Phenomenological theory of mortality evolution: Its singularies, universality, and superuniversality

(mortality curves/universality/evolution)

MARK YA. AZBEL'†

School of Physics and Astronomy, Tel Aviv University, Tel Aviv 69978, Israel

Communicated by Yakir Aharonov, University of South Carolina, Columbia, SC, December 28, 1998 (received for review May 12, 1998)

ABSTRACT The probability to survive to the age x universally increases with the mean lifespan $\bar{x}$. For species as remote as humans and flies, for a given x the rate of its evolution with $\bar{x}$ is constant, except for the narrow vicinity of a certain $\bar{x} = x^*$ (which equals 75 years for humans and 32 days for flies and which is independent of age, population, and living conditions). At $\bar{x} \cong x^*$ the evolution rate jumps to a different value. Its next jump is predicted at $\bar{x} \cong 87$ years for humans and $\cong 59$ days for flies. Such singularies are well known in physics and mathematics as phase transitions. In the considered case different population "phases" have significantly different survival evolution rates. The evolution is rapid—life expectancy may double within a lifespan of a single generation. Survival probability depends on age x and mean longevity $\bar{x}$ only (for instance, survival curves of 1896 Swedes and 1947 Japanese with approximately equal $\bar{x}$ are very close, although they are related to different races in different countries at different periods in their different history.) With no adjustable parameters, its presented universal law quantitatively agrees with all lifetable data. According to this law, the impact of all factors but age reduces to the mean lifespan only. In advanced and old age, this law is superuniversal—it is approximately the same for species as remote as humans and flies. It yields survival probability that linearly depends on the mean lifespan $\bar{x}$. As a result, when human $\bar{x}$ almost doubles (from 35.5 to 69.3 years), life expectancy at 70 years increases from 8 to 9.5 years only. Other implications of the universal law are also considered.

1. Survival Evolution: Its Universality and Rate

Arguably, mortality is the most universal and, at least for humans, the best quantified phenomenon in biology. The human mortality rate in developed countries is well documented for the last two centuries—see, for example, 494 lifetables (yearly for adults and daily, weekly, and monthly for children) for Sweden (1, 2), Germany (3), and Japan (4). In 1825 Gompertz presented a formula (5) for mortality increase between the ages of 20 and 60 years. Later he argued (6) that there may be four different laws of mortality (for 0–1, 1–20, 20–60, and 60–100 years). Consequently, the Gompertz law was refined to be applicable to the older ages (7–9); Strehler and Mildvan (10) stated that there exists a species-specific lifespan limit (see also refs. 11–13 and reviews in refs. 14–17). Pearl (18) suggested the unitarity of the Gompertz law for different species. However, large fly populations (19–22) demonstrated mortality levelling off and decreasing at older ages, in sharp contrast to the (refined) Gompertz law and to the limited lifespan paradigm. Mortality decrease was related to genetic heterogeneity (19–27). Living conditions affect the

mortality laws and their age intervals. During this century human survival curves (1–4) have approached a rectangular shape, and the long quasi-plateau from 20 to 40+ years practically disappeared in the mortality curves. Also, relative mortality increase slowed down in old age (11–13, 28–33), and the probability to survive to 85 years has increased 15-fold (1–4). The changes are country-, time-, and age-specific. This should be anticipated. In a given country in a given calendar year, the probability to die at, for example, 50 years, depends on social, medical, historical, and a variety of other factors, which affected the health and fitness during the previous 50 years. Yet, I prove that the impact of all of these factors on mortality reduces to the mean life expectancy at birth $\bar{x}$ only. Indeed, consider the probability‡ $\ell_x(\bar{x})$ to survive to a given age x as a function of the mean life expectancy at birth $\bar{x}$ for 1891–1995 Swedish (1, 2), 1871–1994 German (2), and 1981–1990 Japanese (4) male and female lifetables. Independent of calendar year, country, race, and sex, all data (for any given x) follow the same dependence on $\bar{x}$. (Fig. 1*A* demonstrates it for $x = 30$, 60, and 90 years.) The choice of $\bar{x}$ as a variable allows for the study of the $\ell_x(\bar{x})$ universality for any animal species. Fly lifetables (19–22) present the largest nonhuman populations under different conditions. Fly mean lifespan changes with conditions and genotypes almost threefold in the cohorts of different families of medflies (19, 21) (598,118 males and 605,529 females in overcrowded cages; 11,373 males and 12,590 females in individual cells) and fruitflies [three inbred and three F_1 lines in 3 blocks, each with over 550 males (20) in 4-dram shell vials with weekly transfer to fresh medium; 121,894 genetically heterogeneous males (22) in cages]. For a given age, all of these populations follow the same $\ell_x(\bar{x})$ dependence on the mean lifespan $\bar{x}$ at any age x. (Fig. 1*A* demonstrates it for $x = 20$ and 40 days.)

