

# Behavioural modifications and increased predation risk of *Gammarus pulex* infected with *Polymorphus minutus*

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## Introduction

Parasitic organisms face a major hurdle during their development from egg to patent adult when the life cycle involves transmission from one host to another. Many species have evolved strategies through which infected intermediate hosts are made more readily available to predatory definitive hosts than non-infected conspecifics. Pertinent adaptations involve subtle and complex interactions relating to various aspects of the host-parasite interface, including morphology, physiology, biochemistry, and behaviour (see Barnard and Behnke, 1989). In many of these host-parasite interactions, the invading species manipulate homeostatic regulatory processes of the host, not only to provide a better environment for their growth and reproduction, but, through the resultant changes in host fitness, to control the stability of host and parasite populations (Anderson, 1976). It is not surprising, therefore, that some parasites have usurped and altered the behavioural patterns of the host in order to optimize their own transmission efficiency (Moore, 1984).

## Abstract

Experiments are described which investigated altered behavioural responses in *Gammarus pulex* infected with the cystacanth stage of *Polymorphus minutus*. Infected gammarids were significantly smaller than non-infected individuals, suggesting that growth and development of the host may have been affected by the parasite. Infected gammarids responded to disturbance by movement to the water surface, whereas controls moved along the substratum. Furthermore, infected *G. pulex* spent significantly more time swimming in surface water compared with non-infected individuals, when undisturbed. This latter behavioural modification was depth-dependent. Susceptibility to predation by fish was significantly enhanced by infection with *P. minutus*. These results suggest that *P. minutus* can selectively modify certain aspects of the behavioural repertoire of *G. pulex*, thus increasing the visual profile of the amphipods, and their likelihood of predation by vertebrate predators including the definitive host.

The ability of parasites to elicit drastic and apparently suicidal changes in intermediate host behaviour has attracted considerable attention in recent years (Carney, 1969; Lester, 1971; Holmes and Bethel, 1972; Bethel and Holmes, 1973; Rau, 1983, 1984). Acanthocephalan parasites are a particularly interesting group in this context because the interaction between host and parasite involves little, if any, pathology and is probably mediated biochemically. One of the classic studies in this context is the work by Holmes and Bethel (1972) and Bethel and Holmes (1973) which looked at the effects of *Polymorphus paradoxus*, *P. marilis*, and *Corynosoma constrictum* on the behaviour of lake-dwelling amphipods (*Gammarus lacustris* and *Hyaella azteca*). While earlier work published in this journal (Brown and Thompson, 1986) has extended these studies to *Pomphorhynchus laevis* and *G. pulex*, no studies have yet been made of the effects of *Polymorphus* on other gammarid hosts. Here, we report a series of experiments which examined the behavioural effects of *P. minutus* on the *G. pulex* inhabiting feeder streams between a series of lakes. The work was conducted over a period of four years (1983-1987), during Easter Vacation (April) Terrestrial Zoology field courses at Woodchester Park in Gloucestershire, UK. The results illustrate the occurrence of selective changes in the behavioural repertoire of gammarids infected with the cystacanths of *P. minutus* and suggest that altered host behaviour is associated with a greater vulnerability to predation by a subset of vertebrate predators which includes the likely avian definitive hosts in this area (mallard, *Anas platyrhynchos*, and tufted ducks, *Aythya fuligula*).

## Material and methods

### Location

The work described in this paper was carried out in Woodchester Park Valley, where there is a chain of artificial lakes with interconnecting streams. The lakes have a resident population of water fowl including mallard, coots (*Fulica atra*), moorhens (*Gallinula*

*chloropus*), and tufted ducks. *Gammarus pulex* were found mainly in the interconnecting streams. The study was conducted in mid-April (1984–1987) for a period of 10 days each year.

