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The effect of mermithid parasitism on predation of nymphal *Baetis bicaudatus* (Ephemeroptera) by invertebrates

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Abstract We investigated how infection by the mermithid nematode *Gasteromermis* sp. affected predation on its nymphal mayfly host, *Baetis bicaudatus*, by two invertebrate predators – the stonefly nymphs of *Kogotus modestus* and the caddisfly larvae of *Rhyacophila hyalinata*. Predation trials and behavioral observations were conducted in stream-side, flow-through experimental chambers. When parasitized and unparasitized prey were offered in equal numbers, *K. modestus* consumed significantly more parasitized than unparasitized nymphs. *R. hyalinata* consumed equal numbers of both prey types. Behavioral observations of foraging *K. modestus* on parasitized and unparasitized prey suggested that the increased consumption of parasitized nymphs was due to differences in the behavior of infected mayflies in response to the predator. Specifically, parasitized nymphs drifted less often to escape an approaching predator (non-contact encounters) compared to unparasitized nymphs, which increased the number of contact encounters and attacks that occurred between *K. modestus* and parasitized prey. Because all hosts are castrated, these behavioral alterations affect only the fitness of the parasite, which is killed along with its host by invertebrate predation. We present a number of hypotheses to explain why the parasite causes increased predation on its host. These include the large size of the parasite affecting the sensory abilities of the host, the larger energetic costs of escape behavior for parasitized individuals, and natural selection from fish predation against drifting behavior by parasitized individuals.

Key words Predation · Parasitism · Mayfly · Behavioral alterations · Mermithid

Introduction

Invertebrate predators are important components of many aquatic communities (Zaret 1980; Sih et al. 1985). These predators may have direct (consumption of prey items), sub-lethal (alterations in prey behavior, reduction in prey fecundity) and indirect (on other, non-prey species) effects on their prey (e.g., Kerfoot and Sih 1987; Cooper et al. 1990; Lancaster 1990; Huang and Sih 1991; Werner 1991; Peckarsky et al. 1993; Sih and Wooster 1994; Kerans et al. 1995).

A factor that has largely been overlooked in the analysis of predator-prey interactions in stream communities is the observation that many prey species harbor parasites (Aho and Kennedy 1987; Cummins and Wilzbach 1988; Söderström and Johansson 1988; Pritchard and Zloty 1995; Vance and Peckarsky 1996). In addition to causing host mortality directly (Cummins and Wilzbach 1988; Vance and Peckarsky 1996), parasites can drastically alter the behavior and escape responses of their host (Moore and Gotelli 1990; Horton and Moore 1993), and can therefore have significant impacts on predator-prey relationships between the host and its potential predators (Bethel and Holmes 1977; Webber et al. 1987; Benton and Pritchard 1990).

In this study we report the effects of parasitism by a mermithid nematode *Gasteromermis* sp. (Nematoda: Mermithidae) on predation of its mayfly nymphal host, *Baetis bicaudatus* (Ephemeroptera: Baetidae) by two co-occurring invertebrate predators *Rhyacophila hyalinata* (Trichoptera: Rhyacophilidae) and *Kogotus modestus* (Plecoptera: Perlodidae). While *B. bicaudatus* mayflies are reproductively dead once infected, the fitness consequences of interactions between predators and the host are of great significance to the parasite. We first present the results of predation trials conducted with each predator to investigate different predator-induced mortality rates on parasitized versus unparasitized prey; and, second, we present the results of experiments investi-

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gating the behavioral mechanisms underlying the observed differences in predator-induced mortality.

Study site and populations

B. bicaudatus, *K. modestus* and *R. hyalinata* were collected from the East River and its tributary, Copper Creek, both high elevation streams flowing through the Rocky Mountain Biological Laboratory, Gunnison County, Colorado where all three species are abundant. The mayfly nymphs graze periphyton off the rocks in the stream (Cowan and Peckarsky 1994), and both *K. modestus* and *R. hyalinata* are active predators on a variety of invertebrates including *B. bicaudatus* (Peckarsky 1985; Muotka 1993; Sangpradub and Giller 1994). Parasitic infection by a mermithid nematode in the genus *Gasteromermis* occurs in this region with a prevalence ranging from 2 to 80% in late instar hosts (Vance and Peckarsky 1996). Early instar nymphs are infected by free-living juvenile parasites. Parasites develop in the haemocol of the mayfly resulting in complete castration and later death of the adult host (Vance 1996). Mermithids require a single mayfly host individual to complete parasitic development and do not survive consumption by invertebrate predators (Ignoffo et al. 1973).

