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Autor: Christie, J.D. / Edward, J. / Goolaman, K.
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¹ Research and Control, P.O. Box 93, Castries, St. Lucia

² University of Texas Medical Branch, Galveston, Texas 77550, USA

Interactions between St. Lucian *Biomphalaria glabrata* and *Helisoma duryi*, a possible competitor snail, in a semi-natural habitat*

J. D. CHRISTIE^{1,2}, J. EDWARD¹, K. GOOLAMAN¹, B. O. JAMES¹, J. SIMON¹, P. S. DUGAT², R. TREINEN²

Summary

In artificial drains similar to those used in banana culture on St. Lucia, *Helisoma duryi*, the rams-horn snail, controlled *Biomphalaria glabrata*, intermediate host of schistosomiasis on that island. Time required for elimination of *B. glabrata* depended on environmental temperature and numbers of *H. duryi* initially introduced in the drains. Best fit to the data was given by the equation for the logistic curve rather than by an equation for unlimited growth. Multiple regression analyses of natality and mortality rates of both species of snails indicated that populations of *B. glabrata* were regulated by temperature rather than by density-dependent means while numbers of *H. duryi* were strongly influenced by numbers of rams-horn snails already present in the drains. Fitting of snail shell growth to von Bertalanffy equations showed that *H. duryi* shell diameter was uninfluenced by environmental temperatures or presence of *B. glabrata* while growth of the intermediate host was strongly affected both by temperature and numbers of *H. duryi*.

Key words: biological competition; ecology; control; schistosomiasis; *H. duryi*; *B. glabrata*.

Introduction

Helisoma duryi, a planorbid snail, has been mentioned as a possible competitor of the intermediate hosts of *Schistosoma mansoni* and *S. haematobium* (Frandsen and Madsen, 1979). In Puerto Rico, members of an un-named spe-

* This paper is dedicated to Elizabeth and Fergus McCullough, two of the "Wild Geese" of Ireland, who, after leaving that land, enriched the rest of the world during their travel.

cies of *Helisoma* were introduced into several ponds containing *Biomphalaria glabrata* (Ferguson, 1977). In some of these areas, *B. glabrata* disappeared after introduction of *Helisoma*, while, in other habitats, the latter snail failed to establish itself successfully. No control ponds were included in these experiments however. Furthermore, no attempt was made to discover the reasons behind success or failure of *Helisoma* either to gain a foothold in the static water habitats or to eliminate the intermediate host of schistosomiasis.

Both Abdallah and Nasr (1973) and Rasmussen (1974), working in Egypt and Tanzania respectively, claimed that *H. duryi* controlled medically important snails by inhibiting laying and hatching of their eggs. However, the Egyptian study merely summarized results without including evidence for these conclusions, while the Tanzanian experiments lacked adequate controls. In more recent work, Madsen and Frandsen (1979), and Madsen (1979a, b) demonstrated that *H. duryi* caused a marked inhibition of growth and reproduction of *B. camerunensis* and *B. alexandrina* possibly by food competition and mechanical interference with the eggs of the schistosome host snail.

Clearly, carefully controlled studies under field conditions are needed to evaluate the potential of the rams-horn snail, *H. duryi*, as a possible agent for control of medically important snails and thus schistosomiasis transmission. This work demonstrates that interactions between St. Lucian *B. glabrata* and a Dominican strain of *H. duryi*, which may be environmentally controlled, result in elimination of the former snail from drains similar to those used for banana cultivation in St. Lucia.

Materials and methods

Five banana drains, each 1.2 m long by 0.5 m wide, were dug in a plot of ground and were enclosed by a chicken wire fence in an attempt to make the area rat-free. The excavations were lined with plastic sheeting and were filled to a depth of 0.1 m with filtered river water. Twenty *B. glabrata* (first-generation laboratory offspring of St. Lucian field stocks) were placed in each of four drains (numbers I, III, IV, and V). Three of these four drains (numbers III–V) also received 5, 10, or 20 *H. duryi* (Dominican strain). Twenty *H. duryi* of the same mean diameter as the other rams-horn snails were added to the remaining drain (number II). Guppies (*Lebistes reticulatus*), which prey on mosquito larvae, were also placed in the water.

Initially, the snails were fed boiled dasheen leaves (*Colocasia esculenta*) in proportion to the number of animals present. However, after 10 weeks of the experiment, all the animals received the same amount of food, given in excess. Every two weeks, the water was changed, the number of snails of each species was determined, and the diameter of every snail greater than 5.0 mm was measured to the nearest 0.1 mm using vernier calipers. Other than this biweekly change of water, addition or removal occurred only when the water depth fell below 0.1 m or when the drains were in danger of flooding.

This experiment was replicated once. The first trial was started in February near the end of winter while the second replicate was initiated in June in the middle of summer. The only other difference between the two sets of experiments was that the mean diameters of the initial *B. glabrata* and *H. duryi* in the first replicate were 8.8 and 6.4 mm respectively as opposed to 8.5 and 7.0 mm in the second trial. In both species of snails, specimens of these respective sizes have started egg-laying.

Daily rainfall was obtained from records kept by the department while temperature records were provided by the meteorological service of a local airport. Heat accumulation, in terms of

number of degree-hours greater than 25° C per fortnight, was determined from the temperature data by the method of Baskerville and Emin (1969).

Regression analyses were performed to fit the raw data to two equations for population growth. The first model described a situation of unlimited growth:

$$dN/dt = rN \quad \text{or:} \quad \ln N_t = \ln N_0 + rt$$

while the second model presents a situation in which there is a limit to growth and is represented by the logistic curve:

$$dN/dt = rN (K-N/K) \quad \text{or:} \quad \ln \left\{ \frac{K-N_t}{N_t} \right\} = c-rt$$

In these equations, N_t is the number of snails at a time t in two week intervals; N_0 is the initial number of snails; K is the carrying capacity of the environment and also the maximum number of snails that can be present in a particular situation; r is the intrinsic rate of natural increase and represents the difference between birth and death rates; and c is an integration constant (Poole, 1974).

Since the first equation is first order, logarithmic transformation puts the data in a form suitable for linear regression analyses (Snedecor and Cochran, 1967). Fitting the data to the second equation involved reiteration of K combined with least squares analyses until a maximum value of the coefficient of determination (r^2) was reached. This reiteration was performed using a program in basic language designed for the Wang 2200 computer. Initial value of K for reiteration was one greater than the maximum value in the raw data series, and a maximum of 100 reiterations were performed. For data which would have yielded a negative intrinsic rate of natural increase, the values were coded by subtracting them from an arbitrary constant. The model with the highest coefficient of determination was then chosen as the most satisfactory fit for a particular set of values.

The ages of the snails were deduced from comparison of growth curves of the initial cohorts of the snails and those of laboratory animals (Christie, unpublished data), and by following modes on the size-frequency distribution from successive fortnights (Webbe, 1962; Dazo et al., 1966). These age determinations were used to ascertain fortnightly birth and death rates and to compare growth rates under the different treatments.

