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An experimental test of antagonistic effects of competition and parasitism on host performance in semi-natural mesocosms

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The mechanisms by which parasites can mediate the interactions between species have received increased interest in recent years. Nonetheless, most research has focused on the role of shared parasites as mediators of interspecific competition. Here, we explore the relative effects of *Gyrodactylus* specialist ectoparasites of Trinidadian guppies *Poecilia reticulata* on competition between their host and juveniles of the killifish *Rivulus hartii*. In mesocosms that replicate natural streams, we exposed guppies to only competitors, to only parasites, to both parasites and competitors, or the absence of both. Consistent with previous studies, we found that female guppies grew significantly less where only *Gyrodactylus* were present, and this was regardless of infection status or parasite load. Surprisingly, this effect of *Gyrodactylus* on the growth of female guppies was greatly reduced when both parasites and competitors were present in the mesocosms. We conclude that guppies can mediate the effects of *Gyrodactylus* on competition with *Rivulus*, by adaptively fine-tuning their phenotype when simultaneously facing multiple enemies.

Every species coexists with many other species, and thus inevitably faces competition, predation and parasitism (Hatcher et al. 2006). To date, however, ecological research examining interactions between these effects has focused mainly on predation and competition (Chase et al. 2002). Although increasing attention is being given to the influence of parasitism on predator–prey interactions (Lafferty and Morris 1996, Raffel et al. 2010, Marino and Werner 2013, Marino et al. 2014), the interaction between parasitism and competition has been largely neglected (Hatcher et al. 2006, Pedersen and Fenton 2007). An important exception is "apparent competition" where two species may have deleterious effects on each other through shared parasites (Holt 1977, Hudson and Greenman 1998). In the present paper, we will consider a different type of interaction between parasitism and competition: how a non-shared parasite can influence competition through its effects on the host.

Specialist parasites, evidently, can only modify competitive interactions through their effects on their particular host (Hatcher et al. 2006), but are also likely to be strongly influenced by the effect of the competitor on its host, as they greatly depend on host density. Theoretical and empirical studies have shown that the presence of competitors can reduce parasite transmission by reducing the host population density (Keesing et al. 2006, Brunner and Ostfeld 2008, LoGiudice et al. 2008, Hall et al. 2009) or can increase transmission by enhancing host–parasite encounters owing to differential use of space, increased activity, and/or foraging behavior (Hatcher et al. 2006). In such cases, a host's response to competition might reduce its capacity to deal with parasites, but at the same time, parasite-induced changes in host traits can negatively impact the ability of the host to deal with competitors. Depending on the risk and fitness costs associated with each of these threats (i.e. relative effects), hosts should show a stronger response to the more costly interaction (Relyea 2002, Raffel et al. 2010). These reciprocal effects of competition influencing parasitism, and parasitism influencing competition, can modify the net effect of both interactions (i.e. interactive effects), yet they have been largely under-explored in experimental research (Raffel et al. 2010). Understanding the relative importance of parasites, in the realm of the interactions to which the host is exposed, is of utmost importance (Price et al. 1986, Minchella and Scott 1991, Hatcher et al. 2006, Dunn et al. 2012), particularly because both density- and trait-mediated effects can affect competitive and consumer–resource relationships, and propagate through trophic levels within the community (Dunn et al. 2012).

In this paper, we explore the relative and interactive effects of parasitism and competition by comparing fish growth in the presence of specialist parasites and/or competitors. We do so in artificial streams that replicate natural streams, and we take advantage of a well-known study system: the Trinidadian guppy *Poecilia reticulata*, its competitor *Rivulus hartii*, and a guppy-specific ectoparasite of the genus *Gyrodactylus*.

