

true preferences, including those for child health. This is an important area for further exploration because it implies that seemingly paternalistic policies, or expenditures that change outcomes relative to what would be chosen independently, may help people to arrive at outcomes that they would themselves choose in the absence of scarcity.

Banerjee and Duflo (15) have recently made the case for improving well-being by reducing the number of decisions that people have to make. They argue that in the United States, people do not have to decide whether to chlorinate their drinking water—it comes that way; similarly, many employers enroll people into retirement plans by default, lessening the need to actively make a choice to save. In developing countries, on these topics

as well as others, people must make choices, decisions, and trade-offs. The evidence from Shah *et al.* provides another argument for why having so many choices can result in bad outcomes; scarcity makes quality decision-making difficult. Under such circumstances, defaults and guide rails, such as default option retirement plans, make quality decision-making easier and can have big payoffs for well-being.

#### References

1. T. W. Schultz, *Transforming Traditional Agriculture* (Yale Univ. Press, New Haven, London, 1964).
2. D. Kahneman, A. Tversky, *Econometrica* **47**, 263 (1979).
3. A. Tversky, D. Kahneman, *Science* **211**, 453 (1981).
4. E. Duflo, in *Understanding Poverty*, A. Banerjee, R. Banerjee, D. Mookherjee, Eds. (Oxford Univ. Press, Oxford/New York, 2006), chap. 24.
5. A. K. Shah *et al.*, *Science* **338**, 682 (2012).
6. *World Bank World Development Report 2011*, (World Bank and Oxford University Press, Washington, DC, 2011).
7. E. Miguel, M. Kremer, *Econometrica* **72**, 159 (2004).
8. A. V. Banerjee, E. Duflo, R. Glennerster, D. Kothari, *BMJ* **340**, c2220 (2010).
9. J. Cohen, P. Dupas, *Q. J. Econ.* **125**, 1 (2010).
10. M. Kremer, J. Leino, E. Miguel, A. P. Zwane, *Q. J. Econ.* **126**, 145 (2011).
11. A. Ahuja, M. Kremer, A. P. Zwane, *Annual Review of Resource Economics* **2**, 237 (2010).
12. M. Kremer, E. Miguel, *Q. J. Econ.* **122**, 1007 (2007).
13. P. Dupas, *Appl. Econ.* **3**, 1 (2011).
14. H. Holla, M. Kremer, in *What Works in Development? Thinking Big and Thinking Small*, J. Cohen, W. Easterly, Eds. (Brookings Institution Press, Washington, DC, 2009), ch. 4.
15. A. Banerjee, E. Duflo, *Poor Economics: A Radical Rethinking of the Way to Fight Global Poverty* (Public Affairs, New York, 2011).

10.1126/science.1230292

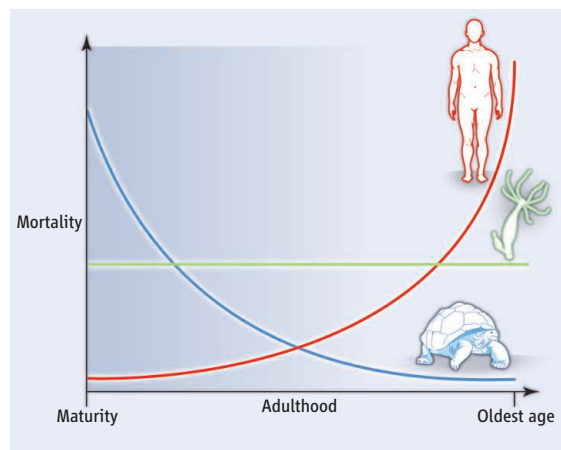
## EVOLUTION

# Getting to the Root of Aging

Annette Baudisch<sup>1,2</sup> and James W. Vaupel<sup>2,3,4</sup>

As people live longer, the question arises of how malleable aging is and whether it can be slowed or postponed. The classic evolutionary theories of aging (1–4) provide the theoretical framework that has guided aging research for 60 years. Are the theories consistent with recent evidence?

At the heart of the theories lies the observation that the old count less than the young: Unfavorable traits are weeded out by evolution more slowly at higher ages (2); traits that are beneficial early in life are selected for despite late life costs (3); and resources are used to enhance reproduction at younger ages instead of maintaining the body at ages that do not matter much for evolution (1). The decline in the force of selection with age is viewed as the fundamental cause of aging (4). It is why, starting at reproductive maturity, senescence—increases in susceptibility to death and decreases in fertility—should be inevitable in all multicellular species capable of repeated breeding (4). Yet, this is not the case. Increasing, constant, and decreasing mortality (and fertility) patterns (see the figure) are three generic variants that compose the rich diversity of life trajectories observed in nature. For vertebrates, reproductive tra-



**Aging patterns.** The illustration is a schematic view of how species age in radically different ways. The life courses of humans and of many mammals and birds, at least at the oldest ages, are generally marked by rising mortality. For the tortoise *Gopherus agassizii* (17) and many other reptiles, amphibians, fish, and plants, mortality decreases throughout adult life. For the freshwater polyp *Hydra vulgaris* (18) and various other species across the tree of life, daily survival is more or less constant with age.

jectories are commonly hump-shaped, and death rates may start rising much later than reproductive maturity (5). Thus, a new view on the fundamental causes of aging is needed to explain the clash of theory and data.

