seum, Argentina. Lynda Gibbons provided access to the collections of the International Institute for Parasitology, St Albans, U.K. This work was supported, in part, by the Mississippi Agriculture and Forestry Experiment Station (MAFES) under project no. MISV-3080. This paper is MAFES publication no. J-9566.

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Differential Parasite (Trematoda) Encapsulation in *Gammarus aequicauda* (Amphipoda)

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ABSTRACT: Because resistance to parasites usually has a cost for host species, it is theoretically expected that, in case of multi-infection, host immune responses should vary according to the levels of parasite pathogenicity. The crustacean gammarid *Gammarus aequicauda* is the second intermediate host of 4 trematode species. Three of these parasites always encyst in the abdomen of gammarids and have no particular effect on the host. However, 1 of these species is sometimes able to encyst in the cerebroid ganglia of the gammarid and strongly alter its behavior in a way that increases its predation risk by aquatic birds, the definitive hosts. In accordance with the hypothesis that the level of parasite pathogenicity influences the likehood and the degree of host reaction, cases of melanization in our gammarid collection almost exclusively concern the cerebral metacercariae. Our results also indicate that this melanization is able to cancel the behavioral alterations induced by the parasite, suggesting that the cause of the manipulation is not the physical presence of metacercariae in the brain.

Increasingly, evidence is accumulating about the way in which investment in defenses against parasites is costly for hosts and frequently traded against investment into survival, growth, or fecundity (Hochberg, 1997; Langand et al., 1998; Agnew et al., 1999; Boot and Haraguchi, 1999; Fellowes et al., 1999; Webster and Woolhouse, 1999; but see Williams et al., 1999). Under natural conditions, free-living species are usually infected by several parasite species. Because pathogenicity levels often differ from one parasite species to another, trade-offs

TABLE I. Prevalence, mean abundance, and mean intensity of the 4 trematode species in males and females.

	Microphallus papillorobustus		*Microphallus hoffmanni*	*Levinseniella tridigitata*	*Maritrema subdolum*
	Cerebral	Abdominal			
Prevalence (%)					
Males	56 (17.7%)	73 (23.1%)	23 (7.3%)	5 (1.6%)	21 (6.6%)
Females	32 (17.4%)	35 (19.0%)	12 (6.5%)	2 (1.1%)	6 (3.3%)
Mean abundance ± SD					
Males	0.63 ± 2.21	0.42 ± 1.09	0.12 ± 0.57	0.02 ± 0.20	0.10 ± 0.52
Females	0.67 ± 1.99	0.29 ± 0.78	0.09 ± 0.37	0.01 ± 0.10	0.04 ± 0.25
Mean intensity ± SD					
Males	3.57 ± 4.16	1.82 ± 1.62	1.65 ± 1.43	1.4 ± 0.89	1.57 ± 1.36
Females	3.84 ± 3.24	1.51 ± 1.17	1.33 ± 0.65	1 ± 0	1.33 ± 0.52

between fitness costs associated with infection and fitness costs associated with resistance are theoretically expected to vary with the nature of the infection. The magnitude of host immune responses against parasites should then have some correlations with the respective pathogenicity levels of parasites.

The crustacean gammarid *Gammarus aequicauda* (Martynov, 1931) is the second intermediate host of at least 4 trematode species (Rebecq, 1964; Helluy, 1981): *Maritrema subdolum* (Jägerskiöld, 1909), *Levinseniella tridigitata* (Creplin, 1837), *Microphallus hoffmanni* (Rebecq, 1964), and *Microphallus papillorobustus* (Rankin, 1940). All these parasites complete their life cycles in aquatic birds (Helluy, 1981). Whereas the first 3 species always encyst in the abdomen of the gammarid and seem to have no particular effect on the host (Helluy, 1981; Thomas, Lambert et al., 1995; Thomas et al., 1996a, 1998), the situation is more complex concerning *M. papillorobustus*. Indeed, when cercariae of this parasite enter the cuticle of young gammarids, the parasites then migrate toward the anterior part of the host and encyst in the cerebroid ganglia (Helluy, 1983). Gammarids infected with cerebral metacercariae display a positive phototaxis, a negative geotaxis, and an aberrant evasive behavior (Helluy, 1981, 1983). Because of these behavioral alterations, infected gammarids (commonly named crazy gammarids) are more vulnerable than other individuals to predation by aquatic birds, the definitive hosts of the parasite (Helluy, 1984). However, when cercariae of *M. papillorobustus* infect older gammarids, they encyst in the abdomen and, as the 3 other trematode species, have no particular effect on the host behavior (Helluy, 1983; Thomas, Renaud, Rousset et al., 1995).