Empirical system

The upstream reaches of rivers in Trinidad are commonly inhabited by only guppies and *Rivulus* – because upstream migration of most fishes is prevented by a series of waterfalls. Adult *Rivulus* (maximum total length ~100 mm) are much larger than adult guppies (maximum total length ~ 45 mm) and are strict predators, foraging mainly on invertebrates and small fish, including juvenile guppies (Gilliam et al. 1993, Mattingly and Butler 1994, Fraser et al. 1999). Juvenile *Rivulus,* on the other hand, are of similar size as guppies, and directly compete with guppies for shelter and food (i.e. aquatic invertebrates) (Dussault and Kramer 1981, Gilliam et al. 1993, Palkovacs et al. 2009). In addition to these effects of *Rivulus* on guppies, reciprocal effects also occur. For example, the presence of guppies decreases the growth rate of juvenile *Rivulus* (Gilliam et al. 1993) – through resource competition – but dramatically increases the growth rate of adult *Rivulus* (Walsh et al. 2011) through guppy predation on *Rivulus* young, and the release of adult *Rivulus* from intra-specific competition (Walsh et al. 2011, Fraser and Lamphere 2013). An indirect effect, the importance of which will become clear later, is that both guppies and *Rivulus* impose strong selection on each other for rapid juvenile growth so as to avoid inter-specific predation (Seghers 1973, 1974, McKellar and Hendry 2011, Gosling and Rodd 2007).

The above guppy–*Rivulus* interactions might be strongly influenced by specialist monogenean *Gyrodactylus* ectoparasites that complete their life cycle on guppy hosts (Kearn 1994, Cable and Harris 2002, Harris et al. 2004). In Trinidad, three species of *Gyrodactylus* are known to infect guppies: *G. poeciliae, G. turnbulli* and *G. bullatarudis* (Harris and Lyles 1992, van Oosterhout et al. 2003, Xavier et al. 2015). The genus is characterized by an extreme progenesis and hyper-viviparity: adults give birth to fully-grown offspring that in turn has a developing embryo in utero (Cohen 1977). Newborn *Gyrodactylus* are fully-grown and directly attach to the host, and feed on host mucus and epithelial cells in a manner similar to other surface-browsing monogeneans. Transmission between guppy hosts occurs through direct contact and infections can cause high guppy mortality in the laboratory (Scott and Anderson 1984, Cable and van Oosterhout 2007) and in nature (van Oosterhout et al. 2007). Sub-lethal effects also occur: guppies exposed to *Gyrodactylus* show reduced foraging behavior (van Oosterhout et al. 2003), and reduced growth perhaps due to a potential reallocation of resources to immune responses (Pérez-Jvostov et al. 2012). Although differences in virulence have been reported for *G. turnbulli* and *G. bullatarudis* in one river (van Oosterhout et al. 2003), guppy immune response seems not to be species-specific (Richards and Chubb 1996).

For the above reasons, the guppy–*Gyrodactylus*–*Rivulus* system is well suited for testing the role of non-shared parasites in mediating interactions between competing species, a subject that has been largely unexplored experimentally. We predict that *Gyrodactylus* will modify guppy–*Rivulus* competitive interaction in favor of *Rivulus* through its detrimental effects on guppy growth and behavior. Thus, our objective is to quantify the relative and interactive effects of parasitism and guppy–*Rivulus* competitive interactions on the performance (i.e. growth) of both fish species.

Material and methods

Fish collection and treatment

In July 2013, we collected mature guppies (17–40 mm) and juvenile *Rivulus* (20–45 mm) from the Paria River in Trinidad (P7 in Millar et al. 2006) and transported them in 2-l containers to the laboratory in Trinidad where they were scanned for *Gyrodactylus* infections using a dissecting microscope. Infected and uninfected fish were then separated into species, sex and size specific groups (small, medium and large). All guppies, regardless of infection status, were then treated for *Gyrodactylus* infections with an application of N-cyclopropyl-1,3,5-triazine-2,4,6-triamine (cyromazine; 'lice and anchor worm treatment', Ecological Laboratories Inc.) – some infected guppies were set aside for use as a source of infection for the mesocosm experiments. The successful elimination of *Gyrodactylus* was verified four days later by scanning all guppies using a dissecting microscope. *Gyrodactylus* infections have been reported to survive for ~ 5 h on *Rivulus* (King and Cable 2007, King et al. 2009, Cable et al. 2013), so all *Rivulus* were also treated.

