On the Biodemography of Aging: A Review Essay*

S. JAY OLSHANSKY

Human aging is a subject of interest to everyone. Although scientists have known for some time that most forms of life age in a predictable way with the passage of time, the mechanisms involved in regulating the metronome of aging or senescence have remained largely a mystery. Actuaries and demographers have developed sophisticated mathematical tools to characterize the dying-out process of humans. Evolutionary biologists have worked almost exclusively with nonhuman species to test hypotheses on why senescence occurs. Researchers from the biological sciences are attempting to understand the mechanisms involved in the aging process, and physicians and other health care workers have sought to identify methods for altering the course of aging and treating its consequences. As readers of this excellent new volume will discover, the emergence of the biodemography of aging is much like the effort in physics to create a unified theory. This is an exciting time for those studying various elements of the aging process—with biodemography representing an important new development that should attract scientists and students from all of the scientific disciplines involved in research on aging.

What is the origin of the term biodemography and what are the scientific antecedents to research in this emerging field? Does the theoretical and empirical research in this volume follow from biodemography's historical roots, or does this book signal the birth of a new discipline? One might think these would be the first questions asked and answered in the first book ever written on biodemography. Surprisingly enough, a definition of biodemography is nowhere to be found, and the fascinating history from which modern biodemography arose is essentially ignored. As a re-

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sult, the uninitiated might be led to the mistaken belief that the term originated with these authors. Despite these omissions, demographer Kenneth Wachter and molecular biologist Caleb Finch (in the opening and ending chapters, respectively) do explore the central questions at the core of biodemography—which are appropriately captured by the graphic title, *Between Zeus and the Salmon*. Zeus, the principal (immortal) god of the Greek pantheon, and salmon, genetically programmed to die shortly after they reproduce, represent the extremes that bound the study of aging and longevity.

I will first define the concept of biodemography of aging and present a brief history of the discipline so the reader can see how this volume follows from biodemography's colorful roots. Both of these pieces of background information will be used as a gauge for evaluating the "biodemographic content" of the individual chapters.

The origin of the biodemography of aging

Although scientists from a variety of disciplines study just about every conceivable aspect of aging, only a handful of truly big questions have emerged. Why do we age—or perhaps more appropriately, why are we not immortal? How do we age—that is, what are the biological mechanisms that lead a fertilized egg through gestation to organisms that experience growth, development, reproduction, and accumulated damage to the components of cells, tissues, organs, and organ systems that in turn lead to the changes we see in the mirror and ultimately to death? The third big question is When do we age—that is, why do aging and death occur when they do in various species and what explains the great variation in ages at death among individual members of the same species?

The Why question has been the focus of research in the fields of evolutionary biology and genetics for over a century. This rich literature is a major force behind the development of biodemography (e.g., Charlesworth 1994; Kirkwood 1977; Medawar 1952; Rose 1991; Weismann 1891; Williams 1957). The How question has been the preoccupation of scientists from a variety of disciplines including genetics, medicine, epidemiology, and molecular biology (e.g., Finch 1990). Much of the focus of modern medicine has been on efforts to understand what fails in living organisms and how to prevent or delay these changes and treat them once they occur. The How question is a critical element in the puzzle of aging—viewed by the public as vitally important because the scientists and physicians who address this question deal on a day-to-day basis with the practical application of biomedicine in the war against diseases. Manipulation of the aging process, if it comes to pass, will derive from researchers addressing the How question. The When question has been addressed mostly by actuaries, demographers, and epidemiologists whose focus has been on empirical observations of the timing of death and the diseases and disorders of aging that precede it.

Biodemography is an explicit effort to answer the When question of mortality for individuals and populations by moving beyond purely empirical efforts toward a combination of traditional demographic analysis with theoretical and experimental elements from evolutionary biology, ecology, genetics, molecular biology, anthropology, and other scientific disciplines involved in research on aging. The focus of most biodemographic research published so far has been on the theoretical and mathematical attributes of mortality and the biological basis for age patterns of death in populations. However, as this volume illustrates, the biodemography of aging should be defined broadly to include the study of all attributes of a species' life history and the social/behavioral impact of that history on aging and longevity, including such attributes as fertility, menopause, and intergenerational transfers.

Benjamin Gompertz, a nineteenth-century English actuary, is the intellectual father of biodemography. Gompertz was the first to speculate on the presence of what he referred to as the "law of mortality" (Gompertz 1820, 1825, 1862, 1872).[1] Although Gompertz did not have the benefit of evolutionary theory, he nevertheless inquired whether there was a biological basis for the regularity he observed in the life tables of humans.