Fig. 1*A* presents the universal evolution of the survival probability with $\bar{x}$. The rate of this evolution $\ell_x(\bar{x})/d\bar{x}$ is the slope in Fig. 1*A*. It is constant for a given age x until a narrow vicinity of a certain $\bar{x} = x^*$. There it jumps to a significantly different constant value. The survival evolution rate decreases before 68 years for humans (e.g., 5.4-fold for $x = 30$ years in Fig. 1*A*) and before 39 days for flies; it increases thereafter (e.g., 15-fold for 90-year-old humans). The change may be nonmonotonic and accompanied by a jump in the survival probability (see, for example, $x = 40$ days for flies in Fig. 1*A*). The crossover lifespan x^* (75 years for humans and 32 days for flies) is universal and independent of age, population, and living conditions. The better the statistics (e.g., humans vs. flies) and the more homogeneous the population (e.g., Swedish females vs. all humans) are, the narrower the crossover and

---

†e-mail: Azbel@TAUNIVM.TAU.AC.IL
‡Human lifetables (2–4) present the mathematical expectation ℓ_x to survive to a given age x (with yearly age intervals) for "all cause" mortality for a given calendar year. The mortality rate $q_x = -d\ell n\ell_x/dx$ is calculated as $q_x = \ell n(\ell_x/\ell_{x+1})$. The mean life expectancy at birth $\bar{x} = -\int x d\ell_x = \int \ell_x dx$ is calculated as $\bar{x} = 0.5 + \sum_{x=1} \ell_x$. Fly lifetables list the daily number of survivors N_x (to the age x) in a cohort, $\ell_x = N_x/N_0$.
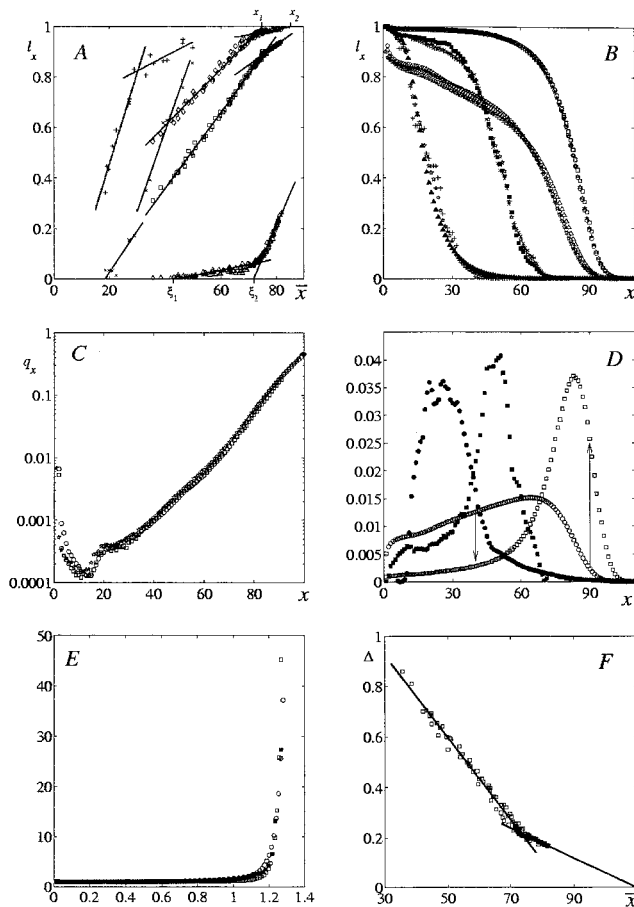
FIG. 1. (*A*) Evolution of the survival probability $\ell_x(\bar{x})$ with the mean lifespan $\bar{x}$. The age $x = 30$ ($\diamond$), 60 ($\square$), and 90 ($\triangle$) for 1890–1995 Swedish, 1871–1994 German, and 1981–1990 Japanese males and females; $x = 20$ (+) and 40 (x) for heterogeneous male, female, and combined medflies in cages and cells, and genetically heterogeneous and homogeneous fruitflies; top level ages x_1 and x_2 are denoted for human $x = 30$; bottom level ages ξ_1 and ξ_2 are denoted for human $x = 90$. In all