Interaction between the Intermediate Host of Schistosomiasis in Brazil *Biomphalaria glabrata* (Planorbidae) and a Possible Competitor *Melanoides tuberculata* (Thiaridae): I. Laboratory Experiments

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The biological control of Biomphalaria glabrata*, intermediate host of* Schistosoma mansoni*, is one the accepted options to fight schistosomiasis. One of the most promising candidates to control* B. glabrata *is the snail* Melanoides tuberculata*, a potential competitor. However, the mechanisms of interaction between the two species are not clear. Our objective is to determine if* M. tuberculata *indeed compete with* B. glabrata*, using two laboratory experiments. In Experiment 1, we tested the effect of the presence of* M. tuberculata *on the fecundity and mortality rates of* B. glabrata*. In Experiment 2, we tested if there was a direct or indirect interaction between the two species. In Experiment 1,* M. tuberculata *was eliminated after the peak in reproductive activity of* B. glabrata*. In Experiment 2,* B. glabrata *produced more egg masses when raised with* M. tuberculata*. The conditions leading to this unexpected positive effect of* M. tuberculata *on the fecundity of* B. glabrata *need further clarification, but emphasize that detailed studies of the interaction between these species in the conditions of the local environment should be considered.*

Key words: *Biomphalaria glabrata* - *Melanoides tuberculata* - competition - schistosomiasis

Certain pulmonate snails are intermediate hosts of *Schistosoma* spp., the digenetic trematode responsible to schistosomiasis in man. Competitors of pulmonate snails have been used for biological control of host populations (WHO 1984, Madsen 1990, Sturrock 1995, Pointier & Giboda 1999). In the West Indies, the thiarid *Melanoides tuberculata* was effective in the elimination or reduction of populations of *Biomphalaria glabrata*, the intermediate host in the cycle of schistosomiasis (Pointier et al. 1989, 1991a, Pointier & McCullough 1989, Pointier & Guyard 1992, Pointier 1993, Schlegel et al. 1997). However, in Venezuela *M. tuberculata* was introduced in 20 sites, but only in three sites was *Biomphalaria* spp. eliminated or effectively reduced (Pointier et al. 1991c). In Brazil, the first occurence of *M. tuberculata* was reported in 1967, in Santos, State of São Paulo. After that, this snail has spread to other localities, probably as a result of successive accidental introductions associated with fish farms (Vaz et al. 1986). However, there are few reports of interaction between *M. tuberculata* and species of the genus *Biomphalaria* in Brazil.

Gomez et al. (1990) observed a negative effect of thiarids on *B. glabrata* in a laboratory experiment, which was attributed to an undetermined substance liberated by thiarids. Conversely, Moné et al. (1986) observed a positive effect of *M. tuberculata* on *B. glabrata*. When raised with *M. tuberculata* and other mollusks, *B. glabrata* reached a larger size and produced more cercaria of *S. mansoni* (Moné 1991). These results point to the dangers of species introductions for biological control based on poor knowledge and weak assumptions of species interactions. The effectiveness of *M. tuberculata* for biological control of *B. glabrata* in a specific environment can be evaluated only when the ecology of these species and the nature of their interactions are understood.

Here, our objectives were to test two hypotheses: that *M. tuberculata* has a negative effect on the growth and demography of *B. glabrata* (H1), and that a substance liberated by *M. tuberculata* causes this negative effect (H2). The second hypothesis was proposed previously for *Thiara granifera*, another thiarid (Prentice 1983, Gomez et al. 1990, Perez et al. 1991). Two laboratory experiments were performed to test these hypotheses.

MATERIALS AND METHODS

Individuals of *M. tuberculata* and *B. glabrata* were collected in streams of two valleys in the municipality of Sumidouro, RJ, Brazil (22º02'59"S, 42º40'29"W). In laboratory, these individuals were raised in 74 x 237 x 330 mm plastic containers with 2 l of dechlorinated tap water. Dehydrated lettuce and rodent food pellets (3-4 mm large) were provided ad libitum, and temperature varied between 22 and 27ºC during the study. Containers were checked at least every two days to remove dead individuals, to guarantee ad libitum food, and that rodent pellets stayed on the bottom. The water was changed every fortnight to avoid any crowding effect, when the number of egg masses, embryos, young and adults was counted. These

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Received 26 June 2001
Accepted 19 December 2001

were the experimental conditions of the following experiments.