The fortnightly death rate d was derived from the equation (Webbe, 1962):

$$l_x = e^{-dx}$$

where l_x was the proportion of snails of a specific size surviving from one sampling to the next interval; e was the base of natural logarithms; and x was the time interval, in this case, two weeks. The birth rate, m , was the number of offspring per each sexually mature snail. From laboratory growth curves, we found that sexually mature *B. glabrata* and *H. duryi* were approximately equal to or greater than 8.0 and 6.0 mm in size respectively.

The relationship of birth or death rate of each species alone, or in combination with the other species, to rainfall, degree-hours greater than 25° C, numbers of *H. duryi*, and numbers of *B. glabrata* were examined by step-up multiple regression analyses (Armitage, 1971).

Finally, growth changes during the first 14 weeks of the trials were determined for both species of snails by means of the von Bertalanffy equation (Walford, 1946):

$$L_t = L_\infty (1 - e^{-kt})$$

where L_t was the maximum diameter of the animal at a specified time; L_∞ was the value of L for a zero growth rate; k was a characteristic growth constant; and t was the age of the animal. Values for this equation were ascertained by plotting L_t on the abscissa and L_{t+1} on the ordinate and fitting a line to the points by the method of least squares. The slope of such a line represented e^{-k} while L_∞ is the point at which the line crosses a representation of the curve $L_{t+1} = L_t$. All of the regression equations were compared by means of Bartlett's test, analyses of variance, analyses of covariance, and "t" tests for homogeneity of variances, equality of slopes, coincidence of lines, and differences among slopes and y-intercepts respectively (Armitage, 1971).

Results

Changes in snail numbers

The outcome of interactions between *H. duryi* and *B. glabrata* for the replicate experiments is depicted in Figs. 1 and 2. In the first replicate, the trial in drain V was abandoned after fourteen weeks because of predation of rats.

As can be seen by a comparison of the two figures, the initial growth of the control *B. glabrata* populations (drain number I) differed drastically in the two replicates. In the first experiment, populations increased rapidly until twelve weeks after the start of the trial when there were 920 *B. glabrata* in the artificial banana drain. On the other hand, in the second replicate, *B. glabrata* increased slowly in the first fourteen weeks. Although not readily apparent from Fig. 2, from the beginning of the experiment until week 12, almost a whole new generation of *B. glabrata* had replaced those snails present at the beginning of the experiment.

Populations of *H. duryi* in their control drains (number II) differ in many respects from those of *B. glabrata*. First of all, populations of these rams-horn snails do not reach the high numbers that *B. glabrata* populations attain. At week 12 in the first replicate, *B. glabrata* in their control drain numbered 920 while in the *H. duryi* control drain, only 226 of the latter animals could be found. *H. duryi* also does not seem to be as sensitive to environmental fluctuations, especially temperature changes, as does *B. glabrata*. Once reaching an asymptotic level, populations of the rams-horn snail tend to stay there. Only at extremely high levels of heat accumulation does *H. duryi* die, and it does so more slowly in drains also containing *B. glabrata* than in control drains (II).

Data from the first 20 weeks of the second trial show that, not only did *H. duryi* reproduce while *B. glabrata* did not increase in numbers during the initial period of high temperatures, but, even after temperatures decreased, the initial dominance by the rams-horn snail over the intermediate host continued. In the first replicate, in drains III, IV, and V, *B. glabrata* established an initial superiority in numbers over *H. duryi* in the first twelve weeks when a low thermal accumulation prevailed. After week 12, both species of snails began to decrease in numbers due to a zero birth rate and mortality of the snails already present, both caused by high temperatures. However, at week 24 of the first trial, *H. duryi* started to reproduce again in drains III and IV while *B. glabrata* populations continued to decline. Once *H. duryi* had established numerical dominance due to this burst of egg-laying, *B. glabrata* in drains III and IV did not start to reproduce again even when temperatures decreased. In the first trial, *B. glabrata* was eliminated from drains III and IV at weeks 60 and 70 respectively while, in the second replicate, *B. glabrata* was completely controlled by 38 weeks after the start of the experiment.

