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On the Biology of *Simulium damnosum* Theobald, 1903, the Main Vector of Onchocerciasis in the Mahenge Mountains, Ulanga, Tanzania

W. HÄUSERMANN

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1. Introduction

As was shown in a first survey of the vectors of onchocerciasis in the Ulanga district, Tanzania, transmission of this disease is restricted largely to the area of the Mahenge mountains (HÄUSERMANN, 1966). The vectors, mainly *S. damnosum* and occasionally *S. woodi*¹, are breeding throughout the year in numerous mountain streams and rivulets which are often difficult to approach even by foot. These conditions make vector control extremely difficult and it was decided to continue with a study of the biology of the main vector *S. damnosum* during a longer period, in order to assess the possibilities for vector control in selected, densely populated areas.

Following the results of several onchocerciasis surveys carried out by staff members and students of the Rural Aid Centre, Ifakara, and the St. Francis

¹ My thank for this final identification goes to Dr. D. J. Lewis, British Museum, Natural History, London.

Hospital, Ifakara, the highest incidence of onchocerciasis is to expect in the eastern valleys of the Mahenge mountains (GEIGY, COLAS & FERNEX, 1965; COLAS, 1966) which are inhabited by altogether about 30,000 persons. Among these valleys the Mselezi valley was finally selected for a closer investigation of the vector biology, for it combined distinct topographical conditions with the great advantage of a practicable road.

This study was made possible by two grants, one from the "Stiftung für experimentelle Zoologie" of the Zoological Institute, Basle, the other from the "Geigy Jubiläumsstiftung" of the J. R. Geigy Ltd., Basle.

I take this opportunity to express my thanks to Prof. Dr. R. Geigy, Director of the Swiss Tropical Institute, Basle, and the Rural Aid Centre, Ifakara, for his supervision and continuous encouragement, his help in finding financial means and the permission to use one Landrover and other facilities of the Rural Aid Centre, Ifakara. My thank goes also to Mr. J. N. Raybould from East African Institute of Malaria in Amani, Tanzania, and to Mr. A. W. McCrae from the Vector Control Division in Kampala, Uganda, for the stimulating discussions I could have at the beginning of this study. I have to extend my thanks also to the district administration in Mahenge for its permission to settle in Mselezi valley, to the Capuchin Fathers of the Roman Catholic Missions Kwirowa and Ruaha, to Mr. A. Mpenda, a native of Mselezi valley who developed in this period to a reliable field assistant, and to my neighbours for their complaisant assistance in every kind of work during the whole sojourn of nearly 2 years in Mbangayao village.

2. Description of the Area

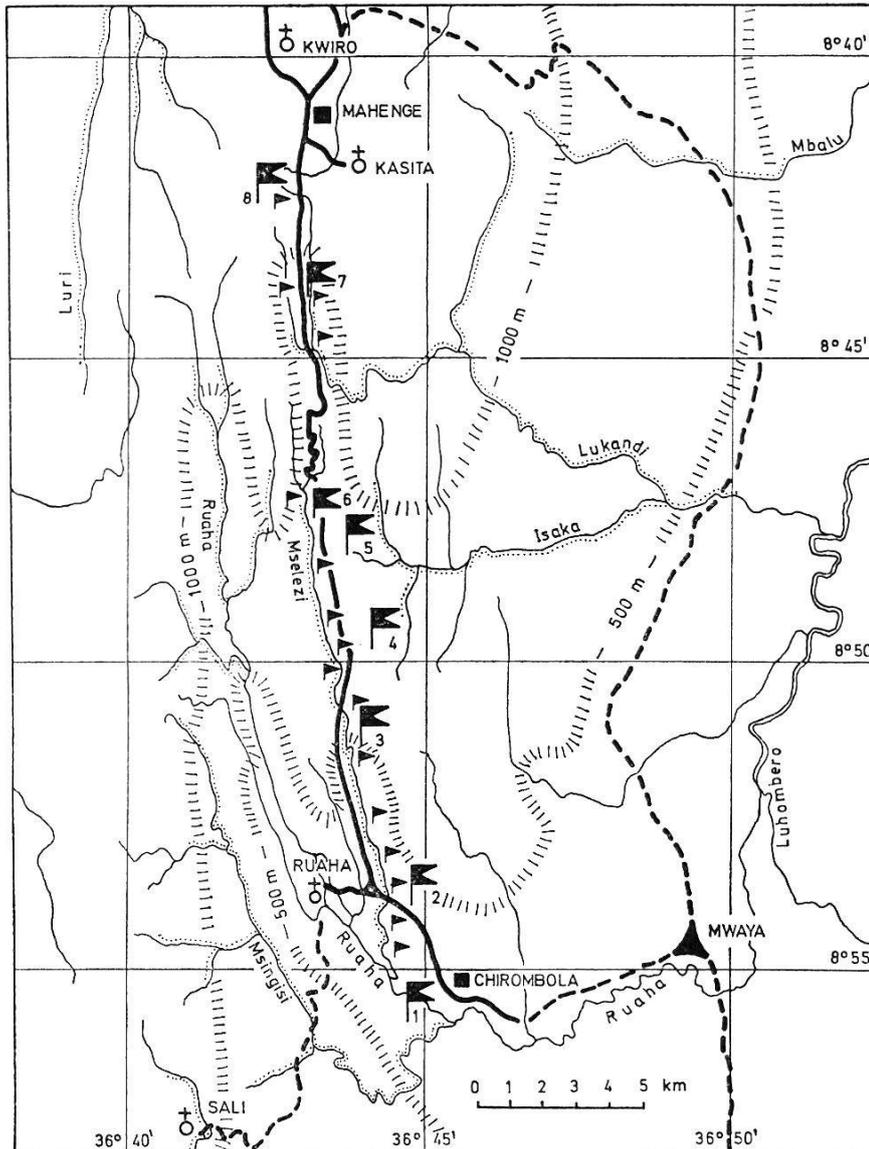
2.1. General description of the Mahenge mountains

The area of the Mahenge massif comprises some 5000 km² between 8°24' and 9°00' S. and 36°00' and 37°00' E. It is formed by Usagaran (precambrian) well foliated gneisses of sedimentary origin. The top layer of the Usagaran rocks comprises the limestone group of Mahenge with crystalline dolomitic limestone and gneisses and is still visible in the eastern part of the Mahenge massif. Numerous crags and cliffs of crystalline dolomitic limestone give the area a characteristic appearance. In the east of the Mselezi valley and the Mahenge plateau is a major fault extending from north to south and forming the boundary between the Usagaran rocks of the Mahenge massif and the Karoo rocks of the undulating country in the Selous game reserve.

Topographically the eastern part of the Mahenge massif is formed by numerous ridges of hills all running from north to south. The area is drained principally by the stream Luri in direction north, by the streams Mbalu, Lukandi and Isaka in direction east and the streams Msingizi, Ruaha and Mselezi in direction south. All streams and their tributaries shown on map 1 are perennial.

Rainfalls, though possible throughout the year, concentrate mainly in a rainy season lasting from December to May, the heaviest rains falling in December or January and again in March and April. The total of annual rainfall ranges between 120 cm in the foothills and some 200 cm in the highest valleys of the Mahenge massif. The mean minimum temperature for the area is about 18°C, the mean maximum temperature about 28°C (comp. FREYVOGEL, 1960).

The primary vegetation types of the Mahenge massif range from mixed deciduous forest to woodland and wooded grassland. The forest is preserved in forest reserves mainly on the higher ridges in the eastern part of the massif.



Map 1. The topographical situation of the Mselezi valley in the eastern Mahenge mountains and the distribution of the perennial rivers, in which *S. damnosum* is breeding.

-  Catching stations of the flyround: 1. Chirombola, 2. Mselezi chini, 3. Lupanga shule, 4. Chiwambu, 5. Liatu, 6. Mbangayao, 7. Nasanji, 8. Isongo juu
-  Collecting sites for larvae on the larval round
-  Non perennial rivers
-  Perennial river in which *S. damnosum* breeds
-  Road
-  Frontier

Woodland, only partly consisting of typical myombo (*Brachystegia*) is still widespread in uninhabited areas in the foothills. Secondary bush or grassland with outstanding *Chlorophora excelsa*, *Sterculia appendiculata*, *Khaya nyasica* and *Vitex cuneata* are common in inhabited areas, indicating forest as climax vegetation. Some of the drier ridges of the massif are covered with pure grassland of *Hyperrhenea cymbaria*, others with uniform woodland of *Albizzia spec.*

Dominant among the human population of the Mahenge massif is the Pogoro tribe, interspersed, however, hamlets of newly settled Ngoni and Ngindo people can be found.

As food crops, rice, sorghum, maize, groundnuts, beans, pulses, cassava, sweet potatoes and bananas are planted. Shifting cultivation is practiced widely for all main crops. Maize is harvested two or three times a year, all other crops only once. After old Pogoro habit rice is cultivated mostly on slopes. As main cash crop cotton is planted in the lower parts of the valleys and in the foothills. Cashew nuts, coffee or tobacco as cash crops are rare. Recently the government introduced wheat as cash crop in higher altitudes, which are unfavourable for cotton. Cattle is kept by the missions only. Although the native Pogoro peasants keep sometimes sheep or goats and always poultry, their diet is normally poor on animal proteins.

2.2. The Mselezi valley

The Mselezi valley extending within 8°47' and 8°55' S and 36°42' and 36°45' E is the most eastward of the valleys running south, and with the length of about 15.5 km also the shortest. The air temperatures measured in this valley range between 7°C in the upper parts shortly before sunrise and 36°C on sunexposed slopes and in the lower parts. At the camp in Mbangayao temperatures below 10°C or exceeding 31°C were never observed. As total rainfall in Mbangayao 162 cm were recorded from March to December 1966 and 266 cm from January to December 1967. As a rule the higher annual rainfalls are recorded in higher altitudes, the reverse, however, is also possible according to observations of the Capuchin Fathers from Kwiwo and Ruaha. The Mselezi stream approximates some 20 km in length of the water course. It discharges about 1500 l/sec at the height of the rainy season and about 100 l/sec at the end of the dry season into the Ruaha river. Floodings of estimated 5000 l/sec were observed. In the dry season the water discharge is bigger in the middle part of the valley than in the lower part. Most of the numerous small tributaries flow only in rainy season and bring between 30 to 100 l/sec. The very few annual tributaries are shown on map 2.

The Mselezi valley is naturally divided into three parts for which special native names exist.

The upper part called Mselezi juu is about 600 m above sea level. It lies wide open between two major ridges ascending to some 800 and 900 m above sea level and extends over 5.5 km. The river meanders strongly in this part but never forms a swamp. Stretches of gravel and sand follow frequently to each other. Only one little rapid exists.

In the middle part of the valley, called Lupanga, the main ridges still of the same height diverge wider apart and a smaller ridge ascending only some 50 m over the bottom of the valley is detached from the left hand major ridge, thus narrowing the valley itself. The stream descends here rather fast in rapids and waterfalls from pool to pool to about 450 m above sea level. This descent extends over about 4 km.

The lower part of the valley, called Mselezi chini, is again about 5.5 km long. Here no longer major and minor ridges can be distinguished. Numerous hills standing up to 50 m over the surrounding country and all arranged in south-southeastern direction characterize the landscape in which the Mselezi unites with the Ruaha. For this last distance the Mselezi stream flows steadily except for 10 little waterfalls 30 to 50 cm high which follow each other rather regularly in distances from 400 to 800 m.

In the Mselezi valley all the vegetation types already mentioned for the Mahenge area can be found. A forest reserve extends on both sides of the valley from Mselezi juu to Lupanga. A dense deciduous forest is formed in the wet side drains. The drier parts of the slopes are covered with woodland or even shrubs. The most conspicuous trees of the forest reserve are from the author's point of view *Khaya nyasica*, *Anthiaris usambarensis*, *Cordia ovalis* and *Stereospermum kunthianum*. On numerous crags and cliffs towering above the forest an extremely xerophytic vegetation with different species of *Euphorbia* is observed. In Mselezi chini the hills are covered with woodland or bush. Uncultivated land is covered with secondary bush or grass. Most characteristic trees of Mselezi chini are *Borassus flabellifer* and some few *Chlorophora excelsa*.

Scattered relics of riverine forest mainly consisting of *Ficus* species are found bordering the Mselezi stream.

As regards the fauna of Mselezi valley Sykes monkey (*Cercopithecus mitis*), Red- and Blueduikers (*Cephalophus harvey* and *C. monticola*) and Tree- and Rockhyraxes (*Dendrohyrax arboreus* and *Procavia capensis*) can be mentioned as common for Mselezi juu and Lupanga. The vervet, *Cercopithecus aethiops* and the yellow baboon *Papio cynocephalus* are the most common and conspicuous mammals in Mselezi chini.

The human population in the Mselezi valley consisting mainly of Pogoro and some few newly settled Ngindo people amounts to approximately 700 persons. Favourite crops of the population in Mselezi juu and Lupanga are sorghum, maize and groundnuts planted at the bottom of the valley and rice planted on slopes in clearings of the forest or, where the forest is protected, on slopes of the neighboured Isaka valley. In Mselezi chini the cultivation of cotton sponsored by the government occupies a good deal of the productive soil. Rice is planted on the hills. The people always keep chicken and sometimes also goats or sheep. A pack of dogs is kept in each hamlet.

