

**ESTIMATION AND SENSITIVITY OF
ALLOMETRY MODEL PARAMETERS**

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Abstract: Studies in the evolutionary biology of aging in the context of size-dependent mortality rate require good estimates of the size exponent parameter in a general allometric relationship. In this paper, using a fish stocking model for illustration, we introduce an alternative algorithm for estimating this size exponent parameter when the individual life spans of members in an original population are not known explicitly. Restraints on other model parameters to assure solution uniqueness and sensitivity of the estimates to changes in their values are also considered.

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1. Introduction

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, see [4].

Within a class, the most significant evolution has been not of bill shape or dentition, not of color or ecological niche, but of body size. This is because body size has the greatest effect on an animal's opportunities to exploit the resources available in the environment. Quantitative requirements for energy and space depend primarily upon how large the animal is that must be fed. The "study of size and its consequences" is allometry [4], literally "of different measures".

This makes body size a good choice for baseline analysis, using the scaling (heterogonic or allometric) equation of Huxley [12] and Kleiber [14]:

$$Y = am^b, \tag{1}$$

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 .

We should point out that although keeping variables in familiar physical units does have certain conceptual advantages, an analysis is much more flexible and robust if the variable Y is scaled by a related intrinsic parameter of similar physical dimension such that the dependent variable is an intrinsic dimensionless entity; and likewise if the variable m with a physical dimension of mass is similarly scaled by an intrinsic mass characteristic of the system such that the size-related independent variable is also a dimensionless entity. In such circumstances the coefficient a is entirely characteristic of the taxonomic classification of the organism and the dimensionless variables can be used as arguments of mathematical functions such as logarithms which transform pure numbers without physical dimension. Furthermore, semantic confusion over the use of kg as a weight or as a mass is avoided.

2. Applications of Allometric Scaling Law

2.1. Linear Growth

Stocking is widely used in the management of freshwater and, to a lesser extent, coastal-marine fisheries (e.g., [9]). A key problem in the management of stocked fisheries is the optimization of release size (e.g., [5]). The optimal release size depends on the contribution that fish of a particular size will make to the catch or fishable stock and on the resources required to produce seed fish of that size. Of the data required to assess optimum size, the survival of seed fish of different sizes to the fishable stock (and/or contribution to the catch) are the most difficult to obtain. Systematic assessments have been either entirely empirical (release – recapture of marked seed fish of different sizes) or based on detailed ecological studies [27]. However, the costs and effort involved in both approaches restrict their use to a small number of fisheries, and the results are not readily generalized. An alternative approach that implies a simple generalization is the use of allometric mortality-size relationship [19]. Provided that natural mortality in stocked fish is subject to a consistent allometry, then an estimate of mortality for a single reference size is sufficient to predict survival for a range of different release sizes.

Theoretical and empirical studies [8,9] point to the existence of an allometric relationship between natural mortality and body weight, of the form

$$M_w = M_u W^b, \quad (2)$$

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 $(unit\ weight)^{-b}$. Note that a mathematical structure of this form would also apply to a system transformed to corresponding dimensionless variables as mentioned in Introduction.

2.1.1. Survival Model

The survival model follows that developed by Lorenzen [10] in which the allometric relationship between natural mortality and body length may be described by the

$$M(l) = M_r \left(\frac{l}{l_r} \right)^b, \quad (3)$$

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 [10]), 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 sufficiently large enough to be approximated as a continuous variable, is described by the differential equation

$$\frac{dN(t)}{dt} = -N(t)M_r \left(\frac{l(t)}{l_r} \right)^b, \quad (4)$$

where $l(t)$ is length 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 fish is small relative to the reported maximum sizes in all stocking experiments analyzed by Lorenzen [10]. A model of the form

$$l(t) = l_0 + ut \quad (5)$$

is used, where t is the time since stocking, and u is the linear length growth rate. Substitution of equation (5) into equation (4), integration, and division by N_0 on both sides gives the following equation to predict survival, $S(t)$ (proportion of stocked fish surviving), from the time of stocking to time t :

$$S(t) = \frac{N(t)}{N_0} = e^{-\frac{M_r \left(-l_0 \left(\frac{l_0}{l_r} \right)^b + (l_0 + ut) \left(\frac{l_0 + ut}{l_r} \right)^b \right)}{(b+1)u}} \quad (6)$$

as was derived by Lorenzen [10] 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 [11], [12], [13], [14]. 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

$$MRD = \frac{2^{\frac{1}{b}} l_r - l_0}{u}. \quad (7)$$

In the presence of mortality data by age, the allometric scaling parameters M_r and b have been estimated by using various statistical methods like maximum likelihood, linear regression, and nonlinear regression [15]. 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 [15], [16] to estimate the model parameters.