Experiment 1: growth and demography of *B. glabrata* raised with *M. tuberculata* - This experiment was designed to test H1, that *M. tuberculata* has a negative effect on *B. glabrata*. Three groups with three replicates each were formed: B 10 *B. glabrata;* M: 10 *M. tuberculata;* BM: 5 *B. glabrata* and 5 *M. tuberculata.*

A replicate was a plastic container with ten young individuals. Only young of the two species were used. Individuals of *M. tuberculata* with less than 3 mm of length and individuals of *B. glabrata* less than 2 mm in diameter were used, corresponding to about 15 days old. All snails were raised in the laboratory, and were allowed to grow and reproduce freely during the experiment. Only dead individuals were removed in Experiment 1. The diameter of *B. glabrata* and the length of *M. tuberculata* were measured every fortnight, followed by the water change in the containers. The number of egg masses, embryos, young and dead adults of *B. glabrata* also was counted every fortnight, and divided by the number of individuals present providing three measures of fecundity and one of mortality. *M. tuberculata* is a viviparous species, and thus only the numbers of young and dead adults were counted.

Experiment 2: mortality rates and fecundity of *B. glabrata* raised in direct and indirect contact with *M. tuberculata* - This experiment was designed to test H2, that *M. tuberculata* liberates a substance that affects *B. glabrata* negatively. Only individuals of *M. tuberculata* with more than 19 mm of length and individuals of *B. glabrata* with more than 15 mm in diameter were used, corresponding to adult individuals. Six groups with two replicates each were formed. The containers of the replicates were divided in two by a wire mesh of $1mm^2$, except for group BMU, as follows: BM: 10 *B. glabrata* at one side and 10 *M. tuberculata* on the other side, to determine indirect effects of individuals of other species; BB: 10 *B. glabrata* at one side and 10 *B. glabrata* on the other side, to control for indirect effects of individuals of the same species; MM: 10 *M. tuberculata* at one side and 10 *M. tuberculata* on the other side, to control for indirect effects of individuals of the same species; B: 10 *B. glabrata* all at one side, the other side empty. A control for any indirect effects of individuals on the other side of the container, regardless of the species; M: 10 *M. tuberculata* all at one side, the other side empty. A control for any indirect effects of individuals on the other side of the container, regardless of the species; BMU: 10 *B. glabrata* and 10 *M. tuberculata* in an undivided container, without the wire mesh, to compare direct and indirect effects between the two species.

The number of adult individuals was kept constant during Experiment 2 by removing newborn individuals and by replacing dead by new adults. The number of adult individuals replaced, and the number of egg masses, embryos, and young of *B. glabrata* was counted every fortnight. Mortality was not measured directly in Experiment 2, but can be inferred from the absolute number of replaced individuals per fortnight. The number of egg masses, embryos, and young was divided by the number of adult individuals present, providing three measures of fecundity for *B. glabrata*. Because *M. tuberculata* is a viviparous species, only the number of young and dead adults was counted.

Statistical analyses - Except for survival in Experiment 1, demographic variables of *B. glabrata* were compared between groups by Analysis of Variance (ANOVA) with replicates nested within groups. There was a marked difference in the fecundity measures of *B. glabrata* before and after the 4th fortnight. Thus, in addition to group and replicate a third factor, named "period", was introduced to consider potential differences between these periods. Survival in Experiment 1 had a linear relationship with time, hence only for this variable time was treated as a covariate, comparing groups by Analysis of Covariance (ANCOVA). In ANCOVA, the effect of time is removed by a process similar to regressing each variable against time and then comparing the intercepts of the regression lines of each variable. Tukey test was used for pair wise comparisons (Sokal & Rohlf 1995). Survival in Experiment 1 was measured as a proportion, and hence was arcsin-square root transformed prior to statistical analyses. The other fecundity variables were counts of dead individuals, egg masses, and young, and hence were log-transformed (Sokal & Rohlf 1995).

