

Life histories have a history: effects of past and present conditions on adult somatic growth rates in wild Trinidadian guppies

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Summary

1. Environmental conditions in the present, more recent past and during the juvenile stage can have significant effects on adult performance and population dynamics, but their relative importance and potential interactions remain unexplored.

2. We examined the influence of food availability at the time of sampling, 2 months prior and during the juvenile stage on adult somatic growth rates in wild Trinidadian guppies (*Poecilia reticulata*).

3. We found that food availability during both the early and later parts of an individual's ontogeny had important consequences for adult growth strategies, but the direction of these effects differed among life stages and their magnitude, in some cases, depended on food levels experienced during other life stages. Current food levels and those 2 months prior to growth measurements had positive effects on adult growth rate; though, food levels 2 months prior had a greater effect on growth than current food levels. In contrast, the effects of food availability during the juvenile stage were higher in magnitude but opposite in direction to current food levels and those 2 months prior to growth rate measurements. Individuals recruiting under low food levels grew faster as adults than individuals recruiting during periods of high food availability. There was also a positive interaction between food levels experienced during the juvenile stage and 2 months prior such that the effects of juvenile food level diminished as the food level experienced 2 months prior increased.

4. These results suggest that the similar conditions occurring at different life stages can have different effects on short- and long-term growth strategies of individuals within a population. They also demonstrate that, while juvenile conditions can have lasting effects on adult performance, the strength of that effect can be dampened by environmental conditions experienced as an adult.

5. A simultaneous consideration of past events in both the adult and juvenile stage may therefore improve predictions for individual- and population-level responses to environmental change.

Key-words: carry-over effects, delayed quality effects, early conditions, life history, phenotypic plasticity, seasonality

Introduction

Most organisms encounter considerable environmental variation throughout their lifetime. For example, numerous species have life cycles in which juveniles and adults live in distinctly different habitats and capitalize on different resources (Moran 1994). Migratory species experience vastly

different conditions during migration and while residing on their breeding and wintering grounds (Webster *et al.* 2002). Many species also face temporal variation within a given habitat through stochastic fluctuations or regular seasonal changes in factors, such as temperature and food availability (Poulin, Lefebvre & McNeil 1992; Farley & Fitter 1999).

Among these organisms, there is increasing evidence that past conditions can have lasting effects on individual performance. Behavioural and reproductive decisions, such as where to forage and when to reproduce, depend on current conditions but are also contingent on the individual's history

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of environmental exposure (Metcalfé & Monaghan 2001; Lummaa & Clutton-Brock 2002; Harrison *et al.* 2011). These delayed effects are thought to occur because environmental conditions at any given time influence the internal state of the individual – such as its body size and condition – which in turn affects its performance in the future (McNamara & Houston 1996).

Conditions experienced during early growth and development can have long-term consequences for the adult phenotype (Henry & Ulijaszek 1996; Monaghan 2008). For example, a suite of traits – including metabolic, cardiovascular, behavioural, reproductive and immune functions – has been shown to vary with nutrition during early growth and development (Bateson 2001; Jasienska, Thune & Ellison 2006; Schilder & Marden 2006) and have lasting effects on individual life-history traits and subsequent reproductive success (Descamps *et al.* 2008; Hamel *et al.* 2009; Auer *et al.* 2010). Long-term effects of early environments on individual and cohort performance – called ‘delayed life-history effects’, ‘delayed quality effects’ or ‘developmental effects’ – have been demonstrated in numerous organisms and are thought to play an important role in population dynamics (Beckerman *et al.* 2002; Lindström & Kokko 2002; Benton, Plaistow & Coulson 2006).

Adult performance is also influenced by more recent conditions experienced in the adult stage (Bearhop *et al.* 2004; Brommer, Karell & Pietiäinen 2004; Harrison *et al.* 2011). ‘Carry-over effects’ or ‘seasonal interactions’ can occur when events in one season affect the state of the individual and its success during the following season (Harrison *et al.* 2011). For example, winter food quality can have positive effects on reproductive success in the upcoming breeding season (Robb *et al.* 2008). Environmental conditions can also have more immediate consequences for individual performance within a season (Stephens *et al.* 2009). For example, some organisms rely on energy acquired in the recent past to finance reproduction (Reznick & Yang 1993; Warner *et al.* 2008). Like the long-term effects of juvenile environments, these delayed effects on individual and cohort performance are thought to play an influential role in population dynamics (Norris & Marra 2007; Harrison *et al.* 2011).

