The direct and indirect effects of guppies: implications for life-history evolution in *Rivulus hartii*

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Summary

1. Ecological factors that alter mortality rates, such as predation, can cause evolutionary change. However, in addition to killing prey, predators can reduce prey abundance and increase food to survivors. Such indirect effects may also cause evolution. Predictions from theory that models how life histories evolve in response to increased mortality rates often change when they include indirect effects. Thus, indirect effects need to be evaluated to couple theory with natural systems.

2. Trinidadian killifish, *Rivulus hartii*, are found in communities with and without guppies *Poecilia reticulata*. *Rivulus* densities decline when guppies are present, which may be due to competitive or predatory interactions with guppies that increase *Rivulus* mortality rates. We previously showed that *Rivulus* from sites with guppies begin reproduction earlier and have increased reproductive allotment compared to *Rivulus* from sites with just *Rivulus*. Such divergence is inconsistent with theory that considers changes in juvenile mortality alone, but is consistent with theory that incorporates indirect effects. Here, we explored the mechanism of divergence with mark–recapture studies that compared the population biology of *Rivulus* between communities that are and are not sympatric with guppies.

3. *Rivulus* were 50% less abundant when guppies were present but guppies were not associated with increased adult mortality rates. Related experiments show that the declines in density are likely due to guppy predation on young *Rivulus*. Guppies do not appear to negatively impact *Rivulus* growth via competition. *Rivulus* with guppies grow $> 3\times$ faster than *Rivulus* from sites upstream, above waterfalls that exclude guppies. If guppies competed with *Rivulus* for resources, then we would instead expect to see their presence be associated with a decline in *Rivulus* growth rates. When *Rivulus* were transplanted from above to below this barrier, their growth accelerated to match the residents. This response instead argues that the differences in growth are mediated by an environmental factor, likely lower population densities, which allow *Rivulus* from sites with guppies to grow faster.

4. These results imply that an indirect effect of guppy predation on young *Rivulus*, which is the presumed agent of selection, improves the fit of empirical findings with theoretical predictions.

Key-words: mark–recapture, killifish, predator–prey interactions, trophic cascade

Introduction

One facet of life-history theory models how changes in age- or size-specific mortality, due to such factors as predation, influence the trajectory of evolutionary change (Gadgil & Bossert 1970; Law 1979; Charlesworth 1980; Taylor & Gab-

riel 1992). Age/size-specific theory predicts that mortality targeted at adult age-classes or large individuals selects for earlier maturation and increased reproductive effort, while the opposite trends are predicted when extrinsic mortality targets immature age- or size-classes. However, this theory models the effects of age- or size-specific mortality independently of other factors. Natural systems are inherently complex and it has long been assumed that ecological factors such as competition, density dependence, and food availability may also influence the evolution of life histories

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(Lack 1954, 1968; MacArthur & Wilson 1967). Predators commonly have indirect effects because they can reduce the abundance of prey and thereby increase the amount of food available to survivors (e.g. Power 1990; Wootton & Power 1993; Wootton 1994; Pace *et al*. 1999). Life-history theory that incorporates such indirect effects yields predictions that can be similar to, or oppose those of theory that just considers changes in mortality (Gadgil & Bossert 1970; Charlesworth 1980; Abrams & Rowe 1996; Gardmark & Dieckmann 2006). Thus, data regarding age/size schedules of mortality as well as the ecological consequences of this mortality are often needed when evaluating the causes of life-history evolution in a natural setting.

In Trinidad, the killifish, *Rivulus hartii*, is found across series of fish communities that differ in predators and competitors (Gilliam, Fraser & Alkins-Koo 1993; Fraser, Gilliam & Yip-Hoi 1995; Fraser *et al*. 1999; Gilliam & Fraser 2001). Two such communities are habitats where *Rivulus* live with guppies, *Poecilia reticulata* ('*Rivulus*/guppy' sites) and those where *Rivulus* is the only species of fish present ('*Rivulus*-only' sites). These communities are often found just tens of meters apart separated by barrier waterfalls that prevent the upstream movement of guppies. Previous work has shown that these sites do not differ in physical habitat or several environmental variables (Walsh & Reznick 2009). There is evidence for an impact of guppies on the population dynamics of *Rivulus*. *Rivulus* are 3× more abundant in *Rivulus*-only compared with *Rivulus*/guppy sites, but this decline in *Rivulus* density is not matched by a commensurate gain in guppy biomass (Gilliam, Fraser & Alkins-Koo 1993). One potential cause for this decline in density is that guppies prey upon young *Rivulus*. Small *Rivulus* are susceptible to predation by guppies because *Rivulus* do not exhibit parental care and *Rivulus* hatchlings [~7 mm in total length (TL)] are believed to inhabit the substrate at the bottom of stream, where guppies frequently forage. This predatory role by guppies has been demonstrated in aquaria (Gilliam, Fraser & Alkins-Koo 1993) and field experiments (D. Fraser, unpublished data). Alternatively, guppies may be competitors with *Rivulus*. Guppies and *Rivulus* exhibit some overlap in their diets as both species consume benthic invertebrates. Guppies also suppressed the growth of smaller size-classes of *Rivulus* in field experiments conducted in enclosures (Gilliam, Fraser & Alkins-Koo 1993). Studies in other fish communities have shown that increased competition can alter rates of recruitment and patterns of abundances (Werner & Gilliam 1984; Mittelbach 1988; Bystrom, Persson & Wahlstrom 1998). Regardless of the mechanism, such interactions have the potential to impact life-history evolution in *Rivulus* (Charlesworth 1980).

