Adaptive Changes in Life History and Survival following a New Guppy Introduction

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ABSTRACT: Numerous studies of wild populations have shown that phenotypic traits can change adaptively on short timescales, but very few studies have considered coincident changes in major fitness components. We here examine adaptive changes in life-history traits and survival rates for wild guppies introduced into new environments. Female life-history traits in the derived (Damier River) populations diverged from the ancestral (Yarra River) population, as a result of adaptation to predation regime (high vs. low) and other aspects of the local river. Moreover, some components of the derived Damier populations, particularly juveniles, now show higher survival in the Damier than do contemporary representatives from the ancestral Yarra population. These results suggest that adaptive change can improve survival rates after fewer than 10 years (fewer than 30 guppy generations) in a new environment.

Keywords: adaptive divergence, fitness, *Poecilia reticulata*, contemporary evolution, mark recapture, life-history evolution.

Introduction

Many environments are changing at rates that render local populations at risk of extinction (Pimm et al. 1995; Hughes et al. 1997; Vitousek et al. 1997). For these threatened populations to persist, they will need to either alter their geographic distribution or undergo in situ adaptive change. The first of these options is often unattainable, such as when populations are isolated by physical barriers, and so the rate and nature of adaptive change becomes critical (Lynch and Lande 1993; Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Boulding and Hay 2001; Price et al. 2003; Kinnison and Hairston 2007; Orr and Unckless 2008). Most studies addressing this topic have focused on specific phenotypic traits, often finding evidence of adaptive responses over timescales as short as a few generations (reviews: Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Stockwell et al. 2003).

The adaptive phenotypic changes documented thus far should have consequences for individual fitness and population dynamics (Hairston et al. 2005; Saccheri and Hanski 2006; Kinnison and Hairston 2007), but these consequences are rarely quantified in nature. Instead, most studies either (1) document changes in phenotypic traits and assume these changes will alter individual fitness and population dynamics or (2) document changes in individual fitness or population dynamics and assume these are the result of adaptation (as often is inferred for invasive species). The few studies of wild populations that have actually quantified the consequences of phenotypic change for population dynamics have mostly concentrated on adaptation to gradual environmental change (Forchhammer et al. 2001; Hanski and Saccheri 2006; Pelletier et al. 2007), whereas we are here interested in responses to abrupt environmental change (see also Kinnison et al. 2008).

Abrupt environmental change should cause optimal trait values to quickly shift away from observed trait values in the current population (Stockwell et al. 2003). The resulting maladaptation should decrease the fitness of individuals, with potentially negative implications for population growth (theory: Lynch and Lande 1993; Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Boulding and Hay 2001; Orr and Unckless 2008; empirical: Both et al. 2006). Adaptation should then work to improve individual fitness and thus potentially increase population size or productivity. Laboratory studies have elegantly shown these dynamics, by comparing the performance of ancestral and derived populations in their respective en-

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vironments (Lenski et al. 1991; Travisano et al. 1995; Elena and Lenski 1997; Rainey and Travisano 1998). We suggest that a similar approach might be profitably applied to wild populations (see also Kinnison et al. 2008), thus extending inferences from adaptation in the laboratory into the more complex natural world.

Our study focused on adaptation in wild Trinidadian guppies (*Poecilia reticulata*) that experienced a dramatic shift in selection caused by their introduction into new environments. Taking the basic design of laboratory experiments as our guide, we performed the initial introduction, waited 8–9 years, verified selective environments, quantified changes in life-history traits, and then used a transplant experiment to assess survival rates of the ancestral and derived populations in the new environments. Laboratory studies of microorganisms can sometimes compare derived or descendant populations to their actual ancestors (e.g., by resurrecting *Escherichia coli* frozen at the time of introduction), but studies of macroorganisms must compare derived populations to contemporary representatives of the ancestral population. Our study organism required the latter approach, which assumes that comparatively little evolution took place in the ancestral population. This assumption seems appropriate in our study, given the lack of obvious changes in the ancestral population's physical environment and its phenotypic traits (D. N. Reznick, unpublished data). For simplicity, we refer to contemporary representatives from the ancestral population as the "ancestors" of the derived populations.

Natural guppy populations can be divided into two basic types (Endler 1995; Reznick et al. 1996*a*; Rodd and Reznick 1997; Magurran 2005). High-predation populations are usually found in the downstream reaches of rivers, where they coexist with predatory fishes that have strong effects on guppy demographics. Low-predation populations are typically found in upstream tributaries above barrier waterfalls, where strong predatory fishes are absent. This broad contrast in predation regime has driven the evolution of many adaptive differences between the two guppy types in color, morphology, behavior, and life history (reviews: Endler 1995; Houde 1997; Magurran 2005). These differences have evolved independently in many different watersheds (Reznick et al. 1996*b*; Alexander et al. 2006), thus providing convenient replication and allowing robust a priori predictions.