An individual’s current state and its ability to respond to change may therefore reflect an integrated history of exposure to past environments in both the adult and juvenile stages. However, because the delayed effects of environmental variation within and across life stages have been studied in isolation, their relative influence, interactions and subsequent importance remain unexplored. On one hand, conditions during critical stages of early growth and development can affect the structure and *modus operandi* of the developing organism and may have permanent effects on the emergent phenotype and its performance (Henry & Ulijaszek 1996; Metcalfé & Monaghan 2001). On the other hand, phenotypic plasticity in life-history strategies or subsequent environmental heterogeneity may weaken or obliterate these earlier effects over time (Auer 2010). In the latter case, more recent conditions may have a larger effect on the present state of the

adult organism and how it responds to variation in the current environment. In predicting individual responses to environmental change and their subsequent effect on population dynamics, it remains unclear if we need to account for the entire histories of individuals within a population or if events at one life stage or time are better predictors of individual performance than others.

We examined the effects of early, recent and current environmental conditions on adult somatic growth rates in cohorts of wild Trinidadian guppies (*Poecilia reticulata*). Guppies are small, livebearing fishes that inhabit freshwater streams on the island of Trinidad, West Indies. Food availability in these streams fluctuates on a seasonal basis through distinct alternating wet and dry periods (Kohler 2010). Because food availability can change substantially within only a few months, growth conditions can vary widely throughout the lifetime of a guppy. Studies demonstrate that guppy growth rates are highly sensitive to variation in both past and current environmental conditions (Grether *et al.* 2001; Auer 2010). Somatic growth rates are known to have important consequences for individual fitness and for the demographic structure and dynamics of guppy populations because of their effect on body size and vital rates (Rodd & Reznick 1997; Bronikowski *et al.* 2002). Conditions during both the early and later stages of life, therefore, have the potential to show delayed effects on adult growth and subsequent population demographics.

Here, we present data on seasonal variation in adult growth rates of wild guppy females. We focused only on female guppies because males cease growing at maturity. Using bimonthly estimates of food availability coupled with longitudinal measurements of female body size, we examined adult female growth responses to current environmental conditions and investigated how conditions 2 months prior as well as in the juvenile stage affected those growth rates. We explored alternative models for adult growth and evaluated the relative importance of past and current environments as predictors of adult growth.

Materials and methods

STUDY AREA

We conducted the study in a small tributary to the upper reaches of the Guanapo River in the Northern Range Mountains of Trinidad, West Indies where a population of guppies was introduced in March 2008 and has been monitored since. The tributary is a small, first-order stream with a distinct pool-riffle structure. It is located above a barrier waterfall that excludes all but one fish species, Hart’s killifish (*Rivulus hartii*) that may prey on smaller guppies (Liley & Seghers 1975). As part of a large-scale study on the feedbacks between ecological and evolutionary processes, 38 pregnant female and 38 male guppies were transplanted to this natural upstream tributary in March 2008 from a downstream site. Each female and male was tagged with a unique colour combination of subcutaneous visible implant elastomer marks (NorthWest Marine Technology, Shaw Island, WA, USA). This marking technique allows identification of individuals without sacrificing their chances of survival in the field (Reznick *et al.*

1996). The introduction area comprises approximately 100 m of stream between two waterfalls.

STUDY DESIGN

We examined adult growth responses to current and previous food availability in recruits from this founding population. Guppies were netted each month and brought back into the laboratory. All recruits were individually marked once they reached 14 mm. Standard length was measured from photographs taken of each fish upon its initial capture and each successive recapture. For each photograph, the fish was anaesthetized in a neutrally buffered solution of MS-222 and straightened over a plate next to a ruler. Its picture was then taken with a digital camera mounted on a tripod above. Standard length was then determined using the program *IMAGE J* (US NIH, Bethesda, MD, USA). Guppies were tracked from May 2008 to July 2009, the first cohorts recruiting 2 months after the initial introduction in March 2008.

Food availability was estimated by sampling both benthic algae and benthic invertebrates that guppies are known to prey on (Bassar *et al.* 2010). Three transects were established in pools 30–50 m apart and were sampled on a bimonthly basis from March 2008 to July 2009. Pools are the habitat most used by guppies and were defined as those deeper sections of stream that accumulated fine material and leaves under low flow velocities.

