Mem. Inst. Oswaldo Cruz, Rio de Janeiro, Vol. 83(2): 165-174, abr./jun. 1988

RHEOTAXIS OF *BIOMPHALARIA GLABRATA* ON VERTICAL SUBSTRATES AND ITS ROLE IN THE RECOLONIZATION OF HABITATS TREATED WITH MOLLUSCICIDES

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The authors observed specimens of Biomphalaria glabrata *climbing up the vertical wall of a ditch against the current. The snails that showed this behavior during application of a molluscicide in the breeding site survived and probably played a role in repopulation, which was observed three months later. These observations motivated field and laboratory investigations which led the authors to conclude that: a) this species is able to climb vertical surfaces both in field and laboratory situations; b) the current of water, as a physical stimulus, is sufficient to trigger this behavior (rheotaxis); c) rheotaxis on vertical surfaces depends on the presence of a necessarily moderate current; d) there are indications that* B. glabrata *may undergo habituation with respect to rheotaxis on vertical walls; e) the relationship between rheotaxis and habituation should be considered as a factor causing snail grouping in water bodies which may contribute to their localization in the field; f) rheotaxis on vertical surfaces may facilitate population dispersal, and its occurrence should be considered when campaigns for the control of schistosomiasis transmission are planned. The authors present some proposals to avoid the manifestation of this behavior in some field situations.*

Key words: *Biomphalaria glabrata* – schistosomiasis – molluscicide – rheotaxis – behavior and control

The occurrence of *Biomphalaria glabrata* in head water habitats may be explained in some situations by the ability of these snails to migrate upstream even along vertical surfaces. However, in the literature there are only reports of *B. glabrata* up and downstream migration along non-vertical surfaces (Lutermoser & Castellanos, 1945; Pimentel et al., 1957; Scorza et al., 1961; Paulini, 1963; Etges & Frick, 1966; Jobbin & Ippen, 1964).

In 1983, we observed that *B. glabrata* specimens climbed vertically, the walls of a rainwater draining ditch and of a spring located at the campus of the Fundação Oswaldo Cruz (Rio de Janeiro, Brazil), against a current of water originating from flooded areas upstream. Bayluscide was applied some time later inside the ditch, apparently killing all the snails present. At that time we noticed that the molluscs present in the headwater marshes and those that climbed against the water current along the wall of the ditch at the time of application, survived and certainly contributed to the repopulation of the breeding site, which was noted three months later.

The objectives of the present study were: 1) to demonstrate the climbing behavior of *B. glabrata* against water currents along vertical surfaces and to discuss the role of this behavior in dispersal and its implications in the population of bodies of water as well as in the repopulation of breeding sites treated with molluscicides; 2) to study the causal stimuli of this behavior; 3) to investigate the responses to different types of water outflow; 4) to propose solutions to prevent the dissemination of these snails against vertical currents; and 5) to determine the occurrence of habituation in snails repeatedly subjected to the presence of a vertical water current.

MATERIALS AND METHODS

Demonstration of the behavior

In the field – This stage of the study was conducted in a ditch 196m long and 1m wide with walls varying in height from 60 to 200cm because of an inclination and of the presence of two 25cm steps inside the ditch (Fig. 1).

This work was supported by FINEP and CNPq/PIDE VI.

Received July 23, 1987.
Accepted November 11, 1987.