A common type of defense in crustaceans against invading pathogens and parasites is the formation of a capsule-like envelope around foreign objects, i.e., encapsulation (Götz, 1986; Johansson and Söderhäll, 1989; Söderhäll and Cerenius, 1992). This cellular defense reaction is often accompanied by melanization (Johansson and Söderhäll, 1989). The main objectives of the present study was to determine whether or not *G. aequicauda* is able to encapsulate and melanize metacercariae of trematodes and to investigate the different levels of host immune responses in regard to the 4 parasite species. We predict that cerebral metacercariae of *M. papillorobustus* should be the most frequently encapsulated metacercariae because, compared to those from the abdomen or those of the other trematodes, they severely reduce the host fitness by increasing its probability of predation by aquatic birds. Our study was designed to determine whether or not the melanization of cerebral metacercariae of *M. papillorobustus* is able to cancel the behavioral alterations in crazy gammarids.

To perform this study, a large sample (S1) of *G. aequicauda* (n = 500, 316 males and 184 females) was collected during spring 1999 (Palavas les Flots, southern France, 43°25′N, 3°35′E). Gammarids were randomly sampled in the aquatic vegetation and in water no more than 40 cm in depth. All individuals were immediately preserved in alcohol (70%) and were later sexed, measured for length (from head to tip of telson),

TABLE II. Prevalence, mean abundance, and mean intensity of melanization among gammarids infected with cerebral metacercariae in S1 and S2–S3.

	S1		S2 and S3	
	Males	Females	Males	Females
Prevalence of melanization (%)	35.7	34.4	42.8	44.2
	Fisher's exact test $P = 0.99$		Fisher's exact test $P = 0.90$	
Mean abundance (± SD) of melanized metacercariae	0.62 ± 1.12	0.69 ± 1.4	0.97 ± 1.57	0.97 ± 0.53
	Mann–Whitney U-test, $Z = -0.04$, $P = 0.97$		Mann–Whitney U-test, $Z = -0.23$, $P = 0.81$	
Mean intensity (± SD) of melanized metacercariae	1.75 ± 1.25	2.0 ± 1.79	2.26 ± 1.69	2.2 ± 1.61
	Mann–Whitney U test $Z = -0.40$, $P = 0.69$		Mann–Whitney U test, $Z = -0.02$, $P = 0.98$	

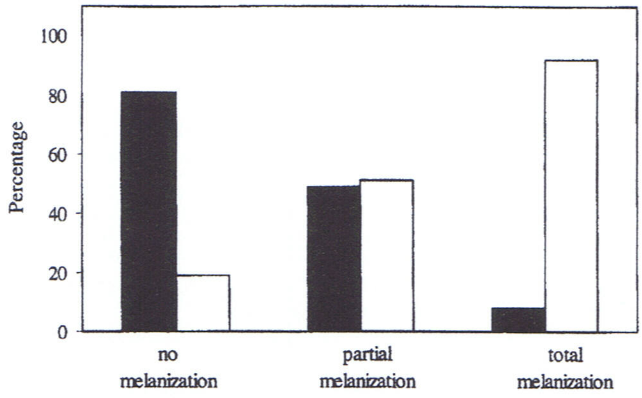

FIGURE 1. Proportion of gammarids with different infection status in S2 (closed bars) and S3 (open bars).

and dissected to count melanized and unmelanized parasites. Metacercariae of the 4 trematode species, i.e., *M. papillorobustus, M. hoffmanni, M. subdolum,* and *L. tridigitata,* can be identified from the size and the form of their cysts (Rebecq, 1964; Helluy, 1981).

