

CONTENTS

Foreword by James W. Vaupel xxi

Preface xxv

- Perspective xxv
- Organization of the book xxvi
- Editorial strategies xxvii
 - Data selection* xxvii
 - Tabulation and visualization* xxviii
 - Concepts and models* xxviii
 - Epistemological* xxix
- Human Demography in Tree of Life Context xxix
 - Human biology shaped mainstream demography* xxix
 - Demographic characteristics* xxx
 - Databases* xxx
- Acknowledgments xxxi
- Permissions xxxii

Introduction 1

- Historical Perspectives on Biodemography 1
 - Biology and demography* 1
 - Early developments* 2
 - Traction* 3
 - Coalescence* 3
- Classical Demography 4
- Usefulness of Demography 5
 - Conceptual unification* 5
 - Projection and prediction* 5
 - Control, conservation, and exploitation* 5
- Demographic Abstractions 5
 - Age* 6
 - Process* 6
 - Flow* 6

Chapter 1: Demography Basics 7

- Basic Formalization 7
 - Demographic levels and traits* 7
 - Age and the life course* 8
 - Types of data* 8

Population Characteristics	9
<i>Population size</i>	9
<i>Population distribution</i>	9
<i>Population structure</i>	10
<i>Population change (size)</i>	12
<i>Population change (space)</i>	13
Basic Demographic Data	13
<i>Exploratory data analysis and summarization</i>	14
Visual inspection of raw data	14
Standard deviation	14
Histograms	15
Box plots	16
<i>Lorenz curves and Gini coefficients</i>	18
<i>Lexis diagrams</i>	19
Concept	19
Lexis diagram: Example applications	21
<i>Demographic time: Extensions beyond age-period-cohort</i>	22
Variants of age-period-cohort (APC)	22
Variants of thantological age-period-death cohort (TPD)	22
Variants of thantological age-chronological age-life span (TAL)	23
Variants of life span-chronological age-death year (LCD)	23
Cohort Concepts	24
Ratios, Proportions, and Rates	25
Chapter 2: Life Tables	26
The Basic Life Table	26
<i>Life table radix</i>	27
<i>Life table rate functions</i>	27
<i>Construction of cohort life table</i>	30
<i>Parameter visualization</i>	35
<i>Life table censoring</i>	35
<i>Period life tables</i>	37
Background	37
Construction	37
<i>Primacy of life expectancy</i>	38
The Abridged Life Table	39
<i>Notation, concepts, and columns</i>	39
<i>Construction of abridged cohort life table</i>	40
<i>Comparison of abridged and complete life table</i>	43
<i>Period and cohort life table concepts</i>	43
Gaps and lags	43
Cross-sectional average length of life (CAL)	47
Metrics of Life Tables	49
<i>Measures of central tendency</i>	49
<i>Central death rate</i>	49
<i>Life table aging rate</i>	50

<i>Life table entropy</i>	50
<i>Sensitivity analysis</i>	51
<i>Example single-decrement processes</i>	53
<i>Life Table as Stationary Population</i>	53
Consider Further	56
Chapter 3: Mortality	59
Discrete Mortality	60
Continuous Mortality: The Calculus of Mortality	62
<i>The Force of Mortality</i>	62
<i>An empirical model</i>	64
<i>Smoothing age-specific mortality rates</i>	65
Mortality Models	66
<i>De Moivre model</i>	67
<i>Gompertz model</i>	67
<i>Makeham model</i>	68
<i>Exponential model</i>	69
<i>Weibull model</i>	69
<i>Logistic model</i>	69
<i>Siler model</i>	70
Mortality Drives the Life Table	70
Demographic Heterogeneity and Selection	71
<i>Model derivation for demographic heterogeneity</i>	73
<i>Distribution of frailty</i>	74
<i>Example of two sub-cohort heterogeneity model</i>	74
<i>Compositional interpretation of the Medfly mortality</i>	75
Mortality Metrics	77
<i>Average lifetime mortality</i>	77
<i>Mortality change indicators</i>	77
<i>Mortality scaling</i>	78
<i>Threshold mortality</i>	80
<i>Standard deviation of mortality</i>	81
<i>Mortality in the human population</i>	81
Consider Further	82
Chapter 4: Reproduction	84
Background	84
<i>Overview of terms and concepts</i>	84
<i>Patterns of Reproduction</i>	84
Basic Concepts	85
Birth Intervals and Rates	86
<i>Basic age-specific birth metrics</i>	86
<i>Lexis diagram: Births by age and period</i>	87
<i>Per capita reproductive rates</i>	87
Daily rates	87
Lifetime rates and mean ages	88

