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Autor(en): **Marti, H.P. / Tanner, M. / Degrémont, A.A.**

Objektyp: **Article**

Zeitschrift: **Acta Tropica**

Band (Jahr): **42 (1985)**

Heft 2

PDF erstellt am: **14.05.2024**

Persistenter Link: <https://doi.org/10.5169/seals-313467>

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¹ Swiss Tropical Institute, Socinstrasse 57, CH-4051 Basel, Switzerland

² Swiss Tropical Institute Field Laboratory, P.O. Box 53, Ifakara, Tanzania

Studies on the ecology of *Bulinus globosus*, the intermediate host of *Schistosoma haematobium* in the Ifakara area, Tanzania*

H. P. MARTI¹, M. TANNER², A. A. DEGRÉMONT¹, T. A. FREYVOGEL¹

Summary

During a period of 2 years, the ecology of *Bulinus globosus* was studied in 8 habitats in two streams near Ifakara, SE-Tanzania. The relative *Bulinus* densities were followed monthly. Two different methods for estimating snail densities (man/time vs. palmleaf traps) gave comparable results. *Bulinus* densities were constantly low throughout the year in the stream, but they showed distinct seasonal fluctuations in adjacent pools, with a density-peak at the end of the small rainy season. *B. globosus*, identified by starch gel electrophoresis, was found to be the only intermediate host for urinary schistosomiasis in the investigated streams. A correlation of the *Bulinus* densities with several abiotic and biotic factors revealed that pH, temperature and conductivity had little effect on the *Bulinus* population, as they oscillated within the tolerated limits. No correlation of the distribution of *B. globosus* and other snail species was found. Rainfall patterns have a distinct influence on snail densities. They determine the duration of desiccation and affect the snails by fluctuations of the water level and by the fast increase of water velocity after heavy rains. *B. globosus* shows a clear predilection for the sedge *Cyperus exaltatus* as support for oviposition. It is also preferred as food and/or food-support. During the dry season, oviposition of *B. globosus* is concentrated in clearly defined sites ("breeding pockets"), which, due to the lowering of the water level, become isolated from the stream or retain only a small connection to it. These sites form important reservoirs of *B. globosus*, from where the snails are spread when the sites are flooded during the subsequent rainy season. The significance of these observations for control measures is discussed.

* This study forms part of a PhD thesis by the first author. The complete thesis entitled "Population dynamics and ecology of *Bulinus globosus* (Mollusca, Gastropoda) in selected habitats in the Ifakara area, Tanzania" is available upon request at the library of the University of Basel, Switzerland

Key words: *Bulinus globosus*; *Schistosoma haematobium*; ecology; breeding sites; Tanzania.

Introduction

The present study was carried out near Ifakara, the capital of the Kilombero district. The Kilombero valley, described in detail by Jätzold and Baum (1968), is situated in the southeastern part of Tanzania, some 300 km from the Indian Ocean coast, at an altitude of about 230–260 m. The climate is characterized by a change between dry and rainy season. The latter roughly extends from the end of November until the middle of May, with maximum precipitation usually recorded during April and with a short interruption in February. The human population consists of several Bantu tribes (mainly Ndamba, Pogoro, Bena, Ngindo, Mbunga) which depend on farming (rice, maize, cassava, cotton) or fishing (Jätzold and Baum, 1968).

Malaria is holoendemic (Freyvogel and Kihaule, 1968) and intestinal helminths are common (Tanner et al., 1982). Studies carried out on schistosomiasis in the Kilombero valley are few. Sturrock (1965) investigated primary school-children near the Kilombero irrigation scheme. He found prevalences of 7.7% for *S. mansoni* and 22.5% for *S. haematobium*. No intermediate hosts for intestinal schistosomiasis could be found, but *B. nasutus* and *B. globosus* were recovered. The latter was found to be infected. A study carried out 12 years later (Matovu, 1977) in the same area, revealed a *S. mansoni* prevalence of 2.2% and an overall *S. haematobium* prevalence of 19.7% among local primary school children. The infection rate in different schools varied between 6.3 and 41.4%.

At Ifakara, the Swiss Tropical Institute Field Laboratory (STIFL) has undertaken several studies on urinary schistosomiasis. A *S. haematobium* morbidity study carried out at the St. Francis Hospital (Furrer, 1981) showed a significant number of cases originating from the villages Kapolo and Kikwawila north of Ifakara. At these same villages Zumstein (1983) found a high prevalence of urinary schistosomiasis (56–71%) among primary school children. Although the median egg output was only 28 eggs/10 ml urine, dip stick tests revealed a frequency of haematuria and proteinuria of 85.5% and 82.1%, respectively (Tanner et al., 1983).

The mapping of the snail intermediate hosts in the Ifakara area was carried out by Zumstein (1983). *Bi. pfeifferi* was found only in one stream 30 km west of Ifakara, which explains the rarity of intestinal schistosomiasis seen at the St. Francis Hospital in Ifakara (1984, 58 cases out of 26 920 stool examinations). The observed distribution pattern of *B. globosus* correlated with the prevalence pattern of urinary schistosomiasis among school children from different primary schools of the Ifakara area. North of Ifakara, near the foothills of the Iringa mountains, prevalences were highest (up to 71%) and correspondingly

numerous waterbodies containing *B. globosus* were found. Also several transmission sites were identified. Further south, *B. globosus* was found less frequently and disappeared near the Kilombero river. The prevalence rates of urinary schistosomiasis at Ifakara were below 15%. *B. nasutus* was found in only three waterbodies west of Ifakara.

