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Introduction

> The relation of our disciplines has not been symmetric. Biology textbooks incorporate short courses in demography, an attention that is not reciprocated. But that . . . by no means forecloses work at the boundary of population and biology.
>
> Nathan Keyfitz (1984, 7)

Biodemography is an emerging interdisciplinary science concerned with identifying a universal set of population principles, integrating biological concepts into demographic approaches, and bringing demographic methods to bear on population problems in different biological disciplines (Carey and Vaupel 2005). It is also an interdisciplinary science in the sense that it uses theories and analytical methods from classical (human) demography and population biology to study biological systems at levels of organization from the individual, to the cohort, to populations. In so doing, biodemography provides quantitative answers to questions at the whole-organism level concerned with birth, death, health, and migration.

Biodemography does not have university-level departments of its own, but it has presence across departments within the fields of demography, economics, sociology, gerontology, entomology, wildlife and fisheries biology, ecology, behavior, and evolution. Research efforts in biodemography are often initiated by scientists who were traditional ecologists, demographers, economists, and gerontologists by training. It is concerned with the study of populations of organisms, especially the regulation of populations, life history traits, and extinction. Depending on the exact definition of the terms used, biodemography can be thought of as a small, specialized branch of classical demography, or as a tool with which to investigate and study ecology, evolution, and population biology.

Historical Perspectives on Biodemography

Demography began as the study of human populations and literally means "description of the people." The word is derived from the Greek root *demos*, meaning "the people," and was coined by a Belgian, Achille Guillard, in 1855 as "demographie"—elements of human statistics or comparative demography (Siegel and Swanson 2004). He defined demography as the natural and social history of the human species or the mathematical knowledge of populations, of their general changes, and of their physical, civil, intellectual, and moral condition.

Biology and demography

The field has had multiple points of contact with biology, as well as mathematics, statistics, the social sciences, and policy analysis. Population biology and demography share common ancestors in both T. R. Malthus (1798) (i.e., populations grow exponentially but resources do not) and Charles Darwin (1859) (i.e., differential birth and death rates resulting from variation in traits). The biology-demography interface also served as the research foundation for two distinguished demographers in the early decades of the twentieth century—Alfred J. Lotka (1880–1949) and Raymond Pearl (1879–1940). Lotka developed concepts and methods that are still of fundamental importance in biological demography, and his two most significant books are *Elements of Physical Biology* (1924) and *Theorie Analytique des Associations Biologiques* (1934). Pearl (1924, 1925) pioneered biological-demographic research on several species, including flatworms, the aquatic plant *Ceratophyllum demersum*, the fruit fly *Drosophila melanogaster*, and humans. He founded two major journals, the *Quarterly Journal of Biology* and *Human Biology*, and helped found both the Population Association of America (PAA) and the International Union for the Scientific Investigation of Population Problems (which later became IUSSP—the International Union for Scientific Study of Population).

Following the pioneering work of Lotka and Pearl in the 1920s and 1930s, there was very little interest among demographers in integrating biology into any part of the discipline until the 1970s. There were a few chapter entries on population studies in crosscutting disciplines such as demography and ecology (Frank 2007), demography and anthropology (Spuhler 1959), and genetics and demography (Kallmann and Rainer 1959), all of which are in the seminal book *The Study of Populations* by Hauser and Duncan (1959). These and other similar chapters served more as illustrations of how demographic methods were used by different disciplines than as sources of knowledge for demography.

Early developments

In the early 1970s a group of population biologists and demographers, including Nathan Keyfitz, launched the journal *Theoretical Population Biology* (TPB). The journal was intended to be a forum for interdisciplinary discussion of "the theoretical aspects of the biology of populations, particularly in the areas of ecology, genetics, demography, and epidemiology." This description is still used by the publisher to describe the journal, but the publisher describes the audience of the journal as "population biologists, ecologists, evolutionary ecologists," with no mention of demographers (or epidemiologists). In the late 1970s IUSSP members expressed concern that demography was at risk of isolating itself and becoming more a technique than a science. Demographer Nathan Keyfitz (1984b, 1) lamented that "*demography has withdrawn from its borders and left a no man's land which other disciplines have infiltrated.*" Hence in 1981 a workshop titled "Population and Biology" was organized at the Harvard University Center for Population Studies (Keyfitz 1984a) to explore the possible impact of biological "laws" on social science (Jacquard 1984; Lewontin 1984; Wilson 1984), the selective effects of marriage and fertility (Leridon 1984), the autoregulating mechanisms in human populations (Livi-Bacci 1984), and the concepts of morbidity and mortality (Cohen 1984). 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, was itself significant—the good intentions of top scientists are not enough to integrate two fields with fundamentally different disciplinary histories, professional cultures, and epistemological frameworks.