To estimate algal abundance, epilithon samples were collected using a modified version of a Loeb sampler (5.07 cm², Loeb 1981). Epilithon was sampled from five to ten randomly-selected areas in the vicinity of each transect and combined into a single slurry. Quantitative subsamples taken from each slurry were used to estimate biomass as ash free dry mass (AFDM). AFDM was analysed by filtering a known amount of homogenous sample through a preweighed ashed (at 450 °C for 2 h) 47-mm Whatman GF/F filter. The material was dried in an oven at 50–55 °C until constant dry mass was achieved and then placed in a desiccator until analysis. The material and filter together were weighed, ashed in a muffle furnace at 500 °C for 1 h and reweighed to calculate AFDM per square metre (Steinman, Lambert & Leavitt 2006).

To estimate benthic invertebrate abundance, macroinvertebrate samples were collected from pools on the same bimonthly basis as the epilithon samples described earlier using a Hess sampler with a basal area of 0.032 m² and 250-µm mesh size (Wildlife Supply Company, Yulee, FL, USA). The substratum was disturbed by hand to suspend invertebrates which were then collected in a downstream net. The samples were rinsed through a 250-µm sieve, and retained materials were rinsed into a sample bag and preserved with ≥70% ethanol containing rose bengal dye to facilitate sorting. In the laboratory, samples were rinsed through stacked 1-mm and 250-µm sieves to separate coarse (> 1 mm) and fine (> 250 µm, < 1 mm) fractions. All invertebrates were removed from coarse fractions, whereas fine fractions were subsampled if necessary. Subsampling was accomplished using a Folsom plankton splitter (Aquatic Research Instruments, Hope, ID, USA) to divide samples (up to 1/8), and subsampled fractions were processed completely to acquire the target of 100 organisms (75 minimum). Sorted invertebrates were identified to the lowest practical taxonomic level (usually genus), counted and measured to the nearest millimetre using a stage micrometre. AFDM was quantified using length-mass regressions calculated following the procedures described by Benke *et al.* (1999) or from published values (Benke *et al.* 1999; Sabo, Bastow & Power 2002; Baumgartner & Rothhaupt 2003; Hall, Dybdahl & VanderLoop 2006; Miyasaka *et al.* 2008).

Guppies are known to feed on both algae and invertebrates (Bassar *et al.* 2010), so the mean of the summed AFDM of both invertebrates and algae per month across the three transects was used as a measure of total food availability. Because guppy population density increased throughout the study period and could affect per capita food availability, density was also estimated each month (Statistical analysis section).

STATISTICAL ANALYSES

We examined how food availability during the current adult, recent adult and juvenile stages affected adult growth rates while controlling for temporal changes in population density. We calculated adult growth on a monthly basis as $[(SL_{\text{recapture}} - SL_{\text{last capture}}) / (\text{the number of days between captures})] * 30 \text{ days (mm month}^{-1})$. Food conditions experienced in the current adult, recent adult and juvenile stage were defined as follows: current conditions were those present during each monthly adult growth measurement; recent adult conditions were those that had occurred during the previous food sampling episode 2 months prior; juvenile conditions were those that had occurred at the time of first capture (Fig. 1). Population densities for each month were estimated by fitting the data to a Cormack–Jolly–Seber capture–recapture model for open populations (Cormack 1989). This was implemented in R package 'RCAPTURE' (Baillargeon & Rivest 2007) which uses Cormack's (1989) log-linear approach.

We considered only those measures of growth that spanned a regular monthly recapture interval (26–33 days) and that were taken during the months for which food availability estimates were available. In addition, we considered only those individual females that were first captured at a standard length smaller than 21 mm because size at maturation ranges from 15 to 20 mm in the field and juvenile conditions could therefore not be reliably assigned to larger individuals (Reznick & Endler 1982). Because the juvenile stage in guppies is known to range from 1.5 to 2 months in duration (Reznick & Bryga 1996; Auer *et al.* 2010), individuals that first recruited during and directly after a month in which food was measured were considered part of the same cohort (Fig. 1). For example, we assumed that individuals recruiting in June had also experienced conditions present in May during their 2 month stage as juveniles. Finally, to examine the effects of food availability 2 months prior in the adult stage, we considered only older females that had been tracked for at least 3 months

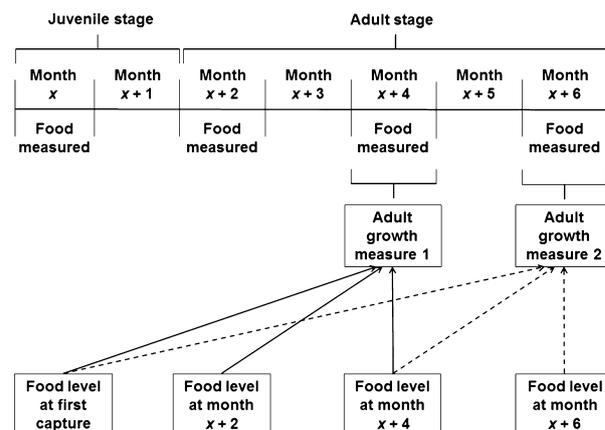


Fig. 1. Schematic illustration of the schedule of adult growth measurements for an individual fish, as well as food conditions during the juvenile stage, 2 months prior, and in the present that could influence the individual's growth rate during the adult stage.

after they were first captured. This prevented temporal overlap between measures of food 2 months prior and those measured at first capture. For example, growth rates for females first captured in May were analysed from September onwards so that the effects of food availability 2 months prior did not overlap with juvenile conditions in May.

