Bull. Org. mond. Santé }
Bull. Wld Hlth Org. } 1962, **27**, 59-85

The Transmission of *Schistosoma haematobium* in an Area of Lake Province, Tanganyika

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This paper records the results of detailed studies carried out over a two-year period on the transmission of Schistosoma haematobium *in an area of Lake Province, Tanganyika. The ecology of a variety of snail habitats is described ; and data on the biology of the principal molluscan host (*Bulinus (Physopsis) nasutus productus*), on seasonal fluctuations in its population density and associated cercarial infection rates, on its response to desiccation and on other aspects of population dynamics are presented and discussed.*

Taking into consideration the seasonal fluctuation in snail numbers which occurs in the area and the snails' capacity to survive desiccation, it is considered that a substantial reduction in transmission of S. haematobium *might be effected by application of a molluscicide timed so as to lower the population density before aestivation begins, followed by a second treatment when the habitats have been refilled by rainfall to reduce yet further the population that has survived the first treatment and subsequent desiccation. It is also suggested that a combination of methods directed against two stages in the schistosome life-cycle—the snail and the miracidium—by application of molluscicides and treatment of infected persons might be more efficacious than an attempt merely to reduce snail density and alter the population structure.*

It would seem axiomatic that any attempt to control the growth of a snail population in the field should be based upon a thorough knowledge of the population dynamics, ecology and biology of the particular species. However, many present-day methods of control which have been directed against what is generally regarded as this vulnerable link in the life-cycle of the schistosome have frequently failed or have enjoyed only moderate success in reducing transmission, owing in part to the shortcomings of the chemicals used, but often owing largely to inadequate information about the biology and bionomics of the snail host and to a lack of proper understanding of snail-parasite relationships. Fundamental biological and ecological studies might also reveal other possibilities of control—for instance, by the use of environmental changes which, where practicable, might be superior to molluscicides—or they might even indicate that a combination of methods directed against more than one link in the schistosome's life-cycle should be used.

The present paper records observations on the transmission of *Schistosoma haematobium*, the biology and ecology of the principal molluscan host, seasonal fluctuations in snail population densities and associated *S. haematobium* infection rates, and other population dynamics.

1. GENERAL CONSIDERATIONS AND ECOLOGY OF SNAIL HABITATS

LOCATION

The main observations were made in a 6-square-mile (15 km²) area of Mwanza District of Lake Province in Tanganyika, some 12 miles (20 km) due south of Mwanza, near the minor settlement of Usagara (latitude 2°3′ S, longitude 33° E). This area is topographically typical of a major portion of the Sukumaland area of Lake Province. Sukumaland is an area of some 14 000 square miles (about 22 500 km²) and the greater portion is situated

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at an altitude of 3500-4000 feet (1070-1220 m) above sea level, gradually rising towards higher ground both in the east and the west and bordered on the north by Lake Victoria. The general impression is of flat, rolling, almost treeless country, with granite outcrops and low ridges of hills as the main features. Fig. 1 shows the area in which the observations were carried out.

GEOLOGY AND SOILS

The geology of the area is characterized by large-scale emplacement of "younger" granite into

FIG. 1

AREA OF LAKE PROVINCE, TANGANYIKA, IN WHICH THE OBSERVATIONS WERE MADE

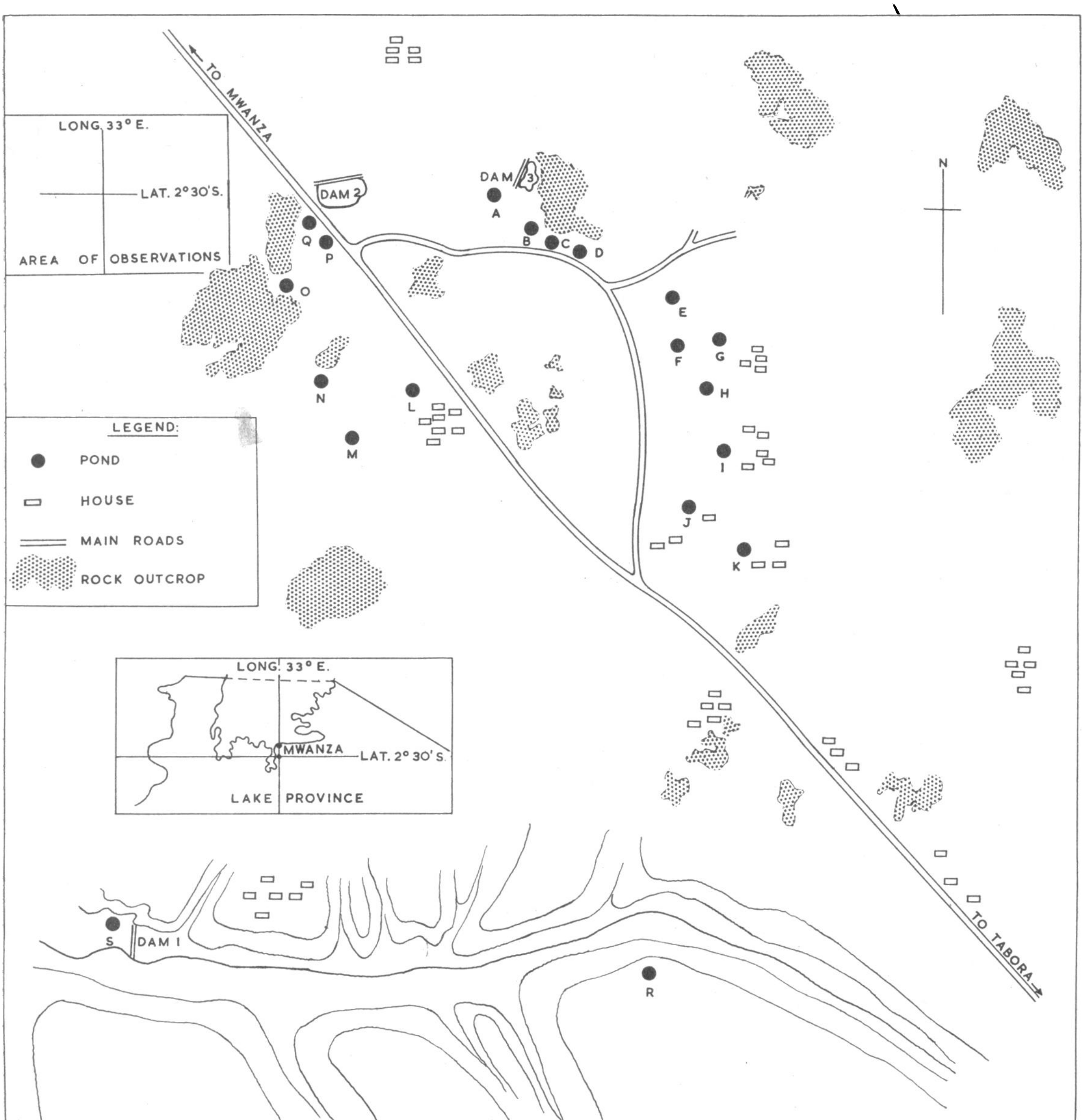
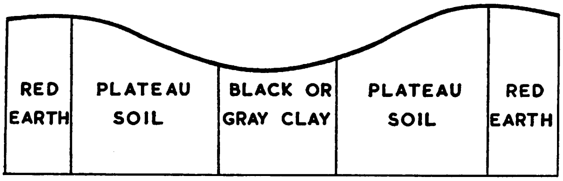


FIG. 2
USUKUMA SOIL CATENA [a]



[a] Red earths may not be present.

Nyanzian and Kavirondian rocks, particularly south of Lake Victoria. The Usukuma soil catena which is shown in Fig. 2 is generally characteristic of the undulating countryside, which may be described as follows.

Laterized red earths are very freely drained, leached, acid soils, which have a uniform open structure and a friable light texture independently of the clay content.

Plateau soils, which are light-coloured soils (grey-yellow or yellow-brown) of sluggish drainage or receiving excess subsoil water seasonally, are usually found on locally transported material lying at a slight slope on a naturally eroded topography or where rock tables check percolation. They are free from calcium carbonate but often have concretionary iron-stone " murram " in the subsoil.

Black or grey clays are dark, ill-drained soils, plastic when wet and cracking deeply when dry. The group is well known as " black-cotton " soil; low-lying areas of " black-cotton " soil, known locally as " Mabuga ", are liable to flooding during the rains.

Vegetation, including annual and perennial crops, pastures and fields, is actively fostered by the local population.

CLIMATE

The annual rainfall is in the neighbourhood of 30-40 inches (75-100 cm), but, since this falls in localized storms of quite considerable intensity and of uneven distribution, the effect on the vegetation is not as great as might be thought. The rainy season is from mid-November to May with some intermission in January and February, most rain falling in March and April. The long dry season is from June to mid-November. The mean annual number of days of rain is 75-100; the mean annual vapour pressure (isopleths in millibars) in the area of observations lies between 20 and 21; the mean annual maximum temperature is 80°F-85°F (27°C-29°C) and the mean annual minimum temperature 60°F-65°F (16°C-18°C).

ECOLOGY OF SNAIL HABITATS

When the observations commenced in September 1959 very dry conditions prevailed throughout the area, following a poor rainy season. Within the area shown in Fig. 1 only three dams (Dams 1, 2 and 3) and the roadside pool shown as Pond Q contained water. Following the onset of the rains in November many other situations under observation were filled with water, and snails were found in some of these within a matter of days.

Dams 1, 2 and 3, the small pools shown in Fig. 1 as Ponds A to S, and two habitats outside the main area of observations and designated Dam 4 and Pond T may be described as follows.

