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Reflexion

Biodemography comes of age

Kenneth W. Wachter

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Kenneth W. Wachter[1]

Abstract

Biodemography has emerged and grown over the last fifteen years, with loyal and far-sighted support from its patrons. As it enters what might be called its adolescence as a field, it faces challenges along with abounding opportunities. One challenge is to continue to generate knowledge that contributes to human health and well-being. A second is to insist on high standards of quality control within its cross-disciplinary environment. Opportunities appear in a variety of directions, including mathematical modeling, genomic analyses, and field studies of aging in the wild.

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[1] Department of Demography, University of California, Berkeley, U.S.A.
E-mail: wachter@demog.berkeley.edu

1. Progress in Biodemography

The last 15 years have witnessed remarkable scientific progress in the emerging field of biodemography. Research in the biodemography of longevity has brought about a whole change in attitude with respect to future progress against mortality at extreme ages, shifting prevailing views from an emphasis on limits and diminishing returns to an emphasis on plasticity. The effect is seen in the solid consensus that has now crystallized around forecasts that posit a continuation of extensions in longevity, with strong implications for the future of social insurance systems in the United States, Europe, Japan, and other developed and developing countries.

The development of biodemography was made possible from the beginning by investments on the part of what is now the Behavioral and Social Research Division of the U.S. National Institute on Aging (N.I.A.) under the leadership of Richard Suzman. Its progress can be traced through a series of workshops funded by the N.I.A. and associated volumes sponsored by the N.I.A. under the auspices of the Committee on Population of the U.S. National Academy of Sciences.

Progress in the biodemography of longevity has been paced by a 1988 workshop at Berkeley organized by Sheila Johansson and chaired by Kenneth Wachter, a pair of workshops in Irvine, California and Washington, D.C. and a 1997 volume *Between Zeus and the Salmon* edited by Kenneth Wachter and Caleb Finch, and a workshop on the Greek island of Santorini and 2003 volume *Life Span* edited by James Carey and Shripad Tuljapurkar. Scientific results have been summed up in a 2002 volume entitled *Longevity* by James Carey. Parallel work on the biodemography of fertility and family formation has led to workshops and a 2003 volume *Offspring* edited by Kenneth Wachter and Rodolfo Bulatao, sponsored by the U.S. National Institute of Child Health and Human Development. Today support for the field has become more international and includes an active program in evolutionary demography at the Max Planck Institute in Rostock, Germany.

Current thinking about trends in mortality draws on biodemographic insights, as in Wilmoth (2007). Complementary viewpoints from behavior genetics may be found in the collection edited by Rodgers and Kohler (2002). A perspective on the evolutionary questions addressed by biodemography has been offered by Flatt and Promislow (2007). Basic sources remain Finch (1990), Charlesworth (1994), Rose (1991), and Vaupel *et al.* (1998).

On a fundamental level, research in biodemography has challenged classical formulations of the evolutionary theory of longevity, both through experimental and observational data and through mathematical and theoretical developments. Initiatives in biodemography have also induced demographers and behavioral social scientists to learn about basic tenets and new findings in the genetics and biology of aging and begin to make biological realism a priority in models. Demographic perspectives have influenced research strategies for a select group of biologists who have come to recognize the value of large population studies for generating lifetable estimates, along with the need for comparative formal modeling. The experience of grappling with the evolutionary theory of longevity has led demographers into collaboration with anthropologists and helped recast our assumptions about the evolutionary environment in which genetic and biological determinants of age-specific vital rates have been shaped.

2. Challenges

The field of biodemography is now moving beyond its heady founding days into a period of consolidation. This period brings new challenges. Two such challenges loom large for the coming years. First is the need to keep research in biodemography in tune with the broader goals which have sustained it, the mission to promote the health and well-being of the human population. Second is the need to keep a high standard of quality control, as interdisciplinary researchers step out beyond their original base of expertise.

First comes the question of mission. The richness of biodemography has been enhanced by a broad view of mission on the part of the funding agencies and their unwavering commitment to fundamental science. Such a broad view remains essential for the future. Nonetheless, relevance is not irrelevant.

Human demography, data collection, validation, and modeling played a large role in the early program projects in biodemography, and especially in the founding program project led by James Vaupel. The amount of human demography included in more recent research programs, for instance under the rubric of “Evolutionary Demography”, is starting to be less. In non-human demography, some studies of the vital rates and lifecycles of other species tell us about fundamentals of the nature of aging. Others can be rather specific to particular species. Strategies for survival among pond-hopping salamanders can be fascinating biology, but the subject stretches the mandate of biodemography.

