Experimental demonstration of a behavioural modification in a cyprinid fish, *Rutilus rutilus* (L.), induced by a parasite, *Ligula intestinalis* (L.)

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Abstract: Behavioural changes in parasitized hosts have been experimentally investigated by comparing the swimming behaviour of roach, *Rutilus rutilus*, infected by the tapeworm *Ligula intestinalis* with that of uninfected roach when they were exposed to the same overhead heron stimulus. Before the stimulus was presented, infected fish swam close to the surface and uninfected fish were preferentially found near the bottom of the tank. The stimulus clearly induced a change in the vertical distribution of infected fish only. On the other hand, infected roach were less active than uninfected fish before, during, and after the stimulus was presented. Proximate mechanisms of these behavioural changes are discussed. These behavioural differences, i.e., roach surfacing, swimming, and response to stimulus, probably favour the predation of infected roach by avian predators.

Résumé : Les modifications du comportement chez des organismes parasités ont été étudiées expérimentalement par comparaison du comportement de nage chez des gardons *Rutilus rutilus* infectés par le cestode *Ligula intestinalis* et chez des gardons sains, particulièrement quand ils étaient exposés au même stimulus, un héron en surplomb. Avant l'introduction du héron, les poissons infectés nageaient près de la surface et les poissons sains semblaient préférer le fond de l'aquarium. Le stimulus a déclenché un changement dans la répartition verticale, mais seulement chez les poissons infectés. Par ailleurs, les poissons infectés étaient moins actifs que les poissons sains avant, pendant et après l'introduction du prédateur. Les mécanismes immédiats qui régissent les changements de comportement sont examinés. Ces différences de comportement, retour en surface, nage et réponse au stimulus, favorisent probablement la prédation des gardons infectés par des oiseaux prédateurs.

[Traduit par la Rédaction]

Introduction

Phenotypic changes in parasitized animals have been reported in a large range of host–parasite systems (Moore 1984; Barnard and Behnke 1990; Combes 1991, 1995; Adamo 1997; Poulin 1998; Poulin and Thomas 1999; Arnott et al. 2000). Although the adaptive value of these changes is sometimes difficult to assess (e.g., Poulin 1995), many have been considered adaptations for parasite transmission (e.g., Holmes and Bethel 1972; Curtis 1987; Combes 1991; Moore 1993; Maitland 1994; Poulin 1994; Vance 1996; Kuris 1997). Behavioural changes making intermediate hosts more susceptible to predation by the parasite's next host have been documented in some trophically transmitted parasites (see Poulin 1994; Lafferty 1999), but in most cases the ecological results of behavioural changes have not been examined. For instance, parasitized intermediate hosts may experience a higher risk of predation by final hosts because of impaired motor performance (e.g., Hay and Aitken 1984), increased or decreased activity levels (e.g., Gotelli and Moore 1992; Poulin et al. 1992), or direct movement toward the microhabitats of foraging predators (e.g., Helluy 1984; Lafferty and Morris 1996; Thomas and Poulin 1998; Berdoy et al. 2000).

The tapeworm *Ligula intestinalis* has a three-host life-cycle (Rosen 1920). The coracidium larva penetrates the gut wall of a copepod microcrustacean and develops into the procercoid form in the haemocoel. The infected copepod is ingested by a planktivorous cyprinid fish and the procercoid then develops into a plerocercoid larva located in the host's abdominal cavity. The cycle of the parasite is completed when the fish is preyed upon by a piscivorous bird, and the plerocercoid then matures in the host's intestine. Several studies have shown that plerocercoids have severe effects on fish viability and behaviour (Moisan 1956; Arme and Owen 1968, 1970; Sweeting 1975, 1976; Taylor and Hoole 1989; Wyatt and Kennedy 1989). Field observations suggest that

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L. intestinalis is able to alter the spatial distribution of fish, making them prefer shallower and more inshore areas than non-infected conspecifics (Bean and Winfield 1992; Loot et al. 2001*a*). Other field studies have reported that fish harbouring plerocercoids of *L. intestinalis* also experience an increased risk of being preyed upon by avian predators such as black-headed gulls, *Larus ridibundus* (Harris and Wheeler 1974), or cormorants, *Phalacrocorax carbo* (Van Dobben 1952). These findings support the hypothesis that *L. intestinalis* alters the behaviour of fish in a way that favours its transmission to avian definitive hosts.

