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MODIFICATION OF ANTIPREDATOR BEHAVIOR OF *CAECIDOTEA INTERMEDIUS* BY ITS PARASITE *ACANTHOCEPHALUS DIRUS*[1]

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Abstract. The isopod *Caecidotea intermedius* serves as the intermediate host for the acanthocephalan *Acanthocephalus dirus. C. intermedius* is preyed upon by the northern creek chub, *Semotilus atromaculatus,* which also serves as the definitive host for *A. dirus.* The effects of the parasite on the antipredator behavior of *C. intermedius* were examined. We tested the hypothesis that behavioral changes induced in *C. intermedius* by the parasite are by-products of increased energy demands induced by the parasite (i.e., increased hunger). Infected and uninfected *C. intermedius* were placed in a divided aquarium with 0, 1, or 2 creek chubs. Leaf discs provided both a food source and a refuge from the predator. In the presence of the creek chubs, uninfected *C. intermedius* avoided the predator, and were found more frequently in refugia as the number of creek chubs increased. However, infected *C. intermedius* were associated with the side of the aquarium containing the predator, and spent significantly more time out in the open away from the refuge regardless of the number of creek chubs. These data show that the antipredator behavior exhibited by *C. intermedius* is altered by *A. dirus,* and that such alterations are unlikely to be simply products of increased energy demands. Parasite-induced behavioral changes appear to increase *C. intermedius*' vulnerability to predation, thereby increasing the likelihood of *A. dirus* completing its life cycle. We find little evidence for greater foraging need as the mechanism indicating changes in antipredator behavior.

Key words: Acanthocephalus dirus; *antipredator behavior;* Caecidotea intermedius; *isopod; parasite–host relationship; parasite transmission;* Semotilus atromaculatus.

INTRODUCTION

For parasites that must pass through intermediate and definitive hosts, any effects of the parasite that increase rate of parasite transmission to the definitive host may be favored by natural selection. For example, if the parasite alters the intermediate host's behavior, morphology, or physiology so that the intermediate host is more vulnerable to predation by the definitive host, the parasite is more likely to complete its life cycle. Parasites may alter the phototaxis (Graham 1966, Holmes and Bethel 1972, Bethel and Holmes 1973, 1977, Moore 1983*b*), or humidity preference (Moore 1983*a, b*) of their intermediate host, increasing the degree of spatial overlap between the host and its predator (Holmes and Bethel 1972). Altered activity, such as increased movement (Moore 1983*b*) and erratic behaviors (Muzzall and Rabalais 1975, Camp and Huizinga 1979), or altered substrate preference (Hindsbo 1972, Moore 1983*a*) brought about by the parasite may cause the host to be more conspicuous to its predator (Holmes and Bethel 1972).

Traditionally, such behavioral modifications have been viewed as specific adaptations to increase transmission (Moore 1983*b,* but see Moore and Gotelli 1992). Alternatively, some of these behavioral modifications may instead be by-products of increased energy requirements in parasitized intermediate hosts (Milinski 1985, Godin and Sproul 1988). The developing parasite may increase host energy demand, forcing the intermediate host to tolerate greater risks of predation and to increase foraging movements, and this in turn may lead to increased risk of predation (Milinski 1985, Godin and Sproul 1988).

The purpose of this study was to test whether (1) the antipredator behaviors of the isopod *Caecidotea intermedius* are modified by its parasite *Acanthocephalus dirus*; (2) *C. intermedius* responds to quantitative differences in risk of predation; (3) such quantitative responses are eliminated or changed when parasitized; and (4) any parasite-induced behavioral changes are produced by simple increases in foraging due to increased energy demands, or are specific adaptations to increase likelihood of predation.

