Life-table experiments with *Helisoma duryi* (Wetherby) and *Biomphalaria pfeifferi* (Krauss) at constant temperatures

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In an effort to find an ecological homologue that could be utilized as a biological control agent of the intermediate host species of economically important helminth parasites, age-specific life-table experiments with *Helisoma duryi* (Wetherby) and *Biomphalaria pfeifferi* (Krauss) (intermediate host of *Schistosoma mansoni*) were carried out at a series of constant temperatures in a laboratory. The results showed that the lifespan and net reproduction rate of *H. duryi* were higher than those of *B. pfeifferi* over the whole range of temperatures investigated (18–35°C). The conclusion is reached that *H. duryi* should theorectically be capable of establishing viable populations in most of the habitats occupied by *B. pfeifferi* in South Africa.

In 'n poging om 'n ekologiese homoloog te vind wat as 'n biologiese beheeragent van die tussengasheerslakspesies van ekonomies-belangrike helmintparasiete aangewend kan word, is ouderdomspesifieke lewenstabeleksperimente met *Helisoma duryi* (Wetherby) en *Biomphalaria pfeifferi* (Krauss) (tussengasheer van *Schistosoma mansoni*) by 'n reeks konstante temperature in die laboratorium uitgevoer. Die resultate het getoon dat die lewensduur en netto voortplantingskoers van *H. duryi* by die hele reeks ondersoekte temperature (18–35°C) hoër as by *B. pfeifferi* was. Die gevolgtrekking word gemaak dat *H. duryi* teoreties in staat behoort te wees om lewensvatbare bevolkings in meeste van die habitats wat deur *B. pfeifferi* in Suid-Afrika beset word, te kan vestig.

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Up to now, most of the components used as molluscicides have been biocidal over a wide spectrum. Consequently, non-chemical methods of snail control are increasingly being sought. From a biological point of view, the ideal method of control should be based on competitive displacement by an ecological homologue which should not only possess similar ecological needs but a higher biological potential and adaptability as the vector species (Frandsen & Madsen 1979). Furthermore, the competitor species should not itself act as an intermediate host of economically important parasite species. After observing that *H. duryi* successfully outcompeted several intermediate host species, including *B. pfeifferi* in his laboratory in 1941, Dr. G. Mandahl-Barth of the Danish Bilharzia Laboratory suggested it as a biological control agent of the intermediate host snails of schistosomes (Madsen 1984).

Helisoma duryi an invader species from North America is already found in widely distributed localities in Africa including cooling dams at the Mandini paper mill in Natal (Brown 1967), a storage tank on a farm in Namibia (Van Bruggen 1974) and the Liesbeeck River in Cape Town (Appleton 1977). Of the 41 entries of *H. duryi* in the data base of the National Freshwater Snail Collection at the Potchefstroom University, only 15 were recorded from natural habitats (marshes, swamps, springs, rivers, streams). The fact that this species already occurs in natural habitats in South Africa eliminates from the start the problems usually encountered in importing an exotic species.

Since the observations of Mandahl-Barth in 1941 (Madsen 1984), several researchers (Ayad, Mousa, Ishak, Yousif & Zaghloul 1970; Abdallah & Nasr 1973; Madsen 1979a & 1979b) showed experimentally that *H. duryi* is particularly well adapted to laboratory conditions and that it can control several intermediate host species under such conditions. These promising results and the fact that *H. duryi* is not susceptible to schistosome infection led to the suggestion by Madsen (1981) that field trials with it should be encouraged.

To outcompete and eventually eliminate other freshwater snail species in natural habitats, *H. duryi* should possess outstanding assets such as a higher innate capacity of increase, a faster growth rate and a longer lifespan under different temperature regimes. It has already been observed that *B. pfeifferi* can be outcompeted by *H. duryi* under certain laboratory conditions (Madsen 1984). However, it is not known how the population statistics of *H. duryi* and *B. pfeifferi* in life-table experiments would compare under carefully controlled laboratory conditions, or under which temperature conditions a local race of *H. duryi* would be capable of establishing viable populations. Consequently, an age-specific life-table experiment with *H. duryi* and *B. pfeifferi* was undertaken at a series of constant temperatures ranging from 18–35°C.

Apart from its medical importance as an intermediate host of the intestinal bilharzia parasite, *Schistosoma mansoni*, *B. pfeifferi* was selected for this evaluation because its geographical distribution in South Africa has been documented thoroughly and its population dynamics under various controlled conditions have been studied intensively (Shiff & Garnett 1967; De Kock & Van Eeden 1981; De Kock &

Van Eeden 1986). The population statistics calculated during life-table experiments with *B. pfeifferi* have already been compared with its geographical distribution (Shiff & Husting 1966; Harrison & Shiff 1966; De Kock & Van Eeden 1981). It is expected that the results of the present study could contribute to meaningful predictions regarding the establishment potential of *H. duryi* in different natural habitats in South Africa.

