Evolution of fitness in the wild

Swanne P. Gordon
Biology Department
McGill University, Montreal

Submitted October, 2005

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of M.Sc.

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-24681-8
Our file Notre référence
ISBN: 978-0-494-24681-8

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Abstract

Environments are changing rapidly, which renders many local populations susceptible to extinction unless they can adapt to these changes. Studies of rapid adaptation commonly document the evolution of individual traits. Overall adaptation however, is a function of fitness itself, rather than the individual traits that contribute to fitness. Although numerous studies provide evidence for the evolution of specific traits on contemporary time scales, no published studies of wild animal populations have examined the evolution of a major fitness component following environmental change. My research demonstrates that an introduced population of guppies (*Poecilia reticulata*) has adapted to its new environment in less than ten years (13-26 generations). This adaptation consists of several phenotypic traits that have changed in the expected direction. Most critically, the introduced population now has higher survival than its ancestral source population when both are tested together in the introduction site. These results show that important components of fitness can evolve rapidly in populations, and that this evolution might influence the persistence of populations in the face of environmental change.

Résumé

L’environnement change rapidement, rendant les populations susceptibles de disparition, à moins qu'elles ne s’adaptent. La capacité d’une population à persister face à des changements environnementaux est déterminée par sa valeur adaptative, qui dépend de plusieurs traits. Alors que plusieurs études ont démontré l’évolution de traits sur de courtes périodes, aucune à ce jour n’a encore examiné l’évolution de la valeur adaptative totale. Ma recherche démontre qu’une population de guppies (*Poecilia reticulata*) introduite s’est adaptée à son nouvel environnement en moins de dix ans. Cette adaptation est le résultat du changement de plusieurs traits phénotypiques dans la direction prédite. Plus précisément, les individus de la population introduite ont maintenant une plus grande chance de survie que les individus de la population d'origine lorsqu'ils sont ensemble au site d’introduction. Ces résultats montrent que des composantes importantes de la valeur adaptative peuvent évoluer rapidement dans des populations qui subissent des changements environnementaux.

Table of Contents

Abstract 2

Résumé 3

Table of Contents 4

Preface 5

Acknowledgements 7

List of Tables 9

List of Figures 10

General Introduction 11

Manuscript: Evolution of Fitness in the Wild 21

- **Abstract** 22
- **Text** 23
- **Methods** 30
- **Literature Cited** 33
- **Table** 37
- **Figures** 38

General Conclusions 42

Appendices 44

- **Appendix 1: Maps of Trinidad** 44
- **Appendix 2. Mark-recapture methods** 46
- **Appendix 3. Damier habitat features** 47
- **Appendix 4. Divergence in specific traits** 49
- **Appendix 5. Program MARK analyses of individually marked adults** 52
- **Appendix 6. McGill University Animal Use Protocol Approval** 56
- **Literature Cited** 57

Preface

This thesis was prepared in accordance with the Faculty of Graduate and Postdoctoral Studies Office's "Thesis Submission Guidelines"

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted, or to be submitted, for publication, or the clearly-duplicated text (not the reprints) of one or more published papers. These texts must conform to the "Guidelines for Thesis Preparation" with respect to font size, line spacing and margin sizes and must be bound together as an integral part of the thesis. (Reprints of published papers can be included in the appendices at the end of the thesis.)

The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with a logical progression from one chapter to the next...As manuscripts for publication are frequently very concise documents, where appropriate, additional material must be provided (e.g., in appendices) in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.

*In general, when co-authored papers are included in a thesis the candidate must have made a substantial contribution to all papers included in the thesis. In addition, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. This statement should appear in a single section entitled "**Contributions of Authors**" as a preface to the thesis."*

My thesis was completed under the guidance and supervision of Dr. Andrew P. Hendry at McGill University. This research was generously supported by the National Science Foundation (DEB 0235605: APH), the Natural Sciences and Engineering Research Council of Canada (Discovery Grant to APH and Postgraduate Scholarship to SPG), the Fonds Québécois de la Recherche sur la Nature et les Technologies (Postgraduate Scholarship to SPG), and McGill University (APH, and SPG).

Contributions of Authors

I attest to the originality of the thesis and to my role as the principal researcher. The thesis, including the manuscript for submission, was written by myself, and I held the major role in all aspects of it. The research was done with the help of other researchers listed in the manuscript as co-authors. Dr. Andrew Hendry, Dr. Michael Kinnison (UMaine), Nathan Millar, Dylan Weese, and Dr. David Reznick (UCR) provided help in the field, funding, and/or aided in the development of comments, and ideas. Dr. Katja Räsänen and Michael Bryant provided help with useful analyses of the data.

Acknowledgements

It is with great pleasure that I acknowledge the many people whose assistance and encouragement have made this thesis possible. In particular, my heartfelt appreciation goes out to my supervisor Dr. Andrew Hendry for his guidance, support, and enthusiasm. Through him I have learned the amount of dedication, effort, and confidence required for successful research. It has truly been a privilege being one of his students. My thanks are also extended to the members of my supervisory committee, Dr. Gregor Fussman and Dr. Andrew Gonzalez, for the guidance and valuable comments they have provided throughout my research.

For the past two years I have been fortunate to work with, and be inspired by many different individuals. In particular I would like to thank Dr. David Reznick, Dr. Edward Maly, and Dr. Michael Kinnison for the knowledge, patience, kindness, and most importantly, the humour that have bestowed upon me. My special thanks go out Dylan Weese, Nathan Millar, Dr. David Reznick, Dr. Michael Kinnison, and Dr. Andrew Hendry, the dedicated crew of people who helped make my field research seasons in Trinidad so successful and extremely fun. Thank you also to the members of the Hendry lab for all their encouragement and warmth.

For helping with specific parts of the thesis I am forever indebted to Amy Schwartz, Jean-Sébastien Moore, Xavier Thibert-Plante, Nathan Millar, Naila Karim, Cristian Correa, and Michael Bryant. For everything, especially her support, guidance, calmness, and for editing earlier versions of this thesis my deepest appreciation goes out to Dr. Katja Räsänen.

Last, but definitely not least, I would like to thank my family and friends for all the love and support that they have shown me. To my immediate family, this work is dedicated to you. Thank you for understanding the late nights, early mornings, and for always being there when I needed help in the lab, a word of encouragement, praise, or a good 'kick in the butt'. It is an understatement to say that I could not have gotten this far in life without you.

To those I have mentioned above, and to those I may have forgotten, this thesis is possible because of you, so with all my heart, thanks.

List of Tables

Manuscript:

Table 1. Results of statistical analysis of the 2004 survival data for adults comparing the Damier high and low predation environments (using local fish)....................................37

Appendices:

Table 1. Comparison of habitat features between high predation and low predation environments in the Damier..47

Table 2. Comparisons of the major features of male colouration between high predation and low predation environments in the Damier..49

Table 3. Comparisons of female life history traits between high predation and low predation environments in the Damier..50

Table 4. Results of Program MARK analyses of survival data in the 2005 mark-recapture transplant experiment...54

List of Figures

Manuscript:

Figure 1. Survival of females and males in high predation and low predation environments in the Damier....39

Figure 2. Life history phenotypes of females from the Damier high-predation and low-predation environments....40

Figure 3. Survival of females, males, and juveniles of each population in high predation and low predation environments in the Damier....41

Appendices:

Appendix 1: Maps of Trinidad showing the Yarra and Damier rivers used in my research....44

General Introduction

Many organisms are currently experiencing environmental change (Reed et al. 2003). If they are to persist as viable populations, they will need to alter their geographic distribution (i.e. migrate to more benign environments), or adapt to the changes. However, as many populations cannot alter their distribution owing to natural environmental barriers (e.g. mountains or waterfalls), or human caused habitat fragmentation, their ability to adapt becomes critical to their persistence. The study of how, and how fast, organisms adapt to new environments can help us better understand how environmental change and evolutionary potential might limit, generate, and sustain biological diversity.

Since Darwin published 'On the Origin of Species' in 1859, many studies have measured the strength of natural selection in the wild, finding that it can sometimes be strong (reviews: Endler 1986; Kingsolver et al. 2001). Accordingly, many populations appear to have undergone contemporary evolution, often called 'rapid' evolution, demonstrating that organisms can rapidly adapt to changing environments (reviews: Hendry and Kinnison 1999; Kinnison and Hendry 2001; Reznick and Ghalambor 2001; Stockwell et al. 2003). Instead of requiring thousands of years, organisms have the potential to adapt in twenty years or less. For example, Losos et al. (1997) showed that over a 10-14 year period certain populations of lizards (*Anolis sagrei*) rapidly diverged from each other following experimental introductions to different islands. In another example, Grant and Grant (1995) studied the adaptation of a population of medium ground finches (*Geospiza fortis*) to environmental changes in their habitat (brought on by a severe drought). The drought caused size-selective mortality as a result of changes in the food supply: larger birds with deeper beaks survived better (i.e. had higher fitness) than smaller birds because they were able to eat the larger and harder seeds that were available after the drought. In yet another classic example, Reznick et al. (1996) introduced guppies (*Poecilia reticulata*) that were adapted to a high predation environment into a novel low predation environment. The introduced populations were then allowed to adapt for approximately 11 years (20-40 generations). Subsequent sampling showed that the introduced guppies had evolved adaptive differences (e.g. increased size and older age at maturity) that paralleled those generally seen in low predation guppies (Reznick et al. 1996). Adaptive evolution of other traits such as colour (Endler 1980; Endler and Houde 1995; Houde 1987; and Houde 1997) and behaviour (Magurran 1998) has also been documented in guppies.