METHODS

Study animal

Caecidotea intermedius (formerly *Asellus intermedius*) serves as an intermediate host for the acanthocephalan *Acanthocephalus dirus. A. dirus* grows and develops from the egg stage through the acanthella stage, to the cystacanth stage, within the isopod (Camp and

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Huizinga 1980). Only the cystacanth stage is capable of infecting a definitive host if the isopod is eaten (Camp and Huizinga 1980). The creek chub, *Semotilus atromaculatus,* feeds readily on *C. intermedius* and serves as the definitive host for *A. dirus.* Previous studies have shown that infected *C. intermedius* are lighter in color (Seidenberg 1973, Oetinger 1977, Camp and Huizingna 1979) and are more active (Camp and Huizinga 1979) than uninfected *C. intermedius,* making them more conspicuous to predators. Camp and Huizinga (1979) observed that the number of infected *C. intermedius* eaten by *S. atromaculatus* was significantly greater than the number of uninfected *C. intermedius* regardless of substrate color.

C. intermedius and creek chubs were collected from Sugar Creek, Normal, Illinois. *C. intermedius* were maintained in plastic tubs with ≈6 L of aerated water and fed a diet of leaf litter. Leaf litter was collected from *Acer saccharum* and *Platanus occidentalis* and soaked in deionized water to allow for fungal colonization and removal of tannins. A proportion of these leaves were cut into 2 cm leaf disks to be used for the experiment, while the rest was used for colony maintenance. *C. intermedius* fed readily on this diet. Creek chubs were maintained in 39-L aquaria and fed a diet of commercial fish food.

Infected *C. intermedius* were easily distinguished from uninfected *C. intermedius* by their lighter color (Oetinger 1977, Camp and Huizinga 1979, 1980). All light-colored individuals contained at least one acanthocephalan in either the acanthella or cystacanth stages, whereas no dark individuals contained acanthocephalans. All *C. intermedius* used in the experiment were dissected after the experiment for verification of parasite stages.

Experimental design

The experimental chamber consisted of a 2-L aquarium, with the lower 15 mm of the aquarium partitioned from the upper portion by netting. One *C. intermedius* was placed in the lower portion in which it could move throughout the entire length of the aquarium. Twenty leaf disks were placed at each end to act as a refuge and food source for *C. intermedius.* The upper portion of the aquarium was divided into two equal compartments by an opaque glass plate. Creek chubs were placed in the upper portion of the aquarium in one of three treatments: (1) zero fish, (2) one fish randomly placed on either side, (3) two fish, one on each side. For statistical analysis, within the one-fish treatment, the side with the fish was designated side A, whereas the side without the fish was designated side B. For the zero- and two-fish treatments, one side was arbitrarily designated side A, whereas the other side was designated side B. The experiment was conducted in a windowless room under fluorescent lights (light : dark = 16:8, with 1.5 h dawn and dusk periods). Room temperature ranged from 22° to 27°C.

We tested for effects of fish treatments and parasitism on two types of behavior of *C. intermedius*: avoidance was determined by recording the choice of side (A vs. B) by *C. intermedius* in the aquarium. Hiding was determined by recording whether *C. intermedius* were under leaf litter (completely hidden), or partially or totally exposed.

Because there were no differences between sides A and B for zero- and two-fish treatments, *C. intermedius* had no choice between sides and therefore would be expected to be distributed at random between sides. In the one-fish treatment, *C. intermedius* could avoid the predator by choosing side B.

Twelve aquaria were run concurrently. Either a light or dark *C. intermedius* was placed in the bottom portion of each aquarium and an appropriate number of fish were added to the top portion. Trials were run for 16 h so that final observations of *C. intermedius* could be taken at the end of the dark phase. Individual *C. intermedius* were observed once, then dissected to determine parasite stage and number. A total of 256 uninfected and 89 infected *C. intermedius* were observed.

We tested for avoidance of fish using a maximum-likelihood contingency table analysis (SAS 1987, Procedure CATMOD), with treatment, parasitism, and interaction as effects. Because we were primarily interested in whether parasitism alters the effects of fish treatments on behavior of *C. intermedius,* we focused on the interaction effect. Contrasts were used to compare treatments in which *C. intermedius* had no choice (zero- and two-fish treatments) with treatments where *C. intermedius* had the choice of exposure to the predator on side A vs. no exposure on side B. Contrasts were performed separately on each level of parasitism in *C. intermedius,* at an overall $\alpha = .05$, using the Bonferroni method (Neter and Wasserman 1974). G tests were used to test for uniform distribution between sides for the choice or no-choice treatments.

