AGING

A Natural History

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Saddleback tortoises of Pinzon Island, in the Galapagos Archipelago, may achieve ages of more than a century. This extreme longevity emphasizes the variation in life spans among animals.

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A Natural History of Life Span

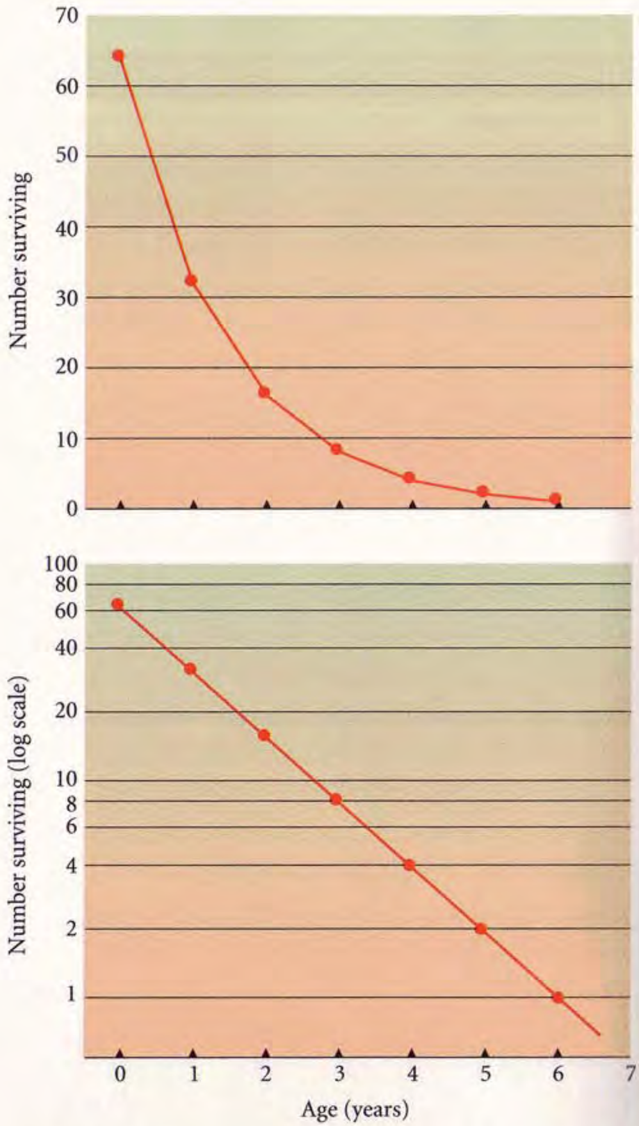
The phenomenon of aging is obvious to anyone over the age of 30. Personal experience alone is enough to convince most of us of its importance as a biological process and of the need for experimental research to determine how aging occurs—and how its worst effects might be prevented! What is less apparent, however, is that our understanding of the aging process has been broadened by looking at aging in different species—what we might call the natural history of life span. Such comparisons are especially helpful for developing and testing evolutionary theories of why we age. These theories attempt to explain not only why the phenomenon of aging exists, but why differences have evolved in the rate of aging among species.

Although we know a great deal about aging in humans and a few organisms raised in the laboratory, our understanding of aging in wild populations is limited. What we do know suggests a rich variation among species in the pattern of aging and allows us to make some educated guesses about the underlying causes of these differences. In this chapter, we show how observations of the natural history of aging reveal interesting patterns that seem to require explanation, but that also suggest some mechanisms that may lie behind senescence.

The Gompertz Pattern of Aging

As we have seen, senescence is a pervasive deterioration of the body's functioning with age. We all recognize the declining health and gradual loss of vitality that come with aging. But for the scientist wishing to compare species, these physiological signs of aging are difficult to measure in most animals and even more difficult to compare. An easier way to depict the advance of senescence within a population is to track the increase in the death rate at progressively older ages. Like the body in general, reproductive systems function less well with age, and so another way to follow the course of aging is to record the decline in the reproductive rate, or fecundity, of individuals at progressively older age. Thus, to portray senescence from a demographic point of view, the scientist tabulates birth and death rates for large samples of individuals that have been followed from birth to the maximum age observed in the population. Until recently, biologists have focused their attention mostly on mortality rate and have largely ignored fecundity. The reason is partly that it is easier to measure mortality than fecundity, especially in males, and partly that we humans are more preoccupied with our own mortality than with the number of our progeny, which nowadays is usually not limited by biological considerations.

Senescence appears as a mortality rate that increases with age. In a population whose members never aged, individuals would still die, of course, but the mortality rate would be identical for all age

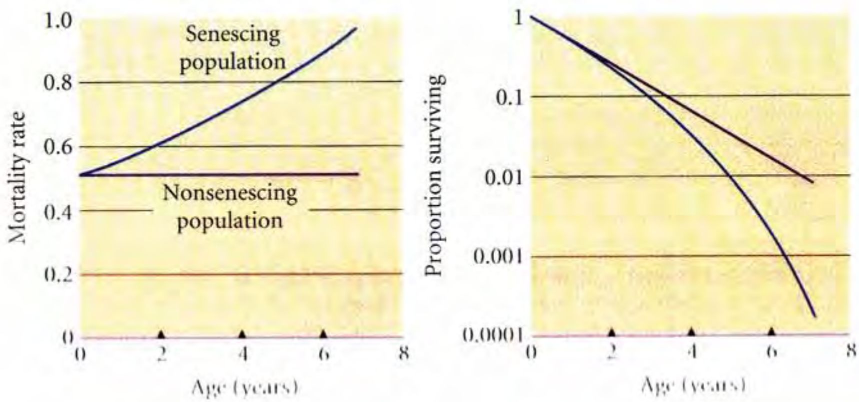


Even if aging did not exist, the number of survivors would decrease exponentially with age. Here the survival function of a cohort of 64 individuals with an annual mortality rate of 50% is plotted on a linear scale above, producing a curve, and on a logarithmic scale below, producing a straight line. In mathematical terms, for a constant mortality rate *m*, the fraction of individuals alive at age *x* decreases exponentially with age. That is, $S_x = e^{-mx}$. When this equation is log-transformed, one obtains $\log_e S_x = -mx$, which, in words, means that the natural logarithm of the fraction surviving decreases as a linear function of age with slope $= -m$.