We are utilizing a multi-step approach consisting of field and laboratory components to determine the evolutionary impacts of guppies on *Rivulus*. We first measured correlations between fish communities and life-history phenotypes from five river drainages to evaluate whether there is a consistent association between community type and life history across a wide geographic area. *Rivulus* from *Rivulus*/guppy sites exhibited a smaller size at maturation, increased fecundity, smaller eggs, and a greater investment in reproduction than those from *Rivulus*-only sites (Walsh & Reznick 2009). There is a genetic basis to these differences as the laboratory studies using second generation lab reared fish showed that *Rivulus* from *Rivulus*/guppy habitats are younger at maturity, lay smaller eggs, produce eggs at a higher rate, and have higher overall rates of investment in reproduction (Walsh & Reznick 2010). Such divergence in life histories does not agree with the predictions from theory that only considers changes in mortality rates. If the sole impact of guppies is to increase the mortality of immature/small *Rivulus* via size-specific predation or competition, then life-history theory predicts that guppies will instead select for delayed maturity and decreased reproductive effort (Law 1979; Charlesworth 1980). However, interactions with guppies may also incur indirect effects. One possibility is that guppies depress *Rivulus* population density and hence cause an indirect increase in resources for *Rivulus*. Such an interaction could be mediated by contrasting diet preferences between *Rivulus* and guppies. Terrestrial organisms, such as ants, are a large component of the diet of *Rivulus*, but not guppies (Gilliam, Fraser & Alkins-Koo 1993), and a lower density of *Rivulus* in sites with guppies could potentially reduce the intensity of intraspecific competition for this resource. More importantly, theory shows that some combinations of direct and indirect effects can lead to the evolution of the differences in life histories similar to those seen between *Rivulus* from *Rivulus*-only and *Rivulus*/guppy habitats (Charlesworth 1980; Abrams & Rowe 1996). Thus, to better understand the cause of life-history evolution in *Rivulus* and thereby differentiate between the applicability of evolutionary theories, we must characterize the comparative ecology and population dynamics of *Rivulus* from these different habitats.

Here we use mark–recapture studies to explore predatory and competitive interactions with guppies by quantifying differences in population biology between populations of *Rivulus* found above and below barrier waterfalls that exclude guppies. We use repeated sampling events to evaluate variation in *Rivulus* mortality and growth rates, in addition to differences in abundance (Gilliam, Fraser & Alkins-Koo 1993), between *Rivulus*/guppy and *Rivulus*-only sites. We expect *Rivulus* to be at lower abundances in *Rivulus*/guppy habitats (Gilliam, Fraser & Alkins-Koo 1993). To test the hypothesis that these differences in density have impacts on rates of individual growth, we also performed a transplant experiment. In this experiment, we quantified changes in growth when *Rivulus* were transplanted from a *Rivulus*-only environment to the downstream *Rivulus*/guppy site. Our characterizations of growth (population comparisons and transplant experiment) are important because *Rivulus* exhibit similar rates of growth when reared on equal, controlled rations in the laboratory (Walsh & Reznick 2008; unpublished data) and, more importantly, previous work on guppies in this system has shown that individual growth rates are correlated with resource availability (Grether *et al*. 2001; Reznick, Butler IV & Rodd 2001). Thus, such approaches provide a means to investigate

whether *Rivulus* compete with guppies and/or guppy predation causes significant indirect effects on *Rivulus*. If the dominant influence of guppies is to compete with *Rivulus*, then we predict that *Rivulus* from *Rivulus*-only localities will exhibit faster rates of growth than *Rivulus* from *Rivulus*/guppy sites. We also predict that guppies will suppress the growth rates of the transplanted *Rivulus*. If the dominant influence of guppies is instead to indirectly increase resource availability by reducing the abundance of *Rivulus*, then we predict that *Rivulus* growth rates will be higher in *Rivulus*/guppy than *Rivulus*-only populations and that *Rivulus* growth rates will accelerate when transplanted from a *Rivulus*-only site into the downstream section of river that contains guppies.

Materials and methods

We performed two, 24-day mark–recapture studies, one each in the Aripo and Arima Rivers, and one 14-day mark–recapture in the Aripo River to compare growth and survival rates of *Rivulus* from *Rivulus*/guppy and *Rivulus*-only communities. Work in the Arima River and the 14-day study in the Aripo River. was performed during January and February 2007, while the 24-day study in the Aripo R. was conducted in September and October 2008. For all studies, the *Rivulus*/guppy and *Rivulus*-only sites were located in the same stretches of river, but were separated by a barrier to upstream guppy movement.

All study sites were monitored for the presence of additional species. *Rivulus* was the only fish species observed in the *Rivulus*-only localities in both streams. *Rivulus* and guppies were the only fish species present in the study sites on the Aripo River. Additional fish species are occasionally present in the *Rivulus*/guppy locale of the Arima River. One such species is the catfish *Rhamdia sebae*; the impact of *Rhamdia* on guppies or *Rivulus* is unknown, although an evaluation of stomach contents did not reveal evidence for piscivory by *Rhamdia* on guppies or *Rivulus* (Gilliam, Fraser & Alkins-Koo 1993). The piscivorous, *Hoplias malabaricus* has previously been observed in this tributary (Fraser, personal observation). Neither *Rhamdia* nor *Hoplias* were observed during the present study, which included repeated surveys done during the day and at night. The eel, *Synbranchus marmoratus*, is potentially present at low abundances throughout these streams but none were captured or observed during these studies.

To minimize differences in sample size between populations, the reaches sampled in the *Rivulus*/guppy sites were longer than the paired sections in the *Rivulus*-only sites. The specific stretches of river sampled in each study were: (i) Arima River: *Rivulus*/guppy = 190 m, *Rivulus*-only = 100 m; (ii) 14-day Aripo River: *Rivulus*/guppy = 120 m, *Rivulus*-only = 80 m; and (iii) 24-day Aripo River: *Rivulus*/guppy = 100 m, *Rivulus*-only = 70 m. *Rivulus* were collected with dip-nets at night between the hours of 18.00–22.00. We also sampled during daylight hours with seines. All *Rivulus* captured in a given site were measured for TL and wet weight and marked with an injection of elastic polymer that fluoresces under ultraviolet illumination (Northwest Marine Technology Incorporated, Shaw Island, Washington, USA). To generate unique marks, a two-dot code was used on each *Rivulus* via five colors and six body positions (see Fraser *et al.* 1999; Gilliam & Fraser 2001). We also sexed each *Rivulus* by evaluating individuals for the presence and absence of male coloration; male *Rivulus* exhibit white/gold bars along the top and bottom of the caudal fin, while females do not. Developing males typically exhibit signs of tail coloration by $\sim$29 mm TL (Walsh & Reznick 2008, 2010) and we, thus, classified individuals below this size as immature. *Rivulus* were returned to the location from which they were collected. *Rivulus* were recaptured on two separate occasions with intervals of 12 days in the 24-day studies and once in the 14-day study.

