SUSCEPTIBILITY OF RODENTS TO INFECTION WITH *SCHISTOSOMA MANSONI* IN RICHARD-TOLL (SENEGAL)

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Summary :

The susceptibility of *Arvicanthis niloticus, Mastomys huberti, Mastomys erythroleucus and Mus musculus* was studied to assess the capacity of these rodents to transmit *Schistosoma mansoni*. The susceptibility was determined by the percentage of adult schistosomes recovered, the number of eggs per gramme of faeces, the viability of these eggs and the capacity of the rodents to maintain the life cycle of *Schistosoma mansoni*. The percentages of adult worms recovered were respectively 18 %, 11.5 %, 8.4 % and 20.5 % in *A. niloticus*, *M. huberti*, *M. erythroleucus* and *M. musculus*. After infection, they liberate in the environment viable eggs whose miracidia are infectious for the intermediate host *(Biomphalaria pfeifferi)*. The mean egg load was 300 ± 327.8 in *A. niloticus*; 664 ± 673.5 in *M. huberti*; 240 ± 304.8 in *M. erythroleucus* ; 400 ± 361.5 in *M. musculus*.

KEY WORDS : *Arvicanthis niloticus, Mastomys huberti, Mastomys erythroleucus, Mus musculus*, Richard-Toll, rodents, Senegal, *Schistosoma mansoni*.

Résumé : SUSCEPTIBILITÉ DES RONGEURS À L'INFESTATION PAR *SCHISTOSOMA MANSONI* À RICHARD-TOLL (SÉNÉGAL)

La susceptibilité de Arvicanthis niloticus, Mastomys huberti, Mastomys erythroleucus *et* Mus musculus *à l'infestation par* Schistosoma mansoni *a été étudiée pour évaluer la capacité des Rongeurs à jouer un rôle dans la transmission de la schistosomiase intestinale à Richard-Toll. La susceptibilité de ces rongeurs a été déterminée par le pourcentage de vers adultes récupérés après infestation, le nombre d'œufs par gramme de fèces, la viabilité de ces œufs et la capacité des rongeurs à maintenir le cycle de développement de* Schistosoma mansoni. *Les pourcentages d'adultes récupérés sont, respectivement, 18 %, 11,5 %, 8,4 % et 20,5 % chez* A. niloticus, M. huberti, M. erythroleucus *et* M. musculus. *Après infestation, les Rongeurs libèrent, dans le milieu extérieur, des œufs viables dont les miracidia sont infestants pour l'hôte intermédiaire* (Biomphalaria pfeifferi). *Le nombre moyen d'œufs libérés est de 300 ± 327,8 chez* A. niloticus, *664 ± 673,5 chez* M. huberti, *240 ± 304,8 chez* M. erythroleucus *et 400 ± 361,5 chez* M. musculus.

MOTS CLÉS : Arvicanthis niloticus, Mastomys huberti, Mastomys erythroleucus, Mus musculus, *Richard-Toll, Rongeurs, Sénégal,* Schistosoma mansoni.

INTRODUCTION

In Richard-Toll, North Senegal, the presence of *Schistosoma mansoni* among rodents was reported for the first time in 1990, two years after the emergence of a new focus of intestinal schistosomiasis. Duplantier *et al.* (1992) had shown that two species of Muridae, *Arvicanthis niloticus* and *Mastomys huberti*, were naturally infected.

The present work was undertaken to study the susceptibility of *A. niloticus* and *M. huberti* to infection with *S. mansoni*. Two other species of rodents *(Mastomys erythroleucus* and *Mus musculus)* were studied as controls. *M. erythroleucus* belongs to the same genus and has the same activity as *M. huberti*. *M. musculus* is commonly used in laboratory. In order to determine the degree of susceptibility of these rodents to *S. mansoni* infection, we have studied the percentage of adult worms recovered after perfusion, the fecundity of the female schistosome harbored, and the capacity of the hosts to maintain the life cycle of *S. mansoni*.

The susceptibility of *A. niloticus* to infection with *S. mansoni* had already been shown by Stirewalt *et al.* (1951), Kuntz & Malakatis (1955), Dumon & Quilici (1976), Karoum & Amin (1985) and Mbieuleu-Nkouedeu (1990).

Although the susceptibility of *Mastomys natalensis* to infection with *S. haematobium* was studied by Pitchford & Visser (1962) and Gear *et al.* (1966), the susceptibility of *M. huberti* and *M. erythroleucus* to infection with *S. mansoni* of African origin has never been studied before.