The tradition of incorporating biology into the analysis of life tables has a long history in actuarial research following Gompertz's lead. Makeham (1867: 335), for example, predicted that Gompertz's "law of mortality" should be particularly well-suited for describing mortality from diseases whose intensity depends "upon the gradual diminution of the vital power." Brownlee (1919) mentioned the "biology of a life table," and Greenwood (1928) inquired whether a life table reflected underlying biological processes or was simply a useful working tool for actuaries. Biologically comparable points within the lifespan were used by Pearl (1921, 1922) and Pearl and Miner (1935) as a scaling device in the first scientific effort to reveal a "fundamental law of mortality" that extended beyond humans to other species. Stimulated by Gompertz's formula for a "law of mortality," various other forms of biodemography surfaced during the twentieth century, including those based on biochemistry (Brody 1924; Brownlee 1919; Greenwood 1928; Loeb and Northrop 1916) and on efforts to perform interspecies comparisons of age patterns of mortality (e.g., Deevey 1947; Finch and Pike 1996). Later, physiologically based models were established on the experimental use of senescence accelerators (e.g., Brues and Sacher 1952; Failla 1958; Lorenz 1950; Mildvan and Strehler 1960; Sacher 1956; Sacher and Trucco 1962; Szilard 1959), studies were conducted of age patterns of mortality at older ages for nonhuman species (e.g., Brooks, Lithgow, and Johnson 1994; Carey et al. 1992; Curtsinger et al. 1992), and life history models were introduced from the fields of ecology and evolutionary biology (e.g., Orzack and Tuljapurkar 1989; Tuljapurkar 1990).

To my knowledge, the term "biodemographic" first appeared in the scientific literature in an article by the influential ecologist G. Evelyn

Hutchinson (1948). Hutchinson suggested that variation in the size of populations of humans and other species is influenced, in a circular causal loop, by physical characteristics of the environments within which species reside—with notable examples including prey–predator and host–parasite relationships. The term itself and the philosophical basis for it surfaced again some 40 years later with the birth of modern biodemography in a book published by Gavrilov and Gavrilova (1991)[2] and a series of articles published by Weiss and colleagues (e.g., see Connor, Weiss, and Weeks 1993; Weiss 1989, 1990; Weiss, Ferrell, and Hanis 1984). I think of these two bodies of work as the rebirth of biodemography because they were heavily influenced by the Gompertz/Pearl "law of mortality" paradigm that linked age patterns of mortality, interspecies comparisons of death rates, and biological explanations for why such patterns exist.

The biodemographic content of the present volume

Between Zeus and the Salmon is organized into three main sections that are preceded by an Introduction and followed by a discussion of data for the future and a summary chapter. The Introduction by Kenneth Wachter is an excellent overview of the importance of an interdisciplinary perspective on aging and the logic behind the formation of modern biodemography. It is here that the reader is first exposed to important reminders for all scientists involved in interdisciplinary research on aging—including the fact that today we are not studying humans within the relevant evolutionary environment, and that scientists are only beginning to understand the great plasticity in the aging process.

The first main section—The Empirical Demography of Survival—contains chapters by demographers James Vaupel and John Wilmoth that strike me as inappropriate to this book because neither is informed by biology (either theoretically or empirically). Vaupel makes two unsupported arguments—the first is what he describes as a new discovery that the Gompertz formula fails to portray mortality dynamics in older regions of the lifespan, and the second is that misguided conventional wisdom implies that death rates at older ages are intractable. These arguments are inappropriately portrayed as lying at the heart of biodemography, yet they recur in several other chapters in the book portrayed as conventional wisdom.

According to Vaupel (p. 17), "Various subsequent researchers [following Gompertz], especially in biology and gerontology, have viewed Gompertz' observation as a law that describes the process of senescence in almost all multicellular animals at all ages after the onset of reproduction." He continues, "Until recently, it was impossible to determine whether this exponential rise continued to advanced ages." This is a puzzling observation since Gompertz himself, as well as numerous other scientists of the nineteenth and twentieth centuries, stated explicitly that his equation did not apply, and in fact was never intended to apply, to older regions of the lifespan. For example, both Gompertz (1825, 1872) and Makeham (1867) recognized that the rise in human mortality decelerates at older ages. Makeham (1867: 346) stated that for humans "the rapidity of the increase in the death rate decelerated beyond age 75." Brownlee (1919: 58) asked whether it is "possible that a kind of Indian summer occurs after the age of 85 years is passed, and that conditions improve as regards length of life on the grounds either of greater care being taken, or that the second childhood relieves nervous strain and thus permits some recuperative effect?" Perks (1932: 15) identified a "curious peak in the rate of increase in q_x round about age 80" and observed that "the graduated curve [of mortality] starts to decline in the neighborhood of age 84" (p. 30). More recently, Strehler (1960: 311) argued that one of the four distinct phases of the human mortality curve was "a period of departure from the Gompertzian relationship at great ages so that mortality rises more slowly than anticipated after age 85–90." Mildvan and Strehler (1960: 224) extended this to other species by noting that "at extremely advanced age, the mortality rate curves of several species rise at a rate progressively lower than exponential."

