Demographic Consequences of a Changing Environment on a Population of Trinidadian Guppies (*Poecilia reticulata*)

A thesis submitted for the degree of Masters of Science by Research

by

Lara Veylit



University of Oxford

Wolfson College

Trinity Term 2016

Supervisors: Prof. Tim Coulson, Dr. Ronald Bassar

Thesis Abstract

Demographic Consequences of a Changing Environment on a Population of Trinidadian Guppies (*Poecilia reticulata*) - a MSc by Research Thesis by Lara Veylit

Wolfson College, University of Oxford, Michaelmas Term 2016

Ecologists are interested in the complex relationships between populations and their environment. Feedbacks from ecological interactions can change the biotic and abiotic landscape, impacting numerous aspects of a population. Selective pressures on phenotypic traits from processes such as predation and intraspecific competition can change the structure of populations. Structured models can be used to predict how individual level processes can determine population level responses and build an overall understanding of population dynamics. When these models are structured by fitness related phenotypic traits, they can simultaneously be used to provide insights into phenotypic change.

In this thesis, I explore ecological drivers of the population and body size dynamics of Trinidadian guppies (*Poecilia reticulata*) following a change in predation environment. I used individual based data to explore how the life history of individuals across size classes is determined by population density and size-dynamics in a varying environment. I (i) used a modelling approach to determine how much female body size, population density, and the interaction between body size and density explain the temporal variation in demographic rates of individuals (ii) parameterized and analysed a density-dependent Integral Projection Model to make predictions about population dynamics. This thesis contributes to our understanding of the factors that determine phenotypic trait dynamics and population demography in a seasonally fluctuating environment. Understanding how populations respond to environmental variation over the long term has important implications as anthropogenic forces rapidly disrupt seasonal dynamics, with serious consequences for populations.

Acknowledgements

I am very grateful to have two incredibly amazing advisors that have given me so many opportunities. Tim Coulson and Ron Bassar not only helped me improve my writing and develop my understanding of quantitative methods, but provided me with continual support and guidance in my life. I feel very lucky to have both of their support. Secondly, the E2D team is not just a collaborative and smart group of people, they are my dear friends. I would like to especially thank Erik Sandvig, Rocío Pozo, Jack Massey, Severin Dreßen, Jacques Deere, Sarah Cubaynes, Jeremy Cusack, Josie Mahony, Marc Brouard, Susanne Vogel, and Leejiah Dorward. I would also like to thank David Morgan for introducing me to Tim-I never thought your recommendation would change my life so much. I would also like to thank AmeriCorps and the National Science Foundation for providing me with much appreciated funding for my time in Oxford and Trinidad respectively.

I am thoroughly indebted to Professor David Reznick for letting me use such a robust dataset for my thesis and hiring me to work in Trinidad. Thank you for letting me be part of this fabulous project. When I was in Trinidad, I learned so much during my three months splashing in streams with the gupsters. So thank you to all the lovely people I met and worked with. There is a whole team of people at the University of California, Riverside I have never met, but I am very thankful for their work. In Oxford, I saw how many hours Marc Brouard worked on the database, whose work I certainly benefitted from.

My family has been forever available and supportive of my crazy plans from going to Trinidad to doing a Masters at Oxford. I love you Mom, Dad, and Chloé. To all the other mad Veylits who fed and housed me countless times: I would not be in Oxford without you. The support of the people around me both at home and in the department has made my time at Oxford so much more rewarding and fun. At home I have had the compassionate Martin Cusack to share adventures and breakfast with. I feel very lucky to have spent the last year with him on Gipsy Lane. Lastly, Emily Simmonds is my ridiculously patient colleague, my caring flatmate, and the best friend anyone could ever hope for. So, thank you Em. I could not have done it without you.

A Note on Relative Contributions

The guppy mark recapture project is an international collaboration between researchers from the University of California, Riverside (UCR) and the University of Oxford. Interns hired by UCR conduct the mark-recapture study each month in the focal streams located on the island of Trinidad. Morphological data is recorded both by interns in Trinidad and technicians at UCR. I conducted field work in Trinidad as part of the intern team for three months (March-June 2015) to develop an understanding of the study system. Subsequently, I completed all analysis and writing between Michaelmas Term 2015 and Trinity Term 2016.

Contents

Thesis Abstract **i**

Acknowledgements **ii**

A Note on Relative Contributions **iii**

Chapter 1: General Introduction **1**

Chapter 2: Analysing temporally varying life-history characteristics **9**

Chapter 3: Predicting population-level responses to environmental change across population densities **27**

Chapter 4: General Discussion **41**

References **45**

Chapter 1: General Introduction

1.1 How do populations respond to change?

Phenotypic traits are not solely determined by an organism's genotype but also by interactions between the genotype and the environment (Agrawal et al. 2001, Lande 1994). When environmental change occurs, individuals can respond by expressing a specific phenotype that alters survival and reproduction within the new environment (Via et al. 1985). This plasticity is adaptive if it increases survival and reproductive rates, or non-adaptive otherwise (Ghalambor et al. 2007, Ghalambor et al. 2015, Meyers et al. 2002). Studies on the yellow-bellied marmot (Ozgul et al. 2010), bighorn sheep (Traill et al. 2014), and North American wolves (Coulson et al. 2011) have demonstrated how plastic body size can be in populations of free-living organisms that experience environmental change. Empirical studies such as these can be used to determine how populations respond to environmental change.

There are a number of processes that determine how a population can respond to their environment. Seasonal environmental changes often determine resource availability and may play a crucial role in in the demography of many populations (Letcher et al. 2002). The growth and development of individuals is determined by both past and present patterns in resource availability. The past environment has effects on the current fitness of individuals, so resource limitations on young individuals may have persistent effects into adulthood (Mousseau et al. 1998, Benton et al. 2001). Resource availability may alter life-histories as growth rates and reproductive capacity are dependent on past and current food availability as well as an individual's ability to compete for resources. In tropical regions characterized by wet and dry periods, seasonality plays a vital role in determining the life-history strategy of organisms (Winemiller et al. 1992, Janzen 1967). For example, growth and reproduction is seasonal for many tropical fish species. This is most likely due to rainfall strongly influencing food availability (Winemiller et al. 1989). Extreme climatic events may also influence the distribution of phenotypes. Finches in the Galapagos provide an example of how large scale events may change selective pressures acting on phenotypic traits (Grant et al. 1993). A survival advantage exists for finches with beak sizes that match available seed types. Increases in El Niño events with associated effects on plant communities influence the availability of different seed types and therefore an individual's ability to survive and reproduce. Finches with beak sizes that match seed types available following El Niño events are selected for during this period, even if this beak size would be disadvantageous during normal years. The Galapagos finches

therefore provide an important example of the interconnected relationship between resource availability, environmental variation and the dynamics of phenotypic traits.

Population density is an important factor determining how individuals will respond to resource availability. Population density may have positive or negative effects on the population growth rate and other measures of fitness. Many models focus on negative density-dependence resulting from competition for resources (Hassell 1975). 'Scramble' and 'contest' are descriptions of types of intraspecific competition. In scramble competition, resources are equally partitioned between members of the same species. When resources are limited and insufficient to support all individuals within the population, there is a large amount of mortality. Contest competition describes a scenario where successful members of a species acquire sufficient resources, and unsuccessful animals do not (Varley et al. 1973). However, population growth may not just be negatively affected by increases in population density (Courchamp et al. 1999). Warner Allee proposed the theory of inverse density dependence, when 'undercrowding, as well as overcrowding may be limiting' (Allee 1949). Antipredatory behaviors such as schooling in fish demonstrate the Allee effect as this behavior is dependent on the population reaching a certain threshold (Sæther et al. 1996, Clark 1974). Below this density threshold, fish are more likely to be predated; above the threshold, fish are more likely to survive. The ecological success of individuals is therefore connected to the population density in a number of ways which vary with both the study system and environmental condition.

The body size of an individual is an important phenotypic trait directly related to an individual's ability to compete for resources and successfully survive and reproduce. Intraspecific and interspecific competition have size-dependent effects on mortality. For example, predation risk and environmental stress are two size-dependent drivers of mortality (Menge et al. 1987). As an individual grows over its lifetime, the resources they exploit change, partially due to their ability to compete for resources against smaller sized individuals (Byström et al. 2003). The niches organisms occupy therefore change as organisms develop (Werner et al. 1984, Wilson 1975). Males often select larger females in promiscuous mating systems (Andersson 1994). This preference makes biological sense, as fecundity increases with body size. Therefore males who mate with larger females are more likely to have more offspring (Metcalf 1986). Therefore, larger, more fecund individuals contribute unequally to the genetic composition of a population. Body size is therefore linked to not just the individual's life history strategy, but their genetic contribution to the population.

1.2 Difficulties and solutions for studying environmental change

Ecologists interested in studying how populations respond to perturbations of their environment face several challenges when seeking systems to study. Robust datasets that capture phenotypic change are relatively rare due to the difficulty and expense of conducting long term capture-mark-recapture studies. For existing datasets, low recapture rates may lead to an underestimation of population densities (Cubaynes et al. 2010). Monitoring individuals and their offspring from birth to death at a high recapture rate is essential to determine accurate survival and gene transmission rates. This has proven either challenging or exceedingly expensive for many species (Wilson et al. 2001). Species with short generation lengths that reproduce several times during their life are favoured in studies aimed at understanding phenotypic change. These fast reproducing species present an opportunity to follow individuals and their progeny through time. Selecting a system that has these advantages makes it easier to construct models that accurately capture how populations respond to their environment.

Models are used to represent facets of complex processes which would otherwise be difficult to understand. For example, predictive ecological models provide a method for capturing how interactions between species and their environment may change. These models can be used to describe biological phenomena and build an understanding of relationships that are not easily determined by observations in the field. One example is the matrix model, which can be used to understand aspects of a system by combining observational data and matrix multiplication (Caswell 2001). Ecological models can be used to describe dynamic systems in ways that are impossible with observational data alone through the use of simulations.

The Integral Projection Model (IPM) is a relatively simple modelling framework popular in ecology. The IPM can be used to make population level predictions based on how an individual's state influences their vital rates (Easterling et al. 2000, Ellner et al. 2006). Population level responses to ecological change have been addressed using IPMs in a number of study systems (Coulson et al. 2011, Plard et al. 2014, Simmonds et al. 2015, Bassar et al. 2016). Long term datasets are used to parameterize an IPM and project population dynamics. Size-dependent competitive ability can be determined by modelling changes in phenotypes across size classes (Childs et al. 2003). The inclusion of body size as a continuous state variable in the IPM makes it possible to compare size-dependent life-history changes that occur in a population. Density-dependence can also be incorporated into models, making

it possible to determine how individuals across a continuous phenotypic trait respond to different population densities. IPMs are used by ecologists to take individual based data and make predictions about populations that can be used to further our understanding of the mechanisms behind ecological change.

The IPM is composed of four fundamental functions describing how a phenotype is associated with (1) survival, (2) growth, (3) reproduction, and (4) inheritance (Easterling et al. 2000). Each of these functions is parameterized using observational data of a continuous character as well as fixed or random independent variables. The IPM is used to project the distribution of the continuous character at time $t + 1$ given its distribution at time t. This is done by discretizing the continuous character and then constructing a matrix for each function. These matrices are then combined using matrix multiplication forming the projection kernel multiplied by the distribution function:

$$N(z', t+1) = \int (G(z'|z,t)S(z,t) + I(z'|z,t)R(z,t))N(z,t)dz \quad (1)$$

where $N(z',t+1)$ gives the expected distribution of the continuous character, I, R, G, and S represent the Inheritance, Recruitment, Growth, and Survival functions, and $N(z,t)$ describes the initial distribution of the continuous character. Sensitivity analysis of density-dependent IPM parameters can be used to determine the role vital rates play on population predictions such as population growth rate and reproductive value at different population densities (Coulson 2012). Comparisons of the contribution of these four life history characteristics can be used to understand the relative contribution of each function to model predictions.

1.3 A brief introduction to the guppy study system

The freshwater guppy (*Poecilia reticulata*) is a small, widely distributed tropical fish and a popular study species in ecology. The life history of guppies is well studied and presents opportunities to study ecological interactions. Guppies are *ovoviviparous* livebearers that produce large numbers of offspring during their lifetime (Wourms 1981). Females produce offspring in broods, which can vary in size from a single offspring to more than one hundred (Magurran 2005). Differences in litter sizes can be attributed largely to female body size as well as evolutionary changes in response to predation risk (Reznick et al. 1982, Reznick et al. 1987). Females reproduce continually throughout the year, although

reproductive investment is seasonal (Reznick 1989). Once a female has reached sexual maturity, they may reproduce continuously until death. Male guppies prefer to mate with larger females as female fecundity increases with body size following sexual maturity (Reznick 1983, Dosen et al. 2004). A typical guppy diet is composed mostly of algae, diatoms, and invertebrates (Dussault et al. 1981). Guppies exert a preference for invertebrates as they are more nutritious than benthic algae (Zandonà et al. 2012). At high population densities when they are stressed, guppies are known to cannibalize their young (Thibault et al. 1974). These details about the life history of guppies can be used to understand how the environment affects the population.

The island of Trinidad has been a center for field experimentation using the guppy study system since the 1950s due to the relative ease the system presents for studying ecological processes (Haskins et al. 1951). Streams in the Northern Range Mountains (Figure 1) serve as a natural laboratory for experiments as natural barrier waterfalls separate fish communities (Endler et al. 1995). This system presents a rare opportunity to regularly collect robust individual based life-history data in the field. As females contuinually produce large broods of offspring, changes to the distribution of traits can be followed across generations. Studies have even shown evidence for adaptive evolutionary divergence between populations of guppies (Ghalambor et al. 2015, Reznick et al. 2009). The distinct life histories of guppies reflect different developmental and reproductive strategies in response to their environment (Reznick et al. 2001, Reznick et al. 1987). The guppy system is useful for study as guppies respond to environmental change on a time scale measurable by human researchers.

