## Realistic stage-structured models alter the optimum expectation of classic life-history trade offs.

- Karthik Ram and Perry de Valpine.
- Environmental Science, Policy & Management. University of California, Berkeley. Berkeley, CA 94720
- karthik.ram@berkeley.edu

## Introduction

Components of the life history of an organism, such as the time it takes to reach maturity, stage-specific survival rate etc. are of considerable interest to both theoretical and applied ecologists alike. Trade offs between such traits allow organisms, especially ones with complex life histories, to choose an optimal strategy that maximizes their reproductive fitness over a range of environmental conditions (Houssard et al., 1991). 11 The diversity of strategies observed in nature are in large part the result of of such tradeoffs between vital 12 traits (Law, 1979). Understanding trade offs has been fundamental to understanding conditions that favor 13 the evolution of iteroparity versus semelarity (Cole, 1954; Gadgil et al., 1970; Stearns, 1989). Ecologists have 14 examined trade-offs to solve applied problems such as the spread of infectious diseases and pests under global 15 change (Woodhams et al., 2008).

Although there are various methods to understand tradeoffs, mathematical models provide a particularly 17 versatile and powerful way to examine the importance of vital rates, and how trade offs between rates alter the evolutionary trajectory of a species. Matrix population models, especially, have proved extremely useful 19 both in a theoretical and applied context (Caswell, 2001). These models can be applied to a variety of 20 organisms such as plants and insects that transition through distinct development stages, but can also be 21 applied to organisms that mature through distinct size classes, which can be treated abstractly as stages 22 (Caswell, 2009). Matrix models have been provided numerous insights into conservation issues (Morris et al., 23 2002, ) and evolutionary ecology (Lande, 1982), the popularity driven primarily by its simplicity and ease of 24 interpretation.

Despite its popularity, matrix population models fail to incorporate an adequate level biological realism that characteize most populations in nature. For example, matrix models fail to capture variation in development 27 time among individuals both within and between stages (de Valpine, 2009). Stage structured models typically 28 assume that time spent in a stage is geometrically distributed, an assumption that is not realistic for most organisms. Therefore, ecologists looking to incorporate more realism must look beyond simple matrix models 30 (de Valpine, 2009). Several authors have provided modifications to the matrix model to overcome such 31 limitations (Caswell, 2001) althogh not all have been widely adopted (de Valpine, 2009). (Need to include a 32 fleshed out section describing the IPM generalization of the matrix model).

These new methods and implementation techniques provide an easy-way to incorporate variable development into matrix models and revisit ecological theory. In particular, this new technique provides an opportunity to 35 reexamine classic life history trade offs, such as the one between growth rate and survival, or fecundity and maturation rate, under more complex assumptions. Here we reassess classic ecological trade offs between 37 maturation (both adult and juvenile) and growth rate (Takada, 1995). 38

In this paper, we investigate the role of incorporating additional complexity in matrix population models, such 39 as realistic assumptions about time spent in a stage, and add further complexity in the form of correlation among stages. We used the Lefkovitch matrix model to describe stage structured population models with 41 reproduction and survival. To maintain a simple story, we also restrict our efforts to a two-stage model 42 (juveniles and adults) in a density-independent case, although our analyses could easily be extended to larger 43 number of classes. We analyze the outcome with varying levels of compelxity, from the simple matrix case all the way to incorporating variation in development time within stages and correlation between stages. We 45

then compare how the optimal trade off strategy shifts as a result of these new assumptions.

$$_{47} \quad M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

## 48 Model Description

## 49 Literature Cited

- 50 Caswell, H. 2001. Matrix Population Models: Construction, Analysis and Interpretation. Sinauer Associates
- <sup>51</sup> Inc., Sunderland, MA.
- 52 Caswell, H. 2009. Stage, age and individual stochasticity in demography. Oikos 118:1763–1782.
- <sup>53</sup> Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology
- <sub>54</sub> 28:218–228.
- 55 Gadgil, M., & Bossert, W. H. 1970. Life history consequences of natural selection. The American Naturalist
- <sub>56</sub> 102:52–64.
- 57 Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation.
- 58 Copeia 1998:367–375.
- <sup>59</sup> Houssard, C., & Escarre, J. 1991. The effects of seed weight on growth and competitive ability of Rumex
- acetosella from two successional old fields. Oecologia 86:236–242.
- Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 63:607-615.
- <sub>62</sub> Law, R. 1979. Ecological determinants in the evolution of life histories. In B. D. T. &. L. R. T. R. M.
- 63 Anderson (Ed.), Population Dynamics (pp. 81–103). Blackwell Science, Oxford.
- 64 Morris, W. F., & Doak, D. F. 2002. Quantitative conservation biology: Theory and practice of population
- viability analysis. Sinauer Associates Inc., Sunderland, MA.
- 66 Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.
- <sub>67</sub> Takada, T. 1995. Evolution of Semelparous and Iteroparous Perennial Plants: Comparison between the
- Density-independent and Density-dependent Dynamics. Journal of Theoretical Biology 173:51–60.
- 69 Woodhams, D. C., Alford, R. a, Briggs, C. J., Johnson, M., & Rollins-Smith, L. a. 2008. Life-history trade-offs
- <sub>70</sub> influence disease in changing climates: strategies of an amphibian pathogen. Ecology 89:1627–39.
- de Valpine, P. 2009. Stochastic development in biologically structured population models. Ecology 90:2889–
- 72 2901.