Although numerous studies provide evidence for the contemporary adaptation of specific traits, few studies examine the rate of overall adaptation (i.e. the evolution of fitness). Yet, it is this composite rate that will determine whether or not a population can persist in the face of environmental change. Fitness is perhaps the best single measure of contemporary adaptation (Barker 1963; Travisano et al 1995; McGraw and Caswell 1996), and it is one of the most central concepts in evolutionary biology (Barker 1963; Brommer at al. 2004). However over the past few decades it has been defined in a number of ways (De Jong 1994; McGraw and Caswell 1996). Here, I define fitness as the differential contribution of individuals or genotypes to future generations (Barker 1963), which will be a function of variation in viability and/or reproductive success.

Theory describes the evolution of fitness as a cycle of increase from natural selection and decrease from various degrading forces such as mutation, immigration, or environmental change (Fisher 1958; Burt 1995). This cycle continues until a relative constant mean population fitness is achieved and the best way to quantify this is to measure mean fitness as it changes in populations experiencing the degrading forces.

The few studies that have measured the evolution of fitness have been done so in a laboratory, greenhouse, or other types of controlled setting (e.g., Bennett et al. 1992; Rainey and Travisano 1998). The model systems typically used have been bacteria and *Drosophila* because these organisms are easy to study in the lab due to their small size and short generation times (e.g., Elena and Lenski 1997; Lenski et al. 1991; Travisano et al. 1995; Travisano and Lenski 1996). For example, Lenski et al. (1991) assessed the rate at which fitness changed in *Escherichia coli* populations. Twelve replicate populations were founded from a single bacterial strain (ancestral source) and allowed to evolve for approximately 2000 generations in a novel environment. The authors concluded that mean fitness increased by about 37 % from the ancestral source, and therefore showed that fitness does indeed evolve when organisms experience environmental change. Some studies have also measured the reverse evolution of fitness, revealing the return of adapted organisms to their ancestral phenotypic states (Burch and Chao 1999; Crill et al. 2000; Teotonio et al. 2001, 2002).

The results of these laboratory studies have enriched our understanding of how fitness evolves. However, if we are to understand how fitness evolves in nature we must study adaptation in natural populations. One powerful method for such work is to examine adaptive evolution in organisms introduced to new, but natural, environments. In such experiments, the evolution of fitness can be assayed by comparing the fitness of the introduced population to that of the ancestral source population, when both are tested together in the introduction site. This approach is valid under the assumption that the source population is a good representative of the ancestral population (from where the introduced population were derived). This is the case if the source population has not undergone any major environmental changes, and if the population is large enough to prevent substantial genetic drift. No published studies thus far have explored this method however, because it is difficult to find systems in the wild where it is possible to compare source and derived populations at the same time. Advantages of this method, compared to laboratory studies, include the ability to make predictions based on traits in populations that have already naturally colonized the same environments, and the assurance that the observed evolution is ecologically relevant. An experimental introduction of guppies between neighbouring watersheds in Trinidad performed nine years ago currently provides an outstanding opportunity to study the evolution of fitness in the wild. This is the goal of my thesis.

There are several advantages to studying Trinidadian guppies (*Poecilia reticulata*) in the wild. Guppies in nature have relatively short generation times (110-210 days), small body sizes, and are easily captured and observed. In addition, guppies have shown demonstrable evidence of adaptation to different selective environments (Endler 1980, 1995; Houde 1997; and Reznick and Endler 1982). Specifically, they can be separated into two basic types: high predation and low predation (Endler 1995; Reznick et al. 1996). High predation populations coexist with predatory fishes that have a strong effect on guppy survival, whereas low predation populations are exposed only to weak predators that have little influence on guppy survival (Reznick and Bryga 1987; Reznick et al. 1996; Reznick et al. 1997).

My research focused on two rivers on the Northern Range mountains in Trinidad: the Yarra and the Damier (see map in Appendix 1). In 1996, D. Reznick transplanted guppies from the Yarra to the Damier (which previously lacked guppies) in three controlled introductions. The first two introductions were of low predation Yarra guppies into the high-predation environment in the Damier, but these were unsuccessful, and the fish were extinct within a year (D. Reznick pers. obs.). The third introduction was of high-predation Yarra guppies into the low-predation environment in the Damier. By the following year, guppies had colonized not only the low predation environment, but they had also moved over a barrier waterfall and colonized the high predation environment below it. These guppies have thus been adapting to their new selective environments for about 9 years: i.e. 15-30 generations (depending on the life history characteristics of Damier guppies). This introduction thus gave me the rare opportunity to examine the evolution of fitness by comparing the survival of the ancestral (Yarra) and introduced populations of Yarra fish (hereafter termed Damier fish) when tested together in the introduction (Damier) site.

This thesis examines the adaptive evolution of specific traits and of important components of fitness using three steps. First, I confirm that the high and low predation environments in the Damier do indeed differ in parallel with those in previously studied watersheds. Second, I test for the adaptive divergence of male colour and female life history traits by examining wild-caught individuals from the two Damier environments. Third, I test for the evolution of fitness by comparing the survival of the introduced populations (Damier) to that of the source population (Yarra), when both are tested together in the Damier.

The methods, discussion, and results for each step are compiled in the following manuscript submitted to the journal *Nature*. As manuscripts submitted to certain competitive peer-reviewed journals have to be very concise, I have added various material as appendices at the end of the thesis to provide more information about certain sections of the paper.

Literature Cited

Barker, J. S. F. 1963. The estimation of relative fitness of *Drosophila* populations. II Experimental evaluation of factors affecting fitness. Evolution 17:56-71.

Bennett, A. F., R. E. Lenski, and J. E. Mittler. 1992. Evolutionary adaptation to temperature. I. Fitness responses of *Escherichia coli* to changes in its thermal environment. Evolution 46:16-30

Brommer, J. E., L. Gustafsson, H. Pietiäinen, and J. Merilä. 2004. Single-generation estimates of individual fitness as proxies for long-term genetic contribution. The American Naturalist 163:505-517.

Burch, C. L., and L. Chao. 1999. Evolution by small steps and rugged landscapes in the RNA virus Φ6. Genetics 151:921-927.

Burt, A. 1995. The evolution of fitness. Evolution 49:1-8.

Crill, W. D., H. A. Wichmann, and J. J. Bull. 2000. Evolutionary reversals during viral adaptation to alternating hosts. Genetics 154:27-37.

Darwin, C. 1859. Origin of Species. John Murray. London.

de Jong, G. 1994. The fitness of fitness concepts and the description of natural selection. Quarterly Review of Biology 69:3-29.

Elena, S. F., and R. E. Lenski. 1997. Long-term experimental evolution in *Escherichia coli*. VII. Mechanisms maintaining genetic variability within populations. Evolution 51:1058-1067.

Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata.* Evolution 34:76-91.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, N. J.

Endler, J. A. 1995. Multiple trait coevolution and environmental gradients in guppies. Trends in Ecology and Evolution 10:22-29.

Endler, J. A., and A. E. Houde. 1995. Geographic variation in female preference for male traits in *Poecilia reticulata*. Evolution 49:456-468.

Fisher, R. A. 1958. The genetical theory of natural selection, 2nd ed. Dover, New York.

Grant, P. R., and R. B. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. Evolution 49:241-251.

Hendry, A. P., and M. T. Kinnison. 1999. The pace of modern life: Measuring rates of contemporary microevolution. Evolution 53:1637-1653.

Houde, A. E. 1987. Mate choice based upon naturally occurring color-pattern variation in a guppy population. Evolution 41:1-10.

Houde, A. E. 1997. Sex, color, and mate choice in guppies. Princeton University Press, Princeton, N. J.

Kingsolver, J. G, H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. American Naturalist 157:245-261.

Kinnison, M. T. and A. P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. Genetica 112/113:145-164

Lenski, R. E., M. R. Rose, S. C. Simpson, and S. C. Tadler. 1991. Long-term experimental evolution in *Escherichia coli*. I. Adaptation and divergence during 2,000 generations. American Naturalist 138:1315-1341.

Losos, J. B., K. I. Warheit, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387:70-73.

Magurran, A. E. 1998. Population differentiation without speciation. Phil. Trans. R. Soc. Lond. 353:275-286.

McGraw, J. B., and H. Caswell. 1996. Estimation of individual fitness from life-history data. American Naturalist 147:47-64.

Rainey, P. B., and M. Travisano. 1998. Adaptive radiation in a heterogeneous environment. Nature 394:69-72.

Reed, D. H., E. H. Lowe, D. A. Briscoe, and R. Frankham. 2003. Fitness and adaptation in a novel environment: Effect of inbreeding, prior environment, and lineage. Evolution 57:1822-1828.

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

Reznick, D. N., and H. Bryga. 1987. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. Evolution 41:1370-1385.

