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Altered host behaviour in a cockroach–acanthocephalan association

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Abstract. The effects of parasitism by the acanthocephalan *Moniliformis moniliformis* on the behaviour of two ecologically similar intermediate cockroach host species (*Periplaneta americana* and *Blattella germanica*) were compared. Open field activity, substrate orientation, substrate colour choice, photophilia, phototaxis and photokinesis were measured for infected cockroaches and uninfected controls in a series of laboratory arena experiments. Parasitism had significant effects on activity and substrate use, but not on photic responses. Compared with control animals, parasitized animals of both species showed a decrease in travel velocity and distance, and an increase in the use of horizontal surfaces. Other behaviour patterns were also altered by parasitism, but the direction and magnitude of the alteration depended on species, sex and light regime. Similar responses of the two species to parasitism may reflect common selective pressures on the host–parasite interaction, including ecological similarities of the host species and shared predators. Interspecific differences in the response to parasitism may reflect phylogenetic differences, physiological limitations, or constraints due to body size differences.

Parasites often alter the behaviour of the hosts that they inhabit (Holmes & Bethel 1972; Moore & Gotelli 1990). These alterations include changes in response to humidity, substrate colour, light and alterations in levels of activity. Altered host behaviour often has important ecological consequences for the parasite and the host, and a variety of evolutionary scenarios have been proposed to account for it (Moore & Gotelli 1990).

Altered host behaviour may enhance parasite transmission by increasing host vulnerability to predation (Holmes & Bethel 1972). From the host's perspective, altered behaviour may be a form of host suicide that prevents parasite transmission to kin (Smith Trail 1980). Altered behaviour may also be an expression of a host-induced physiological fever, or other nutritional or physiological changes associated with parasitism (Beckage 1985; Lawrence 1986). Dawkins (1982) suggests that intermediate host behaviour is a 'shared phenotype', controlled by both parasite and host genes and that behavioural alterations are an evolutionary compromise between conflicting host and parasite strategies.

To date, most studies of altered host behaviour have focused on single host–parasite associations. As a consequence, a comparative perspective is somewhat lacking in this literature (but see Bethel & Holmes 1977; DeMont & Corkum 1982; Helluy 1983). Alternative hypotheses, such as phylogenetic or physiological constraints on host behaviour, can only be investigated by comparing the behaviour patterns of different host species infected with the same parasite (Moore & Gotelli 1990).

The association between acanthocephalans (thorny-headed worms) and their intermediate cockroach hosts is an ideal system for such a comparative study. Acanthocephalans often alter the behaviour of their intermediate hosts in ways that make them more vulnerable to predation by a definitive host (Moore 1984a). Furthermore, cockroaches exhibit a variety of complex behaviour, including escape responses (Camhi et al. 1978), activity patterns (Roberts 1960) and substrate orientation (Silverman & Bell 1979), that may affect their vulnerability to predation.

In this study, we compare the behaviour of two intermediate cockroach host species, *Periplaneta americana* and *Blattella germanica*, infected with the acanthocephalan *Moniliformis moniliformis*. *Periplaneta americana* is the intermediate host species most commonly used in laboratory studies of *M. moniliformis*. Other intermediate host species may also be used by *M. moniliformis* in the field,

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although there is almost no information on natural infection rates of different cockroach species. The definitive host of *M. moniliformis* is the Norway rat, *Rattus norvegicus*.

Periplaneta americana and *B. germanica* exhibit a number of ecological similarities that might suggest similarities of altered behaviour. Cochran (1982) summarizes the biology of these species. Both are highly successful invaders from tropical Africa that have achieved a nearly cosmopolitan distribution due to their close association with human dwellings. *Periplaneta americana* and *B. germanica* are generalist feeders. Both species prefer warm temperatures (20–30°C), although they are active and can survive over a large temperature range. *Blattella germanica* is probably more cold tolerant than *P. americana*, and its range appears to extend further northward.

In spite of these ecological similarities, *P. americana* and *B. germanica* differ greatly in body size, reproductive behaviour, and phylogeny. *Periplaneta americana* is a large-bodied (35–40 mm adult body length) Blattid roach. The adult lifespan averages 1 year or longer, and females hold unrotated ootheca for 24 h before depositing the egg case. In contrast, *B. germanica* is a small-bodied (10–15 mm adult body length) Blattellid roach. Adult lifespan is normally greater than 100 days, but may be much shorter under favourable conditions. Females rotate the ootheca 90° before deposition (Roth 1970). Although the age of the cockroach–acanthocephalan association is not known, *P. americana* is the more primitive of the two host species (McKittrick 1964; Roth 1970).

