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Behavioural impacts of trematodes on their snail host: Species-specific effects or generalised response?

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Abstract

Behavioural changes induced by parasites are extremely common, but their ultimate causes are often difficult to determine: they may represent adaptive manipulation by the parasite, adaptive responses by the host, or non-adaptive side-effects of infection. Contrasting the impacts of different parasites on the same host species offers an opportunity to test for species-specific changes in host behaviour, which are less likely to be general side-effects. Here, we tested the impacts of three trematode species (*Apatemon* sp. I, Plagiorchioid sp. I, and *Maritrema poulini*) on movement, microhabitat choice and responses to predator cues of their common intermediate host, the freshwater snail *Potamopyrgus antipodarum*. All three trematodes cause the castration of their host, and thus adaptive host responses to infection can be ruled out. In laboratory trials, snails infected with *Apatemon* sp. I moved a shorter total distance during the experimental period than uninfected control snails. However, all three trematode species similarly neutralised the attraction to lighted areas shown by uninfected snails, and none of the trematodes affected the time spent moving by their host or its responses to predator cues. Overall, there was little evidence for species-specific effects on host behaviour by the three different trematode species in the same snail host. The single difference in induced behavioural change, involving one trematode species and one specific behavioural measure, is insufficient to reject the hypothesis that the behavioural impacts on the snail host are general and non-adaptive by-products of trematode infection.

KEYWORDS
microhabitat choice, movement tracking, parasite, phototaxis, *Potamopyrgus antipodarum*, predator evasion

1 | INTRODUCTION

Changes in host behaviour are extremely common consequences of infection by parasites (Moore, 2002). In many cases, these changes represent adaptive manipulation of host behaviour by the parasite to maximise its transmission success (Moore, 2002; Poulin, 2010; Thomas, Adamo, & Moore, 2005). For example, there are now hundreds of documented cases of host manipulation by trophically transmitted parasites, that is, those transmitted by ingestion of a prey intermediate host by a predatory definitive host (Poulin & Maure, 2015). In cases where behavioural manipulation is not occurring, there are two alternative explanations for behavioural changes in infected hosts: they may be instances of adaptive responses by the host to compensate for the effects of infection, or they may simply be pathological side-effects of infection with no adaptive value for either host or parasite (Moore, 2002). Distinguishing between these explanations is not always easy. One approach that is rarely used would be to contrast the behavioural changes induced in the same host species by different parasite species. Depending on whether or not the different parasites have similar life cycles, how they modify

host behaviour can be indicative of parasite manipulations, adaptive host responses or pathological side-effects.

Snails and their trematode parasites are good models for this kind of comparative approach, as often the same snail species serves as intermediate host to a suite of different trematode species. The vast majority of trematodes use snails as their first intermediate host, in which they multiply asexually to produce cercariae, the free-swimming dispersal stages that usually leave the snail to seek the next host in the life cycle (Galaktionov & Dobrovolskij, 2003). Almost invariably, trematode multiplication results in the complete and permanent castration of the snail host. Therefore, any subsequent change in snail behaviour is unlikely to represent an adaptive host response, as selection could not favour any response manifested after total loss of reproductive abilities. In some trematode species, cercariae remain within the snail and must await predation by their definitive host to complete their life cycle. In this situation, changes in host behaviour that increase their susceptibility to predators are easily interpreted as adaptive manipulation by the parasite (e.g., Wesolowska & Wesolowski, 2014). In the majority of trematode species, however, cercariae must leave the snail host and seek their next target host, which may be an invertebrate, an amphibian or a fish, depending on the trematode species. Prior to cercarial release, infected snails sometimes display shifts in their spatial distribution, on scales ranging from centimetres (Lowenberger & Rau, 1994) to several metres (Curtis, 1987), bringing them into microhabitats nearer that of the parasite's next host. This phenomenon is compatible with host manipulation, as the release of cercariae closer to the target host is more likely to lead to successful transmission. In many other cases, however, changes in the behaviour of infected snails include decreased activity and impaired orientation (e.g., Miller & Poulin, 2001; Mouritsen & Jensen, 1994; O'Dwyer, Kamiya, & Poulin, 2014), which are more likely to represent pathological by-products of infection arising from energy demands exerted by the parasite. Also, infected snails sometimes show different responses to perceived predation risk than those of uninfected snails, possibly indicating that parasites modify the trade-off between predator avoidance and foraging in infected snails (Bernot, 2003; Kamiya & Poulin, 2012).

