THE USE OF BEHAVIOUR PATTERNS OF LARVAL SCHISTOSOMES IN ASSESSING THE BILHARZIA POTENTIAL OF NON-ENDEMIC AREAS*

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Useful information regarding the field transmission of larval schistosomes from snails can be obtained in a number of ways, such as filtration of, or rodent immersion into, field waters. However, nothing is learnt about the longevity of shedding snails, nor of the effect of varying incubation periods and changing temperatures. The artificiality of laboratory studies makes field application difficult or impossible.

During the normal course of maintaining the same strains of *Schistosoma mansoni, S. haematobium* and *S. mattheei* under outdoor conditions at Nelspruit from 1961, it was soon evident that a very constant pattern of exposed snails and larval schistosome development was being presented each year. It was also possible to correlate these findings with the field transmission of *S. mansoni* and *S. mattheei* as was shown by rodent immersion into natural waters in the neighbourhood of Nelspruit.[1,2]

It was felt that the method of exposing snails to miracidia and studying the subsequent behaviour patterns under outdoor conditions in non-endemic areas might provide some information regarding the bilharzia potential of these areas. In many areas bilharzia follows agricultural development or other ecological change as a *sine qua non;* however, occasionally it might be advantageous to know in advance whether, as a result of human activities and consequent snail introduction, schistosomes would be likely to flourish.

MATERIALS AND METHODS

Schistosome eggs from the mashed, sieved livers of laboratory-infected rodents (*Praomys* (*Mastomys*) *natalensis* and *Saccostomus campestris*) were hatched in water. Batches of 6 - 8-week-old Nelspruit laboratory-bred snails of the appropriate species were exposed singly for 6 - 8 hours in serology plates to 5 miracidia of Transvaal strains of *S. mansoni, S. haematobium* and *S. mattheei.* The snails were then placed in outdoor asbestos aquaria, 4 - 5 inches deep, containing 3 - 4 gallons of water and 3 - 4 feet above ground level. Tap water was used in areas where bilharzia host snails were present, and raw field water in areas not harbouring intermediate hosts.

*Date received: 18 December 1968.

Snails were removed, the water changed and aquaria scrubbed out weekly. No more than 15 snails were placed in each aquarium and shedding snails were kept until dead.

Snails were individually examined for cercariae in test-tubes, but not in direct sunlight. Initially this was done twice a week but was later reduced to once a week. Daily maximum and minimum aquarium temperatures, and where possible continuous field water temperatures, were recorded.

Sites

1. *Nelspruit* is situated at 30° 58′ E, 25°28′ S, at an altitude of 2,350 feet above sea-level, in the Eastern Transvaal Lowveld. Bilharzia infection rates, based on one stool and urine examination, of over 90% *S. mansoni* and over 80% *S. haematobium* in man, and over 70% *S. mattheei* in stock carcasses examined at abattoirs, have been recorded (Fig. 1).

Field transmission of *S. mansoni* from snails determined by rodent immersion was seasonal, and either started or increased significantly in the spring (September) with peak transmission in mid-summer, falling in late summer (January) with an occasional sharp peak in autumn (April/May). For the remainder of the year there was comparatively little or no transmission.[1,2]

In those areas which supported sufficient cattle, transmission of *S. mattheei* occurred throughout the year, with greatly increased transmission in spring and summer. In areas with few cattle, transmission was erratic and unpredictable. No good field transmission picture was obtained for *S. haematobium*.[1,2]

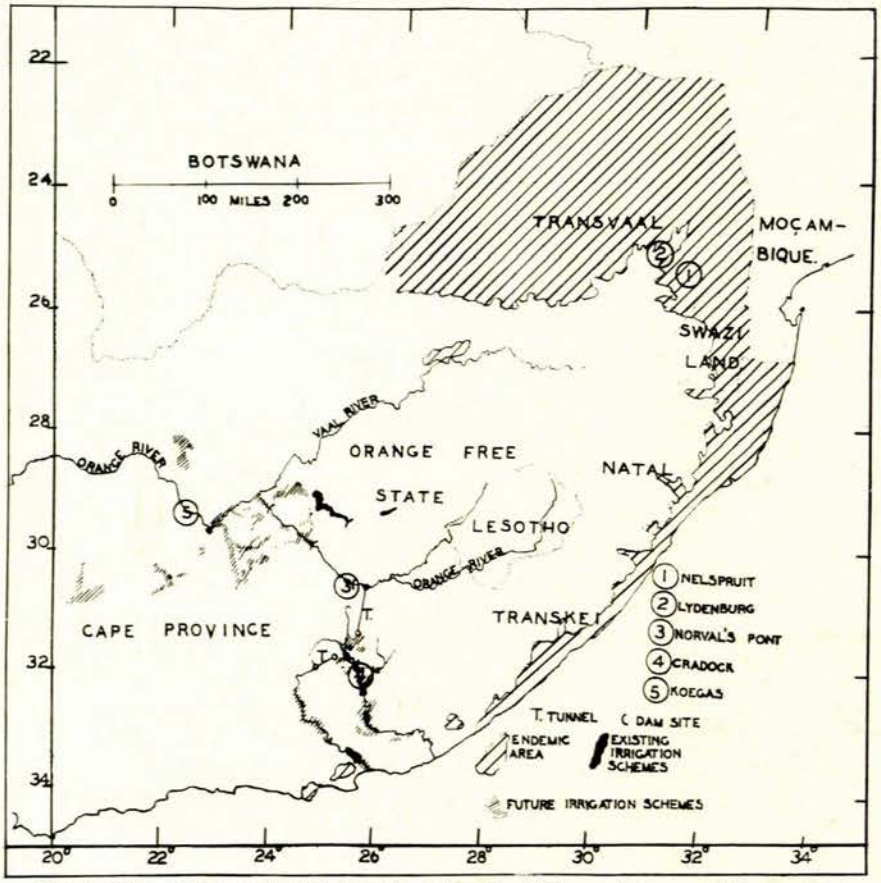

Fig. 1. Map of the endemic bilharzia in South Africa and some of the present and proposed irrigation schemes.

