# EFFECTS OF THE EYEFLUKE, *DIPLOSTOMUM SPATHACEUM*, ON THE BEHAVIOUR OF DACE (*LEUCISCUS LEUCISCUS*)

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**Abstract.** The behaviour of dace infected with *Diplostomum spathaceum* was investigated in the laboratory. As the number of parasites present in the eye increased, the efficiency with which the fish fed on *Gammarus pulex* declined. The loss of efficiency was compensated for by an increase in the time devoted to feeding. Heavily infected fish spent more time in the surface layers of the water. This may increase the likelihood that a gull might eat the fish and thereby continue the life-cycle of the parasite. The parasite modifies the behaviour of its host in a way that increases the parasite's chances of survival at the expense of the host.

The life-cycle of many parasites involves a dispersal or transport stage in an intermediate host. In many trematodes of the Order Digenea, further development of the parasite occurs only when an appropriate final host eats that part of the intermediate host where the parasite is located. In some cases the infected intermediate host shows behaviour which is markedly different from that of uninfected individuals. Animals which differ in behaviour or appearance, or are diseased and weak, are often more vulnerable to predators (Hornocker 1970; Neill & Cullen 1974). The significance of this phenomenon, as suggested by Rothschild (1962), is that there will be selection for characteristics of parasites which result in an increase in the chances that the intermediate host will be eaten by the final host.

There is increasing evidence that parasites can influence the behaviour of their hosts. The growing literature in this field has been reviewed by Holmes & Bethel (1972), who suggested a number of ways in which the behaviour of intermediate hosts may be changed by parasites so that vulnerability to predation is increased. These include reducing the stamina, increasing the conspicuousness, disorientating and altering the responses of the intermediate host.

We chose to investigate the effects of the eyefluke *Diplostomum spathaceum* (Rudolphi) on the behaviour of the dace, *Leuciscus leuciscus* (L.) because the host is an active fish with several potential predators and any of the possible effects on behaviour listed above could occur. A larval form of the parasite (Fig. 1) lives in the crystalline lens of many species of fresh-water fish. The adult parasites live in gulls and terns (Laridae) which have eaten a parasitized fish (Sudarikov 1964; Crowden in preparation). The *Diplostomum* eggs pass out with the host faeces and hatch in water to a miracidium larva, which penetrates a lymnaeid snail and develops in the digestive gland as a sporocyst. The sporocysts give rise to many cercariae which leave the snail and, if they succeed in attaching to a suitable fish host, penetrate its epidermis and migrate to the eyes, where they develop into metacercariae. It has been noted that some fish species are consistently found to harbour greater numbers of eyeflukes than others (Betterton 1974). Up to 900 parasites have been found in the eyes of a roach *Rutilus rutilus* (L.) (Petrushevski & Shulman 1961). The presence of large numbers of parasites can cause the lens to become opaque (Erasmus 1958). This has resulted in a complete lack of responsiveness to visual stimuli in heavily infected trout (Ferguson & Hayford 1941). The dace feeds on aquatic invertebrates (Hellawell 1974), which it appears to detect visually (Crowden in preparation). It is often parasitized by *Diplostomum* and it thrives in the laboratory.

## Methods

Thirty-two dace 9.5 to 10.5 cm in length were selected from seine net catches from the River Thames at Reading. At the time of the experiments the number of *D. spathaceum* present in the eyes of individual fish was not known. This was determined when autopsies were carried out at the end of each series of tests.