To investigate whether or not the melanization of cerebral metacercariae was able to cancel the behavioral alterations in crazy gammarids, we examined 2 other samples (S2, n = 180 and S3, n = 180) of *G. aequicauda* 1 mo later, using 2 different sampling techniques. For S2, we only collected gammarids with an aberrant behavior at the surface of the water. Conversely, for S3, we collected gammarids living under algae, just at the surface of the mud, i.e., individuals with a normal behavior. Previous studies in the same area showed that the behavior of gammarids sampled in these ways is significantly repeatable in the laboratory (Thomas et al., 1996b, 1997). As before, all these gammarids were preserved in alcohol to be sexed, measured for length, and dissected to count melanized and unmelanized cerebral metacercariae of *M. papillorobustus.* All statistical tests were performed following Sokal and Rohlf (1995) and Siegel and Castellan (1988).

In the first sample (S1), we found the metacercariae of the 4 trematode species with different levels of prevalence (Table I; Fisher's exact test on table r × k, $P < 0.0001$ for both males and females) and abundance and intensity (Table I; Kruskal–Wallis ANOVA, $P < 0.0001$ for both males and females). For each parasite, prevalence of infection did not significantly differ between males and females (Fisher's exact test, $P > 0.05$ in each case). There also was no significant difference between sexes for the mean abundance or the mean intensity of each parasite (Mann–Whitney *U*-test, $P > 0.05$ in all cases).

Fifty-seven metacercariae of the 613 found in the collection were melanized. With no exception, this cellular response was addressed against *M. papillorobustus* and almost exclusively against the cerebral metacercariae of this parasite (56 for cerebral metacercariae vs. 1 for abdominal parasites; Fisher exact test, $P < 0.00001$). Among gammarids infected with cerebral metacercariae, the prevalence of melanization was not significantly different between males and females (Table II). The mean number of cerebral metacercariae was not significantly different between individuals harboring melanized metacercariae (mean intensity ± SD, 3.29 ± 3.25, n = 31) and those harboring only intact metacercariae (mean intensity ± SD, 3.93 ± 4.15, n = 56) (Mann–Whitney *U*-test, $Z = -0.29$, $P = 0.77$). There also was no size difference between these 2 categories of individuals (mean size ± SD, individuals harboring melanized metacercariae: 12.4 mm ± 2.0, n = 31, or individuals with only intact metacercariae: 12.5 ± 2.9 mm, unpaired *t*-test, $t = 0.20$, $P = 0.84$). Among gammarids harboring cerebral metacercariae, the mean abundance and the mean intensity of melanized metacercariae were not significantly different between males and females (Table II). Finally, among gammarids harboring melanized metacercariae (n = 31), melanization was complete, i.e., all the metacercariae, for 16 individuals and only partial, i.e., not all the metacercariae, for 15 individuals (on average, 46.6% of the metacercariae). The fact that melanization can be partial or total was not related to the size of gammarids (mean size ± SD, individuals with partial melanization: 12.8 ± 2.08, n = 15, individuals with total melanization: 12.0 ± 1.94, n = 16, unpaired *t*-test, $t = -1.09$, $P = 0.28$) or to their sex (Fisher's exact test, $P = 0.46$). However, the mean number of cerebral metacercariae was significantly higher when melanization was only partial than when it was total (mean intensity ± SD, individuals with partial melanization: 5.0 ± 3.82, n = 15, individuals with total melanization: 1.69 ± 1.35, n = 16, Mann–Whitney *U*-test, $Z = -3.7$, $P = 0.0002$).

Among gammarids infected with cerebral metacercariae in S2 and S3 (187 males and 104 females), the prevalence of melanization was not significantly different between males and females (Table II). The mean number of cerebral metacercariae was slightly higher in individuals harboring melanized metacercariae than in those having only intact metacercariae (mean intensity ± SD, individuals harboring melanized metacercariae 4.62 ± 3.45, n = 126, individuals with only intact metacercariae 4.28 ± 4.11, n = 165, Mann–Whitney *U*-test, $Z = -2.25$, $P = 0.02$) . Among these infected gammarids, the mean abundance and the mean intensity of melanized metacercariae were not significantly different between males and females (Table II). Among the 126 individuals harboring melanized metacercariae, 37 melanize all the metacercariae, whereas for 89 individuals, the melanization was only partial (on average, 44.7% of the metacercariae). As before, the mean number of cerebral metacercariae was significantly higher when melanization was only partial as compared to when it was complete (mean intensity ± SD, individuals with partial melanization: 5.67 ± 3.55, individuals with complete melanization: 2.08 ± 1.11, Mann–Whitney *U*-test, $Z = -6.91$, $P < 0.00001$).