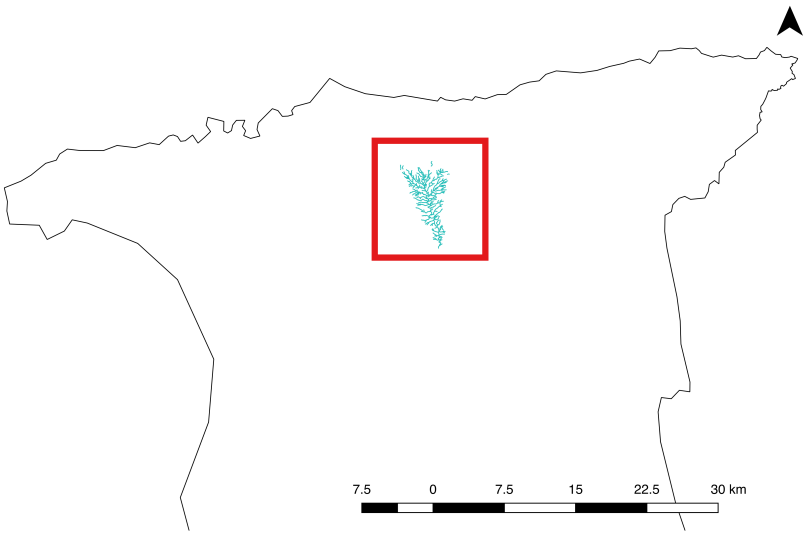


Figure 1 A map of the north of Trinidad. The red rectangle denotes the Guanapo Watershed in the Northern Range Mountains.[1]

Predation regimes characterize the phenotypes guppies express. High Predation (HP) guppies co-occur with a number of piscivores, including the pike cichlid (*Crenicichla spp.*). HP guppies are thought to naturally colonize upstream guppy-free stream reaches infrequently but with cascading ecological effects (Seghers 1973). Colonizing populations in Low Predation (LP) stream reaches are only exposed to a single predator: Hart's killifish (*Rivulus hartii*). *Rivulus* only depredate small body sized guppies as they primarily forage terrestrial invertebrates (Giliam et al. 1993). Guppy populations colonizing reaches characterized by *Rivulus* increase in density rapidly. This has a feedback effect, producing changes in pressures acting on the population and in the life-history of individuals (Bassar et al. 2013).

Seasonality may play a key role in determining guppy life-history strategy. Food availability in Trinidadian streams fluctuates seasonally over wet and dry periods (Auer et al. 2012). Stream

[1]The map layers are available at maps.tt (rivers and base layer). The map was made using Quantum GIS version 2.14.

washouts during periods of heavy rainfall may not just lead to population emigration downstream but also reduced resource availability, thereby altering forage available to remaining members of the population (Zandonà et al. 2011). Decreases in resource availability during high stream flow may also have effects on reproduction. Previous studies have recorded decreases in reproductive allotment and fecundity for guppies during the rainy season (Reznick 1989, Winemiller et al. 1993). Environmental conditions, partially shaped by seasonality, determine which resources are available for the growth and development of guppies throughout their life. Delayed life-history effects can change the fitness of individuals in the late stages of life (Auer et al. 2012). Changes in season, and therefore resource availability, has both direct and indirect effects on the life-history of guppies.

Previous projection models that have been constructed for Trinidadian guppy populations have only captured aspects of population dynamics due to inherent limitations. Previous models of the Trinidadian guppy system use data from mesocosm studies (Bassar et al. 2015, Bassar et al. 2013, El-Sabaawi et al. 2015). These studies have the advantage of semi-controlled conditions, but the drawback of only being conducted during the dry season. The inclusion of the rainy season may have important consequences on ecological models for this system. Collecting continuous data for a long period is informative as lagged and immediate environmental effects can be incorporated into analyses. Although previous models have been used to understand aspects of the guppy study system, many questions that could provide insight into ecological effects of environmental change remain unadressed in this system.

1.4 Using the guppy system to answer ecological questions

I used a long term mark-recapture study of Trinidadian guppies to describe their population dynamics in a changing environment using a modeling approach. In 2008, individuals captured from HP stream reaches were introduced to four LP stream reaches. These four reaches - Lower Lalaja, Upper Lalaja, Caigual, and Taylor – are tributaries of the Guanapo river located in the Northern Range Mountains. Individual guppies from the focal streams are marked and recaptured monthly. A pedigree has been constructed allowing researchers to trace changes to traits across generations. The goal of the mark-recapture project is the creation of a robust individual based capture-mark-recapture dataset beginning with an experimental manipulation that includes seasonal variations and captures phenotypic change. This dataset can be used to parameterize projection models and make predictions

about the population, and therefore the mechanisms that determine how a population can change. The application of modeling techniques to a long term mark-recapture dataset that also includes accurate parental assignment is novel. The experimental origins of the data allows for the study of evolution in relation to ecological change as traits can be mapped to the introduced population and their progeny.

Chapter 2

In Chapter 2, I analyzed life-history characteristics of the guppy population using the long term mark-recapture dataset. I modelled female survival, growth, and recruitment rates as well as the inheritance of maternal body size. I focused on how population density, body size, and their interaction impacted individuals across size classes. I predict different size classes will compete unequally for resources, which will change over the course of the study due to fluctuations in biotic and abiotic seasonal conditions. The linear models I used in this analysis were then used to parameterize my IPM.

Chapter 3

In Chapter 3, I focused on how population density determined population dynamics. I used a density-dependent IPM to project the effects of density on population dynamics. I use the mean reproductive contribution, the population growth rate, and equalibrium population density as measures of the population in different conditions. I expect seasonal resource availability to primarily explain changes in the population parameters over the course of the study. The strength of density effects will therefore depend on the year of the study. These results will give us a novel perspective on how density and size-based competitive ability interact in the guppy study system when environmental fluctuations are included. These model projections can then be used to understand how populations as a whole respond to a variable environment.

Chapter 2: Analysing temporally varying life-history characteristics

Abstract

Environmental change can be either rapid or gradual. It can be challenging to predict how environmental change will impact life-history because the ability of individuals to compete for resources is size- and state-dependent. I investigated how life-history characteristics of Trinidadian guppies (*Poecilia reticulata*) responded to a rapid increase in population density in a seasonal environment. Using a long term mark-recapture dataset, I statistically analysed the survival rate, growth rate, recruitment rate, and inheritance of body size as a function of maternal body size. Temporal variation in vital rates support the conclusion that environmental variability 8plays an important role in determining resource availablity, with effects on the growth and development of individuals. I expected larger females would have higher survival and reproductive rates then their smaller peers. However, large females experienced some of the highest mortality and slower growth rates than smaller guppies. My results provide insight into the how environmental change can impact populations.

Introduction

Variations in resource availability can influence the life-history of species. Effects on life-history linked to environmental variability include the determination of sex ratios (Conover et al. 1987), migration patterns (Holdo et al. 2009), age at sexual maturity, growth rate, and brood size (Winemiller 1993). These effects can be delayed, as growth and reproduction is partially fueled by energy stored from previous environmental conditions (Auer et al. 2012). Compensatory growth is one example of a lagged effect from previous environmental conditions. This occurs when growth rates are accelerated after a period of growth restriction followed by improved conditions. This requires a tradeoff as litter size is negatively affected by accelerated growth (Auer et al. 2010). Unfavorable conditions can also have immediate effects including elevated mortality, depending on the body size and condition of the individual. In this chapter I examine the life-history characteristics of a population during a rapid increase in population density in a seasonally fluctuating environment.

The Trinidadian freshwater guppy (*Poecilia reticulata*) is an ideal system to study the consequences

of environmental change. In mountain streams, guppies live with a number of predators in High Predation (HP) reaches. In contrast, guppies also live in the absence of all predators except Hart's killifish (*Rivulus hartii*) in Low Predation (LP) reaches. High and low predation reaches occur in the same streams, separated by waterfalls that act as a barrier to predators, but not always to guppies. Once HP guppies are transplanted to a LP environment, the population density of guppies increases rapidly, leading to a decline in resources, such as invertebrates, that were once abundant in their environment (Zandonà et al. 2011, Marshall et al. 2012). Resource availability in streams fluctuates seasonally and temporally based on long and short term climatic events. This has immediate and lagged effects on the population, depending on future environmental conditions. During the wet season, large storms can deplete resources when stream flow is high and also change the stream morphology. Stream inhabitants are impacted by the biotic and abiotic results of these changes, although individuals are not affected equally. Guppies can be used to study the effects of changes in population density on individuals of varying body sizes and competitive ability in a seasonal environment.

Data from a mark-recapture study were used with the aim of testing the consequences of a rapid increase in population density. Individually marked HP individuals were transplanted to LP stream reaches in the Northern Mountain Range of Trinidad. Progeny were marked and recaptured monthly over an eight-year long period. Previous studies were limited to a single dry season, making this study unique in its longevity and in the inclusion of seasonality (Gordon et al. 2009, Reznick et al. 2007, Reznick et al. 2009). The effects of an increase in density and environmental variation on demographic rates such as survival, growth, reproduction, and the inheritance of a phenotypic trait can be determined in these natural conditions. Environmental variations may have short or long term effects on the life-history of guppies as conditions experienced in early growth and development can have consequences into adulthood (Monaghan 2008). From mesocosm studies, we know at high densities, guppies compete asymmetrically across body sizes for resources (Bassar et al. 2016). Therefore we analysed the effects of changes in density and the environment as a function of an individual's size.

In this study, we used longitudinal data on females to determine long term consequences of environmental change. Based on short-term studies of guppies, we expect (i) larger females to experience lower mortality than smaller females, and for density to play a significant role in determining survival for smaller individuals in particular (Minto et al. 2008) (ii) density to have a negative effect on growth rates due to resource limitations, with larger fish less affected than smaller individuals by increases in density (Lorenzen et al. 2002) (iii) larger individuals to produce larger offspring, that are

therefore more likely to survive to recruit into the census population (Miller et al 1988). Overall, we expect larger individuals to ecologically outperform smaller individuals (Kooijman 2000). We also expect the rapid change in population density to change selective pressures acting on body size. As seasonal variations will have both biotic and abiotic effects on the stream, we predict these natural environmental flucutations will determine the quality and quantity of food available for individuals.

This study is novel as it follows the invasion of a species in a new environment followed by the natural regulation of the population around carrying capacity. Further, as there is a pedigree that includes the introduced population and their progeny, the variance in reproductive success and the attributes of individuals can be quantified. This is useful as recruitment estimates used in fisheries management are prone to high measurement error (Walters 1981), making this study unique due to its accuracy in associating traits to parents and offspring. This analysis can then be used as part of a comprehensive analysis of evolution occuring in response to ecological change. The statistical determination of patterns in the observational data from these functions will be used to parameterize future models that will be used to make projections about demographic consequences of rapid increases in population density.

Methods

2.1 Experimental design

In 2008, guppies from HP streams were captured and introduced into a LP reach of the Guanapo River constrained by natural and constructed waterfall barriers. The focal stream, Lower Lalaja, is located in the Guanapo River drainage. Following the initial introduction of 50 unique females, individuals were marked and recaptured each month. The first five years of data accounts for between 3-4 generations of females. Guppies were removed from streams using butterfly and dip nets, sexed, and placed in buckets with stream water. Fish were then transported to the field station in stream water treated with antibiotics to control for bacterial infections. Antibiotic treatments were rotated monthly between tetracycline at 0.187 g per 20L and furon at 1.25g per 20L to reduce virulence in bacterial strains.

Guppies were added to plastic tanks containing spring water ranging in size from 0.5L to 2L at approximately 1.5 fish per litre of water once transported back to the lab. Tanks received constant aeration and were subject to ambient temperature and light levels. If guppies were kept in the lab

for longer than two days, their water was changed and re-treated. The guppy's standard length (SL), defined as the distance between the tip of the snout to the posterior end of the hypural plate in the tail, was recorded to the nearest 0.01 mm. Technicians from the University of California, Riverside measured SL using high resolution photos of individuals taken at the field station in Trinidad. Each guppy was given a unique identifying mark if a newly captured individual had a SL greater than 14mm. Fish were anaesthetised during marking with MS-222 using subcutaneous coloured elastomer implants (Northwest Marine Technologies, WA, USA). Marking begin at 14mm as larger fish are easier to mark and less likely to experience mortality from marking. Birth size is around 6-7mm and fish usually reach a markable size within two to three months. Scale samples are collected when fish are first marked to provide a source of DNA for parental assignment. Fish were weighed to the nearest 0.01mg. We did not include age in our model as SL and age are highly correlated in wild guppies ($r^2 = 0.72$) (Reznick et al. 2007). Guppies were re-released in the same pool or riffle in the stream where they were originally captured.

2.2 Statistical analysis

The first five years of data from the long term mark-recapture dataset were used for our statistical analyses. The five years of data represent the first 56 recapture events for the long-term study. All analyses were conducted using R statistical software (version 3.2.2, R Development Core Team 2009). We used data for transplanted females and their progeny from the Lower Lalaja focal stream. As data collection and SL measurements are ongoing, it was not possible to use data from the last three years of data collection. I ran analyses of survival, recruitment, development and inheritance as these are required for the construction of an Integral Projection Model (IPM). SL and population density (total number of individual female guppies captured divided by the total stream benthic area) were included as continuous covariates, year of capture was included as a fixed categorical variable, and the interaction between population density and SL was included as a fixed effect. A squared term was included when a quadratic term improved model fit. Terms that were non-significant were retained as their effects could combine across functions to generate significant patterns at the population level. Mixed models with individual ID and sampling session included as random effects were compared to linear regressions for analysis of growth, recruitment, and inheritance. These mixed models did not explain more variance than standard linear regressions. To maintain simplicity and consistency for IPM

construction, linear regressions rather than mixed models were therefore used for parameterization.

Survival

We estimated the recapture probability of individuals using a closed Cormack-Jolly-Seber model in the program MARK. Because recapture rates were close to unity, results from generalized linear models were nearly identical to those obtained from mark-recapture methods. I consequently used a generalized linear model to analyse the survival of guppies as a function of their somatic size from time *t* to *t+1*. Due to the binary nature of survival data, a binomial error structure and a logit canonical link function were used. Significance of variables included in the model was assessed using Alkaike information criterion (AIC) values (Appendix).

Growth

For the growth analysis, a linear model was used to regress an individual's growth (in mm) given their initial SL at time t. As the residuals were heteroskedastic, comparisons were made to generalized least squares (GLS) models using AIC values. The best GLS model fit did not explain significantly more deviance than the ordinary least squares linear model (Table 1 Appendix). In addition, neither the residuals nor the quantiles of the standardized residuals were significantly improved and the AIC was substantially greater for the GLS model (ΔAIC = 1777.14). Therefore, a linear model with normally distributed errors was used for the growth analysis. AIC values were used to determine which variables to include in the linear model (Appendix).