**Parasite and intermediate host**

Infected gammarids were easily identified by the bright orange colour of the cystacanth (Hyman, 1951). Some cystacanths were allowed to hatch and the parasite was confirmed as *Polymorphus minutus*. The prevalence of infection varied from one year to the next, but in most years 100 or more infected gammarids were available for experimentation. The infected and non-infected specimens were caught by hand nets, transferred to glass jars, and transported to the field centre where they were maintained indoors in separate aerated plastic aquaria. A small quantity of detritus and vegetation was added to both tanks and the water was changed regularly. Prior to each experiment, gammarids were removed at random from these stock-holding tanks.

**Measurement of *G. pulex***

Single gammarids were transferred individually to a 7 cm Petri dish with a drop of water. Each gammarid was allowed to adopt its usual ‘crescent’ shape prior to its length being measured with a piece of 1 mm ruled graph paper, placed under the dish.

**Experiments**

Most of the experiments were carried out indoors in plastic tanks or trays. The temperature of the water was measured at regular intervals and generally did not exceed 14 °C. When necessary, ice cubes were added to reduce water temperature to below 14 °C.

**Fish**

In 1987, a stock of commercially purchased goldfish was used to monitor the relative susceptibility of infected versus non-infected gammarids to predation. The fish were maintained in a conventional manner but were fed mainly on gammarids for a few days before being starved in preparation for the experiments.

**Statistical analysis of results**

When the sample sizes permitted, data were compared via a two-tailed Student’s *t*-test. When the data did not conform to that required for parametric analysis or when sample sizes were too small, the non-parametric Mann–Whitney U-test was employed. Two-sample Kolmogorov–Smirnov tests were used to compare frequency distributions. Differences between groups were considered to be significant when  $P < 0.05$  (Sokal and Rohlf, 1969).

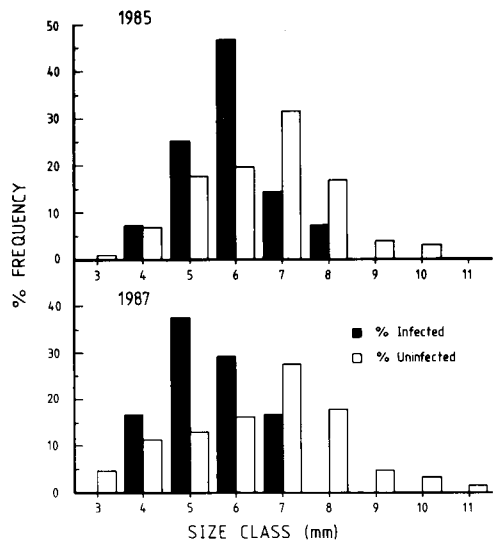
**Experimental design and results**

**The effect of *P. minutus* on the size of the intermediate host**

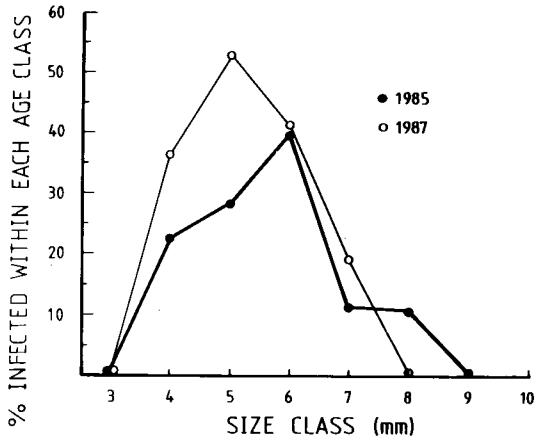
From observations both in the field and laboratory, it was readily apparent that the majority of infected gammarids were smaller than non-infected conspecifics. The frequency distribution of gammarids in size classes ranging from 3 to 11 mm are presented in figure 1, and the data show that in both years (1985 and 1987) infected *G. pulex* were significantly smaller. Figure 2 shows the percentage of gammarids within each age class infected with *P. minutus* and again emphasizes that peak infection rates were observed in the 4–6 mm size class, whereas most non-infected gammarids at this time of the year were 6–8 mm in size. Larger individuals (8 mm+) were generally not infected. The mean values recorded and the size of the populations sampled in each year are given in table 1. On all occasions the mean length for infected hosts was smaller than the mean for the non-infected group and significant differences were obtained in three of the four years. It is also interesting that throughout the four-year period of observation no infected gammarids were ever encountered *in copulo*.