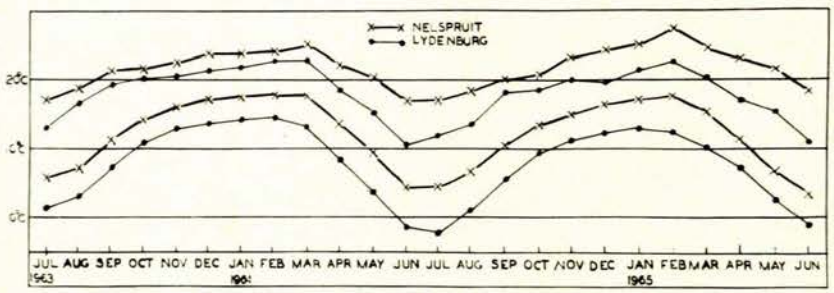

Fig. 2. Mean monthly maximum and minimum aquarium temperatures. Nelspruit and Lydenburg.

Light frosts occasionally occur along some Lowveld rivers during winter, but there is no freezing of field waters. The lowest temperature recorded in the Nelspruit aquaria from 1961 to 1967 was 1·5°C. Field temperatures up to 36°C have been recorded in canals and creeks during summer; the highest temperature recorded in the aquaria was 32·5°C, but aquaria were never subjected to direct sunlight for the whole day. Mean monthly maximum and minimum aquarium temperatures for various years are shown in Figs. 2 and 3.

2. *Lydenburg* lies at 30°27′ E, 25°06′ S, at an altitude of 4,500 feet above sea-level, about 40 miles north-west of and about 1,200 feet higher than Nelspruit. Bilharzia has not been found, in spite of the presence of both snail hosts, *Biomphalaria sp.* and *Bulinus* (*Physopsis*) *sp.*, in small numbers. The nearest endemic area to Lydenburg was about 10 - 15 miles to the north-west and north-east (Official Records of the State Health Department) at an altitude of 3,000 - 3,500 feet above sea-level.

Heavy winter frosts occur annually, with freezing of small field waters. Snow falls occasionally. The monthly mean aquarium temperatures are shown in Fig. 2. The lowest temperature recorded in the aquaria was −6·5°C and the highest 27°C over a 2-year period. Field temperatures were not recorded.

3. *Norval's Pont* lies on the Orange River (25°28′ E, 30°38′S) about a mile downstream from the large Hendrik Verwoerd Conservation Dam presently under construction, at an altitude of 3,910 feet. The dam is one of several to be built for irrigation lower down the river, and, in addition, various irrigable areas in the Eastern Cape Province which to date have no connection with the Orange River will be supplied with water by a 50-mile-long syphon from the dam. The dam will almost certainly be used for recreational purposes.

The nearest endemic area of *S. haematobium* and *S. mattheei* lies about 250 miles east and south-east in the Transkei, where, in addition, *Biomphalaria sp.* was found without *S. mansoni.*[3] *S. mansoni* has been found about 400 miles away in Natal east of the Drakensberg. Neither snail species has been reported nearer than the above-mentioned sites but *Bulinus (Physopsis) sp.* was found in the Southern Transvaal and Northern Orange Free State tributaries of the Vaal River (Official Records of the State Health Department). This river flows into the Orange River 150 miles west of, and below, Norval's Pont. *B. tropicus* was commoner in the areas surrounding Norval's Pont.

Heavy frosts occur annually until early October, with snow during winter. Mean monthly aquarium temperatures are shown in Fig. 3. The lowest temperature recorded in the aquaria was −5·0°C and the highest 41·0°C. Continuous water temperatures were recorded in the Orange River just below the dam site (Fig. 4).

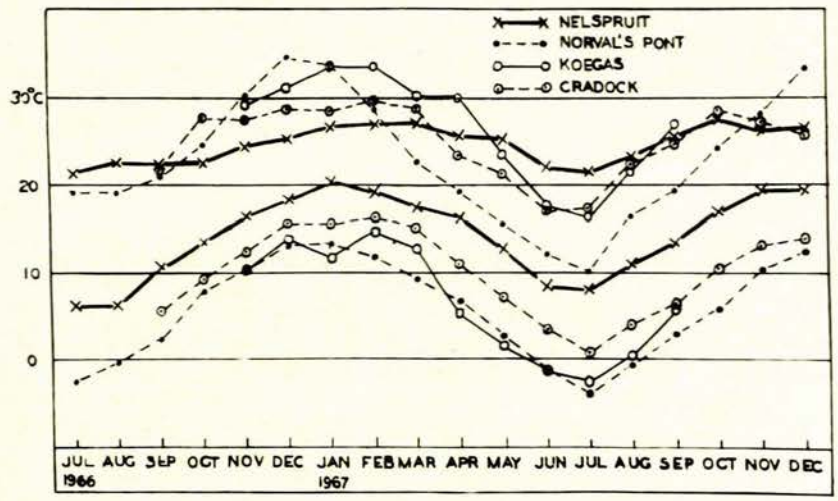

Fig. 3. Mean monthly maximum and minimum aquarium temperatures. Nelspruit, Norval's Pont, Koegas and Cradock.

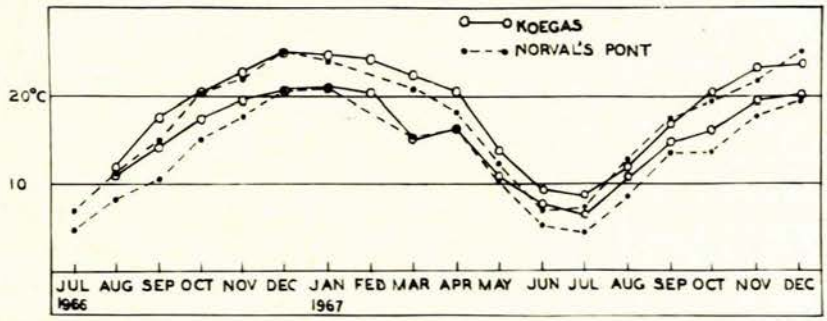

Fig. 4. Mean monthly maximum and minimum temperatures of the Orange River water at Norval's Pont and Koegas.

The height of the dam will be 280 feet and sluice gates open from the bottom of the wall. This might be of some future importance by causing a reduction in water temperatures of the Orange River below after storage in the dam. For all practical purposes the Orange River at the dam site receives all its water from the mountains of Lesotho which are regularly covered with snow during winter. Floods occur during summer and the river is turbid for most of the year, with a heavy deposit of silt and mud. Except for a few individual schemes no large-scale irrigation is practised within a radius of 60 miles from Norval's Pont. Chemical analysis of Orange River water is shown in Table I.