Predation trials

Methods

Experiments were carried out in August 1993 and 1994 using 15-cm-diameter cylindrical plexiglass flow-through chambers housed under ambient conditions in a streamside weatherport and fed by filtered stream water (see Peckarsky and Cowan 1991 for further details). The chambers (80 in all) were provisioned with a layer of coarse gravel and six small stones collected from the river. Flow rates were maintained at 15–20 cm/s and water depth was 12–14 cm.

Individual predators (either *K. modestus* or *R. hyalinata*, $n = 30$ for each) were added to chambers and left to acclimatize overnight (12 h) without prey. Each chamber received either a *K. modestus* or a *R. hyalinata* allocated randomly. Six unparasitized and six parasitized stage II or III mayfly nymphs were added to each chamber. *B. bicaudatus* were determined to be parasitized or unparasitized by inspecting individual live nymphs under a field dissecting microscope and looking for the nematode through the semi-transparent ventral cuticle of the abdomen. Detection was 98% accurate (determined from previous dissections – Vance 1996). Survival from this inspection technique was high (96%) and all nymphs were maintained for at least 12 hours under ambient conditions before being used in the experiments. After addition of prey the chambers were left undisturbed for 36 hours. At the end of this time, remaining live prey

were preserved in 70% alcohol for dissection to determine if they were parasitized or unparasitized. From these data the number of parasitized nymphs minus the number of unparasitized nymphs (NP–NU) killed by each individual predator was calculated.

Results

Overall the number of *B. bicaudatus* eaten (parasitized and unparasitized combined) was significantly greater for *R. hyalinata* (mean = 6.7, SE = 0.35, $n = 30$) than for *K. modestus* (mean = 4.2, SE = 0.37, $n = 30$), (Fig. 1a; unpaired two-tailed t -test of the number of prey eaten by *K. modestus* versus *R. hyalinata*, $t_{58} = -5.00$, $P = 0.0001$). Predators of neither species consumed either all prey or no prey items in a trial.

Under the null hypothesis that neither predator consumed or killed a different number of parasitized (NP) versus unparasitized (NU) nymphs, the mean value of NP–NU would be zero. For each predator species, therefore, the actual values of NP–NU were tested against a population mean of zero using a two-tailed one group t -test. Predation by *K. modestus* showed a significant bias towards eating more parasitized than unparasitized nymphs (Fig. 1b, one group, two-tailed t -test of

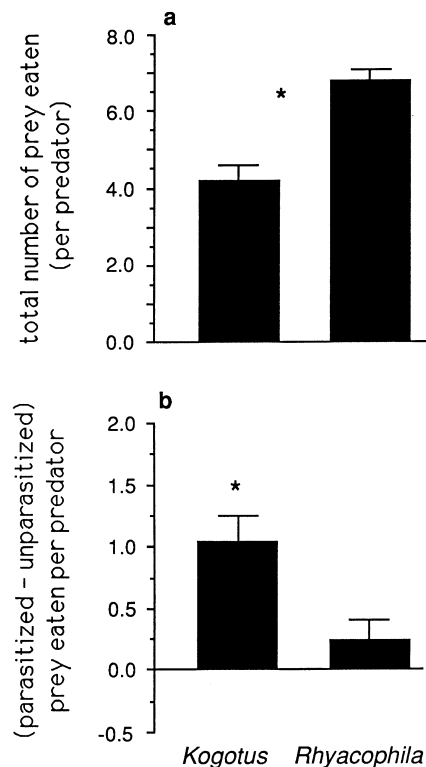


Fig. 1 Predation by *Kogotus modestus* and *Rhyacophila hyalinata* on parasitized and unparasitized *B. bicaudatus* nymphs. **a** Predation rate (total mayfly nymphs eaten during 36 h) shown as mean + SE, $P < 0.05$ indicated by *; $n = 30$. **b** NP–NU (number of parasitized – number of unparasitized nymphs eaten) shown as mean + SE. NP–NU significantly greater than zero are indicated by *; $n = 30$

NP–NU versus zero, $t_{29} = 3.43$, $P = 0.0018$). For *R. hyalinata* there was no significant difference from zero suggesting that they consume parasitized and unparasitized nymphs at the same incidence (Fig. 1b; one group, two-tailed t -test of NP–NU versus zero, $t_{29} = 1.366$, $P = 0.1823$).