The model residuals were squared and regressed against SL in a second linear model. The linear relationship for the squared residuals took the form of

$$\sigma^2(z') = a + bz \tag{2}$$

where σ^2 represents the variance squared, z' represents the distribution of standard lengths in the population at time $t + 1$, and $a + bz$ is the linear relationship for the variation of SL's initial distribution in the census population. This model will be used to incorporate variance into the future growth function (Coulson 2012) that will have the form

$$G(z'|z,t) = \frac{1}{\sqrt{2\pi\sigma^2(z)}} e^{\frac{(z'-E(z)^2)}{2\sigma^2(z)})} \tag{3}$$

where *G(z'|z,t)* represents the expected amount an individual grows conditional on their size at time *t*, σ^2 represents the variance squared, *z* represents the distribution of the continuous trait (standard length) at time *t*, *E(z)* is the linear regression of growth and SL, and *z'* represents the distribution of SL in the population at time *t+1*.

Recruitment

A pedigree was used to assign parentage to offspring and determine the number of offspring per mother that recruited into the census population. The pedigree was constructed using genetic information obtained from individuals in the field. Scale samples were used to genotype individuals using 43 loci using microsatellites. The program COLONY was used to determine the maximum likelihood for the pedigree based on inferred parent and sibling relationships (Bryant et al. 2004). Samples with fewer than 20 identifiable microsatellites were not used as parentage could not be accurately determined. An individual was determined to be a recruit into the census population if the individual successfully reached a SL of 14mm, generally defined as the point when female guppies reach sexual maturity. Recruits were assumed to be progeny of transplanted HP guppies as barrier waterfalls restrict immigration to the census population.

A generalized linear model with a quasi-Poisson error distribution was used to determine the relationship between the number of offspring that recruited into the census population based on mother's initial SL. Quasi-likelihood methods were implemented due to overdispersion in the data. The number of offspring recruited was regressed against their mother's size during the time step during which the offspring recruited to the population. Residual degrees of freedom and deviance explained by nested models were used to determine which variables to include in the reduced model.

Inheritance

Parent-offspring trait correlation was determined by regressing offspring size at *t+1* by their mother's size at *t*. The inheritance model is used to determine the phenotypic correlation between mothers and daughters at an arbitrary point of development for the parameterization of the projection model. Trait correlation was determined using a linear model with a normal error distribution. Parental assignment was determined using pedigree data. Data included in the analysis are for females after the introduction. The variance from the linear model was regressed against mother's SL for future model construction following the same form as growth (Equation 3). Significance of variables was determined by comparing AIC values for nested models.

Results

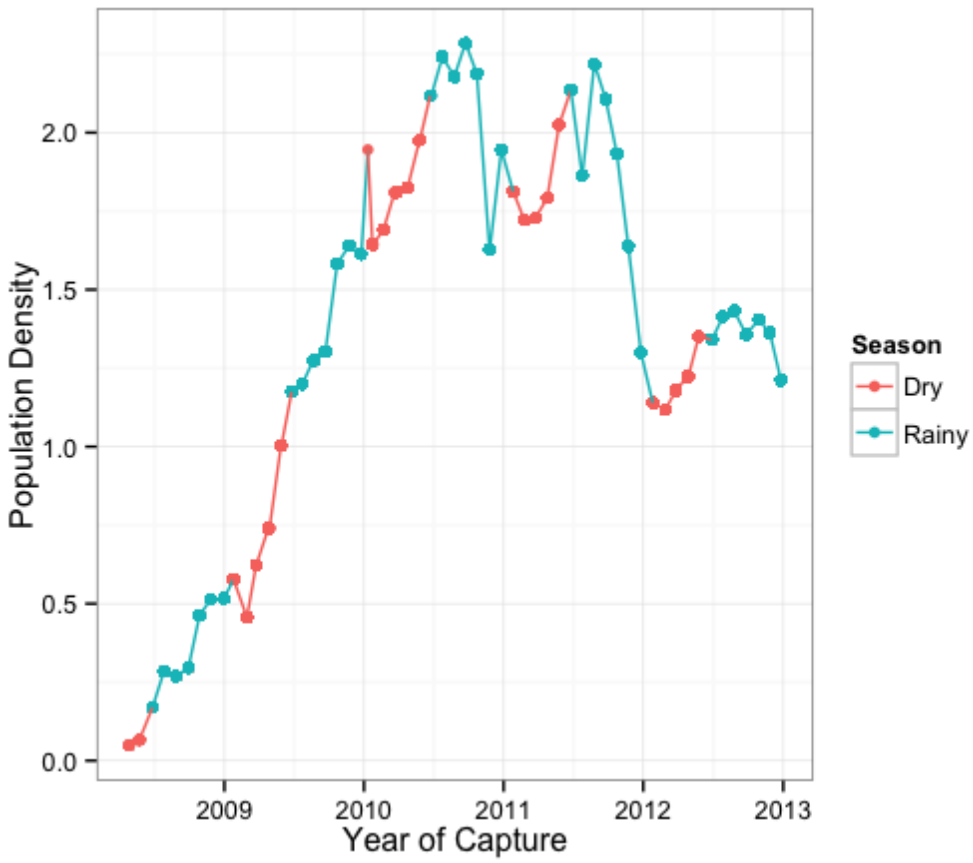


Figure 1 Population density for each month of the mark-recapture study. Population density was estimated as the total number of individual females captured divided by the total stream benthic area. Following the introduction to the LP reach, the population rate increased dramatically then fluctuated based on seasonal and annual variations. The dry season is defined as roughly from January to May, while June to December is defined as the wet season.

3.1 Seasonal effects

Following the initial introduction of guppies to the streams at the beginning of the study, the population density increased dramatically then fluctuated annually with smaller undulations coinciding with seasonal change (Figure 1).

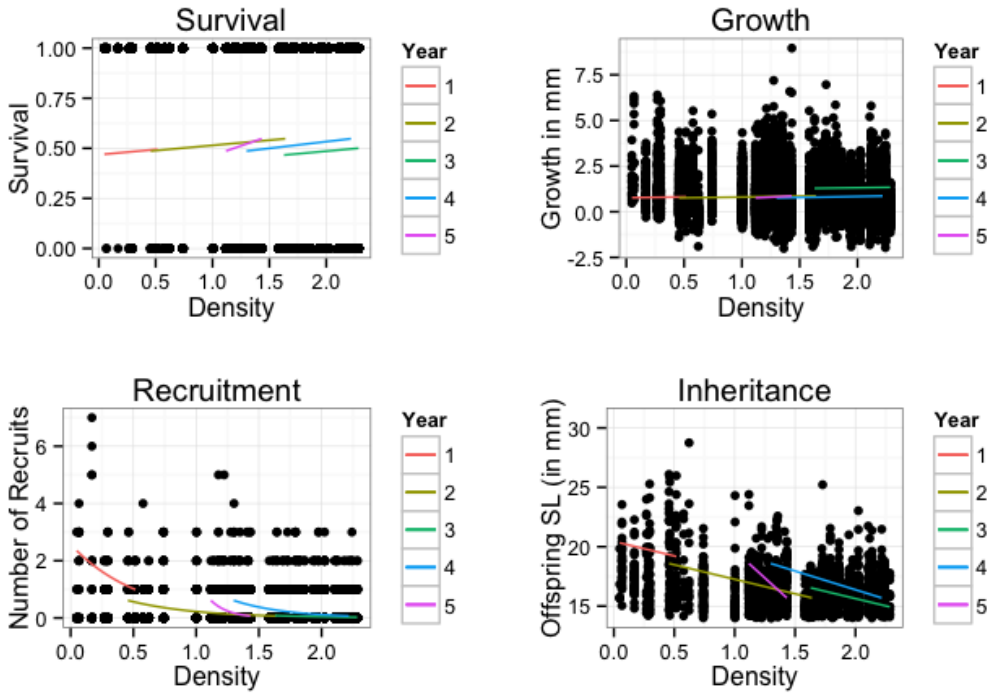


Figure 2 These plots are of the predicted vital rates at the recorded range of densities for each year of the study.

3.2 Survival

The recapture rate from the Cormack-Jolly-Seber model was 91%-sufficiently close to unity that estimates of survival obtained from a generalized linear model would not be substantially biased compared to those obtained from a mark-recapture analysis. The average monthly survival rate was estimated as 84% from the mark-recapture analysis.

Survival of guppies increased with body size ($F_{1,23876} = 65.773$, $P < 0.01$, Appendix Table 2). However, the survival of guppies decreased at the largest size classes. The negative curvature in the data was captured through the inclusion of a quadratic term ($F_{1,23876} = 127.913$, $P < 0.01$), meaning the survival of individuals increased with body size but decreased for larger individuals (Figure 3). Density did not have a significant effect on survival ($F_{1,23876} = 2.635$, $P = 0.105$). Survival decreased over the course of the study ($F_{4,23876} = 286.084$, $P = <0.01,$). The interaction between somatic size and density was not significant ($F_{1,23876} = 0.003$, $P = 0.960$).

3.3 Growth

As female individuals grew, their somatic growth rate decreased ($F_{1,18562} = 3276.6$, $P < 0.01$, Appendix Table 2). The quadratic term captured the positively increasing growth rate of individuals at the largest sizes ($F_{1,18562} = 1512.2$, $P < 0.01$). Growth was significantly negatively affected by increases in population density ($F_{1,18562} = 1137.5$, $P < 0.01$). In the model, year had a positive effect on growth some years, and a nonsignificant negative effect on others ($F_{4,18562} = 276.1$, $P = 0.155$). Larger fish were significantly less impacted by an increase in population density ($F_{1,18562} = 136.4$, $P< 0.01$). From the residuals model, SL was negatively correlated with the growth model ($F_{1,18569} = 696$, $P < 00.1$, Appendix Table 3).

3.4 Recruitment

Larger fish had more offspring that recruited into the census population ($F_{1,24478} = 336.9$, $P < 0.01$, Appendix Table 2). From the general linear model, the number of offspring that survived to recruit to the population as a function of mother's size follows a bell shaped curve as the quadratic term had a slightly negative impact on the slope of the model ($F_{1,24478} = 128.4$, $P< 0.01$). Density had a significantly positive effect on recruitment ($F_{1,24478} = 28.0$, $P < 0.05$), indicating more fish per mother recruited to the population at higher densities. Recruitment decreased over the course of the study ($F_{4,24478} = 4.2$, $P < 0.01$). The interaction between density and SL is negative, indicating larger fish were less affected by an increase in population density than their smaller counterparts ($F_{1,24478} = 62.2$, $P< 0.01$).

3.5 Inheritance

Female offspring of guppies were larger than their mother's size at birth ($F_{1,1897} = 24.2$, $P < 0.01$, Appendix Table 2). Density had a positive effect on offspring size ($F_{1,1897} = 60.8$, $P < 0.01$). Year had a significant effect on offspring size ($F_{4,1897} =19.4$, $P < 0.01$). Offspring size for larger mothers was less impacted by increasing density than for smaller mothers ($F_{1,1897} = 52.3$, $P < 0.01$). The squared residuals from the inheritance model are positively correlated ($F_{1,1903} = 26.7$, $P < 0.01$, Appendix Table 3) with mother's SL.

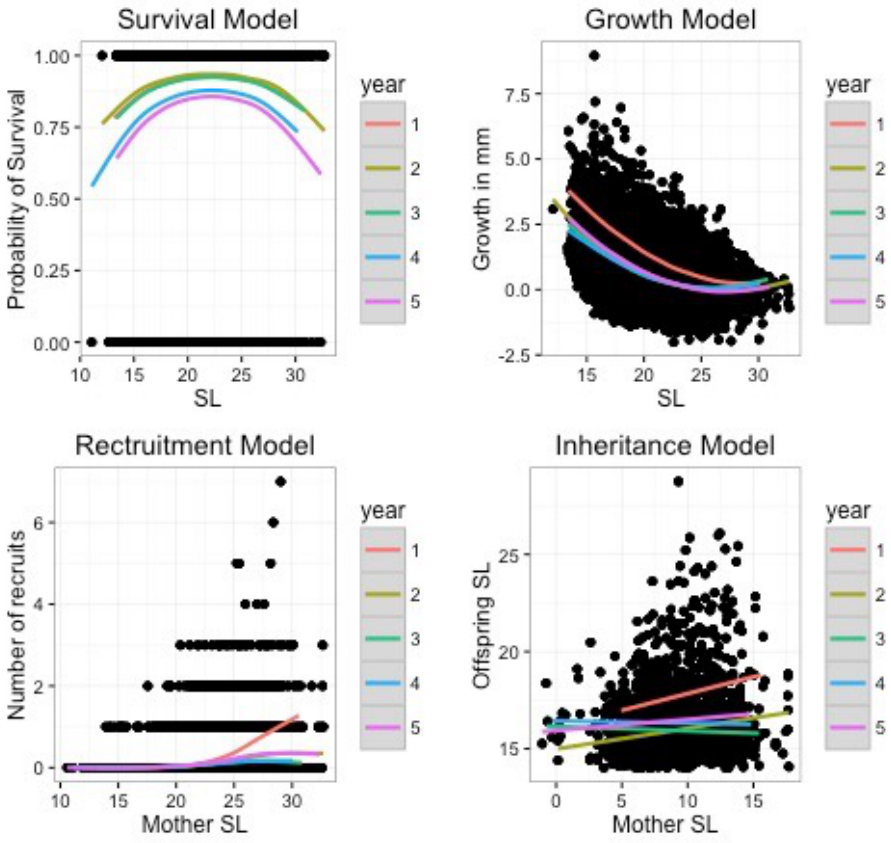


Figure 3 Predicted values of the vital rates from the linear models for each year of the study. Estimates from the models were plotted against fish standard length, which predicts the majority of the variation in the rates. Models include both temporal and ecological variables.

Discussion

My goal was to quantify demographic changes to a population of guppies following an experimentally induced change in selective pressures in a variable environment. The mark-recapture study supports the experimental finding that ecological changes impact the demography of populations. Our results are consistent with directional selection acting on guppy body size, changing the life-history of individuals in the population.

4.1 Survival

The largest and smallest guppies had the highest mortality rates, giving the data its curvilinear form. Mortality of smaller guppies is thought to be driven by intraspecific competition (Meffe et al. 1981). This effect is also expected to be linked to seasonality as during wet periods when benthos is quickly washed downstream, smaller individuals do not have the same fat reserves that larger individuals can rely on when food is scarce. The high mortality rates of the largest individuals was unexpected, though has been found before (Reznick et al. 1996). A possible explanation for high death rates in larger individuals is the correlation between age and body size. Senescence is known to affect guppies (Reznick et al. 2004), possibly due to the accumulation of deleterious mutations (Kirkwood 2002) or through a 'fitness cost' of aging (Abrams 1991). Density was not a significant factor in the survival model, but year effects were significant. This suggests mortality rates were not attributable to density effects. The nonsignificant interaction between body size and population density also seems to support the conclusion that increasing density did not impact mortality significantly. Seasonal and annual differences in resource availibity appear to be the primary driver of mortality across size classes, not density effects.