4. *Cradock* lies about 100 miles almost due south of Norval's Pont in the eastern Karoo at an altitude of 2,855 feet (25°38′ E, 32°10′ S). The Great Fish River flows southwards through the town and empties into the Indian Ocean about 150 miles further on. The Brak River, a tributary of the Fish River, was dammed several decades ago about 30 miles north of Cradock to supply irrigation water along the Fish River. In spite of this the winter flow of the Fish River is very poor or non-existent. With the advent of the syphon from the Hendrik Verwoerd Dam the Fish River will flow permanently and much more land will be placed under irrigation, both above and below Cradock (Fig. 1). Chemical analysis of the Fish River at Cradock is shown in Table I.

None of the 3 species of schistosomes has ever been reported from the Fish River Valley nor have host snails been found (Official Records, State Health Department).

Hard frosts occur during the winter, and occasionally snow falls on the hills in the vicinity. Mean monthly aquarium temperatures are shown in Fig. 3. The highest temperature recorded in the aquaria was 36·0°C and the

TABLE I. CHEMICAL ANALYSIS OF ORANGE RIVER AND FISH RIVER WATERS, MAY 1966

Source	*Turbidity*	*Conductivity*	*pH*	*Alkalinity*	*Ca*	*Mg*	NH_3	NH_2	*Cl*	SO_4	*Na*	*Fl*
Orange River	174	195	8·5	102	63	37	0·01	0·1	3·25	3·4	8	0·3
Fish River	21	3,200	8·3	440	210	390	0·14	0·26	650	380	647	0·95

lowest −3·0°C. Field temperatures were not recorded, because during the winter there was no easily accessible field water which might have been representative of natural waters surrounding Cradock. Cradock was chosen because of the future irrigation extension in its immediate vicinity, and because it was thought that it would be reasonably representative of the whole of the Fish River Valley.

5. *Koegas* (22°22′ E, 29°18′ S, altitude 2,800 feet above sea-level) lies on the Orange River some 300 miles downstream from Norval's Pont and about 200 miles to the north-west as the crow flies. The summers are hot, with a little rain, and the winters are mild with occasional frosts. It was only possible to record weekly maximum and minimum aquarium temperatures (Fig. 3). Some irrigation is practised at Prieska, about 40 miles south-east of Koegas. Future plans include extensive expansion of irrigation over large tracts of country along the Orange River once the dams have been completed.

Several cases of *S. haematobium* have been reported in Whites from Prieska. These patients have, however, all given a history of having spent holidays or lived in endemic areas of Natal or the Transvaal. Recent examinations of local Bantu schoolchildren were all negative (State Health Department, Official Records). The snail hosts have not been reported and much of the field water in the neighbourhood is brackish.

Field temperatures of Orange River water at Koegas are shown in Fig. 4. Flood water at Norval's Pont arrives between 2 days and 2 weeks later at Koegas, depending on the state of the river. It is likely that the reduction of the Orange River water temperature below the dam at Norval's Pont will also be evident at Koegas.

SOME CLIMATIC AND TOPOGRAPHIC FACTORS OF IMPORTANCE IN RELATION TO BILHARZIA AT THE ABOVE FIVE SITUATIONS

Temperature

Although the trend of aquarium temperatures at Nelspruit and Lydenburg was the same (Fig. 2), Lydenburg was considerably cooler in both summer and winter, regularly showing recordings below freezing-point during winter.

The trend of aquarium temperatures at Norval's Pont, Koegas and Cradock was the same, but they all differed from Nelspruit and Lydenburg in a greater range between day and night and between summer and winter (Fig. 3).

The temperatures of the Orange River at Norval's Pont and Koegas were very similar (Fig. 4) although it is

TABLE II. *Biomphalaria sp.* EXPOSED TO *S. mansoni* AT NELSPRUIT

Month exposed	*Number snails exposed*		*Snails surviving to shedding*			*Shedding snails*			
			Number		*%*	*Number*		*% of exposed*	*% of survivors*
Autumn									
March	324		120			51			
April	389	983	177	454	46	55	164	16	36
May	270		157			58			
Winter									
June	360		267			115			
July	210	780	129	538	69	48	223	28	41
August	210		142			60			
Spring									
September	259		209			120			
October	339	598	186	395	66	106	226	37	57
Summer									
November	315		30			9			
December	270	585	80	110	18	38	47	8	42
January	356	741	159	282	38	88	150	20	53
February	385		123			62			

TABLE III. LENGTH OF INCUBATION PERIODS OF *S. mansoni*, *S. haematobium* AND *S. mattheei* DURING EACH MONTH AT NELSPRUIT

	S. mansoni			*S. haematobium*			*S. mattheei*		
Month	*Length of incubation period (days)*	*Mean*	*No. groups*	*Length of incubation period (days)*	*Mean*	*No. groups*	*Length of incubation period (days)*	*Mean*	*No. groups*
Jan.	30– 41	34	12	37– 49	43	6	34– 42	38	10
Feb.	31– 53	42	9	40– 61	50	9	34– 56	42	10
Mar.	32– 53	45	7	49– 64	58	5*	35– 71	55	12
				146–210	184	3			
Apr.	60– 76	70	3*	106–188	155	10	71–154	105	9
	91–175	132	11						
May	98–143	118	7	118–172	147	8	111–147	126	8
June	78–124	108	11	109–142	130	6	86–111	97	8
July	70– 90	80	6	79– 95	86	5	71– 90	82	4
Aug.	56– 89	68	7	74– 81	78	4	60– 81	73	7
Sept.	45– 63	55	9	63– 76	69	7	49– 70	58	6
Oct.	37– 55	45	10	49– 73	58	12	45– 56	51	10
Nov.	39– 46	43	3	42– 57	50	10	41– 67	48	15
Dec.	35– 42	38	4	41– 49	44	9	34– 49	39	10

* Early April or early March exposures.

known that Koegas summer air temperatures rise earlier and fall later.

Chemical Constitution of Water

There is an obvious difference between the chemical composition of the Orange and Fish Rivers which may have some effect on snail life over a long period.

RESULTS

Nelspruit

1. *Biomphalaria sp.* exposed to *S. mansoni.* The cumulative total of snails exposed to miracidia each month from early 1961 until the beginning of 1967 shows that the survival to shedding and the shedding rates of exposed snails increased from the first half of summer (November, December) to spring (Table II).

Incubation periods (time from exposure to shedding) varied with the seasons and was longest in those snails exposed in autumn (April). Thereafter they gradually shortened to spring (August/September) (Table III).

