

Conflict between co-occurring manipulative parasites? An experimental study of the joint influence of two acanthocephalan parasites on the behaviour of *Gammarus pulex*

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SUMMARY

When two parasite species are manipulators and have different definitive hosts, there is a potential for conflict between them. Selection may then exist for either avoiding hosts infected with conflicting parasites, or for hijacking, i.e. competitive processes to gain control of the intermediate host. The evidence for both phenomena depends largely on the study of the relative competitive abilities of parasites within their common intermediate host. We studied the effects of simultaneous infection by a fish acanthocephalan parasite, *Pomphorhynchus laevis*, and a bird acanthocephalan parasite, *Polymorphus minutus*, on the behaviour of their common intermediate host, the amphipod *Gammarus pulex*. We compared the reaction to light and vertical distribution of individuals infected with both parasites to those of individuals harbouring a single parasite species and uninfected ones under controlled conditions. Compared to uninfected gammarids that were photophobic and tended to remain at the bottom of the water column, *P. laevis*-infected gammarids were attracted to light, whereas *P. minutus*-infected individuals showed a modified vertical distribution and were swimming closer to the water surface. The effects of both *P. laevis* and *P. minutus* appeared to be dependent only on their presence, not on their intensity. Depending on the behavioural trait under study, however, the outcome of the antagonism between *P. laevis* and *P. minutus* differed. The vertical distribution of gammarids harbouring both parasites was half-way between those of *P. laevis*- and *P. minutus*-infected individuals, whereas *P. laevis* was able to induce altered reaction to light even in the presence of *P. minutus*. We discuss our results in relation to the occurrence of active avoidance or hijacking between conflicting manipulative parasites and provide some recommendations for future research.

Key words: *Pomphorhynchus laevis*, *Polymorphus minutus*, *Gammarus pulex*, parasite increased trophic transmission, manipulation.

INTRODUCTION

Many parasites have complex life-cycles including a transient phase in an intermediate host, followed by passive transfer to the definitive host through a predator-prey system. In some species, the transmission to the definitive host can be enhanced through the ability of the parasite to alter its intermediate host's behaviour (parasite-induced trophic transmission, Lafferty (1999) and see Dobson (1988) and Poulin (1994) for reviews). This phenomenon of manipulation is particularly common in acanthocephalan parasites (e.g. Bethel & Holmes, 1977; Moore, 1983; Hechtel, Johnson & Juliano, 1993; Hays & Ojeda, 1998).

In some cases, more than 1 species of trophically transmitted parasite may exploit the same intermediate host in sympatry. Recently, Lafferty (1999) has described the various qualitative interactions

that may occur when 2 different parasites rely on the same species as intermediate host. Of particular interest is the situation that occurs when the 2 parasite species have different definitive hosts. A non-manipulative species that becomes associated with a manipulative one whose destination is a different definitive host can then be considered as an 'unlucky passenger'. If both parasites are manipulators, there is a potential for conflict between them. Lafferty (1999) suggested that there may be selection for either avoiding hosts infected with conflicting parasites, or for competitive processes to gain control of the intermediate host, what he described as 'hijacking'. So far, potential conflict between parasites has been documented for only a few species (Lafferty, 1999). For instance, the rat tapeworm *Hymenolepis diminuta* and the chicken tapeworm *Raillietina cesticillus* depend on the same beetles as intermediate hosts for trophic transmission, and both parasites can alter beetle behaviour to enhance their transmission (Graham, 1966; Robb & Reid, 1996). *R. cesticillus* has been shown to prevent the

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establishment of *H. diminuta* (Gordon & Whitfield, 1985), a possible case of hijacking defence (Lafferty, 1999).