The aim of the present study was to examine the influence of *L. intestinalis* on roach, *Rutilus rutilus* (L.), behaviour under experimental conditions. For this purpose we monitored the behaviour of uninfected and infected specimens in the laboratory before, during, and after an overhead predator stimulus was presented by recording (*i*) the vertical distribution of the fish, (*ii*) distance swum, and (*iii*) swimming speed. We discuss our results in relation to current ideas on how parasites alter the behaviour of their hosts and increase trophic transmission.

Material and methods

Animals

Roach specimens were seine-netted in the Lavernose-Lacasse gravel pit near Toulouse in southwest France in mid-March 2000. They were kept in a 200-L aquarium in the laboratory with a 12 h light : 12 h dark photoperiod, a constant temperature of 19°C, and constant oxygen concentration in the water (6.5 mg/L). Fish were kept in these conditions for 14 days to acclimatize them. Storage and experimental tanks were located in the same room, providing identical conditions for fish after their transfer.

All roach specimens used were 3 years old. The lengths of infected and uninfected roach (118.19 ± 1.3 mm (mean ± SD) vs. 120.64 ± 1.3 mm) were not significantly different (*t* test, $P = 0.17$). There was, however, a significant mean difference in mass between infected (18.28 ± 0.23 g (mean ± SD) and uninfected roach (17.07 ± 0.44 g) (*t* test, $P = 0.008$). The mean number of plerocercoids was 9.17 ± 1.49 (mean ± SD), contributing up to about 29% of the total mass of infected fish used in the experimentation.

Procedure

After the 2 weeks' acclimation, 12 infected and 12 uninfected roach were used in the experiment. We carried out the same experiment three times, transferring four infected and four uninfected fish to an experimental tank (100 × 50 × 50 cm; the height of the water was 40 cm) 24 h before starting the experiment. The overhead predator stimulus was standardized by suddenly lowering the head of a stuffed heron into the experimental tank so that the tip of the bill hit the water surface. We recorded fish behaviour for 14 min: 7 min before, 1 min during, and 6 min after the overhead predator stimulus was presented, using two video cameras placed in front of two perpendicular tank sides to provide a 3D recording of each fish. The far wall was marked with a 5 × 4 grid of 10-cm squares for side 1 and a 10 × 4 grid of 10-cm squares for side 2. The grids were used to plot, second by second, the position of each fish's eye using three coordinates (x, y, z). The position of the fish was used to quantify the vertical distribution of fish within the water column, to measure the distance swum and the swimming speed before, during, and after presentation of the stimulus.

The vertical distribution of fish was expressed as the time (in seconds) spent by each roach in four 10-cm layers of the water column (L1–L4). The distance swum by the fish was measured by summing the vector norms. Swimming speed was calculated as the mean of the vector norms between two fish positions, excluding vectors equal to zero. As the behaviour of the eight fish may have differed from one experiment to another, as a basis for comparison we used an index consisting of the ratio of the measurement for a given individual and the mean measurement for the seven other individuals in the same experiment. We used non-parametric statistics, i.e., Friedman's test and Nemenyi's multiple comparisons, to test the vertical distribution and compare indices before, during, and after the stimulus was presented, and a Mann–Whitney test to compare fish position, distance swum, and swimming speed between infected and uninfected fish (Zar 1996). All the tests were two-tailed and the results were considered to be significant at the 5% level (Sokal and Rohlf 1995). All analyses and statistical graphics were performed using SPSS release 8 for Windows (Norusis 1993).

