Functional Ecology

British Ecological Society

Functional Ecology 2011, **25**, 964–973 doi: 10.1111/j.1365-2435.2011.01865.x

Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies

Eugenia Zandonà[1,*], Sonya K. Auer[2], Susan S. Kilham[1], Jason L. Howard[1], Andrés López-Sepulcre[2], Michael P. O'Connor[1], Ronald D. Bassar[2], Arthela Osorio[2], Catherine M. Pringle[3] and David N. Reznick[2]

[1]*Department of Biology, Drexel University, 3141 Chestnut St, Philadelphia, Pennsylvania 19104, USA;* [2]*Department of Biology, University of California, 1229 Spieth Hall, Riverside, California 92521, USA; and* [3]*Odum School of Ecology, University of Georgia, 140 E. Green St, Ecology Bldg, Athens, Georgia 30602-2202, USA*

Summary

1. Life histories evolve as a response to multiple agents of selection, such as age-specific mortality, resource availability or environmental fluctuations. Predators can affect life-history evolution directly, by increasing the mortality of prey, and indirectly, by modifying prey density and resources available to the survivors. Increasing survivor densities can intensify intraspecific competition and cause evolutionary changes in their selectivity, also affecting nutrient acquisition.

2. Here, we show that different life-history traits in guppies (*Poecilia reticulata*) are correlated with differences in resource consumption and prey selectivity. We examined differences in wild-caught guppy diet among stream types with high (HP) and low predation (LP) pressure and how they are related to benthic invertebrate biomass. Fish and invertebrate samples were collected from two HP and two LP reaches of two distinct study rivers in Trinidad.

3. Our results reveal a strong association between life history and diet. Guppies from HP environments mature earlier and have higher fecundity and reproductive allotment than those from LP environments. Prior work revealed that their population densities are lower and that they grow faster than their LP counterparts. Here, we show that these life-history differences are repeated and that HP guppies feed primarily on invertebrates. In contrast, guppies from LP sites feed primarily on detritus and algae, which are a poorer quality food. LP guppies fed on invertebrates according to their availability, while HP guppies were selective towards those invertebrates with the lower carbon/nitrogen body ratio and thus with higher nutritional value.

4. Our study suggests that as predators shape the life histories of their prey and alter prey population densities, they can also indirectly shape their prey's foraging and diet selectivity. This is, to our knowledge, the first report on how intraspecific differences in life-history traits are correlated with prey selectivity, where prey stoichiometry is included. Although there are clear limitations of association data, our study suggests that the patterns of resource use and life history evolve in concert with one another. However, further research is needed to investigate the possible causal links between risk of predation, the indirect effects of predators on guppy population density, the evolution of life-history traits and nutrient acquisition.

Key-words: C/N ratio, eco-evolutionary feedback, gut content analysis, indirect effects of predation, *Poecilia reticulata*, resource use, trophic ecology, tropical streams

Introduction

Early models of life-history evolution envisioned extrinsic, age-specific mortality as the dominant agent of selection in the evolution of life histories (reviewed in Charlesworth 1980; Roff 1992; Stearns 1992). Those early theories were formulated in a density-independent context and predicted that the effect of increasing adult mortality could lead to the evolution of increased reproductive effort and earlier age of maturation (e.g. Gadgil & Bossert 1970; Law 1979). Conversely, increased mortality of young favour individuals with lower reproductive effort and delayed maturity.

*Correspondence author. E-mail: eugenia.zandona@gmail.com

© 2011 The Authors. Functional Ecology © 2011 British Ecological Society

However, natural populations rarely experience complete density independence and are likely to be limited at some point by biotic or abiotic factors (Cappuccino & Price 1995). Population growth can be limited by top-down (predation) or bottom-up forces (resource availability). Removal of predators from a system previously regulated through predation may increase the density of the prey and, in doing so, decrease the per capita resource availability (Wootton 1994). Increased density of conspecifics may thus strengthen intraspecific competition for high-quality resources, leading to a change in their diet selectivity (e.g. Werner & Hall 1974). Under resource scarcity, it may be optimal to consume resources more indiscriminately and include a higher proportion of lower quality food in the diet (e.g. Gende, Quinn & Willson 2001). Such shifts in diet preference might be accommodated by concomitant changes in physiology (e.g. Olsson *et al.* 2007), morphology and behaviour, which may further act to affect these interactions (Werner & Peacor 2003). While the ecological consequences of such indirect effects of predation are well known, their evolutionary consequences have received little attention (Walsh & Reznick 2008).

Variation in the mortality regime, density and resource availability may all influence the evolution of life histories (Gadgil & Bossert 1970; Abrams & Rowe 1996; Reznick, Bryant & Bashey 2002; Walsh & Reznick 2008, 2009). However, there is no consensus (Gadgil & Bossert 1970; Kozlowski & Wiegert 1987) and little experimental evidence (e.g. Walsh & Reznick 2008) on how resource availability influences life-history evolution. When food is scarce, an animal can be forced to adjust some of its life-history traits, such as to trade-off development time with adult size (Roff 1992; Stearns 1992). Less explored are the effects of diet and resource quality on life-history traits, which can respond to the quantity but also the quality of resources consumed (Twombly, Clancy & Burns 1998; Jensen & Verschoor 2004). For instance, low-quality food could affect individual fitness, alter reproductive allocation, decrease growth rates and weight at maturation, or prolong development time (e.g. Twombly, Clancy & Burns 1998; Mayntz, Toft & Vollrath 2003). When animals feed on nutrient-imbalanced diets, they can be forced to make some trade-offs and modify some of their life-history traits, to cope with the nutrient limitation (Mayntz & Toft 2001). However, responses to nutrient imbalance can be species-specific, depending on a species' physiology, life cycles or ecological interactions (Jensen *et al.* 2011). Thus, the responses of single or multiple life-history characteristics to low food quality are not predictable, likely due to differences in nutritional requirements for different functions and between organisms (Twombly, Clancy & Burns 1998).

Here, we examined whether there is an association between life-history traits and diet quality in wild populations of guppies (*Poecilia reticulata*) from Trinidad. Guppies are found in two types of environments, referred to as high predation (HP) and low predation (LP), in which they have evolved different life-history traits (Reznick & Endler 1982; Reznick 1989). In HP sites, they experience strong predation pressure mostly by the wolfish (*Hoplias malabaricus*), the pike cichlid (*Crenicichla* sp.) and characins. In LP sites, guppies coexist with only one other fish species, the Hart's killifish (*Rivulus hartii*), which occasionally prey on juvenile guppies (Mattingly & Butler 1994).

Age-specific mortality has typically been considered the agent of selection determining life-history evolution in guppies (Reznick & Endler 1982; Reznick 1989). If guppies are mainly preyed upon as adults in HP sites and as juveniles in LP sites, density-independent life-history theory predicts that HP guppies should mature earlier and have higher reproductive allotment than LP guppies (Reznick, Bryant & Bashey 2002). These predicted differences in life histories have been observed in many replicates of natural populations (Reznick & Endler 1982; Reznick 1989; Reznick, Rodd & Cardenas 1996) and confirmed by laboratory common garden experiments (Reznick 1982; Reznick & Bryga 1996). However, there are some inconsistencies between all available evidence about guppies and the theory of age-specific mortality as the sole agent of selection. For example, density-independent life-history theory predicts that evolutionary changes can only occur when there are changes in juvenile relative to adult mortality (Gadgil & Bossert 1970; Law 1979; Charlesworth 1980). Mark–recapture experiments on wild guppy populations have shown that, although predation was indeed higher in HP sites, the pattern of size-specific predation was similar in both environments (Reznick *et al.* 1996). This suggests that other factors may be playing a role in guppy life-history evolution.