The demographic relevance of studies of non-human species to human aging has to a large extent been mediated through mathematical modeling of commonalities in the shapes of age-specific schedules of vital rates. Gompertz patterns in hazard functions at medium-old ages and plateaus at extreme ages, shared among a range of organisms, have been a focal point. It is at the level of general evolutionary mechanisms, not specific adaptations, that what we learn about the demography of flies and worms, bacteria and baboons, becomes relevant to humans. This role of mathematics is seen throughout the Santorini volume, Carey and Tuljapurkar (2003), and spelled out in the concluding chapter. A valuable side-effect of programs in biodemography has been to increase the familiarity of social scientists with evolutionary theory and the mathematical genetics of mutation accumulation and antagonistic pleiotropy.

Along with mathematics, in the coming years genome science is likely to open up connections through which research on non-human species uncovers results with analogues for humans. Biodemographers will need to stay abreast of progress made by biologists in identifying mutations, sequencing wild-type and mutant alleles affecting survival, mapping out networks, tracing biochemical pathways of gene action and characterizing patterns of gene expression.

The central role of mathematics and the coming role of genome science in establishing relevance highlight a second newly urgent challenge for biodemography, the issue of quality control. By the standards of mathematicians and mathematical geneticists, most demographers do not know very much mathematics. Among many working in biodemography, knowledge of formal models for evolutionary processes is at best impressionistic. A working grasp of new areas of genome science is just as limited, or more so. But the biodemographic community is now large enough that much work is being evaluated and reviewed within the community itself, and accepted and assimilated by researchers who do not necessarily have the qualifications or incentives to tell what is sound from what is unsound. These are the kind of circumstances which can breed junk science.

This danger coexists with opportunity. Cross-disciplinarity is a strength of biodemography, New ideas often come when researchers reach out and, as they try to master fields in which they have not been trained, struggle with and question prevailing assumptions. Good science, however, also requires good quality control. The continued health of biodemography depends on the ability to enlist and respect expertise in critical specialities, especially in mathematics, mathematical genetics, and genome science.

A special N.I.A. program to attract highly qualified mathematicians and biologists into the biodemography of aging mounted between 1999 and 2006 met with some notable successes. The task of cross-disciplinary recruitment, however, is a difficult one. Persistent efforts are required to build pools of mathematically qualified reviewers and of reviewers with strengths in genetic specialties, both for grant applications and for manuscripts. The incentive structure works against the willingness of people to serve outside their specialties. There is a pressing need for recruitment and retention of reviewers, advisers, and commentators with high standards and appropriate technical expertise.

3. Opportunities

The issues of relevance to human aging and of quality control are challenges that cut across the subject areas of biodemography. They help to structure the following ideas about areas of research that hold out promise.

The sector of biodemography devoted to human demography, which has recently been losing prominence, merits renewed emphasis and investment. Numerous opportunities are being opened up by the collection of biological indicators in conjunction with sample surveys and longitudinal studies rich in background social characteristics.

Biological indicators promise breakthroughs on a number of fronts. Genotype data for human population samples with sufficient representation among the extremely old should allow the identification of alleles concentrated among centenarians. The process of selective survival by genotype serves to amplify and presumably simplify some pathways of genetic influence. What we know about heritability of components of mortality risk and survival from twin studies has remained ambiguous and hard to interpret, especially in terms of age-specific gradients. Conventional demographic data combined with genotypes should help sort out the picture, where gene-environment interactions are likely to be critical. Steps might be taken toward quantifying the extent of mutational load, or at least some components of it. This information is crucial for attempts to account for Gompertzian hazard functions and assess future prospects for continued gains in survival.

Current thinking about questions that may be illuminated through the combination of biological indicators and social surveys is presented in two volumes from the Committee on Population of the U.S. National Research Council, *Cells and Surveys,* edited by Finch, Vaupel, and Kinsella (2001) and *Biosocial Surveys,* edited by Weinstein, Vaupel, and Wachter (2008). Relevance to gene-environment interactions in behavior genetics is treated by Rutter (2003). A range of opportunities opening up for demographers and social scientists interested in causal pathways, many involving biodemography, is surveyed by Hobcraft (2006).

