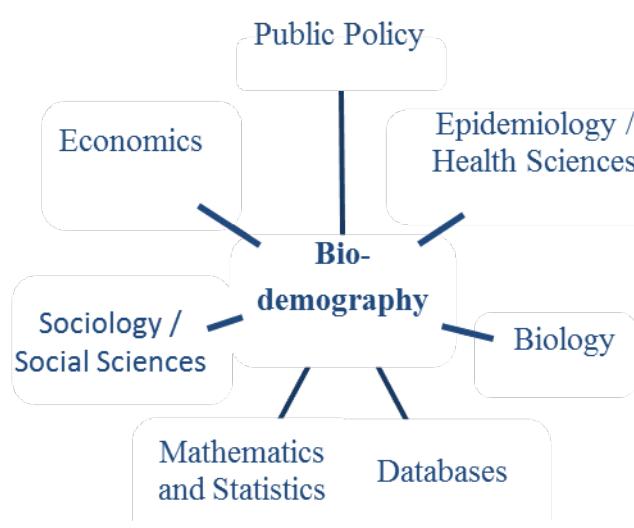


# Report on the Max-Planck Odense Center, 13 December 2016

## I. Overview

The Max-Planck Odense Center on the Biodemography of Aging (MaxO) aims to publish pathbreaking, interdisciplinary research—on humans and on species across the tree of life—that advances fundamental understanding of the nature of aging and thereby fosters the development of the nascent discipline of Biodemography.



The chart summarizes MaxO's place in the world of ideas. Demography is a mathematical discipline: demographers prove theorems. Furthermore, demographers have made and continue to make important contributions to mathematical statistics. Large, accurate databases constitute the second pillar on which Demography rests; MaxO's research is built on analysis of human databases and creation and use of new databases for nonhuman species. Demographers often collaborate with (and have university degrees as) economists and social scientists. The main goal of MaxO is to foster collaboration with Epidemiology and other Health Sciences and with Biology. Demographic findings, including findings about aging, are often relevant to public discussions.

MaxO is a joint venture between the Max Planck Society (henceforth MPG, its German abbreviation) and the University of Southern Denmark (henceforth SDU, its Danish abbreviation). Support from MPG comes from the Max Planck Institute for Demographic Research (henceforth MPIDR) and some of MaxO's research is carried out at MPIDR. Additional support comes from the central headquarters of MPG in Munich (henceforth MPG Munich or just Munich). Sometimes we will refer to SDU as Odense, especially when we want to emphasize that the research is carried out at the Odense campus of SDU. Sometimes we will refer to MPIDR as Rostock, especially when we want to emphasize research done in collaboration with the University of Rostock.

The Staff List in section IV below provides details about MaxO personnel. To concisely provide background information about those associated with MaxO we use these codes:

- **bold red:** Leaders of MaxO at SDU not paid by MaxO
- **red:** Researchers at SDU paid by MaxO
- **red underlined:** Close current or former ties to SDU
- **blue:** Researchers at MPIDR paid by MaxO
- **light blue:** Collaborators at MPIDR not paid by MaxO
- **blue underlined:** Close current or former ties to MPIDR
- **green:** Main external collaborators
- **italics:** EDSD graduates
- **Vaupel** is bold red double underlined in blue as Director of MaxO and MPIDR.

The 19 full, Assoc. and Asst. Professors and postdocs plus the 17 Ph.D. students working in MaxO at SDU (the 36 “core” MaxO SDU researchers) are associated with the Faculty of Health Sciences (20), the Faculty of Natural Sciences (13 in Biology and 2 in the Institute of Mathematics and Computer Science) and Economics (1 Ph.D. student). Three researchers have left MaxO. Of the 36 current core SDU researchers, 28 are paid by MaxO's budget at SDU, 3 are paid by MaxO's budget at MPIDR, and 5 (**Baudisch, Canfield, Christensen, Lindahl-Jacobsen** and **Vaupel**) are paid directly by SDU or Max Planck Munich.

MaxO researchers are united by their goal of advancing Biodemography. Appropriately they come from disparate academic backgrounds—some have degrees in Public Policy, Economics and Sociology; others in Mathematics and Statistics; some are M.D.’s or Ph.D. epidemiologists; some have studied various aspects of Biology, particularly Ecology and Evolution. Most have substantial knowledge of Demography, although some studied mainline human demography, others are strong in formal (mathematical) demography, and still others are population biologists with interest in evolutionary theory (because as noted in **II.B**, evolution drives and is driven by demography). Hence the greatest challenge facing MaxO has been to unite the members of the group into an interdisciplinary team with a common vocabulary and an appreciation for each other’s knowledge. MaxO has done so by holding well-attended joint research meetings once a week (every Monday from 10 to 11.) Furthermore, smaller, more informal meetings are frequent, often over lunch.

These MaxO discussions have led to a growing number of joint publications. Two-page descriptions of six of these articles are given in section **II**. The 157 most collaborative publications are listed in section **V**. Of these, 14, 9 and 18 were published in 2013, 2014 and 2015: most MaxO publications in these three years had a single author or non-MaxO coauthors. In 2016 the number of collaborative MaxO articles, published or accepted, jumped to 34. Moreover 16 additional articles were submitted in 2016 and are under review. A further 66 manuscripts were started, mostly in 2016, by partnerships of at least two and usually more MaxO researchers; only 11 articles with a single MaxO author are currently in preparation. MaxO has become an engine for innovative, interdisciplinary research by MaxO teams.

To provide structure for these teams, MaxO has developed 8 Research Clusters that are described in section **III**. The members of each Cluster regularly meet with each other to discuss ongoing or prospective research; each Cluster makes several presentations per year at the weekly MaxO meetings.

MaxO publications have gotten substantial attention, in some cases from a wide range of newspapers, popular journals and radio and TV stations, as documented in section **VIII**. More generally, MaxO has put considerable emphasis on outreach by MaxO researchers and through MaxO’s partnership with Population Europe; again this is described in section **VIII**.

In addition to publications, MaxO’s research output includes the education of Ph.D. students: as detailed in section **VII**, 16 are currently completing their dissertations at MaxO SDU, 4 at MPIDR and 1 jointly at both locations. MaxO will foster the generation of demographers after them by hosting the one-year European Doctoral School of Demography in 2017-8 and 2018-9. Several MaxO researchers, including [Baudisch](#), [Canudas-Romo](#), [Christensen](#), [Lenart](#), [Oeppen](#) and [Vaupel](#), have taught in the EDS program in previous years.

The two fuels that power MaxO are math and data. Nearly all the full, Assoc. and Asst. Professors as well as the postdocs at MaxO have strong mathematical and statistical skills; most have profound comprehension. This is also true of the Ph.D. students. Indeed, the breadth and depth of quantitative competence at MaxO are extraordinary.

The second lifeblood of MaxO is data. Researchers at MaxO make intensive use of large, accurate databases that researchers at MaxO have helped to create. Some pertain to humans. [Vaupel](#) has fostered the Human Mortality Database since its inception; work on this database is a main activity of the Datalab at MPIDR. He has also led efforts to create IDL, a database on people age 110+ that is now being expanded to 105+. These databases are being used by members of the Pace and Shape, Age-Trajectories and Forecasting Clusters. Also important is the Survey of Health, Aging and Retirement in Europe (SHARE) database. [Andersen-Ranberg](#), who oversees SHARE’s medical and genetic data, is a member of the Epidemiology, Biostatistics and Biodemography Unit. Under the leadership of [Lindahl](#),

**Jacobsen** and Linda Ahrenfeldt, several researchers at MaxO are analyzing SHARE data as are other researchers at SDU.

MaxO has a unique setting in Denmark, a country with the most registered population in the world. Total population registries on cancer (since 1943) causes of death (since 1943), population (since 1968), health (since 1974) and social conditions (since 1972) permit analysis of micro observations at the individual level to deepen understanding of macro population structures and dynamics—and *vice versa*. The Health-Sciences part MaxO at SDU is part of the unit on Epidemiology, Biostatistics and Biodemography (EBB) led by **Christensen**. EBB has in-house the Danish Twin registry with, lifestyle factors, health, survival, genetic markers, and social information on all twins in Denmark as well as similarly detailed data on the oldest old cohorts of Danes born in 1895, 1905, 1910 and 1915.

In addition to these exceptional databases on humans, MaxO uses—and has played the key role in creating—large, reliable databases on nonhuman species, as described in section **III.G**.

Why is the broad canvas of MaxO research needed to more deeply understand human aging? Conversations among demographers, epidemiologists, biologists and others working in interdisciplinary teams are necessary to achieve deep understanding of the very difficult questions of how and why we age and how long we will live in the future. Crucially-important molecular studies, such as those notably being carried out by the Max Planck Institute for Biology of Ageing in Cologne, have to be augmented by the population-level studies being carried out at MaxO. The wide-ranging and ambitious initiatives at MaxO are risky because it is time-consuming for researchers to learn to talk with and collaborate with researchers with very different backgrounds. To maximize numbers of research publications, researchers are better advised to stick to narrow topics within well-established subdisciplines. The researchers recruited to MaxO are putting their careers at stake in a high-risk but high-payoff initiative. Progress since 2013 has been remarkable and the future is promising.

Another approach to understanding the structure and dynamics of MaxO is to examine the expenditures and revenues given on the back page of this Report. Total expected expenditures of MaxO over the five years from 2013 through 2017 are just over €12 million. Some 90% of these expenditures were at SDU; the remaining 10% were at MPIDR. The expenditures at MPIDR were all in 2013, 2014 and the first half of 2015. Following the contract between MPG and SDU, there were no official MaxO expenditures at MPIDR afterwards but there was close collaboration between MaxO and parts of MPIDR (especially **Vaupel's** department but also [Anna Oksuzyan's](#) Research Group and the secretariat of Population Europe); the magnitude of additional expenditures at MPIDR that were associated with activities directly or indirectly related to MaxO is, very roughly and as an upper bound, given in the last column of Table **XI.1** as somewhat less than €5 million over the five years 2013-2017.

The total revenues of MaxO over 2013-2017 are the same as the total expenditures, just over €12 million. Exactly €5 million were contributed by MPG; about three-quarters of this amount came from MPIDR's budget and the remaining quarter from MPG Munich. When the contract between MPG and SDU was being negotiated, it was envisioned that MPIDR and MPG Munich would each contribute €2.5 million. A budget crisis caused by a deficit in the MPG building budget, however, required MPG Munich to cut expenditures in 2013, 2014 and the first half of 2015. MPIDR picked up the shortfall in MaxO's budget.

The revenues of MaxO were increased by €2.1 million from external grants. It can be seen in Table **XI.2** that this funding was modest (but increasing) in 2013-5, jumped in 2016 and doubled in 2017 from 2016 levels. Funding from external grants will increase MaxO expenditures by 50% in 2017. We expect that substantial external funding will contribute to MaxO activities in 2018 and afterwards. Indeed, much of this funding is already in place, as can be seen in the list at the bottom of the Budget page.

## II. Summaries of 6 Research Articles

**II.A Lancet 382:1507-13 (2013), Physical and cognitive functioning of people older than 90 years: a comparison of two Danish cohorts born 10 years apart by Kaare Christensen, Mikael Thinggaard, Anna Oksuzyan, Troels Steenstrup, Karen Andersen-Ranberg, Bernard Jeune, Matt McGue, and James W. Vaupel**

A rapidly increasing proportion of people in high-income countries are surviving into their tenth decade. Concern is widespread that the basis for this development is the survival of frail and disabled elderly people into very old age. In younger elderly people (ages 65–85 years) mixed results about health have been reported, but generally more recent birth cohorts have more diseases (partly because of improved diagnostics), possibly better physical functioning, and consistently better cognitive functioning than do earlier birth cohorts—the latter designated as the Flynn effect (Christensen et al. Lancet 2009, Flynn AmPsychol 1999). However, some researchers have suggested that cohort differences that exist in younger elderly people could be eliminated at older ages by mortality-related processes. In this study, we investigated two complete Danish birth cohorts of nonagenarians born 10 years apart, in 1905 and 1915. The 1905 cohort study took place from August to October, 1998, and included all Danes born in 1905 who lived in Denmark at the time of the survey, a total of 3600 people aged 92–93 years. The 1915 cohort study took place 12 years later, from September to November, 2010, and included all Danes born in 1915 who lived in Denmark at the time of the survey, a total of 2509 people aged 94–95 years (see Figure). The two surveys used the same design and survey instrument. No exclusion criteria were applied: all individuals born in Denmark and living in Denmark during the relevant study periods were approached, irrespective of type of residence, health, or cognitive status.

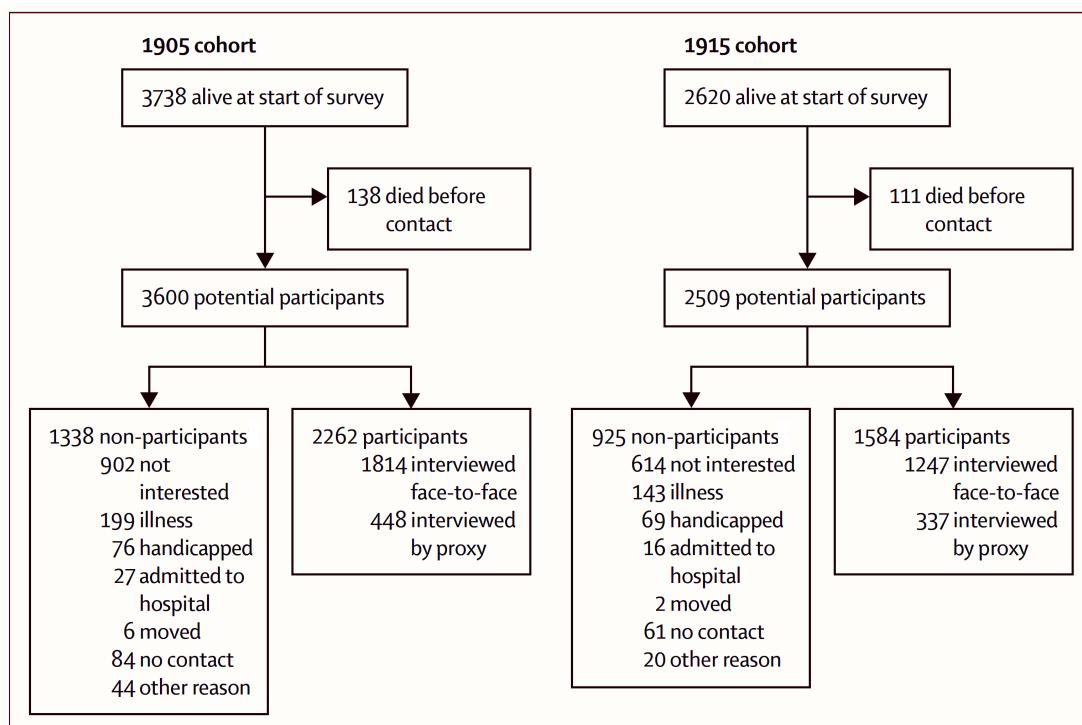


Fig. Study profile for 1905 and 1915 cohorts

On the basis of the Danish cohort life tables (Human Mortality Database accessed March 25, 2013), the chance of surviving from birth to age 93 years was 28% higher in the 1915 cohort than in the 1905 cohort (6.50% vs 5.06%), and the chance of reaching 95 years was

32% higher in the 1915 cohort (3.93% vs 2.98%). The study showed that the general cognitive improvement seen in younger elderly people does continue into very old age as 95-year-olds born in 1915 were doing significantly better cognitively than 93-year-olds born in 1905 (see Table). We also found an improvement in activities of daily living (ADL), but no consistent differences in the physical performance tests between the two cohorts. This finding suggests that the basis for the improved ADL in the later cohort is improved cognitive functioning and living conditions in elderly people, as well as better aids to support mobility and independence.