Given this historical record documenting decelerating mortality at older ages for humans and other species, Vaupel's statement that "[m]ortality decelerations came as a surprise, indeed as a shock, to many biologists and gerontologists" (p. 25) makes no sense. This false line of reasoning has led others in the scientific community (e.g., Barinaga 1992) as well as authors in this volume to speculate on the so-called failure of the Gompertz model. For example, Michael Rose (p. 104) suggests that because Gompertzian models of mortality fail to account for plateaus in old-age mortality, "conventional demographic models are in need of repair." Yet based on his own analysis Rose concludes appropriately that the Gompertz equation works well for the majority of the age range of species but begins to fail at extreme old ages when few individuals remain alive—the same conclusion that Gompertz came to in the nineteenth century.

Vaupel's second argument, that mortality at older ages is intractable, reappears variously in the book as "an ethos of limit theories" (Wachter, p. 6) and a "limited-life-span hypothesis" (Wilmoth, p. 48). This argument can be traced back to a single article by Fries (1980), but has inappropriately been attributed to others, this author included (e.g., Olshansky, Carnes, and Cassel 1990). Demonstrating that death rates have been declining at older ages in many countries (e.g., Kannisto et al. 1994; Wilmoth and Lundström 1996), seemingly overturns an article of "conventional wisdom." For example, Vaupel argues in this volume and elsewhere that "demographers conjectured that mortality at advanced ages was intractable" (1997a) and that "there is one and only one cause of death at older ages. And that is old age. And nothing can be done about old age" (1997b).[3] Vaupel then extended this line of reasoning to make the following assertion: "The belief that old-age mortality is intractable remains deeply held by many people. Because of its implications for social, health, and research policy, the belief is pernicious. Because the belief is so prevalent, forecasts of the growth of the elderly population are too low, expenditures on life-saving health-care for the elderly are too low, and expenditures for biomedical research on the deadly illnesses of old age are too low" (1997b).

There are three problems with this line of reasoning. First and foremost, it leads the reader down a false path to "conventional wisdom" about old-age mortality that does not exist. Although my colleagues and I have been aligned with the ethos of limit theories, it is hardly pessimistic to suggest (a) that most of the rise in life expectancy in modern times is attributed to declining old-age mortality (Olshansky and Ault 1986), and (b) that it is plausible to expect death rates from all causes combined to decline by 50 percent at every age within the twenty-first century (Olshansky, Carnes, and Cassel 1990). The second problem is that some other authors in this volume accepted Vaupel's idea of "conventional wisdom," which in turn influenced the content of their articles. Finally, there are policy implications associated with this line of reasoning that, as Vaupel suggests, have a direct bearing on projections of the future size of the elderly population and expenditures associated with health care and biomedical research.

The only remaining problem I have with this book also appears in the chapter by Vaupel. The discussion of evolutionary theories of senescence would ordinarily have contributed to the biodemographic content of this chapter, but these well-known theories were incorrectly interpreted to mean that "the age-trajectory of mortality should shoot up at postreproductive ages" (p. 18) and that a "black hole of bad alleles . . . should preclude survival much past this [postreproductive] age" (p. 32). Although arguments developed by the evolutionary biologists Peter Medawar (1952) and George Williams (1957) suggest that some inherited lethal diseases should appear within and near the end of the reproductive window of a species, there is no biological basis to assume that selection operates with the precision of a time bomb, nor did either author attempt to extend this view to age patterns of mortality in populations as implied by Vaupel. Later in this volume Linda Partridge effectively dismisses Vaupel's suggestion that a black hole of genetic diseases exists at the end of the reproductive window, stating that "evolutionary theories of aging do not necessarily predict Gompertzian-type increases in postreproductive mortality rates. Nor does the mutation-accumulation theory necessarily predict catastrophic increases in mortality when reproduction ceases" (p. 84). These problems of interpretation in the first chapter could have been avoided through a more careful reading of the historical literature on Gompertzian mortality dynamics and evolutionary theories of senescence and the contemporary literature on old-age mortality among humans.

