J. Social Biol. Struct. 1980 3, 317–329

Kinetics of metazoan mortality[†]

Angelos C. Economos

Department of Biological Sciences, School of Science,
San Jose State University, San Jose, California 95192, USA

In contrast to the well-known generalization that force of mortality and probability of death in aging populations increase exponentially with age ('Gompertz's law'), analysis of mortality kinetics data from a variety of metazoan species that have now become available indicates that Gompertz's law is only an approximation, not valid over a certain terminal part of the lifespan, during which force of mortality levels off. A previously introduced simple paradigm which describes mortality kinetics more accurately is analyzed mathematically; its applicability and usefulness for experimental gerontology are illustrated. It is shown mathematically that this paradigm is equivalent with Gompertz's law over the initial age range in which this law is generally valid.

Introduction

Over one and a half centuries ago, a British actuary, Benjamin Gompertz, hypothesized that force of mortality[‡] increased exponentially with age in human populations of his era (Gompertz, 1825). This hypothesis was subsequently accepted as a general 'law' of mortality kinetics.

However, doubts as to the general applicability of Gompertz's law have been occasionally expressed (e.g. Henderson, 1915; Beard, 1959). Though an indefinitely increasing force of mortality came to be considered synonymous to manifestation of population aging, some investigators had probably observed, for isolated species, that some populations which undoubtedly exhibited aging did not obey Gompertz's law, e.g. the house fly, *Musca domestica* (Rockstein, personal communication).

Unlike in human populations, where there is considerable childhood mortality, in laboratory animal populations there is none, because of the selection process which discards the genetically misfit individuals. The survivorship curve[§] of such populations generally has an inverted-S shape. Such data can be fitted with the so-called 'logistic curve'. This was first attempted by Perks in 1932 (quoted by Beard, 1959), and other authors have used a logistic curve for fitting particular survivorship data (e.g. Kunstyr & Leuenberger, 1975).

[†] An abstract (*Age* 1, 74, 1978), and a short report (Economos, 1979) have appeared.

[‡] Force of mortality in an aging population is defined as the ratio of the number of individuals dying in a short age interval, over the number of survivors at the beginning of that interval.

[§] A survivorship curve is obtained by plotting *vs.* age the percentage of an aging population that survives at each age.

0140–1750/80/040317 + 13 $02.00/0

Some proposed mathematical models

From the definition of force of mortality $M(t)$ (see footnote ‡, p. 317) follows

$$M(t) = -\frac{1}{s(t)}\frac{ds(t)}{dt}, \quad (1)$$

where $s(t)$ is the survivorship as a function of age t.

Gompertz postulated that

$$M(t) = M_0 e^{at}, \quad (2)$$

where M_0 is the (hypothetical) force of mortality at birth ($t = 0$) and a is a constant. From equations (1) and (2) we obtain

$$s(t) = e^{M_0 - (M_0/a)e^{at}}. \quad (3)$$

A 'power law', proposed by Rosenberg, Kemeny, Skurnick & Bandurski (1973) states that

$$M(t) = At^n, \quad (4)$$

where A, n are constants. From equations (1) and (4) follows

$$s(t) = e^{-At^{n+1}/n+1}. \quad (5)$$

The logistic equation for force of mortality has the form (Beard, 1959):

$$M(t) = \frac{Be^{bt}}{1 + De^{bt}}, \quad (6)$$

where B, D, b, are constants.

Finally, Fukuda and Yago (1976) have recently proposed the following equation for survivorship:

$$s(t) = \frac{1 + e^{-a}}{1 + e^{-(a-bt)}} \quad (7)$$

However, equation (7) is equivalent to equation (6) as can be seen by substituting $s(t)$ from equation (7) into equation (1):

$$M(t) = \frac{be^{bt}}{e^{bt} + e^{a}} \quad \text{or} \quad M(t) = \frac{be^{-a} \cdot e^{bt}}{1 + e^{-a} \cdot e^{bt}},$$

which is reduced to equation (6) by putting $be^{-a} = B$ and $e^{-a} = D$. However, equation (7) is less general than equation (6) because it imposes the additional restriction: $B/D = b$.

Various other equations have been proposed based on specific assumptions as, e.g., by Johnson & Pavelec (1972) who described survivorship by the equation

$$s(t) = 1 - (1 - e^{-kt})^p, \quad (8)$$

derived from the 'multihit theory' of radiation injury (k, p are constants).

Like the Gompertz (2) and power (4) equations, equation (8) has two parameters, one less than the logistic equation (6); the latter equation is, therefore, in general superior to two-parameter equations in fitting mortality data. Atlan, Miquel, Helmle & Dolkas (1976) concluded that the 'multihit equation' represents certain mortality data of *Drosophila melanogaster* better than either the Gompertz or the power law.