**Table: Cognitive measures, activities of daily living and physical performance scores for the 1905 and 1915 cohorts\***

	1905-cohort (n=2262)	1915-cohort (n=1584)	P-value
<b>Age</b>			
Mean (SD)	93.1 (0.3)	95.3 (0.3)	<0.001 <sup>†</sup>
<b>Men</b>			
Number (%)	584 (26%)	394 (25%)	0.523 <sup>§</sup>
<b>Cognitive composite score</b>			
Mean (SD)	0.01 (3.6)	0.49 (3.6)	0.0003 <sup>†</sup>
<b>Mini-mental state examination</b>			
Mean (SD)	21.4 (6.0)	22.8 (5.6)	<0.0001 <sup>‡</sup>
<b>Activities of daily living score</b>			
Mean (SD)	1.8 (0.7)	2.0 (0.8)	<0.0001 <sup>‡</sup>
<b>Grip strength</b>			
Mean (SD)	16.1 (6.6)	16.2 (6.6)	0.608 <sup>†</sup>
<b>Cannot stand from chair</b>			
Number (%)	132 (7.7)	127 (10.4)	0.012 <sup>§</sup>
<b>Gait speed (time to walk 3 m in s)</b>			
Mean (SD)	6.5 (3.1)	6.1 (2.7)	0.004 <sup>‡</sup>

\* Higher scores in each of these continuous measures indicate better functioning except for gait speed. <sup>†</sup>Test of equal mean, with an assumption of equal variance (test of equal variance is not rejected). <sup>‡</sup>Test of equal mean, without an assumption of equal variance (test of equal variance is rejected). <sup>§</sup> Test of equal proportions (Fisher's exact test).

As early as 1977, Gruenberg proposed that increased longevity as a consequence of decreasing mortality from chronic diseases (due to improvements in medical treatment of those with chronic diseases) would induce a decline in the health of elderly people (Gruenberg Milbank Mem 1977). He called this development the failure-of-success. The present study does not support this hypothesis. On the contrary, the 1915 cohort performed better on the cognitive tests and on the ADL score than the 1905 cohort despite being 2 years older. This suggests that more people are living to older ages with better overall functioning which could be due to early diagnosis and improved treatment of prevalent diseases and the health benefits of improved standards of living, increased educational achievement, and healthier lifestyles - a success-of-success.

**Citations** (as of 12 December 2016) ISI Web of Science: 66; Google Scholar: 151

**II.B NATURE** 505: 169-173(2014), **Diversity of ageing across the tree of life** by [Owen R. Jones](#), [Alexander Scheuerlein](#), [Roberto Salguero-Gómez](#), Carlo Giovanni Camarda, [Ralf Schaible](#), Brenda B. Casper, [Johan P. Dahlgren](#), Johan Ehrlén, María B. García, Eric Menges, Pedro F. Quintana-Ascencio, [Hal Caswell](#), [Annette Baudisch](#), [James W. Vaupel](#)

Evolution drives and is driven by demography. A genotype moulds its phenotype's age-patterns of mortality and fertility in an environment, and these patterns determine the genotype's fitness in that environment. Therefore, to understand the evolution of ageing, we must compare age-patterns of mortality and reproduction for species across the tree of life. Nevertheless, few studies have done so, and those few have been taxonomically limited, for example focusing on a single group like mammals.

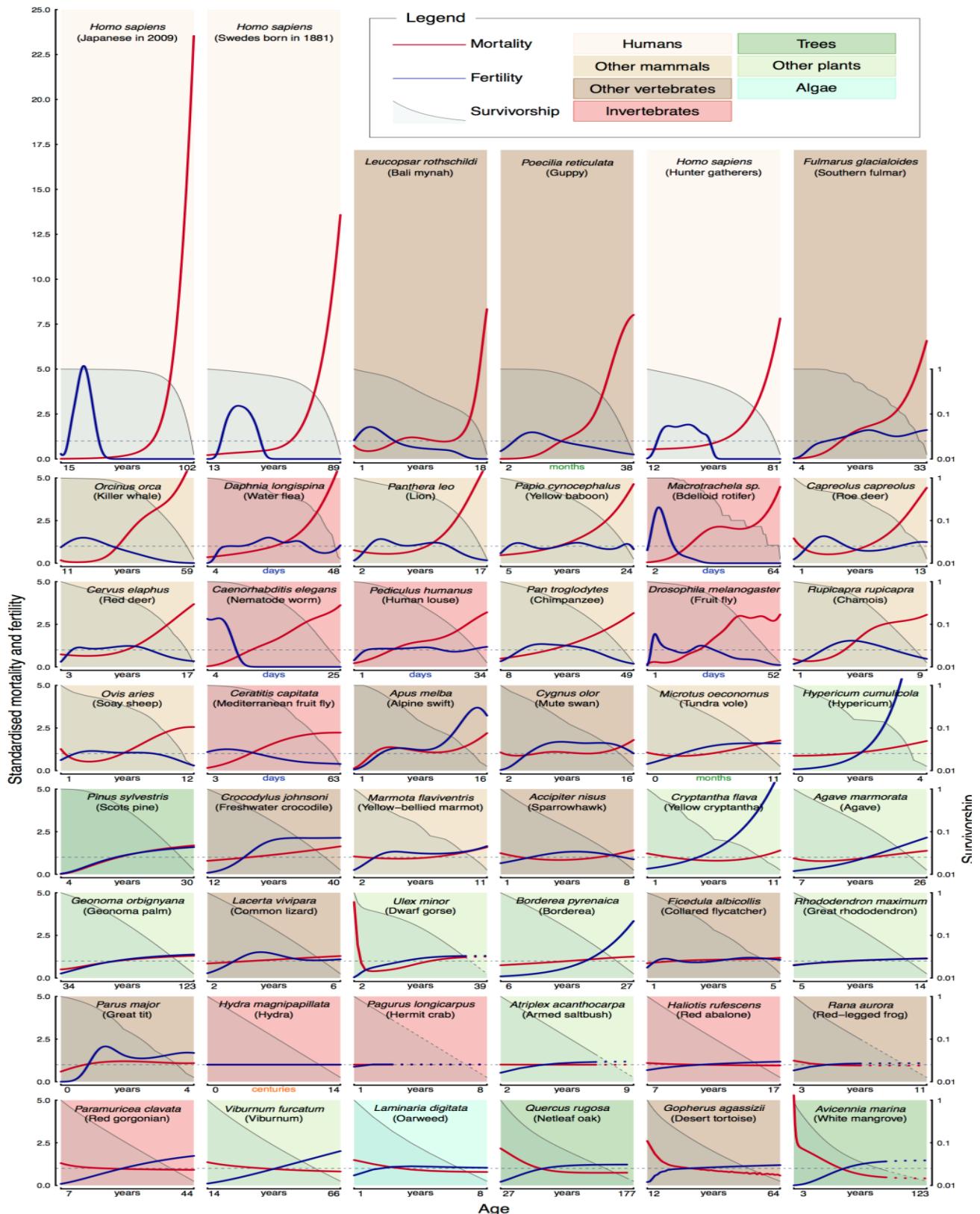
In our ground-breaking study we rectify this by examining the standardised age-patterns of mortality and fertility for a large diversity of species -- 11 mammals, 12 other vertebrates, 10 invertebrates, 12 vascular plants, and a green alga. What we found was remarkable. Our species showed an extraordinary variety in trajectories of mortality and fertility, including increasing, constant, decreasing, humped and bowed trajectories for both long and short-lived species. Our Figure (on the next page) orders species by the amount of relative mortality experienced at the end of the life course and thus illustrates a continuum from positive to negligible to negative senescence.

This surprising diversity is at odds with the canonical evolutionary theories of aging – mutation accumulation, antagonistic pleiotropy, and disposable soma – which provide explanations solely for age patterns of increasing mortality and decreasing fertility from maturity.

Besides the diversity itself, perhaps the most striking pattern in the Figure is the mortality trajectory for post-industrial humans, exemplified by Japanese women in 2009. The steep rise with age in relative mortality for these women is extreme even compared to historical populations such as the Swedish 1881 cohort and to hunter-gatherers whose mortality experience may be typical of humans over most of our existence. The increased steepness of the rise of human mortality has largely occurred over the past century, indicating that it was behavioural and environmental change (including advances in health care) and not genetic change that moulded the current pattern. Our close relatives, chimpanzees and baboons also show a rise in mortality with age but far less than that for hunter-gatherers.

There are clear indications that phylogenetic relatedness plays a role in determining mortality and fertility patterns: All mammals are clustered in the upper part of the Figure, while birds are somewhat more scattered. Amphibians and reptiles are found in the lower half of the panel, with flat mortality shapes and almost no overlap with mammals. In contrast, invertebrates are scattered across the continuum of senescence. The plants we analysed tend to occur lower in our ordering with many species appearing to escape senescence. Such clustering within broad taxonomic levels of kingdom (plants, animals), or class (mammals, birds), suggests that primitive traits related to the bauplan of species may play a pivotal role in determining patterns of ageing.

The diversity illustrated in this work challenges theoreticians to develop broader perspectives on the evolution of ageing and empiricists to study the demography of more species. A deeper understanding of the evolutionary demography of ageing depends on the compilation of demographic data on diverse species and on the development of more inclusive theories that can account for negligible and negative senescence as well as for the steepness of deterioration with age in senescent species. In such empirical and theoretical studies, researchers should guard against anthropocentric intuition about ageing: humans, especially modern humans, are extreme outliers.



**Fig.** Demographic trajectories. Relative mortality (red) and fertility (blue) as functions of age, from maturity to the age when only 5% of the adult population is still alive; mortality and fertility are scaled relative to their means. Subplots are arranged in order of decreasing relative mortality at the terminal age. Survivorship (on a log scale) from maturity is depicted by the shaded areas.

Citations (as of 9 December 2016) ISI Web of Science: 105; Google Scholar: 205

**II.C PNAS 112: 15701-15706 (2015), Constant Mortality and Fertility over Age in *Hydra***  
by Ralf Schaible, Alexander Scheuerlein, Maciej J. Dańko, Jutta Gampe, Daniel E. Martínez,  
**James W. Vaupel**

Senescence, the increase in mortality and decline in fertility with age after maturity, was thought to be inevitable for all multicellular species capable of repeated breeding. Recent theoretical advances and compilations of data suggest that mortality and fertility trajectories can go up, down or remain constant with age, but the data are scanty and problematic.

Constant mortality in a population can arise even if the risk of death rises with age for all surviving individuals in the population- if some individuals are frailer than others with a higher chance of death at any specific age. In this case, ageing of the survivors will increase average mortality while the death of frailer individuals will lower average mortality for the surviving cohort: the two processes can balance each other. To determine whether individuals are deteriorating with age it is informative to study ageing on the individual level. This cannot be done by observing deaths alone because individuals die only once. Individual ageing can, however, be studied by observing repeated reproductive events. If an individual's fertility is constant or increasing with age, then this is strong evidence that the individual is not deteriorating with age. Hence we carefully studied the fecundity of individual *Hydra*. Deaths for *Hydra* under laboratory conditions are so rare that it is unlikely that compositional change could account for constant mortality over age, but evidence that fertility does not decline with age would reinforce the conclusion that *Hydra* do not suffer senescence.

