

Infection with acanthocephalans increases the vulnerability of *Gammarus pulex* (Crustacea, Amphipoda) to non-host invertebrate predators

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SUMMARY

Phenotypic alterations induced by parasites in their intermediate hosts often result in enhanced trophic transmission to appropriate final hosts. However, such alterations may also increase the vulnerability of intermediate hosts to predation by non-host species. We studied the influence of both infection with 3 different acanthocephalan parasites (*Pomphorhynchus laevis*, *P. tereticollis*, and *Polymorphus minutus*) and the availability of refuges on the susceptibility of the amphipod *Gammarus pulex* to predation by 2 non-host predators in microcosms. Only infection with *P. laevis* increased the vulnerability of amphipods to predation by crayfish, *Orconectes limosus*. In contrast, in the absence of refuges, the selectivity of water scorpions, *Nepa cinerea*, for infected prey was significant and did not differ according to parasite species. When a refuge was available for infected prey, however, water scorpion selectivity for infected prey differed between parasite species. Both *P. tereticollis*- and *P. laevis*-infected gammarids were more vulnerable than uninfected ones, whereas the reverse was true of *P. minutus*-infected gammarids. These results suggest that the true consequences of phenotypic changes associated with parasitic infection in terms of increased trophic transmission of parasites deserve further assessment.

Key words: host manipulation, *Pomphorhynchus laevis*, *Pomphorhynchus tereticollis*, *Polymorphus minutus*, trophic transmission.

INTRODUCTION

Several parasites critically rely on trophic transmission from an intermediate host to a final host to complete their complex life-cycle (Moore, 2002). Any influence of the parasite on its intermediate host phenotype that results in increased trophic transmission to an appropriate final host is thus thought to be favoured by natural selection (Dawkins, 1982; Poulin, 1995). Accordingly, several helminth species have been shown to bring about phenotypic changes in their intermediate hosts that appear to enhance trophic transmission to final hosts (Moore, 2002; Thomas *et al.* 2005). However, it is not clear whether such alterations in host phenotype specifically enhance transmission to appropriate final hosts, or actually increase the susceptibility of intermediate hosts to a large range of predators, including non-host species (Cézilly and Perrot-Minnot, 2005). Mouritsen and Poulin (2003) observed that the intertidal cockle *Austrovenus stutchburyi* infected with the bird trematode *Curtuteria australis* was actually exposed to a high risk of attack by a benthic feeding fish, *Notolabrus celidotus*. Quantitative estimations

indicated that only 2.5% of the parasite population in manipulated cockles was transmitted to appropriate bird final hosts, whereas 17.1% was lost to fish (Mouritsen and Poulin, 2003). Similarly, Ness and Foster (1999) observed that three-spine sticklebacks, *Gasterosteus aculeatus*, parasitized by the bird tapeworm *Schistocephalus solidus*, showed increased susceptibility to visually hunting predators, appropriate hosts and non-hosts (e.g. trout) alike. By contrast, Seppälä *et al.* (2006a) found that uninfected rainbow trout (*Oncorhynchus mykiss*) and trout infected with the eye fluke *Diplostomum spathaceum*, did not differ in their susceptibility to predation by a non-host species, the pike, *Esox lucius*. However, experimental evidence of increased susceptibility of eye fluke-infected fish to predation by appropriate final hosts (e.g. birds) remains ambiguous (Seppälä *et al.* 2006b). Cost of predation by non-hosts might be reduced if a fraction of non-host predators are themselves preyed upon by appropriate final hosts (Nickol *et al.* 2006). Parasites may eventually survive in such paratenic hosts, although the importance of paratenic hosts in the evolution of complex life-cycles remains unclear (Choisy *et al.* 2003). However, it is likely that in most cases predation of the intermediate host by a non-host species will constitute a dead end for the parasite (Marriott *et al.* 1989; Mouritsen and Poulin, 2003). This is particularly true of non-host predators that do not swallow their

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prey, but feed on them through sucking their body fluids, such as some heteropteran insects, or pull them into pieces such as some crustaceans.

