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FISH PARASITOLOGY - ORIGINAL PAPER

Hunger games: foraging behaviour and shelter use in fish under the context-dependent influence of parasitism

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Abstract
Diseases, and the parasitic organisms that cause them, can impact aspects of ecosystems ranging from altering food web connectivity to population dynamics. Apart from interspecific interactions, parasites can affect how their hosts behave with conspecifics, such as during competition for resources. Fish are important hosts to a variety of parasite taxa that can, through physical impairment or invasion of sense organs, affect how they interact with conspecifics for food, territory, or mates. In New Zealand, the common bully *Gobiomorphus cotidianus* plays host to a variety of parasites, encysting throughout the body (*Apatemon* sp.) or residing within the eyes (*Tylodelphys darbyi*). We hypothesized that fish with lower levels of infection would secure territories closer to a food patch and be more likely to tolerate sharing that territory. Our experiments show that parasites infecting different areas may have variable impacts on how far the host positions itself from a food patch and the likelihood that it shares its territory. Fish with higher intensities of *T. darbyi* tended to be closer to the food patch, but *Apatemon* sp. did not show a similar pattern. Higher infection levels of both parasites were statistically associated with bullies being less likely to share territory. Further, bigger fish were less likely to share their territory at higher intensities infection, and we observed individual variation in a fish's response between trials. Our findings support that parasites matter in ecological interactions but also emphasize the context dependence of their effects.

Keywords Host–parasite interaction · *Gobiomorphus cotidianus* · Competition · Diplostomid · Eye fluke · Fish ecology

Introduction

The impacts of parasitic organisms are now considered important processes in ecosystems, capable of influencing aspects from population dynamics to food web structure (Anderson and May 1978; Dobson and Hudson 1986; Holmes and Bethel 1972; Hudson et al. 2006; Lafferty et al. 2008; Scott and Dobson 1989). Some, like the rinderpest virus, cause high mortality of their hosts and in so doing can alter entire ecosystems (Sinclair 1979). Metazoan parasites (e.g. parasitic helminths) on the other hand, often impact populations, communities, and ecosystems through behavioural alterations or physical impairment rather than outright host mortality (Hudson et al. 2006; Poulin 2010). These impacts tend to result in the infected individual being ingested by a subsequent host in the parasite's life cycle or even a non-host predator, increasing food web connectivity within the community (Chen et al. 2008; Fredensborg and Longoria 2012; Lafferty 2008; Lafferty et al. 2008; Lafferty and Morris 1996; Mouritsen 2002; Mouritsen and Poulin 2003; Poulin 2010). However, not all interactions in an ecosystem are interspecific, as organisms often must interact with others of their species for resources (e.g. food, mates, shelter), and indeed parasites can impede these interactions as well.

Fish are important hosts in aquatic ecosystems for a variety of parasite groups (e.g. trematodes, cestodes) that can likewise affect how they interact with conspecifics (Barber et al. 2000; Barber and Poulin 2002; Barber and Wright 2006; Cureton II et al. 2011; Maan et al. 2006). Increasing parasitic helminth intensities have been shown to negatively impact mating success in male fish by reducing territory size (e.g. *Pundamilia nyererei* cichlids) and overall ability to pursue females (e.g. mosquitofish *Gambusia affinis*) (Maan et al. 2006; Cureton II et al. 2011). As with competition for

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other resources, the impacts of parasitism on foraging can be a result of reduced physical condition. For example, cestode-infected sticklebacks *Gasterosteus aculeatus* spend more time foraging and ingest less food when placed in direct competition with uninfected individuals (Barber et al. 1995; Barber and Ruxton 1998). Further, minnows (i.e. *Phoxinus phoxinus*), also infected with cestodes, position themselves on the outside of shoals where it is easier to obtain food, but it also puts them at greater risk of predation (Barber and Huntingford 1996).

Food acquisition can also be impaired when parasites invade sensory organs (e.g. eyes), affecting the ability of the host to perceive food in the environment (Kalbe and Kurtz 2006; Seppälä et al. 2004, 2005, 2008; Ubels et al. 2018; Voutilainen et al. 2008, 2010). Diplostomid trematodes use fish as second intermediate hosts in their life cycles where they can infect various parts of the eyes (e.g. lens, humours) (Chappell 1995; Barber 2007; Barber and Wright 2006). When *Diplostomum* spp. reside in the lens, they can generate cataracts, as a result of waste products being released, affecting the host's vision and associated behaviours (Karvonen et al. 2004; Owen et al. 1993). For example, *Diplostomum spathaceum* infection reduces the reaction distance to prey and can cause infected individuals to spend more time foraging than uninfected shoal mates in several fish species (Crowden and Broom 1980; Voutilainen et al. 2008). The closely related *Tylodelphys clavata*, which inhabits the liquid parts of the eye (i.e. the humours), also affects competitive ability of the host (Muñoz et al. 2017, 2019). European perch *Perca fluviatilis* L. 1758 show reduced reaction distance and ingest fewer prey with increasing intensity of *T. clavata* infection, while uninfected individuals have higher foraging success rates (Muñoz et al. 2017, 2019).

Tylodelphys darbyi is the only described diplostomid trematode in New Zealand and at present is known exclusively from mountain lakes on the South Island (Presswell and Blasco-Costa 2020). As with other diplostomids, *T. darbyi* exhibits a complex lifecycle requiring an invertebrate (i.e. a snail) and two vertebrate hosts, a fish followed by a bird, to reach maturity and reproduce (Blasco-Costa et al. 2017; Presswell and Blasco-Costa 2020). The fish host for *T. darbyi* is the common bully *Gobiomorphus cotidianus*, an endemic species widespread throughout New Zealand. In bullies, *Tylodelphys darbyi* resides in the eyes where it moves freely within the humours, can occur at high intensities (> 20/eye), and be quite large (> 1 mm); however, despite this, there is no evidence of pathology (i.e. no damage to retina, lens) related to infection (Stumbo and Poulin 2016). Common bullies are small, benthic fish that use submerged structures (e.g. rocks, woody debris) for shelter (per observation; McDowall 1990). It has been reported that *G. cotidianus* will guard their chosen shelter from conspecifics; however, whether they choose structure preferentially over open space has not been tested (McDowall 1990).

Recently, it has been demonstrated that as *T. darbyi* intensity increases, bullies spend more time actively moving in the open away from shelter (Ruehle and Poulin 2020). It was suggested this behaviour could be due to fish with higher infection levels needing to explore their environment for resources, such as food, more than those with fewer parasites. Additionally, *G. cotidianus* hosts the trematode *Apatemon* sp. that encysts throughout the muscle tissues and body cavity; this parasite could also impact resource acquisition due to physical impairment. In the present study, we wanted to test whether infection by both parasites impacts the ability of *G. cotidianus* to locate a food source and acquire the shelter nearest to it when placed in direct competition with conspecifics. The objectives are to determine whether (1) infection impacts the ability of individuals to identify and hold the territory nearest a food patch and (2) fish are more likely to tolerate sharing a territory if they harbour fewer parasites. We hypothesize that fish with lower levels of infection will secure better territories nearer the food patch and be more likely to tolerate sharing a territory.