Reznick, D. N., M. J. Butler IV, H. F. Rodd, and P. Ross. 1996. Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. Evolution 50:1651-1660.

Reznick, D. N., H. F. Rodd, and M. Cardenas. 1996. Life-history evolution in guppies (*Poecilia reticulata:* Poeciliidae). IV. Parallelism in life-history phenotypes. American Naturalist 147:319-338.

Reznick, D. N., F. H. Shaw, H. F. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934-1937.

Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptation: what do empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112/113:183-198.

Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends in Ecology and Evolution 18:94-101.

Teotonio, H., and M. R. Rose. 2001. Reverse Evolution. Evolution 55:653-660.

Teotonio, H., M. Matos, and M. R. Rose. 2002. Reverse evolution of fitness in *Drosophila melanogaster*. Journal of Evolutionary Biology 15:608-617.

Travisano, M., J. A. Mongold, A. F. Bennett, and R. E. Lenski. 1995. Experimental tests of the roles of adaptation, chance, and history in evolution. Science 267:87-90.

Travisano, M. J., and R. E. Lenski. 1996. Long-term experimental evolution in *Escherichia coli*. IV. Targets of selection and the specificity of adaptation. Genetics 143:15-26.

Manuscript: Evolution of Fitness in the Wild

Swanne P. Gordon[1], David N. Reznick[2], Michael T. Kinnison[3], Michael J. Bryant[2], Katja Räsänen[1], Dylan J. Weese[3], Nathan P. Millar[1] and Andrew P. Hendry[1].

[1]*Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke St. W., Montréal, Québec, Canada, H3A 2K6.* [2] *Department of Biology, University of California, Riverside, CA, U.S.A..* [3] *Department of Biological Sciences, University of Maine, ME, Orono, U.S.A.*

Keywords: Evolution, Adaptation, Fitness, Mark-recapture, Introduced Species, *Poecilia reticulata*

Correspondence:

Swanne Gordon swanne.gordon@mail.mcgill.ca

Redpath Museum, McGill University

859 Sherbrooke Street West

Abstract

Environments are changing rapidly, which renders many local populations susceptible to extinction[1] unless they can adapt to these changes. Whether or not a population is able to persist in the face of environmental change is primarily determined by its overall adaptation (i.e. fitness), a composite function of many individual traits. Although numerous studies provide evidence for the evolution of individual traits on contemporary time scales[2-4], no published studies of wild animal populations have examined the contemporary evolution of fitness. We here demonstrate that an introduced population of guppies (*Poecilia reticulata*) has adapted to its new environment in less than 10 years. This adaptation consisted of several phenotypic traits that have changed in the expected direction. Most critically, the introduced population now has higher survival than its ancestral source population when tested in the introduction site. These results show that important components of fitness can evolve rapidly in populations that experience changing environments.

Text

Theory predicts that selection constantly increases fitness whereas mutations and environmental change constantly decrease fitness, leading to a relatively constant mean population fitness at equilibrium[5,6]. Here we are concerned with a situation where the environment changes dramatically, such as when a population is introduced to a new environment or when the local environment changes abruptly. Both of these scenarios are common in human-disturbed landscapes. When environmental change is too extreme, the reduction in fitness may cause population extinction[7]. Under less dire conditions, fitness should steadily improve through time as selection drives adaptive evolution. This increase in fitness should proceed at a rate approximately equal to the additive genetic variance for fitness[5,6]. But can this process actually be observed in natural populations facing abrupt environmental change?

Previous work on the evolution of fitness components has been conducted in laboratory, greenhouse, or other controlled settings. The model systems typically used are bacteria and *Drosophila* because these organisms are small and have short generation times[8-11]. Although these studies have enriched our understanding of how fitness can evolve, an understanding of how natural populations adapt to environmental change requires studies in nature. One powerful method for doing so is to introduce organisms to new, but natural, environments and then measure associated changes in major fitness components.

We used such an experimental introduction to study the adaptation of wild guppies experiencing a dramatic shift in selection. Natural guppy populations can be divided into two general types, those that experience high levels of predation and those that experience low levels of predation[12,13]. High predation populations are usually found in the downstream portions of rivers, where they coexist with predatory fishes that have a strong effect on guppy demography. Low predation populations, in contrast, are typically found above barrier waterfalls, where they coexist with few predators that rarely prey on guppies[13,14]. This contrast in predation regime has driven the evolution of a broad suite of differences in morphology, behaviour, and life history[12]. For example, high predation males are less colourful than low predation males, presumably because crypsis reduces predation[15]. High predation females mature at an earlier age and have more but smaller offspring than do low predation females[16]. This adaptive divergence between high and low predation guppy populations has proceeded in parallel in many separate watersheds, which provides convenient replication and allows testable predictions regarding evolutionary change.

In prior experimental introductions[15,17,18], guppy populations showed expected patterns of adaptation for specific traits (such as life-history traits) after 4-11 years (6.9-18.1 guppy generations)[17]. The present paper details evolution in a previously unstudied introduction, the first on the north slope of the Northern Range mountains of Trinidad. In 1996, D. Reznick transplanted around 100 guppies from the high predation environment of the Yarra River into the low predation environment of the Damier River, which previously did not contain guppies. Within a year, guppies had become established in the low predation environment and also colonized the high predation environment below a barrier waterfall. By 2004, Damier guppies had been adapting to these environments for 9 years, i.e. 15-30 generations depending on the specific life history characteristics of Damier guppies.

We used this Damier introduction to quantify the evolution of a major fitness component (survival), as well as several specific traits that may influence adaptation. Our first task was to confirm that the low and high predation environments in the Damier differ in mortality rates consistent with the predation dichotomy in previously studied watersheds (i.e., divergent selection was the same as in other studies). Our next task was to examine adaptive divergence between the Damier environments in a set of traits (male colour and female life history) that previous work has shown to respond to divergent selection between high and low predation environments. Our final task was to test for the evolution of a major fitness component by comparing the survival of the introduced populations (Damier high and low predation) to that of their ancestral source population (Yarra high predation) in the introduction sites (Damier).

If divergent selection in the Damier is consistent with that in other streams, guppies should have substantially lower survival rates in the high predation environment than in the low predation environment[19]. Mortality in the high predation environment would primarily be the result of fish predation, whereas mortality in the low predation environment could result from predation by birds, prawns, or killifish (*Rivulus hartii*), or from starvation owing to greater competition[20]. To test whether survival differed as expected, we conducted a within-site mark-recapture study[13] in March of 2004 (see Methods). Consistent with previous work in other rivers[13,19], we found that guppies in high predation sites did indeed have lower survival than guppies in low predation sites (Fig. 1, Table 1). Also consistent with previous work[13], males had lower survival than did females (Fig. 1, Table 1). Given that divergent selection in the Damier is similar to that in other streams, so too should be the pattern of phenotypic divergence.

Based on previous work and adaptive expectations, we predicted that several phenotypic traits would diverge between the two Damier environments. Since we studied wild-caught individuals, the observed patterns might reflect a combination of genetic and environmental effects. Genetic differences do seem likely, however, given that phenotypic differences in previous studies had a genetic basis[14,15,21]. First, we predicted that male colour, particularly orange and black, would be more pronounced in the low-predation environments because sexual selection would favor increased colour in the absence of opposing natural selection [15,22]. Analysis of wild caught males suggested no appreciable divergence in orange ($P = 0.072$) and a slight divergence in the amount of black ($P = 0.035$), but in the opposite direction from predicted (analysis in Appendix 4). Second, we predicted that adult females from low predation environments would produce more but smaller offspring, and have higher reproductive allotment[16,23]. Consistent with this prediction, high predation Damier females produced significantly more ($P = 0.001$) and smaller ($P < 0.001$) embryos than did low predation Damier females (see Methods; Fig. 2; Appendix 4). More specifically the two populations had similar embryo numbers for small females, but significantly different embryo numbers for large adult females. This result is hence agreeable with previous studies. In contrast, the two populations did not differ in female reproductive allotment ($P = 0.708$, Fig. 2; Appendix 4). Reproductive allotment however, has not been proven consistently in past studies and thus could explain why it was the only life-history trait that had not diverged significantly in our system[14,24].

Phenotypic divergence in the Damier thus matched adaptive expectations for two important life-history traits (offspring size and number) but not for female reproductive allotment and male colour. This lack of divergence suggests the intriguing possibility that the details of selection in our system differed somewhat from that in other studies. One possible reason for such differences is that the north slope (our introduction) and south slope (most previous work) differ in the specific predator species (main predator species in the north slope is the Giant Goby *Gobiomorous dormitator,* main predator in the south slope is the Pike Cichlid *Crenicichla* alta)[25], which may impose qualitatively different selection on some traits. Another possibility is that differences in canopy openness between the two Damier environments (Appendix 3) influences productivity, and may therefore influence the evolution of male colour or female reproductive allotment[14,20].

