MONILIFORMIS MONILIFORMIS INCREASES CRYPTIC BEHAVIORS IN THE COCKROACH *SUPELLA LONGIPALPA*

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ABSTRACT: We measured the behavioral responses of the domiciliary pest cockroach *Supella longipalpa* to infection by the archiacanthocephalan *Moniliformis moniliformis*. In black and white behavioral arenas, infected animals spent significantly less time on white horizontal surfaces than did controls. Use of black horizontal, black vertical, and white vertical surfaces was not affected by parasitism, although use of these surfaces was affected by white vs. red light. In a separate experiment, there was no effect of parasitism on the percentage of time animals were active, the total distance traveled, or the average velocity during time of travel. Activity and distance traveled by both control and parasitized animals were reduced sharply in white vs. red light.

In response to directed light (phototaxis), control and parasitized animals did not differ in the direction of movement. However, control animals were more likely to move in response to directional light (photokinesis) than were parasitized animals. Finally, when offered a choice of shade or light (photophilia), there was a tendency for parasitized animals to spend more time in shade than controls.

If *S. longipalpa* is a natural intermediate host, these cryptic behaviors are unlikely to increase the transmission of *M. moniliformis* through predation. This is the first report of an acanthocephalan infection that decreases host conspicuousness to visual predators.

The propensity of acanthocephalans for altering intermediate host behavior is well documented (Moore, 1984). Among these hosts, the American cockroach, *Periplaneta americana,* has been shown to increase activity and positive response to light when infected with *Moniliformis moniliformis* (Moore, 1983; Wilson and Edwards, 1986; Edwards, 1987). We report here the behavioral responses of the domiciliary brown-banded cockroach, *Supella longipalpa,* to parasitism by *M. moniliformis.*

Cochran (1982) reviewed the natural history of *S. longipalpa,* a small (10–14 mm) cockroach of African origin that is now cosmopolitan. In houses, it tends to be distributed more widely than some other domestic species, and it can use nutrients that are not limited simply to the kitchen (e.g., wallpaper paste). Although often considered a tropical or subtropical species, it colonizes dwellings readily; introduced in Florida early in the twentieth century, it had spread to 47 states by 1967.

Moniliformis moniliformis has not been reported from naturally infected *S. longipalpa,* but this may merely reflect lack of parasite surveys of this cockroach species. *Supella longipalpa* habitat is similar to that of *P. americana* and *Blattella germanica,* and *S. longipalpa* may well be exposed to *M. moniliformis* eggs in the same

way. In this study we compare the behavioral responses of infected and uninfected cockroaches. Our laboratory experiments tested for effects of parasitism on substrate orientation, color choices, open field activity, and photic responses.

MATERIALS AND METHODS

Infection and maintenance

Moniliformis moniliformis exhibits a typical acanthocephalan life cycle, involving a rat definitive host and a cockroach intermediate host. Development to infective cystacanth in the cockroach takes 7–8 wk (Moore, 1946; Olsen, 1974). According to Schmidt (1964), *Moniliformis* has been reported from naturally infected *P. americana.* To our knowledge, wild *S. longipalpa* has not been surveyed for acanthocephalans. We were able to infect a rat with cystacanths from *S. longipalpa* and recover mature worms, including gravid females, almost 10 wk later. This experiment confirms that *M. moniliformis* can successfully complete its life cycle with *S. longipalpa* as an intermediate host.

Supella stock was acquired from D. Cochran, Virginia Polytechnic Institute and State University, and was maintained in the laboratory (22 C, 50% RH, 12:12 LD photoperiod) in Plexiglas containers, provisioned with Agway rat chow and cotton-stoppered water vials. A total of 20–40 adult males was taken randomly from the stock culture and provided with only water for 5 days. They then were combined (disrupting any dominance hierarchies that might influence access to food), randomly assigned to parasitized and control treatments, and given applesauce; in the case of the infected treatment, this contained *M. moniliformis* eggs. Roaches then were maintained as before for 8 wk until infections matured.

Behavioral arenas

The polyurethane arenas were 30.5 cm deep and 61 cm in diameter, with the top 2–3 cm lubricated to

prevent escape. Observations were performed on in-
dividual cockroaches between 1 and 3 hr after scoto-
phase commencement; cockroaches are more active at
this time (Roberts, 1960; Barth, 1964). No cockroach
was tested more than once per day. Acclimation pe-
riods were 20 min (15 min for phototaxis). Sequential
observations were made every 15 sec for 15 min; each
roach furnished 60 observations per test. Arenas were
cleaned with a sponge and 10% ethanol between tests.
Parasite intensity was determined by dissection upon
completion of behavioral tests.

