Earth Systems Science 163/363: Demography and Life History Theory

Instructor: James Holland Jones

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Time: MWF, 9:30-10:20 Location: 320-107 Winter Quarter 2017

1 Course Description

Life history theory is the branch of evolutionary biology that attempts to understand patterns of investment in growth, reproduction, and survival across the life cycle. It is the theory that explains the major transitions that mark individual organisms' life cycles from conception to death. The diversity of life reflects a tremendous diversity in life histories. Some organisms live very short lives and reproduce in large numbers. Others spread a modest amount of reproduction out over a long lifespan. Still others live an extraordinarily long time and still manage to reproduce in massive numbers. Why do organisms differ so much in traits such as age at maturity, age-specific fertility, life expectancy, or clutch size? Why would a biological entity ever voluntarily reduce its reproductive output and, presumably, its fitness? How do humans fit into this diversity?

Of central importance, from the perspective of Earth Systems Science, life history theory — and its attendant tools of formal demography and decision theory — provides a framework for understanding both the ecological context and the evolutionary underpinnings of human decision-making in the realms of subsistence, reproduction, and the many domains with which these intersect. Key problems such as population growth, ecological rationality, time preferences, and resilience have their foundations in the evolution of human life histories.

Life history theory lies at the very heart of evolutionary explanation because it deals with the mechanics of natural selection. If you want to argue that a trait – any trait – evolved via natural selection, you need to have at least a rudimentary understanding of life history theory.

In this class, we will focus on the central themes of life history theory and how they relate to specific problems of the human life cycle. Our class reading will focus on classic works that should be in the bibliography of any evolutionarily-informed student of human behavior. The approaches that we discuss will not be exhaustive, but instead will focus on the more explicitly demographic models of life history evolution. In addition to the classic questions of life history theory (e.g., evolution of reproductive effort, size vs. quality, etc.), we will discuss some peculiar issues that relate specifically to humans. In particular, we will explore the intersection of life history theory and more classical economic approaches to decision theory and rational choice. This will include an exploration of the evolution of economic transfers and their implications for demographic transitions, ecological resilience, and the consumption of natural resources. This discussion will explore how an understanding of life history theory might help in promoting investments in future welfare or developing policies that promote sustainability.

2 Expectations

This course uses mathematics to describe processes relevant to the study of human biology and social behavior. It is not, however, a course in mathematics. You will not be expected to do mathematical proofs or derive complex formulae. You will be expected to understand the demographic, social, and biological theory contained in the mathematics as described in class lectures and in the readings.

Students will propose and execute an original analysis on a topic in demography and life history theory. The written form of the project should be on the order of 10-15 pages and composed in the form of a scientific research paper, complete with full citations. The paper should be organized into the following sections: Introduction, Methods, Results, Discussion.

3 Learning Outcomes

In addition to learning about life history theory, students will exit this class knowing how to calculate a period and cohort life table, how to use model schedules for vital rates to fill in for missing demographic data, how to perform simple deterministic and stochastic projections of age-structured populations, how to perform an eigenanalysis of population projection matrices, how to construct and analyze integral projection models, and how to find the optimal sequence of actions in finite-time-horizon dynamic optimality models. Hopefully, the R skills of students completing the class will also be strong.

4 Grading

The breakdown of grading for this class will be as follows:

- 50% Weekly problem sets designed to reinforce lectures and readings and build confidence in your analytic skills. Problem sets will be due on Tuesday at the beginning of class each week. Late work will lose a third of a grade per day past due.
- 15% Take-Home Midterm Exam. This cumulative exam must reflect your own work.
- 25% Final Project.
- 10% Class Participation. This is a small class. If you have questions, ask them in class. Show me that you are actually working to understand the material.

5 Prerequisites

I expect that you have a basic understanding of ecology and evolution and, specifically, natural selection. We will employ mathematical tools in developing the theory discussed in this class. Mathematical preparation at the level of calculus is necessary to understand the material presented. While we will use some techniques from linear algebra, students should be able to acquire an instrumental understanding sufficient for this class without having any specific background.

6 Readings

The primary text for this class will be my manuscript, *The Ecology and Evolution of Human Life Histories* (EEHLH), which is accessible electronically via the secure class website. In addition, readings will be taken from the primary scientific literature. Many of these readings are "classics" – frequently cited and rarely read. Some of the readings are listed under the heading "Optional." These readings fall into one of two classes: (1) important classics that should be known by any student but which are either redundant with other readings or have been substituted by important recent work, and (2) more anthropological (typically less technical) applications of life history theory.

All readings are available in electronic format, and can be accessed at the secure readings section of the class website.

While I have endeavored to summarize the work of the classics in the field in EEHLH, the serious student of demography and life history theory will want some important reference materials for his or her personal library. The first two are authoritative accounts of the methods and theories of mathematical demography. The others are classics of the field, long out of print, but important both for their historical impact on the field and their lasting applicability.

