Demographic Research a free, expedited, online journal
of peer-reviewed research and commentary
in the population sciences published by the
Max Planck Institute for Demographic Research
Konrad-Zuse Str. 1, D-18057 Rostock · GERMANY
www.demographic-research.org

DEMOGRAPHIC RESEARCH

VOLUME 19, ARTICLE 50, PAGES 1749-1758
PUBLISHED 30 SEPTEMBER 2008
http://www.demographic-research.org/Volumes/Vol19/50/

Reflexion

Biodemography:
Research prospects and directions

James R. Carey

This publication is part of the proposed Special Collection "Reflections on the Future of Biodemography", edited by Erica Spotts.

Table of Contents

Biodemography: Research prospects and directions

James R. Carey[1]

Abstract

The purpose of this opinion report is to outline what I consider to be the most promising areas for future biodemographic research and to suggest ways in which the field can be moved forward. I suggest ideas grouped around five major themes including biodemography of disability, ecological, developmental, behavioral and evolutionary biodemography, biodemography of sociality, genomic and genetic biodemography, and biodemographic modeling and analysis. At the end I briefly discuss biodemography in both interdisciplinary and epistemological contexts.

[1] Department of Entomology, University of California, Davis, California 95616 USA; and Center for the Economics and Demography of Aging, University of California, Berkeley, California 94720 USA. Telephone: 530-752-6217 E-mail: jrcarey@ucdavis.edu

1. Introduction

Biodemography as an emerging discipline at the interface of biology and demography is unique in at least two respects (Carey & Vaupel 2005). *First*, it is one of a small number of subdisciplines arising from the social sciences that has embraced biology (e.g. evolutionary psychology; neuroeconomics). However, unlike the others which focus more narrowly on biological sub-areas (neurology) or concepts (evolution), biodemography has no explicit biological boundaries thus making it not only a more all-encompassing interdisciplinary concept, but also one that has deeper biological roots. *Second*, the hierarchical organizations that are inherent to both biology (cell, organ, individual) and demography (individual, cohort, population) form a chain in which the *individual* serves as the link between the lower mechanistic levels and the higher functional levels. Biodemography is thus ideally suited to complement, engage and inform research on human aging through theory building using mathematical and statistical modeling, hypothesis testing using experimental methods, and coherence-seeking using genetics and evolutionary concepts. In short, biodemography serves as both a looking glass through which researchers in the social and biological sciences can see each other's worlds, and a Rosetta stone for interdisciplinary communication and cooperation. Research in the biological-demographic hybrid-zone has been neglected due partly to the conservatism that is inherent to science, and partly to differences between the two paradigms (and thus in the questions asked).

2. Promising areas of biodemographic research

The main challenge in formulating research policy for biodemography is to develop a strategy that balances the need to build on its main historical strengths and at the same time support novel, creative, and, at times, high-risk research that may point the field in exciting new directions. A useful strategy for developing a research agenda in biodemography would be one which involves aging as the main but not sole organizational concept, which expands the scope to engage new topics, invites new researchers, integrates research at mechanistic and functional levels as well as in laboratory and field contexts, and uses genetics and modeling as cross-cutting themes. In this section I describe five thematic areas, the characteristics of which are consistent with these general guidelines just described. The grouping of many of the example topics within a thematic area is arbitrary.

2.1 Biodemography of disability

Inasmuch as whole organisms are highly, intricately, and precisely integrated networks of entities and interactions, any disruption in either the design or the components will disrupt the whole and thus decrease the quality of life and increase the likelihood of death.

Whereas understanding underlying *mechanisms* is the central focus in research on the biology of aging with death as the singular end point, understanding *function* in daily life is the main focus of research on disabilities with loss of function(s) as the endpoint(s). Thus the results of research on the biodemography of disabilities will complement research in health demography (Lamb & Siegel 2004). Biodemographic research concerned with disabilities is an important new area of research not only because experiments on impairment using model animals (insects) will shed light on universal properties and characteristics of disablement processes that are relevant to disabilities in humans, but also because the results of impairment research on non-human species will provide depth, context, and scope for studies in ecology, evolution and behavior. Promising new areas of biodemographic research in this area include empirical studies of the natural history of disability (e.g. age-specific processes involved in acquiring disabilities and co-morbidities), experiments designed to test hypotheses concerned with characteristics of disablement processes, and investigations on impact of disabilities on sex-specific mortality that determines the gender gap. Examples of recent research concerned with the biodemography of disability includes studies on trends in elderly health (Crimmins 2004), on the influence of early-life social conditions on men's mortality (Hayward & Gorman 2004), on functional abilities in Danish twins aged 75 years (Christensen et al. 2000), and on historical effects on human lifespans of inflammatory exposure (Finch & Crimmins 2004).

