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# Patterns of intermediate host use and levels of association between two conflicting manipulative parasites

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## Abstract

For many parasites with complex life cycles, manipulation of intermediate host phenotypes is often regarded as an adaptation to increase the probability of successful transmission. This phenomenon creates opportunities for either synergistic or conflicting interests between different parasite species sharing the same intermediate host. When more than one manipulative parasite infect the same intermediate host, but differ in their definitive host, selection should favour the establishment of a negative association between these manipulators. Both *Polymorphus minutus* and *Pomphorhynchus laevis* exploit the amphipod *Gammarus pulex* as intermediate host but differ markedly in their final host, a fish for *P. laevis* and a bird for *P. minutus*. The pattern of host use by these two conflicting manipulative parasites was studied. Their incidence and intensity of infection and their distribution among *G. pulex* were first examined by analysing three large samples of gammarids collected from the river Tille, Eastern France. Both parasites had low prevalence in the host population. However, temporal fluctuation in the level of parasitic infection was observed. Overall, prevalence of both parasite species was higher in male than in female *G. pulex*. We then assessed the degree of association between the two parasites among their intermediate hosts, using two different methods: a host-centred measure and a parasite-centred measure. Both measures gave similar results; showing random association between the two acanthocephalan species in their intermediate hosts. We discuss our results in relation to the selective forces and ecological constraints that may determine the pattern of association between conflicting manipulative parasites. © 2002 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

**Keywords:** *Gammarus pulex*; *Polymorphus minutus*; *Pomphorhynchus laevis*; Host manipulation; Conflict of interests; Species associations

## 1. Introduction

Most organisms are host to a diverse community of parasites and this raises all the classical ecological questions about the ways in which communities are structured and organised (Begon et al., 1996). The number and identity of parasite species in an infracommunity (i.e. the assemblage consisting of all parasites of different species in the same host (Holmes and Price, 1986) may depend on many factors such as competition for food or space between individuals (see Sousa, 1994 for a review). Infracommunities can range from purely stochastic assemblages of species to highly structured and predictable sets of species (Poulin, 1998). In the last case, interactions between parasite species are one of the main forces that can shape an infracommunity and give it a structure departing from randomness (Sousa, 1994).

Although descriptive analyses of parasite community

structure are now available for a wide variety of vertebrate hosts (Kuris, 1990), the parasite communities of invertebrate hosts have received less attention. Many invertebrates, particularly molluscs and arthropods, serve as intermediate hosts for parasites that complete their development in a vertebrate host (Kuris, 1990). Several of these parasites, e.g. larvae of helminths, consume few host resources and depend upon the ingestion of their intermediate host by their definitive host to complete their life cycle (Lafferty, 1999; Poulin et al., 2000). These parasites often alter the behaviour or appearance of their intermediate hosts in order to increase the risk of the intermediate host being predated by the definitive hosts (Combes, 1995; Lafferty, 1999). This phenomenon creates opportunities for either synergistic or conflicting interests between different parasite species sharing the same intermediate host (Lafferty, 1999; Cézilly et al., 2000; Poulin et al., 2000) and can potentially result in the structuring of infracommunities. For example, if both parasites have the same final host, they have a shared interest in transmission. If one parasite species is an efficient manipulator of the intermediate host behaviour, it is

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expected that, under certain conditions, the other parasite species could increase their probability of transmission simply by preferentially infecting an already manipulated host, making no investment in the manipulation themselves (Lafferty, 1999). Thomas et al. (1997) (see also Mouritsen, 2001; Thomas and Helluy, 2001) provide some evidence for such a ‘hitch-hiking’ parasite strategy. The trematode *Marietrema subdolum* increases its transmission to aquatic birds, their definitive hosts, by preferentially infecting gammarids manipulated by the other trematode *Microphallus papillorobustus*. A different situation occurs when two manipulating parasites exploit the same intermediate host, but differ in the final host they attempt to reach. For instance, the rat tapeworm *Hymenolepis diminuta* and the chicken tapeworm, *Railietina cesticellus* have different definitive hosts but use the same range of coleopterans as intermediate hosts. Both species induce similar behavioural changes in their intermediate host (Graham, 1966; Hurd and Fogo, 1991; Robb and Reid, 1996), suggesting that a potential conflict of interest may have led to a hijacking defence. There are many systems in which either common interests or conflicting interests exist between parasite species sharing the same invertebrate host population, but there have been very few studies of patterns of host use among such parasites (Lafferty et al., 2000).