**The effect of infection with *P. minutus* on the proportion of time spent swimming by the host**

Brown and Thompson (1986) found that gammarids infected with *Pomphorhynchus laevis* were more likely to be seen swimming in open water than non-infected



**Figure 1** The percentage frequency distribution of infected and non-infected *G. pulex* in size classes. A, results obtained in 1985 ( $n =$  infected 28 and non-infected 102). B, results for 1987 ( $n =$  infected 24 and non-infected 62).



**Figure 2** The percentage of *G. pulex* within each age class, infected with *P. minutus*. Data from 1985 and 1987.

individuals. Experiments to determine whether gammarids infected with *P. minutus* spent more time swimming were carried out in plastic tanks or trays filled with water to a depth of 5–10 cm. Various substrata were used including sand, fine pebbles, and stones. The gammarids were introduced into these test arenas and were given 5 minutes to settle before observations were initiated. The total amount of time allocated to swimming in the subsequent 5 minutes was recorded. Water in the tanks was aerated in between each experimental run. Infected and non-infected gammarids were alternated until the entire sample had been assessed.

In three such tests carried out over successive years, infection with *P. minutus* did not affect the percentage of time spent swimming. The mean values for non-infected versus infected gammarids were 36 per cent vs 24 per cent ( $n = 10, 17$ ), 30 per cent vs 31 per cent ( $n = 10, 10$ ), and 66 per cent vs 60 per cent ( $n = 30, 30$ ) respectively. A fourth test gave 74.8 per cent vs 63.2

**Table 1** Comparison of the size of *G. pulex* infected with *P. minutus* with non-infected individuals from the same location

Year	Mean length (mm) ± SEM (n)		$P^1$
	Non-infected	Infected	
1984	8.1 ± 0.3 (80)	7.3 ± 0.2 (60)	0.05
1985	6.5 ± 0.1 (100)	5.9 ± 0.2 (50)	<0.05
1986	6.3 ± 0.6 (70)	6.1 ± 0.7 (70)	NS
1987	6.5 ± 0.2 (61)	5.4 ± 0.2 (26)	<0.001

<sup>1</sup>Groups were compared using the Student's *t*-test. NS = not significant.

per cent ( $n = 20, 20$ ) which represents a significant difference ( $P < 0.01$ ).

**The effect of infection with *P. minutus* on the total time spent swimming by the intermediate host in surface water**

During the course of the initial experiments measuring total swimming time, we observed that when they did swim, infected gammarids were more likely to swim near to the surface of the water than non-infected individuals. This observation was explored further in four experiments (table 2). In each experiment a plastic tank was filled with water to a given depth. A line was then drawn around the tank at exactly half the total depth. Gammarids were introduced, given 5 minutes to adjust, and then observed for a further period of 5 minutes. The total swimming time spent above the half-way mark was monitored. In Experiments 3 and 4, the total times spent swimming were also recorded. The data in table 2 show that infected gammarids spent 2 to 4 times as much of their swimming time in the surface water as did the non-infected amphipods and the difference was significant in three of the four experiments.

**Table 2** The effect of *P. minutus* on the proportion of time spent by *G. pulex* swimming in surface water

Experiment <sup>1</sup> (n1,n2)	Height of <sup>2</sup> water	Mean duration of swimming in surface water in seconds ± SEM (percentage)		$P^4$
		Non-infected	Infected	
1 (10,10)	5	14.0 ± 3.3 (4.7) <sup>5</sup>	57.7 ± 9.5 (19.2)	<0.001
2 (20,20)	5	12.6 ± 3.5 (4.2)	63.2 ± 20.3 (21.1)	0.05
3 (20,20)	10	21.5 ± 3.7 (7.2)	46.8 ± 7.8 (15.6)	0.01
4 (20,20)	20	17.7 ± 5.9 (5.9)	30.6 ± 5.7 (10.2)	NS
Mean% ± SEM of total swimming time, spent in surface water				
3 <sup>3</sup>	10	9.9 ± 1.7	24.4 ± 3.9	<0.05
4	20	10.7 ± 3.7	24.4 ± 4.9	0.01

<sup>1</sup>Experiments 1, 2, and 3 were conducted in 1985, 1986, and 1987 respectively. Experiment 4 was also in 1987.