We tested for hiding from fish using a similar maximum-likelihood contingency table analysis. As before, we focused on the interaction effect. This was followed by all possible pairwise comparisons between treatments within each level of parasitism (overall $\alpha = .05$).

Results

Avoidance

The parasite × treatment interaction was significant ($\chi^2 = 14.37$, df = 2, $P = .0008$), indicating that the effect of fish treatments on avoidance behavior of *C. intermedius* differed between infected vs. uninfected individuals. When given a choice, 63.33 ± 5.08% (mean ± 1 SE) of uninfected *C. intermedius* chose side B away from the fish (Fig. 1). This departed significantly from a uniform distribution of *C. intermedius* between sides A and B ($G = 6.48$, df = 1, $P < .25$). When no choice was provided (zero- and two-fish treatments), the distribution of uninfected *C. intermedius* could not be

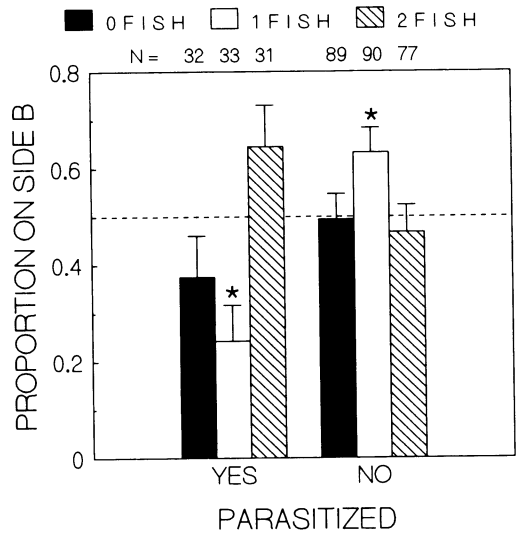

FIG. 1. Proportion of uninfected and infected *Caecidotea intermedius* (mean and 1 SE) on side B of the aquarium (fish absent, in trials with only one fish) for each treatment. *Proportion on side B in the one-fish treatment (choice) was significantly different from that in the zero- and two-fish treatments (no choice), and was significantly different from 50% (– – –); overall $\alpha = .05$.

distinguished from uniform ($G = 0.218$, df = 1, $P \gg .50$). The contrast between choice and no-choice treatments for uninfected *C. intermedius* distribution was significant ($\chi^2 = 5.38$, df = 1, $P = .02$).

When given a choice, only 24.24 ± 7.46% of the infected *C. intermedius* chose side B away from the fish (Fig. 1). This departed significantly from the null hypothesis of a uniform distribution of *C. intermedius* between sides A and B ($G = 9.193$, df = 1, $P < .005$). Thus, infected *C. intermedius* chose to be on the side with the fish. When no choice was provided (zero- and two-fish treatments) the distribution of infected *C. intermedius* could not be distinguished from uniform ($G = 0.0159$, df = 1, $P \gg .50$). The contrast between choice and no-choice treatments for infected *C. intermedius* was significant ($\chi^2 = 5.99$, df = 1, $P = .01$).

There were no significant parasite or treatment main effects on avoidance behavior of *C. intermedius*.

Hiding

The parasite × treatment interaction was significant ($\chi^2 = 7.01$, df = 2, $P = .03$), indicating that the effect of fish treatments on hiding behavior of *C. intermedius* differed between infected vs. uninfected individuals. The proportion of uninfected *C. intermedius* under cover differed significantly between treatments (Fig. 2). The proportion of uninfected *C. intermedius* under cover was significantly different between the zero- and two-fish treatments ($\chi^2 = 13.56$, df = 1, $P = .0002$). However, the proportion of infected *C. intermedius* under cover did not differ among treatments (Fig. 2).

The parasite effect was significant ($\chi^2 = 91.05$, df = 1, $P < .001$). Uninfected *C. intermedius* were under cover significantly more often than infected *C. intermedius* (Fig. 2). This implies that parasitized *C. intermedius* are less likely to be in a food source than unparasitized *C. intermedius*, and thus refutes the prediction of the energy-demand hypothesis. The treatment effect was also significant ($\chi^2 = 7.58$, df = 1, $P = .02$). *C. intermedius* were under cover significantly more often when two fish were present than when zero fish were present, though this latter effect was clearly due to the strong pattern shown by uninfected *C. intermedius* (Fig. 2).