figures x and $\bar{x}$ are in years for humans and in days for flies. Straight lines are linear interpolations, whose mean square deviation from experimental data is less than 0.01. (*B*) Survival curves $\ell_x(\bar{x})$ vs. age x for 1896 Swedish (1) ($\triangle$, the mean lifespan $\bar{x} = 53.65$) and 1947 Japanese (4) ($\diamond, \bar{x} = 53.96$); 1980 Japanese (4) ($\circ, \bar{x} = 78.77$) and 1994 German (3) ($\square, \bar{x} = 78.96$) females; genetically heterogeneous female medflies ($\blacktriangle$) in overcrowded cages (24, 26) (with the mean lifespan $\bar{x} = 18.6$) and genetically homogeneous male fruitflies (+) in vials (25) (with $\bar{x} = 19.1$); different crosses of male fruitflies (25) with $\bar{x} = 46.3$ ($\blacksquare$) and $\bar{x} = 46.5$ (x); and $\ell_x(\bar{x})$ according to the universal law (with no adjustable parameters, $\star$). (*C*) Mortality rates q_x for 1980 Japanese (4) ($\circ$) and 1994 German (3) ($\square$) females from Fig. 1*B* on a semi-logarithmic scale, which is conventional in demographic studies. Note the mortality minimum, the Gompertz linear region; the slowing down of the mortality rate increases in very old age, and the agreement between experimental and universal data ($\star$) over four orders of q_x magnitude. (*D*) Survival evolution rates a_1 ($\circ$, human; $\bullet$ fly) and a_2 ($\square$, human; $\blacksquare$, fly) vs. age x. The rates are in year^{-1} for humans, in day^{-1} for flies. Downward and upward arrows correspondingly demonstrate the decrease ($x = 40$) and increase ($x = 90$ years) in human evolution rate at $\bar{x} \cong x^*$ in Fig. 1*A*. (*E*) Human–fly universality: $x_1/75$ vs. $x/75$ ($\circ$), $x_2/82$ vs. $x/82$ ($\square$) for humans, $x_1/37$ vs. $x/37$ ($\bullet$), $x_2/56$ vs. $x/56$ ($\blacksquare$) for flies; x_1 and x_2 are (top) level ages. (*F*) Species-specific decrease in the $\bar{x}$ relative mean fluctuation with the mean longevity $\bar{x}$ for male and female 1891–1995 Swedes, 1891–1990 Japanese, and 1781–1992 Germans. Straight lines are linear interpolations.