Previous and remaining reproduction	90
Rate generalizations	93
Reproductive Heterogeneity	93
<i>Birth intervals</i>	93
<i>Reproductive parity</i>	98
Daily parity	98
Cumulative parity	98
Individual-level Reproduction	99
<i>Event-history graphics</i>	99
Cohort versus individual patterns	101
Importance of individual-level data	102
<i>Models for individual-level reproduction</i>	103
Model 1: Three adult stages	103
Model 2: Reproductive clock	103
Model 3: Working and retired flies	105
Parity Progression	105
Fertility Models	107
Consider Further	110
Chapter 5: Population I: Basic Models	113
Foundational Concepts	113
<i>Population rates</i>	113
<i>The balancing equation</i>	114
<i>Doubling time and half-life</i>	116
<i>Population growth: Subpopulations and sequence</i>	116
Subpopulations	116
Sequence of Growth Rates	118
The Stable Population Model	118
<i>Background</i>	118
<i>Uses and assumptions of the model</i>	119
<i>Derivation</i>	119
<i>Population Parameters</i>	121
Intrinsic rates: Birth (b), death (d) and growth (r)	121
Intrinsic rate of increase: Analytical approximations	125
Intrinsic birth and death rates	127
Net reproductive rate	128
Stable age distribution	128
Mean generation time	130
<i>Population projection</i>	130
Leslie matrix	130
Example iteration	131
Projection for <i>Drosophila melanogaster</i>	132
<i>Questions to consider when evaluating matrix models</i>	137
Fundamental Properties of Populations	138
<i>Age structure transience</i>	138
<i>Convergence to a stable state</i>	139

<i>Independence of initial conditions</i>	139
<i>Fertility and mortality</i>	139
<i>Changing schedules and unchanging age structure</i>	139
<i>Determinants of age structure</i>	140
<i>Effect on r of reproductive timing</i>	140
<i>Speed of Convergence</i>	141
<i>Population Momentum</i>	142
Consider Further	142
Chapter 6: Population II: Stage Models	145
Model Construction and Analysis	145
<i>Basic stage-structured model</i>	145
<i>Perturbation analysis</i>	147
Stage-Based Models for Modular Organisms: Plants	148
<i>Model I: Growth and renewal</i>	148
<i>Model II: Growth, shrinkage, and dormancy</i>	149
<i>Model III: Connecting populations</i>	151
Stage-based Vertebrate Models	153
<i>Model I: Sea turtles</i>	154
Model construction of a threatened species	154
Matrix projection	154
Perturbation analysis	154
<i>Model II: Killer whales</i>	155
Model construction of a species with a post-reproductive life stage	155
Perturbation analysis	156
Beyond the Basic Stage Model	157
<i>Extensions and refinements of the model</i>	157
<i>Integral projection model</i>	158
Relationship between Leslie Matrix and Lefkovitch Models	158
<i>Model construction using the same data</i>	159
Life cycle graphs and life tables	159
Fertility parameterization: Leslie and Lefkovitch models	159
Constructing the Leslie matrix	160
Constructing the Lefkovitch matrix	161
<i>Model synthesis</i>	165
Lotka equation as the foundation	165
Life tables as stationary population models: Single-decrement life tables	165
Life tables as stationary population models: Multiple-decrement and multistate life tables	166
Stationary population models as life tables: Leslie model	167
Stationary population models as life tables: Lefkovitch model	168
<i>Comparison of model properties</i>	170
Consider Further	170

Chapter 7: Population III: Extensions of Stable Theory 171

Two-sex Models	171
<i>Basic two-sex parameters</i>	171
<i>Sex ratio at age x and intrinsic sex ratio</i>	171
<i>Age-specific sex ratio</i>	172
Stochastic Demography	174
<i>General background</i>	174
<i>Environmental variation in vital rates</i>	177
Stochastic rate of growth	179
Strong and weak ergodicity	180
Multiregional Demography	182
<i>Location aggregated by birth origin</i>	183
<i>Location disaggregated by birth origin</i>	184
<i>Age-by-region projection matrix</i>	186
<i>Comparison of models</i>	190
Hierarchical Demography	190
<i>Background</i>	190
<i>Honeybee: Individual-to-colony</i>	192
Concept of superorganism	192
Assumptions	192
Growth limits	193
Colony-level dynamics	194
Population-level dynamics	197
General properties	199
Consider Further	200