Examination of the infection status of gammarids in S2 and S3 revealed that individuals harboring only intact metacercariae were significantly less common among individuals with normal behavior, i.e., in S3, than those with partial melanization (Fig. 1; Fisher exact test, $P < 0.0001$), suggesting that partial melanization significantly reduces the effect of the parasite on behavior. This phenomenon is stronger when melanization is complete because individuals harboring only melanized metacercariae were significantly more common among gammarids with normal behavior than those with partial melanization (Fig. 1; Fisher exact test, $P < 0.0001$).

These findings first support the hypothesis that the level of parasite pathogenicity is important in determining the likelihood and the degree of host reaction. Indeed, cases of melanization in our gammarid collection almost exclusively concern the cerebral metacercariae of *M. papillorobustus*. This parasite, in this location, is by far the most detrimental for the host because the resulting behavioral alterations strongly increase the probability of gammarid death through predation by aquatic birds (Helluy, 1981, 1984). In addition, *M. papillorobustus* was the most frequent parasite in our study. Thus, even if resistance is costly, investment in a defense against this parasite is likely to be favored by natural selection. Because *M. hoffmanni, L. tridigitata, M. subdolum,* or the abdominal metacercariae of *M. papillorobustus* do not, a priori, cause important fitness reduction in gammarids, hosts may have probably not been selected to invest energy in resistance against these parasites. Previous studies on gammarids support the idea that the pressures exerted by manipulative and nonmanipulative parasites do not have the same potential to select for particular traits in gammarids: males that abandon females (and fertilized eggs in the broodpouch) soon after copulation have some ability to detect and to avoid females infected by cerebral metacercariae of *M. papillorobustus* as a sexual partner (Thomas, Renaud, Derothe et al., 1995; Thomas, Renaud, and Cézilly, 1996). However, such avoidance is not observed when females only harbor the metacercariae of the nonmanipulative species *M. hoffmanni* (Thomas, Lambert et al., 1995). Further studies would be necessary to determine the cue involved to detect and to melanize specifically the cerebral metacercariae of *M. papillorobustus*.

An important implication of our results also concerns the cause of the manipulation exerted by *M. papillorobustus* on gammarids. Because only cerebral metacercariae alter the host behavior, the behavioral changes in infected individuals could, a priori, result from brain damage due to the physical presence of metacercariae in the cerebroid ganglia (e.g., Szidat, 1969; Poulin, 1994). However, our results do not support this hypothesis because melanized metacercariae that are still located in the brain have a reduced effect on the host behavior compared to intact metacercariae. For this reason, we believe that the behavioral alterations induced by *M. papillorobustus* probably rely on chemicals as suggested by Helluy and Holmes (1990). Further experiments are, however, needed to understand why abdominal metacercariae are not able to alter the host behavior.

The most striking result of this study remains, however, the fact that partial melanization seems to partly cancel the behavioral alterations induced by *M. papillorobustus*. Indeed, several studies including laboratory experiments clearly showed that the behavioral alteration in gammarids is not related to the parasite load: the intensity of the altered behavior is similar when gammarids harbor 1, or more than 1, cerebral metacercariae of *M. papillorobustus* (Helluy, 1981, 1983; Thomas et al., 1997). In this context, we do not expect partial melanization to partially cancel the behavior of the gammarids because, a priori, at least 1 metacercariae is still active.