Having documented divergent selection and concurrent adaptive divergence of some traits we would expect the evolution of major fitness components. To test for this possibility, we performed a mark-recapture transplant experiment in the spring of 2005 (see Methods). Here we released high and low predation guppies from both the Damier and Yarra rivers into the Damier. Three groups of fish were released into the Damier low predation environment: Damier low predation fish (DL), Yarra high predation fish (YH), and Yarra low predation fish (YL). Similarly, three groups were released into the high predation environment: Damier high predation fish (DH), YH fish, and YL fish. Two and four weeks after release, the experimental fish were recaptured and identified by their marks.

If fitness has evolved as expected in the Damier, several predictions should hold. In the Damier high predation environment, DH fish should have the highest survival owing to local adaptation. YH fish should have the next highest survival because they are adapted to a high predation regime, but not to the specific river. YL fish should have the lowest survival because they are adapted to a different predation regime and to a different river. In the Damier low predation environment, the same logic predicts that DL fish would have the highest survival, followed by YL fish, and then by YH fish. If fitness has not evolved, Damier fish should have similar survival as their ancestral source population (YH) in each environment.

Our results are generally consistent with the evolution of fitness (Fig. 3). For adults, we evaluated these predictions by fitting alternative models to the data with the Program MARK[26] (see Methods; Appendix 5). Two models were nearly equivalent in their ability to explain our results. Properties common to both models were that survival was lower in the high predation locality than in the low predation and lower in males than in females, patterns consistent with earlier studies[13,19]. In the best model, DH and YH fish had significantly higher survival than YL fish in the high predation locality. This result is explained by the fact that the DH and the YH fish are already adapted to a high predation locality so their survival is much higher than the YL fish that are adapted to the alternate predation regime. There is no significant survival difference between the DH and YH fish in the high predation environment probably due to the Damier fish not being completely adapted to their environment (However the DH females did have approximately 8 percent higher survival than the YH females, no difference for males (Figure 3)). Fish from all three localities (DL, YH, and YL) had equivalent survival in the low predation locality. In the second best model, which fit the data essentially as well as the "best" model ($\Delta QAIC_c = 1.1$), DL and YL fish had higher fitness than YH fish in the low predation environment probably because of the same excuse listed above. Juvenile survival data were based on groups, not individuals, and on a single recapture interval, so data were analyzed with generalized linear models (see Methods; Fig. 3). In the high predation environment, DH juveniles tended to have the highest (although marginally non-significant) survival (DH vs. YL, $P = 0.059$; DH vs. YH, $P = 0.089$), whereas the two Yarra groups did not differ in survival ($P = 0.912$). In the low predation environment, DL and YL juveniles had higher survival than the YH juveniles (DL vs. YH, $P = 0.004$; YH vs. YL, $P = 0.006$), whereas the two low predation groups did not differ in survival ($P = 0.887$).

In summary, observed patterns of survival suggest the adaptive evolution of a major fitness component in response to predation regime: DL fish had higher survival than their ancestors (YH fish) in the low predation environment. This fitness component also appears to have diverged in response to river-specific selection: DH fish had (marginally) higher survival than their ancestors (YH fish) in the high predation environment (Fig. 3). The changes in survival were presumably driven by the adaptive evolution of specific traits, and indeed some traits (offspring size and number) diverged in the expected direction. And yet some traits (male colour and female reproductive allotment) did not diverge as expected. Perhaps the adaptive evolution of some traits is constrained (for currently unknown reasons), or occurs under more sporadic phases of strong selection that have not yet acted. If so, future adaptive changes in such traits should yield additional improvements in components of fitness. In addition we only looked at a small number of traits, other potential traits which could have diverged based on previous studies include behavioural traits, swimming ability and various reproductive traits [18,27,28].

Our study was motivated in part by curiosity as to the circumstances under which adaptive evolution might allow population persistence in the face of environmental change. A number of studies have documented the adaptive evolution of specific traits following a disturbance[2-4] but such observations do not allow predictions regarding population persistence. The reason is that changes in individual traits may contribute little to changes in overall fitness. To make predictions about population persistence, we need data on changes in fitness itself, or at least some major components of fitness. In the present study, we have shown how such information can be gathered by comparing the survival of ancestral and descendent populations in the descendent population's home environment. Although survival is clearly a major component of fitness, other fitness components are also important. Lifetime reproductive success, for example, should be particularly critical[29]. Future genetic assignment of parents to offspring may allow analyses based on this more inclusive fitness surrogate.

Understanding the evolution of fitness in disturbed populations might ultimately allow a predictive framework for evolutionary conservation biology. For example, the relative contributions of evolution and environmental change to the vital rates of populations could be compared[30], thus revealing whether evolution can offset environmental change. Studies of the adaptive evolution of specific traits remain useful but these are insufficient for this more inclusive predictive framework. For the moment, it seems critical for more studies to examine how major fitness components in natural populations evolve following environmental disturbance.

Methods

Selective regimes in the Damier were characterized in April 2004. We collected 268 fish (182 females and 86 males) from three pools in the low predation environment, and

181 fish (120 females, 61 males) from five pools in the high predation environment. Collections were made on three consecutive days and we attempted to collect all the fish in each pool (see Appendix 2)[13]. Adults were anesthesized (MS-222 [3-aminobenzoic acid ethyl ester]), digitally photographed on a grid-ruled background with standard illumination[25], and individually marked by subcutaneously injecting an elastomer dye[13]. The marked fish were allowed to recover for two days in tanks and were then released back into their capture sites on April 1, 2004. The same sites were then resampled and the captured fish identified two weeks later over three consecutive days. To sample any emigrants, we also collected fish from pools above and below the study sites. The data were analyzed using generalized linear models with PROC GENMOD in SAS (version 8.02) with a logit link and a binomial error structure.

Data on male colouration was obtained from the above digital photographs following established methods[25]. In brief, we used the program Scion Image to measure fish body length and area, and the number and size (length, height, and area) of all spots of a given colour. The total area of the body covered with orange spots and with black spots (each ln transformed) was then compared between Damier high predation (N= 52 fish) and Damier low predation (N= 75 fish) males in ANCOVA with total body area as a covariate.

Characterization of life-history phenotypes also followed standard methods[13]. In March 2004, female guppies were collected, killed with an overdose of anaesthetic (MS222), and preserved in 5% formalin. They were then dissected and their embryos removed and classified according to stage of development[14]. For each female, we then determined fecundity (number of developing embryos), embryo size (average dry mass of individual embryos), and reproductive allotment (total dry mass of embryos / (total dry mass of embryos + total somatic dry mass of female))[14]. Life history data were analyzed using ANCOVAs with site (Damier high predation vs. Damier low predation) as a fixed factor and either ln-somatic mass (embryo number) or stage of development (embryo weight and reproductive allotment) as covariates.

The mark-recapture transplant experiment was conducted March to April 2005. Three pools in the high predation environment and three pools in the low predation environment were chosen. Capture, marking and recapture methods were the same as in 2004. In total, 150 YH adults (75 males and 75 females) and 150 YL adults (75 males and 75 females) were marked and released into both the high and the low predation environments in the Damier. Damier fish (94 from the high predation environment and 111 from the low predation environment) were released back into the same environment they were collected from. However, to control for pool effects, each Damier fish was placed in a different pool from the one in which it was initially captured. All adult fish were released March 17, 2005, and were then recaptured over three consecutive days at two recapture intervals (starting March 30, 2005 and April 15, 2005). We also gave 206 juveniles (fish less than 14 mm and greater than 10 mm) a cohort mark to distinguish them by body size and population. We released 47 DL juveniles, 42 YL juveniles, and 18 YH juveniles into the low predation environment. We released 54 DH juveniles, 28 YL juveniles, and 17 YH juveniles into the high predation environment. All juvenile fish were released on March 17, 2005, and were recaptured over three consecutive days starting on March 30, 2005.

Data for individually-marked adults for the 2005 experiment were analyzed with the Program MARK[26], which takes advantage of the two recapture intervals to generate an independent estimate of mortality rate, as well as the probability that an individual was alive but not recaptured during the first time interval. To apply this program, we fit alternative models to the data, then judged the best model on the basis of the Quasi-Akaike-Information-Criteria corrected for sample size ($QAIC_c$). Two models turned out to be nearly equivalent based on the small difference in $QAIC_c$ values (see Appendix 5), so the results for both are interpreted. Data for batch marked juveniles for the 2005 experiment were analyzed using generalized linear models with PROC GENMOD in SAS (version 8.02) with a logit link and a binomial error structure.

Literature Cited

1. Reed, D. H., Lowe, E. H., Briscoe, D. A. & Frankham, R. Fitness and adaptation in a novel environment: Effect of inbreeding, prior environment, and lineage. *Evolution* **57,** 1822-1828 (2003).
2. Hendry, A. P. & Kinnison, M. T. The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* **53,** 1637-1653 (1999).
3. Stockwell, C. A., Hendry, A. P. & Kinnison, M. K. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* **18,** 94-101 (2003).
4. Reznick, D. N., & Ghalambor, C. K. The population ecology of contemporary adaptation: what do empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112/113,** 183-198 (2001).
5. Fisher, R. A. *The genetical theory of natural selection*, 2nd ed (Dover, New York, 1958).