The evidence for both active avoidance of hosts infected with conflicting parasites and hijacking depends largely on the study of competitive abilities of parasites within their common intermediate host. However, so far, to our knowledge, no study has quantified the behaviour of hosts infected with conflicting manipulators. Here we present results from the first quantitative study of the effect of simultaneous infection by a fish acanthocephalan parasite, *Pomphorhynchus laevis*, and a bird acanthocephalan parasite, *Polymorphus minutus*, on the behaviour of their common intermediate host, the amphipod *Gammarus pulex*. The aim of the present study was to compare the behaviour of uninfected, *P. laevis*-infected, *P. minutus*-infected, and doubly-infected gammarids in response to light and gravity. Species belonging to the genera *Polymorphus* and *Pomphorhynchus* are known to alter responses to light in their intermediate hosts (Hindsbo, 1972; Bethel & Holmes, 1973; Kennedy, Broughton & Hine, 1978; Bakker, Mazzi & Zala, 1997; Maynard *et al.* 1998). Infected individuals tend to move towards light, whereas uninfected ones tend to remain in the shade. In addition, *G. lacustris* infected with *P. minutus* tend to swim closer to the surface (Hindsbo, 1972) where they become an easy prey for dabbling ducks, a definitive host for the parasite. We thus studied separately reaction to light and vertical distribution in singly- or doubly-infected, and uninfected gammarids under controlled conditions in the laboratory. We discuss the relevance of our results as empirical support for the occurrence of active avoidance or hijacking between conflicting manipulative parasites in the wild.

MATERIALS AND METHODS

P. laevis is a non-specific parasite and adults have been recorded in a large range of freshwater fish species (Hine & Kennedy, 1974). *P. minutus* can use various species of waterbirds as definitive hosts (Hynes & Nicholas, 1958). Both *P. laevis* and *P. minutus* modify the appearance of their gammarid intermediate host. The cystacanths of *P. laevis* are yellow–orange, whereas those of *P. minutus* are orange–red. Both parasites can be seen through the cuticle of infected gammarids that then show conspicuous orange dots. In addition to modified appearance, cystacanths of *P. laevis* are known to induce various changes in their intermediate host's phenotype. Infected gammarids show reduced O₂ consumption (Rumpus & Kennedy, 1974), increased haemocyanin concentration (Bentley & Hurd, 1993, 1996), and altered reaction towards light (Kennedy *et al.* 1978; Bakker *et al.* 1997). The extent of

physiological and behavioural modifications induced by *P. minutus* on *G. pulex* has received less attention. Crompton (1970) found, however, that infected *G. pulex* had to increase food consumption and ventilation rate to compensate for glucose uptake and oxygen consumption by the parasite. Hindsbo (1972) observed in the closely-related species *Gammarus lacustris* that individuals infected with *P. minutus* showed a higher positive phototropism compared with uninfected individuals.

Infected and uninfected *Gammarus pulex* were freshly collected with a hand net in the river Ouche at the Parc de la Colombière (Dijon, eastern France) in April and May 1999. There, the prevalences of *P. laevis* and *P. minutus* were about 10 and 5% respectively (F. Cézilly, unpublished results). We actively searched for infected individuals in order to collect about the same numbers of individuals harbouring a single species and of uninfected individuals. However, due to their relative scarcity in the field, we could collect only a limited number of individuals infected by both parasites. In the laboratory, gammarids were kept in an aquarium (40 × 20 × 30 cm) filled with 5 litres of water taken in the Ouche mixed with 2 litres of tap water. The temperature in the aquarium was kept constant (15 ± 1 °C). All individuals were used in 2 distinct experiments (with randomized order of presentation) within 48 h following their capture. At the end of the experiments, individuals were killed, sexed, measured in length, and dissected to evaluate precisely their parasite load.

Vertical distribution

We studied the swimming position of individual gammarids in cylinders made of translucent plastic film measuring 5 cm in diameter and 30 cm in height. During an experiment, a cylinder was placed in an aquarium (80 × 40 × 30 cm) filled with water at 15 °C, filtered and aerated between experiments. A graduation was marked with permanent ink on the cylinders to define 6 levels of equal height (5 cm). Ambient light was provided by 60 W daylight fluorescent tubes 2 metres above the aquarium. The bottom and the top of the aquarium were covered with black plastic to avoid attraction to the source of light. Preliminary measurements using a photosensitive cell showed that light intensity was then uniform within the cylinder. At the beginning of each trial, a single individual was introduced in the cylinder. After 5 min of acclimation, the position of the individual was recorded each 30 s, and a score ranging from 1 (bottom level) to 6 (top level) was given according to the swimming position within the water column. The overall performance of each individual was estimated from the sum of scores. Each individual was used only once in this setup.