The duration of the incubation periods (Table IV) did not affect: (*a*) the survival to shedding rate, with the possible exception of incubation periods longer than 147 days; (*b*) the shedding rates, with the possible exception of groups with incubation periods longer than 112 days; or (*c*) the longevity of shedding snails.

The longevity of shedding snails was prolonged in those snails which started to shed during the coldest months, irrespective of the length of the incubation period (Table V).

The cumulative total of snails, corrected to 300 exposed per month (Table VI), shows that (*a*) there was a marked increase of total shedding snails during September and October; (*b*) peak shedding occurred during October, November and December; and (*c*) there was a fall in shedding snail numbers in January. These findings are explained, firstly, by the gradual shortening of the incubation periods from April until August, resulting in more or less simultaneous shedding in September/October; secondly, by the rapid shortening of the incubation periods from September to February/March, combined with high shedding rates and long life of snails exposed between June and September (Table V), resulting in peak shedding in October - December; and thirdly, by the high pre-shedding mortality of groups exposed during November and December, resulting in a decrease in shedding snail numbers in January.

The above pattern corresponds almost exactly with the field pattern of *S. mansoni* transmission to immersed rodents in this part of the Transvaal. It does not, however, explain an occasional increase in field transmission shortly after the January fall.[2] But, assuming that the majority of field transmission to snails results from eggs being washed into the water by rain, then field exposure of snails during the dry season (June, July and August) will be minimal. By deducting all shedding snails which were exposed during these months (Table VI) only one change in the general pattern occurred; shedding snail numbers decreased in January with a relative increase during February, March and April corresponding with

TABLE IV. SURVIVAL AND SHEDDING RATES AND LONGEVITY OF *Biomphalaria sp.* EXPOSED TO *S. mansoni* AT NELSPRUIT IN RELATION TO INCUBATION PERIOD

Incubation period (days)	*Month exposed*	*No. exposed*	*Alive at shedding*		*Shedding snails*		*Length of survival of 50% of shedding snails (weeks)*
			Number	*%*	*Number*	*%*	
30– 35	Dec. Jan. Feb. Mar.	316	236	74	119	37	5– 6
36– 42	Oct. Nov. Dec. Jan. Feb. Mar.	367	207	56	117	31	2– 3
43– 49	Sep. Oct. Nov. Feb. Mar.	286	156	54	93	32	6– 7
Total 30– 49	Sep. Oct. Nov. Dec. Jan.	655	393	60	222	34	1– 2
	Feb. Mar.	314	205	65	107	34	9–10
50– 77	Feb. Mar. Apr.	209	79	37	11	5	13–14
50– 63	Aug. Sep. Oct.	409	291	71	145	35	4– 5
64– 77	Jul. Aug.	180	118	65	49	27	4– 5
78–112	Apr. May. Jun. Jul. Aug.	450	344	76	146	32	10–11
113–126	Apr. May. Jun.	300	200	67	71	24	7– 8
127–147	Apr. May.	120	76	63	20	17	7– 8
148–175	Apr.	120	34	28	9	7	0– 1

TABLE V. LONGEVITY OF SHEDDING SNAILS IN RELATION TO TIME OF YEAR WHEN SHEDDING STARTED

Month shedding commenced	*S. mansoni*		*S. haematobium*		*S. mattheei*	
	No. shedding	*Time in weeks when 50% still alive and shedding after shedding commenced*	*No. shedding*	*Time in weeks when 50% still alive and shedding after shedding commenced*	*No. shedding*	*Time in weeks when 50% still alive and shedding after shedding commenced*
April/May/June	56	10–11	111	7– 8*	246	11–12
July/Aug./Sept.	170	9–10	116	10–11†	260	8– 9
October	198	6– 7	92	4– 5	281	6– 7
November	98	5– 6	121	7– 8	114	6– 7
December	54	<1– 1	167	6– 7	207	4– 5
January	52	4– 5	124	4– 5	170	5– 6
Feb./March	152	3– 4	100	6– 7	233	6– 7

* April/May only. No group started shedding in June.

† Only one group started to shed in each of July and August.

field findings. These, therefore, are probably the result of January and early February exposures, with high shedding rates, short incubation periods and short shedding lives (Table IV).

2. *Bulinus (Physopsis) sp.* exposed to *S. mattheei*. The cumulative total of snails exposed each month from early 1961 until the beginning of 1967 shows that the survival and shedding rates were high throughout the year (Table VII).

The duration of the incubation periods of this parasite showed the same trend as *S. mansoni*, but were never longer than 154 days for winter exposures. Survival and shedding rates in relation to the incubation periods (Table VIII) were consistently high, with the exception of groups with incubation periods longer than 112 days (some April/May exposures).

As with *S. mansoni*, the longevity of the shedding snails was prolonged when shedding commenced during

TABLE VI. MONTHLY CUMULATIVE TOTAL OF SHEDDING *Biomphalaria sp.* EXPOSED TO *S. mansoni* AT NELSPRUIT (CORRECTED TO 300 EXPOSED PER MONTH)

Month exposed	*Actual number exposed*	*Number of snails shedding cercariae each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	356		43	43	7								
February	385			21	43	26	24	22	22	20	16	8	
March	324				24	44	42	28	20	21	6	2	
April	389						2	17	33	39	20	11	2
May	270	1							7	50	57	40	18
June	360	17	7	4						40	91	82	50
July	210	30	11	7						6	67	60	54
August	210	10	4	3	3						81	76	30
September	259	10	1								37	136	90
October	339	30	18	10	7	2						22	63
November	315	3	2	1									6
December	270	31	36	17	4								
Total	3,687	132	122	106	88	72	68	67	82	176	375	437	313
Deducted for exposure during dry months Jun., Jul. and Aug.:		57	22	14	3	0	0	0	0	46	239	218	134
Total after deduction		75	100	92	85	72	68	67	82	130	136	219	179

TABLE VII. *B. (Physopsis) sp.* EXPOSED TO *S. mattheei* AT NELSPRUIT

Month exposed	*Number snails exposed*		*Snails surviving to shedding*			*Shedding snails*			
			Number		*%*	*Number*		*% of exposed*	*% of survivors*
Autumn									
March	384		320			189			
April	285	909	181	631	69	120	396	43	62
May	240		130			87			
Winter									
June	241		203			126			
July	180	618	130	497	80	87	328	52	66
August	197		164			115			
Spring									
September	172	503	147	394	78	93	263	52	66
October	331		247			170			
Summer									
November	410		335			223			
December	290	1,232	210	974	79	141	610	49	62
January	254		202			120			
February	278		227			126			

