Complementary Gompertz Survival Models: Decreasing Alive Versus Increasing Dead

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The survival patterns of many animals can be classified into one of two asymmetric sigmoid forms: One group can be predicted from the standard, classical Gompertz assumption that, with age, the number of individuals alive in the population decreases exponentially at an exponentially increasing rate. The other can be predicted from the alternative Gompertz assumption that, with age, the number of individuals that have died increases exponentially at an exponentially decreasing rate. The two models have similar mathematical forms, but the curves are not the same. In contrast to the standard, the alternative form has an early rapid fall and terminates in a gradual decay of the number of live individuals. It fits “non-Gompertzian” survival plots that are not predicted by the number-alive assumption. Analyses of published data show one or the other survival mode in various animal populations, depending on sex, genetic strain, nutrition, or activity.

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THANKS to the variety of deleterious genetic programs, random environmental insults, and variously hazardous lifestyles, individual humans and other animals die at different ages. According to the standard (classical) Gompertz model of human survivorship, the number of individuals alive in a population decreases exponentially with age at an exponentially increasing rate (1). The model fails for the very young, whose mortality is greater than, and for the very old, whose mortality is less than that predicted by the standard model. The model performs as poorly for many other animals.

For example, an especially prominent “non-Gompertzian” tail has been described in the survival function of Mediterranean fruit flies (medflies, Ceratitis capitata) (2). Easton (3) demonstrated, however, that the older members of the medfly population and of populations of some other animals (4) die off at the same changing rate as the other members of the population, if an alternative Gompertz assumption is used. That assumption is that the number of dead individuals increases at a decelerated exponential rate.

No theoretical, biologic, or mathematical imperative, but only the inertia of convention, appears to require application of the standard Gompertz model to non-Gompertzian survivorship curves. Expanding on earlier observations (3,4), I here call attention to the occurrence of the two survival patterns among different animal species in a variety of circumstances.

DERIVATION OF THE STANDARD AND THE ALTERNATIVE GOMPERTZ SURVIVORSHIP EQUATIONS

Conventionally, the survival curve of a population is plotted in terms of the relative number of individuals remaining alive as a function of age. That convention will be retained here; that is, the number alive, \( n = N_0 - N \), where \( N_0 \) is the total population and \( N \) is the number dead. In the standard model, the rate constant, \( r \), for rate of proportional decrease in number of live individuals, is commonly called the “mortality rate” and is an exponentially rising function. In the alternative model, the rate constant, \( R \), for the rate of proportional increase in number of dead individuals, is an exponentially falling function. For \( R \), I appropriate the designation “death rate,” a term sometimes used synonymously with mortality rate. Mortality rate and the (here defined) death rate vary with age, but each is a particular value (a rate constant) at a particular age. That is the usual usage and is followed here. The derivations show the relation of the standard and the alternative survival models:

### Standard Gompertz Survival Model (symbols lower case)

Number alive, \( n \), decreases exponentially at an exponentially increasing rate, \( r \), with respect to age \( x \):

\[
\frac{dn}{dx} = r \cdot n \quad \text{where} \quad r = r_o \cdot e^{k \cdot x} \quad (1A, B)
\]

where \( k \) is the rate at which the mortality rate, \( r \), increases with respect to age.

Substitute equation (1B) into equation (1A) and integrate between \( n_0 \), \( x = 0 \) and \( n \), \( x \) to obtain:

\[
n = n_o \cdot e^{b(1-e^{k \cdot x})} \quad (2)
\]

where \( n_o \) is the initial number of survivors at point \( x = 0 \).

Function \( r(x) \) is the theoretical mortality rate. Observed mortality rate is calculated from the equation:

\[
r(data) = -2 \left( \frac{n_j - n_{(j-1)}}{n_j + n_{(j-1)}} \right) \quad (2A)
\]

where \( n \) is tabulated number of survivors at point \( j \).
Alternative Gompertz Survival Model (symbols upper case)

Number dead, \( N \), increases exponentially at an exponentially decreasing rate, \( R \), with respect to age \( x \):

\[
\frac{dN}{dx} = R \cdot N \quad \text{where} \quad R = R_0 \cdot e^{-Kx} \quad (3A, B)
\]

where \( K \) is the rate at which the death rate, \( R \), decreases with respect to age.