There were a total of 207 females that met these criteria. The analysed data included one to six growth measurements per female with an average of 2.3 growth measures per female, totalling 483 nonindependent data points. The number of females analysed for each food sampling period was as follows: in 2008, 25 in September and 55 in November; in 2009, 70 in January, 85 in March, 104 in May and 144 in July.

We used a linear mixed model approach to examine effects of food availability in the past and present on adult rates of monthly growth. Each female was characterized by one measure of juvenile food availability, so food level at first capture during the juvenile stage was included as a time-invariant covariate. Current food level and food levels 2 months prior changed throughout the female's lifetime, so they were modelled as time-varying covariates. Correlation coefficients between current food availability, food availability 2 months prior and juvenile food availability were all < 0.3 (all $P > 0.5$), so measures of past and present conditions provided independent measures of food availability.

Because population density increased throughout the study period, correlation coefficients between densities during the juvenile stage, 2 months prior in the adult stage and in the present were all > 0.43 (all $P < 0.05$). However, correlation coefficients between current population density and current food, food 2 months prior and juvenile food were all < 0.7 (all $P > 0.1$). Thus, only current population density was included as a time-varying covariate to control for its effects on per capita food availability. Female identity was nested within cohort and included as a random effect to control for the non-independence of repeated measures on the same female and to control for conditions unique to each cohort that were not measured (Singer & Willett 2003). Standard length and its square at the beginning of each month served as covariates for all measurements of monthly growth because growth is known to be a convex decreasing function of length (Reznick & Bryant 2007). Parameter estimates were centred around a standard length of 23 mm, the mean standard length of adults across all growth measurements (*sensu* Singer & Willett 2003). Residuals were normally distributed, so growth was analysed using the Mixed procedure in SAS version 9.3 (SAS Institute, Cary, NC, USA).

We used an information-theoretic approach to evaluate 20 candidate models that included standard length and its square, current population density, and different combinations of food availability at the different time periods and the two- and three-way interactions between food availability at different time periods in the past and present (Table S1; Burnham & Anderson 2002). We used Akaike's Information Criterion for smaller sample sizes (AICc) to assess the explanatory value and parsimony of each candidate model. The strength of each model was determined by the difference in AICc values between each model and the best fitting model, ΔAICc . Akaike weights, w_i , were then computed to determine the weight of evidence of each model relative to the set of candidate models (Burnham & Anderson 2002). Akaike weights can range from 0 to 1, the best fitting model being the one with the highest weight. We created a confidence set of models by including models with Akaike weights within 10% of the highest value, which is comparable with the minimum cut-off point suggested by Royall (1997). To account for model selection uncertainty, we then calculated the model-averaged estimates

for those parameters, their standard errors and 85% confidence intervals included in the confidence set of models (Burnham & Anderson 2002). Parameter estimates in the final averaged-model were considered reliable predictors of adult growth if their 85% confidence intervals did not include zero (Arnold 2010). AICc and w_i values of the different models were evaluated using maximum likelihood estimation, but estimates presented for the final averaged-model are based on restricted maximum likelihood (Zuur *et al.* 2009).

Results

During the study period, food availability fluctuated significantly, in some instances increasing or decreasing 12-fold across a span of 2 months (Fig. 2a). Population density also changed through time, but generally increased with only minor fluctuations in its upward trend (Fig. 2b).