Human analogues exist for many of the genes carrying the mutations being discovered in model organisms by experimental geneticists examining longevity extension. As knowledge is gained about gene products and physiological pathways of interest, it will be valuable to measure population-level allelic frequencies in human samples and examine their correlations with reported behaviors and social characteristics.

A speculative but exciting area opened up by the collection of genetic indicators is the search for possible associations between certain genotypes or gene expression profiles and behavioral tendencies. Risk taking, altruism, bonding propensities, and addictions are examples. Careful validation of candidate associations could give insight into retirement planning, health regimen compliance, and other major concerns of economic and social demographers. The difficulty of sound research in this area is balanced by the potential directness of its relevance.

Lines of new investigation are sure to emerge from current work on biological indicators focused on cumulative stress, allostatic load, and social support. The striking raw correlation in U.S. data between frequency of religious attendance and probabilities of survival points up the need for deeper studies of social connectedness.

Building on confirmatory studies regarding early-life influences on late-age mortality, future research needs to zero in on possible biological mechanisms. One hypothesis relates to inflammatory responses. Non-genetic biological markers tied to detailed retrospective or longitudinal life histories could further such investigations.

An essay by Linda Partridge (2006) in *Daedalus* explains new genetic findings and their relevance to human studies of aging. An introduction to "Geno-economics" and the search for associations between geneotypes or gene-expression profiles and behavioral tendencies is found in *Biosocial Surveys* Chapter 15 by Benjamin *et al.* (2008). Hummer *et al.* (1999) is a good source for covariates of survival. An example of discoveries relating to allostatic load is found in Seeman, Glei, *et al.* (2004). Inflammatory responses and their late-life influences are featured in Crimmins and Finch (2006).

Biodemographic theory relies heavily on whatever knowledge can be gained about the evolutionary environment under which human vital schedules and life history characteristics evolved. Interaction between biodemographers and anthropologists engaged in fieldwork among the last remaining bands of human hunter-gatherers has been a key to conceptual progress. Promoting continuing collaboration is a high priority for investment. This work represents behavioral and social research *par excellence.*

An example would be further field-work on age-specific profiles of investment in skills and other kinds of human capital and measurements of returns on these investments associated with fitness components. Life-history optimization models are hampered by the absence of independent information on the constraints under which tradeoffs occur. Some clues about constraints might come from comparisons of human hunter-gatherers with data on wild populations of primates which have been observed over substantial periods of time.

In the recent past, one of the most active subjects of study has been relationships between social support, intergenerational transfers, and evolutionary influences on the shape of age-specific vital schedules. However, there have been serious problems with this field. A fallow period might help the field toward recovery.

One of the enduring puzzles about human longevity is the historical connection between enriched nutrition, greater physical stature, and longer life over the last two centuries. Humans seem to have been pre-adapted to be able to take advantage of diets far richer in calories and micronutrients than anything common over the course of evolutionary time. Current concerns over obesity and interest in caloric restriction need to be integrated with the contrasting lessons of the historical record.

Evolutionary game theory has burgeoned in the last few years. The work is not yet being widely discussed by demographers. It fits naturally into several intersecting themes of biodemography. It may be able to supply an evolutionary background for understanding behavioral correlations with genetic indicators for surveys. It connects to anthropological studies of the human evolutionary environment.

Demographic thinking about evolutionary environments has been strongly influenced by the chapter by Hillard Kaplan (1997) in *Between Zeus and the Salmon.* Progress with the collection and interpretation of data is summed up by Kaplan, Hill, *et al.* (2000) and by Kaplan, Lancaster, and Robson (2003). Hofbauer and Sigmund (1998) provide an introduction to evolutionary game theory.

On the mathematical side, high on the agenda is the consolidation of the breakthroughs that have been made in modeling age-specific mutation accumulation. Frailty modeling is entering a period of transition, as fixed-frailty models are succeeded by changing frailty models, for instance by stochastic vitality models, to which general results on quasi-stationarity can be applied. Directions for new research will depend to a considerable extent on the kind of empirical information that experimental genetics proves able to supply. Estimates of age-specific profiles of gene action and mutational loads are eagerly awaited.

Optimization models of life histories would benefit from empirical information on the nature and origin of constraints under which optimization might occur. Such empirical information may be some time in coming. Complete freedom to posit constraints that achieve particular forms of solutions currently limits the approach. New thinking about segregation of damage and reparability has been stimulated by experimental studies of "aging" in *E. coli.* Differential equation models for cellular aging developed by biologists may be worth assimilating by biodemographers. As biological indicators attached to social survey data become available, new statistical approaches will be required.