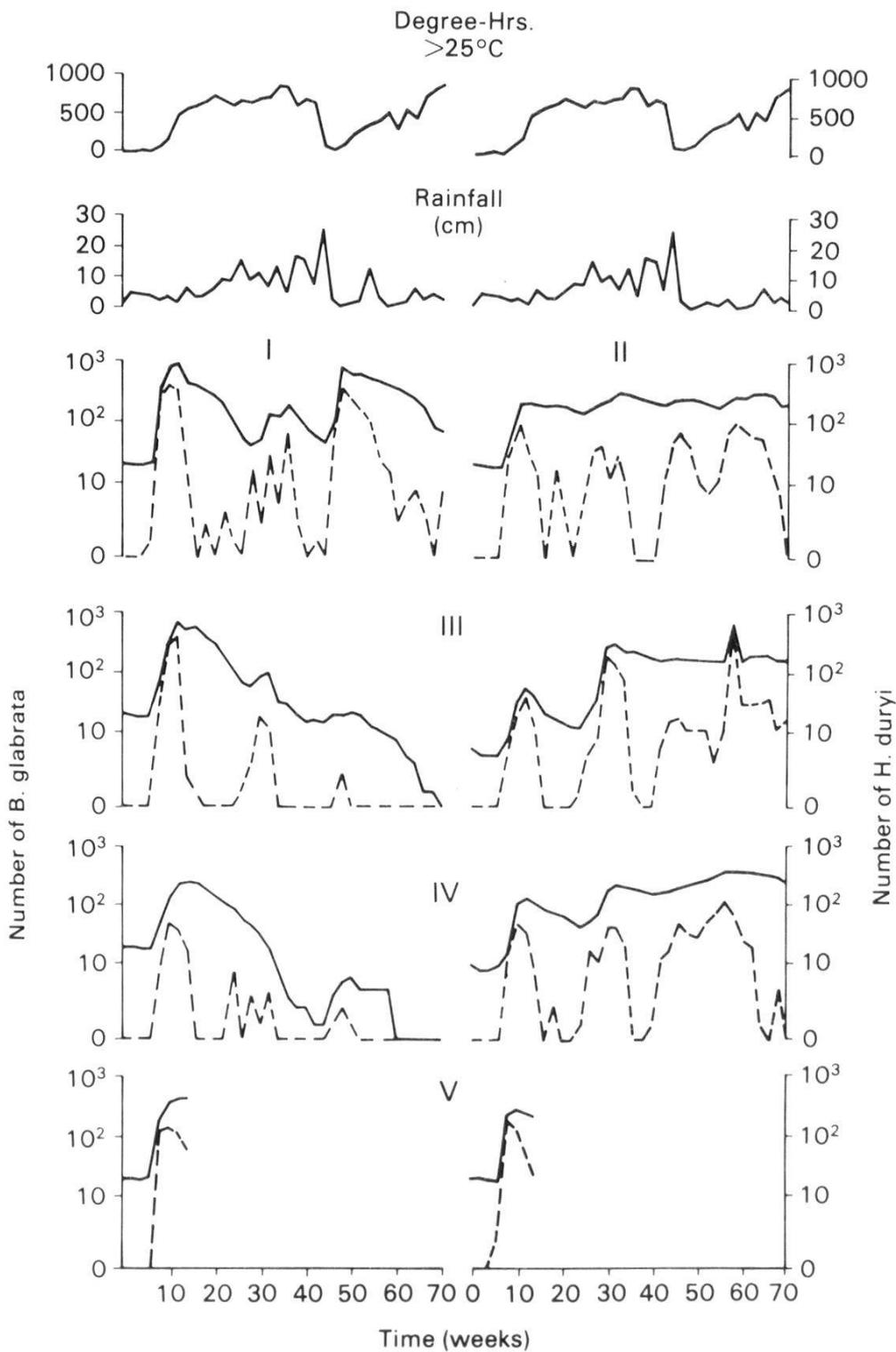


Fig. 1. Rainfall, temperature (in degree-hours greater than 25° C), and numbers of *H. duryi* and *B. glabrata* in different drains in first replicate. In depicting snail populations, solid lines represent total numbers of each species while dashed lines represent numbers of each species less than 5 mm in diameter. Counting was discontinued in drain V due to predation by rats.

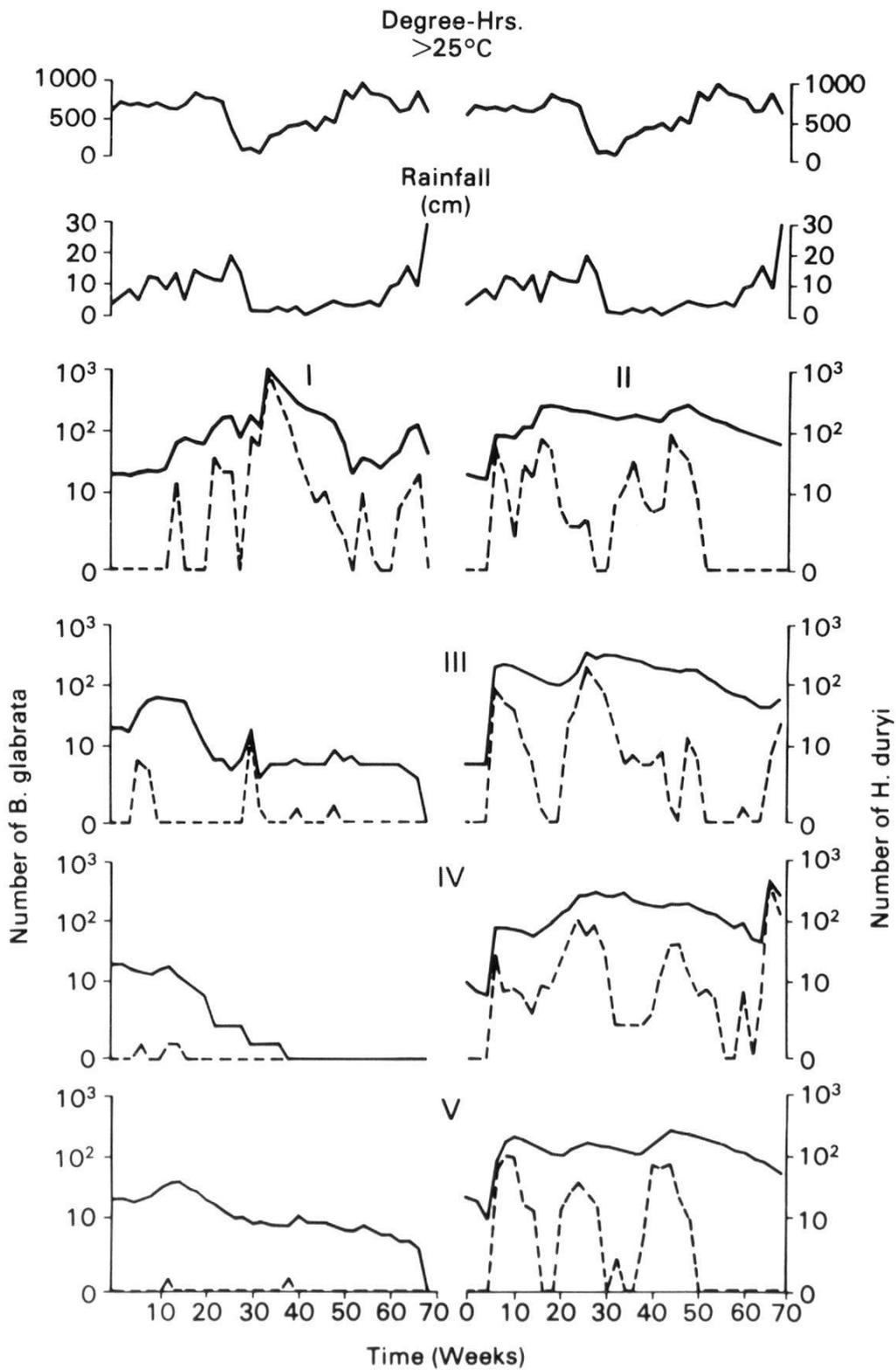


Fig. 2. Rainfall, temperature (biweekly accumulation of degree-hours greater than 25°C), and numbers of *H. duryi* and *B. glabrata* in different drains in second replicate. In depicting snail populations, solid lines represent total numbers of each species while dashed lines represent numbers of each species less than 5 mm in diameter.

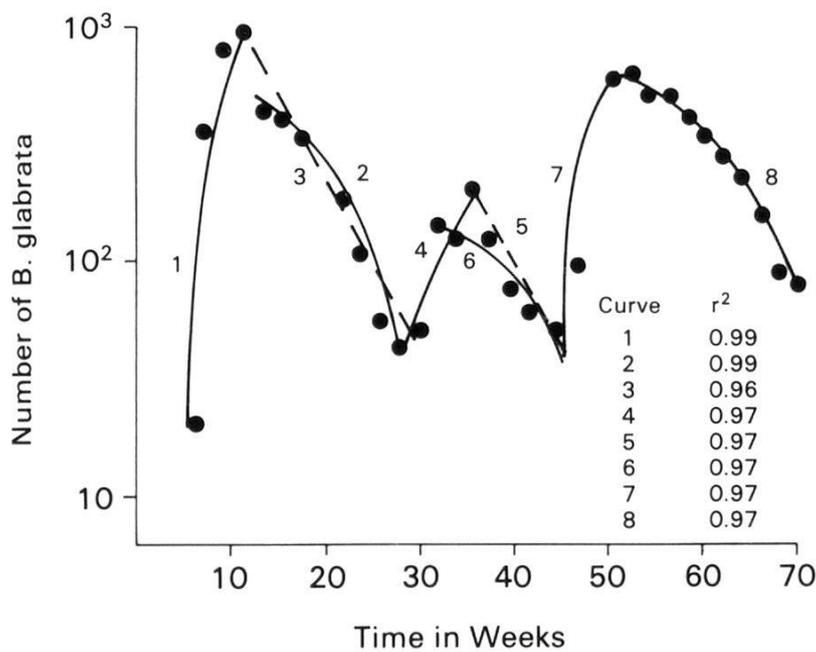


Fig. 3. Fit of regression lines for logistic or unlimited growth equation to numbers of *B. glabrata* found in drain I in first replicate. Solid lines represent logistic curves while dashed lines depict regression of the equation from unlimited growth.

