Testing for local host–parasite adaptation: an experiment with *Gyrodactylus* ectoparasites and guppy hosts

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A B S T R A C T

Hosts and parasites are in a perpetual co-evolutionary "arms race". Due to their short generation time and large reproductive output, parasites are commonly believed to be ahead in this race, although increasing evidence exists that parasites are not always ahead in the arms race – in part owing to evolutionary lineage and recent ecological history. We assess local adaptation of hosts and parasites, and determine whether adaptation was influenced by ecological or evolutionary history, using full reciprocal cross-infections of four *Gyrodactylus* ectoparasite populations and their four guppy (*Poecilia reticulata*) host populations in Trinidad. To consider effects of evolutionary lineage and recent ecology, these four populations were collected from two different river drainages (Marianne and Aripo) and two different predation environments (high and low). The highest infection levels were obtained when parasites from the Aripo lineage infected guppies from the Marianne lineage, indicating a higher infectivity, virulence and/or reproductive success of the Aripo parasites. Aripo lineage guppies were also better able to limit *Gyrodactylus* population growth than guppies from the Marianne River, indicating their strong "resistance" to *Gyrodactylus* regardless of the source of the parasite. Predation environment had no detectable influence on host–parasite population dynamics of sympatric or allopatric combinations. The much stronger effect of evolutionary lineage (i.e., river) than recent ecological history (i.e., predation) emphasises its importance in driving co-evolutionary dynamics, and should be explored further in future studies on local host–parasite adaptation.

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1. Introduction

Adaptation in host–parasite systems is a dynamic "arms race" in which adaptive peaks for the host and the parasite continuously shift in response to evolution of the opposing party (Ebert, 1994; Kaltz and Shykoff, 1998; Gandon and Michalakis, 2002; Kawecki and Ebert, 2004). Parasites are generally considered to be ahead in this arms race due to their shorter generation times which should increase their evolutionary speed (see Lively, 1999; Gandon and Michalakis, 2002; Greischar and Koskella, 2007; Hoeksema and Forde, 2008), and because hosts are usually exposed to many parasite species which makes adaptation to any one species more difficult (Kawecki and Ebert, 2004). Consistent with this, many studies have found that parasites show stronger signals of

local adaptation to their hosts than hosts do to their parasites (reviewed in: Greischar and Koskella, 2007; Hoeksema and Forde, 2008) as evidenced by higher infection levels for a given parasite population on sympatric hosts than on allopatric hosts (Ebert, 1994; Saarinen and Taskinen, 2005). However, other studies have not found evidence of local parasite adaptation, or have found apparent local maladaptation of parasites: e.g., infection levels are higher on allopatric than sympatric hosts (Lemoine et al., 2012; Roth et al., 2012; Konijnendijk et al., 2013; Sternberg et al., 2013).

One set of potential reasons for these varied results is methodological. First, many studies have measured parasite fitness (e.g., infection levels) without also measuring host fitness (e.g., survival or growth) which means that local adaptation cannot be considered independently for both host and parasite. Second, many studies have been conducted in the laboratory whereas very different results might be obtained in the natural environment (Brockhurst and Koskella, 2013). Third, many studies have not performed full reciprocal cross-infection experiments which makes it

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difficult to separate the confounding influences of virulence and resistance co-evolution (Greischar and Koskella, 2007).

Another set of potential reasons for varied results in local host–parasite adaptation studies is untested interactions with other factors related to evolutionary history or ecological context (Thompson, 1994, 1999; Morgan et al., 2005). Evolutionarily, different host lineages and their co-evolved parasites could have had different histories of selection, genetic bottlenecks, drift and founder events which might have strongly shaped co-evolutionary trajectories. Ecologically, recent ecological history whereby different host–parasite populations have experienced different biotic or abiotic conditions could have imposed selection that directly or indirectly influenced co-evolutionary trajectories (Thompson, 1999). As one example, environments with high predation-induced host mortality are likely to select both for parasites that reproduce more quickly (and thus might be more virulent), and for hosts that invest less in parasite defence (Lively, 1999; Gandon and Michalakis, 2002). Of course, the inverse might occur if parasitism increases susceptibility to other sources of mortality (Choo et al., 2003).

The Trinidadian guppy is frequently used in evolutionary studies due to its capacity for rapid and repeatable adaptation to different ecological environments (see reviews: Endler, 1995; Houde, 1997; Magurran, 2005; Dargent et al., 2013). The ecological force that has received the most attention is predation intensity, with guppy populations commonly classified as either high predation (HP), with many dangerous predatory fishes that have major effects on guppy survival, or low predation (LP), with fewer and less dangerous predatory fishes that have only minor effects on guppy survival (Reznick et al., 1996a; Gordon et al., 2009; Weese et al., 2010). In response to these different mortality regimes, HP and LP guppies have evolved a number of behavioural, life history and morphological differences (see reviews: Endler, 1995; Houde, 1997; Magurran, 2005). As one example, HP guppies show earlier maturation and increased reproductive investment, with more frequent reproductive events and many but smaller embryos (Reznick, 1982; Reznick and Endler, 1982). Moreover, this evolution occurs rapidly following experimental introductions in nature (Reznick and Bryga, 1987; Reznick et al., 1990, 1997; Gordon et al., 2009) and is repeatable across watersheds colonised by very divergent guppy lineages and with different predator faunas (Reznick and Bryga, 1996; Reznick et al., 1996b).