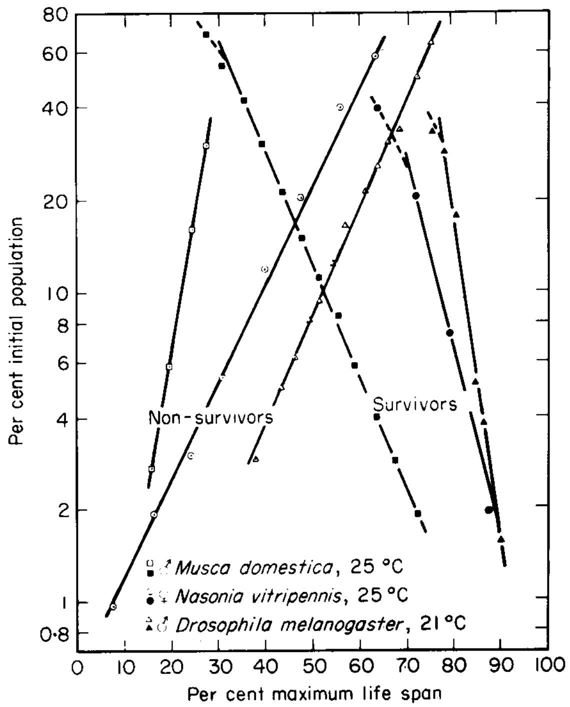

Fig. 1. Mortality kinetics of three insect species represented by pairs of straight lines on a semi-logarithmic plot, one for cumulative mortality ('non-survivors'), the other for survivorship ('survivors'). The data are from Rockstein & Lieberman (1959), Davies (1975) and Miquel, Lundgren, Bench & Atlan (1976); they were obtained from a population of 4627 Musca domestica (maximum lifespan 50 days), 975 Nasonia fed Calliphora pupae (maximum lifespan 25 days), and 590 Drosophila melanogaster (maximum lifespan 120 days)

A simple model

A survey of recent gerontological literature indicated that practically all mortality data for a great variety of metazoan species have been published in the usual form of free-drawn survivorship curves. There have been only sporadic cases of a Gompertz function fitted on the mortality data from species other than humans, but the validity of the Gompertzian model in such cases was usually assumed rather than tested.

Using the published mortality data from a variety of species, we found that the Gompertz equation generally fits mortality kinetics only in an initial part of the age range; force of mortality usually levels off over the terminal 20–70 per cent of the lifespan (Economos, 1979). We also observed that if one plotted a survivorship curve on a semilogarithmic plot, one would obtain a curve consisting of a convex part over a large part of the lifespan, and ending in an apparently straight line segment over the terminal part of the lifespan. If one did the same with the corresponding cumulative morality curve, which gives the total deaths at each age, a complementary picture would be obtained: a long straight line segment followed by a shorter convex part.

Therefore, it could be possible to represent mortality kinetics accurately with two straight lines on a semi-logarithmic plot (see Fig. 1), one, the line of non-survivors, representing cumulative mortality in an initial age interval, the other, the line of survivors, representing

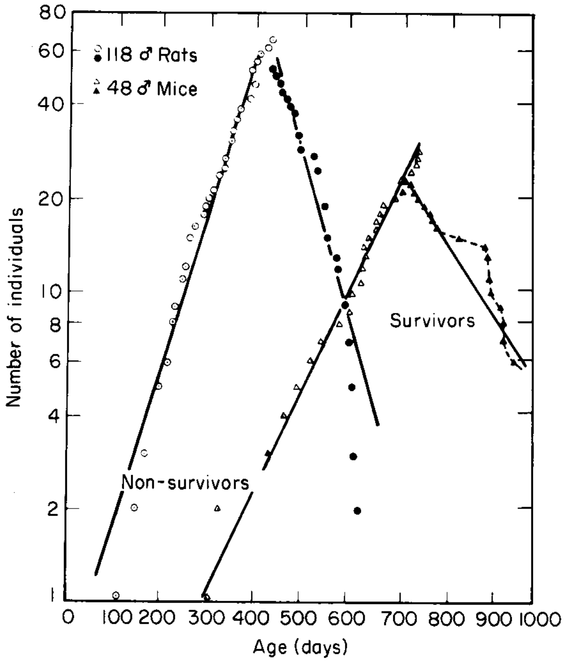

Fig. 2. Mortality kinetics in two small rodent populations; the data are from Ross, Lustbader & Brass (1976) and Economos & Miquel (unpublished). The large irregularity in the survivors line of mice in the interval 1000–1150 days may be due to an initial rise of room temperature from 23 °C to 25 °C (hot summer) and subsequent decrease to 22 °C; this small fluctuation in ambient temperature had a dramatic effect on the survivorship of the remaining very old and thus temperature 'sensitive' mice

survivorship in the terminal age interval. The point of transition from one line to the other corresponds to the inflection point on the cumulative mortality and survivorship curves plotted using linear scales; this is also their intersection point when they are plotted on the same linear plot. In large populations, like those of Fig. 1, the transition between the lines is sharp, over a small age interval; furthermore, the fit of the data with the two straight lines is remarkably accurate.† In relatively small populations, the transition between the lines is less sharp and there is a small scatter of the data around the lines (see, e.g., Fig. 2).