Fitting of data to population growth equations

The outcome of fitting the two populations growth equations to numbers of *H. duryi* or *B. glabrata* present at each sampling interval is shown in Fig. 3 and Tables 1 through 6. In most cases, the equation for limited growth provided a better fit, as determined by size of the coefficient of determination, to the data than did the equation for unlimited population expansion. Thus, for further discussion in this paper, we shall use the equation which expresses a limit on population growth. For some of the data, the time intervals for data fitting were slightly different than those detailed in Tables 1 through 6, but differences were minimal.

For *B. glabrata*, intrinsic rate of increase (r) and carrying capacity (K), during the first twelve weeks, were less in the second replicate than in the first replicate. Comparison of the r and K values of *H. duryi* and *B. glabrata* populations during the first 12 weeks of the experiment shows that there was no difference between the r values for control populations of each of these snails during the first replicate, but this parameter was greater for *H. duryi* than for *B. glabrata* during the initial portion of the second trial. For values of K during the same interval, the situation was slightly different; in the first trial, K was substantially larger for the *B. glabrata* control population than it was for the *H. duryi* control population, while for the second replicate, the situation was reversed. A comparison of r and K values for the control *H. duryi* populations indicates that these values were less in the trial starting in the hot season than those from the replicate originating in the cold season.

Table 1. Effect of presence of *H. duryi* on intrinsic rate of increase (r) of *B. glabrata**

Drain No.	Time (weeks)												
	First replicate						Second replicate						
	6-12	12-28	28-36	36-44	44-52	50-70	4-12	12-18	20-30	28-34	34-52	52-66	
I-0	<i>H. duryi</i>	2.78	-0.73	0.77	-1.79	2.43	-0.45	0.20	0.54	1.20	1.49	0.56	0.33
III-5	<i>H. duryi</i>	1.88	-0.85	-0.64	-0.78	0.10	-0.31	0.83	-0.40	-0.05	-1.48	-0.16	-0.05
IV-10	<i>H. duryi</i>	1.63	-0.48	-0.74	-0.24	0.38	-0.11	0.33	-1.10	-0.30	-0.05		
V-20	<i>H. duryi</i>	2.26**						0.57	-0.34	-0.42	-0.44	-0.08	-0.03

* based on logistic curve fitted to data

** terminated due to predation by rats

Table 2. Effect of presence of *H. duryi* on environmental carrying capacity (K) for *B. glabrata**

Drain No.	Time (weeks)											
	First replicate						Second replicate					
	6-12	12-28	28-36	36-44	44-52	50-70	4-12	12-18	20-30	28-34	34-52	52-66
I-0 <i>H. duryi</i>	928	33	230	44	619	9	29	111	179	994	8	226
III-5 <i>H. duryi</i>	775	46	113	13	65	-2	71	-45	-26	-44	4	-51
IV-10 <i>H. duryi</i>	247	25	-2	-1	29	-1	19	5	0	-8		
V-20 <i>H. duryi</i>	423**						42	-17	6	6	5	-53

* based on logistic curve fitted to data

** terminated due to predation by rats

Table 3. Effect of presence of *B. glabrata* and initial numbers of *H. duryi* on intrinsic rate of increase (r) of *H. duryi*, first replicate*

Drain No.	Time (weeks)									
	6-12	12-24	24-32	32-42	42-48	48-54	54-64	62-70		
II-20 <i>H. duryi</i>	2.74	-0.23	0.36	-0.75	1.47	-0.76	0.57	-0.52		
0 <i>B. glabrata</i>										
III-5 <i>H. duryi</i>	1.26	-0.76	2.65	-0.75	0.16	-0.64	0.16	-1.27		
20 <i>B. glabrata</i>										
IV-10 <i>H. duryi</i>	2.40	-0.38	0.81	-0.27	0.36	0.35	2.25	-0.82		
20 <i>B. glabrata</i>										
V-20 <i>H. duryi</i>	4.15**									
20 <i>B. glabrata</i>										

* based on logistic curve fitted to data

** terminated due to predation by rats

Table 4. Effect of presence of *B. glabrata* and initial numbers of *H. duryi* on intrinsic rate of increase (r) of *H. duryi*, second replicate*

Drain No.	Time (weeks)						
	4-12	10-18	18-32	32-36	36-42	42-48	48-68
II-20 <i>H. duryi</i>	1.04	1.12	-0.85	0.20	-0.53	0.93	-0.54
0 <i>B. glabrata</i>							
III-5 <i>H. duryi</i>	2.01	-0.74	0.49	-0.70	-0.72	-0.17	-0.39
20 <i>B. glabrata</i>							
IV-10 <i>H. duryi</i>	1.84	0.25	0.33	-1.90	-1.51	0.17	-0.33
20 <i>B. glabrata</i>							
V-20 <i>H. duryi</i>	2.56	-0.54	0.30	-0.45	0.48	-2.08	-0.33
20 <i>B. glabrata</i>							

* based on logistic curve fitted to data

In the first replicate, during the initial twelve weeks, the intrinsic rates of natural increase and carrying capacities of *B. glabrata* populations from drains also containing *H. duryi* (drains III, IV, and V) were less than values for *B. glabrata* alone (drain I). However, the decrease in both these parameters was not linearly related to the number of *H. duryi* present initially as *B. glabrata* populations from drain V, which contained 20 *H. duryi* at the start of the experiment, had higher r and K values than *B. glabrata* in drain IV, which contained 10 *H. duryi* at the start of the experiment. In the second replicate, r and K values were greater for *B. glabrata* populations interacting with *H. duryi* than they were for *B. glabrata* populations alone.

If one looks at drains II and V in both replicates, he can note that the presence of *B. glabrata* in drain V increases the values of intrinsic rate of natural increase and carrying capacity of *H. duryi* for the first twelve weeks compared to drain II where *H. duryi* is found alone. Moreover, examination of r and K values from drains III through V for the same period of the experiment indicates that a change in number of *H. duryi* present at the start of the experiment changes the worth of these parameters, but this change is not linearly related to the number of the rams-horn snails added to the drains initially.

