

Figure 1. *Helobdella stagnalis* carrying three young which have fed on a *Tubifex*. Note that the gut of the young but not the gut of the parent is coloured dark with the blood of the *Tubifex*. The view is through a glass pane onto the ventral side of the animal.

Adult *Helobdella stagnalis* and *Glossiphonia complanata* are approximately the same size (15–20 mm). Despite being carried by the parent for the same period of time, the juveniles of *H. stagnalis* are much larger than those of *G. complanata* when they finally start to lead an independent life (5–6 mm versus 1–2 mm), probably due to the fact that they are fed by the parent. Presumably, their larger size results in increased juvenile survival.

Within the Hirudinea, only members of the family Glossiphoniidae show extensive parental care. Sawyer (1971) arranged the degree of protection given to the offspring in a series of increasing complexity as follows: (A) *Glossiphonia*, *Placobdella*, *Theromyzon* and *Hemiclepsis* species attach the cocoons to the substrate and cover it with their body until they hatch; (B) *Helobdella*, *Oculobdella*, *Anoculobdella* and *Batracobdella* species attach the cocoons directly to their ventral surface; (C) *Marsupiobdella* transfer the cocoons into a permanent ventral brood pouch, where the young develop. In both (A) and (B) the newly-hatched young cling to the ventral surface of the parent and are carried around by it. *Helobdella stagnalis* apparently have gone one step further: they feed the young they carry.

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The Effects of Parasitic Infection on the Behaviour of an Intermediate Host, the American Cockroach, *Periplaneta americana*, infected with the Acanthocephalan, *Moniliformis moniliformis*

The life-cycle of some parasites involves a period of development in one or more intermediate hosts before maturing in the final host (e.g. Crompton & Joyner 1980). Recent studies have suggested that, in some cases at least, the parasite does not simply rely on chance consumption by a suitable definitive host to ensure its transmission, but may influence the first host's behaviour in such a way as to facilitate it (e.g. Holmes & Bethel 1972). Trail (1980) described four types of host-parasite relationship and discussed situations in which altered host behaviour might be expected to evolve.

Eleven species of acanthocephalan worm (Acanthocephala) are known to induce behavioural changes in their intermediate hosts (see Moore 1983a for references). Moore (1983b) found that American cockroaches (*Periplaneta americana*) infected with *Moniliformis moniliformis* (Bremser 1811) were hyperactive and positively phototactic. These behaviours are likely to make the animal more conspicuous to the parasite's definitive host, the brown rat (*Rattus norvegicus*). Moore (1983b) measured activity using a running wheel apparatus. In a short series of experiments, we have measured activity on a horizontal substrate and extended comparisons of infected and uninfected individuals to aspects of their social behaviour; both sets of experiments indicate that aspects of cockroach behaviour were altered as a result of infection with *M. moniliformis*.

Ten male cockroaches were starved for 48 h before being given laboratory rodent pellets coated with shelled *M. moniliformis* acanthors suspended in 30% sucrose solution (King & Robinson 1967). A further 10 males were sham-infected using sucrose solution alone. Both sets of cockroaches were maintained at 25°C on a light-dark shifted routine such that the dark period was from 0700–1900 hours. At this temperature the larvae mature to the infective cystacanth stage in around 60 days and lie dormant in the haemocoel of the cockroach until ingested by the definitive host. Testing began 77 days post infection (PI) in October 1984 and continued for 20 weeks. At 33 weeks PI the cockroaches were dissected and the number of mature cystacanths present counted. The infected animals were found to harbour 1–10 cystacanths (mean = 4.44 ± 1.12 SE, $N=9$). The sham-infected animals were parasite free. Each group was housed in a plastic tank measuring 30 cm \times 20 cm \times 20 cm. Food and water were provided ad libitum and an inverted wax cup provided shelter. Tests were performed during the dark period between 0900–1800 hours, under a 60-W red lamp (Barth 1964). In their nocturnal environment, American cockroaches maintain group cohesion by olfaction (e.g. Bell et al. 1972). Both sexes produce an aggregation pheromone in their faeces which is detected by receptors on the antennae. Several studies (e.g. Milinski 1977) have shown that predators attack solitary prey in preference to denser groups of individuals. One way of increasing host vulnerability might be for the parasite to reduce cockroach responsiveness to aggregation pheromone. We tested this on male cockroaches by the use of a T-maze. Females were excluded from the study as they also produce a sex pheromone which attracts males (e.g. Rust et al. 1976) and this could have led to confusion between the effects of the two pheromones.