Dam 1 covers an area of two acres (0.8 ha) at the highest water level and is situated in a low-lying area of " black-cotton " soil. The vegetation is composed of grasses and sedges varying in density and including *Potamogeton* sp.; there is some floating vegetation consisting largely of water-lilies and water-lettuce. About 90% of the area is completely open water subject to fairly strong action by wind and waves. There is a concrete water-trough for watering animals below the wall of the dam; the body of the dam is used for cattle watering in the dry season. Human contact is sporadic. The snail population consists of *Bulinus (Physopsis) globosus* (Morelet), *Bulinus (Bulinus) coulboisi* (Bourguignat), *Bulinus (Bulinus) forskalii* (Ehrenberg), *Lymnaea natalensis natalensis* (Krauss) and *Anisus natalensis* (Krauss).

Dam 2 is also two acres in extent at the highest water level and is situated in a transitional area between plateau soil and " black-cotton " soil. The marginal vegetation consists of grasses and sedges, and there is 70% coverage of floating vegetation, composed of water-lilies, water-lettuce and *Potamogeton* sp. The dam is used regularly for watering cattle and humans are frequently observed bathing at the roadside end of the dam, which is also frequented by wild aquatic birds. The snail population consists of *Biomphalaria pfeifferei* sp., *Bulinus (Bulinus) tropicus toroensis* (Mandahl-Barth), *Bulinus (Bulinus) forskalii, Lymnaea natalensis natalensis* and *Anisus natalensis.*

Dam 3 covers an area of one acre (0.4 ha) at the highest water level and is situated just above an area of " black-cotton " soil. The marginal vegetation is composed of papyrus, grasses and sedges; and there is 80% coverage by floating vegetation, mainly water-lettuce with some water-lilies. The dam is used constantly for cattle watering and is heavily polluted; some human contact has been observed, and the water is frequented by wild aquatic birds. The snail population is made up of *Lymnaea natalensis natalensis*, *Anisus natalensis*, with *Bulinus (Bulinus) forskalii* sporadically.

Dam 4, which covers a quarter-acre (0.1 ha) at the highest water level, is known locally as a " hafir " dam. It is situated 6 miles (nearly 10 km) east of Mwanza in open country on a smooth, gentle gradient just above low-lying "black-cotton" soil. It is subject to considerable fluctuations in the water level and usually dries out seasonally. There is sparse emergent vegetation at the edges, composed of grasses and sedges and some floating vegetation, including water-lettuce and *Potamogeton* sp.; 95% of the surface area is completely open water. The water is used constantly for cattle watering and considerable human contact (bathing, washing, etc.) has been observed. The snail population consists of *Bulinus (Physopsis) nasutus productus* (Mandahl-Barth) and *Lymnaea natalensis natalensis*, and, sporadically, *Bulinus (Bulinus) forskalii* and *Anisus natalensis*.

Ponds A to T are all small, temporary pools of seasonal duration ranging in area from 10 square yards to 300 square yards ($8\ m^2$-$250\ m^2$). They vary in nature from grassy seepages below rock outcrops on plateau soil to open pools in the low-lying black clays. Some have a sparse emergent vegetation at the edges; none have floating vegetation except algae; all have a rich microflora. Considerable human contact (bathing, washing, etc.) has been observed, particularly at the end of the rainy season, and they may be used for watering cattle if other sources dry out, although some are used only by humans. All the ponds have a snail population of *Bulinus (Physopsis) nasutus productus* and sporadically of *Bulinus (Bulinus) forskalii* and *Anisus natalensis*.

Fig. 1 does not show Dam 4, already described, and Pond T, which is situated some 3 miles (about 5 km) south of the main area of observation; these two localities were observed concurrently with the other habitats so that snail population data and associated schistosome infection rates from the main area might be kept in perspective to conditions prevailing over a wider area.

Microflora

Dams and, particularly, the small temporary pools contained a rich microflora. Specimens were taken for examination from rock surfaces, the stems of emergent grasses, bottom mud and the surface of the water. The following identifications were made.

Spirogyra sp. was present in all specimens except those from Ponds M and T and predominated wherever found except in Pond J, where *Draparnaldia* sp. was present in larger quantities. Other green algae found in small quantities in most habitats included *Oedogonium* sp., *Zygnema* sp., *Tribonema* sp. and *Mougeotia* sp. Blue-green algae, found in Dams 2 and 3 and in all ponds except E and T, included *Ullothrix* sp., *Anabaena* sp., *Oscillatoria* sp., *Merismopedia* sp. and *Nostoc* sp. Diatoms and desmids were found in all specimens except those from Pond L; although not present in appreciable quantities, they showed considerable variety. The diatoms commonly found included *Gomphonema* sp., *Navicula* sp. and less commonly *Cymbella* sp. and *Synedra* sp. The desmids commonly found included *Closterium* sp. and *Cosmarium* sp.; less commonly *Pleurotaenium* sp., *Euastrum* sp., *Staurastrum* sp., *Selenastrum* sp., *Scenedesmus* sp. and *Ophiocytium* sp. were observed. Among the flagellates, *Euglena* sp., *Eudorina* sp., *Phacus* sp. and *Trachelomonas* sp. were found sporadically in all dams and some ponds.

While the rich and varied nature of the microflora found in these habitats was evident, no causal relationship was apparent between a particular species of alga or diatom and aquatic snails, as breeding populations of *Bulinus* snails were found in all habitats at some time, though the appearance of *Bulinus B. forskalii* in Dam 3 was sporadic. The presence of blue-green algae, however, often in appreciable quantities in habitats containing thriving snail populations, was surprising as these are generally considered inimical to the same *Bulinus* and *Biomphalaria* species bred in laboratory aquaria. Malek (1958), who examined the digestive tracts of some pulmonate snails, concluded that they had no preference for any particular species of microflora and that so long as green or blue-green algae and diatoms were represented in the diet the food supply appeared to be suitable. He considered that it was not the type of diet but its quantitative composition which was important in conditioning the habitats of snails and that the density of the snail population and the size of the individuals were directly correlated with the amount of food available and probably with some other factor, such as volume of water, as well. As the result of seasonal fluctuation in the quantity of microflora consequent upon changes in rainfall and temperature and in other ecological factors controlled by these, one might expect the density of the snail population to vary.

Chemical and physical analyses

Chemical analyses of water samples taken from the different habitats in the area were made by the Government Chemist. The results, given in Table 1, show that the chemical nature of these waters was broadly the same, with one notable exception. Turbidity was a general and striking characteristic of all the small temporary pools, some having a milky appearance; values ranging from 11.5 p.p.m. to more than 1000 p.p.m. were recorded, the dams being the least turbid of the habitats investigated. A range of pH values of from 6.3 to 8.1 was recorded, most waters being markedly acid. Carpenter (1927) suggested that a low pH might be harmful to molluscs, coagulating the mucus on exposed skin surfaces. Boycott (1936), however, considered that there may be an appreciable diurnal variation in the reaction of the water depending on the carbon dioxide concentration. Malek (1958) suggested that the pH was rarely a limiting factor in the distribution of intermediate hosts of bilharziasis and that the combined effect of other factors correlated with pH was more important than pH considered alone.

Values for calcium and magnesium ranged from 3.2 p.p.m. to 212.8 p.p.m. and from 1 p.p.m. to 90.3 p.p.m., respectively; comparatively high values for sodium and potassium were recorded in two habitats. Snails appeared to thrive even when concentrations of calcium were low, although this may have affected the density of some populations and may also have been responsible for differences in the thickness of snail shells from different habitats. Magnesium, which is generally considered necessary for the snail and for chlorophyll-bearing microflora which form its food supply, may be unfavourable in excess.

Measurements of salinity (total concentration of electrolytes), of which electrical conductivity provides a reasonable assessment, gave values ranging from 77.1 to 2544.0 micromhos per cm at 25°C. Work carried out elsewhere has indicated that a conductivity of 25 micromhos or less is associated with some inhibiting factor and a consequent absence of freshwater snails. In the Bukoba district of West Lake Province, Tanganyika, no snails were found in waters for which conductivities of 8-19.7 micromhos per cm at 25°C were recorded. Harry and co-workers (1957), working in Puerto Rico, found that water having less than 150 p.p.m. of dissolved solids, represented by a conductivity of about 222 micromhos per cm at 25°C-32°C, were free of established colonies of *Australorbis glabratus* (Say) but that other molluscs were found in waters which had conductivities ranging from 87 to 222 micromhos per cm. The effect may be due to a low concentration of one or more electrolytes, so that a particular species cannot maintain its salt balance when the external concentration of a given ion or ions is below a certain value.

Temperatures were recorded periodically in different habitats but regular observations were not possible owing to the repeated disturbance by local inhabitants of apparatus left in the field. The highest water temperature recorded during the investigations was met in June 1960, when the maximum temperature taken at a depth of 8 inches (20 cm) in Pond E during a 24-hour period was 34.5°C; the lowest temperature recorded in April 1960 at the same depth during a 24-hour period in Pond Q was 21.9°C. The average diurnal range of temperature recorded in small temporary pools during the period March to June 1960 was 23.5°C-33°C, and during the period April to July 1961, 22.5°C-33.4°C. The average weekly temperature taken at a depth of 8 inches in the small pools at 10 a.m. during the period February to July 1960 was 24.6°C, and 25.1°C during the period February to July 1961. The average diurnal range of temperature recorded in Dams 1 and 2 at a depth of 12 inches (30 cm) during the period November 1959 to July 1960 was 23.8°C-30.1°C. The high temperatures frequently recorded in these habitats were of short duration and occurred only between noon and about 4 p.m. daily. The snails were evidently able to withstand these high temperatures and the quite severe diurnal temperature range to which they were sometimes subjected.