2.3. *Human onchocerciasis in the Mselezi valley*

An onchocerciasis survey was conducted in order to put entomological findings of the vector survey in relation to the human infection rates in the different parts of the valley and to provide the necessary dates for comparison with other areas of endemic onchocerciasis in Africa.

For the survey only natives and residents living for more than 5 years in the valley were accepted. Small children were only examined when they were able and willing to come by themselves; thus the range of the youngest age group was kept between 2–4 years. In many cases the age of a person had to be estimated after its relationships to other persons of known age. After establishing its membership to one of the 6 age groups a person was surveyed for scratch lesions of the skin indicating pruritus, for depigmentation of the skin over the tibiae and for skin atrophy on shoulders, arms and legs. A search for nodules was carried out over knees, hipbones, ribs, neck, shoulderblades and elbows at the same time. Each person was skinsnipped once on the right shoulderblade.

Immediately afterwards the skinsnip was examined for microfilariae under the high power microscope in a drop of saline. If after half an hour and several checkups the skinsnip still failed to produce microfilariae, the person was regarded as skinsnip negative. In most of the cases, however, the microfilariae appeared within 1–2 minutes after the skin snip was taken.

The visual acuity was tested with Snellen's visual acuity chart in the proper manner prescribed for this table. A visual acuity within 8–6 is listed as normal, one within 5–3 as reduced and an eye with a visual acuity between 2–0 is listed as virtually blind. In addition to this the eyes were also examined with a focussed torch for alterations of cornea, iris and lens. The test for visual acuity was performed whenever possible. Some persons of the younger age groups, however, especially females were unable to undergo this test due to lack of comprehension. On the other side also some old women refused this test, but in this group it may partly also be due to poor vision.

The results of the survey are shown on separate tables for Mselezi juu, Lupanga and Mselezi chini (Tab. 1 a, 1 b and 1 c).

Table 1 a. Human onchocerciasis in Mselezi juu

Sex	Age groups	No. of persons skinsnipped	No. of persons with pos. skinsnip	No. of persons with nodules	Skin changes			Test for visual acuity						
					Pruritus	Depigmentation	Atrophy	No. of persons tested	right eye			left eye		
									normal	reduced	± blind	normal	reduced	± blind
♂	2–4	8	4	1	6	–	–	2	2	–	–	1	1	–
	5–9	9	3	–	3	–	–	6	5	1	–	3	3	–
	10–14	16	14	–	9	–	3	16	15	1	–	15	1	–
	15–29	27	21	3	12	1	14	25	24	1	–	23	2	–
	30 +	24	24	4	14	17	23	23	14	6	3	9	11	3
	Total	84	66	8	44	18	40	72	60	9	3	51	18	3
+♀	2–4	9	1	–	3	–	–	–	9	–	–	9	–	–
	5–9	15	2	–	8	–	–	9	9	–	–	9	–	–
	10–14	9	2	–	6	–	1	8	7	1	–	8	–	–
	15–29	35	20	1	18	–	14	33	31	2	–	29	4	–
	30 +	23	23	4	15	7	21	20	9	8	3	7	9	4
	Total	91	48	5	50	7	36	70	56	11	3	53	13	4
Total	2–4	17	5	1	9	–	–	2	2	–	–	1	1	–
	5–9	24	5	–	11	–	–	15	14	1	–	12	3	–
	10–14	25	16	–	15	–	4	24	22	2	–	23	1	–
	15–29	62	41	4	30	1	28	58	55	3	–	52	6	–
	30 +	47	47	8	29	24	44	43	23	14	6	16	20	7
	Total	175	114	13	94	25	76	142	116	20	6	104	31	7

Table 1 b. Human onchocerciasis in Lupanga

Sex	Age groups	No. of persons skinsnipped	No. of persons with pos. skinsnip	No. of persons with nodules	Skin changes			Test for visual acuity						
					Pruritus	Depigmentation	Atrophy	No. of persons tested	right eye			left eye		
									normal	reduced	± blind	normal	reduced	blind ±
♂	2-4	2	-	-	1	-	-	-	-	-	-	-	-	-
	5-9	6	4	-	2	-	-	4	3	1	-	3	1	-
	10-14	7	5	-	2	-	-	7	7	-	-	5	2	-
	15-29	9	9	-	4	2	6	9	8	1	-	7	2	-
	30 +	6	5	3	2	5	6	6	4	2	-	3	3	-
	Total	30	23	3	11	7	12	26	22	4	-	18	8	-
♀	2-4	6	1	-	4	-	-	-	-	-	-	-	-	-
	5-9	7	1	-	5	-	-	5	5	-	-	3	2	-
	10-14	5	3	-	2	-	-	3	3	-	-	2	-	-
	15-29	11	7	-	8	-	4	10	10	-	-	9	1	-
	30 +	13	10	2	10	1	13	10	4	4	2	6	2	2
	Total	42	22	2	29	1	17	28	22	4	2	21	5	2
Total	2-4	8	1	-	5	-	-	-	-	-	-	-	-	-
	5-9	13	5	-	7	-	-	9	8	1	-	6	3	-
	10-14	12	8	-	4	-	-	10	10	-	-	8	2	-
	15-29	20	16	-	12	2	10	19	18	1	-	16	3	-
	30 +	19	15	5	12	6	19	16	8	6	2	9	5	2
	Total	72	45	5	40	8	29	54	44	8	2	39	13	2

As the tables 1 a, b and c clearly indicate, the incidence of onchocerciasis is considerably higher in the upper part of the valley than in Mselezi chini. The tables also show a distinctly higher incidence of the disease in males, and that males normally acquire the disease in an earlier age group than females. As was to expect, the highest infection rate with 84% overall was found in the age group of 30 years and more.

Clinical symptoms others than pruritus occur mainly in adults over 15 years of age, and here again these symptoms are more common and distinct in males. 43 nodules were observed in 28 persons (17 ♂♂ and 9 ♀♀). They were more often situated on knees and ribs than on shoulderblades or hipbones, and never found on necks or elbows. In size the nodules ranged between peas and walnuts but were more frequently like peas. In general nodules were found on adults only, but a single one was encountered on a boy of less than 4 years. In no case a person with a nodule was found to be skinsnip negative.

As regards the visual acuity, the percentage of poor vision is higher in skinsnip positive persons in age groups over 10 years. The difference, however, is

Table 1 c. Human onchocerciasis in Mselezi chini

Sex	Age groups	No. of persons skinsnipped	No. of persons with pos. skinsnip	No. of persons with nodules	Skin changes			Test for visual acuity						
					Pruritus	Depigmentation	Atrophy	No. of persons tested	right eye			left eye		
									normal	reduced	± blind	normal	reduced	± blind
♂	2-4	4	-	-	3	-	-	-	-	-	-	-	-	-
	5-9	16	2	-	11	-	1	7	7	-	-	5	2	-
	10-14	17	10	-	8	-	2	17	16	1	-	16	1	-
	15-29	20	12	2	5	5	10	20	17	3	-	17	1	2
	30 +	34	24	6	17	10	25	34	23	7	4	23	7	4
	Total	91	48	8	44	15	38	78	63	11	4	61	11	6
♀	2-4	6	-	-	1	-	-	-	-	-	-	-	-	-
	5-9	31	-	-	16	-	-	18	14	4	-	14	4	-
	10-14	12	4	-	6	-	-	12	11	1	-	11	1	-
	15-29	33	13	-	26	1	17	33	29	4	-	28	5	-
	30 +	29	22	2	21	5	22	25	15	8	2	15	8	2
	Total	111	39	2	70	6	39	88	69	17	2	68	18	2
Total	2-4	10	-	-	4	-	-	-	-	-	-	-	-	-
	5-9	47	2	-	27	-	1	25	21	4	-	19	6	-
	10-14	29	14	-	14	-	2	29	27	2	-	27	2	-
	15-29	53	25	2	31	6	27	53	46	7	-	45	6	2
	30 +	63	46	8	38	15	47	59	38	15	6	38	15	6
	Total	202	87	10	114	21	77	166	132	28	6	129	29	8

Table 2. Visual acuity in skinsnip positive and negative persons

Skinsnip	No. of persons	Visual acuity						Alterations of eye connected to re- duced vision or blindness			Virtu- ally blind No. of persons
		right eye			left eye			No. of persons	right eye	left eye	
		normal	reduced	± blind	normal	reduced	± blind				
pos.	234	175	46	13	165	56	13	46	34	38	12
neg.	128	114	12	2	108	17	3	7	5	6	2
Total	362	289	58	15	273	73	16	53	39	44	14

not statistically significant if tested in each single age group. Without special means and special skill visible alterations of cornea, iris and lens in connection with diminished vision was observed in 72 eyes of 46 persons with positive skinsnips and in 11 eyes of 7 persons with negative skinsnips. Out of 362 persons tested for visual acuity 14 can be regarded as virtually blind since both their eyes had a visual acuity of 2 or less. 12 of these 14 persons had a positive skinsnip. Total blindness of one or both eyes was encountered in 5 persons. All had a positive skinsnip. The importance of onchocerciasis as an eye disease in the Mselezi valley can be concluded from table 2, where the visual acuity in skinsnip positive and skinsnip negative persons is compared.

3. Organisation of the Survey

After a team for the survey was recruited and finally settled in a tent and a mudhouse in Mbangayao village, in the uppermost part of the Mselezi valley, the network of observation of *S. damnosum* consisted of a flyround with 8 catching stations and a larval round with 16 stations (see map 1 and 2). Fly-round and larval round were carried out alternatively every fortnight. In addition to this an eleven and half hour (from 6.45 to 18.15 h) catch of Simuliids feeding on man was carried out every week, once in Mbangayao village and a ten hour catch at a second catching place selected arbitrarily among the other catching points of the flyround. Thus for every month a sample of flies was collected which may be regarded as sufficiently representative for the valley in that month.

On the flyround adult Simuliids were caught with three flyboys aged between 10 and 16 years. The catching time at each station was 20 minutes, i.e. with three boys one hour per station. The catching points were visited always in the same order and at the same daytime, in order to make the conditions of collection as similar as possible for each flyround.

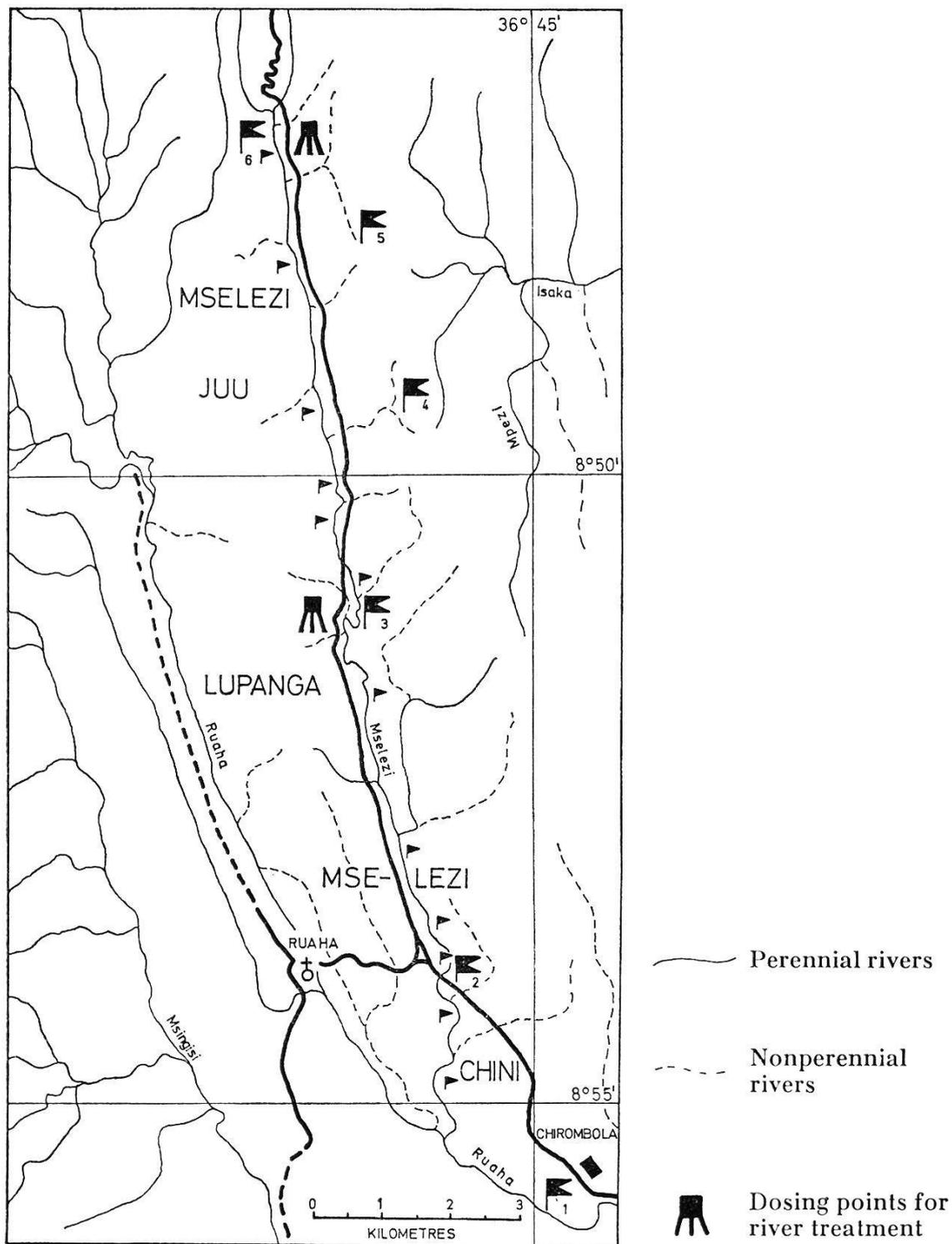
For the 11½-hour periods of catching two boys were employed, catching alternatively for one hour from 6.45 h in the morning to 18.15 h in the evening. All Simuliids settling on the flyboys were collected individually in little glass tubes. The time of each capture was recorded and each fly given a number. Every quarter hour air temperature and air humidity were measured with a sling psychrometer. Light conditions, cloudiness, wind and rain were estimated, always by the same person and also recorded.