The straight lines of non-survivors and survivors can be constructed rigorously by least-square linear regression of the logarithms of cumulative mortality and survivorship *vs.* age, after the transition point has been determined by plotting the cumulative mortality curve and the corresponding survivorship curve on the same linear plot over a convenient middle age interval. This transition point can be also determined approximately by plotting on a semi-logarithmic plot both the initial part of the cumulative mortality curve and the terminal part of the survivorship curve; the transition age is usually relatively evident from this plot.‡

---

† The correlation coefficients from fitting the data with the two straight lines by a least-square linear regression of log per cent population *vs.* age are close to one (see also 'Addendum').

‡ Occasionally, in small populations, the data points for the first few dead individuals or the last few survivors (up to about five per cent of the population or less than 5 individuals), may be clearly off the non-survivors and survivors straight lines and could be neglected in the construction of the straight lines to avoid an apparent bias for those few data points (which gain disproportionate significance on a semi-logarithmic plot).

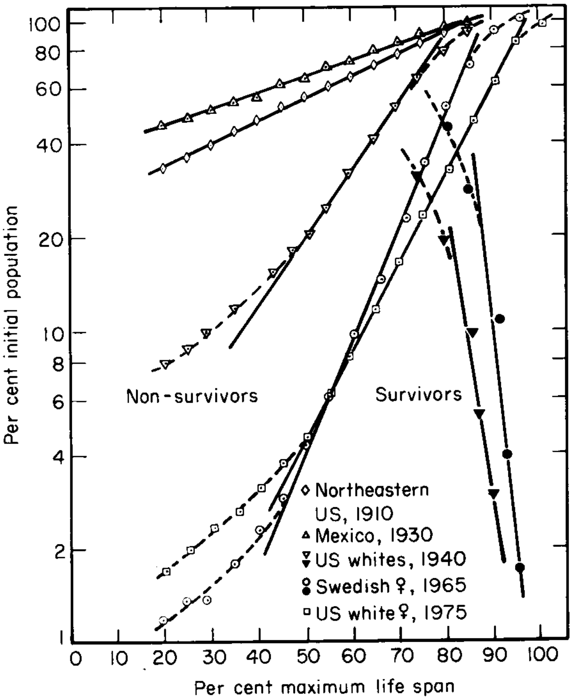

Fig. 3. Mortality kinetics of human populations. The data are from populations of 100,000 individuals, except for Northeastern U.S., 1910, for which ages at death of 1,981,892 individuals were analyzed

Fitting of mortality kinetics with this simple model was described previously for three rodent species and four invertebrate species (Economos, 1979), for one insect species (*Drosophila melanogaster*) at three different ambient temperatures, three oxygen tensions and three radiation levels (Economos & Miquel, 1977), and for mice and *Drosophila* receiving dietary antioxidants which extend natural lifespan (Economos & Miquel, 1979) or lifespan of *Drosophila* under starvation (Economos, Burns, Miquel & Fleming, 1979). The last two applications also demonstrated the usefulness of this model in experimental aging research: the effect of an environmental condition or a dietary chemical on mortality kinetics can be evaluated quantitatively using this model, because the effect is reflected in a shift and/or change of slope of the lines of survivors and non-survivors.

Mortality data for various human populations, plotted according to the new paradigm, are shown in Fig. 3. The data for Mexico, 1930 and US whites, 1940 are from Comfort (1956); the data for Northeastern US, 1910 are from Henderson (1915); the data for Swedish females, 1965 are from Kohn (1973); finally the data for US females, 1975 are from the *Vital Statistics Report* (1977). The human data show some interesting aspects. The entire mortality kinetics after about the period of lowest childhood mortality (around 15 years) for both Northeastern United States, 1910 and Mexico, 1930 can be represented by a single straight line, the line of cumulative mortality or line of 'non-survivors'. US Whites, 1940 and Swedish females, 1965 have mortality kinetics similar to other metazoan animals examined earlier, though the survivors straight lines span a relatively short period; this straight line has practically disappeared for US females, 1975.†

---

† Note the deviation of the data points up to about age 45 years for the last three populations; this lack of fit of the simple model in this age interval is shared by the Gompertzian model too.