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MATERIALS AND METHODS

From each species of rodents, twenty adults, 10 males and 10 females, were experimentally infected. Some of the *A. niloticus* used for this study were trapped in the « Niayes », Dakar, where intestinal schistosomiasis has never been reported as far as we know. However, to be sure they did not harbor any *S. mansoni* infection, they were isolated for four weeks, and tested for infection. All the *M. huberti*, the *M. erythroleucus*, and the *M. musculus* (Swiss mice) were born and bred in the laboratory.

Using the paddling method, all rodents species were exposed to cercaria shed by *B. pfeifferi* from Richard-Toll for 15 min. The number of cercaria used was 600 for *A. niloticus, M. huberti* and *M. erythroleucus* and 150 for *M. musculus*. The infected rodents were kept at the animal house. Seven weeks later, they were perfused in accordance with the Duwall and Dewitt (1967) method and the schistosomes recovered counted to assess the percentage of adults worms. After perfusion, the liver, the mesenteric veins and the lungs were removed and examined under light microscope to see whether adult worms were trapped in.

The fecundity of *S. mansoni* was randomly studied among 10 individuals in *A. niloticus, M. huberti, M. musculus* and *M. erythroleucus* without sexual distinction. The number of eggs per gramme of faeces was counted by the modified Kato-Katz method (Stelma *et al.*, 1993) and their viability tested by hatching them. Weekly fecal examination was also carried out to establish the pre-patent period.

To study the capacity of rodents to maintain the life cycle of *S. mansoni* from Richard-Toll we just evaluate their ability to be infected, to develop adult parasite and then to pass, in the nature, viable eggs insuring the continuity of the cycle. The *S. mansoni* strains used to maintain the life cycle in *A. niloticus* and *M. huberti* were isolated respectively from these two species. Meanwhile, *M. erythroleucus* and *M. musculus* were infected with cercaria shed by naturally infected *B. pfeifferi*. All the rodents and the snails *(Biomphalaria pfeifferi)* used throughout the study of the life cycle were born in the laboratory. At each passage twenty snails were exposed individually to three or four miracidia overnight. Cercaria shed by the positive snails were used to infect different species of rodents. Eight weeks later, perfusion was performed to recover adult worms from rodents. The liver and the faeces were analysed in search of viable eggs. These last were used to infect other snails and so on. In order to find out whether the passage of the parasite strain from one rodent species to another could influence the infectivity of the miracidia, other species were cross-infected at each passage. For example, *M. huberti, M. erythroleucus* and *M. musculus* were exposed to cercaria of first and second generations, shed by *B. pfeifferi* infected with miracidia of *A. niloticus* origin and descent.

RESULTS

Percentage of adult worms recovered

The number of adult *S. mansoni* recovered from rodents varied greatly between different species, and between individuals within species (Table I).

The 20 *A. niloticus* exposed harbored a total of 2,159 schistosomes, 1,506 males and 653 females, with a mean worm load of 108 ± 130.5 and a worm return of 18 %. The sex-ratio of male to female is 2.3. No substantial differences were observed between the number of schistosomes recovered from male and female rodents (χ^2 = 2.89, P > 0.05). Considering the mean worm load, the results between males and females were comparable (Table II).

In total, the *M. huberti* harbored 1,380 *S. mansoni* among which 834 males and 546 females, representing a worm return of 11.5 % and a mean parasite load of 69 ± 47.2. The sex-ratio of male to female was 1.5. The difference observed between male and female rodents was barely significant (χ^2 = 4.408, P = 0.05). However, the mean worm load did not vary significantly between male and female *M. huberti* (Table II).

The 20 *M. erythroleucus* harbored 1,013 schistosomes, 712 males and 301 females. The worm return was 8.4 % with a mean parasite load of 50.5 ± 41.7. The sex-ratio of male to female was 2.4. The number of adult *S. mansoni* recovered from *M. erythroleucus* males was significantly higher than that recovered from females (χ^2 = 25.3, P < 0.001). On the contrary, the mean worm load was not different between male and female rodents (Table II).

The 20 *M. musculus* harbored 616 schistosomes, 394 males and 222 females. The worm return was 20.5 % with a mean parasite load of 30.8 ± 30.4. The sex-ratio of male to female is 1.8. The number of adult schistosomes recovered was significantly higher among male than female rodents (χ^2 = 48.02, P < 0.001). The mean load worm was higher in male than female *M. musculus* (Table II).

