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PROPERTIES AND FITTING OF THE VON BERTALANFFY GROWTH CURVE

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A discussion of the elementary mathematical properties of the von Bertalanffy growth curve shows the very special properties of this sort of growth and suggests a measure of the intrinsic physiological age of an animal. A computer program is presented to fit this curve conveniently to recapture data as well as to conventional age-size data.

INTRODUCTION

The von Bertalanffy growth curve is a curve of the decaying exponential type which has wide application in biology, particularly as a model for animal growth. Von Bertalanffy (1960) reviews the literature in the field of growth, pointing out the good fit obtained with this curve in a wide variety of cases, and presents a physiological model which gives rise to this curve.

Many papers have been published on methods of fitting exponential growth curves, but the methods are mostly either approximate or are restricted to special circumstances. A common graphical approach is described in von Bertalanffy (1960), and a very ingenious graphical method is given by Walford (1946). Von Bertalanffy (1960) also states the normal equations for the least squares but does not discuss the difficulty of solving them. Stevens (1951) and Tomlinson and Abramson (1961) give sophisticated computational schemes and tables for use with them, but the methods are restricted to data involving only a rather small number of equally spaced ages.

With large-scale electronic computers now available in almost every university center, graphical and approximate methods of fitting curves are pointless, for their *raison d'être* was the lessening of arithmetic computation. What is needed now is a flexible, general scheme for fitting the curve by means of an electronic computer.

All of the above cited schemes, and also a computer program proposed by Hayo and Wilcoxson (1963), are concerned with cases in

which weights or lengths are available for animals of known age. Growth data for many animals are most easily obtained by measuring tagged and released animals at subsequent recapture dates, so that if there are no morphological features indicative of age, absolute age cannot be determined and only the time differences are available for estimating the growth parameters. Decaying exponential growth curves bear a special relation to this type of data, as two of the three parameters are completely independent of absolute age and may be fitted easily without knowing it. Gulland and Holt (1959) took advantage of this special suitability to present a graphical method for fitting the von Bertalanffy curve to data from tagged and recaptured animals. Their method is especially convenient if the interval between tagging and recapture is small. Donnelly (1962) derived equations for a least-squares fitting of the von Bertalanffy curve to recapture data, and also derived some approximate methods suitable to special circumstances. It was in response to requests from zoölogists for explanations of Donnelly's work and for a program to run the general method on standard computers that this paper was begun. Section 5 was also partly motivated by some informal discussions with Donnelly.

This paper begins with a review of the principles of curve fitting and the theoretical background of the von Bertalanffy growth curve. In sections 3-5 it discusses the mathematical property of this curve which results in its special applicability to the fitting of recapture data and which also results in a natural solution to the traditional problem of the "physiological age" of an animal.

The remainder of the paper presents a program for fitting the curve to any set of recapture or age-size data. The program, listed in section 10, is in the artificial language Fortran, and is suitable for running on most modern computers, without requiring the biologist to learn programming or the computer operator to learn biology. The operation and preparation of data for the program are described in sections 6 and 7, and in section 8 there is an example illustrating the fitting of the curve and the determination therefrom of the physiological parameters of the von Bertalanffy model.

1. *Basic Principles*

A *growth curve* is a mathematical relation between the size of an animal and time. Suppose x is some measure of linear size, for ex-

ample, length, girth, square root of surface area, cube root of weight or volume, etc., and t is the age of the animal in any convenient units of time. The growth curve we are studying can be characterized by the statement that the growth rate with time is largest at birth and decreases exponentially in time. It can be expressed by the formula

$$x = a(1 - b e^{-kt}). \quad (1.1)$$

The quantities a , b , and k in the formula are *parameters*. They are numbers which are characteristic of the animal being studied: They do not change as the animal grows, but they would have different values for different taxa or for different choices of units or methods of measuring x and t .

Fitting the growth curve means assuming that the growth of the animals under study obeys the given relation for some values of the parameters and then estimating from field or laboratory data what the values of the parameters must be. One can then make statements like "The growth formula for *Hoplodactylus duvauceli* is

$$x = 117(1 - 0.56 e^{-0.00083 t}),$$

where x is the length in millimeters and t is the number of days of growth." We have replaced the symbols a , b , and k by specific numbers appropriate to *Hoplodactylus duvauceli*.

If we could find values of the parameters such that all the values of size and age in the data agreed with formula (1.1), our job would be done. This is seldom possible, however, so we must assume that the observed values of x are values from the formula plus errors made up of individual variation, measurement errors, etc. Fitting then consists of choosing values of the parameters which make the curve come as near as possible to passing through all the points, i.e., so that the errors we have to assume are as small as possible. Graphical or computational schemes can be used to accomplish this fitting. The graphical schemes depend on the eye of the user to determine the best fit and hence are subject to personal differences. Most computational schemes, including the one presented in this paper, choose the values of the parameters which minimize the sum of squares of the errors we have to assume. (A crucial assumption behind this "method of least squares" is that the errors we are assuming all have the same variance, like the errors in measuring various volumes in a graduated cylinder.

Because the method of least squares gives equal weight to each point of the data, it should not be applied without modification to data like the measurements of a range of volumes in an old style conical graduate. There the larger volumes tend to have larger errors and so should be given less weight. Such questions are usually skipped over in elementary texts and assumed to be already understood in advanced ones. For one who already knows some statistics, a good book about pitfalls is Acton, 1959. The beginner might consult Hoel, 1962.)

Saying that a curve fits certain data "well" means that it is possible to find values of the parameters that make the errors we have to assume mostly quite small. It has already been said that the values of the parameters are chosen to make these deviations as small as possible, but if entirely the wrong sort of curve were tried, if for example we tried to fit growth data with a straight line, then we would not be able to make all the deviations small no matter what values of the parameters we chose. Included in this concept is the principle that the observed values group evenly around the fitted curve and do not show any definite tendency away from it; for, if they did, there would be another curve which would fit the data much better.