the more pronounced its singularities are. In physics and mathematics, singularities of static and dynamic characteristics are known as critical phenomena, and phase transitions and are extensively studied. Fig. 1*A* demonstrates an "evolution

phase transition" between population "phases" (with different values of survival evolution rate) at the universal "critical" mean lifespan x^*. (Of course, the elucidation of their biological meaning is beyond the scope of phenomenological theory.) The $\ell_x(\bar{x})$ linear dependence on the mean value $\bar{x}$ is unusual for stochastic phenomena [and is presumably related to strong long-range correlation (28, 34–37) between mortality rates at different ages and of different generations of ancestors and their descendants]. It yields, in particular, a weak dependence of the life expectancy in old age on $\bar{x}$: e.g., at $x = 70$ years it was 8 years for 1800 Swedish (1) (with $\bar{x} = 35.5$) and 9.5 for 1970 Japanese (4) (with almost twice larger $\bar{x} = 69.3$ years, in both cases $\bar{x} < x^*$) males. In the last section, I demonstrate that the universal evolution law predicts the next "evolution phase transition" at human $\bar{x} \cong 87$ years and fly $\bar{x} \cong 59$ days.

Survival evolution is very rapid—Japanese and German $\bar{x}$ more than doubles (3, 4) in 70 years, i.e., within the mean lifespan of a single generation. According to Fig. 1*A*, the age x and the mean lifespan $\bar{x}$ uniquely determine the human and fly $\ell_x(\bar{x})$, which is approximated in the next section. So, the populations with the same $\bar{x}$ should yield identical survival and mortality curves, and the approximation allows one to calculate these curves with no adjustable parameters and provides their change with population and living conditions. This is demonstrated in Fig. 1*B* with the survival curves of 1896 Swedish ($\bar{x} = 53.65$ years) and 1947 Japanese ($\bar{x} = 53.96$ years) females (different races in different countries, at half a century different periods of their different history); of 1994 German (2) ($\bar{x} = 78.7$ years) and 1980 Japanese (4) ($\bar{x} = 78.8$ years) females; of different families of genetically heterogeneous female medflies (19, 21) and inbred (20) (3 × 3, block 2) male fruitflies under different conditions (cages and vials), with $\bar{x} = 18.6$ and 19.1 days correspondingly; of different crosses (20) (3 × 2 and 2 × 1, block 1 in both cases) of male fruitflies with $\bar{x} = 46.3$ and 46.5 days; and of their calculations according to the universal law. Fig. 1*C* demonstrates the agreement of experimental and universal human mortality rate q_x over four orders of its magnitude; the deviation determines the upper limit for the premature mortality, which is surprisingly low.

In the next section, I establish the universal $\ell_x(\bar{x})$ law. In the last section, I study its implications.

2. Universal Laws of Survival Evolution

The linear approximations $\ell_x^*(\bar{x})$ of the $\ell_x(\bar{x})$ dependence on the $\bar{x}$ for all human and fly lifetables yield

$$\ell_x^*(\bar{x}) = 1 - a_1(x_1 - \bar{x}) \text{ if } \bar{x} \leq x_1^*;$$
$$\ell_x^*(\bar{x}) = 1 - a_2(x_2 - \bar{x}_2) \text{ if } \bar{x} \geq x_2^*. \qquad [1]$$

Here $a_1(x), a_2(x)$ are the approximation slopes and $x_1(x), x_2(x)$ are their "top" level ages: $\ell_x^*(x_1) = \ell_x^*(x_2) = 1$ (see Fig. 1*A*); for humans $x_1^* = x_2^* = 75$; for flies $x_1^* = 29$, $x_2^* = 35$; the crossover $x^* = (x_1^* + x_2^*)/2$. Eq. **1** analytically describes the evolution of survival probability $\ell_x^*(\bar{x})$ with $\bar{x}$. For a given age x, the survival evolution rate $d\ell_x^*(\bar{x})/dx$, by Eq. **1** and consistent with Fig. 1*A*, is constant at $\bar{x} \leq x_1^*$ and equals a_1. At $\bar{x} \cong x^*$ the rate jumps from a_1 to a different constant a_2. Since‡ $\ell_o(\bar{x}) = 1$ and $\ell_\infty(\bar{x}) = 0$ (nobody lives forever), so, by Eq. **1**, $a_1(0) = a_2(0) = 0$ and $a_1(\infty) = a_2(\infty) = 0$. Thus, the evolution rate must be zero for newborns, must reach maximum at a certain age, and then decrease to zero. This is verified with Fig. 1*D*, which presents $a_1(x)$ and $a_2(x)$ dependencies on x. For humans, for example, the evolutionary rate $a_1(x)$ is maximal at $x \cong 62$ years, whereas the rate $a_2(x)$ is maximal at $x \cong 83$ years. To compare human and fly mortality, introduce dimensionless variables. Consider, for example, dimensionless level age x_1/x^* vs. age x/x^* for humans with $\bar{x} < x^*$; in all other cases chose the variables that provide maximal proximity of human and fly

plots. Then Fig. 1*E* exhibits human–fly superuniversality. Similar superuniversality in advanced and old age ($x > 25$ years for humans, $x > 15$ days for flies) is exhibited by the dimensionless "bottom" level ages $\xi_1(x)$, $\xi_2(x)$, where $\ell_x^*(\xi_1) = \ell_x^*(\xi_2) = 0$. The tables of $a_1(x)$, $a_2(x)$, which are plotted in Fig. 1*D*, and of $x_1(x)$, $x_2(x)$ in Fig. 1*E* allow one, by Eq. **1**, to calculate complete survival $\ell_x(\bar{x})$ and mortality $q_x(\bar{x}) = \ell n[\ell_x(\bar{x})/\ell_{x+1}(\bar{x})]$ curves, given the values of x and $\bar{x}$ only. The calculations agree with experimental data with no adjustable parameters (see Fig. 1 *B* and *C*). Thus, these (superuniversal in advanced and old age) lifetables may quantitatively replace all hundreds of human and fly lifetables.