Gordon and co-workers (1934), working in Sierra Leone, found that the optimum temperature for *Bulinus (P.) globosus* was 27°C-33°C, but that the species was capable of surviving for long periods at a slightly higher temperature and for short periods at a markedly higher temperature. Mozley (1939) considered that the temperatures commonly met in the East African coastal region did not appear to have any marked effect upon the distribution of molluscs but that relatively high temperatures during

TABLE 1

RESULTS OF PHYSICAL AND CHEMICAL ANALYSES OF WATER SAMPLES FROM SELECTED HABITATS IN THE AREA UNDER OBSERVATION

	Dam 1	Dam 2	Pond C	Pond E	Pond F	Pond I	Pond J	Pond O	Pond Q	Pond T
pH	7.3	8.1	6.8	6.8	6.9	7.7	6.8	7.3	7.2	6.3
Conductivity (micromhos per cm at 25°C)	110.0	274.0	77.1	119.3	155.8	222.6	2544.0	144.7	274.0	107.0
Turbidity (p.p.m.)	17.0	11.5	82.0	78.0	62.0	200.0	200.0	123.0	Over 1000	30.0
Oxygen (p.p.m.) absorbed from N/80 $KMnO_4$ at 80° F (26.7°C)	7.4	8.2	10.0	4.6	9.2	24.0	310.0	3.4	10.6	5.4
Chloride (p.p.m.)	Nil	24.0	4.0	4.0	16.0	32.0	20.0	4.0	24.0	4.0
Fluoride (p.p.m.)	0.5	0.4	0.8	0.6	0.6	0.9	0.4	0.4	1.6	6.0
Free ammonia (p.p.m.)	Nil	Nil	Nil	Nil	Nil	1.04	0.88	3.52	Nil	1.28
Albuminoid ammonia (p.p.m.)	1.3	1.3	1.6	0.8	1.2	2.4	4.0	2.6	0.16	1.14
Nitrite nitrogen (p.p.m.)	Trace	Trace	Trace	Trace	Nil	Nil	Nil	Nil	Nil	Trace
Nitrate nitrogen (p.p.m.)	Trace	Trace	Nil	Nil	9.46	Trace	16.94	Nil	Trace	Trace
Alkalinity, as $CaCO_3$ (p.p.m.)	44.0	104.0	44.0	60.0	60.0	104.0	1216.0	76.0	52.0	44.0
Carbonate hardness (p.p.m.)	34.0	38.0	16.0	16.0	18.0	58.0	908.0	18.0	52.0	44.0
Non-carbonate hardness (p.p.m.)	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	8.0	Nil
Total hardness, as $CaCO_3$ (p.p.m.)	34.0	38.0	16.0	16.0	18.0	58.0	908.0	18.0	60.0	18.0
Calcium (p.p.m.)	11.2	11.2	4.8	4.8	4.0	12.8	212.8	3.2	12.0	4.0
Magnesium (p.p.m.)	1.92	2.4	1.0	1.0	1.9	6.3	90.3	2.4	7.2	1.9
Sodium (p.p.m.)	11.5	44.0	—	—	—	—	—	—	47.5	28.0
Potassium (p.p.m.)	4.0	48.0	Nil	Nil	Nil	Nil	Nil	Nil	21.0	Nil
Silica (p.p.m.)	16.0	14.0	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil

the periods of minimal rainfall resulted in the drying up of many ponds, with the result that the annual period during which it was possible for freshwater snails to be active was greatly reduced. This situation was well illustrated during the present observations when many breeding sites of *Bulinus (P.) nasutus productus* dried out completely during the period July to November 1960.

Values recorded for oxygen absorbed from N/80 $KMnO_4$ in four hours at 80°F (26.6°C) ranged from 3.4 p.p.m. to 310 p.p.m. The existence of micro-habitats, however, supported by their own micro-climates in relation to temperature differences cannot be ruled out. In such circumstances much higher concentrations of oxygen may be available than those recorded for general water samples. The work of Carter (1931), Von Brand, Nolan & Mann (1948), Von Brand & Mehlman (1953) and Chernin (1957) has shown that the heart-beat and oxygen consumption of snails may be influenced by temperature. Wright (1956) considered that this evidence indicated that in nature oxygen tension rather than temperature is likely to be the factor of most importance to snails.

DISCUSSION

Mandahl-Barth (1960) described the subspecies *Bulinus (P.) nasutus productus*, a form occurring in Uganda and Western Tanganyika, there being a remarkable difference in the shape of its shell compared with that of *Bulinus (P.) nasutus nasutus* (Martens), from the type-locality on the East African coast. The widespread distribution of this form, as already described, was in association with small temporary collections of water, almost completely devoid of higher plant life but generally having rich microflora, and it was also found in the " hafir " type of dam, which closely simulates the smaller pools. It is noteworthy that *Bulinus (P.) globosus* was found in only one habitat, Dam 1, where it made a temporary appearance. McClelland (personal communication) previously found *Bulinus africanus* in this habitat. Elsewhere in the Sukumaland area, *Bulinus globosus* and *Bulinus africanus* were always found in large permanent bodies of water, which usually contained rich aquatic vegetation, but the distribution of both species was limited. *Bulinus forskalii* was found in every type of habitat immediately after rain and often in large numbers, but its distribution, though widespread, was sporadic. Other bulinid snails, including *Bulinus coulboisi* and *Bulinus tropicus toroensis*, were associated with large permanent waterbodies and moderately rich aquatic vegetation, as was *Biomphalaria pfeifferi* sp.

Hubendick (1958) commented on the paucity of precise information and the establishment of so few distinct relationships in snail ecology, and considered that this was due largely to natural conditions themselves, freshwater snails as a rule (like many other freshwater creatures), being decidedly euryok, that is, having a wide ecological tolerance and therefore less adaptation to special conditions than most marine and terrestrial animals. Further, this author pointed out that the general euryok character of freshwater snails also means that, to a great extent, various species react similarly to the same environmental influence, their ecological requirements being qualitatively similar but quantitatively different. This applies to most African intermediate hosts of bilharziasis, and it is very difficult to identify and estimate the importance of an individual environmental factor—whether physical, chemical or biological—when all may be mutually affecting one another and their combined effect influencing a certain species.

The description of the snail habitats recorded above shows that they have many environmental factors in common; and no direct causal relationship was established between a particular chemical or biological factor and a given species of snail. It is considered, however, that one distinct ecological relationship was established by this study. *Bulinus (P.) nasutus productus* was found only in temporary habitats of seasonal duration, whether small open pools or a " hafir " type of dam, as distinct from permanent water bodies, such as the large dams. Conversely, other bulinid species, with the exception of *Bulinus forskalii*, were not found in temporary waters in the area. Evidence will be presented which suggested that seasonal drying out of the habitat of *Bulinus (P.) nasutus productus* is an inherent feature of its biology and one that has enabled it to spread into a rather specialized ecological niche—the temporary pool— which, in turn, has influenced its part as an intermediate host of *S. haematobium* in the area.

2. BIOLOGY AND CERCARIAL INFECTION OF THE PRINCIPAL MOLLUSCAN HOST

In addition to the data on the distribution and ecology of bulinid snails given above, information has also been published on bilharziasis in the area of Lake Province under consideration by Jordan (1961). This author has studied the incidence of *S. haematobium* in the area and has found an infection rate of 78% in the 6-12-year age-group. He has also shown that roughly 50% of the population in the older age-groups was infected.

Comparison of the widespread distribution of *Bulinus (P.) nasutus productus* in a large number of habitats with the limited and rather sporadic distribution of other bulinid snails indicated that this species might be an important intermediate host of *S. haematobium* in the area. Further, observed human contact with the favoured habitat of this snail strongly suggested this. Cridland (1955), working in Uganda, examined naturally infected specimens of *B. (P.) nasutus* and by animal inoculation identified *S. haematobium* infection. McClelland (personal communication) examined naturally infected *B. (P.) nasutus productus* collected from small pools in the Mwanza area, and by inoculation into mice also identified *S. haematobium* infection. No naturally infected specimens of *Bulinus (P.) globosus* have been found in many hundreds of snails examined from this area; and of 6721 *Bulinus (B.) forskalii*, collected over a wide area and examined for schistosome infection, two specimens shed non-schistosome cercariae.

This section of the present paper describes the biology of *B. (P.) nasutus productus*, seasonal fluctuations in population densities and associated cercarial infection rates and the response of this snail to desiccation.

METHODS

Snail habitats in the area of observations were examined fortnightly over a two-year period, the snail populations being sampled and the material being examined in the laboratory for schistosome infection. In selecting a suitable method for sampling snail populations, due consideration was given to the nature of the habitats involved and to the long-term requirements of the observations. Consideration was first given to a form of quadrat method which, if used systematically, might have provided information not only on the relative population density but also on the total snail population. There were, however, certain practical and theoretical disadvantages in relation to the area of observations. In a given habitat snails tend to be unevenly distributed so that numerous quadrat samples would be necessary. It was considered that such a method would upset and quickly destroy the biological balance of the small pools which constituted the greater proportion of the habitats, and would make long-term observations on population densities and cercarial infection rates impossible. The method finally adopted may be described as follows.

The snail population of a marked area in the habitat was estimated by counting the number of snails collected by one person, in a uniform manner, for a fixed period of time. In the case of small pools the whole area was used, being uniformly and systematically searched with a hand net (made of wire mosquito gauze, 16 meshes per inch, or 6.5 per cm) for 10 minutes, the number being expressed as the number collected per man per unit of time. Care was taken to disturb the habitat as little as possible and all snails were returned to their respective sites within 48 hours of the sampling. Olivier & Schneiderman (1956) evaluated this method and stated " the observed day-to-day variations in the number of snails collected by one man from the same place indicate that a single collection made according to the described method can provide a reasonably reliable estimate of the probable snail population density. The reliability is improved as the number of snails counted is increased. Repeated collections from the same places would also increase the reliability of the results and the most reliable data are obtained when all collections from a given place are made by one man or a group of men." The limitations of the method, however, must not be overlooked. Some of these are due to the snails not being uniformly distributed and being free to move about in the environment; others derive from variations in the collecting skill and reliability of the collector. They are, however, inherent and encountered with any sampling method.