We chose to examine a number of host behaviour patterns that may affect the cockroach's conspicuousness and vulnerability to predation. These patterns of behaviour include open field activity time, travel velocity and distance, substrate orientation (horizontal, vertical) and substrate colour choice (black, white). We made observations under both red and white light, because cockroaches are relatively insensitive to the red portion of the visible spectrum (Seelinger & Tobin 1981). We also measured freeze time (photokinesis) and directional movement in response to a point light source (phototaxis), and the use of shaded versus lighted substrates (photophilia). These patterns of behaviour are all relevant to predator vulnerability, but they may also reflect other aspects of cockroach biology that can be affected by parasitism, including host metabolism and sexual behaviour.

MATERIALS AND METHODS

Life Cycle of *Moniliformis moniliformis*

Moniliformis moniliformis lives as an adult in the small intestine of the rat. Eggs pass out with the faeces. When the eggs are eaten by a cockroach, the larval acanthocephalan hatches and burrows into the haemocoel of the insect, where it develops into an infective stage called a cystacanth in 7–8 weeks. When a rat eats an infected cockroach, the life cycle is completed (Moore 1946; Olsen 1974).

Periplaneta americana is typically used as a laboratory intermediate host for *M. moniliformis*, and wild populations have been reported to harbour the infection (Schmidt 1964). Gonzalez & Mishra (1976, Table I) reported that a cystacanth had been recovered from naturally infected *B. germanica*, but the text of their paper indicated cystacanths from *P. americana* only. We successfully introduced cystacanths from *B. germanica* into rats and obtained gravid female worms. This experiment confirmed that *M. moniliformis* could complete its life cycle in both species of cockroaches.

Cockroach Populations

We maintained in the laboratory two stock populations each of *P. americana* and *B. germanica* in Plexiglas or metal containers measuring approximately 36 × 26 × 16·5 cm. We provided each population with Agway rat chow and water ad libitum in cotton-stoppered vials. Every 2–3 months, we culled stock populations at random to one-third or one-half of their size to prevent crowding. We maintained populations at room temperature (22°C) and relative humidity (50%) on a 12:12 h light:dark cycle. Animals for all experiments were drawn randomly from these populations. Only mature adults with all appendages intact were used. We did not control for differences in female reproductive cycles.

Acanthocephalan Populations

Eggs of *M. moniliformis* were obtained originally from rats collected at the Houston Zoo. To maintain the life cycle in the laboratory, we provided starved individuals of *P. americana* with apple sauce saturated with eggs of *M. moniliformis*. After feeding, the cockroaches were maintained with ad libitum food and water for 8 weeks, then dissected in physiological saline solution. Twenty-five mature cystacanths were fed to anaesthetized white rats.

Mature female worms were dissected, and eggs were washed, centrifuged, and stored in tap water at 5°C. We mixed acanthocephalan eggs derived from several different worms and rats to provide the experimental stock. Cockroaches used to maintain the acanthocephalan life cycle were never used in behavioural tests.

Experimental Infections

Unless otherwise stated, both species of cockroach were treated identically. We selected randomly a total of 20–40 cockroaches, provided them with water and starved them for 5 days. They were then assigned to the control or parasitized treatments. The parasite treatment group was given one teaspoonful of apple sauce containing the eggs of *M. moniliformis*. Control animals were also given apple sauce. We combined subgroups of animals at the time of exposure to disrupt any dominance hierarchies that might have interfered with feeding. We allowed both groups to feed until the apple sauce was consumed. After feeding, cockroaches were placed in individual half-pint labelled jars, provided with food and water ad libitum, and maintained for 8 weeks on a 12:12 h light:dark cycle until the infections matured.

Behavioural Arenas

Each experimental arena measured 61 cm in diameter × 30·5 cm deep. We coated the top 2–3 cm of each arena with petroleum jelly or fluon (an industrial lubricant) to discourage cockroach escapes. Cardboard arenas were used for testing substrate choice and activity of *B. germanica*. Sanded polypropylene arenas of the same dimensions were used to test substrate choice and activity of *P. americana* and light responses of both species. Substrate material did not appear to greatly alter individual cockroach behaviour, and we therefore concluded that the differences would not confound our comparisons.