The mudsnail *Potamopyrgus antipodarum* is the most abundant freshwater snail in New Zealand, and it serves as first intermediate host to a wide range of trematode species with different life cycles (Hechinger, 2012; Winterbourn, 1973). In one of them, *Microphallus* sp., cercariae do not leave the snail, but instead they encyst within the snail (as metacercariae) and await transmission to waterfowl definitive host through predation. Earlier studies have showed that snails infected by *Microphallus* sp. move more slowly (Levri & Fisher, 2000) and spend more time in the shaded underside of rocks during the day (Levri, 1999) than uninfected conspecifics. However, the response of *Microphallus*-infected snails to chemical cues from a fish predator, the common bully *Gobiomorphus cotidianus*, was not different from that of uninfected snails (Levri, 1998). In some of these earlier studies (Levri, 1999; Levri & Fisher, 2000), snails infected by trematode species in which cercariae must leave the snail to infect a second intermediate host were seen to exhibit behaviours generally not different from those of uninfected snails; however, the trematode species were not identified and/or data were pooled across species, preventing any detailed examination of species-specific effects. Here we investigate the specific effects of three trematode species on the behaviour of the snail *P. antipodarum*. Uniform changes in host behaviour across different species of trematodes in the same host species may suggest pathological side-effects of infection by castrating parasites, whereas species-specific alterations in snail host behaviour by parasites whose cercariae target different host species would be more indicative of adaptive manipulations of host behaviour.

Our specific goals were to compare movement patterns, attraction to light versus dark areas, and responses to predator cues among uninfected snails and snails infected with three different trematode species, with distinct cercarial dispersal behaviour and/or second intermediate host targets. Similar behavioural changes, if any, induced by infection by all three trematode species would strongly suggest that the responses are simply side-effects of pathology and reduced energy levels.

2 | MATERIAL AND METHODS

2.1 | Study species

The New Zealand mud snail, *Potamopyrgus antipodarum*, serves as first intermediate host for a diverse guild of trematode parasites (Hechinger, 2012). In our study, we focused on snails infected with three of the most common trematode species in our region (Lagrue & Poulin, 2015): *Apatemon* sp. I, *Maritrema poulini* and Plagiorchioid sp. I. These three species have different cercarial swimming and dispersal patterns (Selbach & Poulin, 2018) and target different second intermediate hosts (Table 1).

2.2 | Field collection and parasite identification

Mudsnails (*Potamopyrgus antipodarum*) were collected with dip nets from sediment, macrophytes and stones along the shoreline of Tomahawk Lagoon (45°54′06.0″S, 170°33′02.2″E), New Zealand, in February 2018. Snails were transported to the laboratory and placed in 24-well plates filled with small amounts of filtered lake water and exposed to light for 48 hr to induce cercarial release. Cercariae were identified under a microscope based on morphological characteristics, using the keys of Winterbourn (1973), Hechinger (2012) and Presswell, Blasco-Costa, and Kostadinova (2014). Snails were separated according to their trematode species and maintained under controlled conditions in aquaria with aerated lake water and macrophytes for food on a 12-hr/12-hr light/dark photoperiod at 20°C prior to laboratory experiments. Only uninfected snails and snails infected with one of the three focal trematode species (Table 1) and with 4.2–4.9 mm shell length (from shell apex to aperture lip) were retained for the experiments; all were collected on the same day to avoid behavioural differences due to size or time in captivity. All