Curve fitting may yield theoretical results or may be just a means of summarizing data. If the growth curve is derived from a theoretical model, so that the parameters have physiological meaning, then we may be interested in determining their values for theoretical purposes, or at least in determining that a good fit is possible, thus adding support to the validity of the model. On the other hand, a growth curve of no theoretical significance might be fitted merely because of the convenience, for comparisons of taxa etc., of having the data summarized in the values of just a few parameters. (See, for example, Richards, 1959.) The von Bertalanffy growth curve is popular because it fits the growth data of a wide variety of animals quite well and so is useful for purely descriptive purposes (see von Bertalanffy, 1960, or Beverton and Holt, 1957), and also because it can be derived from an interesting model which gives physiological significance to the parameters. This derivation, originally due to von Bertalanffy (1960), is summarized in the next section.

2. *The von Bertalanffy Model and Curve*

The rate of growth in weight of an animal may be thought of as the difference of an anabolic and a catabolic rate. It is natural to

assume that the rate of breaking-down of tissue would be more or less constant, so that the rate of total weight loss in the animal due to catabolism would be proportional to the weight of the animal. One might also assume that the tissue buildup would be limited by the capacity for respiration and ingestion and hence by the surface area, either external or of the lungs, gut, etc. (the "surface rule"). Thus, if we also assume that the shape of the animal does not change as it grows, the anabolic growth rate would be proportional to the two-thirds power of the weight. These assumptions constitute von Bertalanffy's first metabolic type model, which may be expressed,

$$Dw = \eta w^{2/3} - \alpha w, \quad (2.1)$$

where w is the total weight of the animal, Dw is the rate of change of weight with time, and η and α are the anabolic and catabolic constants for the particular taxon under study.

Since the model assumes that the shape of the animal does not change, it is no additional restriction to say that any linear dimension x (which might be length, girth, the cube root of volume, etc.) will be proportional to the cube root of weight, i.e., that

$$x = q w^{1/3},$$

where q is a constant which is characteristic of the taxon. If, following Donnelly (1962), we rewrite the differential equation (2.1) in terms of the variable x , instead of w , and solve it, we get the formula

$$x = \frac{q\eta}{\alpha} - \left(\frac{q\eta}{\alpha} - c \right) e^{-\alpha t/3}, \quad (2.2)$$

where the new parameter c arises in the solution because the differential equation says nothing about the actual value of x , specifying only its rate of change. The form of equation (2.2) has been chosen so that $x = c$ when $t = 0$; that is, c is the size of the animal at birth.

If x is the cube root of weight, then $q = 1$, and we can rewrite (2.2) as the growth formula for weight,

$$w = \left[\frac{\eta}{\alpha} - \left(\frac{\eta}{\alpha} - c \right) e^{-\alpha t/3} \right]^3$$

which is the form given by von Bertalanffy (1960) except that he

erroneously identifies c with w_0 , the weight at time $t = 0$. Substitution of $t = 0$ in this equation immediately gives the correct result, that

$$c = \sqrt[3]{w_0}.$$

We can simplify formula (2.2) by choosing new parameters:

$$\begin{aligned} a &= q\eta/\varkappa \\ b &= 1 - \varkappa c/q\eta \\ k &= \varkappa/3. \end{aligned} \quad (2.3)$$

Then

$$x = a(1 - be^{-kt}). \quad (2.4)$$

We shall work with formula (2.4) because it is simplest. The new parameters a , b , and k have a descriptive significance, giving asymptotic size, etc., rather than being physiologically significant like the parameters in (2.2), but we get exactly the same relation between x and t by fitting either (2.2) or (2.4). If we wish the values of the physiological constants, they can be obtained immediately by solving the equations (2.3) for them, giving

$$\begin{aligned} \varkappa &= 3k, \\ \eta &= 3ak/q, \\ c &= a(1 - b). \end{aligned} \quad (2.5)$$

The constant $q = x/\sqrt[3]{w}$ has to be worked out from a comparison of corresponding values of x and w in the animals studied. The determination of q and of \varkappa and η is illustrated in the example worked out in section 8.

The graph of the growth curve for linear size has the appearance of Figure 1. The rate of growth is highest at birth and decreases continually. The size approaches an asymptote whose value is the value of the parameter a in (2.4). The size x gets closer and closer to a as the animal gets older; x never stops increasing, but never passes a . The parameter k in (2.4) is an indication of the rate of proportional growth of the animal: at age $\ln 2/k$ the animal is halfway between his initial size c and his asymptotic size a . (The quantity $\ln 2$ is the natural logarithm of 2; it is approximately equal to 0.69.) The detailed behavior of the curve and the meaning of the parameters will become clearer when we discuss the exponential property, in the next section.