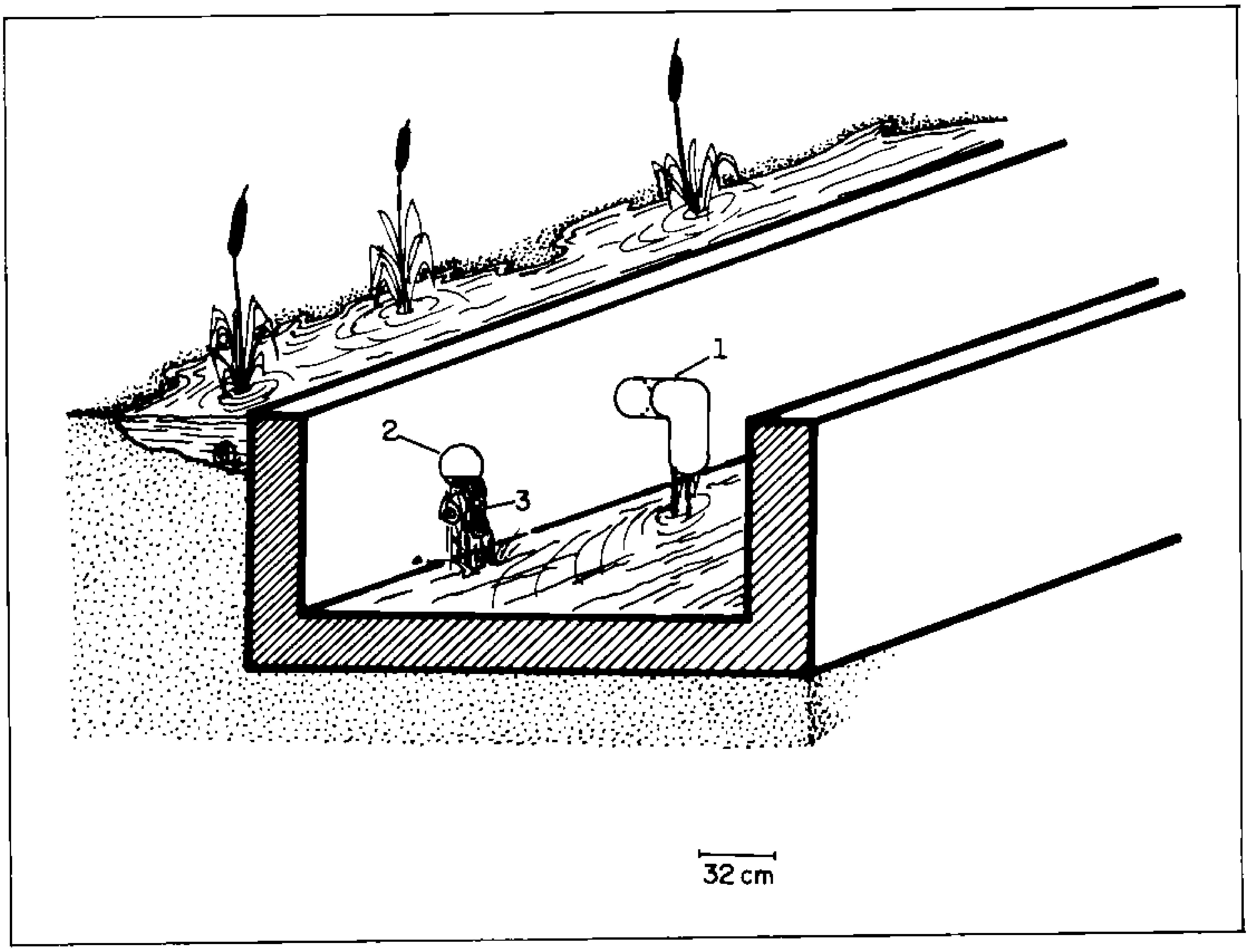

Fig. 1: Schematic representation of a man-made ditch showing the water being drained from the upper drenched areas. 1. ordinary drainage tube; 2. drainage tube coupled with a curved end; 3. vertical migration of the snails on the wall of the ditch.

Permanent water flow is provided by a spring, whose water runs through the ditch after passing through PVC tubes 10cm in diameter (Fig. 2).

The *B. glabrata* population originates from specimens introduced in 1917 (Magalhães, 1966). Populations of *Physa* sp., *Pomacea* sp. and of a species of the family Thiaridae are also present at this site.

To determine migration with and against the current, we set up the apparatus shown in Fig. 2 constructed with PVC tubing and 2 glass flasks separated by a screen. The apparatus was coupled to the exit of one of the drains, permitting normal water flow but interrupting snail migration to the headwater marsh. The animals that moved upstream were captured in flask B, and those moving downstream were captured in flask A.

We also held direct and indirect observation sessions with time-lapse cinematography (Jurberg, 1978) and videotape.

In the laboratory – We performed 4 experiments with replications (30 snails per experiment for a total of 240 snails measuring 10 to 20mm in diameter). In the first two experiments, we used snails from the ditch, and in the other two, snails from the breeding colony of the Department of Biology, Oswaldo Cruz Institute, originally obtained from Touros, RN, Northeastern Brazil.

The equipment (Fig. 3) consisted of an aquarium (60 x 40 x 40cm) divided vertically by two fibrocement plates into three compartments (A, B and C). Water flowed constantly on the experimental plate, forming a vertical current. The control plate was kept moist by dripping water.