TABLE 1 Trematode species infecting *Potamopyrgus antipodarum* used in the behavioural experiments

Trematode sp.	Family	First intermediate host	Second intermediate host	Final host
Apatemon sp. I	Strigeidae	*Potamopyrgus antipodarum*	Fishes	Fish-eating birds
Maritrema poulini	Microphallidae	*Potamopyrgus antipodarum*	Amphipods, isopods	Waterfowl
Plagiorchioid sp. I	Undetermined	*Potamopyrgus antipodarum*	Probably arthropods	Unknown

snails were screened again before and after the individual experiments to ensure infected specimens retained their infections and uninfected specimens did not show patent infections. To avoid confounding effects of time of day, all experiments were carried out in the early afternoon.

2.3 | Experiment 1: Movement and use of light versus dark areas

To investigate snail movement patterns and their attraction to open versus shaded areas, and how these are affected by trematode infection, we quantified the phototactic behaviour of infected and uninfected snails using automatic video tracking. The experiment was performed in petri dishes (diameter: 8.3 cm) which were half covered with a dark, opaque material to provide a choice between dark and light microhabitats. The petri dishes were placed in an opaque box that had a translucent plexiglass cover on top to allow unidirectional illumination by a 100 W lamp placed 0.5 m above the petri dishes. The set of petri dishes was raised on a clear plexiglass sheet to allow filming and tracking of snail movement from below, using a GoPro Hero 6 camera.

At the beginning of each experimental trial, one individual snail from each of the four groups (uninfected controls, infected with *Apatemon* sp. I, infected with Plagiorchioid sp. I, infected with *Maritrema poulini*) was placed in separate petri dishes, on the border between the dark and light zone at the centre of the dish. Snails were given a two-minute acclimatisation period and then filmed to track their movement. Petri dishes were rotated by 180 degrees after half the trials to avoid confounding effects or the orientation of the light and dark areas. Clean petri dishes were used each time, filled with fresh filtered lake water (20°C) before each trial. A total of 19 individuals from each of the four snail groups were filmed for 10 min (600 s) each, resulting in a data set of 190 min of recorded movement per group. Snails which did not move during the 10 min were excluded from the analysis, resulting in 18 snails infected with *Apatemon* sp. I, 15 snails infected with *Maritrema poulini*, 19 Plagiorchioid sp. I infected snails and 18 uninfected control snails for the movement analysis.

Using the videos, the individual snail movement and behavioural pattern were automatically tracked using EthoVision XT 11.5 (Noldus Information Technologies), a system previously used in our laboratory (Selbach & Poulin, 2018). The following movement and behavioural patterns were assessed and analysed: total horizontal distance moved (mm), time spent in light zone versus dark zone (s), and the relative movement duration (time spent moving vs. time not-moving). For the last parameter, individual snails were considered to be moving when their velocity was ≥0.2 mm/s and considered not-moving when the velocity was ≤0.1 mm/s. System noise and small movements "within" the animal ("body wobble") were reduced by using the program's track smoothing tool (Lowess) with five sample points in the half window size.

2.4 | Experiment 2: Response to predator cues

In order to test the potential effect of trematode infection on predator evasion, we quantified the emergence time of snails from their shell in the presence or absence of fish predator cues, using the same predator as Levri (1998). For this, we prepared predator cue water, by keeping four common bullies, *Gobiomorphus cotidianus*, in a 14 L aquarium (32 × 19 × 24 cm) filled with artificial lake water (1/3 saltwater, 2/3 freshwater) for 7 days. Prior to the experiment, snails were taken out of the natural lake water in which they were maintained, and acclimatised for 24 hr at 20°C in predator-free artificial lake water to avoid behavioural change due to different water compositions. Snails were then carefully dabbed dry with tissue paper and individually placed in wells of a 24-well flat bottom plate filled with either 1 ml of predator cue water or untreated water. As soon as individual snails were placed in the well, emergence time was determined as the time until the snail's head and foot fully emerged from the shell.