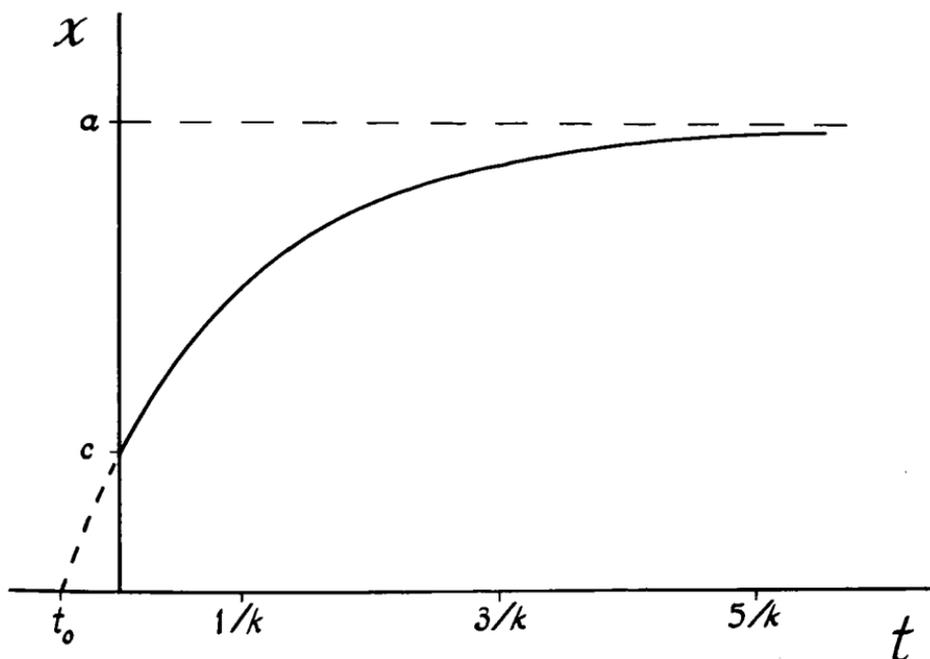


FIGURE 1

Growth in linear size.

The curve for weight growth,

$$w = [a (1 - b e^{-kt})]^3,$$

in terms of the new parameters, is similar in appearance to the one for linear size, but, because of the cubic relationship, it has a slight reverse curvature at the beginning with an inflection point at $w = \frac{8}{27} a^3$ i.e. at eight twenty-sevenths of the asymptotic weight (unless, of course, the animal already weighs $\frac{8}{27} a^3$ or more when it is born).

The von Bertalanffy curve should not be confused with the "monomolecular" curve, which is another type of decaying exponential growth curve in which formula (2.4) is used to describe growth in weight instead of growth in linear size (cf. Medawar, 1945). The monomolecular curve of weight growth has no inflection and lacks the physiological motivation of the von Bertalanffy curve. Since, how-

ever, it also depends on formula (2.4), the discussion in the following sections and the computer program could be applied to it by reading "weight" wherever this paper has "linear size."

3. *The Exponential Property*

The exponential function occurring in decaying exponential growth curves endows them with a special property, the understanding of which is essential to the full appreciation of the nature of this sort of growth and of the special applicability of these curves to recapture data.

By the exponential function we mean the function f whose value for any number t is

$$f(t) = e^t,$$

where e is the base of natural logarithms, $e = 2.7183 \dots$. Any other number besides e could be used here; we could just as well talk about the exponential function based on 2,

$$g(t) = 2^t,$$

or the one based on 10, etc., and the property we are going to discuss would be unchanged. (The only difference would be to change the values of k in the growth formula by a constant factor.) The number e is used because some formulae, particularly in the calculus, are simplest when based on e and therefore e has become standard for mathematical discussions of exponentials, and tables of exponentials are based on it.

The interesting property of this function is that, irrespective of the initial value of the argument t , a given change in the value of the argument always produces the same *percentage* change in the value of the function. For example, if

$$e^{(10+a)} = b e^{10},$$

then

$$e^{(100+a)} = b e^{100},$$

and similarly, for any number n ,

$$e^{n+a} = b e^n.$$

Adding the same number to t always *multiplies* e^t by the same factor.

This is of course obvious from the rule of exponents in elementary algebra,

$$e^{n+a} = e^n e^a,$$

but its being familiar should not lead us to underestimate its importance. This property in reverse (exponentials are but antilogarithms) is what makes logarithms useful for computations: adding the logarithm of two numbers corresponds to multiplying the numbers.

A very familiar example of the exponential property is unrestricted bacterial growth. If the food supply etc. is unrestricted, the colony doubles its size at regular time intervals. The formula for the growth is

$$x = e^{kt},$$

where the time it takes to double x is the time t^* such that $e^{kt^*} = 2$, or $t^* = \ln 2/k$, approximately $0.69/k$. The same growth formula could also be written

$$x = 2^{t/t^*},$$

and it is tempting to do so, since it seems simpler here. But e is more convenient elsewhere (particularly in the formulae in section 9) and is so standard that it is better in the long run to put up with the unattractive factor of 0.69.

The same formula with a negative exponent,

$$x = e^{-kt},$$

is familiar as the law of radioactive decay. Here the quantity of material present x is *halved* every $0.69/k$, this period of time being known as the "half-life" of the particular radioactive element.

It is important to notice the way in which the future behavior of x is independent of the past in these growth and decay curves. In *any* time period of length $0.69/k$, x is doubled or halved, regardless of how long the process has been going on or at what value x started. Conversely, if we come on the scene at time t_1 and find $x = 16$, and at time $t_2 = t_1 + d$ we find $x = 32$ (or 8), then we know immediately that $k = 0.69/d$, but no amount of study of future values of x and t will give us any clue as to how old the colony (or sample of radioactive material) is. (Such is the nature of the models we have described: They are macroscopic views of bacterial growth and radioactive decay in which it is assumed that x varies continuously and can be arbitrarily

small. In reality we could work out a rough estimate of the maximum possible age of a colony because we know that we could not ever have had less than one bacterium. But in no way could we determine the age or original size of the radioactive sample unless we are given one of these two quantities from some other information.)