Traction

In the mid-1980s two separate meetings were organized that brought scientists together to address more circumscribed and focused questions that lie at the interface between biology and demography. The first workshop that brought biologists and demographers together during this period was organized in 1987 by Sheila Ryan Johannson and Kenneth Wachter at the University of California, Berkeley, titled "Upper Limits to Human Life Span," and supported by the National Institute on Aging (NIA). Although there were no publications and/or proceedings from this workshop, it was important historically because it was the first meeting to bring biologists and demographers together to focus expressly on a circumscribed topic of great importance to demographers, biologists, and policy makers—aging and longevity. This workshop set the stage for virtually all the subsequent research developments in the biological demography of longevity and aging.

The second workshop that helped frame biological demography was organized in 1988 at the University of Michigan by Julian Adams, Albert Hermalin, David Lam, and Peter Smouse, titled "Convergent Issues in Genetics and Demography" (Adams 1990). This resulted in an edited volume that included sections on the use of historical information, such as pedigree and genealogical data in genetics and demography, on the treatment and analysis of variation in the fields of genetics and demography, on epidemiology as common ground for the convergence of demography and genetics, and on issues in genetics and demography that have attracted the attention of scientists in both fields, such as two-sex models, minimum viable population size, and sources of variation in vital rates. This workshop on genetics and demography was significant because it revealed the importance of organizing research at the interface between biology and demography around a circumscribed topic, in this case genetics.

Coalescence

The Berkeley and Ann Arbor workshops set the conceptual stage for the organization of a cluster of three highly successful workshops held between 1996 and 2002. The first of these was a workshop titled "Biodemography of Longevity," organized and chaired by Ronald Lee of the Committee on Population of the US National Research Council, and held in Washington, DC (April 1996). This meeting fostered an interchange of demographic and biological ideas and was one of the seminal developments in biological demography because of the new insights and perspectives that emerged on the nature of aging and life span. The workshop led to the book *Between Zeus and the Salmon: The Biodemography of Longevity* edited by Kenneth Wachter and Caleb Finch (1997). This volume includes papers on the empirical demography of survival, evolutionary theory and senescence, the elderly in nature, post-reproduction, the human life course, intergenerational relations, the potential of population surveys in genetic studies, and synthetic views on the plasticity of human aging and life span.

The second workshop concerned with biological demography was organized by James Carey and Shripad Tuljapurkar. Titled "Life Span: Evolutionary, Ecological, and Demographic Perspectives," it was held on the Greek Island of Santorini in 2001. This workshop was a follow-up to the 1996 meeting on biological demography but with a greater emphasis on life span rather than aging per se. The edited volume from this workshop (Carey and Tuljapurkar 2003) included papers on conceptual and/or theoretical perspectives on life span and its evolution, ecological and life history correlates, and genetic and population studies of life span in both in humans and nonhuman species.

The third workshop, held at the National Academies in Washington, DC (June 2002) and 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. Like the others preceding it, this workshop brought together demographers, evolutionary biologists, geneticists, and biologists to consider questions at the interface between the social sciences and the life sciences. Topics in the resulting volume (Wachter and Bulatao 2003) included the biodemography of fertility and family formation and the genetic, ecological, and evolutionary influences on human reproduction.

At the beginning of the twenty-first century, biological demography is reemerging as the locus of cutting-edge demographic research. It is clearly accepted that fertility, mortality, morbidity, and other processes of profound interest to demographers have a basic biological component. Moreover, biology is fundamentally a population science and there is growing recognition that biological studies can benefit greatly from demographic concepts and methods. From a biologist's perspective, biological demography envelops demography because it embraces research pertaining to any nonhuman species, to populations of genotypes, and to biological measurements related to age, health, physical functioning, and fertility. Within this vast territory, several research foci are noteworthy and are briefly described in the next section.