RESULTS

Experiment 1 - All individuals of *M. tuberculata* in group BM raised with *B. glabrata* died at the 4th fortnight of the experiment, right after the peak in production of young by *B. glabrata*. In the control group M, where *M. tuberculata* was raised alone, populations persisted 21 months after the beginning of the experiment in variable degrees (50%, 70%, and 90% of the original populations in the three replicates). In the group M, mortality begun only at the 15th and 17th fortnights in two replicates, and at the 4th fortnight in one replicate. *M. tuberculata* did not reproduce in any group.

Mortality of *B. glabrata* in the control group B and in the experimental group BM began at the 4th fortnight (Fig. 1a). After that, survival was significantly higher in group B (Table I, Fig. 1a). Populations of *B. glabrata* were monitored until the 13th fortnight, when the last surviving individuals died.

In the first four fortnights, the production of egg masses, embryos, and young of *B. glabrata* was higher in the experimental group BM than in the control group B (Figs 1b,c,d), but this difference was not significant (Table I). In all groups, egg masses and embryos of *B. glabrata* appeared at the 2nd fortnight, and adults at the 3rd fortnight of the experiment. The peak of egg mass and young production occurred one fortnight after their first appearance (Figs 1b, c, d).

Experiment 2 - There was no mortality of *M. tuberculata* in any of the groups during the 11 fortnights of the experiment. Group M, where *M. tuberculata* was raised alone on one side of the container, differed from the others by a higher production of young between the 3rd and 4th fortnights (Fig. 2c). Accordingly, there was a significant difference between groups in the production of young, and a significant interaction groups x period (Table II). Tukey *a posteriori* tests detected significant

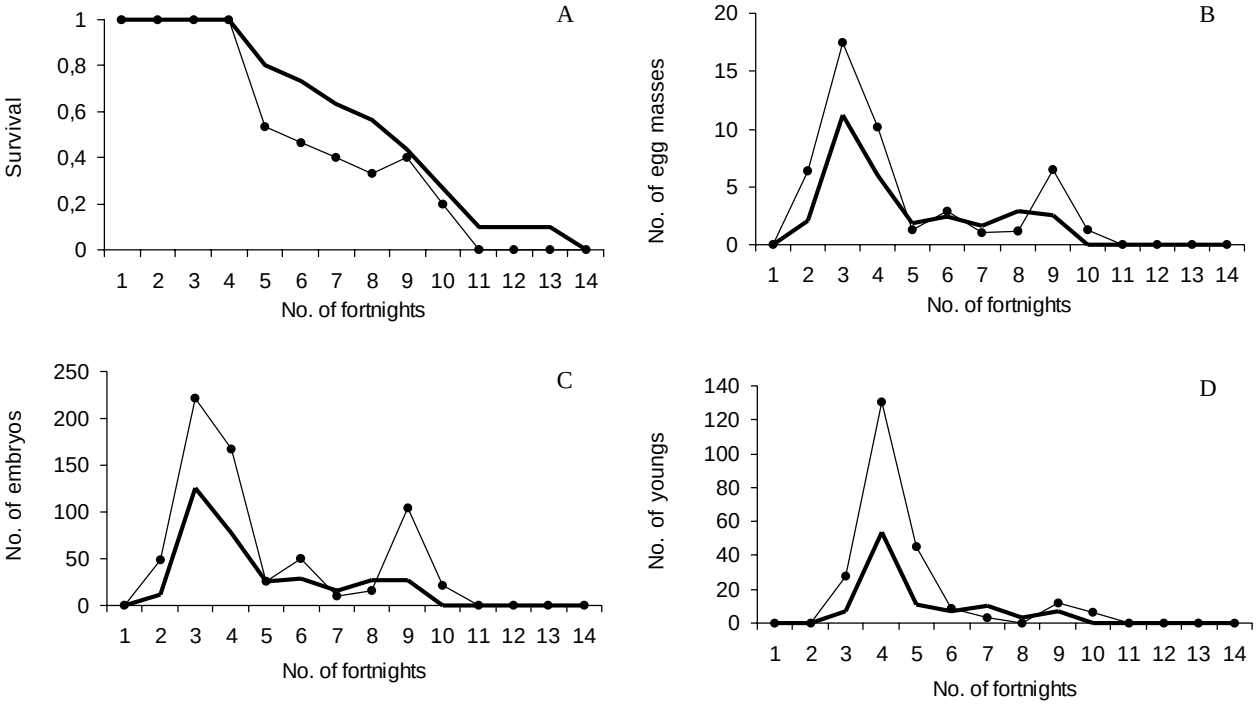

Fig. 1: survival (A), number of egg masses (B), embryos (C) and young (D) of *Biomphalaria glabrata* raised alone (group B) and with *Melanoides tuberculata* (group BM), during the 14 fortnights of the first experiment. Mean value of the replicates was used for each variable.