Emergence time of snails in the presence or absence of predator cue was assessed for a total of 40 snails, 10 from each of the four groups (uninfected controls, infected with *Apatemon* sp. I, infected with Plagiorchioid sp. I, infected with *Maritrema poulini*). Each snail was tested in presence and absence of predator cues. Half of the snails from each group were first exposed to non-predator water, then to predator water; the other half was first exposed to predator water and then to non-predator water. Between the two trials, snails were kept in artificial lake water for 24 hr at 20°C to avoid acclimation to predator cues.

2.5 | Statistical analyses

Statistical analyses were performed with GraphPad Prism (V.7) to test for differences in movement, time spent in the light area, and

emergence time among the four groups of snails. For the total distance moved, we compared the means of the distances among the four groups, using an ANOVA followed by post hoc Tukey's tests. As the data for the relative time spent moving was not normally distributed, we used a Kruskal–Wallis test to compare the medians for that variable among the groups. For the time spent in the light or dark zone, we used paired *t* tests to compare the means of the absolute time spent in each zone for each snail group.

For the responses to predator cues, we compared the emergence time of snails by using a two-way ANOVA to determine if emergence time was influenced by fish odour or by the snail's infection group (uninfected controls, *Apatemon* sp. I, Plagiorchioid sp. I, *Maritrema poulini*). Post hoc Dunnett's tests were performed to compare emergence times between the four groups.

3 | RESULTS

Movement and attraction to the light zone of a total of 70 snails were assessed via automatic video tracking, focusing on the time spent in the light zone compared to dark zone (Figure 1a), the total distance moved (Figure 1b) and the relative time spent moving (Figure 1c). Paired *t* tests showed that only uninfected snails spent significantly more time in the light area ($t = 2.775$, $df = 17$, $p = 0.013$), whereas all infected snail groups did not show a significant preference for either the light or dark area as they spent a similar amount of time in each zone (all $p > 0.36$). However, there was an overall significant difference among snail groups regarding their total distance moved (ANOVA: $F_{3,66} = 4.261$, $p = 0.0082$). Post hoc Tukey's tests showed that uninfected snails moved significantly further than snails infected with *Apatemon* sp. I ($p = 0.0047$), while no significant difference in distance moved could be found among other snail groups (all $p > 0.1$). Moreover, there was no difference in movement duration among the four different snail groups (Kruskal–Wallis test: $p = 0.467$).

In the second experiment (Figure 2), emergence time of snails from their shell was not significantly influenced by predator cues (two-way ANOVA: $F_{1,67} = 0.004095$, $p = 0.9492$), and did not vary among snail groups (two-way ANOVA: $F_{3,67} = 2.53$, $p = 0.0645$).

4 | DISCUSSION

Determining the ultimate cause of behavioural alterations induced by parasites has proven challenging (Moore, 2002; Poulin, 2010). When multiple parasite species induce the same basic physiological change in a shared host species, similarities in parasite-induced changes in host behaviour may simply be non-adaptive consequences of altered host physiology. Here, we investigated the impact of three different trematode species on the behaviour of the snail *Potamopyrgus antipodarum*. All three trematodes cause the castration of their host and may result in similar overall pathology and energy drain. Our results show that all three trematodes neutralise the attraction to lighted areas normally shown by the snail (when uninfected), and none of the trematode species affected the time spent moving by their host

