

RESEARCH ARTICLE

It's a worm-eat-worm world: Consumption of parasite free-living stages protects hosts and benefits predators

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Abstract

1. Predation on parasites is a common interaction with multiple, concurrent outcomes. Free-living stages of parasites can comprise a large portion of some predators' diets and may be important resources for population growth. Predation can also reduce the density of infectious agents in an ecosystem, with resultant decreases in infection rates. While predator–parasite interactions likely vary with parasite transmission strategy, few studies have examined how variation in transmission mode influences contact rates with predators and the associated changes in consumption risk.
2. To understand how transmission mode mediates predator–parasite interactions, we examined associations between an oligochaete predator *Chaetogaster limnaei* that lives commensally on freshwater snails and nine trematode taxa that infect snails. *Chaetogaster* is hypothesized to consume active (i.e. mobile), free-living stages of trematodes that infect snails (miracidia), but not the passive infectious stages (eggs); it could thus differentially affect transmission and infection prevalence of parasites, including those with medical or veterinary importance. Alternatively, when infection does occur, *Chaetogaster* can consume and respond numerically to free-living trematode stages released from infected snails (cercariae). These two processes lead to contrasting predictions about whether *Chaetogaster* and trematode infection of snails correlate negatively ('protective predation') or positively ('predator augmentation').
3. Here, we tested how parasite transmission mode affected *Chaetogaster*–trematode relationships using data from 20,759 snails collected across 4 years from natural ponds in California. Based on generalized linear mixed modelling, snails with more *Chaetogaster* were less likely to be infected by trematodes that rely on active transmission. Conversely, infections by trematodes with passive infectious stages were positively associated with per-snail *Chaetogaster* abundance.
4. Our results suggest that trematode transmission mode mediates the net outcome of predation on parasites. For trematodes with active infectious stages, predatory *Chaetogaster* limited the risk of snail infection and its subsequent pathology (i.e. castration). For taxa with passive infectious stages, no such protective effect was observed. Rather, infected snails were associated with higher *Chaetogaster*

abundance, likely owing to the resource subsidy provided by cercariae. These findings highlight the ecological and epidemiological importance of predation on free-living stages while underscoring the influence of parasite life history in shaping such interactions.

KEYWORDS

Chaetogaster, consumer–resource, infection, parasites, predator–prey, snail, transmission, trematode

1 | INTRODUCTION

Beyond their classical roles within hosts, parasite species are often involved in competitive, facilitative and predatory interactions with a diverse array of non-host taxa, highlighting their importance in ecosystems and food webs (Tompkins et al., 2011). For instance, some parasites have complex, multi-host life cycles that include mass-produced free-living infectious stages, many of which are consumed before reaching their intended hosts (Kaplan et al., 2009; McKee et al., 2020). Therefore, parasites function as important prey taxa and energy pools within some ecosystems (Preston et al., 2013). In freshwater systems, for example, cyclopoid copepods selectively consume free-living larval parasites, which have been documented as energetically valuable prey for invertebrate predators (McKee et al., 2020; Mironova et al., 2020). Indeed, parasites can comprise a large portion of some predators' diets, enhancing individual growth rates and augmenting population sizes (Hopkins et al., 2013; Kagami et al., 2007). Taken together, such studies emphasize how predation on the infectious stages of parasites can alter consumptive interactions and energy flows, thereby influencing both predator populations and food web structure (Johnson et al., 2010; Kuris et al., 2008; Lafferty et al., 2006).

Alongside energetic considerations, predator–parasite interactions are also important for parasite transmission: predation on infectious stages can reduce the density of parasite propagules and thus the risk of infection for hosts (Johnson et al., 2010; Thieltges et al., 2008). For example, through predation of trematode cercariae, damselfly larvae reduced infection of frog hosts by 50% in laboratory trials (Orlofske et al., 2012). Similarly, in mesocosms, consumption of trematode infectious stages by intertidal crabs and shrimps reduced parasitic transmission to mollusc hosts by over 50% (Thieltges et al., 2008). Such predator–parasite interactions contrast with trophic transmission, in which predation of infected hosts advances the life cycle of the parasite (Choisy et al., 2003). That is, although both trophic transmission and predation of free-living stages provide predators with valuable energy (derived from hosts and/or parasites; Lafferty, 1992; McKee et al., 2020), the former promotes parasite life cycles and increases prevalence among hosts, while the latter terminates transmission and reduces prevalence. By limiting infection among potential hosts, predation on free-living infectious stages of parasites (or, 'protective predation') may have

cascading impacts on host fitness and population densities (Johnson et al., 2010). Collectively, these observations suggest that predator–parasite interactions are critical in shaping both ecological and epidemiological processes of ecosystems.

