PRIMARY RESEARCH PAPER

Parasite infection reduces predation risk by dragonfly larvae in crustacean prey

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Abstract Parasites can modify the phenotype of their hosts, altering host vulnerability to predation. Trophically-transmitted parasites often use host manipulation to increase their probability of transmission to the next host or reduce their chances of being consumed by the wrong species. However, phenotypic changes may actually increase the host's vulnerability to other predators that are 'dead-ends' for the parasite, reducing parasite fitness while potentially impacting host populations. The isopod *Austridotea annectens* serves as intermediate host to *Maritrema poulini* (trematode) and display behavioural changes when infected that may increase parasite transmission. We tested the role of parasite infection on predation risk of isopods by a dragonfly nymph, a 'dead-end' parasite host. Size-matched isopod pairs were exposed to nymphs and observed until one was captured; subsequently isopod parasite abundance was determined.

Isopods with lower parasite abundance were significantly more likely to be caught. Several mechanisms may explain this; behavioural modification by the parasites may be altering isopod behaviour to avoid predation by dead-end hosts, or, alternatively, increased activity may allow heavily infected isopods to avoid predation by sit and wait predators. Assessing the effects of parasites on their host's ability to avoid predation is crucial in understanding how parasites may affect ecosystem dynamics and structure.

Keywords Predation · Predator–prey interactions · Parasite-mediation · Dragonfly · Isopods

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Introduction

Intra- and interspecific interactions are influenced by a variety of biotic and abiotic factors, shaping species abundance and population dynamics. The presence of parasites may modify these interactions, affecting the ability of individuals to avoid predation, as well as influencing the outcome of competition (Park, 1948; Price et al., 1986; Hudson & Greenman, 1998; Tompkins & Begon, 1999; Reisinger et al., 2015; Friesen et al., 2018). Parasite effects may include modifications in host behaviour or physical appearance, such as activity levels, phototaxis, aggressiveness or boldness, microhabitat use and body

colouration (Levri, 1998; Mikheev et al., 2010; Rauque et al., 2011; Lagrue et al., 2016; Friesen et al., 2017). Many of these alterations can lead to changes in predation levels on infected individuals relative to uninfected ones (Lagrue et al., 2007, 2013; Reisinger et al., 2015). Differential vulnerability to predation may have extended consequences for the community, by changing resource use and relative species abundances, and determining the likelihood of co-existence (Price et al., 1986; Hatcher & Dunn, 2011).

Interactions between predators and prey are a key component of transmission dynamics in parasites that move between trophic levels (Raoul et al., 2010). Parasites that are trophically transmitted often alter their hosts' behavioural phenotypes, ultimately increasing infected hosts' vulnerability to predation (Poulin, 1995; Klein, 2005; Thomas et al., 2005; Sparkes et al., 2006; Seppälä & Jokela, 2008). Many behavioural changes observed in infected hosts have been documented in the literature (Barber et al., 1995; Poulin, 1995; Klein, 2005; Thomas et al., 2005; Sparkes et al., 2006). These modifications may increase the chance of parasite transmission to the next host (Poulin, 1995). For instance, grass shrimp (*Palaemonetes pugio* Holthuis, 1949) infected by the trematode *Microphallus turgidus* Leigh, 1958 spent more time swimming near a predator, and were thus more likely to be preyed upon by the parasite's definitive host (Kunz & Pung, 2004).

Models have suggested that when behavioural modifications are not specific to the next host, they need to very effectively increase predation risk to actually increase parasite transmission (Seppälä & Jokela, 2008). Therefore, if the host has a naturally low risk of predation, behavioural manipulations can be adaptive to parasites (Seppälä & Jokela, 2008). However, as is the case in many communities, if predation risks are high, parasite-induced behavioural modifications must be more specific to the appropriate host to provide any benefits to the parasite in terms of transmission rate (Seppälä & Jokela, 2008). Yet, parasite-mediated trophic relationships and predation risks are seldom investigated in complex ecosystems, particularly when various species may serve as both intermediate and definitive hosts.