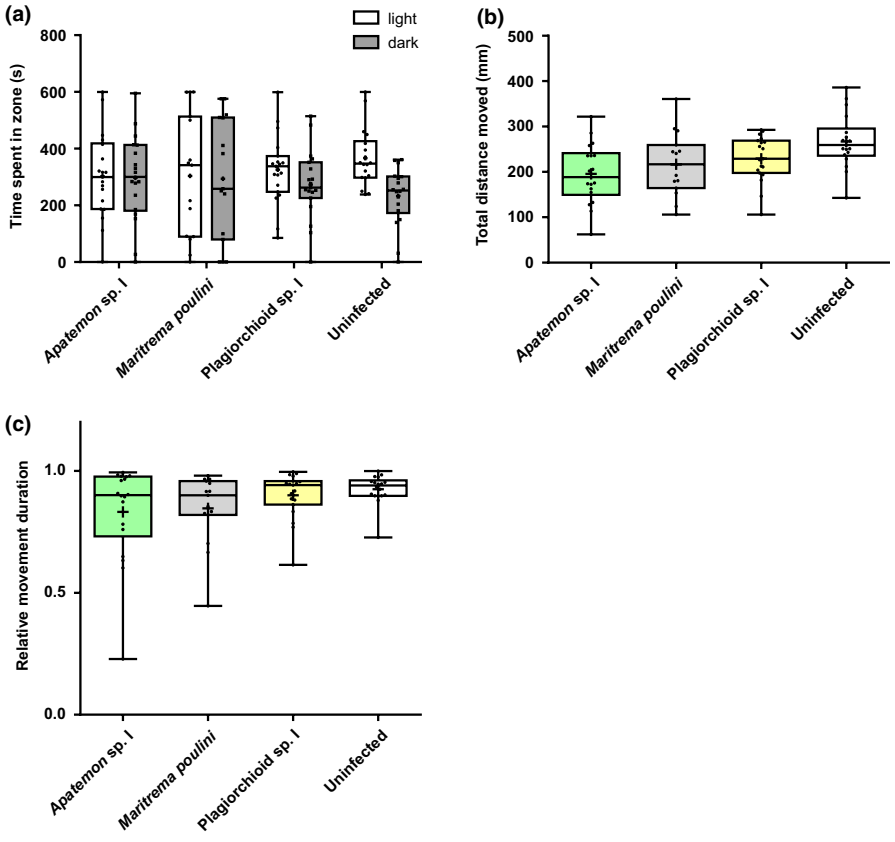

FIGURE 1 Movement and attraction to light versus dark zones of *Potamopyrgus antipodarum* infected with *Apatemon* sp. I ($n = 18$), *Maritrema poulini* ($n = 15$), Plagiorchioid sp. I ($n = 19$) or uninfected snails ($n = 18$). Time spent in light versus dark zone (a), total distance moved (b) and relative movement duration (c) were analysed by using EthoVision XT 11.5. Each boxplot shows interquartile range, maximum and minimum values and individual data points. The line across the plot indicates the median and the mean is represented by the + [Colour figure can be viewed at wileyonlinelibrary.com]

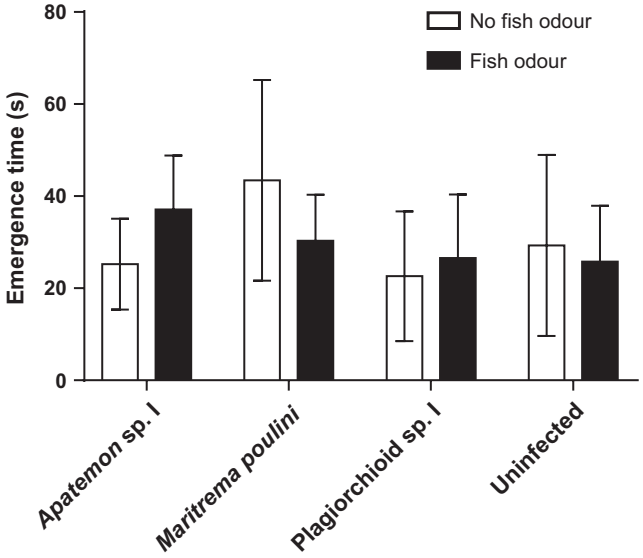

FIGURE 2 Mean emergence time of snails from their shell for each of the four snail groups (n = 10), both in the presence and absence of fish odour. Error bars are standard deviations

or its responses to predator cues. The only significant effect we observed was that snails infected with *Apatemon* sp. I moved a shorter total distance during the experimental period than uninfected control snails. This minor difference aside, overall our findings do not support any strong species-specific effects of trematode parasites on the snail *P. antipodarum*, and suggest instead a more generalised, non-adaptive and minor impact on host behaviour.