Our study focused on guppies introduced from the Yarra River into the Damier River, adjacent watersheds on the north slope of the Northern Range Mountains in Trinidad (fig. 1). Multiple visits to the Damier in the early 1990s confirmed that guppies were historically absent from the watershed (D. N. Reznick, unpublished data). Then, in 1996, D. N. Reznick collected 200 high-predation guppies

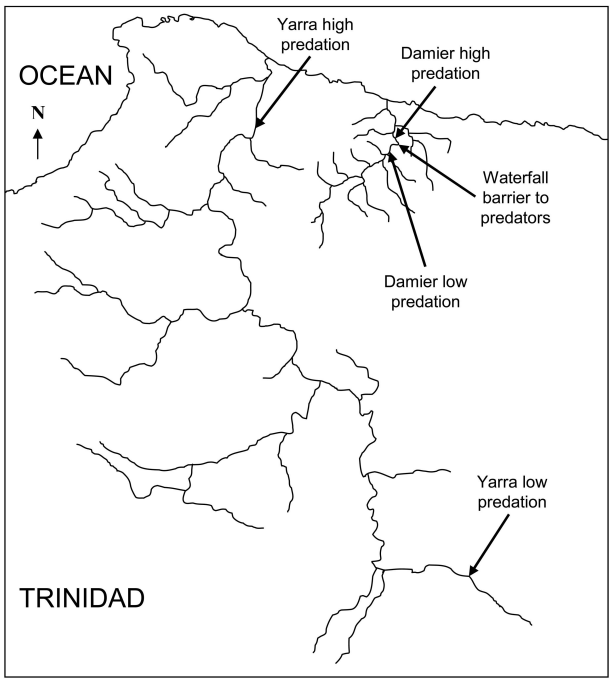

Figure 1: Map of the study sites on the north slope of the Northern Range Mountains of Trinidad.

from the Yarra and introduced them above a barrier waterfall in the Damier. We have never seen major predatory fishes above this waterfall, suggesting a low-predation environment. Qualitative surveys of the Damier in 1997 revealed that the introduced guppies had become established above the waterfall and had also spread downstream to become established below the waterfall. We frequently see potential predatory fishes (*Dormitator maculatus*, *Eleotris pisonis*, *Gobiomorus dormitor*) at this latter site, suggesting a high-predation environment. By the time the current work commenced in 2004, the Damier populations had been separated from their Yarra ancestors for 8 years, which corresponds to 13–26 guppy generations, depending on the particulars of their life history (Reznick et al. 1997). More details on the original Damier introductions are provided in Karim et al. (2007).

Our first step in the present study was to test whether the difference in predatory fishes between sites in the Damier has caused the same difference in survival rates seen in other rivers (e.g., Reznick et al. 1996*a*). It is this difference in mortality, per se, that then drives the evolution of key life-history differences between high- and low-predation guppy populations (Reznick and Endler 1982; Reznick and Bryga 1987; Strauss 1990; Reznick et al. 2001). Mortality rate differences in the Damier would thus lead us to expect adaptive divergence between the high-

Table 1: Possible scenarios for differences in survival among release groups (DH, DL, YH, and YL) in the Damier

Scenario/null hypothesis	Description	Prediction
A	Adaptation depends on the broad contrast in predation regime (high vs. low), independent of other characteristics of the local river (Damier vs. Yarra)	(1) Damier high-predation test site: DH = YH > YL; (2) Damier low-predation test site: DL = YL > YH
B	Adaptation depends on characteristics of the local river, independent of the broad contrast in predation regime	(3) Damier high-predation test site: DH > YH = YL; (4) Damier low-predation test site: DL > YL = YH
C	Adaptation depends on both the broad contrast in predation regime and other characteristics of the local river	(5) Damier high-predation test site: DH > YH > YL; (6) Damier low-predation test site: DL > YH > YL
H_{0A}	Survival probabilities are equal for all release groups, irrespective of the Damier release environment	DH = DL = YH = YL
H_{0B}	Survival differences are due to the river of origin, irrespective of the Damier release site	(DH = DL) ≠ (YH = YL)
H_{0C}	Survival differences are due to the predation regime of origin, irrespective of the Damier release site	(DH = YH) ≠ (DL = YL)
H_{0D}	Survival differences are due to the Damier release site only	(DL = YH = YL in low predation) ≠ (DH = YH = YL in high predation)

Note: DH, Damier high predation; DL, Damier low predation; YH, Yarra high predation; YL, Yarra low predation.

predation and low-predation populations to parallel that seen between these environments in other rivers. In addition to predation, adaptive divergence in guppies is also driven by other environmental features, such as stream size and canopy openness (Grether et al. 2001; Reznick et al. 2001). We therefore also quantified these features in the derived and ancestral environments.

Our second step was to test whether female life-history traits diverged as expected, based on the differences in survival rate and based on previous comparisons in other rivers. First, high-predation females should invest more resources into current reproduction because a high rate of mortality decreases the chance of future reproduction (Reznick et al. 1996*a*, 1996*b*, 2001). Second, low-predation females should produce larger embryos because these are more competitive in the resource-limited environments typical of low-predation sites (Bashey 2002, 2008). Third, low-predation females should produce fewer embryos because they invest fewer resources in current reproduction and have larger embryos (Reznick et al. 1996*a*). In addition to predation effects, females at larger (width and depth) sites with more open canopies can have larger broods of smaller young (Grether et al. 2001).

Evidence of expected divergence in phenotypic traits would confirm that adaptation had occurred in the Damier, which would then lead us to expect changes in major fitness components. We focused on survival. Although more complete fitness surrogates would have been better, these are much more difficult to assay with confidence in natural populations. Our third step was therefore to compare the survival rates of Damier guppies to their ancestral population (Yarra high predation) when both Damier and Yarra fish were tested together in the Damier. The general prediction was that local Damier fish should show equal or higher survival to their ancestors. More detailed predictions then depended on whether adaptation was driven by predation differences or by other habitat features that might differ among the sites (table 1). We distinguished between predation and local river effects by also examining the survival of low-predation guppies from the Yarra River when tested in the Damier. Given that the survival of females, males, and juveniles may respond differently to adaptation, we examined all three of these population components in our experiments.