In comparing values of the intrinsic rate of natural increase and carrying capacity for the duration of the experiment, it is interesting to note the range of these parameters for the control *H. duryi* and *B. glabrata* populations. While populations of both snails show similar maximum r values, *B. glabrata* has a lower minimum value for the intrinsic rate of natural increase than does *H. duryi*. Additionally, *H. duryi* carrying capacities do not fluctuate as much or reach as great maximum or minimum values as do those for *B. glabrata*. A general inspection of all r and K values for *B. glabrata* populations, whether

Table 5. Effect of presence of *B. glabrata* and initial numbers of *H. duryi* on environmental carrying capacity (K) for *H. duryi*, first replicate*

Drain No.	Time (weeks)									
	6-12	12-24	24-32	32-42	42-48	48-54	54-64	62-70		
II-20 <i>H. duryi</i>	227	57	428	201	259	157	346	97		
0 <i>B. glabrata</i>										
III-5 <i>H. duryi</i>	88	11	319	167	235	154	257	167		
20 <i>B. glabrata</i>										
IV-10 <i>H. duryi</i>	130	24	275	108	288	431	404	159		
20 <i>B. glabrata</i>										
V-20 <i>H. duryi</i>	280**									
20 <i>B. glabrata</i>										

* based on logistic curve fitted to data

** terminated due to predation by rats

Table 6. Effect of presence of *B. glabrata* and initial numbers of *H. duryi* on environmental carrying capacity (K) for *H. duryi*, second replicate*

Drain No.	Time (weeks)						
	4-12	10-18	18-32	32-36	36-42	42-48	48-68
II-20 <i>H. duryi</i> 0 <i>B. glabrata</i>	122	311	173	274	140	302	66
III-5 <i>H. duryi</i> 20 <i>B. glabrata</i>	237	94	385	253	173	110	33
IV-10 <i>H. duryi</i> 20 <i>B. glabrata</i>	113	-12	394	298	277	274	24
V-20 <i>H. duryi</i> 20 <i>B. glabrata</i>	215	68	163	90	278	233	22

* based on logistic curve fitted to data

Table 7. Regression and changes in correlation coefficients for environmental variables and birth rate (m_x) of *B. glabrata*

Variable	Regression coefficients	Change in correlation coefficient	
	Value / Standard error	Value	Significance
Degree-hours	$-1.8 \times 10^{-2} \pm 2.8 \times 10^{-3}$	0.510	$p < 0.01$
(Degree-hours) ²	$1.3 \times 10^{-5} \pm 2.9 \times 10^{-6}$	0.100	$p < 0.01$
No. of <i>H. duryi</i>	$-1.8 \times 10^{-2} \pm 3.8 \times 10^{-3}$	0.063	$p < 0.01$
(No. of <i>H. duryi</i>) ²	$2.0 \times 10^{-5} \pm 9.1 \times 10^{-6}$	0.004	$p > 0.05$
No. of <i>B. glabrata</i>	$-7.6 \times 10^{-3} \pm 3.4 \times 10^{-3}$	0.006	$p > 0.05$
(No. of <i>B. glabrata</i>) ²	$7.3 \times 10^{-6} \pm 4.4 \times 10^{-6}$	0.006	$p > 0.05$
Rainfall	$-3.5 \times 10^{-2} \pm 1.2 \times 10^{-1}$	0.000	$p > 0.05$
(Rainfall) ²	$1.4 \times 10^{-3} \pm 5.7 \times 10^{-3}$	0.000	$p > 0.05$

alone or with *H. duryi*, reveals that, except for the initial parts of the two replicates, intrinsic rates of natural increase and carrying capacities are less in drains III, IV, and V where *B. glabrata* are interacting with *H. duryi* than in drain I, where *B. glabrata* exists alone. No such pattern exists for *H. duryi* populations.

Step-up multiple regression analyses of birth and death rates of B. glabrata and H. duryi

The most important factor connected with variation in birth rate of *B. glabrata* is the number of degree-hours greater than 25° C, with the remainder of the measured variables ordered as shown in Table 7. Addition or removal of the various independent variables indicates that only number of degree-hours,

Table 8. Regression and changes in correlation coefficients for environmental variables and death rate (d_x) of *B. glabrata*

Variable	Regression coefficients	Change in correlation coefficient	
	Value / Standard error	Value	Significance
No. of <i>B. glabrata</i>	$9.1 \times 10^{-4} \pm 9.7 \times 10^{-4}$	0.159	$p < 0.05$
No. of <i>H. duryi</i>	$6.4 \times 10^{-4} \pm 5.9 \times 10^{-4}$	0.037	$p > 0.05$
Rainfall	$-4.6 \times 10^{-2} \pm 3.6 \times 10^{-2}$	0.002	$p > 0.05$
(Rainfall) ²	$1.9 \times 10^{-3} \pm 1.6 \times 10^{-3}$	0.009	$p > 0.05$
Degree-hours	$6.2 \times 10^{-4} \pm 7.9 \times 10^{-4}$	0.010	$p > 0.05$
(Degree-hours) ²	$-4.5 \times 10^{-7} \pm 8.4 \times 10^{-7}$	0.004	$p > 0.05$
(No. of <i>B. glabrata</i>) ²	$-2.8 \times 10^{-7} \pm 1.8 \times 10^{-1}$	0.000	$p > 0.05$

the square of number of degree-hours, and the number of *H. duryi* are associated with the observed changes in natality. Forty-seven percent of the variation of birth rate can be linked with inclusion of all the measured factors with the relationship between natality and temperature, in the form of degree-hours greater than 25° C, best fitted by a second-degree polynomial curve. The analysis indicates that as the numbers of *H. duryi* increase, birth rate of *B. glabrata* decreases with the number of *B. glabrata* not associated with variations in natality.

Although step-up analysis of death rates of *B. glabrata* arranges the independent variables in the order given in Table 8, only the number of *B. glabrata* is significantly linked with variations observed in mortality. None of the other factors is associated significantly with changes in death rate, with all of the variables connected with only 5% of the observed variation in mortality.

Variation in *H. duryi* natality is most correlated with the number of *H. duryi*, with the square of numbers of *H. duryi*, degree-hours greater than 25° C, number of *B. glabrata*, and square of degree-hours greater than 25° C being other variables which are associated significantly with changes in birth rate (Table 9). Forty-eight percent of the variation in natality is associated with addition of all the independent variables with the relationship between birth rate and temperature or numbers of *H. duryi* best fitted by second-degree polynomial curves. Once again, as the numbers of one snail, *B. glabrata*, increase, the birth rate of the other mollusk, *H. duryi*, decreases.