For at least eight weeks after capture the fish were kept in groups of five in glass-sided aquaria 120 × 45 × 45 cm. These were illuminated on a 12 hour light/12 hour dark schedule by means of a 60 W bulb positioned 40 cm above each tank. The water temperature was maintained between 14 C and 16 C. The fish were fed daily on a mixture of *Gammarus*, *Tubifex* and *Daphnia*, which was readily taken. Two weeks before
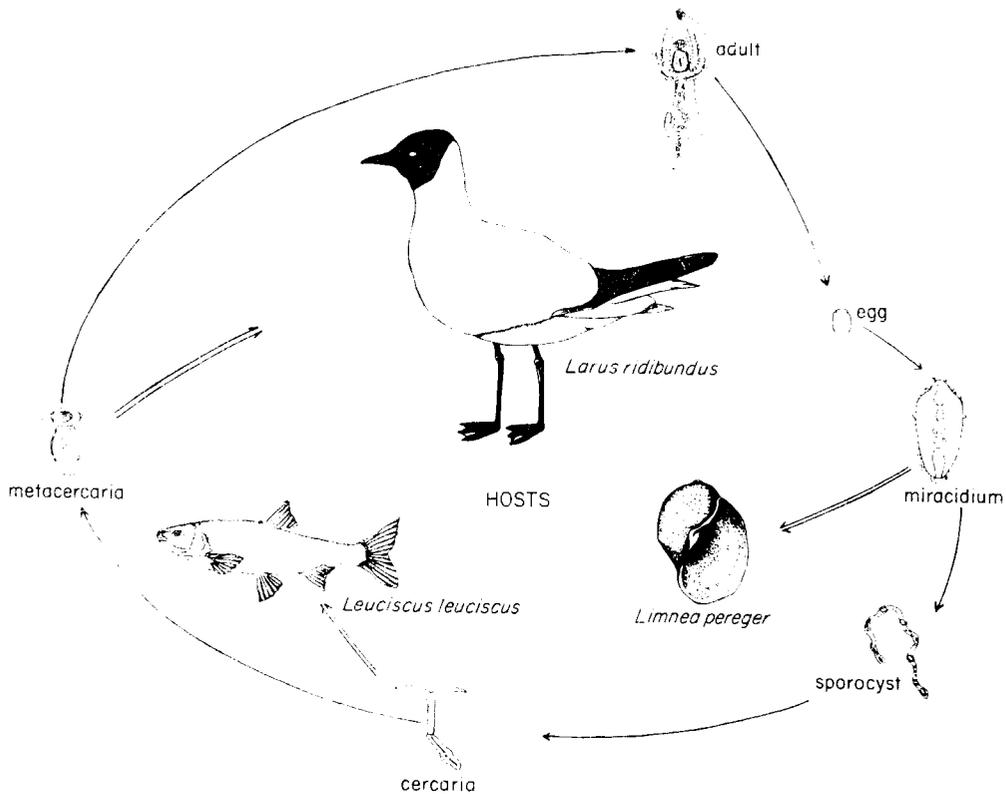
Fig. 1. The life-cycle of *Diplostomum spathaceum* in the River Thames at Reading.

experiments began fish were transferred to individual tanks 120 × 35 × 35 cm, filled with water to a depth of 30 cm. The far wall of each tank was marked with a grid of thirty-six 10 cm squares, each further divided by vertical lines 2 cm apart. This scale was used as an aid when estimating all distances quoted in the results section. Observations were made from inside a portable hide fitted with a large plastic window which acted as a one-way screen, the observer in the hide being in darkness while the tank was illuminated.

The experimental treatment consisted of presenting the fish with live *Gammarus* 6 to 8 mm in body length, and recording the subsequent feeding activities. Each fish was observed once in each of five test situations, the order of which was randomized. In tests 1–3, 50, 25 or 10 prey were introduced into a bare tank, whilst in tests 4 and 5 cover was available and 50 prey were used. The cover consisted of pieces of brown plastic floor tiling 5 × 1 × 0.2 cm, spread evenly over the tank floor to cover 25% (test 4) or 50% (test 5) of the bottom area. *Gammarus* were able to find cover beneath the floor tiles. Tests were begun after 48 h of food deprivation by introducing the *Gammarus* at the water surface. Observation and recording started immediately and continued for 45 minutes. The fish were observed continuously and a note of their behaviour made on a check sheet. The activities recorded were as follows.

(i) **Success.** Capture and swallowing of prey. Each capture was recorded and, if possible, an estimate made of the distance at which the fish first orientated to, or accelerated towards, the prey (the reactive distance).

(ii) **Mistaken responses.** Feeding movements directed towards apparently inedible objects floating in the water or lying on the tank bottom. Many responses were also made in the absence of any visible objects.

(iii) **Missed.** Approach and snap directed towards a *Gammarus* which failed to make contact with the prey.

(iv) **Reject.** Successful capture of prey followed immediately by its rejection.