The total biting catch was dissected and divided into nulliparous and parous. All parous females were stored in alcohol 85% in their individual glass tubes and later on stained with Myer's acid haemalaun and dissected for sausage and infective larvae of filarial parasites.

The larval collections were carried out with three boys for five to twenty minutes per collecting place. Afterwards these collections were sorted out into pupae, last larval instars and younger larvae. Pupae and last larval instars of each species were counted.

Once this network of routine observation was well established and the age grading became less time consuming due to growing experience and decreasing fly density, time could be spared for further observations.

The water discharge of Mselezi river was measured every month with a current meter (made by Alfred J. Amsler & Co., Schaffhausen, Switzerland). Time by time a system of landmarks was established at some narrow rocky passages which allowed to estimate roughly the river discharge in the upper and lower part of the valley on each larval round.



Map 2. Topography of the Mselezi valley with exact position of catching stations and collecting sites.

At the end of the dry season 1966 and beginning of rainy season 1967 some marking experiments were conducted with adult *S. damnosum* in order to gain some information on dispersal and longevity. In the beginning the flies were marked individually on the thorax with a fine brush and oil paint. Later on the flies were marked with Sparvar spraypaint, made by Valley Forge Products Co., Norristown, Pa. (USA). The flies were caught by 6–10 flyboys in small bottles with a funnel shaped bottom and a hole at the end of the funnel, always 25 flies per bottle. The flies were then released in a tin closed at the bottom with a fine nylon-gauze. When the tin was kept with the gauze against the light, the flies kept crawling on the gauze and could be sprayed for about 1 second from the darker open end. Afterwards the flies were released in a wide bowl with a rim of 8 cm height. All flies which managed to fly off over this rim were counted as marked, whereas flies handicapped by the paint were kept back and later on discarded. It was obvious that in general the flies were not much disturbed by the paint for often they tried immediately after marking to bite again. For recaptures the routine flyrounds and routine daily biting catches plus three additional flyboys — one posted in Mselezi juu, one in Lupanga and one in Mselezi chini — were employed. In order to enlarge the chance of recaptures the local population was informed and encouraged to collect marked flies, which, however, did not work.

To gain more information about larval development under natural conditions, control experiments were conducted in the Mselezi river in April and May 1967. The dosing technique employed in these experiments is mentioned in chapter 4.7.

4. Results

4.1. *The Simuliidae of the Mselezi valley*

From March 1966 to March 1967 pupae and larvae of some 16 species of the genus *Simulium* have been collected in regular larval rounds carried out every fortnight in the Mselezi stream and occasional larval collections in tributaries in the Mselezi valley.

4.11. *List of species found in larval collections in the arrangement of species given by FREEMAN & DE MEILLON 1953:*

Group I

S. occidentale Freeman & de Meillon 1953 (= *S. alcocki* f. *occidentale*), *S. johannae* Wanson 1947, *S. geigy* Garms & Häusermann 1968, *S. weyeri* Garms & Häusermann 1968, *S. mcmahoni* de Meillon 1940.

Group II

S. cervicornutum Pomeroy 1920, *S. unicornutum* Pomeroy 1920, *S. unicornutum* f. *rotundum* Gibbins 1936.

Group III

S. ruficorne Macquart 1938, *S. aureosimile* Pomeroy 1920.

Group IV

S. hirsutum Pomeroy 1922, *S. adersi* Pomeroy 1922.

Group VII

S. hargreavesi Gibbins 1934 (= *S. medusaeforme f. hargreavesi*), *S. vorax* Pomeroy 1922, *S. ? taylori* Gibbins 1938², a species of the *S. bovis* complex, *S. damnosum* Theobald 1903.

4.12. *Breeding activities*

S. ruficorne and a species of the *S. bovis* complex were found only once and both seem to be rare in the whole area of the Mahenge mountains. All other species mentioned in the list above can be found at any time of the year in the Mselezi valley.

Some species are more, others less dependent on the environmental changes brought about by the annual seasons. *S. adersi* e.g. is found in abundance on some rapids in Mselezi chini only during the last months of the dry season, when the waterlevel is at its lowest and the water temperature reaches up to 28°C in the early afternoon. Otherwise the species is very rare throughout the year.

S. ? taylori is found in great abundance in the small tributaries in the last months of the rainy season, but it is very rare in the few perennial tributaries during dry season and scarcely found in the Mselezi stream.

Some other species are more ubiquitous and shifting from larval habitats in the tributaries during the rainy season to larval habitats in the Mselezi stream during the dry season, especially all the species of groups I and II, *S. aureosimile* and *S. hargreavesi*. *S. aureosimile* shows a clear preference for shadowy larval habitats where it often is the dominant species in late dry season.

Other species like *S. damnosum* and *S. vorax* are less ubiquitous and shift from larval habitat to larval habitat in the Mselezi stream only according to the season. *S. damnosum* is occasionally found in tributaries but then in small numbers only.

A general increase in the numbers of larvae is observed with species of group VII at the end of the rainy season, among which *S. damnosum* is then the most abundant. Later in the year *S. mc-mahoni* becomes the most abundant species in the Mselezi stream. In higher altitudes *S. mc-mahoni*, however, is extremely rare and *C. cervicornutum* follows *S. damnosum* as most abundant species.

² Pupae and larvae of this species clearly belong to group VII and resemble closest to *S. taylori* Gibbins 1938, though the pupal respiratory organ differs slightly from that of the type form. The question mark indicates that close taxonomic examination might give evidence for a new species.

In some larval habitats which look then still favourable for *S. damnosum* larvae, the larvae of *S. hargreavesi* are found in great abundance and *S. damnosum* is rare.

4.13. Association of the common species, preference for larval habitats and room competition amongst the developmental stages

In the course of the numerous larval collections almost each species could once be found associated at the same substratum with any of the other species.

In rainy season *S. damnosum* is found in a wide range of different larval habitats, rapids, turbulent stretches with gravel and boulders and stretches with laminar flow with vegetation dipping into the water. As substratum serve stones, beards of roots, sticks, water vegetation, moss and grass dipping into the water in laminar or only slightly turbulent current. During dry season, however, *S. damnosum* is found in the rapids of the Mselezi stream only. *S. damnosum* is mainly associated with *S. vorax*, *S. hargreavesi*, *S. mcMahoni* and *S. cervicornutum*.

S. vorax prefers faster flowing water than *S. damnosum* and is found more often on stones and sticks than on swaying and easily afloated matter. It is associated with *S. damnosum*, *S. hargreavesi* and *S. cervicornutum*.

S. hargreavesi is found in an even wider range of larval habitats than *S. damnosum*. Often it is associated with *S. damnosum*, *S. vorax*, *S. cervicornutum*, *S. mcMahoni*, *S. hirsutum*, *S. aureosimile*, and *S. ? taylori*.

S. ? taylori is found in small rivulets splashing from rock to rock in the forest area and fixed on roots and grass hanging into the water and on the rocks of the river bed. Very often it is the only species in this larval habitat. Sometimes, however, it is associated with *S. hargreavesi* or species of the *S. alcocki* group.

S. cervicornutum is found mainly in altitudes of 600 m and more above sea level and inhabits there a wide range of larval habitats from rapids to only slightly broken water where grass or branches of trees are dipping into the surface. As substratum serves mostly dead or living plant material, exceptionally also overflowed stones. It is associated with *S. hargreavesi*, *S. damnosum*, *S. hirsutum*, *S. unicornutum* and species of the *S. alcocki* group.

S. unicornutum and *S. unicornutum f. rotundum* were found mostly together and associated with species of the *S. alcocki* group or *S. cervicornutum* on dead or living grass and leaves in slightly broken, not too fast flowing water.

S. aureosimile was the only species which was found exclusively in shadowy larval habitats. As substratum serve mainly dead

leaves near the water surface. It was associated sometimes with *S. mcMahoni* or other species of the *S. alcocki* group, *S. hirsutum* or *S. cervicornutum*. Often, however, the species was occupying a larval habitat completely for itself.

S. hirsutum is found in the same places as *S. cervicornutum* and *S. mcMahoni* but rarely as dominant species. It is found also associated with *S. damnosum* and *S. hargreavesi*.

S. mcMahoni is the most common and widespread species in lower altitudes and found in nearly all habitats suitable for Simuliid larvae. It is found more often on fresh and decaying vegetable matter than on stones and prefers not too fast running water. It is found associated with species of groups I and II, *S. damnosum*, *S. hargreavesi* and in late dry season with *S. adersi*.

S. adersi prefers also not too fast running water and vegetable matter as substratum. It is mostly associated with *S. mcMahoni*, but found only in the Mselezi stream.

The four species of the *S. alcocki* group with ten respiratory filaments in the pupal stage are found in nearly all streams of the area on living and decaying vegetable matter in not too fast running water. They were never abundant but always present with few larvae and even fewer pupae. They were often associated on the same substratum with *S. mcMahoni* and species of the *S. cervicornutum* group.

In general the species of the groups I–IV (Division A) prefer slower flowing water than those of group VII (Division B). Though they mix sometimes with species of group VII on the same substratum they cannot be regarded as room concurrents. A wide range of substrata and larval habitats and practically no tendency to crowd prevents any serious room competition between species of the first four groups and group seven. Only the pupae of *S. adersi* and *S. mcMahoni* are found sometimes crowded on a leaf and it might be that these two are room concurrents, when the general breeding conditions are equally favourable to both species.

Among group VII, larvae and pupae of all species are sometimes found in dense clusters covering the substratum in a lawn-like fashion. In most cases these clusters consist of one species. It seems that the species of group VII stand in some competition for surfaces which allow a very high larval density and that for ecological differences a certain substratum is occupied predominantly by one species. *S. damnosum* e.g., which could occupy a wide range of larval habitats, may be limited in its expansion during the season of massbreeding by *S. vorax* on larval habitats with fast flowing water and by *S. hargreavesi* and *S. ? taylori* in the range of lower water speed. Especially in the tributaries where *S. damnosum*

occurs sporadically, but never in great numbers, it may be that vast numbers of *S. hargreavesi* prevent *S. damnosum* larvae to settle successfully on substrata otherwise suitable for them.

4.14. *Adult Simuliids caught on man, on animals and in traps*

Two species only were caught biting on man, *S. damnosum* Theobald and *S. woodi* de Meillon. The latter species was caught only rarely and larvae could never be found in the Mselezi stream although hundreds of crabs were checked in all seasons. It seems that the breeding area of this species is restricted to the higher altitudes (Sali and Muhulu, HÄUSERMANN, 1966), where larvae have been collected, and that the few specimens caught have immigrated from there over a distance of at least 10 km and across two valleys.

Three other unidentified species of Simuliids belonging to group I, II or IV were caught after landing on man. Biting was not observed on man but occasionally on young chickens.

In swarms of Simuliids surrounding cattle and goats predominantly *S. vorax* and occasionally *S. damnosum* and a species of group I, II or IV were caught with the hand net. Biting was observed for *S. vorax* but not for the two other species. Landing of *S. damnosum* was also observed on a vervet (*Cercopithecus aethiops*) kept in captivity. Biting, however, was never seen. An antelope (*Sylvicapra grimmia*), kept in captivity near the camp, seemed never to be molested by any kind of Simuliids.

In a shade trap of black cloth suspended over a rectangular frame and with a hole in the centre of the top, covered by a funnel leading into a bottle, *S. damnosum* was caught in big numbers, up to 100 per day during the season of high population density, but seldom only in other times. In this trap also three non-identified species belonging to group I, II or IV were caught, probably the same as the ones caught on man.

4.15. *Predators*

6 species of small fishes were collected in Mselezi stream. Five of these are quite common and could be identified as *Amphilius krefftii*, *Chiloglanis deckenii*, *Labeo victorianus*, *Barbus kurumani* and *Kneria angolensis*².

The gut contents revealed that only two of these, *B. kurumani* and *A. krefftii*, feed on waterinsects. The proportion of Simuliid

² For the identification I have to thank Mr. M. H. Atkinson, Senior Fisheries Officer in Dar es Salaam.

larvae, however, was very small and the fishes seem not to be serious predators of Simuliids.

Unidentified species of crabs and fresh water prawns are also present in the Mselezi stream. Examination of the gut contents of some few specimens (5 crabs, 1 prawn) produced no signs of predation on Simuliid larvae or other insects as recorded by WILLIAMS 1962 for the crabs in the rivers of Mt. Elgon. Predation by crabs on Simuliid larvae is certainly not very important in the Mselezi valley.