Now the growth curve we are studying can be expressed, by rearranging formula (2.4) slightly, as

$$a - x = ab e^{-kt},$$

so we can see that here it is the difference between a and the size x which is halved every $0.69/k$ units of time. With this in mind we can describe the curve in Figure 1 a little more fully. Starting at an initial size c , when it reaches age $0.69/k$ the animal has grown halfway to the asymptotic size a ; that is, its size is $(c + a)/2$ or $c + (a - c)/2$. At twice this age it has grown three quarters of the way to its asymptotic size, i.e. to size $c + 3(a - c)/4$; after three periods of length $0.69/k$ it is seven eighths of the way to a , etc. After $5/k$ units of time, if it lives that long, the animal is within less than 1% of its asymptotic size. Moreover, in any particular length of time, no matter when in the animal's life it occurs, the animal grows the same proportion of the remaining distance to a , and animals of different taxa which happen to be characterized by the same value of k , though they be of widely differing sizes and characterized by widely different values of a and b , will accomplish the same proportion of their growth to asymptotic size in exactly the same periods of time. Thus k may be regarded as a measure of the intrinsic growth rate of the animal.

4. *Fitting Recapture Data*

There are two very important results of this special property of the exponential growth curves. The first is as follows: In the growth curve it is $a - x$ instead of x which is changing exponentially, but the independence of the past is the same as in the previous examples. Given k and a , from the present size of the animal we can predict its entire future growth without any knowledge of how old it is, and, by the same token, k and a can very easily be determined from data only on sizes at known time differences, with no knowledge of absolute age. It is this which makes the curve so convenient to fit to recapture data.

One more equation will perhaps clarify the discussion. Let us write

a formula for the size y of the animal at time $t + d$ in terms of its size x at time t . At time $t + d$, from formula (2.4),

$$\begin{aligned} y &= a (1 - b e^{-k(t+d)}) \\ &= a (1 - b e^{-kt} e^{-kd}). \end{aligned}$$

But
$$x = a (1 - b e^{-kt}),$$

so
$$b e^{-kt} = 1 - \frac{x}{a}.$$

Thus
$$\begin{aligned} y &= a \left[1 - \left(1 - \frac{x}{a} \right) e^{-kd} \right], \\ &= a - (a - x) e^{-kd}, \end{aligned}$$

or
$$y = x + (a - x) (1 - e^{-kd}). \quad (4.1)$$

The important thing to notice about this equation is that both t and b have disappeared. Thus, as we claimed, the new size depends only on the old size, the time elapsed, and the parameters a and k . Recapture data typically consist of pairs of sizes with a time difference, each "observation" being a value of x , a value of y , and a value of d . Such data can be applied to (4.1) and k and a determined therefrom by least squares.

The converse of these remarks is less pleasant: The third parameter b , which is related to the size of the animal at birth, can never be estimated from recapture observations alone. Some observations of sizes at known ages (a few sizes at birth, for example) must be supplied to determine b from formula (2.4) and complete the fitting. In an extreme case the size at birth might be estimated merely as being somewhere between the smallest size observed and zero, or, if births are known to be restricted to a fairly short season, the age of this year's crop might be accurately estimated. It is worth noting, however, that b is often less important than k and a : the intrinsic time scale, the asymptotic size, and the physiological constants α and η all depend only on k , a , and q , which are all determinable without knowledge of absolute age. For this reason, the computer program presented at the end of this paper computes the values of k and a from the recapture form of data and prints them out before accepting additional data to calculate b . If only the physiological constants, say, are wanted, b need not be determined at all.

5. Physiological Time

We have seen in the above discussion that the parameter k determines the time scale of the growth curve. Physiologists have long wanted an intrinsic time scale by means of which the stage of growth of different animals could be compared. The second important result of the exponential property of this growth curve is that, for animals growing according to it, such a scale is both natural and practical. Just as the half-life is the natural unit for describing the age of a sample of a radioactive element, the period $\ln 2/k$, in which the animal achieves half its remaining linear growth, is a natural unit for the age of an animal growing according to this curve. Names such as "half-growth period" immediately suggest themselves, but as it is really half of the *remaining* growth toward an asymptote (which the size will never actually reach), such terms are likely to be confusing as well as unwieldy. I suggest that this period be called a *chron*, after the familiar Greek root $\chi\rho\omicron\nu\omicron\varsigma$, "time." (In modern Greek, even more appropriately, $\chi\rho\omicron\nu\omicron\varsigma$ means "year.") This word is short enough to be used conveniently with metric prefixes. One chron is $\ln 2/k$ units of ordinary time, so that

$$\text{time in chrons} = \text{ordinary time} \cdot (k/\ln 2).$$

In one chron, any animal will grow half the distance from his present linear size to his asymptotic size a . Two animals of the same age in chrons, irrespective of differences in taxon or age in years, are at corresponding points along their respective growth curves: at three chrons they have both accomplished seven eighths of their linear growth; at five chrons they are both within less than one thirty-second of their asymptotic size a .

The above discussion is about linear sizes such as length, girth, etc. Since weight is not a linear size, the time for the weight to change from w to $(w + w_\infty)/2$, half way to the asymptotic weight, will not be one chron, but will, in fact, depend on the initial weight w . In one chron, the weight will change from w to $(w^{1/3} + w_\infty^{1/3})^3/8$, as can be seen by realizing that $w^{1/3}$ is a linear size. However, the value of k , and hence of the size of a chron, can be obtained by fitting (2.4) to data on any linear dimension or by fitting (2.6) to weight data, and the values obtained must be essentially the same. If they are not, it does not indicate that the derivations are wrong, but that the wrong

model has been used. It indicates that the basic von Bertalanffy assumption of constant shape, the assumption that the weight of the animal is proportional to the cube of any linear dimension, is not satisfied, and hence the von Bertalanffy model is not applicable.

(It suggests itself immediately that the time in chrons since the extrapolated time of zero size,

$$t_0 = \ln b/k \text{ units of time}$$

or
$$t_0 = \ln b / \ln 2 \text{ chrons}$$

(see Figure 1) might be an even more appropriate measure of intrinsic age, since in this "rationalized" system an animal one chron old has size exactly $a/2$, at two chrons the size is exactly $3a/4$, etc. But this probably seems less natural than age since birth, and for an animal whose size at birth is small compared with its asymptotic size, the difference is small.)

