

# Distribution and habitats of *Biomphalaria pfeifferi*, snail intermediate host of *Schistosoma mansoni*, in South Africa

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## Abstract

As intermediate host for *Schistosoma mansoni*, *Biomphalaria pfeifferi* plays a major role in the transmission of intestinal bilharziasis in the endemic areas of South Africa. This article focuses on the geographical distribution and habitats of this species, as reflected by the 1 639 samples on record in the database of the National Freshwater Snail Collection of South Africa. This snail is well represented in the Northern Province, Mpumalanga and the coastal areas of KwaZulu-Natal, that represent the bilharzia endemic areas of South Africa. Details of each habitat, as well as mean altitude and mean annual temperature and rainfall of each locality, were processed to determine chi-square and effect size values and to construct an integrated decision tree that makes a selection of those variables that could maximally discriminate between this snail and all the other species in the database. The results indicated that temperature and type of water-body are the major factors determining the distribution of *B. pfeifferi* in South Africa. These findings support the results of demographic studies reported by several authors that led them to the conclusion that *B. pfeifferi* does best under warm stable conditions. The importance of four isolated and persistent foci occurring further west than the western arm of its range of distribution and far removed from the bilharzia endemic areas, is discussed. Two of these localities are popular holiday resorts and the fact that specimens from both these localities showed a high compatibility with a local strain of *S. mansoni* is cause for concern.

**Keywords:** geographical distribution, habitat preferences, experimental infection, epidemiology of schistosomiasis, *Biomphalaria pfeifferi*

## Introduction

*Biomphalaria pfeifferi* is the most important intermediate host in tropical Africa for *Schistosoma mansoni*, the parasite causing intestinal bilharzia in man (Brown, 1994). It was first described from specimens collected in the Umgeni Valley, KwaZulu-Natal. The oldest sample of this species on record in the National Freshwater Snail Collection (NFSC) of South Africa, dates back to 1952. This report focuses on the geographical distribution and habitats of this snail as reflected by the samples on record in the NFSC. The ecological implications of the range of values reported by various authors for the demographic parameter  $r$  (intrinsic rate of natural increase) are also discussed. Attention is drawn to four persistent populations of this species occurring in isolated foci outside the bilharzia endemic areas in South Africa. Details are given of snail habitats as described by the collectors at the time of collection and also of the mean altitude and mean annual rainfall and mean annual air temperature of the loci ( $1/16$  square degree) in which the collections were made.

## Materials and method

Data pertaining to the geographical distribution and habitats of *B. pfeifferi* were extracted from the database of the NFSC. Only those samples for which the collection sites could be pinpointed on the 1:250 000 topo-cadastral map series of South Africa, were

