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## Research

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## Community ecology

# Pace of life, predators and parasites: predator-induced life-history evolution in Trinidadian guppies predicts decrease in parasite tolerance

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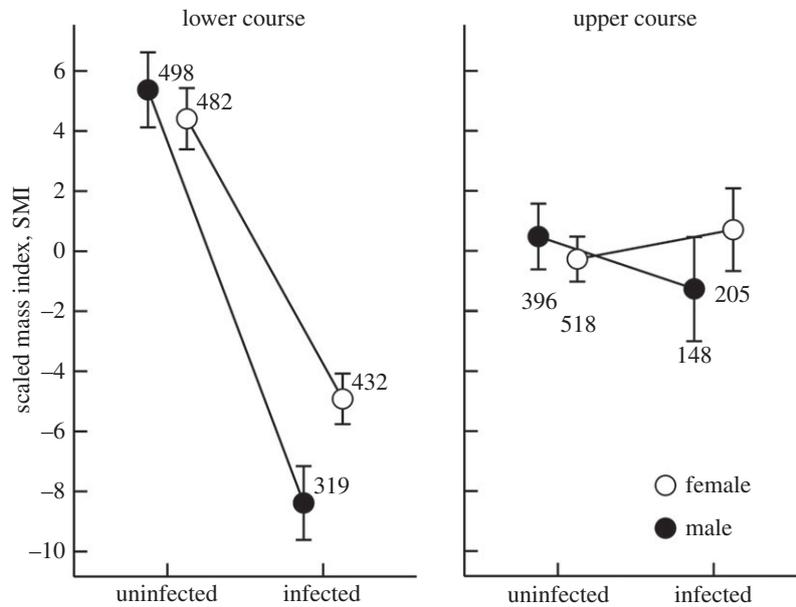
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A common evolutionary response to predation pressure is increased investment in reproduction, ultimately resulting in a fast life history. Theory and comparative studies suggest that short-lived organisms invest less in defence against parasites than those that are longer lived (the pace of life hypothesis). Combining these tenets of evolutionary theory leads to the specific, untested prediction that within species, populations experiencing higher predation pressure invest less in defence against parasites. The Trinidadian guppy, *Poecilia reticulata*, presents an excellent opportunity to test this prediction: guppy populations in lower courses of rivers experience higher predation pressure, and as a consequence have evolved faster life histories, than those in upper courses. Data from a large-scale field survey showed that fish infected with *Gyrodactylus* parasites were of a lower body condition (quantified using the scaled mass index) than uninfected fish, but only in lower course populations. Although the evidence we present is correlational, it suggests that upper course guppies sustain lower fitness costs of infection, i.e. are more tolerant, than lower course guppies. The data are therefore consistent with the pace of life hypothesis of parasite defence allocation, and suggest that life-history traits mediate the indirect effect of predators on the parasites of their prey.

## 1. Introduction

That predation pressure can drive the evolution of faster life histories has been demonstrated both theoretically [1] and empirically [2]. More recently, theory [3] and empirical data have linked the evolution of a faster life history to a decrease in the allocation of resources to defence against parasites: the pace of life hypothesis [4]. Defence against parasites encompasses both ‘resistance’, the ability of hosts to limit the extent of infection, and ‘tolerance’, host ability to limit the fitness cost of a given infection [5]. Immunological responses, proxies for resistance, decrease with increasing pace of life both between [6] and within [7] species. To our knowledge, Johnson *et al.* [8] present the single such study to use a measure of tolerance: the degree of pathology caused by trematode infection across amphibian species is positively correlated with pace of life.

The tenet that predation pressure increases pace of life, which in turn is negatively correlated with parasite defence, leads to the specific, untested prediction that populations of the same species experiencing divergent levels of predation pressure differ in their ability to defend against parasites. The Trinidadian guppy, *Poecilia reticulata*, provides an unprecedented opportunity to test this prediction. Because waterfalls prevent the upstream migration of their major aquatic predators, guppy populations in the lower courses of rivers experience higher levels of predation pressure, and have thus evolved faster life histories, than



**Figure 1.** Exclusively in lower course, high predation populations, *Gyrodactylus*-infected guppies were of a lower body condition than uninfected guppies, and this effect was more pronounced in males (black circles) than females (white circles). Error bars are the standard error of the mean and the numbers give the sample sizes.

those in the upper courses [2,9]. Despite clear differences in life history between guppy populations, previous studies have failed to find consistent evidence for the predicted differences in parasite defence, as quantified using parasite infection load as measure of resistance (e.g. [10–12]). The inconsistencies between these studies may be because infection loads are easily confounded by differences in exposure to parasites between courses [8]. Owing to the unidirectional flow of rivers, lower course guppy populations will be exposed to a higher number and diversity of parasites than will upper course populations [13]. By contrast, measures of tolerance can be considered ‘the integrated product of parasite exposure and host defences over time and across space’ [8].

Here, we tested whether data from field surveys of natural populations of guppies and their parasites conform to the prediction that populations experiencing higher predation pressure, and hence those with faster paces of life, invest less in defence against parasites. We have previously illustrated that predator-driven changes in shoaling indirectly affect the guppy–*Gyrodactylus* spp. host–parasite interaction [14]. We suggest that life history is a second trait mediating the indirect effects of predators on the parasites of their prey.

## 2. Material and methods

### (a) Data collection

The data collection has been described elsewhere [14], and further details are given in the electronic supplementary material (S1.1). In brief, 2998 sexually mature adult guppies were collected at 23 upper course and 28 lower course sites of 24 rivers in Trinidad between 2003 and 2009 (electronic supplementary material, table S1). The fish were killed on site, preserved individually in ethanol and later examined for *Gyrodactylus* spp. (hereafter *Gyrodactylus*) using a dissection microscope with fibre-optic illumination.