Snail samples from the different habitats were brought to the laboratory, the size distribution of each one being determined by measuring the height of all snail shells (the distance from base to apex) to the nearest 0.5 mm. Snails referred to hereafter as " young ", " middle-aged " and " old " corresponded to the size groups 0-7.5 mm, 8-14.5 mm and 15-20 mm respectively. Snails were then examined for cercarial infection, each one being placed in a 3-inch × 1-inch (7.5 × 2.5 cm) specimen tube and exposed to artificial light for four hours on each of two successive days. At the end of this examination the total number of snails shedding " mammalian-type " cercariae was noted and the infection rate of different samples calculated accordingly.

Proof of the identification of schistosome species was obtained by exposing laboratory-bred hamsters (*Mesocricetus auratus*) and white mice to cutaneous penetration by actively swimming cercariae shed by snails from different habitats. Each animal was exposed to the pooled discharge of a number of snails to avoid unisexual infections. Counts were made of the number of cercariae to which each animal was exposed by taking a small sample of the suspension of cercariae and filtering it with a filter paper 4.25 cm in diameter. The cercariae which were retained on the paper were stained with ninhydrin, and counted using a dissecting microscope. An animal to be infected was placed in a 500-ml beaker, and water at 26°-29°C added, bathing the animal to half-way up the abdomen. The beaker was then covered and left for 20 minutes to allow the animal to void excretory products (white mice were left for 10 minutes only). The animal was then placed in a clean beaker and water at 26°-29°C added, again bathing the animal to half-way up the abdomen, and the suspension of cercariae was then added. Hamsters were exposed to the infected water for 60 minutes and mice for 30 minutes only. Identification of *S. haematobium* was made by confirming the presence of the terminal-spined eggs in the uteri of female worms and in the liver tissue of the animal host.

The biology of the snail was studied in the field and in laboratory aquaria, and observations were made on breeding, presence or absence of egg masses, and growth rates.

Snails from different habitats were marked with the radioactive isotope cobalt-60, and returned to their respective habitats just before these became completely dry, in order to obtain evidence concerning the capacity of the snail to survive desiccation and the period for which it might do so. Snails were immersed in an aqueous solution of cobalt-60 (1000 μc per litre) for a period of 24 hours, then placed in a beaker containing clean water for a further 24 hours before being returned to the field. Collections of snails were then made soon after these habitats were again filled by rainfall. These were examined for radioactivity in the laboratory, using a scintillation counter. One habitat was dug up periodically, in order to locate aestivating snails, investigate their depth of penetration and find the proportion of snails of different age-groups surviving over a prolonged period.

Rainfall figures are those from the established meteorological station at Ukiriguru, latitude 2° 42′ S, longitude 33° 1′ E.

OBSERVATIONS

All data hereafter refer to *Bulinus (P.) nasutus productus*.

Biology of the molluscan host

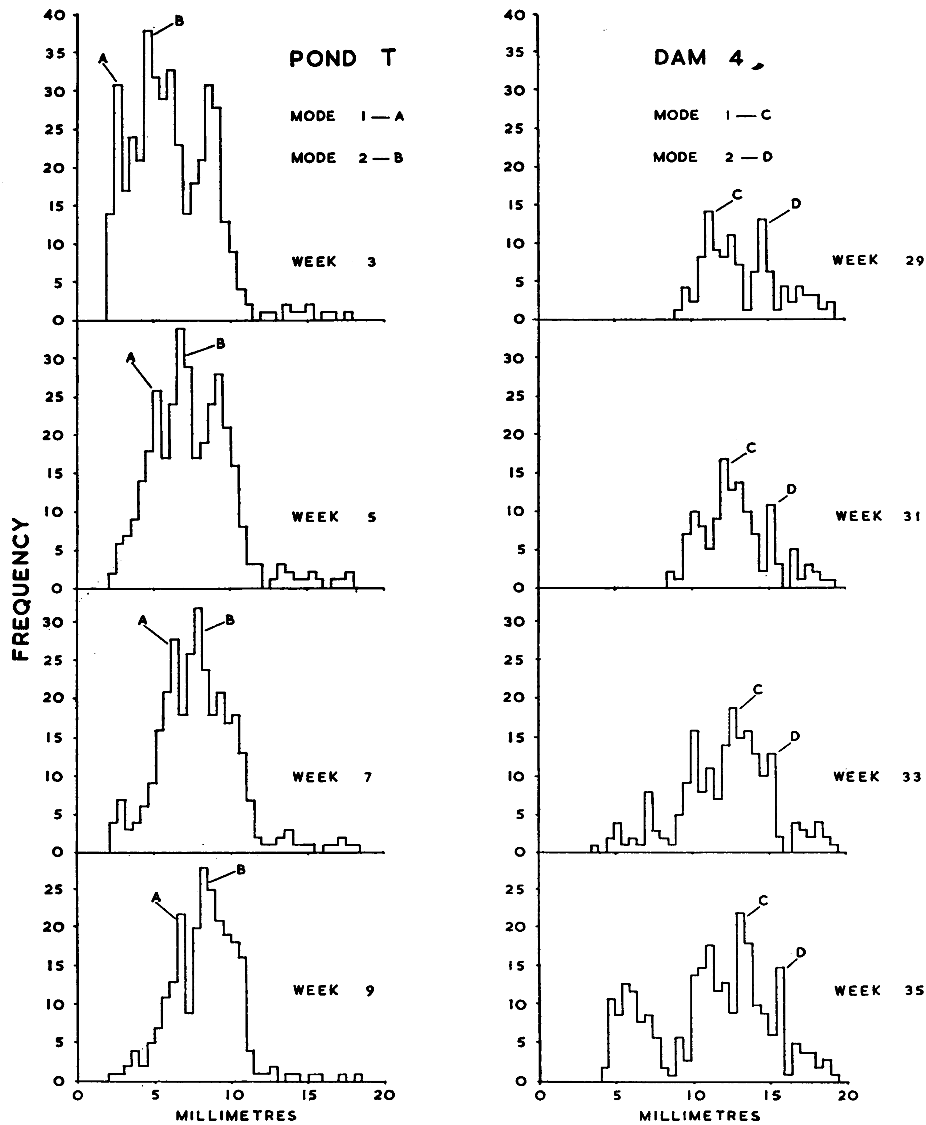
McMullen (1947) observed the growth of *Oncomelania quadrasi* (Mollendorf), and, making fortnightly collections of snails and measuring all specimens collected, was able to follow apparent broods over several weeks, by comparing the modes of successive size-frequency curves. This technique has been applied in the present study to field data collected from fortnightly samples in nine habitats over a period of one year (November 1959 to December 1960).

Fig. 3 shows size-frequency histograms of successive fortnightly snail samples in Pond T and Dam 4; and modes 1 and 2, in the size-frequency histograms of samples from each habitat on week 3 and week 29, respectively, can be followed for successive samples. Some observations which were difficult to make under field conditions on egg-laying, hatching and age at maturity were made in laboratory aquaria. From all the data combined a growth curve was drawn (Fig. 4) and a table made (Table 2) which represent the best estimate of the average growth rate of *B. (P.) nasutus productus* under field conditions in the area of observations.

In appearance the egg mass of the snail was oval and its length varied from 4 mm to 8 mm. The whole egg mass contained some 5-22 egg sacs. McClelland (personal communication) counted 21 egg masses laid by young snails approximately two months old, and found an average of 14.5 egg sacs per mass. The number of egg sacs per mass, however, appeared to increase with the age of the parent snail. Mature snails continued to lay eggs throughout their life-span and cross-fertilization appeared to be customary. Snails hatched from the

FIG. 3

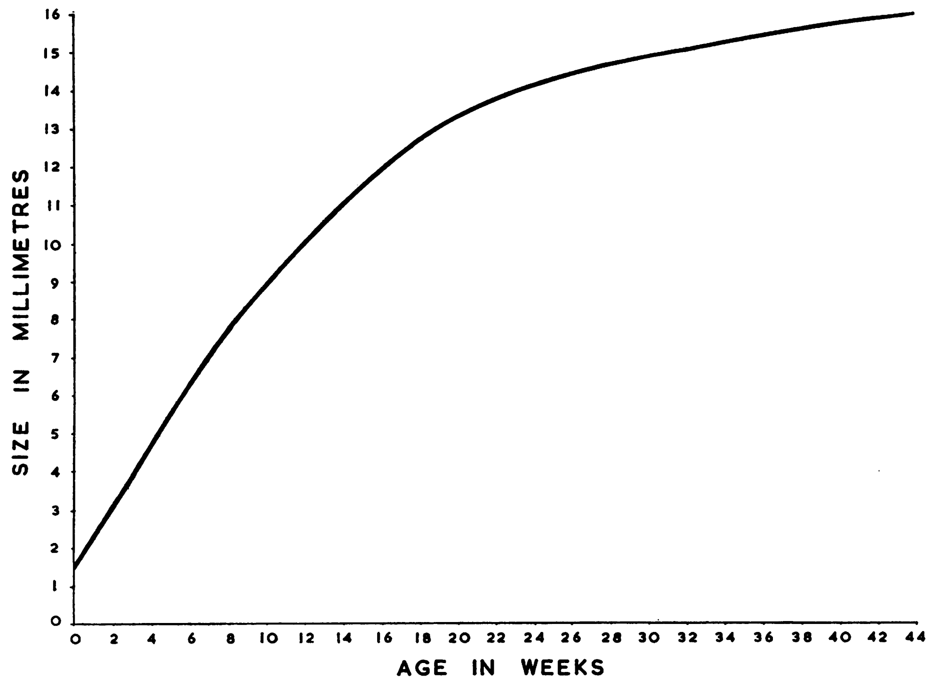
SIZE-FREQUENCY HISTOGRAMS OF SUCCESSIVE FORTNIGHTLY SNAIL SAMPLES COLLECTED IN POND T AND DAM 4



egg capsules 10-11 days after an egg mass was laid, the height of the shell being about 1.5 mm. Thereafter a snail grew about 0.8 mm per week until it measured 7-8 mm (approximately two months old), at which stage most snails were mature. The growth rate then dropped sharply and was about 0.5 mm per week for about 10 weeks, 0.25 mm per week for about five weeks, 0.125 mm per week for about four weeks, 0.1 mm per week for about 10 weeks and 0.07 mm per week for about seven weeks, at which time the height of the shell was about 16 mm and the snail about 44 weeks old. Specimens were occasionally found measuring 20.5 mm, and combined field and laboratory data indicated that the average snail of this species attained its full size not less than 12 months after hatching. Evidence which

FIG. 4

GROWTH CURVE, BASED ON COMBINED FIELD AND LABORATORY DATA, REPRESENTING THE BEST ESTIMATE OF THE AVERAGE GROWTH RATE OF *BULINUS (P.) NASUTUS PRODUCTUS*



will be presented subsequently shows that, in the area studied at any rate, most snails which completed maximum growth did so after one or even two periods of aestivation.