3. Universal Law: Implications and Prediction

Universal law (**1**) of mortality evolution is based on the available data and statistics. Human statistics are rather reliable, except for early ages in developed countries with very low mortality (e.g., 50,208 girls were born and 6 died in their 9th year in 1995 Sweden; ref. 2) and for old ages in the vicinity of and beyond 100 years. Flies allow for genetically homogeneous populations (20), but the latter exceeded a thousand in one case only. Only two (med- and fruitfly) different families were studied. Clearly, comprehensive verification of the implications and predictions of the universal law is important, whereas for young and old ages it may be crucial.

(*i*) The universality of $\ell_x(\bar{x})$ implies another law of mortality evolution—the universal dependence of the $\bar{x}$ mean square fluctuation Δ_2 on $\bar{x}$. Fig. 1*F* demonstrates the universal decrease of the relative fluctuation $\Delta = \Delta_2/\bar{x}$ with $\bar{x}$ for humans (with good statistics). The decrease is linear everywhere, except for the narrow vicinity of the same critical age as in Eq. **1**. With the mean accuracy of 0.02, Δ is approximated by the equations

$$\Delta = 0.016(88.4 - \bar{x}) \text{ if } \bar{x} < 75 \text{ years,}$$

$$\Delta = 0.006(109.7 - \bar{x}) \text{ if } \bar{x} > 75 \text{ years.} \qquad [2]$$

The slope 0.006 year^{-1} agrees with the value 0.005 year^{-1} calculated according to ref. 26. The extrapolation of Eq. **2** to the minimal $\Delta = 0$ yields the maximal mean lifespan $\bar{x}_{\max} = 109.7$ years, which is consistent with the calculation in ref. 26.

The fluctuations of the mean lifespan of genetically homogeneous populations over 550 fruitflies (20) are $\approx 10\%$; in one case only (with the largest Δ), they reach 30%. Together with the universality of Fig. 1 *A* and *F* for genetically homogeneous populations, this suggests that under given conditions a genome uniquely determines§ its $\bar{x}$ and Δ. The validity of Eq. **1** for genetically homogeneous populations implies its validity for a heterogeneous population, where all or almost all genotypes have either $\bar{x} < x_1^*$ or $\bar{x} > x_2^*$, but may not imply it otherwise. This is consistent with the irregular evolution rate of heterogeneous flies in cups (19, 21) ($\bar{x} \cong 32$). In a heterogeneous population with $\bar{x} < x^*$, only the subpopulations with progressively larger $\bar{x} > x^*$ survive to the age significantly beyond x^*, dominate its mortality, and yield deviations from Eq. **1** in very old age. This is consistent with

refs. 26 and 27, with the significant slowing down of the heterogeneous fly $a_1(x)$ decrease in Fig. 1*D* and x_1 increase in old age (beyond $x = 41$ days). However, then their x_1 data are statistically unreliable (and are not included in Fig. 1*E*).

(*ii*) In human young age $\ell_x(\bar{x}) \cong 1$. Thus, by Eq. **1**, $\ell n \ell_x^*(\bar{x}) \cong -a_s(x_s - \bar{x})$, where $s = 1$ or $s = 2$. In early age, according to Fig. 1 *D* and *E*, $a_s(x)$ changes much quicker than $x_s(x)$ does. So,

$$q_x = d\ell n \ell_x/dx \cong a_s'(x) \cdot (x_s - \bar{x}). \qquad [3]$$

Thus, the relative mortality $q_x/q_y = a_s'(x)/a_s'(y)$ (where y is a fixed, arbitrarily chosen young age) depends on age x only and is universal. This was indeed demonstrated (27) with all 272 available child lifetables (2–4) (yearly up to 10 years and daily, weekly, and monthly up to 1 year).

(*iii*) Suppose $\bar{x}$ in Eq. **1** is less than x_1^*. Because survival probability (for $x \neq 0$) never reaches 1, $\bar{x}$ must always remain smaller than $x_1(x)$ according to Eq. **1**. Thus, when $\bar{x}$ approaches $x_1(x)$, the latter must increase to a different value $x_2(x)$. Indeed, when, for example, $x = 40$ years, the human $x_1 \cong 76$ years. It rapidly switches to $x_2 \cong 87$ years at $\bar{x} \cong 75$ years, slightly before $x_1 \cong 76$ years. Likewise, at $x = 20$ days the fly $x_1 \cong 35$ days switches to $x_2 \cong 59$ days at $\bar{x} \cong 32$ days, somewhat before $x_1 \cong 35$ days. Currently, maximal human (1–4) $\bar{x} \cong 82$ years and fly (19–22) $\bar{x} \cong 49.9$ days. I predict the next rapid change from $x_2(x)$ to the larger $x_3(x)$ in the vicinity of $\bar{x} \cong x_2 \cong 87$ years for humans (if $x \sim 40$ years) and $\bar{x} \cong x_2 \cong 59$ days for flies (if $x \sim 20$ days). It may be followed by further jumps at higher $\bar{x}$.

