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Why Biodemography Should be Included

in Demography Coursework

by

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Presented at:

XXIVth IUSSP General Population Conference

Salvador, Bahia, Brazil

18-24 August, 2001

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ABSTRACT

Integrating biology in general and biodemographic principles in particular into the demography curriculum is important because the principles provide an important foundation for understanding human birth and death rates, because the principles can help frame questions concerning future directions, and because the preliminary list of principles will encourage biologists and demographers to identify other general demographic patterns. In this paper I consider the biodemography of aging and longevity in epistemological, comparative, and predictive contexts to illustrate why incorporating biological perspectives into the demography curriculum will help strengthen and renew the field.

INTRODUCTION

The seminal book edited by Hauser and Duncan (1959) considered demography as belonging to that group of empirical sciences whose data are produced by the observation and recording of events occurring naturally in the external world rather than whose data are generated by experiments under controlled conditions. Consequently they considered demography as analogous to astronomy, geology, and paleontology rather than to sciences such as physics, chemistry and biology. With some notable exceptions (e.g. Pearl and Parker 1924), this demographic paradigm accounts for why most of the information flow between demography and biology has been from the former (demography) to the latter (biology). The reason for this unidirectional flow of information and ideas is partly due to historical differences in the disciplinary roots and partly due to practical considerations—many demographers do not believe that biology provides answers to the types of questions with which they were concerned. Rather demographers usually consider social, political and economic answers to be more relevant to the questions they address than are biological perspectives.

In contrast to the earlier times when non-biological considerations in demography superceded biological ones, in the late-1980s and early 1990s interest began to grow in integrating biology into demography (i.e. biodemography) in the context of aging and longevity (Wachter and Finch 1997) and, in turn, of social and economic policies concerned with aging populations. Arguably the single most important question that was raised in this context that encouraged demographers to seriously consider biology was "*What is the upper limit to human life span?*" The reason this question was important is that it needs to be considered in biological as well as demographic contexts—human life

span is inherently biological inasmuch as it is a positively selected (evolved) life history trait of the species. Statistical and/or actuarial analysis alone is inadequate for considering the question concerning 'limits' since strictly analytical approaches cannot shed light on how humans will respond to new environments. As Keyfitz (1970) noted, turning points in demography cannot be predicted from extrapolation alone and models to predict these turning points cannot be developed without a fundamental understanding of the phenomena being modeled.

The broad purpose of this paper is to provide an overview of why incorporating biodemography into demographic pedagogy is important. Although I use examples from research on the demography of aging, the concepts are general and thus apply to a number of other areas where the integration of biology into demography will foster deeper insights and provide more secure scientific foundations for demographic policy.

EPISTEMIOLOGICAL CONSIDERATIONS

Coherence, Understanding and Prediction

There are at least three general ways by which including biodemographic concepts in demography coursework can strengthen the field (from Carey and Judge 2001). *First*, biodemographic principles provide a scientific *coherence* that is lacking in conventional texts on demography and actuarial science. Biodemography has the potential for integrating biology into the pedagogical framework of classical demography in much the same way as basic biology is integrated into biomedicine. The focus on humans is retained but the epistemological foundations are strengthened, the biological scope is expanded, and the demographic perspectives broadened. *Second*, biodemographic principles can provide *explanations* for life table patterns in human populations that are

not evident in the absence of broader biological concepts. For example, biodemographic principles link senescence and sexual reproduction. The principles suggest explanations of sex differentials in life expectancies, why older individuals may grow old more slowly, whether life span limits exist, whether post-reproductive life is common or rare, and if and how post-reproductive life spans in other species increase fitness. *Third*, biodemographic principles can be used as a more secure foundation for qualitative *predictions* in the context of old-age mortality, upper limits of life span (or lack thereof), and the magnitude and sign of the gender gap (Wilmoth 1998; Judge and Carey, 2000). For example, it was not known until the results of animals studies were reported showing similar patterns whether slowing of mortality at older ages in humans was an artifact of small numbers of observations, a period effect, or real (Vaupel et al. 1998).