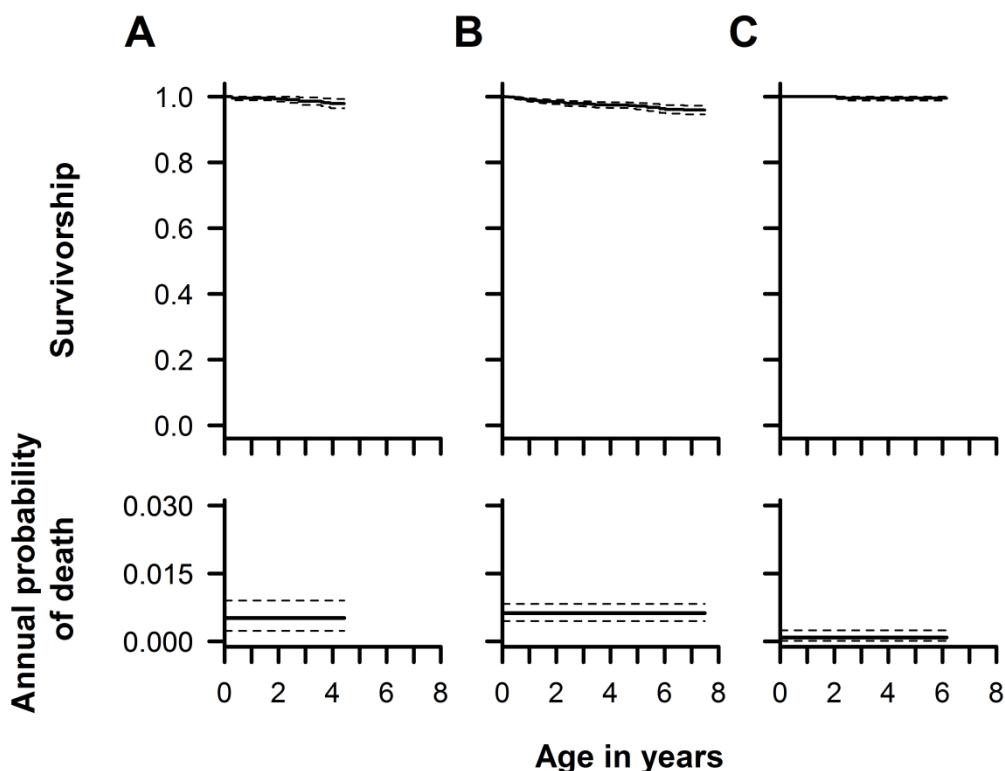
Here we present compelling evidence for constant age-specific death and reproduction rates in *Hydra*, a basal metazoan, in a set of experiments comprising more than 3.9 million days of observations of individual *Hydra*. Our data show that 2,256 *Hydra* from two closely-related species in two laboratories in twelve cohorts, with cohort age ranging from 0 to more than 41 years, have extremely low, constant rates of mortality (see Fig.). Fertility rates for *Hydra* did not systematically decline with advancing age (see Table). This falsifies the universality of the theories of the evolution of aging that posit that all species deteriorate with age after maturity. The non-senescent life history of *Hydra* implies levels of maintenance and repair that are sufficient to prevent the accumulation of damage for at least decades after maturity, far longer than the short life expectancy of *Hydra* in the wild. A high proportion of stem cells, constant and rapid cell turnover, few cell types, a simple body plan and the fact that the germ line is not segregated from the soma are characteristics of *Hydra* that may make non-senescence feasible. Non-senescence may be optimal because lifetime reproduction may be enhanced more by extending adult lifespans than by increasing daily fertility.

The title of Martínez's pioneering study of 1998 (*ExpGerontol*) is “*Mortality Patterns Suggest Lack of Senescence in Hydra*”; in contrast, the title of this article is “*Constant Mortality and Fertility over Age in Hydra*.” The earlier study was suggestive; this study is conclusive over the period of observation. The earlier study focused on mortality; this study shows that both mortality and fertility are constant. Researchers could dismiss the earlier study as small, incomplete, and inconclusive—and could continue to assert, citing Hamilton (*JTheorBiol* 1966), that for all multicellular organisms with repeated reproduction mortality inevitably rises with age starting at maturity and fertility inevitably falls. This view is no longer tenable.

**Table. Individual fertility.**

	1 <sup>st</sup> : 2 <sup>nd</sup> Quarter	2 <sup>nd</sup> : 3 <sup>rd</sup> quarter	3 <sup>rd</sup> : 4 <sup>th</sup> Quarter
Decreasing fertility	8%	2%	4%
Constant fertility	80%	76%	89%
Increasing fertility	12%	22%	7%
	100%	100%	100%

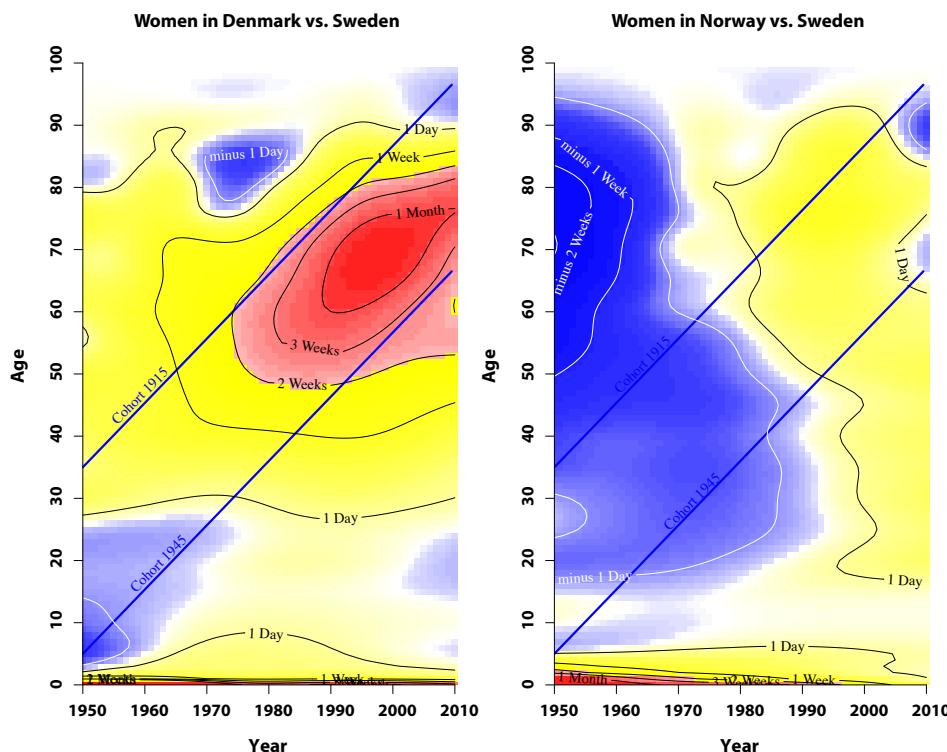
We compared, for all cohorts combined, the number of buds produced by an individual between consecutive quarters of the observation period. Using Chi-square we tested for equality and established for how many individuals budding significantly (at the 95% level) increased or decreased.



**Fig.** The figure shows the survivorship (Kaplan-Meier estimator; upper panels) and annual probability of death (lower panels) in twelve *Hydra* cohorts. (A) Combined data of the 3 Pomona cohorts Cohort P1: *H. vulgaris* strain AEP first generation, 22 individuals derived from fertilized eggs, observed after they were fully grown at 30 days of age; combined with 98 individuals that were raised from buds of the first generation. Cohort P2: 150 *H. vulgaris* strain ARG45a. Cohort P3: 150 *H. vulgaris* buds from strain AEP. (B) Combined data of a subset of Rostock cohorts that had the same annual probability of death as the Pomona cohorts. R1-R3 and R6-R9: (1428 individuals, *H. magnipapillata* strain 105). (C) Rostock cohorts R4 and R5 (408 individuals, *H. magnipapillata* strain 105) that differed from the other Rostock and all Pomona cohorts.

**II.D PNAS 113: 4015-20 (2016), Rise, stagnation, and rise of Danish women's life expectancy by [Rune Lindahl-Jacobsen](#), [Roland Rau](#), [Bernard Jeune](#), [Vladimir Canudas-Romo](#), [Adam Lenart](#), [Kaare Christensen](#), and [James W. Vaupel](#)**

Health conditions change from year to year, with a general tendency in many countries for improvement. These conditions also change from one birth cohort to another: some generations suffer more adverse events in childhood, smoke more heavily, eat poorer diets, etc., than generations born earlier or later. Because it is difficult to disentangle period effects from cohort effects, demographers, epidemiologists, actuaries, and other population scientists often disagree about the relative importance of cohort effects. In particular, some advocate forecasts of life expectancy based on period trends; others favour forecasts that hinge on cohort differences. A few birth cohorts have been identified with clear-cut cohort patterns: those of Britain in the late nineteenth and early twentieth centuries (Smith & Lynch *EurJEpid* 2004, Kermack et al. *IntJEpid* 2001); those of Japan in the early twentieth century (Willets *BrActuarialJ* 2004 ); and cohorts born in Britain in the 1930s, often referred to as the “golden generations” (Murphy *PopDevRev* 2010). In this study we presented another example of cohorts influencing mortality patterns, namely the case of the interwar generations of Danish women. We used a combination of age decomposition and exchange of survival probabilities between countries to study the remarkable recent history of female life expectancy in Denmark, a saga of rising, stagnating, and now again rising lifespans.

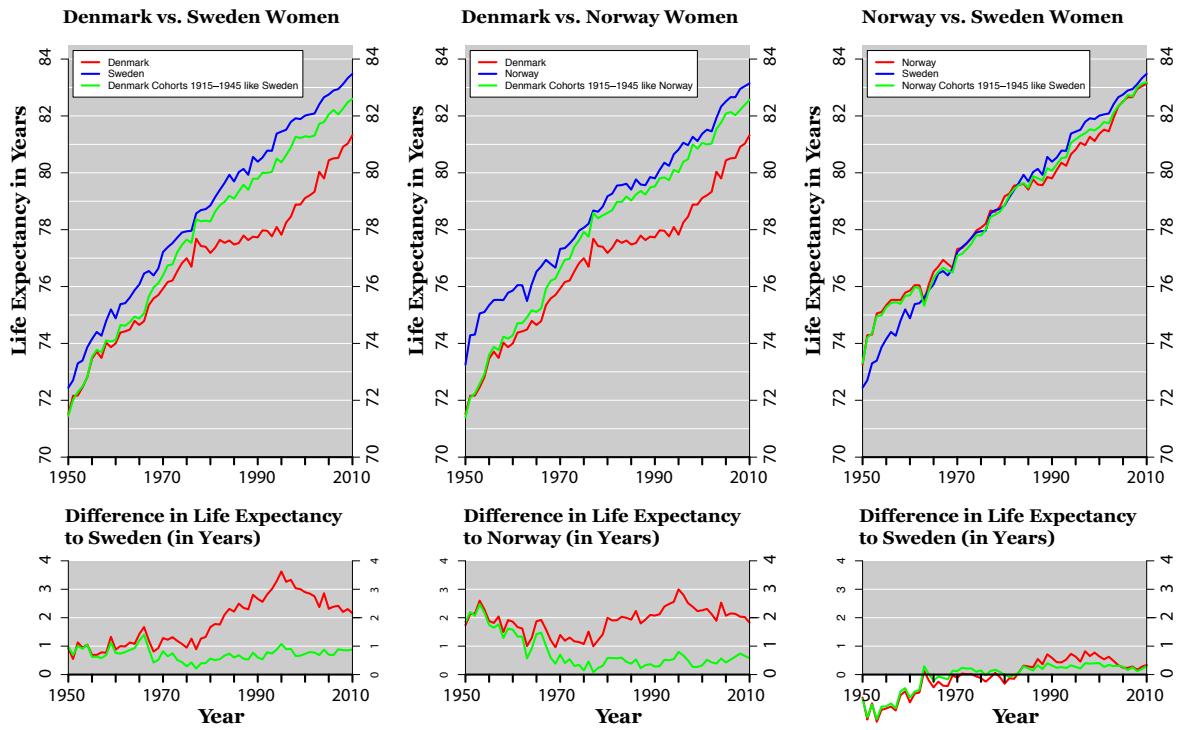


**Fig. 1.** Contour Lexis map plot of differences in life expectancies when comparing Danish and Swedish women and Norwegian and Swedish women

Our study illustrated a clear cohort effects on the life expectancy of Danish women. The decrease and later increase seen in life expectancy compared with Swedish women was driven by the high mortality of Danish women born 1915–1945 (see Figure 1).

If these Danish interwar women had had a mortality pattern similar to that of Swedish or Norwegian women in the period of stagnation, then no stagnation would have occurred (see Figure 2). As predicted by Jacobsen et al. (*EurJEpid* 2004), the dying out of the 1915–1945

generations in the three Scandinavian countries has triggered a more rapid increase in the life expectancy of Danish women compared with Swedish and Norwegian women.

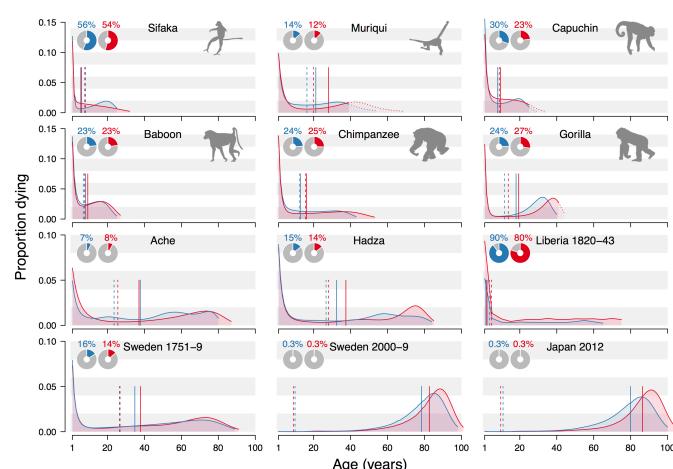


**Fig.2.** Trends and differences in life expectancy for Danish, Norwegian, and Swedish women since 1950 and hypothetical life expectancy of Danish and Norwegian women when assuming survival probabilities of Danish and Norwegian women born 1915–1945 equal those of Swedish women born 1915–1945.

The previous suggested explanation for the higher mortality of Danish women was a higher smoking rate throughout life in Danish women born between the two world wars compared with Danish women born before and after the two world wars (Jacobsen et al. *EurJEpid* 2004). Sweden and Norway did not experience the same stagnation in women's life expectancy. This finding supports the conclusion that smoking was a major explanation for the difference in life expectancy between Danish women and Swedish and Norwegian women, because markedly lower smoking rates throughout life were found for Swedish and Norwegian women (Jacobsen et al. *EurJEpid* 2004). Our findings illustrated the importance of incorporating the cohort in studies of changes in life expectancy and presented an important new example of cohort effects on population mortality patterns. Also, our study showed that the lower Danish female life expectancy was caused by the interwar cohorts and was not attributable to period effects.

**II.E PNAS 113: E7681-E7690 (2016) The emergence of longevous populations by Fernando Colchero, Roland Rau, Owen Jones, Julia Barthold, Dalia A. Conde, Adam Lenart, Laszlo Nemeth, Alexander Scheuerlein, Jonas Schöley, Catalina Torres, Virginia Zarulli, Jeanne Altman, Diane K. Brockman, Anne M. Bronikowski, Linda M. Fedigan, Anne E. Pusey, Tara S. Stoinski, Karen B. Strier, Annette Baudisch, Susan Alberts and James W. Vaupel**

Longevous populations have two characteristics: the average length of life is long and relative variation in lifespans is low. For example, lifetables for contemporary Sweden and Japan indicate that most deaths occur at ages between the late 70s and early 90s. Our primate relatives, in contrast, have lifespans that are highly variable in length but short on average and rarely longer than 30 years. (Fig. 1). An association between the average length of life and its variability has been found for industrialized societies. However, detailed knowledge is lacking about whether and how this association varies across species separated by millions of years of primate evolution, or whether it has changed over the past several centuries of unprecedented social progress in human populations. Fuller comprehension of the relationship between rising lifespans and reduced lifespan variability across evolution and history holds potential insights that might illuminate past, current and future longevity.