ABUNDANCE

Rivulus abundance was estimated using two approaches: (i) via the Lincoln–Peterson formula: N = (C*M)/R, where N = population size, C = is the total number of *Rivulus* caught during the recapture episode, M = No. of *Rivulus* initially marked, and R = No. of marked *Rivulus* that were recaptured; and (ii) via the closed captures model in program MARK. This latter approach requires multiple recapture events and, therefore, only data from the two 24-day studies were included. Differences in *Rivulus* density (No. of fish per m^2) were evaluated between *Rivulus*/guppy and *Rivulus*-only sites using a Kruskal–Wallis test.

SURVIVAL

To estimate survival, Cormack–Jolly–Seber based mark–recapture models, implemented with the program MARK, were used (Lebreton *et al.* 1992). These models consider two possibilities when marked *Rivulus* are not recaptured: (i) that a *Rivulus* died since the last recapture (survival, ϕ); or (ii) that a given *Rivulus* is alive but was not recaught (recapture probability, *P*). Since multiple recapture events are required to estimate these parameters, we only included data from the 24-day studies. Our general approach to estimating survival and recapture probability was to compare complex models with simpler models that contained fewer terms. The 'best' model is the one with the lowest QAIC$_c$ value (Quasi-Akaike Information Criteria; Aikaike Information Criteria values corrected for overdispersion; Anderson, Burnham & White 1994). A simplified model was considered to be a better fit if the QAIC$_C$ value is smaller. Strong evidence for a difference between models is generally defined by a ΔQAIC$_C$ > 7 (Burnham & Anderson 2001).

We began our model selection approach by evaluating the dispersion in the data set. Overdispersion can occur if some individuals are more likely to be recaptured than other individuals, which can impact model selection. To evaluate the degree of overdispersion, a parametric bootstrap goodness-of-fit test with Φ and *p* parameterized with river (Aripo, Arima) and fish community (*Rivulus*/guppy, *Rivulus*-only) effects was used. The results of this test produce a correction factor, c-hat, for overdispersion and the corrected QAIC$_c$ values were subsequently used for model selection. This correction factor, c-hat, was calculated after 10 000 simulations by dividing the observed c-hat by the mean bootstrapped c-hat (1·62/1·004). This process revealed slight overdispersion (c-hat = 1·61). Corrections for values less than three are considered acceptable (Lebreton *et al.* 1992).

Our approach to estimating recapture probability and survival closely follows similar methodology applied to guppies in this system (see Bryant & Reznick 2004; Gordon *et al.* 2009). Since we only have two recapture events, we cannot independently estimate survival or recapture probability in the second recapture event (see Lebreton *et al.* 1992) and we therefore ignored time effects. To estimate recapture probabilities we compared QAIC$_c$ values among a model fitted with stream (Arima, Aripo) and fish community (*Rivulus*/guppy, *Rivulus*-only) effects vs. simpler models that contained either fish community effects or no effects. Survival rate was fully parameterized with stream and fish community effects in the models used to arrive at

the best fit model of recapture probability. Based upon this approach, the most parsimonious model of recapture probability was a function of fish community effects alone (see Results).

To estimate survival, we again began with a fully parameterized model. Survival was parameterized with stream and fish community and we then compared this full model with two simpler models that were parameterized with (i) fish community, and (ii) no effects. This process yields the most parsimonious model of survival. Initial fish length was entered as a covariate for all phases of model selection.

GROWTH RATE

We calculated instantaneous per day growth rates as

$$[(\ln(\text{Wet weight}_{\text{recap}}) - \ln(\text{Wet weight}_{\text{initial}}))/(\text{day}_{\text{recap}} - \text{day}_{\text{initial}})].$$

For our analyses we examined per week (daily growth × 7) growth rates but report mean per day values in the tables and figures. We used a linear mixed model to test for differences in growth between *Rivulus*-only and *Rivulus*/guppy locales. All three studies were included in a single analysis and all recaptured individuals were included in the data set. We used the longest duration possible to calculate the growth of an individual. For example, when an individual was caught and marked, and then recaptured twice, we used the change in mass from the marking event and second recapture event to calculate the weekly growth rate. We treated river (Arima, Aripo), fish community (*Rivulus*/guppy, *Rivulus*-only), sex, and their interactions as fixed effects, and the initial length of each fish was included as a covariate. To account for the potential non-independence among individuals within a study, we included a 'replicate' term (i.e. Aripo River study No. 1, Aripo River study No. 2, Arima River study No. 1) that was entered as a random effect and was nested within the river × fish population interaction. We used between-within subjects degrees of freedom in all tests of fixed effects with the random effect of replicate nested within river × fish population used as the subject. This method partitions residual degrees of freedom into between and within subject degrees of freedom and allows the fixed effects of sex and its interactions to have degrees of freedom that reflect the fact that sexes and individuals are not independent within a replicate (Schluchter & Elashoff 1990). We used separate error variances for each population type because a likelihood ratio test on the full fixed effect model showed that the error variances were not equal among populations ($\chi^2 = 80{\cdot}69$, d.f. = 1, $P < 0{\cdot}001$). All fixed effects and covariates were initially entered along with interactions and we then subsequently removed nonsignificant interactions using maximum likelihood. The final model was fit using restricted maximum likelihood to avoid biases in the estimates of within- and between-population variances. Heterogeneity of slopes was tested by examining the fish population × initial fish length interaction. When significant interactions between main effects were present, we used tests of simple main effects to test for differences of one factor at each level of the other in the interaction (Winer 1971). We recaptured four individuals that could not be reasonably classified as either male or female and were thus considered immature [Arima *Rivulus*-only (1), Aripo *Rivulus*-only 14-day study (1) Aripo *Rivulus*/guppy 24-day study (3)]. To fully evaluate differences between the sex and interactions between sex and the other factors, we removed these individuals from the analyses.