In the absence of age specific mortality data, in this paper we have developed 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 .

2.1.2. Estimation of Parameters

When attempting to estimate allometric scaling parameters it is difficult, in general, to decide upon a particular value of t to use in the expression for $(S(t))$ given in equation (6). However if we are examining the issue of evolution of longevity, then choosing $t = t_m^{(*)}$, a known maximum lifespan for the species, is a reasonable starting value. Finally for ease of analysis we may use the finite lifespan procedure of Witten and Satzer [17] and set $S(t_m) = \frac{1}{N_0}$ (the population contains only one individual left from an original population size N_0). We obtain the following equation for t_m (the time at which the population has only one individual and which approximates the maximum lifespan $t_m^{(*)}$)

$$t_m^* \simeq t_m = \frac{1}{u} \left[(l_r)^{\frac{b}{b+1}} \left(\frac{(b+1)u \ln N_0}{M_r} + l_0 \left(\frac{l_0}{l_r} \right)^b \right)^{\frac{1}{b+1}} - l_0 \right]. \tag{8}$$

Equation (8) gives,

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

or

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

Hence, the above equation implies that

$$b = -1 + \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b - l_0 \left(\frac{l_0}{l_r} \right)^b \right]. \tag{10}$$

The basic equation (10) is transcendental, involving an exponential integral, and hence, its solution may not be unique. Therefore, it is necessary to investigate the uniqueness of b in the solution of (10).

2.1.3. Uniqueness

A Necessary Condition for Uniqueness

Theorem 1. *To have a unique solution of equation (10), it is necessary that*

$$\frac{M_r t_m}{\ln N_0} < 1.$$

Proof. Suppose b_1 and b_2 are two solutions of equation (10), that is,

$$\begin{aligned} b_1 &= -1 + \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^{b_1} - l_0 \left(\frac{l_0}{l_r} \right)^{b_1} \right], \\ b_2 &= -1 + \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^{b_2} - l_0 \left(\frac{l_0}{l_r} \right)^{b_2} \right]. \end{aligned}$$

Consider

$$\begin{aligned} b_1 - b_2 &= \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^{b_1} - l_0 \left(\frac{l_0}{l_r} \right)^{b_1} \right] \\ &\quad - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^{b_2} - l_0 \left(\frac{l_0}{l_r} \right)^{b_2} \right] \\ &= \frac{M_r}{u \ln N_0} \left[\frac{(l_0 + ut_m)^{b_1+1} - l_0^{b_1+1}}{l_r^{b_1}} - \frac{(l_0 + ut_m)^{b_2+1} - l_0^{b_2+1}}{l_r^{b_2}} \right]. \end{aligned}$$

Hence,

$$|b_1 - b_2| \leq \frac{M_r}{u \ln N_0} \left| \frac{(l_0 + ut_m)^{b_1+1} - l_0^{b_1+1}}{l_r^{b_1}} - \frac{(l_0 + ut_m)^{b_2+1} - l_0^{b_2+1}}{l_r^{b_2}} \right|.$$

Therefore,

$$|b_1 - b_2| \leq \frac{M_r}{u \ln N_0} \left| \frac{\frac{b_1 ut_m}{\frac{(l_0 + ut_m)^{b_1+1} - l_0^{b_1+1}}{l_r^{b_1+1}}}}{\frac{b_2 ut_m}{\frac{(l_0 + ut_m)^{b_2+1} - l_0^{b_2+1}}{l_r^{b_2+1}}}} \right|.$$

