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HITCH-HIKER PARASITES OR HOW TO BENEFIT FROM THE STRATEGY OF ANOTHER PARASITE

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Parasites have evolved various behavioral adaptations to find hosts and locate sites of infection within them (Combes 1991; Esch and Fernandez 1993). In many complex parasite life cycles, parasites have been shown to modify the behavior of their intermediate hosts to enhance the probability of predation by the definitive host (Bethel and Holmes 1973; Camp and Huizinga 1979; Barnard and Behnke 1990; Combes 1991). It has been predicted (Combes 1991) that a new category of parasites, unable to modify the behavior of their intermediate host, will favor their transmission through preferentially infecting hosts previously infected by a debilitating parasite. Thus, through so called hitch-hiking such parasites would benefit from the efficient mechanisms of "favorization" (Combes 1991).

In the amphipod *Gammarus insensibilis*, infective larvae (i.e., cercariae) of *Microphallus papillorobustus* (Trematoda, Microphallidae) systematically migrate into the amphipod's brain, encyst in the cerebroid ganglia (Rebecq 1964) and consequently strongly alter their host behavior by inducing a positive phototaxis, a negative geotaxis and an aberrant-suicidal evasive behavior (Helluy 1983a,b). Infected individuals, named 'mad gammarids', are more vulnerable than uninfected ones to predation by aquatic birds, the definitive hosts of *M. papillorobustus* (Helluy 1983a,b). *Maritrema subdolum* is another microphallidae trematode, sympatric and syntopic with *M. papillorobustus*, with a similar life cycle involving the same intermediate and definitive hosts (Helluy 1983a). Unlike *M. papillorobustus*, *M. subdolum* always encysts in the amphipod abdomen and, in addition, is unable to favor its own transmission to the definitive host since it never alters the host behavior (Helluy 1983a).

The aim of the present study was to analyze several aspects of the *M. subdolum* lifecycle to evaluate the evidence for hitchhiking. We first analyzed for the two trematode species the frequencies of infection in the molluscan first intermediate hosts (*Hydrobia acuta* and *H. ventrosa*). Then, we examined in the field the distribution of the two trematode parasites in the population of the amphipod host. Finally, the mechanisms underlying infection processes were studied in the laboratory, through recording the behavior of the amphipod host and of the cercariae of the two parasite species.

MATERIALS AND METHODS

First Intermediate Hosts

A large sample of *Hydrobia* was randomly sampled at the Thau lagoon (Southern France, 43°25'N, 3°35'E) during March 1995. Cercarial emission allowed us to detect infected individuals. Cercariae of *M. papillorobustus* and *M. subdolum* were identified following the description of Rebecq (1964). To avoid confusion related to morphoanatomical criteria, identification of infected molluscs (*H. acuta* and *H. ventrosa*) was based on three electrophoretic loci (*Pgm* EC 2.7.5.1, *Mpi* EC 5.3.1.8, and *PepB* 3.4.13, substrate Leu-Gly-Gly), previously found to be diagnostic. Electrophoresis techniques used are described in Pasteur et al. (1987). We compared the frequencies of infection of each mollusc species by each trematode species.

Second Intermediate Host

To analyze the ecological association between the two parasites in the second intermediate host, a large sample of *G. insensibilis* ($n = 567$) was collected during spring 1994 in the Thau lagoon, following the methodology described in Thomas et al. (1995). Gammarids were randomly sampled in the aquatic vegetation and in no more than 40-cm water depth. All individuals were preserved in alcohol (70%), measured in length, and dissected to count metacercariae of *M. papillorobustus* and of *M. subdolum*. Gammarids were placed in five length classes ranging from 4 mm to 13 mm. Estimation of the ecological association between the two parasites was addressed through computing in each length class the correlation coefficient for binary data (r_{ϕ}) described in Janson and Vegelius (1981).

Behavior of Amphipods

We collected a new sample of 181 *G. insensibilis* in the Thau lagoon during spring 1994. The behavior of uninfected gammarids ($n = 81$) and gammarids infected by *M. papillorobustus* ($n = 100$) was analyzed through checking their location each minute during 30 min in a water column (length: 40 cm, width: 5 cm, height: 35 cm) filled with aerated sea water (38‰). From these data, we computed the mean height of each gammarid in the water column. We then com-

TABLE 1. Proportions of *H. acuta* and *H. ventrosa* infected with *M. papillorobustus* and *M. subdolum*.