TRANSPLANT EXPERIMENT

We performed a transplant experiment at the conclusion of the study in the Arima River to measure changes in growth when *Rivulus* are moved from the *Rivulus*-only locale into a *Rivulus*/guppy site. We have previously shown that these sites are similar in habitat structure and do not differ in several potentially confounding environmental variables that could impact growth rates, including water temperature (Walsh & Reznick 2009). This transplant experiment therefore evaluates the impact of guppies, and their associated ecological consequences, on *Rivulus* rates of individual growth. Eighty marked fish, whose growth history for the previous 24-day was known, were moved from the *Rivulus*-only section into the corresponding *Rivulus*/guppy section. An equal number of resident *Rivulus* were removed from the *Rivulus*/guppy section. The transplanted *Rivulus* were then randomly placed at the same locations in which the resident *Rivulus* were removed. As a result, ambient fish density was unchanged. These fish and a control group of marked resident *Rivulus* were recaptured *c.* 6 weeks later. Differences in instantaneous growth were compared between the pre-transplant and post-transplant period for the transplanted and resident *Rivulus* using a linear mixed model repeated measures approach with time period (pre-transplant, post-transplant) as our repeated effect on fish ID (random effect). We used a compound symmetry variance structure to constrain the variances across repeated effect levels to be equal. Fish population (resident *Rivulus*/guppy, transplanted *Rivulus*-only) was entered as fixed effects and initial fish size was used as a covariate. We initially included all of the main effects and their interactions, but subsequently removed nonsignificant interactions using maximum likelihood. Sexes were analysed separately because our initial analyses of growth rate indicated that their patterns of growth between communities were different (see Results). If the transplanted *Rivulus* respond by accelerating their growth rate to match that of the resident *Rivulus*, then we will see this response as a significant time period × fish population interaction. We used post-hoc Tukey–Kramer tests at the mean value of the covariate to determine if there were significant differences in growth in the resident and transplanted fish between the pre- and post-transplant period.

Results

ABUNDANCE

Based upon the number of fish per m^2, *Rivulus* were significantly (Kruskal–Wallis: $H_{1,10} = 3{\cdot}94$, $P = 0{\cdot}047$) more
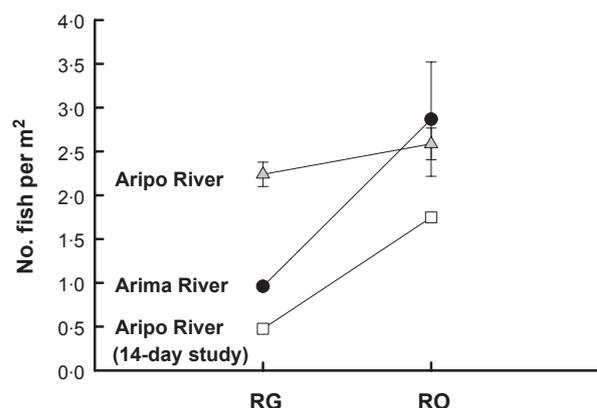
Fig. 1. Differences in abundance between *Rivulus*/guppy and *Rivulus*-only locales. Significant differences were found between fish communities ($H_{1,10} = 3{\cdot}94$, $P = 0{\cdot}047$). These data are from the Lincoln–Petersen method for estimating population size.

abundant in *Rivulus*-only sites compared with *Rivulus*/guppy localities (Fig. 1). On average, the number of fish per m^2 was approximately 2× higher in the *Rivulus*-only sections of river. We also used Program MARK to estimate abundance in the two studies with more than one recapture event. This approach did not reveal significant differences in density between sites with and without guppies (Kruskal–Wallis: $H_{1,4}$ = 0·6, P = 0·44; Mean no. of fish per m^2: *Rivulus*/guppy = 0·69 ± 0·3; *Rivulus*-only = 0·98 ± 0·11), although the trend towards higher densities in the *Rivulus*-only localities remained. This latter result is not significant because it excludes the 14-day Aripo River study and thus has lower power, but also because smaller differences in abundance were observed in the 24-day Aripo River study (see Fig. 1).

RECAPTURE PROBABILITY AND SURVIVAL

The best fitting model for recapture probability included fish community effects only (QAIC$_c$ = 1009·8 for model with fish community effects vs. 1014·7 and 1015·3 for models with stream + fish community effects, and no effects respectively). These differences in QAIC$_c$ values (ΔQAIC$_c$ = 4·9) indicate modest support for a difference between models. Estimates for recapture probability (P ± SE) between *Rivulus*/guppy and *Rivulus*-only locales were 0·45 ± 0·07 and 0·72 ± 0·05, respectively. These differences in recapture probability are likely a by-product of *Rivulus* in *Rivulus*/guppy localities being found at lower abundances, spread out over longer distances, and are thus generally more difficult to recapture than they are in *Rivulus*-only localities.

The most parsimonious model for survival included no effects (Table 1), although there was only modest support for a difference in QAIC$_c$ values between this model and the one containing fish community effects (ΔQAIC$_c$ = 3·79). Survival estimates differed little between *Rivulus*/guppy and *Rivulus*-only communities (*Rivulus*/guppy Φ = 0·80 ± 0·071 vs. *Rivulus*-only Φ = 0·76 ± 0·042; Table 2), and there were no significant differences in survival when all populations were considered ($H_{1,4}$ = 0·6, P = 0·44; Table 2). Note that these estimates pertain primarily to adult survival; our sample of immature individuals was quite small (∼2–3% of marked individuals, Table S1, Supporting information).

Table 1. Model selection for survival from mark–recapture analyses. All models include size as a covariate. The best fitting model did not include any parameters, thus indicating little divergence in survival between *Rivulus* communities with and without the presence of guppies. Recapture probability was constrained by 'fish community' for all models

Model effects	No. of parameters	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	QAIC$_c$ deviance
No effects	6	1002·2	0	0·852	990·1
Fish community	8	1005·9	3·79	0·128	989·8
Fish community, river	12	1009·7	7·59	0·023	985·4

QAIC, Quasi-Akaike Information Criteria.

Table 2. Apparent survival and recapture probability estimates (± 1 standard error) from the two 24-day studies. There were no significant differences between fish communities (P > 0·05)

	Apparent survival (Φ)	Recapture probability (P)
Arima River		
Rivulus/guppy	0·87 (0·12)	0·4 (0·09)
Rivulus-only	0·7 (0·05)	0·78 (0·07)
Aripo River		
Rivulus/guppy	0·8 (0·09)	0·48 (0·08)
Rivulus-only	0·84 (0·07)	0·65 (0·08)

GROWTH RATE

Female and male *Rivulus* from *Rivulus*/guppy communities grew at rates that were approximately 5 and 3× faster than their counterparts from *Rivulus*-only sites, respectively (Fig. 2; Tables 3 and 4). This larger difference in the growth of females than males between *Rivulus*/guppy and *Rivulus*-only sites caused a significant fish community × sex interaction (Table 3). Tests of simple main effects between the sexes within this interaction term revealed significant differences in growth between *Rivulus*/guppy and *Rivulus*-only sites for females ($F_{1,4}$ = 9·04, P = 0·04) but not males ($F_{1,4}$ = 0·09, P = 0·406). Even though there is a 3× difference in the growth of males between localities with and without guppies, this result is not significant because (i) power was lower and (ii) we utilized a conservative statistical approach in which the denominator degrees of freedom are based upon the number of studies and not the number of individuals. There were significant differences in growth between the sexes as females grew faster than males (Table 3; Mean instantaneous growth in grams per day ±1 SE: Female = 0·0021 ± 0·0003, Male = 0·001 ± 0·0003). There were no significant (P < 0·05) growth rate differences between rivers (Table 3) nor was our random effect (replicate term) significant (Estimate ± 1 SE = 5·39 × 10^{-5} ± 5·2 × 10–5, Wald z = 1·03, P = 0·15).