(*iv*) Because Fig. 1 *A* and *F* and Eq. **1** are universal, all relevant characteristic times—the reproductive age, mean and maximal mean longevity, mean longevity fluctuation, and mean time of mortality evolution adjustment to changing external conditions—must be of the same order of magnitude. Indeed, human $\bar{x}/75$ years changes from 0.5 to 1.2; fly $\bar{x}/32$ days increases from 0.6 to 1.7; Japanese and German mean lifespan approximately doubled in 70 years. Eq. **1** universally relates survival probability $\ell_x(\bar{x})$ to the mean longevity $\bar{x}$. Thus, to quantify the evolution of ℓ_x in real time t, it is sufficient to determine the rate $d\bar{x}/dt$. Phenomenologically, this rate depends on $\bar{x}, t$. The dependence of $d\bar{x}/dt$ on $\bar{x}$ is related, in particular, to the properly averaged (with respect to age) $\ell_x(\bar{x})$, which is universal and is nonlinear in $\bar{x}$ in the narrow crossover region $\bar{x} \cong x^*$. (The dependence on t is related to changing conditions and is nonuniversal). In mathematics, it is well known that the behaviour of nonlinear equations is very rich. They may have several solutions, which diverge at the branching points. Possibly, human $x^* \cong 75$ years and fly $x^* \cong 32$ days in Fig. 1*A* are such universal branching points (cf. bifurcations in ref. 48). Branching points yield singularities, instabilities and higher fluctuations. These are indeed evident at these ages in Fig. 1*A*.

(*v*) The universality of Fig. 1*A* and *F* for genetically homogeneous fruitfly populations suggests that the heterogeneous mean lifespan $\bar{x}$ and its fluctuation are related predominantly to the population genetic composition. [Note that $\bar{x}$ of different inbred fruitfly lines (20) differs more than 2.5-fold.] I speculate that although individual chances of survival heavily depend on accidental fortunes or misfortunes, the population probability to survive to a given age is strongly correlated with its genetics, which affects immunity, physical fitness, and many other factors. Mortality exterminates genomes (that are "unwanted" under a given set of conditions) on the mean longevity timescale (see point *iv*) and changes the genetic composition (polymorphism) of the population. This might quantitatively explain very rapid microevolution and is consistent with ref. 49. Rare mutations may be responsible for relatively slower macroevolution on a much larger time scale.

---

§It is not difficult to imagine that any system may display stochastic behavior. It is, however, more difficult to see how this is deliberately or actively determined by the genome. Because this is a crucial point, consider an example where the answer is well known. According to quantum mechanics, the nuclear potential of a radioactive nucleus determines its probability to survive to a given time. This probability (which is related to the laws of nature, and which may be denoted as "intrinsic stochasticity") determines the nucleus mean lifespan, and its fluctuation $\Delta(\bar{x})$ for homogeneous and heterogeneous "nuclei populations." The evidence that genes influence aging and longevity is abundant (15, 38–40). It includes the identification of longevity genes and lifespan extension mutants (38–46), artificial selection for postpones senescence, and heritability of human longevity (47).

Conclusions

The human and med- and fruitfly probability $\ell_x(\bar{x})$ to survive to the age x depends on x and life expectancy at birth $\bar{x}$ only, and is independent of the population and its living conditions. Fig. 1*B* demonstrates it for 1896 Swedish ($\bar{x}$ = 53.65 years) and 1947 Japanese ($\bar{x}$ = 53.96 years) females (i.e., for different races in different countries at very different periods of their different history), for different families of genetically heterogeneous medfly females ($\bar{x}$ = 46.3 days) in overcrowded cages, and for inbred fruitfly males ($\bar{x}$ = 46.5 days) in 4-dram shell vials (i.e., in different conditions).