6. Burt, A. The evolution of fitness. *Evolution* **49,** 1-8 (1995).
7. Bürger, R., & Lynch, M. Evolution and extinction in a changing environment: A quantitative- genetic analysis. *Evolution* **49**, 151-163 (1995).
8. Rainey, P. B. & Travisano, M. Adaptive radiation in a heterogeneous environment. *Nature* **394,** 69-72 (1998).
9. Lenski, R. E., Rose, M. R., Simpson, S. C. & Tadler, S. C. Long-term experimental evolution in *Escherichia coli.* I. Adaptation and divergence during 2,000 generations. *Am. Nat.* **138,** 1315-1341 (1999).
10. Travisano, M., Mongold, J. A., Bennett, A. F. & Lenski, R. E. Experimental tests of the roles of adaptation, chance, and history in evolution. *Science* **267,** 87-90 (1995)
11. Elena, S. F. & Lenski, R. E. Long-term experimental evolution in *Escherichia coli.* VII. Mechanisms maintaining genetic variability within populations. *Evolution* **51,** 1058-1067 (1997).
12. Endler, J. A. Multiple trait coevolution and environmental gradients in guppies. *Trends Ecol. Evol.* **10,** 22-29 (1995).
13. Reznick, D. N., Butler IV, M. J., Rodd, H. F. & Ross, P. Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* **50,** 1651-1660 (1996).
14. Reznick, D. N. & Bryga, H. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* **41,** 1370-1385 (1987).
15. Endler, J. A. Natural selection on color patterns in *Poecilia reticulata. Evolution* **34,** 76-91 (1980).

16. Reznick, D. N., Rodd, H. F. & Cardenas, M. Life-history evolution in guppies (*Poecilia reticulata:* Poeciliidae). IV. Parallelism in life-history phenotypes. *Am. Nat.* **147,** 319-338 (1996).
17. Reznick, D. N., Shaw, F. H., Rodd, H. F. & Shaw, R. G. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* **275,** 1934-1937 (1997).
18. Magurran, A. E. Population differentiation without speciation. *Phil. Trans. R. Soc. Lond.* **353,** 275-286 (1998).
19. Rodd, H. F., Reznick, D. N. & Sokolowski, M. B. Phenotypic plasticity in the life history traits of guppies: Responses to social environment. *Ecology* **78,** 419-433 (1997).
20. Reznick, D. N., Butler IV, M. J. & Rodd, H. F. Life history evolution in guppies. VII. The comparative ecology of high and low predation environments. *Am. Nat.* **57,** 126-140 (2001).
21. Reznick, D. Genetic determination of offspring size in the guppy (*Poecilia reticulata*). *Am. Nat.* **120,** 181-188 (1982).
22. Houde, A. E. *Sex, color, and mate choice in guppies*. (Princeton University Press, Princeton, New Jersey, 1997).
23. Reznick, D. N., Bryga, H. & Endler, J. A. Experimentally induced life-history evolution in a natural population. *Nature* **346,** 357-359 (1990).
24. Reznick, D. N. The impact of predation on life history evolution in Trinidadian guppies:genetic basis of observed life history patterns. *Evolution* **36**, 1236-1250 (1982).

25. Millar, N. P., Reznick, D. N., Kinnison, M. T. & Hendry, A. P. Disentangling the selective factors that act on male colour in wild guppies. *Oikos* (In press).

26. White, G. C. & Burnham, K. P. Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46 Supplement**, 120-138 (1999).

27. Magurran, A. E. & Seghers, B. H. Population differences in predator recognition and attack cone avoidance in the guppy *Poecilia reticulata. Animal Behaviour* **40,** 443-452 (1990).

28. O'Steens, S., Cullum, A. J., & Bennett, A. F. Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **56,** 776-784 (2002).

29. Benton, T. G. & Grant, A. Evolutionary fitness in ecology: Comparing measures of fitness in stochastic, density-dependent environments. *Evol. Ecol. Res.* **2,** 769-789 (2000).

30. Hairston, Jr., N. G., Ellner, S. P., Geber, M. A., Yoshida, T. & Fox, J. A. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* **8,** 1114-1127 (2005).

Table 1: Results of statistical analysis of the 2004 adult survival data comparing the Damier high and low predation environments (using local fish). First shown are results of the full model; with males, females and their interaction. Second shown are results comparing predation regimes in separate analyses for males and females.

Source	χ^2	*P*
Full model		
Predation	20.22	< 0.001
Sex	7.05	0.008
Interaction	1.00	0.318
Effects of predation in sex-specific models		
Males	12.64	<0.001
Females	7.61	0.006

Figures

Captions:

Figure 1. Survival of females (white bars) and males (black bars) from high predation (H) and low predation (L) environments in the Damier, when tested over a two week period in their home environments. The bars are standard errors.

Figure 2. Life history phenotypes of females captured from the Damier high predation (squares) and low predation (circles) environments. The top panel shows the number of embryos with respect to the size of the female. The middle panel shows the average size of embryos dissected from females with respect to their stage of development. The bottom panel shows reproductive allotment (proportion of dry body mass composed of embryos) with respect to stage of development. Lines are least-squares regressions through each population separately. Raw values are shown here but statistical inferences are based on natural logarithms (see Supplementary Information).

Figure 3. Survival of females (white bars), males (black bars), and juveniles (grey bars) in high predation (upper panel) and low predation environments (lower panel) in the Damier. Experimental groups are Damier high predation fish (DH), Damier low predation fish (DL), Yarra high predation fish (YH), and Yarra low predation fish (YL). Survival estimates for the individually marked adults were derived from a Program MARK analysis that included all main effects and interactions. Survival estimates for the batch marked juveniles were derived using generalized linear models with PROC GENMOD in SAS (version 8.02).

Figure 1.

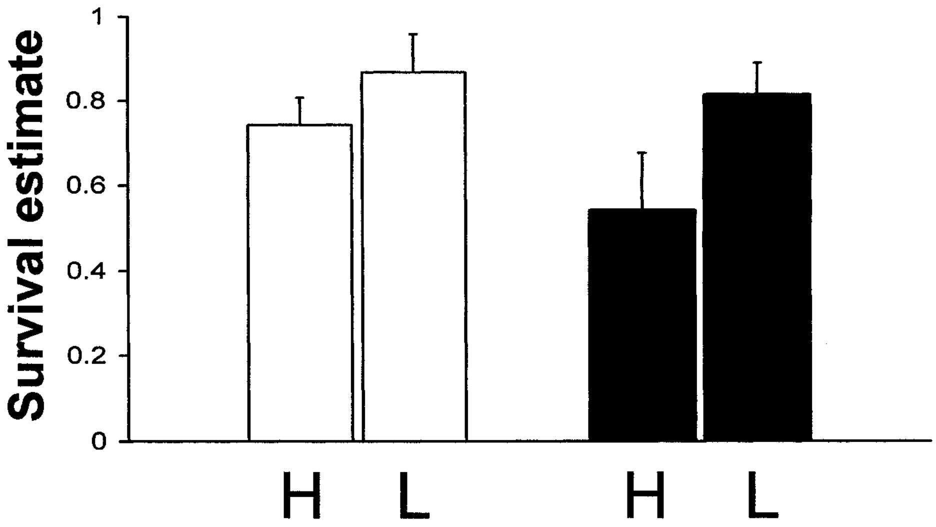


Figure 2.