The occurrence and strength of predation on aquatic parasite stages is hypothesized to be mediated in part by life-history characteristics of both parasites and predators that influence their contact rates and spatio-temporal overlap (e.g. Born-Torrijos et al., 2020; Kaplan et al., 2009). For parasites, these characteristics include the behaviour, life-form and habitat use of infectious stages (Thieltges, Jensen, et al., 2008). Among nematodes, for instance, the degree to which predation reduces infection depends on transmission mode (i.e. whether transmission relies on vectors, eggs or larvae): species that use motile larvae for transmission are often consumed by invertebrate predators, while nematodes that rely on sessile eggs are not (Carvalho et al., 2009; d'Alexis et al., 2009; Wharton, 1980). Similarly, for trematodes, variation in predation risk can arise from species-level differences in cercarial space use (e.g. benthic vs. limnetic) and behaviour (e.g. swimming style and aggregation; Born-Torrijos et al., 2020, 2021; Selbach et al., 2019). Incorporating such trait-based information in laboratory experiments has greatly improved our understanding of variability in predator–parasite interactions (Orlofske et al., 2015). Yet few studies have identified how life-history variability within parasite guilds mediates such interactions in natural communities. Using observational data to quantify predator–parasite interactions in natural systems is thus needed to further elucidate the ecological roles of parasites within ecosystems.

Owing to their high biomass (Preston et al., 2013), trematode parasites are consumed by a diverse array of vertebrate and invertebrate predators (e.g. Kaplan et al., 2009; Mironova et al., 2020). In some systems, trematode biomass can rival or eclipse that of major free-living species (Kuris et al., 2008; Thieltges, De Montaudouin, et al., 2008). Much of this biomass occurs within snails (Hechinger et al., 2009), which often function as first intermediate hosts for trematodes and from which abundant free-living cercariae emerge (Esch & Fernandez, 1994; Kuris et al., 2008). Infection by trematodes typically castrates snail hosts (Esch & Fernandez, 1994) and precipitates the conversion of host biomass into parasite biomass (Preston et al., 2013). Given the immense secondary production by trematodes within snail hosts, factors that limit infection of snails are especially influential in determining the role of trematodes in

aquatic food webs. Importantly, trematodes infect snails in one of two ways: (a) active transmission by a swimming ciliated stage (miracidium) or (b) passive transmission via snail ingestion of trematode eggs (Esch & Fernandez, 1994; Figure 1). These strategies vary across, but not within, trematode taxa. Among trematodes with active transmission, infection success may depend on the risk of consumption by predators, such as *Chaetogaster limnaei limnaei* (hereafter '*Chaetogaster*')—an episymbiotic worm that occupies the head and mantle cavity of aquatic snails (Gruffydd, 1965). Previous research has emphasized the vulnerability of trematode miracidia

to consumption by *Chaetogaster* worms, which can reduce infection success (Figure 1a; Khalil, 1961; Michelson, 1964; Wajdi, 1964). In contrast, passively transmitted eggs resting on the benthic habitat are much less likely to spatially overlap with (i.e. contact) *Chaetogaster* when being ingested by snails (Figure 1b; McKoy et al., 2011), suggesting that the degree to which predation limits trematode infections in snails could depend on transmission mode (Ibrahim, 2007; McKoy et al., 2011; Rodgers et al., 2005).

In addition to limiting infection in snails ('protective predation'), predator–parasite interactions in this system can also