Resource availability, which can also shape life histories, varies considerably among natural populations of guppies (Grether *et al.* 2001). Resource levels, however, often covary with predation gradient, as HP sites are generally located downstream and are commonly wider streams with less canopy cover and higher primary productivity compared with LP sites (Reznick, Butler & Rodd 2001). Increased resource levels could be an indirect effect of increased predation (Wootton 1994). Guppy biomass is higher, and individual growth rates are lower in LP communities relative to HP communities (Rodd & Reznick 1997; Grether *et al.* 2001). These trends suggest that there are lower resources per capita, and consequently, increasing competition for food in LP communities. Food availability may therefore represent another selective factor leading to differences in guppy growth rates, as well as other life-history traits such as size at maturity and reproductive allotment (Gadgil & Bossert 1970). However, even if resources are more abundant in HP sites, they might not be reflected in what guppies consume. Predators may affect guppy habitat use by forcing them to occupy only the margins of pools (Fraser & Gilliam 1992), thus limiting available foraging areas, which may in turn cause them to feed on suboptimal resources (Werner *et al.* 1983); however, Reznick, Butler & Rodd (2001) found that guppies from HP localities have higher growth rates, which suggests that food is not limiting in those localities. Furthermore, Bassar *et al.* (2010) found that HP guppies ate more invertebrates and less detritus and algae than LP fish when they were compared in

artificial streams that presented them with uniform resource availability. This result suggests that guppies from HP sites have evolved a preference for higher-quality food items, which may promote the evolution of increased investment in growth and reproduction (Walsh & Reznick 2008). Nevertheless, differences among guppies from HP and LP localities in resource consumption have not yet been examined in natural populations.

This study investigates how a suite of life-history traits covaries with resource consumption and prey selectivity in wild-caught guppies across sites in Trinidad that differ in their predation regime. We collected guppies from HP and LP sites from two different drainages and examined how the patterns in their diets, life-history traits and invertebrate availability in the stream are associated in natural environments. We also examined prey selectivity for the two phenotypes and asked whether it was correlated with the prey's nutritional quality, expressed as the ratio of carbon to nitrogen (C/N) of their body content. This study is aimed to fill in the gaps about the guppy's trophic ecology, understanding how resource use in natural environments could be associated with the evolution of different life-history traits in this important study system.

Materials and methods

We conducted this study in montane streams draining the Northern Range of Trinidad. Our study streams belong to two different drainages, Aripo and Guanapo, which are both part of the Caroni River system on the south slope of the Northern Range. In each drainage, we sampled a LP and a HP site. LP environments are generally found upstream of barrier waterfalls, which prevent the dispersion of many fish species (Gilliam, Fraser & Alkins-Koo 1993). The catfish *Rhamdia quelen* is also present in the LP Guanapo site. However, this species does not appear to represent a real threat to guppies (Gilliam, Fraser & Alkins-Koo 1993). Fish community composition was based on observations and captures during multiple years. Stream width and canopy openness were measured for three randomly chosen pools in each site. Canopy openness was measured with a hemispherical densitometer (Table 1).

We collected samples during 18–24 March 2007, which corresponds to the dry season in Trinidad. In each site, we collected guppies and benthic invertebrates from three pools and, within each pool, from locales with different stream velocity (low, medium and high) to ensure sampling of most microhabitats found in the stream. We sampled 56–136 individuals per pool ($N = 1003$ individuals across all sites), but this was always less than the total number present in the pool. All samples from a given site were collected on the same day. Fish were collected with hand nets and euthanized immediately with an overdose of MS-222. Guppies were then measured for standard length, weighed, and guts were removed for the diet analysis. Guts and guppies were preserved in 5% formalin solution.

LIFE-HISTORY MEASUREMENTS

We measured the following life-history traits for all guppies collected: size at maturation in males and females, fecundity, offspring size and reproductive allotment (see Reznick & Endler 1982; Reznick 1989 for detailed description of the procedures). Males stop growing at maturity, so for mean male size at maturation, we randomly sampled 25 mature males from each site collection and measured their standard length (to the closest 0·05 mm) and wet weight (to the closest 1 mg). For female reproductive traits, we separated females into 2-mm-size classes and selected a minimum of three females from each size class from each pool ($N = 16$–48 individuals per pool). We determined the number of embryos and their stage of development according to Reznick & Endler (1982). Developing embryos and reproductive tissues were separated from the female and, along with the female soma, were dried overnight in an oven and weighed the following day. For the minimum female size at maturation, we determined the pregnancy status of all females and found the smallest reproductive female in

Table 1. Stream characteristics for the four study sites

Stream characteristics	Aripo HP	Guanapo HP	Aripo LP	Guanapo LP
Invertebrate biomass (mg m^{-2})	177 (37·5)[a]	20·9 (11·6)[b]	19·7 (7·0)[b]	19·2 (4·1)[b]
Invertebrate abundance (no. of individuals)	122 (33·3)[a]	29 (7·4)[b]	29·7 (9·9)[b]	42·3 (18·2)[b]
Total number of invertebrate families	17	14	14	10
Fish community	*Poecilia reticulata*, *Rivulus hartii*, *Hoplias malabaricus*, *Crenicichla* sp., Characidae (many species), *Rhamdia quelen*, *Aquidens pulcher*, *Ancistrus cirrhosus*, *Hypostomus robinii*, *Cichlasoma bimaculatum*, *Synbranchus marmoratus*	*P. reticulata*, *R. hartii*, *Hoplias malabaricus*, Characidae (many species), *R. quelen*, *Aquidens pulcher*, *Ancistrus cirrhosus*, *Hypostomus robinii*	*P. reticulata*, *R. hartii*	*P. reticulata*, *R. hartii*, *R. quelen*
Canopy openness (%)	31·5 (8·4)[a]	12·4 (1·9)[a]	30·4 (12·7)[a]	16·3 (3·7)[a]
Stream width (cm)	917 (159)[a]	653 (52·7)[a,b]	387 (30·3)[b]	403 (103·9)[b]

Values of the environmental variables have been averaged across the three pools. Values with the same superscript letter are not significantly different (as assessed by LSD *post hoc* comparisons). Fish species reported are the ones that have been observed and caught in the sites during multiple years. Differences in average % canopy and stream width were calculated with a Kruskal–Wallis test. Values indicate means (± 1 SE).
HP, high predation; LP, low predation.

each pool. Fecundity was determined by counting the number of offspring in pregnant females. Mean offspring size for each female was calculated as the litter dry weight divided by the number of offspring in the litter. Reproductive allotment was estimated as the summed dry weight of offspring and reproductive tissues. Only females carrying developing embryos were considered (Reznick & Endler 1982).