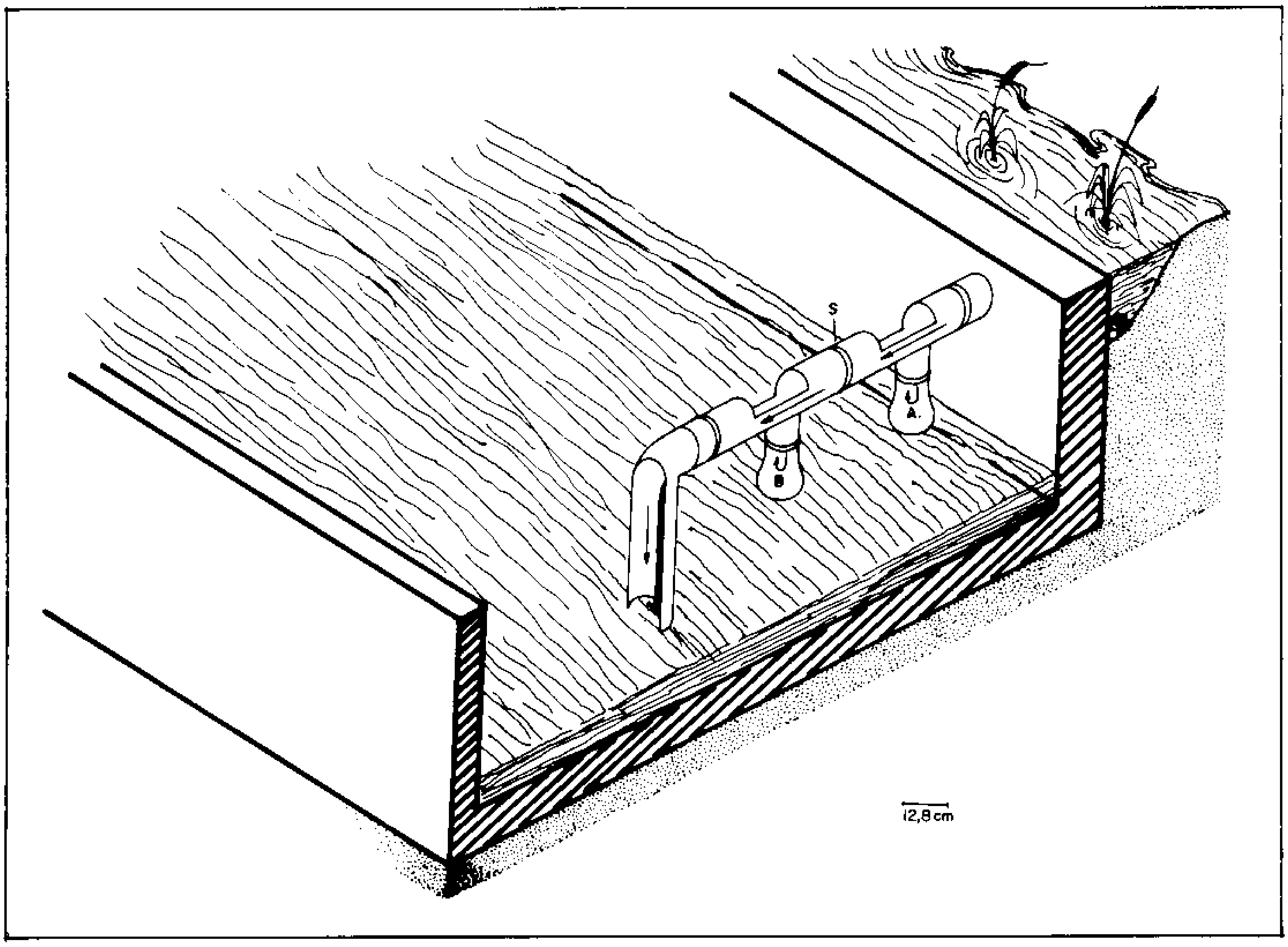

Fig. 2: Schematic representation of an apparatus for monitoring upstream and downstream migration by *Biomphalaria glabrata* in a man-made ditch. The snails moving down from the upper drenched area were caught in flask A whereas those moving vertically upstream were caught in flask B. The arrows indicate the water flow in the apparatus and (S) is the screen between the two flasks.