The computer program presented below automatically prints out the conversion factor from the time units of the data to chrons and *vice versa* after the determination of k and a .

6. Operation of the Program

In section 10 of this paper is listed a program for fitting the von Bertalanffy growth curve (2.4) by means of a large-scale computing machine. The program is written in the artificial language Fortran, which can be used directly or with slight modifications on most computers. In order to be as flexible as possible, the program is written to take advantage of the principles discussed in section 4 and to calculate k and a from recapture data. If the data available are actually sizes at known ages, they can easily be recast in the recapture form.

The program will accept as size data either linear sizes (length or width of the whole or a part of the animal, girth, etc.) or weights. If weights are used, the curve fitted is (2.4) with $x = \sqrt[3]{w}$; the cube root of each weight is automatically taken as it is read by the machine.

The program is in three parts. Part A calculates the parameters k and a . Each piece of data for this part is a number triple (x, y, d) , x and y being two sizes of a particular animal and d the time interval between the measurements. Any number from 2 to 400 of such "observations" may be used; the more there are, the more accurate will be the

estimates of k and a . Some of these data may arise from several successive measurements of one animal, n successive measurements giving rise to $n - 1$ "observations."

The parameters k and a are calculated by an iterated least squares method, the equations for which are derived in section 9. The equations for the least squares estimates of k and a cannot be solved explicitly, so the program determines approximate values for k and a and then applies a Newton-Raphson formula to improve the estimates. The formula is used again to produce further improvement and the process is repeated until successive estimates differ by less than 2×10^{-6} , when the final values are truncated to five significant figures and punched out. This will usually take six or less iterations (a few minutes on an IBM 1620 computer, less on larger machines). If for any reason the estimates should fail to converge in fifteen iterations, the machine will give the values of k and a for five successive iterations and the difference at the twentieth iteration and proceed to part B of the program. The values of k and a can then be accepted if the difference is small enough for the purposes at hand, or the trouble can be diagnosed by examining the successive iterates.

When the calculation of k and a is complete and their values are punched out, the machine proceeds to part B, where it calculates the parameter b . Here there is an explicit formula, also derived in section 9, and no iterations are required. Each piece of data for part B consists of a size x and an age t . One or more (up to 400) of such "observations" may be used. If the average size of the animals at a particular age is known, one might feed only one observation to part B and the value of b will be calculated so that the curve passes through that point. If more than one observation is fed to part B, the value of b found will be the least squares estimate.

Since at advanced age the animal grows slowly as it nears its asymptotic size, values of size at known advanced ages give information mostly about the parameter a and are poor data to use in estimating b . Therefore, if just one observation is fed to part B of the program, an estimated average size at some known age, it should preferably be for as early an age as possible. An estimate of the average size at birth is ideal.

In C, the last part of the program, the machine selects 36 ages spread over the growth of the animal, calculates the size x at each

age, and punches out these ages and sizes so that the growth curve may be easily plotted if desired.

As it is listed in section 10, the program punches all of its output into cards so that machine time is not wasted in typing. If no card listing machine is available in the computer center or the computer is equipped with a high speed printer output, it may be desired to have the machine print the output directly. This can be easily arranged by merely changing all the commands "Punch" in the listed program to "Print."

7. Preparation of Data

The computer program presented in this paper runs automatically throughout with no attention or decisions needed during the run. All the biologist needs to do to run the program is to prepare the data cards described below and give them to the machine operator along with the program listing from section 10.

On the data cards, ten columns are allotted each data entry (size, time difference, or age). The numbers are punched into the cards in standard decimal notation with a decimal point (i.e. twenty must be entered as "20.", not "20"), and may be placed anywhere in the ten columns allotted. Each card begins with a *control digit* in column 1.

The first card in the deck is the *control card*. If the data are to be linear sizes, this card has a 1 in column 1. If the run is to be done on weights (so that the machine takes the cube root of all the sizes as it reads them), column 1 has a 2 instead. The card is otherwise blank.

Following the control card are the *A data cards*, each bearing one observation (two sizes and the time interval between). On every card column 1 must have a 1 or a 2, agreeing with the digit on the control card, and columns 2-11, 12-21, and 22-31 are allotted to the first size x , second size y , and time interval d , respectively.

Following the last card of the part A data, there must be the *end of A data card*. This is like an A data card but with zeroes (written "0.") instead of the data entries and with a 3 in column 1. When the machine reads this card it stops reading data and proceeds to the calculation of k and a .

One or more cards of part B data follow the end of A data card. Each *B data card* begins with a 4 or a 5 in column 1, depending on whether the run is on linear sizes or weights (a 4 if the control card

had a 1 and a 5 if the control card had a 2). Columns 2-11 are allotted to a size and 12-21 to the corresponding age.

Following the last card of the B data there must be an *end of B data card*, bearing a 6 in column 1 and two zeroes for data. This is the last card in the deck. Upon reading it the machine proceeds to calculate b and the values for plotting (part C).

The control digits on the A and B data cards are intended to help prevent errors due to mixing up linear size with weight data or part A with part B data, especially when several runs are being made. If any one of the control digits is wrong, the machine will punch out "Data Error in Card —," giving the number of the offending card as counted from the beginning of the deck, and will then stop. The correct cards should be put in the data deck and the program begun again.

8. An Example

As an example of the procedure, we present the results of two runs made on recapture data collected by R. E. Barwick of the Australian National University on the New Zealand gekkonid lizard *Hoplodactylus duvauceli* (Duméril et Bibron) over a period of several years. Both lengths and weights had been recorded so it was possible to do a run on each and compare the results. Fifty-two pairs of sizes with the intervening time intervals were used as part A data for each run. Barwick had previously determined an average length and weight for an absolute age of 105 days of growth (the winters, when the animals effectively do not grow, are not counted in their age), so this was used as the whole data for part B.