Chapter 8: Human Life History and Demography 201

Biodemographic Synopsis	201
<i>Human demography as evolutionary legacy</i>	201
<i>Developmental stages</i>	202
<i>Reproduction</i>	204
Basic intervals	204
Case study: French-Canadian women	205
<i>Family evolution</i>	205
Background	205
Juvenile help	207
Human family	208
<i>Human life span</i>	208
<i>Actuarial properties</i>	209
Human mortality	209
Human life table	211
Migration patterns	212
Health Demography I: Active Life Expectancy	212
<i>Concepts</i>	213
<i>Basic life table model</i>	214
<i>Worked problem</i>	215

Health Demography II: The Multiple-Decrement Life Table	215
<i>Background</i>	215
<i>Worked problem</i>	217
Cause-of-death data	217
Probability of dying of cause i	218
Competing risk estimation	219
Elimination of cause tables	220
Family Demography	221
<i>Family life cycle</i>	222
<i>Example: Charles Darwin's family</i>	223
Kinship	230
<i>Concepts</i>	230
<i>Types of Kin</i>	230
Examples of relationships	231
Biological pathways	231
<i>Pedigree charts</i>	232
Lineal kin	232
Colineal kin	232
Ablineal kin—same generation	232
Ablineal kin—different generation	232
<i>Pedigree Collapse</i>	232
Consider Further	234
Chapter 9: Applied Demography I: Estimating Parameters	236
Estimating Population Numbers	237
<i>Complete counts</i>	237
<i>Incomplete counts</i>	237
<i>Indirect counts</i>	237
<i>Mark-recapture</i>	238
<i>Hunting effort</i>	239
<i>Change-in-ratio method</i>	240
Estimating Survival: Mark-Recapture	241
<i>Methods</i>	241
Marking and tagging individuals	241
Incomplete data	242
<i>Models</i>	243
Cormack-Jolly-Seber model	243
Worked example	245
Multistate models	245
Mark-recapture as cohort analysis	248
<i>Visualization</i>	249
Estimating Population Growth Rates	253
<i>Growth rate from population number</i>	253
<i>Growth rate from age structure</i>	254
Estimating Population Structure	256
<i>Importance of age data</i>	256
<i>Age structure</i>	257
<i>Stage structure</i>	259

Extracting Parameters from Captive Cohorts	260
<i>Captive cohort life table</i>	261
<i>Mortality equivalencies</i>	261
<i>Survival curve analysis</i>	262
<i>Population structure</i>	265
Frailty structure	265
Age structure	267
Consider Further	271

Chapter 10: Applied Demography II: Evaluating and Managing Populations 275

Comparative Demography	275
<i>Basic metrics</i>	276
Survival and mortality curves	276
Life table metrics	276
Gompertzian analysis	277
<i>Comparative mortality dynamics</i>	278
Mortality slopes	278
Mortality ratios	278
Mortality contributions to e_0	280
Mortality proportional equivalences	282
Health and Health Span	282
<i>Condition scoring: African buffalo</i>	284
Condition indices	284
Health multistate life table	284
<i>Active life expectancy: Fruit flies</i>	288
Biomarker of aging	288
Event history chart	288
Evaluation of active health expectancy	289
<i>Invasion status as health classification for cities</i>	289
Background	289
Application of life table methods	290
<i>Biological control as health demography</i>	293
Irreplaceable mortality	294
Multiple-decrement life table of a pest	294
Population Harvesting	296
<i>Insect mass rearing</i>	296
Single-age/stage harvesting	297
All-age/stage harvesting	298
<i>Culling: African elephants</i>	299
Background	300
Culling as management actuarial strategy	300
Conservation	302
<i>Hunting</i>	302
Age- and season-specific hunting	302
Rear and release	303

Trophy hunting: African lions	304
<i>Poaching: Rhinoceroses</i>	308
Background	308
Competing risk model	309
<i>Captive breeding in conservation biology</i>	312
Background	312
Demography captive breeding: African lion	312
Consider Further	314