Substrate and activity tests were conducted under
red light (4 25-W red bulbs; 350 lux) and white light
(4 GE CHROMALINE full-spectrum bulbs; 700 lux).
Arenas were positioned so that shadows did not fall
on arena floors. The walls and floor of the substrate
arena were half black and half white, and we recorded
color (black/white) and orientation (horizontal/verti-
cal). The fraction of time on each of the 4 surfaces was
the response variable.

A grid of 5-cm squares was drawn on the floor of
the white activity arena. A pair of cartesian coordinates
was associated with each square and recorded for each
observation. In the case of animals on vertical surfaces,
the coordinates of the nearest grid square were record-
ed. These coordinate data were converted to total dis-
tance moved (cm), mean velocity (cm/sec) for those
observations that involved movement, and proportion
of observations that recorded a shift in location.

Photophilia tests (presence in light vs. shade) were
performed in a black arena under white light. One half
of the arena was covered by a black polyurethane sheet
15.2 cm above the arena floor; this height provided
shade but did not confound a preference for shade with
positive thigmotaxis.

Phototaxis measurements (movement towards light)
were conducted in a white arena. The animal was placed
in the center of the arena under an opaque, 5-cm (di-
ameter) cup with lubricated inside walls. The accli-
matization period was under red light except for the
last minute, when a white lightbulb on the upper edge
of the arena was lit. The cup was lifted rapidly at the
beginning of the test. Freeze time for each animal was
the time in seconds between the cup removal and an-
imal locomotion. Direction of movement is reflected
in a score for each animal ranging from 0 (movement
directly toward the light) to 6 (movement 180° away
from light). Animals that managed to climb the walls
of the cup or to fall on their backs were tested another
day.

Statistical tests

Our experiments were designed to evaluate the si-
multaneous effects of light and parasitism on cockroach
behavior. For each behavioral response variable, the
statistical design is a repeated measures analysis of
variance because each animal was tested separately
under red and white light. The within-subjects factor
is light (red or white), and the between-subjects factor
is parasitism (control or parasitized). This design takes
into account the fact that each animal was tested under
both red and white light.

To test for the effects of parasite intensity on behav-
ior, we calculated the correlation coefficient (Pearson's
r) between mature cystacanth number and behavioral

scores of parasitized animals. We used a chi-square
analysis to determine whether movement was affected
by parasitism in the phototaxis experiment.

Percentages were arc-sine square-root transformed
before analysis, and distance and velocity data were
logarithmically transformed to normalize the data. In
the figure and tables, means and standard deviations
are presented for untransformed data to ease the in-
terpretation.

RESULTS

Responses to substrate

Parasitized animals spent significantly less time
on white horizontal surfaces than did controls
($F_{1,48} = 11.31$; $P < 0.01$, Fig. 1). However, there
was no relationship between the intensity of the
infection (number of cystacanths) and the use of
white horizontal surfaces ($r = 0.06$, $P > 0.50$).
Parasitism had no effect on the use of black ver-
tical ($F_{1,48} = 0.31$; $P > 0.10$), white vertical ($F_{1,48}$
$= 1.17$; $P > 0.10$), or black horizontal ($F_{1,48} =$
0.35; $P > 0.10$) surfaces. Under both red and
white light, there was a tendency for parasitized
animals to spend more time on vertical surfaces
than controls did (Fig. 1).

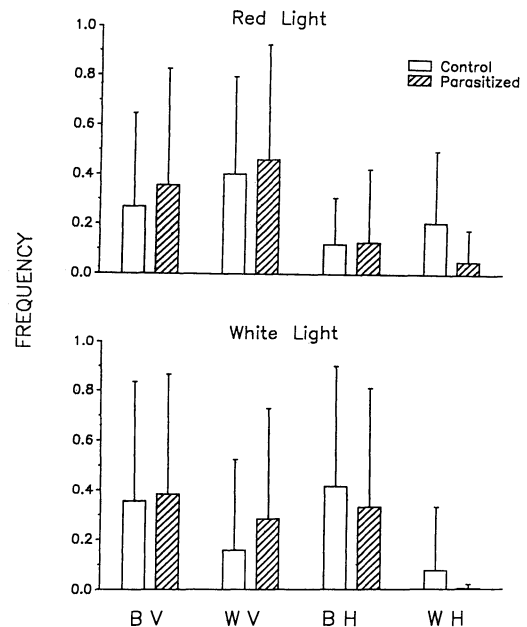Control animals under red light spent the most