H. duryi mortality is also most linked with numbers of *H. duryi* with all of the independent variables except rainfall and the square of precipitation associating significantly with variations in death rate (Table 10). Approximately one quarter, 23%, of the mortality is connected with use of all the measured factors in the analysis. The relationships between mortality and numbers of *H. duryi*, temperature, or numbers of *B. glabrata* can be fitted best by second-degree polynomial curves.

Table 9. Regression and changes in correlation coefficients for environmental variables and birth rate (m_x) of *H. duryi*

Variable	Regression coefficients	Change in correlation coefficient	
	Value / Standard error	Value	Significance
No. of <i>H. duryi</i>	$-2.2 \times 10^{-2} \pm 6.0 \times 10^{-3}$	0.466	$p < 0.01$
(No. of <i>H. duryi</i>) ²	$5.6 \times 10^{-5} \pm 1.8 \times 10^{-5}$	0.106	$p < 0.01$
Degree-hours	$-6.0 \times 10^{-3} \pm 1.8 \times 10^{-3}$	0.064	$p < 0.01$
No. of <i>B. glabrata</i>	$4.1 \times 10^{-2} \pm 4.3 \times 10^{-2}$	0.030	$p < 0.05$
(Degree-hours) ²	$4.2 \times 10^{-6} \pm 1.8 \times 10^{-6}$	0.023	$p < 0.05$
(Rainfall) ²	$-2.8 \times 10^{-3} \pm 4.5 \times 10^{-3}$	0.002	$p > 0.05$
Rainfall	$4.2 \times 10^{-2} \pm 9.4 \times 10^{-2}$	0.001	$p > 0.05$
(No of <i>B. glabrata</i>) ²	$-1.7 \times 10^{-4} \pm 1.4 \times 10^{-3}$	0.000	$p > 0.05$

Table 10. Regression and changes in correlation coefficients for environmental variables and death rate (d_x) of *H. duryi*

Variable	Regression coefficients	Change in correlation coefficient	
	Value / Standard error	Value	Significance
No of <i>H. duryi</i>	$-2.1 \times 10^{-2} \pm 6.0 \times 10^{-3}$	0.283	$p < 0.01$
Degree-hours	$5.8 \times 10^{-3} \pm 1.8 \times 10^{-3}$	0.057	$p < 0.06$
(No. of <i>H. duryi</i>) ²	$5.3 \times 10^{-5} \pm 1.8 \times 10^{-5}$	0.049	$p < 0.05$
(Degree-hours) ²	$-4.8 \times 10^{-6} \pm 1.8 \times 10^{-6}$	0.004	$p < 0.05$
No. of <i>B. glabrata</i>	$1.2 \times 10^{-1} \pm 4.3 \times 10^{-2}$	0.036	$p < 0.05$
(No. of <i>B. glabrata</i>) ²	$-3.2 \times 10^{-3} \pm 1.4 \times 10^{-3}$	0.046	$p < 0.05$
(Rainfall) ²	$3.8 \times 10^{-3} \pm 4.5 \times 10^{-3}$	0.001	$p > 0.05$
Rainfall	$-7.1 \times 10^{-2} \pm 9.4 \times 10^{-2}$	0.005	$p > 0.05$

Use of the von Bertalanffy equation to describe growth of *B. glabrata* and *H. duryi*

Fig. 4 depicts a fit of the equation to part of our data for snail growth and indicates by the high coefficient of determinant, 0.98, the closeness of fit obtained by this method. In Table 11 is represented the final regression equations after statistical analysis and combination of data which are not significantly different from each other. Most importantly, all of the equations for *H. duryi* are indistinguishable statistically and can be represented as one formula for growth.

The equations for *B. glabrata* length changes also possess a common slope, 0.72, which is significantly different at the 0.001 probability level from the slope of the von Bertalanffy equation for the growth of *H. duryi*. The y-intercepts of the two replicate regression equations for *B. glabrata* growth also differ significantly at the 0.001 probability level. Therefore, temperature, which varied in

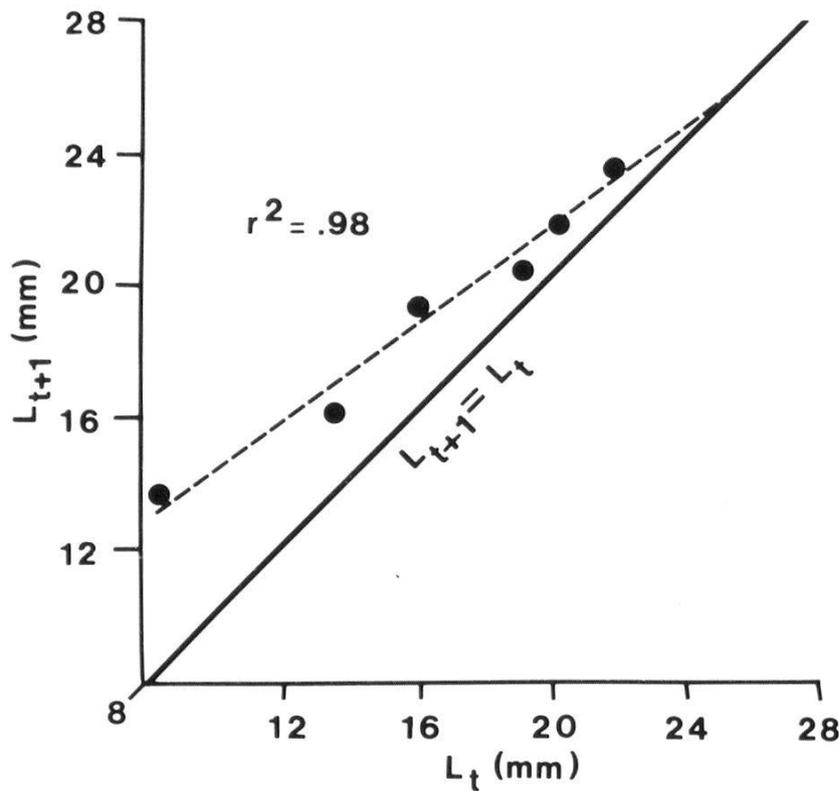


Fig. 4. Fitting of regression equation for calculation of k and L in the von Bertalanffy equation. L_{∞} is the point at which regression line crosses line depicting the equation $L_{t+1} = L_t$; e^{-k} is the slope of the regression equation.