2.2 Evolutionary, ecological and behavioral biodemography

Because demography is deeply imbedded in the fields of evolution, ecology and behavior, a framework for biodemographic research emerges from each area by considering the demographic components. Thus *evolutionary biodemography* is concerned with the demographic changes that occur in organisms over time and with how these evolved forms are better adapted for coping with the demands of their environment; *ecological biodemography* is concerned with theoretical, experimental, and comparative approaches to understanding the demographic characteristics and determinants of plants and animals in the wild; *behavioral biodemography* is concerned with how ecological and evolutionary processes explain the occurrence and adaptive significance of behavior patterns and the use of behavioral processes to predict demographic patterns; and *evolutionary biodemography of development* is concerned with questions related to how genotype and phenotype interact over generational and gestational time spans. Examples of promising research topics in the biodemographic aspects of ecology, evolution and behavior include studies concerned with eco-gerontological rules that describe the relationship between the variation in life spans and a species' environment, with aging in evolutionarily-relevant (i.e. field) environments, with the relationship between aging and both fertility and reproduction, with the biodemography of behavior throughout the life course, with phenotypic plasticity as a potential means of adaptation to divergent environments, and with the biodemography of the Tree of Life (e.g. allometric rules of lifespan, lifespan legacies of different 'ground plans'). Examples of recent research concerned with the biodemography of ecology, evolution and/or behavior include papers on the translation of stage structure to age structure in variable environments (Tuljapurkar & Horvitz 2006), the evolution of aging and life span (Orzack 2003), the evolution of aging and post-reproductive lifespan in guppies (Reznick et al. 2006), negligible senescence during reproductive dormancy in *Drosophila melanogaster* (Tatar et al. 2001), mortality sex differentials in humans (Austad 2006), and sexual conflict and sensescence (Promislow 2003).

2.3 Biodemography of sociality

The *biodemography of sociality* is concerned with ecological, behavioral and evolutionary determinants of cooperative behavior including the biological and social value of cooperation and care giving, theory of the family (Emlen 1995), and theories based on genetic (i.e. inclusive fitness/selfish gene), mutual cooperation (i.e. reciprocal altruism) and group selection (e.g. unrelated individuals help in defense of group) arguments. Thus like humans, many species of social animals (e.g. eusocial insects) have clearly defined "occupations" that can be studied in the context of their effects on sociality and life span (Amdam, et al 2006). For example, complex social behavior in honeybees can be linked to reproductive status which, in turn, can be linked to foraging behavior and ultimately to differential mortality. Promising research topics concerned with the biodemography of sociality involve studies on the behaviorial genetics of sociality, on the linkages of non-human (e.g. primates) and human models of sociality, and on mathematical modelling of sociality. Examples of recent research concerned with the biodemography of sociality include papers on complex social behavior derived from maternal reproductive traits in honeybees (Amdam et al. 2006), on the developmental architectures of social design (Page & Amdam 2007), on the hierarchical demography of social insects (Al-Khafaji et al. 2008), and on the comparative longevity of hunter-gatherers (Gurven & Kaplan 2007).

2.4 Genomic and genetic biodemography

Inasmuch as genetics is the basis for the science of the individuals (Childs, Wiener and Valle 2005) that binds the field of biology into a unified discipline and that some believe may eventually rival the physical sciences, it follows that principles of genetics and genomics need to be integrated into biodemography if this field is to become a unifying force in demography and biology. Demography is itself well positioned to engage in genomic-related research because no other discipline focuses on the individual in quite the same way or to the same degree (Mortimer and Shanahan 2004)-the individual is the quintessence of biological relevance since all discoveries at lower levels of biological organization must ultimately be tested and understood at this level. Promising areas of research in this thematic area include studies concerned with age-specific changes in gene expression, the biodemography of cloning and reproductive genetics, the genetics of family structure, in vivo expression systems, and the effects of epigenetic modifications on aging and fertility. Some of the most innovative work concerned with the genetic aspects of biodemography include papers on the genetic determinants of longevity (Finch & Ruvkun 2001; Johnson 2005; Christensen et al. 2006), on the APOE gene and differences in human longevity (Ewbank 2004), and the evolutionary genetics of aging in the wild (Wilson et al. 2008).