For all traits, we examined the effects of predation regime and drainage using a linear mixed model approach. Drainage and predation were modelled as fixed effects, while pool was modelled as a random effect within predation × drainage to control for nonindependence of individuals measured within the same pool. When there was a significant interaction between drainage and predation, we used tests of simple main effects to compare life-history traits between predation regimes within each drainage (Winer 1971). Female dry mass was included as a covariate in the analyses of fecundity and offspring size. Because offspring dry weight declines as development progresses (Reznick & Endler 1982), the stage of development was also included as a covariate in the analysis of offspring size. To analyse reproductive allotment, we used the summed dry weight of offspring and reproductive tissues as the dependent variable and female dry weight as a covariate.

RESOURCE AVAILABILITY

We collected benthic invertebrates from three pools in each site. Within each pool, we sampled invertebrates from three benthic areas with different water velocities (high, medium and low) ($N = 36$). We collected benthic invertebrates using a PVC pipe sampler (12·065 cm diameter). Invertebrates were picked and identified to the lowest taxonomic level (Perez 1996; Merritt, Cummins & Berg 2007). We used mass–length regression equations (Benke *et al.* 1999) to calculate total invertebrate biomass (mg of dry mass m^{-2}). Differences in benthic invertebrate biomass m^{-2} between drainages and predation level were tested with a two-way ANOVA.

DIET ANALYSIS

A total of 80 guppies were analysed for diet content. Only the anterior part of the gut (stomach and a small part of the foregut – at the point where the gut turns 180°) was analysed, because here food has not been fully digested. Invertebrates were identified at the most inclusive taxonomic level possible, usually the family category (following Perez 1996; Merritt, Cummins & Berg 2007). The selected portion of the gut was placed onto a gridded slide, where ten squares (out of 64) were randomly chosen for quantification of the gut content under a compound microscope. Invertebrates and detritus proportions were estimated for each square. Individual diatoms and filamentous algae were counted because they are too small to estimate their proportion coverage in each box. An average size for diatoms and one for filamentous algae was subsequently assigned to calculate the area they occupied in the 10 squares. The area taken by each food category was estimated for the whole slide (64 squares). Plant matter, inorganic material and other algae have not been included in the analysis as their occurrence was very low.

We performed a multivariate analysis of covariance (MANCOVA) to test for differences in guppy diet across drainages and predation regimes. Proportions of invertebrates, detritus and algae (diatoms and filamentous algae) were the dependent variables of our general linear model (GLM). We included drainage (Aripo and Guanapo) and predation level (HP, LP) and their interaction as fixed factors. We used fish standard length as a covariate and included the interaction between fish length and drainage in the model. We also included pool number nested within the interaction between predation and drainage as a random effect to remove nonindependent effects associated with sampling multiple individuals within a pool and thereby provide the proper error term for comparisons between drainage and predation regime. In addition, we tested the proportion of each diet class in the guts using three univariate ANCOVAS. Proportion of each food item was included as a dependent variable, and the independent variables were the same as they were for the MANOVA. Guppies from HP and LP sites used for the diet analysis did not significantly differ in length.

Finally, to assess whether the benthic invertebrate abundance in the stream had an effect on the amount of invertebrates found in the fish guts, we ran a two-way ANCOVA. Our dependent variable was the proportion of invertebrates found in the fish guts, predation and drainage were fixed factors, and pool benthic invertebrate biomass (mg m^{-2}) was set as a covariate. Fish standard length was not included in the GLM as it did not have a significant effect.

PREY SELECTIVITY

To investigate whether guppies are selectively choosing to feed on specific invertebrate taxa, we calculated an index of prey selectivity as follows:

$$L_i = r_i - p_i$$

where L_i is the index of prey selectivity for the taxa i, r_i is the relative abundance of invertebrate prey i in the fish gut, and p_i is the relative abundance of the invertebrate prey i in the pool where the fish was caught (Strauss 1979; Palkovacs & Post 2008). The index L_i can have values from +1 to −1. If $L_i > 0$, the fish is actively selecting prey i; if it is less than 0, the fish is avoiding prey i; and if $L_i = 0$, the fish is selecting prey i in proportion to its abundance. We chose nine different invertebrate taxa, which are all the ones found in the guppy guts, as our prey items and for each of them, we calculated guppies' selectivity index. The chosen taxa were Ephemeroptera, Trichoptera (excluding Helicopsychidae and Glossosomatidae as they have never been found in guppy guts), Odonata, Chironomidae, other Diptera larvae (Ceratopogonidae, Tipulidae, Simuliidae), Elmidae (only larvae), Psephenidae, Ostracoda and Copepoda.

We created random diets with a Monte Carlo simulation for each of the pools ($N = 12$) where the fish had been caught. The simulated random diets were used to test the significance of the selectivity indices L_i for each of the nine invertebrate taxa. The programme first calculated a pooled diet for all fish from the same pool, with the purpose of comparing it to the invertebrate abundance in the environment. The simulation created random diets for each pool by randomly drawing invertebrate items based on the abundances from the same pool. The randomly simulated diets had the same number of prey items as in the actual diets. Benthic invertebrate taxa were drawn, with replacement, from each of the pools, creating 10 000 random diets for each pool. The programme calculated a selectivity index from the simulated diets for each of the nine prey taxa in all the 12 pools, thus creating a null distribution of L_i. If the selectivity index of the individual fish was within the 95% confidence interval of the null distribution, the fish was feeding according to availability. If it was significantly above or below the limits of the confidence interval, fish respectively selected or avoided that particular taxa. The Monte

Carlo simulation was performed using MATLAB 7.6.0. (Mathworks, Natick, MA, USA)

We also ran a linear mixed-effects model to investigate whether guppies were selecting invertebrate taxa according to their quality, referred to as their elemental composition (body stoichiometry). Typically, prey with a relative high nitrogen content represent good-quality food items, so we characterized the invertebrate taxa based on their carbon to nitrogen ratio (C/N) body composition. C/N ratios indicate the balance between energy and nutrient (nitrogen) acquisition: high C/N values indicate low nitrogen content and thus low-quality food, while low C/N values characterize high nitrogen content and high quality. We calculated the C/N body composition of invertebrate samples we collected during a stream survey in Trinidad in 2007–2008. To obtain the invertebrates' per cent carbon and nitrogen contents, samples of each taxa were dried at 50–60°, ground to fine powder and analysed using a Finnigan Delta C mass spectrometer connected to a Carlo Erba 1500 CHN analyser at the University of Georgia. C/N data were available for seven of the nine invertebrate taxa (not for Copepods and Ostracods). We also excluded Psephenidae from the analysis, because it was the only taxa showing very low occurrence in both diet (1%) and in the environment (2%) in all sites. For this analysis, we thus used the remaining six taxa (Ephemeroptera, Trichoptera, Odonata, Chironomidae, other Diptera and Elmidae), chosen both for the availability of their C/N values and for being the most abundant taxa found in guppy guts and in the environment. In the model, our response variable was the selectivity index calculated by the Monte Carlo simulation, and the explanatory variables were invertebrates' C/N body composition, predation level and the interaction between predation and C/N. The invertebrate taxa identity was set as a random effect to account for other random factors that may affect their selectivity (e.g. species-specific anti-predatory adaptations).

