BIOLOGICAL DEMOGRAPHY

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Summary

Biological Demography (Biodemography) is an emerging area of classical demography consisting of two subcategories including biological demography and biomedical demography, the former concerned primarily with the experimental demography of non-human species such as fruit flies, nematode worms, and laboratory rodents, and the latter concerned with health demography of humans. In this chapter we define biodemography, provide a historical perspective of this new field, and outline some of the main principles that have been identified over the last several decades from the results of research from biological demography including the indeterminacy and adaptive qualities of lifespan and the deceleration and sex-specificity of age-specific mortality. At the end we describe briefly the developments in selected new areas within this new field including evolutionary demography, genetic and genomic demography, paleodemography, ecological biodemography, and biomedical biodemography. We conclude that both the biomedical-demography branch of biodemography and the biological-demography branch are vibrant areas of demographic research that are rapidly growing and that have great potential to enrich and enlarge the domain of demography. Not only can demographers learn much from biologists and epidemiologists, but demographers can contribute much to research on life in general (as opposed to humans in particular) and to research on population health.

1. Introduction

Biodemography can be compared with a tree with two main branches, each with many smaller branches, and with deep historical roots, a tree that currently is relatively small but burgeoning rapidly. Although still a modest sub-field within demography, biodemography is arguably the fastest growing part of demography and the most innovative and stimulating. The two main branches today involve: (1) biological-demographic research directly related to human health, with emphasis on health surveys, a field of research that might be called biomedical demography (or "epidemography" because it is a cross between demography and epidemiology), and (2) research at the intersection of demography and biology (as opposed to biomedicine), an endeavor we will refer to as biological demography. The first branch is characterized by demographers engaging in collaborative research with epidemiologists. This is very important, for both fields and for deeper understanding of human health. Researchers in the second branch face an even bigger challenge. Demographic and epidemiological concepts and methods are fairly similar, whereas the underlying paradigms of demography and biology are less related.

Both of the two main branches of biodemography have many smaller branches. As in any innovative, rapidly-growing interdisciplinary field, these smaller branches form tangles and thickets. Consequently, it is difficult to present a coherent structure for the evolving research in biodemography. One way to proceed is to make use of the hierarchical ordering of knowledge within biology. This hierarchical ordering provides a basis for ordering the research subdivisions that range from the molecular and cellular to the ecological and evolutionary. This ordering of biodemography by levels is useful because, as the eminent physiologist George Bartholemew (Bartholomew 1964) noted over four decades ago: *"…each level [of biological integration] offers unique problems and insights, and …each level finds its explanations of mechanism in the levels below, and its significance in the levels above."* For example, the results of studies on different APOE gene alleles shed important light on a molecular mechanisms for different risks of ischemic heart disease, Alzheimer's disease and other chronic conditions and thus provides information on a person's individual risk of these chronic diseases and, in turn, informs the design of population surveys and model construction for epidemiological forecasting (Ewbank 2004).

We used this organizational concept in Table 1 to summarize what we believe are the main disciplinary sub-areas of biodemographic research within each of three broad levels of biological organization—Level I (molecular to physiological), Level II (individual to kin), and Level III (population to evolutionary processes). Although several of the research categories in Table 1 are arbitrary and the range of research examples cited in each is incomplete, we believe that the information contained in this table captures the emerging scope and complexity of the field and highlights the considerable potential for scientific synergy through interdisciplinary research.

The sub-disciplines listed within each of the three levels have the potential to be mutually informing both within and between categories and levels. There are also a number of instances where closely-related concepts were independently derived in population biology and demography. For example, the early work by Andrei Rogers on

multiregional demography (Rogers 1984; Rogers 1985) is conceptually identical with recent work on meta-population analysis in conservation biology (Hastings and Harrison 1994). The studies involving 'geographic structure' in wild populations of animals (Roderick 1996) are similar to studies concerned with many of the same questions and the use many of the same genetic tools as those in epidemiological demography (Ewbank 2000; Finch and Tanzi 1997; Finch et al. 2000; Wallace 1997; Wallace 2000). Although applied in much different contexts, at their roots the use of the concept of natural selection (Meagher and Futuyma 2001) has parallels with the concept of demographic selection (Vaupel et al. 1979) since both involve a winnowing process.