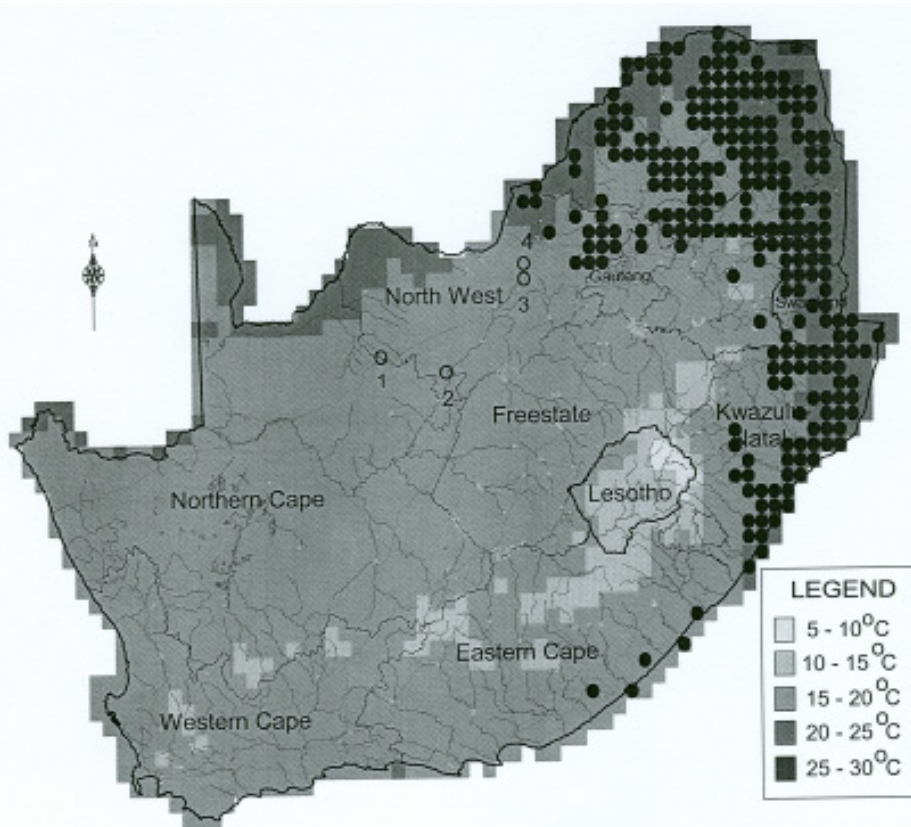
included in the analysis. The majority of these samples were collected during surveys conducted by staff of government and local health authorities and then sent to the former Snail Research Unit at the Potchefstroom University for identification and to be added to the NFSC. Details of the habitats were documented by collectors during surveys by selecting the relevant options on forms compiled by the staff of the Snail Research Unit. The number of loci in which the collection sites were located was distributed in intervals of mean annual rainfall and air temperature, as well as intervals of mean altitude, and the results tabled to illustrate the frequency of occurrence in specific intervals. Rainfall, temperature and altitude data were obtained from the Computing Centre for Water Research, University of Natal. A temperature index was calculated for all mollusc species in the database from their frequencies of occurrence in the selected temperature intervals and the results used to rank them in order of association with low to high climatic temperatures. This was done by allocating numeric values, ranging from one for the coolest to five for the warmest, to five selected temperature intervals. The proportion of the total number of loci of each species falling in a particular temperature interval was then multiplied by the value allocated to that specific temperature interval. This was done for each temperature interval in which the species was recorded and the sum of these scores was then taken as the temperature index for that particular species ( $I = \sum_{i=1}^5 ip_i$ ) and the results presented in a table. This analysis was recommended by Brown (2002). Chi-square values were calculated to determine the significance of the difference between the frequency of occurrence in, on, or at the different options for each variable, such as type of water-body, type of substratum and temperature interval. Furthermore, an effect size was calculated for all the different variables discussed in this paper.

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**Figure 1 (left)**  
The geographical distribution of *Biomphalaria pfeifferi* in  $1/16$  square degree loci and mean annual air temperature in South Africa. Loci of the four persistent populations: 1 = source of the Kuruman River, 2 = Blue Pool at Buxton, district of Taung, 3 = source of the Harts River at Lichtenburg and 4 = source of the Molopo River.

The effect size is an index which measures the degree of discrepancy between the frequency distribution of a given species in the set of alternatives of a given variable such as water-bodies, as compared to the frequency distribution of all other mollusc species in the database in the set of alternatives of the same variable (Cohen, 1977). According to this author values for this index in the order of 0.1 and 0.3 indicate small and medium effects respectively, while values of 0.5 and higher indicate practical significantly large effects (Cohen, 1977). A value for this index in the

**TABLE 1**  
**Types of water-bodies in which *Biomphalaria pfeifferi* was found in 1 639 collection sites recorded during surveys**

Water-bodies	A	B	C	D
Channel	6	0.4%	169	3.6%
Concrete dam	53	3.2%	221	24.0%
Dam	451	27.5%	8400	5.4%
Ditch	21	1.3%	636	3.3%
Irrigation furrow	5	0.3%	113	4.4%
Pan	20	1.2%	306	6.5%
Pond	63	3.8%	1566	4.0%
Quarry	2	0.1%	122	1.6%
River	445	27.2%	7507	5.9%
Spring	8	0.5%	301	2.7%
Stream	212	12.9%	7211	2.9%
Swamp	32	2.0%	2076	1.5%
Vlei	1	0.1%	103	0.8%
Pool	3	0.2%	225	1.3%

Effect size  $w = 0.5$  (large effect)

A Number of times collected in a specific water-body  
 B % of the total number of collections (1 639) on record for this species  
 C Number of times any mollusc was collected in a specific water-body  
 D % occurrence of this species in the total number of collections in a specific water-body

order of 0.5, calculated for the frequency distribution of a given mollusc species in the different types of water-body, for instance, would indicate that this factor played an important role in determining the geographical distribution of this particular species as reflected by the data in the database.