Several species of acanthocephalan parasites are known to manipulate their intermediate hosts in order to enhance their own transmission to their final host. The manipulation may involve both physiological (Harris-Warwick et al., 1989; Helluy and Holmes, 1990; Thompson and Kavaliers, 1994) and behavioural alterations (Hindsbo, 1972; Moore, 1984). In Burgundy (Eastern France), both *Polymorphus minutus* and *Pomphorhynchus laevis* exploit the amphipod *Gammarus pulex* (Amphipoda) as intermediate host. The two species differ markedly in their final host, a fish for *P. laevis* and a bird for *P. minutus*, and in their effect on the host phenotype. Compared with uninfected gammarids that are photophobic and tend to remain at the bottom of the water column, *P. laevis*-infected gammarids are attracted by the light, whereas *P. minutus*-infected individuals swim close to the water surface (Cézilly et al., 2000). Recently, Cézilly et al. (2000) showed that 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*. In this respect, the mixed infection seems to decrease the probability of successful transmission to definitive hosts and then the cost of associating inside the intermediate host might be high for both parasite species. For this reason, we should expect limited co-occurrence of *P. laevis* and *P. minutus* inside the same intermediate host, resulting in a negative association between their abundances (Lafferty, 1999). However, amphipods with those few double infections should have lower mortality rates (i.e. the joint manipulation is not effective), thereby increasing life span of double

infected gammarids relative to single infections. What sort of net pattern should be generated is difficult to predict. Thus, this is a two-tailed prediction of association.

The aim of this study was to test this prediction by using data on infections in field-collected amphipods. For this purpose, we first determined the infection parameters and the distribution of both parasites in the host population. We then assessed whether the two parasite species really are negatively associated in wild *Gammarus* populations. Methods commonly used to quantify the level of pairwise association often consider the host individual (e.g. Kuris, 1990; Lafferty et al., 1994). They provide an estimate of the association between two species relative to their prevalences in the host sample but they do not consider the distribution of the parasites population per se. In the present case, a host-centred measure is probably insufficient since the effect of the conflict on the population dynamics of the two manipulators strongly depends on the number of parasite individuals present in the same intermediate host. Thus, we developed a new measure of association to assess the phenomenon at the parasite population level.

## 2. Materials and methods

Three large samples of *G. pulex* were collected on different dates (August 1997, March 1999, June 1999) in the River Tille in Burgundy (East of France). All individuals were randomly collected in the aquatic vegetation using the kick-sampling method described by Hynes (1954) and were immediately preserved in 70% alcohol. In the laboratory, *G. pulex* individuals were sexed and dissected to count the number of *P. minutus* and *P. laevis* cystacanths. Following Margolis et al. (1982), we measured the prevalence, the mean abundance, and the mean intensity of each parasite within each sample. These indices of infection were tested against two fixed effects, host sex and sampling date (and their interaction). Analysis was carried out by means of generalised linear models using the S-plus statistical software (MathSoft). Observed distributions of *P. minutus* and *P. laevis* in the host populations were then compared with both Poisson and Negative Binomial distributions. The  $k$  values of Negative Binomial distributions were calculated using maximum likelihood techniques. Tests of significance were carried out by means of goodness-of-fit test (G-test), using the procedure FREQ of the SAS statistical software (SAS Institute).

The levels of association between the two acanthocephalan parasite species were first assessed by using a host-centred measure based on the prevalences of the two species (i.e. presence-absence data). If double infection of a gammarid results from independent random co-occurrence of the two parasite species, then the expected number of double infections is  $N_c = N_h p_1 p_2$ , where  $N_h$  is the number of host individuals examined and  $p_1$  and  $p_2$  represent the prevalences of parasite species 1 and 2, respectively. Depar-

tures from random association may be detected by comparing  $N_e$  with the observed number of double infections,  $N_o$ .

