Mermithid Nematode Infections and Drift in the Mayfly *Deleatidium* spp. (Ephemeroptera)

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ABSTRACT: Alterations in host phenotype induced by parasitic infection are often interpreted as either host or parasite adaptations, depending on which of the two appears to benefit. Mermithid nematodes typically castrate their insect hosts and, therefore, any change in host behavior has no further fitness consequences for the host; the adaptive value of the modified behavior must be assessed with respect to parasite fitness only. In a New Zealand stream, mermithid-infected nymphs of mayflies in the genus *Deleatidium* were disproportionately represented in drift samples compared with benthic samples, suggesting that infection by mermithids results in an increased tendency to drift. Drifting mayflies face a higher predation risk from trout, and the mermithid nematodes they harbor die if ingested by a fish. The change in mayfly behavior induced by mermithids thus appears to have negative fitness effects for the parasite, and one possible explanation for this phenomenon is that it is a nonadaptive, pathological side effect of infection.

Parasites of all kinds modify the phenotype of their hosts. For instance, insect hosts often display altered morphological, physiological, and behavioral traits after infection by parasites (see Hurd, 1990; Beckage, 1993; Horton and Moore, 1993). Because changes in host phenotype can affect the fitness of either host or parasite, they are subject to selection and would normally be expected to represent either an adaptive manipulation of the host by the parasite, or an adaptive response of the host against the parasite. Indeed, the great majority of published examples of parasite-induced changes in host phenotype have been interpreted as adaptations, usually parasite adaptations (Poulin, 1995, 1998). In this context, examples of changes in host phenotype that result in fitness losses for both host and parasite are interesting, especially when involving parasite taxa that include species capable of adaptively manipulating their host. Such counterexamples would suggest that adaptive explanations are not always applicable, and that disadvantageous pathological side effects can also exist.

Mermithid nematodes are common parasites of insects and other arthropods (Poinar, 1991). Typically, these worms develop in the hemocoel of their host until they reach adulthood; at this point, adult worms emerge from the host and live freely in water, where they lay eggs. Larvae hatched from these eggs will penetrate a new host and begin the cycle anew. If the host is mostly terrestrial, worms that are ready to emerge can induce marked ‘hydrophilia’ in their host and force them to return to water (e.g., Maeyama et al., 1994). If the host has an aquatic larval phase with only adult females returning to water to oviposit, as in mayflies, mermithid worms infecting male hosts can feminize them and induce them to adopt a female behavior and return to water (Wülker, 1964; Vance, 1996a). Mermithid nematodes are, therefore, capable of manipulating the phenotype of their hosts to their own advantage. Because parasitized insects are usually castrated by mermithids before the onset of these changes (Poinar, 1991; Pritchard and Zloty, 1994), the behavioral alterations have no further fitness consequences for the host. In addition to manipulating the behavior of their host to ensure their return to water, mermithids can also modify host behavior to reduce the risk of the host being consumed by a predator. For example, the parasite *Gasteromermis* sp. decreases the frequency of drifting in its stream-dwelling hosts, nymphs of the mayfly *Baetis bicaudatus* (Vance, 1996b). This reduces the mortality of the parasite via predation

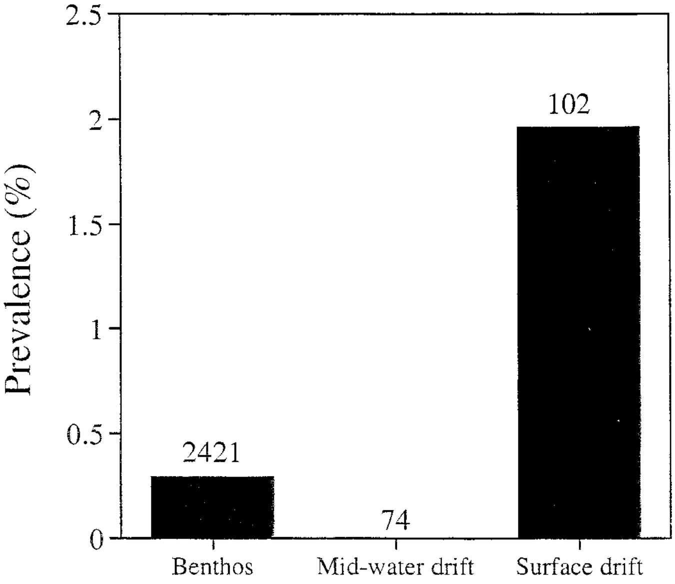

FIGURE 1. Prevalence of mermithid infections in mayfly nymphs *Deleatidium* spp. from benthic, mid-water drift, and surface drift samples taken in Sutton Stream. Numbers indicate sample sizes.

on mayflies by stream fishes such as salmonids, which feed mainly on drifting invertebrates. In the present study, the frequency of mermithid infections among nymphs of mayflies, *Deleatidium* spp., caught in the drift was compared with the frequency of infections in mayflies from benthic samples to test the hypothesis that mermithid nematodes reduce the probability of their host drifting. *Deleatidium* mayflies are among the most abundant and ubiquitous of New Zealand stream invertebrates, but identification of nymphs to species has proved almost impossible (Towns and Peters, 1996).