Besides observations on the specific distribution pattern of the bulinid snail populations, no other data about *Bulinus* spp. – a prerequisite for the planning of preventive measures – were available. The aim of this further study thus was to investigate the ecology and the population dynamics of *B. globosus*. In the high transmission focus of Kikwawila one stream was selected as a representative biotope and studied for a period of two years. Eight habitats were investigated monthly; a number of biotic and abiotic parameters were recorded and the breeding places of *B. globosus* were identified. In addition, field experiments with caged snails were carried out to determine population parameters such as fecundity, growth and mortality rates of *B. globosus* (Marti, in prep.) and the effect of the water current on the snails was determined (Marti and Tanner, in prep.). These data taken together should provide a basis for control measures which will be carried out in the near future under the aegis of a project currently being undertaken at Ifakara which investigates the interactions between nutritional levels, immune status, the patterns of parasitic infections and the local environmental factors.

Material and Methods

Habitats

The stream selected has its source in the Iringa mountains, some 20 km north-east of Ifakara. It flows in a north-south direction, crossing the Tanzania-Zambia Railway and, in Kikwawila village, the road Ifakara-Mikumi. Some 300 m south of Kikwawila, which is situated on the embankment, the stream ends in a swamp which drains into the Kilombero river. Between Kikwawila and Kilama to the north, the area is covered by grassed woodland, partly cleared for the cultivation of rice.

From the 7 habitats selected along the stream, habitat I was situated close to the Iringa mountains, while habitat VII was situated in the Kilombero plain. The distance between these two habitats measured about 3.5 km. The other habitats were situated in between. Five habitats (I–III, V, VII) were situated in the stream itself. Two habitats (IV, VI) were pools adjacent to the stream. They are separated from the stream during the dry season, but connected to it during the rainy season. One additional habitat (VIII) was selected for comparison in a parallel stream situated 1 km farther east.

Identification of Bulinus species

Every 3 months a randomized sample (sample ratio 1/1–1/15) of *Bulinus* spp. from the investigated habitats was brought into the laboratory. The distinction between *B. globosus* and *B. nasutus*, which occur both together in the Ifakara area (Zumstein, 1983), was then determined by starch gel electrophoresis according to Jelnes (1981). The enzyme stained were xanthine dehydrogenase (XDH) and 3-hydroxybutyrate dehydrogenase (HBDH). The relative mobility values (r_m -values) were calculated in reference to the snail haemoglobin.

Snail surveys

Each of the 8 selected habitats was surveyed monthly over a period of 2 years (April 1981 to March 1983). The following parameters were determined: *pH* (Aquamerck mixed indicator no. 11137, scale 0.5 units, E. Merck, Darmstadt, FRG), *water temperature* 10 cm below the surface, *water conductivity* (WTW LF 56 field conductivity meter), *water velocity* with a C2 current meter (A. Ott GmbH, Kempten, FRG), *depth of the water*. The most abundant *plants* were recorded, too. The site was then carefully searched for *snails* by two experienced men for 20 min with a long handled kitchen sieve (diameter 18 cm). Care was taken that always the same men searched, at around the same time of day, at the same place within the habitats. The number of *B. globosus* collected was recorded and their relative density was calculated as snails found per man per 10 min (s/m/10', Oliver and Schneidermann, 1956). Immediately afterwards the snails were scattered over the searching area again. Other species than *B. globosus* were recorded qualitatively only. Attention was paid also to eggmasses. Their distribution within the habitat and their supports were recorded.

During one year the snail collecting method described above was compared to the estimation of relative snail densities by use of snail traps. Dried palmleaves, which proved to be more attractive for snails than banana leaves or bamboo traps (unpublished observations), were woven into a square measuring 50 cm each side (total 0.25m²). Immediately after the monthly survey 10 traps were put into the water at habitats II and VI. One week later the traps were removed and the number of *B. globosus* attached to them was counted. The relative snail density was calculated as the average number of snails found per 0.25 m².

Results

Identification of Bulinus species

A total of 321 *Bulinus* spp. were analysed by starch gel electrophoresis. All turned out to be *B. globosus*. For XDH, this species showed a relative mobility value (r_m -value, calculated in reference to the snail haemoglobin) of 2.62 (SD ± 0.09). It could be easily distinguished from *B. nasutus*, which showed no bands at all (Jelnes, 1982).

For HBDH, *B. nasutus* showed a single band with a r_m -value of 2.53 (SD ± 0.03). *B. globosus* showed a polymorphism. In homozygotic snails the r_m -values were either 2.09 (SD ± 0.11) or 3.02 (SD ± 0.07), while in heterozygotic individuals both bands showed up, together with a third band with a r_m -value of 2.57 (SD ± 0.11).

The migration of the snail haemoglobin varied between 8 and 14.5 mm for runs of 3 h duration. These differences can be attributed to variations in the thickness of the gels, leading to differences in electrical resistance and possibly to unequal warming, and furthermore to fluctuations in the current supply.

