Editorial

Editorial for the Special Issue: Biodemographic determinants of lifespan

1. Introduction

Biodemography has been recognized as a stand-alone area of scientific inquiry for well over two decades (Carey and Vaupel, 2005; Vaupel, 2010) with many papers involving biodemographic concepts, mathematical models, and experimental methods appearing in prominent gerontology journals including Experimental Gerontology. Despite shared interests in studies of aging, survival, and lifespan, interactions between biogerontologists and biodemographers have been limited. This is primarily because historically the former has been primarily concerned with physiological, genetic and molecular mechanisms, and the latter has been mainly interested in individual-, cohort- and population-level phenomena. However, as biodemography "comes of age" (Wachter, 2008) involving, not only mathematical modeling and experimental demography of model organisms, but investigations concerned with gene expression, "geno-economics," and behavioral genetics, opportunities arise for cross-fertilization involving these two fields.

The main purpose of this Special Issue is to bring together the eight papers that summarize, synthesize, and/or extend research conducted by scientists involved with the NIA-funded P01 Biodemographic Determinants of Lifespan that were presented at a workshop in Napa, California in late 2011. A secondary goal is to lay the groundwork for greater exchange of information and collaboration between biogerontologists and biodemographers. It will be useful for us to first present a historical background on the emergence of biodemography as a distinct field. We then present a brief summary of each of the papers, and end with a short commentary concerned with prospects for increased complementarity of biodemography and biogerontology.

2. Biodemography—historical background

Demography and biology (including gerontology) share a deep history as is evident from the early pioneering works of Thomas Malthus (1798), i.e. populations grow exponentially but resources do not; Charles Darwin (1859), i.e. selection on birth and death rates result from the struggle for existence; Benjamin Gompertz (1825), i.e. a person's resistance to death decreases with age; Raymond Pearl and

Parker (1924), i.e. life table studies of *Drosophila*); and Alfred Lotka (1924), i.e. Elements of Physical Biology. Although many biological disciplines including ecology (e.g. life history theory), evolutionary biology (e.g. fitness concepts) and gerontology (e.g. Gompertz model) subsequently integrated these and many other demographic concepts, ideas, and tools into their respective paradigms, there was little interest among demographers in incorporating biology into any part of the discipline until the last quarter of the 20th century (Carey and Vaupel, 2005).

In the late 1970s members of the International Union for the Scientific Study of Population (IUSSP) expressed concern that demography was at risk of isolating itself and becoming more a technique than a science. Nathan Keyfitz lamented that "demography has withdrawn from its borders and left a no man's land" (Keyfitz, 1984; Forward). Hence in 1981 a workshop titled Population and Biology was organized at Harvard University (Keyfitz, 1984) to explore various topics at the interface of biology and demography such as the possible impact of biological "laws" on social science (Jacquard, 1984; Lewontin, 1984; Wilson, 1984), the autoregulating mechanisms in human populations (Livi-Bacci, 1984), and the concepts of morbidity and mortality (Cohen, 1984). It was itself significant that no notable papers or concepts emerged from this meeting between biologists and demographers, many of whom were among the most prominent scientists in their respective fields (Carey and Vaupel, 2005). The good intentions of top scientists are not enough to integrate two fields with fundamentally different disciplinary histories, professional cultures, and epistemological frameworks. To make progress it is imperative to layout a clear set of important (and ultimately fundable) questions that lie at the disciplinary interface. This is particularly important for integrating disciplines with disparate historical roots, such as demography with its roots in the social and analytical sciences and biology with its roots in the natural and experimental sciences.

In the mid-1980s two separate meetings were organized that brought scientists together to address the more circumscribed and focused questions that lie at the interface between biology and demography including: (1) Upper Limits to Human Life Span organized in 1987 by Sheila Ryan Johannson and Kenneth Wachter at the University of California, Berkeley, in 1987, supported by the National Institute on Aging (NIA); and (2) Convergent Issues in Genetics and Demography organized in 1988 by Julian Adams, Albert Hermalin, David Lam, and Peter Smouse at the University of Michigan (Adams et al., 1990). These two workshops set the stage for the organization of a cluster of three highly successful workshops held between 1992 and 1996 under the leadership of Ronald Lee who chaired the Committee on Population of the U.S. National Research Council. A series of planning and discussion meetings culminated in a workshop in Washington D.C. in April 1996 co-chaired by Kenneth Wachter and Caleb Finch. This workshop was one of the seminal developments in

biological demography because of the new insights and perspectives that emerged as well as coinage of the term "biodemography" and creation of the field.

This workshop led to the book Between Zeus and the Salmon: The Biodemography of Longevity, edited by Watcher and Finch (1997). A second workshop, organized and chaired by Kenneth Wachter and Rodolfo Bulatao, focused on fertility and was designed to complement the workshop on the biological demography of longevity (Wachter and Bulatao, 2003). A third workshop concerned with biological demography, held in 2001 on the Greek Island of Santorini, was organized by James Carey and Shripad Tuljapurkar and titled Life Span: Evolutionary, Ecological, and Demographic Perspectives. This meeting yielded two important outcomes: (1) an edited volume that included papers on conceptual and theoretical perspectives on life span and its evolution, ecological and life history correlates, and genetic and population studies of life span in nonhuman species and in humans (Carey and Tuljapurkar, 2003); and (2) creation of a prospective research program consisting of multiple projects funded by the National Institute on Aging (NIA) over a 9-year period starting in 2003 (also included funds from the American Recovery and Reinvestment Act of 2009).