Two days prior to the beginning of the experiment, all collected *Rivulus* and guppies were anaesthetized using 0.02% tricaine methanesulfonate (Finquel MS-222) (1: 8000) buffered to a neutral pH using $NaHCO_3$, weighed (nearest mg), measured (standard length to the nearest mm), and given a distinct intra-dermic mark using an elastomer dye. This marking procedure is standard for guppies and has been used in many studies within minimal mortality (Weese et al. 2010, Bassar et al. 2010, Pérez-Jvostov et al. 2012).

The experiment

The experiment was performed in experimental stream channels (mesocosms) that have been used in previous work on guppies (Palkovacs et al. 2009, Bassar et al. 2010, Pérez-Jvostov et al. 2012). These channels (0.5 m wide by 3 m long by 0.2 m deep) received flowing water from a tributary to the Arima River that had neither guppies nor *Rivulus,* and they were covered with netting to prevent bird predation. Two weeks prior to introduction of fish, river gravel was added to the channels making them available for natural colonization by the invertebrates and algae that provide food for both guppies and *Rivulus*.

The experiment consisted of three replicates of each of five experimental treatments: guppies only (GO); guppies and *Gyrodactylus* (GG); guppies, *Gyrodactylus*, and *Rivulus* (GGR); guppies and *Rivulus* (GR); and *Rivulus* only (RO). Single species treatments (RO, GO, GG) consisted of ten randomly selected *Rivulus* (six small, two medium and two large *Rivulus*: RO) or twelve randomly selected guppies (four large males, four medium females and four large females: GO and GG). The largest *Rivulus* used in the experiment measured 45 mm and the largest female guppy measured 39 mm. Mixed species treatments (GR and GGR) consisted of five *Rivulus* and two male and four female guppies in the same size distribution as in single species treatments and typical in guppy–*Rivulus* experiments (Palkovacs et al. 2009). In addition, to minimize any potential familiarity between fish, we specifically ensured that fish that were kept together prior to the experiment were introduced into different mesocosms.

In the parasite treatments (GG and GGR), one of the male guppies and one of the female guppies used for each mesocosm was selected from the group of fish collected from the field but not treated. Each of these guppies had only 2–3 *Gyrodactylus* located only on the caudal fin. This increased the likelihood that only one species of *Gyrodactylus* (presumably *G. turnbulli* based on location) was used in the experiment (Harris 1989, Harris and Lyles 1992).

The mesocosms were checked daily for dead fish which were immediately removed and identified based on their elastomer marks. After 20 days, all remaining fish were collected, identified, and weighed, and all *Gyrodactylus* were counted by scanning guppies using a dissecting microscope.

Statistical analysis

Growth was calculated as the difference in mass as a proxy for performance, and was analyzed with generalized linear mixed models (GLMMs) with post hoc Tukey's honestly significant difference (HSD) tests to examine pairwise differences between treatments. The model included treatment, sex and their interaction as fixed factors; replicate (1 to 3) was nested as a random factor within treatment. Juvenile *Rivulus* cannot be differentiated based on sex, and so this factor was removed from the *Rivulus* model. Starting mass of individual fish was included in all initial models but was later removed owing to non-significance. These analyses were used to address three key questions. First, we evaluated the effect of competition by comparing the growth (change in mass) of guppies and of *Rivulus* in the competition treatment (GR) with growth in the respective single species treatments (GO and RO). Second, we examined the effect of *Gyrodacytlus* infection on guppies in the absence of *Rivulus* by comparing the growth of guppies between treatments with and without parasites (GG versus GO). Third, we examined the interactive effects of parasitism and competition by comparing growth of guppies and *Rivulus* between treatments with and without *Gyrodactylus* (GR versus GGR; GG versus GGR).