TRANSPLANT EXPERIMENT

The results of the transplant experiment revealed a significant time period-by-fish community interaction for males and females (Table 5). The growth rates of the resident *Rivulus* in the *Rivulus*/guppy habitats declined slightly between the pre- and post-transplant periods (Fig. 3) and post-hoc comparisons between time periods revealed nonsignificant differences in the growth rates of males (Tukey: t_{12} = 0·26, P = 0·994) and females (Tukey: t_{19} = 2·05, P = 0·205). In contrast, female and male *Rivulus* transplanted from a *Rivulus*-only community into the *Rivulus*/guppy community downstream accelerated their growth rates. Transplanted fish grew at a rate that was several-fold faster in the *Rivulus*/guppy environment when compared with their rate of growth in the *Rivulus*-only locality. Differences in growth in the transplanted fish between pre- and post-transplant time periods were highly significant for females (Tukey: t_{19} = −12·22, P < 0·001)
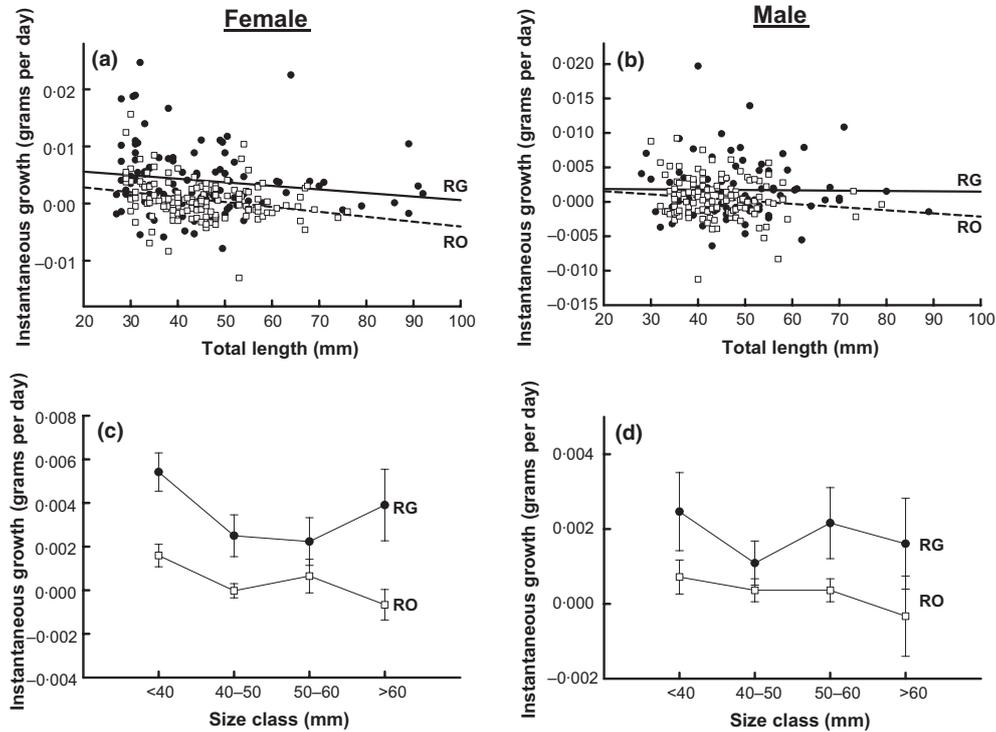
Fig. 2. Female (a, c) and male (b, d) growth rates (in grams per day) from localities with *Rivulus* plus guppies vs. sites with just *Rivulus*. Data from all three mark-recapture studies are included. Female *Rivulus* from *Rivulus*/guppy environments grew significantly (*P* < 0·05) faster than fish from *Rivulus*-only environments in all three studies. Growth rate differences were similar for males but not significant (*P* > 0·05). (a, b) Closed circles, Solid regression line – *Rivulus* from sites with guppies, Open squares, Dashed regression line – *Rivulus* from sites with just *Rivulus* (*Rivulus*-only). (c, d) Closed circles – *Rivulus* with guppies, Open Circles – *Rivulus* alone. RG, *Rivulus* plus guppies; RO, *Rivulus*-only. Error bars = ±1 SE.

Table 3. Growth rate analyses between *Rivulus*/guppy and *Rivulus*-only localities. A significant (*P* < 0·05) interaction between fish community and sex for in rates of instantaneous growth (grams per week) between *Rivulus*/guppy and *Rivulus*-only communities was observed. The growth differences between *Rivulus*/guppy and *Rivulus*-only sites are associated with the 'Fish community' effect

	Numerator d.f.	Denominator d.f.	*F*-value
Covariate:			
Total length	1	457	14·37***
Main effects:			
Fish community	1	3	4·35^{NS}
River	1	3	0·54^{NS}
Sex	1	4	9·46*
Fish × Sex	1	4	8·79*

***P < 0·001, *P < 0·05, ^{NS}P > 0·05.

and males (Tukey: t_{12} = −6·75, P < 0·001). There were no differences between the post-transplant growth rates of resident and transplanted fish (Female Tukey: t_{19} = −0·98, P = 0·763; Male Tukey: t_{12} = −1·49, P = 0·473), so the transplanted fish accelerated their growth rate to match that of the residents. It was this acceleration in the growth of transplanted *Rivulus* in the face of little change in growth of resident *Rivulus* before and after the transplant that caused the significant time × population interaction (Table 5). The repeated, random effect was not significant for females (Wald z = 1·53, P = 0·53) or males (Wald z = 0·76, P = 0·45).