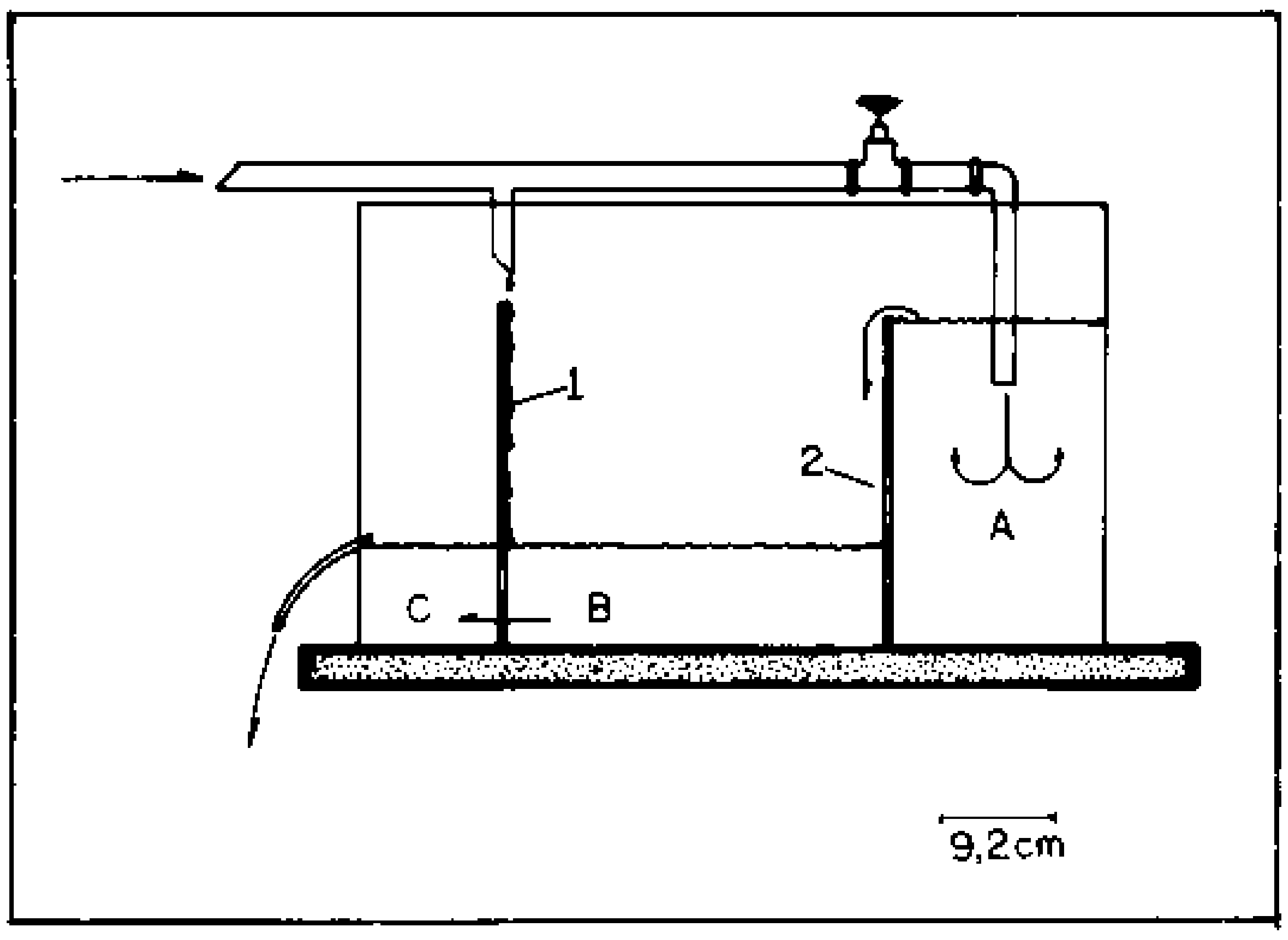

Fig. 3: Schematic representation of an apparatus for monitoring vertical rheotaxis and habituation in *Biomphalaria globrata*. A, B and C comportaments; 1. control wall; 2. experimental wall. See a detailed explanation in the text.

Water filled compartment B and flowed along the experimental wall filling compartments A and C to a height of 10cm. During this stage, flow was constant at 1 l/min.

We performed experiments with the two groups of snails in the presence of food (fresh lettuce ad libitum) in compartments A and B, and under conditions of food deprivation. Individuals were placed in compartment A and their positions were recorded every 12 hours in 48 hours. Snails that reached compartment B were considered to have climbed up vertically.

Study of causal stimuli

In the field – To determine whether the stimulus inducing upstream migration was related to differences in conductivity, pH, total hardness, hardness of calcium, chlorides and temperature, we analyzed these physico-chemical parameters in water samples collected from the upper drenched areas, in the drainage tubes and inside the ditch.

In the laboratory – The role played by searching for food in vertical migration against currents of water was evaluated using the data obtained in the four previously cited experiments in the laboratory.

Effect of different water flow rates – We used water flow rates of 2 l/min, 4 l/min and 6 l/min in the same aquarium, modified so that the water would flow only on a 10cm width of the experimental wall.

We used 30 *B. glabrata* specimens from the ditch for each flow rate and repeated the same experiment as in the previous section, with replication (n = 180) and with food supply.

Proposed control of behavior in the field – To determine the possibility of preventing the snails from climbing up the ditch wall we coupled 10cm long PVC tubes with a curved end to the outflow tubes so that the water would fall away from the margin without forming a current on the wall (Fig. 3).

Occurrence of habituation – We conducted an experiment consisting of two stages of 3 days each, separated by a 3-day interval using 30 snails in the experimental aquarium at a flow of 1 l/min. We placed the snails in compartment B and observed their positions 6,18 and 24 hours later. At the end of the last observation session of each day, the snails were returned to the original position and another identical 72 hour stage was started.

To determine whether the possibility of a snail starting to climb up was the same as the possibility of no climbing behavior occurring we used the MacNemar test (approximation by chi-square distribution with correction of continuity) (Siegel, 1975). If the animals showed lack of climbing behavior more than initiation of climbing behavior, this would be a sign of the occurrence of habituation.

RESULTS

Demonstration of behavior

In the field – Over a period of 17 days of observation, 54 specimens of *B. glabrata* moved downstream, being caught in flask A, 2 specimens moved upstream, being caught in flask B, and 9 climbed the vertical wall of the apparatus, but without reaching flask B. We also observed 8 specimens of *Physa* sp. climbing upstream along the vertical wall of the apparatus and reaching the collection flask. On several occasions we recorded locomotion of *B. glabrata* and of the other mollusks both on the wall of the ditch and on the steps.

When it rained, the volume of water leaving the tubes increased and the snails only were able to climb up along the borders of the flow (where the intensity of the current was lower). On these occasions, the portions of the ditch walls, that were normally dry, started to have a moderate current which favored the climbing behavior of the snails. Those that succeeded in climbing up and leaving the ditch bed escaped from being washed downstream by the rainwater, which increased the outflow inside the ditch.

