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ALTERED BEHAVIOR IN TWO SPECIES OF BLATTID COCKROACHES INFECTED WITH *MONILIFORMIS MONILIFORMIS* (ACANTHOCEPHALA)

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ABSTRACT: *Moniliformis moniliformis*-infected *Periplaneta australasiae* and *Blatta orientalis* were less active than uninfected controls in behavioral arena tests under both red and white light regimes. There was a strong interaction between light regime and parasitism for substrate use by *P. australasiae.* Under red light, parasitism decreased the use of black horizontal surfaces, whereas under white light, parasitism increased the use of black horizontal surfaces. In contrast, *B. orientalis* substrate use was unaffected by parasitism, although infected animals were less active than uninfected conspecifics under both light regimes. For both species, parasitism did not change the percentage of time spent in light, the freeze time, or the directional response to light.

Altered behavior is commonly observed in arthropods infected with acanthocephalans (Moore, 1984), and this has been shown to be true for a number of domiciliary cockroach pests infected with *Moniliformis moniliformis* cystacanths (Carmichael and Moore, 1991; Gotelli and Moore, 1992). When the cystacanth and its host are consumed by a rat, the acanthocephalan matures in the rodent small intestine, producing eggs that are shed along with feces. Roaches acquire the infection upon ingesting these shelled acanthors (Moore, 1946).

Altered behavior in intermediate hosts has been hypothesized to favor parasite transmission in at least some cases by increasing the likelihood of predation by definitive hosts (Moore, 1983). If this is true, then similar behavioral alterations might be expected among related intermediate hosts with similar ecological niches. We therefore compared the behaviors of *Periplaneta australasiae* and *Blatta orientalis* infected with *M. moniliformis* to those of uninfected conspecifics, using tests similar to those performed earlier on *Periplaneta americana* and *Periplaneta brunnea,* related species (Carmichael and Moore, 1991; Gotelli and Moore, 1992). All 4 species are blattine cockroaches and are pests in human domiciles.

MATERIALS AND METHODS

We used only male cockroaches in order to minimize potential behavioral variation often observed in female cockroaches (Lipton and Sutherland, 1970). These animals were exposed to eggs from stock that originated in wild rats from the Houston Zoological Gardens. Resulting cystacanths proved infective to laboratory rats, demonstrating the suitability of *P. australasiae* and *B. orientalis* as intermediate hosts (Freehling and Moore, 1993). Details of experimental maintenance and exposure methods were as described by Gotelli and Moore (1992). Our *B. orientalis* stock originated from cultures at the University of Florida and Fairleigh Dickinson University; *P. australasiae* came from cultures at Virginia Polytechnic Institute and State University.

A white arena under red light was used to examine phototaxis. Because cockroaches are thought to be largely insensitive to red light (Seelinger and Tobin, 1982), such illumination simulates darkness while allowing behavioral observation. A 5-cm-diameter inverted opaque cup was placed over a cockroach in the center of a 61-cm-diameter circular arena. After acclimation, a bright white light was turned on at 1 point along the arena perimeter and the cup was lifted. The time that elapsed between the cup movement and the first major movement of the animal was the freeze time; direction of movement was scored from 0 (toward the light) to 6 (away from the light), with 3 indicating a perpendicular movement.

Photophilia tests were done under white light in a black arena. A semicircular sheet of black Lexan was placed 15 cm above one half of the arena floor. We recorded roach location (light or dark side of the arena) at 15-sec intervals for 15 min. The response variable was the percentage of time each animal spent in the light.

Activity and substrate choice tests for each animal were conducted in separate experiments under both white and red light. Measurements were taken at 15-sec intervals for 15 min. To measure activity, insect location was recorded on a Cartesian coordinate grid (5-cm squares, white arena). The nearest horizontal square determined vertical location. These data yielded number of movements, distance travelled, and average velocity (cm/sec). For the activity study, animals that never moved were excluded from the analysis.

Substrate-choice tests were conducted in an arena in which one half the floor and adjacent walls were black, the other half, white. The fraction of time that each roach spent on each of the 4 possible color and orientation combinations (black vertical, white horizontal, etc.) were recorded.