- Caswell, H. 2001. Matrix Population Models: Construction, Analysis and Interpretation. 2nd ed. Sunderland, MA: Sinauer.
- Keyfitz, N., and H. Caswell. 2005. *Applied Mathematical Demography*. 3rd ed. New York: Springer.
- Keyfitz, N. 1977. Introduction to the Mathematics of Populations. 2nd ed. Menlo Park: Addison-Wesley.
- Sheps, M.C., and J. Menken. 1973. Mathematical Models of Conception and Birth. Chicago: University of Chicago Press.
- Coale, A.J. 1972. The Growth and Structure of Human Populations: A Mathematical Investigation. Princeton: Princeton University Press.
- Tuljapurkar, S. 1990. Population Dynamics in Variable Environments. Edited by S. A. Levin. Vol. 85, Lecture notes in biomathematics. Berlin: Springer-Veralg.

7 Software

We will use a freely-available software package called R. R has a number of advantages: (1) it is free, (2) it is essentially platform independent, (3) R represents the cutting-edge in statistical computation, (4) there is extensive (free) documentation and a large online community of users to provide support, (5) it is used overwhelmingly by professional statisticians and therefore learning R facilitates conversations with statisticians for consulting and collaborative purposes. Did I mention it's free?

The many examples of demographic computation, model optimization, and simulation presented in EEHLH are supported by extensively-documented R code. Furthermore, the R package demogR contains many functions to support work in age-structured demographic analysis (Jones 2007).

8 Course Outline (Subject to Change)

Week 1 The Measurement of Vital Rates

- 1. The life table
- 2. The natural history of human mortality
- 3. Measures of mortality
- 4. Measures of fertility
- 5. Incomplete data and model schedules of mortality and fertility

Readings: EEHLH 4 & 5

Assignment: Problem Set 1

Week 2 Population Renewal

- 1. Lotka's equation
- 2. Stable population theory

Readings: EEHLH 8, Jones (2011) Optional: Coale (1957)

Assignment: Problem Set 2

Week 3 Reproductive Effort

- 1. Cole's Paradox
- 2. Gadgil & Bossert's Framework
- 3. Cole's Paradox Resolved
- 4. Variable Environments and Unstructured Models
- 5. Arithmetic Means, Geometric Means, and Bet-Hedging

Readings: EEHLH 2, Gadgil and Bossert (1970), Charnov and Schaffer (1973), Schaffer (1974) Optional: Hirshfield and Tinkle (1975)

Assignment: Problem Set 3

Week 4 Clutch Size, and State-Dependent Life Histories

- 1. Quality-quantity trade-off
- 2. Lack Clutch

Readings: EEHLH 3, Smith and Fretwell (1974), Milner-Gulland et al. (1996), Mace (1996) Optional: Bogin (1997)

Assignment: Problem Set 4

Week 5 Matrix Models for Structured Populations

- 1. Motivation and model formulation
- 2. Relationship to other models
- 3. Eigenvalues, eigenvectors, etc.
- 4. Sensitivities and elasticities

Readings: EEHLH 9, Hamilton (1966), Caswell (1978), Jones (2009)

Assignment: Problem Set 5

Week 6 More Matrix Models 2: New Directions

- 1. Uses of sensitivities and elasticities
- 2. Second derivatives
- 3. Elasticities and trade-offs
- 4. Integral projection models

Readings: Coulson et al. (2011), Coulson (2012), Caswell (1996), Jones and Tuljapurkar (2015)

Assignment: Problem Set 6

Week 7 Matrix Models 3: Variable Environments

- 1. Types of variable environments
- 2. Autocorrelation, covariance
- 3. Stochastic elasticities

Readings: EEHLH 10, Orzack and Tuljapurkar (1989), Tuljapurkar et al. (2004), Haridas and Tuljapurkar (2007)

Assignment: Problem Set 7

Week 8 Risk

- 1. Risk and risk aversion
- 2. Expected utility/expected loss, Prospect theory
- 3. Arrow-Pratt

Readings: EEHLH 11, Friedman and Savage (1948), Winterhalder and Leslie (2002), Jones et al. (2013) Optional: Kuznar (2002), Henrich and McElreath (2002)

Week 9 Ecological Rationality, Preferences, and Decision-Making

- 1. Behavioral economics
- 2. Rational choice
- 3. Biases and heuristics
- 4. Ecological rationality
- 5. Evolutionary origins of ecological rationality

Readings: Tversky and Kahneman (1974), Gigerenzer and Gaissmaier (2011), Price and Jones (2016)

Week 10 Economic Transfers

- 1. Demographic transition theory
- 2. Economic transfers
- 3. Embodied capital

Readings: EEHLH 6, Lee (2003), Kaplan and Robson (2002), Jones (2015)

References

Bogin, B. (1997). Evolutionary hypotheses for human childhood. Yearbook of Physical Anthropology 40, 40–1997.