The appearance of the machine output for the run on linear sizes is shown in Figure 2. The numbers are in scientific notation with "E" standing for "times ten to the." Thus k is $8.3250\text{E}-04 = 8.3250 \times 10^{-4}$. Similarly, $a = 116.55$ and $b = 0.55950$. The run on weights gave $k = 9.5785 \times 10^{-4}$, $a = 3.1510$, and $b = 0.50572$. Thus the growth curve for length in millimeters and age in days of growth is

$$x = 117 (1 - 0.56 e^{-0.00083 t}),$$

and for weights in grams and age in days of growth it is

$$w = [3.15 (1 - 0.51 e^{-0.00096 t})]^3,$$

FITTING THE DECAYING EXPONENTIAL GROWTH CURVE

$$X = A(1 - B \text{EXP}(-KT))$$
 where X is linear size

PART A 52 OBSERVATIONS

Final Values (3 Iterations)

 $K = 8.3250E - 04$ $A = 1.1655E + 02$

1 Chron = 8.326E + 02 Units of Time.

1 Unit of Time = 1.201E - 03 Chrons.

PART B 1 OBSERVATIONS

B = 5.5950E - 01

PART C CALCULATED VALUES FOR PLOTTING

Age	Linear Size
0.000	5.134E + 01
6.000E + 01	5.452E + 01
1.200E + 02	5.754E + 01
1.800E + 02	6.042E + 01
2.400E + 02	6.315E + 01
3.000E + 02	6.575E + 01
3.600E + 02	6.823E + 01
4.200E + 02	7.058E + 01
4.800E + 02	7.282E + 01
5.400E + 02	7.495E + 01
6.000E + 02	7.698E + 01
7.200E + 02	8.074E + 01
8.400E + 02	8.415E + 01
9.600E + 02	8.723E + 01
1.080E + 03	9.001E + 01
1.200E + 03	9.254E + 01
1.320E + 03	9.482E + 01
1.440E + 03	9.689E + 01
1.560E + 03	9.876E + 01
1.680E + 03	1.004E + 02
1.920E + 03	1.034E + 02
2.160E + 03	1.058E + 02
2.400E + 03	1.077E + 02
2.640E + 03	1.093E + 02
2.880E + 03	1.106E + 02
3.120E + 03	1.117E + 02
3.360E + 03	1.126E + 02
3.600E + 03	1.133E + 02
4.200E + 03	1.146E + 02
4.800E + 03	1.154E + 02
5.400E + 03	1.158E + 02
6.000E + 03	1.161E + 02
6.600E + 03	1.163E + 02
7.200E + 03	1.164E + 02
7.800E + 03	1.165E + 02
8.400E + 03	1.165E + 02
ASYMPTOTE	1.166E + 02

Extrap Zero 8.378E - 01 Chrons Before Birth

FIGURE 2

Machine output for a run on linear sizes.

which gives an asymptotic weight of $a^3 = 31.3$ gm. The curves could be conveniently plotted from the values listed by part C of the program.

Comparison of corresponding lengths and weights in the original data yielded values of the ratio $q = x/\sqrt[3]{w}$ varying from 30 to 35 but giving an average of 33.4 with a standard deviation of 1.9. Taking q as $33.4 \text{ mm/gm}^{1/3}$, we get from the run on lengths, using formulae (2.5),

$$\begin{aligned} \kappa &= 3k = 2.5 \times 10^{-3} \text{ gm/gm day,} \\ \eta &= 3ak/q = 8.7 \times 10^{-3} \text{ gm/gm}^{2.3} \text{ day,} \\ c &= a(1 - b) = 51.3 \text{ mm.} \end{aligned}$$

For the run on weights, $x = \sqrt[3]{w}$, so $q = 1$, and

$$\begin{aligned} \kappa &= 3k = 2.9 \times 10^{-3} \text{ gm/gm day,} \\ \eta &= 3ak = 9.1 \times 10^{-3} \text{ gm/gm}^{2.3} \text{ day,} \\ c &= a(1 - b) = 1.56 \text{ gm}^{1.3}, \end{aligned}$$

or an initial weight of $w_0 = c^3 = 3.79$ gm.

The initial length and weight are also given by the program as the first size listed by part C. The weights in the units for κ cancel out, so one should more correctly write the units just as reciprocal days, making it clear that the value of κ depends on the units of time measurement, but not on the units of weight. The units for η simplify to $\text{gm}^{1/3}/\text{day}$, showing that the value of η depends on the units used for both time and weight.

The program output includes the conversion factors to physiological time and, in case the rationalized system is wanted, the extrapolated time of zero size t_0 . Thus for this animal, 83 days of growth constitute about one decichron. For convenience in keeping track of runs and the behavior of the program, the number of observations used in each part and the number of iterations needed to reach final values for k and a are also given.

9. *The Mathematics of the Fitting*

This section contains the derivation of the formulae for the least squares fitting of the von Bertalanffy growth curve. The derivations follow the general principles of two of the methods given by Donnelly (1962) but yield formulae more suitable for computation, where taking differences late in the calculation must be avoided lest serious rounding errors be introduced. Two approaches are discussed.

The first is an exact but iterative method based on a formula which improves the accuracy of any given estimate of k and a and can be applied again and again to yield any desired degree of accuracy. The second is a direct but approximate method which is used in the computer program to provide a starting estimate for the application of the iterative method. It could also be used to give an approximate answer if a computer were not available. The determination of the third parameter b is straightforward and would be the same for either approach to the estimation of k and a .