Problems with his chapter aside, Vaupel provides a well-written discussion of bio-reliability theory, stressing that the failure times of living organisms and man-made mechanical devices follow comparable paths and that much can be gained by exploring the common design features and failure rates of living and manufactured machines. A more comprehensive presentation of bio-reliability theory upon which this discussion is based was published by Gavrilov and Gavrilova (1991).

The second main section of the book—Evolutionary Theory and Senescence—contains four articles that make significant contributions to the literature. Biologist/demographer Shripad Tuljapurkar boldly formulates an alternative theory of senescence based on the concept of evolutionary equilibrium for a species' life history. Tuljapurkar explains to the reader the rationale behind his theory, setting the stage for a valuable series of testable research hypotheses at the end of the chapter. The traditional view of evolutionary theory is presented in clear language in the subsequent two chapters by evolutionary biologists Linda Partridge and Michael Rose. Particularly interesting is Partridge's use of the reasoning of evolutionary biology to develop a predictive theory of how age-specific death rates might vary as a function of different environments and age compositions. Partridge discusses the importance of distinguishing between external and intrinsic forces that influence vital rates and the difficulty in doing so, but she omits reference to published efforts to make these distinctions (Gage 1991), including the one biodemographic study in which empirical observations were based on partitioning total mortality into its intrinsic and extrinsic components in order to perform interspecies comparisons of age-specific death rates (Carnes, Olshansky, and Grahn 1996). Rose provides a summary of the evolutionary theory of senescence and the experimental evidence linking the force of natural selection to fecundity and longevity. In the end, he teases us with the suggestion that his recent work with colleagues has led to steps toward a theory that explains plateaus in death rates among the oldest-old, but then fails to deliver even a hint of this new development.

The last chapter in this section, by geneticists Thomas Johnson and David Shook, is one of the highlights of the book. The authors carefully explain the language and the methods of determining the genetics of lifespan and life expectancy. This well-crafted essay describes how the genetic study of lifespan is conducted and provides a condensed summary of relevant genetic studies of longevity, either ongoing or completed (with an emphasis on research conducted at the authors' laboratory). Their section on issues in evolutionary theory and demography that can be addressed by identifying genes associated with longevous phenotypes is particularly insightful—pointing the way to numerous testable hypotheses for biodemographers. The premise is that "gerontogenes" exist—a phenotype for longevity made possible by the presence of genes that promote survival. Johnson and Shook's chapter exemplifies successful biodemography that combines theoretical and empirical approaches to aging and longevity from more than one discipline.

The third main section of the book, on The Elderly in Nature, elaborates an intriguing new line of argument that the elderly may play an important role in the population dynamics (including reproduction as well as aging and longevity) of some species. Entomologists James Carey and Catherine Greunfelder suggest that contrary to traditional evolutionary theory, under some conditions the elderly do contribute to a population's fitness. Because the "[l]ife span of animals is not an orderly unfolding of precisely timed events from fertilization to death" (p. 128), the definition of the elderly is nebulous at best. Carey and Greunfelder develop the theoretical and empirical foundation (using a surprisingly large number of case studies) for their argument that the elderly of many species may contribute more to reproductive fitness than is currently believed. Not only will this work influence traditional thinking on the evolutionary theory of senescence, but it appropriately forces both demographers and gerontologists to consider the behavioral ecology of the role of the elderly.

On a related theme, evolutionary biologist Steven Austad examines a phenomenon that is now common among humans but that occurs rarely among animals living in the wild—female menopause. Now that mammals have been reared and followed in captivity for some time, it is evident that menopause is manifest in females when survival is extended beyond the ages normally experienced in the wild. Austad explores "forced" menopause, examines the few species for which postreproductive survival is relatively common (implying that in these cases it occurs as a result of natural selection rather than increased longevity), and presents several hypotheses for the potentially adaptive value of menopause for the few species (e.g., pilot whales and killer whales) in which it occurs naturally. My attention was caught by an account of the intergenerational transfer of "wealth" among bannertail kanagroo rats as a function of the age of the parents. Austad uses language that evokes remarkable similarities to human behavior—"eviction of young from resources controlled by the elderly," "bequeathing resources to young," and "relinquishing resources to offspring." This discussion of how and why menopause occurs and how postreproductive survival can influence the behavior of the young of different species is biodemography at its best.