INDIVIDUAL AND COHORT GROWTH TRAJECTORIES

Standard lengths for adult growth measurements ranged from 17.24 to 32.62 mm and averaged 23.4 mm. Adult growth rates ranged from 0 to 3.64 mm per month and averaged 0.57 ± 0.03 mm per month across all months and all

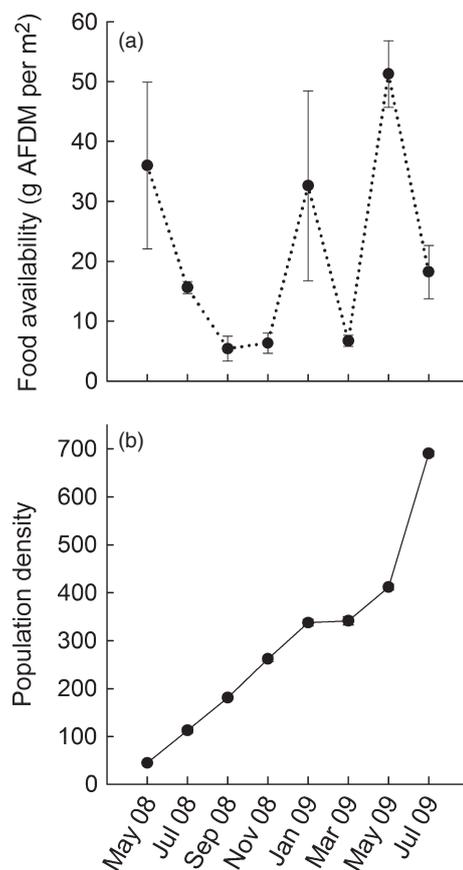


Fig. 2. Temporal variation in (a) food availability and (b) population density in a tributary to the upper Guanapo River in Trinidad, West Indies. Food availability is calculated as the summed ash free dry mass (g) of both algae and invertebrates per square metre. Bars denote ± 1 SE. Estimates of population density do not include individuals smaller than 14 mm in length.

size classes. All cohorts grew rapidly at first and then slowed their growth as they reached larger sizes (Fig. 3a). There was significant variation among cohorts in their asymptotic body size, some slowing their growth appreciably at a mean of

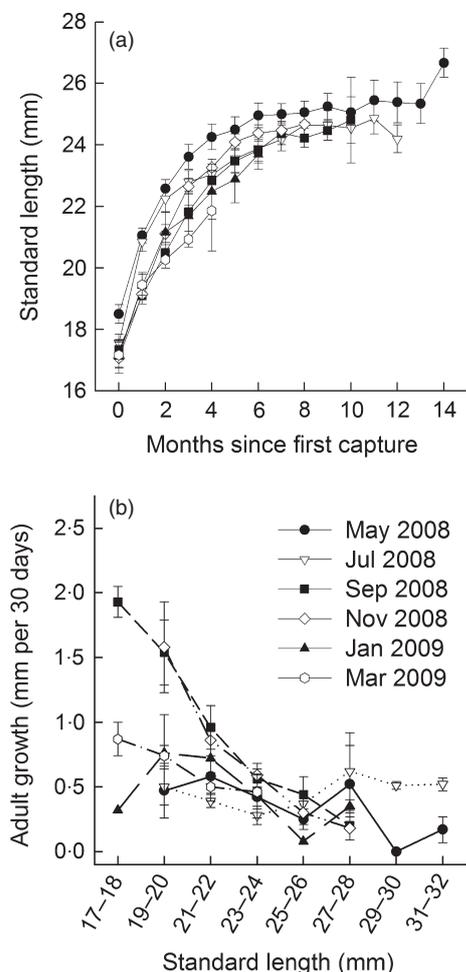


Fig. 3. (a) Size trajectories and (b) growth trajectories of 207 females from six different cohorts born between March 2008 and March 2009 in a tributary to the upper Guanapo River in Trinidad, West Indies. Size trajectories are from the time of first capture, while growth trajectories are only for adult growth rate considered in analyses (starting at adult growth measure 1 as shown in Fig. 1). Bars denote ± 1 SE.

Table 1. Akaike's Information Criterion ranking of models describing the effects of standard length (SL) and its square (SL²), population density (Dens), and food availability in the present (Cur), 2 months prior (2mo) and during the juvenile stage (Juv) on adult somatic growth rates in female Trinidadian guppies (*Poecilia reticulata*). Shown are the number of parameters (k), the difference in Akaike's Information Criterion (Δ AICc) between each model and the top-ranked model, and the Akaike weights (ω_i) of each model in the confidence set ($\omega_i \geq 0.10 \times \omega_{\text{best}}$)

#	Model _i	k	Δ AICc	ω_i
3	SL + SL ² + Dens + Cur + 2mo + Juv + Cur*Juv + 2mo*Juv	11	0	0.407
8	SL + SL ² + Dens + Cur + 2mo + Juv + 2mo*Juv	10	1.0	0.247
2	SL + SL ² + Dens + Cur + 2mo + Juv + 2mo*Juv + Cur*Juv + Cur*2mo	12	2.0	0.150
4	SL + SL ² + Dens + Cur + 2mo + Juv + Cur*2mo + 2mo*Juv	11	2.8	0.100
1	SL + SL ² + Dens + Cur + 2mo + Juv + Cur*Juv + Cur*2mo + 2mo*Juv + Cur*2mo*Juv	13	2.9	0.100

21 mm and others at 25 mm. Size-dependent growth trajectories also differed considerably among cohorts; in the smaller size classes, some cohorts grew four times as much in 1 month as other cohorts (Fig. 3b).