Chapter 11: Biodemography Shorts 315

Group 1: Survival, Longevity, Mortality, and More	315
<i>Survival and longevity</i>	315
S 1. A different way to look at survival—life increments	315
S 2. A 1-year survival pill is most effective near $e(0)$	316
S 3. Redundancy increases system reliability	318
S 4. Five important and useful period measures of longevity	319
S 5. A simple equation for producing survival curves	320
S 6. Computation of life overlap of two or more persons	321
S 7. Mortality of 10-year-old girls is incredibly low	322
<i>Mortality</i>	322
S 8. Reparameterization of Gompertz using modal age, M	322
S 9. Excess mortality rate	323
S 10. Mortality elimination	324
S 11. Quiescent period emerges in cohort but not period mortality	325
S 12. Probability of same-year deaths of sisters is extremely small	325
S 13. Estimating mortality trajectories in supercentenarians	326
S 14. Evidence for the absence of lifespan limits	326
S 15. Advancing front of old-age survival	327
S 16. Actuarially speaking, 92 years old is halfway to 100	328
S 17. Why the oldest person in the world keeps dying	328
S 18. Life span limits: Challenges in data interpretation	329
<i>Life course</i>	331
S 19. Relative age	331
S 20. Retirement age based on remaining life expectancy	331
S 21. Effects of classmate age differences	332
<i>Sport career</i>	332
S 22. Major League Soccer (MLS)	332
S 23. National Basketball Association (NBA)	333
Group 2: Population, Statistical, Epidemiological, and Catastrophic	333
<i>Population</i>	333
S 24. Growth rate required for 40-year-old men	333
S 25. Interaction of mortality and fertility on r	336
S 26. Sex ratio in stable populations is independent of growth rate	337

S 27. Populations can experience “transient” stationarity	338
S 28. Effect on growth rate of female migration	338
S 29. Person-years ever lived	339
S 30. Tempo effects	340
S 31. Birth rates in stable versus stationary populations	340
S 32. Super-exponential growth	340
S 33. Mean age of death in growing population	341
S 34. Equality in stable populations	341
<i>Statistical</i>	342
S 35. Anscombe’s quartet	342
S 36. Descriptive statistics	342
S 37. Comparing lifetime longevity using the t-test	342
S 38. Conditional probability of Alzheimer’s disease (AD)	344
S 39. Peak-aligned averaging	345
S 40. Correlation of ages of death for twins	346
S 41. Two persons having same birthday in a group of 80	346
<i>Epidemiological</i>	349
S 42. Prenatal famine exposure	349
S 43. Direct evidence of demographic selection	350
S 44. Quantal analysis in bioassays	350
<i>Catastrophic</i>	350
S 45. Napoleon’s Grand Armée—March to Moscow	350
S 46. The Donner Party disaster	352
S 47. Actuarial analysis of the Titanic disaster	352
Group 3: Familial, Legal, Actuarial and Organizational	353
<i>Family</i>	353
S 48. Strategy for choosing the “best” spouse	353
S 49. Stopping rules for number of girls	354
S 50. Children already born and left to be born	354
S 51. Family size with boy and girl target numbers	356
S 52. Marriage duration	356
S 53. Contraceptive effectiveness	356
S 54. Likelihood of golden wedding anniversary	356
S 55. What is a life worth? Working life estimation in children	357
<i>Actuarial Science</i>	358
S 56. Yield on deposit, P , at interest rate, r	358
S 57. Payments for financial goal	358
S 58. Monthly mortgage payments for 30-year mortgage	359
S 59. Payments to retire credit card debt	359
S 60. Bank savings for retirement	359
S 61. A small-scale mutual fund concept	360
S 62. A large-scale mutual fund concept	361
S 63. Burden in old-age pension	362
<i>Organization</i>	363
S 64. Rejuvenating organizations	363
S 65. Gender parity in university hiring	363

Group 4: Biomedical and Biological	364
<i>Biomedical</i>	364
S 66. Some persons are cured	364
S 67. Chances of false positives in cancer diagnoses	365
S 68. Visualizing health—hypertension	366
S 69. Trajectories of chronic illness	367
S 70. The Will Rogers phenomenon: Migrating frailty groups	367
<i>Animal biodemography: Selected studies</i>	369
S 71. Whooping crane population	369
S 72. Gorilla population decrease	370
S 73. Longevity minimalists: Force of mortality in mayflies	370
S 74. Dog-to-human year conversions depend on dog breed	371
S 75. Impact of parasitoid insect depends on all-cause mortality	371
S 76. Pace and shape of aging	372
S 77. Population extinction	373
S 78. Spatial mark-recapture	374
S 79. Immortality assumption in vectorial capacity model	375
<i>Evolutionary demography</i>	375
S 80. Intrinsic rate of increase as a fitness measure	376
S 81. Life history trade-offs	376
S 82. The r- and K- continuum	376
S 83. Fisher's reproductive value	377
S 84. Survival curve classification	378
<i>Chronodemography</i>	378
S 85. Fish otoliths as black box recorders	378
S 86. Tree rings: Records of age and injury	379
S 87. Forensic entomology: Insects as crime tools	382