Substitute equation (3B) into equation (3A), integrate between \( N \), \( x \) and \( N_{\infty} \), \( x \to \infty \) to obtain:

\[
N = N_0 \cdot e^{-B \exp(-Kx)} \quad (4)
\]

To express equation (4) in terms of \( n \), the number remaining alive, note that:

\[
n = N - N \quad (5)
\]

\( N_{\infty} \), the total number that die, is the same as \( n_0 \), the total initial live population.

Equation (5) (with equation 4), predicting survivorship in terms of number dead rather than number of living individuals, defines the alternative Gompertz survival model.

The observed death rate is calculated from the equation:

\[
R(\text{data}) = 2 \cdot \frac{(N_j - N_{(j-1)})}{(N_j + N_{(j-1)})} \quad (5A)
\]

Logistic Survival

The Gompertz will be compared with the logistic model, which is based on the differential equation:

\[
\frac{dN}{dx} = K \cdot N \cdot (Nm - N) \quad (6)
\]

One solution of equation (6) is an ascending sigmoid curve, which can serve to describe the increase in number dead, \( N \):

\[
N = \frac{Nm}{1 + A \cdot \exp(-Nm \cdot K \cdot x)} \quad \text{Thus,} \quad S = Nm - N \quad (7A, B)
\]

where \( Nm \) is the total population of dead (or initially alive) individuals, \( K_L \) and \( A \) are constants, and \( S \) the number of survivors. Note that this curve is symmetric, the inflection being at the halfway point, in contrast to the Gompertz models, which are asymmetric, like most survival plots.

METHODS

All the figures are based on other authors’ data, selected from the literature. Where appropriate (Figures 1, 2, and 4), high-precision fitting of the equation to the data was accomplished with the Micromath nonlinear least squares minimization software “Scientist” (Micromath). In the majority of instances (Figures 4–8), the fit was carried out by manual adjustment, to find the pairs of rate constants, \( K, B \) or \( k, b \), that establish the specific slope and horizontal displacement of the curve. A few successive approximations were sufficient to produce a fit that was visually indistinguishable from the machine-assisted result. Data available as a list of numbers (usually number alive vs age) were imported and displayed as a graph in Mathcad 11 (Mathsoft). On such a graph, a line, “best fit” by eye, was then superimposed. The line was calculated from the appropriate equation, with values of parameters adjusted manually. To generate the fit directly from a plotted figure, the graph was scanned into Paint (Microsoft), and a Mathcad graph was set at the same scale and size. The parameter values were then successively adjusted until the resulting line graph, copied and pasted onto the Paint image, showed good visual agreement with the latter. For demonstration of the obvious qualitative differences between the two types of survival curves, machine fitting was not deemed essential.
Examples from a variety of sources are presented, each survival plot fit by the appropriate equation (standard equation 2 or alternative equation 5). Survival curves of the housefly (Musca domestica; figure 1 of Rockstein & Lieberman (5)) illustrate the characteristic differences in form between the standard and the alternative Gompertz models (Figure 1). The females survive in the standard manner (Figure 1A): A gradual fall in numbers alive is terminated by a rapid decline. The males conform to the alternative form: An abrupt fall precedes a slower termination (Figure 1B). In the insets of Figure 1A and B, I have superimposed lines to show how unsatisfactory the best-fitting inappropriate model would be as a predictor of the survival data. The differences in form are diagnostic for each equation, and any particular survival plot can usually be immediately assigned to one or the other category by visual inspection.

**RESULTS**

The survival rates predicted from the models and calculated from the data of Figure 1 are presented in Figure 2. In Figure 2A, the thick line is the predicted mortality rate, \( r(\text{pred}) \), and the solid dots are the calculated mortality rates, \( r(\text{data}) \), for the female flies. The circles and the dashed line show the calculated and predicted death rates for the same population, respectively. Figure 2B shows corresponding results for the male flies. In this instance, solid dots and thick line are the calculated and predicted death rates, respectively; the circles and the dashed line are the mortality rates. The standard mortality rate appears to be appropriate for the younger population and the alternative death rate for the older population. This behavior is consistent with the observation that human survival follows the standard model to about age 85, but the elders follow the alternative model (6).