4.2 Growth

The growth patterns in our model are surprising when considering competitive ability across body sizes. The smallest sized guppies grew at the highest rates before slowing or ceasing to grow, which is expected. However, there are also a number of females 'shrinking', or experiencing negative growth, at the largest body sizes. This is confounding as female guppies grow throughout most of their lifetime (Reznick et al. 1982). This decrease in growth rates may be explained by resource allocation. Large guppies may actually be acquiring sufficient resources, however they may be investing in reproduction rather than growth (Lika et al. 2003). There are also allometric reasons for negative growth due to the definition of standard length being the linear growth, or the mean proportion of growth as length increases. Population density negatively affected growth rates as increasing the number of individuals also increases competition for food. The positive body size and density interaction term indicates larger guppies are abler to compete than smaller sized individuals (see also Bassar et al. 2013). Smaller individuals may grow more quickly as a compensatory response to periods of environmental stress when they were unable to compete for sufficient resources (Metcalf et al. 2001). This compensatory strategy may have tradeoffs later in life, however the speeding up of growth and development could mitigate

effects of poor early growth (Auer et al. 2012). These periods may occur when the population density is high or during wet periods when stream flow is high and individuals rely on fat reserves to survive. These results highlight the differences in life-history strategy for individuals based on their size.

4.3 Recruitment

The model for recruitment mostly captures reproduction for moderately sized individuals as fish that were in the middle of the size distribution were most likely to survive the time step and reproduce. The number of female offspring recruiting to the population may not be representative of the overall number of recruits due to a female sex ratio bias in guppies (Arendt et al. 2014, Rodd et al. 1997, Pettersson et al. 2004). The magnitude of the difference in sex ratios is variable across studies, from 17% to 68% male, indicating the ratio may change annually, depending on environmental conditions. Intraspecific drivers may also play a role in determining the number of offspring that survive to recruit. *Rivulus hartii*, a fish species that co-occurs with guppies in this stream, predates small body sized guppies which may contribute to juvenile mortality (Strauss 1990). Depending on the pressures acting on *Rivulus*, they may consume small guppies more in certain years than others.

Temporal differences in recruitment rates are most likely a product of fluctuations in environmental condition. Density is a strongly significant factor in the recruitment models, indicating reproduction and the survival of offspring is strongly density-regulated. Larger individuals are the most likely to be reproducing, yet larger individuals were less likely to produce offspring that recruited to the census population at high population densities. This may be partially explained by the survival model as the smallest individuals had the highest mortality. Brood size may also explain this trend. Normally larger individuals are more fecund, but larger females may produce smaller brood sizes as a "payback" for accelerated growth rates following periods of environmental stress. Resource limitation during periods high amounts of competition for limited resources could lead to higher competition between offspring, with deleterious effects on later reproduction.

4.3 Inheritance

The relationship between parental and offspring SL is linear, and positively correlated with mother's size. Larger females were therefore more likely to transmit their genetic predisposition to become

larger to their offspring. As larger females also produced more recruits, they contributed unequally to the genetic composition of the population. Larger body sized inviduals were more likely to have larger female offspring at higher densities, but density itself did not affect trait inheritance. Body size inheritance was not significantly explained by density or year effects. The correlation between parental and offspring size is therefore not primarily due to the effects we included in our model.

4.4 Summary

A surprising finding from this analysis was that our results suggest guppies senesce. Previously, it was difficult to detect senescence for wild populations (Kirkwood et al. 2000). With the development of improved mark-recapture models, early-late life trade-offs have been detected in a number of wild populations (Lemaître et al. 2015). The results from the survival and recruitment models suggest senescence is affecting guppies as well. The larger, and therefore older, females experienced lower survival and recruited fewer offspring into the study population. The "shrinkage" of individuals in the growth model may also support the conclusion that guppies senesce. Other long term studies have suggested vertebrates may shrink in response to food availability and energetic stress (Wikelski 2000). These three results may therefore provide evidence of senescence affecting wild guppies.

Larger individuals did not consistently ecologically outperform smaller peers as we expected. This may be due to resource allocation or latent environmental effects. However, larger guppies did produce more recruits than smaller peers and larger mothers had larger children. The genetic contribution of larger females may change the size structure of the population in future generations. This analysis can be used to parameterize a projection model to make statements about the population level effects of density-dynamics.

Appendix

Variables included in Survival, Growth, Recruitment, and Inheritance models

Effects are standard length (SL), the quadratic term or standard length squared (SL^2), Year of the study (Y), and Population Density (D). Models 1-6 were used for analysis of the survival, growth, and recruitment of individuals and models 7-11 were used to analyse the inheritance of maternal SL. Models that were used for our analysis are in bold.

Model	SL	SL^2	D	Y	SLxD
1	X	X	X	X	X
2	X	X	X	X	
3	X	X	X		
4	X	X			
5	X				
6 (NULL)					
7	X		X	X	X
8	X		X	X	
9	X		X		
10	X				
11 (NULL)					

Survival model reduction using AIC values

Model	Residual DF	Residual Dev	AIC	Δ AIC	Weight
1	**23876**	**17197.61**	**17220**	**2.0**	**0.27**
2	23877	17197.61	17210	0	0.73
3	23881	17484.69	17490	279.1	0
4	23883	17486.18	17490	278.6	0
5	23883	17584.4	17580	370.8	0
6 (NULL)	25313	18790	18790.09	1576.5	0

Growth model reduction using AIC values

Model	Residual DF	Residual Dev	AIC	Δ AIC	Weight
1	**18562**	**8874.83**	**39009.73**	**0**	**1**
2	18563	9011.21	39290.94	281.2	0
3	18567	9260.301	39789.31	779.6	0
4	18568	9796.60	40832.83	3203.7	0
5	18569	10553.79	42213.45	3203.7	0
6 (NULL)	18570	15412.249	49243.86	10234.1	0

Recruitment model reduction by comparing deviances

Model	Residual DF	Residual Dev
1	**19146**	**6762.59**
2	19147	6831.35
3	19150	6882.04
4	19151	6984.80
5	19152	7048.84
6 (NULL)	19153	8270.98

Inheritance model reduction using AIC values

Model	Residual DF	Residual Dev	AIC	Δ AIC	Weight
7	**1897**	**5525.90**	**7452.91**	**0**	**1**
8	1898	5578.17	7468.85	15.9	0
9	1935	5900.47	7665.53	212.6	0
10	1936	6346.52	7804.76	351.8	0
11 (NULL)	2924	10692.21	12096.24	4643.3	0

	Generalized Least Squares Model Estimate	Standard Error	*Ordinary Least Squares Model Esti*
SL	-0.855 $***$	0.018	-0.440 $***$
SL^2	0.0144 $***$	0.0004	0.015 $***$
Density	-1.703 $***$	0.082	-1.069 $***$
Year 2	-0.060 $***$	0.036	-0.049 $***$
Year 3	0.260 $***$	0.043	0.373 $***$
Year 4	0.197 $***$	0.042	0.320 $***$
Year 5	-0.070 $***$	0.037	-0.032 $*$
SLxD	0.0515 $***$	0.003	0.058 $***$
(Intercept)	12.964 $***$	0.242	3.557 $***$
Degrees of Freedom	18571		18570 (NULL)
AIC			39010
Residual SE	4022.96		
Residual Deviance			8875
Note : $*$ p $<$ 0.1	$**$ p $<$ 0.05	$**$ p $<$ 0.01	

Table 1 Coefficient estimates for a GLS and linear model fitted for the growth function. The GLS did not significantly differ from the linear model, therefore the simpler linear model was chosen for the analysis.

	Survival	**Growth**	**Recruitment**	**Inheritance**
	logistic	*normal*	*glm: quasipoisson link = log*	*normal*
SL	-0.227 ∗∗∗	-0.440 ∗∗∗	0.970 ∗∗∗	0.223 ∗∗∗
	(0.027)	(0.008)	(0.066)	(0.045)
SL^2	-0.016 ∗∗∗	0.015 ∗∗∗	-0.027 ∗∗∗	
	(0.001)	(0.0004)	(0.003)	
Density	0.195 ∗∗∗	-1.069 ∗∗∗	1.094 ∗∗∗	0.044 (0.323)
	(0.120)	(0.049)	(0.212)	
Year 2	-0.021 ∗∗∗	-0.049 ∗∗∗	-0.589 ∗∗∗	-0.742 (0.210)
	(0.151)	(0.035)	(0.123)	
Year 3	-0.344 ∗∗∗	0.372 ∗∗∗	-0.409 ∗∗∗	0.080 (0.313)
	(0.191)	(0.045)	(0.194)	
Year 4	-0.845 ∗∗∗	0.320 ∗∗∗	-0.612 ∗∗∗	0.339 (0.296)
	(0.183)	(0.043)	(0.184)	
Year 5	-0.916 ∗∗∗	-0.032 ∗∗∗	-0.362 ∗∗∗	-0.139 (0.225)
	(0.150)	(0.035)	(0.138)	
SLxD	0.0006 ∗∗∗	0.058 ∗∗∗	-0.145 ∗∗∗	-0.1245 (0.029)
	(0.012)	(0.003)	(0.020)	
(Intercept)	10.195 ∗∗∗	3.557 ∗∗∗	-7.587 ∗∗∗	15.990 (0.495)
	(0.120)	(0.0489)	(0.443)	
Observations	23885	18571	24487	1905
AIC	17216	39010		
Null Deviance	17627 (23884 DoF)	15412.2 (18570 DoF)	10454.6 (24082 DoF)	
Residual Deviance	17198 (23876 DoF)	8874.8 (18562 DoF)	8577.1 (24074 DoF)	
Note : ∗ p < 0.1	∗∗ p < 0.05	∗∗ p < 0.01		

Table 2 Coefficient estimates for reduced models. SL is centered on 15 mm to obtain more biologically meaningful predictions than an SL of 0 mm.

	Growth Squared Residuals Model	**Inheritance Squared Residuals Model**
SL	-0.071 $***$ (0.003)	-0.324 $***$ (0.061)
(Intercept)	0.912 $***$ (0.019)	4.932 $***$ (0.407)
Observations	18571	1938
Log Likelihood	-29353.160	-6581.524
AIC	58710.320	13167.00
Note : $*$ p $<$ 0.1	$**$ p $<$ 0.05	$**$ p $<$ 0.01

Table 3 Coefficient estimates for the variance of the growth and inheritance models. The squared residuals of the growth and inheritance model were regressed against one and SL was included as a covariate. These results will be incorporated into the parameterization of the functions of a future projection model.

Chapter 3: Predicting population-level responses to environmental change across population densities

Abstract

Environmental change can have serious consequences for the density and structure of populations. However, the long term demographic implications of such changes to population dynamics are often unclear. Here I investigate how density dependence determines population demography following an experimental transplant in a variable environment. I used a long term mark-recapture dataset for a population of Trinidadian guppies (*Poecilia reticulata*) to parameterize an Integral Projection Model. I then estimated population parameters from the model at a range of fixed densities across a range of different environments to explore how the population of guppies responded to different density scenarios. I also conducted sensitivity analysis to evaluate how functions in the model responded to perturbations of model parameters across population densities. The strength of density effects on population descriptors varied as a function of the environment which changed annually. This suggests temporally varying drivers such as climate play a vital role in shaping the abundance of resources available. Resource availability appears to determine the life history of individuals and therefore the population's response to environmental variability. My results contribute to understanding how changes to environmental conditions affect population dynamics.

Introduction

Population density plays a crucial role in determining the structure and dynamics of a population. Predation pressures, seasonal effects, and intraspecific competition for resources can all interact to influence the density of a population. For example, a reduction in predation pressure can lead to an increase in population size in some species, but the magnitude of the increase depends on the environmental condition. In other words, in density-dependent environments, density-independent processes and density-dependence can interact to influence population growth and regulate its size (Gaillard et al. 2000). Past environments, can have long lasting effects on the population (Benton et al. 2001, Lack 1954). Delayed density dependence is one form of maternal effects where an organism's fitness and contribution to the population, is impacted by past conditions. The population density has

short and long term effects on population dynamics, however these effects are not distributed equally in a population.

Structured models provide a useful tool for ecologists to test theories about determinants of stable states in populations where the age or size of individuals determines their life history (Caswell 2001). One kind of structured model, the Integral Projection Model (IPM), provide a simple and powerful way to examine the dynamics of ecological parameters (Easterling et al. 2000). IPMs have been constructed for a range of systems to address questions about density-regulated species (Ellner et al. 2006, Childs et al. 2011, Metcalf et al. 2008). Specific population descriptors can be calculated and compared across densities using IPMs. This allows biologists to determine how a continuous phenotypic trait may be impacted by changes at chosen population densities. The demographic outcomes of changes to the population density can then be predicted.

The Trinidadian freshwater guppy, *Poecilia reticulata*, represents a valuable model organism to study density effects. The strength of the predation pressures guppy populations experience is strongly correlated with population density. Populations of guppies that co-occur with a number of predators generally exist at low densities and populations that co-occur with weak predation pressures exist at high densities (Reznick et al. 2001). Previous experiments have demonstrated changes to body size distribution are not only attributable to size specific differences in mortality rates, but also to density-dynamics (Reznick et al. 1996, Bassar et al. 2013). However, the long term demographic effects of variable availability on population density and size-structure are unknown. By including natural environmental variations into predictions about population dynamics, I can develop a clearer understanding of how populations interact with their environment. As the Trinidadian guppy experiences size-specific differences in life history across densities, this study system can be used to study long-term effects of population density on populations.

Here I examine how density-dynamics impact the demography of a population of Trinidadian guppies in a variable environment. I parameterized a density-dependent IPM using a long term mark-recapture dataset then made predictions about population dynamics at different densities using results described in my previous chapters. I used projected stable size distributions, population growth rates, relative lifetime reproduction contributions, and equilibrium population densities to explore the role of density in determining population demography. I expect environmental conditions will limit population growth through changes to the population size structure (Bassar et al. 2015). This would reflect a dynamic

response to environmental conditions (Rowe et al. 1994, McNamara et al. 1996). To test whether this was the case, I used projected demographic outcomes for different population densities across years of the study. I then perturbed model parameters in the vital rate functions to test predictions about what might happen if these changed. My analysis is unique in its inclusion of seasonal effects, which may have long lasting implications on populations. This has lagged effects on potential population growth. Results from this model can inform future theories on the mechanisms that create differences in populations over time.

