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Evolutionary Theories of Aging

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All living organisms age, from those with a life span of only a couple of days, such as the mayfly, to those with a longevity of centuries, for example, the Arctic whale and certain varieties of carp. In most organisms including humans, phenotypic traits that correspond to the set of individual characteristics (e.g., body mass, physiological performance like immunological parameters) do not remain constant over the life course. For a given trait, the individual performance reaches a peak or a plateau generally between early and mid-adulthood and then declines. These patterns lead to changes that decrease the likelihood of having a child (reproductive senescence) and increase the likelihood of dying (actuarial senescence).

For a very long time, aging has been considered a process that escaped the evolutionary process of natural selection and was thus out of reach by evolutionary processes. Moreover, aging has also been considered to be a specific property of humans and laboratory animals that is only rarely observed in the wild. However, scientific advances made in the last 60 years have changed these beliefs. First, researchers have demonstrated that aging processes are integrative components of life history strategies and subjected to natural selection (i.e., the responses to phenotypic changes across individuals in terms of survival and reproductive success). Second, clear empirical evidence shows that reproductive and actuarial senescence are pervasive in the wild. This entry highlights how aging can be explained in the light of current evolutionary theories and discusses possible implications for human life-span development.

Aging and Evolutionary Processes: From Simple Hypotheses to Elaborated Models

Although identifying the origin of a theory is always a difficult task, the first hypothesis linking aging and evolutionary processes can be attributed to August Friedrich Leopold Weismann at the end of the 19th century. This German physician envisioned living organisms as behaving like machines that display a decline in performance with passing time. He was the first to propose the existence of a biological mechanism subjected to natural selection that limits the number of divisions of somatic cells (i.e., all cells within an organism except the germ line), which allowed removing the oldest individuals in a given population. However, such group-selection arguments for a programmed aging that give priority to the benefit of the group over the benefit to a given individual in that group have been strongly debated and were then mostly rejected in the mid-1960s.

The persistence of aging despite its negative consequences for individual performance was thus viewed as a paradox in the light of evolutionary theory. Any efficient selection should counterselect intrinsic sources of mortality and thereby prevent the evolution of aging. Three seminal and complementary works that still constitute the background of our current evolutionary theories of aging resolved this major paradox. First, in the early 1950s, Peter Medawar's *mutation accumulation theory* stated that the diminution of the strength of natural selection with increasing age is likely to explain why decreased reproduction and decreased survival with increasing age are observed. Indeed, a mutation that will carry deleterious effects is less likely to be counterselected if the deleterious effects are expressed in late life, when the strength of natural selection acting against such mutations is weak. Under this theory, the persistence of aging involves a passive mechanism that prevents aging to be selected against.

Less than 50 years later, William Donald Hamilton, an English evolutionary biologist, formulated a mathematical model demonstrating that this diminution of the strength of natural selection with increasing age is a mandatory outcome of evolution in any age-structured population, which reinforced the view of an inevitable aging. In the late 1950s, George Christopher Williams's *antagonistic pleiotropy* theory of aging set up the argument that for aging to be selected, despite its direct negative influence on survival and reproductive success, the traits may have had benefits earlier in the life cycle (and particularly for reproduction). In addition to considering that the strength of natural selection decreases with increasing age, this theory proposed that a gene responsible for aging should be selected despite its obvious deleterious effects in late life if it provides fitness benefits at much earlier ages. With the *antagonistic pleiotropy* theory, the persistence of aging involves an active mechanism that leads aging to be selected for via reproduction.

These crucial contributions have launched the background for interpreting aging as a biological process subjected to evolution. However, it is only recently (i.e., the current 2010 decade) that the evolutionary theories of aging have been linked to the framework of life history evolution. This theoretical shift has allowed putting forward the crucial role of environmental conditions in shaping the diversity of aging trajectories.

From Aging to Life History Evolution

In the mid-1970s, a new theory of aging, the *disposable soma* theory, took hold. This physiologically based theory relies on the observation that molecular damages accumulate in somatic cells over time, which can progressively lead to cellular death and thus explain the increasing risk of mortality with increasing age. Maintaining molecular integrity in somatic cells is energetically costly and if an individual uses an important quantity of its finite pool of resources for another physiological function, less energy will be available to prevent the deterioration of the cellular machinery, leading damages to accumulate.

Although no direct link with the concept of life-history trade-off was made explicitly in the initial versions of the disposable soma theory, the central role played by energy costs in this theory provided the first theoretical basis for connecting aging and life history evolution. In the early 1990s, the scope of the disposable soma theory was progressively widened to include the trade-off between early- and late-life performance, and the disposable soma theory thus rapidly became complementary to the antagonistic pleiotropy theory. A substantial allocation to growth or reproduction early in life limits the quantity of energy devoted to somatic maintenance, which ultimately leads to decreased survival and/or reproductive performance in late adulthood. These relationships clearly emphasize the tight link between the evolutionary theory of aging and the concept of life history trade-off.