TABLE I

Effect of *Melanoides tuberculata* on the survival and fecundity of *Biomphalaria glabrata* (groups)

	ANCOVA			ANOVA						
	Survival			Egg masses			Embryos		Young	
	d.f.	*F*	*P*	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Groups	1	9.211	**0.004**	1	2.196	0.144	2.624	0.111	1.453	0.233
Replicates (nested)	4	1.130	0.351	4	0.075	0.990	0.257	0.904	0.044	0.996
Time or period	1	330.5	< **0.001**	1	14.021	< **0.001**	3.641	0.061	0.609	0.438
Interaction groups x period				1	0.230	0.634	0.036	0.849	0.024	0.878

Replicates were nested within groups. Time (days) was a covariate for survival, but was treated as a factor with two levels for the other variables (before and after the 4th fortnight). Variables were measured every fortnight. Survival was arcsin-transformed for ANCOVA and variables for ANOVA were log-transformed. Bold type indicates significant values; d.f.: degree of freedom; *F*: F-test; *P*: probability

differences between group M and groups BM and MM (Table III).

For *B. glabrata*, mortality was low in all groups, usually varying between zero and two individuals replaced during the 11 fortnights of the experiment. Nevertheless, there were significant differences between replicates, period (before and after the 4th fortnight), and between groups in the second period (significant period x groups interaction) (Tables IV, V). One of the replicates of group B – where *B. glabrata* was raised alone on one side of the container was the main cause of this significant difference. This replicate differed significantly from the other replicates and groups in Tukey *a posteriori* tests (B1 in Table V).

The production of egg masses and embryos per individual of *B. glabrata* differed significantly between groups, period, and in the interaction groups x period (Table IV). Group BMU (*B. glabrata* raised with *M. tuberculata* in an undivided container) and group BM (container divided by the wire mesh) were significantly more productive than the control groups B and BB. Group BMU produced significantly more egg masses and embryos per individual of *B. glabrata*, whereas group BM produced significantly more embryos per individual (Figs 2a, b, Table VI). The production of *B. glabrata* in group BMU was more pronounced between the 2nd and 4th fortnight of the experiment, whereas in group BM the production was higher than groups B and BB during the whole experiment (Figs 2a, b). Groups BMU and BM differed between each other only in the production of egg masses.

Most groups produced few young *B. glabrata*, yet they differed significantly in the production of young