Material and Methods

Survival and Habitat

In March and April 2004, we used classical mark-recapture methods (Reznick et al. 1996*a*) to evaluate mortality/survival rates in the high- and low-predation Damier sites. Butterfly nets were used to collect adult guppies from three pools in the low-predation site and from five pools in the high-predation site. These fish were transported to our laboratory in Trinidad, anesthetized with MS-222 (tricaine methane sulphonate), and individually marked by subcutaneously injecting unique combinations of colored elastomer dyes. Previous research has suggested that these color marks do not influence susceptibility to predation (Reznick et al. 1996*a*).

The newly marked fish were held in aquaria for 2 days to monitor their health. After eliminating the few fish with problems, we were left with 182 females and 86 males from the low-predation site and 120 females and 61 males from the high-predation site. These fish were released back

into their home pools on April 1, 2004. Following previous work in other streams (Reznick et al. 1996*a*), we waited 2 weeks and then resampled these pools, as well as additional pools upstream and downstream. Each pool was resampled without replacement over three consecutive days, and all captured guppies were held in aquaria. As in previous work (Reznick et al. 1996*a*), this procedure allowed the recapture of nearly all surviving fish: recapture probabilities were high (see "Results"), and only a few fish were captured on the final day of sampling (table A1, in the online edition of the *American Naturalist*). All recaptured fish were individually identified based on their color marks, and any missing marked fish were assumed to have died. Survival rates were compared between sexes and predation environments in generalized linear models with a logit link and binomial error structure (PROC GENMOD in SAS ver. 8.02).

In April 2005, we quantified stream size and canopy openness at each of four sites (fig. 1): Damier high predation (DH), Damier low predation (DL), Yarra high predation (YH), and Yarra low predation (YL). Following previous methods (Millar et al. 2006), we established 11 evenly spaced transects along a 200-m stretch of stream at each site (20 m between transects). Within the Damier, this distance spanned all experimental pools at each site and also extended farther upstream and downstream. At each transect, we measured water depth (cm) at each of three equidistant points across the wetted width (m) of the stream. At eight transects per site, we also measured canopy openness (%) with a concave spherical densiometer (again following methods described in Millar et al. 2006). Densiometer readings at each of these transects were taken facing each compass direction while standing in the middle of the stream channel. Each habitat feature ($\log_{10}$ transformed) was analyzed with a single-factor ANOVA and Tukey tests comparing the four sites (DH, DL, YH, and YL).

Life History

In March 2004, we also collected females from the wild to compare life-history phenotypes among the four sites (DH, DL, YH, YL). The fish were collected with butterfly nets, killed with an overdose of MS-222, and preserved in 5% formalin. Characterization of life-history phenotypes then followed standard protocols (Reznick and Endler 1982; Reznick and Bryga 1987). The females were dissected, and their embryos were removed and classified according to embryonic stage of development. For each female, we then determined embryo number (number of developing embryos), embryo size (average dry mass of individual embryos), and reproductive allotment (total dry mass of a female's embryos divided by the total dry mass of the female including her embryos). Reproductive allotment is thus a measure of a female's current investment into reproduction (Reznick and Bryga 1987). To achieve normality and homoscedasticity, embryo number was $\log_{10}$ transformed.

Each life-history trait was analyzed in a separate ANCOVA (JMP ver. 4.01), with population (DH, DL, YH, YL) as a fixed factor and either somatic mass (for embryo number) or stage of development (for embryo size and reproductive allotment) as a covariate (Reznick and Bryga 1987). We first ran the models with the interaction term included, so as to test whether the different populations had different relationships between the trait and the covariate (i.e., different slopes). We then removed the interaction term to test for differences in trait means standardized for the covariate. Tukey post hoc tests were used to determine which particular populations differed significantly from each other at these covariate-standardized means. Finally, we performed a full-model MANCOVA using the same fixed factor and both covariates, so as to facilitate a general conclusion about the statistical significance of life-history change.

Survival Comparisons

In March 2005, we collected adult males and females from each of the four sites (DH, DL, YH, YL) and individually marked them as described above. At the same time, we collected juveniles (<12 mm and sexually immature) and batch marked them with elastomer dyes specific to their site of origin. The number of fish collected, and therefore the number used in the release experiments (see below), was determined by the number of fish available in the stream. A recent flood had reduced the number of guppies in the Damier, and so we actually used almost all of the fish present at our study sites. Our sample was therefore a good representation of the actual population. So as to maintain comparability with Damier fish, we also limited the number of released Yarra fish to a maximum of 75 of each type at each site. Fewer Yarra juveniles were used because few were found at the Yarra sites.

Into the DH site, we released DH fish (43 males, 68 females, 54 juveniles), YH fish (74 males, 75 females, 17 juveniles), and YL fish (66 males, 74 females, 18 juveniles). Into the DL site, we released DL fish (24 males, 74 females, 47 juveniles), YH fish (72 males, 75 females, 18 juveniles), and YL fish (66 males, 74 females, 42 juveniles). Although Damier fish were thus released back into their original capture sites (low predation or high predation), individuals were not released back into the specific pool from which they had been captured (to reduce potential effects of prior experience). Note that we did not reciprocally translocate Damier fish within the Damier because the shortage of

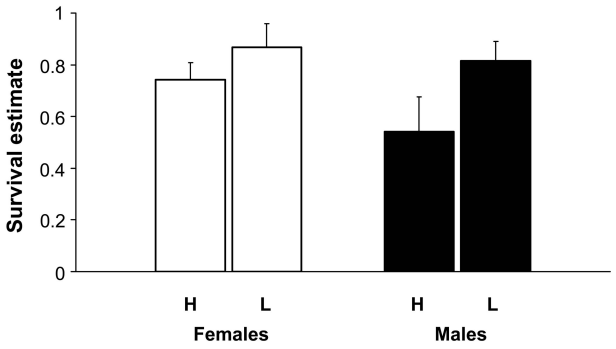

Figure 2: Survival estimates from PROC GENMOD (SAS ver. 8.02) for females (*white*) and males (*black*) in high-predation (*H*) and low-predation (*L*) environments in the Damier. Data correspond to the 2004 experiment in which local fish were released back into their home environment and recaptured 2 weeks later. Detailed statistical results are given in the text. Vertical lines are standard errors.

available fish (see above) necessitated maximizing sample sizes for the key comparison of local Damier fish to their ancestors. Note also that similar experiments were not performed in the ancestral Yarra site, which is too large for mark-recapture methods.