Results

The influence of *L. intestinalis* on the vertical distribution of roach is summarized in Fig. 1. Before the predator overhead stimulus was presented, 10 of the 12 infected roach swam in the upper layer of the water column, while 11 of the uninfected roach only swam in the lower layer and this difference was found to be significant (Fig. 1*a*, Tables 1, 2, and 3A). The overhead predator stimulus clearly induced a change in the vertical distribution of infected fish only. Indeed, the stimulus led to displacement of all infected fish toward the bottom of the tank (Fig. 1*b*), where they spent more time swimming in layers 3, 2, and 1, significantly abandoning the upper layer (Tables 1, 2, and 3A). At the same time the stimulus did not influence the vertical distribution of uninfected fish swimming in the lowest layer (or layer 2 for at least one specimen). From 1 to 7 min after the stimulus was presented, infected fish tended to recover their initial position near the surface of the water (Fig. 1*c*), then the vertical distribution within the four layers was quite similar (non-significant Friedman's test; Table 2). Meanwhile, all uninfected fish remained in the lower layer (Tables 2, 3A).

The influence of *L. intestinalis* on the distance swum by each roach is presented in Fig. 2. There was no significant difference between infected and uninfected fish in the three parts of the recording (Table 2). The distance swum did not differ significantly between infected and uninfected fish before and after the overhead predator stimulus was presented (Table 1). However, during the stimulus, infected roach covered a greater distance than the uninfected fish (Table 1). This difference mainly resulted from a small, nonsignificant decrease in the distance swum by seven uninfected fish and

Table 1. Results of a Mann–Whitney test of the vertical position of infected and uninfected roach, *Rutilus rutilus*, within four layers (L1–L4) in an experimental tank before, during, and after presentation of an overhead predator stimulus, with indices of distance swum and swimming speed.

	U	df	*P*
Fish position			
Before stimulus			
L1	16.5	1	<0.001***
L2	60.5	1	0.510 ns
L3	24.0	1	0.003**
L4	15.5	1	<0.001***
During stimulus			
L1	21.5	1	0.002**
L2	33.0	1	0.024*
L3	24.0	1	0.005**
L4	39.5	1	0.060 ns
After stimulus			
L1	29.0	1	0.012*
L2	37.5	1	0.045*
L3	42.0	1	0.089 ns
L4	40.0	1	0.068 ns
Distance swum			
Before stimulus	49.0	1	0.198 ns
During stimulus	38.0	1	0.050*
After stimulus	63.0	1	0.630 ns
Swimming speed			
Before stimulus	24.0	1	0.005**
During stimulus	17.0	1	0.001***
After stimulus	19.0	1	0.001***

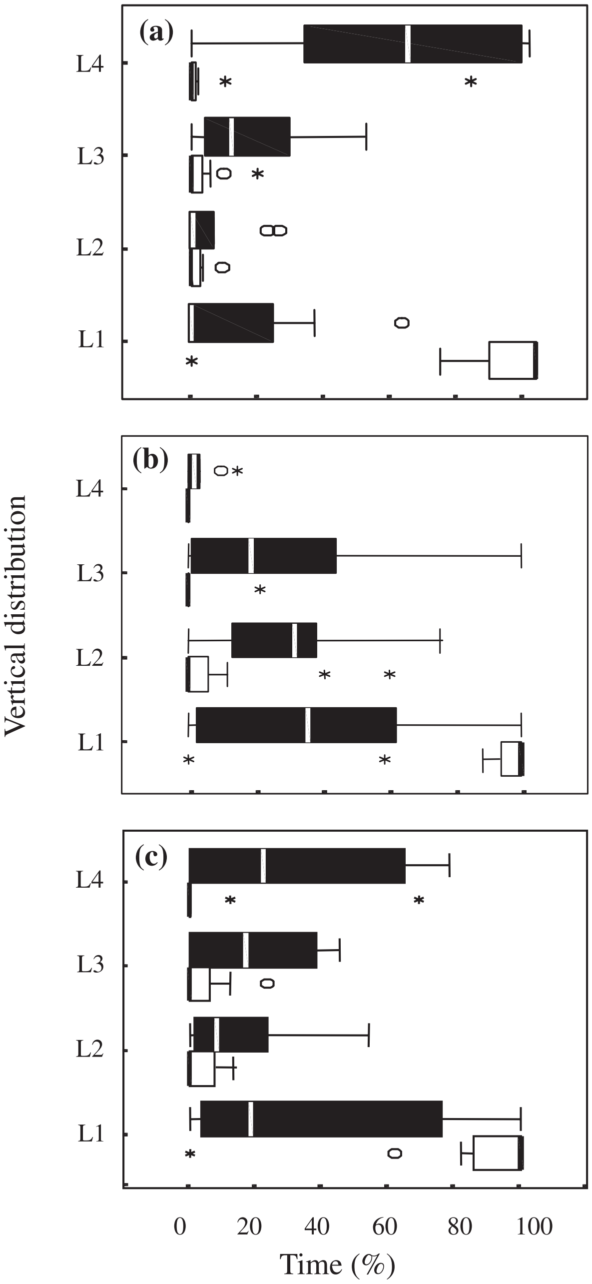
Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