Most previous studies of parasite-induced trophic transmission (i.e. Lafferty and Morris, 1996; Bakker *et al.* 1997; Perrot-Minnot *et al.* 2007) relied on a measure of selective predation on infected hosts by appropriate vertebrate hosts, but neglected to assess the vulnerability of infected prey to predation by non-hosts (see, however, Ness and Foster, 1999; Mouritsen and Poulin, 2003; Seppälä *et al.* 2006b; Kaldonski *et al.* 2007). Amphipods are key elements in the functioning of aquatic ecosystems both as detritivores and predators of other invertebrate species (Dick and Platvoet, 1996; Maltby *et al.* 2002; Elliott, 2005), and as prey to a wide range of predators (Redmond and Scott, 1989; Corona *et al.* 2000; Wilhelm *et al.* 2002; Griffen and Byers, 2006). They are also used by several trematode, cestode and acanthocephalan parasites as intermediate hosts before reaching birds or fish final hosts. Although the phenotypic alterations brought about by parasites on amphipods appear to be consistent with their respective type of final host (Cézilly *et al.* 2000; Perrot-Minnot *et al.* 2007; Kaldonski *et al.* 2007), little is known about their consequences on susceptibility to predation by other, non-host predators. In particular, the effects of infection on vulnerability to predation by aquatic invertebrates remain undocumented.

In this study, we examine the influence of infection with 3 different acanthocephalan parasites on the susceptibility of the amphipod *Gammarus pulex* to predation by 2, non-host aquatic invertebrate predators differing in feeding behaviour and habitat-use. Mouritsen and Poulin (2003) provided evidence that infection with manipulative parasites can increase the vulnerability of intermediate hosts to predation by non-hosts in the field. Here, using experiments in microcosms, we test the hypothesis that phenotypic changes induced by acanthocephalan parasites increase the susceptibility of amphipod hosts to predation by non-host predators.

MATERIALS AND METHODS

Study species

Water scorpion, *Nepa cinerea*, and crayfish *Orconectes limosus* were used as experimental predators. Water scorpions are predominantly surface predators, whereas crayfish are more benthic. Aquatic Hemiptera such as water scorpions, generally hold an intermediate place in food chains, and are often important predators (McCafferty, 1981; Ohba and Nakasuji, 2006). For example, in a study of a fishless spring in Arizona, the heteropteran *Belastoma bakeri* ate more prey (mostly amphipods) than any other top predator (Runck and Blinn, 1994).

Crayfish can have an important predatory impact on aquatic macroinvertebrates (Crawford *et al.* 2006), particularly on amphipods (Stewart *et al.* 1998; MacNeil *et al.* 1999).

Water scorpions had an average length (from tip of rostrum to tail basis) of $18.76 \text{ mm} \pm 1.9 \text{ mm}$ ($n=95$) and crayfish had an average length (from tip of rostrum to distal end of telson) of $61.8 \text{ mm} \pm 0.7 \text{ mm}$ ($n=99$). Both were collected in the same place using the random kick sampling method (Hynes, 1954). These predators were kept separately and fed with gammarids, but were starved for 24 h prior to the experiments.

In Burgundy, eastern France, the amphipod *Gammarus pulex* is exploited as intermediate host by 3 acanthocephalan species. *Pomphorhynchus laevis* and the congeneric *Pomphorhynchus tereticollis* are fish parasites that modify reaction to both light (Cézilly *et al.* 2000; Tain *et al.* 2006) and fish predator's odour in *G. pulex* (Baldauf *et al.* 2007; Kaldonski *et al.* 2007; Perrot-Minnot *et al.* 2007). *Polymorphus minutus* is a bird acanthocephalan that modifies geotaxis in *G. pulex*, but has only weak or no effect on reaction to light or fish odour (Cézilly *et al.* 2000; Kaldonski *et al.* 2007). All *G. pulex* used in the experiments (uninfected, *P. laevis*-, *P. tereticollis*- and *P. minutus*-infected) were collected using the kick sampling method (Hynes, 1954) in the River Ouche in Dijon (Eastern France), during the summer of 2004 (from July to September). There, the density of water scorpions was approximately 5 individuals per linear metre along the bank of the river, whereas the density of crayfish ranged between 1 and 4 individuals per square metre. Only healthy and undamaged adults were kept for the experiments, within sizes ranging from 11 to 15 mm long. Gammarids were maintained in large, separated, well-aerated tanks, filled with dechlorinated tap water and fed with elm leaves and pellet fish food. They were acclimatized to room and water conditions for at least 1 week before the experiments.

Predation experiments

Experiments were conducted in a climate room with a constant temperature of 15 °C and a light:dark cycle of 12:12 h. Observation tanks (35 × 15 × 20 cm) were filled with 7 litres of dechlorinated tap water, oxygenated by an air-stone and illuminated overhead by solar spectra fluorescent tubes (light T° = 9600°K). Aquarium sides were screened with brown plastic to avoid any lateral disturbance. Experiments were conducted in either a simple or a complex microcosm habitat set-up. The simple habitat set-up consisted of washed river sand substrate whereas the complex habitat set-up was composed of the same sand substrate plus a piece of air-brick (21.5 × 10 × 5 cm, designed with eight

1.5 cm² holes) sunk into the sand and 2 *Apiacea* plants where gammarids could find refuge.