The insect fauna of the stream includes larvae of many species of diptera, coleoptera, trichoptera, odonata, plecoptera and ephemeroptera, very often in vast numbers, but no observation of predation on Simuliids were made.

4.16. Parasites

Only very few *S. damnosum* larvae were found to be infected with mermithids. The infections were found accidentally on the same day and place when dissecting larvae for cytotaxonomic examinations. The mermithids might represent two new species (RUBTSOW, per. comm.) but unfortunately all attempts to get further material for final identification failed.

Protozoan infections of larvae as far as discernible by a whitish, swollen abdomen or a speckled appearance of the whole larva, were frequent in some species at certain times and places but rare in *S. damnosum*.

In the course of age grading of adult *S. damnosum* females fungus, protozoan and mermithid parasites were encountered. Some adults were also found to be infested with mites. A collection of diseased specimens was sent to WHO International Reference Centre for diagnosis. Unfortunately, no efforts could be undertaken to rear the more interesting parasites on the spot, and thus no final identifications were possible.

Among some 13 000 females of the *S. damnosum* dissected for age grading only three were found to be infected with mermithids in the abdominal cavity. All three were found in May 1967, when the population was at its peak. Two females caught on May 29, 1967, contained several ciliates in their abdominal cavity which were moving rapidly in the saline solution when the cavity was opened. Such infections were never encountered again.

A fungus infection of the abdominal cavity in association with the ovaries was also observed in May 1967. Of 3516 flies dissected in this month 27 or 0.77% had this infection. The presence of a large fatbody and still opaque malpighian tubules indicated in

each case that the females were nulliparous. The ovaries were always more or less affected by the fungus.

In the second half of May 1967, some nulliparous females were discovered to carry varying numbers of small dark spheres, presumably parasites, surrounded by melanocytes. Of 1565 nulliparous females dissected from May 22 to June 1, 1967, 65 or 4.15% were infected with these organisms. Since never parous females with such an infection were seen, this infection must either disappear or prevent the females of becoming parous.

4.2. *The structure of the S. damnosum population*

As was obvious from a previous survey at least two different races of *S. damnosum*, one nonanthropophilic and one anthropophilic, are present in the Ulanga district. Samples were therefore collected from several larval habitats and sent to Prof. R. W. Dunbar for cytotoxic examination. Up to now three cytotoxic categories are found in Mselezi valley which are provisionally called 'Nkusi', 'Sanje' and 'Ketaketa' according to the local names of their first collection sites (DUNBAR, pers. comm.). Nkusi is a river in Uganda. Sanje is a river in Ulanga north, near Kidatu. Ketaketa is the name of rapids in the Luhombero river in Ulanga south near Ilonga. The species 'Sanje', found mainly in Ulanga north, seems to be zoophilic here and also in the Usambara mountains in northern Tanzania. In the Mselezi sample of larvae, 34 'Nkusi', 1 'Sanje', 1 'Ketaketa', collected on June 23, 1966, the species 'Nkusi' was the most abundant and is very probably the manbiting species of the Mahenge mountains. The biting behaviour of 'Ketaketa' is not known at present, because it was always found in smaller numbers together with 'Nkusi'.

Morphological studies on the biting population, using the same features and methods as LEWIS & DUKE 1966, revealed no significant clues for the presence of two different species in the manbiting *S. damnosum* population of the Mselezi valley, although it contains specimens which can be classified in LEWIS' colour class A and others which belong to colour class B. Mostly those classified under class A have only few dark scales in the basal wing tufts. Of 50 flies examined none could be ranged in class C. As regards tuft ratio and wing length, the flies seem to be of intermediate type. The results of the close inspection of 50 flies are given in table 3.

It seems that as elsewhere minor changes in the size of the flies occur during the year. The smallest sizes are recorded at the peak of the population density.

Another morphological feature, the mesothoracic pattern of

Table 3. Morphological features of manbiting *S. damnosum*, Mbangayao village, Mselezi

Date of capture	Numbers per colour class		Tuft ratio of anterior basitarsi		Wing lengths	
	A	B	mean	range	mean	range
13. 10. 1966	1	6	0.253	0.17–0.30	1.960	1.80–2.15
30. 12. 1966	3	4	0.253	0.17–0.30	2.005	1.92–2.10
27. 1. 1967	1	5	0.266	0.25–0.30	1.927	1.84–2.00
16. 3. 1967	2	8	0.278	0.18–0.42	1.918	1.76–2.05
18. 4. 1967	0	10	0.245	0.17–0.30	1.869	1.78–1.95
2. 6. 1967	3	7	0.289	0.22–0.35	1.907	1.72–2.02
Totals	10	40	0.265	0.17–0.42	1.925	1.72–2.15

males, shows considerable variation in the Mselezi valley. Though no final conclusions are possible at present, further investigations might produce evidence that one of these patterns is unique for one or another cytotaxonomic category.

4.3. Seasonal fluctuations of biting population and premature stages

As it was to be expected from the previous survey in 1965 a clear seasonal pattern in the appearance of adults as well as of immature stages could be observed. The results are best shown in table 4 and figure 1.

It may be seen that at least a few biting females were present throughout the year, the lowest biting numbers being noted in the months September and October, the highest in the months March, April and May. Expressed as number of flies per man-hour, the monthly biting densities are based on one daily catch of 11.5 hours per week, i.e. 4–5 daily catches per month. In spite of the fact that daily biting catches on successive days might produce very different fly totals, the results of 4–5 daily catches per month can be regarded as sufficiently accurate to describe the seasonal fluctuations of the biting population. Figure 1 shows a connection between the drop in biting density and the drops of air temperature and air humidity at the beginning of the dry season. The biting numbers rise again only after the first rains of November and December, notwithstanding the constant rise in air temperature and air humidity since August. Virtually the same seasonal pattern in population fluctuations could be seen at some other places of the flyround, in Mselezi juu and Lupanga, whereas at others the appearance of biting females was restricted to the rainy season.

Table 4. Biting densities at Mbangayao

Year	Month	Environmental conditions				Fly density			Density of pupae and prepupae		
		Mean temperatures of catching sessions °C	Mean vapour pressure of water mm Hg*	Rainfall in Mbangayao mm	Estimated monthly water discharge Mselezi chini	Number of <i>S. damnosum</i> caught	Number of man - hours	Flies per man - hour	Number of pupae and prepupae / man - hour	Number of man - hours	Ratio <i>S. damnosum</i> all species
1966	March	24.6	21	645.3	> 1000	501	11.5	43.5	24.6	1.5	0.39
1966	April	24.7	20	272.0	> 1000	1570	23.0	68.4	50.0	1.5	0.79
1966	May	22.5	17	97.5	700	678	34.5	19.6	20.0	6.0	0.75
1966	June	21.5	15	9.5	300	305	46.0	6.6	3.0	6.0	0.21
1966	July	21.7	12	0.0	200	123	46.0	2.7	12.9	4.5	0.30
1966	August	22.8	14	3.5	150	97	57.5	1.7	5.6	4.5	0.16
1966	Sept.	24.5	15	34.0	100	50	46.0	1.1	0.4	5.0	0.01
1966	Oct.	24.8	16	57.0	100	28	46.0	0.6	15.2	5.0	0.25
1966	Nov.	25.3	18	173.0	100	88	46.0	1.9	3.3	6.0	0.10
1966	Dec.	26.2	19	234.0	200	121	46.0	2.6	13.7	9.0	0.42
1967	Jan.	25.7	19	136.0	250	327	57.5	5.7	42.9	7.5	0.47
1967	Febr.	25.5	19	360.5	500	372	46.0	8.1	40.3	9.0	0.52
1967	March	25.6	21	424.0	1000	429	46.0	9.3	27.6	10.5	0.73
1967	April	25.5	20	518.5	1300	759	46.0	16.5	—	—	—
1967	May	23.7	19	150.5	1000	1471	57.5	25.6	—	—	—
1967	June	21.4	15	43.5	600	476	46.0	10.3	2.0	6.0	0.20
1967	July	21.5	15	50.0	300	192	57.5	3.3	3.5	6.0	0.18

* Calculated from dry and wet bulb temperatures for a mean barometric pressure of 720 mm Hg.

The fluctuations of the immature stages of *S. damnosum* in the Mselezi stream were, though also dependent on the season, more irregular throughout the period of observation. This irregularity cannot be attributed to the sampling method, which after some experiments proved to be the most accurate under the circumstances. The differences in larval densities of *S. damnosum* during the months of the dry season were due to the sporadic appearance of comparatively high numbers of larvae at single larval habitats. The low densities or complete absence in other similar habitats at the same time indicate that these sporadic high densities must be the results of the coincidence of several favourable factors. During rainy season larval densities are occasionally reduced due to floodings in the months of high rainfalls. Highest larval densities were recorded when the current was constant or slowly decreasing and rainfalls frequent but not too heavy at the end of the rainy season, April 1966 and May 1967.

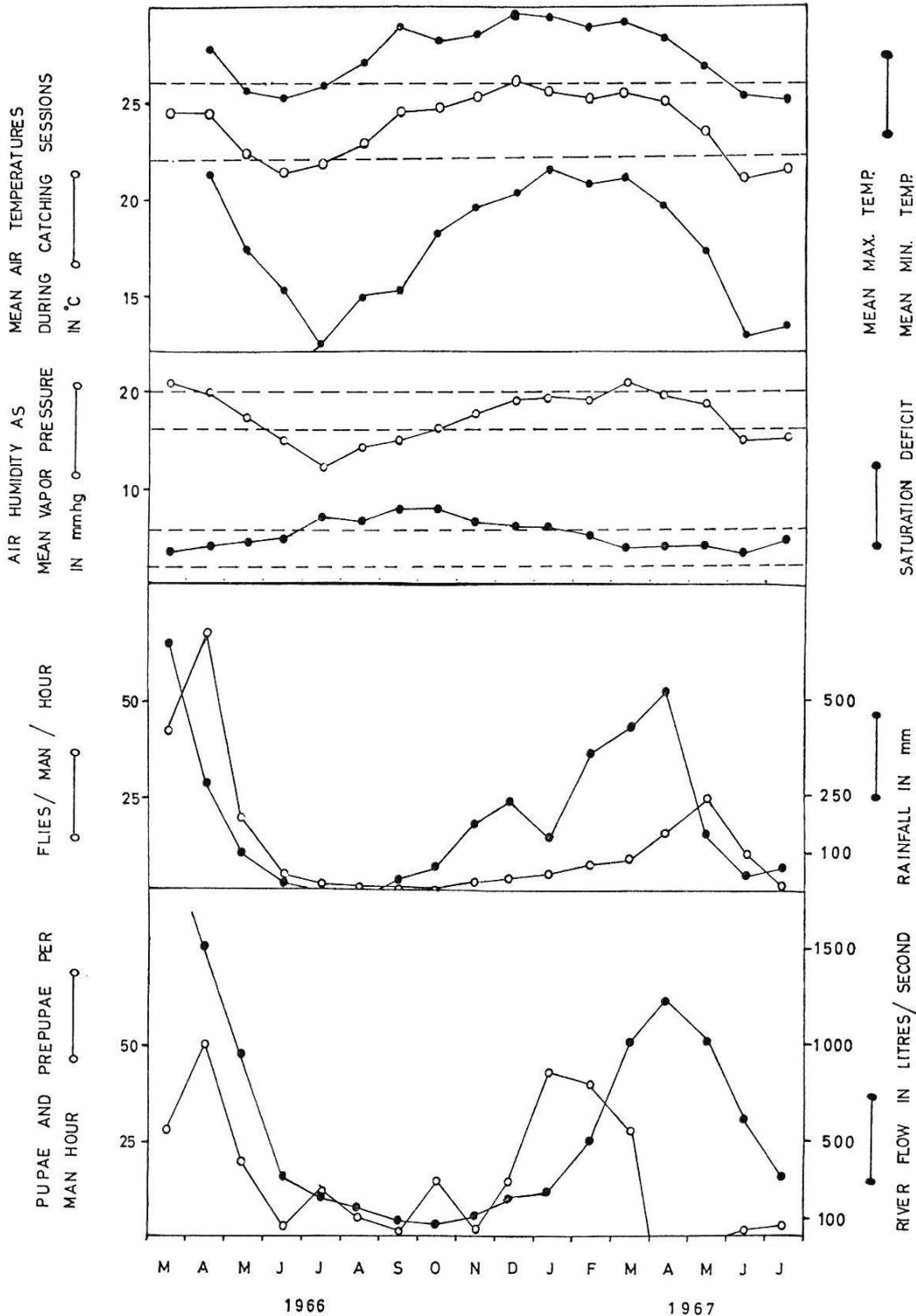


Figure 1. Seasonal fluctuations in the population density of *S. damnosum* and the seasonal variation of some environmental factors.

4.4. Age structure and infection rates of the *S. damnosum* population

4.41. Age grading technique

The age grading technique used in this study was based on the comparison of ovarioles, ovaries, malpighian tubules and fatbodies. It was developed in the first three months, March, April and May

1966. The females were dissected alive in 0.7% saline, first their abdomen for age diagnosis and afterwards their thorax and head separately for infection with sausage and infective larvae. From June 1966 onwards, females regarded as parous were fixed in alcohol 85% and dissected at a later moment, after staining in Myer's acid haemalaun, for sausage and infective larvae. From November 1966 to July 1967 the technician of the Rural Aid Centre in Ifakara, Mr. S. Biringi, was employed for these dissections.