groups. Thus, on a graph of mortality rate versus age, such a population would be represented by a straight, horizontal line, and we would find that the number of individuals surviving decreased exponentially with age. For example, if the mortality rate were 50% each year, a cohort (group of equal age) of 64 individuals would, on average, dwindle to 32, 16, 8, 4, 2, 1, and finally 0 with each advancing year. This relationship between the number of individuals surviving and age is called the survival function. When we plot the number of survivors against age, we see that the absolute rate of decrease becomes less with increasing age because, as the population dwindles, the 50% dying each year make a smaller and smaller number. The effect is the same when we plot, as is often done, the proportion of the original cohort that remains alive at each age, rather than the absolute numbers of individuals. In the analysis of senescence, it is customary to depict the number of individuals alive at each age on a logarithmically transformed scale, which makes the survival function of a nonaging population a straight line. How fast the logarithm of the survival function decreases as age increases (that is called the slope of the line) is equal to the mortality rate of the population. In the foregoing case, the slope of the line has a value of –0.5 (corresponding to 50% mortality per year), and, of course, it is negative because death always removes individuals.

The straight-line survival function is the sign of a hypothetical population that has been spared the decline brought on by aging. In contrast, in a realistic population whose members do experience aging, the mortality rate increases at older age and the line representing the (log-scale) survival function is no longer straight, but curves downward. That is, its slope becomes progressively steeper and more negative. Indeed, senescence can be quantified by how rapidly the mortality rate increases with increasing age. Suppose that individuals in a population were dying at a rate of 50% per year upon reaching adulthood, but that the mortality rate increased exponentially by a factor of 10% each year thereafter, that is, to 55% during the second year of adulthood, 60.5% (55% plus 10% of 55%) during the third year, 66.55% during the fourth year, and so on. By the end of the 5 years, a cohort that aged in this way would dwindle to about 0.8% of its original size, compared with about 3.1% in a nonaging population.

It is common for the mortality rate to increase exponentially with age in natural populations. This pattern of exponential increase is often called the Gompertz pattern of aging. The Gompertz pattern describes the effects of aging on mortality by two



Two, related ways to characterize aging in a population are to plot the mortality rate (left) and the survival function (right). In the nonsenescing population, the mortality rate remains at the minimum, or baseline, mortality rate of 50% per year, the rate when adulthood is achieved. In the senescing population, the mortality rate increases exponentially at a rate of 10% each year. Aging causes the survival function to bend downward at higher ages, reflecting the higher mortality rate numbers that are constant in a given population: the initial or baseline mortality rate, A, and the exponential rate of increase in the mortality rate, G. In the preceding example, the values of A and G were 0.5 and 0.1, respectively. The baseline mortality rate A, which is the mortality rate of young adults, includes death from accidents and other causes not related to aging. The Gompertz constant G measures the rate of aging and may be compared directly between different species. For example, the mortality rate in a captive population of brush turkeys, an Australasian turkeylike bird, increases exponentially at a rate of about 21% per year from a baseline of about 5% per year. The Bali myna, a bird somewhat related to the European starling, has a baseline annual mortality rate of about 9% in captivity, but this rate increases by only 9.6% per year. One can say, therefore, that the myna ages less than half as fast as the brush turkey. Because values of G are not intuitive, scientists often use an inverse measure of G, the mortality rate doubling time (MRDT). MRDT is the age by which the mortality rate has increased to twice its baseline level. For the brush turkey and myna, these values are 3.3 and 7.2 years, respectively.

Gompertz constants vary among species of mammals from as high as about 2.3 (230% per year) in laboratory rats and mice to as little as 0.09 (9% per year) in humans and elephants. These values of G correspond to mortality rate doubling times of 0.3 and 8 years, respectively. Notice that some small

The Gompertz Equation

The expression most commonly employed to compare mortality rates between populations is the Gompertz equation. According to the Gompertz pattern of aging, the mortality rate increases as an exponential function of increasing age. This course of aging is described by the equation

$$m(x) = Ae^{Gx}$$

where $m(x)$ is the mortality rate at age x, A is the initial mortality rate at age 0, and G is the exponential rate of increase in the mortality rate with increasing age. G may be regarded in the same way as the interest rate on a bank account because it governs the rate at which the initial mortality rate (investment) grows with time. The Gompertz law can also be expressed in terms of the proportion of individuals surviving to age x, $S(x)$, according to the equation

$$S(x) = e^{-\frac{G}{A}(e^{Gx} - 1)}$$

Because deaths from childhood diseases and accidents usually decline between birth and the age of sexual maturity, the mortality rate declines as well. For this reason, age 0 is often set as the age of puberty or first bearing of offspring. The initial or minimum mortality rate A is therefore the mortality rate at about the time of puberty. The Gompertz constant (G) also may be expressed as the time required for the mortality rate to double (the mortality rate doubling time, MRDT) according to the expression MRDT = $\log_e(2)/G$.