On the whole, quite separate mathematical models have been developed for the different strands of theory involved in biodemography. Early progress no doubt required a field of mutation accumulation modeling, a field of life history optimization, and a field of reliability and stochastic vitality. But the associated processes must in fact operate in tandem in nature. They are not alternative explanations of commonalities across species. They are complementary components of an explanatory framework. Enough progress has now been made on the separate strands to take up the challenge of combining models. The new demographically structured models for mutation accumulation have opened up opportunities for comprehensive multi-level modeling.

Much of the mathematical work in biodemography has been directed at genetic mechanisms, building on fifty years of progress in mathematical genetics. Future work may profit from more emphasis on behavioral adaptations and processes of adjustment and "learning" over the life course. More attention to environmental interactions may be important to understanding family-level and group effects influencing age-specific vital schedules. The modeling of demographic processes over pre-history can take advantage not only of anthropological clues about the evolutionary environment, but also of the impressive progress that has been made in phylogenetic trees, coalescent processes, and the reconstruction of population bottlenecks from genetic markers. With the new vitality of spatial demography, biogeography and biodemography may have much to contribute to each other, if sufficient mathematical talent can be attracted to the field.

Several kinds of mathematical work in biodemography are featured in the volume by Baudisch (2008) and in papers by Steinsaltz, Evans, and Wachter (2005), Steinsaltz and Goldwasser (2006), Steinsaltz and Wachter (2006), Mueller *et al.* (2007), and Steinsaltz and Evans (2004). Yashin *et al.* (2000), Gavrilov and Gavrilova (1991), and Buerger (2000) are basic sources. Spatially structured models and phylogenetic analysis are treated by Durrett (2002).

For biodemographic work on non-human species, the touchstone needs to be relevance to fundamental processes of aging or to human analogies. Understanding the life-histories and environmental adaptations of any species in evolutionary terms may be of biological interest, but processes are often dominated by the details of the organism and the niche it occupies. It is good for demographers to be aware of such research, but any program in evolutionary demography needs to be able to pick and choose.

Perhaps the highest priority for biodemographic work with non-human species is for research on aging in the wild. Evolutionary accounts of senescence have been based for fifty years or more on untested generalizations about populations in the wild. Questions about the absence or presence of elderly individuals in populations in the wild and about hallmarks of senescence in vital rate schedules are now becoming testable. Because the generalizations of the past have been so sweeping, much may be learned from organisms quite different from humans, including flies and worms, if age-distributions and survival components can be measured. Laboriously collected longitudinal data on primate populations, for example, the Amboseli baboons, represents a treasure trove for biodemographers. When vital-rate estimates of wild, semi-wild, and captive populations of sufficient size can be compared, findings are especially cogent.

Work by experimental geneticists on mutations associated with longevity has been carried out on laboratory strains that have adapted over long periods of time to laboratory environments. Much more information is needed about how the findings play out for organisms in natural environments. Biodemographers need to stay abreast of developments in this area.

Demographers have developed extensive formal theory for studying populations in fluctuating environments. Recently, biologists have been taking advantage of these tools, gathering and interpreting field data for species of plants and animals subject to pronounced and measurable variations in conditions over time. Some findings depend on details of the organism and the field site. One aspect, however, which would have broad implications for overall understanding of aging is the hypothesized relationship between evolutionary benefits of mechanisms associated with caloric restriction and conditions of environmental fluctuation.

Research on aging in the wild can be sampled in Bronikowski *et al.* (2002) and a study of Mediterranean fruit flies by Carey *et al.* (2008). Fluctuating environments come to the fore in Horvitz and Tuljapurkar (2008).

The technology of gene-expression measurements has surged forward, and biodemographers are starting to investigate how this technology can be employed for studying aging. Patterns of changes in gene expression profiles by age, measured simultaneously over large collections of sites, can be expected to be very complex. Presumably they will differ from tissue to tissue. It is early to predict what kinds of general understanding will emerge, but biodemographers should begin to undertake pilot studies. Such studies are important not only to gain a sense of the opportunities and pitfalls, but also to build expertise for interpreting research results from biological laboratories around the world.

In summary, biodemography in 2007 faces challenges and opportunities. Issues of relevance and quality control are taking on new salience. Visionary support has fostered the birth and childhood of this new field. As the field enters what might be called its adolescence, tensions and growing pains go hand in hand with exciting prospects.

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