The universal $\ell_x(\bar{x})$ is determined. It yields survival and mortality curves, which agree with all available experimental data for humans and flies—see examples in Fig. 1 *B* and *C* (note the agreement between human theoretical and experimental mortality rate q_x over four orders of magnitude; their deviation is a quantitative measure of premature mortality at a given age). Theoretical curves exhibit different mortality regions and their change with populations and living conditions—e.g., human minima; quasi-plateaus, which vanish at sufficiently large human $\bar{x}$; and the Gompertz $\ell n q_x$, which linearly increases with x and then slows down at very old age (see, for example, Fig. 1*C*). Survival evolution with $\bar{x}$ (for a given age x) proceeds with a constant rate $a_1(x)$ until the narrow vicinity of a certain critical $\bar{x} = x^*$ (which is independent of age, population, and conditions and equals 75 years for humans and 32 days for flies). At $\bar{x} = x^*$ the rate jumps to a different constant value $a_2(x)$ and proceeds with it thereafter (see Fig. 1*A*). For humans younger than 50 years, $a_2(x) \ll a_1(x)$; humans older than 70 years have $a_2(x) \gg a_1(x)$. The rate significantly changes with age and has a maximum at an advanced age. Survival evolution is rapid: $\bar{x}$ may double within the mean lifespan. Presumably, it is related to the change in the population genetic composition. Such a change may explain a very rapid macroevolution [there were no humans only a few hundred thousand generations ago and no mammals a few dozen million generations ago, whereas a few million billions of intermolecular collisions ("generations") are needed to cool down a cup of coffee] and is consistent with ref. 49. The singularity at $\bar{x} = x^*$ may manifest the emergence of a new population "phase" (with a significantly different mortality evolution rate) in the course of punctured equilibria (50).

Survival probability as a function of dimensionless age and mean lifespan is superuniversal in advanced and old age for different phyla of human and fly (see Fig. 1*E*). Probability to survive to old age little depends on the mean lifespan; for example, at 70 years human life expectancy was 8 years for 1800 Swedish ($\bar{x}$ = 35.5 years) and 9.5 years for 1970 Japanese ($\bar{x}$ = 69.3 years) males. I predict and verify that the mean quadratic fluctuation of mortality depends on $\bar{x}$ only (Fig. 1*F*); that the relative child mortality is independent of conditions. The next jump of the survival evolution rate is predicted in the vicinity of the universal $\bar{x} \cong 87$ years for humans and $\bar{x} \cong 59$ days for flies.

The superuniversality of the survival evolution of species as remote as humans and flies suggests that its law is genetically determined and may be universal for all iteroparous animals. The diversity of life and, in turn, species life histories is so vast that one tends to believe this law is invalid for semelparous species. Yet, one may wildly speculate that it is universal even for animals such as salmon and mayflies, that their survival curves are rectangular at the reproductive age which equals x^*, and that their evolution rate is negative and its value is extremely large beyond $\bar{x} = x^*$.