Material and methods

The experiment was carried out in the throughflow system of aquaria described in detail by De Kock (1985) and De Kock & Van Eeden (1986). Temperatures investigated ranged with three degree intervals from 18–36°C. However, the eggs of neither species failed to hatch at 36°C, thus we tried to compile life-tables at 35°C.

The parental snails of the cohorts of *H. duryi* came from a series of cement and stone dams connected with canals and which are situated in the Amphigarden of the Durban metropolitan area (2931 CC). The parental snails of *B. pfeifferi* came from an earth dam in a tributary of the Harts River in the Lichtenburg urban area (2626 AA). One week after hatching, cohorts of 25 specimens of each species at each temperature were randomly selected for the compilation of life-tables. Mortalities and egg production were noted daily.

The usual population statistics (Table 1) were calculated from the life-tables and calculation methods (described by Southwood (1978) were used.

Results

The population statistics calculated for both species are summarized in Table 2 and the r_m values additionally depicted in Figure 1. It must be kept in mind that these statistics represent a mean value of the performance of a single snail calculated from the egg production and survival of a cohort of 25 individuals. The age specific survival rates per cohort per two-week period are shown in Table 3.

Table 1 The population parameters used to evaluate the response of *H. duryi* and *B. pfeifferi* to the different constant temperatures

Population parameter	Symbol	Explanation
Survivorship	l_x	age-specific survival rate
Natality	m_x	age-specific birth rate
Innate capacity of increase	r_m	increase in numbers of a population in a specific constant environment free from effects of density
Net reproduction	R_o	rate of multiplication in one generation
Finite rate of increase	λ	antilog of r_m ; indicates the number of times a population will multiply per unit time

Table 2 Population statistics recorded for the cohorts of *H. duryi* (H) and *B. pfeifferi* (B) at the different constant temperatures

		Population parameters					
Constant tempera-tures (°C)	Snail species	Hatching time (days)	Hatch-ing %	Days to onset of egg pro-duction	λ	r_m	R_o
18	H	18	88	68	1,89	0,64	664,7
	B	16	85	53	2,27	0,82	140,5
21	H	12	89	37	3,50	1,25	1261,5
	B	11	86	29	5,43	1,69	273,9
24	H	9	95	28	5,13	1,63	1158,1
	B	9	90	24	6,71	1,90	181,8
27	H	7	93	23	9,33	2,23	3718,3
	B	7	82	22	5,94	1,79	150,8
30	H	6	89	22	20,08	2,99	5427,9
	B	6	26	41	0,86	–0,15	0,6
33	H	5	91	20	17,32	2,85	1704,3
	B		0				
35	H	5	34	43	0,67	-0,41	0,2
	B		0				

Discussion

The innate capacity of increase (r_m) is a composite statistic incorporating the results of growth, reproduction and survival (O'Keeffe 1985). Therefore, the r_m values are not independent of the other results — they integrate them into single values. The degree of success should therefore be measured by means of the r_m values for both species at the various temperatures studied. Positive r_m values were obtained for *H. duryi* at temperatures ranging from 18–33°C. This indicates that this species should theoretically be able to establish viable populations under similar temperature regimes in nature ($r_m \geqslant 0$). In contrast, the r_m values calculated for *B. pfeifferi* indicate that this species should have a small advantage over *H. duryi* at temperatures between 18 and 24°C, but that it should have no ability to establish populations at temperatures constantly remaining above 30°C.

The real usability of the parameter r_m according to Shiff & Husting (1966) lies in the range of values obtained under

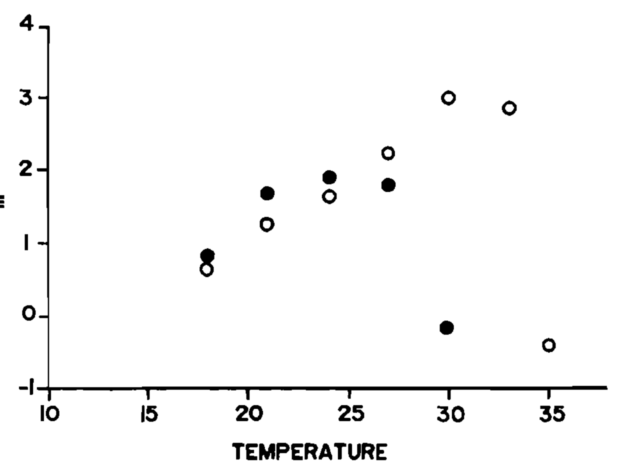

Figure 1 The relationship between r_m and temperature in *Helisoma duryi* (○) and *Biomphalaria pfeifferi* (●).