For the substrate choice and open field activity tests, we observed each individual under white light and under red light. White light tests were conducted beneath a bank of four GE Chromaline full-spectrum bulbs (700 lx). Red light tests were conducted beneath four 25-W red light bulbs (350 lx). Cockroaches are relatively insensitive to short wave lengths (Mote & Black 1981), and these conditions mimic darkness. We positioned the arenas so that shadows did not fall on the arena floors.

Behavioural Tests

We carried out all behavioural tests on individual cockroaches. No animal was tested more than once per day, and no test score was taken more than once. We conducted tests between 1 and 3 h after the start of scotophase, because cockroaches are more active at this time (Roberts 1960; Barth 1964). We allowed individuals to acclimatize for 20 min before any behavioural observations were taken directly by an observer (15 min acclimatization in the phototaxis experiments). We chose an habituation time of 20 min for consistency with other laboratory studies of cockroach behaviour (e.g. Hawkins 1978). We noticed no consistent changes in behaviour during the course of the 15-min observation period, nor did we notice differences between animals sampled early and late in the test period. Between behavioural tests, we wiped the walls and floor of each arena with a sponge dampened with a 10% ethanol solution. After all observations, we dissected each cockroach and counted the numbers of immature acanthors and mature cystacanths. These tests were not conducted blind, because we wanted to ascertain that, whenever possible, both control and exposed animals were tested during the same week. Not all animals exposed to parasite eggs developed an infection; we could not assay the infection until the termination of the experiment (dissection), at which time we discarded data from exposed, uninfected animals. The behavioural tests were unambiguous (black or white, light or dark, etc.) and observer bias was unlikely.

Substrate Colour and Orientation Experiments

The floor and walls of the substrate choice arena were divided into a black and a white side. Adjacent vertical and horizontal surfaces were the same colour. We recorded substrate colour (white or black) and orientation (vertical or horizontal) every 15 s for 15 min. The response variable was the fraction of time an animal spent on each of the four surfaces.

Activity Experiments

The floor and walls of the activity arena were grey (26% reflectance, cardboard arenas) or white (polypropylene arenas). We superimposed a grid of 5-cm

squares on the floor of the arena. Each grid square was marked with a pair of Cartesian coordinates. After an animal had acclimatized, we recorded the Cartesian coordinates of its grid square every 15 s for 15 min. For animals on vertical surfaces, we recorded the coordinates of the closest horizontal grid square.

We converted coordinate data to three measures of activity: (1) total distance travelled in cm; (2) average velocity (cm/s) for consecutive observations during which an animal moved to a new grid square (this could be viewed as average burst speed); (3) the fraction of times that an animal moved to a new grid square during consecutive observations (activity time).

Light Experiments

To measure photophilia (presence in light versus shade), animals were tested in the black/white substrate choice arena. The arena was fitted with a black screen placed 15·2 cm above the black half of the arena. This height ensured that thigmotactic responses to a narrow crevice space were not confounded with the response to light. Although the exposure to light was confounded with substrate colour in this experiment, we were not able to generate enough contrast using a uniformly coloured background. The test was conducted in white light and the response variable was the fraction of time each animal spent in the light. We recorded observations every 15 s for 15 min.

To measure photokinesis (movement in response to light) and phototaxis (movement towards light), we placed each animal in the centre of a white arena beneath an inverted, opaque plastic cup. The outside walls of the cup were covered with black tape and the inside walls were coated with fluon. The cup was 5 cm in diameter for *B. germanica* and 11·5 cm in diameter for *P. americana*. The first 14 min of the acclimatization period were under red light. During the last minute of the acclimatization period, we lit a white lightbulb hung on the upper edge of the arena. When the trial began, we lifted the cup rapidly by an attached string. We recorded the 'freeze time' (a measure of photokinesis) for each animal as the elapsed time in seconds from when the cup was removed to when the animal first began to move in a consistent direction.

To quantify the direction of movement (a measure of phototaxis), we assigned a score to each animal between 0 (movement directly towards the light) and 6 (movement 180° away from the light). Animals that climbed up the inside of the cup, or that were on their backs when the cup was removed were retested on another day.

Statistical Analysis

Ideally, animals would be tested in a sequence that was random with respect to species, sex and treatment. However, this protocol was impossible to follow because of the availability of cockroaches and parasites. We tested substrate choices and activity of *B. germanica* from September 1987 to April 1988, *P. americana* from April 1988 to December 1988, and light responses of both species from January 1989 to May 1990. Within each of these time periods, we tried to test equal numbers of parasitized and control animals, but we were constrained, at times, by the availability of parasitized animals. Parasitism rates were approximately 95% for *P. americana* and 45% for *B. germanica*. Univariate ANOVA showed there were no differences in behavioural scores among batches within a particular treatment. Therefore, we pooled batches to simplify the analysis.