Repeated measures analysis of variance was used for

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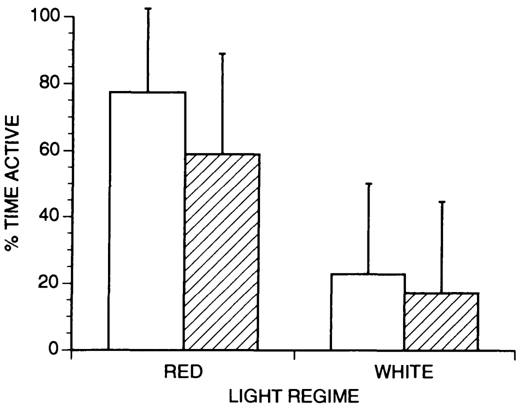

FIGURE 1. Effects of *Moniliformis moniliformis* parasitism on the percentage of time active of *Periplaneta australasiae.* Vertical lines are 1 SD. Light bar, unparasitized (control); shaded bar, parasitized.

each response variable. The between-subjects factor was parasitism and the within-subjects factor was light regime, because each animal was tested under both red and white light. Except where indicated, all reported F-ratios are for main effects. Each cockroach was subjected to each test; no more than 1 test per day was conducted on any given animal. Percentages were arcsine square-root-transformed before analysis, and distance and velocity data were logarithmically transformed to normalize the data. Untransformed data are presented in the figures to ease the interpretation.

RESULTS

Photic responses

Parasitism had no significant effect on photic responses. For both species, there was no difference between control and parasitized animals in the proportion of time an animal spent in the light (*P. australasiae* $F_{1,44} = 0.92$, $P = 0.3437$; *B. orientalis* $F_{1,34} = 2.59$, $P = 0.1169$), freeze time (*P. australasiae* $F_{1,41} = 0.05$, $P = 0.8315$; *B. orientalis* $F_{1,22} = 1.72$, $P = 0.2027$) or the direction of movement (*P. australasiae* $F_{1,40} = 1.45$, $P = 0.2356$; *B. orientalis* $F_{1,22} = 0.34$, $P = 0.5636$).

Activity

Periplaneta australasiae was more active under red light than under white light ($F_{1,25} = 26.36$, $P = 0.0001$). Parasitized animals tended to be less active than uninfected controls ($F_{1,25} = 3.26$, $P = 0.0830$; Fig. 1). Under white light, infected *P. australasiae* activity was negatively correlated with cystacanth number ($r = -0.545$, $P = 0.05$, n = 13). Results were similar for *B. orientalis* under white light: activity was reduced from red light levels ($F_{1,25} = 10.02$, $P = 0.0040$), and parasitized animals were significantly less active than uninfected conspecifics ($F_{1,25} = 4.87$, $P = 0.0367$), but this was not correlated with cystacanth number ($P > 0.50$).

For both species, neither velocity (*P. australasiae* $F_{1,25} = 0.08$, $P = 0.7750$; *B. orientalis* $F_{1,25} = 0.39$, $P = 0.5356$) nor travel distance (*P. australasiae* $F_{1,25} = 0.95$, $P = 0.3380$; *B. orientalis* $F_{1,25} = 1.80$, $P = 0.1915$) was affected by parasitism. Both species travelled less distance under white light than under red light (*P. australasiae* $F_{1,25} = 31.48$, $P = 0.0001$; *B. orientalis* $F_{1,25} = 21.77$, $P = 0.0001$). *Blatta orientalis* also moved at a lower velocity under white light than under red light ($F_{1,25} = 24.02$, $P = 0.0001$), as did *P. australasiae* ($F_{1,25} = 5.137$, $P = 0.0327$).

Substrate use

There was significant effect of parasitism or light regime on substrate use of *P. australasiae.* Under red light, control animals used black horizontal surfaces more than parasitized animals, whereas the pattern was reversed under white light (interaction $F_{1,41} = 8.50$, $P = 0.0057$; Fig. 2), a result that was not related to cystacanth number ($P > 0.50$). Both control and parasitized animals used white horizontal surfaces less under white light than under red light ($F_{1,41} = 23.52$, $P = 0.0001$).

In contrast, there was no effect of parasitism on substrate use by *B. orientalis* ($P > 0.1700$ for all 4 arena surfaces). Both control and parasitized animals used black horizontal surfaces less under white light than under red light ($F_{1,22} = 4.78$, $P = 0.0397$).

DISCUSSION

Moniliformis moniliformis infection affects both substrate use and activity of *P. australasiae.* Parasitized animals move less than controls, and there is an interaction between substrate choice and light regime; under red light, parasitism decreases use of black horizontal surfaces, whereas parasitism increases the use of this substrate under white light.