Reaction to light

In order to evaluate the magnitude of photoreaction, we used an apparatus similar to that used by Kennedy *et al.* (1978) and Bakker *et al.* (1997). The distribution of individual gammarids in response to light was quantified in a plastic aquarium (40 × 20 × 20 cm) filled with 4 cm clear water and providing a choice between light and dark zones. The bottom and sides of the aquarium were covered with opaque, black, plastic. The tank was divided in 2 halves by an opaque, black, plastic partition, positioned 4 cm above the bottom of the tank. The top of 1 half of the aquarium (corresponding to the dark zone) was covered with opaque, black, plastic. The second half of the aquarium (corresponding to the light zone) was left uncovered and was lit by a 40 W fluorescent tube mounted 25 cm above the water surface. The tank was filled with Ouche water at 15 °C which was renewed after 4 h and aerated between each experiment. Each individual was used only once in this setup. At the beginning of each trial, a single individual was placed at the bottom in the middle of the tank. After an acclimation period of 5 min, its position was recorded at 30 s intervals during 5 min (as determined from preliminary experiments). At the end of each trial, the behaviour of the individual was scored from the number of times that it was recorded in the light half of the aquarium. Thus, the score could range from 0 (strongly photophobic) to 10 (highly photophilic). A score of 5 indicated no preference in relation to light.

The distributions of both scores for geotactism and scores for reaction to light did not conform to a normal distribution. Therefore, data were analysed using non-parametric statistics (Siegel & Castellan, 1988). Results were considered significant at $P < 0.05$. Two-tailed tests of significance are used throughout.

RESULTS

Overall, 379 individuals were tested during the experiments. Among those, 116 were uninfected, 142 were infected with *P. laevis*, 86 were infected with *P. minutus*, and 35 harboured at least 1 cystacanth of each species. The number of *P. laevis* per infected host ranged from 1 to 9 (mean ± s.d. = 2.30 ± 1.68), whereas the number of *P. minutus* per infected host ranged from 1 to 4 (mean ± s.d. = 1.13 ± 0.53).

Influence of parasite load and sex of the host

We first considered the influence of parasite load on both vertical distribution and reaction to light. Individuals infected with *P. laevis* were assigned to 3 different categories corresponding to individuals harbouring 1 ($n = 65$), 2 ($n = 28$) or ≥ 3 ($n = 49$)

cystacanths. We found no effect of parasite load on either vertical distribution (Kruskal–Wallis analysis of variance: $H_2 = 4.211$, $P = 0.123$) or reaction to light ($H_2 = 3.176$, $P = 0.204$). Individuals infected with *P. minutus* were assigned to 2 categories corresponding to individuals harbouring 1 ($n = 80$) or ≥ 2 ($n = 6$) cystacanths. We found no difference between these 2 categories for either vertical distribution (Mann–Whitney *U*-test: $Z = -0.341$, $P = 0.204$) or reaction to light ($Z = -0.644$, $P = 0.617$). Therefore, for each parasite species, data from all infected individuals were pooled in subsequent analyses. We found no evidence for an effect of sex, in either uninfected or infected individuals, on vertical distribution (Mann–Whitney *U*-tests, all $P > 0.30$) or on reaction to light (Mann–Whitney *U*-tests, all $P > 0.31$). Therefore, data from each sex were pooled for subsequent analysis.

Influence of infection status on geotactism

There was a significant influence of the infection status on vertical distribution (Fig. 1, Kruskal–Wallis analysis of variance: $H_3 = 68.36$, $P < 0.0001$), with individuals harbouring both parasites showing an intermediate phenotype between *P. laevis*-infected and *P. minutus*-infected individuals. Multiple comparisons between groups (Siegel & Castellan, 1988) confirmed the observed pattern. Uninfected individuals differed significantly ($P < 0.01$ in all cases) from the 3 other groups and *P. laevis*-infected individuals differed from *P. minutus*-infected ones ($P < 0.001$). However, there was no significant difference between individuals harbouring both parasite species and individuals infected with either 1 of the 2 parasites. In addition, the vertical distribution of *P. minutus*-infected individuals was significantly more variable than that of the 3 other groups (Moses test, $P < 0.0085$ to adjust for making $n = 6$ non-independent comparisons).