Monthly surveys

pH

During the whole observation period, the pH showed only very little variation in all habitats. The recorded extremes were 6.0 and 7.5, respectively. 107 records were in the acid range, 75 records were neutral and only 3 were in the alkaline range. The pH of the soil was 6.0 near all habitats. No correlation between pH variation and rainfall was found.

Table 1. Rainfall observations (in mm) in the Ifakara area

	Jan.	Feb.	March	April	May	June
A	185.2	168.9	263.6	339.3	127.5	23.4
B	195.6	209.6	331.8	259.7	84.5	16.7
1981				170.1	120.4	19.2
1982	55.3	131.8	249.8	235.1	183.3	15.1
1983	125.6	175.1	254.0			
	July	Aug.	Sept.	Oct.	Nov.	Dec.
A	7.1	4.4	6.8	12.1	46.8	118.6
B	3.8	10.9	12.3	50.0	88.5	147.3
1981	0	11.1	0.6	8.1	7.3	154.7
1982	12.0	0	1.5	148.3	142.5	167.3
1983						

A = Ifakara town: monthly average of the years 1931–1958 (Freyvogel, 1960)

B = KATRIN agricultural research institute (12 km north of Ifakara): monthly average of the years 1968–1983

1981, 1982, 1983 = Ifakara town: monthly rainfall recorded during the study presented (*April 1981 to March 1983*)

Temperature

The lowest water temperatures were recorded in July with a minimum of 19° C. Later on the temperature rose gradually to around 27–28° C from October till February. The recorded maximum was 33° C in November in habitat IV. In the habitats situated in the stream (habitats I–III, V, VII), the temperature never exceeded 29.5° C. During the heavy rains the temperatures started to decline and reached the minimum in July.

Habitats I and II, situated close to the mountains, were generally 1–2° C cooler than habitats V and VII, located in the Kilombero plain. The pools (habitats IV and VI) were generally 1–2° C warmer than the nearby stream (habitats III and V). In November these differences could even amount to 5° C.

Rainfall

The yearly rainfall in the Ifakara area amounts about 1300 mm (Freyvogel, 1960). The rainfall pattern may vary considerably from year to year. Table 1 summarizes two long-term observations and the rainfall data observed during this study. While in 1981/82 the rains started “in time” (end November/beginning December), their amount was about 250 mm less than in an average year. This led for example to the desiccation of habitat I. In 1982/83 the rains started early, but their amount was in the “normal” range. Yet the relative constance of the parameters recorded over the 2 years’ period indicate that with the excep-

Table 2. Snail species found in the investigated habitats

	Habitats							
	I	II	III	IV	V	VI	VII	VIII
<i>Bulinus globosus</i>	×	×		×	×	×	×	×
<i>Bulinus forskalii</i>		×			×		×	
<i>Lanistes ovum</i>		×	×	×	×	×	×	×
<i>Lymnaea natalensis</i>		×	×	×	×	×	×	×
<i>Pila ovata</i>	×	×	×	×	×	×	×	×
<i>Cleopatra ferruginea</i>								×
<i>Ancylidae</i> sp.		×	×	×	×		×	×
<i>Ceratophallus</i> spp.		×		×	×	×	×	×

tion of habitat I no extraordinary influence on the snail population due to rainfall took place.

Conductivity

The conductivity (at 25° C) showed a distinct seasonal cycle. It was lowest at the end of rainy season (minimum = 43 μ S) and rose gradually during dry season, near the end of which the increase became more pronounced (maximum = 374 μ S). With the start of the rainy season a rapid decline was observed, until the minimum was recorded in April/May after the rains had ceased. At this time there was scarcely any difference in conductivity among the habitats situated in the stream. But at the end of the dry season the conductivities recorded in the south (habitat VII) were nearly twice as high as they were in the north (habitat II). The conductivity in the pools (habitats IV and VI) reached a much higher level than in the habitats in the nearby stream (III and V). No correlation between conductivity and *Bulinus* density was found.

Snail species

Eight different snail species were found in the investigated habitats (cf. Tab. 2). *B. globosus* was found in all habitats with the exception of no. III. *B. nasutus*, although present in the Ifakara area (Zumstein, 1983), was never found in any of the 8 investigated habitats. Concerning the other species found, *Pila ovata* was the only one represented in all habitats, while *Lymnaea natalensis* was most abundant in number. These two species, together with *Lanistes ovum*, were observed very regularly, while *Bulinus forskalii*, *Ancylidae* sp. and *Ceratophallus* spp. were found sporadically and never in large numbers. *Cleopatra ferruginea* was found only four times in the neighbouring habitat VIII.

Bulinus globosus densities

During the two years' survey obvious differences between the *B. globosus* populations in the pools (habitats IV and VI) and in the stream were noted (cf.