Table 11. Values of e^{-k} , k , y-intercept, and L_{∞} for *Biomphalaria glabrata* and *Helisoma duryi* after statistical analyses of initial regression equations

Species, replicate and drain number	e^{-k}	k	y-intercept	L_{∞}
<i>H. duryi</i> :				
All replicates and drains	0.91	0.09	2.54	28.2
<i>B. glabrata</i> :				
First replicate:				
Drain I	0.72	0.33	6.18	22.1
Drains III and IV	0.72	0.33	6.32	22.6
Drain V	0.72	0.33	6.50	23.2
Second replicate:				
Drain I	0.72	0.33	7.23	25.8
Drain III	0.72	0.33	6.83	24.4
Drains IV and V	0.72	0.33	6.97	24.9

the two replicates, did not change k values significantly, but, by its effect on the y-intercept, did alter the final length attained by *B. glabrata*. As demonstrated in Table 11, the presence of *H. duryi* does have an effect on the size of the y-

intercept, and thus on ultimate length of *B. glabrata*. However, within replicates, the y-intercepts, while not identical to each other as demonstrated by analyses of covariance, did not differ significantly from each other as judged by "t" tests between different pairs within a replicate. Finally, *H. duryi* possesses the ability to attain a greater length than does *B. glabrata*, although its rate of attaining that length is significantly less than that of the intermediate host snail.

Discussion

The results of our experiments show that *H. duryi* affects *B. glabrata* population numbers adversely and alters shell growth in a positive or negative manner depending on environmental temperatures. On the other hand, *B. glabrata* interacts with *H. duryi* populations in a positive manner and does not affect shell growth of the rams-horn snail. *Biomphalaria* is eliminated from the artificial drains regardless of the numbers of *Helisoma* present initially. Comparison of numbers of young *B. glabrata* (less than 5 mm in diameter) in the different drains and results of multiple regression analyses indicate that rams-horn snails may cause the disappearance of the schistosome-bearing snails by inhibiting reproduction of adults or increasing mortality of young snails and not by any effects on adult mortality. Using other intermediate hosts of schistosomiasis, several scientists (Abdallah and Nasr, 1973; Malek and Malek, 1978; Madsen and Frandsen, 1979) have found similar results in laboratory studies, although Abdallah and Nasr (1973) and Ayad and his colleagues (1970) also claimed that *H. duryi* caused increased mortality of *Bulinus truncatus* and *Biomphalaria alexandrina* compared to death rates in these latter snails maintained in monoculture. We have found that the time required for complete control of the schistosome intermediate hosts is dependent on temperature and on the numbers of rams-horn snails introduced at the beginning of the experiment. The relationship between numbers of competitor snails and time required for disappearance of *B. glabrata* is not linear as *B. glabrata* in drain IV, where we added 10 *H. duryi* at the start of the experiment, were eliminated before *Biomphalaria* in drains III and V, which contained 5 and 20 *H. duryi* initially.

A more quantitative idea of the effect of *H. duryi* on *B. glabrata* can be gained from a comparison of the r and K values of the snail populations in the different drains. For our control *B. glabrata* populations, the maximum r and K values we calculated using the equation for the logistic curve were not comparable to maxima found by Sturrock (1973) who also utilized that equation for studying population dynamics of St. Lucian *Biomphalaria*. His values developed for periods of population expansion were generally less than ours even when the same initial numbers of snails were used as a starting point for calculations. The discrepancy in carrying capacities (K) may be due to the fact that we conducted our studies in a semi-natural habitat, while Sturrock studied snail populations in different natural sites where additional limiting factors were

probably present. However, that author appears to have calculated r values using the equation for unlimited population growth then fitting a K value by sight. This method would give lower, incorrect values of r than if the logistic equation were described by reiteration of values of carrying capacity until a "best fit" was found. In the first replicate, addition of rams-horn snails to the intermediate host populations caused a decrease in the intrinsic rates or increase and carrying capacities for the first twelve weeks of the experiment. When *B. glabrata* populations started to increase during weeks 28–36 and 44–52 of the first treatment, r and K values were much less for those snail interacting with *H. duryi* than for the *Biomphalaria* alone. In the second replicate, intrinsic rates of increase and carrying capacities of the intermediate host populations were increased by the presence of *Helisoma* compared to the values found in the control population whose reproduction was inhibited by the high environmental temperatures present initially. However, after this time, r and K values for *B. glabrata* were almost always less in the three drains containing both species of snails than in drain II where only the intermediate host snail was present.

We can also measure the effect of *H. duryi* on *B. glabrata* populations by our multiple regression analyses in which birth rate and mortality of *B. glabrata* are the dependent variables (Tables 7 and 8). The number of *H. duryi* is significantly associated with natality of the intermediate host so that as the rams-horn snail population increases, the natality of *Biomphalaria* decreases in a linear fashion. On the other hand, *H. duryi* numbers are not significantly linked with the death rate of *B. glabrata* so that the negative effect of the rams-horn snails on the intrinsic rate of increase of the schistosome-bearing snail is due to action of the former animal on the natality component of r alone.

A comparison of the values for the von Bertalanffy equations indicates that *H. duryi* also causes a change in shell diameter of *B. glabrata*. In the first replicate, ultimate diameter attained by the intermediate host mollusk was increased by the presence of the rams-horn snail over values found in control *Biomphalaria*, while in the second replicate, the opposite effect was found. Thus, whether *H. duryi* increases or decreases *B. glabrata* shell growth depends on the environmental temperatures prevailing at the time of the experiment. Malek and Malek (1978) found that, in their laboratory experiments, *B. glabrata* grew faster when associated with rams-horn snails than when raised alone. Of interest is the fact that these authors' experiments were conducted at 22–24° C which would correspond roughly to the thermal regime prevailing at the start of the first replicate of our work, where we detected an increase in final diameter attained by those *Biomphalaria* raised with *H. duryi* compared to schistosome-bearing snails reared alone. In the experiments of Madsen and Frandsen (1979), shell diameter of *B. camerunensis* interacting with *H. duryi* decreased compared to that in control animals, and the intermediate hosts reared with the rams-horn snails did have a lower organic content and dry weight than did animals living alone.

On the other side of the ledger, inspection of intrinsic rates of increase and carrying capacities of *H. duryi* populations in drains II and V in both replicates indicates that the presence of *B. glabrata* causes an increase in values of both parameters for the rams-horn snails. Thus, we can conclude that *Biomphalaria* actually has a beneficial effect on populations of *H. duryi*. The strength of this conclusion is reinforced by the results of our multiple regression analyses where natality and death rates of *H. duryi* are the dependent variables (Tables 9 and 10). As the number of *B. glabrata* increases, birth rate of the rams-horn snail populations also increases in a linear manner. For *H. duryi* mortality, the situation is slightly more complicated as the relationship between that parameter and the number of *B. glabrata* is second degree polynomial. When the number of *Biomphalaria* exceeds 37, the death rate becomes negative so the numbers of rams-horn snails increase.

Statistical comparison of the values for the slopes and y-intercepts of the von Bertalanffy equations for rams-horn snails in drains II and V shows that neither temperature nor the presence of another snail (*B. glabrata*) has any effect on shell growth of *H. duryi* as opposed to the situation with the intermediate host where both these factors play a role in determining growth. Of course, Madsen and Frandsen (1979) make the very good point that, when determining the effects of interspecific competition between snails, one must examine values of biomass and organic content as well as those of shell diameter. However, from their data or rather from lack of mention in their discussion, it appears that *B. camerunensis* did not have any effect on growth of *H. duryi*.