Methods

Collection, housing, and tagging

Fish, *Gobiomorphus cotidianus* ($n = 32$), were collected from Lake Hayes on the South Island of New Zealand in January 2019, using minnow traps set overnight. The bullies were held in 8 size-matched groups of 4 in 36L aquaria (44 cm × 27.5 cm × 29.5 cm) with filtration, aeration, lit from above on a 12 h day/night cycle, and fed commercial fish pellets ad libitum. Fish were grouped with individuals within ~ 10 mm of their own length (range 43.11–75.07 mm) to reduce the impact of size on experiments and the incidence of intergroup cannibalism. Water in the aquaria was a solution of 1/3 saltwater and 2/3 freshwater, to prevent fungal growth on the fish, and water temperature was kept at ambient levels (i.e. ~ 20 °C). Fish also were provided with enough shelter (e.g. 10 cm × 5 cm PVC pipe pieces) so that each could establish a territory to itself, minimizing conflict between tankmates. After an acclimation period of 72 h, bullies were anaesthetized with MS-222 (5 min, 1 mg/L solution) and tagged with a unique visible implant elastomer implant (2 mm long; Northwest Marine Technologies Inc.) for individual identification. All collection, housing, tagging, and experimental treatment of fish are in accordance with the University of Otago Animal Ethics Committee (permit no. 70/17001).

Experimental procedure

Two test arenas (80 cm × 54 cm × 28 cm) were utilized and a 4 × 3 grid pattern (each cell = 20 cm × 18 cm) drawn on the bottom of each (Fig. 1). Four shelters consisting of PVC tubes (diameter = 4 cm, length = 10 cm) attached to 10 × 10 cm ceramic tiles were placed at distances of 5 cm, 15 cm, 25 cm, and 35 cm from a central point, designated the "food patch", where fish pellets would be introduced during the trial. The shelters were arranged so that an opening was facing the food patch and any visual obstruction was minimized and while the distances remained the same the arrangements differed between the arenas. All 8 groups of fish were tested twice, for repeatability and in different arenas to reduce the likelihood of preference in shelter selection, with their respective group mates in this experiment. All 4 bullies were introduced to the test arena via a plastic jar and allowed 24 h to acclimate to the new surroundings before the trial began. During the acclimation period, 10 fish pellets were introduced via plastic tube to the patch twice (10:00 and 14:00) so the bullies would associate the area with food; this was continued throughout the observation period. Food pellets were introduced simultaneously to give advantage to the first fish to reach the food patch. The grid section of each fish was recorded at 2-h intervals 4 times between 9:00 and 15:00 for 3 days; bullies are benthic fish that are not very active; therefore, this recording scheme suffices to capture their usual location. If the fish was in a shelter, that shelter's distance to the food patch was recorded. If fish were not sitting in the shelter during the observation, if they were in the section with the shelter, it was assumed they were associated with it, and the distance was recorded accordingly. For those that were not in a shelter section, their effective distance was recorded later by measuring from the food patch to the centre of each section, creating 7 possible distance categories: 5 cm, 10 cm, 15 cm, 20 cm, 25 cm, 30 cm, and 35 cm. Following a trial, the fish were returned to their holding tank and allowed to rest for 10 days before being tested again in the second arena. This design allows for 24 observations per fish across both trials (4 times/day × 3 days × 2 trials). Unfortunately, due to technical constraints, only 23 observations were made for fish in group 8.

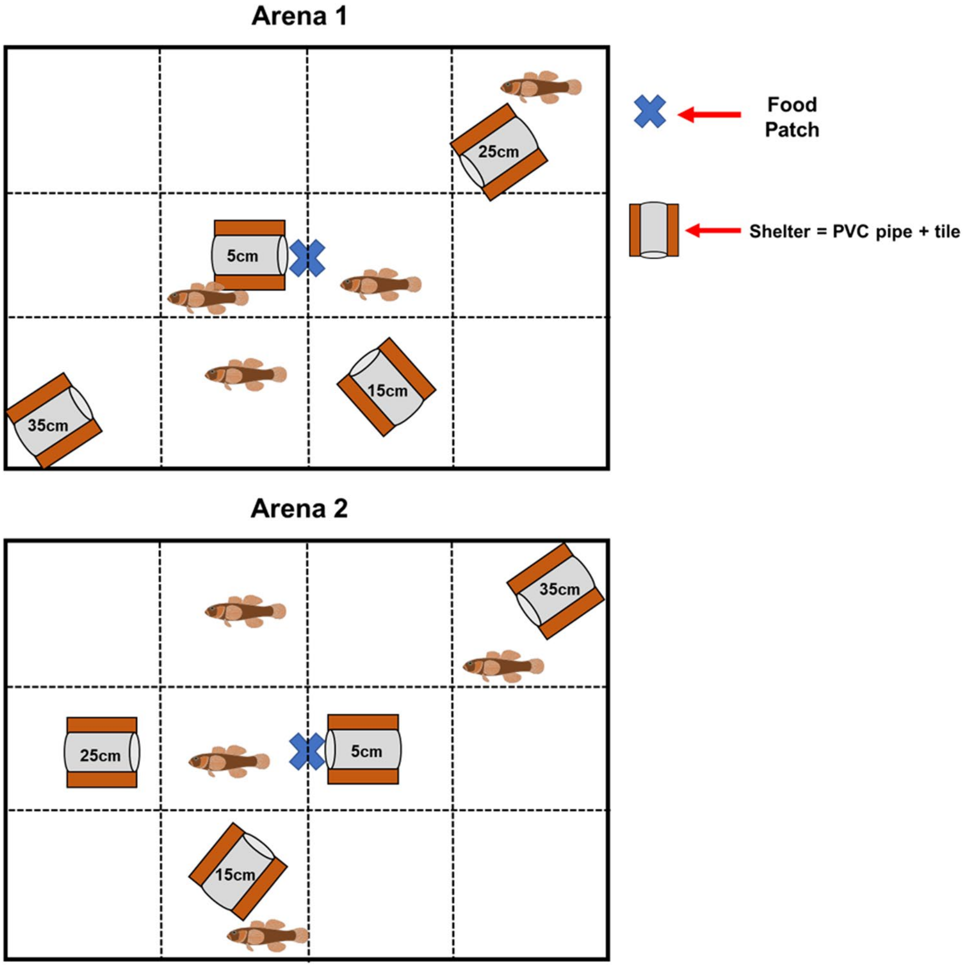


Fig. 1 Diagram of experimental setup showing both arenas

Parasite counts

Following the experiment, all bullies were euthanized by overdose of MS-222 (i.e. 10 mg/L for 5 min) and spinal severance and then measured for standard length (SL). For each fish, we examined both eyes separately for *Tylodelphys darbyi*, with focus on the humours where the parasite is most often found. Three other trematode taxa, *Apatemon* sp., *Telogaster opisthorchis* MacFarlane 1945, and *Stegodexamene anguillae* MacFarlane 1951, are commonly found as metacercariae in bullies from Lake Hayes. All three species are found encysted throughout the muscles, organs, and body cavity, so these were dissected out and the parasites counted. The larval nematode *Eustrongylides* sp. is occasionally found in the body cavity of bullies in association with internal organs, so its presence/absence was noted for each fish.