The data in the database were also adapted and processed to construct an integrated decision tree (Breiman et al., 1984). This is a statistical model that enables the selection and ranking of those variables which can maximally discriminate between the frequency of occurrence of a given species under specific conditions as compared to all other species in the database. This was accomplished by making use of the SAS Enterprise Miner for Windows NT Release 4.0, April 19, 2000 programme and Decision Tree Modelling Course Notes (Potts, 1999).

## Results

The 1 639 samples of *B. pfeifferi* which could be pinpointed on our maps, were collected from 251 different loci (Fig. 1).

This species was present in a wide variety of water-bodies, but the highest percentages were recovered from dams (27.5%) and rivers (27.2%). The frequency of occurrence in these two water-bodies differed significantly from streams ( $\chi^2 = 56.3$ ,  $df = 1$ ;  $p < 0.05$ ;  $\chi^2 = 76.9$ ,  $df = 1$ ;  $p < 0.05$ , respectively), i.e. streams yielded the third highest percentage of samples (12.93%) (Table 1). The largest number of samples (71.5%) was collected in habitats with perennial water and this differed significantly ( $\chi^2 = 130.7$ ,  $df = 1$ ;  $p < 0.05$ ) from the number of samples from habitats with seasonal water (Table 2). The highest percentage of samples was recovered from habitats with standing water, clear water and freshwater (Table 2) and the chi-square values showed that they differed significantly, in each case, from their respective alternative options. The highest percentage of samples (28.6%) came from

	Type		Velocity			Colour		Salinity	
	Perennial	Seasonal	Fast	Slow	Standing	Clear	Muddy	Fresh	Brackish
A	1172	86	91	489	648	909	228	1014	54
B	71.5%	5.3%	5.6%	29.8%	39.5%	55.5%	13.9%	61.9%	3.3%
C	22432	5350	2229	9501	16147	20408	6438	24089	657
D	5.2%	1.6%	4.1%	5.2%	4.0%	4.5%	3.5%	4.2%	8.2%
E	w = 0.3 (medium effect)		w = 0.1 (small effect)			w = 0.1 (small effect)		w = 0.1 (small effect)	

A Number of times collected in a specific water condition  
 B % of the total number of collections (1 639) on record for this species  
 C Number of times any mollusc was collected in a specific water condition  
 D % occurrence of this group in the total number of collections in a specific water condition  
 E Effect size values calculated for each factor

habitats with substrata described as predominantly muddy (Table 3), which differed significantly from all the other substratum types ( $X^2 = 3.2$ ,  $df = 1$ ;  $p < 0.05$  for a stony substratum;  $X^2 = 27.2$ ,  $df = 1$ ;  $p < 0.05$  for a sandy substratum;  $X^2 = 29.5$ ,  $df = 1$ ;  $p < 0.05$  for a substratum of decomposing material). Aquatic plants were reported from 72.3% of the collection sites at the time of survey.

The majority of samples came from sites which fell within the two air temperature intervals that ranged from 15 to 25°C (Table 4) and the chi-square values showed that the frequencies of occurrence in these intervals differed significantly from the frequencies of occurrence in all the other temperature intervals, but not from each other. The highest percentages of samples were recovered from sites that fell within the two intervals of mean annual rainfall ranging from 300 to 600 mm and 600 to 900 mm. The chi-square values showed that the percentages of occurrence in these two intervals differed significantly from all other rainfall intervals, but not from each other. The chi-square values indicated that there were also no significant differences between the frequencies of occurrence recorded for the three altitude intervals ranging from 0 to 500 m, 500 to 1 000 m and 1 000 to 1 500 m.

From the effect size values calculated for each factor, also listed in Tables 1 to 4, a significant positive relationship between the occurrence of *B. pfeifferi* and temperature ( $w = 1.0$ ), altitude ( $w = 0.8$ ) and type of water-body ( $w = 0.5$ ) can be deduced. Although 72.3% of the samples of *B. pfeifferi* were collected in habitats with aquatic vegetation, the effect size,  $w = 0.1$  calculated for this factor, suggests that it should play a relatively unimportant role in determining the presence of this species in a particular habitat.

The integrated decision tree (Fig. 2) constructed from the data shows that temperature was selected from all the variables in the database as the first and type of water-body as the second most important factor determining the presence of this species in a particular area. In the temperature interval ranging from 20 to 25°C, 17.6% of the 4 566 samples on record for all mollusc species in the database were represented by *B. pfeifferi*. In contrast to this, the 880 samples collected in the temperature interval ranging between 15 to 20°C represented only 3.5% of the total number of samples on record for all mollusc species for this particular interval (Fig. 2).