Analyses were conducted in R ver. 2.14.1 (<www.r-project.org>) using the *nlme* package, and the *multcomp* package for paired-wise comparisons in generalized linear mixed effects models (GLMMs). All the levels of significance were set at $p < 0.05$.

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.f5124 > (Pérez-Jvostov et al. 2015).

Results

Overall mortality of guppies (7% − all dead guppies were found) and *Rivulus* (10% of all *Rivulus* were found dead and an additional 6.6% were missing and presumed dead at the end of the experiment) was low. *Gyrodactylus* infections persisted to the end of the experiment in all GG and GGR mesocosms, reaching 33.5% prevalence in the GGR treatments and 25% in the GG treatments (Table 1).

Guppy performance (i.e. growth) was the highest in the absence of *Rivulus* and *Gyrodactylus* (Fig. 1). We detected no evidence that interspecific competition affected growth of either *Rivulus* (RO = GR) ($F_{2,4} = 0.703$, $p = 0.547$) or guppies (GO = GR) ($Z = 1.922$, $p = 0.219$), although a trend for less growth of guppies was evident (Fig. 1, Table 3). However, growth of guppies was negatively influenced by *Gyrodactylus* (Fig. 1). This parasite-induced depression in growth was evident for female guppies in the presence of *Rivulus* (GGR 32% less than GO), and most dramatic in the absence of *Rivulus* (GG 75% less than GO) (Fig. 1, Table 3). In contrast

Table 1. Descriptive statistics. Treatment abbreviations are as follows: GO, guppy-only; GG, guppy–*Gyrodactylus*; GR, guppy–*Rivulus*; GGR, guppy–*Gyrodactylus*–*Rivulus*; RO, *Rivulus*-only. Mixed species treatments consisted of four female guppies, two male guppies and five *Rivulus*. The number of fish was doubled in the single species treatments. Initial and final parasite prevalence (percentage of infected individuals in the mesocosm), mean intensity (average number of parasites per infected fish) and parasite population size (total number of *Gyrodactylus* per mesocosms) were determined on days 1 and 20 of the experiment, respectively.

Treatment	Replicate	Initial prevalence (%)	Final prevalence (%)	Initial mean intensity	Final mean intensity	Initial parasite population size	Final parasite population size	*Rivulus* mortality	Guppy mortality
GO	1	–	–	–	–	–	–	–	–
(12 guppies)	2	–	–	–	–	–	–	–	0/12
	3	–	–	–	–	–	–	–	0/12
GG	1	16.66	25	1.5	2	3	6	–	0/12
(12 guppies)	2	16.66	8.3	2	3	4	3	–	4/12
	3	16.66	25	1	1.66	2	5	–	0/12
GGR	1	33.33	33.3	1.5	3	3	6	1/5	0/6
(6 guppies, 5 *Rivulus*)	2	33.33	16.66	2	5	4	5	0/5	1/6
	3	33.33	33.3	1.5	1.5	3	3	2/5	0/6
GR	1	–	–	–	–	–	–	0/5	1/6
(6 guppies, 5 *Rivulus*)	2	–	–	–	–	–	–	0/5	0/6
	3	–	–	–	–	–	–	2/5	1/6
RO	1	–	–	–	–	–	–	2/10	–
(10 *Rivulus*)	2	–	–	–	–	–	–	1/10	–
	3	–	–	–	–	–	–	2/10	–