TABLE VIII. SURVIVAL AND SHEDDING RATES AND LONGEVITY OF *B. (Physopsis) sp.* EXPOSED TO *S. mattheei* AT NELSPRUIT IN RELATION TO INCUBATION PERIODS

Incubation period (days)	*Month exposed*	*No. exposed*	*Alive at shedding*		*Shedding snails*		*Length of survival of 50% of shedding snails (weeks)*
			Number	*%*	*Number*	*% of exp.*	
30– 35	Dec. Jan. Feb. Mar.	234	179	76	124	53	4– 5
36– 42	Nov. Dec.	290	251	86	158	54	3– 4
36– 42	Jan. Feb.	290	230	79	138	47	6– 7
43– 77	Feb. Mar.	442	383	86	210	47	12–13
43– 63	Aug. Sep. Oct. Nov. Dec.	764	587	76	404	52	4– 5
64– 84	Jul. Aug.	197	168	85	99	50	3– 4
85–112	Apr. May. Jun. Jul.	556	445	80	297	53	6– 7
113–154	Apr. May	240	129	53	81	33	4– 5

the winter and reduced when shedding commenced during the summer (Table V).

The cumulative total of snails corrected to 300 exposed per month shows that the number of shedding snails increased during September, reached a peak during October, November and December, and fell gradually, in contrast to *S. mansoni*, to the lowest numbers during mid-winter. There were considerable numbers of snails shedding throughout the year (Table IX).

In areas with numerous cattle, immersion of rodents showed continuous transmission with a marked increase during the summer, from about September. In areas with few cattle, transmission was unpredictable at any time of the year.[2] The majority of *S. mattheei* miracidia probably reach field snails from faeces deposited directly into water by stock while drinking. Transmission to snails would therefore continue throughout the year and transmission from snails would be increased by the short summer incubation periods of the schistosome in the snail.

3. *Bulinus (Physopsis) sp.* exposed to *S. haematobium*. The cumulative total of snails exposed each month from the end of 1961 until the end of 1966 shows that the survival rate was high with the exception of snails exposed during July and August. Shedding rates of exposed and surviving snails were highest in spring exposures and decreased in winter-exposed snails (Table X).

Incubation periods were consistently longer than those of *S. mansoni* and *S. mattheei*. Survival and shedding rates and the longevity of shedding snails bore little relation to the length of the incubation periods (Table XI). Survival rates were consistently high (77% - 96%); shedding rates varied but were in general higher from summer exposures (short incubation periods).

The tables are not a true reflection of the picture; large numbers of snails stopped shedding during June, July and August; some recommenced shedding during September/October, while others died at various times before this (Tables V and XI). Whether the dead were still infected was not ascertained, and the figures are based on shedding snails only. Longevity was prolonged in snails which started shedding in July, August and September, but the apparent short life of snails which started to shed in April and May was undoubtedly due to temporary cessation of shedding of many snails.

The cumulative total of snails corrected to 300 exposed each month shows that shedding snail numbers increased in September/October and peak transmission occurred from November to February/March; the numbers then

TABLE IX. CUMULATIVE TOTAL OF SHEDDING *B. (Physopsis) sp.* EXPOSED TO *S. mattheei* AT NELSPRUIT (CORRECTED TO 300 EXPOSED PER MONTH)

Month exposed	*Actual number exposed*	*Number of snails shedding cercariae each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	254		54	138	78	43	35	26	10	5	0		
February	278	0		56	134	92	64	44	30	22	10	2	1
March	384	1	0		49	100	133	108	77	60	35	11	5
April	285	0						31	117	118	51	30	5
May	240	2	0						15	69	91	65	7
June	241	21	6	0						88	139	111	46
July	180	13	0								93	137	65
August	197	12	0								137	162	47
September	172	73	2	2	0						36	125	144
October	331	104	40	13	7	5	1	1	0			27	142
November	410	156	70	44	14	7	3	1	0				70
December	290	78	140	92	23	3	0						
Total	3,262	460	312	345	305	250	236	211	249	362	592	670	532

TABLE X. *B. (Physopsis) sp.* EXPOSED TO *S. haematobium* AT NELSPRUIT

Month exposed	*Number snails exposed*		*Snails surviving to shedding*			*Shedding snails*			
			Number		*%*	*Number*		*% of exposed*	*% of surviving*
Autumn									
March	240		197			80			
April	415	1,021	323	751	73	67	230	22	30
May	366		231			83			
Winter									
June	186		130			32			
July	150	523	80	304	58	19	76	14	25
August	187		94			25			
Spring									
September	197		161			72			
October	358	555	286	447	80	161	233	41	52
Summer									
November	323		282			131			
December	253	1,022	204	852	83	92	323	31	37
January	142		117			39			
February	304		249			61			
Total		3,121		2,354	75		862	27	36

fell gradually, as with *S. mattheei*, until June, when the fall became rapid. Delay of peak shedding is accounted for by the long incubation period (Table XII).

Unfortunately no field transmission picture for *S. haematobium* was obtained by rodent immersion,[1,2] but with the good correlation of the laboratory (outdoor) and field pictures of *S. mansoni* and *S. mattheei* there seems sufficient reason to assume that the field picture of *S. haematobium* should be similar to that portrayed by the above findings. These suggest that *S. haematobium* transmission in the field in the Eastern Transvaal would start in October and reach a peak from November to February, with no or negligible transmission during the winter months. However, transmission from man mainly results from swimming and few snails would therefore be exposed from April to August when the water is too cold. By deducting all snails exposed during these 5 months, field transmission from snails would increase during

TABLE XI. SURVIVAL AND SHEDDING RATES AND LONGEVITY OF *B. (Physopsis) sp.* EXPOSED TO *S. haematobium* AT NELSPRUIT IN RELATION TO INCUBATION PERIOD

Incubation period	*Month exposed*	*No. exposed*	*Alive at shedding*		*Shedding snails*		*Length of survival of 50% of shedding snails (weeks)*
			Number	*%*	*Number*	*% of exp.*	
36– 42	Dec. Jan. Feb. Mar.	190	163	85	98	51	5–6
43– 49	Nov. Dec.	296	234	79	118	39	5–6
43– 49	Jan. Feb. Mar.	252	215	85	55	21	5–6
50– 56	Oct. Nov.	270	222	82	114	41	6–7
50– 56	Feb. Mar.	124	111	89	32	25	7–8
57– 63	Sep. Oct. Nov.	207	182	87	83	40	6–7
57– 63	Feb. Mar.	90	87	96	35	38	7–8
64– 77	Jul. Aug. Sep. Oct.	301	240	79	86	28	5–6
78– 91	Jul. Aug.	127	101	79	22	17	6–7
92–105	No observations						
106–142	Apr. May. June	356	303	85	113	31	7–8
143–210	Mar. Apr. May	381	294	77	75	19	6–7