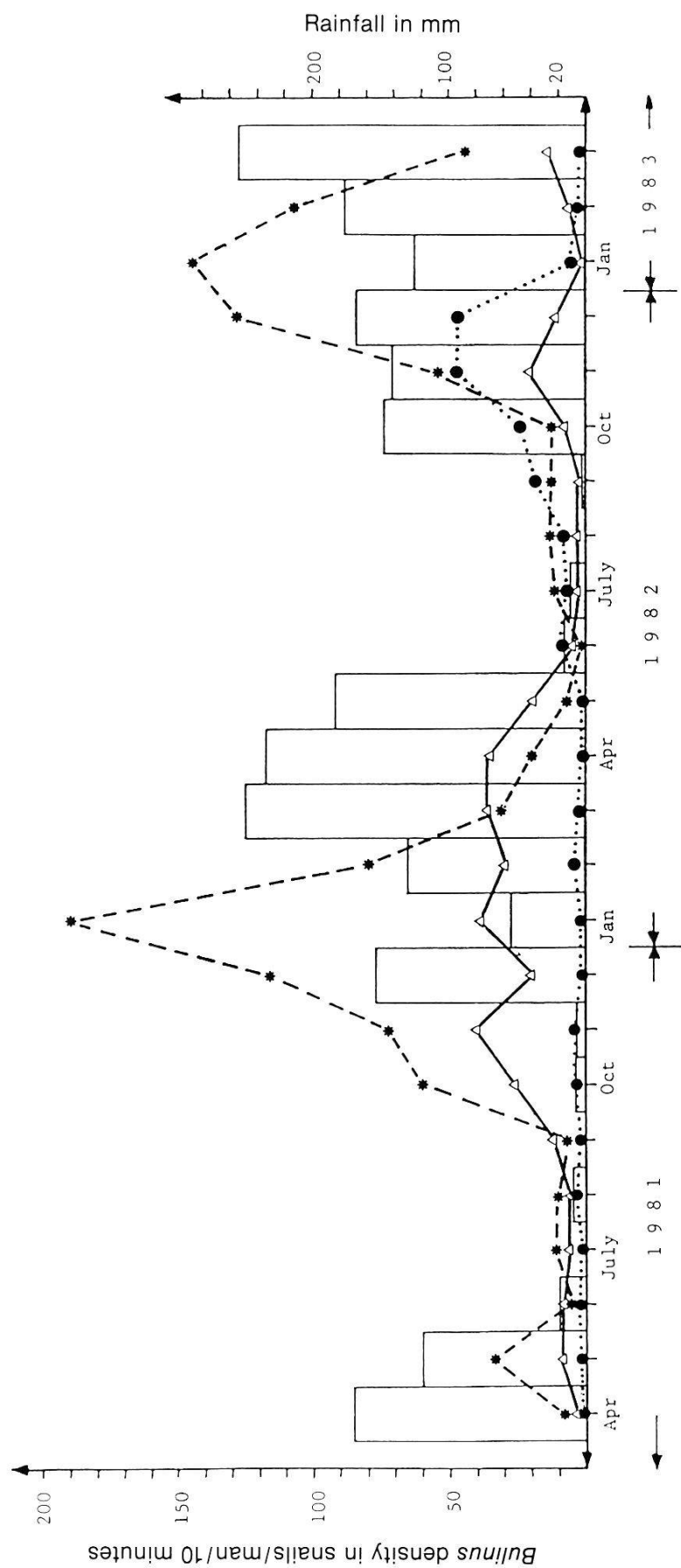


Fig. 1. Relationship between *Bulinus* density and rainfall. Three different habitats are shown as examples:

--★-- = habitat IV ...●... = habitat VI —△— = habitat VIII

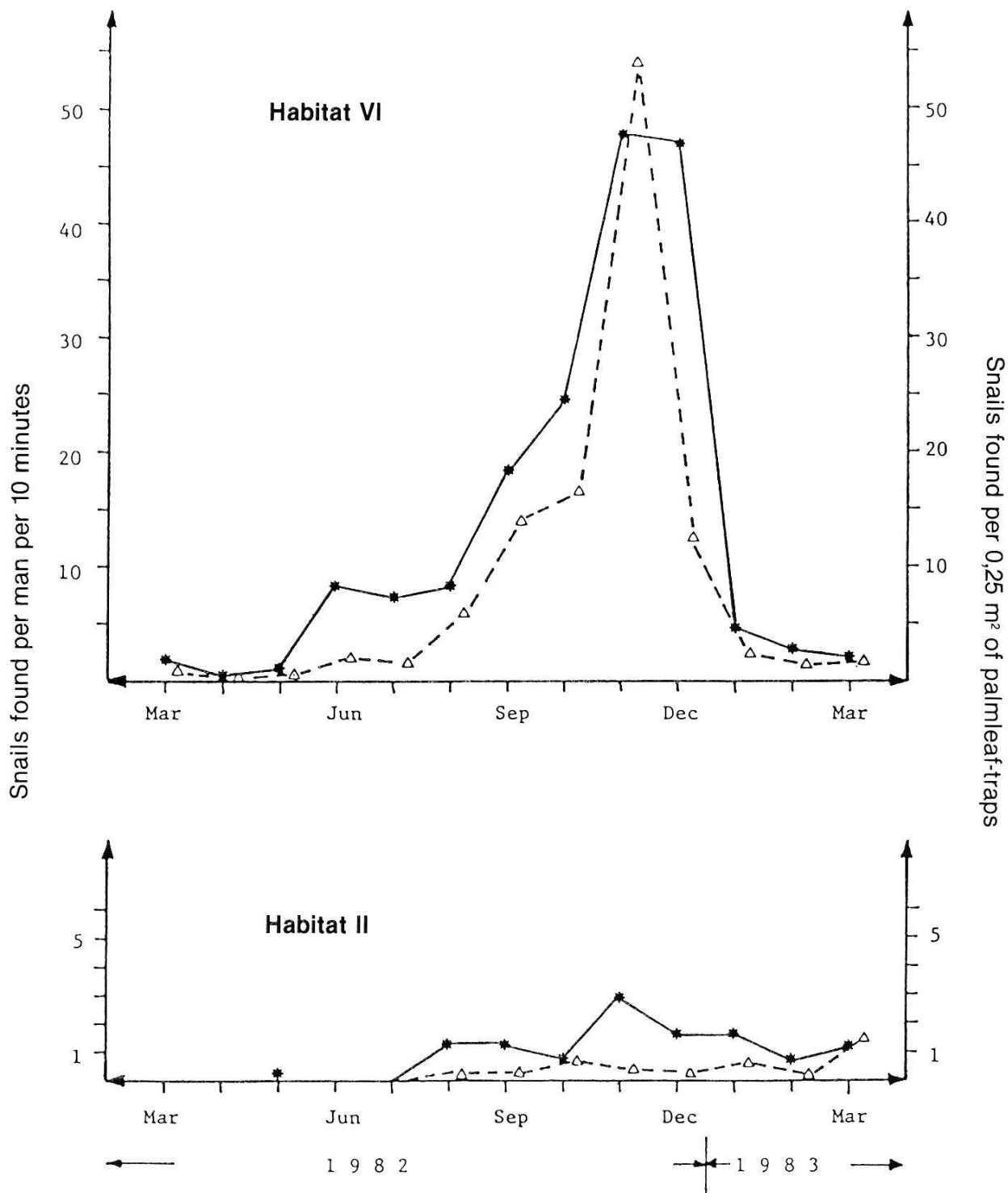
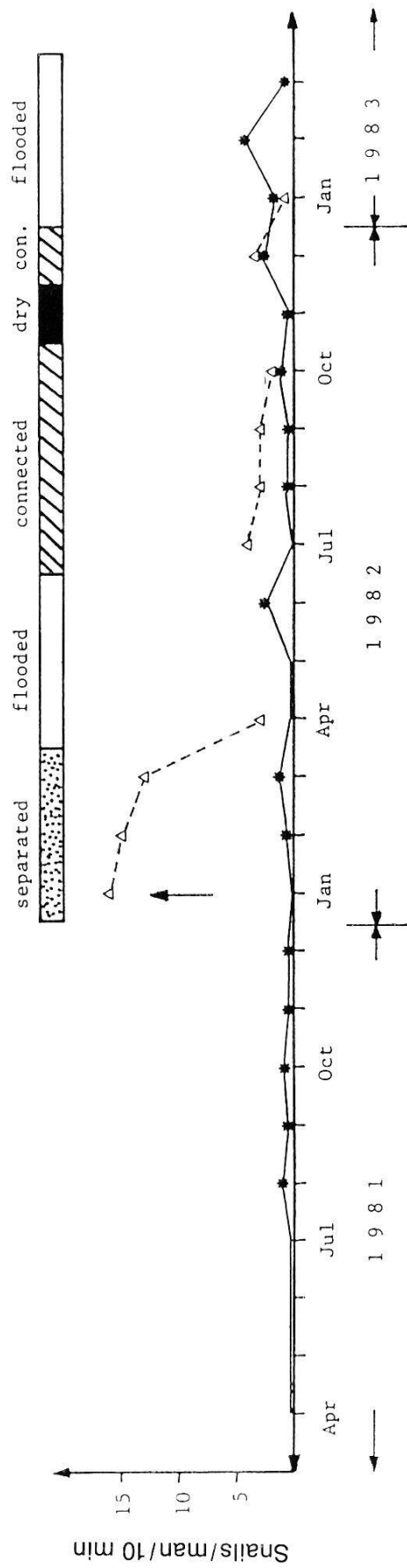


Fig. 2. Comparison of relative *Bulinus* density estimated by two different methods. The habitats were first searched by two men using a long handled kitchen-sieve (expressed as snails per man per 10 min). Immediately afterwards the palmleaf-traps were exposed and checked after 7 days (expressed as snails per 0.25 m² of palmleaf-traps).

— ★ — = *Bulinus* found per man per 10 minutes of search

-- △ -- = *Bulinus* found per 0.25 m² of palmleaf-traps after 7 days of exposure



Tab. 3). While in the stream the *B. globosus* densities remained rather low and constant, in the pools *B. globosus* was much more numerous and showed distinct seasonal fluctuations (cf. Fig. 1).

In the pools, the *B. globosus* density rose sharply towards the end of the dry season/beginning of the rainy season (October/November, cf. Fig. 1). After a brief climax the population was reduced drastically and reached its minimum after the end of the rainy season in June. The *B. globosus* densities then were low until the end of dry season, when they started to rise again. These fluctuations of the *Bulinus* densities were considerable. At the climax the densities were at least 50 times greater than at their lowest level. The absence of a rise in *B. globosus* density in habitat VI in 1981/82 is explained by the fact that in November 1981 some villagers were fishing in the pool using poisonous plants. These plants are well known to the population and often used; they are likely to have affected also the snail population.