Statistical analyses

All statistical tests were performed and figures generated, using the *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2017), *ordinal* (Christensen 2019), and the *tidyverse* (Wickham et al. 2019) suite of packages in R programming. In order to avoid over-parameterization, we ran separate models for each hypothesis using either *T. darbyi* or *Apatemon* sp. intensity as the infection variable; other parasite taxa occurred in low enough prevalences (Table 1) that they were excluded. To test the first hypothesis, i.e. that infection impacts the ability of fish to hold the territory nearest a food patch, we used cumulative link mixed models (CLMMs; *clmm* function) with distance from the food patch as the response, standard length (SL; mm) and trial as fixed factor predictors, in addition to the parasite infection measures above, and fish ID, group number, and day as random factors. We treated distance in this case as an ordered variable because during any given observation, it was not possible for that individual to occupy a different space. For the sharing hypothesis, we calculated the number of neighbours (i.e. other fish in their territory) each fish had during an observation. We then ran generalized linear mixed models (GLMMs; *glmer* function) fitted to the Poisson distribution using the number of neighbours as the response and the same fixed and random factors as the previous models. Finally, we ran a χ^2 test of the number of times each fish was observed in territories with shelter versus those without.

Table 1 Percent prevalence, mean intensity, and range of intensity of parasite taxa

Helminth taxa	Prevalence (%)	Mean intensity	Intensity range	
			Min	Max
Tylodelphys darbyi	100.0	35.8	5	99
Apatemon sp.	100.0	303.7	96	597
Telogaster opisthorchis	68.8	3.9	0	8
Stegodexamene anguillae	71.9	3.6	0	10
Eustrongylides sp.	5.0	1.3	0	2

Ethical note

We used naturally infected fish for our experiments, because the complete life cycle of *Tylodelphys darbyi* is not known. For this reason, we aimed to minimize our sample sizes while keeping them large enough to achieve statistical requirements. *Gobiomorphus cotidianus* is the most abundant and widespread endemic, freshwater fish in New Zealand (McDowall 1990), and > 100 can be recovered in a single trap night, so the numbers we used per experiment (< 40) are not likely to impact the population. In addition, the Lake Hayes population has a *T. darbyi* prevalence of near 100% (Stumbo and Poulin 2016; current study), allowing us to collect smaller numbers of fish and still guarantee infection. Fish were kept in holding tanks at stocking densities of < 2 fish/L and provided with enough shelter (i.e. 10 cm PVC pipes) that each individual had a territory to itself. Common bullies take longer to acclimate (based on their pale colouration) to holding conditions when not in a group and without adequate shelter (author per observation), so these conditions are intended to reduce stress. Fish were held in captivity for no more than 4 months; at the end of each, all individuals were humanely killed via overdose of MS-222 (10 mg/L). These methods were approved by the University of Otago Animal Ethics Committee (No. 70/17001).

Results

All fish examined ($n = 32$) were infected with *Tylodelphys darbyi* and *Apatemon* sp. (Table 1). Both trematodes were found at higher prevalences and at greater intensities (*T. darbyi* = ~36/fish; *Apatemon* = ~304/fish) than the other 3 taxa recovered (Table 1). Within the eyes, *T. darbyi* metacercariae were found exclusively in the aqueous and vitreous humours. *Apatemon* sp. was found encysted throughout the muscles, body cavity, and various organs (e.g. gonads). The other trematodes, *Telogaster opisthorchis* and *Stegodexamene anguillae*, were found in the same tissues as *Apatemon* sp. but at much lower intensities. Larval stages of *Eustrongylides* sp., the only non-trematode recovered, were found in the body cavity in very few individuals (Table 1).

We found that bullies used territories (i.e. grid sections) with shelter significantly more than those without ($\chi^2 = 258.74$, $df_{resid} = 47$, $P < 0.001$) (Fig. 2). There is a negative relationship