Level/Sub-levels	**Concept/Example(s)**
Level I:	**Molecular to Physiological Biodemography** *Level I* is concerned with processes at the lower levels of biological organization from the molecular to the physiological (Finch et al. 2000); includes basic research on aging and longevity with model organisms as well as the results of studies such as clinical assays involving determination of handgrip and lung capacity and body fluids such as urine and blood; demographic approach to health analysis includes some indicators of 'biology' which are biological risk factors (Crimmins and Seeman 2000);
Molecular	Advances in technology will likely make it possible to carry out molecular screening of a large number of molecules in body fluids or tissue samples that may identify genetic variation or be markers of disease processes (Burns et al. 1998; Halter and Reuben 2000); molecular techniques provide tools for investigating questions about the evolution of humans including phylogenetic relationships among subpopulations; demographic implications of medically assisted reproduction and pre-implantation diagnostics (McClure 1996); medical implications of human genome project(Collins 1999) and demographic outcome
Genetic	Use of twins or other related individuals to control for unobserved heterogeneity associated with genetics; analyses of data on the genetics of individuals or gene frequencies for populations including exploration of genes that may explain geographic differences in individual response to medications (Wallace 1997); demographic implications of pre-implantation and fetal diagnosis (Holzgreve and Hahn 2003); determination of the risk of specific diseases in individuals; research on the genetic basis for common diseases and mortality will benefit from application of multistate modeling Also research on the determinants of health and behaviors could expand to include controls for genetic differences (Ewbank 2000); genetic determinants of longevity in model organisms including nematodes (Johnson 1990; Kenyon 1997) and *Drosophila* (Curtsinger et al. 1992; Harshman 2003; Helfand and Inouye

	2002),
Genomic	Include research on origins of human populations and ancient migration streams, the role of evolution in human history, differences in migration patterns of males and females, historical demography of cultures with ancient roots (Cavalli-Sforza et al. 1994; Owens and King 1999). Genome-level basis for disease patterns in human populations; study of population-level genomics—the interface between population genetics, molecular biology and demography (Black et al. 2001; Harpending 2003; Harpending and Rogers 2000)
Cellular	Assays can be used on cells to indicate their health and level of functioning (Halter and Reuben 2000). For example, specific cells can be isolated from blood or tissue samples for testing functional capability such as white blood cells responsible for initiating inflammation, red blood cells for their ability to produce clotting proteins and skin, muscle and fat cells to shed light on their functional characteristics.
Organ	Clinical measurements of body fluids provide important information on the functioning of many organs. For example, blood levels of thyroid hormones provides measures of over- or under-function of the thyroid gland (Halter and Reuben 2000); noninvasive technology documents cardiac arrhythmias and fluctuations in blood pressure; sleep monitoring equipment can be used to document nocturnal activity and sleep patterns; simple mechanical devices are available to estimate pulmonary (lung) function
Physiological	Longevity response of animals to caloric restriction requires an understanding of how animals modulate their metabolic rates when subjected to food shortages (Feder et al. 2000); physiology-to-gene approaches where goal is to find the genetic basis for physiological response underlying longevity; gene-to-physiology approach where goal is to examine the performance and fitness implication of discrete genes or products they encode (e.g. alcohol dehydrogenase on ethanol tolerance); understanding of allostatic load which is the cost of chronic exposure to fluctuating or heightened neural or neuroendocrine response resulting from repeated or chronic environmental challenge that an individual reacts to as being particularly stressful (McEwen and Stellar 1993); late-life influence of pre-natal environment (Barker 1994)
Level II	**Individual-, Cohort- and Kinship-level Biodemography** *Level II* is concerned with processes involving biological organization of whole-organism and three levels or types of groupings—the cohort which is group experiencing same event (e.g. birth; marriage), the family which consists of nuclear, stem and extended family and thus grades into more extensive kinship relations including ablineal and colineal kin.
Individual	Integration of different kinds of ages including biological (e.g. functional capabilities), social (i.e. roles and habits relative to