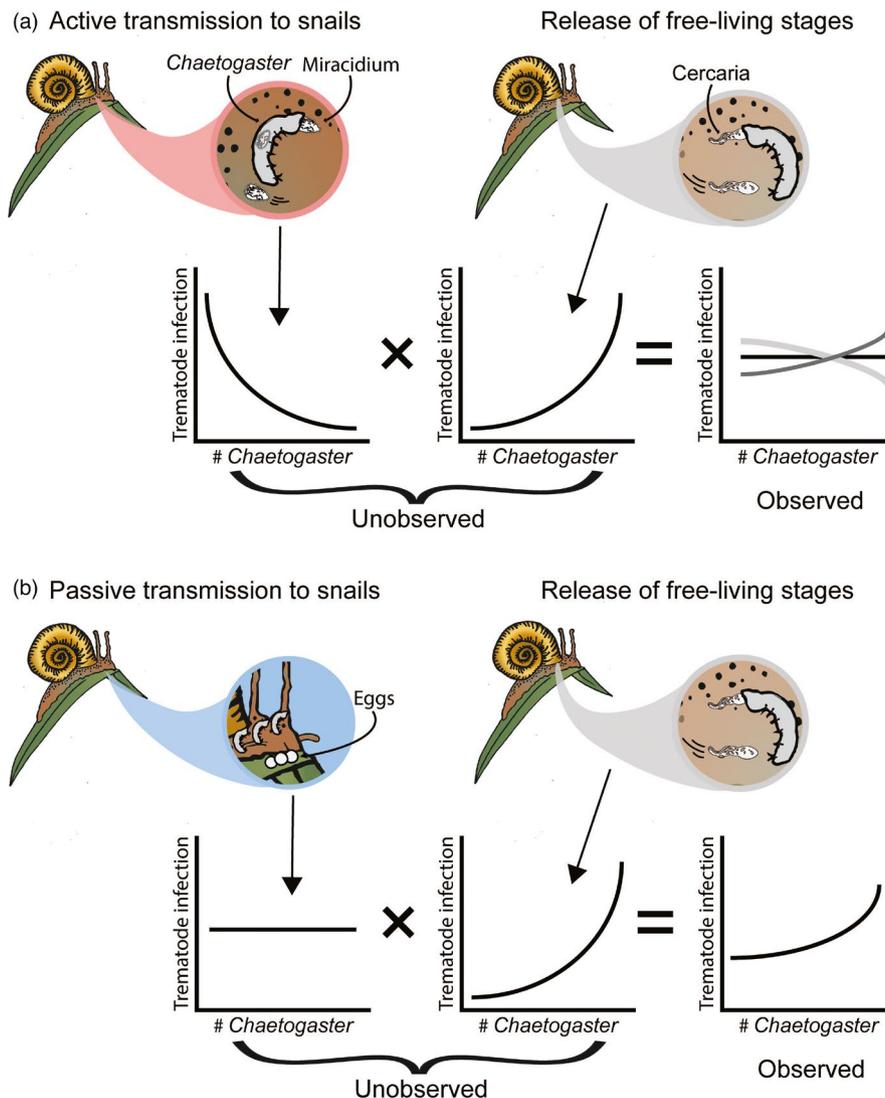


FIGURE 1 Patterns of *Chaetogaster* and trematode co-occurrence reflect the dynamic interplay of transmission limitation and predator augmentation. Here, we provide graphical predictions of how unobserved interactions may shape observed relationships between *Chaetogaster* predators and trematode parasites, and how these relationships may vary based on parasite transmission mode. For trematodes with active transmission (a; in pink), predation of both miracidia (prior to infection) and cercariae (following infection) are predicted to act in concert and in opposite directions. First, during active transmission to snails (by miracidia), transmission limitation may produce a negative relationship between *Chaetogaster* abundance and trematode infections (protective effects). Then, during the release of cercariae (free-living stages), the numerical response from consumption of cercariae may lead to a positive relationship between trematode infection and *Chaetogaster* abundance (predator augmentation). Thus, the observed outcome will depend on the relative strength of the two unobserved processes. Conversely, for trematodes with passive transmission (b; in blue), predation on eggs is rarely expected to occur, generating a null relationship between *Chaetogaster* abundance and trematode infection. Any observed positive relationship between trematode infection and *Chaetogaster* abundance should therefore primarily reflect predation on (and a numerical response to) cercariae

result in predator augmentation (McKoy et al., 2011). Within infected snails, trematodes reproduce asexually and release numerous free-living infectious stages (cercariae; Figure 1; Esch & Fernandez, 1994). Relative to other trematode free-living stages (i.e. miracidia and eggs), cercariae are abundant and nutritious (Esch & Fernandez, 1994); they therefore represent an important food resource for a variety of invertebrate predators, including *Chaetogaster* (Figure 1; Hopkins et al., 2013; McKee et al., 2020; Preston et al., 2013). For instance, individual oligochaete mass and population sizes are linked to cercarial consumption (Schultz & Koprivnikar, 2021), and *Chaetogaster* populations can grow by 65% in response to increased cercariae availability (Fernandez et al., 1991; Hopkins et al., 2013). Thus, alongside their role in protecting snails from initial trematode infection, *Chaetogaster* may also consume cercariae and respond numerically. Importantly, these two phenomena lead to potentially conflicting predictions about the expected relationship between predatory *Chaetogaster* and trematode infection among snails: if *Chaetogaster* consume invading miracidia and prevent infection in snails, we might expect predator protection, or a strong, negative association between *Chaetogaster* abundance and snail infection (Figure 1; 'Transmission to snails'). Alternatively, if *Chaetogaster* feed primarily upon cercariae released by already-infected snails and derive a significant resource subsidy, we might expect predator augmentation, or a positive link between infected snails and *Chaetogaster* abundance (Figure 1; 'Release of free-living stages').

To understand the net effects of predator–parasite interactions for both transmission and predator abundance, we characterized relationships between trematode infection and *Chaetogaster* abundance in an extensive dataset involving 20,759 examined snails and nine trematode taxa. Recognizing the potential for multiple forms of interaction between trematodes and *Chaetogaster*, we specifically sought to test the hypothesis that trematode transmission mode mediates the net outcome of interactions between *Chaetogaster* and trematodes in natural communities. Using data collected from 79 ponds across 4 years in California, we tested how the net relationship between *Chaetogaster* abundance and trematode infection depended on transmission mode (actively vs. passively acquired infection). Importantly, for these observational data, the relationship between trematode infection and *Chaetogaster* abundance is the product of predation on both miracidia and cercariae, which could be occurring simultaneously for some trematode taxa (Figure 1). Therefore, our approach evaluated which pattern emerged across an extensive dataset involving multiple sites, years and species, and assessed which process—'protective predation' or 'predator augmentation'—was the predominant outcome. Our study thus offers insight into how parasite transmission mode mediates vulnerability to predators and modifies their roles as ecological (i.e. as food resources) and epidemiological (i.e. as parasites) members of communities; it also provides a powerful empirical foundation for subsequent experiments that can robustly observe and quantify the predation of miracidia, eggs and diverse cercariae by *Chaetogaster*.

