The Application of the Gompertz Model To Describe Body Growth

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ABSTRACT: Three potential errors in applying the Gompertz growth model are discussed: 1. Restriction of growth data to the subadult or juvenile phase; 2. Confusion of mean growth rate with (mean) maximum growth rate; 3. Improper application of the growth model in cases of sample size variation. These errors are demonstrated on the example of growth data of Zambian common mole-rats (*Cryptomys* sp.).

KEY WORDS: Growth, Growth curve, Gompertz model, *Cryptomys*, Mole-rat

ZUSAMMENFASSUNG: Es werden drei potentielle Fehler diskutiert, die bei der Anwendung des Gompertzmodells zur Beschreibung von Körperwachstum auftreten können: 1. Beschränkung der Wachstumsdaten auf nur einen Teil der Wachstumsperiode (Jugend- oder Subadultphase); 2. Verwechslung von mittlerer Wachstumsrate und (mittlerer) maximaler Wachstumsrate; 3. Unzulässige Anwendung des Wachstumsmodells bei Variation der Anzahl gewogener Tiere. Diese Fehler wurden am Beispiel von Wachstumsdaten sambischer Graumulle (*Cryptomys* sp.) demonstriert.

INTRODUCTION

Growth of animals has been subject of many studies and different methods have been employed to describe and analyze it. In the most simple case periods of almost linear growth can be described by average growth rate (total weight gain divided by time in which it was achieved) (cf., Case, 1978; Millar, 1977; Daly and Patton, 1986) or by determining the slope of the regression line plotted for the linear growth period (e.g., Lunn *et al.*, 1993). Although this procedure may be instructive in special cases it does not allow comparison among species with different body size. Reliable growth parameters which can be used for comparative reasons are provided by curve-fitting procedures, e.g., logistic, von Bertalanffy, Gompertz, Richards' or modified Weibull functions, which all take the adult weight into account. While in 1967 Ricklefs still noted that "the primary reason that curve-fitting has rarely been employed for such studies in the past is its relative difficulty for the non-mathematician," nowadays there seems to be no such problem, and many authors use the curve-fitting procedures for different purposes (e.g., Rosas *et al.*, 1993; Kunz & Robson, 1995; Lima & Páez, 1995).

Zullinger *et al.* (1984) tested three growth equations (logistic, von Bertalanffy and Gompertz) fitting them to growth curves in 331 mammalian species. They found the Gompertz model to be most appropriate for describing parameters of mammalian growth. Since then, the Gompertz equation has been repeatedly used by students of mammalian growth (e.g., Kyriazakis & Emmans, 1992; Derrickson, 1988) and has become a standard method in comparative studies of growth in African mole-rats (Bathyergidae), providing a basis for sociobiological implications (Bennett *et al.*, 1991; Bennett *et al.*, 1994; Bennett & Aguilar, 1995; Mosch, 1995).

In the present paper I demonstrate, however, that several problems can arise (and should therefore be considered) when applying the Gompertz model on the growth curve of bathyergids or other mammals with extended growth. Following critical points leading to potential errors could be identified in the literature:

1. Only a part of the growth period is taken into consideration;
2. The mean growth rate is confused with the mean maximum growth rate (defined as the average of at least two maximum growth rates);
3. The growth parameters are estimated for the mean weights based on different sample sizes.

METHODS

Gompertz model

The non-linear regression using the Levenberg-Marquardt-algorithm estimates three or two parameters (Three-parameter-model or Two-parameter-model), respectively, namely A (g), the asymptotic value, I (days), age at the inflection point, and K ($days^{-1}$), the growth constant. In the Two-parameter-model, the asymptotic value is fixed with the adult weight and only two parameters, I and K, are estimated. The asymptotic value A is obviously an estimation of the adult weight in the Three-parameter-model. At the inflection point (I) the growth curve alters in its curvature (from a right-curvature to a left-curvature); the growth at this point is the fastest. The growth constant K can be regarded as a measure of growth. Because of its independence of adult weight, cross-species comparisons are possible.

The Gompertz equation (Gompertz, 1825; Winsor, 1932) which is fitted to the growth data has the form

$$W(t) = A \cdot e^{-e^{-K \cdot (t-I)}}.$$

where W(t) is the mass at time t.
Therefore the growth rate at time t is described by the function

$$W'(t) = A \cdot K \cdot e^{-K \cdot (t-I)} \cdot e^{-e^{-K \cdot (t-I)}}.$$

Parameters were estimated using the non-linear regression procedure of SPSS. Starting values for A and I were determined visually by means of plotted growth data. A starting value for K was calculated by using both, namely A and I, and one of the data points.