Parasite-induced behavioural modifications may also increase hosts vulnerability to predation by species unsuitable as hosts (i.e. 'dead-end' hosts;

Mouritsen & Poulin, 2003; Seppälä & Jokela, 2008; Seppälä et al., 2008). This is the case in the isopod *Asellus aquaticus* Sket, 1965 infected with the acanthocephalan *Acanthocephalus lucii* Müller, 1776. *Acanthocephalus lucii* modifies the pigmentation and behaviour of isopod hosts, increasing their vulnerability to consumption by both the definitive host and other dead-end predators. However, the increase in vulnerability to predation by the parasite's definitive host is greater than that by dead-end hosts (Seppälä et al., 2008). Alternatively, changes in the behavioural phenotype of infected individuals may cause them to be more effective at evading dead-end predators, increasing the probability of the parasite continuing its life cycle (Levri, 1998; Médoc et al., 2006, 2009; Médoc & Beisel, 2008).

Much of the research on the relationship between phenotypic modifications by parasites has focused on the transmission between hosts, yet most intermediate hosts are also prey to a range of non-host predators within their community (Cézilly et al., 2010). Differential predation levels on infected individuals have potentially substantial consequences for the ecosystem. If parasite-induced behavioural modifications increase predation rate on a given infected host species by a variety of different predators, not just the parasite's next host, it may reduce host population size, alter competition with other species, and ultimately may drive selection for counter-adaptations.

Trophic transmission in trematode parasites provides the opportunity to examine the interplay among parasites, hosts and predators, particularly in complex multi-trophic ecosystems where they are often found. The isopod, *Austridotea annectens* Nicholls, 1937 (Family Idoteidae), serves as intermediate host to the trematode parasite, *Maritrema poulini* Presswell et al. 2014 (Family Microphallidae) and parasite abundance has been shown to be positively correlated with increased activity levels (Friesen et al., 2017). *Maritrema poulini* uses waterfowls as definitive hosts (Presswell et al., 2014). Eggs produced by adult worms pass out with host faeces and are ingested by the first intermediate host, the snail, *Potamopyrgus antipodarum* Gray, 1843. After asexual multiplication within the snail, free-swimming larvae are released in the water where they seek a crustacean second intermediate host (isopod or amphipod), in which they encyst as metacercariae. The life cycle is completed when the infected crustacean host is

consumed by the avian definitive host (Presswell et al., 2014). In addition to changing the activity levels of their isopod host (Friesen et al., 2017), infections by this parasite also provide an example of super extended phenotype, influencing competitive interactions and ultimately the microhabitat use of a congeneric competitor, *Austridotea lacustris* Thomas, 1879 (Friesen et al., 2018). The isopod *A. annectens* is an important prey within its ecosystem and is consumed by a variety of predator species beyond the definitive host of *M. poulini*, including other birds, odonate nymphs, fish, congeners and other macroinvertebrates (Wilhelm et al., 2002, 2007; Kattel & Closs, 2007; Lagrue et al., 2011, 2015).

We investigated whether behavioural differences observed in infected isopods altered their vulnerability to predation by a dead-end predator. To test whether parasite abundance was related to increased vulnerability to predation, due to differential selection behaviour by the predator or changes in behaviour of the host, we paired isopods of similar sizes but harbouring different numbers of parasites, and exposed them to a dragonfly nymph, a dead-end host for the parasite but a natural predator of isopods. If parasite abundance simply increases predation rates, then we expected that captured isopods would harbour consistently higher numbers of parasites. However, if infection alters host phenotype, and therefore behaviour, in host specific ways, we may expect predation rate by a dead-end host to decrease with infection.

Methods

Sample collection

We collected naturally infected *Austridotea annectens* isopods from the littoral zone of Lake Waihola, South Island, New Zealand (46°01′14S, 170°05′05E) and dragonfly nymphs (*Hemicordulia australiae* Rambur, 1842; Family Corduliidae) from Tomahawk Lagoon (45°54′11S, 170°32′33E) between April and May 2017. Although isopods and dragonfly nymphs are found in sympatry in both lakes, due to differences in natural abundance of invertebrates and ease of sampling, isopods and dragonfly nymphs were taken from separate locations. Isopods were caught using dip-nets and dragonfly nymphs were picked by hand from rocks. All animals were transported to the laboratory

in lake water. Isopods were maintained in 10 L tanks containing aerated lake water and aquatic plants (*Myriophyllum triphyllum* Orchard and *Elodea canadensis* Michx.) for food. Dragonfly nymphs were maintained individually in plastic containers with 0.5 L of water, a large rock and some macrophytes for cover. Animals were kept at room temperature (16°C ± 1°C), and under a controlled photoperiod (12 h dark and light) for 14 days prior to their use in predation trials.