2 | MATERIALS AND METHODS

2.1 | Study system

Between 2013 and 2016, we sampled freshwater snail populations within pond ecosystems of the Bay Area of California, USA. We sampled a total of 120 ponds (range of ponds sampled per year: 79–97), most of which occurred on public lands (county and regional parks), were human constructed or modified (e.g. artificially deepened) and which served as water sources for grazing livestock. Ponds spanned broad ranges of perimeter, maximum depth, vegetation structure and water chemistry. Pulmonate snails of the genera *Gyraulus*, *Radix*, *Lymnaea*, *Helisoma* and *Physa* were present within our study area, although we focused on representatives from the last two genera owing to larger sample sizes (i.e. more snails dissected). The distribution of *Helisoma* and *Physa* snails varied among ponds: 73 ponds had both species, 27 had just *Helisoma* and 20 had just *Physa*. *Helisoma* and *Physa* host a diverse suite of digenean trematodes (Esch & Fernandez, 1994; McCaffrey & Johnson, 2017), most often as first intermediate hosts (i.e. the infections studied here) but also as second intermediate hosts for some trematode taxa (e.g. *Echinostoma* spp.). Evidence from field and laboratory studies suggests that *Helisoma* and *Physa* snails often use similar habitats (e.g. Harman, 1972; Turner & Chislock, 2010), though it is possible that differences in preferred habitat (e.g. benthic vs. vegetation substrate) could lead to differing rates of contact with trematode miracidia and eggs. Of the trematodes in this system, most are capable of infecting both *Helisoma* and *Physa* snails (Armatae morphotype, Brevifurcate-apharyngeate morphotype, *Echinostoma* spp., *Halipegus* spp., Strigeid morphotype, *Zygocotyle lunata*); however, *Ribeiroia ondatrae* and *Clinostomum marginatum* can infect only *Helisoma*, and *Haematoloechus* spp. can infect only *Physa* (Ameel et al., 1949; Blair, 1974; Calhoun et al., 2020; Dronen Jr. & Lang, 1974; Fried et al., 2009; Ingles, 1933; Johnson et al., 2002; Lang, 1968; Olsen, 1986; Smyth & Smyth, 1980; Thomas, 1939).

2.2 | Field sampling

We visited each pond twice annually between May and August for snail collection. During visits, we collected snails with dip nets, seine nets and by hand. We targeted a sample size of 50 individuals per species per visit, although low snail densities sometimes precluded this goal. Between collection and dissection, snails were housed at ~4°C in 1-L containers specific to unique site × species combinations. Within 24–96 hr of collection, we dissected all snails ($n = 33,201$ total; *Helisoma*: 19,668; *Physa*: 13,533) after measuring shell width (Richgels et al., 2013). We dissected each snail under a dissecting microscope, first removing its shell and then examining each organ. We used forceps to carefully inspect the head and mantle of snails and estimate the number of observed *Chaetogaster* on the exterior of the snail; very few *Chaetogaster* were observed inside snail shells or organs but because it has been shown that this species can parasitize

snails (Smyth et al., 2015), future work on this system should quantify precise *Chaetogaster* locations within snails. Because *Chaetogaster* abundance was often high and individuals were counted in situ (i.e. on snails), counts were often approximated to the nearest multiple of five. To confirm species identification of *Chaetogaster limnaei limnaei*, we examined wet mounts of *Chaetogaster* individuals under a compound microscope. Some trematode taxa infect *Chaetogaster* as a second intermediate host via trophic transmission (e.g. Khalil, 1961); however, because no trematodes in this study system are known to infect *Chaetogaster*, predation is assumed to lead to cercariae death.

To quantify trematode infections, we dissected the snail gonadal tissue, which trematodes occupy and consume while undergoing several rounds of asexual reproduction prior to the release of cercariae (Schell, 1985). When infections were mature (i.e. cercariae-producing), we identified trematodes to the lowest possible taxonomic unit based primarily on cercaria morphology; in some cases, identification was aided by morphological traits of sporocysts and rediae (larval trematode stages that give rise to cercariae; Schell, 1985). To incorporate transmission mode into our analyses, we categorized each trematode taxon as having either 'active' (i.e. miracidia penetration) or 'passive' (i.e. egg ingestion) transmission mode based on descriptions from previous research. In total, we identified trematodes of nine taxa—six taxa relied on active transmission: *Brevifurcate-apharyngeate-morphotype* (Ameel et al., 1949; Calhoun et al., 2020), *Clinostomum marginatum* (Ameel et al., 1949; Calhoun et al., 2020), *Echinostoma* spp. (Kanev, 1994), *Ribeiroia ondatrae* (Johnson et al., 2002), Strigeid morphotype (Blair, 1974) and *Zygocotyle lunata* (Fried et al., 2009); three taxa relied on passive transmission: Armatae morphotype (Dronen Jr. & Lang, 1974; Ingles, 1933; Lang, 1968; Smyth & Smyth, 1980), *Haematoloechus* spp. (Olsen, 1986; Smyth & Smyth, 1980) and *Halipegus* spp. (Smyth & Smyth, 1980; Thomas, 1939; see Appendix S1 for more information on trematode traits). Cases in which we detected rediae or sporocysts but no mature cercariae were classified as immature and omitted from analysis ($n = 278$).