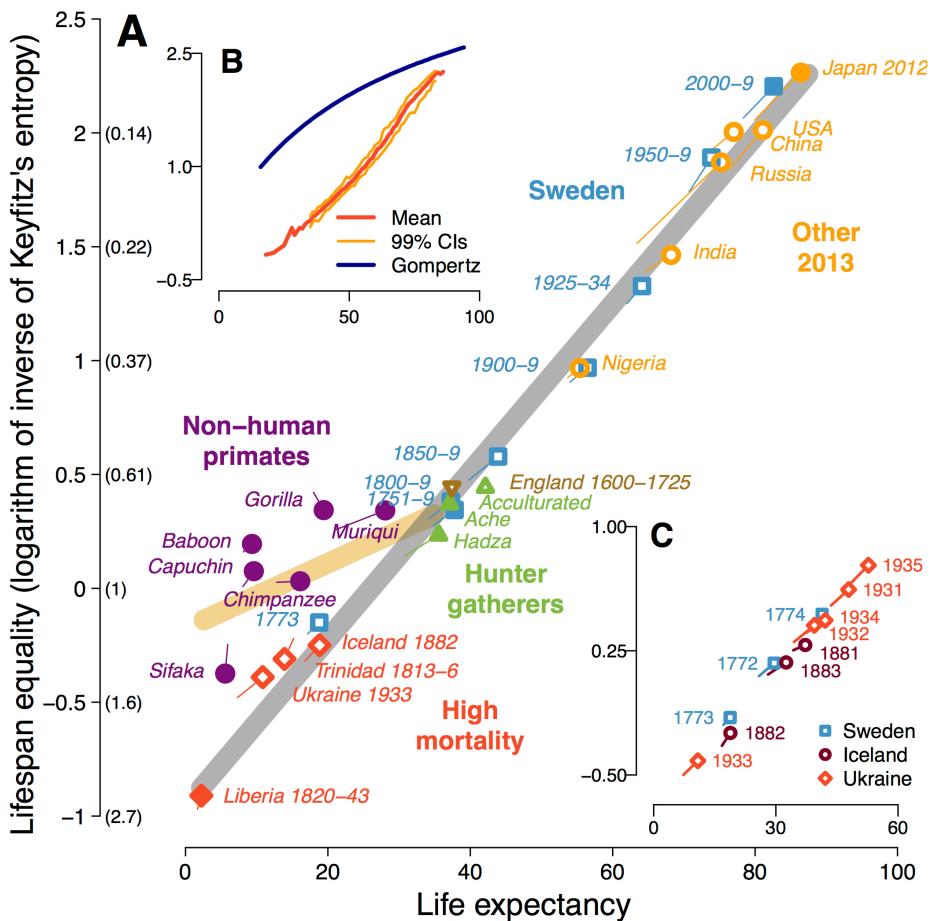
**Fig. 1** Lifespan distributions for males and females. Each panel presents the proportion of individuals dying by age for females (red) and males (blue). Infant mortality (before age 1) is reported in the inset pie charts. The solid vertical lines mark life expectancies for each sex. The dashed vertical lines indicate the average number of years of life expectancy lost due to death. Keyfitz's entropy is given by this value divided by life expectancy.

For the muriqui, capuchin and female gorillas, the curves are extrapolated beyond maximum estimated lifespans within the dataset, as indicated by dotted curves and diagonal shading.

We pose three related questions aimed at filling this knowledge gap: how long and variable are lifespans for humans compared with nonhuman primates, for humans today compared to the past, and for males compared with females? We provide answers to these questions by applying a powerful framework that simultaneously examines changes in both the average length of life in a population or species—the ‘pace’ of life—and relative variation in the length of life, i.e., the ‘shape’ of the distribution of ages at death.

Using data from charismatic primate populations and diverse human populations our study provides key answers to these questions. First, two straight lines describe the joint rise of life expectancy and lifespan equality: one for primates; the second over the full range of human experience from average lifespans as low as 2 years during mortality crises to more than 87 years for Japanese women today (Fig. 2). Second, industrial humans differ more from non-industrial humans in these measures than non-industrial humans do from other primates. Third, in spite of the astonishing progress humans have made in lengthening the lifespan, a male disadvantage in lifespan measures has remained substantial – a result that will resonate with enduring public interest in male-female differences in many facets of life.

Our results are a major achievement for MaxO because they illustrate the power of Biodemography, the nascent, transformational discipline that combines concepts, methods, questions and theories from demography with related ideas from public health and from population biology and its sister disciplines of evolutionary biology, ecology, and life history analysis, adding hybrid vigor to the Aristotelian and Darwinian roots of biology. This analytical strategy will yield further insights when applied at MaxO and elsewhere to other clades across the tree of life. In particular, application of the pace-shape framework to other species, as well as topics other than age at death (e.g., age at childbearing, marriage or dementia) may lead to new results.



**Fig. 2** The continuum of lifespan equality and life expectancy in primates. In all three panels, the y-axis shows our measure of lifespan equality, the log of the inverse of Keyfitz's entropy; corresponding values of Keyfitz's entropy are given in parentheses in Fig. A. (A) The evolutionary-historical continuum in lifespan equality and life expectancy for the 12 focal populations and 16 additional human populations. (B) The continuum for 8,198 human life tables. The blue curved line describes the relationship between lifespan equality and life expectancy if mortality follows Gompertz's law, i.e., if the risk of death rises exponentially, increasing 14%/year. Because of the paucity of observations, the 99% confidence intervals (CIs) are not shown for life expectancies below 35 or over 85. (C) The continuum for three short-term crisis populations when mortality rose sharply and then declined sharply from year to year. In A and C, data for female-male pairs from each population are indicated by a point with a ‘tail’; the point represents female values, with male values at the end of the tail.

**II.F** (In preparation for submission to Nature; preliminary title) **Demographic Knowledge for Species Conservation: A Landscape of Ignorance** by [Dalia A. Conde](#), [Johanna Stärk](#), [Fernando Colchero](#), Hassan Syed, John E. Fa, Eelke Jongejans, [Jonas Schöley](#), Heide Maria Baden, Lionel Jouvet, [Ana Rita Silva](#), Shai Meiri, Jean-Michel Gaillard, Scott Chamberlain, Jonathan Wilcken, [Ulrich Steiner](#), [Owen Jones](#), [Johan Dahlgren](#), Zjef Pereboom, Lucie Bland, Ivan Gomez-Mestre, Jean-Dominique Lebreton, Jaime Gonzalez-Vargas, Nate Flesness, Alexander Scheuerlein, [Vladimir Canudas-Romo](#), [Roberto Salguero-Gómez](#), Onnie Byers, Stephan A. Funk, Hugh Possingham, Sebastian Devillard, Dmitry Schigel, [James W. Vaupel](#), [Annette Baudisch](#)

Extinction is a demographic process: when deaths consistently offset births, then the population of a species dwindles to zero. Extinction is increasingly common and many species are threatened. Effective conservation management for a species requires data on fertility, mortality and population size to inform Population Viability Analyses, which are based on demographic models of the life cycle of a species. PVAs are used to examine the effect of environmental threats and mitigation efforts on extinction probability and mean time to extinction.

Our analysis reveals that available demographic knowledge is insufficient to construct even the simplest PVAs for the vast majority of tetrapods—mammals, birds, reptiles and amphibians. We created a metadatabase from 22 data repositories of life history traits and demographic data of 32,143 tetrapod species (99.2% of all described tetrapods according to the Catalogue of Life). This was a laborious task because of inconsistencies in taxonomy, in definitions of demographic variables and in units of measurement. Using these data, we developed a Demographic Index of Species Knowledge (DISKo) to describe the existing level of demographic knowledge for each species.

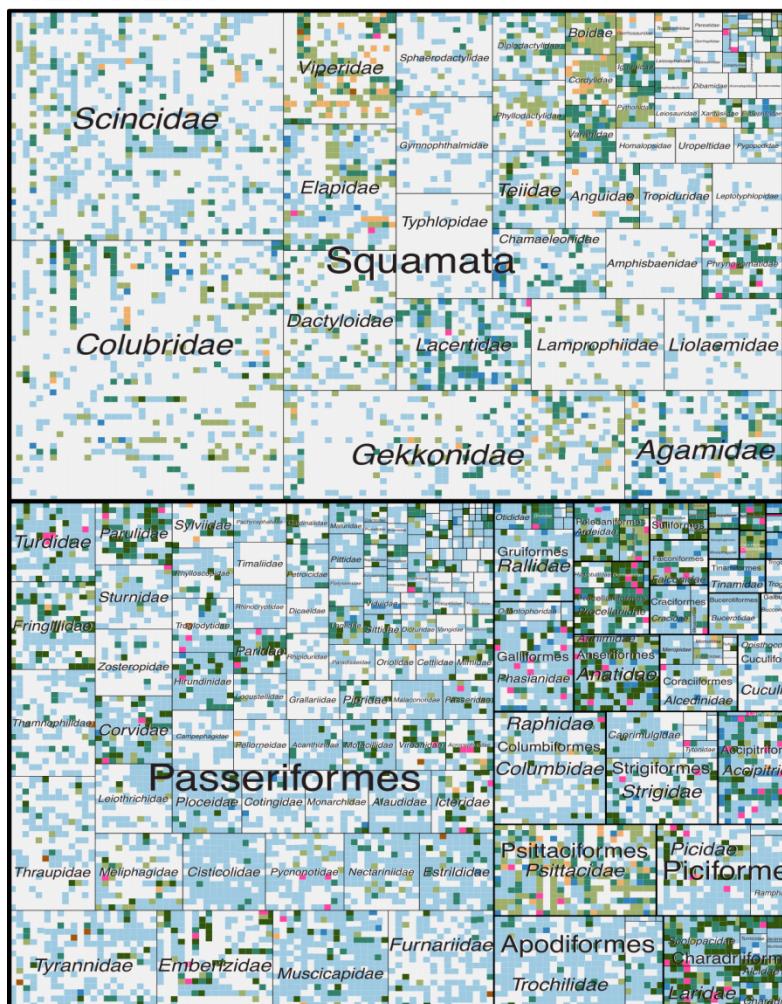
- The most detailed category of data pertains to species with lifetables by age or population matrices by age or stage. Such data are alarmingly scarce. Age-specific or stage-specific mortality and fertility values are available for only 189 of 5,586 described mammals, 3.4%, and only 43 of 1,122 threatened mammal species, 3.8%. For birds, the figures are even lower, with age-specific or stage-specific values available for 113 of 10,333 species, (1.1%) and 12 of 1203 threatened species (1.0%). For reptiles, age or stage data are available for 0.3% of species and for amphibians, 0.2%.
- Otherwise, categories of the index summarize the number of measures available for fertility and mortality for a species. For fertility, the measures are age at first reproduction, inter-litter/inter-birth interval, litter/clutch size, proportion of adult females who are reproductive, and birth or recruitment rate, with recruitment denoting the number of individuals who reach some age or stage (e.g., maturity or leaving the nest). For mortality, the measures are maximum recorded lifespan, mean age of the (adult) population, and crude death rate (of adults), which biologists often call the annual survival rate and which can be calculated as the inverse of another measure sometimes provided, namely, life expectancy at maturity.

The Table and Figure summarize the availability of data. It is also noteworthy that for 78% of the species data available, it is unknown if the data come from wild or captive records. Furthermore, species demographic knowledge is geographically biased with glaring data gaps in the tropics.

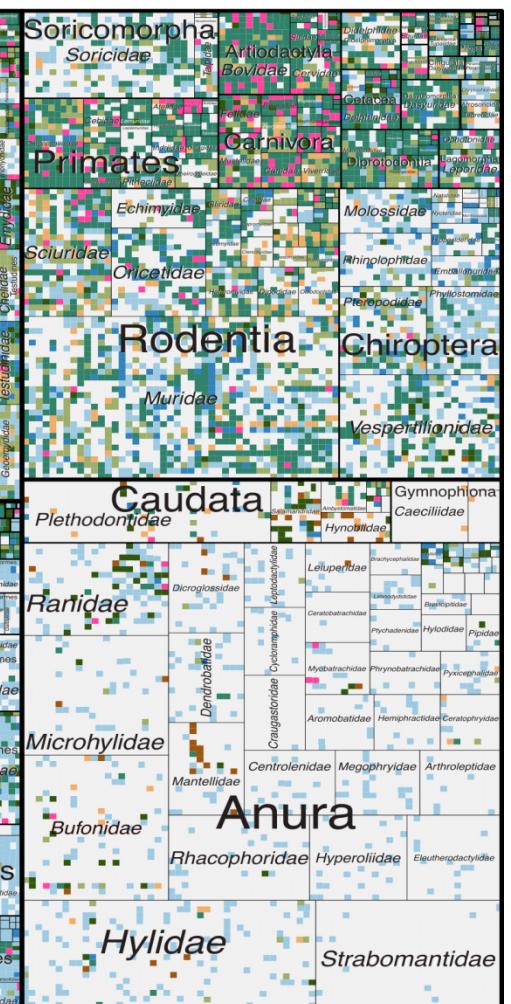
This article, which is in preparation, goes on to discuss opportunities—supplementing more field studies—to fill gaps in the landscape of demographic knowledge about species. For example, information from zoos can be used to estimate values in the wild—if there is knowledge about how zoo and wild values differ. Information about some measures, e.g., the crude death rate or body size, can sometimes be used to estimate other measures, e.g., the

crude birth rate or life expectancy. Information about a species can sometimes be roughly inferred from information about similar species. MaxO will pursue these as adumbrated in the summary of the Conservation Biology Cluster in section III.D.