(v) **Resting.** Time spent inactive, with pectoral, pelvic and caudal fins touching the bottom of the tank.

(vi) **Escape swim.** Time spent swimming vigorously up and down against the sides of the tank.

(vii) **Top 10 cm.** Each visit to the upper 10 cm of the water was recorded, and a note made or its duration.

At the end of each test the subject was removed and transferred to a second tank containing large numbers of *Gammarus*, where it remained undisturbed for 1 h. The surviving *Gammarus* in the test tank were removed and counted as a check on the observed numbers eaten. The tank was cleaned and prepared for the next test (i.e. bare tank or required amount of cover added) and the fish replaced for at least 48 h before retesting.

No tests were continued if any external stimulus disturbed the fish, or more than 10% of the time was spent escape swimming.

### Results

The rate of predation on the *Gammarus* was greatest at the beginning of each feeding trial, and fell in a non-linear fashion (Table I). The prey dispersed rapidly away from the point of introduction, moving towards the bottom, sides and corners of the tank. The dace initially fed in mid-water, later seeking their prey on the bottom of the tank. Feeding was usually vigorous, and there were no indications that any of the fish were suffering any disability. However, analysis of the data reveals significant differences in the performance of individual fish, which were correlated with the number of parasites present in their eyes.

A comparison of linear regressions between individual test data for several of the measures where between-test differences were thought most likely to occur was carried out. No significant differences were found, and the results for the five tests on each fish have therefore been pooled. The results presented are therefore based on a total of 225 min observation of each fish, during which 185 *Gammarus* were available as prey. The results are presented in Figs. 2–7. All dace were infected with at least 17 *D. spathaceum*, but such small numbers occupy only a small proportion of the lens volume.

The number of *Gammarus* eaten by individual fish during the tests varied from 74 to 147, but the numbers eaten were not correlated with the numbers of parasites present (Fig. 2: $r_s = -0.073, P > 0.05$). There was a strong negative correlation between the number of parasites and the maximum distance from which each fish was seen to approach its prey (Fig. 3: $r_s = -0.84, P < 0.01$). The mean value of the reactive distance for each fish was also found to be negatively correlated with the number of parasites ($r_s = -0.57, P < 0.01$).

The fish with most parasites also had high scores for mistaken feeding responses (Fig. 4: $r_s = 0.76, P < 0.01$). The more heavily infected individuals showed ten times as many mistaken responses as those with fewest parasites. Heavily infected fish also missed more often (Fig. 5: $r_s = 0.52, P < 0.01$), usually because the snap was completed before the prey was within range. There was no significant correlation between parasite load and the number of captured prey which were rejected ($r_s = 0.29, P > 0.05$).

The percentage of feeding responses resulting in food capture declined with increasing numbers of parasites, as would be expected from the earlier results (Fig. 6: $r_s = -0.73, P < 0.01$). However, increasing parasite numbers were also associated with an increase in the amount of time spent feeding (Fig. 7: $r_s = 0.81, P < 0.01$).

Table I. Numbers of *Gammarus pulex* Eaten by Dace During Successive 5–minute Periods. Pooled Data for Tests 1 to 5

| | Time period | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 0–5 | 6–10 | 11–15 | 16–20 | 21–25 | 26–30 | 31–35 | 36–40 | 41–45 |
| Total number of *Gammarus* taken (total number 5920) | 2588 | 664 | 338 | 192 | 112 | 73 | 39 | 26 | 15 |
| Number taken as a percentage of number available at the start of each period | 43.7 | 19.9 | 12.7 | 8.2 | 5.2 | 3.6 | 2.0 | 1.4 | 0.8 |

A similar relationship existed for the amount of time spent within 10 cm of the water surface (Fig. 8: $r_s = 0.73, P < 0.01$). The increased time in the surface layers as parasite numbers increased was due to an increase in the number of visits to this part of the tank ($r_s = 0.71, P < 0.01$) as well as an increase in the mean duration of each visit ($r_s = 0.56, P < 0.01$). There were no significant differences between different test situations in the time spent near the surface.