Classical Demography

Classical demography is concerned with basically four aspects of populations (Siegel and Swanson 2004; Poston and Bouvier 2010). These are 1) *size*—the number of units (organisms) in the population; 2) *distribution*—the arrangement of the population in space at a given time; 3) *structure*—the distribution of the population among its sex and age groupings; and 4) *change*—the growth or decline of the total population or one of its structural units. The first three (size, distribution, structure) are referred to as population statics while the last (change) is referred to as the population dynamics. Hauser and Duncan (1953) regard the field of demography as consisting of two parts: *formal demography*—a narrow scope confined to the study of components of population variation and change (i.e., births, deaths, and migration); and *population studies*—a broader scope concerned with population variables as well as other variables, which may include genetics, behavior, and other aspects of an organism's biology. The methodology of demographic studies includes data collection, demographic analysis, and data interpretation.

Demographers conceive the population as the singular object for scientific analysis and research. However, as Pressat (1970, 4) notes, "population" is everywhere and nowhere in the sense that many aspects of demography can be studied simply as component parts of the disciplines considered. He states, "But to bring together all the theories on population considered as a collection of individuals subject to process of evolution, has the advantage of throwing into relief the many interactions which activate a population and the varied characteristics of that population." This is what demography is about, particularly mathematical demography.

Usefulness of Demography

Conceptual unification

Demography can be thought of in two ways. First, as a large collection of mathematical models that can be reduced to a small number of mathematical relationships. Or, as a small collection of metaphors that can be conceptually extended to a large number of biological problems. Both of these ways of thinking about demography provide conceptual as well as functional unification to ecology and population biology. In principle all life history events can be reduced to a series of transition probabilities and all events are interconnected in several ways. Demography provides the tools to connect these events, and most events reduce to one of two things—birth or death. Metaphorically, birth and death can represent a wide range of phenomena. In human demography divorce can be viewed as the death of a marriage, or in epidemiology hospital entry can be viewed as the birth of a case. In insect ecology metamorphosis can be viewed as the "death" of a larva and the "birth" of a pupa. It will become evident later that these perspectives extend beyond the rhetorical.

Projection and prediction

The terms *projection* and *prediction* are often used interchangeably in other disciplines. In demography, however, these terms apply to two distinctly different activities. *Population prediction* is a forecast of the future population. Because things are interconnected, we thus cannot know the future of one variable (population) without knowing the future of every other variable. *Population projection* refers to the consequences of a particular set of assumptions with no intention of accounting for the future population of a specific case (Keyfitz 1985). All predictions are also projections, but the reverse is not necessarily true.

Control, conservation, and exploitation

Caughley (1977) points out that the uses of demography in applied ecology fall into one of three categories. The first is control, where the objective is to reduce population number and growth rate. This obviously applies to the management of plants and animals. The second is conservation, where the goal is to increase growth rate to the point where the number of individuals are no longer threatened by extinction. The third is exploitation, where the purpose is to maintain a breeding stock of fixed size in order to harvest a fraction of their offspring (e.g., insect mass rearing) or gather products that they produce (e.g., honey). All three cases are concerned with conferring a predetermined population size or growth rate by manipulating life history traits. All involve demography.

Demographic Abstractions

Many early demographers tended to view the components of population change and the processes of population change separately, but more recently the trend has been to abstract and extend many of the components and mechanisms. These perspectives are important because they establish a unity among concepts and methods and they permit an easy extension to analysis of life history characteristics that may not currently have a protocol. Three useful abstractions include age, process, and flow.

Age

In conventional demography many events are measured with respect to the progression of age, but age is not the only progression in the life course. By viewing birth as the starting point and life progression as distance, then age becomes distance in time and total births become the distance in births. The general point is that all individuals that live to age 10 must also have lived to age 9, age 8, age 7, and so forth. Likewise, all individuals that live to produce the tenth offspring must also have lived to produce offspring number 9, number 8, number 7, down to number 1. This concept applies to any repeatable life history event.

Process

Demographic processes in which constituent events cannot be repeated are referred to as *nonrenewable processes,* and those events that can be repeated are *renewable processes*. Clearly, attainment of reproductive maturity and mortality are nonrenewable processes, and giving birth and mating are renewable in most species. By specifying the order of events in a renewable process, it is possible to examine the constituent nonrenewable parts using life table methods of analysis.

Flow

Demography provides a methodology for biological accounting. Gathering data in many respects is the measurement of current inventory that describes changes in stocks (individuals) that have occurred over two or more points in time. Changes arise as a consequence of increments and decrements associated with events such as births and deaths and with flows of individuals between ages or between cross-classifications. Hence net changes in birth and death account for changes in numbers, but interstate transitions or flows from what is considered the origin state to the destination state account for population structure.

These abstractions form the core of the biodemographic models and analysis that are presented in the chapters that follow.

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