Seasonal fluctuation in snail population densities

The numbers of snails collected fortnightly under uniform conditions in Ponds C, O and T illustrate the seasonal nature of the habitats and the high cercarial infection rates occurring in individual foci. These data were chosen as being generally representative of conditions prevailing in the majority of habitats in the area during the period of observations.

In Pond C (Fig. 5—which may be taken as illustrative of similar data for other habitats), the population build-up began some 12 weeks after the site was first filled by rainfall, though some snails were found within a few days of the first rain. No snails were found between week 11 and week 21 of 1960, and this was possibly due to the presence of only a small number of snails, which sampling failed to reveal, or to death of the snails first found on weeks 9 and 11 and the subsequent appearance of a new population on week 21. The age structure of the population revealed by sampling between week 21 and week 31 suggests that a large number of old snails was present in the habitat during the period between week 11 and week 21, probably in the mud, and that these emerged owing to some change in the aquatic environment favourable to their normal existence after week 21.

A common feature of small temporary collections of water in the area is the way in which they abruptly dry out. This habitat remained dry from week 33 until week 44, and the first collection of snails was made again during week 45. It then dried out for some three weeks and the next collection of snails was made on week 48. Thereafter continuous fortnightly sampling was carried out until week 29 of 1961. The age structure of samples collected on weeks 49 and 51 of 1960 and on week 1 of 1961 indicated that large numbers of " middle-aged " and a few " old " snails survived the dry period by aestivation. Quite a high mortality occurred in these age-groups, however, as shown by the age structure

TABLE 2

SIZES AND CORRESPONDING AGES OF *BULINUS (P.) NASUTUS PRODUCTUS*, BASED ON GROWTH CURVE DERIVED FROM FIELD AND LABORATORY DATA

Size (mm)	Age (weeks)	Size (mm)	Age (weeks)
1.5	at hatching	9.0	9.9
2.0	0.5	9.5	10.9
2.5	1.3	10.0	11.9
3.0	2.0	10.5	12.9
3.5	2.5	11.0	13.9
4.0	3.0	11.5	15.0
4.5	3.7	12.0	16.1
5.0	4.4	12.5	17.2
5.5	5.0	13.0	19.0
6.0	5.6	13.5	21.0
6.5	6.3	14.0	23.0
7.0	6.9	14.5	27.0
7.5	7.5	15.0	32.0
8.0	8.1	15.5	37.0
8.5	8.9	16.0	44.0

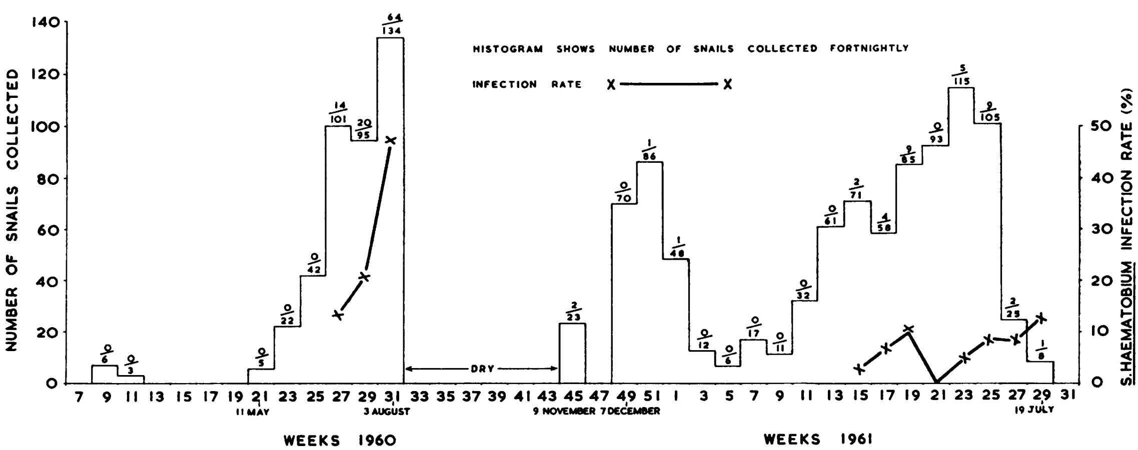
of the samples collected on weeks 3, 5, 7 and 9 of 1961, after which new broods of snails became apparent and the population density increased. The large numbers of infected snails collected in this habitat on weeks 29 and 31 of 1960 were not found during 1961 when population densities were comparable.

Pond O, first sampled on week 13 of 1960, was completely dry before week 35 of 1960. The first samples collected on weeks 13 and 15 showed that a large number of " middle-aged " and " old " snails had survived a long dry period. New broods of snails were soon apparent in subsequent samples, however, a high mortality among " old " snails having occurred. This habitat remained dry for 16 weeks before being filled by rainfall on week 49 of 1960. A collection of snails was made on week 51, after which the habitat dried out again; the next collection was made on week 13 of 1961, and thereafter fortnightly until week 33. This habitat contained water and a breeding population of snails for exactly the same periods during 1960 and 1961. Large numbers of infected snails were collected during June and July 1960, and during the corresponding period in 1961, but the peak cercarial infection rate occurred rather later in 1961.

Pond T was first sampled on week 47 of 1959, and fortnightly thereafter until week 27 of 1960. The age structure of the samples collected on weeks 47, 49 and 51 indicated that an appreciable number of " middle-aged " and " old " snails had survived a period of desiccation and emerged when the habitat was filled by rainfall. The age structure of the samples collected on weeks 1 and 3 of 1960

FIG. 5

NUMBERS OF SNAILS COLLECTED FORTNIGHTLY UNDER UNIFORM CONDITIONS AND NUMBERS INFECTED WITH *S. HAEMATOBIUM* [a] IN POND C



[a] The figures above the histograms represent the numbers of snails shedding " mammalian-type " cercariae over the numbers examined.

indicated that a high mortality of " old " snails had occurred and that new broods of snails were present, and an increase in the population density then began. A large number of cercarial infections were found among " old " snails collected on weeks 49 and 51 of 1960. Unlike the situation in other habitats, however, the infection rate dropped sharply, and large numbers of infected snails were not found subsequently, despite the appreciable increase in the population density. It is thought that this may have been due to the observed use of this habitat for washing clothes and a possible consequent inhibition of infection in the snails owing to the concentration of soap in the water. After week 27 of 1960, the habitat was completely dry for 16 weeks and the next collection of snails was made on week 47 and fortnightly thereafter until week 27 of 1961. It is of interest that during 1961 snail breeding in this habitat was apparent and the age structure of samples showed that numerous broods of snails were produced, but at no time did the population density approach that of the corresponding period during 1960.

Before the snail samples were taken, all habitats were carefully searched for the presence or absence of egg masses on rock surfaces, emergent vegetation and any other likely surface on which eggs might be laid. In the small temporary pools egg masses were difficult to locate, and often the only evidence that breeding was taking place was the appearance of new broods of snails in successive samples.

The number of snails collected monthly in the area (Ponds A-S), the number with cercarial infections and the monthly rainfall figures are shown in Fig. 6. The histogram shows the monthly build-up in the number of snails as habitats were filled by rainfall and as individual population densities rose.

It may be argued that the monthly build-up in the number of snails was simply a function of the increased number of habitats being sampled, and was not necessarily due to an increase in individual population densities. However, the mean monthly densities of snails and the percentage of cercarial infection rates for the period January 1960 to August 1961, shown in Table 3, were calculated from the total numbers of snails collected monthly and the numbers of habitats holding water and available for sampling each month. The results show that increase in population densities occurred and that the number of infected snails found increased with population density, the infection rate lagging behind population build-up.