Thus,

$$|b_1 - b_2| \leq \frac{M_r t_m}{\ln N_0} \frac{|b_1 - b_2|}{\min \left(\frac{\frac{b_1 ut_m}{(l_0 + ut_m)^{b_1+1} - l_0^{b_1+1}}}{l_r^{b_1+1}}, \frac{\frac{b_2 ut_m}{(l_0 + ut_m)^{b_2+1} - l_0^{b_2+1}}}{l_r^{b_2+1}} \right)}. \quad (11)$$

Suppose we have a unique solution of b in equation (10). Then equation (11), which allows distinct solutions, can not hold. From this restriction it follows as a consequence that

$$\frac{M_r t_m}{\ln N_0} \frac{1}{\min \left(\frac{\frac{b_1 ut_m}{(l_0 + ut_m)^{b_1 + 1} - l_0^{b_1 + 1}}}{l_r^{b_1 + 1}}, \frac{\frac{b_2 ut_m}{(l_0 + ut_m)^{b_2 + 1} - l_0^{b_2 + 1}}}{l_r^{b_2 + 1}} \right)} < 1. \tag{12}$$

Since $0 \leq \frac{b ut_m}{(l_0 + ut_m)^{b+1} - l_0^{b+1}} \leq 1, \forall b \geq 0, ut_m > 0$ and $l_0 > l_r$, from (12), we get

$$\begin{aligned} \frac{M_r t_m}{\ln N_0} &< \min \left(\frac{\frac{b_1 ut_m}{(l_0 + ut_m)^{b_1 + 1} - l_0^{b_1 + 1}}}{l_r^{b_1 + 1}}, \frac{\frac{b_2 ut_m}{(l_0 + ut_m)^{b_2 + 1} - l_0^{b_2 + 1}}}{l_r^{b_2 + 1}} \right) \\ &\leq \max \left(\frac{\frac{b_1 ut_m}{(l_0 + ut_m)^{b_1 + 1} - l_0^{b_1 + 1}}}{l_r^{b_1 + 1}}, \frac{\frac{b_2 ut_m}{(l_0 + ut_m)^{b_2 + 1} - l_0^{b_2 + 1}}}{l_r^{b_2 + 1}} \right) \leq 1. \end{aligned}$$

Hence, the above inequality implies that $\frac{M_r t_m}{\ln N_0} < 1$. □

In the following discussion, we will examine parameter sensitivity in the above model formulations.

2.1.4. Sensitivity to Parameter Changes

Sensitivity analysis has become popular in ecology (e.g., [17], [18]) and has been used to manage and conserve wild populations (e.g., [19]). Such analyses usually assume that the population’s state (i.e., the age, stage, or size distribution) remains stable through time (i.e., asymptotically stable), and that the population grows according to a constant, or stable distribution of rates. All else being equal, theory suggests that the stable state assumption in population biology is a safe one [20], [21]. Sensitivity analysis can be used to determine the functional relationship between population size or growth rate and the constituent vital rates (e.g., fecundity, survival, growth, maturation, recruitment, movement), and to project changes in population growth rate and size as vital rates change.

From the work of Witten and Satzer [17] we know that in the standard Gompertz mortality model the age-dependent mortality rate α becomes insensitive to changes in the initial population size N_0 if N_0 approaches a very large

value, but becomes very sensitive to changes in N_0 if N_0 approaches 1. Similarly we would now like to consider how an analogous system, as represented by equation (10), behaves when N_0 , M_r and t_m are large. To do this, we consider the partial derivatives of b with respect to N_0 , M_r and t_m . These are given by

$$\begin{aligned} & \frac{\partial b}{\partial N_0} \\ &= \frac{-(b+1)/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b \ln \left(\frac{l_0 + ut_m}{l_r} \right) - l_0 \left(\frac{l_0}{l_r} \right)^b \ln \left(\frac{l_0}{l_r} \right) \right] \right]}, \end{aligned} \quad (13)$$

$$\begin{aligned} & \frac{\partial b}{\partial M_r} \\ &= \frac{(b+1)/M_r}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b \ln \left(\frac{l_0 + ut_m}{l_r} \right) - l_0 \left(\frac{l_0}{l_r} \right)^b \ln \left(\frac{l_0}{l_r} \right) \right] \right]}, \end{aligned} \quad (14)$$