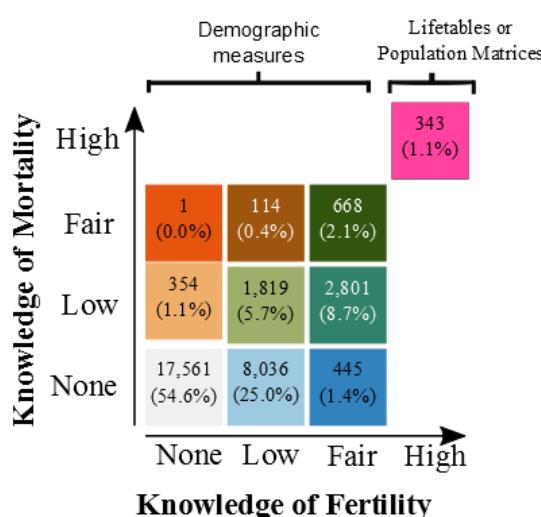
## REPTILIA



## MAMMALIA



## AVES



**Fig.** The landscape of Demographic knowledge for all the described tetrapods. Each pixel represents a species and they are grouped by families and orders. The level of information on fertility and mortality are coded in a two-dimensional colour, with blue shades representing information on fertility and red shades representing information on mortality. Green shades represent if there is information on both fertility and mortality; pink, if there is knowledge on the population level either as a life table or a population matrix, and grey represents no information on any variable. The numbers and percentages in each box indicate the number and relative number of species.

**None:** No demographic knowledge

**Low:** Single variable at species level

**Fair:** Multiple variables at species level

**High:** Population Matrix/Lifetable

### III. Research Clusters

#### A. Pace Shape Cluster (Coordinator: [Annette Baudisch](#))

The pace shape framework was developed at the Max Planck Research Group on Modeling the Evolution of Aging in Rostock ([Baudisch](#) 2011, [Wrycza, Baudisch](#) 2014, [Wrycza, Missov, Baudisch](#) 2015) to facilitate comparing populations that live and die on different time scales. It aims to quantify and explain the pace and shape of age-patterns. Pace captures time scale and is typically represented by mean age at death. Shape captures the scale-free pattern of death and distinguishes between positive, nil or negative aging. Shape is typically measured by relative spread of death over the life course. Hence, shape not only classifies types and degrees of aging, but simultaneously quantifies lifespan equality. It is flexibly applicable to human and non-human populations, supports large scale comparative research and offers a fresh perspective on age-patterns, thereby supporting the main thrust of the Center.

Applying the pace shape framework to human and non-human populations across the tree of life, we aim to help uncover key factors that determine patterns of birth and death. The work of the cluster relies on data availability and valid methods to extract pace and shape values from different data types (see Methods and Databases Cluster, Conservation Demography Cluster).

The pace shape framework has been instrumental in two out of the five major articles of the MaxO Center ([Jones](#) et al. 2014 and [Colchero](#) et al. 2016, summarized in Sections II.A and E.). These studies raise new questions that spark further large-scale collaborative projects involving people from across MaxO, Rostock and several external collaborators.

What is the relationship between pace and shape across species? What species share similar aging types, and can we identify determinants of those types utilizing relationships in the tree of life? While [Baudisch](#) et al. (2013) found a positive relationship between pace and shape within the clade of flowering plants, [Jones](#) et al. (2014) found no relationship across plants and animal species. Theoretical insights ([Barthold, Lenart, Baudisch](#), submitted) and empirical studies on the “Pace and Shape across Species” ([Baudisch, Barthold, Salguero-Gómez](#), et al., [Caswell, Jones](#), in progress) aim to answer these questions.

How variable are patterns of aging within species? [Colchero](#) et al. (2016) suggests that humans may follow a universal pathway to longevity. Hence knowledge of lifespan would predict the distribution of death. This insight opens new routes of developing forecasting methods (see forecasting cluster). It further enables crude classification of countries’ development along the path of longevity progress utilizing a newly developed “pace-shape-index” ([Baudisch, Oeppen, Ebeling](#), EPC 2016). Within non-human species, [Colchero](#) et al. (2016) sparks research on the “Pace Shape within Species” ([Baudisch, Danko](#), et al. Stoustrup) to test how rigidly pace and shape are linked. We developed an R package ([Schöley, Pascariu, Villavicencio](#) et al.) that support pace shape analysis to ensure efficiency and consistency among projects.

Current and future collaborative projects (will) apply the pace shape approach to human data on causes of death ([Ebeling, Bergeron, Baudisch](#), Conference Paper), to crisis populations, to diseases, especially to cancer, and to male/female mortality patterns. Across species, we will quantify the impact of pace vs. shape in captive vs. wild populations (see conservation cluster), which will entail the need for further development of the pace shape framework.

In all those applications we will generally seek to distinguish between simple re-scaling and actual re-shaping effects of age patterns, inspired by our finding (Archer et al. (submitted) that diet composition in *Drosophila* distinctly affects age-patterns: varying carbohydrate re-shapes, varying protein re-scales.

### **III.B. Age-Trajectories Cluster** (Coordinator: [James W. Vaupel](#))

The Age-Trajectories Cluster continues and further develops research endeavors launched in [Vaupel's](#) department at MPIDR. The primary emphasis is on age-patterns of mortality for humans and other species. A secondary emphasis is on age-patterns of morbidity and disability for humans. Mortality, morbidity and disability are studied over age in a population, over age across populations, and over age over time. This research is related to the research being carried out by [Christensen's](#) unit and also associated with research in the Pace-Shape, Male-Female and Forecasting Clusters. The focus in this Cluster is on measures of pace; whereas the Pace-Shape Cluster simultaneously considers pace and measures of shape, e.g., of the relative distribution of lifespans.

[Vaupel](#) hypothesized (in *Nature* 2010) that the rate of increase with age in senescent mortality for humans, sometimes called the rate of aging, was (with little if any variation) invariant across individuals in diverse populations and over time. This hypothesis has turned out to be very difficult to prove—or disprove. Several years of effort at MPIDR and, to a lesser extent, at MaxO SDU, have been punctuated by periods of euphoria, when a decisive test appeared to have been found, followed by periods of depression, when it turned out that “a problem worthy of attack proves its worth by fighting back”. Part of the difficulty is distinguishing between senescent death (resulting from aging) and non-senescent death (resulting from factors that do not hinge on the deterioration of humans with age)—because these two causes of death interact with each other and are difficult to disentangle. Another problem stems from heterogeneity in frailty: the individuals most prone to die tend to die first, leaving a more robust cohort of survivors. Members of this Cluster are still attacking this problem, hoping for a breakthrough. One particularly promising approach, being pursued by [Zarulli](#) and [Lindahl-Jacobsen](#), is to study the increase in mortality with age for smokers vs. nonsmokers. Preliminary results are consistent with the rate-of-aging hypothesis but more work is needed.

A second research thrust is to study whether senescence is being delayed: is 80 the new 70 and 70 the new 60? [Ahrenfeldt](#), [Lindahl-Jacobsen](#), [Steiner](#), [Thinggaard](#) and others are attacking this question using various measures of mortality, morbidity and disability.

The pace of improvement in age-specific mortality is another topic of interest. [Torres](#) is, for example, studying the origins of the revolution in life expectancy starting roughly in 1840 and in Scandinavia by analyzing age-specific rates of improvements in death rates. A somewhat related project, conducted by [Gampe](#) and others, focuses on long-term trends in life expectancy and age-specific mortality from the Paleolithic to the Middle Ages.

Death rates decline from conception to maturity. This improvement is being studied by [Schöley](#), who has developed innovative models based on population heterogeneity.

Age-patterns of causes of mortality and morbidity and their changes over time are of great interest, e.g., with regard to cancer or dementia. A group led by [Wensink](#) is starting to study cancer patterns.

Whether life expectancy can rise above 100 hinges on whether death rates above 100 can be substantially reduced. An egregiously incompetent article in *Nature* recently claimed that this was impossible. The question is still open whether progress can or cannot be made in averting death among the oldest-old. Several researchers in the Cluster, including [Lenart](#) and [Medford](#), are studying this.

Finally, several researchers in this Cluster are analyzing age-trajectories of mortality for nonhuman species. The articles summarized in **II.B** and **II.C** present revolutionary findings about this. Further research along these lines is being carried out by [Dahlgren](#) (about plants), [Steiner](#) (about bacteria) and others.

### **III.C. Male-Female Cluster** (Coordinator: [Rune Lindahl-Jacobsen](#))

Women today have longer life expectancy than men in all countries of the world. Even in extremely harmful environments females tend to outlive males ([Zarulli](#) et al submitted to PNAS). Yet women tend to report poorer self-rated health, have higher disability levels at all ages and perform more poorly on physical tests than men. This is the so-called male-female health-survival paradox: men die while women suffer. Despite substantial research, understanding is deficient about how behavioral and social factors modulate fundamental sex differences in health and mortality. Researchers at MaxO are collaborating with researchers in [Oksuzyan's](#) Independent Research Group (IRG) on Gender Gaps in Health and Survival at MPIDR and elsewhere to disentangle these patterns.

MaxO and the IRG are collaborating on a registry-based research program with integration of data sources from Danish registries and joint employees affiliated with both MPIDR and MaxO. Research thrusts include sex differences among the oldest old by ethnic background, childbearing status and changes in social status, position and connectedness. [Andreas Höhn](#), a joint PhD student affiliated with both [Oksuzyan's](#) Group and MaxO has started his project on examining 'Gender, Hospitalization and Mortality'. [Mine Kühn](#) and [Angela Carollo](#) are joint research scientists in the IRG and MaxO.

The Forecasting Cluster and the Male-Female Cluster collaborate to improve forecasting of health, life expectancy and mortality. Two PhD students ([Bergeron](#) and [Pascariu](#)) use data on age-specific sex gaps in mortality to forecast death rates and life expectancy. Steps have been taken to further extend this collaboration through a joint PhD student Mikkel Bruun-Jensen will start, in 2018, combined MA and PhD study in Economics, working in MaxO to study how changes in male vs. female educational discipline and level in Denmark might influence healthy life expectancy in the future.

A grant on the Demography of Sex Differences in Health and Survival from the U.S. NIH/NIA to [Vaupel](#) is helping to fund several projects in the Male-Female Cluster as well as collaborative projects with [Christensen](#) and with [Alberts](#) and [Zeng](#) at Duke University; an article by [Zeng](#), [Christensen](#) and [Vaupel](#) has recently been accepted by The Lancet. The projects in the Cluster include:

- Analysis of modern male vs. female mortality. It is commonly believed that differences in male vs. female life expectancy are attributable to high male mortality between ages 15 and 35 and are due to the tendency of younger males to take risks, be aggressive and otherwise engage in behavior that increases death rates. Male mortality relative to female mortality is highest between ages 15 and 35 but the life expectancy gap is largely due to excess male mortality after age 65. At MaxO we have developed some preliminary models that capture this and we plan to refine the models over the next five years.
- Analysis of paleodemographic male vs. female mortality. Deep understanding of male-female mortality differences hinges on knowledge about these over the long course of human evolution. At MPIDR in Rostock and in the future at MaxO in Odense, we exploit a uniquely accurate and large dataset on more than 20,000 skeletons assessed for age at death from the Mesolithic to 1500 A.D. to estimate male vs. female age-specific death rates over thousands of years.
- Analysis of male vs. female mortality for animals. Sustained efforts by legions of biologists have now produced male vs. female mortality data for hundreds of species. Preliminary analysis suggests a general tendency for shorter male life expectancy in mammals but longer male life expectancy in birds. We plan detailed further analysis.
- Causes of death for males vs. females. We plan to analyze violent deaths, complications of childbearing and pregnancy, and causes associated with cigarette smoking to gain deeper understanding of male-female mortality differences. We also plan to examine survival after disease onset for various diseases for males and females.

### **III.D. Forecasting Cluster** (Coordinator: [Vladimir Canudas-Romo](#))

“How long will we live?” is the core question of research in the Forecasting Cluster. Our studies on forecasting, which build on research in the Age-Trajectories Cluster, have focused on developing innovative methods to predict longevity over the course of the 21st century.

[Canudas-Romo](#), [Oeppen](#), [Vaupel](#), [Wensink](#) and the 7 Ph.D. students in the Cluster are developing strategies to forecast life expectancy by using data on life expectancy over time:

- We are working on two different approaches to forecast—at birth, age 65 and other ages—record (female) life expectancy, one using time-series methods ([Pascariu](#)) and the other using methods from extreme-value theory and record theory ([Medford](#));
- We are also developing a method to jointly forecast life expectancy and lifespan equality ([Aburto](#), [Baselini](#) and [Kjærgaard](#)), working together with the Pace&Shape Cluster;
- We have developed a time-series method to forecast the gap between female life expectancy in a country of interest and record female life expectancy ([Pascariu](#));
- We have developed a method to forecast the gap between female and male life expectancy in a country and plan to refine this method with the Male-Female Cluster ([Pascariu](#));
- We are developing method to forecasts age-specific death rates for periods and for cohorts based on forecasts of life expectancy.

Several researchers are working on complementary strategies to forecast period and cohort age-specific death rates and to use these rates to forecast life expectancy. In particular, we have devised ways of combining methods of Compositional Data Analysis (CoDa) applied to distributions of ages at death with Lee-Carter and Lee-Li approaches to forecast age-specific death rates for a country and coherently for a group of countries ([Bergeron](#), [Oeppen](#)). We are analyzing ways of determining which grouping of countries is best if one is interested in forecasts for a specific country ([Kjærgaard](#)). In addition, we are developing strategies, based on extreme-value theory and record theory, to forecast maximum lifespans ([Medford](#)).

We plan to take on some additional questions:

- Our research has emphasized period forecasts; in the future we will also focus on cohort forecasts and on ways to combine period and cohort information (e.g., using frailty models);
- We plan to develop cohort and period methods for forecasting health, beginning with forecasts of the incidence and prevalence of and mortality from various causes of death, initially with an emphasis on cancer ([Wensink](#)) and later on dementia; in a related endeavor we are analyzing mortality for smokers vs. non-smokers.
- We are beginning to develop approaches to forecast life expectancy and age-specific mortality for socio-economic groups using lifetable deaths in the CoDa framework mentioned above ([Kjærgaard](#) and [Oeppen](#));
- [Medford](#) and others have started work on forecasting age-specific death rates for centenarians and supercentenarians (110+), with a focus on determining whether these death rates are likely to decline in the future. (This is a key question for life-expectancy forecasting because life-expectancy cannot rise much above 90 unless death rates after 100 significantly decline.)
- We plan to develop approaches to forecasting life expectancy and age-specific mortality in developing countries with poor vital-statistics data (working with the Methods and Databases Clusters and using methods we have developed to forecast life expectancy and then age-specific mortality);
- We will start to explore strategies for forecasting the risk of extinction for nonhuman species, working with the Conservation-Demography Cluster.

This research is partially funded by grants from AXA and SCOR, two large insurance companies. Four members of the team are actuaries as well as demographers; various members of the team have made presentations at actuarial meetings.