Caswell, H. (1978). A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theoretical Population Biology* 14, 215–230.

- Caswell, H. (1996). Second derivatives of population growth rate: Calculation and applications. Ecology 77(3), 870–879.
- Charnov, E. L. and W. M. Schaffer (1973). Life history consequences of natural selection: Cole's result revisited. *American Naturalist 107*, 791–793.
- Coale, A. (1957). How the age distribution of a human population is determined. Cold Spring Harbor Symposia on Quantitative Biology 22, 83–88. Reprinted in D. Smith and N. Keyfitz (1977) Mathematical Demography: Selected Papers. pp. 167-172. Berlin: Springer-Verlag.
- Coulson, T. (2012). Integral projections models, their construction and use in posing hypotheses in ecology. *Oikos 121*, 1337–1350.
- Coulson, T., D. R. MacNulty, D. R. Stahler, B. vonHoldt, R. K. Wayne, and D. W. Smith (2011). Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History. Science 334 (6060), 1275–1278.
- Friedman, M. and L. Savage (1948). The utility analysis of choices involving risk. Journal of Political Economy 56(4), 279–304.
- Gadgil, M. and W. H. Bossert (1970). Life historical consequences of natural selection. American Naturalist 104, 1–24.
- Gigerenzer, G. and W. Gaissmaier (2011). Heuristic Decision Making. Annual Review of Psychology 62, 451–482.
- Hamilton, W. D. (1966). The moulding of senescence by natural selection. Journal of Theoretical Biology 12, 12–45.
- Haridas, C. V. and S. Tuljapurkar (2007). Time, transients and elasticity. *Ecology Letters* 10(12), 1143–1153.
- Henrich, J. and R. McElreath (2002). Are Peasants Risk-Averse Decision Makers? Current Anthropology 43(1), 172–181.
- Hirshfield, M. F. and D. Tinkle (1975). Natural selection and the evolution of reproductive effort. Proceedings of the National Academy of Sciences, USA 72(6), 2227–2231.
- Jones, J. H. (2007). demogR: A package for the analysis of age-structured demographic models in R. Journal of Statistical Software 22(10), 1–28.
- Jones, J. H. (2009). The force of selection on the human life cycle. Evolution and Human Behavior 30(5), 305–314.
- Jones, J. H. (2011). Primates and the Evolution of Long, Slow Life Histories. Current Biology 21(18), R708–R717.
- Jones, J. H. (2015). Resource Transfers and Human Life-History Evolution. Annual Review of Anthropology 44(1), 513–531.

- Jones, J. H., R. B. Bird, and D. W. Bird (2013). To kill a kangaroo: understanding the decision to pursue high-risk/high-gain resources. Proceedings of the Royal Society B: Biological Sciences 280(1767), 20131210.
- Jones, J. H. and S. Tuljapurkar (2015). Measuring selective constraint on fertility in human life histories. Proceedings of the National Academy of Sciences 112(29), 8982–8986.
- Kaplan, H. S. and A. J. Robson (2002). The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. Proceedings of the National Academy of Sciences, USA 99(15), 10221–10226.
- Kuznar, L. (2002). On Risk-Prone Peasants: Cultural Transmission or Sigmoid Utility Maximization? Current Anthropology 43(5), 787–9.
- Lee, R. D. (2003). Rethinking the evolutionary theory of aging: Transfers, not births, shape social species. Proceedings of the National Academy of Sciences, USA 100(16), 9637–9642.
- Mace, R. (1996). When to have another baby: A dynamic model of reproductive decision-making and evidence from Gabbra pastoralists. *Ethology and Sociobiology* 17(4), 263–273.
- Milner-Gulland, E. J., R. Mace, and I. Scoones (1996). A model of household decisions in dryland agropastoral systems. Agricultural Systems 51(4), 407–430.
- Orzack, S. H. and S. Tuljapurkar (1989). Population dynamics in variable environments. VII. Demography and evolution of iteroparity. *American Naturalist* 133(6), 901–923.
- Price, M. H. and J. H. Jones (2016). Hierarchical Evolutionary Preferences Explain Discrepancies in Expected Utility Theory. Submitted.
- Schaffer, W. M. (1974). Optimal reproductive effort in fluctuating environments. American Naturalist 108, 783–790.
- Smith, C. C. and S. D. Fretwell (1974). The optimal balance between size and number of offspring. American Naturalist 108, 499–506.
- Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella (2004). The many growth rates and elasticities of populations in random environments. *American Naturalist* 164(6), 821–823.
- Tversky, A. and D. Kahneman (1974). Judgment Under Uncertainty: Heuristics and Biases. Science 185(4157), 1124–1131.
- Winterhalder, B. and P. Leslie (2002). Risk-sensitive fertility: The variance compensation hypothesis. Evolution and Human Behavior 23, 59–82.