$$\begin{aligned} & \frac{\partial b}{\partial t_m} \\ &= \frac{\frac{(b+1)M_r}{\ln N_0} \left(\frac{l_0 + ut_m}{l_r} \right)^b}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b \ln \left(\frac{l_0 + ut_m}{l_r} \right) - l_0 \left(\frac{l_0}{l_r} \right)^b \ln \left(\frac{l_0}{l_r} \right) \right] \right]}, \end{aligned} \quad (15)$$

respectively. Considering the RHS in (13),

$$\frac{-(b+1)/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b \ln \left(\frac{l_0 + ut_m}{l_r} \right) - l_0 \left(\frac{l_0}{l_r} \right)^b \ln \left(\frac{l_0}{l_r} \right) \right] \right]}, \quad (16)$$

and using (9), we get

$$\frac{-(b+1)/(N_0 \ln N_0)}{\left[1 - (b+1) \left[\frac{(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b \ln \left(\frac{l_0 + ut_m}{l_r} \right) - l_0 \left(\frac{l_0}{l_r} \right)^b \ln \left(\frac{l_0}{l_r} \right)}{(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b - l_0 \left(\frac{l_0}{l_r} \right)^b} \right] \right]}. \quad (17)$$

Since,

$$(b+1) \left[\frac{(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b \ln \left(\frac{l_0 + ut_m}{l_r} \right) - l_0 \left(\frac{l_0}{l_r} \right)^b \ln \left(\frac{l_0}{l_r} \right)}{(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r} \right)^b - l_0 \left(\frac{l_0}{l_r} \right)^b} \right] > 1 \quad (18)$$

$\forall l_0 > l_r$, and $b, u, t_m > 0$, from (17), we get, assuming $N_0 > 1$,

$$\frac{-(b+1)/(N_0 \ln N_0)}{\left[1 - (b+1) \left[\frac{(l_0+ut_m)\left(\frac{l_0+ut_m}{l_r}\right)^b \ln\left(\frac{l_0+ut_m}{l_r}\right) - l_0\left(\frac{l_0}{l_r}\right)^b \ln\left(\frac{l_0}{l_r}\right)}{(l_0+ut_m)\left(\frac{l_0+ut_m}{l_r}\right)^b - l_0\left(\frac{l_0}{l_r}\right)^b} \right] \right]} > 0.$$

Thus,

$$\frac{-(b+1)/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0+ut_m}{l_r}\right)^b \ln\left(\frac{l_0+ut_m}{l_r}\right) - l_0\left(\frac{l_0}{l_r}\right)^b \ln\left(\frac{l_0}{l_r}\right) \right] \right]} > 0.$$

Hence,

$$\begin{aligned} & \frac{\partial b}{\partial N_0} \\ &= \frac{-(b+1)/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0+ut_m}{l_r}\right)^b \ln\left(\frac{l_0+ut_m}{l_r}\right) - l_0\left(\frac{l_0}{l_r}\right)^b \ln\left(\frac{l_0}{l_r}\right) \right] \right]} > 0. \end{aligned}$$

As a consequence of the above inequality, we have

$$\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0+ut_m}{l_r}\right)^b \ln\left(\frac{l_0+ut_m}{l_r}\right) - l_0\left(\frac{l_0}{l_r}\right)^b \ln\left(\frac{l_0}{l_r}\right) \right] \right] < 0.$$

In view of this, equations (14) and (15) satisfy

$$\begin{aligned} & \frac{\partial b}{\partial M_r} \\ &= \frac{(b+1)/M_r}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0+ut_m}{l_r}\right)^b \ln\left(\frac{l_0+ut_m}{l_r}\right) - l_0\left(\frac{l_0}{l_r}\right)^b \ln\left(\frac{l_0}{l_r}\right) \right] \right]} < 0, \end{aligned}$$

and

$$\begin{aligned} & \frac{\partial b}{\partial t_m} \\ &= \frac{\frac{(b+1)M_r}{\ln N_0} \left(\frac{l_0+ut_m}{l_r}\right)^b}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0+ut_m}{l_r}\right)^b \ln\left(\frac{l_0+ut_m}{l_r}\right) - l_0\left(\frac{l_0}{l_r}\right)^b \ln\left(\frac{l_0}{l_r}\right) \right] \right]} < 0. \end{aligned}$$

