
Foreword

What is the ultimate cause of aging? Before Dr. Annette Baudisch began her research on this question, aging was thought to be fundamentally a consequence of the decline with age of the force of Darwinian selection. Only a fraction of individuals survive to older ages and only a fraction of their fertility remains. Consequently, deleterious mutations that act only at older ages will be purged so slowly over successive generations that such mutations will accumulate in the population. This implies that starting at the age of reproductive maturity death rates will begin to increase. As William D. Hamilton put it, "senescence is an inevitable outcome of evolution." This view was biological dogma for half a century – until Dr. Baudisch's compelling critique and radical breakthrough, cogently explained in this monograph.

Dr. Baudisch distinguishes between aging and senescence, defining aging as the pattern of change in mortality over age and senescence as an increase in mortality with age. She shows that for some species mortality goes down with age or stays constant – something she calls sustenance. In this monograph she presents some empirical evidence for this, but mainly she develops the theoretical argument that the age-pattern of mortality is a consequence of a species' optimizing limited resources. Tradeoffs must be made between spending energy on growth, repair and maintenance, on the one hand, and reproduction, on the other. If enough is spent on growth, repair and maintenance, then there is no increase in mortality with age. Senescence results from the cumulative impact of an imbalance between damage and repair. If, as Dr. Baudisch demonstrates, the level of repair and regeneration is sufficient to counter-balance new damage and destruction, then an organism can maintain itself. With this research Dr. Baudisch has made

a major contribution to knowledge and has created a new agenda for research on the evolutionary biology of aging.

The first chapter of Dr. Baudisch's monograph sets the stage by reviewing evolutionary theories of senescence, discussing how senescence and fitness can be measured, outlining the optimal life-history approach, and summarizing some recent research developments. The chapter is much more than a critical survey of the literature: it is a lucid, original account of key research questions and strategies.

The second chapter carefully considers Hamilton's indicators of the force of selection. Insight after insight is gained as Dr. Baudisch probes deeper and deeper. She shows that Hamilton's claim that senescence is inevitable can be disproved even within Hamilton's restricted framework. In particular, she demonstrates that depending on the measure used and on levels of mortality and fertility, the force of selection can increase with age. Furthermore, she explains why and how the age-trajectories of mortality and fertility depend not only on the force of selection but also on the incidence of mutations. Dr. Baudisch's findings in this chapter strengthen the case that demographic schedules of mortality and fertility over most of the life course are largely shaped by optimization of tradeoffs rather than by mutation accumulation. An earlier version of the chapter was published as a single-authored article¹ in *PNAS, the Proceedings of the National Academy of Sciences of the United States*.

In her third chapter, Dr. Baudisch critically explains the limitations of Hamilton's framework. By presenting empirical evidence and by systematically reviewing various theoretical considerations, she develops further reasons why mutation accumulation is of secondary importance in molding age-trajectories of mortality. Instead, the primary force is adaptation: patterns of aging are a byproduct of the optimization of tradeoffs. In addition, Dr. Baudisch shows that Hamilton's notion – that the age pattern of mortality is inversely related to his indicator – is wrong. The relationship between the force of selection and the pattern of mortality is so complicated that sophisticated modeling is required.

Chapters 4 and 5 of Dr. Baudisch's monograph develop two kinds of optimization models, which she analyzes using sophisticated methods of control theory and dynamic programming. In Chapter 4 the focus is on the role of growth. By investing in continued growth, the individuals

¹ Annette Baudisch. Hamilton's Indicators of the Force of Selection. *Proceedings of the National Academy of Sciences, USA*, 102(23):8263–8268, 2005. Copyright (2005) National Academy of Sciences, U.S.A.

in a species can attain greater size. If chances of survival increase as size increases, then death rates can fall with continued growth. Dr. Baudisch shows that it can be optimal to grow rather than to invest more available resources in fertility.

In Chapter 5, she considers a model of vitality, i.e., size adjusted for functioning. Dr. Baudisch shows that various patterns of aging are optimal depending on a species' characteristics. In particular, sometimes senescence is optimal and sometimes it is not. The dichotomy depends on various factors, including the hazardousness of the environment, whether there are economies of scale in investing in growth and maintenance, and whether there are economies of scale in reproduction.