Influence of infection status on reaction to light

There was a significant effect of the infection status on the reaction to light (Fig. 2, Kruskal–Wallis analysis of variance: $H_3 = 77.09$, $P < 0.0001$). Multiple comparisons between groups indicated that individuals harbouring both parasites did not differ from *P. laevis*-infected individuals, and were equally attracted towards light, whereas all other paired comparisons were significant ($P < 0.02$ in all cases). Uninfected individuals were strongly photophobic, whereas *P. minutus*-infected ones were only slightly photophobic. There was no difference in terms of variability in reaction to light between the 4 groups (Moses test, $P > 0.0085$ to adjust for making $n = 6$ non-independent comparisons). Finally, the magnitude of reaction to light was weakly, although

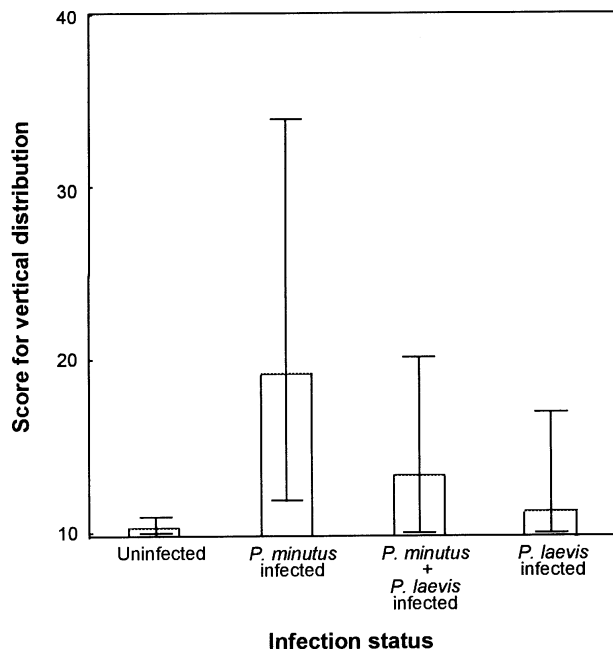


Fig. 1. Median values for vertical distribution of gammarids according to their infection status. Bars show the interquartile range. All paired comparisons are significant ($P < 0.01$), except between doubly-infected individuals and singly-infected individuals of each parasite species.

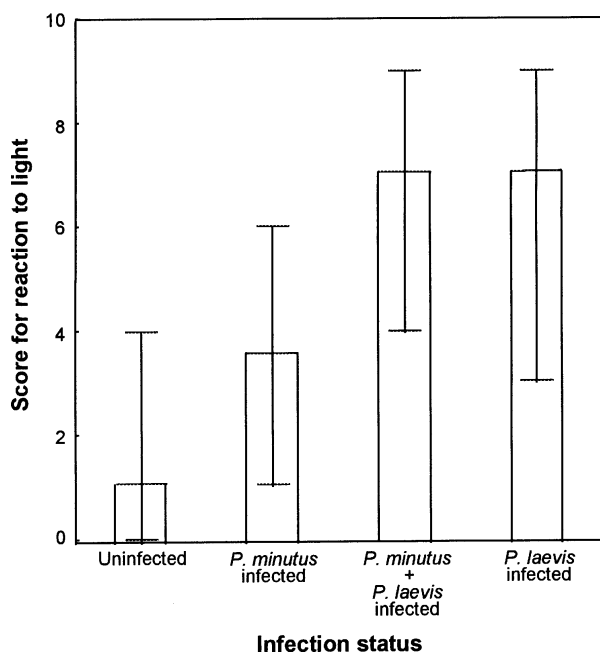


Fig. 2. Median values for the reaction to light of gammarids according to their infection status. Bars show the interquartile range. All paired comparisons are significant ($P < 0.02$), except between doubly-infected individuals and *Pomphorhynchus laevis*-infected individuals.

significantly, correlated with vertical distribution in uninfected individuals (Spearman rank-order correlation coefficient: $r_s = -0.195$, $n = 106$, $P =$

0.046), whereas there was no such evidence for the 3 other groups (*P. laevis*-infected individuals: $r_s = -0.178$, $n = 142$, $P = 0.859$; *P. minutus*-infected individuals: $r_s = 0.106$, $n = 86$, $P = 0.330$; doubly-infected individuals: $r_s = -0.153$, $n = 35$, $P = 0.879$).