Table 2. Results of Friedman's test of the vertical position of infected and uninfected fish within the four layers (L1–L4) of the experimental tank before, during, and after presentation of the stimulus, with indices of distance swum and swimming speed.

	S	df	*P*
Fish position			
Before stimulus			
Infected fish	11.83	3	0.008**
Uninfected fish	21.72	3	<0.001***
During stimulus			
Infected fish	9.53	3	0.023*
Uninfected fish	22.98	3	<0.001***
After stimulus			
Infected fish	1.50	3	0.682 ns
Uninfected fish	20.53	3	<0.001***
Distance swum			
Infected fish	1.17	2	0.558 ns
Uninfected fish	5.17	2	0.076 ns
Swimming speed			
Infected fish	12.50	2	0.002***
Uninfected fish	6.17	2	0.046*

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

Fig. 1. Vertical distribution of 12 infected and 12 uninfected roach, *Rutilus rutilus*, expressed as the time (%) spent by each fish in four 10-cm layers of the water column, L1 (bottom to 10 cm), L2 (10–20 cm), L3 (20–30 cm), and L4 (30 cm to surface), before (7 min), during (1 min), and after (6 min) presentation of a stimulus. The median (the vertical line inside the rectangle), 25th percentile (the left boundary of the rectangle), and 75th percentile (the right boundary of the rectangle) are shown on the box plots. Fifty percent of the cases have values within the box. Open circles represent units in which values were more than 1.5 box lengths from the 75th percentile (outliers). Solid box plots represent infected roach and open box plots represent uninfected roach (*, $P < 0.05$).



a small, nonsignificant increase in the distance swum by most infected fish.

Finally, the influence of *L. intestinalis* on the swimming speed of the roach is presented in Fig. 3. Uninfected roach

Fig. 2. Index of distance swum for infected and uninfected roach before (7 min), during (1 min), and after (7 min) presentation of the stimulus. The median (the vertical line inside the rectangle), 25th percentile (the left boundary of the rectangle), and 75th percentile (the right boundary of the rectangle) are shown on the box plots. Fifty percent of the cases have values within the box. Open circles represent units in which values were more than 1.5 box lengths from the 75th percentile (outliers). Solid box plots represent infected roach and open box plots represent uninfected roach.

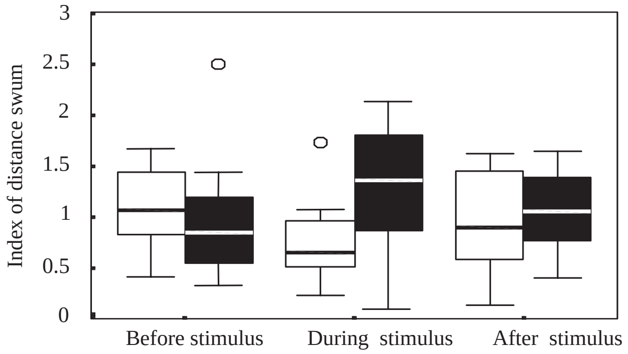


Fig. 3. Index of swimming speed for infected and uninfected roach before (7 min), during (1 min), and after (6 min) presentation of the stimulus. The median (the vertical line inside the rectangle), 25th percentile (the left boundary of the rectangle), and 75th percentile (the right boundary of the rectangle) are shown on the box plots. Fifty percent of the cases have values within the box. Open circles represent units in which values were more than 1.5 box lengths from the 75th percentile (outliers). Solid box plots represent infected roach and open box plots represent uninfected roach.