EFFECTS OF THE PAST AND PRESENT

Food availability at the three time stages – those during the present, 2 months prior and as far back as the juvenile stage – were all important predictors of adult growth rates after controlling for effects of body size and population density (Tables 1 and 2). However, the direction of their effects differed among time stages and their magnitude, in some cases, depended on food levels at other time stages. Current food levels and those 2 months prior to growth measurements had positive effects on adult growth rate; though, food levels 2 months prior had a greater effect on growth than current food levels (Table 2, Fig. 4a,b). In contrast, the effects of food availability during the juvenile stage were higher in magnitude but opposite in direction to current food levels and those 2 months prior to growth rate measurements. Individuals recruiting under low food levels grew faster as adults than individuals recruiting during periods of high food availability (Table 2, Fig. 4c). There was also a positive interaction between food levels experienced during the juvenile stage and 2 months prior such that the effects of juvenile food level diminished as the food level experienced 2 months prior increased (Table 2, Fig. 5). Figure 5 illustrates the interaction among food levels 2 months prior and during the juvenile stage decomposed from the more general relationships shown in Fig. 4. Model-averaged parameter estimates of the remaining two- and three-way interactions between food levels at the three time periods were not reliable predictors of adult growth because their 85% confidence intervals included zero (Table 2).

Discussion

An individual's history of exposure to past environmental conditions in the adult stage and as far back as the juvenile stage is known to affect its decisions in the current environment. However, despite the role that past events in these two life stages are thought to play in processes, such as

Table 2. Model-averaged means (Estimate), their unconditional standard errors (SE) and 85% confidence intervals (85% CI) for the fixed effects of standard length (SL) and its square (SL²), current population density (Dens), and food availability in the present (Cur), 2 months prior (2mo) and during the juvenile stage (Juv) on adult somatic growth rates in adult female Trinidadian guppies (*Poecilia reticulata*). Food availability is calculated as summed ash free dry mass (g per m²) of both algae and invertebrates. SL is centred on 23 mm

Parameter	Estimate	SE	85% CI	
			Upper	Lower
Intercept	1.512	0.259	1.888	1.136
SL	-0.117	0.012	-0.099	-0.135
SL ²	0.012	0.003	0.016	0.007
Dens	-0.003	0.001	-0.002	-0.004
Cur	0.009	0.005	0.016	0.001
2mo	0.014	0.007	0.024	0.005
Juv	-0.020	0.007	-0.011	-0.030
Cur*2mo	-0.00002	0.00030	0.0004	-0.0005
Cur*Juv	0.00012	0.00012	0.0003	-0.0001
2mo*Juv	0.00034	0.00017	0.0006	0.0001
Cur*2mo*Juv	0.000002	0.000003	0.00001	-0.000002

population dynamics, their effects on and relative importance for individual performance have not yet been evaluated simultaneously. Here, we show that past events occurring in the juvenile and adult stage can both have important delayed consequences for adult growth strategies, but the direction of these effects can differ among life stages and their magnitude can depend on food levels at other life stages.

Lower food availability during the juvenile stage led to faster growth during adulthood, while similar conditions in the recent past had negative effects on adult growth. These contrasting effects suggest that the same conditions during the juvenile and adult stages may have different effects on the state of the organism and its subsequent long- and short-term growth strategies, respectively. However, the dampening of juvenile food effects by food levels experienced 2 months prior in the adult stage also suggests that environmental heterogeneity in the adult stage can, in some cases, obliterate the long-term effects of the juvenile environment.

The negative effect of low food experienced 2 months prior that we report here is consistent with effects observed in other studies. Poor food conditions generally have negative effects on physiological condition and subsequent performance (Ratikainen *et al.* 2008; Harrison *et al.* 2011). These negative effects can occur because conditions in the past place constraints on an organism's ability to grow or reproduce, for example by increasing stress levels and decreasing energy reserves (Pickering 1993; Bearhop *et al.* 2004; Kopp & Medzhitov 2009). Recent conditions may also favour reallocation of resources to other functions at the expense of growth. For example, organisms that experience an increase in food levels following a period of food restriction often divert resources to replenish their energy stores before resuming structural growth (Nicieza & Metcalfe 1997; Auer *et al.* 2010).