In the laboratory – In all experiments there were snails that climbed against the water current (Table I). Snails coming from the field (78.3%) climbed up more than the snails proceeding from laboratory experiments (41.4%) (Table II). When field and laboratory animals are considered as a whole, 52.1% climbed up in the presence of food and 68.4% did so in the absence of food (Table III).

In all phases of the study, the snails climbed up against the current of water on a vertical surface using a behavioral pattern similar to crawling with a hanging shell discribed by Jurberg et al. (1987).

Filming permitted us to observe that the animals often climbed up the vertical wall following the trail of other snails that had climbed previously.

Study of causal stimuli

In the field – The physico-chemical analysis of the water revealed differences in conductivity between the ditch water, from which the snails climbed, and the upper drenched areas from which the water came. There was no difference between the steps of the ditch, where vertical climbing by the snails was also observed.

In the laboratory – We analyzed the data by summing the result of each experiment with that of its replication after determining that they did not differ significantly at the 5% level (chi-square, DF = 1, $\alpha = 0.05$).

The snails coming from the field climbed up at a significantly higher frequency than those proceeding from the laboratory (chi-square = 33.609; DF = 2; $\alpha = 0.05$) (Table II).

The frequency of climbing behavior was significantly lower in the presence than in the absence of food (chi-square = 6.521; DF = 2; $\alpha = 0.05$) (Table III).

In all experiments, some of the snails that had climbed up to compartment B climbed down again returning to compartment A (Table IV).

In the presence of food, the frequency of snails that descended was significantly lower than the frequency of those that did not descend both in the experiments with field animals (chi-square = 8.805, DF = 1, $\alpha = 0.95$) and in the experiments with laboratory animals (chi-square = 17.191, DF = 1, $\alpha = 0.05$). In the absence of food there was no significant difference between the frequencies of snails that descended and did not descend in the field experiments (chi-square = 2.283, DF = 1, α = 0.05) or in the laboratory experiments (chi-square = 0.926, DF = 1, $\alpha = 0.05$).

Effect of different water flows – The frequency of climbing up animals was not the same for all water flows. At the lowest flow rate (2 l/min), the frequency of climbing-up behavior was sharply higher than at higher flow rates (4 and 6 l/min), with the latter flow rates giving similar results (Table V).

TABLE I

Frequency (F) and percentage (%) of *Biomphalaria glabrata* which climbed against current reaching the compartment B

Experiment	% in each experiment		% (snails from the same origin	% (snails under name Feeding regimen
1. Field snails with food in compartments A and B	68.3	41	78.3	
2. Field snails without food in compartments A and B	88.3	53		52.1
3. Laboratory snails with food in compartment A and B	35.6	21		68.4
4. Laboratory snails without food in compartments A and B	47.4	27	41.4	

TABLE II

Location of the non-climbing *Biomphalaria glabrata* in different sites of the aquarium

Experiment	Compartment A (initial)	Control wall	Water surface (control)	Compartment C (control)	Experimental wall	Water surface experimental
1	7	1	0	0	9	2
2	0	0	0	2	5	0
3	37	0	0	0	1	0
4	17	2	1	0	7	3

TABLE III

Frequency (F) and percentage of *Biomphalaria glabrata* which went down and which remained up*

Experiment	Went down F	%	Remained up F	%	P
1	11	26.8	30	73.2	0.34**
2	21	39.6	32	60.4	0.1254
3	1	4.8	20	95.2	0.0002
4	16	59.3	11	40.7	0.2311

* These frequencies were obtained from snails which reached the experimental compartment.
** Significant difference (chi-square Test, GL = 1, $\alpha = 0.05$).

TABLE IV

Effects of the absence of food on the frequency of the climbings: chi-square test comparing field and laboratory snails

	With food	Without food	P
Field snails	40	53	0.2119
Laboratory snails	21	27	0.6160

Proposed control of the behavior – With this prolongation of the outflow tubes and the consequent abolition of a water current on the wall, the snails no longer climbed up. However, they apparently started to concentrate where the water dripped.

Occurrence of habituation – The results are given in Table V. When the first two days of the experiment were compared, we found that there was no decrease in the probability of each snail climbing up within 24 hours (chi-square = 1.455; DF = 1, $\alpha = 0.05$).

During the second stage which started 3 days later we confirmed what we had noted during the first, i. e. during the first 24 hours there was no decrease in the probability of each snail climbing up (chi-square = 1.070; DF = 1; α = 0.05) and those that had climbed up at least once during the first 2 days tended to show lack of climbing behavior on the third day (chi-square = 15.588; DF = 1; $\alpha = 0.05$).

When we compared the snails that climbed up during the first stage with those that climbed up on the first day of the second stage, we noted that, after 3 days without any contact with the vertical current of water, the snails started to climb up again regardless of their experience during the first stage (chi-square = 0.000; DF = 1; $\alpha = 0.05$).

Considering the total period of 6 days during which the animals were in contact with the vertical current, we observed that of the 30 snails tested, 10 did not climb up, 8 climbed only once, 6 climbed twice and 6 climbed three times.