Dependent variables and covariates were either arcsin square root transformed (for proportions) or log transformed when appropriate. All statistical analyses, except the Monte Carlo simulation, were performed using SAS (SAS Institute Inc., Cary, NC, USA) and PASWSTATISTICS 18.0 (IBM Corporation, Somers, NY, USA), and the levels of significance were set at 0·05.

Results

LIFE-HISTORY TRAITS

Guppies showed clear life-history differences between HP and LP sites in both drainages. Male guppies were smaller at maturity in HP relative to LP sites ($F_{1,8}$ = 79·7, P < 0·001; Fig. 1a) and there was no significant effect of drainage ($F_{1,8}$ = 1·67, P = 0·23) or the interaction between predation and drainage ($F_{1,8}$ = 3·85, P = 0·08). The marginal interaction arose because the difference in the size of mature males from HP and LP sites on the Guanapo River was larger than on the Aripo River. Females also matured at a smaller size in HP relative to LP sites ($F_{1,8}$ = 26·0, P < 0·001; Fig. 1b) and there were no differences between drainages ($F_{1,8}$ = 3·73, P = 0·08) nor any significant interaction between drainage and predation ($F_{1,8}$ = 1·31, P = 0·28). Female fecundity increased with female body size ($F_{1,150}$ = 194·0, P < 0·001) and was higher in HP than in LP sites ($F_{1,8}$ = 10·99, P = 0·01; Fig. 1c). Fecundity was greater in females from the Guanapo relative to the Aripo drainage ($F_{1,8}$ = 6·33, P = 0·04), but there was no significant interaction between predation and drainage ($F_{1,8}$ = 4·55, P = 0·07). The marginal interaction for fecundity occurred because the difference between HP and LP localities was larger in the Aripo than the Guanapo rivers. Offspring size increased with female body size ($F_{1,119}$ = 22·26, P < 0·01) and decreased with the stage of development ($F_{1,119}$ = 71·8, P < 0·01). There was a significant effect of predation ($F_{1,8}$ = 15·86, P < 0·01, Fig. 1d), but there was also a significant effect of drainage ($F_{1,8}$ = 6·62, P = 0·03) as well as a significant interaction between predation and drainage ($F_{1,8}$ = 68·6, P < 0·01). Offspring were larger in LP relative to HP sites in the Aripo drainage ($F_{1,8}$ = 83·8, P < 0·01; Fig. 1d), but were smaller in LP relative to HP sites in the Guanapo drainage

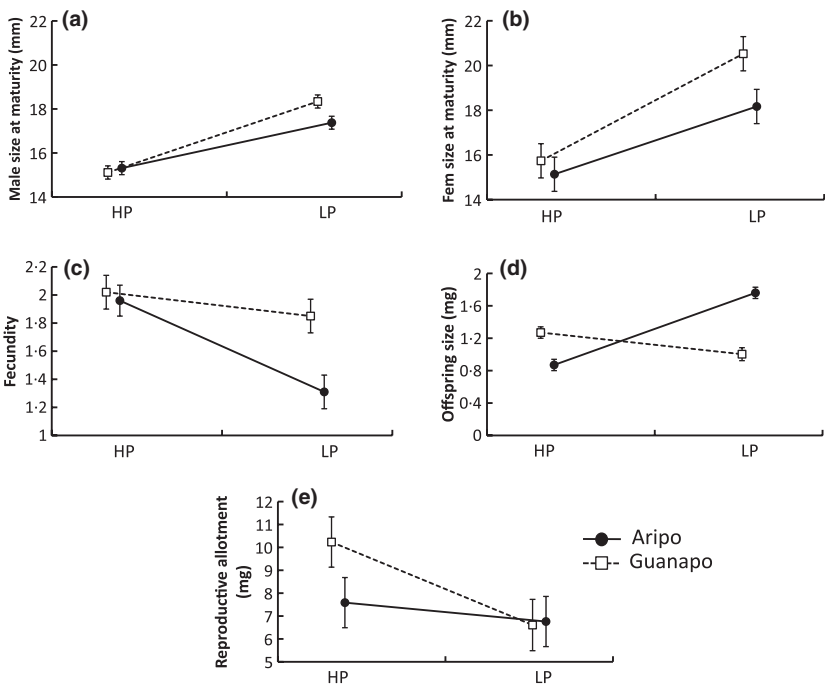

Fig. 1. Differences in life-history traits between high (HP) and low (LP) predation guppies from the Aripo (closed symbols) and Guanapo (open symbols) rivers. Values represent the estimated marginal means calculated by the general linear model as explained in the text. Bars represent ± 1 SE.

($F_{1,8}$ = 5·62, P = 0·04). Finally, reproductive allotment increased with female dry weight ($F_{1,119}$ = 270·7, P < 0·001) and decreased with the stage of development ($F_{1,119}$ = 16·18, P < 0·001). Reproductive allotment was larger in HP relative to LP sites ($F_{1,8}$ = 5·38, P = 0·04; Fig. 1e) and was not affected by drainage ($F_{1,8}$ = 1·57, P = 0·24) or the interaction between predation and drainage ($F_{1,8}$ = 2·08, P = 0·19).

RESOURCE AVAILABILITY

Predation ($F_{1,8}$ = 6·92, P = 0·03), drainage ($F_{1,8}$ = 9·52, P = 0·015) and the interaction between predation and drainage ($F_{1,8}$ = 10·1, P = 0·013) all have a significant effect on benthic invertebrate biomass per area found in the streams. All three effects are caused by the much higher benthic invertebrate biomass in the Aripo HP site relative to the other three sites (Table 1). We ran a one-way ANOVA with site identity as a fixed factor and Least Significant Difference (LSD) *post hoc* analysis to assess the differences in benthic invertebrates between the four sites. We found that the site of origin had a significant effect ($F_{3,8}$ = 8·85, P = 0·006) and that the Aripo HP site had a significantly higher invertebrate biomass m^{-2} than the other three sites (LSD: Aripo HP-Aripo LP P = 0·003; Aripo HP-Guanapo HP P = 0·002; Aripo HP-Guanapo LP P = 0·004; see Table 1). Aripo LP, Guanapo LP and Guanapo HP did not show significantly different averages (Table 1).

DIET ANALYSIS

Guppies from sites with different predation regimes showed significantly different gut content composition. The MANCOVA showed a significant effect of predation ($F_{3,7}$ = 4·34, P = 0·05), fish length ($F_{3,63}$ = 6·99, P < 0·001) and of the interaction between fish length and drainage ($F_{3,63}$ = 5·90, P = 0·001) on the composition of guppy diets. There was no significant effect of drainage ($F_{3,7}$ = 0·71, P = 0·57) nor of the interaction between drainage and predation ($F_{3,7}$ = 1·14, P = 0·40). Univariate tests showed that HP guppies ate significantly more invertebrates than LP guppies ($F_{1,9}$ = 16·69, P = 0·003), which instead fed significantly more on algae ($F_{1,9}$ = 7·82, P = 0·02) and detritus ($F_{1,9}$ = 13·69, P = 0·005) (Fig. 2a and Tables S1 and S2 in Supporting Information). The MANCOVA showed a strong effect of guppy length on diet. The nature of the relationship between length and diet differed among Aripo and Guanapo but not among HP and LP sites within each river. This means that the differences in diet between HPand LP localities are independent of length (Fig. S1).