<sup>2</sup>Each run of experiments was carried out in a standard plastic tank in which the total depth of water was the figure given in this column in cm. Surface water was defined as the top half of each respective total depth.

<sup>3</sup>In Experiments 3 and 4, the data were also calculated as a percentage of the total swimming time, spent in surface water.

<sup>4</sup>Groups were compared using the Mann-Whitney U-test.

<sup>5</sup>The figure in brackets is the percentage of the 5 minute period of observation, spent swimming in surface water.

**The response to light of *G. pulex* infected with *P. minutus***

One explanation for the observations recorded above may reside in an altered response to light during infection with *P. minutus*. Brown and Thompson (1986) found that gammarids infected with *P. laevis* had a reduced tendency to seek darkness compared with non-infected animals. A series of experiments was consequently carried out to see whether this was the case with *P. minutus*. In some experiments tanks were used, in others glass tubes, but in each case half of the experimental arena was blocked off by dark paper. The gammarids were presented, therefore, with a simple choice between swimming or resting in the illuminated or darkened half of the container. Care was taken to minimize the effect of environmental light sources and readings were taken alternating the position of the darkened versus light area and the orientation of the tank in relation to the windows and the position of the sun.

We were unable to detect a significant effect in any of the permutations which were explored. The mean values of percentage time spent in the illuminated half of the arena of non-infected versus infected gammarids were as follows: 21 per cent vs 34 per cent ( $n=5, 10$ ), 26 per cent vs 34 per cent ( $n=10, 10$ ), 27 per cent vs 31 per cent ( $n=20, 20$ ), and 41 per cent vs 45 per cent ( $n=20, 20$ ). None of these were significantly different. These results contrast with those from gammarids infected with other *Polymorphus* species (Bethel and Holmes, 1973).

**The response of *G. pulex* to disturbance**

Experiments were carried out to determine whether the escape response to disturbance of infected versus non-infected gammarids differed. Plastic tanks were filled with water to a depth of 5 to 20 cm. Gammarids were introduced one at a time and, after a 5 minute period of acclimatization, the experimental animal was disturbed by a gentle touch with a glass rod applied to the tip of the abdomen. The distance to the next point of settlement was measured for 10 disturbances of each gammarid tested. When the direct horizontal distance from point of disturbance was measured, significant differences were observed. Thus, in one trial 5 non-infected and 5 infected gammarids travelled, on average  $10.7 \pm 6.0$  and  $7.9 \pm 4.9$  cm respectively ( $P=0.025$ ). In another the values were  $20.2 \pm 6.4$  and  $7.4 \pm 4.7$  ( $P<0.05$ ). In a third trial we plotted the exact course of escaping organisms on graph paper, using grid points marked on the tank. The convoluted trails were subsequently measured precisely and the difference was again significant (non-infected =  $36.8 \pm 15.0$  [ $n=40$ ]; infected =  $22.4 \pm 14.0$  [ $n=40$ ];  $P<0.001$ ).

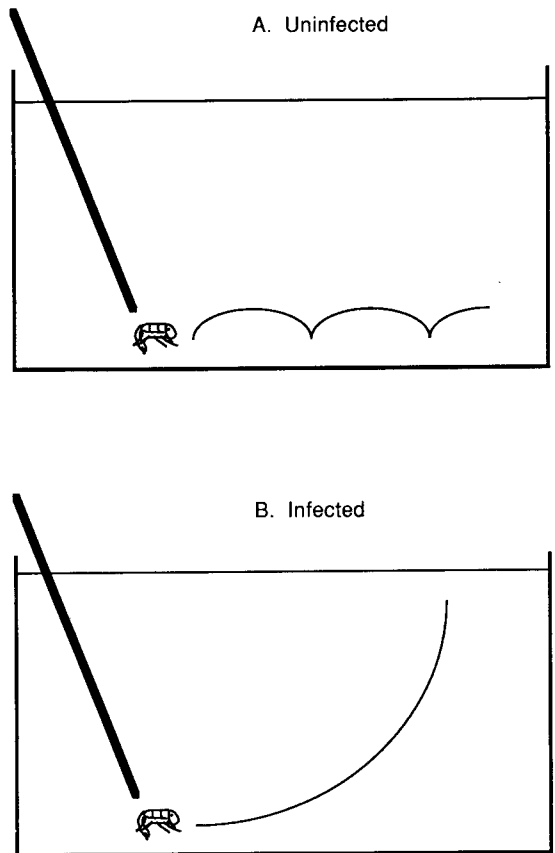
**The duration and height of the escape response of *G. pulex***