Dragonfly nymphs were fasted for 7 days prior to predation experiments. All nymphs were F-5 or F-6 instars and likely young-of-the-year as this species appears to have a 1-year life cycle (Winterbourn & Pohe, 2013). Prior to the experimental treatment, dragonflies were sustained on a diet of isopods. Dragonfly nymphs generally hunt in one of two different styles; some larvae are visually dependent predator and hunt as they move amongst the vegetation (e.g. Superfamily Aeshnoidea) whereas others sit and wait for their prey (e.g. Superfamilies Cordulegastroidea and Libelluloidea) (Pritchard, 1965; Richards & Bull, 1990). The dragonfly nymph used here is from the Superfamily Libelluloidea (Leach 1815), and therefore a sit and wait predator. As such, a behavioural shift, such as parasite-induced changes in activity levels, in infected isopods should impact their probability of being captured by this predator.

Predator trials

We paired isopods by size to reduce any confounding influence of size on prey selection. Isopods were not matched by sex because sexing isopods requires extensive handling and is almost impossible without killing the isopod (Friesen et al., 2018). Two paired isopods were added to each trial container (clear cylindrical plastic containers, 200 mL volume, 90 mm diameter and 40 mm depth) with a sandy substrate and left for 5 min to acclimate to their new environment. A sandy environment is the preferred substrate of this species of isopod in nature (Friesen et al., 2018). This also provided isopods with enough time to bury themselves completely if desired. One dragonfly nymph was then added to each container and monitored until it caught one of the two isopods. The isopod was then retrieved from the nymph before it could be consumed and placed into a labelled vial with 70% ethanol until dissection. The uncaptured isopod was

also recovered, killed in 70% ethanol and stored until dissection. Each dragonfly nymph was only used in up to a maximum of three trials to ensure it did not expend too much energy striking for prey without receiving food.

Total body length of each isopod was determined by measuring from the anterior tip of the cephalic capsule to the posterior end of the uropod. Sex was determined for each individual when possible. Isopods shorter than 7-8 mm in body length were impossible to sex due to the lack of secondary sexual characters and thus considered juveniles (Friesen et al. 2017). Individuals were then dissected to retrieve and count all parasites; only the trematode *M. poulini* was found in isopods used in our study. Parasite abundance was defined as the number of parasites per host including zeros. All dragonflies were euthanized after the trials, measured and dissected to ensure they harboured no parasites.

Statistical analysis

Statistical analyses were performed in JMP® 12 (SAS Institute Inc 2015), R statistical software (http://www.R-project.org) and G*Power (Faul et al., 2007, 2009). Differences in parasite abundance between captured and uncaptured isopods were analysed using a generalized linear mixed model (glmerMod, family = binomial) with parasite abundance as the main predictor, with size and sex as fixed effects, and captured/uncaptured at the binomial response variable. Dragonfly identity was also included as a random factor to control for possible non-independence of trials using the same predator and any individual predator bias. Size was included in the model as previous research has found a positive linear relationship between isopod size and parasite abundance (Friesen et al., 2017). Odds ratios and 95% confidence intervals for each fixed effect were also calculated. The probability of capture was also calculated. Variance explained (R^2) for the model was calculated using the multi-model inference package (r.squaredGLMM) (Nakagawa & Schielzeth, 2013). Effect size of the difference between the parasite abundance of uncaptured versus captured isopods was calculated using Cohen's *d*, to account for the paired nature of the experiment. A post-hoc power analysis was performed on the differences in parasite abundance between captured and

uncaptured isopod pairs. Our post-hoc statistical power analysis indicated a statistical power of 0.99.

Results

We paired 70 *A. annectens* isopods by size (i.e. 35 pairs), ranging in size between 4.9 and 11.5 mm. Isopod sex ratio was 2:1 males to females, with 6 individuals classified as juveniles. Size differences between individuals in a pair ranged between 0 and 2.3 mm, with a mean difference of 0.7 mm.

