln N_c} = 1$  in view of (16) and (17) the survival function (5) takes the form

$$S(t) = \begin{cases} e^{\frac{-M_r - l_0 \frac{l_r^b}{l_r} + (l_0 + ut_c) (\frac{l_0 + ut_c}{l_r})^{-b}}{(b+1)u}} & \text{if } t \leq t_c (N \geq N_c) \\ e^{\frac{-M_r - l_0 \frac{l_r^{-b}}{l_r} + (l_0 + ut_c) (\frac{l_0 + ut_c}{l_r})^{-b}}{(-b+1)u}} & \text{if } t \leq t_c (N \leq N_c). \end{cases} \quad (19)$$

Lemma: S(t) is continuous at  $t = t_c$ .

Proof: Indeed

$$\begin{aligned} \lim_{t \rightarrow t_c - 0} S(t) &= e^{\frac{M_{rc} \left( -l_0 \frac{l_r^{-b_c}}{l_r} + (l_0 + ut_c) \left( \frac{l_0 + ut_c}{l_r} \right)^{-b_c} \right)}{(b_c + 1)u}} \\ &= e^{\frac{-M_{rc} (-l_0 \frac{l_r^{-b_c}}{l_r} + (l_0 + ut_c) \left( \frac{l_0 + ut_c}{l_r} \right)^{-b_c}}{(b_c + 1)u}} \\ &= e^{\frac{-M_{rc} (-l_0 \frac{l_r^{-b_c}}{l_r} + (l_0 + ut_c) \left( \frac{l_0 + ut_c}{l_r} \right)^{-b_c}}{(b_c + 1)u}} \\ &= \lim_{t \rightarrow t_c - 0} S(t) \end{aligned}$$

Now we extend the formula (15) to  $-b_c$  for  $N_0 = N_c$ . When given  $A_{av}, t_m$  and  $N_0$  satisfy (13) with  $N_0 \leq N_c$

And (14) with  $t_c \leq \frac{\ln N_0}{A_{av}}$  Upon substitution  $b_c = b_c$  into (15) we get

$$-b_c + 1 = A_{av} \frac{l_r}{u} \frac{-\ln N_c}{e^{\frac{1}{1 - \left( \frac{l_0 + ut_c}{l_r} \right)^{-b_c + 1}}}} \int_0^u \frac{e^{-z}}{z} dz$$

As such the above integral is unbounded. The unboundedness results in by the substitution  $t_c = 1$  or  $N_0 = 1$  with  $N_0 \leq N_c$  into (15), when  $b_c < 0$ . But inequality (17) implies the existence of  $b_c$ . To overcome this situation, we need to introduce limit age,  $t_{lim}$  of the critical population  $N_c$ . Following Suematsu [32], the limit age can be defined as an age where the final member of the critical population  $N_c$  disappears. Stating mathematically,

$$S(t_{lim}) = e^{\frac{-M_r - l_0 \frac{l_r^b}{l_r} + (l_0 + ut_{lim}) \left( \frac{l_0 + ut_{lim}}{l_r} \right)^{-b}}{(-b+1)u}} \leq \frac{1}{N_0}$$

Clearly, if the population  $N_c$  at an age  $t \leq t_c$  is less than unity, all the members under discussion must, in the statistical mean, vanish. Hence, the limit age can be identified with the minimum age,  $t_{lim}$ , that satisfies

$$S(t_{lim}) \leq \frac{1}{N_0}$$

Taking into account the above arguments, substitute  $N_0 = 0$  ( $N_0 \leq N_c$ ) into the upper limit of (15) when  $b_c < 0$  to get

$$-b_c + 1 = A_{av} \frac{l_r}{u} \frac{-\ln N_c}{e^{\frac{1}{1 - \left( \frac{l_0 + ut_c}{l_r} \right)^{-b_c + 1}}} E_i \left( \frac{\ln N_c}{1 - \left( \frac{l_0 + ut_c}{l_r} \right)^{-b_c + 1}} \right) \quad (21)$$

where

$$E_i(x) = \lim_{n \rightarrow +\infty} \left[ \int_{-x}^{-\eta} \frac{e^{-z}}{z} dz + \int_{\eta}^{\infty} \frac{e^{-z}}{z} dz \right]$$

[ $x > 0$ ]

Clearly, (21) satisfies inequality (17). We could not obtain (17) directly from (21), since the integrand is unbounded at  $z = 0$ .