The results for resting ($r_s = 0.25, P > 0.05$) and escape swimming ($r_s = 0.15, P > 0.05$) showed no correlation with the number of parasites. Escape swimming was comparatively rare and the number of records which were not included in the analysis because the fish spent more than 10% of the 45 min escape swimming was 3 out of 163.

## Discussion

This experiment shows that the feeding behaviour of dace and the likelihood that they will be near the surface of the water are significantly affected by the presence of *D. spathaceum*.

These effects on feeding behaviour and on the time spent near the surface are not likely to be confused by any disturbance caused by the observer. All observations were of fish in a 'home' tank and were made from behind a one-way screen. Escape swimming, which has been used as an indication of distress in fish (Keenleyside 1955; Fenderson & Carpenter 1971; Healey 1972), was rare.

The distance at which predators are able to respond to the presence of their prey is an important determinant of their food searching ability (Blaxter & Staines 1971). An increase in the reactive distance will enhance the rate of discovery of prey (Ware 1972). Several factors are known to affect the reactive distance of fish, including the size of the prey (Brawn 1969), previous experience with the prey (Beukema
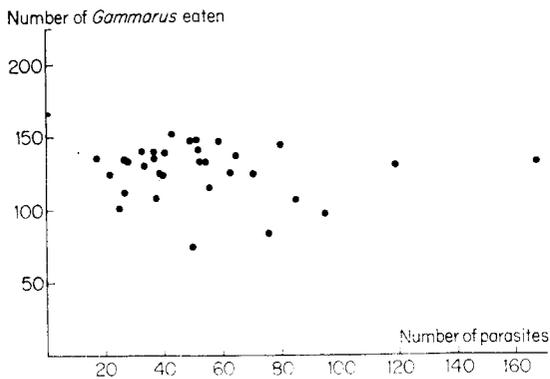


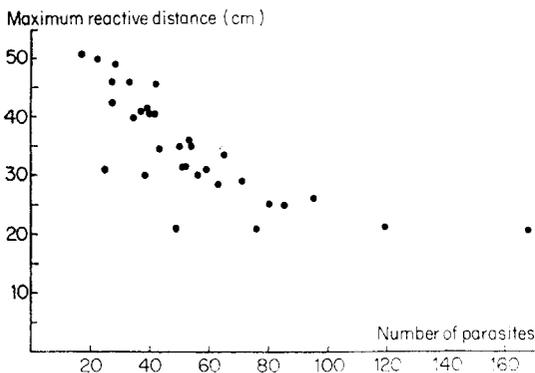Fig. 2. Relationship between numbers of *Gammarus* eaten and the numbers of *D. spathaceum* in the eyes of dace.



Fig. 3. Relationship between maximum reactive distance to prey and numbers of *D. spathaceum* in the eyes of dace.
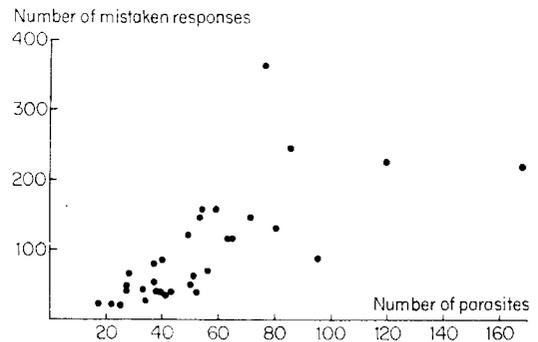


Fig. 4. Relationship between the number of mistaken feeding responses and numbers of *D. spathaceum* in the eyes of dace.
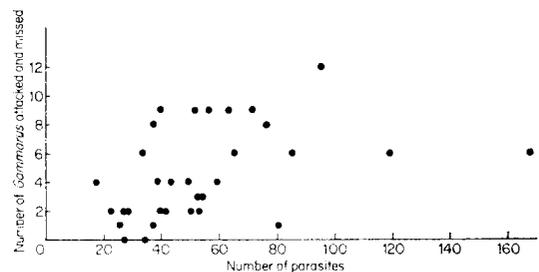


Fig. 5. Relationship between number of *Gammarus* attacked and missed and the numbers of *D. spathaceum* in the eyes of dace.