This association measure has often been used in past studies hosts (e.g. Rhode, 1981; Kuris, 1990; Fernandez and Esch, 1991). However, it focuses on hosts rather than parasites as it considers the frequency of infected hosts but fails to take into account the distribution of parasites among these hosts. Consequently, a gammarid harbouring five individuals of *P. laevis* and three individuals of *P. minutus* would have the same effect in the analysis than a host infected by one individual of *P. laevis* and one individual of *P. minutus*. Because parasites often have an aggregated distribution among their hosts (e.g. Crofton, 1971; Pennycook, 1971; Jones et al., 1991; Boulinier et al., 1996), such a host-centred measure might therefore be insufficient to detect positive or negative associations between parasites. Therefore, we designed an alternative measure of association that takes into account the distribution of parasites among their hosts. This measure compares  $C_o$ , the observed number of parasites exposed to the conflict of co-occurrence, with  $C_e$ , the expected number of parasites exposed to the conflict under the null hypothesis of random association.  $C_e$  is equal to:

$$C_e = \sum_{j=1}^{n_1} \sum_{i=1}^{n_2} [(P_1(i) \cdot P_2(j) \cdot N_h) \cdot (i + j)]$$

where  $n_1$  represents the maximum number of parasite species 1 found in a host and  $n_2$  is the maximum number of parasite species 2 observed in a host;  $P_1(i)$  is the probability of finding  $i$  individuals of species 1 in a host and  $P_2(j)$  is the probability of finding  $j$  individuals of parasite 2 in a host individual;  $N_h$  is the number of hosts examined and  $(i + j)$  is the number of parasites exposed to the conflict in a host harbouring  $i$  parasite of species 1 and  $j$  parasite of species 2.  $P_1(i)$  and  $P_2(j)$  were estimated using the theoretical distributions that best fitted the observed distributions of parasites in the host populations (i.e. Poisson or Negative Binomial distribution).

For each treatment, a G-test was used to compare  $N_o$  with  $N_e$  (i.e. host-centred measure) and  $C_o$  with  $C_e$  (i.e. parasite-centred measure), using the procedure FREQ of the SAS statistical software.

### 3. Results

Prevalence and mean abundance of *P. laevis* and *P. minutus* in gammarids differed significantly among the three samples (Fig. 1). Host sex also had a significant effect on the occurrence of the two parasites, with *P. minutus* and *P. laevis* being more prevalent and abundant in males than in females, especially in August 1997. The mean intensity of *P. minutus* was higher in male gammarids than in female ones, and there was also significant variation in mean intensity of *P. laevis* among the three samples (Fig. 1). Given the significant effects of both host sex and sample date on the

infection parameters of the two parasite species, each subsample was considered separately in subsequent analyses.

Given the low prevalences, frequency distributions of parasites among hosts were strongly skewed, with the zero class (i.e. uninfected hosts) amounting to more than 90% of observations for both parasite species. In all samples, the Negative Binomial fitted the distribution better than the Poisson distribution indicating that parasite individuals were aggregated among their hosts at the population level (Poisson:  $P < 0.05$  in all cases; Negative Binomial:  $P > 0.2$  in all cases). Values of  $k$  ranged between 0.05 and 0.37.

The main result emerging from the association study is that the host-centred and parasite-centred measures revealed variable patterns of association between *P. minutus* and *P. laevis* (Table 1). The host-centred measure detected a significant negative association between the two acanthocephalans within the gammarid females sampled in August 1997, while for the other subsamples, we found no significant difference between the observed number of double-infections and that expected by chance. The parasite-centred measure of association gave similar results for assemblages except for the male gammarids sampled in June 1999 where a positive association between *P. minutus* and *P. laevis* was found.

## 4. Discussion

### 4.1. Patterns of gammarids use by the larval acanthocephalans

The incidence and intensity of infection of *G. pulex* by *P. laevis* and *P. minutus* were low. Infection parameters differed significantly among the three gammarid samples suggesting that levels of infection may vary at different times of the year. Temporal variation in the level of infection has previously been observed for both *P. minutus* (Hynes and Nicholas, 1957) and *P. laevis* (Hine and Kennedy, 1974; Dezfuli et al., 1999). Temporal variations are assumed to be a consequence of seasonal fluctuations in temperature, which, in turn, may influence physiological parameters associated with transmission (Crompton and Nickol, 1985). They may also reflect seasonal variations in the local number of definitive hosts (i.e. waterfowl and fishes).

Overall, *G. pulex* males had higher levels of infection for both *P. minutus* and *P. laevis* compared to those of females. In vertebrates, males are typically more susceptible to parasite infections than females, an observation usually attributed to the immunosuppression associated with testosterone (Poulin, 1996). Because of the absence of this hormone in arthropods, males are not generally supposed to be more prone to parasite infections than females (Sheridan et al., 2000). In *G. pulex*, one factor that may explain sex differences in susceptibility to the two acanthocephalans is sexual size dimorphism: males are normally larger than females.

Consequently, males may have to feed more often, thereby increasing the risk of becoming infected with acanthocephalans. This may be a common phenomenon, since positive

correlations between host size and intensity of infection, regardless of host sex, have been reported in many studies (Sheridan et al., 2000).