	others) and psychological (e.g. adaptive capacities such as memory, learning and emotions) age in life course analysis (Settersten and Mayer 1997); whereas life course currently refers to the "social processes extending over the individual life span…" (Settersten and Mayer 1997), a biodemographic agenda will incorporate an understanding of biological processes as well since the biological (reproduction) and social (marriage; family creation) are inextricably intertwined; rescaling the life cycle as life expectancy increases (Lee and Goldstein 2003).
Birth & reproduction	Encompasses interconnections of the biology of reproduction and the demography of individuals and family formation (Bulatao and Casterine 2001; Wachter and Bulato 2003). Includes genetic influences on fertility (Kohler and Rodgers 2003; Rutter 2003), basic questions regarding pair-bonding in monogamous species (Young 2003), mediation of physiological and behavioral processes (Cameron 2003), fertility patterns and behavioral controls in nonhuman primates (Altmann and Alberts 2003), evolution of primate reproductive rates (Ross and Jones 1999); evolutionary perspectives on human fertility and mating patterns (Campbell 2003; Gangestad 2003; Kaplan et al. 2003; Lam 2003; Worthman 2003), and general syntheses of human fertility and reproduction (Bachrach 2001; Hobcraft 2003; Watcher 2003); biological basis for regional and global fertility declines (Bongaarts 2001; Caldwell 2001)
Mortality & longevity	Trajectories of mortality at post-reproductive and advanced ages (Vaupel 1997; Vaupel 2003; Vaupel et al. 1998); models examining relationship between mortality cause-elimination and human life expectancy (Olshansky et al. 1990); reliability theories of aging and longevity (Gavrilov and Gavrilova 2001); the elderly in nature (Austad 1997; Carey and Gruenfelder 1997; Kaplan 1997; Lee 1997), evolutionary theory and senescence (Johnson and Shook 1997; Partridge 1997; Rose 1997; Tuljapurkar 1997); interspecies differences in life span distribution (Horiuchi 2003); comparative life table analysis (Deevey 1947), primate life tables (Gage 1998), and comparative demography of life spans (Carey and Judge 2000);
Birth-Death Interactions	Re-visitation of cost of reproduction concepts (Bell and Koufopanou 1986; Carey 2003b; Reznick 1985); fundamental relationship between early reproduction and late-life mortality (Müller et al. 2001; Müller et al. 2002); effect of child's death on birth spacing, fertility, and fertility transition (Montgomery and Cohen 1998)
Morbidity/ frailty	Medical demography—the study of chronic disease, disability, and mortality in mature and aging populations including interaction of disability dynamics and mortality (Manton and Stallard 1994); evolutionary (Darwinian) medicine—approaches to human health based on knowledge of human evolutionary history (Trevathan et al. 1999; Williams and Nesse 1991); natural

	history of disease stages and the life cycle; comorbidity; cause-elimination models (Palloni 2001); general need to develop sets of proximate biological factors related to health outcomes based on knowledge of biology and the relationship between bioindicators, demographic variables and health outcomes (Crimmins et al. 1996; Lollar and Crews 2003); use of studies on both captive and free-ranging animals populations for investigating the maintenance of allostasis, the cascade of events leading to allostatic load (McEwen and Stellar 1993), and biopsychosocial, pre-disease pathways to diverse health outcomes (Singer and Ryff 2001); morbidity and aging in non-human species including primate gerontology (DeRousseau 1994) and insect frailty studies (Papadopoulos et al. 2002)
Migration/ movement	Integration of conceptual and empirical framework developed in ecology for dispersal (movement affecting spatial pattern) and migration (mass directional movement) to demography including biological and behavioral basis for age-specific patterns of migration and dispersal {Cade, 2003 #195; Rogers, 1984 #156; Rogers, 1985 #157; Begon, 1996 #158
Family and Kin	Desired family size and the course of fertility (Bacci 2001; Vogler 2000); patterns of availability and access of elderly to kin (Wolf 1994); two-sex demography (Pollak 1986); biodemography of parental care (Clutton-Brock 1991) and parental behavior (Numan 1998); family and population implications of reprogenetics—modification of germ-line DNA (Kollek 2003); comparative socioecology of kinship bonding and mating systems (Foley 1999)
Level III	**Population, Ecological and Evolutionary Biodemography** *Level III* is concerned with levels of organization and processes above the individual including populations (groups of individuals coexisting at a given moment), ecological (interrelationship of organisms and their surroundings), and evolutionary (the descent, with modifications, of different lineages from common ancestors). Biodemography is inextricably linked to all of these organizational groupings since vital rates and population processes underlie the dynamics of change at all levels.
Population principles	Theory of population dynamics (Preston et al. 2001) and applications to both humans (Keyfitz 1977; Shryock and Siegel 1976) and non-human species (Caswell 1989); theoretical basis for evolution of life span and aging (Orzack 2003); demography of growth rate (Mangel 2003);
Human populations	Sociobiological and anthropological perspectives on health (Nguyen and Peschard 2003); evolution of human life span (Kaplan et al. 2003; Kaplan and Lancaster 2003); anthropological demography (Hill and Kaplan 1999) including questions regarding birth and death rates of indigenous peoples, population sex ratios in primitive societies, ages at onset, termination of reproduction and cultural comparisons between foragers versus