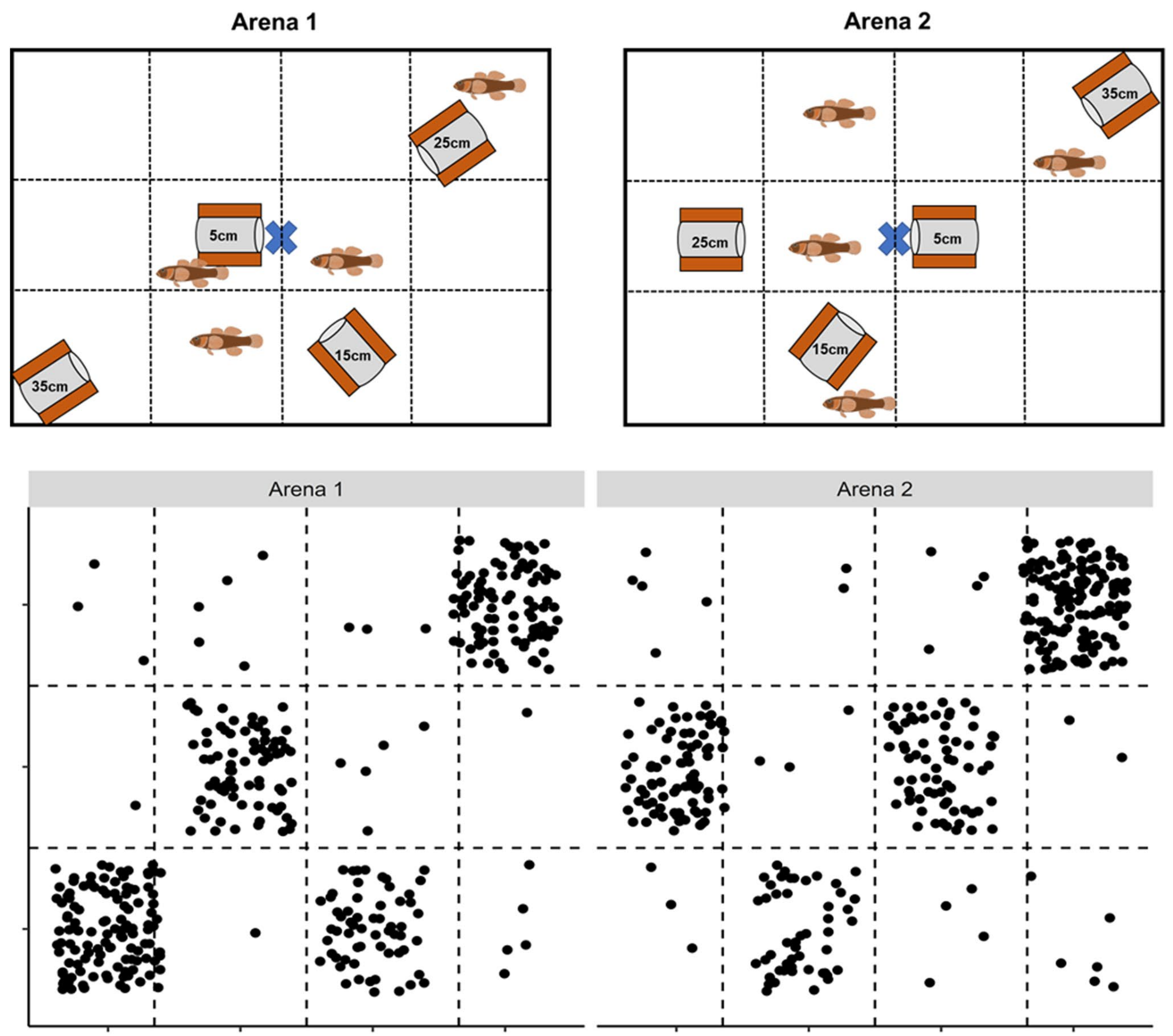


Fig. 2 Diagram of experimental setup showing both arenas (top). Plot showing location records of *G. cotidianus* during the experiment (bottom). Each point represents the grid section in which an individual was observed. Points are jittered for visibility and do not indicate exact physical position of fish during an observation

between *T. darbyi* infection and the mean distance from the food patch at which fish positioned themselves; also, we found that fish frequently recorded in territories without shelter had higher intensities ($z = -2.029$, $df_{resid} = 749$, $P = 0.042$) (Fig. 3). Likewise, smaller fish tended to have fewer *T. darbyi* and situate themselves farther from the food patch, although their mean distance to the food patch differed between trials (Fig. 4; Table 2). *Apatemon* sp. intensities were lower in smaller fish that tended to stay farther from the patch, with some variation between trials (Fig. 4; Table 2). In the model with *Apatemon*, the two-way interaction between SL and Trial significantly predicted distance but did not in the *T. darbyi* model (Table 2).

Between trials, the likelihood of bullies sharing a territory decreased with increasing intensities of *T. darbyi* ($z = 2.699$, $df_{resid} = 749$, $P = 0.007$) (Fig. 5), and larger individuals tended to have fewer neighbours on average (Table 2; Fig. 5). Likewise, the likelihood of a fish sharing territory decreased with higher intensities of *Apatemon* sp., but this was most pronounced in the first trial (Table 2; Fig. 5). For both models, trial was a significant main effect, while the two-way interaction between SL and Trial predicted the likelihood of territory sharing in the *Apatemon* sp. model (Table 2).

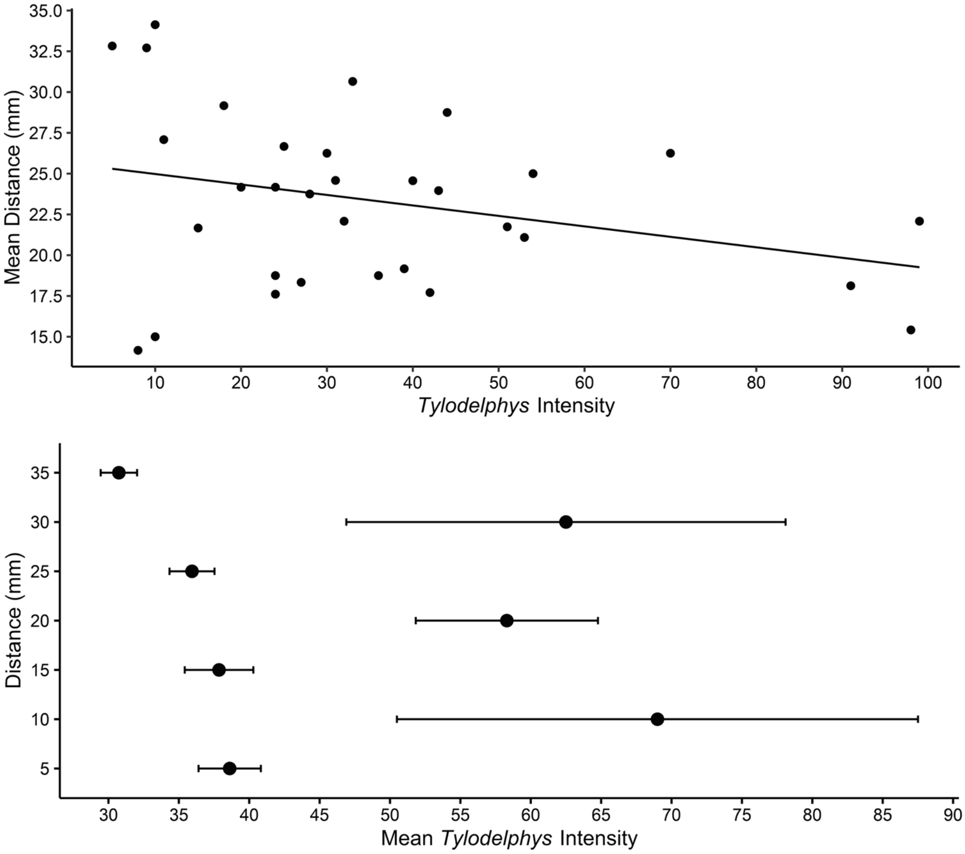


Fig. 3 Relationship between mean distance from the food patch and *Tylodelphys darbyi* intensity for each fish (top). Mean *T. darbyi* intensity of fish observed at each possible distance from the food patch; 5 cm, 15 cm, 25 cm, and 35 cm correspond to distances associated with shelters (bottom)

Discussion

Infection by parasites can impact the ability of the host to search for and obtain resources (Barber et al. 1995; Barber and Ruxton 1998; Maan et al. 2006; Muñoz et al. 2017, 2019). We have shown that parasites infecting different regions of their host's sensory organs and overall body can potentially have variable impacts on how far the host positions itself from a food patch and whether it tolerates sharing a territory. The more *Tylodelphys darbyi* metacercariae a bully has in its eyes, the closer, on average, it positions itself to the food source. In general, higher infection levels, of both *T. darbyi* and *Apatemon* sp., are associated with bullies being less likely to share territory. Some of these effects show an interaction with the fish's size and/or trial with respect to how the host responded during the experiment. Larger fish appear to be less likely to share their territory with increasing intensities of *Apatemon* and *T. darbyi*, and there is individual variation in a fish's response between trials. Overall, the potential influence of parasitic infection was strongly context-dependent, as it varied depending on fish size, on which trial was analysed, and between parasite species. Further, in addition to demonstrating bullies use territories with an available shelter over those without, we showed that mean *T. darbyi* intensity was higher for those fish observed in open spaces, corroborating previous findings (Ruehle and Poulin 2020).