	Substratum types			
	Muddy	Stony	Sandy	Decomposing material
A	469	329	342	50
B	28.6%	20.1%	20.9%	3.1%
C	12835	7934	6523	632
D	3.7%	4.2%	5.2%	7.9%
E	w = 0.2 (small effect)			

A Number of times collected on a specific substratum  
 B % of the total numbers of collections (1 639) on record for this species  
 C Number of times any mollusc was collected in a water-body with a specific substratum  
 D % occurrence of this species in the total number of collections in a water-body with a specific substratum  
 E Effect size values calculated for substrata

The effect size values calculated for the set of temperature indexes of all the mollusc species in the database, indicated practical significant differences ( $w = > 0.5$ ) between the temperature index of *B. pfeifferi* and those of all but 12 of the other mollusc species (Table 5).

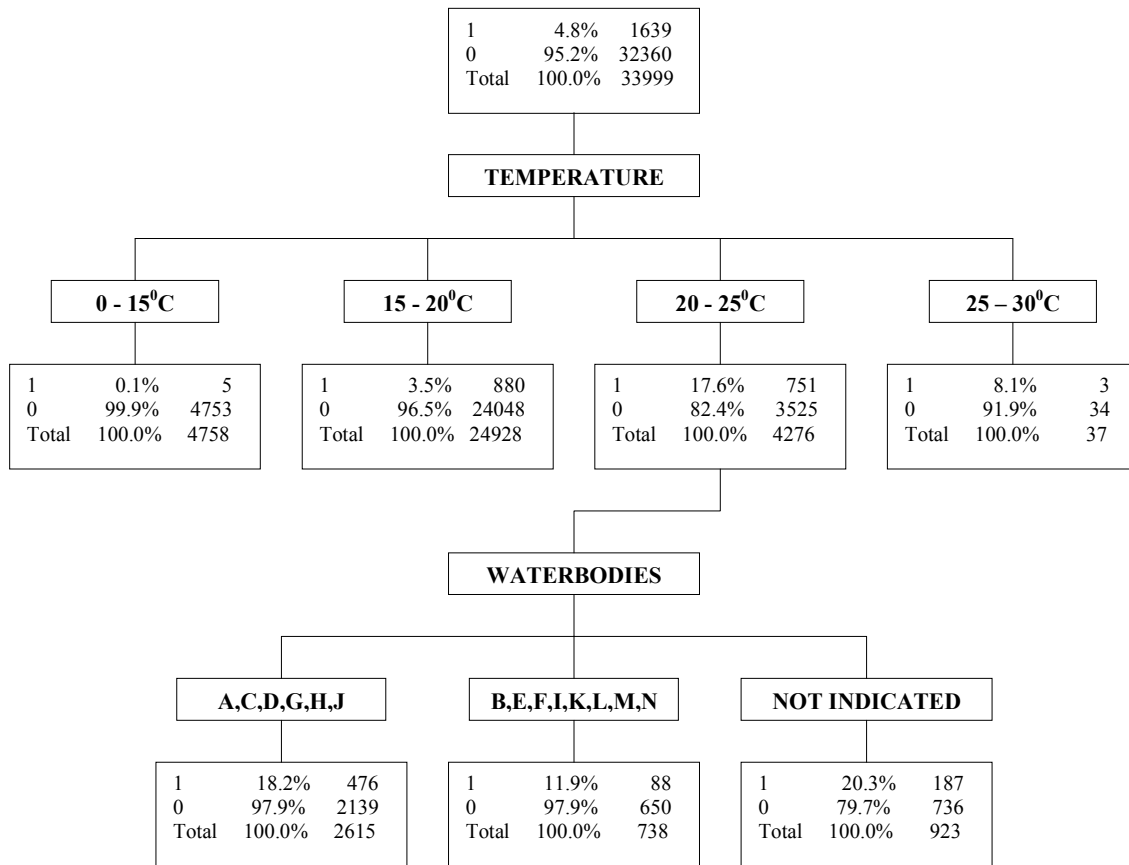
## Discussion

According to Brown (1994) the main present-day range of distribution of *B. pfeifferi* lies southwards of a line passing approximately from Asmara in Ethiopia to the lower Senegal River basin.