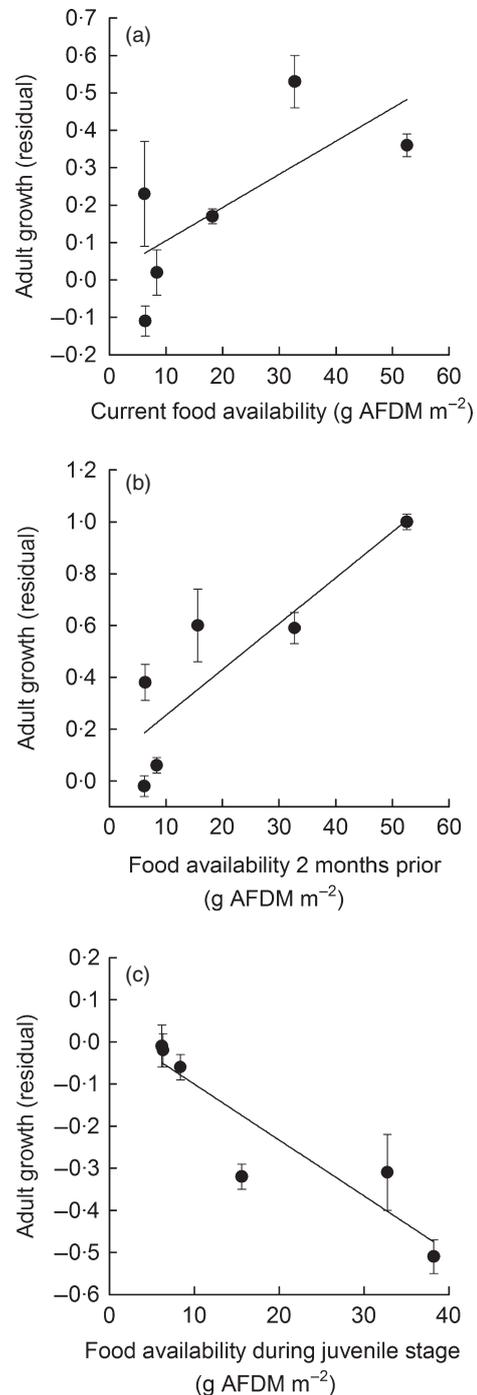


Fig. 4. Adult growth as a function of food availability (a) in the present, (b) 2 months prior and (c) during the juvenile stage in Trinidadian guppies in a tributary to the Guanapo River in Trinidad, West Indies. Food availability is calculated as the summed ash free dry mass (g) of both algae and invertebrates per square metre. Shown are weighted partial residuals after accounting for female body size and all other environmental variables and their interactions.

Why and how low food availability during the juvenile stage led to faster rates of adult growth is less clear. Studies typically find that poor conditions during the juvenile stage, like recent conditions during the adult stage, have a negative effect on the physiological state of the organism at

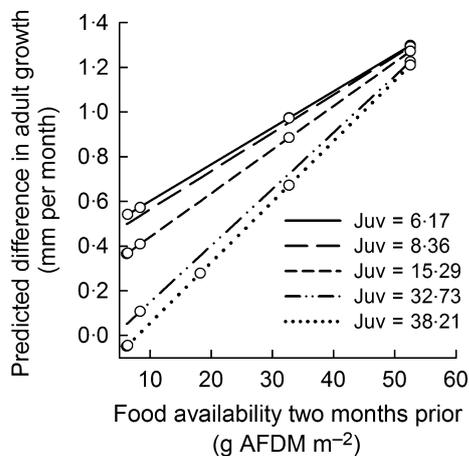


Fig. 5. Predicted difference from mean adult growth rate in response to food availability 2 months prior as a function of food availability during the juvenile stage (Juv) in Trinidadian guppies in a tributary to the Guanapo River in Trinidad, West Indies. Food availability is calculated as the summed ash free dry mass (g) of both algae and invertebrates per square metre. Juvenile food levels of 6.17 and 6.32 g AFDM m^{-2} are shown together because their predicted trajectories overlap. Model-averaged parameters are centred on mean body length = 23 mm, mean current food level = 21 g AFDM m^{-2} and mean density = 370. Points show growth rate predicted for combinations of food levels actually observed.