Behavioral observations

Methods

Based on the results of the first experiment, we conducted behavioral observations to record the details of predatory encounters between *K. modestus* and both parasitized and unparasitized *B. bicaudatus* nymphs. These trials enabled us to determine why more parasitized individuals were killed by the stonefly predator.

Eighty chambers were set up as described above with a single stonefly in each and left with no prey for 12 h. Twelve *B. bicaudatus* nymphs (the 12 were either all unparasitized or all parasitized) were allocated randomly to each chamber, and after 10 min acclimatization time the behavior of the foraging stonefly was recorded for 10 min in the early morning. For half of the stoneflies (20 with parasitized prey, 20 with unparasitized prey) we recorded the number of contact encounters that occurred between the stonefly and its prey; for the other 40 chambers (20 with parasitized prey, 20 with unparasitized prey) we recorded the number of non-contact encounters that occurred between the stonefly and its prey. Contact encounters are defined as physical contact between the predator and prey (Peckarsky 1987). These usually involve lunges by the stonefly towards the mayfly. Non-contact encounters occur when the foraging stonefly comes within 2 cm of the prey. No physical contact occurs between the two, but the mayfly is able to hydrodynamically detect the presence of the predator and respond to its approach (Peckarsky et al. 1994; Peckarsky and Penton 1989b). From these data we calculated the frequency and type of encounters that were occurring between stoneflies and parasitized versus unparasitized prey.

A second observer simultaneously recorded whether mayflies drifted in response to each type of encounter with the predator. For each stonefly we used these response data to calculate the proportion of encounters during the 10-min observation that resulted in the mayfly drifting ($n = 80$ stoneflies). From these data we calculated the proportion of contact and non-contact encounters that resulted in mayfly drift for unparasitized versus parasitized mayfly nymphs ($n = 20$ stoneflies for each). Prey items were not used in more than one trial.

Results

The number of non-contact encounters that occurred between stoneflies and parasitized (mean = 18.85,

SE = 1.14, $n = 20$) versus unparasitized nymphs (mean = 19.4, SE = 1.52, $n = 20$) was not statistically different (Fig. 2a), but the number of contact encounters that occurred between stoneflies and parasitized nymphs (mean = 28.75, SE = 1.41, $n = 20$) was much higher than the number that occurred between stoneflies and unparasitized nymphs (mean = 20.1, SE = 1.20, $n = 20$), (Fig. 2a). A two-way ANOVA (infection \times encounter type) of the number of encounters per observation showed a significant effect of encounter type ($F_{1,76} = 14.7$, $P = 0.0003$), a significant effect of infection ($F_{1,76} = 8.6$, $P = 0.0045$) and a significant interaction effect ($F_{1,76} = 11.1$, $P = 0.0013$). The significant interaction term indicates that the effect of infection was only observed for contact encounters.

The frequency of drift responses to contact versus non-contact encounters with a stonefly showed a pronounced difference for both unparasitized and parasitized mayfly nymphs (Fig. 2b). Regardless of parasitized state, nymphs drifted more frequently to contact than non-contact encounters. Parasitized nymphs drifted as frequently to contact encounters as their unparasitized counterparts (parasitized mean = 0.98, SE = 0.008, $n = 20$; unparasitized mean = 0.98, SE = 0.007, $n = 20$), but showed a significant reduction in their drift fre-