Methods

2.1 Study system

Eight years ago, populations of freshwater guppies found in lowland reaches in Trinidad were experimentally introduced to four upstream reaches of naturalstreams. These reaches are tributaries of the Guanapo River located in the Northern Range Mountains. The original High Predation (HP) population co-occurred with a variety of predators including the pike cichlid, *Crenicichla alta*. Low Predation (LP) stream reaches where guppies were transplanted contain a single fish species, *Rivulus hartii*, which only occasionally preys on guppies (Mattingly et al. 1994). Individuals and their offspring have been marked and recaptured monthly since the initial introduction (the mark-recapture protocol was described in detail in Chapter 2).

Several aspects of the guppy system make it ideal for following a population through time. The introduction sites are at high elevations upstream which eliminates immigration from upstream. Meanwhile, barrier waterfalls limit immigration from downstream fish populations. The system is assumed to be closed as migration plays, at most, only a minor role in determining the number of individuals that leave the population. Migration beyond adjacent pools is typically at a rate of less than 5% (Reznick et al. 1996, Bryant et al. 2004). The low number of migrants relative to the high number of individuals in the mark recapture study (3,677 unique females; 1,189 unique mothers) reduces the impact migrants have on my analysis. The high recapture rate (91%; see Chapter 2 for details on this calculation) supports the conclusion that density estimates are fairly accurate. Loss from the population via mortality and emigration are consequently combined and referred to as mortality. The closed nature of this system and high number of individuals in the study make it possible to make predictions about the population.

2.2 Model construction

The first five years of data from the long term mark-recapture study for one stream reach (Lower Lalaja) were used in my data analysis. All analyses were conducted using R statistical software (version 3.2.2, R Development Core Team 2009). Estimates from the linear models for the four fundamental functions of the IPM — survival, growth, recruitment, and inheritance - were used to parameterize the IPM (see Chapter 2). Female standard length (SL), defined as the distance between the tip of the snout to the posterior end of the hypural plate of the tail, measured to the nearest 0.001 mm, was included in models to track body size dynamics. Temporal variations were also included as categorical fixed year effects, density was included as a continuous effect, and the interaction between SL and density was included as a fixed effect. I standardized the inclusion of effects across models to simplify IPM construction.

I used a discrete-time density-dependent deterministic model in my analysis. For simplicity, I did not include males in the model, but focused on females only. In order to describe the population at different densities, I made each of the functions that compose the IPM dependent on the census population density at time *t*. For example, the survival function takes the form

$$S(N) = \frac{1}{e^{-(a+bN_t)}} \tag{4}$$

where *S(N)* represents survival as a function of the population density at time *t*, $a + b$ represents the linear relationship between the vital rate and body size, and N represents the population density at time *t*. The recruitment function similarly is a function of density, taking the form

$$R(N) = e^{(a+bN_t)} \tag{5}$$

as the number of individuals that are projected to recruit to the population at time *t+1* is dependent on the population density at time t (the equation for the growth and inheritance functions is explained in Chapter 2).

An additive offset was included to the inheritance and recruitment functions. The parental assignment rate for the pedigree was 68%, biasing recruitment numbers downwards. This low parental

assignment rate was a product of damaged genetic samples. I adjusted the inheritance and recruitment intercepts to compensate for the biased recruitment and inheritance number. I shifted the intercept for the recruitment function upwards by 1.31 and the intercept for inheritance downwards by 1.99 from the original estimates (the generalized linear models estimated values for the recruitment and inheritance intercepts are -7.81 and 15.99 and the offset intercepts in my model are -6.50 and 14 respectively). Model predictions (including offsets) for the population density for each month were then compared to observed population densities to determine when the visual fit of the model improved.

2.3 Model analysis

Once a population converges to a stable size distribution, the population grows exponentially at a constant rate of λ (Caswell 2007). The population is growing when λ is greater than one, the population is stable when λ is equal to one, and the population is shrinking in size when λ is smaller than one. I compared λ at a variety of chosen densities at each year of the study in order to determine the population's response to different ecological conditions. I plotted the stable size distribution (SSD) at various simulated population densities to determine the effect population size had on the distribution of body sizes at equilibrium. *R0*, the mean lifetime reproductive success, was used to determine the mean contribution of different sized individuals. The point where *R0* and λ are equal to one is the carrying capacity (K) for the population.

I used perturbation analysis to quantify the effects of slightly increasing parameter values on vital rate functions (Caswell 2000). Sensitivities of λ were compared over a range of population densities to gain insight into the effects of a 1% increase in the body size and density slope terms on model predictions. The sensitivity of a parameter is the partial derivative of λ with respect to the perturbed parameter (Ellner et al. 2016). Sensitivities of λ were also compared between years of the study in order to evaluate whether the year of the study impacted the response of λ to perturbations. Year effects would not be expected to make much of a difference to the sensitivity analysis as year was included as a categorical effect. The first and fifth year were chosen as the difference in carrying capacity for these two years was the greatest. The response of parameters in vital rate functions to perturbations of the density and body size terms can be used to understand how components of the model responded to slight upward perturbations.

Results

3.1 Analysing population parameters

Annually changing population parameters reflect a dynamic environment. This is evident from the distributions of the expected mean lifetime reproductive output *R0*, the population growth rate λ, and the carrying capacity K. The difference between *R0* at low and high densities decreased over the course of the study (Figure 1). The difference in reproductive output between population densities was therefore less variable across population densities. The difference between λ at low and high densities increased over the course of the study. The magnitude of the effect of population density therefore increased. Population density had a negative effect on λ as at the highest densities $\lambda < 1$ for the last two years of the study. Both λ and *R0* can be used to trace demographic outcomes of changes to the population density.

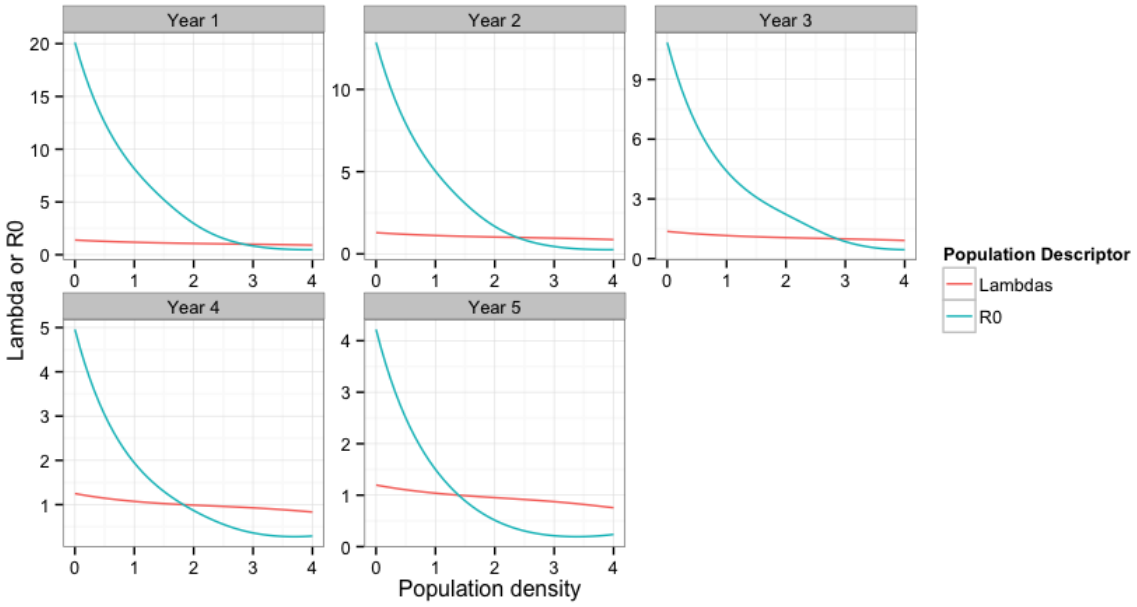


Figure 1 This plot depicts *R0*, or mean lifetime reproductive contribution to the population, and λ, or the population growth rate, for the first five years of the study. The carrying capacity is the point where *R0* and λ are equal to one.

The carrying capacity, or the population density where *R0* and λ are equal to one, changed over the course of the study (Figure 2). Changes to the carrying capacity reflected differences in annual

resource availability. The equilibrium population density fluctuated for the first years of the study then steadily declined ($\Delta\ K = 1.4$). As the environmental condition was different each year of the study, the carrying capacity for the population changed annually.

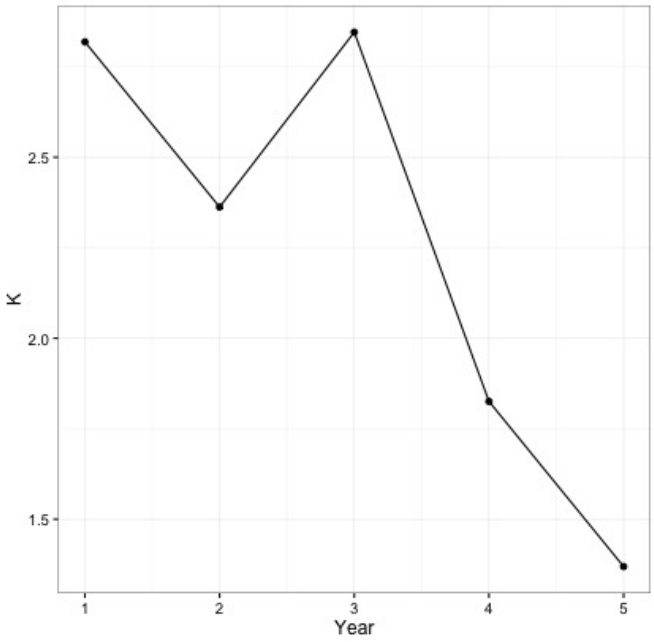


Figure 2 The equilibrium population density, or carrying capacity (K), for the population over the course of the study. The carrying capacity changed each year of the study.

3.2 Stable size distributions

The size-structure of the population was partially determined by the population density. As the population density increased, the cohort of larger sized individuals grew. At higher population densities, the population is growing slowly and the largest cohort is composed of sexually mature individuals (SL $>$ 14 mm) with a smaller but significant cohort of sexually immature individuals (SL $<$ 14 mm). At the average population density recorded over the course of the study, the cohorts were of nearly equal sizes. The number of small and large individuals were therefore roughly similar. At lower population densities, the population is dominated by smaller individuals, with a second distinct cohort of larger sized individuals (Figure 3). The relative sizes of cohorts was shaped by the population density.

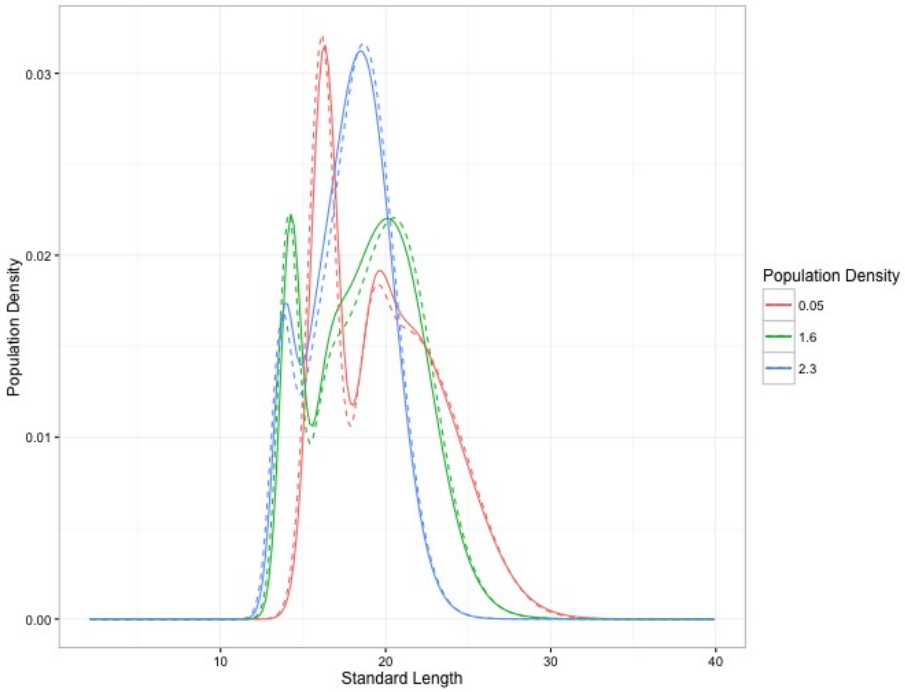


Figure 3 The stable size distribution for the population at the first (solid lines) and fifth (dotted lines) year of the study at different population densities. Densities were chosen based on observed values; 0.05 was the density at introduction, 1.6 was the average density, and 2.3 was the highest recorded population density.

3.3 Sensitivity analysis

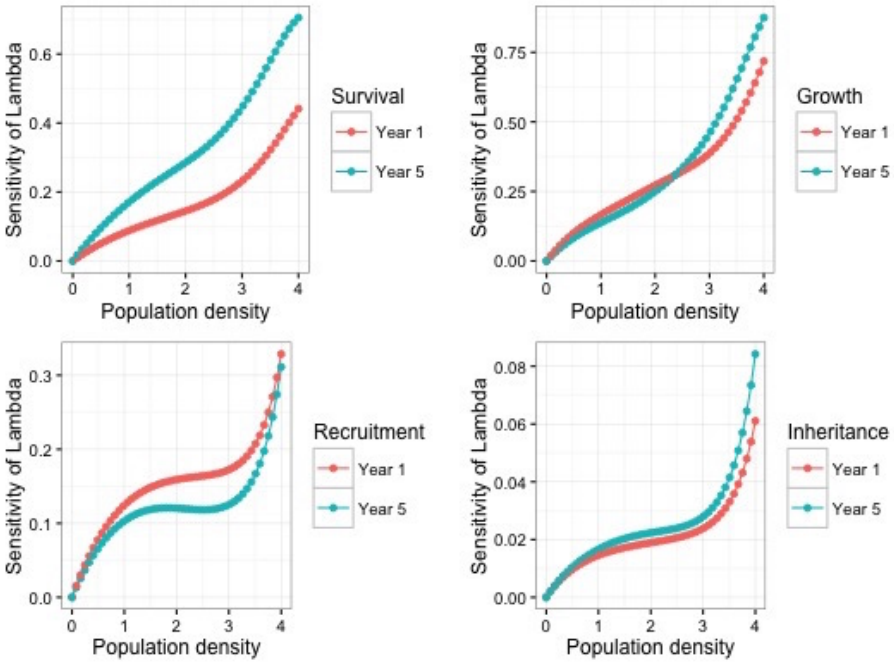


Figure 4 The sensitivity of λ to perturbations of the density parameter in the vital rate functions. Sensitivities were calculated across population densities for the first and fifth year of the study.