In fishes, the length often correlates positively with both intensity of infection and age, with larger fish having more parasites and being older than smaller individuals (Poulin 2000; Winemiller and Rose 1992). So, while it is possible that our results are due in part to bigger fish having more parasites, we find this unlikely as fish were size-matched in each tested group (Appendix Fig. 6). Common bullies, especially larger fish, are territorial and will guard their chosen area from other individuals (McDowell 1990). Therefore, the pattern we observed could be due to larger fish being inherently more territorial than smaller individuals. Furthermore, some of the differences seen between trials could be attributed to the fish habituating to experimental conditions. We tested fish sequentially in two arenas containing different arrangements of shelters in order to reduce this effect, but the food patch was in the same spot in both arenas. Thus, it is possible fish were used to food being presented in that location by the second trial.

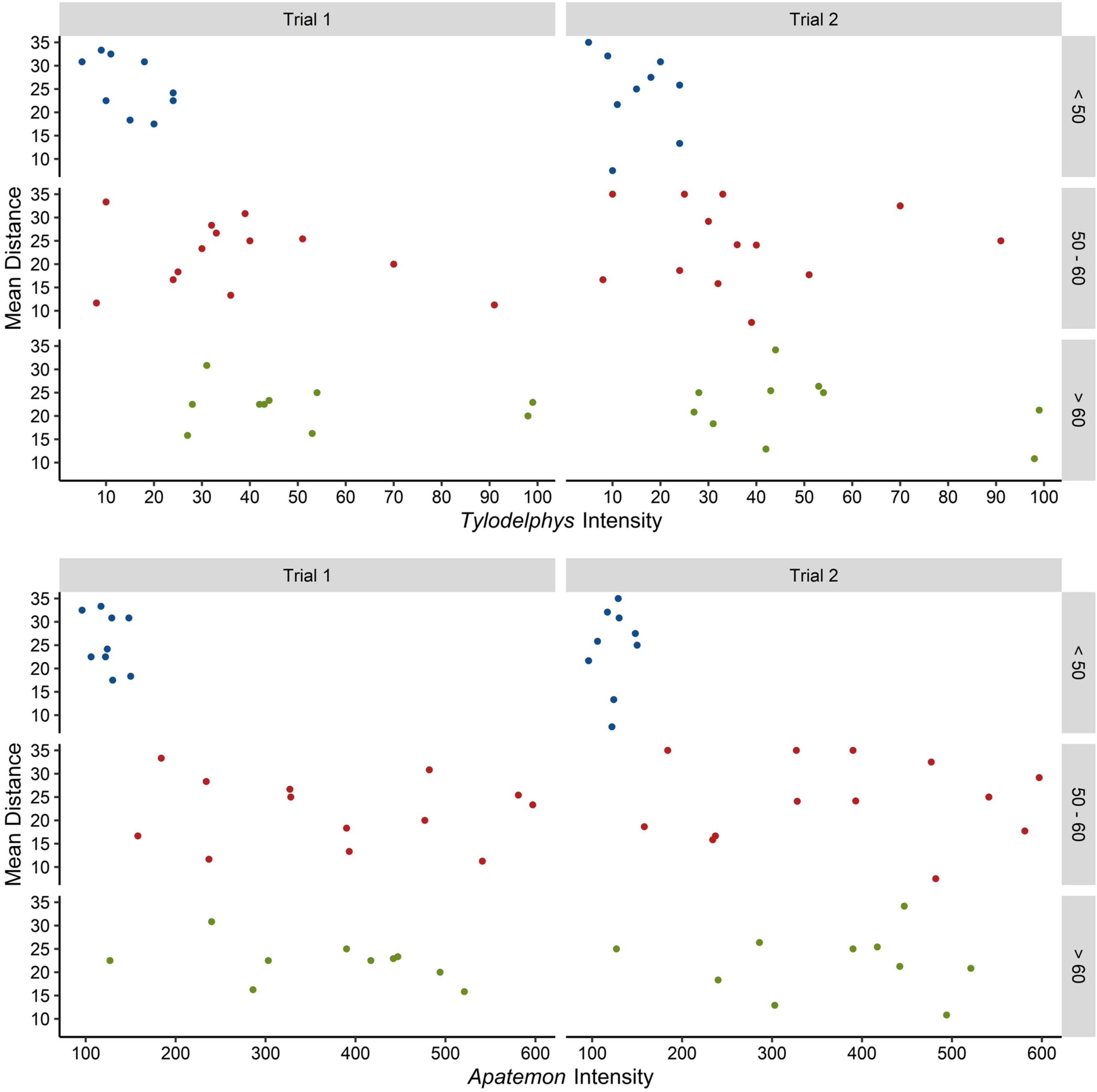


Fig. 4 Relationship between mean distance from the food patch and *Tylodelphys darbyi* intensity (top) and *Apatemon* sp. intensity (bottom) for each fish for both trials. Fish are grouped into size classes for visualization only: < 50 mm (blue), 50–60 mm (red), and > 60 mm (green)

We hypothesized that increased parasite infection would result in bullies being less able to locate and hold the shelter nearest the food patch. However, those with more *T. darbyi* in the eyes positioned themselves closer than those with lower intensities of the parasite. Recent studies on the impacts of *T. clavata* in the eyes of perch *Perca fluviatilis* have shown that reaction distance to prey decreases with higher intensities of the parasite (Muñoz et al. 2017, 2019). Therefore, it is possible that to compensate for reduced visual ability, the highly parasitized fish place themselves closer to the known location of food delivery. The obstruction of the eye by parasites, as with other sensory organs, should make location of prey more difficult for the host (Barber 2007), so bullies with

Table 2 Results from the two model series organized by response variable and parasite predictor. The distance series shows results from CLMMs. The sharing territory series shows results from GLMMs fitted to the Poisson distribution. Significant interactions ($P<0.05$) are indicated in bold