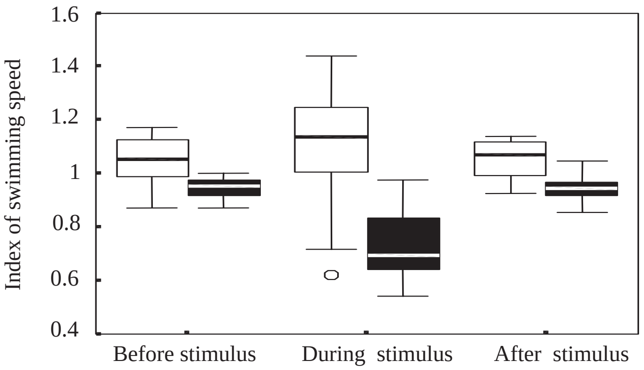


Table 3. Results of Nemenyi's multiple comparisons to test the vertical positions (L1–L4) and index of swimming speed of infected and uninfected fish before, during, and after presentation of the stimulus.

(A) Vertical position.

	Infected fish				Uninfected fish			
	L1	L2	L3	L4	L1	L2	L3	L4
Before stimulus								
L1		0.89	–2.01	–3.35		4.02	5.14	4.69
L2	ns		–2.90	–4.24	***		1.11	0.67
L3	ns	*		–1.34	***	ns		–0.44
L4	**	***	ns		***	ns	ns	
During stimulus								
L1		–0.55	0.44	3.24		3.80	4.69	4.91
L2	ns		1.00	3.80	***		0.89	1.11
L3	ns	ns		2.79	***	ns		0.22
L4	**	***	*		***	ns	ns	
After stimulus								
L1						3.80	4.91	4.69
L2					***		1.11	0.89
L3					***	ns		–0.22
L4					***	ns	ns	

(B) Swimming speed.

	Infected fish			Uninfected fish		
	Before stimulus	During stimulus	After stimulus	Before stimulus	During stimulus	After stimulus
Before stimulus		4.47	0.28		–3.17	–0.28
During stimulus	***		–4.18	**		2.88
After stimulus	ns	***		ns	*	

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

were significantly more active than infected fish before, during, and after the stimulus (Table 1). The overhead predator stimulus had a brief influence on both infected and uninfected fish, inducing a significant decrease in swimming speed of infected fish and a significant increase for uninfected fish (Tables 2C, 3B). Thus, infected fish appeared to be much less active than uninfected fish in escaping predation by birds.

Discussion

This experimental study clearly shows significant differences in the behaviour of roach when infected by plerocercoid larvae of *L. intestinalis*. Before the overhead predator stimulus was presented, infected fish swam close to the water surface, whereas uninfected fish swam near the bottom of the tank. Infected fish covered the same distance as uninfected fish but were less active. When exposed to the overhead heron stimulus, infected fish swam down to the bottom, whereas uninfected individuals remained near the bottom and moved less. Infected roach were also less active than uninfected fish during presentation of the predation stimulus. Finally, after the predation stimulus was presented, infected fish returned to their location near the surface and recovered their initial swimming distance and swimming speed.

Because we used naturally infected fish, our results must be considered with caution, since we cannot exclude the possibility that their modified behaviour is the cause rather than the consequence of the infestation (Poulin 1995). Assuming, however, that the observed changes resulted from the presence of plerocercoids, the results of our experiment suggest that alterations in the behaviour of infected roach are likely to favour the transmission of the parasite to avian predators. Indeed, as infected roach (*i*) swim near the surface, (*ii*) have low mobility, and (*iii*) swim greater distances during predator attack, these three factors are likely to increase capture by visually oriented avian predators. In addition to these behavioural alterations, the swollen abdomens of infected fish display white stripes from a dorsal "predator's eye" view. Various authors have suggested that this characteristic would make infected fish more vulnerable to predation by piscivorous birds (Van Dobben 1952; Sweeting 1976). Further studies using a true predator would be necessary to confirm that the behavioural alterations in infected roach render them more likely to be eaten by avian predators, and also to assess the impact of the interaction between the behaviour and the colour of infected roach on their predation risk (for instance, see Bakker et al. 1997).