Habitat I harboured a dense *B. globosus* population that had been known for several years (Zumstein, 1983). However, this population disappeared in September 1981 and subsequently only very few *B. globosus* were found until the end of the observation period (cf. Tab. 3). The opposite happened in habitat VII, where no *Bulinus* could be found for nearly one year. Only during the rainy season in 1982 were a few snails detected for the first time. This very low density persisted from then onwards. In habitat III only once a single specimen of *B. globosus* was found. It originated from an experiment with caged snails (Marti, in prep.) and escaped when the cage was destroyed by local people.

In habitats II and VI the comparative study between two different snail collecting methods showed very similar results for both methods. No relevant differences between the results for a habitat with a high *B. globosus* density (habitat VI) or a habitat with a low *B. globosus* density (habitat II) could be observed (cf. Fig. 2).

Breeding sites

Except in habitats I and III, egg masses of *B. globosus* could be found everywhere. The kidney-shaped egg masses, which can easily be distinguished from the abundant, long and slender egg masses of *Lymnaea natalensis*, averaged 3.5×5 mm. They contained between 4 and 34 embryos. This coincides roughly with the number of embryos found in eggmasses laid in the laboratory (2–28) or in experiments with caged snails (2–29) (Marti, in prep.).

The egg masses could be found the whole year through, but were observed more frequently in the late dry season. *B. globosus* clearly preferred *Cyperus exaltatus* as a support. Sometimes a dozen or more egg masses could be found on a single leaf. This sedge was also often frequented by adult snails and seems to play an important role in the ecology of *B. globosus* in the investigated area. Egg masses were also found on the leaves of *Nymphaea* spp., but this was more the preferred support of *Lymnaea natalensis*. The following supports were used

Table 3. *Bulinus globosus* densities (s/m/10 min) in 8 habitats in the Kikawila area from April 1981 to March 1983

Habitats	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
I	0.7 0.3	2.2 0	24.8 0	10.7 0	5.7 0.5	0 0.7	0 —	0 —	0 —	— 0.3	— 2.0	— 0
II	0 0	0.9 0.3	0.5 0	0 0	0.3 1.3	0 1.3	0.3 0.8	0.5 3.0	0 1.7	0.3 1.7	0 0.8	0 1.3
BP	n.d. 0.6	n.d. 0	n.d. 1.4	9.0 0	8.0 11.0	18.0 —	—	—	—	—	—	—
III	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0.3	0 0	0 0
IV	2.8 20.3	34.5 7.5	7.5 2.5	7.0 7.0	9.8 7.8	7.7 12.7	59.3 7.3	73.0 54.3	117.3 128.0	189.5 144.3	80.8 106.5	32.3 45.3
V	0 0	0 0	0 2.5	0 0	1.0 0.7	0.3 0.4	0.8 1.0	0.5 0.3	0.3 2.7	0 1.3	0.3 4.0	1.3 0.7
BP	n.d. 3.0	n.d. —	n.d. —	n.d. 4.0	n.d. 3.0	n.d. 3.0	n.d. 1.5	n.d. 0	n.d. 3.0	16.0 1.0	15.0 —	13.0 —
VI	0.5 0.5	2.0 1.0	0.8 8.3	1.5 7.5	2.7 8.3	0.7 18.4	3.0 24.7	4.0 47.7	1.0 46.7	2.2 4.3	4.3 2.7	1.8 2.3
VII	n.d. 0.3	0 0.3	0 0.3	0 0	0 0	0 0	0 0.6	0 0	0 0.3	0 1.3	0 1.0	0.8 0.3
VIII	0.3 35.4	8.5 20.0	8.5 5.8	6.7 3.7	5.0 3.5	12.5 2.8	26.5 8.1	40.5 20.7	20.7 11.4	38.3 0.2	29.8 3.5	36.5 13.8

For each habitat the 1st line indicates the monthly *B. globosus* densities (s/m/10 min) from April 1981 till March 1982 and the 2nd line the monthly densities from April 1982 till March 1983

BP = breeding pockets

— = dry

n.d. = no search for snails

empty spaces = breeding pockets overflowed by the stream

by *B. globosus* occasionally only: the snails' shell, pieces of wood, floating leaves of trees and the leaves of *Phragmites mauritianus*. In habitat VIII egg masses were found on the leaves of banana trees thrown into the water by neighbouring farmers.

Oviposition clearly took place according to a distinct site-distribution pattern. Nearly all egg masses were confined to well defined sites, where the *B. globosus* density was found to be much higher than in the surroundings (cf. Tab. 3 and Fig. 3). During the dry season these sites were normally separated from the stream or were connected only in a minor way; they may thus be described as "pockets". In all these pockets the vegetation was dominated by *C. exaltatus* and outside them egg masses were found only rarely. During the two years' observation period it was found that the separation of these pockets from the stream lasted up to 5 months, until they either dried out or were overflowed during the rainy season.

Such breeding pockets were found in habitats II, V (cf. Fig. 3) and VIII. In habitat VIII two pockets were identified, one of which was destroyed by sand swept in during the rainy season 1983. Habitats IV and VI can be regarded as breeding pockets of habitats III and V, respectively, because habitat V is regularly connected with habitat VI for about 4 months each year and after very heavy rains habitat VI was also connected with habitat III.