Response	*Tylodelphys darbyi*				*Apatemon* sp.			
Distance $df_{resid}=749$	**Predictors**	**Standard error**	***z* value**	***P* value**	**Predictors**	**Standard error**	**z-value**	***P* value**
	T. darbyi	**0.011**	**−2.029**	**0.042**	*Apatemon* sp.	0.001	−1.553	0.121
	SL	0.034	−0.463	0.643	SL	0.030	−0.773	0.439
	Trial	**0.158**	**2.674**	**0.007**	**Trial**	**0.164**	**2.304**	**0.021**
	T. darbyi:SL	0.001	1.707	0.088	*Apatemon*:SL	0.000	0.954	0.340
	T. darbyi:Trial	**0.008**	**2.814**	**0.005**	**_Apatemon_:Trial**	**0.001**	**3.355**	**0.001**
	SL:Trial	0.024	−1.223	0.221	**SL:Trial**	**0.021**	**−2.116**	**0.034**
	T. darbyi:SL:Trial	**0.001**	**−3.482**	**<0.001**	**_Apatemon_:SL:Trial**	**0.000**	**−2.553**	**0.011**
Sharing territory $df_{resid}=749$	***T. darbyi***	0.008	−1.463	0.143	***Apatemon* sp.**	**0.001**	**−3.223**	**0.001**
	SL	0.024	−1.263	0.206	SL	0.022	0.236	0.813
	Trial	**0.135**	**3.355**	**0.001**	**Trial**	**0.131**	**3.653**	**<0.001**
	T. darbyi:SL	**0.001**	**2.699**	**0.007**	*Apatemon*:SL	0.000	1.154	0.248
	T. darbyi:Trial	0.007	−0.653	0.514	*Apatemon*:Trial	**0.001**	**3.283**	**0.001**
	SL:Trial	0.021	1.279	0.201	SL:Trial	0.018	−1.881	0.060
	T. darbyi:SL:Trial	**0.001**	**2.639**	**0.008**	*Apatemon*:SL:Trial	0.000	−1.925	0.054

high infections of *T. darbyi* could be staying in proximity once a food source is located to avoid having to search out another. There is a similar pattern with *Apatemon*, with smaller fish in general having fewer parasites and staying more than 15 mm from the food patch and bigger individuals showing greater variation. Given *Apatemon*'s location throughout the muscle and body cavity, we would expect some degree of physical impairment (Poulin 1993; Lafferty and Shaw 2013). It is possible that providing a shelter for each fish did not adequately generate a situation in which bullies needed to interact with one another for space, and as such, any detrimental effects of infection did not manifest.

Common bullies do not often tolerate sharing a shelter (per observation; McDowall 1990), so we tested whether the combination of parasitism and competition for limited ideal structures would impact this behaviour. Falling in line with our hypothesis, general bullies were more likely to share shelters at lower intensities of infection compared to those with higher infection levels. Parasitism has been shown to affect the shoaling behaviour of other fish species resulting in infected individuals separating themselves from the group (Barber and Huntingford 1996; Krause and Godin 1994). This can be due to infected individuals being incapable of keeping up with the movement of healthy shoal members, particularly in the case of *Apatemon* that encysts in the musculature and body cavity. Alternatively, it may be that infected individuals need to spend more time foraging and as such leave the safety of the shoal more often (Barber et al. 1995). In bullies, it has been shown that as *T. darbyi* intensity in the eyes increases, the host is more active, spending more time moving about in the open (Ruehle and Poulin 2020). Thus, considering that bullies with high intensities also positioned themselves close to the food patch, it is possible that these fish are separating themselves from others in order to increase their chances of taking advantage of this resource. Likewise, the bullies with lower intensities could be more likely to share a shelter in our experiment because shelter availability was limited, especially compared to rocky, nearshore habitats in New Zealand glacial lakes. In general, bigger bullies have fewer neighbours on average than smaller fish, which is likely due to larger individuals being more territorial (McDowall 1990).

One caveat of our study is that because the snail first intermediate host of *T. darbyi* (the source of infective stages) has not yet been identified despite extensive sampling, our experiments use naturally infected fish instead of experimentally infected ones. This makes the direction of causality difficult to ascertain, as fish behaviour may lead to infection just as infection itself might change behaviour; thus, our results inform on correlation rather than causation. However, we feel that infection with *T. darbyi* resulting in changes in fish behaviour is the more plausible explanation, because the presence of the parasite in the eyes of the host provides a clear mechanism by which infection could alter behaviours that rely on vision.

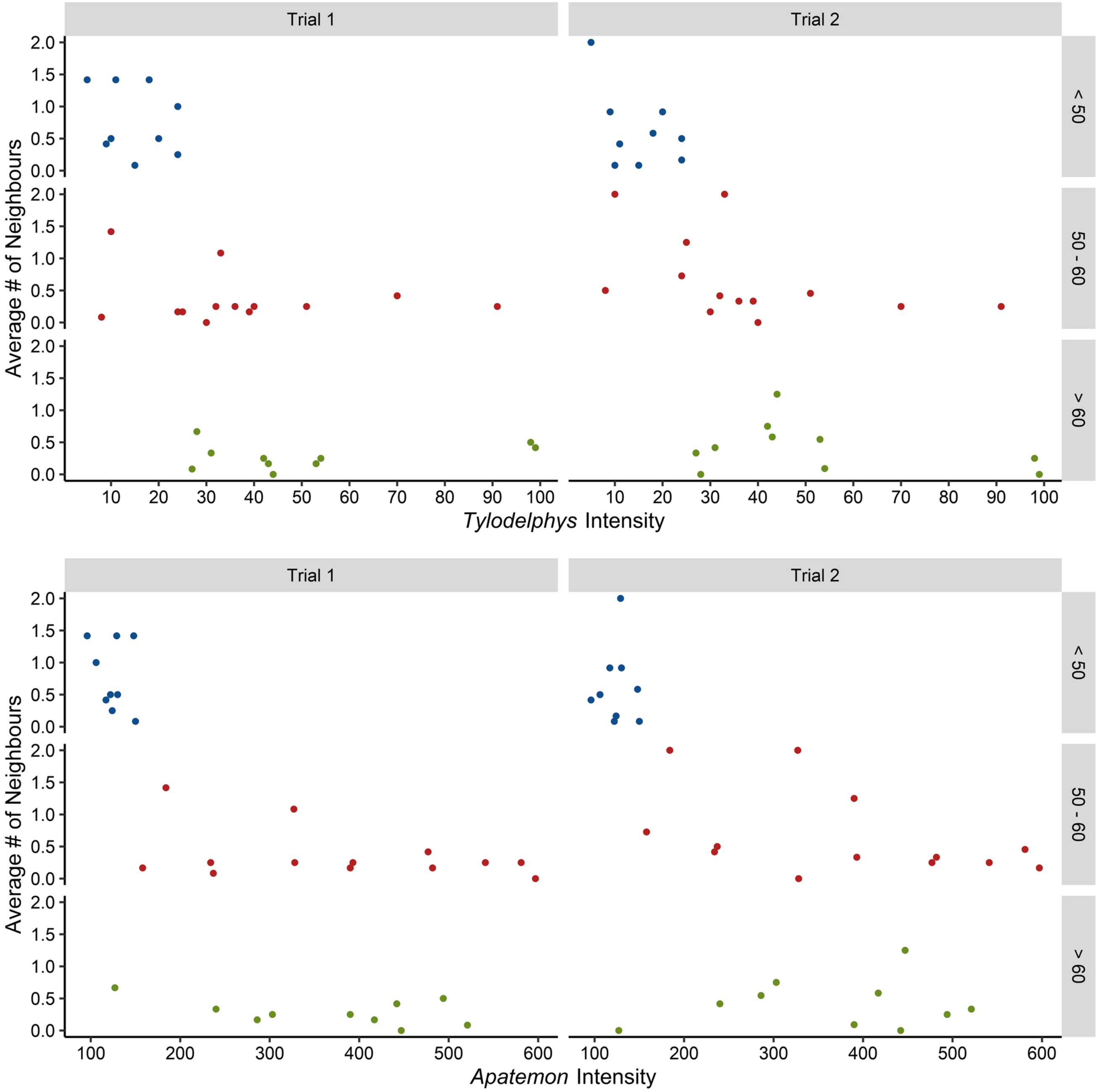
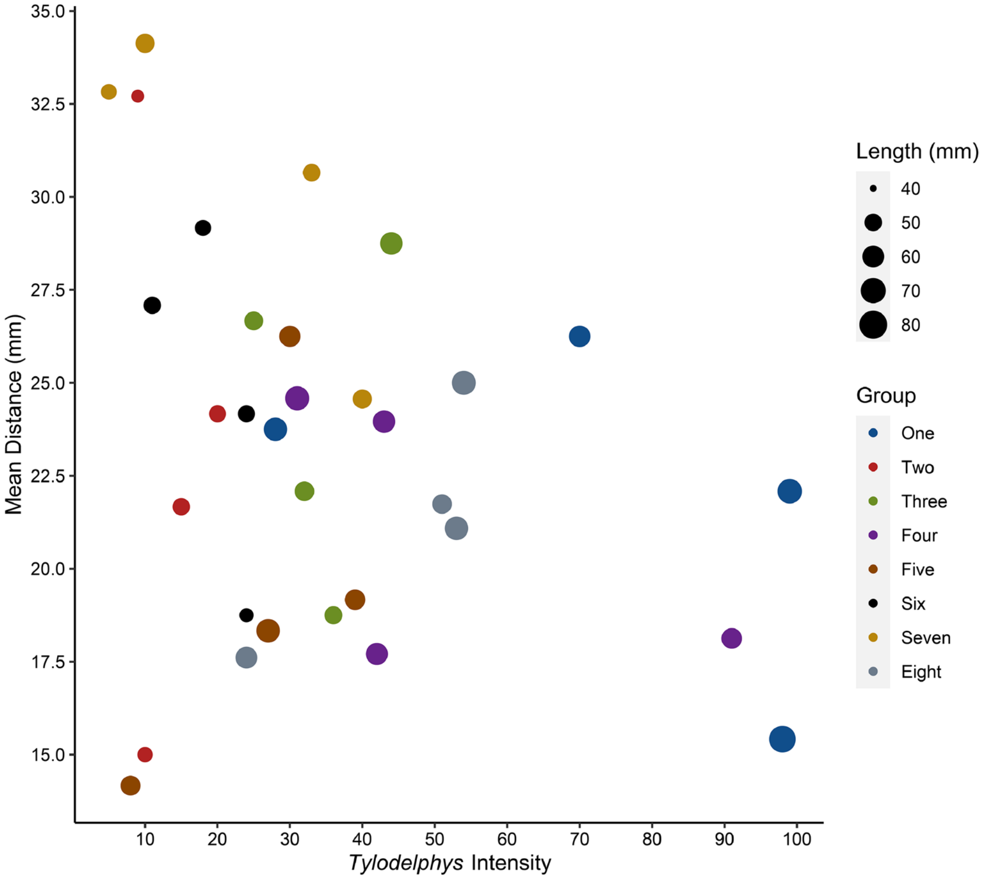