Guppies are commonly infected by the monogenean worm *Gyrodactylus*, a genus of ubiquitous host-specific ectoparasites on fishes (Harris and Lyles, 1992; Kearn, 1994; Harris et al., 2004). *Gyrodactylus* are viviparous and reproduce directly on the host, exhibiting hyperviviparity: a mature female has in its uterus a fully developed embryo that in turn has a developing embryo within its uterus (Kearn, 1994). Transmission between hosts occurs through contact when the parasite 'jumps' to a new host. These characteristics result in a rapid increase in parasite numbers on an individual host and epidemic spread of infection through fish populations (Scott and Anderson, 1984). Infections by *Gyrodactylus* can cause high guppy mortality in the laboratory (Scott and Anderson, 1984; van Oosterhout et al., 2003; Cable and van Oosterhout, 2007a,b) and in nature (van Oosterhout et al., 2007). Not surprisingly, then, some evidence exists that guppy populations have evolved in response to *Gyrodactylus*, particularly through variation in the immune response (van Oosterhout et al., 2003) and at loci of the Major Histocompatibility Complex (MHC) (Fraser and Neff, 2009; Fraser et al., 2010).

In a previous study (Pérez-Jvostov et al., 2012), we used experimental infections in semi-natural mesocosms to test whether adaptation to different predation environments (HP versus LP) influenced *Gyrodactylus*–guppy interactions. We found strong and repeatable differences in *Gyrodactylus* infection dynamics between

host–parasite assemblages taken from different field locations, but we found that the differences were not related to predation regime. However, because each guppy population was infected only with its own local parasite population, we were unable to disentangle the confounding effects between highly resistant hosts and highly virulent parasites, and those from low-resistance hosts and low-virulence parasites, which restricted any potential inferences on local adaptation.

The objective of this study was to assess local adaptation of hosts and parasites, and to determine whether adaptation was influenced by ecological or evolutionary history, using the well-studied ectoparasite *Gyrodactylus* infecting the Trinidadian guppy (*Poecilia reticulata*). Our design allowed us to circumvent methodological limitations (Hoeksema and Forde, 2008) by (i) generating separate measures of parasite and host fitness, (ii) conducting experiments in reasonably natural (mesocosm) environments, and (iii) conducting a full reciprocal cross-infection experiment with four *Gyrodactylus*–guppy populations to disentangle local adaptation from effects of host–parasite co-evolution. We specifically tested whether parasites or hosts showed evidence of local adaptation (higher performance of parasites with sympatric than with allopatric hosts, or higher performance of hosts with sympatric than with allopatric parasites), and whether any local maladaptation was related to drainage of origin (evolutionary lineage) or predation regime (ecological differences).

2. Materials and methods

2.1. Fish collection and treatment

Immature guppies were collected from an HP population and an LP population within each of two rivers in the northern mountain range of Trinidad: the Marianne River (HP, N10°46′30.525″, E-61°18′25.861″; LP, N10°44′51.85″, E-61°17′30.615) on the northern slope and the Aripo River (HP, N10°39′25.832″, E-61°13′39.395″; LP, N10°41′15.496″, E-61°14′4.455″) on the southern slope. These two rivers represent different guppy lineages (and probably separate colonisation events) as genetic distances between them are very large (see Suk and Neff, 2009; Willing et al., 2010). The *Gyrodactylus* populations in these different drainages are probably also distinct (given their host specificity for guppies), but this has not yet been confirmed.

At each site, the fish were collected with butterfly nets and immediately placed in individual 8 oz. whirl-pak bags (Spectrum Nasco, U.S.A.) to prevent movement of parasites among fish. After transfer to our laboratory in Trinidad, all fish were anaesthetised with MS-222 (Finquel MS222 from Fisher Canada; 1:8000 dilution and buffered to a neutral pH using NaHCO$_3$) and then immediately scanned for *Gyrodactylus*, using a dissecting microscope. Infected fish were isolated in individual containers to prevent the spread of infection.

All fish, regardless of whether or not they were initially infected, were treated with N-cyclopropyl-1,3,5-triazine-2,4,6-triamine (cyromazine; Lice And Anchor Worm Treatment, Ecological Laboratories Inc., U.S.A.) which effectively eliminates *Gyrodactylus* (Pérez-Jvostov et al., 2012). When no *Gyrodactylus* were seen on a fish over three consecutive days of visual inspection (as above), the fish was considered parasite-free. Elastomer dyes (Northwest Marine Technology Inc., U.S.A.) were then injected to give each fish a distinct intra-dermic mark, a procedure used effectively in many previous guppy studies (Bassar et al., 2010; Weese et al., 2010; Pérez-Jvostov et al., 2012). The elastomer marks were no longer than 2 mm and no marked fish showed signs of reduced mobility or altered behaviour. Guppies were then held in population- and sex-specific aquaria. No fry were observed in the