To determine a maximum growth rate (g/day) which describes the growth at the inflection point the growth constant K is multiplied by $A \cdot e^{-1}$.

The following analyses deal particularly with the growth constant K because of its important role in comparisons among species (cf., Zullinger *et al.*, 1984).

Growth data of Zambian common mole-rats

The growth data of common mole-rats (*Cryptomys* sp., karyotype 2n=68, population Lusaka, Zambia) were collected over the period of eight years (1986-1993) by weighing each animal at least once weekly with an accuracy of 0.01 g. While the whole set of these data, analyzed from different points of view, is a subject of a separate report (Mosch, 1995; Begall & Burda, 1997), some data are used here to demonstrate some general problems and errors resulting from an uncritical application of the Gompertz model.

The animals were housed in standard cages at an average ambient temperature of 23°C. The food (potatoes, carrots, etc.) was supplied *ad libitum*. For more details concerning the animal keeping conditions see Burda (1989).

RESULTS AND DISCUSSION

In the following the above mentioned critical points (see introduction) will be discussed.

1. Only a part of the growth period is taken into consideration

An error which has often been made while applying the Gompertz growth model, is that the authors considered only a small part of the growth curve (Bennett *et al.*, 1991; Bennett & Aguilar, 1995; Pasternak & Shalev; 1992, though the latter authors did not use their data for comparative studies.) To show the effect of shortened time periods a large data set of one mole-rat was reduced step by step. For each step asymptotic values A were fixed to animal's weight at the end of time period (Two-parameter-model), irrespective of reaching adult weight or not. Development of the estimated growth constants K is illustrated in Figure 1. It is noteworthy that the growth constant rose up to fourfold if the underlying period was reduced arbitrarily.

For example, Bennett *et al.* (1991) took in their study of the growth of *Cryptomys hottentotus* only a period of 80 days into account although the mean time, the animals are supposed to grow up, is 268 days (Bennett *et al.*, 1991). The estimated parameters (based on the Gompertz model) were A = 42,0 g, K = 0,015, I = 12,6 days. In the same article the authors noticed that the adult weight of *Cryptomys hottentotus* amounts to 62 g while in a previous publication (Bennett, 1989) the adult weight of some individuals of *C. hottentotus* was given as 100 g and more (up to 131 g). Apparently, only a very small part of the growth period was taken into consideration.

It is not easy to estimate the amount of the error because the process by means of which the parameters were determined is iterative. However, in order to demonstrate the error I reduced large data sets of two Zambian mole-rats and compared the estimated parameters (see Table 1).

It is obvious that the growth constants (K) remain almost constant after the animals have achieved their full grown size. In the case of the individual C-6 the maximum growth rate is doubled. However, if the time period was reduced just to the subadult or juvenile phases, the estimated parameters became unrealistic and it is not possible to compare these data with growth parameters (particularly growth constants K) in other species. Mostly, the estimated growth constants are too high while the time of inflection is fixed too early by the iterative process.

2. *The mean growth rate is confused with the mean maximum growth rate*

Although the units for the maximum growth rate and the (average) growth rate are the same (g/day) there is no direct connection between these parameters. To obtain the maximum growth rate which describes the growth at the inflection point, the growth constant K is multiplied by $A \cdot e^{-1}$ which may be expressed as $W'(I)=K \cdot A \cdot e^{-1}$.