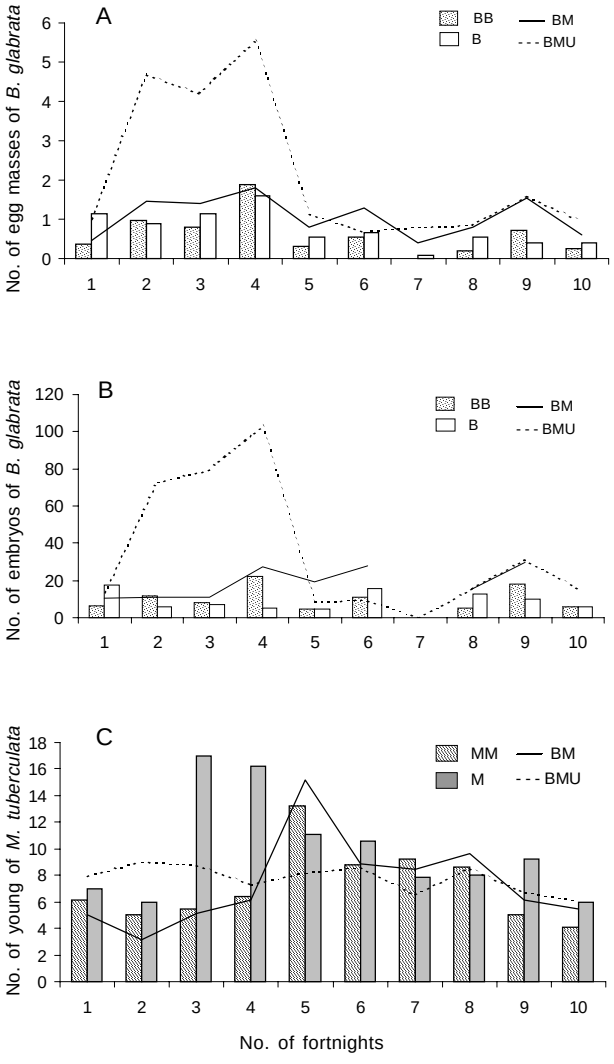

Fig. 2: fecundity of *Biomphalaria glabrata* and *Melanoides tuberculata* in the six treatments of Experiment 2. Two measures of fecundity were used for *B. glabrata*: the number of egg masses (A) and embryos (B). One measure of fecundity was used for *M. tuberculata*: the number of young (C). Containers divided in two sides: B: *B. glabrata*/empty; BB: *B. glabrata*/*B. glabrata*; BM: *B. glabrata*/*M. tuberculata*; M: *M. tuberculata*/empty; MM: *M. tuberculata*/*M. tuberculata.* Containers undivided: BMU: *B. glabrata*/*M. tuberculata*

(Table IV). Similarly to mortality in *B. glabrata*, the same replicate of group B (B1) was the main cause of this significance. It produced significantly more young compared to other replicates of the same group, and compared to other groups as well (Table V).

DISCUSSION

The hypothesis that *M. tuberculata* has a negative effect on *B. glabrata* (H1) was not supported in the conditions of Experiments 1 and 2. In Experiment 1, there was competition for food, but, contrary to expectation, *M. tuberculata* was eliminated by *B. glabrata*. Only the re-

TABLE II

Effect of the direct contact with *Biomphalaria glabrata* on the fecundity of *Melanoides tuberculata* (groups)

		Young (number produced per individual)	
ANOVA	d.f.	*F*	*P*
Groups	3	5.245	**0.003**
Replicates (nested)	4	2.591	**0.044**
Period	1	4.049	**0.048**
Interaction groups x Period	3	5.436	**0.002**

Replicates were nested within groups. Variables were measured every fortnight. Period had two levels, before and after the 4th fortnight. Young was measured every fortnight and was log-transformed. Bold type indicates significant values; d.f.: degree of freedom; *F*: F-test; *P*: probability

TABLE III

Probabilities (Tukey test) for the null hypothesis of no differences between groups in the number of young produced per individual *Melanoides tuberculata* (log-transformed) in Experiment 2

Groups	M	M M	BM	BMU
M	1.000	-	-	-
M M	**0.012**	1.000	-	-
BM	**0.004**	0.983	1.000	-
BMU	0.385	0.404	0.222	1.000

Bold type indicates significant values; containers divided in two sides: BM: *B. glabrata*/*M. tuberculata*; M: *M. tuberculata*/empty; MM: *M. tuberculata*/*M. tuberculata.* Containers undivided: BMU: *B. glabrata*/*M. tuberculata*

TABLE IV

Effect of the direct contact with *Melanoides tuberculata* on mortality and fecundity of *Biomphalaria glabrata* (groups)

ANOVA	d.f.	Mortality		Number of egg masses		Embryos		Young	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Groups	3	2.272	0.088	14.306	< **0.001**	9.104	< **0.001**	6.567	**0.001**
Replicates (nested)	4	6.138	< **0.001**	0.120	0.975	0.319	0.864	4.868	**0.002**
Period	1	9.869	**0.002**	38.967	< **0.001**	5.489	**0.022**	5.381	**0.023**
Interaction Groups x Period	3	3.420	**0.022**	3.909	**0.012**	4.719	**0.005**	1.155	0.333

Replicates were nested within groups. Variables were measured every fortnight. Period had two levels, before and after the 4th fortnight. Mortality was the number of individuals replaced every fortnight, fecundity measures were calculated per individual, and all variables were log-transformed. Bold type indicates significant values; d.f.: degree of freedom; *F*: F-test; *P*: probability

TABLE V

Probabilities (Tukey test) for the null hypothesis of no differences between groups in mortality and in the number of young produced per individual *Biomphalaria glabrata* in Experiment 2