As part of the preceding experiments, the duration of swimming following disturbance was also recorded. A

significant difference was observed, the infected gammarids spending considerably less time in swimming ( $5.6 \pm 4.7$  seconds [ $n=40$ ]) than the non-infected individuals ( $9.5 \pm 6.6$  seconds [ $n=40$ ],  $P<0.05$ ).

From observations made while conducting these experiments, it was noted that infected and non-infected gammarids displayed qualitative differences in evasive behaviour (figure 3). When disturbed from a similar position in the aquaria, non-infected gammarids typically executed a stereotyped evasive response consisting of a series of hemispherical loops, followed by a return to the resting position. In marked contrast, infected gammarids similarly disturbed directed their escape behaviour upwards, usually along a parabolic trajectory, occasionally breaking the surface tension and causing an obvious surface disturbance.

To confirm these observations we recorded the maximum height to which gammarids swam following disturbance. As can be seen from the data in table 3, infected gammarids swam significantly higher. Fre-



**Figure 3** Illustration of a typical escape response by uninfected (A) and infected (B) *G. pulex* to gentle mechanical stimulation

**Table 3** The height of the escape response of infected and non-infected *G. pulex* following gentle mechanical stimulation

Group	No. tested	Mean height of response (cm) ± SEM	P <sup>1</sup>
Non-infected	40	5.16 ± 0.68	<0.01
Infected	50	11.50 ± 0.90	

<sup>1</sup>Groups were compared using the Kolmogorov–Smirnov test.

quency distribution analysis of these data sets (figure 4) emphasized this point further with the response of non-infected gammarids being skewed in the lower direction (peak frequency at 0–2 cm) and that of infected gammarids in the higher direction (peak frequency 18 cm;  $P < 0.01$ ). Only one non-infected gammarid attained a comparable height.

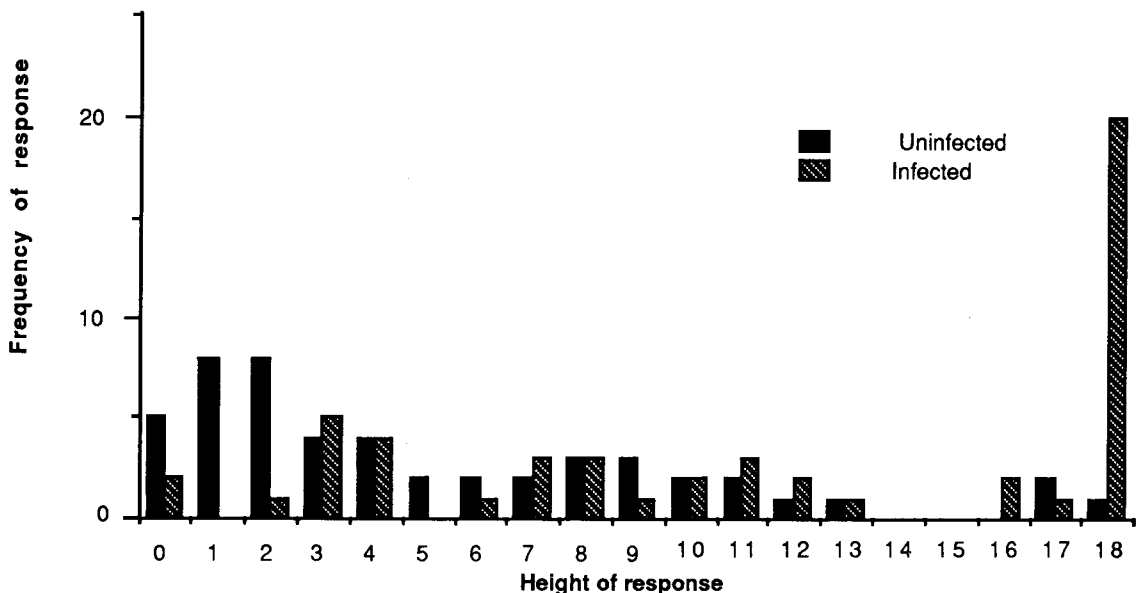
#### The effect of *P. minutus* on predation of *G. pulex* by fish