Discussion

Our results show consistent differences in the population densities and growth rates of *Rivulus* from adjacent sites that

Table 4. Least squares means (±1 standard error) of instantaneous growth rates (grams per day) for the three mark–recapture studies

	Arima River (24-day study)		Aripo River (24-day study)		Aripo River (14-day study)	
	Instantaneous growth		Instantaneous growth		Instantaneous growth	
Population	Female	Male	Female	Male	Female	Male
Rivulus/guppy	0·0034 (0·0007)	0·0026 (0·0008)	0·0041 (0·0005)	0·0012 (0·0005)	0·0057 (0·0016)	0·0048 (0·0015)
Rivulus-only	−6 × 10-6 (0·0005)	−0·0003 (0·0005)	0·0005 (0·0005)	0·00036 (0·0005)	0·0022 (0·0007)	0·0023 (0·0009)

Table 5. Analyses from the transplant experiment. A linear mixed model repeated measures approach was used to examine changes in growth between the pre- and post-transplant period with time period entered as the repeated measures effect and fish population (resident *Rivulus*/guppy, transplanted *Rivulus*-only) entered as a fixed effect

	Female		Male	
	d.f.	*F*-value	d.f.	*F*-value
Time period	1, 19	**48·27*****	1, 12	**8·39***
Fish population	1, 19	**30·32*****	1, 12	0·59^{NS}
Time × Population	1, 19	**98·32*****	1, 12	**11·27****

$*P < 0·05$, $**P < 0·01$, $***P < 0·001$, $^{NS}P > 0·05$.
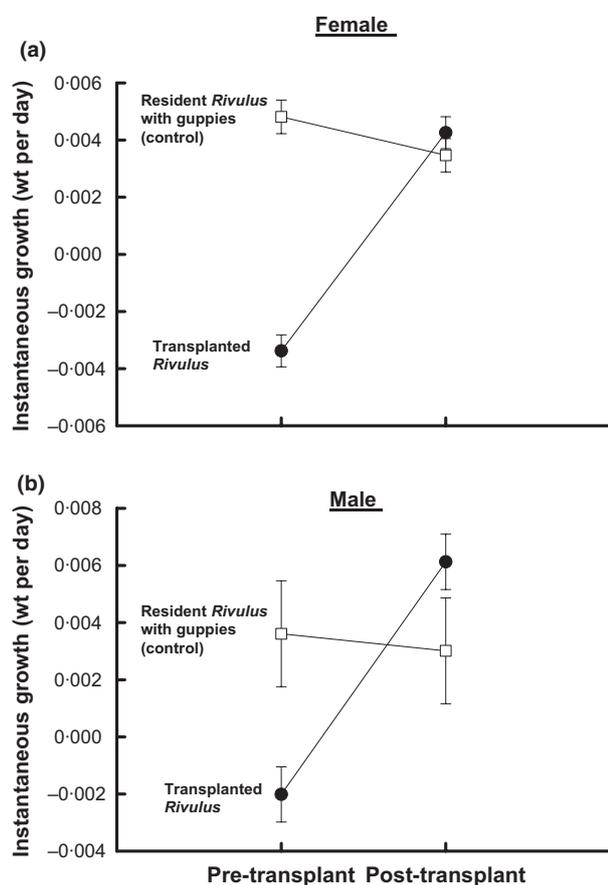
Fig. 3. Results of transplant experiment for (a) females and (b) males. For both graphs: Closed circles – *Rivulus* that were transplanted from site with just *Rivulus* into locality with *Rivulus* and guppies; Open squares – resident *Rivulus* from the sites with *Rivulus* plus guppies. Error bars = ±1 SE. 'Pre-transplant' represents the rates of growth during the initial 24-d study. 'Post-transplant' represents the rate of growth from the end of the 24-day study until the final recapture event. A significant ($P < 0·05$) 'time period-by-fish population' interaction was observed in both males and females as the transplanted fish greatly accelerated their rate of growth in the site with guppies, but the resident fish exhibited little change in growth between the pre- and post-transplant period.

either did or did not have guppies. These patterns suggest that guppies strongly impact the ecology of *Rivulus* and thereby create the opportunity for selection on the evolution of *Rivu-*

lus life histories (Figs 1 and 2). *Rivulus* from *Rivulus*/guppy communities were, on average, less abundant, per unit area of stream than *Rivulus* from *Rivulus*-only sites (Fig. 1). Male and female *Rivulus* from *Rivulus*/guppy communities exhibited rates of individual growth that were at least 3× faster than those from *Rivulus*-only communities (Fig. 2). When *Rivulus* were transplanted from a *Rivulus*-only site into a *Rivulus*/guppy site in one of our focal streams, the transplanted fish greatly accelerated their growth rates to match those of the residents (Fig. 3). Since no changes were observed in the growth of the resident *Rivulus* between pre- and post-transplant periods (Fig. 3) and also since these sites do not differ in habitat structure or several potentially confounding features of the physical environment (Walsh & Reznick 2009), the accelerated growth in the transplanted fish indicates that some feature of the biotic environment (e.g. predation or competition) causes the lower growth rates in the *Rivulus*-only sites. More importantly, the large differences in growth between *Rivulus*/guppy and *Rivulus*-only sites in conjunction with the dramatic changes in growth observed in the transplant experiment show that guppies are unlikely to be a strong competitor of *Rivulus*. The results instead support the hypothesis that guppies increase per capita resource availability to *Rivulus*. Below we compare the results of the present study to prior work and then more fully consider the possible mechanisms for the declines in density and increases in growth observed in *Rivulus*/guppy sites.

The decline in *Rivulus* density in sites with guppies was first reported by Gilliam, Fraser & Alkins-Koo (1993), who compared the densities (measured in grams m^{-2}) of *Rivulus* between adjacent pools that differed in the presence and absence of guppies across four tributaries to the Guanapo River. They showed that the density of *Rivulus* declined by 40–85% with guppies. Gilliam, Fraser & Alkins-Koo (1993) also show similarly consistent declines in the abundance of *Rivulus* in sites with guppies and one or two non- or weakly piscivorous species (*Rhamdia*, *S. marmoratus*, *Hemibrycon taeniurus*) in five other tributaries. The results of the present study, which includes data from two additional rivers, revealed similar differences in *Rivulus* abundance as reported in Gilliam, Fraser & Alkins-Koo (1993). We show that the density of *Rivulus* declined by 15–73% when guppies were present (Fig. 1). The declines in *Rivulus* density reported by us and Gilliam, Fraser & Alkins-Koo (1993), which have now been demonstrated in 11 streams, are compelling because female *Rivulus* from *Rivulus*/guppy localities have a higher rate of egg production (Walsh & Reznick 2009, 2010). Yet, such differences in egg production do not apparently have resultant impacts on adult abundance.