	<i>M. papillorobustus</i>	<i>M. subdolum</i>
<i>Hydrobia acuta</i>	11 (34%)	48 (46%)
<i>Hydrobia ventrosa</i>	21 (66%)	56 (54%)

pared (Mann Withney *U*-test) infected and uninfected gammarids as regard to the mean water height.

Behavior of Cercariae

Behavior of cercariae produced by infected molluscs *H. acuta* and *H. ventrosa*, was analyzed by determining their vertical distribution in a water column (diameter: 9 cm, vertical height: 30 cm). Several infected molluscs were put in a wide-mesh (1 mm) cage placed in the middle of the water column for 20 h. To limit the possible bias induced by dead cercariae, we changed the water every two hours after collecting the bottom (0–1 cm, crawling cercariae) and the top fraction (2–29 cm, swimming cercariae) of the water column separately. The two fractions were filtered to trap cercariae (pore size: 0.22 μ m). After staining (2g KI, 1g I, 100 cc water), cercariae appeared in red and were counted. We conducted this experiment once for each parasite species. This procedure permitted the comparison of, at a given time, the proportion of swimming cercariae of the two trematode species. Statistical tests followed Siegel and Castellan (1988) and Sokal and Rohlf (1981).

RESULTS AND DISCUSSION

Both *M. subdolum* and *M. papillorobustus* rely on the same two mollusc species, *H. acuta* and *H. ventrosa*, as first intermediate hosts. In the field, the frequencies of infection of each mollusc species by either trematode were similar (Table 1, Fisher exact test $P = 0.31$), suggesting that the life cycles of the two parasites are parallel.

There was a close association between the two trematode parasites in their amphipod hosts. Occurrence of metacercariae of *M. subdolum* was positively and significantly associated with that of *M. papillorobustus* (Table 2). The observed association between the two parasites in gammarids could be generated by an heterogeneity in the distribution of infected snails. In such a case, the positive association would result from a passive phenomenon. However, we do not favor this hypothesis for the following reasons: the snails are infected through the excrement of several bird species (larids, small waders, at least 23 species; Rebecq 1964). The depo-

TABLE 2. Ecological association within five size classes of the hosts between abdominal metacercariae of *M. subdolum* and cerebral metacercariae of *M. papillorobustus* in *G. insensibilis*.

	Size classes				
	1	2	3	4	5
<i>n</i>	107	147	123	112	78
r_{ϕ}	0.22	0.23	0.29	0.34	0.34
	*	**	***	***	**

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

TABLE 3. Proportion of swimming versus crawling cercariae of *M. subdolum* and *M. papillorobustus*.

	<i>M. subdolum</i>	<i>M. papillorobustus</i>
Swimming cercariae	342 (26%)	122 (14%)
Crawling cercariae	966 (74%)	731 (86%)

sition of the excrement probably follows a uniform spatial pattern over the sampling zone. The eggs undergo a slow development involving a dispersing phase during 10 days before reaching the miracidium stage that infects molluscs. Moreover, once infected, snails do not start releasing cercariae in the water until several weeks have passed, a time during which snails are likely to move along the substrate. Finally, the association is significant within the five different length classes of gammarids, suggesting that the phenomenon is not due to spatial or temporal association of the two parasites in the first intermediate host. This positive association between the two trematodes within gammarids might result from *M. papillorobustus* cercariae infecting preferentially gammarids previously infected by *M. subdolum*. Although the resulting benefit for *M. papillorobustus* would be unclear in this scenario, we cannot exclude this hypothesis. Another possibility is that *M. subdolum* preferentially infect "mad gammarids."

Overall, gammarids infected by *M. papillorobustus* preferred to swim closer to the surface (on average at 13 cm depth) as compared with uninfected ones (on average at 26 cm) (Mann Withney *U*-test, $U = 1378$, $P < 0.001$). In our experimental conditions, the proportion of cercariae swimming, versus those crawling, was significantly greater for *M. subdolum* (26%) than for *M. papillorobustus* (14%) (Fisher's exact test, $P < 0.0001$, Table 3). Thus, cercariae of *M. subdolum* display a better ability to swim in the water column and are probably more likely to be transported toward the surface by the vertical turbulent diffusion processes (Millet and Cecchi 1992). Due to this behavioral trait, cercariae of *M. subdolum* are probably more likely to encounter modified photophilic gammarids and to increase their probability of transmission by hitch-hiking.

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