We continued exposing animals to parasites until we had accumulated data on approximately 25 parasitized males and 25 parasitized females of each species. Data from animals that did not become infected or that died during the course of the experiments were not used. For the light response experiments, only males of both species were used.

Our experiments were designed to evaluate the simultaneous effects of light, species, sex and parasitism on cockroach behaviour. For each behavioural response variable, the statistical design is a repeated measures analysis of variance. The within-subject factor is light (red or white), because each animal was tested under red and white light. The between-subjects factors are species (*P. americana*, *B. germanica*), sex (female, male), and parasitism (control, parasitized). All factors in the model are fixed, and the analysis uses type III sums of squares (SAS Institute 1985), which are appropriate for designs with unequal sample sizes.

To test for the effects of parasite intensity on behaviour, we calculated the correlation coefficient (Pearson's r) between mature cystacanth number and behavioural scores for each group of parasitized animals.

Percentages were arcsine square-root transformed before analysis. Distance and velocity were

Table I. *P*-values for significant effects of parasitism, sex, species and light on substrate use

	Black		White	
Effects	Vertical	Horizontal	Vertical	Horizontal
P	<0·01			<0·05
S				
Sp	<0·001	<0·001		
L	<0·05	<0·001	<0·05	<0·001
P × Sp				
P × L		<0·05		
P × S			<0·05	
Sp × S				
Sp × L	<0·05	<0·01		<0·05
L × S				
P × L × S				
P × Sp × S				0·05
P × Sp × L				
L × S × Sp				<0·01
P × L × S × Sp				

Each column gives the significance levels for a separate repeated-measures ANOVA of substrate use. P: parasitism; S: sex; Sp; species; L: light.

logarithmically transformed. 'Freeze time' data were analysed with a reciprocal transformation. In the Figures and Tables, means and standard errors are presented for untransformed data to ease the interpretation.

Our analyses ensure that the effects of species, sex, light and parasitism can be evaluated independently of one another. However, the behavioural choices on the different substrates are not independent. That is, the fraction of time an animal spends on black horizontal surfaces is not independent of the fraction of time it spends on black vertical surfaces. However, MANOVAs of these data gave comparable results to the univariate tests we present here.

RESULTS

Responses to Substrate

Effects of parasitism

The use of black vertical substrate differed between parasitized and unparasitized cockroaches of both species, but the degree of difference was influenced somewhat by the light regime (Table I; Fig. 1). Under red light, parasitized animals of both species used black vertical surfaces less than unparasitized animals did. Under white light, there were no consistent differences between parasitized and unparasitized animals. Under red light, parasitized animals used black horizontal surfaces more than did their uninfected counterparts. Under white light, there were no consistent differences in the use of these surfaces for either sex or species.

Finally, white horizontal surfaces were used more frequently by parasitized animals under all conditions, with the exception of *P. americana* males under red light. The use of white vertical surfaces was not affected by parasitism. For all significant effects, there was no relationship between cystacanth number and behavioural score.

Across-species comparisons

Periplaneta americana consistently used black vertical surfaces more frequently than *B. germanica* did. Both species decreased their use of these surfaces under white light, but the decrease was more pronounced for *B. germanica*. On the other hand, *B. germanica* used black horizontal surfaces more than *P. americana* did. Both species increased their use of these surfaces under white light, but the increase was more dramatic for *B. germanica*. Overall, *B. germanica* used white horizontal surfaces more than *P. americana* did. However, differences between light conditions and sexes were not con-