Fig. 5 Relationship between average number of neighbours and *Tylodelphys darbyi* intensity (top) and *Apatemon* sp. intensity (bottom) for each fish for both trials. Fish are grouped into size classes for visualization only: < 50 mm (blue), 50–60 mm (red), and > 60 mm (green)

Previous work has shown that parasitism can impact how hosts view for resources such as food or mates (Barber et al. 2000; Barber and Poulin 2002; Barber and Wright 2006); however, here we demonstrate that the effects of infection are not always so simple. We have shown that parasites infecting different parts of the host can have the potential to influence foraging and territorial abilities. Individuals with the most *T. darbyi* tend to occupy prime feeding locations and are in general less likely to share their territory and show inconsistency in behaviour. Our findings add to the evidence that parasites matter in ecological interactions but also emphasize the context dependence of their effects. The interplay of parasitism with other factors means that the nature of their effects cannot easily be generalized across species but instead requires more nuanced interpretation.

Appendix

Figure 6 Relationship between Tylodelphys darbyi intensity and the mean distance from the food patch for each fish. Point size represents fish length and colour signifies fish tested together in a group



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Declarations

Ethics approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the University of Otago Animal Ethics Committee (No. 70/17001).

Conflict of interest The authors declare no competing interests.

References

Anderson RM, May RM (1978) Regulation and stability of host-parasite population interactions: I. regulator processes. J Anim Ecol 47:219–247

Barber I, Huntingford FA (1996) Parasite infection alters schooling behaviour: deviant positioning of helminth-infected minnows in conspecific groups. Proc Biol Sci 263:1095–1102

Barber I, Huntingford FA, Crompton DWT (1995) The effect of hunger and cestode parasitism on the shoaling decisions of small freshwater fish. J Fish Biol 47:524–536

Barber I, Ruxton GD (1998) Temporal prey distribution affects the competitive ability of parasitized sticklebacks. Anim Behav 56:1477–1483

Barber I, Hoare D, Krause J (2000) Effects of parasites on fish behaviour: a review and evolutionary perspective. Rev Fish Biol Fish 10:131–165

Barber I, Poulin R (2002) Interactions between fish, parasites, and disease. In: Hart PJB, Reynolds JD (eds) Handbook of Fish Biology and Fisheries. Blackwell Publishing, Oxford, UK, pp 359–389

Barber I, Wright HA (2006) Effects of parasites on fish behaviour: interactions with host physiology. Fish Physiol 24:109–149. https://doi.org/10.1016/S1546-5098(05)24004-9

Barber I (2007) Parasites, behaviour and welfare in fish. App Anim Behav Sci 104:251–264. https://doi.org/10.1016/j.applanim.2006.09.005

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Blasco-Costa I, Poulin R, Presswell B (2017) Morphological description and molecular analyses of *Tylodelphys* sp. (Trematoda: Diplostomidae) newly recorded from the freshwater fish *Gobiomorphus cotidianus* (common bully) in New Zealand. J Helminthol 91:332–345

Chappell LH (1995) The biology of diplostomatid eyeflukes of fishes. J Helminthol 69:97–101

Chen H, Liu W, Davis AJ, Jordan F, Hwang M, Shao K (2008) Network position of hosts in food webs and their parasite diversity. Oikos 117:1847–1855. https://doi.org/10.1111/j.1600-0706.2008.16607.x

Christensen RHB (2019). ordinal - regression models for ordinal data. R package version 2019.12–10. https://CRAN.R-project.org/package=ordinal. Accessed 25 June 2021

Crowden AE, Broom DM (1980) Effects of the eyefluke, *Diplostomum spathaceum*, on the behaviour of dace (*Leuciscus leuciscus*). Anim Behav 28:287–294

