

**Evolutionary Theories of Aging**

Martin Reichard, Institute of Vertebrate Biology, Brno, Czech Republic

© 2020 Elsevier Inc. All rights reserved.

**Email me at [reichard@ivb.cz](mailto:reichard@ivb.cz)  
to get the full chapter**

<b>Introduction</b>	<b>57</b>
<b>Defining Evolutionary Theories of Aging</b>	<b>58</b>
Mutation Accumulation	58
Antagonistic Pleiotropy	58
Disposable Soma	59
Conditions for Evolutionary Theories of Aging	59
Predictions of the Three Evolutionary Theories of Aging	59
<b>Empirical Tests for the Evolutionary Theories of Aging</b>	<b>60</b>
Ecological Correlates of External Mortality: Broad Taxonomic Comparisons	60
Demographic associations	60
Comparative genomics	60
Ecological Correlates of External Mortality: Intraspecific Contrasts	61
Support from intraspecific contrasts	61
Contradictions from intraspecific contrasts	61
The importance of condition-dependent survival	61
Contrasts Between Castes in Eusocial Animals	61
Eusocial insects	61
Complex vertebrate societies	61
Artificial Selection and Experimental Evolution	62
Testing antagonistic pleiotropy and longevity-reproduction trade-offs	62
Testing accumulation of mutations	62
Insight to particular genetic pathways	62
Testing the role of condition-dependent survival	62
<b>Extensions and Modifications of Standard Evolutionary Theories of Aging</b>	<b>63</b>
Condition Dependence	63
Positive Pleiotropy and the Modified Mutation Accumulation Theory	63
Indeterminate Growth	63
<b>The Relationship Between Aging and Reproduction</b>	<b>64</b>
Reproductive Senescence	64
Generalized Trade-Offs Between Aging and Reproduction	64
Cost of Gamete Production and Germ Line Maintenance	64
Sexual Selection	65
Sexual Conflict	65
<b>Situations Beyond the Evolutionary Theories of Aging</b>	<b>65</b>
The Lack of a Clear Distinction Between the Germ and Somatic Lines	65
Unicellular organisms	65
Plants	65
Fungi	66
Animals with pluripotent cells	66
Clonal reproduction	66
<b>Summary and Conclusions</b>	<b>66</b>
<b>References</b>	<b>66</b>
<b>Further Reading</b>	<b>67</b>

**strict copyright restrictions apply  
for posting this text online****Introduction**

Demographically, aging is defined as a decline in fitness with increasing chronological age, manifested by an elevated risk of death and a decrease in reproductive success. This demographic change is caused by functional deterioration at multiple levels, providing a mechanical explanation for the manifestation of aging. As to why organisms age, we are faced with an apparent paradox. As aptly articulated by G. C. Williams more than 60 years ago, "It is truly amazing that, after having completed the nearly miraculous feat of embryogenesis, a complex metazoan fails at the seemingly much easier task of simply preserving what was already created" (Williams, 1957). This paradox is best explained by evolutionary theories of aging.

## Summary and Conclusions

The seeming paradox of why aging has not been eliminated by natural selection when it is apparently detrimental to individual fitness is well embraced by standard evolutionary theories of aging. The theoretical treatments of aging are underpinned by the fact that mortality itself is common in nature, irrespective of aging. This makes survival to a particular chronological age negatively associated with time since birth, enabling aging to evolve as a mere side effect of genetic drift (“**Mutation Accumulation**” section) or a consequence of the trade-off between early and late-life fitness income (“**Antagonistic Pleiotropy**” and “**Disposable Soma**” sections).

Not all organisms and not all cell lineages age. Germ cell lines, most prokaryotic organisms and many eukaryotes show no increase in mortality with chronological age. This is sometimes misleadingly interpreted as a failure of evolutionary theories of aging to incorporate their occurrence into their theoretical underpinning. However, evolutionary theories of aging specifically aim to explain situations where basic assumptions are met and are not relevant in other circumstances. Hence, while the current paradigm for the explanation why does aging sometimes evolve is solid, our understanding of how other taxa escape aging is far from settled. New discoveries, comparative analyses and experimental tests keep producing new insights into the evolutionary perspectives of aging, sometimes leading to clarifications and modifications of the prevailing opinions. In short, evolutionary understanding of aging is itself evolving.

## References

- Abrams, P.A., 1993. Does increased mortality favor the evolution of more rapid senescence? *Evolution* 47, 877–887.
- Arbuthnott, D., Promislow, D.E., Moorad, J.A., 2016. Evolutionary theory and aging. In: Bengtson, V.L., Settersten Jr., R. (Eds.), *Handbook of theories of aging*, 1st ed. Springer, New York, pp. 113–136.
- Austad, S.N., 1993. Retarded senescence in an insular population of Virginia opossums (*Didelphis virginiana*). *Journal of Zoology* 229, 695–708.
- Austad, S.N., Hoffman, J.M., 2018. Is antagonistic pleiotropy ubiquitous in aging biology? *Evolution, Medicine, and Public Health*. <https://doi.org/10.1093/emph/eoy033>.
- Baudisch, A., 2011. The pace and shape of ageing. *Methods in Ecology and Evolution* 2, 375–382.
- Blažek, R., Poláčik, M., Kačer, P., et al., 2017. Repeated intraspecific divergence in life span and aging of African annual fishes along an aridity gradient. *Evolution* 71, 386–402.