maturation and its subsequent performance as an adult (Lindström 1999; Lummaa & Clutton-Brock 2002). Low food availability during the juvenile stage can lead to smaller adult body size, reduced energy reserves, higher stress levels and increased susceptibility to starvation, disease and predation (Lindström 1999; Lummaa & Clutton-Brock 2002; Davis & Maerz 2009), which in turn can lead to reduced somatic growth, reproductive success and survival in the adult stage of life (Madsen & Shine 2000; De Block & Stoks 2005; Descamps *et al.* 2008). However, there is also evidence from both cichlids and guppies suggesting that poor juvenile conditions do not always spell doom for adult performance. Mouth brooding cichlids responded to low juvenile food levels in the adult stage by increasing their reproductive rates (Taborsky 2006a) and by producing larger eggs and young (Taborsky 2006b). In a laboratory study of guppies, females reared as juveniles under low food levels were older, smaller and had fewer energy reserves at maturation than females reared on higher food levels, but they were able to compensate for these initial setbacks through phenotypic plasticity in their growth and reproductive strategies during the adult stage. As adults, females reared as juveniles on low food replenished their fat reserves, increased their growth rate to make up for their small body size, and increased their production of babies to compensate for their delayed maturity such that overall they were able to enjoy the same reproductive success as females reared on high food as juveniles (Auer 2010).

Faster growth in adult female guppies reared on low relative to those reared on high food in the laboratory (Auer 2010) suggests that the patterns we observed in this study

represent phenotypic plasticity of adult growth in response to early conditions. However, the faster somatic growth we observed in adults that recruited during periods of low food availability may also be due to sources other than the direct effects of the external environment on the state of the individual. Guppies breed during periods of both low and high food availability (Reznick 1989), but the number of reproductively active females changes seasonally, more females reproducing during the dry season when food levels are highest (Alkins-Koo 2000). Thus, if only high quality females are able to breed under the low food conditions during the wet season, then cohorts born during these rough times may be of higher quality themselves and therefore exhibit higher growth as adults. Alternatively, but not exclusively, the higher growth we observed in females that recruited under poor juvenile conditions may also be due to viability selection causing a temporal shift in genotype frequency within a cohort, whereby only higher quality individuals born in the wet season survive to the size at which we start tracking them.

There is an increasing appreciation that conditions in both the recent and distant past can produce variation in demographic life-history traits among cohorts and individuals and that this heterogeneity in performance can then have important consequences for population size, structure and dynamics (Beckerman *et al.* 2002; Lindström & Kokko 2002; Ratikainen *et al.* 2008). As population dynamics are a consequence of the summed life-history responses of all individual constituents, predicting how populations will respond to changes in the environment therefore hinges on how well we understand the link between the environment and individual performance (Beckerman *et al.* 2002; Benton, Plaistow & Coulson 2006). Previous studies have demonstrated repeatedly that individual performance is influenced by conditions in the recent and distant past, and these effects are now increasingly being incorporated, albeit separately, into demographic models (Lindström & Kokko 2002; Ratikainen *et al.* 2008). While these models typically assume that individual performance is influenced in a positive manner by the quality of conditions in the past, here, we found that this assumption is met with respect to the effect of recent adult conditions but not juvenile conditions on adult growth rates. These differences between guppies and other organisms in how they respond as adults to conditions experienced during the early stages of life underscore the need to better understand how and why responses to early conditions may differ among species. Our study also highlights the importance of simultaneously considering events occurring in both the recent and distant past; depending on their relative magnitude and direction, these past conditions may amplify their total effect on the individual's physiological state and performance or, if operating in opposite directions, may actually cancel out one another's effects.

Many species face new challenges as ecosystems worldwide undergo rapid human-induced changes (Vitousek *et al.* 1997; McCarty 2001; Walther *et al.* 2002). Given these recent changes in climate and habitat size and distribution, there is

an urgent need to better understand how organisms are affected by, and cope with, changes in environmental conditions experienced in different life stages. Here, we show that individual variation in a key demographic trait, adult somatic growth rate, reflects an integrated history of exposure to environmental conditions in both the past and present. However, the mechanisms underlying these individual growth responses and how these growth responses translate into population-level processes still require further attention if we are to improve our predictions for how individuals and populations might be expected to respond to current environmental change.

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Supporting Information

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Table S1. Model parameters, number of parameters in each model (k), difference in AICc value between each model and the model with the lowest AICc value (ΔAICc), and AICc weight (ω_i) for 20 candidate models evaluated for their ability to predict the effects of standard length (SL) and its square (SL^2), current population density (Dens), and food availability in the present (Cur), 2 months prior (2mo) and during the juvenile stage (Juv) on adult somatic growth rates in adult female Trinidadian guppies (*Poecilia reticulata*).

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