DISCUSSION AND CONCLUSIONS

Demonstration of the behavior – The field and laboratory observations showed that both the *B. glabrata* specimens from the ditch and those originating from Touros and maintained in the laboratory for several generations showed the behavior of climbing against a water current on vertical surfaces, demonstrating that this behavior is not limited to the population inhabiting the FIOCRUZ campus or to conditions specifically occurring in that particular ditch.

This behavior represents an adaptative advantage for this species since it may facilitate snail dispersal even at breeding sites with steep walls and may eventually protect the animals from being washed away by rainwater and from the action of molluscicides or of other control

TABLE V

Frequency with which each *Biomphalaria glabrata* climbed against current

Number of snail	Days 1	2	3	1st stage Total climbing/ day/snail		Days 1	2	3	2nd stage Total climbings/ day/snail	Total climbings/ in the 2 stage/ snail
1				0		*			1	1
2	*			1		*	*		2	3
3				0	3				0	0
4		*		1		*			1	2
5				0	D	*			1	1
6	*		*	2	a	*			1	3
7	*	*		2	y		*		1	3
8	*			1	s	*			1	2
9				0					0	0
10	*			1	I	*	*		1	2
11	*			1	n	*			1	2
12	*			1	t				0	1
13				0	e				0	0
14	*	*		2	r		*		1	3
15	*			1	v	*	*		2	3
16				0	a	*			1	1
17				0	l		*		1	1
18				0		*			1	1
19				0					0	0
20		*		1					0	1
21				0					0	0
22				0					0	0
23		*		1		*			1	2
24				0			*	*	2	2
25				0					0	0
26	*			1			*		1	2
27				0					0	0
28				0					0	0
29				0		*			0	0
30				0					0	0
Total Climbings/ Day	10	5	1			13	8	1		

* Occurrence of climbing.

measures. This favors repopulation, since the survival of only one specimen is sufficient to reconstitute an entire population within a short period of time (Paraense, 1972).

The field animals climbed proportionally more than the laboratory animals, probably because these were different populations reared in different environments and subjected to different selective pressures.

Study on the causative stimuli – We observed that a moderate water current, regardless of other factors, stimulates the climbing behavior of these animals along vertical surfaces. This conclusion was reached due to the fact that if the snails climbed up both in the presence and in the absence of lettuce, the search for food probably is not the causative stimulus of this behavior. Since the water was the same at all points in the aquarium as well as above and below the steps inside the ditch, we conclude that the quality of the water was not responsible for snail migration upstream along vertical surfaces. However, the possibility that other factors in addition to the current attracted these snails in a secondary manner should not be ruled out.

With respect to water currents on non-vertical surfaces, Bousfield (1978, 1979), in a laboratory experiment, concluded that in *B. glabrata* positive rheotaxis is triggered by chemoattractants. According to Etges & Frick (1966), the snails show positive rheotaxis in the presence of chemical stimuli, but, in the absence of such stimuli, their movements predominantly follow the current. Paulini (1963) proposed that other stimuli in addition to the current may play an important role in the migration of *B. glabrata* against the current. Radke & Ritchie (1961), after releasing marked *B. glabrata* snails at a given site, found 27% of the animals above and 3% below this site, showing a clear upstream climbing behavior.

Etges & Frick (1966), Bousfield (1978, 1979) and Thomas (1982) relate the attraction for chemical stimuli to the term rheotaxis, which has been defined by Fraenkell & Gunn (1961) as the response to a physical stimulus (the current itself). According to these authors, rheotaxis is "a reaction in which in rapid currents, some animals align their body with the water flow keeping their face turned against the current".

We consider rheotaxis to be locomotion of the snails against the current of water motivated only by the presence of such a current, independently of chemical or social stimuli.

Pimentel et al. (1957) reported that these animals migrate with and against the current, and the downstream locomotion should not be attributed only to "tropism" but also to the physical force of the water. Bovbjerg (1952), in a study of *Campeloma decisum,* Say (Viviparidae), noted that these snails cluster at sites where a water current exists and that they respond to this stimulus either by geotaxis or by an interaction of both stimuli.

In the present study the number of climbing-up behaviors was proportionally larger than the number of descending behaviors, except for the experiment with laboratory animals in the absence of food. The snails probably started climbing up in response to the current and continued climbing. However, when they found no food or any other stimulus that would keep them in the experimental compartment they descended again. This apparent tendency to climb up more than to descend, as well as the observations of snails climbing up the ditch walls on rainy days, may indicate another adaptative advantage which would compensate for the snails being washed away downstream.

It was not possible to determine whether the snails followed the trails of other snails, whether they followed the same trail because of the existence of more appropriate conditions at the sites selected for the climbing up behavior, or if this behavior was oriented by mucus trails (Townsend, 1974). In the present study we found that rheotaxis can occur in the presence of water current as a physical stimulus.