1968) and the degree of contrast between the prey and background (Ware 1971). The size of the visual field has been recognized as an essential component of models which seek to explain why fish feed selectively on prey of a certain size or species (Ware 1973; Confer & Blades 1975; Moore & Moore 1976a, b). The reduction of both maximum and mean reactive distance with increasing parasite numbers may therefore have a fundamental effect on the feeding strategy of the fish. The amount of undirected swimming necessary before prey are detected will increase, and more energy will be expended for each prey sighting.

Once the prey has been detected it still has to be approached, grasped and swallowed. The significant increase, with increasing parasite load, in number of attacks which missed contributes further to the decline in the efficiency of feeding,

as does the increase in the number of mistaken feeding responses. The effects of these changes are summarized by the marked decline in the percentage of feeding attempts which resulted in food capture. The increase in the amount of time spent feeding in the more heavily infected fish explains why the reduced efficiency of their feeding is not reflected in the number of *Gammarus* which they capture per 45-min test.

In the conditions of the experiment the disabilities produced by the parasite are overcome, but these conditions greatly simplify the natural situation. In natural fish populations it is frequently found that there are no detrimental effects resulting from infections (Chappell 1969; Holmes & Bethel 1972) although there are occasional reports of mass mortalities (Sudarikov 1964). *Diplostomum* epizootics appear to be more serious in fish hatcheries, both as a result of massive cercarial invasion and the subsequent development of metacercariae in the eyes (Ferguson & Hayford 1941; Molnar 1974). A suggestion that large numbers of eyeflukes cause the death of the host by starvation or predation has arisen from the observation that heavily infected individuals often disappear from host populations during the winter (e.g. Pennycuick 1971; Kennedy 1975; Kennedy & Burrough 1977). Although Pennycuick (1971) found that a closely related species, *Diplostomum gasterostei* (Williams) impaired the growth of the three-spined stickleback *Gasterosteus aculeatus* (L.), it is generally very difficult to demonstrate differences in the condition of fish as a result of parasitism (e.g. Rabideau & Self 1953; Pitt &
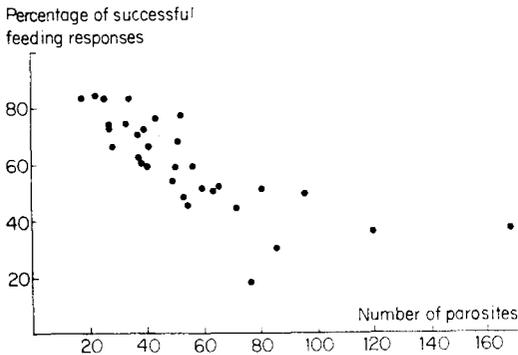


Fig. 6. Relationship between percentage of feeding responses resulting in prey capture and numbers of *D. spathaceum* in the eyes of dace.
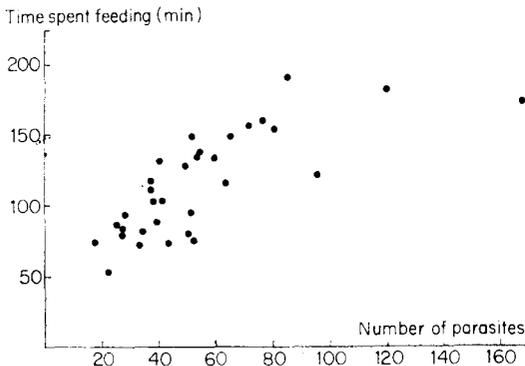


Fig. 7. Relationship between time spent feeding and the numbers of *D. spathaceum* in the eyes of dace.
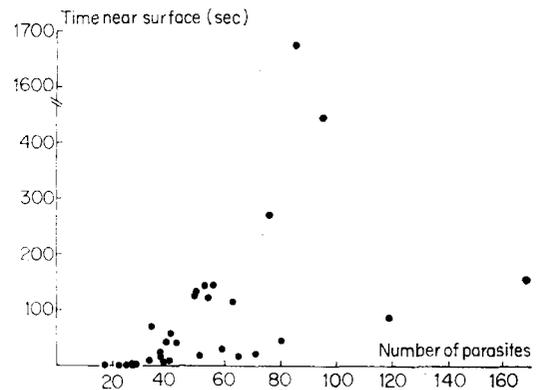


Fig. 8. Relationship between time spent in the top 10 cm of the water and number of *D. spathaceum* in the eyes of dace.