	Groups and replicates	B1	BB1	BM1	BMU1	B2	BB2	BM2	BMU2
Mortality (number of individuals replaced)	B1	1.000	-	-	-	-	-	-	-
	BB1	**0.015**	1.000	-	-	-	-	-	-
	BM1	0.068	0.999	1.000	-	-	-	-	-
	BMU1	**0.018**	1.000	1.000	1.000	-	-	-	-
	B2	**0.004**	1.000	0.983	1.000	1.000	-	-	-
	BB2	**0.048**	1.000	1.000	1.000	0.993	1.000	-	-
	BM2	**0.011**	1.000	0.998	1.000	1.000	1.000	1.000	-
	BMU2	0.998	0.092	0.287	0.097	**0.035**	0.223	0.071	1.000
Young (number produced per individual)	B1	1.000	-	-	-	-	-	-	-
	BB1	<**0.001**	1.000	-	-	-	-	-	-
	BM1	<**0.001**	1.000	1.000	-	-	-	-	-
	BMU1	**0.001**	0.997	0.999	1.000	-	-	-	-
	B2	**0.001**	0.996	0.998	1.000	1.000	-	-	-
	BB2	<**0.001**	1.000	1.000	0.998	0.997	1.000	-	-
	BM2	<**0.001**	1.000	1.000	1.000	1.000	1.000	1.000	-
	BMU2	**0.015**	0.824	0.865	0.994	0.996	0.849	0.963	1.000

Capital letters code for the treatments of Experiment 2, and numbers code for the replicates. Variables were measured every fortnight and were log-transformed. Bold type indicates significant differences. Containers divided in two sides: B: *B. glabrata*/empty; BB: *B. glabrata*/*B. glabrata*; BM: *B. glabrata*/*M. tuberculata*; M: *M. tuberculata*/empty; MM: *M. tuberculata*/*M. tuberculata.* Containers undivided: BMU: *B. glabrata*/*M. tuberculata*

sults of Experiment 1 would not be enough to reject H1, because it could be explained by stronger intraspecific competition in group B (10 *B. glabrata*) than in group BM (5 *B. glabrata* + 5 *M. tuberculata*) during the first 4th fortnights. However, in Experiment 2, fecundity and mortality rates of *B. glabrata* were expected to be lower in the groups BM and BMU because of the negative effect of *M. tuberculata*. Instead, the highest fecundity of *B. glabrata* was in the group BMU.

The hypothesis that *M. tuberculata* liberates a substance that affects negatively individuals of *B. glabrata* (H2) was not supported either. According to H2, fecundity should be lower and mortality higher in the groups BM and BMU because of the presence of *M. tuberculata*. The result was in the opposite direction.

The higher production of egg masses and embryos by *B. glabrata* when raised with *M. tuberculata* in Experiment 2 (groups BMU and BM) could be explained by reduced crowding of *B. glabrata* per unit of volume in group BMU. However, crowding per unit of volume in groups B and BM is the same as in group BMU, but the production of egg masses and embryos was significantly higher in group BMU (Table VI). A second hypothesis is that crowding per unit of area, not volume, is reduced in group BMU, which indeed is true. Although the total density of individuals of the two species is the same in both groups, in the group BM, individuals of each species were restricted to one half of the container. Hence, each species was more crowded than in BMU, where individuals were allowed to use the whole container. Crowding in *B. glabrata* usually is related to volume of available water (Wright 1960), but it also may be related to available surface area (Sturrock & Sturrock 1970). Surface area is not usually considered in the design of experiments with snails. Reduced area could increase chances of hitting other individuals, increasing stress and reducing fecundity and growth (Chernin & Michelson 1959). In this study, crowding in *B. glabrata* probably occurred as an area effect.