**Figure 2.** Standard and alternative Gompertz rate comparisons. (A) Rates from Figure 1A: female survival. Dots: standard mortality rate, \( r(\text{data}) \), calculated from data of Figure 1A (see equation 2A). Thick line: \( r(\text{predicted}) \), from fit of equation (2) to data of Figure 1A. Circles: death rate, \( R(\text{data}) \) calculated from data of Figure 1B (see equation 5A). Dashed line: \( R(\text{predicted}) \) (equation 2B) from fit of equation (5) to data of Figure 1A. (B) Rates from Figure 1B: male survival. Dots, heavy line: \( r \) calculated and predicted. Circles, dashed line: \( r \) calculated and predicted.

**Figure 3.** Logistic survival. (A) Points: same as in Figure 1A. Line: best fit of equation (7). \( N_m = 995 \), \( K_L = 0.000146 \), \( A = 80 \). (B) Points: same as Figure 1B. Line: best fit of equation (7). \( N_m = 1005 \), \( K_L = 0.000283 \), \( A = 132.32 \).
Logistic survival (equation 7), based on number of dead flies, is illustrated in Figure 3. The locus of the female data (Figure 3A) is more symmetrical than that of the male, and the logistic therefore fits the former better than the latter, but the Gompertz models (Figure 1) are superior to the logistic for both sexes.

Interesting data provided by Peter and Parker (7) show the effect of a genetic modification in Drosophila (Figure 4). Both male and female wild-type flies (W) conform to the standard model, but the vestigial-wing (V) flies of both sexes clearly follow the alternative scheme, like the wild-type medflies (3) or the female houseflies (Figure 1A).

Life span in animals can be increased by dietary restriction, an effect commonly attributed to calorie reduction. Recent experiments (8) show that other factors are important. For example, in Drosophila, life prolongation is more favored by decrease in amount of yeast supplied in the diet than by sugar deficiency (Figure 5). For flies on a “normal” control diet (SY), the survival curve is of the alternative form. When the diet is deficient in yeast (Sy), the fly survival curve is shifted markedly to the right (survival is improved) and is converted to the standard form.

A profound effect, attributed to a difference in energy expenditure, is illustrated in Figure 6 (9). The houseflies confined to a space that allowed walking but not flying are longer lived and survive along the standard curve (LA). Those allowed to fly (and therefore presumably expending more energy) die off more quickly, along the alternative pathway (HA).

Most animal survival studies are longitudinal; that is, in a cohort of individuals born at the same time (and reared in a common environment), the number alive is tallied at successive time (age) intervals. For humans, the data are generally “transverse” (cross-sectional); that is, the numbers of individuals at each age in a mixed population are recorded. The human survival curve is of the standard form (eg, Figure 1A). Figure 7 shows transverse data obtained from a tabulation of estimated ages of found skulls of Dall mountain sheep (Ovis d. dalli, Murie, 1944, as cited in Deevey (10)). The curve is of standard form.

For many birds, the survivorship curve appears to be the tail end of an alternative plot, consistent with the very high mortality of the young population (Paynter, in press, and Lack, 1943, both as cited in Deevey (10)). The quail (Coturnix coturnix) is an exception (11), for it follows a full alternative path (Figure 8).

**DISCUSSION AND CONCLUSIONS**

The standard (classical) and the alternative models of survival are different statements of the basic assumptions of Gompertz kinetics: The dependent variable changes exponentially at an exponentially changing rate with respect to time.

**Figure 4.** Survival curves of wild-type and vestigial-wing Drosophila melanogaster. Points are from table I of the study by Pearl and Parker (7). W: survival curve for wild-type male flies. The line is drawn from equation (2) (standard model), $k = 0.067, b = 0.029$. V: survival curve for vestigial-wing male flies. The line is drawn from equation (5) (alternative model), $K = 0.175, B = 7.4$.