If we let $N_0 \rightarrow \infty$ in (13), we get

$$\lim_{N_0 \rightarrow \infty} \frac{\partial b}{\partial N_0} = 0.$$

Next we substitute $\frac{b+1}{M_r} = \frac{-l_0 \left(\frac{l_0}{l_r}\right)^b + (l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r}\right)^b}{u \ln N_0}$ from equation (9) into equation (14), to get

$$\frac{\partial b}{\partial M_r} = \frac{\frac{-l_0 \left(\frac{l_0}{l_r}\right)^b + (l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r}\right)^b}{u \ln N_0}}{\left[1 - \frac{M_r}{u \ln N_0} \left[(l_0 + ut_m) \left(\frac{l_0 + ut_m}{l_r}\right)^b \ln \left(\frac{l_0 + ut_m}{l_r}\right) - l_0 \left(\frac{l_0}{l_r}\right)^b \ln \left(\frac{l_0}{l_r}\right) \right]\right]}.$$

Hence,

$$\lim_{N_0 \rightarrow \infty} \frac{\partial b}{\partial M_r} = 0.$$

Finally, if we let $N_0 \rightarrow \infty$ in (15), we get

$$\lim_{N_0 \rightarrow \infty} \frac{\partial b}{\partial t_m} = 0.$$

Thus, we see that b is relatively insensitive to changes in N_0 . That is, b does not change rapidly as the original population size becomes larger.

On the other hand, if we let $N_0 \rightarrow 1$ in equation (13), we get

$$\lim_{N_0 \rightarrow 1} \frac{\partial b}{\partial N_0} = \infty.$$

because $\frac{1}{N_0 \ln N_0} \rightarrow \infty$ as $N_0 \rightarrow 1$. This, in turn, gives

$$\frac{\partial b}{\partial M_r} \rightarrow -\infty \quad \text{and} \quad \frac{\partial b}{\partial t_m} \rightarrow -\infty, \quad \text{as } N_0 \rightarrow 1.$$

Thus, as the original population size decreases, we see a greater change in the sensitivity of b .

2.2. 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 [22]. 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 [23], [24], continuous growth has rarely been investigated closely [25], [26]. Specifically, little is known of how continuous growth is achieved at a fine 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 [26] and for interpreting the increasing number of studies that seek to identify the molecular and cellular controls of the ecdysozoan growth [27], [28], [29].

Knight et al [22] used the free living nematode *Canenorhabditis elegans* as the best characterized example of continuously growing ecdysozoan [30]. 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 [31]. In view of this we assume that the growth variable $l(t)$ (see equation (4)) is exponential. That is

$$l(t) = l_0 e^{vt}, \quad (19)$$

where v is the allometric exponent.

2.2.1. Survival Model

A model of the form given in (19) is used. Substitution of equation (19) into equation(4), integration, and division by N_0 on both sides gives the following equation to predict survival, $S(t)$,

$$S(t) = e^{-M_r \left(\frac{l_0}{l_r}\right)^b \left(\frac{e^{bvt} - 1}{bv}\right)}. \quad (20)$$

Again as was mentioned for the case of linear growth, in exponential growth the two parameters M_r and b are also of interest to many investigators in biogerontology and the evolutionary biology of aging [11], [12], [13], [14]. 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

$$MRD = \frac{1}{v} \ln \left(\frac{2^{\frac{1}{b}} l_r}{l_0} \right). \quad (21)$$

In the presence of mortality data by age, the allometric scaling parameters M_r and b have been estimated by using various statistical methods such as

maximum likelihood, linear regression, nonlinear regression, see [15]. 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, see [15], [16].

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).