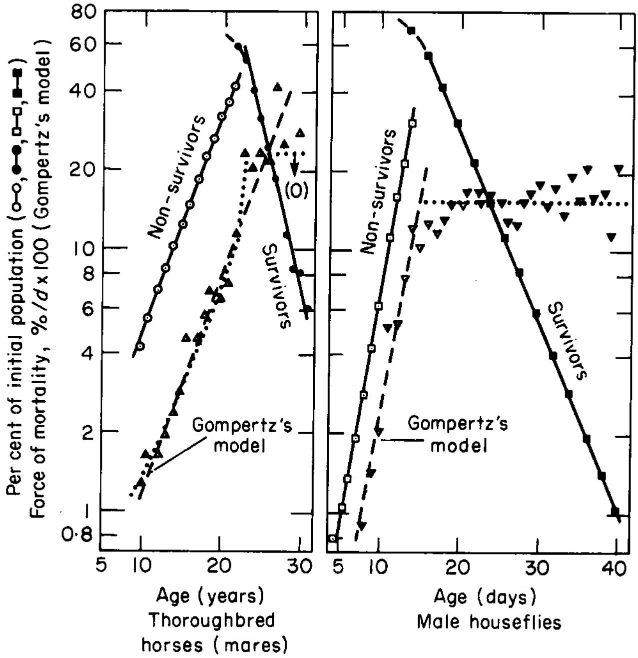

Fig. 4. Comparison of the new paradigm with Gompertz's law in populations from two species, the American male houseflies (4627) of Fig. 1 and 1492 English thoroughbred mares fouled in 1875–1880. The force of mortality data (triangles) were obtained from tables reported by Rockstein & Lieberman (1959) and Comfort (1959)

Comparison with Gompertz's law and logistic equation

In Fig. 4 we have plotted mortality kinetics of two species, thoroughbred mares and male houseflies, *Musca domestica*, at 25 °C, using both the introduced simple paradigm and according to Gompertz's model. These two species represent two opposite extremes for our purposes: thoroughbred mares have a survivors line that spans a short age interval, while the survivors line of houseflies spans a large age interval. The following points emerge from this comparison.

1. The proposed new paradigm fits mortality kinetics of both species accurately (the data points fall almost exactly on the regression lines).

2. The Gompertz model fits only part of the mortality kinetics. Interestingly, the fit 'breaks' at the age at which our survivors straight line starts. This is clear in houseflies where there are many data points in the survivors part of the lifespan. Because the remaining population is small in this period, there is considerable variation around an average force of mortality which tends to a (constant) steady state value.† Further, because we deal with a continuous phenomenon, the transition from the non-survivors to the survivors straight line is not abrupt and discontinuous, and this is reflected in the transition from exponentially

---

† The apparent larger variability in the data for force of mortality compared with the data for survivorship in this age interval can be explained by taking into account that the scale for force of mortality is multiplied by 100. Thus, e.g., two units on the scale correspond to two per cent or about 100 houseflies for survivorship (in a total population of about 5000), while they correspond to 0.02 per cent or only one fly for force of mortality.

increasing to constant force of mortality. In the thoroughbred mares, there are only a few data points in the survivors age range, and the large variability in the force of mortality in this interval does not allow an unequivocal conclusion as to whether the Gompertzian line fits the data over the entire lifespan or the fit 'breaks' at the age of transition from the non-survivors to the survivors line. However, because the actual values of force of mortality in this interval are consecutively 23.28, 20.54, 23.42, 22.22, 40, 0, 25.00 and 28.57, it appears again that force of mortality tends to level off in the terminal part of the lifespan. The survivors line fits the data well in this age interval.

3. A Gompertz straight line can be fitted to the force of mortality data in the first period of the lifespan, i.e. up to the point where our non-survivors straight line terminates. Interestingly, the so obtained Gompertz straight line is parallel to the non-survivors straight line (see Appendix).

4. A mathematical expression for the survivors straight line is:

$$s(t) = s_p \cdot \exp\,[-a'(t-t_p)], \tag{9}$$

where exp stands for exponential function, s_p and t_p are the survivorship and age at the starting point of the survivors straight line, and a' is the slope of this line. From the equation of definition of force of mortality $M(t)$ (equation (1) above) we obtain by substitution of $s(t)$ with the expression given by equation (9):

$$M(t) = a', \tag{10}$$

i.e. force of mortality is constant in this age interval. Because the performed mathematical operations are reversible, the opposite is also true, i.e. a constant force of mortality implies an exponentially decreasing survivorship. This is in agreement with point 2 above.

5. From the logistic equation for force of mortality,

$$M(t) = \frac{Be^{bt}}{1+De^{bt}} \text{ or } M(t) = \frac{B}{D+e^{-bt}} \tag{11}$$

follows that for large t, such that $e^{bt} \gg 1/D$,

$$M(t) \simeq \frac{B}{D},$$

i.e. force of mortality tends to a constant steady state. Therefore, the survivors straight line in the terminal age interval is an approximation of the logistic model in this interval.