From equation (21), on account of 8.214. 2 in [33], we get

$$b_c + 1 = A_{av} \frac{l_r}{u} e^{-r} \left[ C + \ln r + \sum_{k=1}^{\infty} \frac{r^k}{k k!} \right].$$

Where  $C = 0.577215$ , Euler's constant and

$$\tau = \frac{\ln N_c}{1 - \left( \frac{l_0 + ut_c}{l_r} \right)^{-b_c + 1}}$$

Next, we shall obtain a greatest lower bound for  $b_c$ . From the above equation, we get

$$b_c + 1 \geq A_{av} \frac{l_r}{u} e^{-r} [C + \ln r + e^{-r} - 1],$$

Since

$$\sum_{k=0}^{\infty} \frac{x^k}{k k!} < \sum_{k=1}^{\infty} \frac{x^k}{k!} < \sum_{k=0}^{\infty} \frac{x^k}{k!} = e^x - 1.$$

Further

$$\begin{aligned} b_c + 1 &\geq -A_{av} \frac{l_r}{u} e^{-\tau} [C + \ln \tau] - A_{av} \frac{l_r}{u} [1 - e^{-\tau}] \\ &\geq -A_{av} \frac{l_r}{u} e^{-r} [C + \ln \tau] - A_{av} \frac{l_r}{u} \\ &\geq -A_{av} \frac{l_r}{u} [C + 1] - A_{av} \frac{l_r}{u} \max(\ln \tau, e^{-\tau}) \\ &= -A_{av} \frac{l_r}{u} [C + 1] - 0.097 A_{av} \frac{l_r}{u} \\ &\quad (0.097 = \max(\ln \tau, e^{-\tau})) \\ &= -A_{av} \frac{l_r}{u} [1.097 + C]. \end{aligned}$$

On the other hand, from the inequality (17) we get

$$(b_c + 1)ut_c \leq l_0 \left[ \left( \frac{l_0 + ut_c}{l_0} \right)^{b_c + 1} - 1 \right]$$

Combining, finally we get  

$$-A_{av} t_c l_r [1.097 + C] \leq (b_c + 1) u t_c \leq l_0 \left[ \left( \frac{l_0 + u t_c}{l_0} \right)^{b_c + 1} - 1 \right].$$

**Theorem 1:** For every fixed  $A_{av}$ ;  $t_m$  and  $N_0$  satisfying either (13) with  $N_0 \leq N_c$   $t_c \geq \frac{\ln N}{A_{av}}$  or (14) with let I be the interval defined by

$$I = (-A_{av} \frac{l_r}{u} [1.097 + C], 0). \quad !$$

where  $C = 0.577215$ , Euler's constant  
 Suppose there exists a unique solution of (21) in I. Then it is necessary that  $\frac{A_{av} t_c}{\ln N_c} = 1$

Moreover, the following estimation is true

$$b_c + 1 \geq -A_{av} \frac{l_r}{u} [1.097 + C].$$

**Remark 1.** From (18) it is easy to get the asymptotic formula of initial mortality rate using (21).

#### D.Exponential Growth

Two modes of growth have been proposed in the ecdysozoan: "saltational," in taxa in which a tanned cuticle permits size increase only at molts, and "continuous" in taxa with stretchable, collagenous cuticles [34]. Research into these methods of growth has been limited almost exclusively to the arthropods (saltational growth) and nematodes (continuous growth), and even here, despite long standing interest in the details of the saltational growth of arthropod taxa (Alpatov [35], Rice [36]), continuous growth has rarely been investigated closely (Howells and Blainey [37], Wilson [38]). Specifically, little is known of how continuous growth is achieved at a scale, the role of cuticle, and the cells that secrete it. Understanding the details of growth has important implications for understanding the significance of molting as an evolutionary conserved feature of the ecdysozoa (Wilson [38]) and for interpreting the increasing number of studies that seek to identify the molecular and cellular controls of the ecdysozoan growth (Estevez et al.[39], Johnston et al.[40], Oldham et al. [41]).

In [34], Knight et al. used the free living nematode *Caenorhabditis elegans* as the best characterized example of continuously growing ecdysozoan (Riddle et al.[42]). The hatchling worm is 0.25 mm long and grows to 1.4 mm within 5 days, a 6-fold increase in length and over a 100-fold increase in volume. *C. elegans* have an S-shaped growth curve an exponential phase of larval growth and a gradual approach to a plateau in late adulthood (Byerly et al.[43]). In view of this we assume that the growth variable  $l(t)$  (see equation (4)) is exponential. That is

$$l(t) = l_0 e^{vt} \quad (22)$$

where  $v$  is the allometric exponent.