The third article to address the role of the elderly was written by economist Ronald Lee. He makes a persuasive argument that contrary to the current view, the prevalence of postreproductive human females in preagricultural female populations may be as high as 10–30 percent—implying that menopause may be a product of evolutionary intent rather than neglect. Lee explores the economic flow of resources and knowledge between generations as a basis for explaining the utility of a postreproductive population. This discussion is remarkably similar to Austad's presentation of the flow of resources between generations of bannertail kanagroo rats; both authors see an emerging theory of the ecology of resource transfers across generations in various species, including humans. The link between longevity and intergenerational transfers is a fascinating area that should draw the attention of both students and funding agencies.

In the remaining chapter in this section, the anthropologist Hillard Kaplan sets forth an interesting hypothesis about the evolution of life history traits that include a postreproductive period and an extended human lifespan. He speculates that the long lifespan, extended period of juvenile dependence, and support of reproduction by older postreproductive individuals are interrelated outcomes of a feeding strategy unique to humans. This article is a valuable resource for readers interested in the life history attributes of hunter-gatherer populations.

The chapter by the epidemiologist Robert Wallace focuses on the data contained in population surveys sponsored by the National Institute on Aging that may be used for genetic studies of disease in humans. Wallace follows his informative summary of this material with a description of various ways such data may be used to evaluate biodemographic issues of aging and longevity. Publication of a comprehensive summary of databases available for all species that permitted genetic analyses would be useful.

In the final chapter Caleb Finch observes that the modern rise in life expectancy in humans is not unexpected given the plasticity found in the evolution of life histories that influence the longevity of species. Not only is there a broad range of survival opportunities across and between species, but the fact that most postreproductive survival is not a direct product of natural selection implies that senescence can be manipulated through environmental parameters. Just how much humans can modify the process of senescence without intervening in the genetic blueprint of life has yet to be determined, as Finch notes, but observed changes in human survival fall within the range of the expected plasticity in the aging process. As Finch's (1990) treatise did at length, this chapter provides in brief a background on the plasticity of senescence from various biological levels of organization, from genes to populations.

Conclusion

I like many things about this book and object to only a few. The chapters are written almost exclusively by scientists who, while well known within their own disciplines, have also been instrumental in developing and extending the field of the biodemography of aging. The common thread of evolutionary biology appears within most chapters, with implications for aging and longevity then evaluated through various attributes of the life history. I particularly appreciate the fact that most of the authors were careful to explain the language of their discipline. Overall this volume is a valuable contribution to the literature.

The problems with this volume are as follows. First, there is an overemphasis in several of the biologically oriented chapters on explaining decelerating mortality at older ages among humans and other species and the rise in the number of centenarians among humans in modern times. To be sure, both are interesting phenomena. However, they are largely irrelevant in genetically heterogeneous populations like humans where the majority of any birth cohort contains neither the genotype nor the practical means to survive as long as the population's longevity outliers. At this point the interest in centenarians should be at the level of identifying alleles that favor such extreme longevity, as Finch suggests in his chapter. An understanding of postreproductive survival in humans requires a focus on the vast majority who die between the ages of 60 and 100 and on the alleles that influence their deaths rather than on the small segment of every birth cohort with the potential to survive to extreme old age. The other main problems in the book, already discussed at length, concern the purported failure of the Gompertz model to portray old-age mortality, and the erroneous impression that a conventional wisdom exists suggesting that old-age mortality in humans is intractable.

Despite these criticisms, I give this book my strongest endorsement—it is essential reading for anyone interested in biodemography and the study of aging and longevity in humans and other species. With few exceptions, every chapter is well-crafted and uses language that students and scientists from a variety of disciplines can understand and appreciate. *Between Zeus and the Salmon* should invigorate both the science and the funding of modern biodemography.

Notes

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1 For a detailed discussion of the historical search for the "law of mortality" beginning with the work of Gompertz through the present, see Olshansky and Carnes (1997).

2 An earlier version of this book was published in Russian in 1986.

3 This quote was attributed to the gerontologist Leonard Hayflick. According to Hayflick (personal communication), the quote attributed to him is not only false, but he does not believe what the quotation states. In addition, Vaupel (1997a) then went on to attribute the following line of reasoning to us (e.g., Olshansky, Carnes, and Cassel 1990): ". . . the view that mortality at older ages is intractable leads to the conclusion that health-care resources and biomedical research should not be wasted on hopeless attempts to prolong the lives of the elderly." This is not only a false attribution, but my colleagues and I do not believe what the quotation states.

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