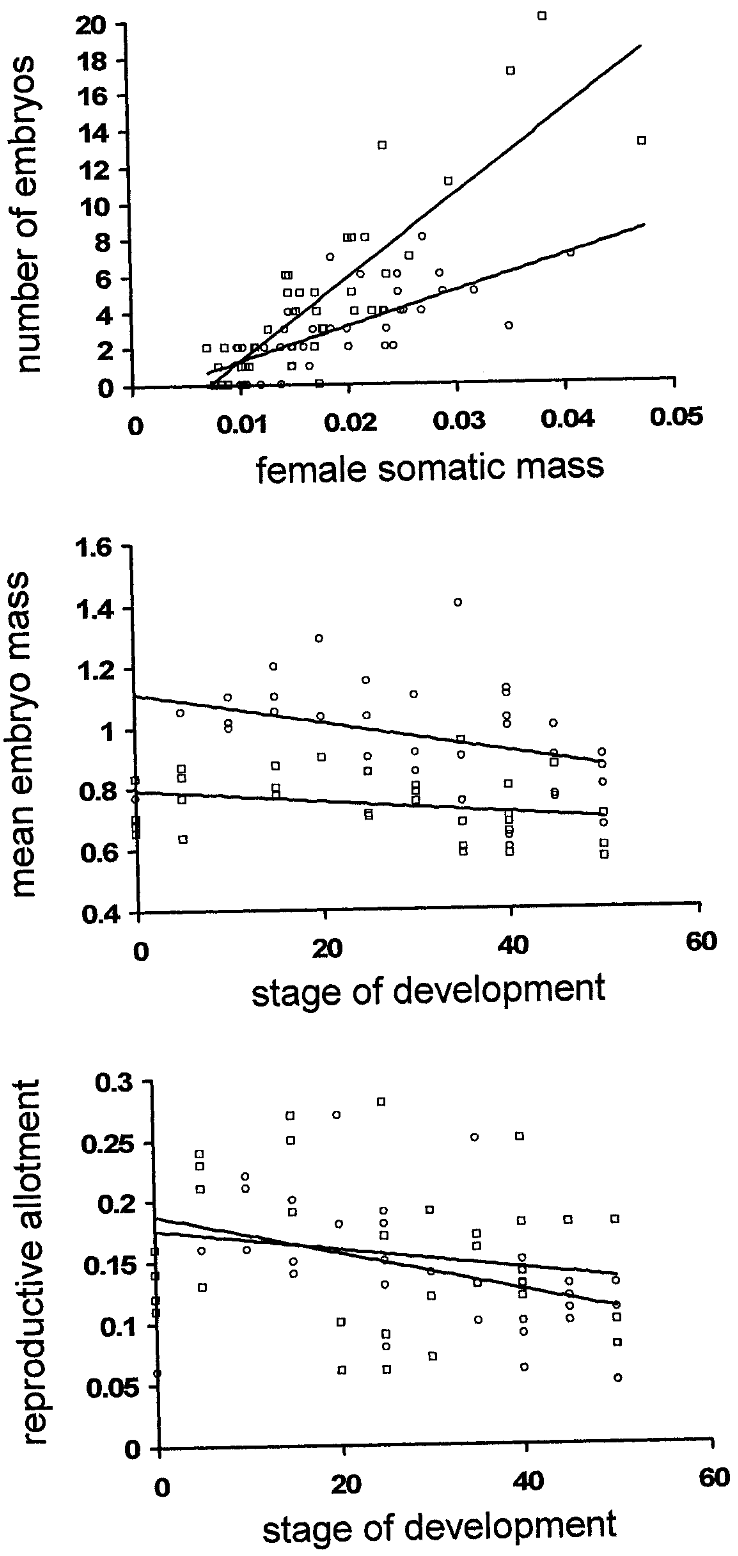
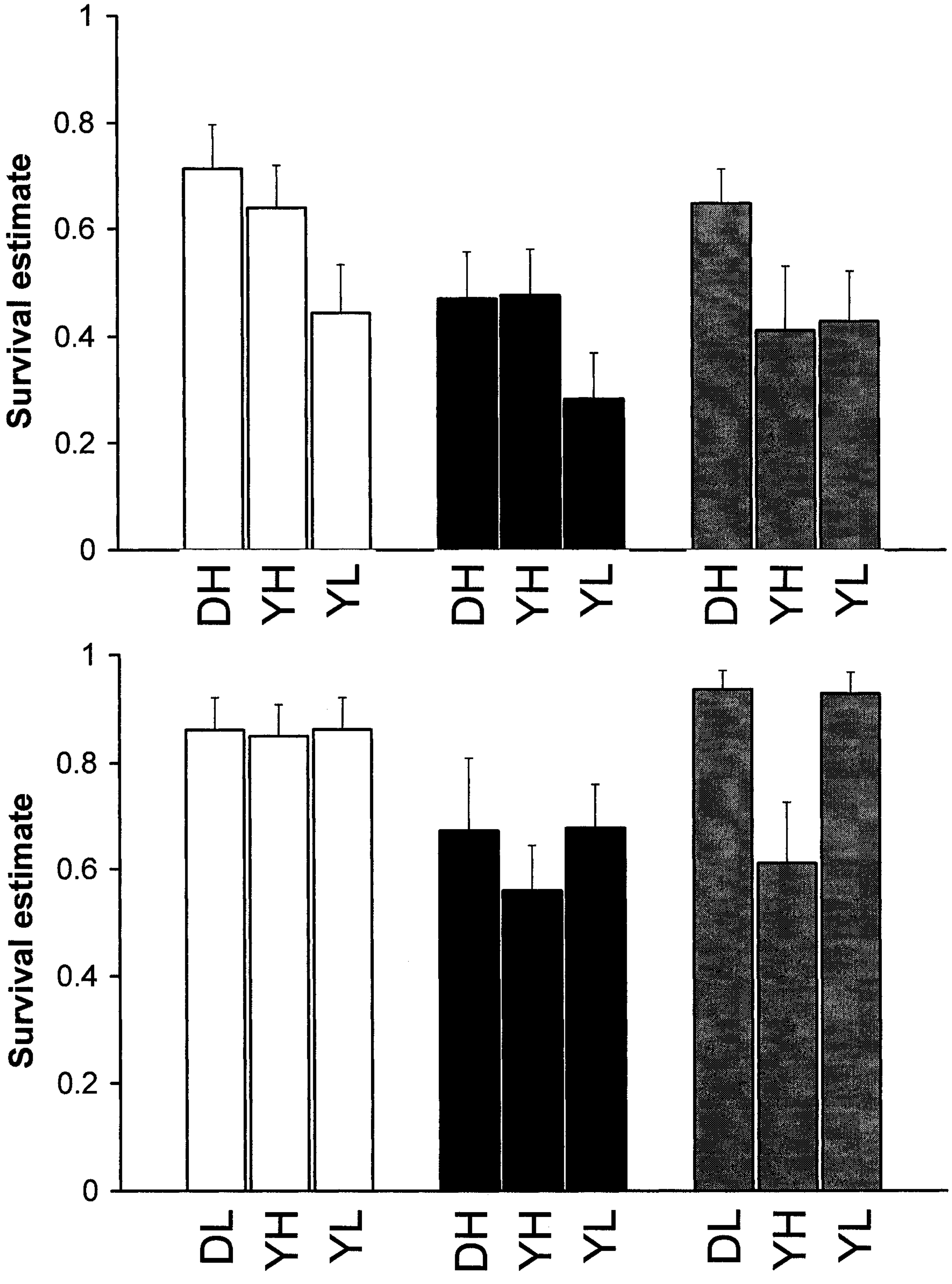

number of embryos
20
18
16
14
12
10
8
6
4
2
0
0
0.01
0.02
0.03
0.04
0.05
female somatic mass
mean embryo mass
1.6
1.4
1.2
1
0.8
0.6
0.4
0
20
40
60
stage of development
reproductive allotment
0.3
0.25
0.2
0.15
0.1
0.05
0
0
20
40
60
stage of development

Figure 3.


Survival estimate
1
0.8
0.6
0.4
0.2
0
DH
YH
YL
DH
YH
YL
DH
YH
YL
Survival estimate
1
0.8
0.6
0.4
0.2
0
DL
YH
YL
DH
YH
YL
DL
YH
YL

General Conclusions

Can adaptation save populations from extinction? My thesis addressed this question by studying Trinidadian guppies introduced into two divergent environments: high predation and low predation. This dramatic and abrupt environmental change caused the adaptive evolution of several traits, particularly offspring size and number. Moreover, the adaptation led to a substantial improvement in survival, and hence fitness, of the introduced fish. This inference was made by comparing the survival of individually-marked guppies from the ancestral (source) population and the derived (introduced) population in the new (introduction) site. The academic merits of the overall study include an increased understanding of how adaptation can save populations experiencing these changes. At present, we have no information on this topic in wild populations, thus my research will improve our knowledge of how environmental change influences biological diversity.

An issue which should be addressed in the future is studying the evolution of fitness using other fitness components such as lifetime reproductive success (LRS). LRS is a major fitness component because it incorporates not only parental survival, but also offspring production, and offspring survival (Benton and Grant 2000). Genetic assignment of parents to offspring could allow future analyses based on this more inclusive fitness surrogate. My previous research has centered on the question of whether fitness really evolves in the wild on short time scales. However, another issue to address in the future would be to compare the rate of the evolution of fitness with the rate of the evolution of individual traits influencing fitness. This will allow us to make predictions regarding how these rates of evolution will influence population persistence in the face of environmental change, which could have major implications for conservational biology.

Literature Cited

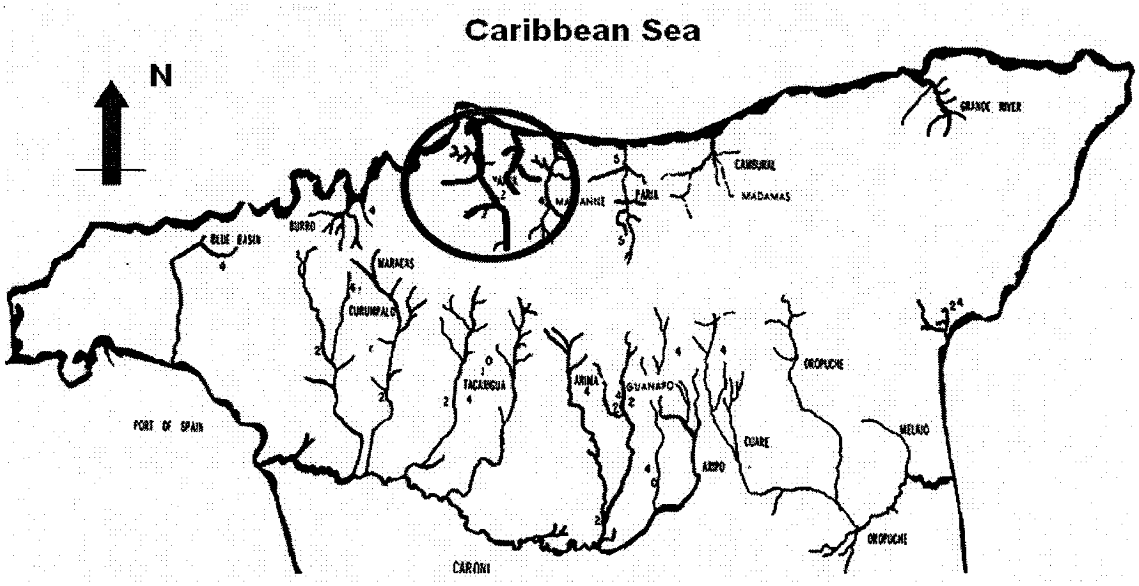
Benton, T. G. and A, Grant. 2000. Evolutionary fitness in ecology: Comparing measures of fitness in stochastic, density-dependent environments. Evol. Ecol. Res. 2:769-789.

