Light-induced eye-fluke behavior enhances parasite life cycle

The animal eye can be infected by a variety of pathogens, such as viruses, bacteria, fungi, protozoans, nematodes,cestodes, and trematodes, all of which can potentially damage vision through the development of cataracts, infections, or permanent blindness (Rushton 1937; Seppälä et al. 2011; Wesołowska and Wesołowski 2014). Some eye parasites, including trematode flukes belonging to the Diplostomidae family, occupy the inner portions of the eye globes of their hosts and are able to "swim" in the eye fluids.

Parasitic Diplostomidae eye-flukes often require two intermediate hosts before reaching their target host. Snails serve as the first intermediate host, from which the parasite’s free-swimming cercariae eventually emerge to search for fish, the second intermediate host. After penetrating the fish’s body, the cercariae develop into metacercariae, which migrate to the interior of the eye. To reach their target avian hosts and complete their life cycle, the parasites have to be eaten by a bird as it preys on an infected fish (Rauch et al. 2005). Diplostomidae parasites are assumed to impair eye functioning, and thereby disrupt visual signals that would otherwise cue anti-predator behavior, possibly making infected fish more susceptible to predation by water birds (Seppälä et al. 2004, 2012; Correa et al. 2014).

In 2013, in southern Brazil’s Upper Paraná River Floodplain, we began our investigation of the interactions between Diplostomidae Austrodiplostomum compactum parasites and their fish hosts. Although several fish species are documented hosts of this particular parasite, we selected the cichlid Satanoperca pappaterra as the focal host because it reportedly experiences a very high eye-parasite burden in the Upper Paraná.

During exploratory expeditions, we sampled individuals of S pappaterra and visually inspected them to determine whether parasites were present. Free-swimming metacercariae – occasionally moving vigorously to or from behind the lenses – can actually be seen inside the eyes of live infected fish. Our first sampling started before sunrise and was disappointing; no parasites were found during visual inspections. Additional sampling continued a few hours later, under intense tropical sunlight. To our surprise, we did see parasites in the eyes of fish caught after sunrise. To our further surprise, when later dissected in the lab, fish that were captured both before (n = 22 fish; mean abundance of parasites per fish = 24.1) and after (n = 25 fish; mean abundance of parasites per fish = 24.3) sunrise contained similar numbers of eye parasites (t45 = 0.07; P = 0.97). Furthermore, fish sampled before sunrise had no parasites in the outer region of their eyes, while fish sampled after sunrise did have flukes in the outer eye region. This led us to wonder whether parasites were migrating from the inner to the outer regions of the eye based on ambient light levels at different times of the day.

With this new question in mind, we sampled more fish to investigate the distribution and movement patterns of the parasites inside fish eyes. We found that when fish were kept in dark experimental conditions, the parasites tended to remain deeper in the eyes, whereas when the fish were briefly exposed to light, parasites were detected in the outer zones of the eyes, indicating light-induced movement (Figures 1 and 2). This movement was a swift response to light, as parasites were observed to move from inner to outer eye zones within minutes of light exposure. We also investigated the anti-predator escape behavior of fish – subjected to a threat by an artificial bird predator – with parasites occupying either inner or outer regions of the eyes; our results indicated that parasites situated in the outer zone of fish eyes, in front of or immediately behind the lenses, are more likely to disturb vision and behavioral responses, probably by physically preventing visual signs from reaching photoreceptor cells at the back of the eye.

Figure 1. After exposure to light, Austrodiplostomum compactum parasites are more concentrated in the outer, front region of the eye of the host fish Satanoperca pappaterra. Photos show a fish eye (a) exposed to (non-intense) light immediately after darkness, (b) exposed to intense light for 1 minute, and (c) exposed to intense light for 2 minutes.
If parasites need their second intermediate hosts to be preyed upon in order to reach their final host, anti-predatory behavioral adaptation in that intermediate host can incur fitness costs to the parasite. Natural selection should therefore benefit parasites that adapt so as to reduce predator avoidance in their intermediate hosts. There are interesting empirical examples of parasite-induced changes in host anti-predator behavior that increase host risk of predation. For instance, chimpanzees (Pan troglodytes troglodytes) infected with Toxoplasma gondii lose their innate aversion toward the odor of leopard (Panthera pardus) urine; leopards are their natural predators (and target hosts for T gondii). As a consequence, infected chimpanzees behave oddly and become more susceptible to predation (Peirotte et al. 2016). Such alteration in host behavior can be seen as an extended phenotype of parasites manipulating hosts (Dawkins 1982; Hughes et al. 2012), and should provide selective advantages by enhancing parasite transmission (Poulin 1995, 2010).

Similarly, A compactum behavior may face selection pressure to move within the eye during dawn conditions into regions that obstruct visual cues and reduce fish anti-predator responses to avian predators. The dawn period coincides with a daily time of high foraging activity in water birds, increasing the probability of infected fish being eaten. Here, we suggest that A compactum behavior may be adaptive, increasing the probability that the parasite will reach the target host, providing an intriguing example of how a parasite manipulates its host’s vision.

Parasitologists have long assumed that the distribution of A compactum inside the eye globes of S papattarea is random, whereas our findings suggest light-induced movement and distribution. Parasite species other than A compactum may also display within-eye movement behaviors to enhance their fitness, and future studies should examine the advantages of such migration. For example, do parasites residing deeper in the eye allow infected fish to forage efficiently while avoiding predators that are not targeted as final hosts by the parasites? Do different parts of the eye supply parasites with resources that vary in quality? An improved understanding of the trade-offs that eye-flukes face not only helps to explain the evolution of extended phenotypes in parasites, but also warrants attention across parasite and host taxa.

Supporting Information

References and additional web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1513/suppinfo

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Figure 2. Schematic distribution patterns of Austrodiplostomum compactum parasites inside the eye of fish hosts in (a) dark and (b) light conditions.