2.3 | Statistical analysis

We used a GLMM to test for an association between *Chaetogaster* abundance and the probability of snail infection by trematodes—and whether such a relationship varied by transmission mode (i.e. active- vs. passive-infecting trematodes). We limited our analyses to pond \times year combinations that had at least one snail with *Chaetogaster* and at least one snail with a trematode infection. For this analysis, we used a 'long data' format, in which each dissected snail had multiple associated rows—one per trematode taxon capable of infecting that snail taxon—that indicated whether a snail was infected by a given trematode. Representatives of most trematode morphotypes/taxa were detected in both *Helisoma* and *Physa* snails, except for *Ribeiroia ondatrae* (*Helisoma* only), *Clinostomum marginatum* (*Helisoma* only) and *Haematoloechus* spp. (*Physa* only). We treated trematode infection as a binomial response (infected or uninfected)

and specified fixed effects for snail species (*Helisoma* or *Physa*), snail size, day of year (as a numeric value), *Chaetogaster* abundance, trematode transmission mode and a *Chaetogaster* \times transmission mode interaction (to allow the effect of *Chaetogaster* on infection to vary by transmission mode). Day of year and *Chaetogaster* abundance were z-standardized prior to model inclusion. Individual snail size was a proxy for snail age (and thus cumulative exposure) and was z-standardized on a per-species basis by subtracting the mean size of that species and dividing by its standard deviation. Effectively, this allowed us to test whether there was an effect of snail size after accounting for snail species (as a fixed effect). We included random intercepts for snail individual (because each snail had nine associated rows of data), trematode taxon (to account for identity effects), site and collection event (e.g. 2013-event 1, 2013-event 2, 2014-event 1, etc.). Including these random intercept terms accounted for any lack of independence within snail hosts, trematode taxa, sites and collection events (within- and among-year; Bolker et al., 2009). For fixed effects, we assessed the weight of evidence against a null model based on approximate p -values obtained from likelihood-ratio test (LRT) χ^2 values (Bolker et al., 2009). To obtain p -values for the slopes describing the relationships between the probability of infection by passive and active trematodes and *Chaetogaster* abundance, we fit models with both active and passive specified as the reference level for the transmission factor. All statistical analyses were performed in the R programming environment (version 3.6.3; R Core Team, 2019) using the statistical analysis package GLMMTMB (Brooks et al., 2017). Script to reproduce models and associated plots can be found in Appendix S2.

3 | RESULTS

Of the 120 sampled sites, 79 supported both *Chaetogaster* and trematode infections in one or more years (annual range: 36–55). Within the 20,759 snails from these sites (*Helisoma*: 11,288; *Physa*: 9,471), we identified 2,515 mature trematode infections, including 2,134 involving trematode taxa with active transmission and 381 involving taxa with passive transmission. Trematode infection prevalence was 0.12 overall (i.e. among all snails) and varied widely between transmission modes, between snail species and among trematode taxa (Table 1). Coinfections were exceedingly rare (<0.1%), as is typical in this study system (Richgels et al., 2013). We detected *Chaetogaster* within 38% of snails, with a mean count of 14.5 individuals per snail. The distribution of *Chaetogaster* among snails was highly aggregated, with many unoccupied snails and relatively few with high abundance (maximum = 109; variance-to-mean ratio = 44.4; Figure 2). Mean *Chaetogaster* abundance was greatest on snails infected by trematodes with passive transmission (mean = 22.2), intermediate on uninfected snails (mean = 14.8) and lowest on snails infected by trematodes with active transmission (mean = 10.4; Figure 2).

The relationship between the probability of infection by trematodes and *Chaetogaster* abundance depended strongly on trematode transmission mode (i.e. active vs. passive; $\beta_{\text{scaled}(\text{Chaetogaster})} \times$

Trematode group/taxa	Prevalence		
	<i>Helisoma</i>	<i>Physa</i>	Overall
Active transmission	0.053 (1,101)	0.050 (1,033)	0.103 (2,134)
Brevifurcate-apharyngeate ^a	0.001 (24)	0.002 (38)	0.003 (62)
<i>Clinostomum marginatum</i>	0.001 (13)	NA	0.001 (13)
<i>Echinostoma</i> spp.	0.023 (477)	0.043 (884)	0.065 (1,361)
<i>Ribeiroia ondatrae</i>	0.015 (310)	NA	0.015 (310)
<i>Strigea</i> spp.	0.011 (230)	0.005 (97)	0.016 (327)
<i>Zygocotyle lunata</i>	0.002 (47)	0.001 (14)	0.003 (61)
Passive transmission	0.013 (268)	0.005 (113)	0.018 (381)
Armatae ^a	0.007 (148)	0.001 (28)	0.008 (176)
<i>Haematoloechus</i> spp.	NA	0.003 (56)	0.003 (56)
<i>Halipegus</i> spp.	0.006 (120)	0.001 (29)	0.007 (149)
Overall	0.066 (11,288)	0.055 (9,471)	0.121 (20,759)

^aMorphotype.