Appendices

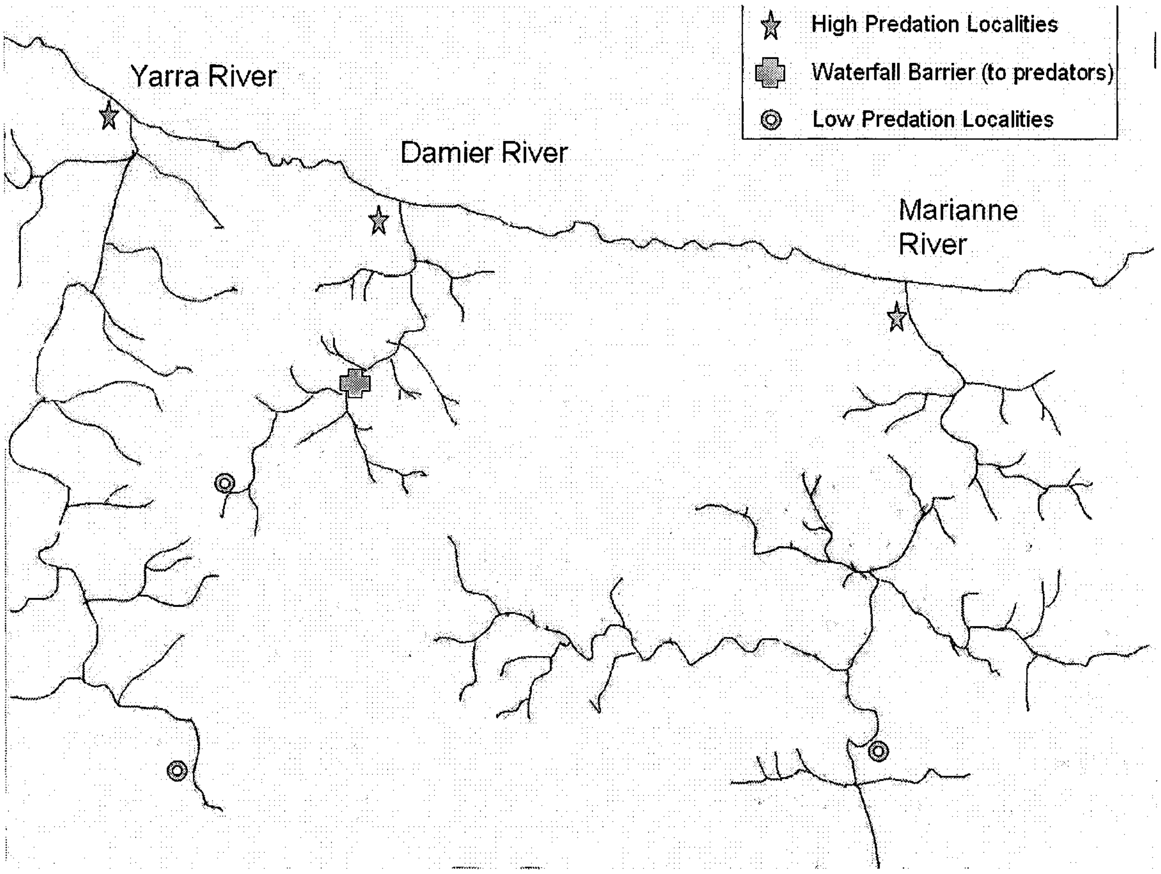
Appendix 1: Map of Trinidad

Map of Trinidad showing research sites. The two study rivers (darker shaded) that are circled in the first picture are the Yarra and the Damier (the third river is the Marianne). The circle is magnified in the second picture. The stars show the locations of the high predation localities, the donuts show the locations of the low predation localities, and the plus shows the location of the Damier waterfall, which acts a barrier to large guppy predators. Similar barriers exist in the much bigger Yarra river.

Picture1:



Picture 2:


High Predation Localities
Waterfall Barrier (to predators)
Low Predation Localities
Yarra River
Damier River
Marianne River

Appendix 2. Mark-recapture methods

Our inferences regarding survival rates in the Damier river were made using mark-recapture methods, which could cause potential sources of bias. The surviving fish were identified by visible marks placed on their bodies, which may bias our results if these marks influence survival. However, previous studies showed that these marks do not affect short-term predation and have little to no effect on the survival of guppies[1,2]. Another potential source of bias is that fish may become difficult to recapture once they are released. However, according to previous work, it is easy to catch essentially all of the fish within a pool or stream (recapture rate is generally > 90 %) [1,2]. Moreover, guppies return to their normal activities quite soon after a disturbance to their environment[3], and their emigration rate over short periods of time in the streams seems to be very low[1]. This allowed us to place guppies in a particular location and later recapture those that remain alive in, or close to, that same location.

Appendix 3. Damier habitat features

High and low predation sites often differ in stream size and canopy openness[4,5], which causes a difference in stream productivity and can influence life-history evolution[4,5]. Damier high and low predation environments did not differ in stream size (neither water depth nor stream width differed), but the high predation environment had a more open canopy than the low predation environment (Table 1).

Physical habitats were quantified in April 2005 using the methods of Millar et al.[6]. In the high predation and low predation sites, we established eleven evenly-spaced transects covering 200 m of stream. This distance spanned all introduction pools and sections upstream and downstream of these pools. At each transect , we measured the wetted width of the stream and water depth. Water depth was measured three times, one at each of three equidistant points along each transect. Canopy openness was measured using a concave spherical densiometer at eight of the transects. Densiometer readings were taken facing each cardinal direction while standing in the middle of the stream channel. The data (log transformed) were analyzed with a single factor ANOVA having two levels (Table 1).

Table 1. Comparison of habitat features between high and low predation environments in the Damier.

	Low Predation	High Predation	F	P
Canopy openness (%)	9.00	17.71	10.015	0.006
Stream width (cm)	385.91	331.82	0.689	0.416
Water depth (cm)	20.15	21.33	0.023	0.881

Table notes: Values in the “low predation” and “high predation” columns are mean values for untransformed data.

Appendix 4. Divergence in specific traits

As a supplement to the information in the manuscript regarding the differences in male colour and female life-history traits, I have added the results from the data analyses. ANCOVAs were used to analyze both male colour (Table 2) and female life history (Table 3). The information generated is listed in the form of two tables. Table 2 shows the comparison of the areas of black and orange spots on male guppies between high and low predation Damier environments. Table 3 shows the comparison of female life history traits between high and low predation fish in the Damier.

Table 2. Comparisons of major features of male colouration between high predation and low predation environments in the Damier.

	Orange area	Black area
N (high/low)	52/75	52/75
<u>With interaction</u>		
Site	1.90	3.94^{b}
Covariate	15.11^{d}	2.95^{a}
Interaction	1.65	4.21^{b}
<u>Without interaction</u>		
Site	1.22	4.55^{b}
Covariate	15.21^{d}	2.71
<u>Adjusted means</u>		
High predation	2.30 mm^2	2.00 mm^2
Low predation	2.11 mm^2	1.58 mm^2

Table Notes: Shown first are sample sizes (high predation site/low predation site), F ratios from the full model with the interaction, F ratios from the model without the interaction, and adjusted means as antilog transformed adjusted means from the analyses of ln transformed data. The covariate in each case is total body area. Significance levels: ^{a} $P < 0.10$, ^{b} $P < 0.05$, ^{c} $P < 0.01$, and ^{d} $P < 0.001$.

Table 3. Comparisons of female life history traits between high predation and low predation environments in the Damier.

	Embryo number	Embryo mass	Reproductive allotment
N (high/low)	35/37	35/37	35/37
With interaction			
Site	9.76^c	18.54^d	0.40
Covariate	92.97^d	10.64^c	6.88^b
Interaction	7.64^c	0.96	0.86
Without interaction			
Site	12.47^c	51.88^d	0.14
Covariate	97.36^d	10.14^c	6.50^b
Adjusted means			
High predation	4.15	0.729 mg	0.139
Low predation	2.83	0.961 mg	0.135

Table Notes: Shown first are sample sizes (high predation site/low predation site), F ratios from the full model with the interaction, F ratios from the model without the interaction, and adjusted means as antilog transformed adjusted means from the analyses of ln transformed data. The covariate for embryo number is female mass and the covariates for embryo mass and reproductive allotment are stage of development. Significance levels: $^a P < 0.10$, $^b P < 0.05$, $^c P < 0.01$, and $^d P < 0.001$.