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Parasite Community Structure in *Pimephales promelas* (Pisces: Cyprinidae) from Two Converging Streams

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Abstract: Parasites of the fathead minnow, *Pimephales promelas,* were examined in fish collected from Elk Creek (40.88534°N, 96.83366°W) and West Oak Creek (40.90821°N, 96.81432°W), Lancaster County, Nebraska. These 2 streams are part of the Salt Valley watershed and flow together approximately 2 km downstream from the collection sites to form Oak Creek. This study examined the extent to which the 2 tributaries constitute a continuous habitat with respect to fish hosts. The parasite community included *Trichodina* sp., *Myxobolus* sp., *Dactylogyrus simplex, D. bychowskyi,* and *D. pectenatus* (all on gills); *Gyrodactylus hoffmani* (gill and body surface); *Posthodiplostomum* sp. (neascus, body cavity); and *Uvulifer ambloplitis* (encysted in skin). Among 46 fish from Elk Creek and 56 fish from West Oak Creek taken on 5 dates during April–July 1998, *U. ambloplitis* was found in Elk Creek fish at prevalences of 44–100% but in only 2 West Oak fish on 1 date. Prevalence and mean abundance of *D. simplex* also differed between the 2 sites. On the basis of these observations, fish populations in the 2 streams were considered to be distinct, with little or no fish movement between the tributaries.

Fish parasite communities in a watershed should vary depending on the extent to which tributaries constitute continuous or discrete habitats. Although streams may eventually converge, surrounding geography and land use may create distinct conditions so that plant and animal communities are characteristic of particular tributaries (Brouder and Hoffnagle, 1997). In the case of fish parasites, prevalences and abundances in these tributaries should vary according to environmental conditions, parasite life cycles, and presence of intermediate hosts (LeBrun et al., 1990; Janovy et al., 1997). In a watershed, fish movement potentially affects the distribution and abundance of parasites in the system. This study attempted to test the above ideas by using parasites to indicate whether 2 tributaries of Oak Creek, Lancaster County, Nebraska, were continuous or distinct habitats with respect to the distribution of *Pimephales promelas* Rafinesque, 1820, the fathead minnow. If the tributaries differed ecologically, then they should provide separate parasite transmission opportunities. If fish movement was restricted, differences in the tributaries' parasite communities could reveal the ecological distinctions, but if fish moved freely throughout the watershed, the parasite communities in the 2 tributaries should be indistinguishable because of host mixing.

The 2 tributaries studied were Elk Creek and West Oak Creek, northwest of Lincoln, Lancaster County, Nebraska (Fig. 1). The streams are part of the Salt Valley Watershed and converge within 2 km of the study sites, forming Oak Creek. Elk Creek is much more sinuous than West Oak Creek, has steeper banks, and is fairly heavily wooded with trees and brush along much of its length. West Oak Creek passes through farmland and, for about 0.5 km on either side of the study site, the banks are treeless. *Pimephales promelas* were collected from Elk Creek (40.88534°N, 96.83366°W) and West Oak Creek (40.90821°N, 96.81432°W) from April to October 1998. Collection dates (sample size) are Elk Creek: 13 April (9), 20 April (11), 20 May (3), 7 June (11), 9 July (12); West Oak Creek: 6 April (8), 20 April (7), 20 May (11), 7 June (15), 9 July (15). Fish were taken to the laboratory alive and dissected within 72 hr. Parasites were identified and nomenclatural decisions were justified using Mizelle (1937a, 1937b), Price (1938), Mizelle and Donahue (1944), Hoffman (1967), and Mayes (1976, 1977). Videotapes were made and digital images were captured

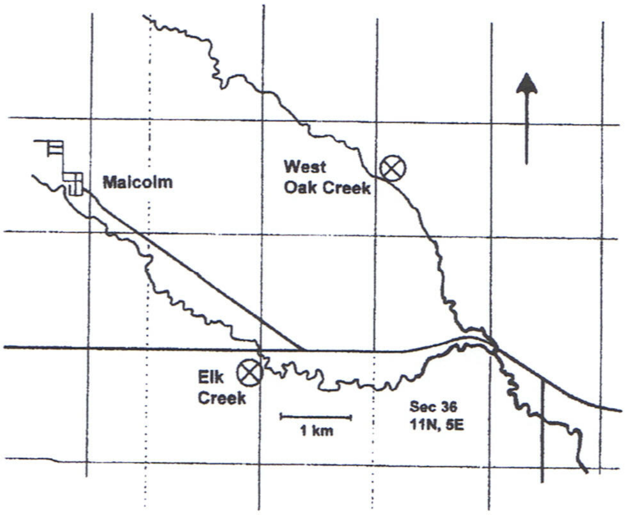

Figure 1. Collection sites west of Lincoln, Lancaster County, Nebraska.