2.5 Biodemographic modeling and analysis

Biology is rapidly becoming a science that demands more intense mathematical analysis than biologists have been accustomed to and, in this context, demographers have much to offer. Inasmuch as mathematics and statistics are the principle means of integrating evolution and genetics (Cohen 2004), and that mathematics and statistics are fundamental to demography, it follows that the future of biodemography must continue to be based on strong analytical components in all areas of empirical research. Promising topics in modeling and analysis include those concerned with evolutionary theories of senescence and altruistic aging (Longo et al. 2006), mathematical models of mutation-selection equilibrium, joint analysis of longitudinal data and event (death) times, plasticity of life tables and hazard rates, and longitudinal trajectories and gene profiles. Some of the most innovative work in biodemographic modeling includes papers on evolutionary demographic models for mortality plateaus (Wachter 1999), on mortality Markov models (Steinsaltz & Evans 2003), on evolutionary theories of aging in demographic contexts (Lee 2003), on frailty of the oldest-old in the past (Yashin et al. 2001), on indicators of the force of selection (Baudisch 2005), on the evolution of lifespan in rock fish (Mangel et al. 2007) and on negative senescence (Vaupel et al. 2004).

3. Biologists, demographers and the rise of biodemography

Several of the biggest jumps forward in the 20th century involved the coming together of two disciplines-genetics and evolution formed *population genetics*, physics and biochemistry formed *molecular biology*, and evolutionary biology and developmental biology formed *evolutionary developmental biology* (i.e. Evo-Devo) (Carroll 2005). The 'parent' disciplines from which each of these new fields were derived were also positively affected e.g. physics brought to biology an attitude that mysteries can be solved (Varmus 1999). Thus the operational concept for considering biodemography's future is to maintain strong ties with both mainstream biology and mainstream demography. The participation of established (senior) researchers from both of the mainstream disciplines provide credibility and authority and thus affirmation to the junior scientists who are working in the area. Participation of these junior scientists will ultimately shape the future of the field.

Whereas less than a decade ago, researchers interested in biodemography were small in number (a few score) and their questions relatively circumscribed (e.g. mortality plateaus), the number of persons concerned with biodemography and the types of questions asked are now rapidly expanding with implications of new findings ramifying across disciplines-from conventional demography and gerontology, to medicine, sociology, economics, animal and plant ecology, behavior, evolutionary biology, and anthropology. Fostering development of the biodemography paradigm is important because, through the use of experimental demography, life history and evolutionary theory, and comparative methods, this emerging field is providing the necessary stepping stones for scientists to bridge biology and demography. This is because biodemography combines the encapsulatable problems of the gene and cell (Sapp 2003) with the focus on *parts* and on *mechanisms* with the holistic problems of evolution and the individual with the focus on the *whole* and on *functions*. Biodemography is beginning to play a key epistemological role in science by serving as a framework for asking questions that otherwise would not be asked and for providing answers to these questions that would otherwise would go unanswered. Biodemography adds value to its respective 'parent' disciplines by suggesting new insights and useful perspectives to old problems as well as by generating new ones relevant to both fields. The nascent field is becoming a force for unifying biology and demography, a platform for interdisciplinary research, a concept for bringing together scholars from different professional cultures, and a theme for inter-institutional support. We are standing at a new scientific boundary with exciting prospects of invitation and challenge.

4. Acknowledgments

Opinion report solicited by Behavioral and Social Research (BSR) Program, National Institute on Aging in response to recommendation from National Advisory Council on Aging (NACA), BRS Report, May 2004. Funding was provided through grants P01 AG022500-01 and P01 AG08761-10. Report strengthened by input from Gro Amdam, Larry Harshman, Tom Johnson, Hans Mller, Rob Page, Debbie Roach, Blanka Rogina, Olav Ruppell, Leslie Sandberg, Judith Stamps, David Steinsaltz, and Jane-Ling Wang. I also thank Erica Spotts for her editorial advice.

References

Al-Khafaji, K., Tuljapurkar, S., Carey, J. R., and Page, R. E. (2008). Life in the colonies: Hierarchical demography of social insects. in press.

Amdam, G. V., Csondes, A., Fondrk, M. K., and Page, R. E. (2006). Complex social behaviour derived from maternal reproductive traits. *Nature*, 439:76–78.

Austad, S. N. (2006). Why women live longer than men: Sex differences in longevity. *Gender Medicine*, 3:79–92.

Baudisch, A. (2005). Hamilton's indicators of the force of selection. *Proceedings of the National Academy of Science*, 102:8263–8268.

Carey, J. R. and Vaupel, J. W. (2005). Biodemography. In Poston, D. and Micklin, M., editors, *Handbook of Population*, pages 625–658. Kluwer Academic/Plenum Publishers, New York.

Carroll, S. B. (2005). *Endless Forms Most Beautiful*. W. W. Norton & Company, New York.

Christensen, K., Johnson, T. E., and Vaupel, J. W. (2006). The quest for genetic determinants of human longevity: Challenges and insights. *Nature Reviews Genetics*, 7:436–447.