Appendices: Visualization, Description, and Management of Demographic Data 383

Appendix I: Visualization of Demographic Data 385

Event History Chart	385
<i>Individual-level data</i>	385
<i>Construction methods</i>	386
Overview of Other Major Graph Types	387
<i>Bar charts</i>	387
<i>Dot plot</i>	387
<i>Histogram</i>	388
<i>Scatter plot</i>	388
<i>Bubble chart</i>	388
<i>Area charts</i>	388
<i>Line charts</i>	389
<i>Box plots</i>	389
<i>Heat maps</i>	390

Strip plots 390
Pie charts 390
Helpful resources for visualizing data 390

Appendix II: Demographic Storytelling 393

Demographic Storytelling: Selected Examples 393
Leonardo Fibonacci: Rabbit breeding 394
Thomas Malthus: Population growth and food supply 395
Charles Darwin: The struggle for existence 396
P. B. Medawar: Actuarial immortality 396
Demography Stories through Graphics or Schematics 397
Demographic transition 397
Age pyramids 398
The greatest walk 398
Helpful Resources for Demographic Storytelling 400

Appendix III: Ten Visualization Rules of Thumb 401

Appendix IV: Management of Demographic Data 403

Data Management Plan and Data Life Cycle 403
Data and Data Documentation 403
Data, data types, and data categories 403
Methods documentation, data dictionaries, and file codes 405
Organization 405
Folder and file naming conventions 405
Storage 406

References Cited 409

Index 437

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 non-human 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.

INDEX

- Abbot's Correction, 350
active life expectancy, 288
activities of daily living (ADL), 213
actuarial aging, 59
actuarial science, 358–60
ADLs. *See* activities of daily living
African buffalo, 284–86
African elephant, 299–306
African lion, 304–13
age: and life course, 8; age class, 9; chronological, 8, 23; definition of, 8; differences, 334; estimation in insects, 258; maximum, 67; models, 130 (*see also* Leslie matrix); periods, 8; pyramid, 11, 172, 398; relative, 331, 332; retirement, 331; structure, 140, 172, 265–67; structure estimation, 256; thanatological, 22, 23
age-period-cohort effects, 19
aging, pace and shape of, 372
aging methods, 258
alfalfa weevil, 295–96
Alzheimer's Disease, 344
Anscombe's quartet, 342–43
area charts, 388
arithmetic rate, 113
aspect ratio, 401
Australopithecus, 210
- balancing equation, 114
Bayesian Theory, 365–66
bioassay, 350
biodemography: data management for, 403; data visualization of, 385; historical perspective, 1; interdisciplinarity, 1
biological control, 293
biomarker, of aging, 288
birth: intervals, 86, 93; per capita, b , 54; rate of, 340
birth origin, location by, 184
birthday, two persons same, 346
black box recorders, 378
box plots, 16, 389
bubble chart, 388
buffalo. *See* African buffalo
- CAL. *See* cross-sectional average length of life
cancer, 365, 366, 368
captive breeding, 312, 313
captive cohort, 55, 236, 260–74
Carey's Equality, 354–55
carrying capacity, 300, 377
cause of death. *See* data
censoring, 35. *See also* Kaplan-Meier
central death rate, 49, 60
characteristic equation. *See* Lotka equation
children subsidy, 208
chronic illness, trajectories of, 367–68
chronodemography, 378
chronodendrology, 379
classmate age, effects of, 332
cohort: analysis, 24, 248; definition of, 7; synthetic, 26
colony (honeybee), 192–99
competing risk, 219, 309
compression of morbidity, 213
condition scoring, 284
consanguinity, 233
conservation, 302, 312
contraception: effectiveness in humans, 356; in elephants, 300
convergence, to stable state, 139–41
Cormack-Jolly-Seber Model, 243
cross-sectional average length of life (CAL), 46, 320
culling, of elephants, 299–301
current. *See* life tables, period
- Darwin, Charles, 223, 396
data: categorical, 8; cause of death, 217; continuous, 8; cross sectional, 24; curation, 406; definition of, 8, 403; dictionaries, 405; discrete, 8; file codes, 405; individual-level, 102; interpretation of, 329; lifecycle, 403; longitudinal, 24; management of, 403; metadata, 404; organization, 405; tabular, 401; types of, 403; visual inspection, 14
death: cause of, 218; central death rate, 49; distribution, $d(x)$, 49; mean age of, 341; per capita rate, d , 54
deer, white-tailed, 304
DeLury Method, 239
demographic rates: age-specific, 25; crude, 25; intrinsic, 25; restricted, 25; by topic, 25