When we incorporated the pool benthic invertebrate biomass as a covariate in the two-way ANCOVA, we found that it did not have a significant effect ($F_{1,79}$ = 0·16, P = 0·69) on the proportion of invertebrates found in the guppies guts. Even with benthic invertebrate biomass as a covariate, the model still revealed a significant effect of predation ($F_{1,79}$ = 17·09, P < 0·001), a marginally nonsignificant effect of drainage ($F_{1,79}$ = 3·47, P = 0·066), and no significant effect of the interaction between drainage and predation ($F_{1,79}$ = 1·18, P = 0·28) (Fig. 2b).

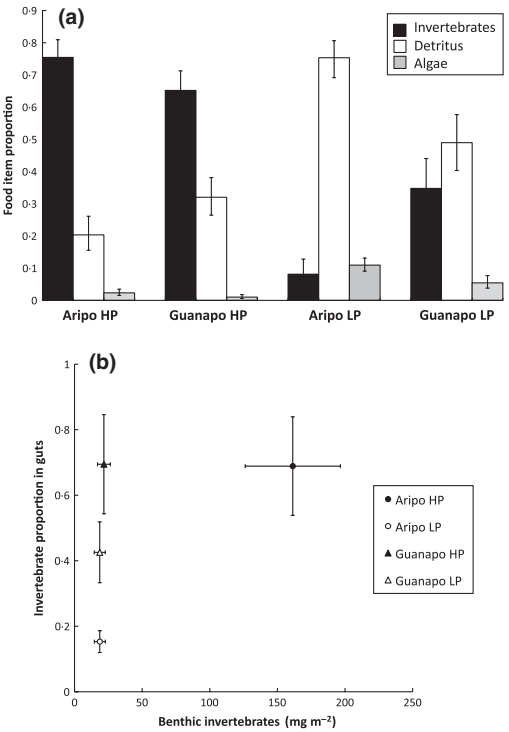

Fig. 2. (a) Proportion diet composition of high predation (HP) and low predation (LP) guppies from the two study drainages, Aripo and Guanapo. Data shown here represent the estimated marginal means calculated by the general linear model on arcsin-transformed data. Estimated marginal means and standard errors have been back-transformed for the graphical representation. Food categories analysed are invertebrates, in dark grey; amorphous detritus, in white; and algae (filamentous and diatoms), in light grey. (b) Relationship between benthic invertebrate density in the environment and proportion of invertebrates found in the fish guts. Aripo fish are indicated with circles and Guanapo with triangles; HP fish are closed symbols, while LP fish are open. Bars represent ± 1 SE.

PREY SELECTIVITY

High predation guppies are more selective when feeding on invertebrates than LP fish, which instead fed more according to availability in the environment (Fig. 3a). Overall, Chironomidae represented 40% of the invertebrate portion of guppy diet. Trichoptera were 14%, other Diptera 13% and Ephemeroptera 8%. Even though Ephemeroptera was the most abundant taxon found in the environment (34%), the Monte Carlo simulation showed that HP guppies tended to avoid them (Fig. 3a). Elmidae and Ostracoda also had relatively high abundance in the environment, with 11% and 19%, respectively, but they were uncommon in the guts (0·5% and 2%, respectively). Some invertebrate taxa commonly found in the benthic samples were never found in the guppy guts. These taxa were Trichoptera with rocky cases such as Helicopsychidae and Glossosomatidae, Oligochaete (Tubificidae) and Gastropoda (Thiaridae).

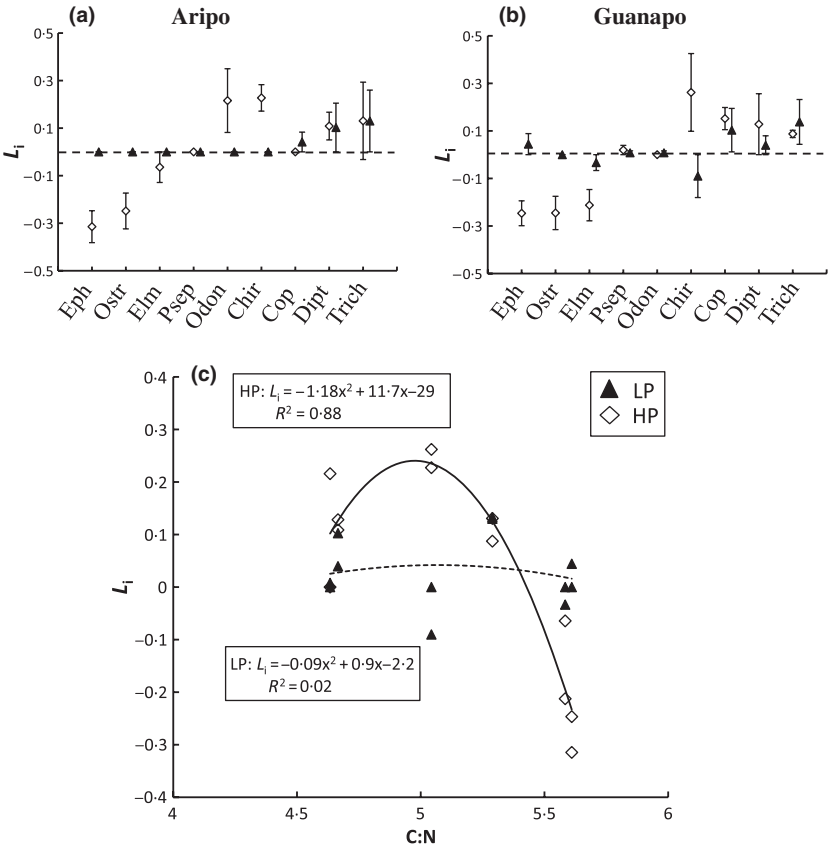

Fig. 3. Selectivity indexes for the nine invertebrate taxa found in the guppy guts for (a) Aripo high predation (HP) and low predation (LP) and (b) Guanapo HP and LP. Positive values indicate positive selectivity, while negative values indicate avoidance. Error bars represent standard errors calculated across the three pools means for each site. (Eph = Ephemeroptera; Ostr = Ostracoda; Elm = Elmidae; Psep = Psephenidae; Odon = Odonata; Chir = Chironomidae; Cop = Copepoda; Dipt = Other Diptera; Trich = Trichoptera). (c) Relationship between C/N (molar) invertebrate body composition and selectivity index (L_i) for HP and LP fish. We have not separated the Guanapo and Aripo in two distinct graphs, because the patterns for the two drainages were very similar. For each of HP and LP, each taxon is thus represented twice (once for the Aripo and once for the Guanapo). Regression equation and R^2 values are shown in graph. In all graphs, open diamonds indicate HP and closed triangles LP.