DISCUSSION

The parasite *A. dirus* not only alters the general behavior of its host, *C. intermedius*, but more specifically alters two kinds of antipredator behaviors of *C. intermedius*. Because predation on the intermediate host is necessary for completion of the parasite's life cycle, and because these behavioral changes are not consistent with the alternative hypothesis of increased energy demand leading to increased foraging, this modification of antipredator behavior may be a direct adaptation on the part of the parasite to increase the likelihood of predation on the intermediate host. In particular, the change from avoidance of fish by uninfected *C. intermedius* to an attraction to fish in infected *C. intermedius* would cause a greater overlap of habitats between infected *C. intermedius* and creek chubs, leading to a higher capture rate by the predator (Holmes and Bethel 1972). *A. dirus* also causes *C. intermedius* to decrease its use of cover, leaving it more conspicuous to the predator. The physiological and behavioral mechanisms by which the parasite induces these changes and whether there is a heritable basis for

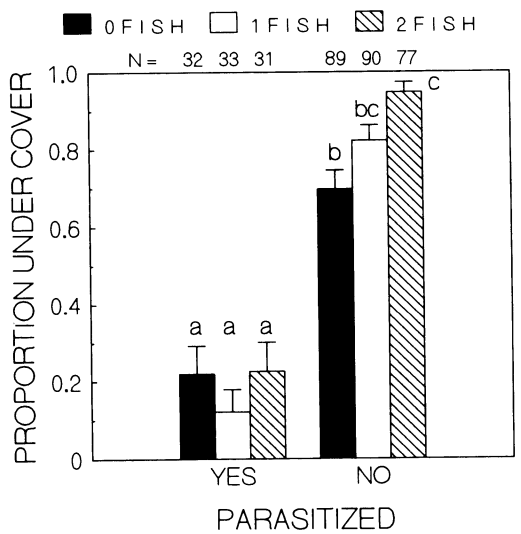

FIG. 2. Proportion of uninfected and infected *Caecidotea intermedius* (mean and 1 SE) under leaf cover for each treatment. Proportions marked by different letters are significantly different; overall $\alpha = .05$.

the ability to induce changes in host behavior are unknown. It seems likely that some kind of tactic or kinetic response by *C. intermedius* is the mechanism underlying avoidance. How *A. dirus* may change these responses is not known.

These behavioral changes appear to be unrelated to foraging needs. Infected *C. intermedius* were more likely to be found away from leaf disks, which were the only food available to isopods in the aquaria. If infected *C. intermedius* were food stressed, we would expect them to be on or in the leaf disks feeding. In very few cases were infected *C. intermedius* found on top of the leaf disks, but in more cases, were found moving across the netting separating the fish from *C. intermedius*. There was little evidence that *C. intermedius* fed on the leaf disks during the experiment. However, the experimental isopods were in the aquaria for only 16 h and were well fed prior to the experiment. Recent studies supporting the foraging need hypothesis have involved cestode parasites of sticklebacks (Milinski 1985, Godin and Sproul 1988), which can be very large, relative to the intermediate host. The results of this experiment on *A. dirus* and *C. intermedius* suggest that either different parasite taxa induce changes in host behavior in different ways, or that larger parasites are more likely to modify intermediate host behavior by increasing energy demand.

These behavioral changes are also inconsistent with nonspecific disruption of typical behaviors. Our study shows that normal avoidance of fish by *C. intermedius* is not simply eliminated but actually reversed by the parasite: infected *C. intermedius* appeared to be attracted to fish. Also, the overall tendency of *C. intermedius* to hide is reduced by *A. dirus* and the increased tendency to hide as the number of fish increases is eliminated.

The normal antipredator behavior of *C. intermedius* has its own complexity. Our results show that uninfected *C. intermedius* increase hiding as the number of potential predators increases. This suggests that *C. intermedius* can perceive quantitative differences in risk of predation and make corresponding quantitative adjustments in its behavior.

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