

The Role of Resources and Mortality in Life-History Evolution: A Model of Optimal Reproductive Effort and Offspring Size in the Trinidadian Guppy

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Goal

To improve understanding of life-history patterns in guppies by developing a model that predicts resource allocation decisions (interbrood interval, reproductive effort, and offspring size).

Background

The work of David Reznick and colleagues on life-history evolution in guppies (*Poecilia reticulata*) is viewed as strong support for age-specific demographic models for the evolution of reproductive effort (cf. Stearns 1992, p. 165). This work compares the life history of guppies from high- and low-predation sites. High-predation environments are those in which guppies co-occur with larger species of fish, such as the pike cichlid (*Crenicichla alta*), that frequently feed on guppies. Low-predation environments are found in the same drainages, but upstream of rapids or waterfalls that exclude the larger species of predators. At these sites, guppies co-occur with just the killifish (*Rivulus hartii*) that is limited to feeding on juvenile guppies (Liley and Seghers 1975). This difference in age-specific mortality risk leads to the prediction that guppies from high-predation locales should mature at an earlier age and have a higher reproductive effort than their counterparts from low-predation environment (following demographic models aligns such as Gadgil and Bossert (1970) and Law (1979)). These predictions have been well supported via comparative studies of the life-history phenotypes of wild-caught guppies (Reznick 1989; Reznick and Endler 1982; Reznick et al. 1996b) as well as through laboratory comparisons of the genetic basis of these life-history patterns (Reznick 1982; Reznick and Bryga 1996). Furthermore, replicated introduction experiments demonstrate that a change in predation environment is associated with the rapid evolution of life-history patterns in the predicted direction (Reznick et al. 1990; Reznick and Bryga 1987; Reznick et al. 1997). Nevertheless, our understanding of guppy life-history evolution is not complete.

In their analysis of age-specific mortality as the mechanism of selection on guppy life histories, Reznick et al. (1996a) found an overall difference in mortality rates between *Crenicichla* and *Rivulus* locales, but no difference in size-specific mortality. Classic demographic theory predicts that in density-independent populations or in populations where density-dependent regulation affects all ages equally, a uniform change in mortality rate will not select for any change in reproductive effort or age at maturity (Gadgil and Bossert 1970; Michod 1979). If size-specific mortality is equated to age-specific mortality, then a specific form of density-dependence must be operating in order for predator-mediated selection to favor the observed changes in life history (Charlesworth 1980).

Moreover, although predation is the dominant factor associated with differences in life-history phenotypes between low- and high-predation sites (Strauss 1990), low- and high-predation sites do differ significantly in factors relating to resource availability (Reznick et al. 2001). What effect does different resource availability have on evolution of life-history traits? Current theory does not yield a general prediction for how changes in resource availability affect the evolution of life-history traits. For example, while Gadgil and Bossert (1970) demonstrated that reduced resource availability would select for a later age at maturity and lower reproductive effort, the opposite change in life history is predicted by Kozłowski and colleagues (Kozłowski and Uchmanski 1987; Kozłowski and Wiegert 1987). The discrepancy between these predictions is due to the use of a different fitness criteria and different assumed relationships between resource availability and age-specific survival and fecundity.

Furthermore, current life-history models focus on *either* reproductive effort/age at maturity or offspring size. However, in the guppy system these traits are strongly correlated. As part of my dissertation work I have been evaluating adaptive hypotheses for the evolution of offspring size. Offspring size varies between populations as well as plastically with populations in response to food availability (Reznick and Yang 1993). The two adaptive hypotheses that I have been evaluating are (1) size-limited predation by *Rivulus* and (2) size-dependent competitive ability. To assess the importance of offspring size differences, I would like to incorporate the results I have on newborn and juvenile growth and survival to assess the effects on the entire life history. Additionally, most offspring-size theory starts with the assumption that reproductive effort is fixed; although, empirical evidence suggests that reproductive effort is more variable than offspring size (Stearns, 1992, p. 174). Only one theoretical study (Winkler and Wallin 1987) specifically examines the interplay between reproductive effort and effort per offspring. They conclude that as the optimal effort per offspring increases, the optimal total effort should decrease. Thus, selection of offspring size could constrain evolution of reproductive effort. Conversely, offspring size may be suboptimal if costs of reproduction are such that reproductive effort faces the higher selective pressure.

Research Questions

I would like to examine the evolutionary interplay of offspring size and reproductive effort in the context of the guppy system. Specifically, I would like to address how three decisions a female guppy must make affect her fitness. In every reproductive cycle, a female guppy must decide (1) how long to forage before fertilizing her litter, (2) how much of her surplus energy to put into her litter, and (3) how to partition that energy among offspring in her litter. These decisions can also be thought of as (1) interbrood interval, (2) reproductive effort, and (3) offspring size. I will explore how different patterns of resource availability and mortality affect the fitness consequences of these decisions.

Methods and Work Plan

To start I will examine the fitness consequences of having a fixed set of life-history decisions. In this oversimplified model, interbrood interval, reproductive effort and offspring size decisions will remain fixed throughout all reproductive cycles. In addition, to assess the fitness of these three decision variables, I will have to include a fourth, age at first reproduction. To find the best set of fixed life-history decisions, I will use numerical techniques to determine the combination(s) that maximize(s) lifetime reproductive success (R_0) and the intrinsic rate of growth (r). I will repeat this exercise with different patterns of size-specific mortality and resource availability. This fixed model will provide a good baseline for comparison with the more complex models that allow flexibility in life-history decisions.

I have used a dynamic optimization approach as outlined by Mangel and Clark (1988) and McNamara (1991; 1993; McNamara and Houston 1996) to develop a model assessing the optimality of reproductive effort and offspring size decisions. My plan for this summer is to revise and expand this model to include interbrood interval using the continuous-time algorithm developed by ADN. The dynamic optimization approach allows each of the three decisions to change at any reproductive cycle. Moreover, it allows for females of different sizes to make different decisions. My goal is to examine how life-history patterns will evolve in response to different mortality and resource availability regimes. This approach will not only allow me to address whether life-history patterns we see across populations of guppies are adaptive, but it can also address scenarios in which plasticity may be advantageous.

The final issue I would like to address is under what conditions density and frequency dependence can affect the fitness of life-history decisions in this system. When density and frequency dependence are introduced into a system, fitness measures like R_0 and r may be misleading and a more robust measure is the invasibility criterion (Metz et al. 1992; Mylius and Diekmann 1995). To this end, I hope to explore how favored life-history decisions change when feedbacks on population size, population structure, resource availability and predation risk are included.

Relevance and Link to ADN's Research Plan

The proposed research will examine how life-history decisions will evolve in response to changes in the environment. From an ecological perspective, accurately predicting changes in life-history traits will allow for better assessment of population growth and viability. From an evolutionary outlook, life-history traits are closely linked to fitness and thus provide the best traits for studying adaptive evolution in action. The proposed research aims to understand the evolution of life-history traits in a fish species that is well studied. By using a well-studied species, the effectiveness of our modeling can be assessed by comparison to empirical data. Furthermore the environmental changes this work addresses, mortality and resource availability, are general and relevant to many anthropogenic disturbances. Thus the goals of the proposed research are closely allied with ADN's interest in Fisheries Management and Evolutionary Conservation Biology.

Expected Output and Publications

The proposed research is expected to result in one chapter of my Ph.D. dissertation. This chapter will be submitted for publication as a jointly-authored paper early in 2002.

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