The question to be discussed now is "What are the mechanisms which cause elimination of *B. glabrata*?" Examination of Figs. 1 and 2 and of the various multiple regression analyses, especially those of Tables 7 and 9, indicates that temperature is the factor which determines the direction of competition. Our data in this paper demonstrate that reproduction of *B. glabrata* is adversely affected by high environmental temperatures while natality of *H. duryi* is much less so. This supposition is borne out by experiments in our laboratory where life tables have been compiled for both species of snails under discussion. While the intrinsic rate of increase of *B. glabrata* is greater than that of *H. duryi* at or below 25° C, at temperature greater than this value, intrinsic rate of increase of populations of the intermediate host snail declines below that of *H. duryi*. Thus when water temperature increases, reproduction of *B. glabrata* declines while birth rate of the rams-horn snail shows a lesser decrease; as the *Biomphalaria* populations age and die without being replaced by its offspring, *H. duryi*, which may share a niche similar to that of the intermediate host, continues to breed with its young filling the gap left by the mortality of the other species. However, in work performed at temperatures between 23 and 28° C, de Andrade (1978a, b) noted that fecundity of *H. duryi* was much greater and mortality much less than for a Brazilian strain of *B. glabrata*. Thus, for these species and strains of snails, *r* values, which are an expression of both mortality

and natality, may be greater for *H. duryi* than for *B. glabrata* through the whole range of environmental temperatures which these two species encounter meaning that *H. duryi* can dominate the interaction between the two mollusks from the start. We shall not touch upon the importance of temperature as a factor in reproduction, growth, and mortality of schistosome-bearing snails except to refer the reader to two reviews (Appleton, 1978; Jordan et al., 1980) where this subject is covered in greater detail. The important point of this discussion is that, in nature, we can expect competition to swing in favor of *H. duryi* only in those geographic regions and micro-habitats where temperatures are high enough and other environmental variables favorable enough to give this species the competitive advantage over schistosome intermediate hosts.

The multiple regression analyses of factors associated with variations in natality and mortality of *B. glabrata* and *H. duryi* indicate that these two species have different ecological strategies and are adapted for different habitats. Birth rate of *B. glabrata* is significantly associated with temperature in a second degree polynomial relationship and with the number of *H. duryi*. Numbers of *Biomphalaria* do not play any role in regulating fecundity of that snail. A consideration of mortality of the schistosome-bearing snail shows that death rate is associated to some degree with numbers of *B. glabrata* present, but this variable only accounts for 16% of the observed variation in mortality. On the other hand, both mortality and natality of *H. duryi* are significantly linked to the numbers of rams-horn snails already present. Thus, *B. glabrata* populations appear to be regulated very strongly by temperature and other environmental factors with little density-dependent regulation of population, while *H. duryi* numbers are regulated in an exactly opposite fashion. These trends can also be seen in Figs. 1 and 2 where *B. glabrata* numbers show large variations, while rams-horn snail populations stay at a plateau whose height varies very little. *B. glabrata* exhibits many of the characteristics of a r specialist while *H. duryi* appears to be a K specialist (Southwood et al., 1974). This differentiation in terms of life-history adaptation has many connotations, but the most important from our point of view is that r-selected organisms are adapted to life in unstable habitats where temporal and spatial heterogeneity is high, while K specialists have evolved to thrive in stable habitats (Southwood, 1977). Thus, if we are to use *H. duryi* as a control agent, it must be in stable environments, where its life history strategy will be of competitive advantage, as opposed to unstable habitats, where the life-history adaptations of the schistosome-bearing snail will give the latter animal a good chance to dominate. We must admit at this point in our discussion that the idea of a r/K continuum with animals being either r or K selected in terms of life history is simplistic especially as each habitat offers a different environment in which the snail must live and reproduce. A more realistic depiction of population changes is that environmental changes act on populations of organisms through an interaction between the micro-habitat and some environmental fluctuations occurring throughout the macro-environment. Whittaker

and Goodman (1979) have developed a model based on this concept, where a species is either utilizing: “a predominantly unfavorable (adversity selection); an unpredictable and intermittently favorable (exploitation selection); or predominantly favorable and fully occupied environment (saturation selection)”. *B. glabrata* appears to be exploitation selected, while *H. duryi* fits in the last category. We have introduced this classification not to be perverse but simply to focus attention on the micro-habitat, where all population and community interactions, whether those of man, snail, or parasitic occur. This fact is sometimes forgotten in the grand design of schistosomiasis control offered to us by granting agencies, modellers, epidemiologists, and control personnel alike.

Does competition play a role in structuring communities found in the micro-habitat? One group of ecologists (Simberloff, 1978; Strong et al., 1979; Connor and Simberloff, 1979) has argued that island colonization, assembly of species communities, and character displacement, which are all considered examples of competition at work, are really due to chance. However, some of these arguments, which have been supported by computer simulations, have been shown to rest on incorrect assumptions (Grant and Abbott, 1980), and almost everyone agrees that competition plays some role in community structure under some circumstances. Two theories of community structure seem to prevail: the community proceeds to equilibrium, which competition helps to maintain (Diamond, 1978); or the community never attains equilibrium, so competition plays no role in maintaining species diversity (Wiens, 1977; Connell, 1978). A reasonable view, which is supported by some experimental evidence from the field (Werner, 1977; Sousa, 1979; Liebermann et al., 1979) is that, in fluctuating and variable habitats, communities never equilibrate, so competition plays little part in governing species assemblies in this situation, but, in relatively stable habitats, communities can come to equilibrium and are structured to a greater or lesser extent by interspecific interactions. Thus, in the habitats which are both temporally and spatially heterogeneous, we must not expect competition to control schistosome-bearing snails, and investigators must look for organisms which fit the niche of that particular habitat better than do the schistosome intermediate hosts. Only in permanent and stable habitats will a species such as *H. duryi* dominate an exploitation specialist such as *B. glabrata*, and even then, the intermediate host may have to be temporarily removed by mollusciciding before the rams-horn snail can gain a foothold.

Finally, we did not start this work because we felt that *H. duryi* was a particularly good biological control agent for schistosome-bearing snails, but rather because we wanted to demonstrate that well-controlled studies in a semi-natural environment are necessary to bridge the gap between laboratory trials and field trials. Such experiments as ours may also help to temper the overwhelming enthusiasm of laboratory-based scientists for use of a particular biological agent. Those of us who attempt to utilize biological control tend to forget the constraints placed upon laboratory systems which are to be used in the field,

and we have been guilty of promising more than we can deliver. On the other hand, funding agencies must realize that all control agents work only under certain circumscribed circumstances, and that delineating these limits takes good biological studies and time. Last but not least, we must remember that, in control of tropical disease, the environment and the micro-habitat dominate interactions between man, snail, parasite, and other organisms.

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