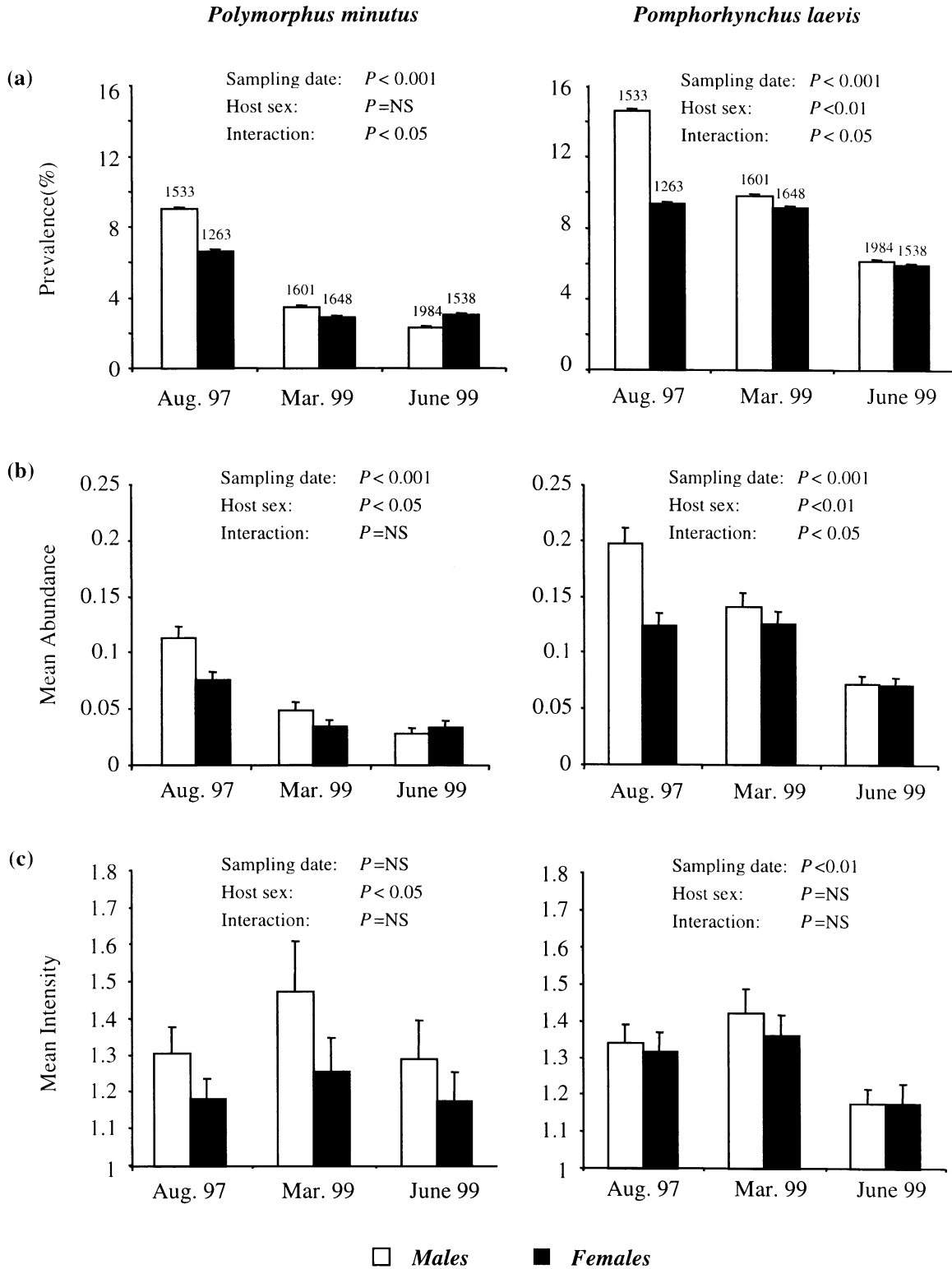


Fig. 1. Effects of sample date and host sex on (a) prevalence, (b) mean abundance, and (c) mean intensity of the two acanthocephalan parasites *Polymorphus minutus* and *Pomphorhynchus laevis* in their intermediate host, *Gammarus pulex*. P is the P value from the generalised linear models. All numbers above the columns refer to host sample sizes in each treatment.