Samples were taken from Sutton Stream, a tributary of the Taieri River, South Island, New Zealand. The only fish found in this stream is the introduced brown trout *Salmo trutta* L., a visual predator that feeds mainly on drifting macroinvertebrates such as mayfly nymphs (Cadwallader, 1975; McLennan and MacMillan, 1984). Three sites were chosen for sampling, each with similar substrate, water velocities, and water depth (approx. 15 cm), and each separated by at least 30 m from the others. Drift samples were collected using 4 nets (9-cm opening diameter, 250-μm mesh) installed at each site; 2 nets were submerged in mid-water and 2 were positioned with half of the opening out of the water to collect near-surface drift. Sampling was carried out over 3 24-hr periods in February–March 1998. Drift samples were removed from the nets every 4 hr during these periods, after which the nets were cleaned and reinstalled. After this, a benthic sample was taken at each site, just downstream from the drift nets. This involved arbitrarily selecting 10 rocks of comparable sizes from a randomly chosen area, turning them over, and washing their surfaces into a 250 μm mesh net.

All drift and benthic samples were preserved in 100% ethanol and returned to the laboratory. During sorting of the stream invertebrates captured, all *Deleatidium* nymphs were counted and individually dissected under a microscope to detect the presence of mermithid nematodes. In the analysis that follows, all benthic, mid-water drift, and near-surface drift samples were pooled within each of these 3 categories rather than treated separately, because of the relatively low frequency of infections.

A total of 2,597 *Deleatidium* nymphs was collected and examined from Sutton Stream. Of these, only 9 (0.35%) were infected with an unidentified species of mermithid nematode. None of the mayflies caught in mid-water drift samples was infected, but the prevalence of infection in mayflies from the near-surface drift samples was more than 5 times greater than that in benthic mayflies (Fig. 1). The frequency of infection in mayflies from the near-surface drift samples was significantly greater than that among benthic mayflies (Fisher's exact test, $P = 0.0059$); this significant difference remained when all drifting mayflies (near-surface plus mid-water) were pooled and compared to benthic ones ($P = 0.0498$). In other words, mermithid-infected mayfly nymphs were disproportionately represented in the drift, particularly the near-surface drift.

Our results are in sharp contrast to those of Vance (1996b), who found that mermithid-infected nymphs of the mayfly *B. bicaudatus* from a stream in Colorado were less likely to drift than uninfected conspecifics. The reduction in the tendency to drift observed by Vance (1996b) was interpreted as an adaptive manipulation of host behavior by the parasite, aimed at reducing fish predation on both host and parasite. Interestingly, in the same system, Vance and Peckarsky (1997) found that parasite-mediated changes in mayfly behavior led to increased predation on the host by a benthic invertebrate predator, the nymph of the stonefly *Kogotus modestus.* By not escaping an approaching stonefly by drifting, a parasitized mayfly faced more attacks from these predators. A similar effect of mermithid infection of mayflies has been reported in a different system (Benton and Pritchard, 1990). Because predation by both fish and invertebrates results in the death of the parasite, the only situation in which a mermithid could benefit by decreasing the drifting tendency of its host would be if predation rates by fish are markedly higher than predation rates by benthic invertebrate predators. In our study system, where mermithids apparently increase the tendency of mayflies to drift, an adaptive explanation could be that predation by stoneflies and other invertebrates is more important than predation by trout, a phenomenon for which information is lacking. Perhaps, in contrast to North American streams where drift-feeding salmonids are native, brown trout in New Zealand have not been present long enough (less than a century) for invertebrate prey to be responsive to their threat. This seems unlikely, however, for two reasons. First, stream insects are known to evolve rapidly in response to introduced fish predators (Flecker, 1992). Second, *Deleatidium* shows a strong tendency toward nocturnal drift (less likely to be predated by fish) in a stream containing brown trout (Sutton Stream) or one containing the native fish *Galaxias eldoni* McDowall, as opposed to a neighboring fishless stream (Williams, 2000). Of course, observational studies like the present one cannot rule out all alternative explanations, and it is still possible that the increased propensity to drift in parasitized mayflies is of benefit to either host or parasite in certain situations.

Previous studies have reported parasite-induced increases in the tendency of stream invertebrates to drift, but only in host–parasite systems where the parasite can benefit. For instance, the acanthocephalan *Pomphorhynchus laevis* makes its amphipod host more likely to drift, but because this parasite must complete its development in the gut of trout or other drift-feeding fish, the behavioral alteration is clearly to its advantage (McCahon et al., 1991; Maynard et al., 1998). In the present system, however, the alteration in host behavior induced by the mermithid parasite has no fitness impact on the host, which is castrated by the parasite (Wülker, 1964; Poinar, 1991; Pritchard and Zloty, 1994), and apparently only negative consequences for the parasite.