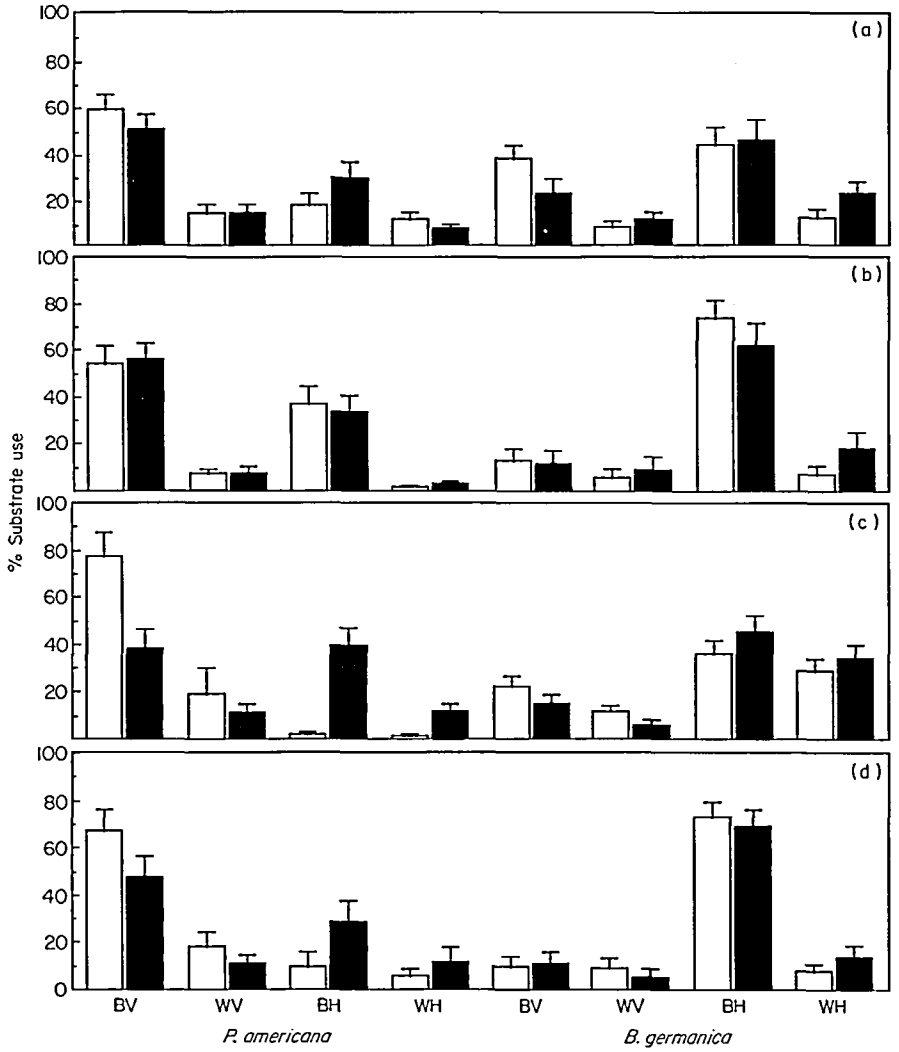

Figure 1. Mean (+SE) per cent substrate use by *P. americana* and *B. germanica*. □: unparasitized; ■: parasitized. (a) Males, red light; (b) males, white light; (c) females, red light; (d) females, white light. BV: black vertical; WV: white vertical; BH: black horizontal; WH: white horizontal. For control males $N=28$ (*P. americana*), $N=25$ (*B. germanica*); parasitized males $N=36$ (*P. americana*), $N=17$ (*B. germanica*); control females $N=10$ (*P. americana*), $N=25$ (*B. germanica*); parasitized females $N=22$ (*P. americana*), $N=25$ (*B. germanica*).

sistent. Finally, the use of white vertical surfaces decreased under white light for all groups.

Activity Measurements

Effects of parasitism

Parasitism had no effect on activity time (Table II; Fig. 2). Under both light conditions, parasitized *B. germanica* moved more slowly than did their uninfected counterparts. *Periplaneta americana* males ran slower when parasitized than did uninfected males, but parasitized females ran faster than uninfected females (Fig. 3). These differences in velocity were statistically non-significant.

As a consequence of these differences in velocity, parasitized *B. germanica* and parasitized *P. americana* males covered significantly less distance than did uninfected counterparts, while parasitized *P. americana* females travelled greater distances

Table II. *P*-values for significant effects of parasitism, sex, species and light on activity

Effect	% Time active	Velocity	Distance travelled
P			<0·05
S			
Sp		<0·05	
L	<0·001	<0·05	<0·001
P×Sp			
P×L			<0·05
P×S			
Sp×S			
Sp×L	<0·01		<0·001
L×S	<0·001		0·01
P×L×S			
P×Sp×S			
P×Sp×L			
L×S×Sp	<0·05		
P×L×S×Sp			

Each column gives the significance levels for a separate repeated-measures ANOVA of activity. Abbreviations as in Table I.

than uninfected females (Fig. 4). Number of cystacanths was negatively correlated with the distance travelled by *Periplaneta* males under red light ($r=-0{\cdot}33$, $P=0{\cdot}046$; $N=36$).