The T-maze was constructed from 40-mm diameter perspex tubing (adapted after Bell et al. 1973) and each of three 150-mm arms could be removed and interchanged. Aggregation pheromone was extracted by soaking pieces of faeces-soiled filter paper in methanol for 24 h. Using a small paint brush, the inside of one arm of the T-maze was painted with the faeces/methanol solution and the other painted with methanol alone. Cockroaches from both groups were placed individually in the starting chamber and allowed to move down the first arm and turn into one of the painted arms. The test was repeated six times with each animal and after each run the painted arms were switched round and the arm chosen by each cockroach noted. At the end of testing, all three tubes were cleaned thoroughly and the experiment repeated for each of the twenty cockroaches.

Figure 1 shows that the uninfected cockroaches were attracted to aggregation pheromone: the frequency distribution for orientations towards the pheromone arm of the T-maze was shifted significantly.

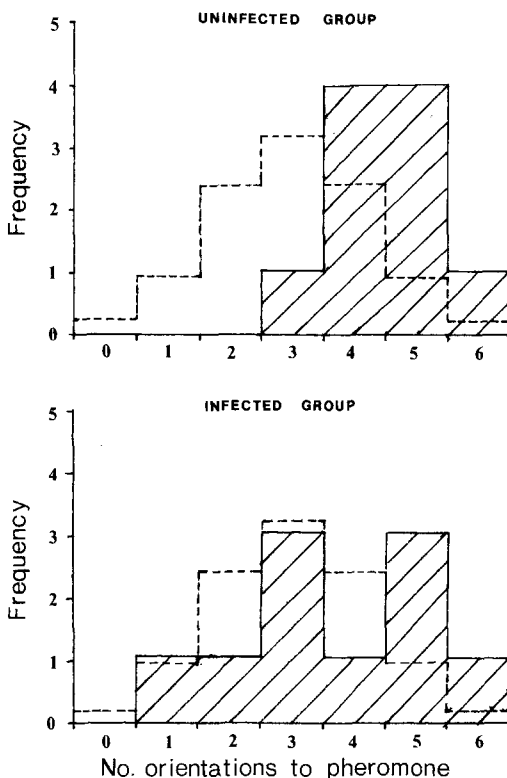


Figure 1. Frequency distribution for the number of orientations towards aggregation pheromone by cockroaches within a T-maze apparatus. Open blocks: expected binomial distribution; hatched blocks: observed frequencies.

cantly to the right of the expected binomial distribution ($D=5.56$, $N=7$, $P<0.05$, Kolmogorov-Smirnov one sample test). However, the distribution for infected cockroaches was not significantly different from the expected random orientation. Three out of 10 infected cockroaches consistently turned left or right in the maze, irrespective of the position of the pheromone arm. None of the uninfected animals behaved in such a manner. The number of orientations towards the pheromone arm declined as the number of cystacanths harboured increased ($r_s=0.451$, $N=19$, $P<0.05$, Spearman rank one-tailed test).

To test for the effect of infection on activity levels, a 1-m diameter arena was used to measure the cockroaches' response to a novel open field environment. Each cockroach was placed in the centre of the arena, released, and its path transcribed onto a scale diagram of the arena floor. The mean distance travelled in 5 min by infected cockroaches (mean \pm SE = 5.46 ± 0.73 m, $N=6$) was significantly greater than that exhibited by uninfected individuals (3.14 ± 0.74 m, $N=6$) over the same period ($U=34$, $N=12$, $P<0.01$, Mann-Whitney U -test). Greater activity was positively correlated with the number of *M. moniliformis* cystacanths harboured ($F=13.64$, $df=1$, 10 , $P<0.01$, ANOVA). There was no significant difference in the amount of time spent active, so the infected individuals moved faster than the uninfected individuals. Moore (1983b), found that infected cockroaches placed on a running wheel spent significantly more time moving than did uninfected cockroaches on a similar wheel. They did not however move any farther, implying that the infected animals moved more slowly than controls. It should be noted that Moore's experiment recorded general activity several hours after exposure to the test apparatus, whereas the experiment described here records the animals' immediate locomotor response to a novel environment. Closer analysis revealed that only in the first minute of each test was there a significant difference between the distances travelled by the two groups ($U=34$, $N=12$, $P<0.005$, Mann-Whitney U -test). Infected cockroaches which are abnormally rapid in their movement may be more vulnerable to predation than uninfected cockroaches. Future studies will test this hypothesis.

These results indicate that *M. moniliformis* may be able to influence the behaviour of *P. americana* by affecting reactions to aggregation pheromone and rate of locomotion. As the cystacanth stage of the parasite is enclosed within a parasite-derived envelope inside the haemocoel of the insect, mechanical damage is unlikely to be the cause of these

aberrant behaviours. The parasites may in some way be interfering with the cockroaches' nervous system or, maybe, interfering with its hormone production.

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