The fish marked as above were then recaptured from the Damier River over three consecutive days in each of two separate periods. In the first recapture period (March 30–April 1), males, females, and juveniles were identified based on their marks and then released back into the pools from which they had been captured. In the second recapture period (April 15–17), only males and females were identified because the juveniles were maturing and could therefore not be unambiguously identified. The juvenile data comprised batch-marked fish recaptured after only a single interval and were therefore analyzed with generalized linear models with a logit link and binomial error structure (PROC GENMOD). The adult data comprised individually marked fish that were recaptured after two intervals and were therefore analyzed in Program MARK (White and Burnham 1999). MARK uses maximum likelihood to distinguish between the probability that an individual died during a given interval and the probability that it was alive but not recaught. For the MARK analyses, Akaike Information Criterion (AIC) was used to formally compare alternative models designed to inform our predictions (see appendix, "Supplementary Information for Program MARK," in the online edition of the *American Naturalist* for more information). The model having the lowest AIC value was inferred as being the best fit to the data set (table 5). Similar procedures have been applied to guppies previously by Bryant and Reznick (2004).

Results

Survival and Habitat

In the Damier, survival was lower for males than for females ($\chi^2 = 7.05$, $P = .008$) and lower in the high-predation site than in the low-predation site ($\chi^2 = 20.22$, $P < .001$; fig. 2), with no interaction between sex and site ($\chi^2 = 1.00$, $P = .318$). These general results were confirmed in the next year's experiment (see below) and were similar to those in other high- versus low-predation comparisons (Reznick et al. 1996*a*).

The YH site had the widest channel, the deepest water, and the most open canopy (table 2). This site also has very low guppy densities and very high periphyton abundance (A. Hendry, personal observation). Together, these observations suggest that the YH site has higher resource levels than our other study sites. Few differences were evident among the other three sites, except that the DL site might have the most closed canopy (table 2).

Life History

For the life-history data (tables 3, 4; fig. 3), we make two types of comparison: between high- and low-predation environments within each river and between the Damier populations and their YH ancestors. In the first type of comparison, YH fish had greater reproductive allotment and significantly more and smaller embryos than did YL fish. A similar pattern was seen in the Damier, but the difference between predation environments was less dramatic (table 3). In the second type of comparison, both Damier populations had lower reproductive allotment (although significantly different only for DL) and significantly fewer and larger embryos than their YH ancestors (table 3). All of these conclusions are robust to some slope

Table 2: One-way ANOVAs testing for differences in habitat features between the study sites

	Stream width*		Water depth**		Canopy openness***	
Site	Mean	SE	Mean	SE	Mean	SE
DH	2.494^{B}	.057	1.144^{B}	.109	1.207^{BC}	.060
DL	2.555^{B}	.057	1.170^{B}	.109	$.950^{C}$	.068
YH	3.064^{A}	.094	1.890^{A}	.181	1.570^{A}	.096
YL	2.381^{B}	.057	$.934^{B}$	.109	1.275^{B}	.072

Note: DH, Damier high predation; DL, Damier low predation; YH, Yarra high predation; YL, Yarra low predation. Mean values are for $\log_{10}$ transformed data. Superscript letters that differ indicate groups of sites that are significantly different from each other in Tukey post hoc tests.

* $F = 13.106$, $P < .001$.

** $F = 6.847$, $P = .001$.

*** $F = 9.929$, $P < .001$.

Table 3: One-way ANCOVAs testing for differences in life-history traits between the study sites

	Embryo size (mg)			Embryo number (log)			Reproductive allotment		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
With interaction:									
Site	161.64	3	<.001	22.25	3	<.001	3.97	3	.010
Covariate	22.56	1	<.001	168.63	1	<.001	10.91	1	.001
Interaction	.51	3	.676	10.35	3	<.001	5.01	3	.003
Without interaction:									
Site	167.20	3	<.001	40.92	3	<.001	4.12	3	.008
Covariate	25.69	1	<.001	128.58	1	<.001	19.37	1	<.001
	Mean		SE	Mean		SE	Mean		SE
Adjusted means:									
DH ($N = 39$)	.766[C]		.026	1.699[C]		.088	.157[AB]		.009
DL ($N = 39$)	1.004[D]		.025	1.403[D]		.081	.146[C]		.008
YH ($N = 44$)	.603[A]		.023	2.174[A]		.076	.184[A]		.008
YL ($N = 43$)	1.350[B]		.041	.659[B]		.133	.148[AB]		.011

Note: DH, Damier high predation; DL, Damier low predation; YH, Yarra high predation; YL, Yarra low predation. Superscript letters that differ indicate groups of sites that are significantly different from each other in Tukey post hoc tests.

heterogeneity that arose due to different relationships in the YL fish (appendix, "Detailed Results for the Analysis of Life-History Data"). That is, the above conclusions for DH, DL, and YH hold regardless of whether YL samples were in the analysis. Finally, MANCOVA results confirmed that life-history traits differ among the populations when they are all considered together in a single model with the covariates (table 4).