**TABLE 4**  
**Frequency distribution of the 1 639 collection sites of *Biomphalaria pfeifferi* in selected intervals of mean annual air temperature and rainfall and mean altitude in South Africa**

	Temperature intervals (°C)				Rainfall intervals (mm)				Altitude intervals (m)			
	10-15	15-20	20-25	25-30	0-300	300-600	600-900	900-1200	0-500	500-1000	1000-1500	1500-2000
A	5	880	751	3	47	714	732	146	550	579	495	15
B	0.3%	53.7%	45.8%	0.2%	2.9%	43.6%	44.7%	8.9%	33.6%	35.3%	30.2%	0.9%
C	4404	24928	4276	37	975	11994	19799	1203	6747	4491	14918	6998
D	0.1%	3.5%	17.6%	8.1%	4.8%	6.0%	3.7%	12.1%	8.2%	12.9%	3.3%	0.2%
E	w = 1.0 (large effect)				w = 0.4 (medium to large effect)				w = 0.8 (large effect)			

A Number of times collected in a locality falling in a specific interval  
 B % of the total number of collections (1 639) on record for this species  
 C Number of times any mollusc was collected in a locality falling in a specific interval  
 D % occurrence of this species in the total number of collections in a specific interval  
 E Effect size values calculated for each factor



**Figure 2**

Decision tree of the frequency of occurrence of *Biomphalaria pfeifferi* for each variable as compared to the frequency of occurrence of all the other species in the database of the NFSC. 0 = percentages and frequencies of all other species, 1 = percentages and frequencies of *B. pfeifferi*. Waterbodies: A = brook, B = channel, C = concrete dam, D = dam, E = ditch, F = irrigation furrow, G = pan, H = pond, I = quarry, J = river, K = spring, L = swamp, M = vlei, N = pool.

The southern limits lie in S. Angola, the Okavango Delta, W. Transvaal (North West Province) and Transkei (Eastern Cape Province). According to this author the absence of *B. pfeifferi* from apparently suitable water-bodies in the Free State Province, Cape

Province and Lesotho seems due to the cool winter climate. This is in general agreement with the geographical distribution plotted from the records of the NFSC which show that this snail is widely distributed in the Limpopo Province, Mpumalanga and the coastal

**TABLE 5**  
**Frequency distribution in temperature intervals and temperature index of *Biomphalaria pfeifferi* as compared to all mollusc species in the database of the national freshwater snail collection**