As a rule the varying conditions of ovaries, malpighian tubules and fatbodies were sufficient to establish the parous state of a female. Presence or absence of follicular relics as final criterion was checked in doubtful cases only.

Three categories of ovaries were distinguished:

1. Nulliparous females: the ovarioles are tightly packed and all of the same shape and size. The ovaries are scarcely spread out under the weight of the coverslip and regain their shape quickly when the slip is shortly pressed. No follicular relics are observed.
2. Parous females: the ovarioles are still tightly packed, but when torn apart after slight pressure, the ovaries seem less elastic in regaining their normal shape. Follicular relics and sometimes also residual eggs are observed.
3. Old parous females: the ovarioles are loose in the ovary; this is not elastic and spread wide apart under the weight of the coverslip. The number of ovarioles per ovary seems less than in females of group 2. The follicular relics are sometimes rather large. Residual eggs or degenerating follicles were occasionally observed, especially with the beginning of the dry season. Once, on April 17, 1967, a female was caught which contained degenerating follicles exclusively.

As regards the malpighian tubules 4 categories were distinguished. The difference being made in their transparency, the four categories can be described as follows:

1. Malpighian tubules opaque except the ends towards the proctodeum.
2. Malpighian tubules still mainly opaque but with some small transparent sections.
3. The malpighian tubules are nearly half transparent and half opaque.
4. The transparent sections in the malpighian tubules prevail clearly. In some cases the tubules are even completely clear.

The tubules of stage 3 and 4 are more slender than in stage 1 and 2.

As regards the fatbody also four categories were distinguished. They can be described as follows:

1. Fatbody fully present in large opaque lobes.
2. Fatbody broken down into smaller less opaque lobules.
3. Fatbody reduced to some small translucent relics.
4. Fatbody completely absent.

The observed changes in ovaries, malpighian tubules and fatbodies obviously indicate rising age. The correlation between the observed categories of each single characteristic, however, does not permit to establish a more elaborate scale of age groups than that already given by OVAZZA et al. 1965a into nulliparous, young parous and old parous females. Females with malpighian tubes of category 2 and fatbodies of category 3 or 4 had usually ovaries of category 2 and were grouped as young parous. Females without fatbody, ovaries of category 3 and malpighian tubes of category 3 or 4 were classified as old parous.

The arrangement into young parous and old parous females based on ovaries and malpighian tubules, however, corresponds only partly with the results of the inspection for sausage, preinfective and infective larvae, the two groups correspond therefore not to groups of mono- and multiparous females.

4.42. Age structure

From March 1966 to July 1967 a total of 13 378 flies were dissected. 2507 or 18.8% of these were parous. From March to May 1966 only nulliparous and parous females were distinguished. Afterwards the parous females were differentiated into young and old parous females according to the appearance of their ovaries and malpighian tubules. The parous rates may differ considerably from day to day, but the results, obtained from 7–12 day-long catching sessions per month, provide a sufficiently large sample to represent the fly population in the valley. The results of the age grading show a clear seasonal pattern corresponding to that of the biting density (table 5, figure 2). The population build-up starts in November and December with practically equal numbers of parous and nulliparous females. The parous rate then decreases with the increase in the population and keeps more or less constant during the dry season when the biting population starts to decrease and breeding is largely reduced.

Table 5. Age structure and infection rates of the *S. damnosum* population in the Mselezi valley (based on 7–12 catching days per month on 2–4 places)

Month	Total No. of flies dissected	No. parous	No. young parous	No. old parous	No. of flies with developing infections	No. of flies with infective larvae in the head
March 1966	66	9	–	–	0	–
April	255	30	–	–	6	0
May	641	123	–	–	63	1 (1) *
June	629	128	110	18	48	5 (3)
July	351	97	67	30	45	5 (4)
August	157	42	18	24	11	0
September	149	32	21	11	11	1 (1)
October	53	15	10	5	10	1 (1)
November	157	77	36	41	22	5 (4) **
December	277	145	55	90	35	5 (4)
January 1967	527	172	53	119	62	11 (10)
February	576	92	42	50	43	7 (7)
March	1,324	223	104	119	73	8 (6)
April	2,384	399	255	143	182	12 (8)
May	3,516	594	470	124	234	18 (16)
June	1,597	240	166	74	58	3 (3)
July	619	89	57	32	22	4 (3)
Total	13,378	2,507			925	86 (71)
Total June 1966 to July 1967	12,416	2,345	1,465	880	856	85

* Figures in brackets = No. of double infections.

** 3 parous females with infective forms in the abdomen are not included in this table.

4.43. Infection rates

The infection rates of parous females differed also considerably on different days, but in this case the combined results of 7–12 catching days per month show no seasonal fluctuations.

940 or 37.5% of all parous flies were infected or infective, i.e. the overall percentage of infected flies was higher than the one observed by DUKE (1968a, b) in the *S. damnosum* population at Bolo in the Cameroon forest and the one observed by RAYBOULD (1967) in Amani on a *S. woodi* population. At the same time the total parous rate and the total infectivity rate were considerably lower than the corresponding rates in Bolo.

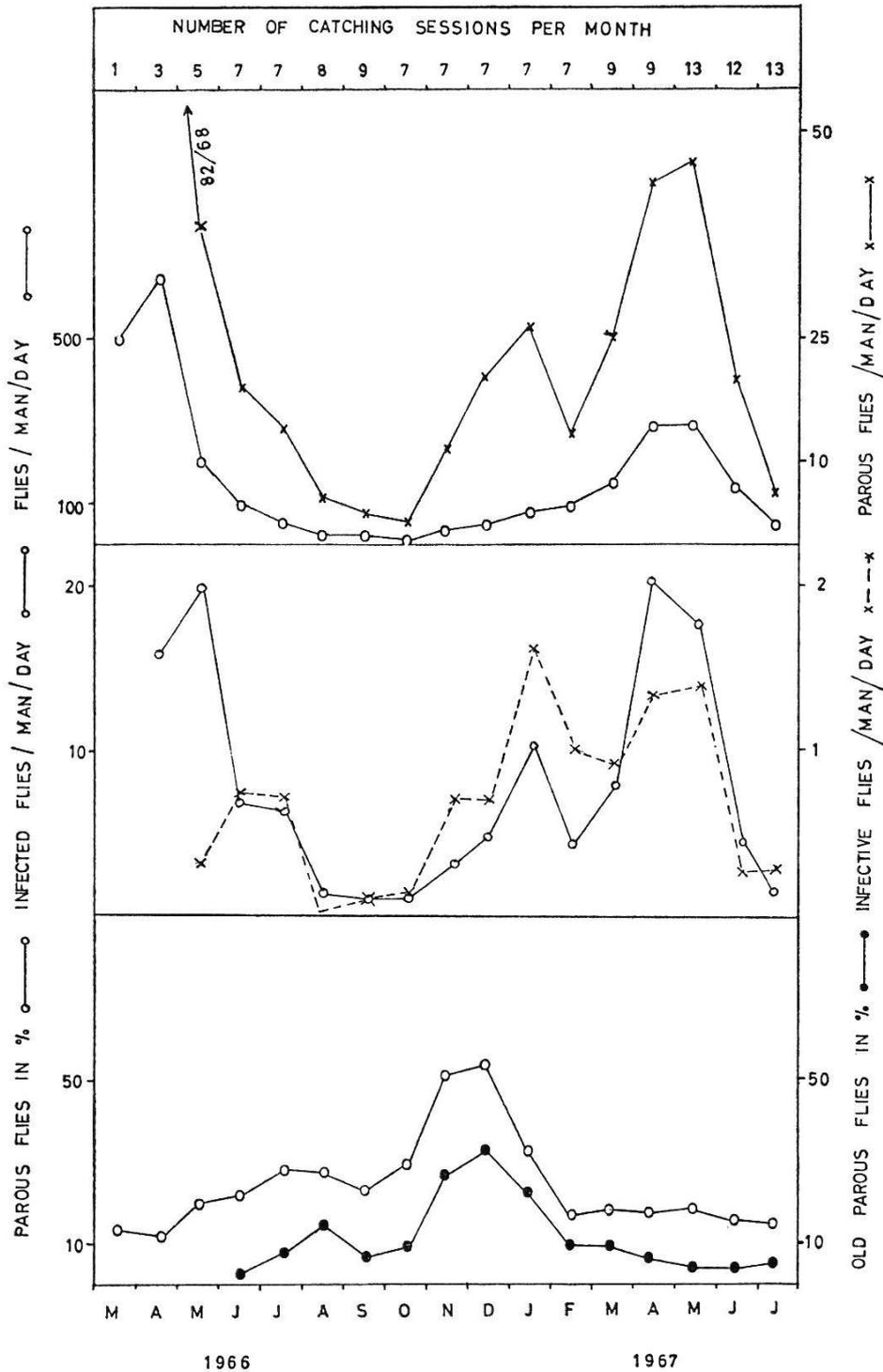


Figure 2. Annual cycles in biting density of the different components of the *S. damnosum* population in the Mselezi valley.

The kind of infection of the 871 infected parous females caught from June 1966–July 1967 is shown in table 6.

It is remarkable that the number of infective flies carrying also developing parasites was 71 or 82% compared to 29% in case of the *S. damnosum* population in the Cameroon forest.

Of the 871 infected parous females 559 were young parous and 312 were old parous. Of the young parous flies 22 had infective

Table 6. Mean numbers and range of parasites in 871 infected parous flies

Number of flies	Sausage larvae	Preinfective larvae	Infective larvae
704	4.8 (1-51)	—	—
39	—	2.2 (1-10)	—
15	—	—	2.5 (1-6)
43	3.6 (1-32)	2.2 (1-8)	—
17	3.5 (1-12)	—	4.2 (1-11)
32	—	1.9 (1-5)	2.1 (1-4)
21	2.9 (1-9)	2.7 (1-6)	3.6 (1-8)

larvae and of the old ones 63. Preinfective larvae were found in 40 young females and 95 old females.

4.5. Environmental influences on biting activity

In the Mahenge mountains as anywhere else (DE MEILLON 1957) *S. damnosum* tends to bite on the lower legs and only rarely attacks arms or exceptionally also face and neck. When the biting density is high, flies often creep also under long trousers and bite above the ankles. The fly boys showed remarkable differences in their attractivity for *S. damnosum*. This attractivity was, however, not a constant feature but seemed dependent on the place, time and general biting activity.

In the season of high population density biting was observed almost anywhere out of doors except in dense forest. With decreasing population density biting stopped first on the bare places in and around the hamlets and in the shadow of the mango trees. All the year round biting was observed in clearings of the forest on the slopes, mostly old abandoned rice fields. At the bottom of the valley biting flies were extremely rare in late dry season.

The relations between biting activity, air temperatures and air humidities are shown in figure 3 a + b, where the mean numbers of biting flies per man-hour are plotted against air temperature and vapour pressure of water. The favourable air temperatures and air humidities under which most biting females were caught lie between 22° and 26°C and 16-20 mm Hg vapour pressure, respectively 2-6 mm Hg saturation deficit. If these results are compared with figure 1 concerning the fluctuations of the population, it becomes obvious that the biting activity and the population in consequence are decreasing when mean air temperature and mean air humidity drop below the favourable range during daytime. In the same time also the minimal temperatures of the nights are more