Survival Comparisons

As in our earlier mark-recapture experiment (see above), survival was lower in the DH environment than in the DL environment (fig. 4). We make this inference because models assuming differences in survival between the Damier release environments (models 1–6 in tables 5, 6) fit the data much better than did models assuming no such difference (models 7–9).

In the DH environment, the different sexes and age classes showed different patterns of survival related to predation regime and river of origin. For males and females, predation effects dominated, with fish from high-predation sites, whether Yarra or Damier, showing the highest survival (prediction 1: DH = YH > YL; fig. 4; tables 5, 6). For juveniles, local river effects dominated, with Damier fish showing higher survival than Yarra fish of both types (prediction 3: DH > YH = YL; fig. 4; table 7). Although this last result had a *P*-value of .089, we interpret it as significant, owing to the large effect size (fig. 4) and the two-tailed significance test of a one-tailed hypothesis.

In the DL environment, the different sexes and ages again showed different patterns of survival. For females, all groups had equally high survival (fig. 4; table 6). For males, predation effects dominated, with fish from the low-predation populations, whether Yarra or Damier, showing the highest survival (prediction 2: DL = YL > YH; fig. 4), although an alternative (equal survival for all released groups) received almost as much support (table 5; see also below). For juveniles, predation effects also dominated, with fish from the low-predation populations, whether Yarra or Damier, showing by far the highest survival (prediction 2: DL = YL > YH; fig. 4; table 7).

We used a Monte Carlo approach to examine how the above conclusions from MARK might be altered if we had larger sample sizes (appendix, "Post Hoc Power Analysis of Mark-Recapture 2005 Data"). For females, increasing sample size would not have altered any of the above conclusions. For males, the only change would be increasing support for the alternative model (YL = DL = YH) in the DL environment.

We now summarize all of these survival results with respect to potentially adaptive change following their introduction in the Damier. In general, local Damier fish always survived as well or better than their YH ancestors. When survival was similar, this was generally to be ex-

Table 4: Full-model MANCOVA testing for differences in life-history traits between the study sites

	Wilks's λ	Exact *F*	df
Covariates:			
Somatic mass		298.2387	3, 111
Stage		17.4801	3, 111
Effects:			
Site	.3117	18.4521	9, 270.3
Somatic mass × site	.5895	7.2827	9, 270.3
Stage × site	.7147	4.4454	9, 270.3
Whole model	.0052	49.1204	33, 327.73

Note: $P < .0001$ for all.

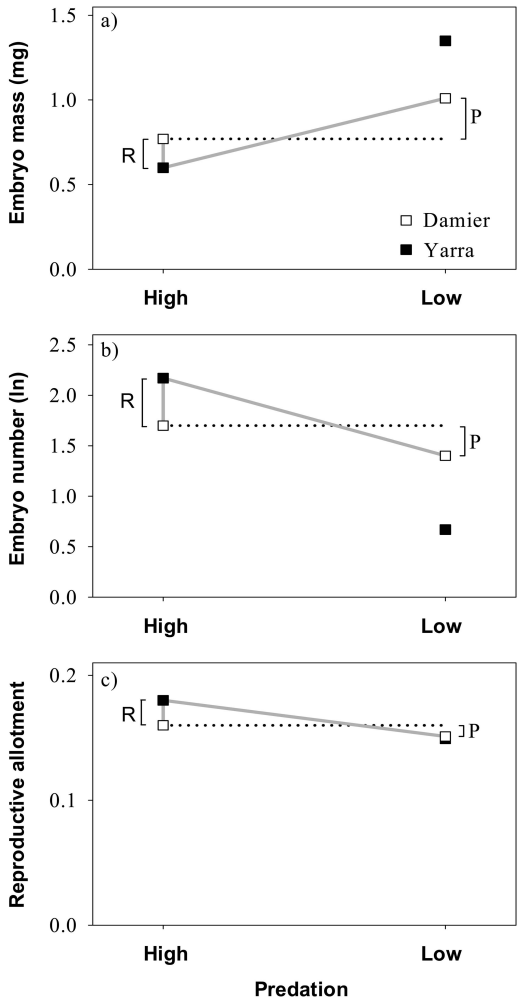

Figure 3: Life-history phenotypes of females captured from the four study sites. All values are least squares means as corrected ("adjusted") for appropriate covariates (see "Methods"). Yarra fish are indicated by the filled squares, and Damier fish are indicated by the open squares. Gray lines are drawn between the Yarra high-predation ancestral fish and each Damier-derived population, thus showing divergence between ancestral and derived fish. Divergence between Yarra high-predation and Damier high-predation fish is due to local river effects (*R*), whereas divergence between the two Damier populations will likely be mainly caused by predation (*P*). Divergence between the Yarra high-predation and Damier low-predation populations will likely be a combination of both river and predation effects. *a*, Average dry mass of individual embryos; *b*, number of embryos (log) per female; *c*, reproductive allotment of females (proportion of dry body mass composed of embryos). Detailed statistical results including post hoc Tukey tests are given in table 2.

pected. For example, both YH and DH fish were originally from high-predation environments and might therefore perform equally well in the DH environment. Moreover, females generally show high survival in all low-predation environments, and so no differences are expected. When the Damier fish did survive better than their ancestors, comparisons to the YL fish suggested the importance of adaptation to predation regime (juveniles, and perhaps males, in the Damier low-predation site) or the local river (juveniles in the high-predation Damier site). Overall, the strongest signatures of improved survival in the Damier came from juveniles.