1. National Central Bureau of Statistics (1974) Statistical Abstracts of Sweden (National Central Bureau of Statistics, Forlaget, Stockholm).
2. National Central Bureau of Statistics (1996) Population Statistics: Life Tables 1891–1995, Infant Mortality 1891–1995 (National Bureau of Statistics, Forlaget, Stockholm).
3. Federal Statistics Office (1996) Statistics Figures for Everyone (Federal Statistics Office, Wiesbaden, Germany).
4. Ministry of Health and Welfare (1994) Life Tables 1891–1992 (Ministry of Health and Welfare, Tokyo, Japan).
5. Gompertz, B. (1825) *Philos. Trans. R. Soc. London* **A115,** 513–525.
6. Gompertz, B. (1872) *J. Inst. Actuaries* **16,** 329–344.
7. Makeham, W. M. (1867) *J. Inst. Actuaries* **13,** 325–358.
8. Brownlee, J. (1919) *J. R. Stat. Soc.* **82,** 34–77.
9. Perks, W. (1932) *J. Inst. Actuaries* **63,** 12–57.
10. Strehler, B. L. & Mildvan, A. S. (1960) *Science* **132,** 14–21.
11. Finch, C. E. & Pike, M. C. (1996) *J. Gerontol. Biol. Sci.* **51A,** B183–B187.
12. Olshansky, S. J. & Carnes, B. A. (1997) *Demography* **34,** 1–15.
13. Vaupel, J. W., Carey, J. R., Christensen, K., Johnson, T. E., Yashin, A. I., Holm, N. V., Iachine, I. A., Kannisto, V., Khazaeli, A. A., Liedo, P., *et al.* (1998) *Science* **280,** 855–860.
14. Fries, J. F. & Grapo, L. M. (1981) *Implications of the Rectangular Curve* (Freeman, San Francisco).
15. Finch, C. E. (1990) *Longevity, Senescence and Genome* (Univ. of Chicago Press, Chicago).
16. Gavrilov, N. S. & Gavrilova, L. A. (1991) *The Biology of Life Span: A Quantitative Approach* (Harwood Academic, Chur, Switzerland).
17. Wachter, K. W. & Finch, C. E. (1997) *Between Zeus and Salmon, The Biodemography of Aging* (Natl. Acad. Press, Washington, DC).
18. Pearl, R. (1922) *Am. Nat.* **56,** 398–405.
19. Carey, J. R., Liedo, P., Orozco, D. & Vaupel, J. W. (1992) *Science* **258,** 457–461.
20. Curtsinger, J. W., Fukui, H. H., Townsend, D. R. & Vaupel, J. W. (1992) *Science* **258,** 461–463.
21. Carey, J. R. (1993) *Applied Demography for Biologists* (Oxford Univ. Press, New York).
22. Pletcher, S. D. & Curtsinger, J. W. (1993) *Evolution* **52,** 454–462.
23. Brooks, A., Lithglow, G. J. & Johnson, T. R. (1994) *Science* **263,** 668–671.
24. Kowald, A. & Kirkwood, T. B. L. (1993) *Science* **260,** 1664–1665.
25. Vaupel, J. W. & Carey, J. R. (1993) *Science* **260,** 1666–1667.
26. Azbel', M. Y. (1996) *Proc. R. Soc. London B* **263,** 1449–1453.
27. Azbel', M. Y. (1998) *Proc. Natl. Acad. Sci. USA* **95,** 9037–9041.
28. Thatcher, A. R., Kannisto, V. & Vaupel, J. W. (1998) *The Force of Mortality at Ages 80 to 120* (Odense Univ. Press, Odense).
29. Beard, R. E. (1971) in *Biological Aspects of Demography*, ed. Brass, W. (Taylor & Francis, London).
30. Kannisto, V. (1988) *Pop. Stat.* **42,** 389–406.
31. Thatcher, A. R. (1987) *J. Inst. Actuaries* **114,** 327–338.
32. Economos, S. (1982) *Age* **2,** 74–76.
33. Riggs, J. R. (1993) *Mech. Ageing Dev.* **72,** 165–167.
34. Coale, A. & Demeny, P. (1983) *Regional Model Life Tables and Stable Populations* (Academic, New York).
35. Lee, R. D. & Carter, L. R. (1993) *J. Am. Stat. Assoc.* **87,** 659–668.
36. Yashin, A. I. & Iachine, I. A. (1997) *Demography* **34,** 31–39.
37. Abrams, P. A. (1991) *Evol. Ecol.* **5,** 343–354.
38. Jazwinski, S. M. (1996) *Science* **273,** 54–59.
39. Luckinbill, L. S., Arking, R., Clare, M. J., Cirocco, W. C. & Buck, S. A. (1984) *Evolution* **83,** 996–1003.
40. Rose, M. R. (1991) *Evolutionary Biology of Aging* (Oxford Univ. Press, New York).
41. Klass, M. R. (1983) *Mech. Ageing Dev.* **22,** 279–286.
42. Friedman, D. B. & Johnson, T. E. (1998) *Genetics* **188,** 75–86.

43. Kenyon, C., Chang, J., Gensch, E., Radner, A. & Tabtiang, R. (1993) *Nature (London)* **366,** 461–465.
44. Larsen, P. L., Albert, P. S. & Riddle, D. L. (1995) *Genetics* **139,** 1567–1583.
45. Wong, A., Boutis, P. & Hekimi, S. (1995) *Genetics* **139,** 1247–1259.
46. Parkes, T. L., Elia, A. J., Dickinson, D., Hilliker, A. J., Phillips, J. P. & Boulianne, G. L. (1998) *Nat. Genet.* **19,** 171–174.
47. Perls, T. T., Bubrick, E., Wager, C. G., Vijg, J. & Kruglyak, L. (1998) *Lancet* **351,** 1560–1563.
48. Jazwinski, S. M., Kim, S., Lai, C.-Y. & Benguria, A. (1998) *Exp. Gerontol.* **33,** 571–580.
49. Cossing, A. (1994) *Nature (London)* **369,** 309–313.
50. Gould, S. J. & Eldredge, N. (1993) *Nature (London)* **366,** 223–227.