DISCUSSION

Parasites can modify a wide range of morphological, physiological and behavioural traits in their hosts (Poulin & Thomas, 1999). Our results on 2 acanthocephalan parasites in sympatry, together with previous studies (Rumpus & Kennedy, 1974; Bentley & Hurd, 1993, 1996) confirm that the same parasite can modify more than 1 trait, as previously observed in other host-parasite systems (LoBue & Bell, 1993; Thomas, Cézilly & Renaud, 1996; Ness & Foster, 1999). Because we used amphipods with natural infections in our experiments, there is a possibility that the observed modified behaviours lead to increased likelihood of infection, rather than the converse. However, previous studies of similar host-parasite systems (e.g. Bethel & Holmes, 1974) have shown that modified behaviours are observed only after the cystacanths have become infective to the definitive host. Therefore, we consider that the observed alterations of infected hosts behaviour are the consequence and not the cause of infection.

The modifications associated with the presence of either *P. laevis* or *P. minutus* in *G. pulex*, as observed in laboratory conditions, are clear-cut and appear to be consistent with their respective definitive hosts. In the field, the increased reaction to light induced by *P. laevis* presumably drives infected gammarids away from shelters and thus makes them more vulnerable to predation by various fish species. On the other hand, the modified vertical distribution of *P. minutus*-infected individuals should make them more prone to predation by waterfowl compared to uninfected individuals. Our results largely confirm previous studies of the behavioural effects of the same or related species of acanthocephalan parasites on crustacean hosts (Hindsbo, 1972; Bethel & Holmes, 1974, 1977; Kennedy *et al.* 1978; Bakker *et al.* 1997; Maynard *et al.* 1998). However, none of these studies has attempted to relate the total parasite load to the magnitude of the difference in behaviour to that of uninfected individuals. Here, we found that the number of parasites present in a host had no significant effect on either reaction to light or vertical distribution. Rumpus & Kennedy (1974) similarly observed that the number of *P. laevis* parasites present in *G. pulex* did not affect the magnitude of the reduction of the host respiratory rate. Thus, the effects of both *P. laevis* and *P. minutus* may be dependent only on their presence, not on their intensity.

It is interesting to note, however, that in our experiments *P. minutus*-infected gammarids were significantly less photophobic than uninfected individuals, while the vertical distribution of *P. laevis*-infected ones was significantly different from that of uninfected individuals. From an evolutionary point of view, it is possible that the modifications brought about by acanthocephalan parasites in crustacean hosts were initially by-products of pathological effects, and have been later amplified in a specific direction depending on which species constitutes an appropriate definitive host. Further experiments and comparative studies are necessary to test this hypothesis.

Since the increased trophic transmission of each acanthocephalan parasite appeared to be targeted at a specific host, our results are suggestive of a potential conflict between them (see Lafferty, 1999). Depending on the behavioural trait under study, however, the outcome of the antagonism between *P. laevis* and *P. minutus* was different. Considering the vertical distribution of infected individuals, the performance of doubly-infected gammarids appeared to be half-way between those of *P. laevis*- and *P. minutus*-infected individuals. In this respect, mixed infection seems disadvantageous to both parasites and selection may exist to avoid each other as suggested by Lafferty (1999). In contrast, *P. laevis* appeared to be able to induce an altered reaction to light even in the presence of *P. minutus*. Thus, if *P. minutus* parasites are unable to counteract the influence of *P. laevis* on the host's reaction to light, they may benefit from avoiding *P. laevis*-infected gammarids. However, additional information must be obtained before any conclusion can be drawn about the outcome of the antagonism between the two parasites. In particular, because infected gammarids were collected in the field, we have no information on the temporal order of infection. It would be interesting to know whether in the case of a mixed infection the relative influence of each parasite depends on the time delay between the establishment of the first parasite and that of the second one. Experiments with controlled infections and detailed survey of the dynamics of infection in local populations are necessary to answer this question. Ultimately, only a quantitative study of the susceptibility of doubly-infected gammarids to predation by fish and birds will indicate whether one parasite species is able to overpower the influence of the other, or if mixed-infection results in hampered transmission to the appropriate definitive host for both parasites.

Although the possibility that interactions between manipulative parasites can result in specific behavioural or physiological adaptations is appealing (Lafferty, 1999), the empirical evidence supporting the idea is weak. Assessment of the consequences of mixed-infection by antagonistic parasites on the

behaviour and susceptibility to predation of their common intermediate hosts requires careful investigations both in the field and in controlled environments. This remains a challenge for future studies. In this context bird and fish acanthocephalans and their crustacean hosts may be a promising biological model.

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