#### E.Survival Model

A model of the form given in (22) is used. Substitution of equation (22) into equation(3), integration, and division by  $N_0$  on both sides gives the following equation to predict survival,  $S(t)$ ,

$$S(t) = e^{-M_r \left( \frac{l_0}{l_r} \right)^b \frac{e^{bvt} - 1}{b_v}} \quad (23)$$

The two parameters  $M_r$  and  $b$  are of interest to many investigators in biogerontology and the evolutionary biology of aging [17 - 21]. Species comparisons in mortality rates are aided by calculations of MRD (mortality rate doubling time) which changes in the same direction as lifespan and is given by

$$MRD = \frac{1}{v} \ln \left( \frac{l_r}{l_0} \right)^{\frac{1}{b}}. \quad (24)$$

In the absence of age-specific mortality data, we have developed a method to estimate  $b$  from the instantaneous mortality rate ( $M_r$ ), original population size ( $N_0$ ), and maximum lifespan ( $t_m$ ).

In [29] we have derived the following result for exponential growth

$$t_m^* \approx t_m = \frac{1}{b_v} \ln \left[ 1 + b_v \frac{\ln N_0}{M_r} \left( \frac{l_r}{l_0} \right)^b \right]. \quad (25)$$

The average mortality rate of a steady state population subject to age specific mortality rates of equation (19) is [20 & 21]

$$A_{av} = \frac{1}{\int_0^{\infty} S(t) dt}, \quad (26)$$

Equation (25) gives

$$\frac{M_r}{b_v} \left( \frac{l_0}{l_r} \right)^b = \frac{\ln N_0}{(e^{b_v t_m} - 1)}, \quad (27)$$

And from equation (27) we get,

$$\frac{1}{A_{av}} = \int_0^{\infty} e^{-M_r \left( \frac{l_0}{l_r} \right)^b \frac{e^{bvt} - 1}{b_v}} dt.$$

A simple substitution in the above integral gives

$$b = \frac{A_{av} \ln N_0}{v (e^{b_v t_m} - 1)} \int_0^{\infty} \frac{\ln N_0}{(e^{b_v t_m} - 1)} \frac{e^{-\tau}}{\tau} d\tau. \quad (28)$$

#### F.Existence of Negative Critical Parameter

Recall that the age at which the mortality rate,  $M_r \left( \frac{l}{l_r} \right)^b$  of initial population  $N_0$  has ceased increasing or, equivalently, it tends to a constant, is called a critical age,  $t_c$  [30]. The remaining population left from an original population size  $N_0$  surviving at this critical age is called critical population,  $N_c$ , and the corresponding Allometry parameter in  $M_r \left( \frac{l}{l_r} \right)^b$  is called Allometry parameter,  $b_c$ .

Since the partials of  $b$  with respect to  $N_0$  and  $t_m$  become zero at

$$b = \frac{A_{av}}{v} \left( \frac{e^{b_v t_m} - 1}{\ln N_0} \right), \text{ and using (27), we get}$$

$$\frac{A_{av} t_m}{\ln N_0} = \frac{b_v t_m}{(e^{b_v t_m} - 1)} \quad (29)$$

From (29) it follows that

$$\frac{A_{av} t_m}{\ln N_0} \begin{cases} < 1 \text{ if } b > 0, \\ = 1 \text{ if } b = 0, \\ > 1 \text{ if } b < 0. \end{cases} \quad (30)$$

The point  $\frac{A_{av} t_m}{\ln N_0} = 1$  at which  $b$  changes sign is said to be critical point of  $b$ .

In human populations, according to published studies (Witten, [20 & 24]), the acceleration of mortality rate slows after 85 years. After 105 years, the mortality rate appears to cease increasing and may even decrease at these extremely advanced ages. Decreasing mortality at advanced ages is described in detail for ies (Curtsinger et al., 1992 [44], Fukui et al., 1993 [45], Carey et al., 1992 [46]). There is an additional evidence for the exponential decay at higher age. Quite recently Wang and co-workers disclosed an elegant experiment for the senescence accelerated mouse (SAM), showing that the mouse mortality function also approaches a constant value at higher age (Wang et al., 1998[47]). All the evidences accumulated so far suggest strongly that the exponential decay of populations at higher age is a general theorem (K.Suematsu et al., 1999 [32]).

