

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

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## 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). The diversity of strategies observed in nature are in large part the result of such tradeoffs between vital traits (Law, 1979). Understanding trade offs has been fundamental to understanding conditions that favor the evolution of iteroparity versus semelparity (Cole, 1954; Gadgil et al., 1970; Stearns, 1989). Ecologists have examined trade-offs to solve applied problems such as the spread of infectious diseases and pests under global change (Woodhams et al., 2008).

Although there are various methods to understand tradeoffs, mathematical models provide a particularly 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 both in a theoretical and applied context (Caswell, 2001). These models can be applied to a variety of organisms such as plants and insects that transition through distinct development stages, but can also be applied to organisms that mature through distinct size classes, which can be treated abstractly as stages (Caswell, 2009). Matrix models have been provided numerous insights into conservation issues (Morris et al., 2002, ) and evolutionary ecology (Lande, 1982), the popularity driven primarily by its simplicity and ease of interpretation.

Despite its popularity, matrix population models fail to incorporate an adequate level biological realism that characterize most populations in nature. For example, matrix models fail to capture variation in development time among individuals both within and between stages (de Valpine, 2009). Stage structured models typically 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 (de Valpine, 2009). Several authors have provided modifications to the matrix model to

overcome such limitations (Caswell, 2001) although not all have been widely adopted (de Valpine, 2009). (Need to include a 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 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 maturation (both adult and juvenile) and growth rate (Takada, 1995). In this paper, we investigate the role of incorporating additional complexity in matrix population models, such 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 reproduction and survival. To maintain a simple story, we also restrict our efforts to a two-stage model (juveniles and adults) in a density-independent case, although our analyses could easily be extended to larger number of classes. We analyze the outcome with varying levels of complexity, from the simple matrix case all the way to incorporating variation in development time within stages and correlation between stages. We then compare how the optimal trade off strategy shifts as a result of these new assumptions.

## Model Description

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