The linear mixed-effects model showed selectivity was on average stronger in HP guppies ($t_{15} = -3{\cdot}37$; $P = 0{\cdot}004$). Moreover, while selectivity was unrelated to C/N ratio in LP guppies ($t_3 = 0{\cdot}40$; $P = 0{\cdot}71$), HP guppies were highly selective on the basis of C/N ratios (interaction predation × C/N; $t_{15} = 3{\cdot}48$; $P = 0{\cdot}003$). The shape of this relationship for HP guppies is quadratic ($t_{15} = -3{\cdot}58$; $P = 0{\cdot}003$), showing stronger preference for invertebrates with a C/N ratio around five and strong avoidance for lower-quality invertebrates (with high C/N ratios; Fig. 3c). LP guppies instead showed no selectivity and fed according to what was available in the stream.

Discussion

Guppies adapted to different levels of predation displayed marked differences in diet and prey selectivity. Fish from HP environments fed on food of higher quality (invertebrates as opposed to detritus or algae; Fig. 2a) and preferred those invertebrate taxa that had higher relative nitrogen content (Fig. 3c). LP guppies were less selective in their diet choice. They mostly ate detritus and algae, which have low nitrogen content, and did not show preferences for specific invertebrate taxa; they instead fed according to what was available in the stream (Fig. 3).

These patterns lend themselves to different causal interpretations. We already know that guppies from HP communities sustain higher risk of mortality and have evolved different life histories (Reznick & Endler 1982; Reznick 1989; Reznick *et al.* 1996). The comparative ecology of HP vs. LP environments (Reznick, Butler & Rodd 2001) suggests that there may be indirect consequences of predation. Guppies from LP environments attain higher population densities and have lower growth rates (Reznick, Butler & Rodd 2001), most likely because food is less abundant. Their less selective diet may be a second indirect response to predation that is independent of life-history evolution (Werner & Hall 1974; Wootton 1994). However, there is also the possibility that the differences in diet are a consequence of correlated, but independent, features of the habitat and that diet has helped shape the evolution of life histories (Walsh & Reznick 2008).

The life-history differences that we observed between HP and LP guppies overall confirmed the results commonly found in other studies on wild-caught guppies (Reznick & Endler 1982; Reznick 1989). HP guppies matured at a smaller size (which has served as an indicator of earlier maturity in prior studies – Reznick & Endler 1982; Reznick 1982; Reznick, Rodd & Cardenas 1996; Reznick *et al.* 1996) and had higher fecundity and reproductive allotment than their LP counterparts. HP fish also typically produce smaller offspring (Reznick 1982; Reznick & Endler 1982; Reznick, Rodd & Cardenas 1996; Reznick *et al.* 1996). The one difference between the current results and those of earlier life-history studies was for offspring size in the Guanapo River. In this case, the LP population produced smaller offspring than the HP population; in all prior studies, it was found that LP populations produced larger babies than their HP counterparts (Reznick 1982; Reznick & Bryga 1996). J. Torres-Dowdall

(unpublished data) found that there is a genetic basis to these offspring size differences in the Guanapo River. Most life-history theory predicts how overall reproductive allocation evolves (e.g. Gadgil & Bossert 1970; Charlesworth 1980) but does not address how this allocation is provisioned to offspring (e.g. many small vs. few large). The evolution of offspring size is represented by independent theory (e.g. Smith & Fretwell 1974; Lloyd 1987) and it is possible that offspring size might evolve independently of other components of the life history. However, multivariate work on Poecilids showed that offspring size is not independent of other life-history traits (Strauss 1990; Johnson & Belk 2001). Theoretical and empirical work argues that fitness consequences of offspring size depend strongly on the competitive environment. Being larger is a big advantage when food is scarce and competition is intense, but of little advantage when food is abundant and competition is lax (Bashey 2008). It is possible that per capita resource availability varies among sites sharing the same predator community, potentially leading to the evolution of different offspring size. We lack the necessary information to address the possible cause of this unexpected result for offspring size on the Guanapo River at this time.

Resource (invertebrate) biomass was not well associated with fish community perhaps because factors other than the fish community can influence invertebrates. Invertebrate biomass can be controlled by bottom-up (light levels, nutrient concentrations) or top-down effects (predators) (Power 1992). We expected higher invertebrate biomass in HP sites than in LP sites for two reasons. First, HP sites are generally bigger streams with more primary productivity (Reznick, Butler & Rodd 2001), which should sustain higher levels of secondary production (Hill, Mulholland & Marzolf 2001). Second, if invertebrate abundance is regulated by predators, then we expect the higher density of guppies in LP sites to reduce invertebrate abundance. We instead found that this expectation was only fulfilled in the Aripo River. The Aripo LP and two Guanapo sites did not significantly differ from each other and all have far lower invertebrate biomass than the Aripo HP site (Table 1). The Aripo HP site had almost nine times the invertebrate biomass m^{-2} of the other three sites. It was also significantly wider, but did not have significantly lower canopy coverage. The higher invertebrate biomass in the Aripo HP could be caused by higher primary, or even the result of more complex trophic cascade effects due to the more diverse fish community present in this site. The absence of the expected differences between HP and LP sites could also be attributed to the reduced number of sites – only four – used for this study, potentially amplifying the effects of the site idiosyncrasies. Nevertheless, there were consistent differences in the diet of guppies from HP and LP sites in spite of there not being consistent differences in invertebrate biomass.

A missing link in our assessment is an estimate of guppy population density and hence per capita food availability. Previous studies reported that the guppy density is lower (Reznick, Butler & Rodd 2001) and size distribution is smaller (Rodd & Reznick 1997; Reznick, Butler & Rodd 2001) in HP sites because of the higher birth and death rates, resulting in one-fourth of the guppy biomass per area found in LP sites (HP mean = 126 mg m^{-3}, LP mean = 530 mg m^{-3}; from Reznick, Butler & Rodd 2001). If our sites replicated these guppy biomass differences, then the per capita invertebrate availability would be lower in LP sites.

Here, we show that there are correlated differences in diet that are consistent with what we would predict if resources were less abundant in LP sites. Optimal diet theory predicts that a predator should have a broader diet in unproductive environments and become more of a specialist on high-quality food when prey density is high (MacArthur & Pianka 1966). For instance, Gende, Quinn & Willson (2001) found that brown and black bears became more specialized in energy-rich salmon (females that had not spawned) when their availability was high. Werner & Hall (1974) found that bluegill sunfish (*Lepomis macrochirus*) were more selective towards bigger size prey when prey density was high; the fish were instead more opportunistic when prey density decreased. In a study on cadmium-intolerant *Drosophila*, Bolnick (2001) found that when cadmium-free food abundance was low and competition for it was high, *Drosophila* evolved tolerance for cadmium-rich food. In HP streams, with low guppy biomass, there are more high-quality resources (invertebrates) available to each guppy (Reznick, Butler & Rodd 2001); thus, the fish can be more selective in what they feed on. HP guppies indeed show higher invertebrate content in their diet and higher selectivity for certain taxa, especially those with intermediate–low C/N values. This pattern suggests that HP guppies can afford to specialize on higher-quality prey, because food is not limiting.