The data for the estimation of k and a are assumed to be of the recapture type, each "observation" consisting of two sizes and the difference of time between their measurement, since, as mentioned above, any other form of data can be easily converted to this form. In the formulae which follow it is also always assumed that x is a linear size. If weight data are to be fitted, one would first take the cube root and then apply the formulae to $x = \sqrt[3]{w}$.

9.1 Least-Squares Estimate of k and a

The data consist of n observations each being two linear sizes x_i and y_i and the time difference d_i between their measurement. Given x_i and d_i , the value we would predict for y_i is, from formula (4.1) derived above,

$$y_i^* = x_i + (a - x_i) (1 - e^{-kd_i}).$$

If we apply the least-squares principle to the y_i , it states that we should choose k and a so as to minimize

$$E = \sum (y_i - y_i^*)^2 = \sum [y_i - x_i - (a - x_i) (1 - e^{-kd_i})]^2,$$

where, as in all the following formulae, the summations are over all the data, $i = 1, 2, \dots, n$. To minimize E we set the partial derivatives with respect to k and a equal to zero. Setting $D_a E = 0$ immediately yields

$$a = \frac{\sum (1 - p_i) (y_i - x_i p_i)}{\sum (1 - p_i)^2}, \quad (9.1)$$

where we have written p_i for e^{-kd_i} to simplify the formula. Differentiating E with respect to k yields

$$D_k E = -2 \sum d_i p_i (a - x_i) [y_i - x_i - (a - x_i) (1 - p_i)],$$

which we also wish to equate to zero. If we drop the factor of -2 and introduce the further simplifying substitutions

$$r_i = a - x_i \text{ and } s_i = a - y_i$$

(where a is calculated from (9.1) so that r_i and s_i are functions of k), we can state that our problem is to find k such that

$$F(k) = \sum d_i p_i r_i (r_i p_i - s_i) = 0. \quad (9.2)$$

Unfortunately, this equation cannot be solved directly for k , but it can be attacked by the Newton-Raphson method, which states that if k_0 is an approximation to the solution, then

$$k_1 = k_0 - F(k_0)/DF(k_0) \quad (9.3)$$

is a better one. Starting with k_1 we can repeat the procedure to get a still better approximation k_2 and so forth, doing as many iterations as necessary to achieve the accuracy we desire. (See, for example, Courant, 1937, pp. 355-7.)

The derivative DF which is required in formula (9.3) follows from the definition of F in (9.2) and is

$$DF(k) = \sum d_i p_i \{Da [s_i + r_i (1 - 2p_i)] + r_i d_i (2p_i r_i - s_i)\},$$

where, from (9.1), the derivative of a with respect to k is

$$Da = \sum d_i p_i [y_i + x_i (1 - 2p_i) - 2a (1 - p_i)] / \sum (1 - p_i)^2.$$

9.2. An Approximate Method for k and a

If we can assume that the time intervals d_i are short compared with the lifetime of the animal, we can avoid the iterations of the previous method and get approximate values of k and a in the following manner: If d_i is small, then $r_i = (y_i - x_i)/d_i$ is approximately the derivative Dx of size with respect to time at size $s_i = (x_i + y_i)/2$.

But since, by differentiating (2.4),

$$Dx = abk e^{-kt} = k(a - x),$$

we have approximately

$$r_i = k (a - s_i).$$

We can now estimate k and a by applying least squares to r_i , that is, by choosing k and a to minimize

$$E = \Sigma [r_i - k(a - s_i)]^2.$$

This is now a standard linear regression problem. The solution is obtained by setting the derivatives $D_k E$ and $D_a E$ equal to zero. We get

$$k = \frac{\Sigma r_i \Sigma s_i - n \Sigma r_i s_i}{n \Sigma s_i^2 - (\Sigma s_i)^2},$$

and

$$\begin{aligned} a &= \frac{1}{nk} (\Sigma r_i + n \Sigma s_i) \\ &= \frac{\Sigma s_i \Sigma r_i s_i - \Sigma r_i \Sigma s_i^2}{n \Sigma r_i s_i - \Sigma r_i \Sigma s_i}. \end{aligned}$$

9.3 Estimation of b

As mentioned in section 4, b cannot be estimated from recapture data. Some data relating size x to absolute age t must be supplied. Once k and a have been calculated and this extra data supplied, however, the determination of b offers no difficulty. The values of k and t_i being given, $p_i = e^{-kt_i}$ is known, so we can write (2.4) in the form

$$x_i = a(1 - bp_i).$$

The value of b to minimize

$$E = \Sigma [x_i - a(1 - bp_i)]^2$$

is found immediately by setting $D_b E = 0$ to be

$$b = \frac{\Sigma p_i (a - x_i)}{\Sigma p_i^2}.$$

10. Listing of the Program

The following is the program in Fortran I as used on an IBM 1620 computer with a Fargo processor. In the Fortran statements the parameter k is called C; other variable names agree substantially with the text.

```

C      FITTING THE DECAYING EXP GROWTH CURVE—FABENS 30 APR 64
      DIMENSION X(401), Y(401), D(401)
1     FORMAT (/45HFITTING THE DECAYING EXPONENTIAL GROWTH
      CURVE)
4     FORMAT (/11HPART A          I4,13H OBSERVATIONS)
6     FORMAT (5HAFTER15, 16H ITERATIONS, K = 1PE11.4,5H, A = E11.4)
7     FORMAT (7HDIFFK = 1PE8.1,9H, DIFFA = E8.1)