### **III.E. Conservation-Demography Cluster** (Coordinator: [Dalia A. Conde](#))

Demographic processes are at the core of understanding species extinctions. When deaths exceed births for a prolonged period of time, populations collapse. The growing number of species that are at risk of extinction has prompted the development of policies and research to tackle this issue. At MaxO we are pioneering a new field of research—Conservation Demography—to develop state of the art demographic methods to help assess actions to reduce the risk of extinction.

As outlined in **II.F**, little is known about the demography of most species: documenting this was the arduous task of the Conservation Demography Cluster until now. In the future the central goal is to augment field studies (by others) by developing strategies to use existing data to fill knowledge gaps we have uncovered.

Our top priority is to exploit data from animals in zoos. We recently established a partnership with the biggest data holder of wild animals in captivity, Species360. [Conde](#) (who is continuing to serve as a MaxO researcher and head of the Conservation Demography Cluster) is now Director of Research of Species360. She is in charge of analyzing over 43 years of records that include 74 million medical and 167 million husbandry records for 6.8 million animals of 21,000 species in more than 800 institutions. We will explore methods to use these zoo data to estimate mortality and fertility for species in the wild.

We are also developing ways to estimate measures by exploiting data on related species. The primate line in the Fig. in Section **II.E** indicates that limited data for a species can be augmented using data for similar species. Furthermore, working with the Problematic Data Cluster, we will (1) assess ways of using some observation for a species, e.g., maximum recorded lifespan or body size, to estimate other measures, such as life expectancy or crude birth rate and (2) extend the Bayesian methods developed at MaxO to estimate age-specific mortality and fertility from limited data.

A central aspect of conservation demography is linking environmental drivers to demographic parameters of plants and animals. This allows detailed management plans for threatened species as well as forecasts of how environmental changes, such as climate warming and land-use changes, will affect future species distributions. [Colchero](#), [Dahlgren](#), [Jones](#), and [Conde](#) are engaged in research on various aspects of this, supported in part by external grants to MaxO.

Forecasts and management plans are crucial elements of species conservation. We are beginning to collaborate with members of the Forecasting Cluster to devise methods of forecasting that go well beyond current methods of Population Viability Analysis (PVA) used to assess the effect of environmental threats and mitigation efforts on extinction probability and mean time to extinction. Led by [Colchero](#), we have started to analyze the impact of PVA assumptions on forecasts, and we plan to develop methods to forecast probability distributions of times to extinction.

In addition, we have launched research on applying methods of prescriptive decision analysis and cost-benefit analysis to help set priorities in allocating limited resources across endangered species. [Vaupel](#) is an expert on these methods and [Conde](#) has recently studied them at Stanford University.

To influence priorities for (1) gathering new data about species and (2) species management plans, the members of the Conservation Cluster, especially [Conde](#), are developing ties with key institutional actors such as the Species Survival Commission of the International Union for Conserving Nature and the Alliance for Zero Extinction. In particular, we are collaborating with TRAFFIC, with the goal of using demographic methods to determine the limits of captive breeding for more than 80 species of turtles and tortoises that are being illegally traded as captive bred.

### III.F. Demographic Methods Cluster (Coordinator: [Fernando Colchero](#))

Most of the researchers associated with MaxO in Odense and in Rostock have strong mathematical and statistical interests and skills, especially [Aburto](#), [Basellini](#), [Baudisch](#), [Canudas-Romo](#), [Caswell](#), [Colchero](#), [Danko](#), [Ebeling](#), [Gampe](#), [Kjærgaard](#), [Lenart](#), [Medford](#), [Missov](#), [Nemeth](#), [Pascariu](#), [Rau](#), [Riffe](#), [Rizzi](#), [Schöley](#), [Steiner](#), [Thinggaard](#), [Vaupel](#) and [Villavicencio](#). The collaborative initiatives of these 23 researchers are coordinated by [Colchero](#).

Demographers often study datasets that are riddled with missing records and partial information. To overcome such limitations, [Colchero](#), when he was at MPIDR, developed the general approach of “Bayesian Survival Trajectory Analysis” and made it publicly available through the now popular R package BaSTA ([Colchero](#) and Clark 2012, [Colchero](#) et al 2012). This framework has been applied, for example, to estimate age-specific mortality from 16<sup>th</sup> Century marriage records ([Villavicencio](#) et al. 2015) and to test hypotheses on the existence of negative senescence in indeterminate growers by treating age and size as latent states ([Colchero](#) & [Schaible](#) 2014). In the PNAS article summarized in Section II.E, a Bayesian hierarchical model that builds on the multi-event framework was applied to estimate age and to estimate age-specific mortality and dispersal for populations in which one or both sexes disperse from the study area.

Another accomplishment of the Cluster is the development of non-parametric methods, based on penalized composite link models ([Rizzi](#) et al. 2015, 2016), for ungrouping coarsely aggregated data to estimate continuous age trajectories.

Members of the Cluster including [Caswell](#) and [Steiner](#) are also interested in expanding classical age-only-structured population methods to age-stage-structured populations to advance our understanding of the interplay between age- and stage-dynamics (e.g., [Steiner](#) et al. 2014).

Demographic data are generally discrete, pertaining to finite populations observed at points in time. Key formulas, however, often assume infinite populations and continuous time. Consider, for example, Keyfitz’s entropy  $-\int_0^\infty \ell(x) \ln \ell(x) dx / \int_0^\infty \ell(x) dx$ . Different numerical approximations can yield very different results. Using simulated data from specified survival functions  $\ell(x)$ , a team of researchers ([Schöley](#), [Pascariu](#), [Villavicencio](#), [Danko](#), [Jouvet](#), [Sherman](#), [Stott](#), [Torres](#) and [Baudisch](#)), from the Methods Cluster and the Pace and Shape Cluster, are developing an R package ([github.com/jschooley/pash](#)) that uses discrete approximations that come closest to the exact value implied by the continuous formula.

High points in the life of the Cluster are when members get together to discuss new results in formal demography. For example, when a death is averted at a young age, lifespan inequality decreases but when a death is averted at an old enough age, lifespan inequality increases: [Aburto](#) and others are developing equations to determine the age separating these two outcomes for various measures of lifespan inequality. [Villavicencio](#) and [Riffe](#) (2016) and [Canudas-Romo](#) and [Zarulli](#) (2016) made further contributions to the study of life lived vs. life left. [Missov](#), [Lenart](#), [Nemeth](#), [Canudas-Romo](#) and [Vaupel](#) (2015) discuss Gompertz curves with the mode as a parameter. [Wensink](#) and [Baudisch](#) working with [Caswell](#) showed “The rarity of survival to old age does not drive the evolution of senescence” (2016) and with [Wrycza](#) there can be “No senescence despite declining selection pressure” (2014).

More generally, most of the publications listed in Section V of this Report are based on sophisticated statistical methods and powerful demographic equations approved (and often developed) by members of the Methods Cluster.

### III.G. Databases Cluster (Coordinators: [Owen Jones](#) and [Alexander Scheuerlein](#))

As emphasized in Section I of this Report, the research of MaxO heavily relies on large databases on human survival and health.

In addition, MaxO is leading the way in collating nonhuman demographic data into several databases. Of these, the **COMPADRE** Plant Matrix Database and **COMADRE** Animal Matrix Database are the most fully-developed. These databases include demographic information in the form of published matrix population models (MPMs) obtained from the literature. An MPM describes the dynamics of a population in discrete time using discrete stages (e.g. age, size classes and developmental stages). From them, a myriad of demographic outputs can be obtained, including rates of senescence, mean and variance of life expectancy, degree of iteroparity (number of reproductive cycles), population growth rates, etc. and they are therefore useful to address a wide range of demographic topics. The latest versions of these sister-databases contain demographic information in the form of over 9,000 matrix population models for 695 plant species and 405 animal species – matrices for a further ~800 plant and >1,000 animal species are in the process of being digitized. We have made these databases Open Access at [www.compadre-db.org](http://www.compadre-db.org). The work to compile the databases was overseen by [Salguero-Gómez](#) and [Jones](#); the data compilation effort was undertaken by student assistants working in [Vaupel's](#) department at MPIDR in Rostock.

To complement these MPM databases the Databases Cluster is collaborating with other researchers to develop an analogous pair of databases known as **PADRINO** and **MADRINA**, which collate data on published Integral Projection Models (IPMs). IPMs are discrete time, continuous state (e.g. size, weight and parasite load) demographic models that incorporate rates of survival and fertility of individuals. They are therefore conceptually similar to MPMs.

**DATLife** (Demography Across the Tree of Life) is a data source for the comparative analysis of age-trajectories of mortality and fertility for many species, currently mostly vertebrates. The database, which is being compiled at MPIDR under the direction of [Scheuerlein](#), is functional but still in test form. The data pertain to:

1. **Age-specific mortality**, mostly in lifetables that are published or that we created from published data smoothed by the method of [Rizzi](#) et al. (2016). DATLife currently holds **2955** lifetables of **364** species, of which **263** are vertebrates.
2. **Age-specific fertility** in **297** fertility tables of **90** species, all of which have corresponding mortality data.
3. **Stage-specific mortality** usually describes annual juvenile and annual adult mortality of animals. DATLife currently includes **4394** values on **496** species.
4. **Maximum observed lifespan**: **5437** values on **2859** species.
5. **Age at sexual maturity**: **9269** values for **2620** species.

For each of these databases an infrastructure for sharing data is provided. Published data are used, but an embargo option allows the inclusion of data before publication. For each data type we record study location, study duration, sex, the end of the study and the number of organisms in the study.

[Steiner](#) and [Jouvet](#) collect demographic data on *E. coli* using high throughput cutting-edge microfluidic technology that permits tracking of thousands of individual bacteria cells throughout their lives. Demographic data include division rate, survival, cell elongation rate, and size at cell division for each individual under tightly controlled environmental conditions. The data provide unprecedented insights into effects of genetics (species to single gene), the environment (temperature, nutrients), and intrinsic stochastic processes on demographic parameters.

An additional database, **DISKo**, was described in Section II.F above.

Collectively, these databases offer unrivalled information for biodemographic research.

### **III.H. Basal Metazoan Cluster** (Coordinators: [Ralf Schaible](#) and [Daniel Levitis](#))

Research in this cluster has focused on whether death rates for basal metazoans—hydra, sponges, jellyfish and some kindred species at the root of the animal tree of life—increase with age or remain more or less constant. The main contribution of the group is a large study showing that age-specific mortality does not increase with age for asexually-reproducing hydra under protected laboratory conditions and age-specific fertility does not decline: see **II.C.** This painstaking research demonstrates that senescence is not inevitable for all species starting at reproductive maturity, a canonical belief in biology since Hamilton (1966).

A study in Rostock by Ph.D. student [Felix Ringelhan](#) focused on *Eleutheria dichotoma*, a marine hydrozoan with a stationary polyp stage (something like hydra or sea anemones) and a free-ranging medusa stage (roughly like the jellyfish that bother bathers). There was suggestive evidence that the polyps do not senesce but medusae suffer increasing deterioration with age. A somewhat parallel study in Denmark by Ph.D. student [Josephine Goldstein](#), investigated the mortality of the jellyfish *Aurelia aurita*, which has a settled, benthic polyp stage in which reproduction is asexual as well as the more familiar pelagic medusa stage in which reproduction is sexual. The evidence suggests that polyps may not senesce whereas medusae deteriorate with age in the wild, perhaps because of food limitations, but not under protected laboratory conditions.

An ambitious project, which was cut short when the key investigator, [Daniel Levitis](#), left MaxO, established a sponge aquaculture in Kerteminde, Denmark, with several hundred breadcrumb sponges (*Halichondria panicea*), to determine age- and size-specific growth and vital rates (mortality, survival and reproduction) of sponge cohorts under natural conditions using monthly SCUBA surveys. The preliminary data over a three-year period before the study was halted suggests that breadcrumb sponges do not senesce with age. A review of other studies by a doctoral student, [Lars Kumala](#), and various experiments carried out by [Paul Dunn](#) are also consistent with the hypothesis that mortality does not systematically increase with age and fertility does not systematically decrease with age for sponges.

A smaller, side project investigated the longest-lived non-colonial species, as far as is known, *Arctica islandica*, the quahog clam, in waters off Iceland and in the Baltic. Annual death rates were lower in the colder waters off Iceland, but in both cases evidence suggests that death rates do not increase with age and possibly decrease as clams grow in size.

The researchers associated with this Cluster attempted to develop a deeper understanding of the biological processes that enabled hydra to avoid senescence and the other species to probably avoid senescence under some circumstances. They carefully considered regulatory and cellular processes involved in the maintenance of constant regeneration capability and stress resistance throughout life. For hydra and, to a lesser extent, the other species, they conducted experiments aimed to identify ways species prevent damage and mutation accumulation to achieve non-senescence. In this line, theoretical models were developed to explore how species can control their damage accumulation. The Cluster researchers started to explore how hydra, sponges and jellyfish fared in the wild vs. in the laboratory. For sponges they experimentally investigate endogenously- and environmentally-driven dynamics of sponge filter-feeding and respiration. For the jellyfish they modeled ecological and demographic drivers of jellyfish blooms. These drivers include the survival and fertility of benthic (asexually reproducing) polyps and pelagic (sexually reproducing) medusae as a function of environmental factors such as food availability, climate change, hydrodynamic processes and interspecific competition.

This research cluster will almost certainly end in December 2017 because it is unlikely that the basal metazoan laboratory will be continued in Rostock and because the University of Southern Denmark has not been able to recruit a new leader of the basal metazoan research in Kerteminde.

#### IV. Staff List

ONat denotes the SDU faculty of Natural Sciences in Odense; OHealth denotes the SDU faculty of Health Sciences in Odense. Asc. P. is an abbreviation for Associate Professor. Only one or two primary research clusters are listed for each researcher; a few researchers are associated with more than two clusters.