In LP sites, where guppy biomass is typically higher and individual growth rates are lower (Reznick, Butler & Rodd 2001), guppies might be under stronger intraspecific competition for scarce, high-quality resources. In such conditions, it is predicted that consumers will become generalists, adapting to feed on a broader variety of food items, even those of lower nutritional quality (MacArthur & Pianka 1966). Indeed, we found that LP guppies have a more omnivorous diet, with high proportions of low-quality food (detritus), and feed on invertebrates according to availability. Bassar *et al.* (2010) found the same patterns; HP guppies preferred to eat invertebrates, while LP guppies had a higher proportion of detritus and algae in their diet. Bassar *et al.* (2010) worked with fish from the same localities as in the current study, but diet was assessed after fish were kept for 28 days in artificial streams that had been uniformly stocked with invertebrates collected from natural streams. Seeing such a pattern in the absence of any difference in resource availability or population density suggests that guppies have specialized diets that might have evolved as a response to different resource levels in their natural environment.

Increased resource availability, when modelled as an indirect effect of predation, represents a factor that can select for the evolution of early age/size at maturity and higher reproductive effort according to some models (Gadgil & Bossert 1970; Abrams & Rowe 1996). On the other hand, chronically

low food levels have been linked to the evolution of slower growth rates, as a strategy to minimize the costs of growth (Sinervo & Adolph 1994; Arendt & Reznick 2005). In a series of studies conducted on the Trinidadian killifish *R. hartii*, Walsh & Reznick (2008, 2009) found that high resource availability was associated with the evolution of earlier maturity, increased reproductive allotment and the production of more, smaller eggs when these fish were compared with killifish from sites where they were the only resident species. In our study system, high resource levels were likewise correlated with smaller size at maturation, higher reproductive allotment and fecundity, while low food levels led to the opposite patterns. For this reason, resource availability, which is indirectly affected by the presence/absence of predators, may also be an important agent of selection in the life-history evolution of guppies. However, laboratory comparisons of the life histories of guppies from HP and LP environments (Reznick 1982; Reznick & Bryga 1996) do not reveal the same interaction with food availability as seen in killifish (Walsh & Reznick 2008, 2009), so there is not an equivalent signal of adaptation to food availability.

ECO-EVOLUTIONARY PERSPECTIVE

Predators can drive community divergence in prey and these changes can feed back to mould the evolution of predators' traits in contemporary time (e.g. trophic morphology; Palkovacs & Post 2008). For instance, natural populations of anadromous and landlocked alewives (*Alosa pseudoharengus*) differently modified the structure and composition of the zooplankton community (Brooks & Dodson 1965). Consequently, the effect of the alewives on the zooplankton community feeds back affecting alewives' trophic morphology, favouring those traits that are more adapted to the modified zooplankton community (Palkovacs & Post 2008). Possibly, eco-evolutionary feedback could have caused divergence between HP and LP guppies. The population densities of the guppies may dictate the nature of resource availability. In LP sites, the higher population densities caused by the lack of predators (Rodd & Reznick 1997) may actively depress the abundance of invertebrates. If such conditions persist, then there follows selection in favour of those individuals that are less selective in their choice of prey. If such diet preferences do indeed evolve, then they could conceivably be accompanied by selection for differences in the digestion and absorption of nutrients from the diet (e.g. modified gut length and intestinal microstructure) and other changes to the metabolism, to external trophic morphology (e.g. gill raker spacing, gape width) and lastly, life-history traits. Preliminary evidence of differences in morphological and physiological traits between natural guppies populations from HP and LP sites is starting to accumulate, suggesting the existence of other forms of adaptation, other than life-history traits. For instance, the gut length of wild-caught appears to be negatively correlated with the proportion of invertebrates in the diet (Zandonà 2010). Guppy trophic morphology is associated with predator community and feeding behaviour and has apparently evolved in response to the transplantation of guppies from a HP site to a previously guppy-free LP environment (Palkovacs, Wasserman & Kinnison 2011). All of this information suggests that guppies will provide fertile substrate for the study of interactions between ecological and evolutionary processes in a natural ecosystem.

Conclusions

Predation can have direct and indirect effects on the evolution of life-history traits of prey (Gadgil & Bossert 1970; Abrams & Rowe 1996; Walsh & Reznick 2008, 2009). Predators directly affect mortality rates and population size structure (Rodd & Reznick 1997) and indirectly influence the amount of per capita resources available to surviving prey (Wootton 1994). In this study, we showed an association between evolved life-history traits in guppies and their diet preferences. Guppies that live in streams with predators display smaller size at reproduction and higher reproductive allotment. They also have more resources available per capita, which is reflected in their feeding habits: they are more specialized in invertebrates and show higher prey selectivity. Guppies from predator-free streams show the opposite pattern in life-history traits and have fewer resources available in the environment. They also have lower individual growth rates (Reznick, Butler & Rodd 2001). They feed more consistently on lower-quality food (detritus), most likely as an effect of the more intense intraspecific competition that they experience. Our results suggest that patterns of resource availability and diet selectivity may be linked to the evolution of life-history traits. Ours is a correlational rather than a mechanistic study and thus only allows limited inferences on the causal link between life-history traits evolution and diet. It is however the first study showing how guppies from HP and LP environments differ in prey selectivity, where prey stoichiometry is included and, as a consequence, it opens the doors to a suite of interesting research questions in this important study system.

Acknowledgements

Thanks to E. Chiu, M. Thury-Drott, J. Holding, K. Sullam for laboratory help. Discussion with R. El-Sabaawi, M. Marshall, E. Palkovacs, J. Russell, J. Spotila, M. Weksler greatly improved the manuscript. We thank the William Beebe Research Center and ASA Wright in Trinidad for providing lodging and research facilities. Fish were collected and handled with the approval of the University of California Riverside IACUC AUP (no. A-20080008) and conforming to the legislation in Trinidad. This research was funded by the NSF FIBR program, grant no. EF-0623632 to DNR and the J. Mozino scholarship to EZ.

References

Abrams, P.A. & Rowe, L. (1996) The effects of predation on the age and size of maturity of prey. *Evolution*, **50**, 1052–1061.

Arendt, J.D. & Reznick, D.N. (2005) Evolution of juvenile growth rates in female guppies (*Poecilia reticulata*): predator regime or resource level? *Proceedings of The Royal Society B*, **272**, 333–337.

Bashey, F. (2008) Competition as a selective mechanism for larger offspring size in guppies. *Oikos*, **117**, 104–113.