TABLE XII. MONTHLY CUMULATIVE TOTAL OF SHEDDING *B. (Physopsis) sp.* EXPOSED TO *S. haematobium* AT NELSPRUIT (CORRECTED TO 300 EXPOSED PER MONTH)

Month	*Actual number exposed*	*Number of snails shedding per month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	142		48	82	52	25	12	0	0	2	2	4	
February	304			10	59	43	18	1	1	2	6	4	2
March	240				10	70	71	37	47	46	34	16	9
April	415	1						2	14	30	28	12	7
May	366	14	1							22	68	62	37
June	186	11	2								25	50	23
July	150										36	38	16
August	187	9	1								11	39	16
September	197	78	15									47	107
October	358	97	41	31	18	11	0	0	2	2	1	26	119
November	323	118	84	33	8	2	1						12
December	253	41	104	78	27	3	1	0	0	0	1	1	
Total	3,121	369	296	234	174	154	103	40	64	104	212	299	348
Deducted during non-swimming months (Apr.–Aug.):	*for exposures*	35	4	0	0	0	0	2	14	52	168	201	99
Total after deduction		334	292	234	174	154	103	38	50	52	44	98	249

TABLE XIII. NUMBER OF *Biomphalaria sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mansoni* EACH MONTH AT LYDENBURG

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	60		17	0									
February	120			76	4/43	4/37	1/34	0		25 Number surviving not shedding			
March	150				110	81	38	0		6/12 Number shedding/number surviving			
April	120					95	41	0					
May	55						53	0					
June	60							0					
July	30								0				
August	0								0				
September	90	3/29	3/26	1/22	18	16	14	0			80	67	54
October	60	12/43	17/42	12/35	7/31	1/25	15	0				57	56
November	90	5	2/4	1	0								68
December	90	23	17	12	10	6	0						

August/September from snails which recommenced shedding after winter, to be followed by a drop in October as a result of these snails dying. Transmission would again increase in November and reach its maximum from December to March, and then fall gradually until June (Table XII).

An additional factor contributing to decreased winter and increased spring transmission in the field of both *S. mansoni* and *S. haematobium* and possibly *S. mattheei* is that the numbers of cercariae shed decrease during winter and increase during the following spring.

Lydenburg

Batches of the appropriate Nelspruit snails were exposed at regular intervals from mid-1963 until mid-1965 at Lydenburg to the Nelspruit schistosome strains. These then developed under outdoor Lydenburg conditions.

Water in the aquaria froze regularly at night in June, July and August, and occasionally during April and May (Fig. 2), resulting in total snail mortality with successive sub-zero temperatures.

Incubation periods of the schistosomes which matured to cercariae varied from 59 to 119 days for *S. mansoni*, from 54 to 119 days for *S. mattheei* for September to February exposures, and from 75 to 127 days for *S. haematobium* for September to December (and probably January) exposures. Complete development to cercariae did not occur in snails exposed during the remainder of the year. None of the 3 schistosome species shed cercariae before January and all shedding ceased during May or June.

1. *Biomphalaria sp.* exposed to *S. mansoni*. There was heavy snail mortality not only during November and December, as in Nelspruit, but also in January. In addition all snails died during the winter due to cold (Tables XIII and XXV).

The shedding of cercariae was generally poor: it started in January with peak shedding in February comparable with Nelspruit autumn. There was no chance of increased shedding after February because the earlier onset of cold weather prolonged the incubation period until such time as the snails died from cold. Under these circumstances it seems unlikely that *S. mansoni* could become established at Lydenburg.

2. *B. (Physopsis) sp.* exposed to *S. haematobium*. Shedding rates of *S. haematobium* were comparatively high from snails exposed from September to December and were comparable with Nelspruit spring (September/October) shedding (Tables XIV and XXV). High shedding rates were however restricted to February, March and April, with peak shedding during March. Because of the longer incubation period it is doubtful whether peak shedding could occur at any other time of the year, but March is somewhat late for human exposure. Transmission to man, if it occurred at all—assuming an even field distribution and optimum chances of exposure of snails from October to January—would probably take place only in February, resulting in light worm loads and low infection rates.

3. *B. (Physopsis) sp.* exposed to *S. mattheei*. Shedding of *S. mattheei* cercariae from snails exposed from October to February was good, and occurred from February to May with the peak in March/April (Tables XV and XXV). Shedding was comparable with Nelspruit shedding from January to June. Because the habits of stock give a greater chance of snail exposure to *S. mattheei* for a longer period than *S. haematobium*, and because of the shorter incubation period of *S. mattheei*, this parasite might become established at Lydenburg, if an increase of the stock population occurred without proper watering facilities. The few cattle (about 20) examined by us at abattoirs at Lydenburg were negative.

Norval's Pont

Snails at this and the following 2 stations were always exposed at Norval's Pont and placed into the field aquaria on the same day at Norval's Pont and either the following day or two days later at Cradock and Koegas. Nelspruit schistosomes and snails were used. When difficulty was experienced with snail breeding it was necessary to supplement directly from Nelspruit. With these exceptions the work routine was the same.

1. *Biomphalaria sp.* exposed to *S. mansoni*. Snail mortality was high throughout the year, except from March to May (autumn) (Tables XVI and XXV). There was total snail mortality during June and July due to the recurrent sub-zero night temperatures. High summer temperatures might have accounted for the high summer mortality. Snails in the outside aquaria did not breed well except during the hottest months (December and January).

Shedding started in November from September exposures and was maintained at a low level (comparable to winter shedding at Nelspruit) until March/April when

TABLE XIV. NUMBER OF *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. haematobium* EACH MONTH AT LYDENBURG

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	0												
February	78			77	72	67	14	0	25 Number surviving not shedding				
March	120				117	99	55	0	6/12 Number shedding/number surviving				
April	136					88	64	0					
May	45						37	0					
June	30							0					
July	30								0				
August	30									0			
September	50	20	5/19	6/18	3/16	15	0				44	39	28
October	75	53	14/52	14/47	14/47	5/30	20	3				75	56
November	120	3/104	19/102	15/94	6/77	50	10	0	0				118
December	30	29	1/25	4/24	4/12	1/12	12	0					

there was a marked increase in shedding snails comparable to Nelspruit spring.