The lack of impact of trematodes on certain snail behaviours is not surprising. For instance, altered responses to predation risk as a result of parasite infection have been reported only in some cases (Bernot, 2003; Kamiya & Poulin, 2012), but not in a previous study on the snail *P. antipodarum* (Levri, 1998). The only behavioural difference we observed among our snail groups was the reduced distance travelled by snails harbouring the trematode *Apatemon* sp. I compared to uninfected snails. Although this parasite targets fish as its next host, whereas the other two species we investigated presumably target arthropods, it is difficult to imagine how reduced snail movement (by only about 20%) could benefit the parasite for either intra-host multiplication or successful cercarial transmission to fish. Species-specific effects of trematodes on the physiology or morphology of their common snail host have been reported before, that is influences on shell shape (Hay, Fredensborg, & Poulin, 2005; Lagrue & Poulin, 2007) or thermal tolerance (Bates, Leiterer, Wiedeback, & Poulin, 2011) associated with certain trematode species but not others. However, without clear a priori predictions linking the phenotypic changes with transmission success in some trematodes but not in others, the most parsimonious explanation is that the changes are not adaptive for either the parasites or (given that snails are castrated by trematode infection) the host.

In contrast, the trematode *Microphallus* sp. has previously been demonstrated to induce several changes in the behaviour of the snail *P. antipodarum* (Levri, 1999; Levri & Fisher, 2000). Unlike the trematode species investigated in our study, *Microphallus* sp. does not have free-swimming cercariae; instead, these remain within the snail host and transmission to waterfowl definitive hosts occurs via direct predation on the snail. Adaptive manipulation of intermediate host behaviour has evolved repeatedly across various taxa of parasites transmitted trophically to their definitive host (Moore, 2002; Poulin, 2010; Poulin & Maure, 2015). It is therefore likely that the different usage of the snail made by *Microphallus* sp. (as vehicle for transmission) compared to other trematodes (strictly as a resource base for asexual multiplication) has resulted in different selective pressures, with adaptive manipulation only arising in the former.

Our methodological approach had some advantages, such as the continuous tracking of snail movement for a full 10 min allowing more accurate and detailed quantification than snapshot observations at regular intervals. However, the experimental set-up also created some artificial behavioural patterns. In particular, snail movement often showed a clear edge effect, with the snails tending to move in circles, always maintaining contact with the sides of the petri dish. This results from thigmotaxis, a common animal response consisting in maintaining contact with solid vertical surfaces during movement. However, we feel that our measures of total distance moved and time spent moving reflect intrinsic activity levels independent of any edge effect. Similarly, the time spent in light and dark zones should not have been biased in any particular way by edge effects during our study. Moreover, our experimental approach using round petri dishes was similar to previous assessments of snail movement and phototaxis (Levri and Fischer, 2000) and should therefore be comparable to these studies.

Whether the behavioural changes we observed are adaptive or mere side-effects, they may still have important ecological consequences. Previous studies have shown that small changes in activity levels or microhabitat choice in snails infected by trematodes can result in altered grazing rates on microalgae, and thus changes in local primary productivity (Mouritsen & Haun, 2008; Wood et al., 2007). The extent of those impacts of course depends on prevalence of infection. In populations of *P. antipodarum* where trematode infections are common, decreased use of well-lit areas may therefore impact algal growth and the broader community.

In conclusion, we find no strong evidence for species-specific effects on host behaviour by three different trematode species infecting the same snail species. All three trematodes caused the same change in the host's preference for light areas, and none of them influenced the time spent moving by their host or its responses to predator cues. One trematode caused a small reduction in the total distance covered by the host, but on its own this result is insufficient to conclude that the behavioural impacts on the snail host are something more than general and non-adaptive by-products of trematode infection.

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