Titled "Biodemographic Determinants of Lifespan," this NIA-funded P01 involved upwards of seven different research projects concerned with empirical, theoretical, and mathematical aspects of aging and lifespan, and a total of 20 different scientists with expertise ranging from experimental biology and field ecology to mathematical demography and statistical modeling. A wide diversity of organisms was studied including honeybees in California and Arizona, tephritid fruit flies in Greece and Mexico, butterflies in Uganda and Colorado, nematode worms in Oregon and Colorado, and indigenous peoples in Bolivia. The range of mathematical models developed on the program was also quite extensive including deconvolution methods for estimating age structure, models exploring questions concerned with antagonistic pleiotropy and mutation accumulation, intergenerational transfer, age-stage structure, and dynamic heterogeneity. Researchers involved with the program published over 70 original research articles, the vast majority of them in either the top science journals such as Nature, Science, PLoS Biology and PNAS or in high-impact disciplinary journals such as Aging Cell, American Naturalist, Bioessays, Theoretical Population Biology, Current Biology, Experimental Gerontology, Ecology Letters, and Ecology. Two workshops were held during the funding period, one in the Azores in the 2007 organized by James Carey and Shripad Tuljapurkar that was titled Biodemography of Aging, Longevity, & Sociality, and a second in Napa, California in 2011 organized by James Carey, Shripad Tuljapurkar and Kenneth Wachter that was titled Evolutionary Ecology of Lifespan. Papers from this second workshop are those contained in this Special Issue.

3. Overview of papers

Each of the papers in this Special Issue is associated with one of the projects in the P01 program Biodemographic Determinants of Lifespan that was supported during part or all of the funding period (2003–12). These include projects involving the biodemography of the nematode (PIs—Thomas Johnson and Patrick Phillips), honeybees (PIs—Rob Page and Gro Amdam), and medflies (PIs—James Carey, Hans-Georg Müller, and Jane-Ling Wang), intergenerational transfers (PI—Ronald Lee), mathematical demography of biodemography (PI—Kenneth Wachter), evolutionary dynamics of lifespan (PI—Shripad Tuljapurkar), and healthspan in Tsimane indigenous people in Bolivia (PIs—Hillard Kaplan and Michael Gurven). Brief summaries of the main findings or overviews of each of these papers are presented below.

Using the nematode worm, *Caenorhabditis elegans*, Deqing Wu, Patricia Tedesco, Patrick Phillips and Thomas E. Johnson explored a question central to evolutionary theories of aging (Wu et al., 2012-this issue)—do fertility/longevity trade-offs exist in populations of randomly mating males and hermaphrodites? The results of experiments involving a large population of young *C. elegans* males and hermaphoridites that were no longer self-fertile showed a significant negative relationship between late-life fertility and individual longevity (i.e. *C. elegans* hermaphrodites can increase their reproductive success via late-life outcrossing with males). Noting that this capacity must therefore either be an evolutionary relic or be still actively maintained within populations, they stress that interpretation of the potential tradeoffs must clearly be considered within the context of both self fertilization and outcrossing.

Many animals are characterized by declining brain function at advanced ages, including *Apis mellifera*, the model system used by Nicholas Baker, Florian Wolschin, and Gro Amdam in their paper concerned with brain aging in this species (Baker et al., 2012). In their experiments they combined manipulations of social development with a measurement of sensory sensitivity, associative learning, and a proteomic technique to address the question of whether learning performance can be recovered in aged individuals. They confirm that sensory sensitivity can remain intact during aging, and that age-associated learning deficits are specific to bees that forage. These initial data go beyond previous findings by showing how foragers age in social groups of different age-composition and size. Their work provides the strongest evidence, thus far, for reversibility of learning deficits in aged honeybees, and indicates that recovery-related brain plasticity is connected to cellular stress resilience, maintenance and repair processes.

Ulrich Steiner, Shripad Tuljapurkar, Timothy Coulson, and Carol Horvitz address some of the challenges associated with understanding structured populations (Steiner et al., 2012-this issue). They note that interest in stage-and age structured models has recently increased because these models can describe quantitative traits such as size that are left out of age-only demography. However, available methods for the analysis of vital rates on lifespan in stage-structured models have not been widely applied because they are hard to use and interpret. Therefore these researchers present easily interpretable expressions for the sensitivities and elasticities of life expectancy to vital rates in age-stage models and illustrate their application with two biological examples, one involving swans and the other involving a tropical treelet. Their approach contributes to the new framework of the study of age- and stage-structured biodemography.

Deborah Roach presents original data from her large-scale experimental system on plants (*Plantago lanceloata*), one of the only plant projects ever to receive NIH/NIA funding (Roach, 2012-this issue). Making use of the appearance of an unplanned extrinsic 3-year stress period during an 11-year study of demographic rates in experimental cohorts, her study investigates how stress interacts with age to determine lifespan and mortality. She shows that it is not simply the environment that can have a major impact on demography in natural plant populations, but rather age, size and growth can interact with the environment to influence mortality and life span when the environment is stressful.

The paper by James Carey, Hans-Georg Müller, Jane-Ling Wang, Nikos Papadopoulos, Alexis Diamantidis and Nikos Kouloussis complements much of their earlier work on the captive cohort method—a technique they developed on their project which uses data gathered on the remaining lifespans of captured medflies to estimate the age structure of the wild population from which they are sampled (Carey et al., 2012). The underlying concept for this new method is that a population's age structure and its death distribution are inextricably and uniquely interconnected. In their paper they re-derive the basic population model in demographic rather than statistical notation to make it more transparent and accessible to demographers and biologists, introduce new graphics to illustrate the basic captive cohort concept, and describe a simplified method for