6. It can be shown that the non-survivors straight line in the initial age interval is an approximation of the logistic curve in that interval, just as it was shown to be the case for the survivors straight line in the terminal age interval. Thus, from the left of equations (11) follows that, for a small t, such that $e^{bt} \ll 1/D$,

$$M(t) = Be^{bt} \tag{12}$$

i.e. Gompertz's law. Given also that, as shown in the appendix, the non-survivors line is equivalent to Gompertz's law in the initial age interval, it follows that the non-survivors straight line is an approximation of the logistic curve in this interval.

7. A striking feature is exhibited by the mortality kinetics of four species of birds in their natural habitat (Fig. 5): the entire mortality kinetics can be represented by an exponentially decreasing survivorship curve. That the mortality kinetics of many wild species in their natural habitat has this form is well known. What is less well known is that this form of mortality kinetics is not obligatory for wild animals as is demonstrated by Fig. 6.

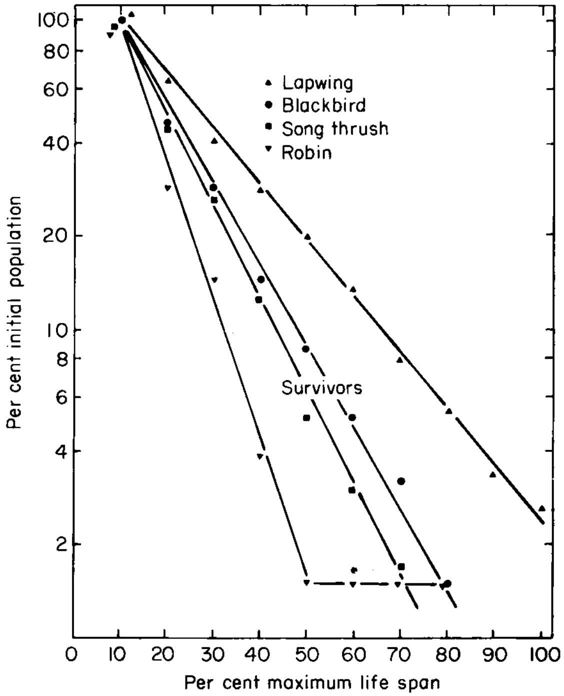

Fig. 5. Mortality kinetics of (presumably) heavily predated populations; the data are from Deevey (1947). Maximum lifespan of these bird species is 9–12 years

Frequency distribution of deaths

Plotting the derivative of cumulative mortality *vs.* age, one obtains the frequency distribution of deaths. Assuming validity of the Gompertz law over the entire lifespan, the distribution function or probability density function is, from equation (3),

$$\frac{\mathrm{d}m(t)}{\mathrm{d}t} = -\frac{\mathrm{d}s(t)}{\mathrm{d}t} = M_0 e^{M_0} \cdot e^{at-e^{at}} \tag{13}$$

This function is not related to any of the known statistical distributions, but it has been shown (Brown & Forbes, 1974) that from a normal distribution one can derive the Gompertz law by approximation. However, frequency distribution of deaths as well as of many other biological and technological characteristics does not resemble a normal curve (Economos, Miquel, Ballard & Johnson, 1980); usually, the distribution curve is asymmetric and tends more toward a lognormal, gamma or related form, as is true of probability density functions for failure of manufactured products (see, e.g., Kapur & Lamberson, 1977).

Underlying mechanisms include influence of a characteristic by several factors which act multiplicatively, or competition for a common resource between the individuals of a population. With the simple paradigm introduced here, the corresponding frequency distribution of deaths is non-Gaussian, asymmetric, resembling a negatively skewed lognormal curve. This is compatible with a theory (Economos, 1978) which expressed mammalian lifespan as the product of a number of constitutional and life cycle parameters (frequency distribution of deaths or ages at death is, of course, identical with frequency distribution of lifespans). Finally, it was shown elsewhere (Economos, 1979) that some manufactured products have failure kinetics that can be accurately represented by the model introduced here, as is for instance the case with copper fuses, relays and heat insulators.