From our earlier work [30], we know that, for a given  $N_0$ ,  $t_m$  and  $A_{av}$  with  $\frac{A_{av} t_m}{\ln N_0} < 1$

$$t_c = t_m \text{ and } N_c = e^{A_{av} t_c}. \quad (31)$$

On the contrary, when  $\frac{A_{av} t_m}{\ln N_0} > 1$

$$t_c = \frac{\ln N_0}{A_{av}}, N_c = e^{A_{av} t_c} \text{ and } t_c \neq t_m \quad (32)$$

Note that  $t_c = t_m$  for any given  $A_{av}$ ,  $t_m$  and  $N_0$ . We also know that [31], the asymptotic solution  $b$  of (28) is a continuous function in the variables  $A_{av}$ ,  $t_m$  and  $N_0$  from puberty through critical life span (or,  $N_0 \geq N_c$ ). What happens to solution  $b$  when  $N_0 \leq N_c$  (below the critical population). As we have already equated  $t_m$  with  $t_c$  when,  $\frac{A_{av} t_m}{\ln N_0} < 1$ , what is then actual (species) maximum life span,  $t_m^*$ ? Such  $t_m^* < t_m$  exists, since the critical population  $N_c$  has not yet diminished to one survivor. How to determine this  $t_m^*$ ? This in turn, leads us to consider negative allometry parameter, since  $\frac{A_{av} t_m}{\ln N_0} \geq 1$  for  $N_0 \leq N_c$ .

To determine the negative allometry parameter consider (31) with  $N_0 \leq N_c$  and (32) with  $t_c \geq \frac{\ln N_0}{A_{av}}$ .

Upon substitution  $N_0 = N_c$  into (28), we get

$$b_c = \frac{A_{av} \ln N_c}{v (e^{b_c v t_c} - 1)} \int_{\frac{\ln N_c}{(e^{b_c v t_c} - 1)}}^{\infty} \frac{e^{-z}}{z} dz \quad (33)$$

Where  $t_c = t_m$  when  $\frac{A_{av} t_m}{\ln N_0} < 1$  and  $t_c = \frac{\ln N_0}{A_{av}}$  when  $\frac{A_{av} t_m}{\ln N_0} > 1$ .

Equation (33) gives

$$b_c v t_c \leq \frac{A_{av} t_c}{\ln N_c} (e^{b_c v t_c} - 1)$$

The above inequality ensures the existence of solution  $b_c$ , provided  $\frac{A_{av} t_c}{\ln N_c} = 1$ .

As a consequence, we get

$$b_c v t_c \leq (e^{b_c v t_c} - 1) \quad (34)$$

A close observation of the inequality (34) reveals that any  $b_c \leq 0$  also satisfies it

This result, in fact, motivates us to consider the negative critical Gompertz parameter. On the other hand, in the neighbourhood of the critical point  $\frac{A_{av} t_c}{\ln N_c} = 1$ , it is necessary that  $\frac{A_{av} t_c}{\ln N_c} > 1$  if  $b < 0$  from (30).

Hence

$$-b_c v t_c \leq (e^{-b_c v t_c} - 1) \quad (35)$$

Is valid for  $N_0 = N_c$  provided  $\frac{A_{av} t_c}{\ln N_c} > 1$ . Clearly  $\frac{A_{av} t_c}{\ln N_c} > 1$  holds when  $t_c > \frac{\ln N_0}{A_{av}}$  in (32). In case of (31)  $\frac{A_{av} t_c}{\ln N_c} > 1$  if  $N_0 < N_c$  and this gives  $t_c > \frac{\ln N_0}{A_{av}} = t_c \frac{\ln N_c}{\ln N_0}$ . We designate

$t_m^* = t_c \frac{\ln N_c}{\ln N_0}$  as the actual maximum life span. Since  $t_m^*$  becomes very large numerically as  $N_0 \rightarrow 1$ , we can choose any finite value greater than  $t_c$  as  $t_m^*$ . Fortunately, we shall not use the numerical value of  $t_m^*$  in our sequel.