The assumption behind the previous experiments was that behavioural alterations in infected gammarids increase the vulnerability of the latter to predators. Experiments with other acanthocephalan relationships suggest that this may be so (Bethel and Holmes, 1977; Brown and Thompson, 1986). To test this more directly here, we carried out some simple experiments using fish as predators. A large glass aquarium (150 cm × 45 cm × 30 cm) was filled to a depth of 25 cm with water. Each of the four sides was obscured with tissue paper to minimize light access from the

sides of the tank, and disturbance to the fish by extraneous influences. Twelve goldfish of different ages and sizes were introduced into the tank and allowed to acclimatize for four days during which time they were deprived of food. At the beginning of the experiment, the goldfish were partitioned off in one half of the tank, and 10 infected and 10 non-infected gammarids were introduced into the other half. After 5 minutes the partition was removed and the fish were allowed to feed on the amphipods. The total number of gammarids remaining was checked approximately half-hourly. The experiments were stopped when approximately seven gammarids had been eaten by the fish. The total number of infected and non-infected gammarids in the remaining population was then assessed. After the fifth trial, the fish were rested for 24 hours prior to continuing with the remaining trials. The results are presented in table 4, from which it is evident that infected gammarids were predated more heavily.

#### Discussion

The investigations reported here demonstrated the occurrence of alterations in the behavioural responses of gammarids infected with larval *P. minutus*, and related the changes to predation risk. Previous authors have similarly presented evidence that infection alters aspects of intermediate host behaviour, so as to move it into a zone of overlap with the feeding habitat of the definitive host (Holmes and Bethel, 1972; Bethel and Holmes, 1977). There are two related but separate components to this phenomenon: (a) actual



**Figure 4** Frequency distribution of the height of the escape response following gentle mechanical stimulation. The data were compared using the two-sample Kolmogorov–Smirnov test and  $P < 0.01$ .

**Table 4** The effect of infection with *P. minutus* on the predation of *G. pulex* by goldfish

Group	Mean no. of gammarids consumed $\pm$ SEM	No. of trials in which losses were higher <sup>1</sup>	<i>p</i> <sup>2</sup>
Non-infected	1.7 $\pm$ 0.6	1	<0.05
Infected	5.5 $\pm$ 0.9	8	

Ten trials were conducted and in each trial 10 infected and 10 non-infected gammarids were presented to the fish. Each trial was terminated when approximately 7 gammarids had been consumed. <sup>1</sup>In one trial losses were equal (3 each). In the trial where non-infected gammarids sustained higher losses, 7 non-infected and 6 infected gammarids were eaten.

<sup>2</sup>Groups were compared using the Mann-Whitney U-test.

translocation in space of the infected host and (b) increased predation, consequent on the changed responses. Though it was not possible to test this latter component with the definitive host, we have nevertheless shown that within this particular host-parasite relationship, both do occur—altered behavioural responses occur which effectively segregate infected *G. pulex* from their non-infected conspecifics and apparently predispose them to increased predation. We do not imply that the parasite-induced alterations in behaviour, reported here, are targeted specifically at a particular definitive host. On the contrary, the changes in the behaviour of *G. pulex* which we observed, would make them more vulnerable to predation by a wide range of potential hosts. This possibility is supported by the study of Crompton and Harrison (1964) who reported adult *P. minutus* in natural infections from 86 avian species and one mammal.