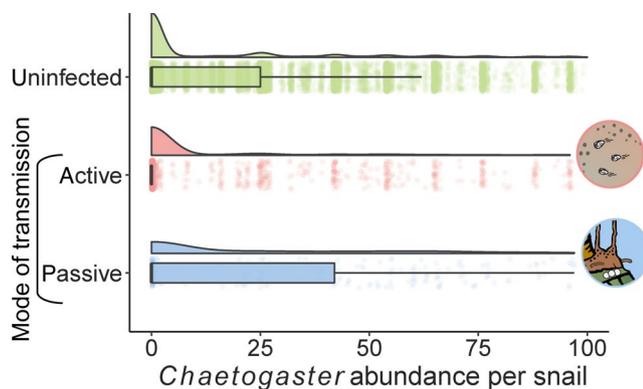


FIGURE 2 *Chaetogaster* abundance per snail was highly aggregated and varied with infection status. Raincloud plots depicting the distribution of *Chaetogaster* abundance among snails that were: uninfected (green), infected by trematodes with active transmission (pink) and infected by trematodes with passive invasion (blue). Boxplots depict median (zero for all), interquartile range (boxes) and full range of values (whiskers). Points depict individual observations (one point per snail) and have been jittered for visual clarity

$\beta_{\text{transPassive}} \pm SE = 0.50 \pm 0.05$; LRT: $\chi^2 = 86$, $p < 0.0001$). Snails harbouring more *Chaetogaster* were less likely to be infected by trematodes with active transmission ($\beta_{\text{scaled(Chaetogaster)}} \pm SE = -0.24 \pm 0.03$; $p < 0.0001$); for every increase of 1 standard deviation in *Chaetogaster* abundance (25.4 individuals), the odds of trematode infection decreased by 21% (Figure 3a,b). In contrast, per-snail *Chaetogaster* abundance and infection by passively transmitted trematodes were positively associated ($\beta_{\text{scaled(Chaetogaster)}} \pm SE = 0.26 \pm 0.04$; $p < 0.0001$); a 1 standard deviation increase in *Chaetogaster* abundance was associated with 30% greater odds of infection (Figure 3c,d). Overall, the probability of infection by trematodes was greater for larger snails

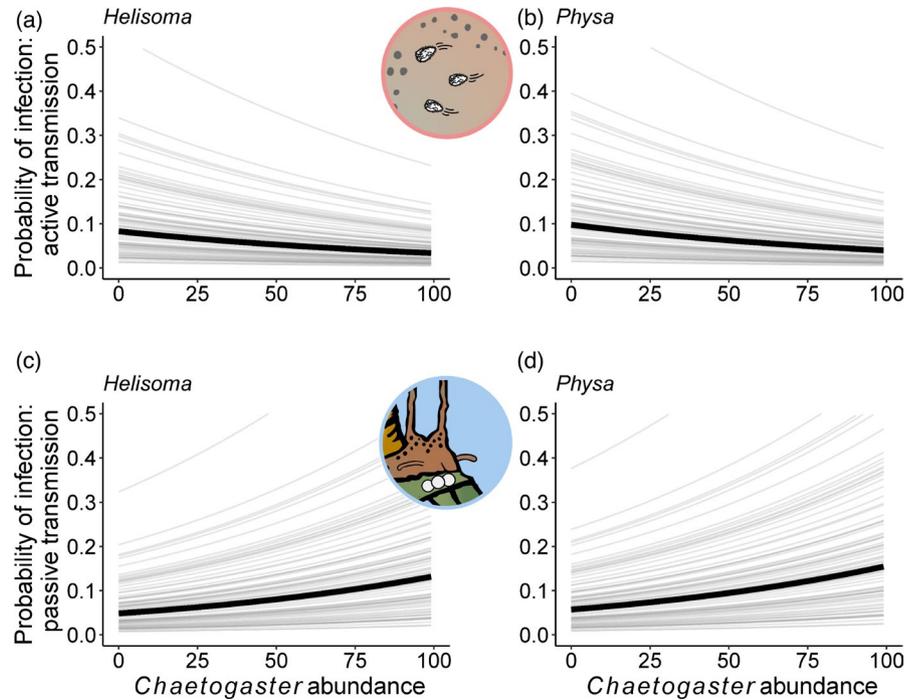
TABLE 1 Trematode infection prevalence varied widely among transmission modes, trematode taxa and snail host species. Column labelled 'Overall' contains the prevalence for all snails (*Helisoma* and *Physa*). Row labelled 'Overall' contains prevalence values across all trematode taxa. All values were rounded to the nearest thousandth. Sample sizes (n) are shown in parentheses after prevalence values. Cells with 'NA' represent incompatible host–parasite combinations (i.e. a given parasite cannot use a given host)

($\beta_{\text{scaled(size)}} \pm SE = 0.85 \pm 0.02$; LRT: $\chi^2 = 1,384$, $p < 0.0001$), collection events conducted later in the year ($\beta_{\text{scaled(doy)}} \pm SE = 0.15 \pm 0.04$; LRT: $\chi^2 = 11.4$, $p = 0.0007$) and for *Physa* snails relative to *Helisoma* snails ($\beta_{\text{snailPhysa}} \pm SE = 0.17 \pm 0.05$; LRT: $\chi^2 = 10.4$, $p = 0.001$). Among random intercepts included in the model, the term for trematode taxon was associated with the most variance (1.49), followed by site (0.83), collection event (0.08) and individual snail identity (4.2×10^{-9}). Collectively, these results reveal both negative and positive associations between *Chaetogaster* and trematodes, and indicate that the net observed outcome ('protective predation' vs. 'predator augmentation') varied with transmission mode.