Numerical experiments show that the transition from  $b_c$  to  $b_c$  is extremely slow. The graphical illustration should enhance the understanding of this idea [19]. Further, it follows from (28) that as

$$b \rightarrow 0 \text{ at } N_0 = N_c, M_r \rightarrow \frac{\ln N_c}{t_c} = A_{av}.$$

As  $b_c$  changes sign, from (27) we obtain

$$\frac{M_r}{-b_c v} \left( \frac{l_0}{l_r} \right)^{-b_c} = \frac{\ln N_c}{e^{b_c v t_c} - 1},$$

Which gives

$$M_r = \frac{b_c v t_c}{e^{b_c v t_c} - 1} \left( \frac{l_0}{l_r} \right)^{-b_c} \frac{\ln N_c}{t_c} \geq \frac{\ln N_c}{t_c}$$

Thus

$$M_r \geq \frac{\ln N_c}{t_c}.$$

### G.Exponential Allometry Survival function

In the neighbourhood of the critical point  $\frac{A_{av} t_c}{\ln N_c} = 1$ , in view of (31) and (32) the survival function (23) takes the form

$$S(t) = \begin{cases} e^{-M_{r_c} \left(\frac{I_0}{I_r}\right)^b \frac{\varepsilon^{bvt-1}}{b_v}} & \text{if } t \leq t_c (N \geq N_c) \\ e^{-M_{r_c} \left(\frac{I_0}{I_r}\right)^{-b} \frac{1-\varepsilon^{bvt}}{b_v}} & \text{if } t \geq t_c (N \leq N_c) \end{cases} \quad (36)$$

Lemma: S(t) is continuous at  $t = t_c$

Proof Indeed

$$\begin{aligned} \lim_{t \rightarrow t_c-0} S(t) &= e^{-M_{r_c} \left(\frac{I_0}{I_r}\right)^b \frac{\varepsilon^{bvt_c-1}}{b_v}} \\ &= e^{\frac{\ln N_c}{\varepsilon^{b_v t_c-1}} (1-\varepsilon^{b_v t_c})} \\ &= e^{\frac{\ln N_c}{\varepsilon^{-b_v t_c-1}} (1-\varepsilon^{-b_v t_c})} \\ &= e^{-M_{r_c} \left(\frac{I_0}{I_r}\right)^{-b} \frac{1-\varepsilon^{b_v t_c}}{b_v}} \\ &= \lim_{t \rightarrow t_c+0} S(t) \end{aligned}$$

Now we extend the formula (33) to  $-b_c$  for  $N_0 = N_c$  satisfy (31) with  $N \leq N_c$  and (32) with  $t_c \geq \frac{\ln N_0}{A_{av}}$

Upon substitution  $b_c = -b_c$  into (33) we get

$$-b_c = \frac{A_{av}}{v} e^{\frac{\ln N_c}{1-\varepsilon^{-b_v t_c}}} \int_0^1 \frac{\ln N_c}{1-\varepsilon^{-b_v t_c}} \frac{\varepsilon^{-z}}{z} dz. \quad (37)$$

As such the above integral is unbounded. The unboundedness results in by the substitution  $t_c = \infty$  or  $N_0 = 1$  with  $N \leq N_c$  into (33), when  $b_c < 0$ . But inequality (35) implies the existence of  $b_c$ .

To overcome this situation, we need to introduce limit age,  $t_{lim}$  of the critical population  $N_c$ .

Following Suematsu [32], the limit age can be defined as an age where the final member of the critical population  $N_c$  disappears. Stating mathematically,

$$S_{(tim)} = e^{M_{r_c} \left(\frac{I_0}{I_r}\right)^{-b} \frac{1-\varepsilon^{-bvt_{tim}}}{b_v}} \leq \frac{1}{N_0}$$

Clearly, if the population  $N_c$  at an age  $t_c$  is less than unity, all the members under discussion must, in the statistical mean, vanish. Hence, the limit age can be identified with the minimum age,  $t_{lim}$ , that satisfies

$$S_{(tim)} \leq \frac{1}{N_0}.$$

Taking into account the above arguments, substitute  $N_0 = 0$  ( $N_0 \leq N_c$ ) into the upper limit of (33) when  $b_c < 0$  to get

$$\begin{aligned} -b_c &= \frac{A_{av}}{v} e^{-\frac{\ln N_c}{1-\varepsilon^{-b_v t_c}}} \int_0^1 \frac{-\ln N_c}{1-\varepsilon^{-b_v t_c}} \frac{\varepsilon^{-z}}{z} dz. \quad (38) \\ &= -\frac{A_{av}}{v} e^{-\frac{\ln N_c}{1-\varepsilon^{-b_v t_c}}} E_i \left( \frac{\ln N_c}{1-\varepsilon^{-b_v t_c}} \right), \end{aligned}$$

where  $E_i(x) = -\lim_{n \rightarrow +\infty} \left[ \int_{-x}^{-\eta} \frac{\varepsilon^{-z}}{z} dz + \int_{\eta}^{\infty} \frac{\varepsilon^{-z}}{z} dz \right]$ ,  $[x > 0]$ .