Life history trade-offs are at the core of life history evolution and correspond to negative relationships between competing traits measuring performance at a given time (e.g., reproduction *vs*. survival, offspring size *vs*. offspring number) or between the same traits measured at competing times (e.g., current *vs*. future reproduction). Such negative relationships prevent the existence of a *Darwinian demon*, an ideal organism that would be able to maximize all performance-related traits at all times. Trade-offs are rooted in the *principle of allocation*, which stipulates that the environment limits the total amount of energy an organism can acquire, so that a given allocation to one biological function (such as growth, survival, or reproduction) should limit the amount of energy that can be allocated to another function (such as maintaining the organism's integrity and functionality throughout life). In most vertebrates studied so far, it has been clearly shown that aging results from the trade-offs between early-life allocation in growth or reproduction and late-life allocation in survival or reproduction. Interestingly, this evolutionary context offers the possibility to study any aging pattern in the wild. Indeed, from this viewpoint, aging, like any other trade-off, can be expressed or not, leaving a key role to environmental conditions in shaping the timing and intensity of aging. Overall, the progressive but recent connection between classic evolutionary theory of aging and life history evolutionary theory enables to better understand the diversity of aging patterns observed among and within species.

Evolutionary Theories of Aging and Human Life-Span Development

The evolutionary framework of aging is particularly relevant to better understand the causes and consequences of the improvement of the human life span. The human population of the earth has surpassed 7 billion, and the societal implications of this exponential increase (in 1950, world population was just over 2.5 billion) stress the importance of a thorough understanding of human population growth. Because population growth is a direct function of age-specific fertilities and survival, a better assessment of the selective forces shaping age-specific trajectories of reproduction and survival is required. This need is especially true for modern societies where life expectancies at birth are currently around 80 years, which provides a key role of aging in shaping population growth.

Because the general increase in life span observed in human populations is associated with a higher proportion of older individuals in a population, it is also particularly important to better understand the origins of age-related diseases. Again, evolutionary theories of aging provide powerful tools to study health at old ages. For instance, there is increasing evidence that some diseases in late life such as cardiovascular diseases or some cancers can be a direct consequence of a selection for high reproductive success during early adulthood, in line with the antagonistic pleiotropy theory of aging proposed by Williams.

Finally, evolutionary theories could provide a suitable theoretical background to understand better the gender gap observed in human populations. In most countries, women outlive men, a feature common to most mammalian species. Various evolutionary hypotheses have been proposed to explain the evolution of sex differences of aging across species. For instance, the heterogametic sex hypothesis states that the sex carrying different sex chromosomes (XY males in mammals or ZW females in birds) should display higher adult mortality than the sex carrying two copies of the same sex chromosome (XX females in mammals or ZZ males in birds). Although our current understanding of evolutionary processes does not allow yet explaining observed survival differences between men and women, there is now clear evidence that evolution provides insightful answers to the striking question of sex differences in aging.

See also Aging; Centenarian; Demography; Ecology; Evolution; Evolutionary Theory; Fertility; Gerontology; Longevity; Old Age; Sex Differences

- theories of aging
- evolutionary theory
- ageing
- life histories
- senescence
- natural selection
- reproduction

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Further Readings

Carter, A. J., & Nguyen, A. Q. (2011). Antagonistic pleiotropy as a widespread mechanism for the maintenance of polymorphic disease alleles. BMC Medical Genetics, 12, 160.
Cody, M. L. (1966). A general theory of clutch size. Evolution, 20, 174–184.
Hamilton, W. D. (1966). Moulding of senescence by natural selection. Journal of Theoretical Biology, 12, 12–45.
Kirkwood, T. B., & Rose, M. R. (1991). Evolution of senescence: Late survival sacrificed for reproduction. Philosophical Transactions of the Royal Society B-Biological Sciences, 332, 15–24.
Lemaître, J. F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F., & Gaillard, J. M. (2015). Early-late life trade-offs and the evolution of ageing in the wild. Proceedings of the Royal Society B: Biological Sciences, 282, 20150209.
Medawar, P. B. (1952). An unsolved problem of biology. London, UK: Lewis.
Nussey, D. H., Froy, H., Lemaître, J. F., Gaillard, J. M., & Austad, S. N. (2013). Senescence in natural populations of animals: Widespread senescence and its implications for bio-gerontology. Ageing Research Reviews, 12, 214–225.
Regan, J. C., & Partridge, L. (2013). Gender and longevity: Why do men die earlier than women? Comparative and experimental evidence. Best Practice & Research Clinical Endocrinology & Metabolism, 27, 467–479.
Shefferson, R. P., Jones, O., & Salguero-Gómez, R. (in press). The evolution of senescence in the tree of life. Cambridge, UK: Cambridge University Press.
Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. Evolution, 11, 398–411.