Model Systems

Inasmuch as demography is concerned with whole-animal phenomena (birth; death), model systems (e.g. nematode worm; fruit flies; laboratory rodents) can be brought to bear on fundamental questions concerning the nature of aging and longevity. However, a stumbling block in mainstream demography for the serious use of these model systems in studying actuarial aging has been the mistaken belief that, because causes of death in humans are unrelated to causes of death in non-human species (particularly in invertebrates such as nematodes and fruit flies), little can be learned from detailed knowledge of age-specific mortality in these model species. This perspective is based on a theory familiar to most demographers—the "theory of the underlying cause" in public health and medicine which states that if the starting point of a train of events leading to death is known (e.g. cancer), death can be averted by preventing the initiating

cause from operating (Moriyama, 1956). For aging research the problem with this perspective is that death is seen as a single force—the skeleton with the scythe. A more apt characterization that applies to deaths in all species is given by Kannesto (1991) who notes that deaths are better viewed as the outcome of a crowd of "little devils"; individual potential or probabalistic causes of death, sometimes hunting in packs and reinforcing each other's efforts, at other times independent. Inasmuch as underlying causes of death are frequently context-specific, difficult to distinguish from immediate causes, and their post-mortem identification in humans is often arbitrary (in invertebrates virtually impossible), studying the causes of death often provides little insight into the nature of aging. If aging is considered as a varying pattern of vulnerability to genetic and environmental insults, then the most important use of model species in both teaching and research on the demography of aging is to interpret their age patterns of mortality as proxy indicators of frailty. The point is this—different model systems can be used to address questions at different levels of demographic generality.

COMPARATIVE BIODEMOGRAPHY

Levels of Specificity

The demographic profile of humans have characteristics typical of a wide variety of organisms due to similarity in evolutionary selection pressures. For example, the characteristic of higher male than female mortality during prime reproductive ages is typical in sexually reproducing animals of a large number of vertebrate and invertebrate species (Carey 2001; Carey and Judge 2001). The pattern is an evolutionary result of sexual selection on males and, as such, is a *general characteristic* of a large number of species. Other observed general characteristics include the variable rate of change in

mortality with age (rates that decline after earliest stage and then increase with age) and a slowing of mortality at the most advanced ages (Vaupel et al. 1998). Given such generalities, there are also characteristics of mortality profiles that pertain more specifically to a particular species (or other taxonomic group). Such species level characteristics are imposed on some general pattern.

The mortality experience for humans can thus be considered at two levels. The *general level* exhibits a decline after infancy, increases through the reproductive life span (the overall U-shaped trajectory), and a sex differential. The *specific level* pertains to details of the mortality experience unique to humans including the actual probabilities of death by age, inflection points of age-specific mortality, the cause-specific probabilities of death, and the age-specific pattern of the sex differential. The observed mortality pattern is a combination of the evolutionary components of the trajectory (which will be common to a large number of species with overlapping life history characteristics) and the proximate age and sex-specific factors contributing to mortality under certain conditions. For example, under contemporary conditions male reproductive competition selects for riskier behavior and results in deaths due to accidents and homicides during early adulthood. The general and specific components of any population's mortality schedule can only be determined through studies using model systems; that is, the use of experimental demography and comparative biology.

Human Life Span

Questions such as *"Is human life span extraordinary or relatively common?" "In what evolutionary context did human longevity evolve?" "Is menopause an artifact of living in a protected environment or an evolved, species-specific traits?"* cannot be

adequately addressed without considering human longevity in the context of comparative demography. For example, analyses of large databases on record life spans in both vertebrates (Carey and Judge 2000) and invertebrates (Carey 2001) suggests that selection for the extended longevity of most species can be grouped into two general categories: (1) *Environmentally-selected.* This category includes animals which live in environments where food is scarce and/or widely dispersed (e.g. cave species; deep-sea tube worms) or where conditions are uncertain and/or predictably adverse part of the time (many desert species such as tortoises and some lizards); and (2) *Socially-selected.* This category includes species which exhibit extensive parental investment (tsetse flies), extensive parental care and/or monogamy (e.g. most birds; bats); and/or a high level of sociality including the eusocial insects (wasps, ants, bees, termites) as well as several mammalian species such as most primates (including humans), cetaceans (whales; dolphins), and elephants. The reason that this classification system is useful in demography is because it situates human life span in the broad context of all animals. Specifically it suggests that the extended longevity of *Homo sapiens* evolved in a socioecological context more similar to non-human primates and eusocial insects than in the context of unfavorable environments such as the extended longevity of solitary desert species. The analysis also reveals that humans are among the longest lived animals in the animal kingdom, both absolutely and relatively (to body size). And comparative analysis by Judge and Carey (2000) of primate life spans and correcting for body and brain size estimated that the evolved life span of humans was likely in the range of 72 to 90 years. This estimate is important because it suggests that, because the estimate exceeds the age of menopause by over 2 decades, that menopause is likely a part of the evolutionary

legacy of our species. Understanding this relationship is important to demography because it delineates a line between the segment of the human life span that evolved (e.g. 75 years) from the segment that is most likely truly an artifact of living in protected environments (e.g. greater than 75 years). The former is sometimes referred to as the "Darwinian" segment and the later as the "Post-Darwinian" segment.