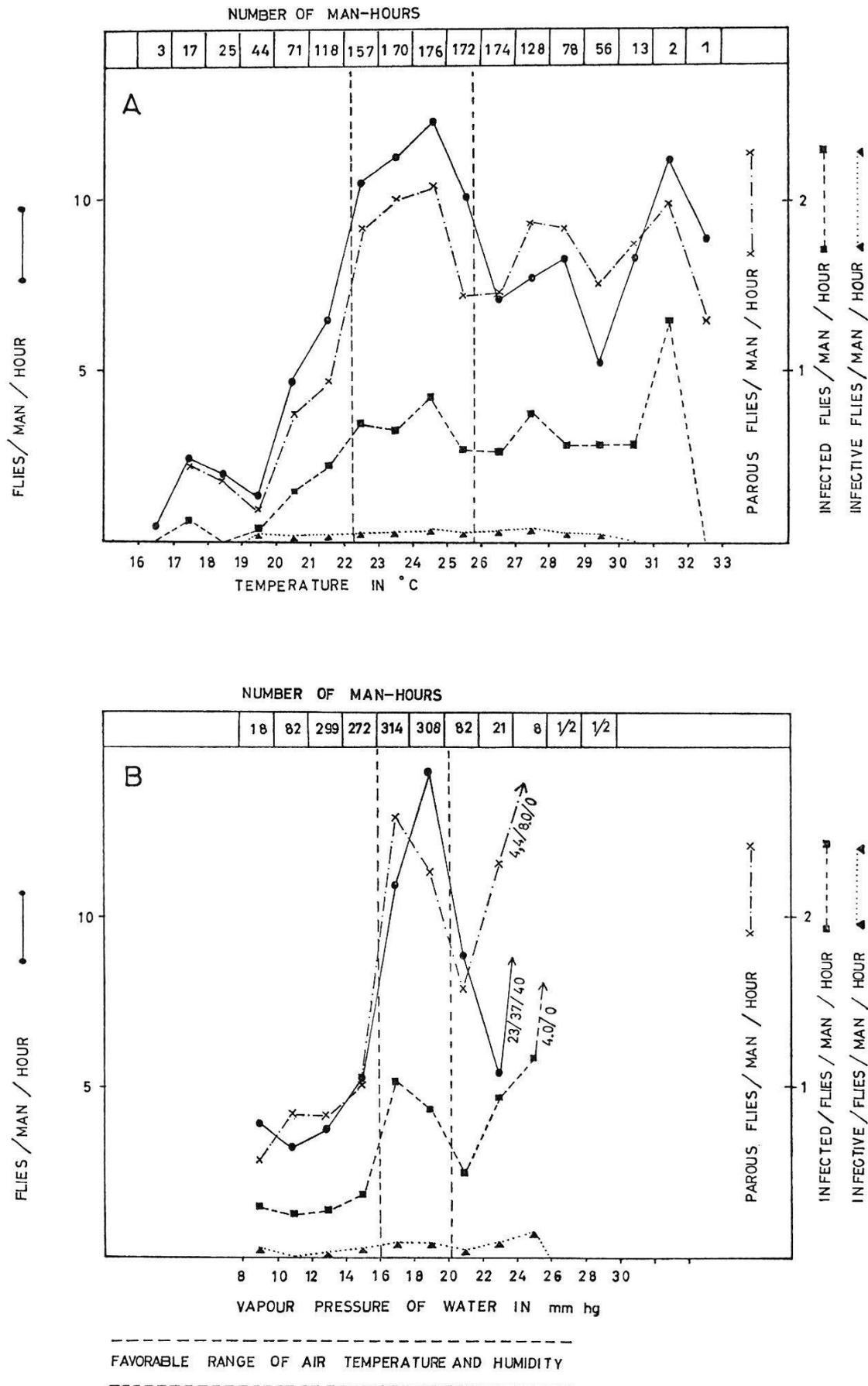


Figure 3. The relations between biting activity and the environmental factors air temperature (A) and air humidity (B).

and more frequently below 16°C, which was the lowest temperature at which biting was observed.

The biting density increases again when temperature and air humidity are in the favourable range and the rainy season starts.

Between different age groups or infected and non-infected flies no differences in biting behaviour can be observed in relation to air temperature and air humidity.

Biting was observed up to temperatures of 36°C, the highest temperature which was recorded in the area.

The daily biting cycles show usually two peak biting periods and a midday lull during months with favourable temperatures, but progressively lose this pattern in the cooler months while the population is decreasing. The pattern then reappears again more and more regular during the months of population increase. Figure 4 shows the biting cycles for the stagnating population with a low biting rate from August to October, for the increasing biting population at the beginning of the breeding season from November to January, for the main breeding season from February to April and for the decreasing population from May to July. For parous, infected and infective flies the biting density was normally higher in the morning except in late dry season, when biting concentrated more on the afternoons.

The light conditions were recorded as sunshine if the fly boys were throwing a shadow or diffuse light, when the sun was completely covered by clouds or behind the mountains and no shadow was thrown. The cloud coverage was estimated in tenths of the whole visible sky. The influence of cloud coverage and light on the biting activity is shown in figure 5, in which the dates of all captures are combined. The figure shows that the biting activity increased rapidly with increasing cloud coverage up to about 6/10 under diffuse light conditions and up to 9/10 in sunshine. The different components of the population differ not remarkably from each other in their reaction to the light conditions.

The wind velocity was estimated according to the movements of the vegetation. Whereas little wind, moving only grass and leaves or little twigs, had no remarkable influence on the biting activity, no biting at all was observed in the few cases when the wind was moving heavier branches of trees. Short drizzling rains had practically no influence on the biting activity and only a short heavy downpour or a longer rain reduced and even stopped the biting numbers for that time.

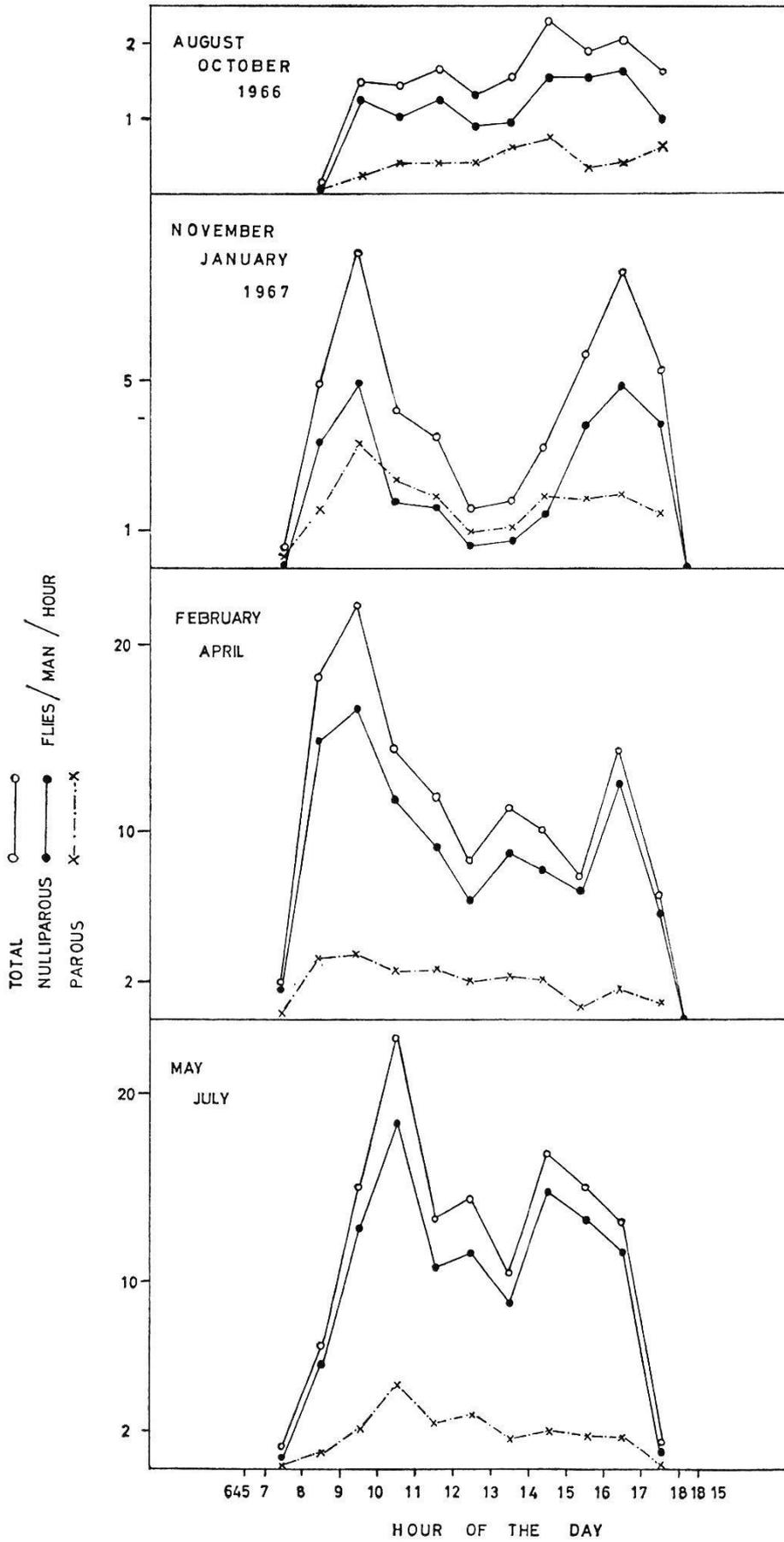


Figure 4. The variation of the biting cycles in the *S. damnosum* population under the influence of seasonal changes.

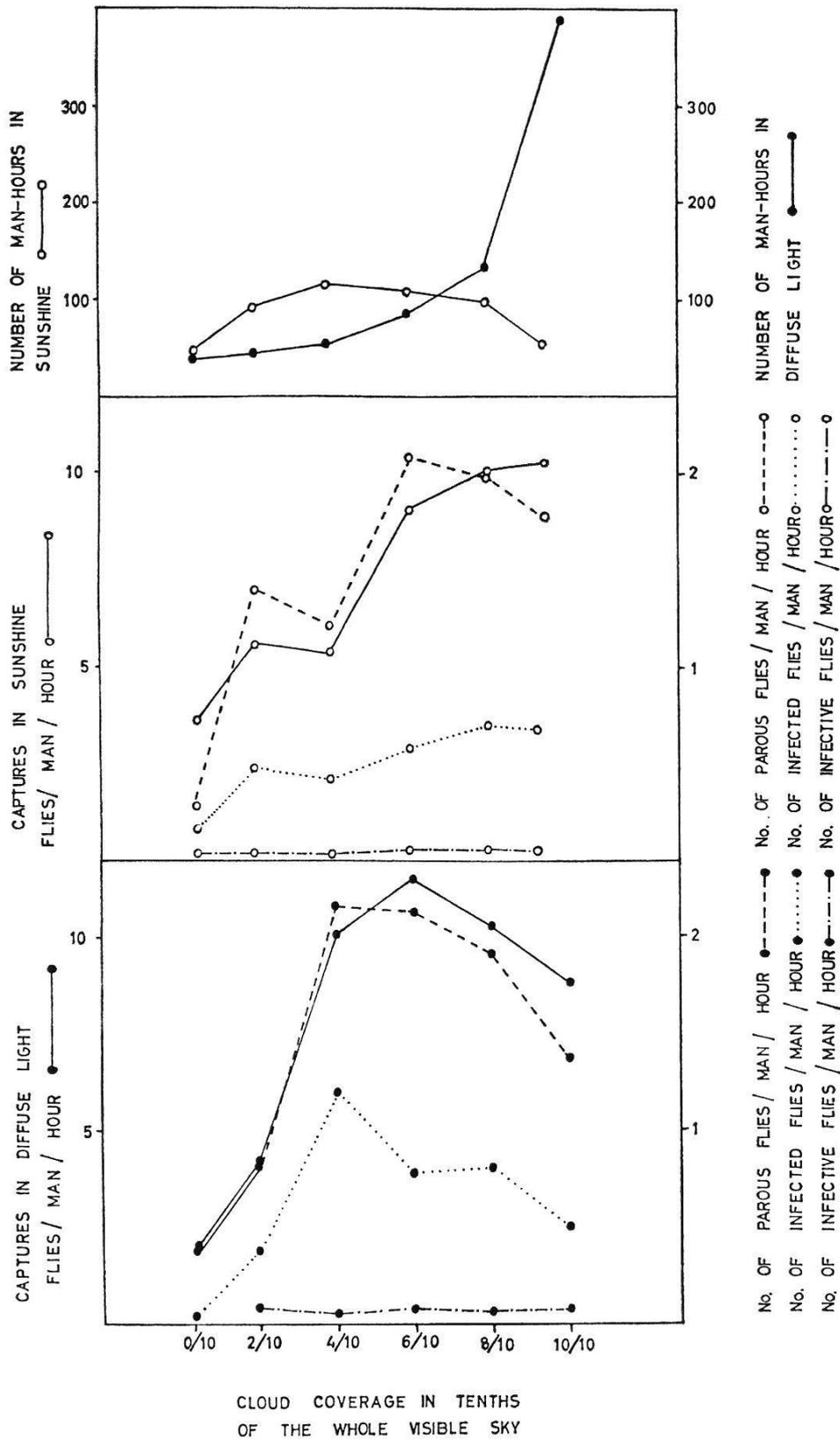


Figure 5. The influence of the light conditions on the biting activity of *S. damnosum*.

4.6. Distribution and dispersal

4.6.1. Distribution

The perennial larval habitats on which *S. damnosum* larvae can be found in late dry season are restricted to rapids in larger streams, mostly in medium and lower altitudes. At the same time biting flies are mainly caught in medium altitudes and not in lower altitudes where the larval habitats are more favourable. When the biting numbers increase after the first rains, the increase is more remarkable in medium altitudes though the larval numbers increase first in the larval habitats of the lower altitudes. Only in the second half of the rainy season, when the upper parts of the streams discharge more water and the non-perennial rivulets start to flow again, the breeding of *S. damnosum* spreads over the whole area of the Mahenge mountains shown on map 1.

Differences in biting numbers between the 8 catching stations of the flyround in different altitudes, shown on table 7, and occasional observations in other localities permit the following generalizations on the distribution of *S. damnosum* in the eastern part of the Mahenge mountains.