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LITERATURE CITED

BECKAGE, N. E. 1993. Games parasites play: The dynamic roles of proteins and peptides in the relationship between parasite and host. *In* Parasites and pathogens of insects, Vol. 1, N. E. Beckage, S. N. Thompson, and B. A. Federici (eds.). Academic Press, New York, New York, p. 25–57.

BENTON, M. J., AND G. PRITCHARD. 1990. Mayfly locomotory responses to endoparasitic infection and predator presence: The effects on predator encounter rate. Freshwater Biology **23:** 363–371.

CADWALLADER, P. L. 1975. Feeding relationships of galaxiids, bullies, eels and trout in a New Zealand river. Australian Journal of Marine and Freshwater Research **26:** 299–316.

FLECKER, A. S. 1992. Fish predation and the evolution of invertebrate drift periodicity: Evidence from neotropical streams. Ecology **74:** 438–448.

HORTON, D. R., AND J. MOORE. 1993. Behavioral effects of parasites and pathogens in insect hosts. *In* Parasites and pathogens of insects, Vol. 1, N. E. Beckage, S. N. Thompson, and B. A. Federici (eds.). Academic Press, New York, New York, p. 107–124.

HURD, H. 1990. Physiological and behavioural interactions between parasites and invertebrate hosts. Advances in Parasitology **29:** 271–318.

MAEYAMA, T., M. TERAYAMA, AND T. MATSUMOTO. 1994. The abnormal behavior of *Colobopsis* sp. (Hymenoptera: Formicidae) parasitized by *Mermis* (Nematoda) in Papua New Guinea. Sociobiology **24:** 115–119.

MAYNARD, B. J., T. A. WELLNITZ, N. ZANINI, W. G. WRIGHT, AND B. S. DEZFULI. 1998. Parasite-altered behavior in a crustacean intermediate host: Field and laboratory studies. Journal of Parasitology **84:** 1102–1106.

MCCAHON, C. P., S. J. MAUND, AND M. J. POULTON. 1991. The effect of the acanthocephalan parasite (*Pomphorhynchus laevis*) on the drift of its intermediate host (*Gammarus pulex*). Freshwater Biology **25:** 507–513.

MCLENNAN, J. A., AND R. W. H. MACMILLAN. 1984. The food of rainbow and brown trout in the Mohaka and other rivers of Hawke's Bay, New Zealand. New Zealand Journal of Marine and Freshwater Research **18:** 143–158.

POINAR, G. O. 1991. Nematoda and Nematomorpha. *In* Ecology and classification of North American freshwater invertebrates, J. H. Thorp and A. P. Covich (eds.). Academic Press, New York, New York, p. 249–283.

POULIN, R. 1995. 'Adaptive' changes in the behaviour of parasitized animals: A critical review. International Journal for Parasitology **25:** 1371–1383.

———. 1998. Evolution and phylogeny of behavioural manipulation of insect hosts by parasites. Parasitology **116:** S3–S11.

PRITCHARD, G., AND J. ZLOTY. 1994. Life histories of two *Ameletus* mayflies (Ephemeroptera) in two mountain streams: The influence of temperature, body size, and parasitism. Journal of the North American Benthological Society **13:** 557–568.

TOWNS, D. R., AND W. L. PETERS. 1996. Fauna of New Zealand: No. 36 Leptophlebiidae (Insecta: Ephemeroptera). Manaaki Whenua Press, Lincoln, Canterbury, New Zealand.

VANCE, S. A. 1996a. Morphological and behavioural sex reversal in mermithid-infected mayflies. Proceedings of the Royal Society of London (B) **263:** 907–912.

———. 1996b. The effect of the mermithid parasite *Gasteromermis* sp. (Nematoda: Mermithidae) on the drift behaviour of its mayfly host, *Baetis bicaudatus* (Ephemeroptera: Baetidae): A trade-off between avoiding predators and locating food. Canadian Journal of Zoology **74:** 1907–1913.

———, AND B. L. PECKARSKY. 1997. The effect of mermithid parasitism on predation of nymphal *Baetis bicaudatus* (Ephemeroptera) by invertebrates. Oecologia **110:** 147–152.

WILLIAMS, J. K. 2000. Influence of abiotic and biotic factors on invertebrate drift. M.Sc. Thesis. University of Otago, Dunedin, New Zealand, 116 p.

WÜLKER, W. 1964. Parasite-induced changes of internal and external sex characters in insects. Experimental Parasitology **15:** 561–597.

J. Parasitol., 87(5), 2001, pp. 1227–1229