It is of interest to compare these results to altered behaviors that have been measured for *P. brunnea* and *P. americana,* 2 closely related species (Carmichael and Moore, 1991; Gotelli and Moore, 1992). Parasitism did not alter any measure of *P. brunnea* activity (Carmichael and Moore, 1991). In contrast, infected *P. americana* travelled less distance than did uninfected con-

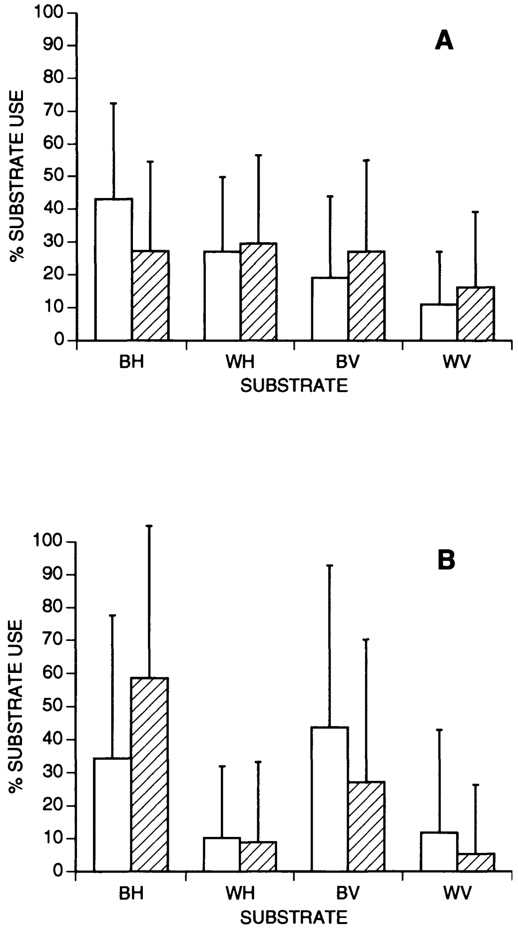

FIGURE 2. Effects of *Moniliformis moniliformis* parasitism on substrate use by *Periplaneta australasiae*. Vertical bars are 1 SD. BH, black horizontal; WH, white horizontal; BV, black vertical; WV, white vertical. Light bar, unparasitized (control); shaded bar, parasitized. A. Red light regime. B. White light regime.

specifics (Gotelli and Moore, 1992). Thus, for 2 of 3 species of *Periplaneta* studied, parasitism has resulted in a decrease in some measures of activity. These results stand in contrast to other studies of arthropod host behavior, which have frequently shown increases in host activity in response to acanthocephalan infections albeit under experimental conditions that differ from those reported here (see Moore and Gotelli [1990] for review).

Although *P. brunnea* decreased freeze time in response to *M. moniliformis* infection (Carmichael and Moore, 1991), neither *P. americana* nor *P. australasiae* changed any response to light as a result of infection (Gotelli and Moore, 1992). Positive responses to light are common, but not universal, among parasitized arthropods (Moore and Gotelli, 1990). In contrast, 3 *Periplaneta* congeners altered substrate and orientation preferences when parasitized, although in slightly different ways. The major change in infected *P. australasiae* was manifested in use of black horizontal surfaces, and this was strongly influenced, in fact, reversed, by light regime, with a decrease in use under red light. In comparison, both infected *P. brunnea* and *P. americana* increased use of white horizontal substrates under both light conditions. In contrast to *P. australasiae,* infected *P. americana* increased use of black horizontal surfaces under red light.

Our experiments revealed only reduced activity in parasitized *B. orientalis,* despite close phylogenetic (subfamilial) relationship to *Periplaneta* species. *Blatta orientalis* differs from *Periplaneta* species in several aspects that may affect its tendency to exhibit similar behavioral shifts. For instance, the absence of footpads limits the ability of *B. orientalis* to climb (Cornwell, 1968). In addition, although it is a domiciliary pest and found associated with human habitation much as *Periplaneta* species are, *B. orientalis* generally prefers cooler temperatures and may frequent unheated areas. These traits could constrain the ability of parasites to influence behaviors related to substrate orientation. Although representatives of the genus *Periplaneta* investigated thus far exhibit some coherence in behavioral responses to acanthocephalan parasitism (e.g., altered substrate choice), an evolutionary explanation of this phenomenon across a larger taxonomic group awaits further exploration.

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