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Parasites grow larger in faster growing fish hosts

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Abstract

Parasites depend on host-derived energy for growth and development, and so are potentially affected by the host's ability to acquire nutrients under competitive foraging scenarios. Although parasites might be expected to grow faster in hosts that are better at acquiring nutrients from natural ecosystems, it is also possible that the most competitive hosts are better at countering infections, if they have an improved immune response or are able to limit the availability of nutrients to parasites. I first quantified the ability of uninfected three-spined sticklebacks *Gasterosteus aculeatus* to compete in groups for sequentially-presented food items, and then exposed either the best or worst competitors to infective stages of the cestode *Schistocephalus solidus*. Fish were subsequently raised in their original groups, under competitive feeding regimes, for 96 days, after which fish and parasite growth was determined. Unexpectedly, pre-exposure host competitive ability had no effect on susceptibility to infection, or on post-infection growth rate. Furthermore, despite a 120-fold variation in parasite mass at the end of the study, pre-infection competitive ability was not related to parasite growth. The closest predictor of parasite mass was body size-corrected host growth rate, indicating that the fastest growing fish developed the largest parasites. Faster growing hosts therefore apparently provide ideal environments for growing parasites. This finding has important implications for ecology and aquaculture.

Keywords: Stickleback; *Schistocephalus solidus*; Competitive ability; Fitness; Host–parasite relationships; Growth

1. Introduction

Within populations, individuals differ in their ability to compete for limited resources (Begon et al., 1990) and the resulting unequal division of nutrients leads to variation in growth rates, body size and nutritional condition (e.g. Rubenstein, 1981; Metcalfe, 1986; Westerberg et al., 2004). Unequal nutrient intake by competitors is also likely to have consequences for any parasites they may harbour, though it is difficult to predict the direction of such effects. On the one hand, because parasites are completely dependent on host-derived energy for growth and development (Bush et al., 2001), infecting better competitors might benefit parasites, particularly those with significant energetic requirements. Alternatively, if the best competitors are either in better nutritional condition as a result of their competitive superiority, or of intrinsically higher genetic quality, then they may be poor hosts for parasites if they have better immune systems or are able to limit the availability of nutrients to growing parasites. Pre-existing variation in the competitive ability of hosts therefore has potentially important implications for parasite infections, but to date no studies have directly tested this.

There is clear evidence from studies of parasitoids (insects with parasitic larvae that feed on the bodies of other arthropods, eventually killing them; Godfray, 1994) that intraspecific variation in host body size and nutritional status, which are likely correlates of competitive ability, can affect parasite growth (e.g. Harvey et al., 1995; Otto and Mackauer, 1998; Paine et al., 2004). If variation in body size and nutritional condition reflects the prior competitive foraging ability of parasitoid hosts these results might suggest that better competitors make the best hosts for parasites. Yet whether the results from parasitoid studies are

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likely to apply to all host–parasite systems, particularly to those involving vertebrate hosts, is questionable. Firstly, although insect hosts are capable of mounting cellular defences against parasitoids (e.g. Strand and Pech, 1995; Kraaijeveld and Godfray, 1997) their antiparasite responses are far less well developed than those higher animals (Wakelin, 1996). Second, unlike parasitoids, the growth stages of ‘true’ parasites do not generally kill their host, being forced to sequester nutrients from living hosts. Given these significant differences, it is important to test whether host competitive ability mediates parasite success in a vertebrate host that has greater potential to control infections.

There is evidence that infection with nutritionally demanding parasites can be associated with altered host foraging strategies, including exploiting risky foraging habitats, altering prey preferences and altering time budgets in order to maximise food intake rates (e.g. Milinski, 1985; Godin and Sproul, 1988; Ranta, 1995). Although behavioural changes associated with infection may allow infected hosts to maximise nutrient intake (Milinski, 1990), it is not clear whether this benefits hosts or parasites, and hence whether changes in host foraging behaviour are host or parasite adaptations (Poulin, 1998). Examining the relationship between the growth rates of hosts and their parasites under competitive feeding conditions can provide insight. If increased food intake benefits hosts by allowing them to mount an immune response or otherwise limit parasite growth a negative relationship between host and parasite growth would be predicted. Conversely, a positive relationship between host and parasite growth rates under competitive foraging regimes would indicate that parasites benefit from increased nutrient intake of hosts. The absence of studies examining growth rates of hosts and their parasites under competitive foraging conditions means that the consequences of host competitive ability and of infection-associated changes in host nutrient intake for host and parasite fitness remain unknown.

Here, I examine how pre-existing variation in the competitive ability of three-spined sticklebacks *Gasterosteus aculeatus* affects the growth of the parasitic cestode *Schistocephalus solidus* following experimental infection, and investigate the relationship between host and parasite growth over a 96-day period of food competition. *Schistocephalus* plerocercoids are common parasites of sticklebacks (Wootton, 1976), which become infected when they eat copepods harbouring infective procercoids. Plerocercoids grow rapidly in the stickleback body cavity, imposing significant energetic demands, and ultimately contribute up to 50% of the infected fish’s mass (Arme and Owen, 1967). *Schistocephalus* can only achieve sexual maturity in the intestine of an endotherm (generally a bird, Smyth, 1985), relying on ingestion of the fish host for transmission. The relative ease with which fish can be experimentally infected, coupled with straightforward host maintenance, makes this an ideal model system for examining host–parasite interactions.

2. Materials and methods

2.1. Husbandry

Sexually mature sticklebacks hand-netted from Inverleith Pond, Edinburgh UK (55°55′N, 03°10′W) in June 1999 were allowed to spawn in aquaria at Glasgow University, and embryos recovered from nests were incubated until hatching (Barber and Arnott, 2000). After 12 weeks of being fed an ad libitum diet of Liquifry™, *Artemia nauplii* and bloodworms (*Chironomus* sp. larvae), 19 groups of six, size-matched juveniles were selected and each group transferred to a 40×20×20 cm (16 L) aquarium. Group members were measured (standard length, SL_0, to 1 mm), weighed (wet weight, W_0, to 0.001 g) and marked with coloured plastic tags attached to the second dorsal spine (Barber and Ruxton, 2000; tag colours did not include red or orange, colours known to elicit aggressive attacks; Rowland, 1994). Mean group SL_0 ranged from 30.2 to 37.7 mm, and within-group size range was always less than ±10% of the mean group SL_0. Aquaria were provided with a gravel substratum and a plastic plant for shelter; water was maintained at 17±1 °C, filtered and aerated with sponge airlift filters and partially replaced on a weekly basis. A lighting regime of 14 h dark:10 h light was used.

2.2. Assigning competitive rank within groups

The relative competitive ability of individual fish in each group was assessed by scoring foraging success in three trials, undertaken on alternate days in December 1999 (d0, d2 and d4). During each trial, 20 bloodworms were introduced to each tank at 5 min intervals, by pipette via a suspended plastic funnel, and the identity of the fish ingesting each prey item was recorded. A screen, fitted with viewing windows, isolated the fish visually from the observer. The proportion of items ingested by each fish on each day was used to rank fish with respect to their competitive ability within the group, generating three daily performance ranks (R_{d0}, R_{d2}, R_{d4}) that were averaged to give a mean rank (R_m). This was then used to assign each fish an overall rank (R) from 1 (best competitor) through 6 (worst competitor) in its group. Where tied R_ms were generated, the fish that ingested the most prey items over all three trials was assigned the more competitive R value.

2.3. Parasite exposure

Infected copepods were generated by exposing individuals to infective coracidia and scoring the number of visible