Across-species comparisons

All cockroaches spent less time moving under white light, except for *P. americana* females, which showed no difference (Fig. 2). All cockroaches ran faster under white light than under red except *B. germanica* males, which ran at similar speeds under both light conditions (Fig. 3). For *P. americana*, males travelled further than females; this was not evident for *B. germanica*. Both male and female *B. germanica* did not move as far under white light as under red light. *Periplaneta americana* males also responded in this way, but females seemed to travel further in white light (Fig. 4).

Responses to light

Effects of parasitism

Parasitism had no effect on the proportion of time an animal spent in the light ($F_{1,132}=0{\cdot}63$, $P>0{\cdot}05$; $N=136$), the freeze time ($F_{1,131}=1{\cdot}02$, $P>0{\cdot}05$; $N=135$), or the direction travelled in response to light ($F_{1,131}=0{\cdot}33$, $P>0{\cdot}05$; $N=135$).

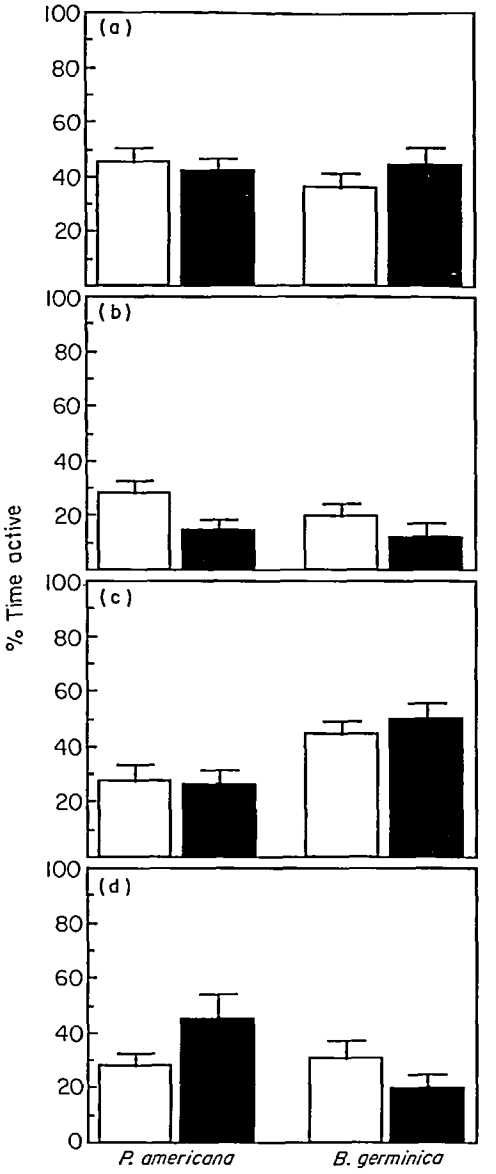

Figure 2. Mean (+SE) activity of *P. americana* and *B. germanica*. The percentage of time active is the percentage of consecutive observations during which animals moved to new grid squares. □: unparasitized; ■: parasitized. (a) Males, red light; (b) males, white light; (c) females, red light; (d) females, white light. Sample sizes for *P. americana* are: control males $N=26$; parasitized males $N=36$; control females $N=10$; parasitized females $N=19$; *B. germanica*: control males $N=25$; parasitized males $N=17$; control females $N=25$; parasitized females $N=25$.