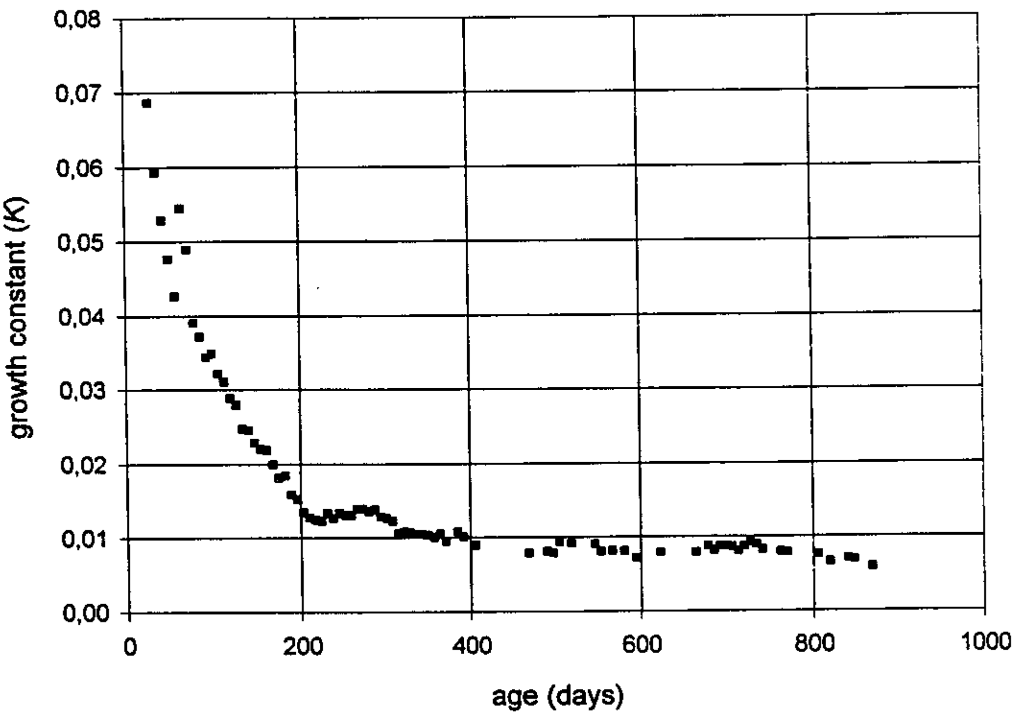

Figure 1: Growth constants (K) estimated according to the Gompertz model for one individual of the Zambian common mole-rat in dependence on the length of the underlying time period.

TABLE 1
Estimated parameters (Gompertz growth model) calculated for a step by step reduced period of time (two individuals of the Zambian common mole-rat)

	length of the period (in days)	actual weight at the end of the period [g]	*A* [g]	*K* [days^{-1}]	*I* [days]	maximum growth rate [g/day]
C-6	1456	143,80	152,64	0,0070	138	0,393
	525*	153,30	154,90	0,0064	139	0,368
	168	71,30	71,30**	0,0276	52	0,724
C-7	2499	150,60	152,34	0,0039	228	0,219
	728*	145,00	166,98	0,0033	260	0,203
	140	41,30	41,30**	0,0209	45	0,316

* animal is fully grown from that point on,
** 2-parameter-model (*A* was fixed with this value)

The confusion of the mean growth rate with the mean maximum growth rate may be based on the following procedure: 1. the maximum growth rates are estimated for several individuals; 2. an arithmetical mean is calculated. At this point I want to emphasize that the obtained value represents a mean maximum growth rate, which is not identical with the mean growth rate. This error occurs in several publications dealing with growth of bathyergids (Bennett *et al.*, 1991; Bennett *et al.*, 1994; Bennett & Aguilar, 1995). However, mole-rat data and cited literature are used as examples of wide-spread problems. Wroot *et al.* (1987) determined growth constants for Columbian ground squirrels (*Spermophilus columbianus*) by means of an exponential growth model and called them growth rates (unit: ln(g)/day) which is misleading.

The amount of the error can be demonstrated on the example of two male mole-rats (C-1 and C-2) which had an almost equal birth weight yet in the age of one year weighed 110 g and 80 g, respectively. Therefore we can assume C-2 had a mean growth rate lower than C-1. However, the maximum growth rate was 0.313 g/day for C-1 and 0.394 g/day for C-2. This result was seemingly unexpected because after one year C-1 had an higher weight achieved than C-2. In Figure 2 the growth trajectories of both individuals are shown and it is apparent that growth at the inflection point of C-1 (I=49 days) is higher than that of C-2 at its inflection point (I=126 days). In general, the growth of C-2 is characterized by phases of fast and slow growth while that of C-1 is more linear. This example shows that the maximum growth rate does not point to the growth course.