	pastorals (Ellison 2001; Hill and Hurtado 1996); extraordinary longevity in human populations (Robine 2003; Robine and Saito 2003; Wilmoth and Robine 2003); limits to world population (Cohen 1995);
Non-human populations	Life history theory in biodemographic contexts (Caswell 1989; Cole. 1954; Tuljapurkar 1990); studies of geographic structure involving both demography and genetics to examine the distribution of genotypes within and between populations (Roderick 1996; Slatkin 1987); use of social insects as models and concepts of sociobiology (Wilson 1971; Wilson 1975) to gain fundamental insights into social aspects of aging, longevity, fertility, and intra- and intergenerational transfer (Lee 2003; Rueppell et al. 2004); ecological correlates of life span and hazard rates (Gaillard et al. 2003; Ricklefs and Scheuerlein 2003; Wachter 2003); senescence and mortality in field and laboratory populations of plants (Roach 2001; Roach 2003)
Ecological biodemography	Conservation biodemography (Young and Clarke 2000b) and biodemography of invasive species (Sakai et al. 2001) including minimum viable populations (Soule 1987), demography of harvesting (Carey 1993; Getz and Haight 1989); metapopulation analysis (Hastings and Harrison 1994; Thrall et al. 2000), demographic toxicology (Stark and Banks 2003), demographic effects of habitat fragmentation (Young and Clarke 2000a)
Evolutionary biodemography	Understanding the processes of evolution informs every area of biology including biodemography; concerned with the interface of demography, genetics and evolution in age-structured populations (Charlesworth 1994); evolution of life history traits and trade-offs between birth and death (Stearns 1992); accounting for the evolution of short or long life span (Carey 2003a); post-Darwinian longevity (Vaupel 2003); understanding the underlying demography related to the unbroken chains of descent of all organisms from viruses to redwoods to humans (Meagher and Futuyma 2001);

Table 1. The emerging research agenda for biodemography with cross-cutting themes from both biological demography and biomedical demography.

The remainder of this chapter is structured as follows. We begin with an extended discussion of the branch of biodemography that we call biological demography. Then we turn to a shorter description of the other main branch, the branch we call biomedical demography. That is, the bulk of this chapter focuses on biological demography. The biomedical branch is at present at least as prominent as the biological branch, with at least as many demographers actively involved. And the biomedical branch is certainly path breaking, with substantial results to date and much promise. In our section on it, we list some of the key researchers and main publications. We decided, however, to emphasize biological demography because the concepts and methods of biomedical demography are quite accessible to demographers whereas the concepts and methods of biological demography are much more foreign and difficult to understand. In particular,

we believe that understanding biological thinking in demography requires appreciation of a set of biological-demographic principles. A major portion of the chapter is devoted to an exposition of these principles and the more general concept of why it is useful and important to think in terms of such principles.

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Biographical Sketches

James R. Carey received the B.S. degree in Animal Ecology from Iowa State University (1973), the M.S. degree in Entomology, from Iowa State University (1975), and the Ph.D. degree in Entomology, from the University of California, Berkeley (1980). He has been a faculty member at the University of California, Davis since 1980. He also served as Vice-Chairman of the Department of Entomology from 1997-1999. He is an elected fellow of the Gerontological Society of America (2003) and an elected fellow of the American Association for the Advancement of Science (2000). He has been a member of the Center for Economics and Demography of Aging (CEDA), UC Berkeley since 1996. His main research focus is insect biodemography (i.e. the marriage of biology and demography) with special emphasis on aging and lifespan. Research in his laboratory focused on the use of insects as models to address questions concerned with lifespan limits, the male-female longevity gap, dietary restriction, aging in wild populations, the effects of anti-aging drugs on longevity, morbidity and mortality dynamics, and the effects of behavior throughout the life course on survival and mortality. The majority of this research is supported by grants from the National Institute on Aging. The first and longest running is Exceptional longevity in fruit flies, a research project within the Duke University-based program project (P01) titled Exceptional Longevity that is directed by James Vaupel, Executive Director of the Max Planck Institute for Demographic Research in Rostock, Germany. The second research project is Aging in the Wild, part of the UC Davis-based program project (P01) that he directs titled The Biodemographic Determinants of Lifespan.

James W. Vaupel studied mathematical statistics, business administration, and public policy at Harvard University, where he received his BA in 1967 and his Ph.D. in 1978. Prof. Vaupel has taught at Duke University, the University of Minnesota, the University of Southern Denmark, and the University of Rostock, Germany. Dr. Vaupel is Founding Director of the Max Planck Institute for Demographic Research in Rostock, Germany as well as being Senior Research Scientist and Head of the Program on Population, Policy, and Aging at the Terry Sanford Institute of Public Policy at Duke University. In 2001, Dr. Vaupel won the Irene Taeuber Award for outstanding accomplishments in demographic research. His research spans the study of humans, including centenarians and twins, nematodes, and Mediterranean fruit flies to further understanding of the determinants of and limits to human life expectancy. He is a leader in the new areas of biodemography and paleodemography.