In altitudes between 500 and 1000 m above sea level the biting densities are the highest throughout the year in this area and the highest biting numbers are recorded for clearings in the forest or

Table 7. Biting densities at different catching stations of the flyround

Catching station	Daytime of visit	FMH *						Total flies per station	FMH for all 34 fly-rounds
		April 1966	May-July 1966	Aug.-Oct. 1966	Nov.-Jan. 66/67	Feb.-April 1967	May-July 1967		
Chirombola	8.00-8.20	1	1.0	0	1.6	0.2	0.3	23	0.7
Mselezi chini	8.40-9.00	26	4.5	0.1	1.1	1.3	1.2	78	2.3
Lupanga shule	9.20-9.40	69	11.1	0.3	2.8	6.5	4.7	227	6.7
Chiwambu	10.20-10.40	130	18.5	0.9	1.8	37.7	24.0	631	18.5
Liatu	11.40-12.00	54	14.3	1.3	1.8	26.3	18.3	421	12.5
Mbangayao	12.40-13.00	63	8.3	0.1	2.1	1.0	9.2	192	5.6
Nasanji	15.20-15.40	29	7.8	1.4	2.9	16.3	1.7	217	6.3
Isongo juu	16.00-16.20	6	0.8	0.7	1.5	0.7	1.5	41	1.2
Total number of flies per period		378	389	34	124	540	365	1,830	6.7
FMH/per quarter of year			8.0	0.6	2.0	11.2	7.6		

* FMH = flies per man-hour.

woodland used for rice cultivation (e.g. Chiwambu, Liatu). On the bottom of the valley the biting numbers are usually smaller (e.g. Lupango shule, Mbangayao), although here record biting numbers are also possible during the period of highest population density. In lower parts of the valley, below about 500 m biting is by far not so frequent, even when the biting population is at its peak, e.g. Mselezi chini, Chirombola. Further in the plains, *S. damnosum* is occasionally caught on man during rainy seasons only and e.g. in Mwaya, 9 km from the next larval habitat, not noticed by the people. In higher altitudes over about 1000 m biting density is again decreasing compared to medium altitudes (Nasanji ca. 950 m, Isongo juu ca. 1050 m), but *S. damnosum* and *S. woodi* are occasionally caught up to 1500 m (highest altitudes in the Mahenge massif).

4.62. *Dispersal*

An upwards directed migration of newly hatched females may extend over 20–40 km – the largest distances between the favourable larval habitats in lower altitudes to biting localities in the upper regions –, whereas the random dispersal from the Mahenge mountains into the surrounding plains seems to be negligible. The extremely low biting density on the catching station Chirombola, within 2 km distance of two favourable larval habitats, demonstrates this. Inside the Mahenge mountains, however, the dispersal activity must be regarded as very intense. Marking experiments were conducted on four different places from March to May 1967 in order to gain some information on dispersal activity. 33 430 flies caught on human bait were marked and released. 312 of these were caught again within 0–9 days after release and in distances of 0–5 km from the point of release. The biggest distance of approx. 5 km was covered by an uninfected parous fly in not more than 6 hours, i.e. at 14.00 h after release of the first batch of 25 marked flies at 08.00 h in the same morning. Another fly was caught 3½ km from the point of release not more than 9¼ hours after marking. The results of the marking experiments are shown in table 8 and on map 3. The recaptures demonstrate that *S. damnosum* covers considerable distances in biting mood, may be in direct pursuit of human bait or following the numerous footpaths connecting the various hamlets with the ricefields on the slopes.

When the biting population started to decrease, suddenly extremely high numbers of biting flies were caught again after some weeks of low biting numbers. It is possible that immigration of larger numbers of flies from other areas, probably from higher

*Table 8. The results of the marking experiments**Table 8 a. Preliminary marking experiments*

Date	Place	Kind of marking	Number marked	Recaptures			
				Date	Number checked	Number marked	Age
14. 9. 66	Lupanga	by hand on thorax	25	15. 9. 66	16	—	old parous
				17. 9. 66	28	1	
				20. 9. 66	7	—	
12. 11. 66	Mbangayao	by hand on thorax	52	14. 11. 66	34	1	nulliparous
				16. 11. 66	36	—	
				18. 11. 66	45	—	
31. 12. 66	Mbangayao	by spray	190	3. 1. 67	127	—	young parous
				5. 1. 67	218	—	
				7. 1. 67	224	—	
				9. 1. 67	216	1	
				11. 1. 67	205	—	
11. 1. 67	Mbangayao	by spray	205	15. 1. 67	264	—	nulliparous
				17. 1. 67	185	2	

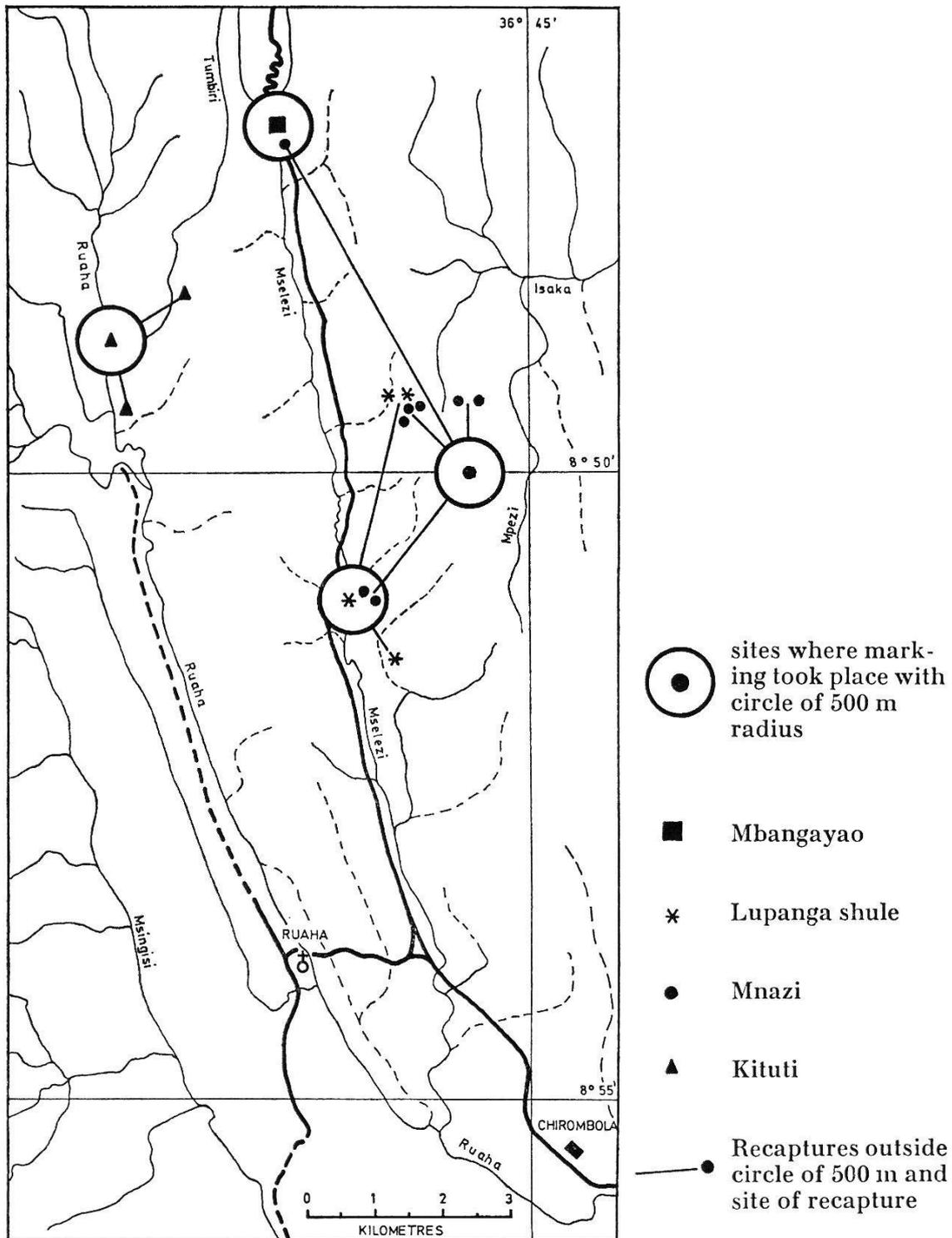
Table 8 b. Marking experiments for dispersal (see also map 3)

Date	Place	Number marked	Marked recaptures in distance from point of release						Date and age of recaptures after end of campaign
			0.5 km	1 km	2 km	3 km	4 km	5 km	
21. 3. to 25. 3. 1967	Mbangayao	5,711	61	—	—	—	—	—	29. 3. 1967 1 nulliparous 1 young parous
12. 4. to 18. 4. 1967	Lupanga	10,385	51	1	—	2	—	—	
27. 4. to 2. 5. 1967	Mnazi	8,261	106	2	3 *	—	2 **	1 ***	4. 5. 1967 1 young parous
9. 5. to 14. 5. 1967	Kituti	9,073	79	2	—	—	—	—	

* All 3 parous.

** 1 parous, 1 nulliparous.

*** 1 old parous.



Map 3. The results of the marking experiments.

altitudes, induced by cooler temperatures, is responsible for this sudden increase in biting in a decreasing population.

The marking experiments demonstrate also that *S. damnosum* females may remain nulliparous for a considerable period after a first unsuccessful attempt to get a bloodmeal. Preliminary marking experiments for testing the marking method carried out in a period of low population density as well as the final experiments about

dispersal in the period of high biting density gave similar results in this connection. The results of all marking experiments are shown in table 8.

4.7. Vector control in the Mselezi valley

From March 31st to May 31st the Mselezi stream was treated with DDT in fortnightly intervals. The application of DDT was carried out with the apparatus shown in figure 6. The apparatus granted a regular outflow and quick distribution of DDT emulsion into the stream for 15 or 30 minutes according to the amount of emulsion prepared in the drum. A 25% DDT emulsifiable concentrate with the designation A-661 B of Geigy Ltd., Basle, was used for all treatments. The concentration for the applications was selected empirically in the first treatment. In rainy season with a water discharge of about 1000 l/sec. the lowest DDT concentration killing all Simuliid larvae for more than 1 km downstream was 0.04 ppm for 15 minutes. River treatment from two points (map 2) with concentrations of 0.12 ppm for 15 minutes was sufficient to kill all Simuliid larvae in the Mselezi from Mbangayao village

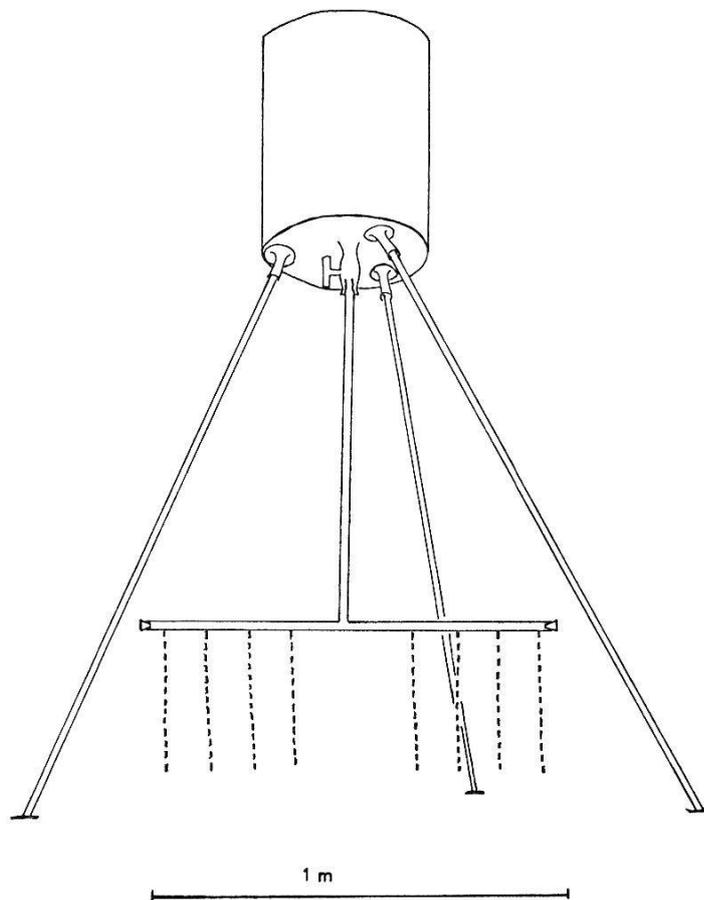


Figure 6. The apparatus for DDT application.

downstream to the junction between Mselezi and Ruaha, but spared all fishes, crabs, freshwater prawns and a small proportion of other insect larvae, especially trichoptera, coleoptera and odonata. With the decrease of the water level a third dosing point became necessary for the last treatment on May 31st. In dry season when the water discharge was about 100 l/sec., a DDT concentration of 1 ppm for 15 minutes killed Simuliid larvae for less than 1 km downstream but killed also all other water insects for this distance and many freshwater prawns and some fish of the species *A. krefftii* and *B. kurumani*. Further experiments for dry season treatment of the perennial larval habitats were not justifiable after these first experiences.