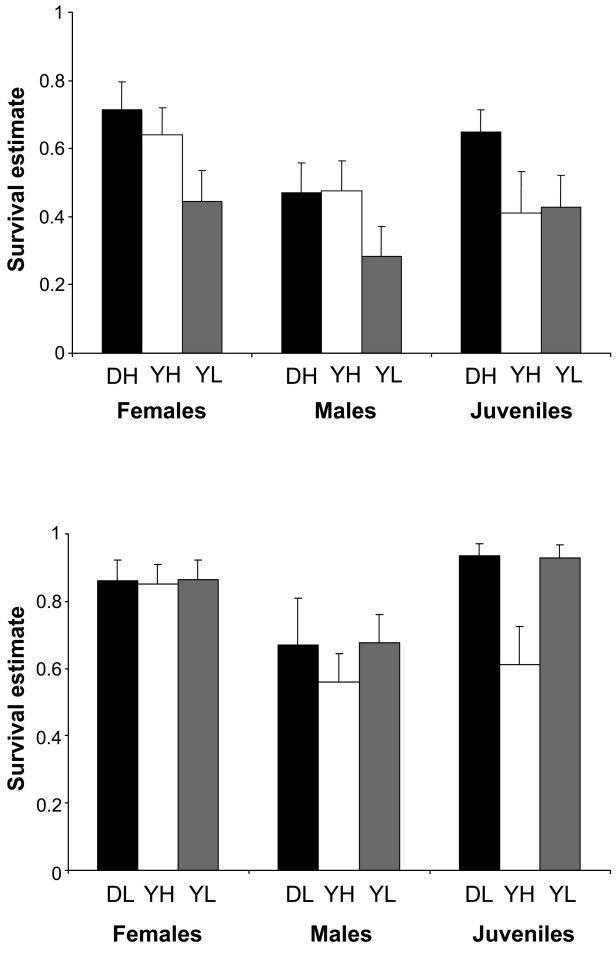

Figure 4: Survival estimates for a 2-week period for females, males, and juveniles in the Damier high-predation (*upper panel*) and the Damier low-predation (*lower panel*) environments. Release groups are Damier high predation (DH; *black*), Damier low predation (DL; *black*), Yarra high predation (YH; *white*), and Yarra low predation (YL; *gray*). These estimates correspond to the 2005 experiment in which the three groups were released into the two Damier sites and recaptured after 2 weeks (males, females, and juveniles) and 4 weeks (males and females). Survival estimates for the individually marked adults were derived from a Program MARK analysis that included all main effects and interactions (tables 5, 6). Survival estimates for the batch-marked juveniles were derived using generalized linear models (table 7). Bars are standard errors.

Table 5: Program MARK analyses of survival data for males from the four release groups (DH, DL, YH, YL) at each Damier release site (high predation or low predation)

Model	Estimated survival parameters (ϕ)		Scenario/prediction (taken from table 1)	AIC	ΔAIC	AIC weights	Model likelihood	Deviance
	High-predation environment	Low-predation environment						
1	DH = YH > YL	DL = YL > YH	Scenario A; predictions 1, 2	753.67	.00	.54	1.00	16.17
2	DH = YH > YL	DL = YL = YH	Scenario A; prediction 1	754.35	1.18	.36	.55	19.39
3	YH > DH > YL	YL > DL > YH	Scenario C; predictions 5, 6	757.32	3.65	.08	.16	15.71
4	DH = YH = YL	DL = YL > YH	Scenario A; prediction 2	758.58	4.92	.05	.09	23.13
5	DH = YH = YL	DL = YL = YH	H_{0D}	759.78	6.11	.03	.05	26.35
6	DH > YH = YL	DL > YL = YH	Scenario B; predictions 3, 4	763.33	9.66	.00	.01	25.83
7	DH = DL = YH = YL		H_{0A}	781.21	27.55	.00	.00	49.82
8	(DH = YH) > (DL = YL)		H_{0C}	782.77	29.40	.00	.00	49.34
9	(DH = DL) > (YH = YL)		H_{0B}	783.22	29.55	.00	.00	49.80

Note: AIC, Akaike Information Criterion; ΔAIC, difference between the AIC for a given model and that for the best model; DH, Damier high predation; DL, Damier low predation; YH, Yarra high predation; YL, Yarra low predation. Program MARK evaluates two-tailed hypotheses regarding whether different groups have different survival rates, rather than one-tailed hypotheses regarding which particular groups have higher or lower survival. We thus report the nature of the model (observed inequalities in the actual survival estimates) that was evaluated by MARK (for more information on our MARK analyses, see appendix, "Supplementary Information for Program MARK").

Discussion

Many studies have documented apparently adaptive phenotypic changes associated with environmental change. We here join the few of these studies (see "Introduction") that have also assessed how this adaptation can influence major fitness components in the wild. We did so by implementing some key design elements of laboratory studies on the evolution of fitness: we (1) introduced organisms (guppies) into new environments, (2) waited for possible adaptation (13–26 guppy generations), (3) verified the expected selection regimes (survival rates; fig. 2), (4) documented adaptive changes in phenotypic traits (female life history; fig. 3), and (5) compared the performance (survival) of ancestral and derived populations in the new environment (fig. 4). In the following paragraphs, we discuss in more detail the divergence in life history and survival, before then discussing some implications.