Name	Start	End	Salary/ Stipend				Current position	Place	Primary Cluster	Second Cluster	
			MPIR		SDU	External					
			MaxO	Other	MaxO	Other					
<i>Aburto, José M.</i>	16	...		*			Ph.D.	OHealth	Pace&Sh	Forecast	
<i>Ahrenfeldt, Linda</i>	16	...			*		Postdoc	OHealth	Age-Tr	M/F	
<i>Alberts, Susan</i>	13	...					Prof.	Duke	M/F	Databases	
<i>Andersen-Ranberg, K.</i>	13	...					Asc. P.	OHealth	Databases		
<i>Baden, H. Maria</i>	14	...				*	Res.Ast.	ONat	Age-Tr	ConsDem	
<i>Barbi, Elisabetta</i>	13	...					External	Rome	Age-Tr		
<i>Barthold, Julia</i>	14	...		*			Postdoc	OHealth	Pace&Sh	M/F	
<i>Basellini, Ugofilippo</i>	16	...		+		*	Ph.D.	Paris/OH	Forecast		
<i>Baudisch, Annette</i>	13	...			*		Prof.	ONat+H	Pace&Sh		
<i>Bergeron, Marie-P.</i>	13	...		*			Ph.D.	OHealth	Forecast	M/F	
<i>Binti Azali, Julia</i>	16	...		*			Lab Ast.	ONat	Age-Tr	ConsDem	
<i>Canfield, Donald</i>	13	...			*		Prof.	ONat	Basal		
<i>Canudas-Romo, V.</i>	13	...		*			Asc. P.	OHealth	Forecast		
<i>Carollo, Angela</i>	15	...	*	+			Res.Sc.	Rostock	M/F		
<i>Caswell, Hal</i>	13	...					Adj. P.	Amsterd.	Age-Tr	Pace&Sh	
<i>Christensen, Kaare</i>	13	...			*		Prof.	OHealth	Age-Tr		
<i>Colchero, Fernando</i>	13	...			*		Asc. P.	ONat	Methods		
<i>Conde, Dalia Amor</i>	13	...		+		*	Asc. P.	ONat	ConsDem		
<i>Dahlgren, Johan</i>	13	...		*			Asc. P.	ONat	Age-Tr	ConsDem	
<i>Danko, Alexandra</i>	13	...	*	*			Ph.D.	Rostock	Basal		
<i>Danko, Maciej</i>	13	...		*			Res.Sc.	Rostock	Pace&Sh	Age-Tr	
<i>Dunn, Paul</i>	13	15					Postdoc	ONat	Basal		
<i>Ebeling, Marcus</i>	15	...		+		*	Ph.D.	Rostock	Pace&Sh		
<i>Edel, Andreas</i>	13	...	*	*			Res.Sc.	Berlin			
<i>Gampe, Jutta</i>	13	...		*			Res.Sc.	Rostock	Age-Tr		
<i>Goldstein, Josi</i>	13	16		*			Ph.D.	ONat	Basal		
<i>Hansen, Lone M.</i>	13	...		*			Secr.	OHealth			
<i>Höhn, Andreas</i>	16	...		*	+		Ph.D.	Rostock	M/F		
<i>Iversen, Ulla</i>	14	...		*			Account.	OHealth			
<i>Jensen, Vibeke</i>	13	...		*			Secr.	ONat			
<i>Jeune, Bernard</i>	13	...					Asc. P.	OHealth	Age-Tr		
<i>Jones, Owen</i>	13	...		*			Asc. P.	ONat	Databases	Pace&Sh	
<i>Jouvet, Lionel</i>	14	...		*			Postdoc	ONat	Age-Tr	Pace&Sh	
<i>Kjærgaard, Søren</i>	15	...		*			Ph.D.	OHealth	Forecast		

<a href="#">Kluge, Fanny</a>	13	...	*			Res. Sc.	Rostock	Age-Tr	
<a href="#">Kühn, Mine</a>	15	...	*	+		Postdoc	Rostock	M/F	
<a href="#">Kumala, Lars</a>	13	...	*			Ph.D.	ONat	Basal	
<a href="#">Lenart, Adam</a>	13	...		*		Asst. P.	OHealth	Age-Tr	Methods
<a href="#">Levitis, Daniel</a>	13	15		*		Asst. P.	ONat	Basal	
<a href="#">Lindahl-Jac., Rune</a>	14	...		+	*	Asc. P.	OHealth	M/F	Age-Tr
<a href="#">Lundgreen, Kim</a>	13	15		*		Res.Ass.	ONat	Basal	
<a href="#">Medford, Anthony</a>	14	...		*		Ph.D.	OHealth	Forecast	Age-Tr
<a href="#">Missov, Trifon</a>	13	...	*			Prof.	Rostock	Age-Tr	Methods
<a href="#">Nemeth, Laszlo</a>	13	16	*			Ph.D.	Rostock	Age-Tr	Pace&Sh
<a href="#">Nørmark, Emil</a>	16	...		*		Ph.D.	OEcon	Age-Tr	
<a href="#">Oeppen, Jim</a>	14	...		*		Asc. P.	OHealth	Forecast	M/F
<a href="#">Oksuzyan, Anna</a>	13	...	*			Leader	Rostock	M/F	
<a href="#">Pascariu, Marius</a>	14	...		*		Ph.D.	OHealth	Forecast	Pace&Sh
<a href="#">Peters, Antje</a>	13	...	*	*		Secr.	Berlin		
<a href="#">Rau, Roland</a>	13	...		*		Prof.	Rostock	Age-Tr	Methods
<a href="#">Riffe, Tim</a>	15	...	*			Res. Sc.	Rostock	Methods	
<a href="#">Ringelhan, Felix</a>	13	16	*			Res. Sc.	Rostock	Basal	
<a href="#">Rizzi, Silvia</a>	15	...		*		Ph.D.	OHealth	Methods	M/F
<a href="#">Salg.-Gómez, Rob</a>	13	...				Res.Fell.	Sheffield	Databases	Pace&Sh
<a href="#">Schaible, Ralf</a>	13	...	*	*		Res. Sc.	Rostock	Basal	
<a href="#">Scheuerlein, Alex</a>	13	...	*	*		Res. Sc.	Rostock	Databases	Pace&Sh
<a href="#">Schöley, Jonas</a>	15	...		*		Ph.D.	OHealth	Age-Tr	Methods
<a href="#">Sherman, Danielle</a>	14	...	*			Ph.D.	ONat	Age-Tr	ConsDem
<a href="#">Shkolnikova, Maria</a>	13	...			*	Res. Sc.	Rostock	Age-Tr	
<a href="#">Shkolnikov, V.</a>	13	...	*			Res. Sc.	Rostock	Age-Tr	Methods
<a href="#">Silva, Ana Rita</a>	16	...		*		Ph.D.	ONat	ConsDem	
<a href="#">Stärk, Johanna</a>	14	...	*			Ph.D.	ONat	ConsDem	
<a href="#">Steiner, Ulrich</a>	13	...		*		Asc. P.	ONat	Age-Tr	Databases
<a href="#">Stott, Iain</a>	16	...	*	+		Postdoc	ONat	Pace&Sh	ConsDem
<a href="#">Sugareva, Venelina</a>	13	...	*	*		Res. Sc.	Rostock	Basal	
<a href="#">Sussman, Meir</a>	13	...	*	*		Res. Sc.	Rostock	Basal	
<a href="#">Thinggaard, Mikael</a>	15	...		*		Postdoc	OHealth	Age-Tr	Methods
<a href="#">Torres, Catalina</a>	15	...		*		Ph.D.	OHealth	Age-Tr	Methods
<a href="#">Vaupel, James W.</a>	13	...	*		+	Dir/Prof	OH+Ros	Age-Tr	Forecast
<a href="#">Villavicencio, Franc.</a>	15	...		*	*	Ph.D.	ONat	Methods	Pace&Sh
<a href="#">Vogt, Tobias</a>	13	...	*			Res. Sc.	Rostock	Age-Tr	
<a href="#">Wastesson, Jonas</a>	15	16		*		Postdoc	OHealth	Age-Tr	
<a href="#">Wensink, Maarten</a>	15	...		*		Asst. P.	OHealth	Age-Tr	Forecast
<a href="#">Wrycza, Tomasz</a>	13	14	*			Ph.D.	Rostock	Pace&Sh	Methods
<a href="#">Zarulli, Virginia</a>	13	...		*		Asst. P.	OHealth	M/F	Age-Tr
<a href="#">Zeng, Yi</a>	13	...				Prof.	Beijing	M/F	Methods
<a href="#">Zimmermann, Ann</a>	13	...	*	*		Res. Sc.	Berlin		

Citizenship at birth:

German 19, Danish 11, USA 7, Italian 5, Mexican 4, British 4, Polish 3, Bulgarian 2, French 2, Hungarian 2, Russian 2, Spanish 2, Swedish 2, Armenian 1, Austrian 1, Barbadian 1, Canadian 1, Chinese 1, Colombian 1, Dutch 1, Israeli 1, Malaysian 1, Portuguese 1, Romanian 1, Turkish 1

**V. Collaborative MaxO Publications 2013-2016** (by at least two authors associated with MaxO (red in Odense or blue in Rostock). Arranged by year, with new years in large bold, and within a year alphabetically by first author. The 157 publications are drawn from the complete list of MaxO publications available at [www.sdu.dk/maxo](http://www.sdu.dk/maxo), which includes 92 additional articles published or submitted and 11 additional articles in preparation. The total is 260 MaxO articles.

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## VI. Governance

MaxO is a joint venture of the Max Planck Society (MPG) and the University of Southern Denmark (SDU). **Vaupel** is the Director, serving in his capacity as Director of MPIDR and also as Professor at SDU. He reports to Martin Stratmann, President of the Max Planck Society, through Angela Friederici, Vice President of the Human Sciences section and Bill Hansson, Vice President of the Biology and Medicine section who is Head of the Max Planck Commission on Max Planck Centers. He reports to Henrik Dam, Vice Chancellor (Rektor) of the University of Southern Denmark through Ole Skøtt, Dean of Health Sciences, and Martin Zachariasen, Dean of Natural Sciences. Marianne Holmer, Jesper Bo Nielsen and Martin Svensson, who are Heads of the Institutes of Biology, Public Health, and Mathematics and Computer Science, oversee MaxO staff associated with their Institutes. **Christensen** and **Canfield** advise **Vaupel** as Co-Directors of MaxO at SDU; because **Christensen** is Head of the Unit of Epidemiology, Biostatistics and Biodemography at SDU, he is closely involved with MaxO activities and has played a major role in encouraging collaborative research.

**Baudisch** is Deputy Director for MaxO researchers in Natural Sciences; **Lindahl-Jacobsen** is Deputy Director for MaxO researchers in Health Sciences **Vaupel** talks regularly with Mikko Myrskyla, Executive Director of MPIDR and briefs him about MaxO. **Vaupel** talks from time to time with other Directors of Max Planck Institutes and has gotten particularly constructive advice from Axel Börsch-Supan. The members of MaxO at SDU meet once a week (on Mondays at 10) and after a research presentation and discussion, MaxO business is discussed. Nearly all important decisions are agreed to by consensus.

## VII. Doctoral Education

### Ph.D. students associated with MaxO

Name	Year	Place	Supervisors (and advisors)	Cluster	Topic
<i>Aburto, José Manuel</i>	2019	Odense	<a href="#">Vaupel</a> , <a href="#">Canudas-Romo</a> , <a href="#">Lindahl-Jacobsen</a> ( <a href="#">Baudisch</a> )	Pace&Sh, Forecast	The relationship between life expectancy and lifespan equality, including joint dynamics and forecasting both simultaneously
<i>Basellini, UgoFilippo</i>	2019	Odense and Paris	<a href="#">Canudas-Romo</a> , Camarda, <a href="#">Baudisch</a>	Forecast, Pace&Sh	Analyzing and forecasting all-cause and cause specific age at death distributions
<i>Bergeron Marie-P.</i>	2017	Odense	<a href="#">Canudas-Romo</a> , <a href="#">Vaupel</a>	Forecast, M/F	Mortality changes in industrialized societies: Past, present and future
<i>Danko, Alexandra</i>	2017	Rostock	Pijanowska, <a href="#">Vaupel</a>	Basal	Environmental effects on life-history traits of polyp and medusa stages of <i>Eleutheria dichotoma</i>
<i>Ebeling, Marcus</i>	2017	Rostock	<a href="#">Rau</a> , <a href="#">Baudisch</a>	Pace&Sh	Dynamic measures in mortality and aging
<i>Goldstein, Josi</i>	2016	Odense	Steiner, Riisgård, ( <a href="#">Vaupel</a> )	Basal	Life-history stages of the jellyfish <i>Aurelia aurita</i> – towards a demographic under-standing of jellyfish blooms
<i>Höhn, Andreas</i>	2019	Odense and Rostock	<a href="#">Oksuzyan</a> , <a href="#">Rau</a> , ( <a href="#">Christensen</a> , <a href="#">Lindahl-Jacobsen</a> )	M/F	Gender, hospitalization and mortality
<i>Kjærgaard, Søren</i>	2019	Odense	<a href="#">Lindahl-Jacobsen</a> , <a href="#">Oeppen</a> , Møller Dahl	Forecast	New multi-population Mortality forecasting models
<i>Kumala, Lars</i>	2017	Odense	<a href="#">Canfield</a> , Riisgård, ( <a href="#">Vaupel</a> )	Basal	Ecophysiology and bio-demography of aging in sponges
<i>Medford, Anthony</i>	2019	Odense	<a href="#">Vaupel</a> , Goegebeur	Forecast, Age-Tr	Maximum life expectancies and lifespans: Insights from extreme value theory
<i>Nemeth, Laszlo</i>	2016	Rostock	<a href="#">Missov</a> , <a href="#">Vaupel</a>	Age-Tr	Models for adult and old-age human mortality: Evidence, applications and consequences
<i>Nørmark, Emil</i>	2019	Odense	Møller Dahl, <a href="#">Lindahl-Jacobsen</a>	Age-Tr	Genetic markers and economic behavior in the context of longevity
<i>Pascariu, Marius</i>	2018	Odense	<a href="#">Canudas-Romo</a> , <a href="#">Vaupel</a>	Forecast, Pace&Sh	Modelling and forecasting age-specific death rates at older ages

<u>Rizzi, Silvia</u>	2017	Odense	<u>Lindahl- Jacobsen, Vaupel</u> , (Thinggaard)	Methods M/F	Age-specific distributions from coarse-count data: Epidemiological and demographic application of a penalized composite link model
<u>Schöley, Jonas</u>	2018	Odense	<u>Vaupel, Oeppen, Lindahl- Jacobsen</u>	Age-Tr, Methods	Selection in fetal and infant mortality
<u>Sherman, Danielle</u>	2018	Odense	<u>Dahlgren, Jones</u>	Age-Tr	Comparative life history and the demography of ageing in plants
<u>Silva, Ana Rita</u>	2019	Odense	<u>Conde, Colchero</u>	Cons- Dem	Filling biodiversity knowledge gaps for decision making in conservation
<u>Stärk, Johanna</u>	2018	Odense	<u>Conde, Colchero</u>	Cons- Dem	Filling knowledge gaps for the development of conservation programs for threatened taxa: Zoo data and Bayesian methods
<u>Torres, Catalina</u>	2019	Odense	<u>Oeppen, Vaupel, Lindahl- Jacobsen</u>	Age-Tr.	Two centuries of rising life expectancy: a comparative analysis of the characteristics and causes of the historical decline in mortality in the Nordic and some other European countries
<u>Villavi- cencio, Francisco</u>	2017	Odense	<u>Colchero,</u> (Cabré), (Missov)	Methods Pace&Sh	Methods to analyze sparse demographic data: from Bayesian inference to agent- based modelling
<u>Wrycza, Tomasz</u>	2015	Rostock	<u>Baudisch, Missov</u>	Pace&Sh	Developing the mathematical framework for the shape-pace approach

The European Doctoral School of Demography (EDSD) will be taught as part of activities of MaxO in 2017-8 and 2018-9. James Vaupel is “Rector” of this program, Annette Baudisch, Vladimir Canudas-Romo and Rune Lindahl Jacobsen will serve as Dean, Dean of Students, and Adminstrative Dean, and almost all MaxO researchers in Odense, including the Ph.D. students at SDU listed above, will contribute to teaching and mentoring. Each year about 20 first-year doctoral students who plan to finish their Ph.D. studies at a European university will spend 11 months in this program, six weeks at MPIDR in Rostock in Sept. to mid Oct. and then in Odense until the end of July. The Ph.D. students completing their research in Odense who graduated from earlier EDSD programs are shown in the above Table in italics.