If snails could maintain themselves in the field at Norval's Pont, with the high summer and low winter temperatures of small waters, *S. mansoni* transmission might occur during March and April as a result of young snails being exposed during December, January and February. However, temperatures begin to fall during March and April and human contact would decrease.

2. *B. (Physopsis) sp.* exposed to *S. haematobium* and to *S. mattheei*. There was total mortality of these snails during June, July and August as a result of repeated night temperatures below zero (Tables XVII, XVIII and XXV). For the remainder of the year (except February - April) mortality was high possibly due to excess heat.

The peak snail-breeding period under outside conditions was a little later than that of *Biomphalaria sp.* but also occurred during December and January, with very little breeding during the remainder of the year.

Shedding of *S. haematobium* was very poor throughout the year and from the results obtained it is doubtful whether the parasite could become established.

Shedding of *S. mattheei* cercariae started during November from September-exposed snails and reached a peak in December/January, more or less comparable to Nelspruit mid-winter. As at Lydenburg, a little *S. mattheei* transmission during mid-summer might occur provided that the snails could establish themselves in the field

TABLE XV. NUMBER OF *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mattheei* EACH MONTH AT LYDENBURG

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	60		59	30/54	33/46	22/34	14/29	0					
February	120			4/115	22/109	27/84	17/29	0	25 Number surviving not shedding				
March	150				134	111	73	0	6/12 Number shedding/number surviving				
April	120					52	34	0					
May	60						57	0					
June	60							0					
July	20								2	0			
August	30									0			
September	50	1/1	1/1								41	16	7
October	90	12/67	26/64	23/55	13/41	2/33	4	0				83	73
November	120	8/95	29/83	17/65	7/49	1/30	6	0					120
December	90	78	31/69	39/66	23/44	11/22	5/8	0					

TABLE XVI. NUMBER OF *Biomphalaria sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mansoni* EACH MONTH AT NORVAL'S PONT

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	30		2/17	9/12	7/9	1	0						
February	60			22/57	23/47	10/31	16	0	25 Number alive not shedding				
March	60				60	27	0		6/12 Number shedding/number surviving				
April	30					22	10	0					
May	40						26	0					
June	85							0					
July	60								0				
August	100	0								55	43	28	7
September	100	1/5	0								88	14/49	15/31
October	150	3/5	0									98	3/43
November	60	0											5
December	60	3/39	5/11	5/11	5/11	7	3	0					

TABLE XVII. NUMBER OF *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. haematobium* AT NORVAL'S PONT

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	0		0										
February	59			2/54	2/44	32	16	0	25 Number alive not shedding				
March	24				24	14	13	0	6/12 Number shedding/number surviving				
April	20					14	2	0					
May	40						25	0					
June	58							0					
July	60								0				
August	100									0			
September	102	1/2	0								79	44	3/35
October	123	1	0									100	6/46
November	50	0											49
December	15	9	7	4	2	0							

under the temperature conditions likely to exist in small waters.

Cradock

All the snails studied at this station were obviously very unhappy a week or two after being placed in the aquaria. Total snail mortality of both species occurred only during July with repeated night temperatures below zero. Maximum breeding in the outside aquaria occurred during January and February.

Shedding of *S. mansoni* (Table XIX) started in January, with peak shedding during March/April as at Norval's Pont. It was comparable to Nelspruit from January to May.

Shedding of the two schistosomes with terminal-spined eggs (Table XX, XXI and XXV) was very poor. No shedding occurred before January.

Under present conditions—unhealthy snails, poor schistosome development and Fish River water—it is thought that none of the schistosomes would be likely to develop in the Fish River Valley. The arrival, in the future, of the Orange River water in the valley might well change conditions.

Koegas

Aquarium temperatures at Koegas were higher for a longer period than those at Norval's Pont and Cradock.

1. *Biomphalaria sp.* exposed to *S. mansoni.* Mortality

TABLE XVIII. NUMBER OF *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mattheei* AT NORVAL'S PONT

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	0		0										
February	39			3/37	8/34	15	4	0	25 Number alive not shedding				
March	24				24	10	6	0	6/12 Number shedding/number surviving				
April	20					14	3	0					
May	40						25	0					
June	85							0					
July	60								0				
August	100									0			
September	52		0								38	1/15	3/10
October	60	11/21	2/5	1/3								49	27/35
November	60	8/20	5/8	5/8	2	0							10/60
December	58	2/30	6/14	5	0								

TABLE XIX. NUMBER OF *Biomphalaria sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mansoni* EACH MONTH AT CRADOCK

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	30		1/12	3/12	3/11	0							
February	60			17/59	19/34	15/19	4	2	0	25 Number alive not shedding			
March	60				50	13	0			6/12 Number shedding/number			
April	30					27	20	4	0				surviving
May	40						13	0					
June	30							13	0				
July	30								0				
August	120									64	38	2	0
September	100	1/5	0								91	27	3
October	150	3/5	0									81	18
November	60	0											13
December	60	12	7/11	6/8	3/4	1/2	0						

TABLE XX. NUMBER OF *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. haematobium* AT CRADOCK

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	0												
February	39			31	14	1/12	6	0	25 Number alive not shedding				
March	24				23	22	20	0	6/12 Number shedding/number surviving				
April	20					16	16	0					
May	35						25	0					
June	15							0	0				
July	30									52	24	3	0
August	120										68	5	0
September	102											86	53
October	134	3	3	0									25
November	50	5	3	0									
December	15	3	3	2	0								

of snails from cold was complete during July only (but it is probable that freezing would not be an annual occurrence); mortality was high throughout the rest of the year possibly due to heat (Tables XXII and XXV).

Shedding started during October and reached a peak in February comparable to the September shedding at Nelspruit. It was however short-lived, and in March fell to mid-winter Nelspruit shedding. Probably because of the higher temperatures at Koegas (compared with Norval's Pont) shedding continued for 8 months of the year and *S. mansoni* might become established, with a little transmission during late summer, provided the snails are able to maintain themselves with the high summer field temperatures.

2. *B. (Physopsis) sp.* exposed to *S. haematobium* and *S. mattheei*. As with *Biomphalaria sp.*, and probably for the same reasons, there was high mortality of *B. (Physopsis) sp.* throughout the year with total mortality during July (Tables XXIII - XXV).