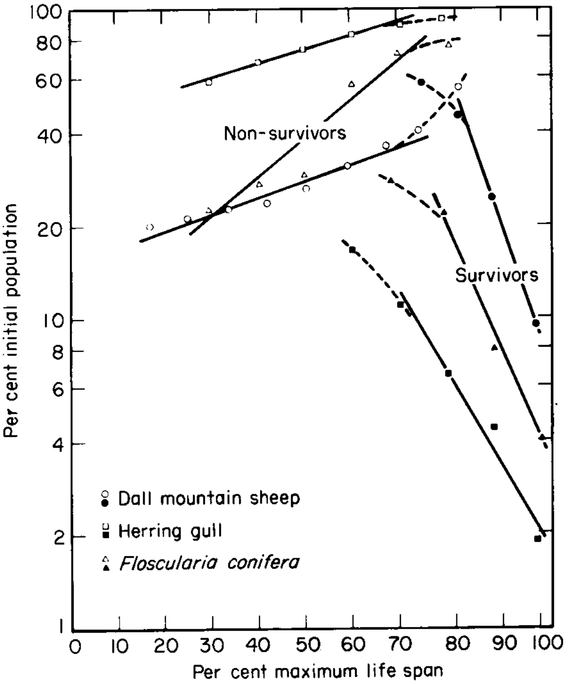

Fig. 6. Mortality kinetics of three species (presumably not-heavily predated, but with high initial mortality) in their natural habitats; the data are from Deevey (1947). Maximum lifespan of the herring gull is 10 years, of the rotifer Floscularia conifera is 10 days and of the Dall mountain sheep is 14 years

We have found only two (related) species whose frequency distribution of deaths resembles a normal probability density function; these mortality data, plotted in Fig. 7 as in previous figures, constitute an exception from the model introduced here. A pair of straight lines was obtained only in the male *Tribolium castaneum*. The survivors lines of female *Tribolium confusum* and *Tribolium castaneum* as well as both the survivors and non-survivors lines for male *Tribolium confusum* are convex. In the same figure is shown the area under the Gaussian frequency distribution curve for comparison. What causes this deviation from the straight lines is not known. Because various environmental factors and drugs or nutrients, applied on populations of animals post-natally, displace or change the slope only (not the form) of the straight line pairs, this different form of the mortality lines may be due to environmental conditions during development or a genetic idiosyncracy of these beetle species.

Concluding remarks

Gompertz was an actuary and his interest in mortality kinetics was confined to human populations, actually only the inhabitants of England at the beginning of the nineteenth century. Data on other metazoan species were not available at that time and the idea of applying the same mathematics to failure kinetics of manufactured products might have been considered unusual or maybe unacceptable by his contemporaries.

Gompertz considered his hypothesis of exponential increase of force of mortality as a fundamental law of human mortality based on the empirical agreement of the hypothesis

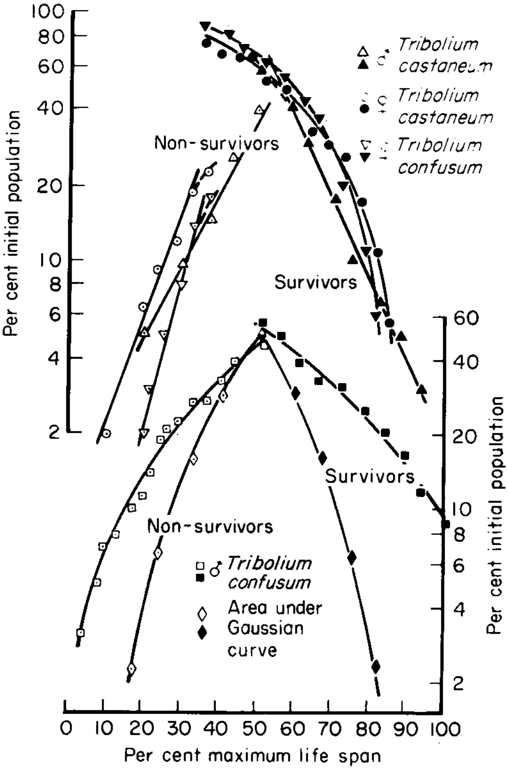

Fig. 7. Mortality kinetics of males and females of two beetle species (200–500 individuals per group, maximum lifespan 400–500 days); the data are from Ducoff (1975). The introduced paradigm fails to represent mortality kinetics in three of the four groups (curved instead of straight lines)

with the data then available (Gompertz, 1825). During the last two or three decades that experimental gerontology was largely expanded to include the study of a great variety of metazoan species, it has been assumed that the same law of mortality would apply to other metazoan species as well, so that the original hypothesis of Gompertz was now thought to apply in general to all metazoans—apparently without careful and extensive testing. In this paper we have documented the fact that the Gompertz law is not a universal law of mortality, but only an approximation.

The finding that force of mortality levels off beyond a certain age in the examined species may appear surprising because, traditionally, it was thought that in an aging population force of mortality increases exponentially until all individuals have died. However, this expectation was an assumption that would only be valid if Gompertz's model were valid over the entire lifespan. The data from many species show that this is not true, however. Instead, after a certain species-characteristic age, force of mortality and probability of death cease to increase exponentially with age and tend toward a (high) constant level for the remainder of the lifespan. This conclusion is not an assumption, it is based on experimental findings.