Principles of Biodemography

Carey and Judge (2001) described a set of general principles of biodemography that apply to a wide range of species including humans, a subset of 10 of which are contained in Table 1. These principles are important because they summarize and synthesize many of the general demographic properties and/or concepts that apply to a wide range of species. Construction of this preliminary set of general principles encourages a greater communication between demographers and biologists by defining a common goal—identifying general demographic patterns. Each of the ten principles listed in Table 1 are general and therefore applies to virtually all species including, of course, humans.

{Table 1 around here}

FRAMING THE FUTURE OF HUMAN LIFE SPAN

An understanding of biodemography can provide a framework for considering the demographic future in ways that are not possible using conventional approaches. For example, consider the question: "*What is the future of human life span?*" There are at least two ways to consider this question. One way is to use conventional demographic methods of extrapolation or projection to delimit the sex-specific rates and causes of death into the future. This is the standard approach used by most actuaries and

demographers and is useful for short and medium-term estimates of life expectancy in the future. Although are numerous problems with using extrapolation to predict the future, one of the main shortcomings is that the approach assumes that trends in the past will continue into the future. Or in the context of life span, it assumes that the rate of aging in humans is essentially immutable but that reductions in different causes of death can be reduced more or less at the same rates as in the future.

A second way to address this question regarding the future of human life span is to consider long-term changes that are thought to be either practically or theoretically possible based on biodemographic principles that were derived from experimental and/or comparative demography (e.g. Table 1). This approach has received little attention because it does not yield results that are useful in day-to-day demography policy making. However, I believe this approach is useful because it frames questions regarding the future of human life span in a different and larger domain than the extrapolation approach. That is, the mortality decrement approach for considering the question of the future of human life span is analogous to weather forecasting whereas the "biodemographic principles" approach more analogous to forecasting broad climatic trends. The former (decrement) approach provides specifics but the later (principles) approach provides long-term constraints on possibilities.

To illustrate how biodemographic principles can be brought to bear on demographic questions concerned with the future, in this section I will address the question "*What is the long-term future of human life span*?" While it is impossible to accurately predict specifics such as the life expectancy in the U.S. males in 2050 or the magnitude of the gender gap, it is possible to frame the question and therefore establish

general constraints. This can be done by drawing on four general biodemographic principles described in the following sections.

Life Span is Open-ended

This concept is derived from the finding from large scale life table studies on model organisms (Vaupel et al. 1998) where mortality slows at older ages. This observation is inconsistent with the idea that life span is fixed; that there is an age in all species (including humans) to which some individuals can survive but none can live beyond. In the context of human longevity, this suggests that life span is a dynamic rather than a static concept; that although there are certainly biological constraints, there are no specific built in limits to our longevity. This general observation is supported by the recent findings (Wilmoth et al. 2001) that the record life span in Sweden has been increasing for the past 130 years.

Sex-specific Mortality Responses Differ

The concept that the mortality response of males and females differ in similar environments stems from the observation in virtually all animals (including humans) that this is true due to differences in behavior and biology. For example, young males in nearly all sexually-reproducing species are risk prone whereas females are risk averse. This behavioral idiosyncrasy alone will ensure that differences exist in the sex-specific mortality response and, in turn, underlie differences in their life expectancies. Thus the general principle with respect to the future of human life span is that the gender gap in humans will almost certainly persist although the magnitude and perhaps even the sign of the sex-specific difference will be constantly changing.