```

```

 9 FORMAT (/14HFINAL VALUES (I4,12H ITERATIONS))
10 FORMAT (/8H      K = 1PE11.4,8H      A = E11.4)
11 FORMAT (/11HPART B      I4,13H OBSERVATIONS)
12 FORMAT (/14H      B = 1PE11.4)
13 FORMAT (/39HPART C      CALCULATED VALUES FOR PLOTTING)
14 FORMAT (25H      AGE      LINEAR SIZE)
15 FORMAT (1PE10.3,4X,E10.3)
16 FORMAT (19HDATA ERROR IN CARD I4)
17 FORMAT (I1,F10.0,F10.0,F10.0)
18 FORMAT (44HX = A(1 - B EXP(-KT)) WHERE X IS LINEAR SIZE)
19 FORMAT (48HCUBE RT(W) = A(1 - B EXP(-KT)) WHERE W IS
WEIGHT)
20 FORMAT (22H      AGE      WEIGHT)
81 FORMAT (/15H      1 CHRON = 1PE10.3,15H UNITS OF TIME.)
82 FORMAT (22H      1 UNIT OF TIME = 1PE10.3,8H CHRONS.)
83 FORMAT (10H ASYMPOTOTE4X,1PE10.3)
84 FORMAT (/11HEXTRAP ZERO1PE10.3,20H CHRONS BEFORE BIRTH/)

```

```

C      READ PART A DATA
      PUNCH 1
      READ 17, J
      LLL = 1
      IF(J-1)73,72,73
72     PUNCH 18
      GO TO 76
73     IF(J-2)75,74,75
75     PUNCH 16,LLL
      GO TO 100
76     N = 1
74     PUNCH 19
22     READ 17, I, X(N), Y(N), D(N)
      LLL = LLL + 1
      IF(I-J)24,77,24
77     IF(J-1)78,23,78
78     X(N) = X(N)**.33333333
      Y(N) = Y(N)**.33333333
23     N = N + 1
      GO TO 22
24     IF(I-3)75,26,75
26     N = N - 1
      PUNCH 4,N

```

```

C      CALCULATE INITIAL K
      F = 0.
      G = 0.
      H = 0.
      P = 0.
      M = 0
      DO 27 I = 1, N
      R = (Y(I) - X(I))/D(I)
      S = (X(I) + Y(I))/2.
      F = F + R
      G = G + S
      H = H + R*S
27     P = P + S**2
      T = N

```

$C = (F * G - T * H) / (T * P - G ** 2)$
 $AP = 1.$

C ITERATE TO IMPROVE K AND A

```

29 F = 0.
   G = 0.
   H = 0.
   M = M + 1
   DO 301 I = 1, N
     P = EXPF(-C*D(I))
     F = F + (1.-P)*(Y(I)-X(I)*P)
301 G = G + (1.-P)**2
     A = F/G
     DO 302 I = 1, N
       P = EXPF(-C*D(I))
302 H = H + D(I)*P*(Y(I) + X(I)*(1.-2.*P) - 2.*A*(1.-P))
       DA = H/G
       F = 0.
       G = 0.
       DO 303 I = 1, N
         P = EXPF(-C*D(I))
         R = A - X(I)
         S = A - Y(I)
         F = F + D(I)*P*R*(S-R*P)
303 G = G + D(I)*P*(DA*(S+R*(1.-2.*P)) + D(I)*R*(2.*P*R-S))
       CP = C - F/G
       F = (CP - C) / C
       C = CP
       G = (A - AP) / AP
       AP = A
       IF (F - 2.E-06) 31, 31, 35
31 IF (-F - 2.E-06) 32, 32, 35
32 IF (G - 2.E-06) 33, 33, 35
33 IF (-G - 2.E-06) 38, 38, 35
35 IF (M - 15) 29, 34, 34
34 PUNCH 6, M, C, A
   IF (M - 20) 29, 37, 37
37 PUNCH 7, F, G
   GO TO 36
38 PUNCH 9, M
   PUNCH 10, C, A
36 F = .69314718 / C
   PUNCH 81, F
   F = 1. / F
   PUNCH 82, F

```

C PART B—READ PART B DATA

```

N = 1
39 READ 17, I, X(N), D(N)
   LLL = LLL + 1
   IF (I - 3 - J) 41, 91, 41
91 IF (J - 1) 92, 40, 92
92 X(N) = X(N) **.33333333
40 N = N + 1
   GO TO 39
41 IF (I - 6) 75, 43, 75

```

```

43  N = N - 1
    PUNCH 11,N
C    CALCULATE B
    F = 0.
    G = 0.
    DO 44 I = 1, N
    P = EXPF(-C*D(I))
    F = F + (A-X(I))*P
44  G = G + P**2
    B = F/(A*G)
    PUNCH 12, B
C    PART C
    PUNCH 13
    IF(J-1)61,60,61
60  PUNCH 14
    GO TO 62
61  PUNCH 20
62  P = .1/C
    I = .43429448*LOGF(P) - 1.0000005
    N = P * .1**I
    P = N
    P = P * 10.**I
    R = 0.
45  T = R*P
    S = A*(1. - B*EXPF(-C*T))
    IF(J-1)63,64,63
63  S = S**3
64  PUNCH 15,T,S
    IF(R-5.)46,47,47
46  R = R + .5
    GO TO 45
47  IF(R-14.)48,49,49
48  R = R + 1.
    GO TO 45
49  IF(R-30.)50,51,51
50  R = R + 2.
    GO TO 45
51  IF(R-70.)52,53,53
52  R = R + 5.
    GO TO 45
53  IF(J-1)54,55,54
54  A = A**3
55  PUNCH 83, A
    F = -LOGF(B)/.69314718
    PUNCH 84, F
100 STOP
    END

```

SUMMARY

The physiological background and the algebraic properties of the von Bertalanffy growth curve are discussed. One result of the properties is that this curve is very convenient to fit to recapture type data. An-

other is a possible solution to the traditional problem of the "physiological age" of an animal. A computer program is presented and explained which makes completely automatic the fitting of this growth curve to any recapture data or to data giving sizes at known ages.

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