It should be emphasized that the often repeated statement that aging necessarily results in a continuously increasing force of mortality, would be correct if a population consisted of identical individuals, whose weighted sum of capacities of physiological functions or health state index ('vitality') in early maturity was the same. However, every population has a certain, usually non-uniform, frequency distribution of vitalities of its individuals; this distribution influences the form of the frequency distribution of deaths and consequently population mortality kinetics. If the frequency distribution of vitalities were changed, e.g. by eliminating from the population the weak, sick or unfit individuals by means of a severe but non-invasive physical examination, the mortality kinetics would be affected accordingly (Economos & Miquel, 1979). Furthermore, if the frequency distribution were such that the number of individuals with the highest vitality score decreased exponentially as a function of that score, then force of mortality in a terminal age interval would level off, although the population still ages in that interval (Economos & Miquel, 1979).[†]

A practical advantage of the described method of representation of mortality kinetics is its simplicity and ease of use; little more effort or time is required for construction of the two straight lines than for the usual graphic representation of mortality kinetics by a hand-drawn curve. Only very simple statistics (:linear regression) are needed. Yet, mortality kinetics are accurately described and in a way that the effect of an environmental factor, nutrient or drug, can be quantitated, namely, in terms of changes in the relative positions and slopes of the straight lines.

References

Atlan, H., Miquel, J., Helmle, L. C. & Dolkas, C. B. (1976). *Mech. Age. Dev.* **5**, 371.

Beard, R. E. *(1959). CIBA Found. Colloq. Age.* **5**, 302.

Brown, K. S. & Forbes, W. F. (1974). *J. Gerontol.* **29**, 46.

Comfort, A. (1956). *The Biology of Senescence*. New York: Hold, Rinehart and Winston, Inc.

Comfort, A. (1959). *CIBA Found. Colloq. Age.* **5**, 35.

Davies, I. (1975). *J. Gerontol.* **30**, 294.

Deevey, E. S., Jr. (1947). *Quart. Rev. Biol.* **22**, 283.

Ducoff, H. S. (1975). *Exp. Gerontol.* **10**, 189.

Economos, A. C. (1978). *Age* **1**, 157.

Economos, A. C. (1979). *Age* **2**, 74.

Economos, A. C. & Miquel, J. (1977). In *Proceed. 30th Ann. Confer. Engng. Med. Biol.*, pp. 448, Bethesda: Alliance for Engineering in Medicine and Biology.

Economos, A. C. & Miquel, J. (1979). *Aviat. Space Environm. Med.* **50**, 697.

Economos, A. C. & Miquel, J. (1979). *Age* **2**, 127.

Economos, A. C., Burns, M. K., Miquel, J. & Fleming, J. (1979). *Age* **2**, 135.

Economos, A. C., Miquel, J., Ballard, R. C. & Johnson, J. E., Jr. (1980). In *Aging and Cell Structure* (J. E. Johnson, Jr., Ed.). New York: Plenum Press (in press).

Fukuda, N. & Yago, N. (1976). *J. theor. Biol.* **58**, 131.

Gompertz, B. (1825). *Philos. Trans. Roy. Soc.* (*London*) ser. AA **115**, 513.

Henderson, R. (1915). *Mortality Law and Statistics*. New York: John Wiley & Sons.

Johnson, H. A. & Pavelec, M. (1972). *Am. J. Pathol.* **66**, 557.

Kapur, K. C. & Lamberson, L. R. (1977). *Reliability in Engineering Design*. New York: John Wiley & Sons.

Kohn, R. R. (1973). *Aging*. Kalamazoo, Michigan: The Upjohn Company.

Kunstyr, I. & Leuenberger, H. G. W. (1975). *J. Gerontol.* **30**, 157.

Miquel, J., Lundgren, P. R., Bensch, K. G. & Atlan, H. (1976). *Mech. Age Dev.* 5, 347.

Rockstein, M. & Lieberman, H. (1959). *Gerontology* **3**, 23.

Rosenberg, B., Kemeny, G., Smith, L. G. & Skurnick, D. (1973). *Mech. Age. Dev.* **2**, 275.

Ross, M. H., Lustbader, E. & Bras, G. (1976). *Nature* **262**, 548.

Vital Statistics Report (1977). (HRA) 77-1120, vol. **25**, No. 11, Supplement.

[†] The Gompertz law requires a faster than exponential decrease in this respect; this can be caused artificially when the old individuals are exposed to a harsh environment. This is exemplified by the Mexico data of Fig. 3; another example is animals exposed to radiation.