Cureton JC II, Martin RE, Lewis RL, Stoops SB, Deaton R (2011) Effects of a trematode infestation on body condition, reproduction and mating behaviors in a livebearing fish. Behaviour 148:967–984

Dobson AP, Hudson PJ (1986) Parasites, disease, and the structure of ecological communities. Trend Ecol Evol 1:11–15

Fredensborg BL, Longoria AN (2012) Increased surfacing behaviour in longnose killifish infected by brain-encysting trematode. J Parasitol 98:899–903. https://doi.org/10.1645/GE-3170.1

Holmes JC, Bethel WM (1972) Modification of intermediate host behaviour by parasites. Zool J Linnaen Soc 51:123–149

Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? Trend Ecol Evol 21:381–385

Kalbe M, Kurtz J (2006) Local differences in immunocompetence reflect resistance of sticklebacks against the eye fluke *Diplostomum pseudospathaceum*. Parasitology 132:105–116

Karvonen A, Seppälä O, Valtonen T (2004) Eye fluke-induced cataract formation in fish: quantitative analysis using an ophthalmological microscope. Parasitology 129:473–478. https://doi.org/10.1017/S0031182004006006

Krause J, Godin JGJ (1994) Shoal choice by banded killifish (emopen *Fundulus diaphanusemclose*, Teleostei, Cyprinodontidae): Effects of predation risk, fish size, species composition and size of shoals. Ethol 98:12–136

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. J Stat Softw 82:1–26. https://doi.org/10.18637/jss.v082.i13

Lafferty K, Morris AK (1996) Altered behaviour of parasitized killifish increases susceptibility to predation by bird final hosts. Ecology 77:1390–1397. https://doi.org/10.2307/2265536

Lafferty KD, Shaw JC (2013) Comparing mechanisms of host manipulation across host and parasite taxa. J Exp Biol 216:56–66

Lafferty KD (2008) Ecosystem consequences of fish parasites. J Fish Biol 73:2083–2093

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PTJ, Kuris AM, Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual M, Poulin R, Thieltges DW (2008) Parasites in food webs: the ultimate missing links. Ecol Lett 11:533–546

Maan ME, van der Spoel M, Jimenez PQ, van Alphen JJM, Seehausen O (2006) Fitness correlates of male colouration in a Lake Victoria cichlid fish. Behav Ecol 17:691–699

McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed MAF Publishing Group, Auckland, NZ

Mouritsen K (2002) The parasite-induced surfacing behavior in the cockle *Austrovenus stutchburyi*: a test of an alternative hypothesis and identification of potential mechanisms. Parasitology 124:521–528

Mouritsen K, Poulin R (2003) Parasite-induced trophic facilitation exploited by a non-host predator: a manipulator's nightmare. Int J Parasitol 33:1043–1050

Muñoz JCV, Staaks G, Knopf K (2017) The eye fluke *Tylodelphys clavata* affects prey detection and intraspecific competition of European perch (*Perca fluviatilis*). Parasitol Res 116:2561–2567. https://doi.org/10.1007/s00436-017-5564-1

Muñoz JCV, Bierbach D, Knopf K (2019) Eye fluke (*Tylodelphys clavata*) infection impairs visual ability and hampers foraging success in European perch. Parasitol Res. https://doi.org/10.1007/s00436-019-06389-5

Owen SF, Barber I, Hart PJB (1993) Low level infection by eye fluke, *Diplostomum* spp., affects the vision of three-spined sticklebacks, *Gasterosteus aculeatus*. J Fish Biol 42: 803-806

Poulin R (1993) Age-dependent effects of parasites on anti-predator responses in two New Zealand freshwater fish. Oecologia 96:431–438

Poulin R (2000) Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. J Fish Biol 56:123–137. https://doi.org/10.1111/j.1095-8649.2000.tb02090.x

Poulin R (2010) Parasite manipulation of host behaviour: an update on frequently asked questions. In: Brockmann HJ (ed) Advances in the study of behavior. Elsevier Inc., Academic Press, pp 151–186

Presswell B, Blasco-Costa I (2020) Description of *Tylodelphys* darbyi n. sp. (Trematoda: Diplostomidae) from the threatened Australasian crested grebe (Podiceps cristatus australis, Gould 1844) and linking of its life-cycle stages. J Helminthol 94.https://doi.org/10.1017/S0022149X19000142

Ruehle B, Poulin R (2020) Risky business: influence of eye flukes on use of risky microhabitats and conspicuousness of a fish host. Parasitol Res 119:423–430. https://doi.org/10.1007/s00436-019-06589-z

Scott ME, Dobson A (1989) The role of parasites in regulating host abundance. Parasitol Today 5:176–183

Seppälä O, Karvonen A, Valtonen T (2004) Parasite-induced change in host behaviour and susceptibility to predation in an eye fluke-fish interaction. Anim Behav 68:257–263. https://doi.org/10.1016/j.anbehav.2003.10.021

Seppälä O, Karvonen A, Valtonen T (2005) Manipulation of fish host by eye flukes in relation to cataract formation and parasite infectivity. Anim Behav 70:889–894. https://doi.org/10.1016/j.anbehav.2005.01.020

Seppälä O, Karvonen A, Valtonen T (2008) Shoaling behaviour of fish under parasitism and predation risk. Anim Behav 75:145–150. https://doi.org/10.1016/j.anbehav.2007.04.022

Shirakashi S, Goater CP (2002) Intensity-dependent alteration of minnow (*Pimephales promelas*) behaviour by a brain-encysting trematode. J Parasitol 88:1071–1074

Sinclair ARE (1979) The eruption of the ruminants. In: Sinclair ARE, Norton-Griffiths M (eds) Serengeti: Dynamics of an ecosystem. University of Chicago Press, Chicago, pp 82–103

Stumbo AD, Poulin R (2016) Possible mechanism of host manipulation resulting from a diel behaviour pattern of eye-dwelling parasites? Parasitology 143:1261–1267. https://doi.org/10.1017/S0031182016000810

Ubels JL, DeJong RJ, Hoolsema B, Wurzberger A, Nguyenm TT, Blankespoor HD, Blankespoor CL (2018) Impairment of retinal function in yellow perch (*Perca flavescens*) by *Diplostomum baeri* metacercariae. Int J Parasitol Parasites Wildl 7:171–179

Voutilainen A, Figueiredo K, Huuskonen H (2008) Effects of the eye fluke *Diplostomum spathaceum* on the energetics and feeding of Arctic charr *Salvelinus alpinus*. J Fish Biol 73:2228–2237

Voutilainen A, Huuskonen H, Taskinen J (2010) Penetration and migration success of *Diplostomum* spp. cercariae in Arctic charr. J Parasitol 96:232–235

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel

DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. J Open Sourc Softw 4:1686. https://doi.org/10.21105/joss.01686

Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. Can J Fish Aquat Sci 49:2196–2218