To assess the selectivity of predators for uninfected or infected gammarids, predation tests were performed in paired choice experiments involving a 30% proportion of infected gammarids, slightly above natural prevalence of parasites in the field (Lagrue *et al.* 2007). Each experimental test consisted of recording the relative numbers of infected and non-infected prey captured by a single predator during a given amount of time. Forty-two uninfected gammarids and 18 infected ones (parasitized by a single acanthocephalan species) were first introduced into the aquarium. After 15 min, 1 individual predator was introduced in the aquarium. The time of exposure of prey to different predators was adjusted to prevent too great a proportion of prey (more than 50%) being eaten (Fullick and Greenwood, 1979). Owing to preliminary experiments, the duration of each trial was set at 3.5 h for crayfish and 72 h for water scorpion. At the end of each trial, predators and remaining prey were removed, surviving gammarids counted, and all material rinsed well with tap water. Only trials where more than 6 prey were eaten were kept for analysis.

Because it was not possible to correctly identify which prey types were captured through direct observation, absolute as well as relative prey densities could not be kept constant over the course of predation trials. Differential of predation between the two prey types was therefore analysed by Manly's alpha probabilistic approach (Manly, 1974; Chesson, 1978). This method allows for prey depletion during the course of the trial, and thus for changes in the proportions of available prey classes as prey are eaten. Manly's alpha (α_i) for variable prey population is calculated using the equation:

$$\alpha_i = \frac{\log p_i}{\sum_{j=1}^m \log p_j}$$

where α_i = Manly's alpha (preference index) for prey type i , p_i and p_j = proportion of prey i or j remaining at the end of the trial, and m = number of prey types. Manly's selectivity index ranges from 0 (when only uninfected prey are eaten) to 1 (when only infected prey are eaten), with a value of 0.5 for absence of preference.

Preference index data were transformed using a Box-Cox function to meet the assumptions of parametric tests. The preference index for each group was tested using a t-test to a specified value (Sokal and Rohlf, 1995) to check whether predator significantly preyed upon infected prey. The influence of infection type, refuge availability, and interaction term were analysed using a two-way ANOVA and pairwise differences were evaluated with Fisher's PLSD. All tests were performed using the *Statistica* statistical software (v. 6.0, Statsoft Inc.).

Table 1. Results of a two-way ANOVA testing for differences in mean selectivity of crayfish in relation to parasite species and refuge availability

Source	SS	D.F.	F ratio	P
Parasite species (PS)	1.572	2	17.620	<0.001
Refuge (R)	0.018	1	0.405	0.526
PS × R	0.056	2	0.630	0.535
Error	4.15	93		

RESULTS

A total of 2388 gammarids were eaten, 1127 by the 99 different crayfish and 1261 by the 95 different water scorpions. Crayfish ate fewer gammarids (mean \pm S.D. = 11.38 ± 4.70) than did water scorpions (mean \pm S.D. = 13.27 ± 5.93) per trial (Mann-Whitney test, $Z = -2.07$, $n_{WS} = 95$, $n_C = 99$, $P = 0.04$). However, for both series of tests, the number of prey eaten had no influence on selectivity of predator toward infected preys, neither for crayfish (Pearson correlation, $r < 0.001$, $P = 0.84$) nor for water scorpions ($r = 0.003$, $P = 0.58$).

Crayfish selectivity

Refuge availability had no effect on crayfish selectivity, irrespective of parasite species (Table 1; Fig. 1a). Crayfish selectivity for infected prey varied, however, significantly between groups (two-way ANOVA: $F_{5,93} = 7.52$, $P < 0.0001$; Fig. 1a). Crayfish selectivity for *P. laevis*-infected prey was highly significant (with refuge: $t_{1,14} = 3.44$, $P = 0.004$; without refuge: $t_{1,16} = 8.96$, $P < 0.001$; Fig. 1a), and differed significantly from selectivity for *P. tereticollis*-infected (Fisher's PLSD: $P < 0.001$; Fig. 1a) or *P. minutus*-infected prey (Fisher's PLSD: $P < 0.001$; Fig. 1a). By contrast, crayfish showed no selectivity for either *P. minutus*- (with refuge: $t_{1,16} = -1.86$, $P = 0.081$; without refuge: $t_{1,16} = -1.32$, $P = 0.207$) or *P. tereticollis*-infected prey (with refuge: $t_{1,17} = 0.29$, $P = 0.726$; without refuge: $t_{1,14} = -0.24$, $P = 0.816$; Fig. 1a). No difference was observed between selectivity for *P. minutus*-infected prey and selectivity for *P. tereticollis*-infected ones (Fisher's PLSD: $P > 0.05$; Fig. 1a).