Appendix

Equivalence of Gompertz's law with the non-survivors straight line

A mathematical expression for the non-survivors line (see Fig. 4) is

$$m(t) = m_0 \exp(at) \tag{A1}$$

where $m(t)$ is cumulative mortality, m_0 is cumulative mortality at $t = 0$ and a is the slope of the non-survivors line on the semi-logarithmic plot. From

$$m(t) + s(t) = 1 \tag{A2}$$

follows

$$s(t) = 1 - m_0 \exp(at). \tag{A3}$$

Guided by the polynomial expansion of the exponential function

$$e^x = 1 + \frac{x}{1} + \frac{x^2}{1.2} + \frac{x^3}{1.2.3} + \ldots, \tag{A4}$$

we rewrite equation (A3) as follows:

$$\begin{aligned} s(t) + m_0 + \frac{(m_0[1-\exp(at)])^2}{1.2} + \frac{(m_0[1-\exp(at)])^3}{1.2.3} + \ldots \\ = 1 - m_0 \exp(at) + m_0 + \frac{(m_0[1-\exp(at)])^2}{1.2} + \ldots. \end{aligned} \tag{A5}$$

The right-hand side of equation (A5) can be rewritten as

$$1 + \frac{m_0[1-\exp(at)]}{1} + \frac{(m_0[1-\exp(at)])^2}{1.2} + \ldots,$$

which, according to equation (A4), is equal to

$$\exp(m_0[1-\exp(at)]). \tag{A6}$$

It can be shown that the quantity added to the left side of equation (A3), see equation (A5), i.e. the quantity

$$Q = m_0 + \frac{(m_0[1-\exp(at)])^2}{1.2} + \frac{(m_0[1-\exp(at)])^3}{1.2.3} + \ldots \tag{A7}$$

is small compared with the values of $s(t)$ in the age interval spanned by the non-survivors line. This can be seen by calculating Q in the examples of Fig. 4; m_0 has the value 0.007 for thoroughbred mares (an unusually high value) and the value 0.001 for houseflies (a value in the usual range). The value of Q is respectively (approximately) 0.08 and 0.07, calculated for the age where the non-survivors line terminates, i.e. the age at which this quantity attains its largest value. Compared with the value of survivorship at the same age, which is roughly 0.6, this error is therefore rather small, about 10–13 per cent; this error decreases rapidly toward zero age.

By ignoring quantity Q from the left side of equation (A5) and replacing the right side of the same equation by equation (A6), we obtain

$$s(t) = \exp(m_0[1-\exp(at)]), \tag{A8}$$

from which we get

$$\ln s(t) = m_0[1-\exp(at)]. \tag{A9}$$

Substituting equation (A8) in the equation of definition of force of mortality, we finally obtain

$$M(t) = m_0 a \exp(at), \tag{A10}$$

which is the Gompertz law. At the same time, from equations (A1) and (A10) follows that the Gompertz straight line is parallel to our non-survivors straight line (they have the same slope a), a conclusion justified by the data of Fig. 4 in both thoroughbred mares and male houseflies.

The above mathematical analysis has demonstrated that Gompertz's law is valid in the age interval spanned by the non-survivors straight line, i.e. in the interval where cumulative mortality is increasing exponentially with age, and that the Gompertz relation can be *derived* analytically from the mathematical expression of the non-survivors straight line. We shall show that the opposite is also true, i.e. in the age interval where Gompertz's law is valid, the non-survivors line is by necessity a straight line, that is, cumulative mortality increases exponentially with age. The proof is straightforward; it actually consists of going through equations (A3)–(A10) backwards, starting from equation (A10), i.e. the Gompertz relation

$$M(t) = m_0 a \exp(at),$$

or equivalently, using the equation of definition of $M(t)$,

$$-\frac{1}{s(t)} \cdot \frac{\mathrm{d}s(t)}{\mathrm{d}t} = m_0 a \exp(at),$$

which can be rewritten as

$$\frac{\mathrm{d}s(t)}{s(t)} = -m_0 a \exp(at)\,\mathrm{d}t. \tag{A11}$$

Integration of equation (A11) between $t = 0$ and t gives

$$\ln s(t) = m_0[1 - \exp(at)],$$

which is identical to equation (A9). From this, equation (A8) follows directly, from which by expansion in series and approximation as with the proof of the direct statement above (equations (A4)–(A6)), equation (A3) is obtained as an expression of survivorship, wherefrom follows the expression of cumulative mortality as an exponential function of age.

Addendum

An abstract has appeared recently (Richie, J. P. & Lang, C. A. (1980). *Fed. Proc.* 39, 604) in which the present model was validated using data from mosquito populations cultured under standard laboratory conditions. For their analysis, the authors made the assumption that the transition from the line of non-survivors to the line of survivors takes place at about the age of median survival (50 per cent mortality). However, this may be approximately true of insects (e.g. see the data of Fig. 1) and mosquitoes in particular, but is not true in general (e.g. mouse data in Fig. 2 and human data, Fig. 3); rather, the transition age should be determined for each studied population, for instance (as mentioned in the text) by determining the crossing point of the survivorship and cumulative mortality curves plotted on the same plot using linear scales. The authors of the abstract stated that the present model '... consistently yielded closer fits with the data with coefficients of determination (r^2) ranging from 0.9–1.0, while the Gompertz method gave lower values ranging from 0.5–0.95'. They concluded that the model '... is a valid, rigorous and simple method for the study of lifespan profiles'.