4 | DISCUSSION

Predation on free-living stages of parasites is a widespread ecological interaction with multiple, potentially concurrent outcomes: consumption of free-living stages can inhibit parasite transmission ('protective predation') while also bolstering predator growth ('predator augmentation'; d'Alexis et al., 2009; Johnson et al., 2010; Lafferty et al., 2006; Mironova et al., 2020; Thielges et al., 2013). Yet, the ecological factors that mediate the outcomes of such interactions remain poorly understood. Using an extensive dataset of predator–parasite co-occurrence that spanned multiple sites, years, host species and parasite taxa, we show that infection by trematodes was strongly linked to the abundance of predatory *Chaetogaster* worms, but that the direction of this relationship varied with parasite transmission mode. Specifically, greater *Chaetogaster* abundance was associated with a lower probability of snail infection by trematodes with active transmission (Figure 3a,b), suggesting that predation of infectious agents by *Chaetogaster* reduced infection of snail hosts by trematodes relying on active transmission (i.e. via swimming miracidia). Conversely, *Chaetogaster* abundance was positively associated with the probability of infection by trematodes

FIGURE 3 The observed relationship between *Chaetogaster* abundance and trematode infection depends on transmission mode. A GLMM revealed that *Chaetogaster* abundance was negatively associated with infection by trematodes with active transmission (a and b), suggesting a protective effect. Conversely, *Chaetogaster* abundance and infection by trematodes with passive transmission were positively associated (c and d), suggesting predator augmentation. The mean probability of infection also varied between *Helisoma* (a and c) and *Physa* (b and d) snails. Black lines depict the overall fixed effect of *Chaetogaster* while grey lines depict site-level random effects



that relied on passive transmission (i.e. via ingestion of parasite eggs; Figure 3c,d). This suggests that while *Chaetogaster* are unlikely to affect the transmission of eggs into their snail hosts, they likely do consume and respond numerically to the trematode cercariae released from infected snails, as reported previously in laboratory studies (Fernandez et al., 1991; Hopkins et al., 2013). Our results thus highlight the consequences and dependencies of predation on free-living parasite stages and contribute to a growing body of evidence that such interactions hold significance for both predator ecology and parasitic infection.

Predation on infectious trematode stages can have important consequences, but quantifying the magnitude of 'protective predation' by *Chaetogaster* in natural systems is challenged by confounding interactions. Specifically, when analysing field patterns (as we did here), the observed associations between *Chaetogaster* abundance and trematode infection are the product of unobserved predation on infectious stages entering the snail (miracidia and eggs) and cercariae released from infected snails (Figure 1). Thus, if infectious stages evade *Chaetogaster* and successfully establish, then the numerical response of *Chaetogaster* to subsequently released cercariae may partially obscure their protective role. It follows that our estimate of *Chaetogaster* 'protective predation' against trematodes with active transmission is likely an underestimate. Conversely, because contact between *Chaetogaster* and trematode eggs is less likely, this confounding effect is weaker and we observed net predator augmentation. By demonstrating the importance of transmission mode in mediating the net outcome of *Chaetogaster*-trematode interactions, our research helps clarify and unite prior findings. Many findings have documented evidence that *Chaetogaster* can partially protect snails from trematode infections in both the laboratory (Michelson, 1964; Sankurathri & Holmes, 1976) and the field (Ibrahim, 2007; Rodgers et al., 2005). Yet, the absence of this pattern

in other *Chaetogaster*-snail-trematode systems has generated uncertainty about whether *Chaetogaster* predation is an important process for trematode infection more broadly (McKoy et al., 2011). McKoy et al. (2011) speculated that the association between *Chaetogaster* abundance and trematode infection may vary with transmission mode, and our study provides quantitative, large-scale insights into when *Chaetogaster* is expected to inhibit transmission of trematodes to snail hosts. Given the ubiquity of snail-trematode-*Chaetogaster* interactions in freshwater habitats (e.g. Ibrahim, 2007), such insights can help improve understanding of parasite and disease dynamics in a range of systems.

Understanding when and to what degree 'protective predation' can reduce trematode transmission to snails has implications for snail population biology; energy flow through food webs; and patterns of disease among humans, livestock and wildlife. Trematodes often occupy and consume the gonads of snails, thus castrating their hosts and eliminating the reproductive potential of infected snails (Esch & Fernandez, 1994). Thus, by helping to shape transmission risk and infection prevalence, *Chaetogaster* may affect snail population dynamics, particularly where baseline trematode infection rates are high (Brown et al., 1988). Because snails are important herbivores in aquatic systems (Rosemond et al., 1993), factors that alter trematode infection may also affect food web dynamics and productivity; such effects could manifest at both the individual scale (e.g. changes to snail behaviour) and the population scale (e.g. changes to snail population size; Morton & Silliman, 2019; Wood et al., 2007). The effects of limiting some trematode infections may extend beyond snails, which are typically just the first of several host taxa infected by trematodes. Downstream hosts—which can include humans, livestock and wildlife species of conservation concern—often suffer pathology and increased vulnerability to predation when infected by trematodes. Indeed, in this system, trematode-induced