2.2.2. Estimation of Parameters

When attempting to estimate allometric scaling parameters it is difficult, in general, to decide upon a particular value of t to use in the expression for ($S(t)$) given in equation (6). However if we are examining the issue of evolution of longevity, then choosing $t = t_m^*$, a known maximum lifespan for the species, is a reasonable starting value. Finally for ease of analysis we may use the finite lifespan procedure of Witten and Satzer [17] and set $S(t_m) = \frac{1}{N_0}$ (the population contains only one individual left from an original population size N_0). We obtain the following equation for t_m (the time at which the population has only one individual and which approximates the maximum lifespan t_m^*)

$$t_m^* \simeq t_m = \frac{1}{bv} \ln \left[1 + bv \frac{\ln N_0}{M_r} \left(\frac{l_r}{l_0} \right)^b \right]. \quad (22)$$

Equation (22) gives,

$$\frac{bv \ln N_0}{M_r} = \left(\frac{l_0}{l_r} \right)^b (e^{bvt_m} - 1)$$

or,

$$\frac{M_r}{b} = \frac{v \ln N_0}{(e^{bvt_m} - 1)} \left(\frac{l_r}{l_0} \right)^b. \quad (23)$$

Hence, the above equation implies that

$$b = \frac{M_r}{v \ln N_0} (e^{bvt_m} - 1) \left(\frac{l_0}{l_r} \right)^b. \quad (24)$$

The basic equation (22) is transcendental, involving an exponential integral, and hence, its solution may not be unique. Therefore, it is necessary to investigate the uniqueness of solution of (22).

2.2.3. Uniqueness

A Necessary Condition for Uniqueness

Theorem 2. *To have a unique solution of b in equation (22), it is necessary that*

$$\frac{M_r t_m}{\ln N_0} < 1.$$

Proof. Suppose b_1 and b_2 are two solutions of b in equation (22), that is,

$$b_1 = \frac{M_r}{v \ln N_0} (e^{b_1 v t_m} - 1) \left(\frac{l_0}{l_r} \right)^{b_1},$$

and

$$b_2 = \frac{M_r}{v \ln N_0} (e^{b_2 v t_m} - 1) \left(\frac{l_0}{l_r} \right)^{b_2}.$$

Consider,

$$\begin{aligned} b_1 - b_2 &= \frac{M_r}{v \ln N_0} \left[\left(\frac{l_0}{l_r} \right)^{b_1} (e^{b_1 v t_m} - 1) - \left(\frac{l_0}{l_r} \right)^{b_2} (e^{b_2 v t_m} - 1) \right] \\ &= \frac{M_r}{v \ln N_0} \left[\left(\frac{l_0}{l_r} \right)^{b_1} \frac{b_1 v t_m}{b_1 v t_m} (e^{b_1 v t_m} - 1) - \left(\frac{l_0}{l_r} \right)^{b_2} \frac{b_2 v t_m}{b_2 v t_m} (e^{b_2 v t_m} - 1) \right] \\ &= \frac{M_r}{v \ln N_0} \left[\frac{b_1 v t_m}{\frac{b_1 v t_m}{(e^{b_1 v t_m} - 1) \left(\frac{l_0}{l_r} \right)^{b_1}}} - \frac{b_2 v t_m}{\frac{b_2 v t_m}{(e^{b_2 v t_m} - 1) \left(\frac{l_0}{l_r} \right)^{b_2}}} \right] \\ &= \frac{M_r}{v \ln N_0} \left[\frac{b_1 v t_m}{\frac{b_1 v t_m \left(\frac{l_r}{l_0} \right)^{b_1}}{(e^{b_1 v t_m} - 1)}} - \frac{b_2 v t_m}{\frac{b_2 v t_m \left(\frac{l_r}{l_0} \right)^{b_2}}{(e^{b_2 v t_m} - 1)}} \right]. \end{aligned}$$

Hence,

$$|b_1 - b_2| \leq \frac{M_r}{v \ln N_0} \left| \frac{b_1 v t_m}{\frac{b_1 v t_m \left(\frac{l_r}{l_0} \right)^{b_1}}{(e^{b_1 v t_m} - 1)}} - \frac{b_2 v t_m}{\frac{b_2 v t_m \left(\frac{l_r}{l_0} \right)^{b_2}}{(e^{b_2 v t_m} - 1)}} \right|.$$

Thus,

$$|b_1 - b_2| \leq \frac{M_r t_m}{\ln N_0} \frac{|b_1 - b_2|}{\min \left(\frac{b_1 v t_m \left(\frac{l_r}{l_0}\right)^{b_1}}{(e^{b_1 v t_m} - 1)}, \frac{b_2 v t_m \left(\frac{l_r}{l_0}\right)^{b_2}}{(e^{b_2 v t_m} - 1)} \right)}. \quad (25)$$