## VIII. Outreach

<b>Presentations/posters at meetings of:</b>	
PAA (Population Association of America	23
EPC (European Population Conference)	19
Evolutionary Demography Society	36
<b>Other presentations at or visits to Universities and research institutions in:</b>	
Germany	39
Other European countries	78
U.S.A.	23
Other countries	12

From January 2013 until 1 December 2016, 88 researchers visited MaxO in Odense and 108 visited [James Vaupel's](#) laboratories at MPIDR in Rostock. The longer-term or more frequent visitors included [Susan Alberts](#), Heather Booth, [Hal Caswell](#), [Roberto Salguero-Gómez](#), Johan Ehrlén, [Zeng Yi](#) and (in 2017) Fanny Janssen.

MaxO uses **Population Europe**, of which it is a partner institute, to reach out to the public, journalists and influential people; MaxO has contributed a total of €585,000 to Population Europe's budget. Population Europe, which was founded in June 2009 under the leadership of [Vaupel](#) and Frans Willekens, currently includes 30 partner institutes and more than 150 eminent researchers throughout Europe. Population Europe has developed various information tools including a website ([www.Population-Europe.eu](http://www.Population-Europe.eu)) [Vaupel](#) serves as Chair of the Board of Trustees, the top governing body of the network; [Baudisch](#), [Canudas-Romo](#) and [Christensen](#) are members of the Council of Advisors. MaxO researchers have contributed since 2013 to

- Conferences of Population Europe in Odense, Berlin and Brussels,
- Policy-relevant talks in Brussels,
- Policy Brief ("Europe's Citizens Should Have a Choice"),
- Population Digests ("Secrets of Longevity"; "Slowing Down the Rush Hour of Life"; "Older but Fitter")
- Population & Policy Bites (Blog): "From Age-Flex to Flex-Work: How Increasing Life Expectancy could contribute to Gender Equality in Leadership Positions",
- Traveling exhibition "How to get to 100 – and enjoy it",
- Videos on Population Europe's YouTube channel.

Population Europe co-organised the Grand Opening of MaxO in Odense in 2013.

Media coverage of MaxO research includes items, often several, in

- FAZ, Süddeutsche Zeitung, Spiegel, Die Welt, Die Zeit, 10 other German newspapers, 3 German TV channels,
- Politiken, Jyllandsposten, Kristeligt Dagblad, Fyns Amt Avis, 3 other Danish newspapers, TV2 news,
- N.Y. Times, Washington Post, Huffington Post, 5 other U.S. newspapers, Scientific American, Discover magazine, National Geographic, the Discovery TV channel, ABC and NBC news,
- The Guardian, BBC and 2 other British TV channels,
- El País and 2 other Spanish newspapers,
- Newspapers in Estonia, Italy, the Netherlands, Norway, Pakistan and Sweden as well as TV and radio channels in Sweden and France.

## **IX. Future Directions and Perspectives**

The diligent exertions of MaxO researchers have not only fostered success in collaborative publications and in mentoring doctoral students; the exertions have also built a platform for future publications and mentoring.

- The increase in output by MaxO research teams suggests a bright future in publishing interdisciplinary biodemographic research. In 2013, 14 collaborative articles were published compared with 50 such articles published, accepted or submitted in 2016. Today 66 more in preparation compared with only 11 manuscripts in preparation with only one MaxO author. It seems probable that the six major articles summarized in section **II** will be augmented by even more high-impact articles in coming years, with emphasis on manuscripts with coauthors from both the Public Health and the Natural Sciences sides of MaxO. There are very good journals beyond Nature, Science, PNAS and The Lancet: MaxO will strive to publish innovative articles in broad-audience journals such as eLife as well as top journals in Demography, Epidemiology and Biology. MaxO will strive not to maximize the number of publications but to maximize innovative joint publications.
- Although MaxO has not, yet, engaged in the most information-intensive “big” data research, MaxO Asst. Prof. [Lenart](#) is currently getting a degree from U.C. Berkeley with a focus on such data and MaxO may move into this field in the future, especially if the zoo data available to [Conde](#) or the registry data of Denmark become big data with genetic, environmental and behavioral information. MaxO has, however, done cutting-edge research on compiling and analyzing “very large” data, as outlined in sections **I** and **III.G**, and will continue this research thrust, with even greater stress on research using SHARE data and the unprecedented nonhuman databases MaxO has compiled.
- The unique concentration at MaxO of demographers who deeply understand relevant parts of mathematics and statistics provides another avenue for trailblazing MaxO research.
- Research on National Transfer Accounts to understand the age-specific expenditures and contributions of the individuals in a population is a hot and productive topic in Demography. MaxO SDU may be able to recruit two younger experts—[Fanny Kluge](#) and [Tobias Vogt](#)—currently in [Vaupel's](#) department at MPIDR. This research may develop into a Research Cluster to replace the Basal Metazoan Cluster.
- A central goal of MaxO will be to build even stronger ties with Max Planck Directors and Research Group Leaders with congruent interests. These Directors and Leaders include
  - Mikko Myrskyla at MPIDR,
  - [Vaupel's](#) successor at MPIDR,
  - [Anna Oksuzyan](#) at MPIDR,
  - Directors at the MPI for Evolutionary Biology,
  - Directors at the MPI for Social Law and Social Policy,
  - Directors at the MPI for Biology of Ageing.
- MaxO has also started reaching out to economists and political scientists at SDU. Furthermore, MaxO will coordinate, under [Baudisch's](#) leadership, an elite program for outstanding students—from all five faculties of SDU—interested in aging. This and other activities at SDU may lead to a teaching program in Demography.
- For demographers concerned about the future of Demography, the most exciting prospect for MaxO is the commitment of SDU to establish 10 (ten!) full Professorships in Biodemography by the end of the second five-year funding period of MaxO. Such a concentration of full Professors, especially given the excellence of those who might be recruited, would greatly further Biodemography and fundamentally help Demography.
- SDU is also interested in a possible Max-Planck Odense INSTITUTE for Biodemography, perhaps funded by major Scandinavian foundations, after the second five-year funding period for MaxO ends in December 2022.

## X. Summary

The Max Planck Society and the University of Southern Denmark ask the Evaluation Committee to assess seven dimensions of MaxO's performance.

1. **Scientific quality.** MaxO scores well on this criterion, as evidenced by the 6 publications adumbrated in Section **II** as well as the fuller list in Section **IV**.
2. **Research output.** MaxO's record is documented in Section **IV** and the online list at [www.sdu.dk/maxo](http://www.sdu.dk/maxo). MaxO has been productive, especially considering that most of its research has been innovative and interdisciplinary, requiring the collaboration of several researchers.
3. **Scientific impact.** MaxO research has been published in Nature, the Lancet and PNAS as well as the main Demography, Epidemiology and Biology journals and is under review or about to be submitted to these various journals as well as Science.
4. **Future directions and perspectives.** Work at MaxO since 2013 has laid the groundwork for even greater scientific quality, research output and scientific impact in the future. Interdisciplinary teams are now in place and are focused on important, innovative questions. MaxO has developed a compelling set of future research directions on frontiers of knowledge about aging that are probably feasible in terms of MaxO talents. The input and feedback of the distinguished members of the Review Committee will be taken very seriously.
5. **International competitiveness.** There is no question that MaxO is the leading institution in the field of Biodemography. There are brilliant researchers elsewhere but no university or institution has more than a handful of them. In collective **Scientific quality**, **Research output** and **Scientific impact**, MaxO is superlative.
6. **Outreach.** On the one hand, MaxO is providing leadership to the community of bi demographers around the world, as well as reaching out to demographers in general and to epidemiologists, biologists and actuaries (4 researchers at MaxO hold actuarial degrees). On the other hand, MaxO is providing perspectives on population aging, one of the key issues of our times, to journalists, opinion leaders and the general public.
7. **Effective utilization of budget.** The output MaxO has produced with its five-year budget is impressive. MaxO has been effective in pursuing path-breaking research that builds on knowledge from different disciplines. MaxO also has a remarkable record of interdisciplinary Ph.D. education, mentoring 21 doctoral students on the frontiers of the nascent field of Biodemography.

In addition, the Max Planck Commission that will recommend whether further funding is justified requests information not only on these but also on some additional factors.

1. **Added value.** The productive activities of MaxO have cost Max Planck Munich an average of €250 thousand/year. MPIDR contributed more to the budget but the combined Max Planck Munich+MPIDR share of the total budget is two-fifths, as documented in section **XI**.
2. **Collaboration.** More than two-thirds of MaxO's publications are collaborative, with at least two and usually more researchers associated with MaxO as coauthors. The publication list in section **V** is a colorful mix of red and blue authors and red and blue underlined authors.
3. **Sharing of new or improved methods.** Two of the primary thrusts of MaxO are to create more powerful demographic methods and to compile uniquely large and accurate databases. These efforts have been shared products of researchers in Odense and in Rostock, as documented in sections **III.E** and **F**.
4. **Unique research through combination of unique fields.** MaxO is the leading engine in the unique, highly productive combination of evolutionary biology, epidemiology and demography, Its research is being published in top journals, as documented in sections **II**, **III**, **V**.
5. **Attract talent, junior to senior.** MaxO has attracted 21 talented doctoral students, listed in section **VII**. The graduates of the European Doctoral School of Demography, which MaxO

will host in 2017-8 and 2018-9, form most of the cadre of future demographers in Europe. Fewer than 200 have graduated so far in the decade since EDSD was established. As documented in the Staff List in IV, MaxO has attracted 14 of these graduates to Odense and another 4 are associated with MaxO activities in Rostock. So roughly 10% of the EDSD graduates (drawn from the best 15-20% of these graduates) have been attracted to MaxO. At the middle level, 4 of the Assistant Professors attracted to MaxO have been promoted to tenured Associate Professors and 2 of the postdocs have been promoted to tenure-track Assistant Professors. At the senior level, MaxO has succeeded in attracting Jim Oeppen, one of the world's most knowledgeable demographers. One of the Associate Professors is under review to become a full Professor. Four highly-regarded full Professors, Baudisch, Canfield, Christensen and Vaupel provide leadership to MaxO. Baudisch, the youngest of the four, has an extraordinary record of publication in Science, Nature, PNAS and other top journals. Canfield and Vaupel are members of the U.S. National Academy of Sciences; Christensen was knighted by the Queen of Denmark for his outstanding research. All four have been extensively cited relative to the standards of their disciplines and their ages.

**6. Joint education programs for junior researchers.** The best education program for first-year doctoral students in Demography is the European Doctoral School of Demography, of which Vaupel is “Rektor” and which receives a large share of its funding and much of its teaching from MPIDR as well as from, increasingly, MaxO SDU. In particular, several of the staff at MaxO SDU teach in the EDSD program, including Baudisch, Canudas-Romo, Lenart, Oeppen and Vaupel; this effort will increase in 2017-19 when EDSD will be located in Odense. EDSD is a key joint educational program, between MPIDR and MaxO Odense and also among the leading demographic research institutions in Europe. Beyond EDSD, researchers at MaxO SDU and MPIDR have jointly advised several doctoral students, as documented by the red and blue colors and underlines in VII.

**7. Joint use of infrastructure.** The required infrastructure for Biodemography has two crucial, hard-to-find elements—(i) state-of-the-art mathematical and statistical methods as well as (ii) large, accurate databases. As outlined in section III.E, MaxO Odense and MaxO Rostock work closely together on (i). And as outlined in sections I and III.F, this is also the case for (ii). Another key element of infrastructure is transportation that facilitates face-to-face contact. Rostock and Odense are roughly 150 km. apart and various means of getting from one place to the other exist. For two decades Vaupel traveled almost every week back and forth between the two and many researchers at MaxO Odense and MaxO Rostock make the trip regularly.

**8. 3<sup>rd</sup> party funding.** Our record of external grants detailed on page 40 speaks for itself. Such grants will increase MaxO expenditures by 50% in 2017.

**9. Increased international competitiveness.** MaxO is the international leader in its field.

**10. Visibility.** The media record of MaxO coverage is outstanding compared with the performance of most other Max Planck Centers and of most Max Planck Institutes.

Despite its excellence on the seven criteria to be considered by the Review Committee and the ten additional criteria to be assessed by the Max Planck Commission on Max Planck Centers, the future of MaxO is uncertain because of a technical problem. Vaupel will step down from his directorship at MPIDR at the end of 2017. It is not yet known who his successor might be. Hence it is impossible for MPIDR to make decisions affecting MaxO in 2018 and beyond. It is possible that Directors of other Max Planck Institutes might play a role in helping guide MaxO in the future. Creative, judicious solutions to these issues will be formulated at the highest levels of the Max Planck Society.