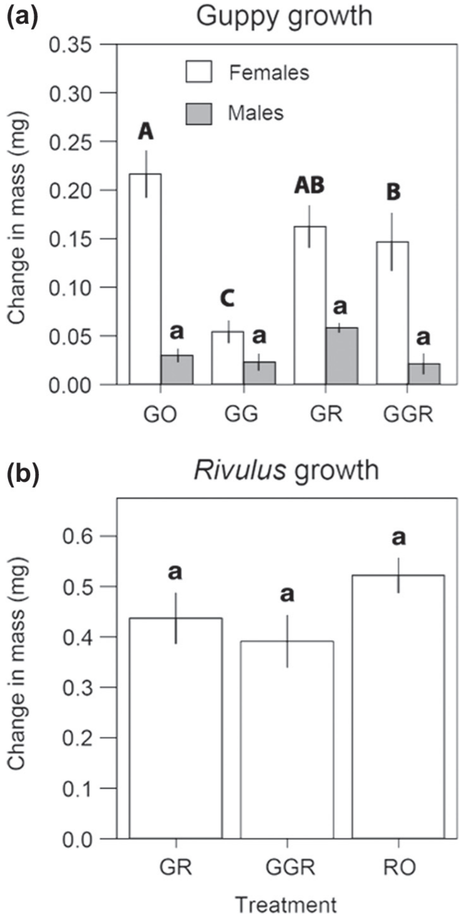

Figure 1. Least square means in growth for (a) female and male guppies, and (b) *Rivulus* pooled across sexes. The five treatments as shown are: GO, guppy-only; GG, guppy–*Gyrodactylus*; GR, guppy–*Rivulus*; GGR, guppy-*Gyrodactylus-Rivulus*; RO, *Rivulus*-only. Specific pair-wise comparisons were performed within each guppy sex. Error bars represent standard errors.

to guppy females, male guppy growth did not differ among any treatments (Fig. 2, Table 3).

Discussion

Our goal was to quantify the effects of parasitism and guppy–*Rivulus* interactions on the growth of both fish species – with particular attention being paid to the relative importance of parasitism and competition, and the nature of any interactions between them. Although no effects of parasitism were detected for *Rivulus* or for male guppies, the presence of *Gyrodactylus* parasites decreased female guppy growth, and this effect was much stronger than the effect of *Rivulus* (Fig. 1). We also found a very strong antagonistic interaction: *Gyrodactylus* reduced female guppy growth in the absence but not the presence of *Rivulus*. In short, the relative effect of *Gyrodactylus* on the growth of female guppies was much greater than that of a competitor (and potential predator), but the two effects were strongly interactive. These results generate several important insights into the nature of guppy–*Gyrodactylus*–*Rivulus* interactions and, more generally, food web interactions.

Table 2. Statistical analysis for guppy growth across the different treatments (GO, guppy-only; GG, guppy–*Gyrodactylus*; GGR, guppy–*Gyrodactylus*–*Rivulus*; GR, guppy–*Rivulus*; RO, *Rivulus*-only). Analyses were performed using linear mixed effects models with replicate nested in treatment.

Explanatory variable	DF	F	p
Sex	1,85	47.122	**<0.001**
Treatment	3,6	12.434	**0.005**
Sex × Treatment	3,85	5.040	**0.002**

Table 3. Specific Tukey's HSD Contrasts for female and male guppies. GO, guppy-only; GG, guppy–*Gyrodactylus*; GGR, guppy–*Gyrodactylus*–*Rivulus*; GR, guppy–*Rivulus*; RO, *Rivulus*-only.

Females	Contrast	Estimate	SE	Z	p
	GG vs GO	−0.162	0.023	−7.125	**<0.001**
	GG vs GR	−0.108	0.028	−3.799	**<0.001**
	GG vs GGR	−0.092	0.028	−3.341	**0.005**
	GO vs GR	0.054	0.028	1.922	0.219
	GO vs GGR	0.070	0.027	2.556	**0.052**
	GR vs GGR	0.016	0.032	0.488	0.962
Males	**Contrast**	**Estimate**	**SE**	**Z**	**p**
	GG vs GO	−0.007	0.033	−0.209	0.997
	GG vs GR	−0.035	0.042	−0.836	0.837
	GG vs GGR	0.002	0.042	0.040	0.993
	GO vs GR	−0.028	0.041	−0.692	0.900
	GO vs GGR	0.009	0.041	0.210	0.997
	GR vs GGR	0.037	0.049	0.759	0.873