Suppose we have a unique solution of b in equation (22). Then equation (25), which allows distinct solutions, cannot hold. From this restriction it follows as a consequence that

$$\frac{M_r t_m}{\ln N_0} \frac{1}{\min \left(\frac{b_1 v t_m \left(\frac{l_r}{l_0}\right)^{b_1}}{(e^{b_1 v t_m} - 1)}, \frac{b_2 v t_m \left(\frac{l_r}{l_0}\right)^{b_2}}{(e^{b_2 v t_m} - 1)} \right)} < 1. \quad (26)$$

Since $0 < \left(\frac{l_r}{l_0}\right)^b \leq 1, \forall b > 0$ and $l_0 > l_r$, from (26), we get,

$$\begin{aligned} \frac{M_r t_m}{\ln N_0} &< \min \left(\frac{b_1 v t_m \left(\frac{l_r}{l_0}\right)^{b_1}}{(e^{b_1 v t_m} - 1)}, \frac{b_2 v t_m \left(\frac{l_r}{l_0}\right)^{b_2}}{(e^{b_2 v t_m} - 1)} \right) < \\ &\min \left(\frac{b_1 v t_m}{(e^{b_1 v t_m} - 1)}, \frac{b_2 v t_m}{(e^{b_2 v t_m} - 1)} \right) < \max \left(\frac{b_1 v t_m}{(e^{b_1 v t_m} - 1)}, \frac{b_2 v t_m}{(e^{b_2 v t_m} - 1)} \right) \leq 1. \end{aligned}$$

Note that $\max \frac{b v t_m}{(e^{b v t_m} - 1)}$ attains 1 only if $b v t_m = 0$. Hence, the above inequality implies that $\frac{M_r t_m}{\ln N_0} < 1$. \square

2.2.4. Sensitivity to Parameter Changes

In Section 2.1.4 we know that in the standard allometry model (with linear growth) the age-dependent mortality rate coefficient (i.e. exponent) b becomes insensitive to changes in the initial population size N_0 if N_0 approaches a very large value, but becomes very sensitive to changes in N_0 if N_0 approaches 1. Similarly we would now like to consider how an analogous system, as represented by equation (22), behaves when N_0 , M_r and t_m are large. To do this, we consider the partial derivatives of b with respect to N_0 , M_r and t_m . These are given by

$$\frac{\partial b}{\partial N_0} = \frac{-b/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r}\right)^b \left[\ln \left(\frac{l_0}{l_r}\right) (e^{b v t_m} - 1) + v t_m e^{b v t_m} \right] \right]}, \quad (27)$$

$$\frac{\partial b}{\partial M_r} = \frac{b/M_r}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r}\right)^b \left[\ln\left(\frac{l_0}{l_r}\right) (e^{bvt_m} - 1) + vt_m e^{bvt_m}\right]\right]}, \quad (28)$$

$$\frac{\partial b}{\partial t_m} = \frac{\frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r}\right)^b b v e^{bvt_m}}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r}\right)^b \left[\ln\left(\frac{l_0}{l_r}\right) (e^{bvt_m} - 1) + vt_m e^{bvt_m}\right]\right]}, \quad (29)$$

respectively. Considering the RHS in (27),

$$\frac{-b/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r}\right)^b \left[\ln\left(\frac{l_0}{l_r}\right) (e^{bvt_m} - 1) + vt_m e^{bvt_m}\right]\right]}, \quad (30)$$

and using (24), we get

$$\begin{aligned} & \frac{-b/(N_0 \ln N_0)}{\left[1 - \frac{b}{e^{bvt_m-1}} \left[\ln\left(\frac{l_0}{l_r}\right) (e^{bvt_m} - 1) + vt_m e^{bvt_m}\right]\right]} \\ &= \frac{-b/(N_0 \ln N_0)}{\left[1 - e^{bvt_m} \left[\frac{b}{e^{bvt_m}} \ln\left(\frac{l_0}{l_r}\right) + \frac{bvt_m}{e^{bvt_m-1}}\right]\right]}. \end{aligned} \quad (31)$$