Mollusc species	No. of samples	5-10°C	10-15°C	15-20°C	20-25°C	25-30°C	<sup>1</sup> Index	<sup>2</sup> SD	<sup>3</sup> CV	Effect size
<i>Pisidium viridarium</i>	636	201	270	163	2		1.947	0.764	39.225	-1.981
<i>Pisidium casertanum</i>	5		2	3			2.600	0.548	21.066	-1.568
<i>Lymnaea truncatula</i>	723	95	281	343	4		2.354	0.709	30.135	-1.558
<i>Pisidium costulosum</i>	425	1	138	282	4		2.680	0.492	18.344	-1.533
<i>Pisidium langleyanum</i>	627	18	173	430	6		2.676	0.544	20.328	-1.439
<i>Bulinus tropicus</i>	8448	32	2326	5860	230		2.744	0.502	18.305	-1.407
<i>Gyraulus connollyi</i>	969		185	777	7		2.816	0.406	14.404	-1.265
<i>Ceratophallus natalensis</i>	1797		299	1430	68		2.871	0.433	15.092	-1.157
<i>Burnupia</i> (all species)	2778	7	287	2384	100		2.928	0.380	12.971	-1.046
<i>Ferrissia</i> (all species)	540		72	420	47	1	2.957	0.476	16.088	-0.987
<i>Bulinus reticulatus</i>	296		6	287	3		2.990	0.174	5.832	-0.923
<i>Assiminea umlaasiana</i>	2			2			3.000	0.000	0.000	-0.904
<i>Tomichia cawstoni</i>	4			4			3.000	0.000	0.000	-0.904
<i>Tomichia differens</i>	10			10			3.000	0.000	0.000	-0.904
<i>Tomichia lirata</i>	2			2			3.000	0.000	0.000	-0.904
<i>Tomichia ventricosa</i>	89			89			3.000	0.000	0.000	-0.904
<i>Tomichia tristis</i>	81			79	2		3.025	0.156	5.162	-0.855
<i>Unio caffer</i>	76		6	63	6	1	3.026	0.461	15.237	-0.852
<i>Physa acuta</i>	755			719	36		3.048	0.213	6.997	-0.810
<i>Bulinus depressus</i>	552			519	33		3.060	0.237	7.755	-0.786
<i>Arcuatula capensis</i>	15			14	1		3.067	0.258	8.420	-0.772
<i>Lymnaea columella</i>	2302		81	1977	243	1	3.071	0.371	12.072	-0.763
<i>Lymnaea natalensis</i>	4721		205	3802	713	1	3.108	0.429	13.789	-0.691
<i>Assiminea bifasciata</i>	17			15	2		3.118	0.332	10.652	-0.672
<i>Gyraulus costulatus</i>	736		20	580	135	1	3.159	0.437	13.836	-0.591
<i>Bulinus forskalii</i>	1209		17	985	204	3	3.160	0.409	12.948	-0.589
<i>Pisidium ovampicum</i>	6			5	1		3.167	0.408	12.892	-0.575
<i>Sphaerium capense</i>	25		1	17	7		3.240	0.523	16.136	-0.419
<i>Bulinus africanus</i> spp. group	2930		9	2155	760	6	3.260	0.450	13.816	-0.391
<i>Corbicula fluminalis</i>	389		1	291	94	4	3.267	0.437	13.384	-0.377
<i>Tomichia natalensis</i>	23			16	7		3.304	0.470	14.238	-0.304
<i>Thiara amarula</i>	10			6	4		3.400	0.516	15.188	-0.114
<i>Assiminea ovata</i>	5			3	2		3.400	0.548	16.109	-0.108
<i>Melanoides victoriae</i>	49			29	19	1	3.429	0.540	15.752	-0.056
<i>Biomphalaria pfeifferi</i>	1639		5	880	751	3	3.459	0.508	14.692	0.000
<i>Septaria tessellaria</i>	2			1	1		3.500	0.707	20.203	0.058
<i>Coelatura framesi</i>	6			3	3		3.500	0.548	15.649	0.075
<i>Neritina natalensis</i>	16			8	8		3.500	0.516	14.754	0.079
<i>Bulinus natalensis</i>	245		2	97	146		3.588	0.510	14.204	0.253
<i>Segmentorbis planodiscus</i>	27			9	18		3.667	0.480	13.101	0.409
<i>Segmentorbis angustus</i>	32			7	25		3.781	0.420	11.108	0.634
<i>Melanoides tuberculata</i>	305			64	237	4	3.803	0.430	11.305	0.678
<i>Pisidium pirothi</i>	23			4	19		3.826	0.388	10.129	0.723
<i>Spathopsis petersi</i>	44			5	37	2	3.932	0.398	10.111	0.931
<i>Aplexa marmorata</i>	9				9		4.000	0.000	0.000	1.065
<i>Bellamya capillata</i>	31				31		4.000	0.000	0.000	1.065
<i>Eupera ferruginea</i>	169			6	157	6	4.000	0.258	6.455	1.065
<i>Lentorbis carringtoni</i>	8				8		4.000	0.000	0.000	1.065
<i>Lentorbis junodi</i>	12				12		4.000	0.000	0.000	1.065
<i>Segmentorbis kanisaensis</i>	9				9		4.000	0.000	0.000	1.065
<i>Spathopsis wahlbergi</i>	28			1	26	1	4.000	0.272	6.804	1.065
<i>Cleopatra ferruginea</i>	73				71	2	4.027	0.164	4.081	1.119
<i>Lanistes ovum</i>	41				38	3	4.073	0.264	6.473	1.209

<sup>1</sup>Index = Temperature index; <sup>2</sup>SD = Standard deviation; <sup>3</sup>CV = Coefficient of variance

areas of KwaZulu-Natal. These areas represent the endemic areas of bilharziasis in South Africa (Gear et al., 1980). All the essentially tropical molluscs have a southern arm of their distribution range, touching the Mpumalanga Province for a greater or lesser distance down the coast, and some have also a western arm in the Limpopo Province and the lower valley of the Vaal River (Brown, 1978). According to this author the first group may be termed 'narrowly tropical' while the species with a western arm of range are generally more widely distributed and may be termed 'broadly tropical'. Among the broadly tropical group are *B. pfeifferi* and the *Bulinus africanus* group of species. However, at least four isolated populations of *B. pfeifferi* exist still further west and far outside the endemic area of intestinal bilharziasis as reported for South Africa. The population in the Blue Pool in the Harts River at Buxton in the district of Taung (2724DA, marked No. 2 in Fig.1) is fed by a perennial spring and has been on record in the NFSC since 1958. Those at the eye (source) of the Molopo River (2526CC, marked No. 4 in Fig. 1), the eye of the Harts River at Lichtenburg (2626AA, marked No. 3 in Fig. 1) and the eye of the Kuruman River (2723AD, marked No. 1 in Fig. 1) have been on record since 1964, 1974 and 1977, respectively.