FIGURE 1.   The frequency of substrate use by con-
trol and parasitized Supella longipalpa. BV, black ver-
tical; WV, white vertical; BH, black horizontal; WH,
white horizontal. Each bar is an average, and the ver-
tical line is 1 SD. Sample sizes are control = 26, par-
asitized = 24. Each animal was tested under red and
white light on separate days.

TABLE I. Distance traveled, percentage of time active, and average velocity for control and parasitized *Supella longipalpa* under red and white light. Standard deviations are given in parentheses, and sample sizes are given in brackets.

	% Time active	Distance traveled (cm)	Average velocity (cm/sec)
Control, red light	27.75	337.26	1.33
	(30.72) [27]	(381.11) [27]	(0.43) [19]
Parasitized, red light	36.94	435.10	1.35
	(30.93) [24]	(361.42) [24]	(0.53) [17]
Control, white light	4.77	58.31	1.22
	(13.64) [27]	(169.31) [27]	(0.62) [5]
Parasitized, white light	0.78	6.70	0.93
	(3.16) [24]	(27.8) [24]	(0.09) [2]

time on white vertical surfaces. Under white light, these animals spent the most time on black horizontal surfaces and showed a significant shift away from white horizontal surfaces ($F_{1,48} = 6.66$; $P < 0.05$). The use of black vertical surfaces was not affected by light or parasitism.

Activity measurements

There was no significant effect of parasitism on the percentage of time an animal was active ($F_{1,49} = 0.15$; $P > 0.10$), the total distance traveled ($F_{1,49} = 0.02$; $P > 0.10$), or the velocity during travel ($F_{1,5} = 0.09$; $P > 0.10$). Variances in these measures were large, and parasitism had inconsistent effects on activity under red and white light (Table I).

For uninfected animals, light had strong effects on the percentage of time active and the total distance traveled. These animals were significantly less active under red light than under white light (Table I). Average velocities during time of travel were somewhat lower under white light, although sample sizes were limited because so few animals were active under white light.

Responses to light

For animals that moved in response to a directed white light (phototaxis) there was no effect of parasitism on the direction of movement ($F_{1,19} = 0.31$, $P > 0.05$). However, parasitism affected the probability of movement. More of the control animals moved in response to light (14/27) than did the parasitized animals (6/26; $\chi^2 = 4.67$, $P < 0.05$).

There was also a marginally nonsignificant effect of parasitism ($F_{1,25} = 3.42$; $P = 0.07$) on the response to shade vs. light (photophila). Control animals spent more time under light ($\bar{x} = 34.0\%$) than did parasitized animals ($\bar{x} = 6.8\%$).

DISCUSSION

Under simulated daylight conditions, *S. longipalpa* is a remarkably quiescent animal. For instance, under white light, *S. longipalpa* is active less than 5% of the time (Table I). This inactivity may have important consequences for the extent to which *S. longipalpa* behavior may be modified by parasitism.

In the case of response to light, for example, freeze times exceeded 4 min for half of the control animals and three quarters of infected ones. These freeze times are substantially longer than those of any species examined to date (Moore, 1983; Carmichael and Moore, 1991; Gotelli and Moore, 1992). In *S. longipalpa,* parasitism does not alter the average freeze time; it does decrease the probability that animals will move when exposed to sudden light. This may not have ecological significance, however, because the majority of animals that moved in both treatments were stationary for at least 30 sec. Under these circumstances, parasitism is unlikely to affect predator–prey interactions, one possible selective basis for altered behaviors (Moore and Gotelli, 1990). In a similar fashion, parasite-induced photophobia exhibited by *S. longipalpa* is unlikely to increase the conspicuousness of the cockroach to a visual predator.