Table 9. The influence of river treatment on Simuliid larvae

Remarks to collections of larvae	Date	Man - hours spent for collecting larvae	Larvae			Prepupae			Pupae		
			<i>S. damnosum</i>	Others	Relation <i>S. damnosum</i> : Total	<i>S. damnosum</i>	Others	Relation <i>S. damnosum</i> : Total	<i>S. damnosum</i>	Others	Relation <i>S. damnosum</i> : Total
Before 1st treatment	30. 3. 1967	1	222	121	0.65	53	30	0.64	53	19	0.74
Treatment I	30. 3.										
1. check	31. 3.	8	6	9	0.38	1	3	0.25	344	138	0.72
2. check	5. 4.	3	28	37	0.43	3	2	0.60	3	6	0.33
3. check	13. 4.	7	724	115	0.85	4	8	0.33	1	3	0.25
Treatment II	13. 4.										
1. check	14. 4.	9	0	0	—	0	0	—	0	21	—
2. check	19. 4.	7	1	84	0.01	1	8	0.11	0	1	—
3. check	27. 4.	1	196	149	0.57	2	12	0.14	0	10	—
Treatment III	28. 4.										
1. check	29. 4.	5	0	1	—	0	0	—	0	36	—
2. check	4. 5.	5	0	6	—	0	3	—	0	1	—
3. check	11. 5.	7	58	456	0.11	2	55	0.04	0	4	—
Treatment IV	12. 5.										
1. check	15. 5.	5	1	13	0.07	1	3	0.25	0	18	—
2. check	22. 5.	4	1	12	0.08	0	0	—	0	2	—
3. check	29. 5.	8	372	807	0.32	3	128	0.02	0	13	—
Treatment V	31. 5.										
1. check	2. 6.	8	1	14	0.07	1	2	0.33	5	33	0.13
2. check	15. 6.	3	22	458	0.05	0	27	—	0	22	—
3. check	29. 6.	8	118	660	0.15	44	101	0.30	55	137	0.29

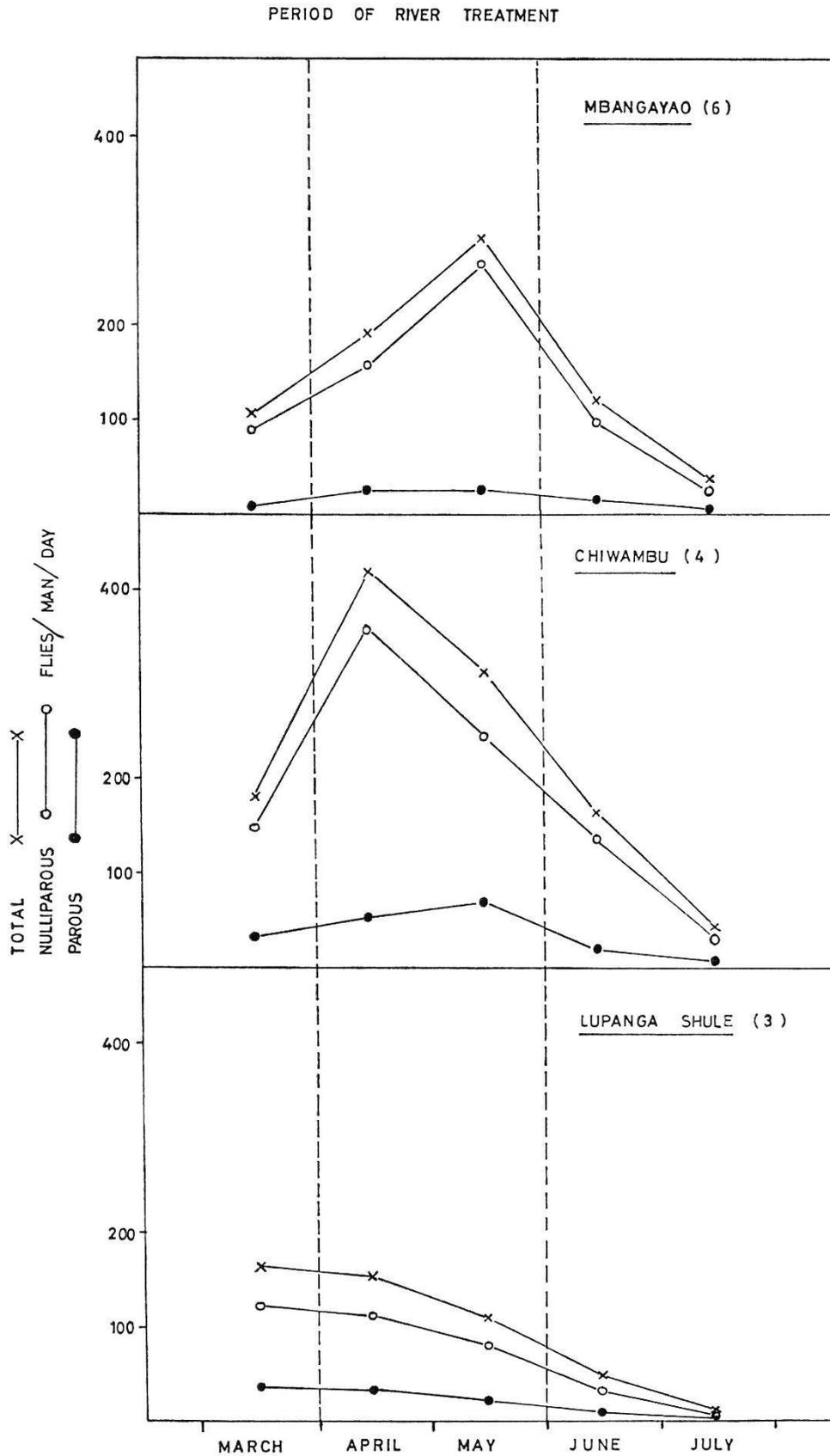


Figure 7. The influence of the river treatment on the biting population at three different places in different distances from the centre of the eliminated breeding area (compare map 2).

The influence of the river treatment on Simuliid larvae and information on the speed of repopulation and development is given in table 9. At the prevailing water temperatures between 20° and 24°C, the first prepupae of *S. damnosum* were found 14 days after the treatment and the first pupae 16 days afterwards. Pupae of the species of the groups I, II and IV were always found earlier, which can be explained by the fact that these species breed also in the tributaries and immigrate continuously into the Mselezi stream.

The DDT treatment in fortnightly terms is therefore automatically more selective for *S. damnosum* and *S. vorax*, which breed with few exemptions in the main stream only.

The influence of the river treatment on the biting population is shown in figure 7, where the biting densities of three catching stations before, during and after the treatment are compared. In the centre of the breeding area the numbers were decreasing since the onset of the treatment, whereas on the periphery the biting numbers were increasing according to the general improvement of breeding conditions in the whole area of the eastern Mahenge mountains. The control experiment restricted to the Mselezi stream demonstrates herewith clearly the dispersal activity from one valley to another.

Figure 1 on the seasonal fluctuations of biting *S. damnosum* shows that in the months of treatment the biting density was lower than in the corresponding months the year before. This lower density, however, cannot be ascribed entirely to the DDT treatment. The first rains in November and December 1966 were not very plentiful and the discharge of the Mselezi stream never reached a favourable level for breeding of *S. damnosum* until mid of March, i.e. the population build-up started very slowly and many larval habitats were not occupied by *S. damnosum* until April. Naturally the elimination of the numerous larval habitats in the Mselezi during the period of highest reproductive activity has reduced the biting density at certain places like Mbangayao or Lupanga shule in addition to lower density in the whole area, but this reduction is certainly less important than the fact that many larval habitats could be occupied by *S. damnosum* two or even three months later than in the previous year.

5. Discussion

5.1. *Factors influencing the seasonal fluctuations of the biting population*

The sporadically high numbers of *S. damnosum* larvae in one or other larval habitat during the dry season prove that in the

Mahenge mountains larval habitats favourable for *S. damnosum* are present throughout the whole year. This indicates that not a lack of suitable larval habitats – as in some areas of West Africa (OVAZZA et al. 1965 a, b, 1968) – is primarily responsible for the reduction of the breeding and biting activity at the beginning of the dry season – at which time more suitable larval habitats are present than at the beginning of the breeding season – but that other environmental factors influence the adult population.

In figure 4 it is attempted to describe the relations between air temperatures, air humidity and biting density and to define the favourable range of these factors. As figure 1 shows increasing or high biting densities and high larval densities are only observed when the monthly means of these factors are within the favourable range. Figure 4 shows how the daily biting cycles change during periods in which the mean values of these factors are outside the favourable range. From May–July biting starts later in the morning and stops earlier in the afternoon and from August to October biting is not only reduced, but the normal two peak biting pattern disappears almost completely because the periods with favourable conditions during the day are short and irregular. It seems that for biting or lastly for the whole reproductive activity in the Mahenge area air temperature and air humidity are limiting factors and influence the daily as well as the annual biting cycle.

The high proportion of parous flies observed at the beginning of the rainy season, when the population started to increase, could be explained by the fact that at this time favourable air humidity and air temperature induced increasing reproductive activity without corresponding increase in nulliparous females due to still unfavourable conditions at most of the larval habitats. As soon as the water level rises and the environmental conditions for the larvae improve, the proportion of nulliparous females increases.

5.2. *Transmissions of onchocerciasis*

The infective density (figure 2) shows distinct seasonal fluctuations, corresponding more or less to the parous and the overall biting density. The main transmission period is the rainy season.

Topographically the highest infective biting densities were observed in medium altitudes where also the highest biting densities were recorded. Since the distances from the next larval habitats are everywhere very short in rainy season, no outstanding differences of the infective biting density are observed in different places. In higher and lower altitudes the infective biting density was lower

as was to be expected from the lower overall biting density. The observation corresponds also with the lower infection rates in the human population, especially remarkable in younger age groups.

Although a large proportion of the human population is infected in the mountain area, serious symptoms e.g. blindness are rare. This could be explained either by the comparatively low infective biting density and consequently slight human infections, or indicate that a forest strain of *O. volvulus* is present, which produces less serious symptoms than the savannah strains of West Africa.

The overall ratio of infective flies to flies with developing infections is with 0.10 considerably lower than the ratio found in the Cameroon forest (DUKE 1968 a). At the same time the proportion of infected parous flies is with 0.37 considerably higher than there. As a possible explanation for these diverging results an unusually high mortality rate of infected females is considered. Such a mortality could also be responsible for the low parous rate, the females being affected before they are ready to bite for a second time. The low mean numbers of developing or infective larvae per fly would support this interpretation, indicating furthermore that flies with lower infections have a better chance to survive.

5.3. *The possibilities of vector control*

A control experiment in the Mselezi stream revealed that it is possible to kill *S. damnosum* larvae with low doses of DDT and to eliminate the stream as breeding ground without serious side effects for the other river fauna. The control resulted also in a slight reduction of the biting density in the centre of the breeding area but was without visible effect on the infective biting density. It demonstrated furthermore the dimensions of the immigration from other breeding areas and made clear that in order to attain a remarkable reduction in biting density in a selected area of the Mahenge mountains, the rivers of a much larger area have to be treated. In the case of the Mselezi valley a control campaign should probably include all breeding streams in map 1.

Since such a control campaign would have to be carried out annually for many years without any prospects for complete vector eradication, it is not justifiable if it is not combined with mass treatment of the disease in the human population.

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Zusammenfassung

1. Die Biologie von *S. damnosum* im Mselezi Valley, einem kleinen Tal im weiten Onchocercose-Gebiet von Mahenge, wurde während mehr als einem Jahr studiert.

2. Es folgen eine allgemeine Beschreibung der Gegend sowie Angaben über die Infektionsraten verschiedener Altersgruppen der einheimischen Bevölkerung.

3. Die verschiedenen Simulien-Arten, die mit *S. damnosum* im selben Gebiet vorkommen, werden aufgezählt und ihre Beziehung zueinander und zur Umwelt diskutiert.

4. Die Struktur der *S. damnosum*-Population wird untersucht, und es wird festgestellt, welche der vom *S. damnosum*-Komplex bekannten Rassen und Arten im Gebiet vorkommen.

5. Jahreszeitliche Fluktuationen der Stechaktivität werden aufgezeigt und mit den Umweltfaktoren in Zusammenhang gebracht.

6. Die meisten stechenden Weibchen sind nullipar. Die Stechaktivität von paren Weibchen ist niedrig, und nur wenige von diesen erweisen sich als infektiös.

7. Der Umweltseinfluß auf die Stechaktivität und der Stechzyklus werden beschrieben.

8. Auf Grund von Larven- und Adultfängen aus dem ganzen Gebiet sowie von Markierungsexperimenten werden Verbreitung und Dispersion der Art besprochen.

9. Die Aussichten einer Bekämpfung werden abgeschätzt auf Grund von Resultaten eines auf das Mselezi-Tal beschränkten Versuches.

Résumé

1. Pendant plus d'une année, la biologie de *S. damnosum* a été étudiée à Mselezi Valley, une petite vallée dans la vaste zone d'onchocercose de la région de Mahenge.

2. L'aspect géographique de la région et le taux d'infestation de différents groupes d'âge de la population indigène sont décrits.

3. On énumère les différentes espèces de Simulies rencontrées dans la même région que *S. damnosum* et on discute leurs relations écologiques.

4. La structure de la population de *S. damnosum* est étudiée et les races et espèces présentes du complexe *S. damnosum* sont déterminées.

5. Les fluctuations saisonnières de l'activité des Simulies (fréquence de l'acte de piquer) sont démontrées et mises en rapport avec la nature des milieux.

6. La plupart des femelles piquantes sont nullipares. Les femelles pares piquent peu et seul un petit nombre d'entre elles se sont révélées infectieuses.

7. L'influence du milieu sur l'acte de piquer ainsi que les cycles journaliers de cette activité sont décrits.

8. La distribution et la dispersion de l'espèce sont discutées sur la base de captures de larves et d'adultes, ainsi que sur des expériences menées avec des femelles marquées.

9. La possibilité d'une lutte est évaluée d'après des résultats obtenus lors d'un essai limité à la vallée de Mselezi.