Shedding of *S. haematobium* was poor when it occurred and was comparable to mid-winter Nelspruit shedding. In contrast the shedding of *S. mattheei,* though poor, continued for 7 months from November to May.

It is not thought that *S. haematobium* or *S. mattheei* would be able to become established under present field conditions at Koegas.

If, after the completion of the dams, the temperature of the Orange River water at Koegas falls appreciably,

TABLE XXI. NUMBER OF *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mattheei* AT CRADOCK

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	0												
February	34			35	2/31	8/17	6	0	25 Number alive not shedding				
March	24				24	0			6/12 Number shedding/number surviving				
April	20					18	14	0					
May	35						29	6					
June	30							13	0				
July	30								0				
August	120									37	11	0	
September	102	0									58	14	6
October	85	0										49	19
November	60	3/8	2	0									41
December	58	10	6	4	0								

TABLE XXII. NUMBER OF *Biomphalaria sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mansoni* EACH MONTH AT KOEGAS

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	30		14/20	6/12	0								
February	60			7/52	17/42	9/18	8	0	25 Number alive not shedding				
March	60				56	25	19	0	6/12 Number shedding/number surviving				
April	30					21	12	0					
May	40						40	5	0				
June	15							13	0				
July	30								0				
August	120									101	2/36	1/5	0
September	60	0									60	49	4
October	120	0										115	1/23
November	60	0											19
December	60	5/53	6/11	0									

TABLE XXIII. NUMBER *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. haematobium* AT KOEGAS

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	0												
February	39			36	22	6/8	3	0	25 Number alive not shedding				
March	24				24	11	5	0	6/12 Number shedding/number surviving				
April	20					16	10	0					
May	35						26	13	0				
June	30							0					
July	30								0				
August	120	8	0							76	39	19	15
September	102	5	0								88	49	32
October	122	28	0									112	74
November	50	6/48	5	0									50
December	15	11	0										

TABLE XXIV. NUMBER OF *B. (Physopsis) sp.* EXPOSED TO, SURVIVING AND SHEDDING *S. mattheei* AT KOEGAS

Month exposed	*Number exposed*	*Number shedding and surviving each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
January	0												
February	39			1/36	7/34	3/14	5	0		25 Number alive not shedding			
March	24				24	18	7	0		6/12 Number shedding/number surviving			
April	20					20	12	0					
May	35						29	7	0				
June	45							7	0				
July	30								0				
August	120	0								79	60	1/27	6/10
September	52	9	0								42	1/33	3/28
October	60	8/17	0									57	12/46
November	60	24/49	3	0									58
December	58	52	1	0									

TABLE XXV. CUMULATIVE TOTAL OF SNAILS SHEDDING EACH MONTH AT THE VARIOUS SITES CORRECTED TO 300 EXPOSED PER MONTH

Schistosome species	*Site*	*Number of snails shedding cercariae each month*											
		Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
S. mansoni	Nelspruit	132	122	106	88	72	68	67	82	176	375	437	313
	Lydenburg	70	101	63	45	15	2	X	X	X?	0	0	0
	Norval's Pont	24	45	235	210	50	X	X	0	0	0	42	51
	Cradock	9	45	145	140	80	0	X	0	0	0	0	0
	Koegas	25	170	95	65	45	0	X	0	0	5	3	3
S. haemato-bium	Nelspruit	369	296	234	174	154	103	40	64	104	212	299	348
	Lydenburg	7	143	190	129	30	0	X	X	X	0	0	0
	Norval's Pont	3	0	10	10	0	X	X	X	0	0	0	24
	Cradock	0	0	0	0	7	0	X	0	0	0	0	0
	Koegas	48	0	0	0	46	0	X	0	0	0	0	0
S. mattheei	Nelspruit	460	312	345	305	250	236	211	249	362	592	670	532
	Lydenburg	66	268	409	357	223	129	X	X	X	0	0	0
	Norval's Pont	111	65	59	60	0	X	X	X	0	0	6	203
	Cradock	15	0	0	15	60	0	X	0	0	0	0	0
	Koegas	160	0	7	52	21	0	X	0	0	0	7	93

X = Total mortality of snails.

the field temperatures of irrigation dams and canals would possibly be more suitable to snails during summer but less so during winter.

SUMMARY AND CONCLUSIONS

Different groups of *Biomphalaria sp.* and *Bulinus (Physopsis) sp.* were exposed to *S. mansoni*, *S. haematobium* and *S. mattheei*, respectively, and observed under outdoor conditions in a highly endemic area (Nelspruit) for a 6-year period. The behaviour pattern of the snails and the developing schistosomes repeated itself each year and the summation of the findings reflected, with minor modifications, the field transmission picture of *S. mansoni* and *S. mattheei*.

No field picture had been obtained for *S. haematobium*. It was, however, assumed that the results of *B. (Physopsis) sp.* exposure and further development of this parasite under outdoor conditions would, in general, reflect the field transmission picture in the area surrounding Nelspruit.

Development of the 3 parasites in snails was studied under outdoor conditions in 4 non-endemic areas, of which only Lydenburg presently harbours both snail species. The other 3 places, Norval's Pont, Cradock and Koegas, although they do not harbour the intermediate hosts, were studied in anticipation of future irrigation schemes. Altitudes of the 5 places varied from 2,350 feet above sea-level at Nelspruit to 4,500 feet above sea-level at Lydenburg.

Aquarium temperatures at Nelspruit and Lydenburg varied in degree only—the general pattern being the same. The other 3 places all differed from Nelspruit, showing greater seasonal and daily variation.

With the exception of Nelspruit, all snails died during the winter as a result of night temperatures repeatedly below freezing. Snail mortality was high throughout the year at Norval's Pont, Cradock and Koegas, except in autumn.

It was concluded that: (*a*) at Lydenburg, *S. mattheei* might become established in stock under certain conditions, but the other two parasites would not; (*b*) at Norval's Pont, provided both snail species were able to maintain themselves in the unfavourable field conditions, *S. mansoni* and *S. mattheei* might become established; (*c*) at Cradock none of the 3 parasites would become established; and (*d*) at Koegas *S. mansoni* might become established but neither of the other two species, provided again that the snails were able to maintain themselves in the field.

Reduction of temperature of the Orange River water after completion of the dams might have some adverse effect on snails and their schistosome parasites during the winter, but an advantageous effect might result during the summer.

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