This shift toward cryptic behavior is seen also in the response of parasitized *S. longipalpa* to substrate color. Parasitized animals avoid white horizontal surfaces. They also tend to use vertical surfaces more when parasitized. These behaviors could present a 2-fold problem for potential predators: parasitized *S. longipalpa* may be more difficult to see and (on vertical surfaces) more difficult to catch.

Of course, we do not know for certain that *S. longipalpa* serves as a natural intermediate host for *M. moniliformis.* This is likely, however, given its overlap in habitat with other natural intermediate hosts. We also do not know which rodent species acquire *M. moniliformis* in this way. The altered behaviors would render *S. longipalpa* less noticeable to almost any visual predator, however, by decreasing contrast with substrate and decreasing time spent in lighted areas.

These results stand in stark contrast to responses of other cockroaches to *Moniliformis* infection. Comparisons with *B. germanica* are of particular interest because the German cockroach is similar to *S. longipalpa* in size and association with human dwellings. *Blattella ger-*

manica is 10–15 mm long, of African origin, and a successful colonist (Cochran, 1982). Uninfected *B. germanica* and *S. longipalpa* also exhibit similar substrate choices, especially in the time they spend on white horizontal surfaces (white light: 7% for each species; red light: approximately 10% and 20%, respectively).

Despite these similarities, *B. germanica* response to *M. moniliformis* parasitism is completely different from that of *S. longipalpa* (Gotelli and Moore, 1992). Parasitized German cockroaches increase use of white horizontal surfaces whereas parasitized brown-banded cockroaches avoid them, despite similar control responses. Parasitism does not affect light responses in German cockroaches whereas parasitized brown-banded cockroaches become more cryptic. Finally, parasitism decreases velocity and travel distance in *B. germanica* but has no effect on *S. longipalpa* activity (Gotelli and Moore, 1992; Table II).

In most cockroaches examined to date, *Moniliformis*-induced behaviors increase visual conspicuousness. Activity may be altered (Moore, 1983; Wilson and Edwards, 1986), and for 3 other species (*Periplaneta brunnea, P. americana,* and *B. germanica*), parasitized animals increase their use of white horizontal surfaces.

Acanthocephalan infections commonly enhance host conspicuousness in a variety of host–parasite associations and often are associated with demonstrably increased predation (Holmes and Bethel, 1972; Moore, 1984). Given the behavioral alterations we describe here, increased risk of predation seems to be unlikely in *S. longipalpa* infected with *Moniliformis,* even though *S. longipalpa* habitat easily could overlap with rat predators, as does the habitat of *P. americana* and *B. germanica.* In fact, we do not know the intermediate host that contributes most to *M. moniliformis* transmission in nature. The majority of laboratory work has been done with *P. americana,* in large part because it is easy to rear and manipulate. Other cockroaches that live near *Moniliformis* egg sources also may be candidates. Nonsignificant results must be interpreted cautiously because the large variance in the data (Table I) reduces the power of the statistical test (Toft and Shea, 1983). Nevertheless, if consistent effects of parasitism cannot be demonstrated in a controlled laboratory setting, they are unlikely to be important in the field.

Vector biologists have acknowledged that the behavioral attributes of a species may be as im-

TABLE II. Effect of *Moniliformis moniliformis* parasitism on the behavior of *Supella longipalpa* and *Blattella germanica.* Results from *B. germanica* are summarized from Gotelli and Moore (1992).

	S. longipalpa	*B. germanica*
Substrate choice	Avoid white horizontal	Increase use of black and white horizontal, decrease use of black vertical
Light responses	Avoid light, decrease probability of movement	No effect
Activity	No effect	Decrease velocity, distances

portant as susceptibility in the potential of that species to transmit disease. *Supella longipalpa* is highly susceptible to *M. moniliformis* infection; 93% of exposed cockroaches developed mature cystacanths. Yet our results suggest that *S. longipalpa* is unlikely to be important in *Moniliformis* transmission. Of course, this has yet to be tested in predation experiments, but given the nearly opposite responses of *S. longipalpa* and *B. germanica,* they are probably not encountering predators at the same rate.

There are examples of parasitoids inducing cryptic host behavior (Brodeur and McNeil, 1990), and these behaviors may promote parasitoid survivorship. The host moves to a protected place where the parasitoid can develop and emerge. This is the first report of an acanthocephalan infection that does not appear to increase intermediate host conspicuousness to predators and that induces crypticity instead. The ecological implications of such alterations remain to be investigated.

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