The coexistence between guppies and *Rivulus* has been commonly viewed as a balance between predation and competition, with guppies being the better competitors (Gilliam et al. 1993), but large adult *Rivulus* actively preying upon juvenile guppies (Fraser and Lamphere 2013). So why was *Rivulus* unaffected by the better competitor in this experiment? Although we did find a trend for a decrease in growth of *Rivulus* in the presence of size-matched guppies, this was not significantly different from the *Rivulus*-only control, and similar results have been reported in a previous mesocosms experiments (Palkovacs et al. 2009), where changes in biomass did not differ between mixed and single species treatments. It is possible that under these experimental conditions competition is lessened due to relatively low fish density per mesocosms; however, an alternative possibility is that *Rivulus* grow larger than guppies and shift their diet towards terrestrial prey that are too large for guppies to eat, releasing them from resource competition (Fraser and Lamphere 2013). Indeed, at the end of the experiment *Rivulus* in the mixed-species treatment were almost three times larger than female guppies, despite being of similar size as the largest females in the mesocosms at the beginning of the experiment. Our results, thus, support the notion that guppies compete with size-matched *Rivulus* until these are large enough to feed on alternative prey types, and avoid resource competition.

Why might the growth of female guppies be lower in infected compared with uninfected mesocosms? It is important to point out that the parasite-induced reduction in female guppy growth observed here was consistent with our previous mesocosms experiment of eight guppy populations (Pérez-Jvostov et al. 2012). In that experiment, the reduction in female growth was not influenced by parasite load or infection status, but rather by the presence of *Gyrodactylus*. We suggest that guppies exposed to *Gyrodactylus* face an energetic tradeoff between growth and the activation and the maintenance of the immune response – as has been frequently documented in birds and mammals (Rauw 2012). Crucially, the reduction in guppy growth is not due to any pathological effects of the infection, but rather an immunoprophylactic response in which guppies invest in resistance at the expense of growth. This would also help explain the strong reduction in growth despite the low infection levels observed at the end of the experiment in the GG treatment (Table 1), and reinforce the notion that it is not the pathology commonly associated with high *Gyrodactylus* infection levels, but rather a phenotypic response of the host.

How did the interactive effect arise, whereby female guppies exposed to *Gyrodactylus* grew better in the presence of a competitor? We suggest two potential mechanisms. *Gyrodactylus* transmission is positively density-dependent, so the per capita risk of infection should be higher at higher guppy densities (Anderson and May 1981). Thus, it is predicted that guppies will increase their investment in *Gyrodactylus* resistance mechanisms as population density increases. Under this scenario, differences in guppy density between treatments could explain the strong reduction in female guppy growth in the GG (12 guppies) compared to the GGR treatment (6 guppies), as the risk of infection is larger in the higher-density GG treatment. This density-dependent-prophylaxis has been extensively reported in insects (Wilson and Cotter 2009), but whether it plays an important role in vertebrates is still largely unknown (Sadd and Schmid-Hempel 2009). Alternatively, intraguild predation provides a more feasible explanation for the observed differences in female growth between treatments. As an apparently adaptive response to reduce *Rivulus* predation on juvenile guppies, these increase their growth rate when exposed to chemical cues from adult *Rivulus* (Gosling and Rodd 2008). Guppies might thus show a phenotypic response to *Rivulus* as a potential predator. Even though the *Rivulus* in our experiment were not large enough to eat the guppies, the presence of small *Rivulus* is presumably a reliable cue of the likely presence of larger *Rivulus*. If guppies increased their growth in response to chemical cues signaling the presence of *Rivulus,* this would have partially counteracted the negative effects of parasitism on guppy growth, consistent with our observation that female guppy growth in the presence of *Gyrodactylus* and *Rivulus* was intermediate between guppy-only and guppy–*Gyrodactylus* treatments.