No worm was found in the lungs od *A. niloticus, M. huberti, M. erythroleuceus* and *M. musculus*.

Fecundity of *S. mansoni* female

14.3 % of the *A. niloticus* began to excrete eggs six weeks post infection. All of the *M. huberti, M. ery-*

Rodents	Number of worms recovered											
	A. niloticus			*M. huberti*			*M. erythroleucus*			*M. musculus*		
	SmM	SmF	Total	SmM	SmF	Total	SmM	SmF	Total	SmM	SmF	Total
	8	3	11	4	5	9	3	3	6	13	3	16
	1	11	12	11	0	11	4	4	8	13	6	19
	11	7	18	17	0	17	14	4	18	13	8	21
	22	3	25	21	9	30	23	11	34	19	3	22
Males	9	24	33	33	8	41	35	20	55	19	6	25
(n = 10)	19	18	37	70	0	70	32	31	63	13	18	31
	45	36	81	58	46	104	43	30	73	36	8	44
	74	58	132	57	51	108	43	28	71	39	24	63
	207	107	314	58	67	125	53	35	88	62	31	93
	264	113	377	103	33	136	157	15	172	75	52	127
	10	8	18	1	4	9	7	11	18	4	4	8
	17	14	31	1	4	5	12	8	20	8	2	10
	17	20	37	15	18	33	11	11	22	6	5	11
	27	11	38	47	22	69	21	8	29	9	2	11
Females	38	19	57	29	42	71	17	13	30	8	6	14
(n = 10)	26	41	67	61	29	90	22	8	30	7	8	15
	35	45	80	41	53	94	28	5	33	9	9	18
	112	49	161	73	32	105	28	5	33	12	8	20
	112	52	164	39	67	106	84	18	102	9	12	21
	452	14	466	95	56	151	75	33	108	20	7	27

Table I. — Number of worms recovered from 10 males and 10 females of the rodents *Arvicanthis niloticus, Mastomys huberti, Mastomys erythroleucus* and *Mus musculus*, seven weeks after exposure to *Schistosoma mansoni* furcocercaria; SmM = *S. mansoni* male, SmF = *S. mansoni* female.

Rodents species	Sex	*Schistosoma mansoni* mean ± s.d.	Test *t* de Student d.f. = 18
A. niloticus	Male	104 ± 133.4	0.132 NS
	Female	111.9 ± 13.6	
M. huberti	Male	65.1 ± 4.7	0.361 NS
	Female	79.9 ± 46.9	
M. erythroleucus	Male	58.8 ± 49.1	0.868 NS
	Female	42.5 ± 33.4	
M. musculus	Male	46.1 ± 37.4	2.558 *
	Female	15.5 ± 5.9	

Table II. — Mean number of *S. mansoni* adult recovered from male and female rodents; d.f. = degree of freedom, NS = not significative, * = significative.

throleucus, M. musculus and 71 % of the *A. niloticus* began to excrete eggs in their faeces seven weeks after infection. The number of eggs per gramme of faeces and of miracidia hatched per 24 h varied considerably in different individuals. The mean egg load and the mean miracidia hatched per 24 h are shown in Table II. In all rodents species the number of eggs per gramme correlated significantly with the number of female worms recovered, apart from *A. niloticus*.

The eggs recovered from the liver and the faeces were viable and infective.

MAINTENANCE OF LIFE CYCLE

S. mansoni was maintained for at least three generations in *M. musculus* (Swiss mice), two generations in *A. niloticus* and *M. erythroleucus* and only one generation in *M. huberti*.

Snails exposed to miracidia of first generation isolated from eggs excreted by one *A. niloticus* naturally infected, began to produce cercaria four weeks later. *A. niloticus, M. huberti, M. erythroleucus* exposed to these cercaria of first generation develop adult worms. Miracidia of second generation isolated from their liver and faeces were used to infect other snails which give birth to infective cercaria of second generation. As far as *S. mansoni* of *A. niloticus* origin and descent are concerned, only *S. mansoni* males were recovered from *A. niloticus* and *M. huberti* at the end of the second passage. The cercaria of *A. niloticus* origin and *M. huberti* or *M. erythroleucus* descent were infective. They develop into adult worms and pass viable eggs in nature.