Effect of different water flows – Environments with moderate water currents are considered to be more favorable for the development of *B. glabrata* (Cridland, 1958; Andrade, 1959). Scorza et al. (1961), in a study on *Australorbis glabratus (= Biomphalaria glabrata),* observed that the velocity of the current was the main factor causing a habitat to become populated, with currents of more than 29cm/s representing a limiting factor for the establishment of these snail populations. Luttermoser & Castellanos (1945) observed experimentally that *B. glabrata* specimens can move against a water current having a maximum velocity of 50cm/s, and are paralized and washed away by currents above this limit. Harry & Cumbie (1956) concluded that "populations of *Australorbis glabratus,* the vector for *Schistosoma mansoni* in Puerto Rico, are not maintained in reaches of streams steeper than 20 meters fall per 1000 meters of length".

The present results, concerning a water current on a vertical surface were similar to data reported in the literature about horizontal or slanted locomotion, since in the experiment with lower water flow the frequency of climbing behavior was much higher.

Proposed control of behavior – Sanitation engineering measures have been proposed for the control of water speed (Lutermoser, 1945; Jobin & Ippen, 1964), and changes in water levels in canals (Jobin, 1970) and water distribution in sewers (McJunkin, 1975) have been proposed for the control of these snails.

As an additional contribution to snail control, on the basis of our results we suggest that draining ditches, water tanks and other water reservoirs for human use should be constructed taking into consideration rheotaxis along vertical surfaces. This would prevent the occurrence of favorable conditions for the intercommunication of these environments with breeding sites of vector snails, since the presence of a moderate water current even on vertical surfaces facilitates the dispersal of these animals. In the particular case of water drainage tubes, we suggest that they should be prolonged and their ends curved.

Occurrence of habituation – The present study suggests the occurrence of habituation after 48 hours, since after this period of time the snails tended to avoid climbing up. Experiments of longer duration and including more than one stimulus would be needed to exclude with certainty the occurrence of fatigue.

After a 3-day interval following the first 72-hour stage, the snails responded to the water current as if they were facing it for the first time. This fact also indicates the occurrence of habituation, because, according to Willows (1973), "Spontaneous recovery of the response occurs over time when the habituating stimulus is no longer presented".

Habituation is a form of learning which is extensively diffuse among several taxa. In mollusks, habituation has been detected in various groups, as reported in reviews by Willows (1973) and Carey & Samley (1986).

Habituation may be of great adaptative value for planorbids which are vectors for schistosomiasis in relation to upstream climbing, since it may act by reducing permanent dispersal towards biotopes located above the breeding sites. Thus, if on the one hand climbing against the current may facilitate the occupation of a body of water, on the other, habituation moderates this behavior by preventing upstream concentration by the snails.

The relationship between rheotaxis and habituation should be considered as a factor causing snail clustering in water collections, although Simpson et al. (1973) and Thomas (1977) consider clustering to be due to environmental heterogeneity, to social attraction or to a combination of the two.

RESUMO

Reotaxia de *Biomphalaria glabrata* em superfícies verticais e seu papel no repovoamento de habitats tratados com moluscicidas – Os autores observaram exemplares de *Biomphalaria glabrata* subindo contra corrente em uma parede vertical de uma vala, constatando que os caramujos que apresentavam esse comportamento durante a aplicação de moluscicida neste criadouro sobreviveram e, provavelmente, tiveram papel no repovoamento, que foi observado três meses após. Essas observações suscitaram investigações de campo e de laboratório, através das quais concluiram que: a) esta espécie é capaz de subir em superfícies verticais em situações de campo e de laboratório; b) a corrente da água enquanto estímulo físico, é suficiente para desencadear esse comportamento (reotaxia); c) a reotaxia em superfícies verticais depende da existência de uma corrente de água necessariamente moderada; d) há indícios de que *B. glabrata* sofra habituação em relação à reotaxia em paredes verticais; e) a reotaxia em superfícies verticais pode facilitar a dispersão das populações, devendo sua ocorrência ser considerada no planejamento das campanhas de controle da transmissão da esquistossomose. Os autores apresentam propostas para evitar a manifestação desse comportamento em algumas situações de campo; f) a relação entre a reotaxia e habituação deve ser considerada um fator de agrupamento dos caramujos nas coleções d'água, que pode contribuir para sua localização.

Palavras-chave: *Biomphalaria glabrata* – esquistossomose – moluscicida – reotaxia – comportamento e controle

ACKNOWLEDGEMENTS

We wish to thank Dr. Wladimir Lobato Paraense, for providing the snails and Dr. Otavio Sarmento Pieri for this critical discussions on the work.

REFERENCES

ANDRADE, R. M., 1959. Ecologia. *Rev. Bras. Mal e Doenças Tropicais, 11* (2/3): 171-217.

BOUSFIELD, J. D., 1978. Rheotaxis and chemoreception in the freshwater snail *Biomphalaria glabrata* (SAY): Estimation of the molecular weights of active factors. *Biol. Bull., 154* (3): 361-371.