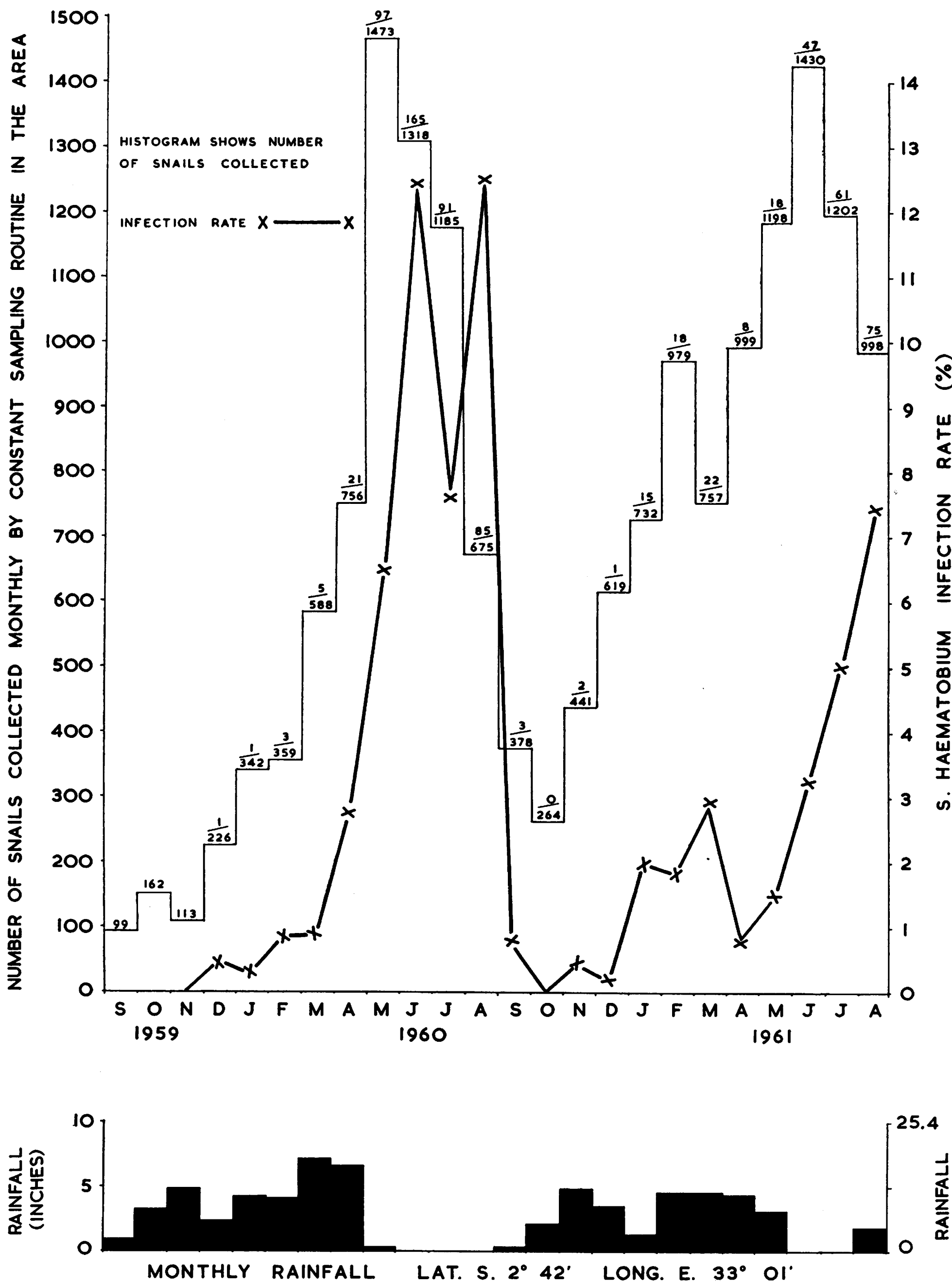
The peak population density in the area during 1960 occurred in May, after a burst of breeding activity and the production of large numbers of snails, following the rains in March and April; and the highest numbers of snails infected with *S. haematobium* were found during the following months of June, July and August. During 1961 the peak population density occurred in June, following an erratic rainy reason which extended well into May, while the highest numbers of cercarial infections were again found in June, July and August; but the total was only a little more than half the number found during the corresponding period of the previous year.

The results show that the main transmission period in this area lasted for some four to five months, corresponding to the end of the main rains and the period immediately afterwards—i.e., April-August—when the maximum number of snail habitats contained water and population densities were high. This picture was, of course, dependent upon rainfall, and may be expected to vary slightly from year to year. This was shown during 1961, when rapid population build-up occurred in January, February and March, and relatively large numbers of cercarial infections were found following appreciable rainfall in November and December 1960 and normal rains earlier that year.

Infected snails were found in all the small temporary pools sampled in the area, but in several of them only very occasionally, even though they contained thriving snail populations. No physical, chemical or biological difference was apparent between these habitats and others in which large numbers of cercarial infections were found, except their use by local inhabitants. Ponds G, I, L, M and N were all so used, and were apparently reserved solely for human use by inhabitants in the immediate vicinity. It is presumed that the infected snails occasionally collected from them were the consequence of pollution by strangers, probably itinerant cattle-boys. Small boys between the ages of 6 and 14 years were most frequently observed bathing and washing in the small temporary pools, while the older persons were often seen using the dams for these purposes. Observations on the use of different bodies of water, however, were unfortunately restricted and those recorded are not necessarily true for other areas. Cattle were observed watering in a variety of habitats during September and October, when conditions were generally dry and water very restricted, though the dams were focal points for this purpose throughout most of the year.

FIG. 6

NUMBERS OF SNAILS COLLECTED MONTHLY UNDER UNIFORM CONDITIONS IN OBSERVATION AREA (PONDS A-S) AND NUMBERS INFECTED WITH *S. HAEMATOBIUM*,[a] TOGETHER WITH MONTHLY RAINFALL FIGURES



[a] The figures above the histograms represent the numbers of snails shedding " mammalian-type " cercariae over the numbers examined.

TABLE 3

MEAN MONTHLY DENSITIES OF *BULINUS (P.) NASUTUS PRODUCTUS* AND *S. HAEMATOBIUM* INFECTION RATES,[a] JANUARY 1960 THROUGH AUGUST 1961

Month	No. of habitats	Mean monthly snail density	Mean monthly *S. haematobium* infection rate (%)
1960			
January	6	57.0	0.3
February	14	25.6	0.8
March	15	35.2	0.9
April	17	44.5	2.8
May	17	86.6	6.6
June	19	69.3	12.5
July	17	69.7	7.7
August	13	51.9	12.6
September	11	34.4	0.8
October	9	57.5	0
November	12	36.7	0.5
December	16	38.7	0.2
1961			
January	18	40.7	2.0
February	16	61.2	1.8
March	16	47.3	2.9
April	17	58.8	0.8
May	17	70.5	1.5
June	19	75.3	3.3
July	18	66.8	5.1
August	15	66.5	7.5

[a] Calculated from the total number of snails taken monthly (Fig. 6), and taking into consideration the number of habitats holding water and available for sampling each month.

Size-frequency histograms for snails with cercarial infections are shown in Fig. 7 for two consecutive periods. The ages of these snails were calculated from the growth-rate data already given in Fig. 3 and 4 and in Table 2. Most infected snails were two months and more old, and the majority of infections occurred in snails eight months old. No infected specimens were found which were less than six weeks old.

Transmission experiments

Table 4 shows the results obtained when laboratory animals were exposed to " mammalian-type " cercariae shed by naturally infected snails collected in different habitats.

A total of 828 adult worms was recovered from the autopsy of 18 hamsters; 53% of the worms were males. The proportion of cercariae used for infection which developed to maturity was never high, but, even when the number of days from first exposure to autopsy was the same, considerable variation occurred. In one experiment 7.3% of 792 cercariae developed to maturity after an interval of 112 days, while in another experiment only 1.5% of 792 cercariae from the same pool developed to maturity after the same interval of time. Of 990 cercariae to which two other hamsters were each exposed, 11.6% and 7.2% respectively developed to maturity after an interval of 96 days.

In hamsters worms were recovered from the portal vein, the intrahepatic veins and the mesenterics. An infected liver was invariably enlarged and friable and usually contained a characteristic pigment which gave it a dark bluish-grey appearance. Eggs were numerous in infected liver tissue and were occasionally found in the spleen, which was sometimes enlarged.

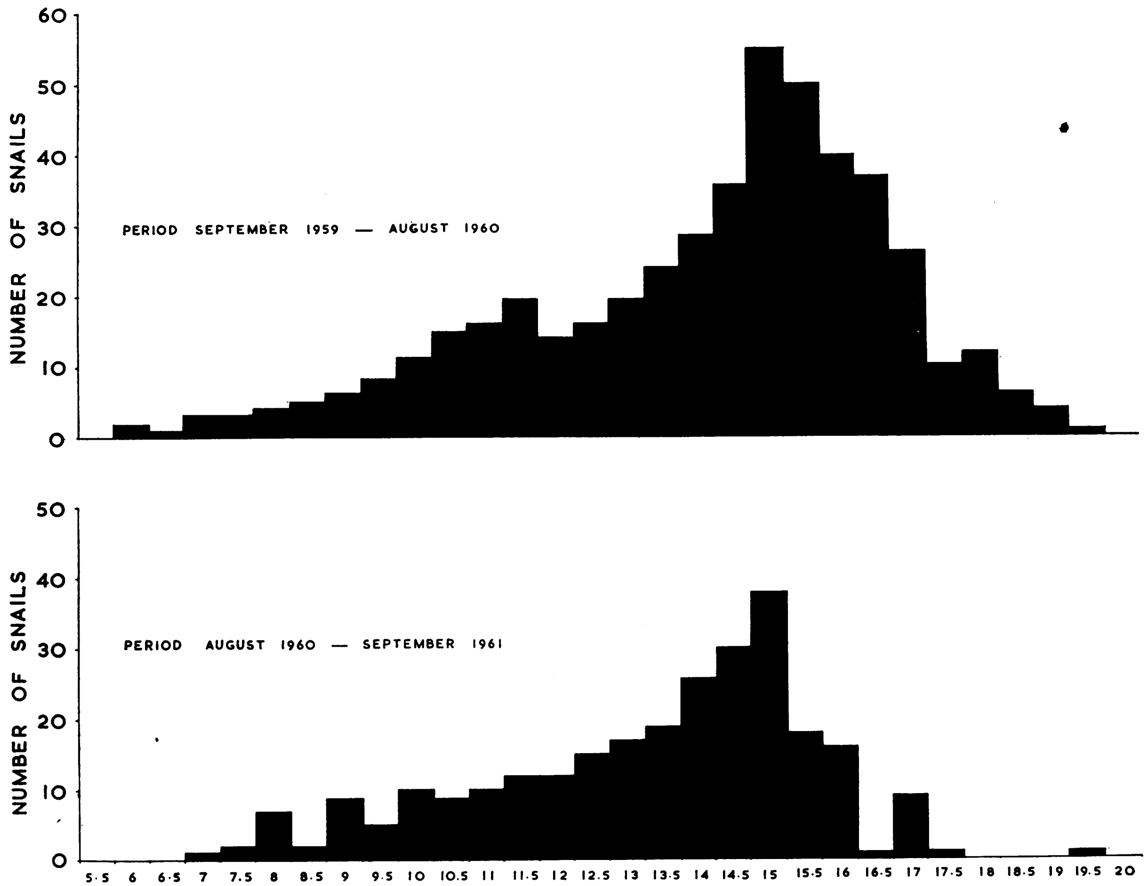
A total of 24 adult worms was recovered from the autopsy of three mice; 54% were males. The proportion of cercariae used for infection which developed to maturity was very low. Of 400 cercariae to which three mice were each exposed, 1.8%, 3% and 1.3%, respectively, developed to maturity after an interval of 224 days.