- demographic selection, 71–74, 102, 279, 350
demographic transition, 386, 397–98
demography: applied, 236; biomedical, 364;
classical, 4; comparative, 275; health, 212–15,
282, 286; multiregional, 182–83, 190–91;
multistate, 145, 167–69, 214, 247, 285
DeMoiivre model. *See* mortality models
dependency ratio, 331
development stages, human, 202
disability, 213–16, 286, 289
disability-free life expectancy, DFLE_x, 214
dispersal, 151
dog-to-human year conversions, 371, 372
Donner Party disaster, 352–53
dormancy, 148–52
dot plot, 387
doubling time, 116, 137, 278, 314
Drosophila, 76, 275, 280; age-by-sex distribution
for, 172; age distribution estimates for, 172, 273;
captive cohort of, 271; fertility models for, 110;
intrinsic rate of increase for, 123–24; life table
for, 30–35, 42–43, 276; metadata for, 405;
mortality of, 279; parity progression ratios for,
108–9; population projection of, 135; population
structure of, 137–41; projection for, 132;
reproduction of, 15–18, 90–92, 98–99, 111
- earning potential, lifetime, 357
eigenvector, 147
elasticities. *See* stage models
elephant. *See* African elephant
encounter histories, 374
entropy. *See* life table parameters, entropy
ergodicity, 132, 138, 170; strong, 180–82;
weak, 180–82
estimation: change-in-ratio, 240; complete counts,
237; frequency of capture, 239; hunting effort
model, 239; incomplete counts, 237; indirect
counts, 237; mark-recapture model, 238;
population growth, 253–54; population
numbers, 237; survival, 241
European dipper, 246–48
event history chart, 288; construction of, 386;
example, 386
events, age-specific, 93
evolutionary demography, 375
extinction, 6, 152–53, 177, 312, 329, 373–74
- false positives, 365
family: Charles Darwin, 223, 227–30; demogra-
phy, 221; evolution of, 205–8; extended, 230;
juvenile help in, 207; life cycle, 222, 226; net
values of children, 207; nuclear, 230; stem, 230;
target number of children, 356
famine exposure, prenatal, 349
fecundability, 84, 204
fecundity, 84. *See also* reproduction
fertility, 84. *See also* reproduction
fertility models: Coale-Trussel, 110; parameter
calculation, 160; Pearson Type I, 110
Fibonacci numbers, 395
force of mortality, 50–51, 62–65, 73, 260, 323,
340, 370
forensic entomology, 380–82
formal demography, 7
frailty, 74, 77, 265–7
- gap, life table, 43–45
gender parity, 363
geometric rate, 113
gestation, 204
Gini index, 18
golden ratio, 395
Gompertz model. *See* mortality models
Gompertz-Makeham. *See* mortality models
gorillas, 370
graph types: area chart, 388; bar charts, 387;
box plot, 389; bubble chart, 388; dot plots, 387;
heat maps, 390; histogram, 388; line chart,
389; pie charts, 390; scatter plot, 388; strip
plots, 390
“greatest walk, the,” 398–99
growth limits, 193
growth trajectory, human, 203
- half-life, 116
harvest, lions, 307
harvesting, 296, 300, 307
hazard. *See* mortality, age-specific
health demography. *See* demography
health expectancy, active, 289
health span, 282, 283, 284
health transition, 213
heat maps, 390
heterogeneity, demographic, 71–76
hierarchical demography, 190–200
hiring strategies, for gender parity, 363
histogram, 15, 388
Hominoidea, 202
Homo species, 202, 208
honeybee, 191–96
human stages, 204
hunting, 240, 302–9
hypertension, 366