Discussion

For the estimation of relative *Bulinus* densities, the man/time method (Olivier and Schneidermann, 1956) was chosen for this study. Its biggest advantages are the simple equipment and the exclusion of interference of local people with equipment left at the sites. The well known disadvantages of the method due to variations in individual skill and motivation or uneven distribution of the snails, were at least partly eliminated by carrying out the surveys as uniformly as possible. Always the same two men searched the same places within the habitat at around the same time of day. Interference by additional factors, however, can not always be prevented. For example, a rise of water level after heavy rains with the number of snails remaining constant, may result in a lower capture rate due to the dispersal of the snails over a larger area and thus falsely indicate a decrease in snail density. Also predominantly larger snails may be caught because they are more easily recognized by the searcher (Dazo et al., 1966). Thus, to check the reliability of the results obtained, a comparative study using palm leaf traps was carried out in two habitats.

Fig. 2 shows a high coincidence between the two curves in a habitat with a high relative snail density (habitat VI). Slight differences may be due to the fact that the results of the palm leaf traps were read one week after the man/time method. The coincidence of the curves was slightly reduced in a habitat with a low snail density (cf. Fig. 2, habitat II). With the man/time method a larger area

will be surveyed than by the exposure of traps. If only a few snails are present in the habitat, they will more likely be discovered by the man/time method. However, with one exception snails were always detected by both methods. The main advantage of the palm leaf traps is that they are not influenced by the searcher and even untrained assistants can use them. They will also yield a larger fraction of very small snails as demonstrated by Teesdale (1962). However, they fail to reveal possible predilections of the snails for certain plants or sites for oviposition. Conclusively it can be stated that both methods revealed fluctuations in snail densities in a similar manner. The appropriate method has to be chosen for each study depending on the sites to be searched, on the objectives of the survey and on the skill of the available manpower (Chu and Klumpp, 1978).

Of the 8 snail species found, *B. globosus* is responsible for the transmission of urinary schistosomiasis in the Ifakara area (Zumstein, 1983), but *B. nasutus*, the main intermediate host in NW-Tanzania (Webbe, 1962), is also present. However, it was never found in one of the investigated habitats and in laboratory experiments this species has been shown to be refractory to the local *S. haematobium* strain (Zumstein, 1983).

Concerning the distribution of *B. globosus* along the stream (cf. Tab. 3), no characteristic differences between the north (habitats I, II) and the south (habitats V, VII) could be detected. The densities in the stream were low and very constant throughout the investigated period. Only habitat I harboured a larger population as recorded by Zumstein (1983). However, the snails disappeared after the vegetation (mainly *C. exaltatus*) beside the stream and on the banks was cleared for a rice field. As this sedge was clearly favoured by *B. globosus* (cf. below), its removal significantly disturbed the ecology of the snail. Additionally, in January 1982 the habitat exceptionally dried out for a period of three months. Desiccation is well known to be lethal (Appleton, 1978), although a few snails, usually young adults, may survive. After the period of desiccation, *B. globosus* was very rare.

The snail populations in the stream and in the adjacent pools were different. In the latter higher densities and marked seasonal fluctuations (highest at the end of the small rainy season and lowest after the heavy rains) were observed. In addition, differences in population parameters were revealed during experiments with caged snails (Marti, in prep.).

In order to explain these observed differences, several abiotic factors were examined. The *pH* (hydrogen-ion concentration) tolerated by freshwater gastropods varies within a range of about 4.5–10.0 (Malek, 1980). In Liberia, *B. globosus* were found within a *pH* range of 4.6–7.5 (Saladin et al., 1980). In habitats in northern Tanzania, Webbe and Msangi (1958) recorded small fluctuations between *pH* 6.0 and 7.5 and long periods with a constant *pH* (minimum at 5.5). Our observations together with those of others indicate that the *pH* had no influence on the distribution and biology of *B. globosus* in the investigated area.

The intermediate host of *Schistosoma* spp. can tolerate a wide range of temperature, extending approximately between 18 and 32° C (Appleton, 1978). Optimum growth and highest net reproductive rate were observed around 25–26° C for *B. truncatus* and *Bi. alexandrina*. With increasing or decreasing temperature the onset of egg laying is delayed and fecundity decreases. The survival of adult snails is affected only by extreme temperatures (Mousa and Abou el Hassan, 1972; El Emam and Madsen, 1982). Additionally, *B. globosus* is able to seek out the temperature nearest its optimum by vertical movements (Shiff, 1966). During our studies at Ifakara the temperature stabilized for about 5 months at 27–28° C. This value is close to the experimentally recorded optimum of 25° C for *B. globosus* (Shiff, 1964), indicating that only slight effects of temperature on reproduction could be expected for a very limited period.