Within pairs, uncaptured isopods had higher *M. poulini* abundance than captured individuals in 77% of all trials (mean parasite abundance uncaptured, mean ± SE, 16.8 ± 2.2, captured, 9.7 ± 1.1, mean difference between captured and uncaptured, 7.09 ± 2.1; Figs. 1 and 2). The probability of an
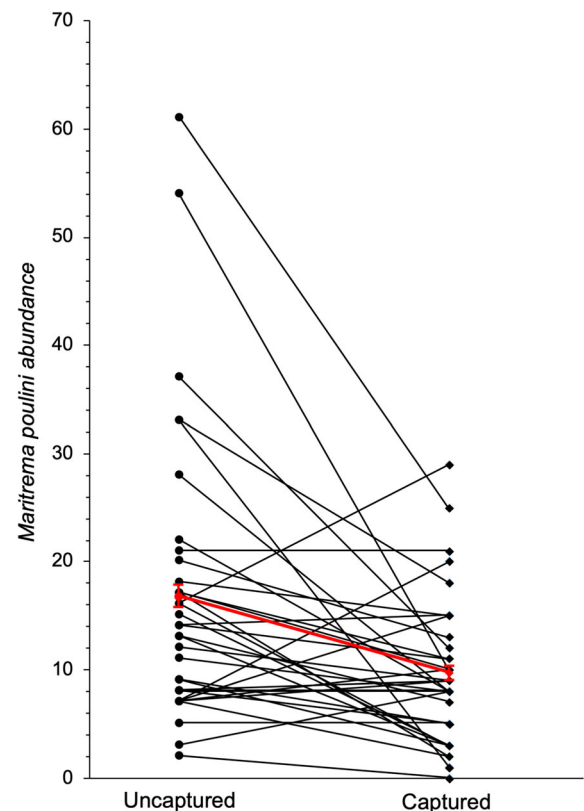
Fig. 1 Parasite (*Maritrema poulini*) abundance in matched pairs of captured and uncaptured isopods (*Austridotea annectens*). The mean abundance and standard error of both uncaptured and captured isopods are shown in red. Figure was produced using JMP and MSOffice
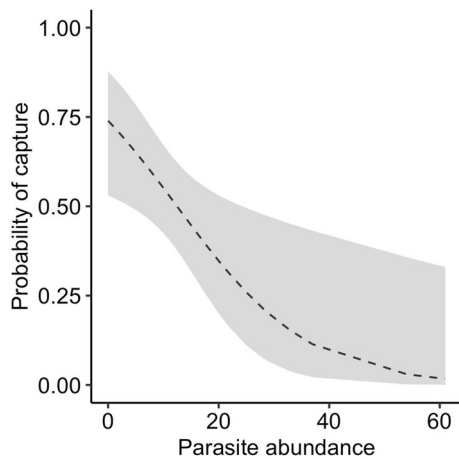
Fig. 2 The probability of capture as a function of an isopod's (*Austridotea annectens*) parasite (*Maritrema poulini*) abundance. The shaded area represents the 95% confidence interval. Figure was produced using R statistical software

individual being captured was negatively related to parasite abundance, with each additional infection reducing the probability of capture by $\sim 0.6\%$, with an increased probability drop when infection levels are low (Fig. 2). Consistently, uncaptured isopods had a higher abundance of *M. poulini* than captured individuals when controlling for the possibility of individual predator bias (Parasite abundance, $z = -2.35$, $P = 0.019$; Table 1). The effect size of the difference in parasite abundance between uncaptured and captured isopods was 0.68 (Cohen's *d*). The marginal R^2 for the model was 0.28 (Nakagawa & Schielzeth, 2013).

Across all pairs of isopods, there was no difference in body size between the individual captured by the predator (mean $\pm$ SE, 8.3 $\pm$ 0.24 mm) and the one that was not (8.3 $\pm$ 0.26 mm; Table 1; Size, z-value = 0.039, $P = 0.97$). We also found no relationship between the sex of an isopod and its

probability of being captured (Sex, z-value = 1.13, $P = 0.26$; Table 1).

A total of 16 different dragonfly nymphs were used during the trials, ranging in size between 20 and 24 mm. All individuals were dissected after the trials and no macroparasite was found in any dragonfly individual.