Allocation theory, which seeks to explain how resource limitations determine life-history patterns, provides a possible, promising perspective (6). Nature strikes compromises in allocating limited resources to growth ver-

Why do patterns of aging differ widely across the tree of life?

sus maintenance versus reproduction versus escaping predators and pathogens. The scarcity of resources available for competing needs requires that an organism “makes difficult choices” at every moment of life. For instance, more energy dedicated to growth at one moment may reduce reproductive output but improve chances of survival to the next breeding opportunity, when conditions might be better and reproductive potential (because of growth) higher (6). Current theory of aging acknowledges the necessity of such compromises (7) but neglects their fundamental importance. Because the declining force of selection with age dominates evolutionary thinking about aging, classic theory focuses on life-history choices that specifically confer early-life advantages at the cost of late-life losses.

By widening horizons to consider not only early- versus late-life compromises but all the difficult choices an organism must make in allocating limited resources to competing needs over its life span, it is possible to gain insights into the diverse demographic patterns observed in nature (6, 8, 9). Even the effects of purely deleterious mutations that act only

<sup>1</sup>Max Planck Research Group for Modeling the Evolution of Aging, Rostock, Germany. <sup>2</sup>Max Planck Institute for Demographic Research, Rostock, Germany. <sup>3</sup>University of Southern Denmark, Odense, Denmark. <sup>4</sup>Duke University, Durham, NC 27705, USA. E-mail: baudisch@demogr.mpg.de

at older ages can be accounted for by appropriate allocation models (10). In such models, the force of selection declines with age, but though important, this decline is not decisive in molding fertility and mortality patterns.

What is decisive is the “option set” of a species, which can be summarized by the feasible combinations of survival and reproduction at all ages over the life span. Option sets differ widely: For some species, extra investment in repair and maintenance substantially reduces fertility; for other species there is little impact; for yet other species enhanced repair and maintenance decrease current but increase future fecundity. The details of such option sets shape age patterns of growth, fertility, and mortality (8, 11).

Little is known about what types of constraints favor a pattern of aging with increasing mortality and decreasing fertility (senescent) versus alternative patterns with constant or declining mortality and constant or increasing fertility (nonsenescent). Life-history models suggest that the marginal costs and benefits of energy allocation play a central role (8, 11). To test this and to explore other hypotheses, it would be informative to compare plants, for which growth and reproduction flexibly adapt to environmental conditions (12), to animals, for which growth and reproduction are more rigid and distinct (8). In contrast to vertebrates, plants capable

of vegetative reproduction can create offspring by splitting off body parts. Thereby an investment in growth effectively becomes an investment in reproduction. Species that are small but long-lived (such as hydra in the laboratory), that can reproduce either sexually or asexually (such as daphnia), or that face highly uncertain environments [such as desert plants (12)] may also be good candidates for studies of how allocation options shape patterns of aging.

Research on the evolution of aging should focus on unraveling those differences in species’ option sets that lead to senescent versus nonsenescent aging patterns. A major barrier in accomplishing this has been the lack of laboratory, zoo, and field evidence about age patterns of growth, maintenance, fertility, and mortality for species across the tree of life. New statistical methods and software now permit the extraction of mortality patterns from field data that are sporadic or are missing observations (13). Further development of life-history models hinges on more extensive and reliable data as well as on experiments to reveal how much allocation of additional resources to, say, faster growth or a more effective immune system affects lifetime fertility and survival. Fundamental understanding of why humans deteriorate so sharply (14) compared with other species, why human mortality has fallen so

dramatically (15), and whether aging can be further delayed or even slowed (16) depends on knowledge of why some species senesce and others do not.