- IADLs. *See* instrumental activities of daily living
- immortality assumption, 375
- instrumental activities of daily living (IADL), 213
- integral projection model, 158
- interquartile range, 16
- intrinsic rate of increase, r , 121–25, 140–42, 179, 313, 362, 376
- intrinsic rates, 121; analytical approximations, 125; birth, 121, 127; death, 121, 127; growth, 174; of increase, r , 121; sex ratio, 172
- invasion biology, 289
- irreplaceable mortality. *See* mortality, irreplaceable
- iteroparous, 85, 204
- Kaplan-Meier, 37
- key factor analysis, 294
- killer whales. *See* stage models
- kinship: ablineal, 231–32; biological pathways, 231; colineal, 230–32; collateral, 230; concepts, 230; lineal, 232; lineal kin, 230; pedigree charts, 232; types, 230
- lag, life table, 43, 45
- LAR. *See* life table aging rate
- lead time bias, 369
- Lefkovitch models: assumptions of, 146; elasticities for, 147, 156; for killer whales, 155–57; with metapopulations, 151; model properties, 170; modularity in, 148–49; parameter calculations, 164; perturbation analysis of, 147; for plants, 148–53; for sea turtles, 154–56; with size class, 145–49, 158; for vertebrates, 153
- Leslie matrix, 130, 145, 158–60; age-by-region, 186; construction of, 160; *Drosophila* population projection with, 132; as life table model, 167; parameterization of, 159–61; projection of, 131–33; stochastic, 179; transition matrix, 162
- Lexis diagrams, 7, 19–22, 48, 61, 82, 248–49, 256, 380
- life course, 8, 35, 66, 204, 221, 279, 331, 366, 386
- life cycle graphs, 159
- life expectancy: average weighted cohort, 320; cross-sectional (CAL), 319; period, 319; tempo adjusted, 320. *See also* life table parameters, expectation of life
- life expectancy, active, 212
- life history: components, 7; data, 160; effects of changes on r , 140; human, 201; primate, 201; trade-offs, 376
- life increments, 315–17
- life overlap, 321
- life table parameters: cohort survival, $l(x)$, 27; death distribution, $d(x)$, 28; disability free life expectancy, 216; entropy, H , 50, 51; expectation of life, $e(x)$, 29, 38; healthy life expectancy, HLE, 214; life table aging rate, LAR, 50, 278–79; period mortality, $q(x)$, 27; period survival, $p(x)$, 27
- life tables: abridged, 39; for African buffalo, 287; applied to cities, 289–93; background, 26; for captive cohort, 261; cause of death, 220–24; cohort, 26, 30, 35; construction of, 30; fruit fly metrics, 276; for health, 212; for human, 211; identity, 55; Lefkovitch analog, 169; Leslie matrix analog, 168; multiple decrement, 166, 215, 294–95, 310–11; multistate, 166, 284; period, 37, 38; plant, 150–52; radix, 27; single decrement processes, 54; as stationary population, 54; survival bonus, 44; types of, 26
- life worth, 357
- life-lived and left, 341, 354
- lifespan: in demographic time, 22; in fertility model, 103; and health span, 283; human, 201, 208–9; limits, 326, 329; mark-recapture estimates of, 249; post-capture, 252; predicted, 210; reproductive, 205
- Lincoln index, 238
- line charts, 389
- lion. *See* African lion
- logistic model. *See* mortality models
- Lorenz curve, 18–19
- Lotka equation, 119, 165, 172
- Makeham. *See* Gompertz-Makeham
- marking. *See* tagging
- mark-recapture, 238–52, 374
- marriage duration, 356
- mass rearing, insects, 296
- mayfly, 370, 371
- Medfly, 15, 275, 279, 290; captive cohort, 262–64; intrinsic rate of increase, 338; life table for, 276, 337, 342–44; lifespan of, 104; reproduction for, 15–17, 88, 95–96, 101, 104, 337; supine behavior in, 291
- Mediterranean fruit fly. *See* Medfly
- metapopulation, 151, 247
- Mexfly, 15, 275, 280, 290; intrinsic rate of increase, 338; life table for, 276, 337–44; reproduction, 15–17, 337
- Mexican fruit fly. *See* Mexfly
- midhinge, 17