3. The growth parameters are estimated for mean weights based on different sample sizes

The application of the Gompertz growth model is in fact rather easy. It is possible to estimate the growth parameters *A, K* and *I* numerically in an iterated process by several computer programmes like SPSS, SAS or BMDP. To determine these parameters for a larger number of animals, most authors apply the growth model to average body weights which is a fast and easy method. However, in some

TABLE 2
Comparison of two methods of determining growth parameters (method 1: Gompertz model applied to mean values of the animals' body weight with variation of sample size among measurements; method 2: means calculated of individuals' growth parameters);
N = number of measurements during the growth period.

	C-3	C-4	C-5	method 1	method 2
A	82,09	134,28	156,38	108,2	124,25 (SD = 38,15)
K	**0,0042**	**0,0044**	**0,0065**	**0,0072**	**0,0050** (SD = 0,00127)
I	76,44	192,23	141,52	128,90	136,73 (SD = 58,04)
N	61	65	37	81	
r^2	0,93503	0,97115	0,96494	0,86	

cases this method does not provide the correct parameters, e.g. if not all the animals were weighed at the same age. Thus for example, animals may be weighed once a week and all the animals are weighed at the same day of the week: due to the fact that the examined animals were not born at the same day, a shifting in time takes place (e.g., one litter is weighed on days 5, 12, 19, etc. and another one on days 2, 9, 16, etc.). There may be still many other reasons why the growth data of an animal could be

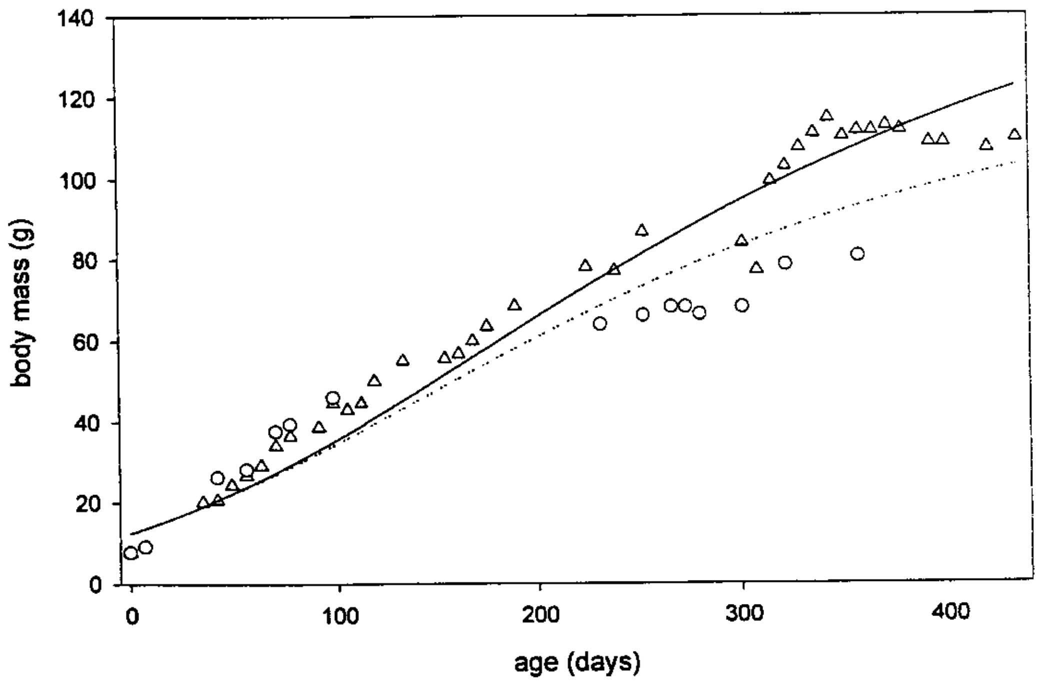

Figure 2: Growth curves of two Zambian male mole-rats: C-1 triangle (full line), C-2 circle (broken line).

incomplete. If the Gompertz function is to be applied to mean weights then only such mean values which were based on comparable measurements should be considered. That means that some (or a lot of) growth data cannot be employed. Therefore it may be better to fit the growth curves for each animal separately and then to calculate means of the growth parameters. However, in practice usually all growth data (mean values) are considered even if not all animals were weighed at the same age. This is evidenced in many figures which show that the number of animals per measurement was not constant (Bennett *et al.*, 1994, Prestrud & Nilssen, 1995).