Table 3 Age-specific survival of the cohorts of *H. duryi* and *B. pfeifferi* at the different constant temperatures

Pivotal age	Species	l_x values at the different constant temperatures 18°C	21°C	24°C	27°C	30°C	33°C	35°C
0,5	H+	1,0	1,0	1,0	1,0	1,0	1,0	1,0
	B++	1,0	1,0	1,0	1,0	1,0	*	*
1,5	H	1,0	1,0	1,0	1,0	1,0	1,0	0,6
	B	1,0	1,0	1,0	1,0	1,0		
2,5	H	1,0	1,0	0,8	1,0	1,0	1,0	0,1
	B	1,0	1,0	1,0	1,0	1,0		
3,5	H	1,0	0,9	0,6	0,9	1,0	1,0	1,0
	B	1,0	1,0	0,9	0,5	0,4		
4,5	H	1,0	0,9	0,6	0,8	1,0	0,9	**
	B	1,0	0,6	0,6	0,5	0,2		
5,5	H	1,0	0,9	0,6	0,8	1,0	0,9	
	B	1,0	0,5	0,4	0,3	0,2		
6,5	H	0,9	0,9	0,6	0,8	1,0	0,9	
	B	0,9	0,5	0,4	0,3	**		
7,5	H	0,9	0,8	0,6	0,8	1,0	0,9	
	B	0,8	0,4	0,2	0,2			
8,5	H	0,9	0,8	0,6	0,8	1,0	0,9	
	B	0,6	0,4	0,1	0,2			
9,5	H	0,8	0,8	0,5	0,8	0,9	***	
	B	0,6	0,4	0,1	0,2			
10,5	H	0,8	0,8	0,5	0,8	0,9		
	B	0,6	0,4	0,1	0,2			
11,5	H	0,8	0,8	0,5	0,7	0,9		
	B	0,5	0,4	0,1	0,1			
12,5	H	0,8	0,8	0,5	0,7	0,9		
	B	0,4	0,3	**	**			
13,5	H	***	0,8	0,4	0,7	0,8		
	B	***	0,3					
14,5	H		0,8	0,4	0,7	0,8		
	B		0,3					
15,5	H		0,7	0,4	0,7	***		
	B		0,3					

+ = *Helisoma duryi*
++ = *Biomphalaria pfeifferi*
* = Egg clutches failed to hatch
** = All snails died
*** = Experiment terminated

specific experimental conditions. These values calculated for *H. duryi* are not only higher than those for *B. pfeifferi*, but show a clear peak at 30°C (Figure 1). In contrast, the values for *B. pfeifferi* do not reach a distinctive peak. The ecological implications of similar differences, interpreted in the light of the views of Shiff & Husting (1966) and Harrison & Shiff (1966), are that temperature should play a larger part in the geographical distribution of *H. duryi* and that it should be better adapted to occupy habitats with unfavourable environments, than *B. pfeifferi*. The relatively longer reproduction period, reflected in the considerably higher net reproduction rate (Table 2) and the excellent survival rate, resulting in a longer lifespan, indicate that *H. duryi* is more *K*- and less *r*-selected than *B. pfeifferi*. This should act in the favour of *H. duryi* in a competition for natural resources, because, according to Pianka (1970), *K*-selected species are usually severe and efficient competitors.

As far as we know, no experimental investigations regarding competition between *H. duryi* and *B. pfeifferi* have been carried out under natural conditions in South Africa. The most important conclusions that could be reached from experiments carried out in Tanzania were that *H. duryi* reduced the numbers of *B. pfeifferi* under certain conditions and that it did well in the tropics under the same biophysical and chemical conditions as the particular host species (Frandsen & Madsen 1979). It was also experimentally demonstrated by Frandsen (1976) that *H. duryi* was capable of attracting miracidia of *S. mansoni* and thus reducing the infection and production of cercariae in *B. pfeifferi*.

In spite of the fact that *H. duryi* has been distributed right across South Africa by the aquarium industry, and the first records of finds in nature were made 25 years ago, it had not yet been able to spread significantly. This could be attributed to a poorer ability to aestivate, as reported by McCullough (1981), or to the fact that self-fertilization does not occur in the species. However, according to Madsen (1981), this inability to self-fertilize does not make *H. duryi* unsuitable for biological control because it implies that non-intentional distribution can be controlled much more easily.

The results of the present study indicate that, as far as temperature is concerned, *H. duryi* should be able to survive in most of the habitats occupied by *B. pfeifferi* in South Africa. The degree of success achieved elsewhere in the world under laboratory as well as field conditions in biological control experiments with *H. duryi* and the results of our own study hold promise. Follow-up experiments in the laboratory as well as trials under natural conditions should be encouraged.

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