Among factors governing the distribution of this species, type of water-body, total dissolved chemical composition, or salinity, of the water, current velocity, stream geology and temperature, amongst others, are important.

*Biomphalaria pfeifferi* was reported from all the types of water-body on record in the database, but the results in Fig. 2 indicate that streams, concrete dams, dams, pans, ponds and rivers were selected as water-bodies which were favoured by this species as compared to the other species in the database at the temperature interval ranging between 20 and 25°C. The effect size calculated for water-bodies ( $w = 0.5$ ) suggests that this factor should play a significant role in the distribution of this species in South Africa. The largest percentage of samples of this species was collected in dams, rivers and streams (Table 1) which is in general agreement with the water-bodies mentioned by Brown (1994) for this species in its range of distribution in Africa.

Mineral content of the water can be limiting, both when values are too high or too low (Williams, 1970; Jennings et al., 1973; Jennings, 1976). However, the effect size calculated for the frequency of occurrence in either fresh or brackish water ( $w = 0.1$ ) in the present investigation points to a minor role played by this factor in the distribution of this species in South Africa.

Intermediate host snails of schistosomiasis have been found to have a remarkably narrow tolerance range to current velocity. Most habitats in which they occur are lentic, but established, persistent populations occur also in very slow-flowing water, up to a limit of approximately 0.3 m/s. (Frank, 1964; Appleton, 1975). The effect size ( $w = 0.1$ ) calculated for this factor, likewise suggests that it should play a relatively unimportant role in the distribution of this species in South Africa.

During surveys in the Gladdespruit and Komati River (Mpumalanga Province) by Appleton (1975) a potentially useful association was found between the occurrence of permanent lentic habitats produced by the weathering of bedrock with a hardness above 5 in Moh's Scale of Hardness and the longitudinal distribution of persistent populations of the intermediate host snails *B. pfeifferi* and the *Bulinus africanus* group. Appleton and Stiles (1976) mention the phenomenon that host snails have been found at many isolated and sometimes small outcrops of hard rock, surrounded by large areas of unsuitable soft rocks, supporting the suggestion that during earlier periods of increased rainfall, snails occurred over a wide area in which they now survive as apparently

relict populations in only scattered, particularly suitable habitats, e.g. the occurrence of the persistent population of *B. pfeifferi* at Taung. These authors come to the conclusion that practically the entire endemic area of the bilharzia intermediate host snails *B. pfeifferi* and the *B. africanus* group in South Africa is over rock formations which are resistant to erosion. Although accepting that waters flowing over such rocks tend to provide permanent pools which serve as refuges for snails, Brown (1978) is of opinion that this effect is no more than locally significant. This author points to the fact that large parts of the area from which *Biomphalaria* and the *Bulinus africanus* group are absent, contain apparently suitable habitats and consequently it seems that unfavourable climatic temperature is likely to be a factor of overriding influence in excluding these snails and a number of other freshwater molluscs.

Many authors have assumed that climatic temperature influences the distributions of aquatic invertebrates in Southern Africa, but investigations in natural habitats and in the laboratory to confirm the ideas deduced from distribution patterns have been confined to only a few species of snail (Brown, 1978). The values recorded for the demographic parameter  $r$  (intrinsic rate of natural increase) for cohorts of *B. pfeifferi* in life-table experiments by several authors, did not differ much at constant temperatures ranging from 20 to 27°C (Shiff and Husting, 1966; Shiff and Garnett, 1967; De Kock and Van Eeden, 1981). The ecological implications of the phenomenon that no clear peak value for the parameter  $r$  was recorded at any of the constant temperatures investigated, are that this species would do best in warm stable conditions. With regard to stability of its habitats, this snail is not found in briefly-filled rain pools, although it can survive moderate periods of drought in a state of aestivation (Brown, 1994). Its relatively low reproduction potential per time unit, as reflected by its long generation time and low intrinsic rate of natural increase ( $r$ ) reported from the results of life-table experiments by the authors mentioned above, is probably the main reason for its inability to colonise temporary habitats.