Life History

Previous work on guppies, starting with Reznick and Endler (1982), has shown that low-predation females tend to have fewer offspring, larger offspring, and lower investment in current reproduction than do high-predation females. We documented a broadly similar pattern of divergence between predation environments within the Damier (fig. 3). Our assay for this divergence was phenotypic in the sense that it was based on wild-caught individuals. We nevertheless expect that the observed differences have a genetic basis because life-history differ-

Table 6: Program MARK analyses of survival data for females from the four release groups (DH, DL, YH, YL) at each Damier release site (high predation or low predation)

Model and rank (not corrected)	Estimated survival parameters (ϕ)		Scenario/prediction (taken from table 1)	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weights	Model likelihood	Q deviance
	High-predation environment	Low-predation environment						
1 (1)	DH = YH > YL	DL = YL = YH	Scenario A; prediction 1	325.30	.00	.56	1.00	10.97
2 (2)	DH = YH > YL	DL = YL > YH	Scenario A; predictions 1, 2	327.30	2.00	.20	.37	10.94
3 (5)	DH = YH = YL	DL = YL = YH	H_{0D}	328.51	3.21	.11	.20	16.21
4 (4)	DH > YH = YL	DL > YL = YH	Scenario B; predictions 3, 4	329.93	4.64	.05	.10	13.58
5 (6)	DH = YH = YL	DL = YL > YH	Scenario A; prediction 2	330.51	5.21	.04	.07	16.18
6 (3)	DH > YH > YL	YL > DL > YH	Scenario C; predictions 5, 6	330.99	5.70	.03	.06	10.56
7 (8)	DH = DL = YH = YL		H_{0A}	343.24	17.94	.00	.00	32.95
8 (7)	(DH = DL) > (YH = YL)		H_{0B}	343.73	18.93	.00	.00	31.43
9 (9)	(DL = YL) > (DH = YH)		H_{0C}	345.26	19.96	.00	.00	32.95

Note: QAIC, quasi–Akaike Information Criterion ($QAIC_c$); DH, Damier high predation; DL, Damier low predation; YH, Yarra high predation; YL, Yarra low predation. Columns are the same as for table 5, except that the information criterion used is the $QAIC_c$, which has been corrected for overdispersion. The first column also reports (in parentheses) the rank order of models when the correction for overdispersion is not applied.

Table 7: Generalized linear models comparing survival of juveniles among the four release groups (DH, DL, YH, YL) at the two Damier release sites (high predation or low predation)

			Pairwise comparisons (*P*)		
Group	χ^2	*P*	(DH or DL) versus YL	(DH or DL) versus YH	YH versus YL
High predation	5.10	.078	.059	.089	.912
Low predation	11.17	.004	.887	.004	.006

Note: DH, Damier high predation; DL, Damier low predation; YH, Yarra high predation; YL, Yarra low predation. Owing to interactions among main effects (results not shown), separate analyses were performed for each predation environment (high or low). *P* values for pairwise comparisons among three groups at each release site are shown in the last three columns. DH was released into the DH site only. DL was released into the DL site only.

ences are maintained in common-garden experiments with guppies from the Damier (S. Gordon, A. Hendry, and D. Reznick, unpublished data) and other rivers (Reznick et al. 1990, 1996*b*). In short, Damier guppies show the expected pattern of divergence in life-history traits between high- and low-predation environments. Despite the broad similarity of life-history divergence in the Damier to that in other rivers, two nuances warrant further discussion.

One interesting nuance is that divergence in the Damier was less dramatic than the divergence in most other rivers (including the Yarra; see fig. 3; table 3). Some unlikely explanations for this weaker divergence include (1) limited time for divergence (rebuttal: greater divergence has been documented over similar time frames in other guppy introductions [Reznick et al. 1990]), (2) limited genetic variation for adaptation (rebuttal: 200 fish were introduced and trait variation remains high), and (3) high gene flow in the Damier (rebuttal: this will not explain why the isolated DL population has shown limited divergence). A more promising explanation for limited divergence in the Damier is that divergent selection is weaker than in other rivers. The northern slope of Trinidad boasts a different suite of predators than the southern slope sites used in previous guppy introductions. In addition, other environmental factors that influence life histories (Grether et al. 2001; Reznick et al. 2001) are much less divergent between predation environments in the Damier than they are in the Yarra (table 2) and in other rivers (Reznick et al. 2001).

Another interesting nuance is that both Damier populations have diverged from their YH ancestors: both moved closer to a low-predation phenotype (fig. 3). One potential explanation is that gene flow from the DL population above the waterfall (gene flow in the other direction would be very low) may be constraining adaptation of the high-predation population below the waterfall. Another potential reason is again a difference in selection: the DH site has fewer predators and more closed canopies than does the YH site. Overall, these patterns suggest that both local river and predation effects might influence trait adaptation (fig. 3) and therefore might also contribute to survival differences.

Survival Comparisons

Supporting our general prediction (see "Introduction"), Damier fish survived as well as or better than their YH ancestors when both groups were tested together in the Damier (fig. 4; tables 5–7). Support for the more detailed predictions (table 1) then depended on the specific Damier test environment (high or low predation) and the specific population component (females, males, juveniles). In the DH environment, adaptation by males and females was driven by predation (prediction 1), whereas adaptation by juveniles was driven by local river effects (prediction 3). In the DL environment, no survival differences were seen for females, presumably because their large size allows high survival in such environments (Seghers 1973), whereas adaptation by juveniles and (perhaps) males was driven by predation (prediction 2). With respect to change since the introduction, Damier fish showed higher survival than their ancestors for juveniles and (perhaps) males in the DL environment (predation effects) and for juveniles in the DH environment (local river effects).

Overall, then, Damier adults showed only modest divergence in survival rates from their ancestors. This general result suggests that the adaptation of guppy adults to an extreme high-predation environment (Yarra) also makes them suitable in a less extreme high-predation environment (Damier) and does not dramatically compromise their survival in a nearby low-predation environment (Damier). For juveniles, the story was very different. Here, Damier fish in both populations survived at higher rates than did their ancestors. This result fits expectations that juvenile performance is under strong divergent selection (Bashey 2002, 2008; Bronikowski et al. 2002) and can have dramatic impacts on population dynamics (Taborsky 2006). For these reasons, we conclude that adaptation in the Damier has made an important contribution to individual fitness and perhaps to population dynamics.