Sensitivities of λ to perturbations of the density parameter were similar for the first and fifth year of the study (Figure 4). The survival function showed the largest difference in sensitivies of λ between years, while in the inheritance term the differences between sensitivities across years was smallest. At high densities, the growth function was most sensitive to perturbations, while the inheritance function was least sensitive to perturbations at high densities. At low densities, the sensitivity of λ in the recruitment function changed at the highest rate.

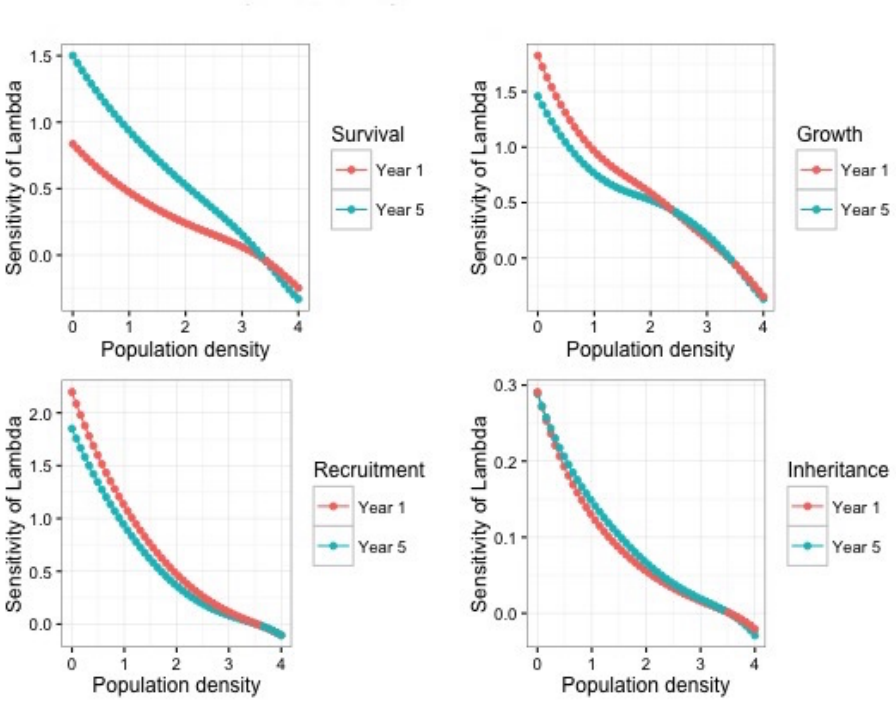


Figure 5 The sensitivity of λ to perturbations of the body size parameter in the vital rate functions was evaluated over a range of population densities. Sensitivities were evaluated at the first and fifth year of the study.

The sensitivity of λ when the body size slope term was perturbed was similar for the first and fifth years of the study (Figure 5). The differences between years was greatest in the survival function at low densities. As density increased, the differences between years decreased. The recruitment function played the greatest role in determining the population's response to perturbations of the body size effect at low densities. Perturbations of the body size slope parameter has the most negative effect on the sensitivity of λ in the growth function at high densities. Perturbations of the body size slope term in the model had a variable effect across years and functions.

Discussion

4.1 Interannual variations in population parameters

The distribution of λ and *R0* values over population densities changed each year of the study. Temporal variability for population parameters are likely not only due to density effects, but also to fluctuations in the biotic and abiotic landscape. The population is most likely responding to annually varying resource availability rather than directly to population density. From the sensitivity analysis it became clear the relative effects of perturbing parameters at different densities varied across years of the study. Annual differences to the environment had population-level consequences.

The changes in population parameters may in fact be a lagged response to resource availability during previous years. Resource availability has long and short term effects on populations (Auer et al. 2012, Monaghan 2008). Individuals respond to changes in resource availability through changes in life history strategy. Tradeoffs in development and reproduction affects individuals even after the environmental condition has improved (Metcalfe et al. 2001). The life-history strategy of individuals is therefore influenced by not only available resources, but past conditions. My results show past conditions may have lagged effects on the guppy population. Perturbations to the density term show the growth of individuals are most affected by change at high densities. As density increases and competition for resources increases, the growth and development of individuals is most affected. Perturbations of the body size slope parameter in the model suggest changes to the effect of body size has the strongest negative effect on the inheritance of maternal body size. The population growth rate is therefore becoming smaller as the body size effect in the inheritance function becomes larger. Individuals and their offspring may face long term consequences of changes to resources availability based on the population density and their relative competitive ability.

Environmental conditions impact different sized individuals unequally. My results reflect a fitness advantage for larger individuals able to compete for food. From the SSD, at higher densities the population is primarily composed of larger fish. This is consistent across years of the study. Larger individuals have higher energy reserves and lower metabolisms, suggesting they would be more likely to survive starvation conditions (Shuter et al. 1990, Schultz et al. 1999). During wet periods in the tropics, stream level and flow increases. Food availability in streams is scarce and individuals must compete for the benthos that is not washed downstream. I would expect larger individuals, which are abler to compete for resources, would be more likely to survive the wet season when food availability was limited. Higher survival by larger individuals during periods of environmental stress would explain the increasing size of the cohort of larger individuals with population density.

4.2 Size-related competitive ability shaping the SSD

Traditional scramble competition models assume individuals are able to compete equally, so an increase in density has an equal effect on all individuals in a population (Hassell 1975). My model suggests this is not true when certain traits, such as body size, allow for an advantage in competitive interactions. Mismatched competitive ability may explain the wider distribution of sizes at higher densities and the smaller cohort of younger guppies in the SSD (Bassar et al. 2016). The larger body sized individuals that were abler to compete for resources would be more likely to survive than smaller individuals. The kind of competition individuals experience also changes with their body size and size of their cohort. I would expect smaller individuals would experience contest competition white larger individuals may experience scramble competition. Smaller individuals are more likely to face mortality if they are unsuccessful at acquiring food as they have lower fat reserves they can rely on than larger individuals. Larger individuals would not have a fitness advantage when resources are readily available, however food availability fluctuates throughout and between years.

The population size-structure is likely determined by a combination of competitive ability and the quality of food available in the environment. Guppies are known omnivores (Grether et al. 2001, Zandonà et al. 2015) that prefer high-quality invertebrates to less nutritious benthos. As different sized individuals inhabit different niches, larger individuals likely are able to rely on invertebrates while smaller individuals may be relegated to exploiting what lower quality food is available. The relative abundance of each kind of resource available would determine the magnitude of competition between individuals. If there is sufficient invertebrates available, small and large fish would be able to grow and develop quickly. However, during periods of resource depletion individuals have to compete.

Density-dependent selection is one example of how an ecological change can have evolutionary consequences. Previous models have demonstrated density-dependent effects impact individuals as a function of their body size (Bassar et al. 2013). This relationship may be a product of asymmetrical competitive ability (Bassar et al. 2016), which in turn impacts life history speed. I would therefore expect the speed of evolutionary change to be impacted by the population density. My results support density-dependent selection acting on this population. Changes in density influenced the size structure of the population, which influences the population growth rate as body size and reproductive success are directly related. Future analyses of the full mark-recapture dataset could be used to determine long term demographic consequences of density-dependent selection.

4.4 Opportunities for future research

My results indicate environmental heterogeneity is interacting with population density to determine population dynamics. The inclusion of variables such as stream morphology and the relative ratio of wet and dry seasons may provide insights into the specific effects of changes to the abiotic environment (Strauss et al. 1990, Palkovacs et al. 2009). Changes to stream morphology and climatic variability influence the relative abundance of invertebrates and benthos, which has cascading effects on the fish that inhabit streams. As temporal fluctuations in resource availability appear to be determining population density, determining what factors constrain resource availability would be useful for projecting the population density in future years. This and future studies can be used to develop an expanded understanding of the relationship between the environment and population dynamics.

Appendix

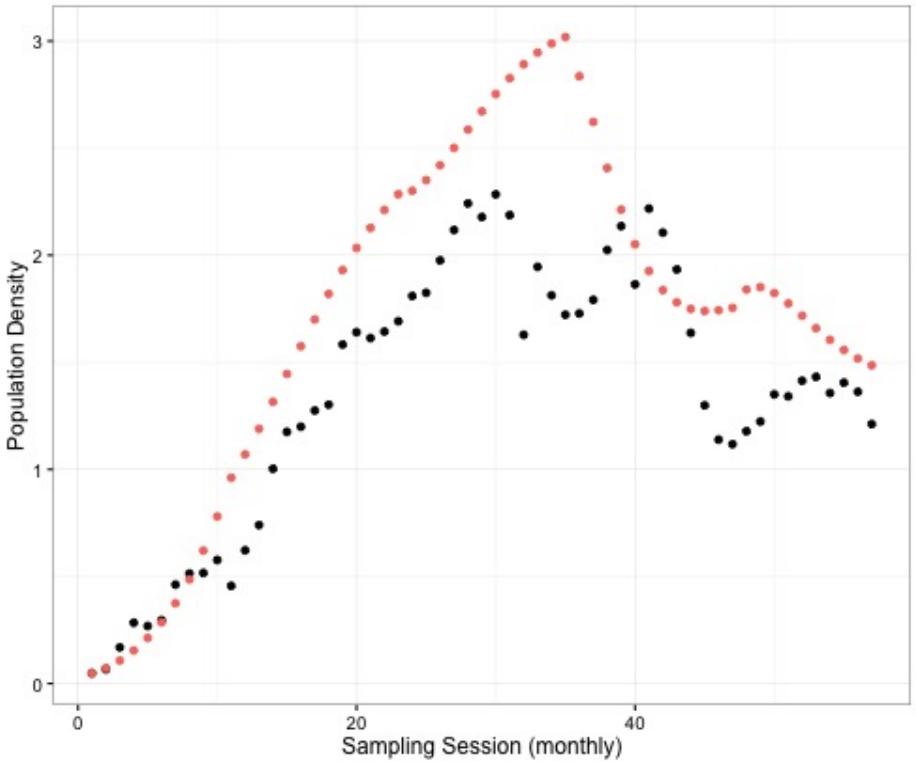


Figure A Observed density values in black and the projected population density from the model in red. Projected population densities were calculated based on the number of individuals at each body size in the matrix model.

Chapter 4: General Discussion

The interactions between populations and their environment are determined by a number of factors including predation pressures, resource availability, and competition. My goals for this thesis were to (i) describe the life-history of a population of *Poecilia reticulata* following a rapid increase in population density in a variable environment (ii) parameterize and analyse an Integral Projection Model to explore the role of population density in determining population dynamics. My results can be used to understand how a population's life history strategy responds to environmental variability. I demonstrate the population density and variable resource availability both are determinants of the life history of individuals. All individuals were not affected equally, however, these indirect effects affect individuals as a function of their body size. Population parameters are also influenced by the indirect effects of changes to the population density and resource availability. λ and K both changed temporally, likely due to changes in the population density and resource availability, leading to variable amounts of competition. In this discussion I will link my results to the broader literature on the individual and population level response to environmental change.

In my IPM, λ is determined by the population density and the environmental condition. An increase in population density will have different effects on the population depending on the population size structure as size and fitness are correlated. In populations dominated by smaller, less fecund individuals, the population will grow more slowly than populations with a dominant cohort of large individuals. Fluctuations in resource availability will affect these two populations very differently. Temporal differences in carrying capacity are partially attributable to the quantity of resources available and the size structure of the population at the previous time step. Seasonal resource availability will determine the quality and quantity of resources individuals are competing for. The population structure will determine the relative success of individuals to compete for these resources, depending on the kind of competition and an individual's competitive ability. The strength of environmental effects on population parameters is therefore partially determined by the population structure, and partially determined by environmental condition.

1.1 Is resource availability creating differences in life histories over the course of the study?

Variations in resource availability has important effects on survival rates. Seasonal mortality during

periods of low resource availability in particular drive interannual differences in mortality (Lahti et al. 1998). Mortality would be expected to be higher during periods of low resource availability such as during the wet season or over winter with the strength of seasonal effects being determined by body size. Mild winters with abundant food availability are correlated with lower mortality rates (Källander 1981). Seasonal mortality does not affect individuals equally, however. In studies of salmon (Xu et al. 2010), juvenile mortality was higher than adult mortality. Results from my analysis are consistent with mortality rates varying across size classes and years. The difference in mortality across years of the study is likely driven by the duration and magnitude of wet and dry periods. Size-dependent mortality shapes the size-structure of populations with long term demographic consequences.

The growth rates of individuals are determined by resource availability as well as predation risk. Size-refuge from predation may drive faster growth rates. However, in environments with many kinds of predators or very low predation risk there is no size-refuge and therefore no advantage for rapid growth (Arendt 1997). In the guppy system, predation risk by *Rivulus* appears to play a minor role in determining growth rates. Juvenile guppies are only likely to be predated upon in years when insufficient terrestrial invertebrates are available for *Rivulus* to forage (Gilliam et al. 1993). Resource availability, not predation risk, appears to be determining the growth of individuals (Mattingly et al. 1994). From my analysis, availability of resources and competitive ability for limited resources is likely to be the main determinant of the growth rate of individuals.

Resource availability influences the reproductive ability of individuals. Compensatory strategies from past resource limitations include changes to sex ratios (Pettersson et al. 2004) and decreased litter sizes from juvenile compensatory growth (Auer et al. 2010). These strategies have lagged effects on the population, as the population density will decrease if litter size is reduced for several years and changes to the sex ratio will change the population demography. Temporal fluctuations in resource availability also impacts the condition of offspring (Rowe et al. 1994). Increases in juvenile mortality rate and reduced population density would be expected to induce the evolution of early maturation and increased juvenile allotment (Gadgil et al. 1970, Abrams et al. 1996). Life history evolution is one consequence of changes to population density and variations in resource availability. The fecundity of individuals in partially determined by current and past resource availability as well as density-effects.

1.2 Can competition explain the differences in individuals across size classes?

The magnitude of competition for limited resources may be determined by resource availability (Briones et al. 1998). Increases in population density leads to resource depletion, with variable consequences depending on an individual's size and state. At high population densities, juvenile mortality was high. This may be attributable to smaller individuals being less competitive for food than larger individuals, leading to juvenile mortality during periods of low resource availability. Sexual selection and fecundity are also determined by competitive ability. Larger females are preferred by males due to their higher fecundity, potentially contributing to smaller females producing fewer recruits (Dosen et al. 2004). This preference may contribute to the inheritance of maternal body size as larger females are more likely to reproduce and transmit her genes. When competitive ability varies across a trait, the fitness of individuals is determined by their competitive ability.