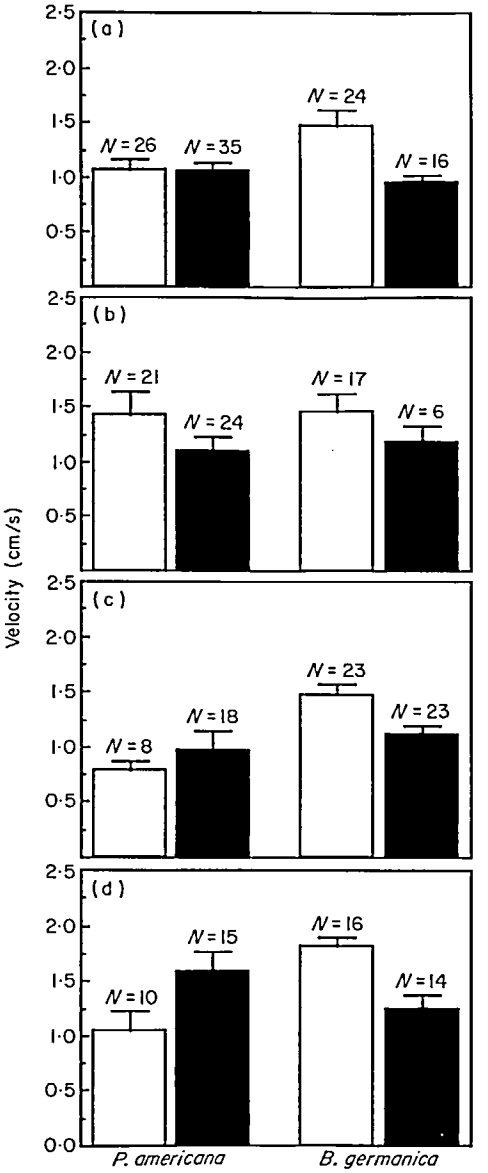

Figure 3. Mean (+SE) travel velocity (cm/s) of *P. americana* and *B. germanica*. Velocities were calculated for consecutive observations during which animals moved to a new grid square. □: unparasitized; ■: parasitized. (a) Males, red light; (b) males, white light; (c) females, red light; (d) females, white light. Sample sizes are shown above standard error bars.

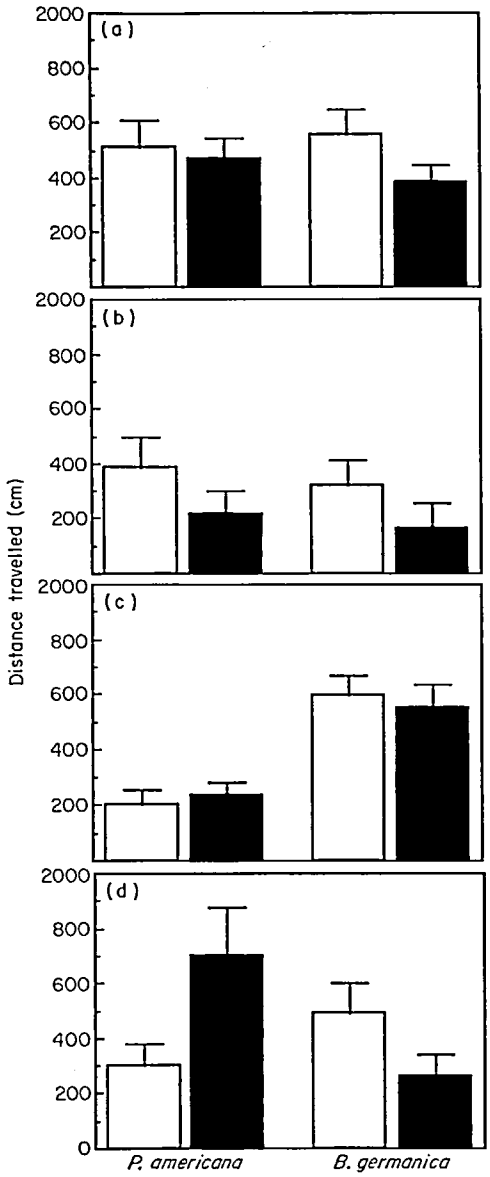

Figure 4. Mean (+SE) total distance travelled (cm) by *P. americana* and *B. germanica*. □: unparasitized; ■: parasitized. (a) Males, red light; (b) males, white light; (c) females, red light; (d) females, white light. Sample sizes are given in Fig. 2.

Across-species comparison

Blattella germanica spent significantly more time in the light and had a shorter freeze time than did *P. americana*. There were no differences between species in the average direction travelled (Table III).

DISCUSSION

Acanthocephalan effects on arthropod movement are not uncommon. For example, infected aquatic isopods spend more time moving than uninfected isopods (Muzzall & Rabalais 1975; Camp & Huizinga 1979) and infected terrestrial isopods

Table III. Average (±SE) behavioural scores for light response experiments

Species	Treatment	% Time in light*	Freeze time (s)†	Direction‡
P. americana	Control	8·07	29·45	3·46
(*N*=25)		(3·73)	(3·55)	(0·37)
P. americana	Parasitized	16·53	46·54	3·76
(*N*=25)		(3·31)	(10·24)	(0·33)
B. germanica	Control	34·15	9·38	3·87
(*N*=53)		(4·69)	(1·29)	(0·23)
B. germanica	Parasitized	32·73	13·01	3·21
(*N*=33)		(5·29)	(8·45)	(0·77)

Only males were used in these experiments.
*The average percentage of time spent in the light in a shading experiment.
†The average 'freeze time' (s) of cockroaches exposed to a point light source.
‡The average directional score (0 = towards light; 6 = away from light).

tend to move further than do uninfected ones (Moore 1983b). Our study appears to be the first to report a decrease in distance travelled in arthropod hosts of acanthocephalans, although decreases in velocity have been inferred (Moore 1983a). Moreover, this decrease is not restricted to *P. americana*. We find comparable results with a co-occurring, ecologically similar host (*B. germanica*). In a congener, *Periplaneta brunnea*, however, *M. moniliformis* parasitism had no significant effect on activity (Carmichael & Moore 1991). However, both species were tested at temperatures below their optimum, which may account for differences in their activity patterns (Delcomyn 1971) and their responses to parasitism.