The miracidia isolated from viable eggs excreted by one *M. huberti* trapped in Richard-Toll were used to infect *B. pfeifferi*. Four weeks post-infection, the snails shed cercaria which were used to infect one *A. niloticus*, one *M. huberti* and one M. *erythroleucus*. Eight weeks later, all *S. mansoni* adult recovered were long, thin and tangled of shape. It was difficult to distinguish the male and the female schistosomes.

Rodents	Number of *S. mansoni* female	Sex-ratio	Number of eggs epg	Number of eggs epg/Smf	Number of miracidia /24 h	Number of miracidia /24 h/Smf
A. niloticus						
MBA 648	3	7.3	0	0	0	0
MBA 670	3	2.7	60	20	0	0
MBA 558	14	32.3	0	0	0	0
MBA 671	41	0.6	80	1.9	0	0
MBA 667	58	1.3	180	3.1	0	0
MBA 669	52	2.1	280	0	0	0
RET 87	49	2.3	980	20	40	0.8
RET 108	107	1.9	400	3.7	12	0.1
RET 104	113	2.3	740	6.5	134	1.2
E 199/I	14	1.2	280	20	6	0.4
Mean ± s.d.	45.4 ± 39.7		300 ± 327.8		192 ± 42.2	
Mastomys huberti						
E 81/II	9	2.3	560	62.2	50	5.5
E 81/II	67	0.9	640	9.6	270	4
E 81/II	8	4	260	32.5	0	0
E 106/II	22	2.1	880	40	0	0
E 97/II	0		0	0	0	0
E 97/II	0		0	0	0	0
E 97/II	0		0	0	0	0
E 78/II	67	0.6	1,780	26.6	13	0.2
E 97/II	53	0.8	720	13.6	162	3.1
E 194/I	42	0.7	1,800	42.9	111	2.6
Mean ± s.d.	26.8 ± 27.9		664 ± 673.5		60.6 ± 92.7	
Mastomys erythroleucus						
E 94/II	15	10.5	700	46.7	391	26.1
E 94/II	20	1.75	40	2	9	0.45
MBA 589	13	1.3	80	6.2	14	1.1
E 105/III	35	1.5	880	25.1	0	0
MBO 209	11	1	0	0	0	0
E 105/III	5	5.6	0	0	0	0
MBA 633	8	2.6	80	10	0	0
E 96/III	8	1.5	200	25	28	3.5
E 96/III	8	11	160	80	0	0
E 96/II	18	4.7	260	5.7	23	1.3
Mean ± s.d.	14.1 ± 8.8		240 ± 304.8		46.5 ± 121.5	
M. musculus						
S 1	52	1.4	1,260	24.2	0	0
S 2	31	2	260	8.4	0	0
S 6	8	4.5	200	25	153	19.1
S 23	6	1.3	80	13.3	7	1.2
S 25	2	4.5	200	100	0	0
S 23	8	1.5	640	80	0	0
S 29	4	1	300	75	0	0
S 30	12	0.8	680	56.7	13	1.1
S 26	18	1	180	20	1	0.1
S 32	8	0.9	200	25	16	2
Mean ± s.d.	14.9 ± 15.5		400 ± 361.5		19 ± 47.5	

Table III. — Number of *Schistosoma mansoni* female (Smf), number of egg per gramme of faeces (epg) and number of miracidia hatched per 24 h, s.d. = standard deviation.

One *M. erythroleucus* was exposed to cercaria shed by *B. pfeifferi* recolted in Richard-Toll. Eight weeks later, the rodents was perfused and snails were infected with miracidia isolated from the liver and faeces. One *M. erythroleucus,* one *M. huberti,* one *M. musculus* and one *A. niloticus* were exposed to cercaria from these snails. *S. mansoni* male and female were recovered from *M. erythroleucus* and *A. niloticus* after the second passage. Viable eggs were found in the liver and faeces of these rodents. Only *S. mansoni* males were recovered from *M. huberti* and *M. musculus.*

In *M. musculus,* the strain of *S. mansoni* was maintained for three generations. *M. musculus* was infected with cercaria from *B. pfeifferi* naturally infected. Eight

weeks later, *M. musculus* was examined, adult worms recovered and then snails bred in the laboratory were exposed to miracidia from the liver and the faeces. After five weeks, one *M. erythroleucus,* one *M. huberti,* one *M. musculus* and one *A. niloticus* were infected with cercaria shed by these snails. These rodents develop *S. mansoni* adults and eliminate viable eggs with faeces.