Only under particular conditions do Dr. Baudisch's models in Chapters 4 and 5 lead to senescence. Her simpler models imply sustenance; senescence is optimal only in more complicated, restricted models. Not only is senescence not inevitable: senescence is a special case. In her sixth and final chapter, Dr. Baudisch points to directions for future research. Some of the suggestions concern the burning questions she would like to address next. Other suggestions pertain to the development of the field of evolutionary demography. This is an exciting, insightful chapter, full of ideas presented in a judicious balanced manner. It will guide other researchers: it adumbrates an important new field of inquiry.

The monograph builds on Dr. Baudisch's doctoral dissertation. In particular, Chapter 5 has been substantially revised and strengthened, in part of a result of an insight of Arthur Robson, Professor of Economics at Simon Fraser University, and comments from and subsequent interchanges with Kenneth Wachter, Professor of Demography and Mathematical Statistics at the University of California Berkeley, member of the U.S. National Academy of Sciences. Prof. Linda Partridge, an evolutionary biologist at University College London who was recently appointed Director of the new Max Planck Institute for the Biology of Aging, and I served as her dissertation advisors. Annette Baudisch received her doctorate after being examined in June 2006 by Michael Murphy, Professor at the London School of Economics and past President of the British Population Association and Brian Charlesworth, Professor at the University of Edinburgh and Fellow of the Royal Society, an evolutionary biologist who has focused much of his research on evolutionary theories of aging.

Kenneth Wachter emailed Dr. Baudisch: "I read your dissertation. . . . It is the most thought-provoking and comprehensive dissertation I have

read in many years.” This judgment was confirmed when the Max Planck Society in June of this year awarded Dr. Baudisch the Otto Hahn Medal, the Society’s highest prize for doctoral research.

The pathbreaking research of Dr. Annette Baudisch in her dissertation, further developed in this monograph, fundamentally alters understanding of the evolution of aging. Numerous researchers will spend years exploring the field she has opened up, trying to understand why some kinds of species suffer senescence whereas others enjoy sustenance. Her dissertation is exceptionally important, stimulating and insightful. This monograph is even better.

The series of Demographic Research Monographs is under the editorial supervision of the Max Planck Institute for Demographic Research. I am Editor-in-Chief. I am advised by an Editorial Board that currently consists of Prof. Elisabetta Barbi (Messina University, Italy), Prof. Gabriele Doblhammer (Rostock University, Germany), Dr. Jutta Gampe (Max Planck Institute), Prof. Joshua Goldstein (Max Planck Institute), and Prof. Bernard Jeune (University of Southern Denmark). Additional members of the Editorial Board will be appointed as needed to review manuscripts submitted for possible publication. The current manuscript was reviewed and accepted by James Vaupel, Joshua Goldstein and Jutta Gampe.

The Demographic Research Monographs series can be considered the successor to the series called Odense Monographs on Population Aging, edited by Bernard Jeune and James Vaupel. The volumes in this now-terminated series were first published as hardcover books by an academic publisher, Odense University Press, and subsequently made available online at www.demogr.mpg.de/books/odense. The nine Odense Monographs on Population Aging include two collections of research articles that focus on specific subjects on the frontier of demographic research, three volumes by senior researchers that present path-breaking findings, a review of research on a topic of emerging interest, a presentation of a new method for analysis of demographic data, an outstanding doctoral dissertation, and a unique collection of important demographic data on non-human species.

The series of Demographic Research Monographs will continue this mix, with books that are often under 200 pages in length, that have a clear focus, and that significantly advance demographic knowledge. Research related to population aging will continue to be a focus on the series, but it will not be the only one. The series will embrace all of demography, broadly defined. As indicated by the first volume in the series, an important subject will be historical demography. We also

plan to publish research on fertility and family dynamics. Mathematical demography is the core of the population sciences and we will strive to foster monographs that use mathematics and statistics to further develop the theories and methods of demography. Biodemography is a small but rapidly growing and particularly innovative branch of demography: we will seize opportunities to publish monographs at the intersection of biology and demography, pertaining both to human and other species, and including demographic research with ties to such fields as epidemiology, genetics, evolutionary biology, life-history biology, experimental demography, and paleodemography.

Each volume in the Demographic Research Monograph series will have a substantial link to the Max Planck Institute for Demographic Research. As well as being published as hardcover books by Springer-Verlag, the volumes of the Max Planck series of Demographic Research Monographs will subsequently be available at www.demogr.mpg.de/books/drm. The online version may include color graphs, supplemental analyses, databases and other ancillary or enhanced material. Parallel publication online and in print is a significant innovation that will make the monograph series particularly useful to scholars and students around the world.

Rostock,
August 2007

James W. Vaupel
Editor-in-Chief