Since,

$$e^{bvt_m} \left[\frac{b}{e^{bvt_m}} \ln\left(\frac{l_0}{l_r}\right) + \frac{bvt_m}{e^{bvt_m-1}} \right] > 1$$

$\forall l_0 > l_r$, and $b, v, t_m > 0$, from (31), we get

$$\frac{-b/(N_0 \ln N_0)}{\left[1 - e^{bvt_m} \left[\frac{b}{e^{bvt_m}} \ln\left(\frac{l_0}{l_r}\right) + \frac{bvt_m}{e^{bvt_m-1}}\right]\right]} > 0.$$

Thus,

$$\frac{-b/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r}\right)^b \left[\ln\left(\frac{l_0}{l_r}\right) (e^{bvt_m} - 1) + vt_m e^{bvt_m}\right]\right]} > 0.$$

Hence,

$$\frac{\partial b}{\partial N_0} = \frac{-b/(N_0 \ln N_0)}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r}\right)^b \left[\ln\left(\frac{l_0}{l_r}\right) (e^{bvt_m} - 1) + vt_m e^{bvt_m}\right]\right]} > 0.$$

As a consequence of the above inequality, we have

$$\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r} \right)^b \left[\ln \left(\frac{l_0}{l_r} \right) (e^{bvt_m} - 1) + vt_m e^{bvt_m} \right] \right] < 0.$$

In view of this, equations (28) and (29) satisfy

$$\frac{\partial b}{\partial M_r} = \frac{b/M_r}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r} \right)^b \left[\ln \left(\frac{l_0}{l_r} \right) (e^{bvt_m} - 1) + vt_m e^{bvt_m} \right] \right]} < 0,$$

and

$$\frac{\partial b}{\partial t_m} = \frac{\frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r} \right)^b b v e^{bvt_m}}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r} \right)^b \left[\ln \left(\frac{l_0}{l_r} \right) (e^{bvt_m} - 1) + vt_m e^{bvt_m} \right] \right]} < 0.$$

If we let $N_0 \rightarrow \infty$ in (27), we get

$$\lim_{N_0 \rightarrow \infty} \frac{\partial b}{\partial N_0} = 0.$$

Next we substitute $\frac{b}{M_r} = \frac{(e^{bvt_m} - 1)}{v \ln N_0} \left(\frac{l_0}{l_r} \right)^b$ into equation (28), to get

$$\frac{\partial b}{\partial M_r} = \frac{\frac{(e^{bvt_m} - 1)}{v \ln N_0} \left(\frac{l_0}{l_r} \right)^b}{\left[1 - \frac{M_r}{v \ln N_0} \left(\frac{l_0}{l_r} \right)^b \left[\ln \left(\frac{l_0}{l_r} \right) (e^{bvt_m} - 1) + vt_m e^{bvt_m} \right] \right]}.$$

Hence,

$$\lim_{N_0 \rightarrow \infty} \frac{\partial b}{\partial M_r} = 0.$$

Finally, if we let $N_0 \rightarrow \infty$ in (29), we get

$$\lim_{N_0 \rightarrow \infty} \frac{\partial b}{\partial t_m} = 0.$$

Thus, we see that b is relatively insensitive to changes in N_0 . That is, b does not change rapidly as the original population size becomes larger.

On the other hand, if we let $N_0 \rightarrow 1$ in equation (27), we get

$$\lim_{N_0 \rightarrow 1} \frac{\partial b}{\partial N_0} = \infty$$

because $\frac{1}{N_0 \ln N_0} \rightarrow \infty$ as $N_0 \rightarrow 1$. This, in turn, gives

$$\frac{\partial b}{\partial M_r} \rightarrow -\infty \quad \text{and} \quad \frac{\partial b}{\partial t_m} \rightarrow -\infty, \quad \text{as } N_0 \rightarrow 1.$$

Thus, as the population size decreases, we see a greater change in the sensitivity of the size-dependent exponent parameter b .

3. Closing Comments

The purpose of this discussion has been to address the issue of parameter sensitivity of a new method for estimating the *size - dependent* mortality rate exponent b of the allometry model. Such a method is necessary when attempting to estimate allometry mortality rate parameters in the absence of mortality data by age.

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