DISCUSSION

All four rodent species studied were susceptible to infection with *S. mansoni* and are thus potential hosts. The parameters which determine the susceptibility of rodents to infection with *S. mansoni* vary considerably between species and between individuals of a same species.

Differences in the number of adult worms recovered may result from variation occurred either when the cercariae penetrated the host skin or when the schistosomula migrated and became mature. Warren and Peters (1967) showed that the cercarial penetration was not directly responsible for the variation in the number of adult schistosomes recovered from hamster, mouse, guinea pig, rabbit and rat. Earlier results suggest that the number of *S. mansoni* recovered is related to the capacity of migration and maturation of the schistosomula rather than the capacity of penetration of cercariae. However, as far as *A. niloticus, M. huberti,* and *M. erythroleucus* are concerned the question of whether the variation in worm return is related to differences in cercariae penetration or migration of the schistosomula remains open.

It has been shown that the percentage of worms recovered may be influenced by production of host antibodies (Auriault *et al.,* 1984; Capron, 1989). Some authors like Stirewalt *et al.* (1951), Kuntz and Malakatis (1955), Smithers and Terry (1965), Imbert-Establet (1986) observed a mortality of adult schistosmes related to duration of infection.

In the work presented here, *M. huberti* had the greatest number of eggs per gramme of faeces, whereas he did not have the highest worm load. The heavily infected rodents did not necessarily passed the greatest number of eggs. According to Kuntz (1961) the relationship « hosts with the greater number of parasites passed larger quantities of eggs » is not always valid and on several occasions good hosts with only a few schistosomes passed numerous eggs.

Except for *A. niloticus,* the two species of *Mastomys* and *M. musculus* showed a significant correlation between the number of female *S. mansoni* and the eggs recovered in faeces. This indicates that the number of eggs excreted with faeces does not depend only on the number of females recovered; other factors may influence the excretion of eggs with faeces. These would include intrinsic or extrinsic factors to the parasites. In fact, schistosomes have to migrate through the blood-stream to the liver, then pair before maturing and continue their migration to the mesenteric veins where the oviposition takes place. The host species could influence the development, the evolution and the fecundity of *S. mansoni* female. As shown by Basch (1981 *a, b*) and Basch and Humbert (1981) the species of host is relevant with regard to development of female *S. mansoni.* They believe that « a specific developmental stimulus, present in permissive animal host, is necessary for proper maturation of schistosomes of both sexes ». Imbert-Establet (1986) highlighted a low worm return, high adult worm mortality, low fecundity and total absence of *S. mansoni* eggs in faeces among *Rattus norvegicus.*

According to Imbert-Establet (1986) the pulmonary localisation of growing schistosomes could prevent the spreading of eggs. After staying in the mesenteric veins the schistosomes are able to migrate towards the lungs; this capacity of migration may play an important role in the elimination of eggs with faeces as eggs deposited in pulmonary tissue will not be excreted. Eggs associated with an inflammatory reaction and bilharzial tubercles developed in relation to ova were respectively observed in the lungs of *A. niloticus* and *Mastomys natalensis* by Gear *et al.* (1966). These rodents were experimentally infected with *Schistosoma haematobium* for one year. In the present work, no bilharzial lesions of the lungs were found in *A. niloticus, M. huberti, M. erythroleucus* and *M. musculus.*

The physiological state of the intestinal mucus can also cause the differences observed among *A. niloticus, M. huberti, M. erythroleucus* and *M. musculus.* Eggs ponded in mesenteric veins must migrate through the intestinal wall before being excreted by the faeces. When eggs are numerous, they may cause lesions and form intestinal nodules which make migration difficult. This phenomenon was observed in *A. niloticus* naturally infected at Richard-Toll (Sène, 1994).

We succeeded in maintaining the *S. mansoni* strain in each species of rodents for at least one generation. However after a certain number of successive passages a cessation of life cycle was observed. This sudden stop, when related to a degradation or a sterilization of the parasite strain, may be explained by an alteration of the cercariae infectivity. Even if they mature the cercariae only develop into male parasites. This phenomenon of sterilisation has already been observed among *Rattus rattus* by Jourdane and Imbert-Establet (1980).

In short, *A. niloticus, M. huberti, M. erythroleucus* and *M. musculus* are susceptible to infection with senega-

lese *S. mansoni.* They are capable of being infected and of passing viable and infective eggs. Consequently, the species *(A. niloticus* and *M. huberti)* found naturally infected are potential natural reservoirs.

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