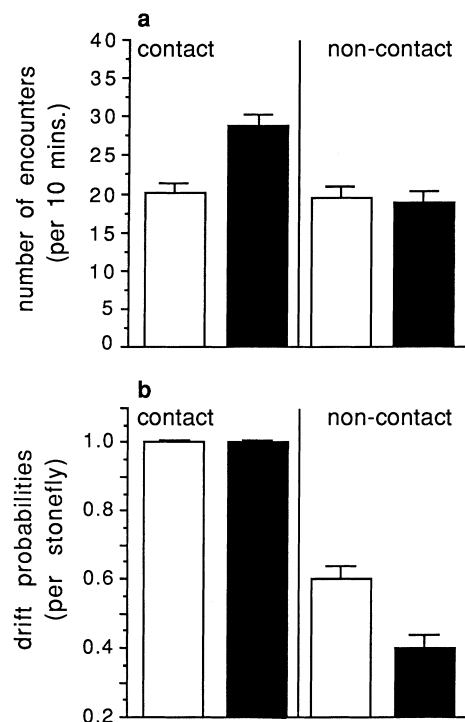


Fig. 2 Encounters between *K. modestus* and either parasitized (filled bars) or unparasitized (open bars) *Baetis bicaudatus*. **a** Frequency of contact and non-contact encounters (per 10 min) shown as mean + SE. ANOVA, $P < 0.05$ for effect of encounter, effect of infection and interaction effect; $n = 20$ **b** Proportion of drift responses (per stonefly) of mayflies (either parasitized or unparasitized) to contact and non-contact encounters shown as mean + SE. ANOVA, $P < 0.05$ for effect of encounter, effect of infection and interaction effect; $n = 20$

quency to non-contact encounters (parasitized mean = 0.36, SE = 0.04, $n = 20$; unparasitized mean = 0.61, SE = 0.04, $n = 20$). A two-way ANOVA (infection \times encounter type) of the arcsin $\sqrt{\text{proportion of drift responses per stonefly}}$ transformed data showed a significant effect of encounter type ($F_{1,76} = 454.3$, $P = 0.0001$), a significant effect of infection ($F_{1,76} = 17.2$, $P = 0.0001$) and a significant interaction effect ($F_{1,76} = 13.8$, $P = 0.0004$). The significant interaction term indicates that this effect of infection was only observed for non-contact encounters.

We observed several stonefly nymphs ($n = 6$) catching and eating parasitized mayfly nymphs. In all of these cases the stonefly extracted the parasite from its host and ate it separately. The parasites did not survive passage through mouth parts and were often ripped and bitten into pieces.

Discussion

Parasites that increase the predation risk of their hosts are commonly observed (Moore and Gotelli 1990), but few studies have incorporated more than one predator in their analysis (Bethel and Holmes 1977; Webber et al. 1987). By comparing the effects of different predators (if this is relevant to the system under study), a more complete assessment of predation on infected versus uninfected prey can be made. In this study predation by only one of two invertebrate predators, the stonefly *K. modestus* was biased towards parasitized versus unparasitized *B. bicaudatus* nymphs. In contrast, the caddisfly predator *R. hyalinata* killed both parasitized and unparasitized *B. bicaudatus* nymphs at the same frequency. Predation by caddisfly larvae on parasitized hosts has not, to our knowledge, been previously reported. However, Benton and Pritchard (1990) reported an increase in stonefly predation on infected *Ameletus* mayfly nymphs, but the underlying mechanisms involved were very different from those observed in this study (see discussion below). The observed differences in predation pressure on parasitized mayfly nymphs between the two predators may be explained by examining their different prey capture behaviors.

The predator-prey relationship between *K. modestus* and its mayfly prey is a complex interplay of contact and non-contact encounters based on hydrodynamic and tactile cues perceptible to both the stonefly and the mayfly nymphs (Peckarsky 1987; Williams 1987; Peckarsky and Penton 1989a; Peckarsky and Wilcox 1989). Such a complex interaction allows many opportunities for differences in behavior of prey items to be translated into differences in mortality rates. In this study, parasitized nymphs were less responsive [drift rates reduced; cf. Benton and Pritchard (1990) who report increased activity rates] to non-contact encounters with foraging stoneflies. Drifting in response to these encounters carries some risk since stoneflies are attracted to the hydrodynamic signature of a swimming mayfly (Peck-

arsky and Wilcox 1989). If the mayfly can react soon enough, however, non-contact encounters can operate as an early warning system for the mayfly, giving them enough time to detect and drift out of the way of a foraging stonefly (Peckarsky 1987; Williams 1987; Peckarsky and Penton 1989b; Peckarsky et al. 1994). i.e. drifting in response to non-contact encounters is an effective means of escape; drifting in response to contact encounters is dangerous since it evokes attack.

A reduced drift frequency in response to these non-contact encounters, as shown by parasitized nymphs in this study, therefore appears to decrease the mayfly's ability to avoid stoneflies and hence increase the number of contact encounters that occur between the predator and prey (also found by Benton and Pritchard 1990). Since it is these contact encounters that result in capture of the prey (Peckarsky and Penton 1989b), we suggest that the decreased sensitivity of parasitized mayflies to approaching stoneflies leads to an increase in the number of contact encounters, which in turn increases their mortality rate from stonefly predation.