Water scorpion selectivity

Water scorpion selectivity for infected prey differed between trials (two-way ANOVA: $F_{5,89} = 15.15$, $P < 0.001$; Fig. 1b). A significant interaction between parasite species and refuge availability indicates that infected prey differed in their vulnerability to predation according to microcosm type (Table 2; Fig. 1b). When no refuge was available for prey,

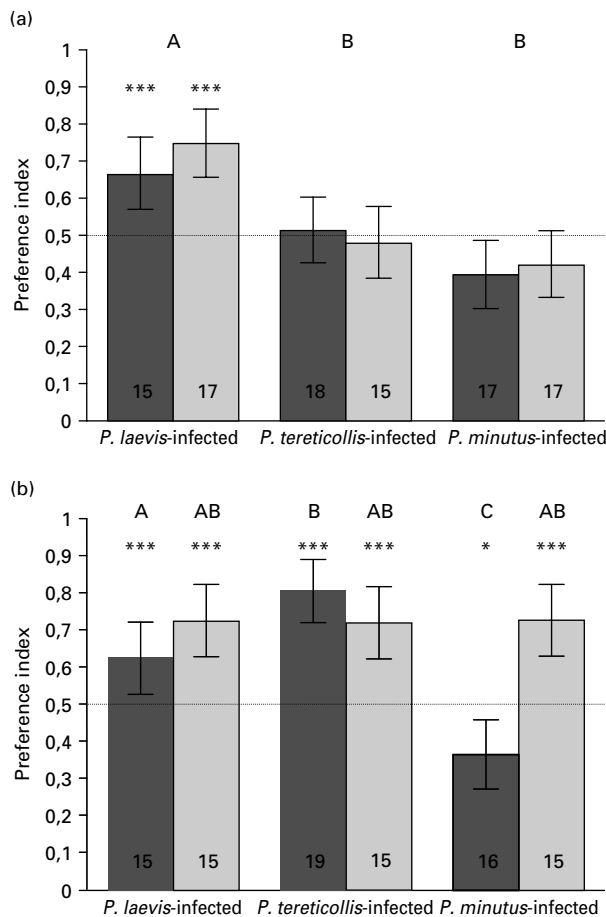


Fig. 1. Mean (\pm 95% confidence interval) of preference index showing selectivity of (a) crayfish and (b) water scorpions toward uninfected versus gammarids infected by 3 different parasite species, either in a complex microcosm type setting (dark bars) or in a simple one (light bars). Values above the dashed line indicate over consumption of infected prey. Stars above the bars indicate a significant difference from equal susceptibility of infected and uninfected prey and bars not connected by the same letter are significantly different.

water scorpions' selectivity for infected prey was significant ($t_{1-14} = 6.66, 4.80, \text{ and } 6.00$ for *P. laevis*, *P. tereticollis* and *P. minutus* respectively, $P < 0.001$ in all cases; Fig. 1b) and did not differ according to parasite species (Fisher's PLSD: $P > 0.05$; Fig. 1b). When a refuge was available for infected prey, however, water scorpion selectivity for infected prey differed markedly between parasite species (Fig. 1b). Both *P. tereticollis*-infected gammarids ($t_{1-18} = 10.74, P < 0.001$) and *P. laevis*-infected ones ($t_{1-14} = 3.13, P = 0.007$) were more predated than uninfected individuals, whereas the reverse was true of *P. minutus*-infected gammarids ($t_{1-15} = -2.74, P = 0.015$; Fig. 1b).