Grundmann 1957). The most commonly used measure in this connection is the condition factor, which compares the relationship between weight and length for individual fish (see Ricker 1971). However, condition factor is affected by the age, sex and habitat of the fish and by the time of year, so parasite effects are readily masked. There is no evidence that *D. spathaceum* affects the condition of Thames dace (A. D. Berrie, personal communication; Crowden in preparation). This is consistent with the experimental observations indicating that over the range of parasite numbers encountered, individual dace are able to modify their feeding to maintain a constant food intake. It therefore seems unlikely that many Thames dace starve as a result of parasitism by *D. spathaceum*. It is possible, however, that in adverse conditions the impaired feeding efficiency of the heavily parasitized dace might result in more of them dying. Some of those which die might be eaten by gulls. Individuals which are weakened by inadequate feeding or which can see less well than less heavily parasitized fish may be more likely to be caught by gulls or terns if they visit the surface of the water. Heavily infected fish did visit the water surface more frequently, and for longer periods, than did lightly infected fish. Dace often feed at the surface (Wheeler 1969) but they usually make brief visits to the surface. The parasitized fish either remained motionless or moved slowly around just below the surface without attempting to feed. The proportion of time spent near the surface was still small compared to the time spent at lower levels, but the increase might well be enough to cause a significant increase in vulnerability to avian predators. The main definitive host in the study area is believed to be the black-headed gull (*Larus ridibundus* L.) (Crowden in preparation). This bird does not dive as terns do but it is capable of submerging briefly by plunge-diving (Haviland 1915). It has been suggested, therefore, that only those fish swimming within 12 cm of the surface are vulnerable to gull predation (Collinge 1927, quoted by Vernon 1972).

It appears that *D. spathaceum* can be considered as another example of a parasite whose presence can result in a change in the host's behaviour such that the total number of parasites reaching the next host is increased. Dawkins (1978) has described effects of this type in terms of parasite genes manipulating the behaviour of the host so that they spread in the parasite popu-lation. How much the frequency of such phenotypic effects is the result of the direct action of natural selection and how much they have arisen as beneficial side effects of selection acting on some other characteristic of parasite or host is a matter for speculation. One important difference from other known examples of such parasite effects is that many *Diplostomum* have a greater effect than a few. Ants infected with metacercariae of *Dendrocoelium dendriticum* (Rudolphi) have radically altered behaviour, apparently caused by the presence of one or two metacercariae encysted near the suboesophageal ganglion (Carney 1969). Gammarids infected with a single *Polymorphus paradoxus* (Connell & Corner) show marked alterations of their normal responses to light and disturbance (Bethel & Holmes 1973). Fish infected with single *Ligula intestinalis* (L.) have distorted inflexible bodies (Harris & Wheeler 1974) and are sluggish, less gregarious and found in shallower water than uninfected fish (Dence 1958; Holmes & Bethel 1972). Similar results have been obtained for sticklebacks *G. aculeatus* infected with as few as one *Schistocephalus solidus* (Muller) (Lester 1971). The changes reported in this paper are greatest for the larger parasite numbers. Small numbers of parasites appear to have very little effect. This is an important consideration, since in areas where this parasite is found, a very large proportion of the fish population may become infected (e.g. Chappell 1969; Pennycuick 1971; Wootten 1974; Crowden in preparation). The parasite population is usually aggregated in the host population, with a small number of hosts supporting a disproportionately large number of parasites (Kennedy & Burrough 1977; Crowden in preparation). In the case of *D. spathaceum*, where the effects of the parasite are cumulative, this means that potentially harmful effects are confined to relatively few hosts. This minimizes the harm to the host population and the death of a single heavily infected host removes a large number of parasites from the population. This form of statistical distribution determines the regulatory influences of the parasite on host population growth as well as the stability of the host–parasite interaction (Anderson 1978; Anderson & May 1978; Anderson et al. 1978).

A measure of the success of this parasite is its almost ubiquitous distribution in the fish populations of still and slowly moving water bodies of the northern hemisphere.

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