The hamster generally proved a more satisfactory experimental animal than the mouse for S. *haematobium* transmission experiments. In addition to the animals used for the transmission experiments shown in Table 4, a further 43 hamsters were exposed to pooled cercariae from snails collected in the different habitats during the course of the observations, and proof of *S. haematobium* infection was obtained in all experiments. No *S. bovis* infection was found in any of the transmission experiments carried out.

Aestivation of snails

The populations of *B. (P.) nasutus productus* in the area studied may be subjected to prolonged periods of desiccation owing to the seasonal character of the main habitat of this snail. The widespread distribution of the species in a variety of temporary situations quite soon after rainfall cannot be account-

FIG. 7
SIZE-FREQUENCY HISTOGRAMS OF SNAILS WITH CERCARIAL INFECTIONS FOR TWO CONSECUTIVE PERIODS



ed for by passive dissemination from a few foci which may not have dried out. Further, measurement of snails from newly rain-filled sites, together with growth-rate studies, showed that large numbers of snails of different ages survived dry conditions by aestivation.

Snails from six different habitats were marked with the radioactive isotope cobalt-60 and were returned to their respective sites just before these dried out. Two snails collected from a habitat only seven days after it was again filled by rainfall were found to be radioactive, thus proving that they had survived dry conditions for a period of 130 days. It was considered that the small recovery of marked snails was mainly attributable to their being returned to the different habitats too late for the majority to survive the final process of drying out.

In one habitat, which was dug up periodically, snails were found at the bases of grass roots around the perimeter of the dried-out, saucer-like depression, but not in the middle portion. No snails were found at depths greater than 2 cm. It was observed that snails were rarely collected from a situation which was in the last stages of drying out and this, together with the fact that aestivating specimens were found around the perimeter of the site, only suggested that snails did not follow the receding waterline and finally burrow in a central muddy pool, but were stimulated to begin aestivation some time before severe contraction of the water-body occurred.

The size structure of successive two-monthly samples of live snails recovered from the dry habitat is shown in Fig. 8. The results show that a progressive diminution in the survival of " old "

TABLE 4
RESULTS OF EXPOSING LABORATORY ANIMALS TO " MAMMALIAN-TYPE " CERCARIAE OBTAINED FROM NATURALLY INFECTED *BULINUS (P.) NASUTUS PRODUCTUS*

Snail habitat	Laboratory animal	No. of snails used	Total cercariae applied	Days from first exposure to autopsy	Result of autopsy
Pond A	Hamster	7	918	109	9 male and 7 female *S. haematobium*
	Hamster	7	918	109	6 male and 6 female *S. haematobium*
Pond C	Hamster	64	990	96	60 male and 55 female *S. haematobium*
	Hamster	64	990	96	37 male and 34 female *S. haematobium*
	Hamster	64	990	116	53 male and 48 female *S. haematobium*
Pond I	Hamster	4	900	118	34 male and 30 female *S. haematobium*
	Hamster	4	900	90	23 male and 20 female *S. haematobium*
Pond J	Hamster	3	1 125	91	27 male and 25 female *S. haematobium*
	Hamster	3	1 125	119	15 male and 14 female *S. haematobium*
Pond K	Hamster	6	882	90	22 male and 22 female *S. haematobium*
	Hamster	6	882	112	28 male and 25 female *S. haematobium*
Pond O	Hamster	26	450	157	14 male and 15 female *S. haematobium*
	Hamster	26	900	166	19 male and 17 female *S. haematobium*
Pond S	Hamster	4	750	141	12 male and 11 female *S. haematobium*
	Hamster	4	750	141	12 male and 9 female *S. haematobium*
Pond T	White mouse	8	400	224	4 male and 3 female *S. haematobium*
	White mouse	8	400	224	7 male and 5 female *S. haematobium*
	White mouse	8	400	224	2 male and 3 female *S. haematobium*
	Hamster	8	800	226	34 male and 32 female *S. haematobium*
Dam 4	Hamster	8	792	112	30 male and 28 female *S. haematobium*
	Hamster	8	792	112	6 male and 6 female *S. haematobium*

snails occurred; and that towards the end of the eight-month period few were found alive, the majority being " young " and " middle aged " specimens.

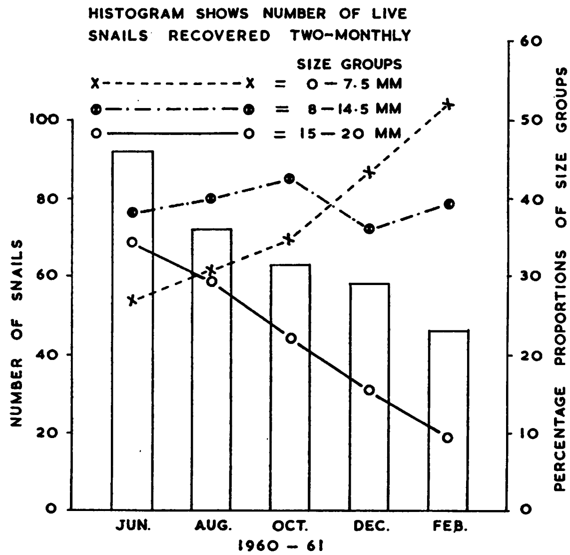
Two snails, in a collection made six days after Pond C was refilled by rainfall (having been dry for 98 days), shed " mammalian-type " cercariae. A hamster exposed to 450 cercariae shed by these snails and autopsied 101 days later was found to contain adult male and female *S. haematobium* worms, thus proving that *S. haematobium* infection was carried in the snails from one wet season to the next. It is of interest that eight days before this habitat dried out, 47.7% of a sample of 134 snails were found to be infected with *S. haematobium.*

DISCUSSION

Studies on the molluscan hosts of bilharziasis have been made in various parts of the African continent, and consideration has been given to factors which may influence population density and composition. Smithers (1956), working in the Gambia, described the ecology of pools formed on a laterite plateau and the seasonal build-up of populations of *Bulinus*

FIG. 8

SIZE STRUCTURE OF LIVE SNAIL SAMPLES COLLECTED IN ALTERNATE MONTHS FROM A HABITAT WHICH REMAINED DRY FOR A PERIOD OF EIGHT MONTHS



(B.) senegalensis (Müller) in these laterite pools. McCullough (1957), working in Ghana, recorded the highest counts of *B. (P.) globosus* at the beginning of the dry season (December and January) and very few snails in March and April after heavy rains had flooded the habitats. This author considered that the principal factors which appeared to govern the density of snail populations were drying, flooding, seasonal changes in aquatic vegetation and competition with other molluscan genera, while variations in temperature and in chemical constituents of the water were insignificant. Barlow & Abdel Azim (1946) and Gaud (1958), working in North Africa, studied seasonal fluctuations in the fertility and growth of intermediate hosts of bilharziasis. The evidence presented by these authors shows that the factors responsible for seasonal fluctuations are multiple, and that the existence of an internal rhythm, whether of species or race, seems to be excluded.

Mozley (1939), working in Zanzibar, recorded that *B. (P.) globusus* bred rapidly, with generations both during and after the main rains (April-May) and with another generation at the time of the short rains (November-December). Cridland (1957a) concluded that while periodic drying of a habitat was the most significant factor in reducing numbers of *B. (P.) nasutus*, trematode infection caused a reduction in the number of snails before the habitat dried up. Cridland (1957b, 1958) recorded seasonal fluctuations in population densities of *Biomphalaria* sp. with sudden increases in the numbers of young snails after the main rains in April. Webbe & Msangi (1958), working near the coast in Tanganyika, found that seasonal fluctuation occurred in the numbers of bulinid snails, and that breeding peaks closely followed the "long" and "short" rains in April-May and November-December, respectively. These authors found that populations of bulinid snails followed an average growth curve, the maxima and minima of which were related to rainfall and temperature and to the ecological changes brought about by them. Webbe (1960) concluded that although rainfall may under certain conditions produce bursts of breeding activity followed by large numbers of young forms (particularly in areas with well-defined seasonal rainfall alternating with periods of drought), a snail population may be adversely affected by flooding owing to rapid change in the water level and the many consequent limnological changes.

The present observations show that major seasonal fluctuations in snail population density occurred which were mainly consequent upon rainfall and temperature and the ecological changes brought about by them, high temperatures during periods of minimum rainfall resulting in the rapid drying of temporary water collections and high snail mortality. Apart from these seasonally operating extrinsic factors, the density and age structure of a snail population is controlled by intrinsically operating factors, such as birth-rate, natural mortality and environmental resistance, which are not constant for a population and will vary with the size and composition of different populations and environmental conditions. Further consideration will be given to these factors in the final part of this paper.