Positive responses to light are a common effect of acanthocephalan parasitism and have been reported in at least eight arthropod–acanthocephalan associations (see Moore 1984b; Moore & Gotelli 1990, for review). Among these is *P. americana* infected with *M. moniliformis* (Moore 1983a; Wilson & Edwards 1986; see also Edwards 1987). In contrast, we were unable to demonstrate any significant parasite effects on either phototaxis or photophilia in either cockroach (Carmichael & Moore 1991, obtained similar results for *P. brunnea*). However, variances in these data were large, and we note that in *P. americana*, parasitized animals spent, on average, twice as much time in the light as did uninfected animals, and had a longer freeze time (but see Moore 1983a).

Substrate responses showed complex interactions with light, species and sex. None the less, there was a general response to parasitism: under most conditions, parasitized animals of both species shifted to horizontal substrates.

At least three factors may contribute to this shift. First, cockroaches on horizontal surfaces may be more vulnerable to predation by the final host (Silverman & Bell 1979). Thus, the behavioural alteration may contribute to parasite transmission. It is, at least, consistent with that hypothesis.

Second, standing on a horizontal surface may require less energy than clinging to a vertical surface. Preliminary data suggest that infection with *M. moniliformis* may alter oxygen consumption by *P. americana* (B. Full, personal communication). Thus, the behavioural alteration may reflect energetic constraints on infected hosts.

Finally, vertical orientation of *P. americana* is related to sexual behaviour. Male cockroaches usually perch above females on vertical surfaces; this enhances their ability to encounter females when they move down in response to sex pheromone (Silverman & Bell 1979; Bell & Tobin 1981). Infection with *M. moniliformis* may reduce sensitivity to sex pheromone (as measured by activity counts per min) in *P. americana* males (M. Carmichael, J. Moore & N. J. Gotelli, unpublished data) and may therefore have effects on sex-related behaviour as well, including use of vertical surfaces. Parasites and parasitoids interact in a complex fashion with arthropod host endocrinology and biochemistry (Thompson 1983; Beckage 1985; Lawrence 1986). Such interactions may mediate at least some of the alterations we have observed.

Substrate colour choice has not been examined in many acanthocephalan–host associations. Moore

(1983b) showed that dark terrestrial isopods parasitized with *Plagiorhynchus cylindraceus* spent more time on light-coloured substrates than did uninfected isopods. Pigmentation dystrophy has also been reported in some crustacean hosts (see Moore 1984b for review). In such a situation, the host might be more conspicuous to a predator against its normally chosen substrate.

Despite numerous descriptions of altered behaviour associated with acanthocephalan infection, comparative studies are rare. Bethel & Holmes (1973, 1977) observed one host, *Gammarus lacustris*, infected with either *Polymorphus paradoxus* or *Polymorphus marilis*, and found that the species of parasite influenced the response of gammarids to environmental stimuli; these responses affected risk of mallard predation. DeMont & Corkum (1982) showed that each of two species of ostracod infected with *Octospiniferoides chandleri* responded more positively to light than did uninfected conspecifics. Other stimuli were not tested.

Our comparative study has shown that two ecologically similar cockroach species, which are both intermediate hosts, show some similar responses to parasitism by *M. moniliformis*. These shared responses may reflect shared selective pressure on the parasite–host association. Nevertheless, each species showed some unique behavioural responses to parasitism, and these differences were often mediated by sex and light regime. Interspecific differences in behavioural responses may result from divergent histories, physiological limitations, or constraints due to body size differences. Body size differences, in particular, may have profound effects on host behaviour, physiology and metabolism (Calder 1984), and probably contributed to at least some of the behavioural differences between *P. americana* and *B. germanica*.

However, it is difficult to know which of the differences between host species are responsible for divergent behavioural responses when only two host species are compared. By introducing *M. moniliformis* into several different cockroach species, we hope to reveal consistent effects of ecology, phylogeny and body size on host behavioural responses to parasitism.

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