Christensen, K., McGue, M., Yashin, A., Iachine, I., Holm, N. V., and Vaupel, J. W. (2000). Genetic and environmental influences on functional abilities in Danish twins aged 75 years. *Journal of Gerontology: Biological and Medical Sciences*, 55:M446–M451.

Cohen, J. E. (2004). Mathematics is biology's next microscope, only better; biology is mathematics' next physics, only better. *Public Library of Science*, 2:2017–2023.

Crimmins, E. M. (2004). Trends in the health of the elderly. *Annual Review of Public Health*, 25:79–98.

Emlen, S. T. (1995). An evolutionary theory of the family. *Proceedings of the National Academy of Sciences*, 92:8092–8099.

Ewbank, D. C. (2004). The APOE gene and differences in life expectancy in Europe. *Journal of Gerontology: Biological Sciences*, 59A:16–20.

Finch, C. E. and Crimmins, E. M. (2004). Inflammatory exposure and historical changes in human life-spans. *Science*, 305:1736–1739.

Finch, C. E. and Ruvkun, G. (2001). The genetics of aging. *Annual Review of Genomics* *and Human Genetics*, 2:435–462.

Gurven, M. and Kaplan, H. (2007). Longevity among hunter-gatherers: A cross-cultural examination. *Population and Development Review*, 33:321–365.

Hayward, M. D. and Gorman, B. K. (2004). The long arm of childhood: The influence of early-life social conditions on men's mortality. *Demography*, 41:87–107.

Johnson, T. E. (2005). Genes, phenes, and dreams of immortality: The 2003 Kleemeier Award lecture. *Journal of Gerontology: Biological Sciences*, 60A:680–687.

Lamb, V. L. and Siegel, J. S. (2004). Health demography. In Siegel, J. S. and Swanson, D. A., editors, *The Methods and Materials of Demography*, pages 341–370. Elsevier Academic Press, Amsterdam.

Lee, R. D. (2003). Rethinking the evolutionary theory of aging: Transfers, not births, shape senescence in social species. *Proceedings of the National Academy of Sciences*, 100:9637–9642.

Longo, W. D., Mitteldorf, J., and Skulachev, V. P. (2006). Programmed and altruistic ageing. *Nature Reviews Genetics*, 6:866–872.

Mangel, M., Kindsvater, H. K., and Bonsall, M. B. (2007). Evolutionary analysis of life span, competition, and adaptive radiation, motivated by the pacific rockfishes (Sebastes). *Evolution*, 61:1208–1224.

Orzack, S. (2003). How and why do aging and life span evolve? In Carey, J. R. and Tuljapurkar, S., editors, *Life Span: Evolutionary, Ecological, and Demographic Perspectives*, 29. Population Council: Supplement to Population and Development Review, New York.

Page, R. E. and Amdam, G. V. (2007). The making of a social insect: Developmental architectures of social design. *BioEssays*, 29:1–10.

Promislow, D. (2003). Mate choice, sexual conflict, and evolution of senscence. *Behavior genetics*, 33:191–201.

Reznick, D., Bryant, M., and Holmes, D. (2006). The evolution of senescence and post-reproductive lifespan in guppies (Poecilia reticulata). *Public Library of Science*, 4:0136–0143.

Sapp, J. (2003). *Genesis: The Evolution of Biology*. Oxford University Press, Oxford.

Steinsaltz, S. and Evans, S. N. (2003). Markov mortality models: Implications of quasistationarity and varying initial distributions. *Theoretical Population Biology*, 65:319–337.

Tatar, M., Chien, S. A., and Priest, N. K. (2001). Negligible senescence during reproductive dormancy in Drosophila melanogaster. *American Naturalist*, 158:248–258.

Tuljapurkar, S. and Horvitz, C. C. (2006). From stage to age in variable environments: Life expectancy and survivorship. *Ecology*, 87:1497–1509.

Varmus, H. (1999). Plenary talk at centennial meeting of the American Physical Society: The impact of physics on biology and medicineed. Atlanta: American Physical Society, pp. 7.

Vaupel, J. W., Baudisch, A., Dolling, M., Roach, D. A., and Gampe, J. (2004). The case for negative senescence. *Theoretical Population Biology*, 65:339–351.

Wachter, K. (1999). Evolutionary demographic models for mortality plateaus. *Proceedings of the National Academy of Sciences*, 96:10544–10547.

Wilson, A. J., Charmantier, A., and Hadfield, J. D. (2008). Evolutionary genetics of ageing in the wild: Empirical patterns and future prospects. *Functional Ecology*, 22:431–442.

Yashin, A. I., Ukraintsev, S. V., and Anisimov, V. N. (2001). Have the oldest old adults ever been frail in the past? A hypothesis that explains modern trends in survival. *Journal of Gerontology: Biological Sciences*, 56A:B432–B442.