Bassar, R.D., Marshall, M.C., López-Sepulcre, A., Zandonà, E., Auer, S.K., Travis, J., Pringle, C.M., Flecker, A.S., Thomas, S.A., Fraser, D.F. & Reznick,

D.N. (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences USA*, **107**, 3616–3621.
Benke, A.C., Huryn, A.D., Smock, L.A. & Wallace, J.B. (1999) Length-mass relationships for freshwater macroinvertebrates in north america with particular reference to the southeastern united states. *Journal of the North American Benthological Society*, **18**, 308–343.
Bolnick, D.I. (2001) Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature*, **410**, 463–466.
Brooks, J.L. & Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28–35.
Cappuccino, N. & Price, P.W. (1995) *Population Dynamics: New Approaches and Synthesis*. Academic Press, San Diego.
Charlesworth, B. (1980) *Evolution in Age-Structured Populations*. Cambridge University Press, Cambridge, UK.
Fraser, D.F. & Gilliam, J.F. (1992) Nonlethal impacts of predator invasion – facultative suppression of growth and reproduction. *Ecology*, **73**, 959–970.
Gadgil, M. & Bossert, W.H. (1970) Life historical consequences of natural selection. *American Naturalist*, **104**, 1–24.
Gende, S.M., Quinn, T.P. & Willson, M.F. (2001) Consumption choice by bears feeding on salmon. *Oecologia*, **127**, 372–382.
Gilliam, J.F., Fraser, D.F. & Alkins-Koo, M. (1993) Structure of a tropical stream fish community – a role for biotic interactions. *Ecology*, **74**, 1856–1870.
Grether, G.F., Millie, D.F., Bryant, M.J., Reznick, D.N. & Mayea, W. (2001) Rain forest canopy cover, resource availability, and life history evolution in guppies. *Ecology*, **82**, 1546–1559.
Hill, W.R., Mulholland, P.J. & Marzolf, E.R. (2001) Stream ecosystem responses to forest leaf emergence in spring. *Ecology*, **82**, 2306–2319.
Jensen, T. & Verschoor, A. (2004) Effects of food quality on life history of the rotifer *Brachionus calyciflorus* Pallas. *Freshwater Biology*, **49**, 1138–1151.
Jensen, K., Mayntz, D., Toft, S., Raubenheimer, D. & Simpson, S.J. (2011) Prey nutrient composition has different effects on *Pardosa* wolf spiders with dissimilar life histories. *Oecologia*, **165**, 577–583.
Johnson, J.B. & Belk, M.C. (2001) Predation environment predicts divergent life-history phenotypes among populations of the livebearing fish *Brachyrhaphis rhabdophora*. *Oecologia*, **126**, 142–149.
Kozlowski, J. & Wiegert, R.G. (1987) Optimal age and size at maturity in annuals and perennials with determinate growth. *Evolutionary Ecology*, **1**, 231–244.
Law, R. (1979) Optimal life histories under age-specific predation. *American Naturalist*, **114**, 399–417.
Lloyd, D.G. (1987) Selection of offspring size at independence and other size-versus-number strategies. *American Naturalist*, **129**, 800–817.
MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, **100**, 603–609.
Mattingly, H.T. & Butler, M.J. (1994) Laboratory predation on the trinidadian guppy – implications for the size-selective predation hypothesis and guppy life-history evolution. *Oikos*, **69**, 54–64.
Mayntz, D. & Toft, S. (2001) Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia*, **127**, 207–213.
Mayntz, D., Toft, S. & Vollrath, F. (2003) Effects of prey quality and availability on the life history of a trap-building predator. *Oikos*, **101**, 631–638.
Merritt, R.W., Cummins, K.W. & Berg, M.B. (2007) *An Introduction to the Aquatic Insects of North America*, 4th edn. Kendall/Hunt Publishing Company, Dubuque, Iowa.
Olsson, J., Quevedo, M., Colson, C. & Svanback, R. (2007) Gut length plasticity in perch: into the bowels of resource polymorphisms. *Biological Journal of the Linnean Society*, **90**, 517–523.
Palkovacs, E.P. & Post, D.M. (2008) Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits? *Evolutionary Ecology Research*, **10**, 699–720.
Palkovacs, E.P., Wasserman, B.A. & Kinnison, M.T. (2011) Eco-evolutionary trophic dynamics: loss of top predators drives trophic evolution and ecology of prey. PLoS ONE 6(4): e18879. doi:10.1371/journal.pone.0018879.
Perez, G.R. (1996) *Guía para el estúdio de los macroinvertebrados acuáticos del Departimento de Antioquia*. Universidad De Antioquia, Colombia.
Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology*, **73**, 733–746.
Reznick, D. (1982) The impact of predation on life-history evolution in trinidadian guppies – genetic-basis of observed life-history patterns. *Evolution*, **36**, 1236–1250.
Reznick, D.N. (1989) Life-history evolution in guppies. 2. Repeatability of field observations and the effects of season on life histories. *Evolution*, **43**, 1285–1297.
Reznick, D., Bryant, M.J. & Bashey, F. (2002) r- and k-selection revisited: the role of population regulation in life-history evolution. *Ecology*, **83**, 1509–1520.
Reznick, D.N. & Bryga, H.A. (1996) Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). 5. Genetic basis of parallelism in life histories. *American Naturalist*, **147**, 339–359.
Reznick, D., Butler, M.J. & Rodd, H. (2001) Life-history evolution in guppies. Vii. The comparative ecology of high- and low-predation environments. *American Naturalist*, **157**, 126–140.
Reznick, D. & Endler, J.A. (1982) The impact of predation on life-history evolution in trinidadian guppies (*Poecilia reticulata*). *Evolution*, **36**, 160–177.
Reznick, D.N., Rodd, F.H. & Cardenas, M. (1996) Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). 4. Parallelism in life-history phenotypes. *American Naturalist*, **147**, 319–338.
Reznick, D.N., Butler, M.J., Rodd, F.H. & Ross, P. (1996) Life-history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. *Evolution*, **50**, 1651–1660.
Rodd, F.H. & Reznick, D.N. (1997) Variation in the demography of guppy populations: the importance of predation and life histories. *Ecology*, **78**, 405–418.
Roff, D.A. (1992) *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York.
Sinervo, B. & Adolph, S.C. (1994) Growth plasticity and thermal opportunity in sceloporus lizards. *Ecology*, **75**, 776–790.
Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506.
Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford Universigy Press, Oxford, UK.
Strauss, R.E. (1979) Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society*, **108**, 344–352.
Strauss, R.E. (1990) Predation and life-history variation in *Poecilia reticulata* (Cyprinodontiformes: Poeciliidae). *Environmental Biology of Fishes*, **27**, 121–130.
Twombly, S., Clancy, N. & Burns, C. (1998) Life history consequences of food quality in the freshwater copepod *Boeckella triarticulata*. *Ecology*, **79**, 1711–1724.
Walsh, M.R. & Reznick, D.N. (2008) Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. *Proceedings of the National Academy of Sciences USA*, **105**, 594–599.
Walsh, M.R. & Reznick, D.N. (2009) Phenotypic diversification across an environmental gradient: a role for predators and resource availability on the evolution of life histories. *Evolution*, **63**, 3201–3213.
Werner, E.E. & Hall, D.J. (1974) Optimal foraging and the size selection of prey by the bluegill sunfish *Lepomis macrohirus*. *Ecology*, **55**, 1042–1052.
Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.
Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.
Winer, B.J. (1971) *Statistical Principles in Experimental Design*. Mcgraw-Hill, New York.
Wootton, J.T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, **25**, 443–466.
Zandonà, E. (2010) *The Trophic Ecology of Guppies (Poecilia reticulata) From the Streams of Trinidad*. PhD thesis. Department of Biology, Drexel University, Philadelphia.

Received 14 December 2010; accepted 7 April 2011
Handling Editor: Jonathan Blount

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Correlations between diet items and length.

Table S1. Univariate ANCOVA results for diet analysis.

Table S2. Proportions of the three food items for each site.

Table S3. Invertebrate's selectivity index and C/N values.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Copyright of Functional Ecology is the property of Wiley-Blackwell and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.