Behavioural segregation between infected and non-infected *G. pulex* is well illustrated by their differential distribution and activity and in their responses to escape stimuli. The data establish that infected gammarids spend a significantly greater proportion of their time high in the water column. At increased depth, however, the vertical distribution did not differ although a significant difference was found to occur in the percentage of time spent actively swimming in surface water. Thus, although a two-fold increase in depth suppressed the amount of time spent nearer to the surface, the proportion of swimming time spent in surface water was still significantly higher in infected gammarids.

A particularly pronounced segregative behaviour was that elicited in response to an escape stimulus. The markedly polarized distribution of the two classes of individuals in their respective evasive behaviours was consistent with that reported by others (Bethel and Holmes, 1973). In our system, infected gammarids directed their swimming response to a disturbance in an upward direction, towards the surface of the water, occasionally breaking the surface tension and causing a surface disturbance that

was clearly noticeable. Similar behaviour has been reported for *G. lacustris* infected with *P. paradoxus* (Bethel and Holmes, 1973) although in this system, in addition to swimming upwards, infected gammarids showed strong clinging behaviour to items floating on the surface. In our experience *G. pulex* infected with *P. minutus* do not exhibit comparable behaviour.

It is probable that these segregative behaviours which we have observed will have profound implications for the transfer efficiency of the parasite to the definitive host. Bethel and Holmes (1973) reported that mallards reared from birth on commercial pellet food still actively predated gammarids when they were made available, suggesting that this was an innate feeding behaviour. Since mallards are 'dabblers' feeding primarily at the surface (Perrins, 1987), the elevated distribution of infected gammarids may lead to their preferential predation. Bethel and Holmes (1977) also observed that ducks were particularly orientated towards surface disturbances such as bubbles, and actively investigated such occurrences during feeding. Thus, the heightened locomotory activity and surface-directed escape behaviour, elicited perhaps by fish, the ducks themselves, or by other events on the stream bed, may serve to accentuate the visual profile of the infected gammarids by translocation into an area of overlap with the surface feeding behaviour of the definitive host.

The manipulation of the behaviour of the intermediate host by the parasite thus intuitively suggests a causal relationship between altered behavioural responses and a greater vulnerability to predation. Evidence to support this hypothesis was provided by experiments in which fish were used as predators. A significantly greater proportion of infected *G. pulex* was caught and consumed by fish when tested against their non-infected conspecifics. With respect to this latter experiment two points require further expansion. Firstly, it should be noted that although many species of acanthocephala utilize carrier or paratenic hosts (Cheng, 1986), it was not our intention to evaluate the role of fish in such a context. Rather the significance of this experiment resides in its value as a model system whereby the net effects of infection can be related to increased susceptibility to predation. Secondly, with respect to the adaptive significance to the parasite of interventive mechanisms that increase predation by animals in which the parasite cannot continue development, it is our contention that increased predation by non-definitive and definitive hosts respectively are not necessarily mutually exclusive. Clearly, the heightened activity, elevated distribution, and upwardly directed evasive behaviour will all increase the conspicuousness of infected gammarids to many predators, but they should also make the parasite available to suitable definitive hosts, contact with which would otherwise be precluded by the largely benthic habits of uninfected *G. pulex* (Hughes, 1970) and the surface feeding behaviour of the definitive host.

Although it was not possible in the available time to separate the relative contributions made by altered behavioural responses and/or the formation of a search image related to the bright colour of the cystacanths (Tinbergen, 1960; Bethel and Holmes, 1977) on increased predation, this experiment nevertheless demonstrated that under near-field conditions infected *G. pulex* suffered relatively higher mortality. This, taken in the context of behavioural modifications that potentially increase contact between infected intermediate and the definitive hosts, suggests that *P. minutus* can selectively modify certain aspects of the behavioural repertoire of *G. pulex* in a manner conducive to increased predation by a subset of vertebrate predators which includes the definitive host.

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