One would expect that the growth parameters estimated for the mean body weights (method 1) are about the same as the mean of growth parameters estimated for single individuals (method 2). However, a simple example shows that method 1 fails, if all data were considered irrespective of variation in numbers of particular measurements (e.g., day 0: 26 animals, day 7: 21 animals, etc.): Growth parameters of the Gompertz model applied to growth data of three mole-rats (C-3, C-4, C-5) which were not weighed at the same days of age are listed in Table 2 (see also Figure 3). Obviously, the parameters estimated according to method 1 and 2 differ and, astonishingly, the growth constant K according to method 1 is higher than the K-values for each of the individuals.

Indeed, method 2 is more time-consuming but if the animals cannot be weighed at the same ages, the effort is profitable.

The three sources of errors demonstrated in this paper can lead to variation in growth parameters. Due to the fact that the present paper only deals with examples demonstrating that those errors do exist, analyses showing the sensitivity of results depending on methodical errors are necessary.

Fitting growth equations to animals' growth should not be based on authors' personal preference and arbitrariness. Growth models are efficient tools for comparing growth of animals and therefore care must be taken to avoid mistakes in the application of mathematical formula. According to the described error sources the following items should be considered: 1. sigmoid parameters should not be estimated for data sets that are not sigmoid in shape (e.g., inadequately short time segments of sigmoid growth), 2. exact usage of (mathematical) terms in order to avoid confusion, 3. estimation of growth parameters

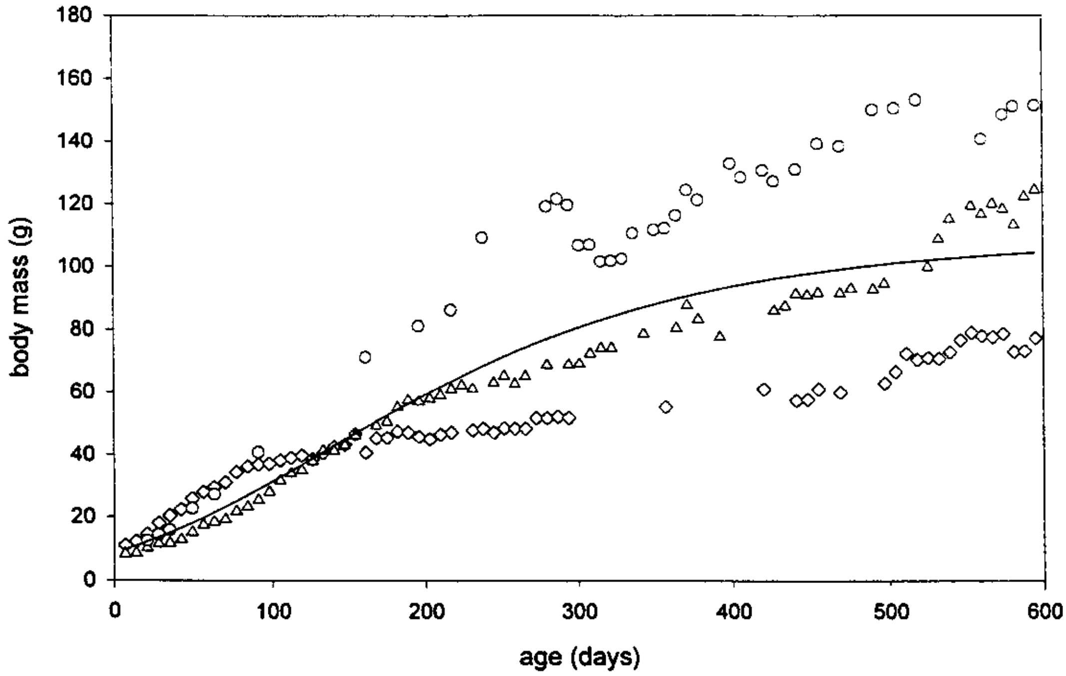

Figure 3: Growth of three Zambian common mole-rats (C-3 circle, C-4 triangle, C-5 rhombus) and a Gompertz curve fitted to the mean body weights of these individuals (line).

for each individual separately or at least avoidance of sample size variation.

Furthermore, fitting growth equations to growth data should be done using current software and methods of parameter determination. Growth equations, which comprise a fourth parameter describing the shape of a curve (e.g., Richards or Janoschek function), as well as other current techniques used to estimate parameters (e.g., Neafsey and Lowrie, 1994) may lead to better results.

One should take care not to draw speculative conclusions apparently supported by mathematics which has been, however, improperly employed.

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