TABLE VI

Probabilities (Tukey test) for the null hypothesis of no differences between groups in the number of egg masses and embryos produced per individual *Biomphalaria glabrata* in Experiment 2

	Groups	B	BB	BM	BMU
Egg masses	B	1.000	-	-	-
	BB	0.830	1.000	-	-
	BM	0.434	0.094	1.000	-
	BMU	< **0.001**	< **0.001**	**0.003**	1.000
Embryos	B	1.000	-	-	-
	BB	0.997	1.000	-	-
	BM	**0.023**	**0.037**	1.000	-
	BMU	< **0.001**	**0.001**	0.524	1.000

Capital letters code for the treatments of Experiment 2. Variables were measured every fortnight and were log-transformed. Bold type indicates significant differences. Containers divided in two sides: B: *B. glabrata*/empty; BB: *B. glabrata*/*B. glabrata*; BM: *B. glabrata*/*M. tuberculata*. Containers undivided: BMU: *B. glabrata*/*M. tuberculata.*

Crowding of *B. glabrata* per unit of area does not explain the significantly higher production of embryos in group BM compared to groups BB and B. Crowding per

unit of area was the same in these three groups, and a logical hypothesis is that *M. tuberculata* is facilitating the production of embryos by *B. glabrata*. *M. tuberculata* could be releasing a nutrient for *B. glabrata*, or could be producing a substance that would stimulate growth of *B. glabrata* directly. Gomez et al. (1990) observed a decline in numbers of *B. glabrata* raised with *T. granifera* in the laboratory, the opposite result of this study. Conversely, Moné (1991) observed higher growth rates of *B. glabrata* raised with *M. tuberculata*, in agreement with this study. Moné (1991) also discussed the possible causes and suggested that *M. tuberculata* could liberate a nutritive substance that would stimulate growth of *B. glabrata* directly. Such substance may also stimulate the fecundity of *B. glabrata* as observed in this study. The same phenomena have been reported in other studies of competition between freshwater snails, but these observations have not received adequate attention (Santos et al. 1989, Stryker et al. 1991). It is possible that *M. tuberculata* indeed liberates a substance that affects *B. glabrata*. This substance might have a negative effect on *B. glabrata* in some conditions (e.g. Gómez et al. 1990) or positive in others (this study and Moné 1991). Therefore, the result of this interaction might be affected by environmental conditions. For example, Pointier et al. (1991b, 1992) observed that the efficiency of *M. tuberculata* in the elimination of *B. glabrata* depended on the type of habitat where the two occurred.

The advantage of *B. glabrata* over *M. tuberculata* in Experiment 1 was a result of the early reproduction, high reproductive rate and the high number of young *B. glabrata* produced at the 4th fortnight of the experiment. As soon as rodent food pellets were provided, individuals of *B. glabrata* would aggregate over the food, covering it completely and making it unavailable for *M. tuberculata*. Conversely, in Experiment 2 *B. glabrata* was prevented from monopolizing food in the same manner by a low number of adults and a wire mesh dividing the container.

M. tuberculata did not reproduce in Experiment 1, and reproduced only intermittently in Experiment 2. Mortality of *M. tuberculata* is usually low (Dudgeon 1986, Freitas et al. 1987), but it reproduces continuously (Bedê 1992, Pointier et al. 1992). It is possible that the source population of *M. tuberculata* reproduces late in the development. Indeed, age of first reproduction of *M. tuberculata* in Brazil was 710 days (Bedê 1992), whereas in Hong Kong it varied between 90 and 120 days (Dudgeon 1986), and in Malaysia between 100 and 200 days (Berry & Kadri 1974). Fecundity of *M. tuberculata* did not differ between groups, hence, the presence of *B. glabrata* did not affect *M. tuberculata* in the conditions of the experiment.

In conclusion, our results confirm the differences in demographic strategies between *B. glabrata* and *M. tuberculata* reported in the literature. Individuals of *M. tuberculata* reproduce later and grow slower than *B. glabrata*, resulting in the elimination of *M. tuberculata* by *B. glabrata* in laboratory conditions. These results may not hold in the field because of the complexity of natural conditions.

M. tuberculata does not seem to inhibit *B. glabrata* producing chemical substances. Actually, in the conditions of the experiment of this study *M. tuberculata* might even facilitate the reproduction of *B. glabrata*. The conditions leading to this result need further clarification and field evidence. Nevertheless, detailed studies of the interaction between these species in the conditions of the local environment are necessary prior to introductions. Such introductions could lead to a result opposite to that expected, i.e., the increase in the size of populations of *B. glabrata*. Additional complications are the fact that *M. tuberculata* transmits other parasites that cause diseases in humans (Pointier 1999), and that it may have unpredicted effects on the endemic fauna.

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