### (b) Data analysis

All data analyses were performed in R (v. 3.0.2; [15]), and used course (upper versus lower) as a proxy for the predation regime

faced by guppies (see the electronic supplementary material, S1.2). In order to investigate guppy tolerance of *Gyrodactylus* infection in natural populations, the scaled mass index (SMI) was calculated for each fish using the lmodel2 package [16] and the equation given in [17], standardized such that within upper and lower courses both males and females had a mean SMI of 0 to account for differences in body shape between the sexes, and between lower and upper course populations experiencing different predation regimes [9]. Standardized SMI was used as the response variable in a general linear mixed model in the lme4 package ([18]; Gaussian error family and identity link function). Sample site was included as a random term (see the electronic supplementary material, S1.3). Fixed terms included: presence and number (log transformed) of *Gyrodactylus*, fish sex, course, fish weight (size) and the two-way interactions between these variables. Model simplification involved removing non-significant fixed effects (number of *Gyrodactylus* and all interactions involving this term; see the electronic supplementary material, S1.4 for further analyses and discussion of these parasite count data) from the full model to minimize the Akaike Information Criterion (AIC).

## 3. Results

Infected guppies were of a lower condition (lower SMI) than uninfected guppies, but this difference was only evident in lower course, high predation, populations (figure 1; course  $\times$  infection status interaction:  $F_{1,2986.4} = 21.49$ ,  $p < 0.0001$ ). Across all populations, this correlation between infection and body condition was greater among males than among females (figure 1; sex  $\times$  infection status interaction:  $F_{1,2958.5} = 6.32$ ,  $p = 0.012$ ).

## 4. Discussion

Guppies infected with *Gyrodactylus* were of a lower condition than uninfected guppies, but this difference was only evident in lower course, high predation populations (figure 1). This correlation between infection and condition was stronger among males than among females. Although we cannot confirm a causal relationship, the result suggests that *Gyrodactylus* infection

has a more negative impact on the condition of lower course guppies than on those from the upper courses. Lower course guppies therefore appear less tolerant of infection, and as they are faster lived than upper course guppies, our results support the pace of life hypothesis of pathogen defence allocation [4]. The data furthermore support the existence of a trade-off in defence against the two classes of enemy, predators and parasites [19], which is consistent with the observation that upon release from predation pressure (via translocation), guppies evolve increased resistance, and perhaps tolerance, to *Gyrodactylus turnbulli* [20] (but see [21] for other potential explanations).

Stressors other than predators, both biotic and abiotic, differ between upper and lower courses and may affect guppy tolerance of *Gyrodactylus* infection. Lower course guppies are more likely to be co-infected by multiple strains and species of parasite [13,14]. The synergistic effects of multiple infections, if they commonly occur with *Gyrodactylus*, may explain the lower condition of *Gyrodactylus*-infected guppies in the lower courses [19,22]. Additionally, lower courses are subject to more anthropogenic disturbance [9]. Increased water temperatures [23] (due to deforestation [9]), and pollution [24] may diminish *Gyrodactylus* tolerance among lower course guppy populations, relative to that among upper course populations.

An important consideration is that these populations of guppies might not differ in their tolerance of infection, but instead differ in their resistance. If lower course guppies were less resistant to *Gyrodactylus* they would, by definition, develop heavier infection loads, and conceivably bear greater fitness costs relative to upper course guppies as a result. Although we cannot rule it out, we consider this explanation unlikely for two reasons. First, in our data the number of *Gyrodactylus* parasites infecting each fish did not explain significant variation in guppy condition (see the electronic supplementary material, S1.4), and second, despite several previous studies, evidence has not yet been found for a consistent difference in resistance or infection load between predation regimes (e.g. [10–12]).

Predator-driven changes in host traits may indirectly affect parasite traits; our results could reflect differences in the parasite populations infecting upper and lower course guppy populations. Lower course guppies shoal more, an antipredator defence, facilitating *Gyrodactylus* transmission [14]. Increased

transmission is predicted to increase parasite virulence [25], potentially explaining why the condition of guppies infected with lower course parasites was lower than that of those infected with upper course parasites. This explanation is not mutually exclusive with divergence in host defence against parasites; indeed it is most likely that traits of both host and parasite differ between predation regimes.

Females appeared more tolerant of *Gyrodactylus* infection than males across predation regimes, providing further support for the pace of life hypothesis. While, across taxa, males maximize fitness through increasing mating opportunities, females do so through living longer [26], and thus invest more in immunocompetence [27]. Conforming to this principle, wild female guppies live an estimated 1.65 times longer than males [28]. This result could additionally reflect behavioural differences between the sexes: their low shoal fidelity and resulting higher number of contacts [29] mean males may be more likely to become co-infected than females.

In conclusion, although our data are correlational, they support the hypothesis that predator-driven life-history divergence has resulted in divergence in parasite tolerance between guppy populations. While many studies have investigated the role of parasites in predator–prey relationships, this is among the first to explore the potentially equally important role of predators in host–parasite relationships.

**Ethics.** This work was conducted under UK Home Office license (PPL 30/2876) with approval by the Cardiff University Animal Ethics Committee.

**Data accessibility.** Raw data are available from the Dryad digital repository (<http://dx.doi.org/10.5061/dryad.3pf61>).

**Authors' contributions.** J.F.S. designed the study, analysed the data and wrote the manuscript. C.v.O. and J.C. collected the data and contributed to revisions. All authors gave final approval for publication, and agreed to be accountable for all aspects of the work.

**Competing interests.** We have no competing interests.

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