BOUSFIELD, J. D., 1979. Plant extracts and chemically triggered positive rheotaxis in *Biomphalaria glabrata* (SAY), snail intermediate host of *Schistosoma mansoni* (SAMBON). *J. Appl. Ecol., 16:* 681-690.

BOVBJERG, R. V., 1952. Ecological aspects of dispersal of the snail *Campeloma decisum. Ecology, 33* (2): 169-176.

CAREY, J. T. & SAMLEY, C. M., 1986. Intermediate learning and memory from behavior to molecule. *Ann. Rev. Neurosci., 9:* 435-487.

CRIDLAND, C. C., 1958. Ecological factors affecting the number of snails in a permanent stream. *J. Trop. Med. Hyg., 61:* 16-20.

ETGES, F. C. & FRICK, L. P., 1966. An experimental field study of chemoreception and responses in *Australorbis glabratus* (SAY) under rheotactic conditions. *Amer. J. Trop. Med. Hyg., 15* (3): 434-438.

FRAENKEL, G. S. & GUNN, D. L., 1961. *The orientation of animals. Kineses taxes and compass orientation.* Dover Publications Inc. New York, X + 376p.

HARRY, W. H. & CUMBIE, B. G., 1956. Stream gradient as a criterion of lotic habitats suitables for *Australorbis glabratus* in Puerto Rico. *Amer. J. Trop. Med. Hyg., 5:* 921-928.

JOBIN, W. R., 1970. Control of *Biomphalaria glabrata* in a snail reservoir by fluctuation of the water level. *Am. J. Trop. Med. Hyg., 19* (6): 1049-1054.

JOBIN, W. R. & IPPEN, T. A., 1964. Ecological design of irrigation canals for snail control. *Science, 145:* 1324-1326.

JURBERG, P., 1978. Contribuição para o conhecimento da conquiologia, anatomia de *Thausmatus (Thausmatus) taunaisii* (FERUSSAC, 1822). Tese de mestrado, Museu Nacional, 56p.

JURBERG, P.; SCHALL, V. T.; BARBOSA, J. V.; GATTI, M. S. & SOARES, M. S., 1987. Behavior of *Biomphalaria glabrata,* the intermediate host snail of *Schistosoma mansoni,* at different depths in water in laboratory conditions. *Mem. Inst. Oswaldo Cruz, 82* (2): 197-208.

LUTERMOSER, G. W. & CASTELLANOS, J. V., 1945. Observaciones sobre la propagacion del caracol, *Australorbis glabratus* (SAY, 1818), vector de *Schistosoma mansoni* (Bilharzia) em El Valle, D. F. *Rev. Y. Asist. Soc., 10:* 109-148.

MAGALHÃES, L. A., 1966. Estudo de uma população de *Biomphalaria glabrata* (SAY 1818) recentemente introduzida no estado da Guanabara, *Folia Clin. et Biol., 35:* 102-120.

McJUNKIN, F. E., 1975. *Waters engineers development and disease in the tropics.* Agency for International Development Washington, 182p.

PARAENSE, W. L., 1972. Fauna Planorbídica do Brasil. cap. 10: 213-239 – *Introdução a Geografia Médica do Brasil* – Edgard Blucher e USP.

PAULINI, E., 1963. Field observation on the upstream migration of *Australorbis glabratus. Bull. World Hlth. Org., 29:* 838-841.

PIMENTEL, D.; WHITE, P. C. & IDELFONSO, V., 1957. Vagility of *Australorbis glabratus* intermediate host of *Schistosoma mansoni* in Puerto Rico. *Am. J. Trop. Med. Hyg., 12:* 191-196.

RADKE, M. G. & RICHIE, S. L., 1961. Field observations on the migration of marked *Australorbis glabratus* snails. *Journ. parasitol., 47:* 712.

SCORZA, J. V.; SILVA, J.; GONZALEZ, L. & MACHADO, R., 1961. Stream velocity as a gradient in *Australorbis glabratus* (SAY, 1818). *Tropenmed. parasitl., 12:* 191-196.

SIEGEL, S., 1975. *Estatística não-paramétrica para as ciências do comportamento.* McGraw-hill do B_asil, 350p.

SIMPSON, A. W.; THOMAS, J. D. & TOWSEND, C. R., 1973. Social behavior in the freshwater snail *Biomphalaria glabrata* (SAY). *Beh. Biol., 9* (6): 731-740.

THOMAS, J. D., 1977. The sociobiology of *Biomphalaria glabrata* snail host of *Schistosoma mansoni.* Instituto de Biología publicaciones especiales, *4:* 531-542.

THOMAS, J. D., 1982. Chemical ecology of the snails hosts of schistosomiasis: snail-snail and snail-plant interation. *Malacologia, 22* (1-2): 0 81.

TOWNSEND, C. R., 1974. Mucus trial following by the snail *Biomphalaria glabrata* (SAY). *Anim. Behav., 22:* 170-171.

WILLOWS, A. O. D., 1973. *Learning in gastropod mollusc:* 187-274. In: *Invertebrate Learning vol. 2.* 284p, W. C. Corning, J. A. Dyal, A. O. D. Willows.