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EDITOR'S CHOICE

Behave in your parasite's interest

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Any change in the phenotype of an infected host that would lead to an increase in the fitness of the parasite involves *parasitic manipulation* of host phenotype. For many altered host phenotypes, it is intuitive that parasite-induced changes would benefit the parasite, but not the host. This is especially true for the manipulation of host behaviour, appearance, and reproduction by parasites characterized by complex life cycles. These parasites are transmitted via one or more intermediate hosts, in which growth or asexual reproduction of the parasite takes place, to the definitive host, where the parasite reproduces sexually. Changes in infected intermediate hosts that make them more vulnerable to predation by the next host (often the definitive host) in the parasite's life cycle would obviously only benefit the parasite. It is tempting to also refer to this increase in host susceptibility to predation as parasitic manipulation, and according to the definition given above, it is. Yet, an altered host phenotype may be a by-product or side effect of an infection caused by, for instance, activation of the immune system or decreased energy availability. Definitions of direct parasitic manipulation, therefore, also demand that the adaptive alteration of a host phenotype is controlled by the parasite's genotype. Parasitic manipulation must therefore be seen as an extended phenotype of the parasite (Heil 2016).

Doubts about direct manipulation by parasites has particularly been raised in parasite systems in which the parasite extracts high amounts of energy from its intermediate host, as is the case of the cestode *Schistocephalus solidus*. This parasite is transmitted via cyclopoid copepods and three-spined sticklebacks (*Gasterosteus aculeatus*) to fish-eating birds. In the obligatory three-spined stickleback host, the worm grows enormously and may reach half the body mass of the fish (Fig. 1). Infected sticklebacks seem to behave in ways that make them easy prey for birds. When parasitized with fully developed (infective) worms, sticklebacks swim for longer periods of time close to the water surface, and are bolder under predation risk. They also shoal less, and, under simulated bird attack, flee less (Barber and Scharsack 2010). Is this altered host behaviour due to parasitic manipulation or simply a side effect of the increased energetic need and oxygen demand of heavily infected sticklebacks? This is still an open question that has been discussed for several decades (reviewed in Barber and Scharsack 2010).

Talarico et al. (2017), published in this issue of *Behavioural Ecology and Sociobiology*, suggests that the *S. solidus*—stickleback interactions involve parasitic manipulation. Using sticklebacks that were experimentally infected with *S. solidus*, they compared the behaviour of infected and uninfected sticklebacks in two contexts. The first context was without predation risk; feeding in a familiar environment and exploration of a new environment were quantified. In the second context, feeding was quantified under a perceived risk of predation (simulated bird attack). For parasitic manipulation, one would expect behavioural differences between infected and uninfected sticklebacks in the presence of predators but not in their absence. In the case of immunological or other physiological side effects of infection, one would expect differences in both contexts. The results clearly favour parasitic manipulation, with large effects under the condition of risk, but not in the relatively safe situation.

These results contrast with the recent findings on the same parasite system (Hafer and Milinski 2016). Risky feeding

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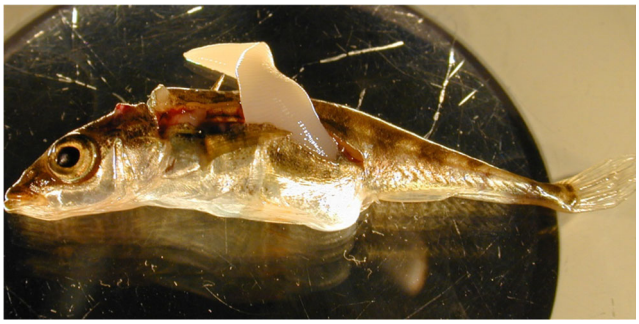

Fig. 1 *Schistocephalus solidus* creeping out of a freshly killed and opened three-spined stickleback. Photo: Martin Kalbe, Max Planck Institute for Evolutionary Biology, Plön, Germany

under simulated predation risk was similarly affected by hunger state in sticklebacks infected with *S. solidus* and uninfected sticklebacks, which was expected when parasite-induced changes are the consequence of energy drain by the parasite. When simultaneously infected by an infective and a non-infective stage of the parasite, risk-taking became even more pronounced than in sticklebacks carrying only the infective stage. Again, this was not expected under direct parasitic manipulation, as the non-infective parasite should avoid being eaten by the definitive host, which is the case when it resides alone in the intermediate host (Hafer and Milinski 2016). In another recent study of the *S. solidus*—stickleback interaction, some but not all parasite-induced changes could be mimicked by physiological interventions (Grécias et al. 2017). These authors concluded that "The behaviour changes observed in infected fish may be due to the combined effects of modifying the serotonergic axis, the lack of energy, and the activation of the immune system." (Grécias et al. 2017). So, the fascinating issue of parasitic manipulation is complex. The present paper of Talarico et al. (2017) highlights the direct manipulative aspect by parasites without excluding other causes for parasite-induced changes.

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