DISCUSSION

Our results provide, for the first time, empirical evidence that infection with acanthocephalan parasites can increase the vulnerability of amphipods to

Table 2. Results of a two-way ANOVA test for differences in mean selectivity of water scorpions in relation to parasite species and refuge availability

Source	SS	D.F.	F ratio	P
Parasite species (PS)	0.689	2	14.491	<0.001
Refuge (R)	0.320	1	13.455	<0.001
PS \times R	0.742	2	15.613	<0.001
Error	2.115	89		

non-host predators. However, the magnitude of the effect may depend on complex interactions between parasite species, the physical complexity of the environment, and predator species (see Holmlund *et al.* 1990; Corona *et al.* 2000). In particular, the observed differences between predators in selectivity for infected prey remain difficult to interpret. Water-scorpions, being poor swimmers, stay motionless at the water's surface for long periods of time, and capture prey using the ambush method, whereas crayfish are more benthic. Differences in hunting methods between the two predators might then contribute to explain the observed differences in selectivity. However, the vulnerability of uninfected and infected gammarids to predation by crayfish or water-scorpions is also dependent on their ability to modify their behaviour in response to the perceived risk of predation.

Overall, refuge availability had no influence on the vulnerability of infected gammarids to crayfish. Uninfected *G. pulex* are known to increase their use of refuge when in the presence of a fish predator (Perrot-Minnot *et al.* 2007; Kaldonski *et al.* 2007), but the effect of crayfish on refuge use by *G. pulex* has not been quantified so far. However, it has been previously observed that uninfected *G. pulex* decrease their activity when exposed to chemicals from predatory fish, but do not react to chemicals from the crayfish, *Pacifascatus leniusculus* (Åbjörnsson *et al.* 2000). It is therefore possible that both infected and uninfected gammarids did not react to the presence of crayfish, thus explaining the absence of an effect of refuge availability on selectivity for infected prey. Actually, only gammarids infected by *P. laevis* showed an increased vulnerability to predation by crayfish compared to uninfected individuals. It has been shown that amphipods infected with *P. laevis* are more active than uninfected ones (Dezfuli *et al.* 2003), thus making them potentially more exposed to sit and await predators such as crayfish. However, no data on activity levels are available for *P. tereticollis*- and *P. minutus*-infected amphipods.

Infection with either *P. laevis* or *P. tereticollis* had a highly significant effect on vulnerability of infected prey to predation by water scorpions, independently of refuge availability. In contrast, *P. minutus*-infected individuals were less vulnerable than uninfected ones to predation by water scorpions only in

the presence of refuges, whereas the reverse was true in the absence of refuges. Data from previous studies (Kaldonski *et al.* 2007; Perrot-Minnot *et al.* 2007) suggest that *P. minutus*-infected *G. pulex* spend more time in refuges, independently of predator presence, compared to *P. laevis*- and *P. tereticollis*-infected individuals. This may explain the difference between host-parasite associations in vulnerability to predation by water scorpions in relation to the presence/absence of refuges, although other factors may have contributed to the observed pattern of predation.

Parasite-induced trophic transmission to final hosts is supported by substantial empirical evidence (Moore, 2002; Thomas *et al.* 2005). However, evidence for specificity in manipulation remains equivocal, such that the importance of parasitic manipulation for the population dynamics of both predators and prey remains unclear. Fitness consequences of parasite-induced behavioural alterations are likely to be complex (Vance and Peckarsky, 1997). On the one hand, increased vulnerability of infected prey is supposed to benefit both the parasite and its final host (Lafferty, 1992; Bakker *et al.* 1997). Final hosts may benefit from feeding and specializing on infected prey if the energy gain associated with the capture of easy prey outweighs the costs associated with the risk of transmission of the parasite from prey to predator (Lafferty, 1992). Even if manipulation does incur a cost to parasites (see Poulin *et al.* 2005), this cost might be largely compensated for by the benefit of enhanced transmission to final hosts. On the other hand, when prey capture is facilitated by parasites and risk of transmission of the parasite from prey to predator is non-existent (as in this study), a large range of predators may benefit from selecting infected prey (Lafferty, 1992), including many non-host species. Acanthocephalan-infected gammarids have previously been shown to be more susceptible than uninfected ones to predation by appropriate final hosts (birds: Bethel and Holmes, 1977; fish: Bakker *et al.* 1997, Perrot-Minnot *et al.* 2007, Kaldonski *et al.* 2007). However, the present results suggest that infection with acanthocephalans might also increase vulnerability to non-host predators, such that the exact balance between benefits and costs of manipulation remains to be evaluated properly. One possibility is that the cost of non-host predation is limited because the overall impact of predation on intermediate hosts by appropriate final hosts is much higher than that by non-host predators. In addition, in the present experiment, each predator was tested in isolation, whereas interactions between predators may affect their selectivity in the wild (Nilsson *et al.* 2000). Future work should then address this important question through combining long-term experiments in mesocosms and modelling (see Duffy *et al.* 2005; Fenton and Rands, 2006).

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