Table 1

Analysis of the interspecific association between the two acanthocephalan parasites *Polymorphus minutus* and *Pomphorhynchus laevis* in their intermediate host, *Gammarus pulex*<sup>a</sup>

Date	Host sex	Measure 1: host population level				Measure 2: parasite population level			
		$N_h$	$N_o$	$N_e$	$P$ value	$N_p$	$C_o$	$C_e$	$P$ value
August 1997	Males	1533	19	20.2	0.847	480	46	53.4	0.433
	Females	1263	1	7.7	< 0.01	253	2	19.4	< 0.01
March 1999	Males	1601	5	5.4	0.901	304	12	16.3	0.407
	Females	1648	8	4.2	0.272	263	18	11.2	0.193
June 1999	Males	1984	7	2.7	0.159	200	18	6.8	< 0.05
	Females	1538	6	2.8	0.274	167	13	6.8	0.147

<sup>a</sup> Two measures of association were used: a host-centred measure and a parasite-centred measure (see text for explanation).  $N_h$  is the number of gammarids examined.  $N_o$  is the observed number of double infections of the both parasites and  $N_e$  is the expected double infections.  $N_p$  is the number of parasites found in the host population.  $C_o$  is the observed number of parasites exposed to the conflict of co-occurrence.  $C_e$  is the expected number of parasites exposed to the conflict under the null hypothesis of random association.  $P$  values are from goodness of fit tests (G-tests).

Finally, the two acanthocephalan species were aggregated within gammarid populations. Aggregated parasite distributions are common (Jones et al., 1991). The biological forces shaping aggregation include stochastic demographic mechanisms in both host and parasite populations (Poulin, 1998). The model proposed by Anderson and Gordon (1982) suggests that heterogeneity in the rates of gain or loss of parasites by hosts is the major cause of aggregation.

#### 4.2. Patterns of association between larval acanthocephalans in gammarids

Both the host-centred and parasite-centred measures of association gave similar results for associations between *P. minutus* and *P. laevis* in their intermediate amphipod hosts except in the male gammarids sampled in June 1999 where the parasite-centred measure estimated a positive association between these two parasites. This result may be explained by the presence of an extreme observation in this subsample: one amphipod harboured five individuals of *P. laevis* and one individual of *P. minutus*. The estimated probability of this co-occurrence was extremely low ( $1.762 \times 10^{-5}$ ). The effect of this observation alone doubled the number of parasites exposed to co-occurrence conflict. This result suggests that when parasite prevalences are low, extreme observations (i.e. heavily infected hosts) have a strong biasing effect on the parasite-centred measure of association. By considering the distribution of parasites in the host population, it is important to note, however, that the parasite-centred measure provides a better estimate of the level of interaction between the two parasites species, one of the main forces that can shape an infracommunity. Therefore, it is a better measure of the phenomenon we have in mind when we refer to species association. However, in order to assess the effect of parasite distribution in the hosts on the association measure, the use of field data with higher prevalences would be useful. Overall, our results suggest that association between *P. minutus* and *P. laevis* is random. Both measures of association detected however a significant negative association between

the two acanthocephalan species within the female gammarid sampled in August 1997. Since we can imagine no suitable explanation for this result, we suggest that this negative association is most likely the result of an uncontrolled sampling heterogeneity.

The theoretical approach of Thomas et al. (1998) suggests that the costs and benefits of avoiding and associating with another parasite species depend upon the prevalences of the two species. Infection of gammarids with *P. minutus* or *P. laevis* is passive (Crompton and Nickol, 1985). Once in the intermediate host, there is no evidence that these acanthocephalans could distinguish already infected hosts from non-infested hosts or that they could avoid development in an already infected host. Moreover, there is also no evidence that one parasite species is able to overpower the influence of the other (i.e. hijacking defence). Even if host avoidance mechanism or hijacking exists, our field data suggest that they would have a low probability of co-occurring with larvae of *P. laevis* (based on the product of both parasite prevalences). Given those odds, hijacking or active avoidance of infected gammarids is probably less advantageous than random host infection.

Our results fail to show any negative association between the two conflicting parasites. One possibility is that prevalences were too low to exert a strong enough selection pressure for active avoidance or hijacking. In other systems in which parasite prevalences are much higher, levels of association between parasite species may involve mechanisms of host location and host acceptance (e.g. Thomas et al., 1997; Poulin et al., 2000; Dezfuli et al., 2000). Further work from both empirical and theoretical viewpoints is then needed to assess the effects of the parasite prevalences on the evolution of mechanisms of both actively seeking for hosts and preferential infection in parasites.

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