#### References and Notes

1. T. B. L. Kirkwood, *Nature* **270**, 301 (1977).
2. P. B. Medawar, in *Uniqueness of the Individual* (Lewis, London, 1952), pp. 44–70.
3. G. C. Williams, *Evolution* **11**, 398 (1957).
4. W. D. Hamilton, *J. Theor. Biol.* **12**, 12 (1966).
5. O. R. Jones *et al.*, *Ecol. Lett.* **11**, 664 (2008).
6. S. C. Stearns, *The Evolution of Life Histories* (Oxford Univ. Press, Oxford, New York, 1992).
7. L. Partridge, R. Sibly, R. J. H. Beverton, W. G. Hill, *Philos. Trans. Biol. Sci.* **332**, 3 (1991).
8. A. Baudisch, *Inevitable Senescence? Contributions to Evolutionary Demographic Theory*, Demographic Research Monographs (Springer, Berlin, 2008).
9. J. W. Vaupel *et al.*, *Theor. Popul. Biol.* **65**, 339 (2004).
10. M. J. Dañko *et al.*, *PLoS ONE* **7**, e34146 (2012).
11. A. Baudisch, *Gerontology* **10.1159/000341861** (2012).
12. R. Salguero-Gómez, B. C. Casper, *J. Ecol.* **98**, 312 (2010).
13. F. Colchero *et al.*, *Methods Ecol. Evol.* **3**, 466 (2012).
14. A. Baudisch, *Methods Ecol. Evol.* **2**, 375 (2011).
15. O. Burger, A. Baudisch, J. W. Vaupel, *Proc. Natl. Acad. Sci. U.S.A.* **10.1073/pnas.1215627109** (2012).
16. J. W. Vaupel, *Nature* **464**, 536 (2010).
17. F. B. Turner, K. H. Berry, D. C. Randall, G. C. White, “Population ecology of the desert tortoise at Goffs, California, 1983–1986. Report No. 87-RD-81” (Southern California Edison Company, 1987).
18. D. E. Martinez, *Exp. Gerontol.* **33**, 217 (1998).

**Acknowledgments:** We thank L. Partridge, F. Colchero, D. Conde, D. Levitis, O. Jones, R. Salguero-Gomez, A. Scheuerlein, and the Evodemo group at the Max Planck Institute for Demographic Research. Supported by NIH grant AG-031719.

10.1126/science.1226467

## EVOLUTION

# How Cichlids Diversify

M. Emília Santos and Walter Salzburger

**H**ow is genetic variation connected to morphological evolution? How did Earth’s spectacular organismal diversity evolve and how is it maintained? To answer these fundamental questions, scientists must understand how organisms function and diversify and how they interact with other organisms and the environment. Recent studies of cichlids, including (1–7), are beginning to provide insights into the basis of diversification in this exceptionally diverse fish family.

Many widely used biological model systems only provide limited insights into organismal diversification. Traditional laboratory-based model organisms tell us little about how

organisms survive, adapt, behave, and reproduce in the wild. Model organisms used in evolutionary and ecological research, on the other hand, are often difficult to breed, their genomes are poorly characterized, and few genetic and developmental tools are available to study them. Furthermore, most established model systems are not very diverse taxonomically and phenotypically. Notable exceptions are instances of adaptive radiation, that is, the rapid origination of a multitude of phenotypically diverse species from a common ancestor through adaptation to distinct ecological niches (8, 9). Famous examples of adaptive radiations include Darwin’s finches on the Galápagos archipelago, silversword plants on Hawaii, anole lizards on islands of the Caribbean, and cichlid fishes in East Africa.

In the case of cichlids, hundreds of endemic species evolved independently in

The extreme diversity of cichlid fishes in East Africa helps to elucidate how and why organisms diversify.

each of the three East African Great Lakes: Victoria, Malawi, and Tanganyika. Cichlids thus form by far the most species-rich extant adaptive radiations. They split up into distinct species in such little time that their DNA is still almost identical, a situation comparable to an experimental mutagenesis screen, yet in a natural environment (10).

Analyses of draft genome and transcriptome sequences have demonstrated the potential provided by such data (1, 2, 5, 7, 11). Loh *et al.* (1), for example, investigated microRNA genes, which are important agents for the regulation of gene expression, and detected signatures of divergent natural selection in microRNA target sites among Lake Malawi cichlids. A comparative transcriptome analysis revealed little divergence at protein-coding sequences but high divergence in untranslated regions that are impor-

Zoological Institute, University of Basel, Vesalgasse 1, CH-4051 Basel, Switzerland. E-mail: emilia.santos@unibas.ch; walter.salzburger@unibas.ch

**Getting to the Root of Aging**

Annette Baudisch and James W. Vaupel (November 1, 2012)  
*Science* **338** (6107), 618-619. [doi: 10.1126/science.1226467]



Editor's Summary

---

This copy is for your personal, non-commercial use only.

---

- Article Tools** Visit the online version of this article to access the personalization and article tools:  
<http://science.sciencemag.org/content/338/6107/618>
- Permissions** Obtain information about reproducing this article:  
<http://www.sciencemag.org/about/permissions.dtl>

*Science* (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright 2016 by the American Association for the Advancement of Science; all rights reserved. The title *Science* is a registered trademark of AAAS.