An interesting result worth exploring is the observed difference in the effect of *Gyrodactylus* between male and female guppies, where only females showed a strong decrease in growth in the presence of *Gyrodactylus*. This could simply be related to behavioral differences that could indirectly reduce the cost of infection. For example, in the wild females tend to school more and invest more time in feeding behavior, which may increase their susceptibility to *Gyrodactylus* infections (Richards et al. 2010). Indeed, female guppies in the wild tend to be more commonly infected than males, with the largest females usually having also the highest parasite loads (Gotanda et al. 2013). Although behavioral differences would help to explain differences in infection levels in the wild, they do not explain the strong reduction in growth in females but not males in our experiment. It has been recently shown that females in low predation localities – such as the ones used here – have 1.6 times longer life span than do males, independently of any extrinsic source of mortality (Arendt et al. 2014). This short male-life span may favor the evolution of higher resistance – given that they have little to no time to waste fighting *Gyrodactylus* infections. Indeed, Dargent et al. (2013) have recently shown that male guppies are overall more resistant to *Gyrodactylus,* than are females. Thus, the observed reduction of growth rate in females, but not in males, seems to be directly related to the intrinsic cost of infection and their reduced capacity to fight *Gyrodactylus* infections (i.e. reduced tolerance and resistance).

A natural question that rises from our results is whether *Gyrodactylus* could change the dynamics and structure of the broader community. It is possible that *Gyrodactylus* are limited in the extent to which they can influence the local community because they can only modify guppy–*Rivulus* interactions through their effects on guppies (i.e. non-shared parasites). Thus, an adaptive response from guppies to *Gyrodactylus* would mitigate any potential effects they could have. Conversely, different environmental conditions to which natural communities are subject to might exacerbate *Gyrodactylus* effects. For example, during the rainy season in Trinidad, heavy flooding could make it more difficult for guppies to find the necessary resources to fight an infection. During these periods infected guppies are more easily swept downstream (van Oosterhout et al. 2007), and this may drastically reduce guppy population density. It is thus possible that the *Gyrodactylus* effects reported here may be more prominent during strong flooding events. In addition, if differential foraging and dietary preference for higher quality items to fight the infection occur, *Gyrodactylus* could have strong top–down effects, and potentially influence the structure and composition of lower trophic levels (i.e. invertebrates and algae). Finally, we used guppies and *Rivulus* that have coevolved in the presence of *Gyrodactylus*; it would be interesting to test how *Gyrodactylus* can influence guppy–*Rivulus* competition and the broader community when neither of the species has previously encountered *Gyrodactylus*, and it would provide to be useful to do so in the wild.

Our results add to the growing evidence that host phenotypic plasticity in response to multiple enemies is fine-tuned to balance opposing phenotypic optima. Although several previous studies have found that parasites can drive interspecific interactions through their effects on host phenotype and survival (Werner and Peacor 2003, Hatcher et al. 2006), in most of these studies parasites had synergistic effects with predators and competitors. The effects of parasitism and competition in our study were antagonistic: increased female guppy growth in the presence of *Rivulus*, and decreased growth in the presence of the parasite. Similar effects have also been reported for amphibians (reviewed by Relyea 2007), where tadpoles of *Bufo americanus* delayed development in the presence of an echinostome-infected snail, but accelerated their development in response to a caged newt predator (*Notophthalmus viridescens*) (Raffel et al. 2010). However, to our knowledge, this is the first time that such antagonistic effects have been reported in a fish system. If we hope to better understand how hosts cope with multiple threats simultaneously, it is critical that we recognize the importance of the interactive effects of competition and parasitism on host phenotype (i.e. antagonistic versus synergistic), as host response to one source of mortality is likely to be contingent on its interaction with the other.

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