mortality of amphibians (second intermediate hosts) can exceed 90% among populations (Wilber et al., 2020). Given that infection of second intermediate hosts (e.g. amphibians; Johnson et al., 2013) is tightly coupled to snail infection prevalence, reductions of infection among snails have potential consequences for a suite of host taxa. Moreover, reducing infection (and associated pathology) among intermediate hosts can affect transmission to the definitive hosts that serve as the source of eggs and miracidia that may ultimately infect snails (Lafferty & Morris, 1996). This suggests that cyclical dynamics could occur in which 'protective predation' generates local feedback cycles of decreasing infection and/or shifts in the relative abundance of parasite taxa with different transmission modes. Although such possibilities remain unexplored, the myriad consequences of 'protective predation' are potentially far-reaching.

Our results also reinforce the notion that parasites can be valuable food resources for predators and contribute to the growing recognition that life history helps shape the vulnerability of free-living stages to predation (Johnson et al., 2010). Previous work has shown that the consumption of free-living parasite stages can increase predator growth rates (Kagami et al., 2007) and even affect predator population dynamics (Hopkins et al., 2013); yet, detecting such outcomes in natural communities is challenged by factors that obscure numerical responses. The positive association between *Chaetogaster* abundance and infection by trematodes with passive transmission suggests that *Chaetogaster* consume and respond numerically to emerging trematode cercariae (free-living stages). This corresponds with a previous finding that *Chaetogaster* densities on snails infected by *Haliplus occidialis*—which uses passive transmission—were significantly greater than densities on uninfected snails (Fernandez et al., 1991). Yet, others have found that *Chaetogaster* populations increase dramatically in response to the cercariae of taxa with active transmission, such as *Echinostoma* spp. (Hopkins et al., 2013). In our observational study, potential numerical responses to *Echinostoma* spp. (and other taxa with active transmission) were numerically obscured by 'protective predation' on miracidia. Beyond the importance of transmission mode, a key future question is to understand how functional traits of emerging cercariae affect their consumption risk for *Chaetogaster*. Cercariae traits such as size, mobility and diurnal timing of activity can influence vulnerability to predation by odonate larvae (Orlofske et al., 2015) and estuarine fishes (Kaplan et al., 2009). Given that *Chaetogaster* specialize on snails, show numerical responses over short time windows and are poor dispersers among snails, this system offers an exciting opportunity to feasibly explore such questions in natural systems (Hopkins et al., 2015). For example, *Chaetogaster* have previously been found to consume cercariae across a range of mobility values and body sizes, but direct comparisons of trait-mediated predation rates have not been made (e.g. Fernandez et al., 1991; Hopkins et al., 2013). An examination of such interactions among a broad range of predators, parasites and life stages will be especially helpful in better understanding how parasites affect energy flow in food webs.

The breadth of the current study (which spanned multiple taxa, sites and ecological conditions) suggests that our results represent

a broad mean state of the system. Future experimental research may extend and validate our findings by examining dynamic interactions between *Chaetogaster* and trematodes in a controlled setting. Notably, our statistical modelling of infection probability implicitly assumed that *Chaetogaster* abundance at the time of dissection was proportional to abundance at the time of infection by trematodes. *Chaetogaster* could preferentially colonize infected snails to capitalize on the release of cercariae, although previous experiments suggest this is unlikely (Hopkins et al., 2015). Similarly, if trematode infection alters snail conspecific attraction (e.g. Friesen & Detwiler, 2021), dispersal of *Chaetogaster* among snails could further depend on trematode infection status. Even so, *Chaetogaster* populations are more likely to increase than decrease in the span between infection and dissection, owing to consumption of cercariae and other prey (Hopkins et al., 2013). Thus, if *Chaetogaster* imperfectly protects against infection by miracidia and numerically responds when infection does occur, 'protective predation' would likely be obscured in observational data. We nevertheless observed a significant negative correlation between *Chaetogaster* abundance and the probability of infection by trematodes that rely on miracidia for transmission. Using this finding as a starting point, future experiments could disentangle pre- and post-transmission dynamics of *Chaetogaster* populations, helping to further clarify the degree to which *Chaetogaster* can affect infection probability among snails. Such trials, by including multiple parasite taxa, could also conduct a detailed and controlled examination of how cercariae traits shape vulnerability and profitability to *Chaetogaster*. Our findings, based on robust observational data, thus provide motivation and groundwork for several avenues of future research that may offer insights relevant to a range of ecologically, economically and medically important systems.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

B.K.H. and P.T.J.J. designed the study with critical contributions from all authors; T.M.-G. and W.E.M. collected the data; B.K.H. analysed

the data with input from all authors; B.K.H. wrote the manuscript; all authors provided feedback on the manuscript and approved its final form for publication.

DATA AVAILABILITY STATEMENT

Data available from Figshare https://figshare.com/articles/dataset/Hobart_et_al_JAnE_csv/15067254 (Hobart et al., 2021)

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