Discussion

Phenotypic modifications of hosts induced by parasites have been documented to increase hosts' vulnerability to predation and therefore parasite transmission to the next host (Poulin, 1995; Seppälä et al., 2004; Cézilly & Perrot-Minnot, 2005; Lagrue et al., 2007; Poulin & Maure, 2015). Yet changes that assist in avoiding dead-end hosts are seldom documented and far less understood (Mouritsen & Poulin, 2003; Seppälä & Jokela, 2008; Seppälä et al., 2008). In our isopods, individuals with a higher abundance of *M. poulini* had a decreased probability of being caught by a predator. As these isopods show higher activity levels with higher abundance of *M. poulini* (Friesen et al., 2017, 2018), the opposite relationship between parasite abundance and the likelihood of being captured by a predator, especially a sit and wait predator like dragonfly nymphs, suggests another mechanism is in place. Our results may be due to a number of factors, indicating that either dragonfly nymphs are avoiding eating highly infected individuals or, more likely, parasites are modifying their intermediate hosts in the presence of a dead-end host to reduce their chances of being eaten by an unsuitable predator.

Parasites may modify isopod behaviour based on the presence of specific predators; altering isopod behaviour to avoid predation by a dead-end host, such as decreasing movement and burrowing (Curtis, 1987;

Table 1 Results of the generalized linear mixed model examining the differences in parasite abundance between captured and uncaptured isopods

Fixed effects	Model estimate	Standard error	*z*-value	Odds ratio	95% confidence intercal	*p* value
Parasite abundance	-0.0999	0.0043	-2.35	0.905	0.15	**0.019**
Sex	0.258	0.229	1.13	1.294	1.25	0.26
Size	0.0211	0.547	0.039	1.021	2.72	0.97

Post-hoc effect sizes (odds ratios) are included. Significant values are shown in bold

Moore, 2002; Médoc & Beisel, 2008; Médoc et al., 2009; Lagrue et al., 2013). Although increased activity levels of the host may increase their encounter rate with a sit and wait predator such as dragonfly nymphs, it may alternatively allow them to avoid predation by the same type of predator through higher rates of avoidance. As the mechanisms behind these changes are not yet fully understood in this system, the changes in behaviour in our isopods may be due to the manipulation by the parasite or a physiological by-product of infection, such as increased activity to compensate for the energetic or pathological consequences of infection (Moore, 2002; Poulin, 2010). Yet, any changes in the behavioural phenotype of infected individuals that make them more effective at evading dead-end predators should be selected for in parasites as they also increase the probability of the parasite continuing its life cycle (Levri, 1998; Médoc et al., 2006, 2009; Médoc & Beisel, 2008).

The possibility that dragonflies select less infected individuals is unlikely but cannot be discounted outright. It is possible, although improbable, that *M. poulini* use the dragonfly nymphs as paratenic hosts (intermediate hosts that may be used to complete a parasite's life cycle but in which no development occurs) (Stigge & Bolek, 2015). However, present dissections and past work on this species failed to reveal any infections or encysted *M. poulini* in dragonfly nymphs, and the use of paratenic hosts by trematodes is very uncommon (Chubb et al., 2010). Furthermore, dragonfly nymphs slough off the epithelium lining of their alimentary canal when excreting waste (Needham, 1897), and adult *M. poulini* are found in the intestine of their definitive hosts (Presswell et al., 2014). As such, *M. poulini* survival within the nymph would depend on being able to survive digestion, and then move through this layer to survive, which is unlikely. It is also possible that infected isopods may release novel or increased levels of chemicals that deter dragonfly nymphs and thus resulting in increased predation of less infected individuals (Wolf et al., 2009; Poulin, 2010). Overall, there is no obvious reason for dragonfly nymphs to avoid consuming highly infected individuals, strongly suggesting that differences in the probability of predation are more likely due to behavioural changes in the isopods themselves.

Increased vulnerability of less infected individuals to predation has the potential to shift ecosystem dynamics. Removing less infected individuals from a community can shift competitive interactions, as is seen between *A. annectens* and its competitor, *A. lacustris* (Friesen et al., 2018). If *M. poulini* affects the vulnerability of its host to predation, it is yet to be understood how these changes may play out with targeted host species, other dead-end hosts, and in complex, multi-trophic interactions (Lagrue & Poulin, 2015). The same changes that allow the more highly infected individuals to be less likely to be captured by the dragonfly nymphs may have indirect consequences on their foraging abilities and competitive interactions. Understanding the effects of parasites on their host's ability to avoid predation is crucial to start to understand how the presence of parasites may affect population dynamics and ecosystem structure.

Data Availability The datasets generated during and/or analysed during the current study will be publicly available in the Dryad Digital Repository, at time of publication.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving animal rights All applicable institutional and national guidelines for the care and use of animals were followed.

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