- midrange, 17
- migration, 183; effect on growth rate, 338; gross in migration, 14; gross out migration, 14; human age patterns in, 212; interchange, 14; net, 14; stream, 14
- momentum, population, 143
- morbidity, 213–15, 349
- mortality: age-specific, 59–60; all-cause, 59; average lifetime, 59, 77; change indicators, 77–9; elimination, 324; equivalencies, 261, 329; excess rate of, 323; human, 81, 209–10; importance of, 59, 60; interaction with fertility, 336; irreplaceable, 294–96; lowest in girls, 322; old-age trajectory, 327; proportional equivalencies, 282; ratio, 278–80; scaling, 78; smoothing, age-specific, 65; standard deviation of, 81; threshold, 80; traveling waves of, 327–28; for US females, 66
- mortality models: 66–67; de Moivre, 67; exponential, 69; Gompertz, 50, 67–71, 77, 210, 277, 304, 322; Gompertz-Makeham, 68–69, 306; logistic, 69; Perks, 69; Siler, 70, 306; Weibull, 69
- multiregional. *See* demography, multiregional
- multistate. *See* demography, multistate
- mutual fund, 361
- Napoleon's Grand Armée, 350–52
- natural enemies, 293
- NRR. *See* net reproductive rate
- odds ratio, 59
- oldest person, 328
- otoliths, 378
- parameterization (Leslie and Lefkovich models), 159
- parasitoid insects, 371
- parental care, 204
- parity: age composition, 205; cumulative, 86, 98; daily, 86, 98; French-Canadian women, 206; progression life table, 105, 354
- paternity functions, 86
- peak-aligned averaging, 345–46
- pedigree chart, 233
- pedigree collapse, 232
- pension, old age, 362
- person years, 339
- perturbation analysis, 154–56. *See* stage models
- pest control, 293
- pheasants, 305
- pie charts, 390
- PMI. *See* postmortem interval
- poaching, 308
- population: change, 12–13; characteristics, 9; distribution, 9; momentum, 142; projection, 130–32; size, 9; structure, 10; study, 7; United States, 10
- population growth rates: deterministically varying, 181; stochastically varying, 181
- postmortem interval, 380–82
- primates, 202
- probability: of animal detection, 374; of becoming oldest person, 328; of breast cancer, 365; conditional, 344; density function, 342; distribution, 15; extinction, 153, 373; family composition, 354; of golden wedding anniversary, 356; lifetime earnings, 358; of marriage duration, 356; of same birthday, 346; of sister deaths, 325
- processes, demographic, 6
- projection: and prediction, 5; comparison, 170; integral model, 158; Leslie matrix, 131; life expectancy, 38; stochastic, 180; subpopulations, 117; two-region, 189
- Q-phase. *See* quiescent period
- quantal analysis, 350
- queen (honeybee), 192–97
- queuing theory, 329
- quiescent period, 325
- r- and K- continuum, 376
- R_0 . *See* net reproductive rate
- rabbit breeding, 395
- redundancy, system, 318
- rejuvenating organizations, 363
- relative risk, 59
- release-pulse cycle, 305
- reliability, 318
- relocation, 300
- reproduction: age schedule of, 85; age-specific, 88–96; birth flow, 159; birth pulse, 159; concentration of, 86; daily, 87; event-history graphic of, 99; gross, 85, 89, 206; heterogeneity, 93–94, 98; individual-level, 94, 99; interval, 86, 204; Lexis diagram, 88; lifetime, 88; mean ages, 88; net, 85–89, 128, 206; parity, 98–99; previous, 90; remaining, 90; schedules, 85
- reproduction models: reproductive clock, 103–6; three adult stages, 103–4; working and retired flies, 105–7
- reproductive strategies, comparative, 209
- reproductive value, 377
- retirement, 359
- rhinoceros, 306–12

- SAD. *See* stable age distribution
- scatter plot, 388
- semelparous, 84
- sensitivity analysis, 51, 138
- sex ratio, 172–74, 337
- Siler model. *See* mortality models
- single decrement processes, 53
- spider mite, 174
- sport career: for Major League Soccer, 332, 335; for National Basketball Association, 333, 335
- spouse, choosing best, 353
- stable age distribution, 118, 129, 132, 141, 165, 172–73
- stable population model, 118; assumptions of, 119; derivation of, 119; intrinsic rate of increase for, 121, 140, 165; properties of, 138; stable age distribution for, 128, 336
- stage models. *See* Lefkovitch models
- stage structure, 137, 181, 259
- stage-frequency analysis, 259–60
- standard deviation, 11, 15–16, 177, 342, 387
- stationary population, 56, 165
- sterilization, elephant, 300
- stochasticity: demographic, 175; environmental, 177–78; rate of population growth, 179
- stopping rules, 354
- storytelling, 393; Darwin—the struggle for existence, 396; demographic transition, 397; Fibonacci—rabbit breeding, 394; “the greatest walk,” 398; Malthus—population growth, 395; Medwar—actuarial immortality, 396
- strip plots, 390
- Sullivan method, 214–16
- supercentenarians, 326
- super-exponential growth, 340
- superorganism, concept of, 192
- supine behavior, 288–89
- survival: bonus, 44–46; curve analysis, 262; curve classification, 378–79; horizontalization of, 262; longevity extension, 262; pill, 316; simple equation for, 320–21; verticalization of, 262
- swarming threshold, 200
- tagging, 241
- TCAL (truncated CAL), 47
- tempo effects, 340
- threshold mortality, 80
- Titanic disaster, 352
- transience, age structure, 138
- transient population stationarity, 338
- trap encounter rate, 374
- tree rings, 379, 380
- trophy hunting, 304
- tsunami, 350
- t-test, 342
- turtles, loggerhead sea. *See* stage models
- twins, ages of death, 346
- two-region population, 183
- two-sex models, 171
- vectorial capacity, 375
- visualization, 385; with event history chart, 385; of individual-level data, 385; mark-recapture model, 249; rules of thumb for, 401
- wedding anniversary, golden, 356
- Weibull model. *See* mortality models
- whooping crane, 369
- Will Rogers phenomenon, 367
- zero population growth, 142–43, 296–97