Why does the abundance of *Rivulus* decline with guppies? The lower abundance of *Rivulus* with guppies is not explained by higher rates of adult mortality, as rates of survival differed little for fish greater than 25 mm between sites with and without guppies (Table 2). One possible explanation is that a bottleneck exists during the early life history of *Rivulus* in *Rivulus*/guppy sites that limits recruitment to the adult stage. There are two logical mechanisms for this bottleneck:

(i) guppies prey upon larval *Rivulus,* and/or (ii) guppies compete with larval/juvenile *Rivulus*, potentially causing higher mortality rates via starvation or increased exposure to predators (see Wilbur, Morin & Harris 1983; Werner & Gilliam 1984; Mittelbach 1988; Post & Evans 1989; Bystrom, Persson & Wahlstrom 1998). The results of the current study provide little evidence that guppies negatively impact the growth of *Rivulus* in nature; *Rivulus* grow faster in *Rivulus*/guppy sites compared with the *Rivulus*-only sites in size-classes that overlap with guppies(< 40 mm; Fig. 2). Thus, the results of the current study do not support the hypothesis that guppies compete for resources with adolescent or adult *Rivulus*. However, recent work shows that guppies reduce rates of egg-to-juvenile survival in *Rivulus* by preying upon very small individuals (Fraser, unpublished data; Gilliam, Fraser & Alkins-Koo 1993). As a result, guppy predation on small *Rivulus* is a viable explanation for the observed differences in abundance between *Rivulus*/guppy and *Rivulus*-only communities. It also remains possible that competition between juvenile *Rivulus* (< 20 mm) and guppies causes increased mortality rates in juvenile *Rivulus*. Under either alternative, the presence of guppies would cause a bottleneck in *Rivulus* recruitment.

There are multiple ecological interactions that can facilitate faster rates of growth in communities with guppies. First, ecological factors, such as environmental productivity, could covary with guppies. This possibility is unlikely because sites with and without guppies are just tens of meters apart and we previously reported that there are no differences in some environmental factors that could impact growth rates, such as temperature, dissolved oxygen, pH, salinity, and habitat structure (Walsh & Reznick 2009). Our prior work also shows that life-history divergence in *Rivulus* between sites with and without guppies is highly repeatable across five drainages in Trinidad (Walsh & Reznick 2009). These rivers differ in habitat type, flow rate, as well as canopy openness, yet there is a consistent association between the presence of guppies and life-history divergence in *Rivulus* within each river regardless of considerable variation among rivers in habitat. For these reasons, we argue that correlated differences in unmeasured ecological factors are unlikely to explain the differences in the growth between guppy-present and guppy-free habitats.

Second, *Rivulus* can prey upon small guppies (Reznick & Endler 1982; Bashey 2002) so guppies could provide an additional source of food that could enhance *Rivulus* growth. However, prior research indicates that *Rivulus* predation on guppies in nature may be infrequent. Some analyses of *Rivulus* stomach contents reveal frequent predation on guppies (Seghers 1973), while others have failed to reveal any guppies in the stomachs of *Rivulus* (Fraser *et al*. 1999). A second, stronger argument against *Rivulus* predation on guppies causing the increase in *Rivulus* growth rates, is that *Rivulus* from *Rivulus*/guppy sites exhibited rates of growth that were faster than *Rivulus* from *Rivulus*-only sites across all measured size-classes (∼25–95 mm TL). This is important because previous work shows that *Rivulus* smaller than 45 mm are unlikely to consume guppies; in mesocosm experiments guppies exhibited survival rates in excess of 95% in the presence of *Rivulus* that were less than 45 mm (Bashey 2002). Thus, having guppies as an added source of food in *Rivulus*/guppy localities is unlikely to explain the growth differences between communities.

Third, the presence of guppies may induce morphological, behavioural, or physiological changes in *Rivulus* that could impact rates of growth. For instance, the predators can cause organisms to forage less (Morrison 1999; Peacor 2002), occupy less productive habitats (Schmitz, Krivan & Ovadia 2004), and alter food assimilation efficiency (McPeek 2004), which can have both positive (Peacor 2002; McPeek 2004) or negative (Morrison 1999) impacts on growth (see also: Werner & Peacor 2003; Schmitz, Krivan & Ovadia 2004; Preisser, Bolnick & Bernard 2005). It is plausible that the presence of guppies could induce such phenotypic changes in *Rivulus*; however prior work has shown that guppies reduced the growth rates of equal-sized *Rivulus* when the two are kept together in mesocosms with no differences in *Rivulus* density (Gilliam, Fraser & Alkins-Koo 1993), thereby indicating that guppies do not appear to indirectly facilitate higher rates of growth or cause physiological or behavioural changes that enhance growth. The present study instead shows that *Rivulus* exhibit faster growth when they co-occur with guppies in natural streams, even when there are less dramatic differences in population density (see 24-day Aripo River study). These latter results may indicate a role for non-lethal impacts of guppies on growth in *Rivulus* and such interactions merit further study.

Finally, the differences in growth may be an indirect effect of guppies mediated by a change in the density of *Rivulus*. It is known that predators can reduce prey abundance, which increases food to survivors (Power 1990; Wootton & Power 1993; Wootton 1994). In our transplant experiment, *Rivulus* moved from the high density *Rivulus*-only site to the lower density site with guppies greatly accelerated their rates of growth to match those of the resident *Rivulus*/guppy fish. This response to a change in habitat (and intraspecific density) indicates that the naturally occurring variation in growth rate between sites with and without guppies is caused by an environmental factor that allows *Rivulus* from the *Rivulus*/guppy localities to grow faster and also invest more in reproduction than *Rivulus* from the *Rivulus*-only localities (Walsh & Reznick 2009). The most plausible explanation is that the faster rates of growth in *Rivulus*/guppy locales are due to some correlate of the lower population densities of *Rivulus* in these sites. The simplest explanation is that the differences in growth are caused by higher levels of food availability that are a density-mediated indirect consequence of guppy-induced mortality in young *Rivulus*. The lower densities of *Rivulus* may increase the per capita availability of terrestrial food items, a major component of *Rivulus* diets (Gilliam, Fraser & Alkins-Koo 1993; Fraser *et al*. 1999), and thus facilitate faster rates of growth. This conclusion is further supported by the negative correlation between population density and individual growth rate observed within the *Rivulus*-only localities (Fig. 1; Table 4). Another plausible explanation is that *Rivulus* from *Rivulus*-only sites invest heavily in costly aggressive behaviours that divert energy away from growth and reproduction.