Several mechanisms could explain the behavioural alterations in infected roach. First, it is possible that such behavioural changes result from important parasite-induced physiological alterations in fish. For instance, Lester (1971) found that the respiratory rate of sticklebacks (*Gasterosteus aculeatus*) infected by the cestode *Schistocephalus solidus* was higher than that of uninfected fish. The greater respiratory requirements may then lead the stickleback to modify its behaviour (Giles 1987). Giles (1983) suggested that the oxygen demand of the parasite might force the stickleback to quickly return to near the water surface to satisfy its oxygen debt after an overhead predator stimulus was presented. This physiological alteration could also explain the decrease in host mobility. Lester (1971) found that heavily infected fish did not swim continuously at speeds over one body length per second, and that the oxygen consumption of infected fish increased dramatically during faster swimming. He suggested that the behaviour of infected fish might be due to their seeking well-oxygenated water and attempting to avoid excessive activity; this could be related to their swollen abdomens increasing water resistance. In our experiment, the oxygen concentration of the water was consistently high, so further experiments would be necessary to assess the relevance of this hypothesis to our system.

An altered response to light might explain the differences in host behaviour that we observed. For instance, Holmes and Bethel (1972) showed that gammarids infected with *Polymorphus paradoxus* clung to material on or near the surface of the water, whereas uninfected gammarids did not. The authors associated these results with positive phototaxis. We do not favour this hypothesis because, regardless of whether the water column was in the dark or illuminated all round, the infected fish still swam close to the surface (G. Loot, personal observation).

Another hypothesis that may explain these behavioural modifications is that *L. intestinalis* stimulates roach foraging behaviour by increasing feeding motivation. For instance, plerocercoid larvae of the cestode *S. solidus*, through a nutrient/energy drain, increased the nutritional demand of infected sticklebacks and stimulated their foraging behaviour (Walkey and Meakins 1970; Pascoe and Mattey 1977; Giles 1983; Milinski 1985; Godin and Sproul 1988). The altered behaviour of infected roach could have resulted from a change of foraging behaviour. The swimming speed of infected roach was slower than that of uninfected fish, possibly because of a change in foraging behaviour. At the site where the fish were sampled, *L. intestinalis* grows markedly in the host's body cavity and can reach 30 cm in length. Three-year-old roach specimens were the most heavily infected, with a parasite abundance of 5.98 ± 0.25 (mean ± SD), making up about 17.5% of the total fish mass. The parasite could therefore substantially increase the feeding motivation of an infected host, making it forage sooner than uninfected fish after an overhead predator stimulus was presented during our experimentation.

A last hypothesis is that roach infected with *L. intestinalis* exhibit altered shoaling behaviour because the parasite changes the costs and benefits involved in this process. For an individual, the two main benefits of joining a shoal of conspecifics are protection against predation (Pitcher and Parrish 1993) and enhanced food detection (Pitcher et al. 1982; Street and Hart 1985). However, the major costs of group living are competition for resources (Bertram 1978) and increased visibility. The decision of fish to join a shoal is likely to depend on the outcome of the trade-offs between the costs and benefits involved (Barber and Huntingford 1995). For infected fish, whose competitive ability is often reduced, moving near the surface may be a way to leave the shoal and limit competition. In accordance with this hypothesis, Orr (1966) found that infected rudd (*Scardinius erythrophthalmus*) did not join spawning shoals. Similarly, Dence (1958) reported that infected shiners (*Notropis cornutus*) were sluggish, less gregarious than uninfected fish, and frequented the shallower, warmer waters by the shore, even when avian predators were near. Further experiments would be necessary to study the interactive behaviour of roach infected and not infected with *L. intestinalis*.

Whatever the exact proximal cause(s) of the behavioural alteration observed in roach, these results demonstrate a relationship between *L. intestinalis* infestation and roach surfacing, swimming, and response to bird attack. The simplest explanation is that these changes are non-adaptive incidental side effects of parasitic infection (see Loot et al. 2001*b*). Nonetheless, the complex nature of certain parasite-induced changes is suggestive of adaptive modification (Dawkins 1986), and although a true predation test and experimental infestation would be useful, our experimental results are in accordance with the hypothesis that the parasite “modifies” the host’s behaviour to enhance its own chances of transmission.

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