Quantity of Life Follows Quality of Life

This concept refers to the principle that longevity (quantity of life) follows from health and vigor (quality of life). This principle is important because it provides context for the "Morbidity Compression" model first introduced by Fries (1980) stating that the prevalence of morbidity in a population can be reduced if (i) life span is fixed; and (ii) the age of onset of irreversible diseases can be postponed to later and later ages approaching this fixed 'maximal' life span. On close examination of this model in a comparative biological context suggests that, although the assumption is valid that quality of life follows (by definition) from improved health and vigor, the assumption that quantity of life is independent of this improved quality is incorrect. The importance of this principle in the context of the future of human life span is that it is virtually certain that morbidity will always be part of the human condition; that it is not possible to separate quality and quantity of life and that a transition period of poor health and infirmity will likely always be part of life's final stages.

Longevity Extension is Self-reinforcing

This concept was first introduced to the literature by Carey and Judge (2001) and is derived, in part, from the idea that long-lived animals such as humans evolved their extended life spans in one-of-two broad ecological or sociological contexts and that the different contexts have a bearing on the dynamics of further extensions in longevity. The first broad category of long-lived animals include those whose longevity evolved through direct natural selection in the context of environmental extremes, for example in deserts where rainfall and thus conditions for reproduction are episodic, or in caves where resources are extremely scarce. In both cases, extended longevity serves as an adaptation

for surviving long periods due to resource limitations and/or unpredictability. Examples include the desert-dwelling species such as tortoises and cave- and deep sea-dwelling species (both invertebrates and vertebrates). The second broad category includes species that exhibit extensive parental care, monogamy and/or advanced sociality (e.g. humans). Longevity in these contexts evolved through natural selection as well as through sexual and kin selection. The importance of this simple classification of animal life spans is that it provides important evolutionary and biological context for human longevity and, in turn, on the processes involved in extending longevity in social species. Specifically it set the stage for developing the idea that longevity extension in social species may be self-reinforcing.

This concept states that events in the human life course at foster improved health and well being at any one age, ramify broad band across all ages. This increases overall life span where the added age increments foster yet additional improvements in health at younger ages. And the cycle feeds on itself. The importance of this principle with respect to the future of human life span is that it underscores the importance of maintaining health in all age classes in order to extend survival at older ages, it changes thinking about life span from aging-oriented to longevity-oriented theory and thus allows consideration of mortality factors not related to aging (e.g. accidents; socio-economic; education) into a more comprehensive model.

DISCUSSION

In its perennial struggle to define and renew itself and to ensure its relevance in an ever-changing world, demography is always faced with decisions regarding whether to move in new directions. As Foster (2000) notes, demography, like other social sciences,

is slowly coming to terms with important truths that the biological sciences have proved beyond any doubt—that both the human mind and human behaviors are as much products of biological evolution as is the human body. Wilson (1998) noted that human beings may be unique in their degree of behavioral plasticity and in their possession of language and self-awareness, but all of the known human systems—biological and social—taken together form only a small subset of these displayed by the thousands of living species. I believe that the integration of biology into demography will provide a deeper understanding of demographic processes and thus will offer insights into which patterns are common to a broad range of organisms and thus which demographic patterns are uniquely human.

Table 1. Selected biodemographic principles derived from research on model organisms and comparative demography (from Carey and Judge 2001).

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Principle	Description
1. Senescence	Senescence is a product of natural selection on survival versus reproduction
2. Death vs failure	Biological organisms die whereas mechanical systems fail. The fundamental distinction between biological systems and mechanical ones is that the former undergo development whereas the later are 'born' de novo.
3. Mortality deceleration	Mortality rates slow in virtually all organisms at older ages. This deceleration implies that a specific upper limit to life span does not exist.
4. Sex-specificity	The mortality response of males and females of virtually all species will be different in similar environments.
5. Mortality plasticity	The trajectory of mortality in all species including humans is "facultative"—a term used in biology to describe life history traits with alternative conditions that vary with environmental conditions.
6. Demographic selection	As populations age they become more selected because subgroups with higher death rates will die out in greater numbers than those with lower death rates thereby transforming the population into one consisting mostly of individuals with low death rates.
7. Subdetectable mortality	Death rate cannot be measured below 1/n where n is the cohort size.
8. Longevity is adaptive	Life span evolved to 'solve' particular ecological problems such as bridging unfavorable periods (droughts) or, for humans and other social species, as a co-adaptation with sociality.
9. Life span is indeterminate	Life span is open-ended and dynamic; it is most usefully considered in the context of a species' ecology and evolutionary biology.
10. Cost of reproduction	A unit increase in reproduction at young ages causes a unit decrement in mortality at older ages. More generally, reproduction and mortality are inextricably linked.

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