The observed patterns of survival could potentially reflect some combination of prior experience, plasticity, selection within a generation, and genetic adaptation. The first three of these effects could have arisen because our experimental fish were captured from the wild. In the case

of prior experience, Damier fish may have been familiar with the local Damier environment. We reduced this possibility by first holding all of the experimental fish for several days in the laboratory and then releasing individuals into different pools from the ones in which they were captured. In the case of plasticity, differential environmental effects in the local environment may have led to adaptive plasticity before we captured the fish for marking. In the case of selection within a generation, differential mortality before capture may have weeded out some maladapted phenotypes/genotypes. Any of these effects could have given the Damier fish a nongenetic survival advantage following release back into the Damier, but we also have various reasons to suspect at least some strong genetic effects. First, adaptive phenotypic divergence in guppies usually has a genetic basis (Endler 1980; Reznick and Bryga 1987; Reznick et al. 1997; Magurran 1998, 2005; O'Steen et al. 2002), and this is known to be the case for at least some traits in the Damier (S. Gordon, A. Hendry, and D. Reznick, unpublished data). Second, the greatest survival differences were evident for juveniles (fig. 4), which would have had less time than adults to accumulate any nonevolutionary effects in their local environments.

The specific traits driving survival patterns in the Damier are not certain. For adults, female life history and male color seem unlikely because females showed the least survival differences (current study) and because Damier males have not diverged strongly in the size and number of color spots (Karim et al. 2007). For juveniles, embryo size may be an important contributor, given that this trait strongly influences juvenile performance (Bashey 2002, 2008) and has changed considerably in the Damier (fig. 3). Also important may be unquantified aspects of behavior, such as microhabitat selection (Seghers 1973), predator detection (Fraser and Gilliam 1987), predator inspection (Dugatkin and Alfieri 1992), shoaling (Magurran and Seghers 1991), and evasive tactics (O'Steen et al. 2002). Divergence in these behaviors is known to have a genetic basis in guppies (see above references), further suggesting that any resulting survival differences may have a genetic basis.

Implications

Contemporary adaptive change can, in theory, aid population persistence in the face of environmental change (e.g., Lynch and Lande 1993; Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Boulding and Hay 2001; Orr and Unckless 2008). Explicit tests of this possibility, however, are lacking for natural populations (review: Kinnison and Hairston 2007). Studies such as ours (see also Pelletier et al. 2007 and Kinnison et al. 2008) take steps in this direction, by examining the response of major fitness components to environmental change. Here, we found evidence that adaptive change improves survival rates for at least some components of a population. The most striking observation is that juveniles showed a 54%–59% increase in survival rate (fig. 4) only 8–9 years after introduction to a new environment.

The limitations of our study are several. First, our survival rate comparison did not have a temporal replicate. Such replicates must now wait until any residual evolutionary effects of the released fish have decayed back to near the starting condition. Second, our sample sizes were relatively small, which was necessitated by the very small populations at the time of our experiment. Thus, we likely have good estimates of population parameters, but these parameters may be influenced by random variation owing to small population size. Third, our overall experiment has been unreplicated in the sense that we examined only a single experimental introduction (Yarra to Damier), and so our inferences are specific to that context. Ideally, we would now replicate our study in another population and site. This limitation, however, also applies to other studies examining the survival consequences of adaptation to altered environments in nature (e.g., Pelletier et al. 2007; Kinnison et al. 2008). Evolutionary biologists are still at such an early stage in addressing this particular question that demonstrations for single populations remain extremely important.

Despite these limitations, the magnitude of observed change in the current study was realistic. First, previous introduction studies have shown even greater changes in guppy life-history traits over similar time frames (Reznick et al. 1990, 1997). Second, behavioral traits likely influencing survival rates, such as predator escape ability, have also been found to evolve in these earlier guppy experiments (O'Steen et al. 2002). Third, our results are roughly comparable to laboratory experiments that show adaptation can increase fitness by 1%–10% per generation (Burt 1995). That is, even our most extreme estimate (54%–59% increase in survival for juveniles over 13–26 generations) is well within this range. Note that direct quantitative comparisons to theoretical models (e.g., Lynch and Lande 1993; Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Boulding and Hay 2001; Orr and Unckless 2008) are not possible, given different assumptions (gradual environmental change in many models) and different response variables (typically the probability of population persistence).

The changes in survival in our study may initially seem encouraging from a conservation perspective, but it is important to remember that the elapsed time frame was 13–26 guppy generations. The current results may therefore provide little solace for biologists and managers concerned with longer-lived species. Yet it is also important to remember that most of the change observed in our study

may have occurred early in the time sequence. Indeed, asymptotic evolutionary approaches toward new optima are expected in theory (Stockwell et al. 2003) and are seen in empirical analyses (Reznick et al. 1997; Kinnison and Hendry 2001). Confirmation, however, awaits fine-scale tracking of evolutionary change immediately following environmental change.

Ultimately, we are interested not only in individual fitness but also in population persistence. This topic is much more difficult to assess in nature because it requires the close monitoring of replicate experimental introductions that ultimately vary in their success. Indeed, our experiment might initially be taken as evidence that adaptation is not important for population persistence, simply because the introduced fish survived through an initial period when local adaptation was not strong. This realization highlights the potential fitness consequences of other factors, such as relaxation from competition and interannual environmental variation. These and other potential effects suggest a rich series of opportunities and challenges for future studies of experimental evolution in the wild.

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Left, guppy predator *Gobiomorus* in natural environment. *Right*, males in display for single female guppy. Photographs by Paul Bentzen.