In contrast, the second invertebrate predator in this study, the caddis larva *R. hyalinata*, is an ambush predator (see also Otto 1993), and hence prey have no hydrodynamic early warning of its presence. Prey also have been shown to be unresponsive to the caddis larva's odor (Malmqvist 1992). Both parasitized and unparasitized nymphs responded to physical, direct contact encounters with stoneflies in the same way. Since direct contact is probably the only type of interaction between an ambush predator and its prey, we suggest that this explains the similar mortality rates of *R. hyalinata* on parasitized and unparasitized *B. bicaudatus* nymphs.

In a system where behavioral alterations in a parasitized host affect the predation rates on that host, the fitness consequences of those alterations are complex. An alteration could benefit, harm or have no impact on the parasite, on the host and also on the predator. In the system studied here, any alterations in behavior or predation rates have no fitness consequence to the infected host. All infected hosts are reproductively dead (castrated) due to the *Gasteromermis* infection (Vance and Peckarsky 1996); and the restrictive conditions necessary for kin selection and adaptive host suicide are not met in the system (McAllister and Roitberg 1987; Vance 1996). For the predator (either *K. modestus* or *R. hyalinata*) eating parasitized prey items also has no negative fitness impact and may even be beneficial. First, the parasite offers no threat to the predators health (Ignoffo et al. 1973) and, second, our data suggest that parasitized *B. bicaudatus* nymphs are an easier prey item to catch for *K. modestus*. In situations where the risk of transmission of the parasite from prey to predator are low (in this study they are non-existent), and prey capture is facilitated by parasites, predators may actually benefit from eating and specializing on parasitized prey (Lafferty 1992). Finally for the parasite in this system, being eaten by a predator is fatal for the parasite. *Gasteromermis* does not survive predation on its host by either *K. mod-*

estus or *R. hyalinata* or any other predator tested to date (Ignoffo et al. 1973). Any alterations that increase the mortality of its host (such as those observed in this study) will therefore be detrimental to the parasite's own survivorship.

If this interpretation of fitness consequences is correct, why does *Gasteromermis* alter the behavior of its host and hence decrease its own survivorship? Both the mermithid parasite in its host and unparasitized mayflies are faced with the same predators, and both benefit from the survival of the nymphs. One would predict there should be selection on the parasite to minimize its effect on host behavior. So why has the parasite evolved to alter the host behavior so that it is different from unparasitized nymphs? There are a number of interacting explanations that address possible differences in the selective forces operating on the parasite compared to the unparasitized nymphs.

First, mermithid nematodes are large parasites occupying much of the abdomen of their hosts (Gordon 1981; Vance and Peckarsky 1996). The presence of such a large parasite may interfere with the sensory mechanisms used by mayfly nymphs to detect stoneflies. Mayfly nymphs with their cerci experimentally removed show a similar increase in mortality rates from foraging stoneflies (Peckarsky and Penton 1989b) as seen in this study of parasitized nymphs. Second, infections by mermithid nematodes also exact a considerable nutritional drain on host nutrients (Schmidt and Platzer 1980; Gordon 1981; Womersley and Platzer 1982). Drifting in response to foraging stoneflies has significant sub-lethal impacts in terms of reduced feeding rates and fecundity (Peckarsky et al. 1993) that the developing parasite may be less able to accommodate than unparasitized nymphs.

Last, stoneflies are only one of the many potential predators that *B. bicaudatus* nymphs must avoid (including *R. hyalinata* in this study that shows no difference in consumption rates between parasitized and unparasitized nymphs). Vance 1996 suggests that while in the water column parasitized *B. bicaudatus* nymphs are more vulnerable to trout predation than unparasitized nymphs. It is therefore possible that this threat overrides the drift response of parasitized nymphs even when they are threatened with stonefly predation. Finally, the direct lethal effects of stonefly predation are low relative to the effects of fish in these systems (Kerans et al. 1995), so it is possible that for parasitized individuals (i.e., for the parasite itself) the benefits of reduced drift in response to a stonefly (decreased trout predation) outweigh the costs of increasing stonefly attacks.

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