The assumption, mentioned earlier, that climatic temperature influences the distribution of aquatic organisms, is supported by the findings of Appleton (1977) and Appleton and Eriksson (1984) that temperature can be limiting for *B. pfeifferi*, both when too cool and too warm. The importance of temperature is also borne out by the results in Fig. 2, from which it is evident that *B. pfeifferi* is sensitive to low temperatures as compared to the rest of the species in the database. Its frequency of occurrence at temperature intervals ranging from 0 to 15°C and 15 to 20°C represented respectively only 0.1% and 3.5% of the total number of frequencies of occurrence of all the other mollusc species (Fig. 2). In contrast to this, it represented 17.6% and 8.1% respectively, of the total number of frequencies of occurrence at the temperature intervals ranging from 20 to 25°C and 25 to 30°C (Fig. 2). The relatively large effect size calculated for temperature ( $w = 1.0$ ) also suggests that temperature could play a significant role in determining the distribution of this species in South Africa.

De Kock and Van Eeden, (1981) reported a value of 0.83 for  $r$  (intrinsic rate of natural increase) and a lifespan of more than eight months for *B. pfeifferi* at a constant temperature of 17°C during life-table experiments in the laboratory. From a regression line fitted to the  $r$  values of these experiments it was deduced that a zero value for  $r$  would be reached at 14°C, implying that this species would be capable of maintaining a population under these circumstances. The persistent population at the source of the Harts River near Lichtenburg (No. 3, Fig. 1) is subjected to severe frost during winter and daily minima water temperatures of less than 8°C were recorded during May and June in this habitat when temperature was

monitored continuously during 1982/1983 (Wolmarans et al., 1986). In this case, the permanency of the habitat would play a decisive role; as mentioned earlier, this water-body is fed by a perennial spring and is therefore stable as far as water supply is concerned. This factor also provides a plausible explanation for the occurrence of the other three persistent populations of *B. pfeifferi* in the three isolated habitats mentioned earlier. These habitats are all closely associated with perennial springs, which usually have a stabilising effect on both the temperature regime and the water supply. Although the temperature in such habitats might be sub-optimal for reproduction for *B. pfeifferi*, as reported by Wolmarans et al. (1986) for the source of the Harts River at Lichtenburg, the negative effect would at least partially be compensated for by the fact that a permanent habitat is ensured by the continuous water supply. The reproduction period would therefore not be dependent on the availability of water. The same argument could be applied in an assessment of the chances of the intestinal bilharzia parasite to complete its life cycle in the snail intermediate host under these circumstances, because in such a stable habitat, in respect of water supply, time would not be a limiting factor. Furthermore, the average lifespan of the snails would be enhanced by temperatures sub-optimal for reproduction (De Kock and Van Eeden, 1981).

Specimens from the population in the Harts River at Lichtenburg, showed a compatibility of over 90% with a local strain of *S. mansoni* in experimental infections in several of our earlier studies (Wolmarans et al., 1986; De Kock, 1992; 1993; 1995) and specimens from the population at the source of the Molopo River likewise showed a compatibility of over 90% with this parasite species under laboratory conditions (De Kock, 1995). Both these localities are popular picnic and camping resorts frequented by people from all over the country, thus creating favourable conditions for establishing transmission foci. A recent study in the Limpopo Province revealed that a prevalence of infection of only 7% in a field population of *B. pfeifferi* was responsible for maintaining a prevalence of over 80% of *S. mansoni* infections in the rural human population (Strauss, 2000). In spite of these seemingly favourable conditions for transmission of bilharziasis, no infected field-collected specimens of *B. pfeifferi*, or cases of intestinal bilharzia, to our knowledge, have yet been reported from either one of these localities. Some field-collected snails from the source of the Harts River at Lichtenburg were occasionally found to shed amphistome cercariae which encysted on the containers in which they were kept, but our efforts to determine the identity of the parasites were unsuccessful (Wolmarans et al., 1986).

In view of the fact that at least two of these persistent foci of *B. pfeifferi* are located in popular picnic and camping resorts, located far outside the bilharzia endemic areas, it is recommended that representative samples of snails from these localities should periodically be collected and screened for possible schistosome infections.

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