Electrical conductivity is an indicator of factors which may limit the distribution of snails, e.g. low concentration of an ion essential for the snails. Snails live in biotopes with wide differences in conductivity. In Liberia, Saladin et al. (1980) found *B. globosus* in waters with a conductivity as low as 20 μ S, while in Madagascar *B. liratus* was found in biotopes with a conductivity as high as 1500 μ S (Degrémont, 1973). Tolerance to conductivity varies by species and life stage. Egg masses and hatchlings are more sensitive to high conductivity than adults (Donnelly et al., 1983). *B. obtusispira* did not establish populations in waters with a conductivity above 600 μ S (Degrémont, 1973). In our study the recorded values varied between 43 and 374 μ S and correlated clearly with rainfall. Conductivity increased during the dry season and decreased in the rainy season. After the onset of the rains the conductivity was in the same range in all habitats, but, in the dry season due to the evaporation, the conductivity in the pools (habitats IV and VI) was much higher than in the adjacent stream. Yet the recorded values were still well within the tolerated limits.

The marked influence of rainfall on aquatic snail populations has been described by several authors. In Tanzania Webbe (1960) working with *Bi. pfeifferi* found a peak density at the end of the “long” rains in May. Later on the density decreased to reach a minimum at the end of the dry season. These observations were confirmed by Baalawy and Moyo (1970) for *B. nasutus*. The peak density was reached in March and thereafter declined. At Ifakara similar observations were recorded. The population density was sparse at the end of the dry season; thereafter it increased, unaffected by the “short” rains, to reach a maximum in January (cf. Fig. 1). A rapid decline during and just after the “long” rains was observed. The influence of the rains can be attributed to two factors; increase of water velocity in the streams (Marti and Tanner, in prep.) and fluctuations of water level. The latter has a negative effect on snail host populations and were exploited for snail control (Jobin, 1970).

Breeding sites

During our surveys an interesting breeding pattern was observed. Nearly all egg masses of *B. globosus* were found in clearly defined sites, or “pockets” which formed during the dry season when they became isolated from the stream or retained but a small connection to it. Such isolation lasted for several months until the onset of the rainy season. Various types of “pockets” were identified. Some were depressions filled with water during the floods (e.g. breeding pocket [BP] near habitat II or habitat IV which might be regarded as BP of habitat III). Others were part of the stream becoming separated as the water level fall (e.g. BP of habitat V) or were established in some of the pools which were formed due to the disintegration of the stream at the height of dry season (e.g. habitat VIII). Outside these “pockets” egg masses were quite rare.

A common feature of these “pockets” was the relative abundance of *Cyperus exaltatus*, which was highly favoured by *B. globosus* as a support for oviposition. This sedge possibly also serves as food and/or food-support and gives the snails a certain protection against the current (Marti and Tanner, in prep.). Yet the presence of large *C. exaltatus* formations in biotopes without bulinid snail populations (cf. also Zumstein, 1983) shows, that the presence or absence of this specific sedge is not a truly reliable indicator of the suitability of a habitat for *B. globosus*. If present, however, *B. globosus* is most easily detected on the leaves of *C. exaltatus*.

The concentration of oviposition coincided with high *Bulinus* densities in the “pockets”. High snail densities in well defined pockets were also observed for *B. nasutus* and *B. africanus* (Kinoti, 1964), *B. rohlfsi* (Klumpp and Chu, 1977), *B. abyssinicus* (Upatham et al., 1981) and *Bi. glabrata* (Jordan, 1977), but only Kinoti (1964) and Upatham et al. (1981) mention the importance of these sites as breeding places.

These “pockets” thus represent a very important niche for the snails. From them the snails are swept into the stream during flood periods, where some can form new colonies (Hira and Muller, 1966; Cantrell, 1981). Fig. 3 shows that the snail density was drastically reduced when the pocket was flooded by the stream. An immediate rise in snail density in the adjacent stream was observed only during the second flooding. Snails, however, may be swept away over a larger distance and do not necessarily settle in the proximity of their breeding pocket (Marti and Tanner, in prep.). The appearance of *B. globosus* in habitat VII was possibly due to snails derived from such a breeding pocket. Additionally, these “pockets” may also play an important role as transmission sites (Kinoti, 1964), as confirmed by a study of human water contact patterns (Marti and Tanner, 1982).

The concentration of *B. globosus* in well defined breeding pockets at the end of the dry season offers promising perspectives for focal snail control by mollusciciding. The use of toxic substances in a confined pocket would not have unwanted side-effects on the fauna of the stream. Transmission control mea-

tures through the elimination of *B. globosus* in these “pockets” with a plant molluscicide combined with selective mass treatment of the population are currently being undertaken.

Acknowledgments

The authors wish to thank Dr. S. Tayari (District Medical Officer, Kilombero District) and Prof. Dr. W. Kilama (Director General, National Institute for Medical Research, Tanzania) for their support of the study. The support of Dr. J. E. Jelnes from the Danish Bilharziasis Laboratory, who partly carried out the identification of the snails and provided the equipment for the starch gel electrophoresis, is gratefully acknowledged. The authors wish to thank Mr. S. Komba for his excellent technical assistance. Research clearance for this project was obtained from the Tanzanian National Scientific Research Council (Director General Prof. Dr. A. Msangi) as per Ref. Nos.: NSR/CONF. R. C. of 22nd August 1981 and NSR/CONF. R. C. of 29th July 1982.

The study was made possible by a grant from the “R. Geigy Stiftung zu Gunsten des Schweiz. Tropeninstituts” and was partly supported by the Swiss Directorate for Development Cooperation and Humanitarian Aid.

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