Intraspecific competition plays an important role in determining the demography of populations. Differences in resource choice by individuals can determine if they experience scramble or contest competition (Dammhahn et al. 2010). The habitat use of individuals changes with growth and development, so the level and kind of competition will be a function of an individual's size and state (Werner et al. 1984). As guppies grow, the resources they depend on changes (Zadonà et al. 2011). The resources individuals are competing for therefore changes with their body size. Body size also determines an individual's energetic requirements. As individuals grow, their energetic maintenance requirement increases (Deb et al. 1975). The amount and quality of resources individuals require and therefore must compete for increases. The magnitude of competiton and agression of guppies competing for resources may therefore increase with body size. The differences in effects of population density across size classes could be a product of relative competitive ability, the kind of competition an individual experience as a function of their size and state, and their relative energetic maintenance requirement.

1.3 Could changes to density and resource availability lead to life history evolution?

Indirect effects of food availability and population density can lead to evolutionary change. In *Rivulus*, indirect effects of resource availability and population density may drive trait variations between populations exposed to some juvenile predation and populations exposed to no predation pressures (Walsh et al. 2011). There is a genetic basis for phenotypic differences between populations of *Rivulus* exposed to different levels of predation (Walsh et al. 2010), suggesting indirect effects on the population

are leading to evolutionary change. Adaptation to indirect effects is a source of evolutionary divergence in a number of populations.

In guppies, indirect effects of predation has also been linked to life-history evolution (Reznick et al. 2001). In high predation streams, guppies experience higher levels of resource availability than in sites with low amounts of predation. Guppies exposed to higher levels of resource availability allocate more resources to reproduction, grow faster, and reach larger sizes than those exposed to environments with constrained resources. The predation regime is also a determinant of the population density. The density-effects a population experiences are therefore correlated with the level of predation. As the census population is in a low predation environment, I would expect the population to respond to changes in density and limitations on resources in a manner consistent with previous studies of high predation populations transplanted to low predation environments (Reznick 1982, Reznick et al. 1982). Evolutionary change from the indirect effects of density and resource variability from my results would be expected in future analyses of the complete mark-recapture dataset.

1.4 Final remarks

This thesis contributes to the expanding body of literature combining empirical datasets and demographic models. Studies that draw on both observational data and modelling techniques are useful for testing theories about the life history strategies of populations in dynamic systems. The life history of an individual is determined by abiotic and biotic interactions and density feedbacks, which influence the environmental condition. The effects of environmental changes are not distributed equally across the population. Competitive ability and life history strategy changes with body size. The size structure of a population drives intraspecific competition for limited resources. Over the long term, changes to the life history of populations as a consequence of indirect effects of density and resource availability may induce evolutionary divergence in populations. Environmental change may therefore have both ecological and evolutionary effects over time. My analysis as well as future studies of this system can be used to better predict how populations will respond to environmental variability. This has important implications as the duration and strength of seasonal effects changes rapidly throughout the world.

References

Abrams, P. A. 1991. "The fitness costs of senescence: The evolutionary importance of events in early adult life." *Evolutionary Ecology* 5, 343–360.

Abrams, Peter A, and Locke Rowe. 1996. "The effects of predation on the age and size of maturity of prey." *Evolution* 50 (3): 1052–61.

Agrawal, A. 2001. "Phenotypic plasticity in the interactions and evolution of species." *Science* 294 (5541): 321–26. doi:10.1126/science.1060701.

Allee, W.C. A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. *Principles of Animal Ecology* Saunders, Philadelphia, Pennsylvania, USA.

Andersson, M. 1994. *Sexual Selection.* Princeton, NJ: Princeton University Press.

Arendt, J. D. 1997. "Adaptive intrinsic growth rates : an integration across taxa." *The Quarterly Review of Biology* 72(2), 149–177.

Arendt, Jeffrey D., David N. Reznick, and Andres Lopez-Sepulcre. 2014. "Replicated origin of female-biased adult sex ratio in introduced populations of the Trinidadian Guppy (*Poecilia Reticulata*)." *Evolution* 68 (8): 2343–56. doi:10.1111/evo.12445.

Auer, Sonya K. and Arendt, Jeffrey D. and Chandramouli, Radhika and Reznick, David. 2010. "Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*)." *Ecology Letters* 13 (9): 998–1007.

Auer, Sonya K., Andres Lopez-Sepulcre, Thomas Heatherly, Tyler J. Kohler, Ronald D. Bassar, Steven A. Thomas, David N. Reznick. 2012. "Life histories have a history: Effects of past and present conditions on adult somatic growth rates in wild Trinidadian guppies." *Journal of Animal Ecology* 81, 818–826.

Bassar, Ronald D, Thomas Heatherly I, Michael C Marshall, Steven A Thomas, Alexander S Flecker, and David N Reznick. 2015. "Population size-structure-dependent fitness and ecosystem consequences in Trinidadian guppies." *Journal of Animal Ecology*, 955–68. doi:10.1111/1365-2656.12353.

Bassar, Ronald D, Michael C Marshall, Andrés López-Sepulcre, Eugenia Zandonà, Sonya K Auer, Joseph Travis, Catherine M Pringle, et al. 2010. "Local adaptation in Trinidadian guppies alters

ecosystem processes." *Proceedings of the National Academy of Sciences of the United States of America* 107 (8): 3616–21. doi:10.1073/pnas.0908023107.

Bassar, Ronald D., Dylan Z. Childs, Mark Rees, Shripad D Tuljapurkar, David N. Reznick, and Tim Coulson. 2016. "The effects of asymmetric competition on the life history of Trinidadian guppies." *Ecology Letters*. doi:10.1111/ele.12563.

Bassar, Ronald, Andres Lopez-Sepulcre, David Reznick, and Joseph Travis. 2013. "Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories." *The American Naturalist* 181 (1): 25–38. doi:10.1086/668590.

Bassar, Ronald D and Ferriere, Regis and López-Sepulcre, Andrés and Marshall, Michael C and Travis, Joseph and Pringle, Catherine M and Reznick, David N. 2012. "Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian Guppy (*Poecilia reticulata*)." *The American Naturalist* 180 45 (2): 167–85. doi:10.1086/666611.

Benton, T. G., Ranta, E., Kaitala, V. & Beckerman, A. P. Maternal effects and the stability of population dynamics in noisy environments. *Journal of Animal Ecology* 70, 590–599 (2001).

Briones, O., Montaña, C., & Ezcurra, E. 1998. "Competition intensity as a function of resource availability in a semiarid ecosystem." *Oecologia* 116(3), 365–372. http://doi.org/10.1007/s004420050599

Bryant, Michael J, and David Reznick. 2004. "Comparative studies of senescence in natural populations of guppies." *The American Naturalist* 163 (1): 55–68. doi:10.1086/380650.

Byström, P., Persson, L., Wahlström, E. & Westman, E. Size- and density-dependent habitat use in predators: Consequences for habitat shifts in young fish. *Journal of Animal Ecology* 72, 156–168 (2003).

Haskins, Caryl and Edna Haskins. 1951. "The inheritance of certain color patterns in wild populations of Lebistes reticulatus in Trinidad." *Evolution* 5 (3): 216–25.

Caswel, Hal. 2001. *Matrix Population Models : Construction, Analysis, and Interpretation*. Sinauer Associates.

Caswell, Hal. 1989. "Analysis of life table response experiments I. Decomposition of effects on population growth rate." *Ecological Modelling* 46 (3-4): 221–37.

Charlesworth, B. 1980. *Evolution in Age-Structured Populations*. Cambridge, U.K.: Cambridge University Press.

Childs, D. Z., T. N. Coulson, J. M. Pemberton, T. H. Clutton-Brock, and M. Rees. 2011. "Predicting trait values and measuring selection in complex life histories: Reproductive allocation decisions in Soay sheep." *Ecology Letters* 14 (10): 985–92. doi:10.1111/j.1461-0248.2011.01657.x.

Childs, Dylan Z, Mark Rees, Karen E Rose, Peter J Grubb, and Stephen P Ellner. 2003. "Evolution of complex flowering strategies: an age- and size-structured integral projection model." *Proceedings of the Royal Society-Biological Sciences* 270 (1526): 1829–38. doi:10.1098/rspb.2003.2399.

Clark, C. W. Possible effects of schooling on the dynamics of exploited fish populations. *Journal du Conseil* 36, 7–14 (1974).

Clutton-Brock, T. H. 1984. "Reproductive effort and terminal investment in iteroparous animals." *The American Naturalist* 123, 212–229.

Conover, D. O., & Heins, S. W. (1987). Adaptive variation in environmental and genetic sex determination in a fish. *Nature* 326(6112), 496–498. http://doi.org/10.1038/326496a0

Coulson, Tim. 2012. "Integral projections models, their construction and use in posing hypotheses in ecology." *Oikos* 121 (9): 1337–50. doi:10.1111/j.1600-0706.2012.00035.x.

Coulson, Tim, Daniel R. MacNulty, Daniel R. Stahler, Bridgett VonHoldt, Robert K. Wayne, and Douglas W. Smith. 2011. "Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history." *Science* 334 (6060): 1275–8. doi:10.1126/science.1209441.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. Inverse density dependence and the Alle effect. *Trends in Ecology and Evolution* 14, 405–410 (1999).

Creel, Scott, and David Christianson. 2008. "Relationships between direct predation and risk effects." *Trends in Ecology and Evolution* 23 (4): 194–201. doi:10.1016/j.tree.2007.12.004.

Cubaynes, Sarah, Roger Pradel, Rémi Choquet, Christophe Duchamp, Jean Michel Gaillard, Jean Dominique Lebreton, Eric Marboutin, et al. 2010. "Importance of accounting for detection heterogeneity when estimating abundance the case of French wolves." *Conservation Biology* 24 (2): 621–26. 46 doi:10.1111/j.1523-1739.2009.01431.x.

S. Deb, R. J. Martin & T. V. Hershberger. 1975. "Maintenance requirement and energetic efficiency of lean and obese Zucker rats." *Journal of Nutrition* 106, 191–197.

De Roos, André M., Lennart Persson, and Edward McCauley. 2003. "The influence of size-dependent

life-history traits on the structure and dynamics of populations and communities." *Ecology Letters* 6 (5): 473–87. doi:10.1046/j.1461-0248.2003.00458.x.

Dosen, L. D. & Montgomerie, R. Female size influences mate preferences of male guppies. *Ethology* 110, 245–255 (2004).

Dussault, G. V. and Kramer, D. L. 1981. Food and feeding behaviour of the guppy, *Poecilia reticulata* (*Pisces: Poeciliidae*). *Canadian Journal of Zoology* 59, 684–701.

Easterling, Michael R., Stephen P. Ellner, and Philip M. Dixon. 2000. "Size-specific sensitivity: Applying a new structured population model." *Ecology* 81 (3): 694–708. doi:10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2.

El-Sabaawi, Rana W., Ronald D. Bassar, Chase Rakowski, Michael C. Marshall, Brynne L. Bryan, Steven N. Thomas, Catherine Pringle, David N. Reznick, and Alexander S. Flecker. 2015. "Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom-up factors." *Oikos* 124 (9): 1181–91. doi:10.1111/oik.01769.

Ellner, S P and Rees, M. 2006. "Integral Projection Models for species with complex demography." *The American Naturalist* 167 (3): 410–28. doi:10.1086/499438.

Ellner, SP, S. Z. Childs, and M. Rees. *Data-driven Modelling of Structured Populations.* 2016. Springer.

Endler, John A. 1995. "Multiple-trait coevolution and environmental gradients in guppies." *Trends in Ecology & Evolution* 10 (1): 22–29. doi:10.1016/S0169-5347(00)88956-9.

Fowler, Charles. 1981. "Density dependence as related to life history strategy." *Ecology* 62 (3): 602–10.

Gadgil, M. & Bossert, W. H. 1970. "Life history consequences of natural selection." *The American Naturalist* 104, 1–24.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. & Toigo, C. 2000. "Temporal variation in fitness components and population dynamics of large herbivores." *Annual Review of Ecological Systems* 31, 367–393.

Ghalambor, Cameron K., Kim L. Hoke, Emily W. Ruell, Eva K. Fischer, David N. Reznick, and Kimberly a. Hughes. 2015. "Non-adaptive plasticity potentiates rapid adaptive evolution of gene expression in nature." *Nature* 525 (7569): 372–75. doi:10.1038/nature15256.

Ghalambor, Cameron, J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. "Adaptive versus non-

adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments." 47 *Functional Ecology* 21 (3): 394–407. doi:10.1111/j.1365-2435.2007.01283.x.

Gilliam, J. F., Fraser, D. F. & Alkins-koo, M. 1993. "Structure of a tropical stream fish community : a role for biotic interactions." *Ecology* 74, 1856–1870.

Gordon, S P, D N Reznick, M T Kinnison, M J Bryant, D J Weese, K Rasanen, N P Millar, and A P Hendry. 2009. "Adaptive changes in life history and survival following a new guppy introduction." *The American Naturalist* 174 (1): 34–45. doi:10.1086/599300.

Grant, R. & Grant, P. 1993. "Evolution of Darwin's finches caused by a rare climatic event." *Proceeding of the Roya Society London, B* 251, 111–117 .

Grether, Gregory F., David F. Millie, Michael J. Bryant, David N. Reznick, and Wendy Mayea. 2001. "Rain forest canopy cover, resource availablity, and life history evolution in guppies." *Ecology* 82 (6): 1546–59. doi:10.1890/0012-9658(2001)082%5B1546:RFCCRA%5D2.0.CO;2.

Hassell, B Y M P. 1975. "Density-dependence in single-species populations." Journal of Animal Ecology 44 (1): 283–95. Janzen, Daniel. 1967. "Synchronization of Sexual Reproduction of Trees Within the Dry Season in Central America." *Evolution* 21 (3): 620–37.

Janzen, D. H. 1967. "Why mountain passes are higher in the tropics." *The American Naturalist.* 101, 233–249.

Källander, H. 1981. "The effects of provision of food in winter on a population of the great tit *Parus major* and the blue tit *P. caeruleus*." *Oikos* 12, 244–248.