**Figure 5.** Diet restriction and survival. Figure scanned from figure 2 of Mair and colleagues (8). Lines: visual fits superimposed on original points. At left, Drosophila melanogaster populations provided with a “normal” diet of sugar and yeast (SY); survival curve is alternative form ($K = 0.16, B = 20$). At right, flies on diet restricted in both sugar and yeast (sy); survival curve is standard form ($k = 0.14, b = 0.0056$). Yeast restriction (Sy), alternative survival ($k = 0.1195, B = 0.0078$); sugar restriction (sY), standard survival ($k = 0.14, b = 19.5$).

**Figure 6.** Activity and survival (Musca domestica). LA: houseflies in confined space were allowed to walk but not to fly. HA: flies in 1-ft³ box were free to fly. Curves generated in Mathcad are superimposed on scanned original figure 7 of Agarwal and Sohal (9). LA, standard model, equation (2), $k = 0.082, b = 0.007$. HA, alternative model, equation (5), $K = 0.19, B = 22$. 
the independent variable. Four combinations can be drawn from this assumption: accelerated exponential growth, decelerated exponential decay, decelerated exponential growth, and accelerated exponential decay. The last two describe, respectively, the alternative and the standard survival curves (cf. (12)). All are represented by the same differential equation and differ only in placement of signs.

For model validation, the plot of survival rate versus age is generally considered a better test than survival versus age. Figure 2 is an example of that test for the Gompertz models. The interesting result is that the standard mortality rate, $r$, appears to be a good predictor at young ages in either instance, whereas the alternative death rate is a good predictor at older ages. The failure of the standard model to account for the elder survival has been well known since the time of Gompertz (1). Easton and Hirsch (6) show that the elder population follows the number-dead model. The calculated mortality rates, $r_{\text{data}}$, behave erratically at great ages, and the death rates, $K$, are erratic at young ages (Figure 2A and B). The decreasing number of survivors, $S$, approaches zero as the population ages, and the annual decrements, $\Delta S$, in number of survivors are also small. The random errors in these small numbers lead to fluctuations in the ratio $\Delta S/S$ involved in calculation of $r_{\text{data}}$. Conversely, at the young end of the survival curve, the cumulative number dead, $D$, and the increments, $\Delta D$, are small, and thus, the calculated ratios $\Delta D/D$ are subject to high random error. At young ages for $r$ and at old ages for $K$, the relatively small error of the denominator compared with the numerator dampens the statistical fluctuation of the calculated ratios.

Survival data sets are generally asymmetrical and can be assigned to one or the other Gompertz model. The members of a small minority are symmetrical and can be predicted as a proper sum of contributions from both functions or by the logistic model. The popular logistic model (13,14) yields a symmetric $S$ curve and is therefore not suitable for asymmetric survival plots. Comparison of Figure 3 with Figure 1 shows that the logistic is less reliable than the Gompertz models in predicting the survival of the flies.

The familiar human survivorship curve (similar to Figure 1A), showing a slow decline terminating in an abrupt fall, is well tracked over most of its path by the standard model but not by the alternative. Older members of the human population survive longer than predicted by the standard model, however. Members of this “longer lived” cohort appear to die off according to the “increasing number dead” alternative model (6). Medfly survival plots, which show a large “non-Gompertzian tail,” are well represented by the alternative Gompertz model (3). What is extraordinary survival according to one model is therefore “normal” behavior in another.

An interesting question is whether any biologic meaning attaches to the observation that survival of some animals in some circumstances is best predicted in terms of the decline in number alive (standard model), whereas other animals succumb according to the increase in the number that die (alternative model). In exponential growth processes such as increase in $N$ members of a reproducing population of organisms, or of $N$ dollars in your bank account, $N$ is itself the source of more $N$, and thus, the growth of $N$ in proportion to $N$ makes intuitive sense. In those instances, a clear causal relation is apparent between $dN/dx$ and $N$. None is evident between $\Delta S$ and $S$ or between $\Delta D$ and $D$.

Reasonable hypotheses can be generated to account for differences in life span, but a biologic justification for the particular mathematical form of the appropriate predictive model for a survival curve remains elusive. A biologic
connection between the number of individuals alive or dead and a decrease or an increase in that number seems unlikely, and both Gompertz models therefore appear to be entirely empirical and without theoretical biologic foundation. For the present, the differential distribution of the standard and the alternative survival models remains an intriguing and unexplained phenomenon.

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