SIZE-SPECIFIC MORTALITY, OVERCOMPENSATION, AND STAGE-SPECIFIC BIOMASS

It is intuitive that increases in mortality, due to predation, should lead to a decrease in population density. However, as previously described, increased mortality can indirectly increase food to survivors. Increases in food availability can also facilitate faster growth, earlier maturation, and higher rates of offspring production. Such phenotypic changes may, in turn, alter the interaction between mortality and the abundances of individuals within certain life-history age- or size-classes (Werner & Gilliam 1984; Benton, Plaistow & Coulson 2006).

Theory that models the size-structure of populations as well as food-mediated patterns of growth, survival, and maturation was recently developed to explore such feedbacks between age- or stage-specific mortality and biomass (de Roos *et al.* 2007; see also de Roos & Persson 2002; de Roos, Persson & Thieme 2003). These models predict that increased mortality can cause decreases in abundance of some age-classes, as well as 'overcompensation', or *increased* abundances in other life-history stages. For example, in a population limited by strong adult competition, increased adult mortality is predicted to decrease adult density, increase per capita rates of reproduction, and thereby increase the biomass of juveniles (de Roos *et al.* 2007). Conversely, increased juvenile mortality is predicted to cause a decrease in the biomass of juveniles, but an increase in the biomass of adults under most conditions. These predictions, thus, run counter to what we see in natural populations of *Rivulus* when guppies are present (for examples of similar trophic cascades in size-structured populations see: Power 1990; Wootton & Power 1993; Pace *et al.* 1999). Furthermore, in a related laboratory experiment on *Heterandria formosa*, a livebearing member of the fish family Poeciliidae, Schroder, Persson & de Roos (2009) imposed different levels of adult and juvenile mortality as an empirical test of this theory. They found that adult population density was insensitive to increase juvenile mortality. This theory and empirical work, thus, seems inconsistent with our result for the guppy-*Rivulus* interaction.

We cannot explain the differences between what we see in the guppy-*Rivulus* interactions and what is expected on the basis of the models of de Roos *et al.* (2007) or the laboratory experiment by Schroder, Persson & de Roos (2009). *Rivulus* and *Heterandria* likely differ in life span, which could alter potential stage-specific biomass compensation. There are also layers of biological complexity associated with the guppy-*Rivulus* interaction that are not represented in these models or the associated laboratory experiment. Adult guppies prey on neonate *Rivulus*, but adult *Rivulus* can prey on juvenile guppies. Adult guppies compete with juvenile *Rivulus*. Both species can be cannibalistic. Both species are flexible in their diet preferences and can switch to diets not consumed by the other species. Both are known to evolve in response to the presence of the other and there is experimental evidence for co-evolution between the two species (Palkovacs *et al.* 2009). Somewhere among all of these interactions that are not part of the models or experiment may lie an explanation for the differences between their predictions and our results.

EVOLUTIONARY IMPLICATIONS

The results of this work are vital to understanding why the life history of *Rivulus* has diverged between *Rivulus*/guppy and *Rivulus*-only fish communities. The present study suggests that guppies cause a decrease in *Rivulus* population density and, as a consequence, cause an increase in resource availability to individual *Rivulus*. Guppy predation on juvenile *Rivulus* impresses us as the most likely cause of these differences. Previous work has shown that *Rivulus* from *Rivulus*/guppy sites are characterized by a smaller size at maturation and increased reproductive allotment compared with *Rivulus*-only communities (Walsh & Reznick 2009), which is inconsistent with the theoretical predictions that consider increases in mortality on very small or young individuals (Law 1979; Charlesworth 1980). Several theories predict that increases in juvenile mortality rate, when combined with the ecological consequences of reduced population density, can instead cause the evolution of earlier maturation and increased reproductive allotment (Gadgil & Bossert 1970; Stearns & Koella 1986; Hutchings 1993; Abrams & Rowe 1996). Thus, the patterns of phenotypic divergence between sites with and without guppies are consistent with theories that consider the indirect effects of changes in mortality rates.

The experiments in which we evaluated the genetic basis of trait variation between *Rivulus*/guppy and *Rivulus*-only sites (Walsh & Reznick 2010) support the conclusion that indirect effects have played an important role in shaping life-history evolution. The field-based growth rate data were incorporated into laboratory experiments by rearing all populations on two levels of food availability that mimic the naturally occurring differences in growth between *Rivulus*/guppy and *Rivulus*-only sites. We found that the life-history differences between *Rivulus* from *Rivulus*/guppy vs. *Rivulus*-only localities are heritable, but that the differences depended strongly on food level. *Rivulus* from *Rivulus*/guppy localities were younger and smaller at maturity and had higher rates of reproduction compared to those from *Rivulus*-only localities, but only when they were reared on high levels of food availability (Walsh & Reznick 2010). These differences disappear, or are even reversed in some cases, when they are instead reared on low rations that sustain growth rates typical of *Rivulus*-only localities. These interactions between indices of fitness and food level indicate that *Rivulus* are adapted to contrasting resource levels (Falconer & Latyszewski 1952). Such results further support the notion that differences in population densities and food availability are important agents of selection on *Rivulus*.

Conclusions

The presence of guppies is correlated with large changes in the population biology of *Rivulus*. Such results provide a link between changes in density and growth and subsequent

evolution in *Rivulus*. These associations are important because evolutionary biologists typically simplify the role of the environment as a selective force; single ecological factors (i.e. predation or competition) have received much attention, yet impacts spanning multiple trophic levels are ignored (Johnson & Stinchcombe 2007; Hughes *et al.* 2008). Our work on *Rivulus* (Walsh & Reznick 2008, present study) argues that a detailed understanding of the ecology of target organisms is necessary to provide robust explanations for mechanisms of evolutionary change in nature.

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Supporting Information

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

Table S1. Raw data of the number of fish marked and subsequently recaptured at each sampling interval for the mark-recapture studies. Each cell represents the number of female (F), male (M), or immature (I) *Rivulus*.

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