Kirkwood, T. B. L., & Austad, S. N. 2000. "Why do we age?" *Nature* 408(6809), 233–238. http://doi.org/10.1038/35041682

Kirkwood, T. B. L. 2002. "Evolution of ageing". *Mechanisms of Ageing and Development* 123(7), 737–745. http://doi.org/10.1016/S0047-6374(01)00419-5

Kooijman, S.A.L.M. 2000. *Dynamic Energy and Mass Budgets in Biological Systems.* Cambridge, U.K.: Cambridge University Press.

Lack, David. 1954. *The Natural Regulation of Animal Numbers.* Oxford, U.K. : Claredon Press.

Lahti, K., Orell, M., Rytkönen, S., & Koivula, K. 1998. "Time and food dependence in Willow Tit winter survival." *Ecology* 79(8), 2904–2916. http://doi.org/10.2307/176525

Lande, Russell, and Susan Shannon. 1994. "The Role of Genetic Variation in Adaptation and Population Persistence in a Changing Environment." *Evolution* 50 (1): 434–37.

Lemaître, J.-F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F., & Gaillard, J.-M. 2015. "Early-late life trade-offs and the evolution of ageing in the wild." *Proceedings. Biological Sciences / The Royal Society* 282(1806), 20150209. http://doi.org/10.1098/rspb.2015.0209

Lika, K., & Kooijman, S. A. L. M. 2003. "Life history implications of allocation to growth versus reproduction in dynamic energy budgets." *Bulletin of Mathematical Biology* 65(5), 809–834. http://doi.org/10.1016/S0092-8240(03)00039-9

Lorenzen, K., & Enberg, K. 2002. "Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons." *Proceedings. Biological Sciences / The Royal Society*, 269(1486), 49–54. http://doi.org/10.1098/rspb.2001.1853

Marshall, Michael C., Andrew J. Binderup, Eugenia Zandonà, Sandra Goutte, Ronald D. Bassar, Rana W. El-Sabaawi, Steven A. Thomas, et al. 2012. "Effects of consumer interactions on benthic resources and ecosystem processes in a neotropical stream." *PLoS ONE* 7 (9). doi:10.1371/journal.pone.0045230.

Mattingly, H. T., & Butler, M. J. 1994. "Laboratory predation on the Trinidadian guppy : implications for the size-selective predation hypothesis and guppy life history evolution." *Oikos* 69(1), 54–64.

McNamara, J. M. & Houston, A. I. 1996. "State-dependent life histories." *Nature* 380, 215–221.

Meffe, Gary K, and Robert C Vrijenhoek. 1981. "Starvation stress and intraovarian cannibalism in livebearers (*Atheriniformes : Poeciliidae*)." Copeia 1981 (3): 702–5.

Menge, B. A. & Sutherland, J. P. "Community Regulation : Variation in Disturbance , Competition , and Predation in Relation to Environmental Stress and Recruitment." *The American Naturalist* 130, 730–757 (1987).

Metcalfe, N. B., & Monaghan, P. 2001. "Compensation for a bad start: Grow now, pay later?" *Trends in Ecology and Evolution* 16(5), 254–260. http://doi.org/10.1016/S0169-5347(01)02124-3

Metcalf, C J E, K E Rose, D Z Childs, A W Sheppard, P J Grubb, and M Rees. 2008. "Evolution of flowering decisions in a stochastic, density-dependent environment." *Proceedings of the National Academy of Sciences* 105 (30): 10466–70. doi:10.1073/pnas.0800777105.

Meyers, Lauren Ancel, and James J. Bull. 2002. "Fighting change with change: Adaptive variation in an

uncertain world." *Trends in Ecology and Evolution* 17 (12): 551–57. doi:10.1016/S0169-5347(02)02633-2.

Miller, T. J., Crowder, L. B., Rice, J. a., & Marschall, E. a. 1988. "Larval size and recruitment mechanisms in fishes: Toward a conceptual framework." *Canadian Journal of Fisheries and Aquatic Sciences*, 45(9), 1657–1670. http://doi.org/10.1139/f88-197

Minto, C., Myers, R. a, & Blanchard, W. (2008). "Survival variability and population density in fish populations." *Nature* 452(March), 344–347. http://doi.org/10.1038/nature06605

Monaghan, P. "Early growth conditions, phenotypic development and environmental change." 1635–1645 (2008). *Philosophical Transactions of the Royal Society, B* doi:10.1098/rstb.2007.0011

Mousseau, T. & Fox, C. The adaptive significance of maternal effects. *Trends Ecology and Evolution* 13, 403–407 (1998).

Ozgul, A, D Z Childs, M K Oli, K B Armitage, D T Blumstein, L E Olson, S Tuljapurkar, and T Coulson. 2010. "Coupled dynamics of body mass and population growth in response to environmental change." *Nature* 466 (7305). Nature Publishing Group: 482–U5. doi:10.1038/nature09210.

Palkovacs, Eric P., Michael C. Marshall, Brad A. Lamphere, Benjamin R. Lynch, Dylan J. Weese, Douglas F. Fraser, David N. Reznick, Catherine M. Pringle, and Michael T. Kinnison. 2009. "Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364 (1523): 49 1617–28. doi:10.1098/rstb.2009.0016.

Pettersson, Lars B., Indar W. Ramnarine, S. Anette Becher, Rajindra Mahabir, and Anne E. Magurran. 2004. "Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulata*." *Behavioral Ecology and Sociobiology* 55 (5): 461–68. doi:10.1007/s00265-003-0727-8.

Plard, Floriane and Gaillard, Jean-Michel and Coulson, Tim and Hewison, A. J Mark and Delorme, Daniel and Warnant, Claude and Bonenfant, Christophe. 2014. "Mismatch between birth date and vegetation phenology slows the demography of roe deer." *PLoS Biology* 12 (4): 1–8. doi: 10.1371/journal.pbio.1001828.

Pozo, Rocío A., Susanne Schindler, Sarah Cubaynes, Jeremy J. Cusack, Tim Coulson, and Aurelio F. Malo. 2016. "Modeling the impact of selective harvesting on red deer antlers." *The Journal of Wildlife Management*, 1–12. doi:10.1002/jwmg.21089.

Reznick, D, and M Bryant. 2007. "Comparative long-term mark-recapture studies of guppies (*Poecilia reticulata*): differences among high and low predation localities in growth and survival." *Annales Zoologici Fennici* 44 (2): 152–60.

Reznick, D.A, H. Bryga, and J.A. Endler. 1990. "Experimentally induced life-history evolution in a natural population." *Letters to Nature* 346 (November 2015): 357–59. doi:10.1038/346183a0.

Reznick, David. 1990. "Plasticity in Age and Size at Maturity in Male Guppies (*Poecilia Reticulata*): An Experimental Evaluation of Alternative Models of Development." *Journal of Evolutionary Biology* 3 (3-4): 185–203. doi:10.1046/j.1420-9101.1990.3030185.x.

Reznick, David N, and Robert E Ricklefs. 2009. "Darwin's bridge between microevolution and macroevolution." *Nature* 457 (7231): 837–42. doi:10.1038/nature07894.

Reznick, David N. 1982. "The impact of predation on life history evolution in Trinidadian guppies : 50 genetic basis of observed life history patterns." *Evolution* 36 (6): 1236–50.

Reznick, David N., Cameron K. Ghalambor, and Kevin Crooks. 2008. "Experimental studies of evolution in guppies: A model for understanding the evolutionary consequences of predator removal in natural communities." *Molecular Ecology* 17 (1): 97–107. doi:10.1111/j.1365-294X.2007.03474.x.

Reznick, D N and Butler, M J and Rodd, F H and Ross, P. 1996. "Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection." *Evolution* 50 (4): 1651–60. doi:10.2307/2410901.

Reznick, David. 1983. "The structure of guppy life histories: the tradeoff between growth and reproduction." *Ecology* 64 (4): 862–73. Reznick, David. 1989. "Life-history evolution in guppies : repeatability of field observations and the effects of season on life histories." *Evolution* 43 (6): 1285–97.

Reznick, David and Butler IV, Mark J and Rodd, Helen. 2001. "Life history evolution in guppies. VII. The comparative ecology of high and low predation environments." *The American Naturalist* 157 (July): 126–40. doi:doi:10.1086/318627.

Reznick, D. N. 1982. "The impact of predation on life history evolution in Trinidadian guppies : genetic basis of observed life history patterns. *Evolution* (N. Y). 36, 1236–1250.

Reznick, D. N. & Endler, J. A. 1982. "The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*)." *Evolution* 36, 160–177.

Reznick, David N and Bryga, Heather. 1987. "Life-history evolution in guppies (*Poecilia reticulata*): 1 . phenotypic and genetic changes in an introduction experiment." *Evolution* 41 (6): 1370–85.

Reznick, D., Butler IV, M. J. & Rodd, H. 2001. "Life history evolution in guppies. VII. The comparative ecology of high and low predation environments." *The American Naturalist* 157, 126–140.

Rodd, F H, and D N Reznick. 1997. "Variation in the demography of natural populations of guppies: the importance of predation and life histories." *Ecology* 78 (2): 405–18. doi:10.1890/0012-9658(1997)078[0405:VITDOG]2.0.CO;2.

Roff, Derek A. 1992. *The Evolution of Life Histories : Theory and Analysis.* Chapman & Hall.

Rowe, L., Ludwig, D. & Schluter, D. 1994. "Time, condition, and the seasonal decline of avian clutch size." *The American Naturalist* 143, 698–722.

Sæther, Bernt Erik, Ringsby, T. H. & Røskaft, E. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* 77, 217–226 (1996).

Seghers, Benoni Hendrik. 1973. "Analysis of geographic variation in the antipredator adaptations of the guppy : *Poecilia reticulata*," 1–261. https://circle.ubc.ca/handle/2429/32288.

Schultz, E. T., Conover, D. O., & Ehtisham, A. 1998. "The dead of winter : size-dependent variation and genetic differences in seasonal mortality among Atlantic silverside (*Atherinidae : Menidia menidia*) from different latitudes." *Canadian Journal of Fish and Aquatic Science* 1157, 1149–1157.

Schultz, E. T. & Conover, D. O. 1999, "The allometry of energy reserve depletion : test of a mechanism for size-dependent winter mortality." *Oecologia* 474–483.

Shuter, B. J. & Post, J. R. "Climate, population viability, and the zoogeography of temperate fishes." 1990. *Transactions of the American Fisheries Society* 119, 314–336.

Simmonds, Emily G., and Tim Coulson. 2015. "Analysis of phenotypic change in relation to climatic 51 drivers in a population of Soay sheep Ovis aries." *Oikos* 124 (5): 543–52. doi:10.1111/oik.01727.

Strauss, Richard E. 1990. "Predation and life-history variation in *Poecilia reliculata* (Cyprinodontiformes: *Poeciliidae).*" Environmental Biology of Fishes* 27 (2): 121–30. doi:10.1007/BF00001941.

Traill, Lochran W, Susanne Schindler, and Tim Coulson. 2014. "Demography, not inheritance, drives phenotypic change in hunted bighorn sheep." *Proceedings of the National Academy of Sciences of the United States of America* 111 (36): 13223–8. doi:10.1073/pnas.1407508111.

Thibault, R. E. Genetics of cannibalism in a viviparous fish and its relationship to population density. *Nature* 251, 138–140 (1974).

Travis, Joseph, David Reznick, Ronald D. Bassar, Andres Lopez-Sepulcre, Regis Ferriere, and Tim Coulson. 2014.*Do Eco-Evo Feedbacks Help Us Understand Nature? Answers from Studies of the Trinidadian Guppy.* Vol. 50. doi:10.1016/B978-0-12-801374-8.00001-3.

Varley, G. C., Gradwell, G. R. & Hassell, M. P. (1973). *Insect Population Ecology.* Blackwell, Oxford.

Via, Sara, and Russell Lande. 1985. "Genotype-environment interaction and the evolution of phenotypic plasticity." *Evolution* 39 (3): 505–22. doi:10.2307/2408649.

Walsh, M. R. & Reznick, D. N. 2010. "Influence of the indirect effects of guppies on life-history evolution in *Rivulus hartii*." *Evolution* (N. Y). 64, 1583–1593. Walsh, M. R., Fraser, D. F., Bassar, R. D. & Reznick, D. N. 2011. "The direct and indirect effects of guppies: implications for life-history evolution in *Rivulus hartii*." *Functional Ecology* 25, 227–237

Walters, C. J., & Ludwig, D. 1981. "Effects of measurement errors on the assessment of stock–recruitment relationships." *Canadian Journal of Fisheries and Aquatic Sciences*, 38(6), 704–710. http://doi.org/10.1139/f81-093

Werner, E. E. 1984. "The ontogenetic niche and species interactions in size-structured populations." *Annual Review of Ecology and Systematics* 15, 393–425.

Wikelski, M., & Thom, C. 2000. "Marine iguanas shrink to survive El Niño." *Nature*, 403(January), 37–38. http://doi.org/10.1038/47396

Wilson, D. S. 1975. "The adequacy of body size as a niche difference." *The American Naturalist* 109, 769–784 (1975).

Wilson, Gavin J., and Richard J. Delahay. 2001. "A Review of Methods to Estimate the Abundance of Terrestrial Carnivores Using Field Signs and Observation." *Wildlife Research* 28 (2): 151–64. doi:10.1071/WR00033.

Winemiller, Kirk. 1989. "Patterns of Variation in Life History Among South American Fishes in Seasonal Environments." *Oecologia* 81: 225–41.

Winemiller, K. O., Rose, K. A. & Rose, K. A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation Patterns of Life-History Diversification in North

American Fishes: Implications for Population Regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49, 2196–2218.

Winemiller, Kirk O. 1993. "Seasonality of reproduction by livebearing fishes in tropical rainforest streams." *Oecologia* 95 (March): 266–76. doi:10.2307/4220436.

Wourms, J. P. 1981. "Viviparity: The Maternal-Fetal Relationship in Fishes." *American Zoologist* 515, 473–515.

Zandonà, Eugenia, Sonya K. Auer, Susan S. Kilham, and David N. Reznick. 2015. "Contrasting 52 population and diet influences on gut length of an omnivorous tropical fish, the trinidadian guppy (*Poecilia reticulata*)." *PLoS ONE* 10 (9): 1–18. doi:10.1371/journal.pone.0136079.

Zandonà, Eugenia, Sonya K. Auer, Susan S. Kilham, Jason L. Howard, Andrés López-Sepulcre, Michael P. O'Connor, Ronald D. Bassar, Arthela Osorio, Catherine M. Pringle, and David N. Reznick. 2011. "Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies." *Functional Ecology* 25 (5): 964–73. doi:10.1111/j.1365-2435.2011.01865.x.