Clearly, (38) satisfies inequality (35). We could not obtain (35) directly from (38), since the integrand is unbounded at  $z = 0$ .

From equation (38), on account of 8.214. 2 in [33], we get

$$\begin{aligned} -b_c &= -\frac{A_{av}}{v} e^{-\frac{\ln N_c}{1-\varepsilon^{-b_v t_c}}} E_i \left( \frac{\ln N_c}{1-\varepsilon^{-b_v t_c}} \right) \\ &= -\frac{A_{av}}{v} e^{-\omega} \left[ C + \ln \omega + \sum_{k=1}^{\infty} \frac{\omega^k}{k k!} \right]. \end{aligned}$$

Where  $C=0.577215$ , Euler's constant  $\omega = \frac{\ln N_c}{1-\varepsilon^{-b_v t_c}}$

Next, we shall obtain a greatest lower bound for  $b_c$ . From the above equation, we get

$$-b_c \geq -\frac{A_{av}}{v} e^{-\omega} [C + \ln \omega + e^{\omega} - 1],$$

Since

$$\sum_{k=1}^{\infty} \frac{x^k}{k k!} < \sum_{k=1}^{\infty} \frac{x^k}{k!} < \sum_{k=1}^{\infty} \frac{x^k}{k!} = e^x - 1.$$

Further

$$-b_c \geq -\frac{A_{av}}{v} e^{-\omega} [C + \ln \omega] - A_{av} [1 - e^{-\omega}]$$

$$\geq -\frac{A_{av}}{v} e^{-\omega} [C + \ln \omega] - \frac{A_{av}}{v}$$

$$\geq -\frac{A_{av}}{v} [C + 1] \geq -\frac{A_{av}}{v} \max(\ln \omega, e^{-\omega})$$

$$= -\frac{A_{av}}{v} [C + 1] - 0.097 \frac{A_{av}}{v}$$

$$= -\frac{A_{av}}{v} [1.097 + C]$$

On the other hand, from the inequality (35) we get

$$-b_c v t_c = \varepsilon^{b_v t_c-1}$$

Combining, finally we get

$$-\frac{A_{av}}{v} [1.097 + C] \leq -b_c v t_c = \varepsilon^{-b_v t_c-1}$$

Summing up, we conclude that

**Theorem 2:** For every fixed  $A_{av}$ ;  $t_m$  and  $N_0$  satisfying either (31) with  $N_0 \leq N_c$  or (32) with  $t_c \geq \frac{\ln N_0}{A_{av}}$ , let I be the interval defined by

$$I = \left( -\frac{A_{av}}{v} [1.097 + C], 0 \right)$$

where  $C = 0.577215$ , Euler's constant.

Suppose there exists a unique solution of (38) in I. Then it is necessary

that.  $\frac{A_{av} t_c}{\ln N_c} = 1$

Moreover, the following estimation is true

$$-b_c \geq -\frac{A_{av}}{v} [1.097 + C]$$

**Remark 2.** From [20], here we listed in Table I the numerical values of  $b_c$  for a comparison with that of positive  $b_c$  for  $N_0 = N_c$ .

**Remark 3.** From (27) it is easy to get the asymptotic formula of initial mortality rate using (38).

**Remark 4.** Kai Lorenzen [16] listed in Tables 1 and 2 the numerical values of each parameter. It is useful to compare our asymptotic formula [30] and the existence of critical and negative critical allometry parameter.

Table I

$A_{av}/\text{Year}$	$-b_c$	$b_c$
Pipepestrell bat 0.36	-0.602	0.244
European robin 0.62	-1.038	0.253
Lapwing 0.34	-0.569	0.177
Starling 0.52	-0.870	0.163
Common swift 0.18	-0.301	0.127
Herring gull 0.34	-0.569	0.180
Human 0.015	-0.025	0.024
Mouse 0.74	-1.239	0.888
Rat 0.64	-1.072	0.845
Japanese quail 0.35	-0.586	0.295

### III. CONCLUSION

It is well known that the average mortality rate differs between males and females. For instance, (Humans) 0.005 for males and 0.015 for females [19-20]. The issue of sex differences is not addressed in this article and presents further complexities. The body size dependent relationships of mortality and longevity are examined for birds and eutherian mammals [W. A. Calder III]. Differences between mass exponents for maximum recorded longevity and survival times for fractions of original adult populations confirm the age dependence of mortality in both classes and a size dependency of population age distribution [16]. It is worth studying further the effect of body size on the mortality rate with sex differences.

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