Appendix 5. Program MARK analyses of individually marked adults

The program MARK[7] can be used to estimate survival rates from individually marked animals that have been censused over at least two recapture intervals. The program uses maximum likelihood methods to distinguish between the probability that an individual died during a given interval versus the probability that it was alive but not recaught. The critical observation over two recapture intervals is an individual that was not recaught after the first interval but was recaught after the second interval, which indicates that it had been alive earlier but evaded capture. Because we had two recapture intervals in 2005, we were able to estimate survival and the probability of being caught if alive for the first recapture interval. Comparisons of survival between the two capture intervals were not made because survival and recapture probabilities are not separable for the last interval.

The first step in the analysis was to fit a fully parameterized model to the data, for both survival and recapture probabilities. The main effects in our model were the introduction site (Damier High (DH), Damier Low (DL)), sex, and the site of origin of the released fish (DH, Yarra High (YH), and Yarra Low (YL) for the DH site; DL, YH, and YL for the DL site). We then analyzed the three two-way interactions and one three-way interaction among these main effects. This yielded a model that estimates survival and recapture probabilities for each of the 12 available combinations of introduction site, site of origin, and sex. To assess the goodness of fit for this model we conducted a bootstrap test with 1000 iterations. All bootstrapped iterations yielded deviances and c-hat values less than the estimated values from the data – indicating significant overdispersion. We calculated a c-hat correction factor of 3.00 (estimated c-hat divided by the mean of the bootstrapped c-hat values: 3.18/1.06). This is an extreme correction factor but one within the acceptable limits. Because of the need to correct for overdispersion, model selection was made by comparing Quasi-Akaike Information Criteria ($QAIC_c$). The rank order of the candidate models was not affected by altering the c-hat correction between values 2.5 and 3.5.

The best models were ones that assumed an equal probability of recapture of the different groups in the two locations. The mean probability of recapture if alive during a single census interval was 89%. Other important main effects were that mortality was higher in the Damier high predation environment than in the Damier low predation environment and higher in males than females. The only significant interaction was between the site of origin and the site of introduction. This interaction occurred because YH fish had higher survival that YL fish in the high predation site, but lower survival in the low predation site. These results simplified our analysis because we could look at the effect averaged across sexes and focus on the predictions that survival in the low predation site would follow the pattern DL > YL > YH and that survival in the high predation site would follow the pattern DH > YH > YL. We therefore present a relevant subset of the models in Table 4.

Model 1 assumes that there is no difference among any of the treatment groups in survival. Model 2 (the full model used for the goodness of fit test) includes all main effects and interactions and allows all recapture probabilities to be unique. Model 3 (I = introduction site, S=sex and O=site of origin) includes all main effects and interactions but assumes that the recapture probabilities are the same for all groups. Note that we ran a series of intermediate models that considered heterogeneity among groups in recapture probability, such as differences among sexes or among fish from high versus low predation environments, and that all of these models fit less well than Model 3. Model 4 is the same as Model 3 except that it excludes the three way interaction. Model 5 includes only the main effects and excludes all interactions. Model 6 includes all main effects and two of the two-way interactions. Model 7 includes all main effects and the interaction between the site of origin and the introduction site. This model comes closest to the a priori predictions stated in the text. The O*I interaction is caused by YH fish having higher survival than YL fish in the high predation locality but lower survival in the low predation locality. Models 8 and 9, which represent the best fit to the data, represent a different way of evaluating the data, since they postulate relative survivorships within each introduction site rather than including the O*I interaction. In both models, we fitted different survival probabilities in the high and low predation introduction sites. In Model 9, we assumed that the survivorships of the YH and DH fish were equal and different from the YL fish in the high predation site, then that the YL, YH and DL fish had equal survivorships in the low predation site. In Model 8, the survivorships if YL and DL were equal and different from YH. By the criteria of White and Burnham (1999)[7], Models 8 and 9 should be considered as equally good descriptions of the data. Model 8 comes closest to the a priori predictions stated in the text, which are that the introduced fish should have the highest fitness in their respective habitats, followed by the Yarra fish derived from a similar predation environment, then the Yarra fish derived from a different predation environment.

Table 4. Results of Program MARK analyses of survival data in the 2005 mark-recapture transplant experiment. Model 8 and 9 which represent the best fit to our data are in bold. See above text for details.

Model	QAICc	ΔQAICc	# Par	QDeviance
9. {Phi(Sex+(YHDH=DHDH+YLDH)+ (YLDL=DLDL=YHDL)p(.)}	579.6	0	5	20.1
8. {Phi(Sex+(YHDH=DHDH+YLDH)+ (YLDL=DLDL+YHDL)p(.)}	580.7	1.1	6	19.2
7. {Phi(S+O+P+O*P)p(.)}	584.6	5.0	8	19.0
6. {Phi(S+O+P+O*P+S*P)p(.)}	585.6	6.0	9	18.0
5. {Phi(S+O+P)p(.)}	585.7	6.1	6	24.2
4. {Phi(S+O+P+S*O+O*P+S*P)p(.)}	589.6	9.9	11	17.9
3. {Phi(S+O+P+S*O+O*P+S*P+S*O*P)p(.)}	593.3	13.6	13	17.5
2. {Phi(g) p(g)}	609.1	29.5	23	12.7
1. {Phi(.)p(.)}	625.7	46.1	2	72.2

Renewd

Guidelines for completing the form are available at www.mcgill.ca/rgo/animal

McGill University
Animal Use Protocol – Research

Protocol #: 4570
Investigator #: 996
Approval End Date: April 30, 2005
Facility Committee: SCI

:le: Natural selection, reproductive isolation, and the evolution of biological diversity.
ıst match the title of the funding source application)

New Application ☒ **Renewal of Protocol #** 4570 ☐ **Pilot** **Category** *(see section 11)*: B

Investigator Data: & email & cond

ncipal Investigator: Andrew Hendry **Phone #:** 398-4086 ext. 00880
ɔartment: Redpath Museum and Dept. of Biology **Fax#:** 398-3185
dress: 859 Sherbrooke St. W., Montreal **Email:** andrew.hendry@mcgill.ca

Emergency Contacts: Two people must be designated to handle emergencies.

me: Andrew Hendry **Work #:** 398-4086 ext. 00880 **Emergency #:** 514-637-9938
me: David Green **Work #:** 514-398-4086 ext: 4088 **Emergency #:** 450-678-2851

Funding Source:		For Office Use Only:
:ernal ☒	**Internal** ☐	ACTION / ✓ / DATE CCS ✓ Apr 26 DB Apr 23 '04 APPROVED
ırce (s): NSERC	**Source (s):** ____	
:r Reviewed: ☒ YES ☐ NO**	**Peer Reviewed:** ☐ YES ☐ NO**	
tus : ☒ Awarded ☐ Pending	**Status:** ☐ Awarded ☐ Pending	
ıding period: June 2002 – June 2006	**Funding period:** ____	

\ll projects that have not been peer reviewed for scientific merit by the funding source require 2 Peer Review Forms to be ıpleted e.g. Projects funded from industrial sources. Peer Review Forms are available at www.mcgill.ca/rgo/animal

posed Start Date of Animal Use (d/m/y): ____ **or ongoing** ☒
ɪected Date of Completion of Animal Use (d/m/y): ____ **or ongoing** ☒

restigator's Statement: The information in this application is exact and complete. I assure that all care and use of animals in this ɔosal will be in accordance with the guidelines and policies of the Canadian Council on Animal Care and those of McGill University. I shall ıest the Animal Care Committee's approval prior to any deviations from this protocol as approved. I understand that this approval is valid ɔne year and must be approved on an annual basis.

ncipal Investigator's signature: **Date:** April 4, 2004

Approved by:

air, Facility Animal Care Committee:		**Date:** April 20, 2004
iversity Veterinarian:		**Date:** April 22, 2004
air, Ethics Subcommittee (as per UACC policy):		**Date:**
proved Animal Use	**Beginning:** MAY 1, 2004	**Ending:** April 30, 2005

This protocol has been approved with the modifications noted in Section 13.

er 2002

22 AVR. 2004

Literature Cited

1. Reznick, D. N., Butler IV, M. J., Rodd, H. F. & Ross, P. Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* **50,** 1651-1660 (1996).
2. Bryant, M. J. & Reznick, D. N. Comparative studies of senescence in natural populations of guppies. *Am. Nat.* **163,** 55-68 (2004).
3. Rodd, H. F., Reznick, D. N. & Sokolowski, M. B. Phenotypic plasticity in the life history traits of guppies: Responses to social environment. *Ecology* **78,** 419-433 (1997).
4. Reznick, D. N. & Bryga, H. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* **41,** 1370-1385 (1987).
5. Reznick, D. N., Butler IV, M. J. & Rodd, H. F. Life history evolution in guppies. VII. The comparative ecology of high and low predation environments. *Am. Nat.* **57,** 126-140 (2001).
6. Millar, N. P., Reznick, D. N., Kinnison, M. T. & Hendry, A. P. Disentangling the selective factors that act on male colour in wild guppies. *Oikos* (In press).
7. White, G. C. & Burnham, K. P. Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46 Supplement**, 120-138 (1999).