Large numbers of snails infected with *S. haematobium* were generally found when snail population densities were high, and most cercarial infections occurred in snails about seven to nine months old. Many infected snails, which were found in some cases only six to eight weeks after habitats were filled by rainfall, were (according to data available for conversion from size to age) between 15 and 48 weeks old and had survived at least one period of desiccation. Infections were possibly established in very young snails, but the evidence suggests that these were frequently fatal and that mature infections generally derived from snails which were already several, if not many, weeks old at the time of infection. It appears, therefore, that the probability of a snail's becoming infected increases with age and is dependent upon the time spent in the aquatic environment and available to inoculation by miracidia.

A high mortality of snails may occur as the result of infection, but Gordon et al. (1934) considered that the effect was small. Cridland (1957b), however, concluded that both changes in snail density and their infection rates might be due to the effect of parasitism. During the present observations the effect of parasitism on snail density was difficult to assess as high cercarial infection rates frequently occurred immediately before complete drying of the habitat and a high mortality of snails of all age-groups. However, infected snails did not appear to survive for long periods, as shown in Fig. 7 by the relative absence of cercarial infections in very old snails compared with those three to nine months old. Radical changes in density as the result of parasitism may, therefore, have occurred in populations which were composed largely of " middle-aged " and " old " snails, and in which birth-rates were low. Coelho (1954) observed a significant reduction in the number of egg masses laid by *Australorbis glabratus* infected with *S. mansoni*, and during the present study parasitism may have been responsible, in part at any rate, for a drop in reproduction which was apparent in some habitats where high cercarial infection rates were observed.

Many workers, including Blacklock & Thompson (1924), Humphreys (1932), Archibald (1933), Barlow & Abdel Azim (1945), Gerber (1952), Olivier (1956a, 1956b) and Shiff (1960) have made observations on the reaction of molluscan hosts of bilharziasis to drying. The capacity of snails to survive out of water for weeks or even months has important consequences in relation to the epidemiology of bilharziasis and to control measures. Infection with schistosomes appears to render snails less tolerant to desiccation. Barbosa & Coelho (1953) observed that sporocysts and cercariae of *S. mansoni* degenerated on the 20th day in *Australorbis glabratus* subjected to desiccation. Olivier, Barbosa & Coelho (1954) found that the effect of desiccation was apparent during the first 20-30 days, but that thereafter deaths among infected snails were no more frequent than among uninfected ones. Barbosa & Coelho (1955) showed that survivors of *A. glabratus* which were subjected to desiccation came out free of infection only when the infection was mature. These authors found that if the infected snails were removed from the water within 25 days of exposure to the miracidia of *S. mansoni*, the snails kept the infection for 90 days or more. From these experiments they concluded that development of the infection stopped. Barbosa & Olivier (1958) found an immature infection under field conditions and suggested that this might have epidemiological significance, since it raised the question whether infection in snails could be carried from one wet season to the next. Cridland (1957a) concluded from laboratory and field experiments that while *B. (P.) nasutus* was capable of surviving periods of drought by aestivation, infected snails of this species did not normally survive over a period of one month. Webbe & Msangi (1958) recorded that *B. (P.) nasutus* shed " mammalian-type " cercariae only 21 days after a pond, which had been dry for five months, was refilled by rainfall; and they concluded that in view of the short period which elapsed between the refilling of the pool and the shedding of mature cercariae by the snails, the cercariae may possibly have contained immature infections. The present observations show that *B. (P.) nasutus productus* containing infections of *S. haematobium* survived drying for a period of 98 days, and it is considered that this may be a relatively common occurrence (dependent upon the stage of maturity of the infection when aestivation begins) in other habitats in the area.

It is concluded that *B. (P.) nasutus productus* is the principal intermediate host of *S. haematobium* in the area studied and that its colonization of temporary pools and its capacity to survive periods of desiccation by aestivation have enabled it to become widespread in distribution, thereby enhancing its importance in the transmission of the disease.

3. SNAIL POPULATION DYNAMICS

The way in which growth-rate and age-composition data were derived for *Bulinus (P.) nasutus productus* has been described above. These data form the basis of some population dynamics discussed in the present part of this paper, which will deal with age-structure in relation to density at different times, reproduction indices, adult mortality rates and their relationship to one another. The possibility of reducing the transmission of *S. haematobium*, in the light of the studies made, will also be discussed.

METHODS

Measurement of size is the only practical method of determining the age of snails collected in the field, and in order to estimate their ability to survive under natural conditions one must know the age distribution of a population at any given time. Measured snails were grouped into three size groups—0-4.5 mm, 5-7.5 mm and 8-20 mm—referred to hereafter as "very young", "juvenile" and "old" snails, respectively; and percentage proportions of the different size-groups were calculated for different population densities. The term "middle-aged", used in the preceding part of this paper, refers to the size group 8-14.5 mm, which was made use of in the observations described there. The term "density" refers to the number of snails of all sizes collected at any sampling. From the successive size-frequency histograms of fortnightly samplings and the growth-rate data derived from them, accurate calculations of the mortality of adult snails in different habitats were made for each interval between sampling. The number of adult snails at any sampling was taken as a starting-point (snails 10 mm and over being considered adult), then by reference to the growth-rate data the size to which the smallest adult would have grown by the time of the next sampling was calculated. The number of snails of this expected size and larger was then subtracted from the number at the first sampling to give the total loss. The average daily mortality rate in a given habitat was then calculated using the following expression:

$$lx = e^{-xd}$$

where lx = the proportion of snails surviving to age x;

x = the number of days between sampling (in this case 14);

d = the daily mortality rate.

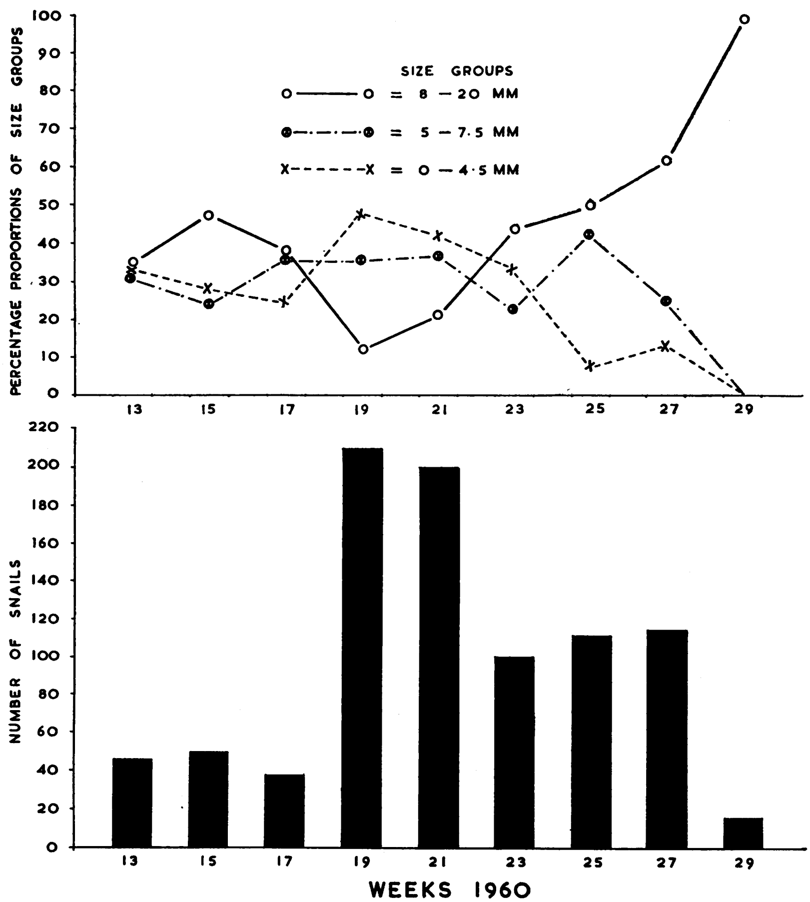


FIG. 9
SNAIL DENSITIES AND PERCENTAGE PROPORTIONS OF SIZE GROUPS AT FORTNIGHTLY INTERVALS IN POND I

Differences in the survival rates of young snails and in reproduction must influence population structure and density, but data on survival of young snails and egg-laying cannot be determined under field conditions with the accuracy of adult mortality rates. An index of a combination of the two was obtained, however, by dividing the number of mature snails (height of shell 8 mm and over) at one sampling into the number of young at the next. The number of young was determined by reference to the growth-rate data, which gave the maximum size that a young snail could have reached if the egg was laid on the day that the mature snails were counted. The ratio thus obtained was divided by the number of days between sampling to obtain a mean daily reproduction index.

OBSERVATIONS

Age-structure and density

On week 13, in Pond I (Fig. 9), " very young ", " juvenile " and " old " snails were present in almost equal proportions, having survived a period of desiccation. The sample collected in week 15 showed that the number of " old " snails had increased at the expense of " very young " and " juvenile " ones, rapid growth having taken place. On week 17, a mortality of " old " snails was apparent and the proportion of " very young " snails was reduced, with a corresponding increase in the " juvenile " group. On weeks 19 and 21, a sharp increase in population density was apparent, the proportion of " very young " snails being correspondingly high; but on week 23 a drop in density occurred which suggested that there had been a high mortality of " very young " snails. On weeks 25 and 27, although population density was relatively high, the proportion of " very young " snails was low. Thereafter the relationship between the different age-groups was evident as growth took place, and the change from an expanding population containing a large proportion of " very young " snails to a declining one with a large proportion of " old " snails was apparent.

On week 47 of 1959, in Pond T (Fig. 10) many " old " and some " juvenile " snails were present, having survived a period of desiccation. On week

FIG. 10

SNAIL DENSITIES AND PERCENTAGE PROPORTIONS OF SIZE GROUPS AT FORTNIGHTLY INTERVALS IN POND T

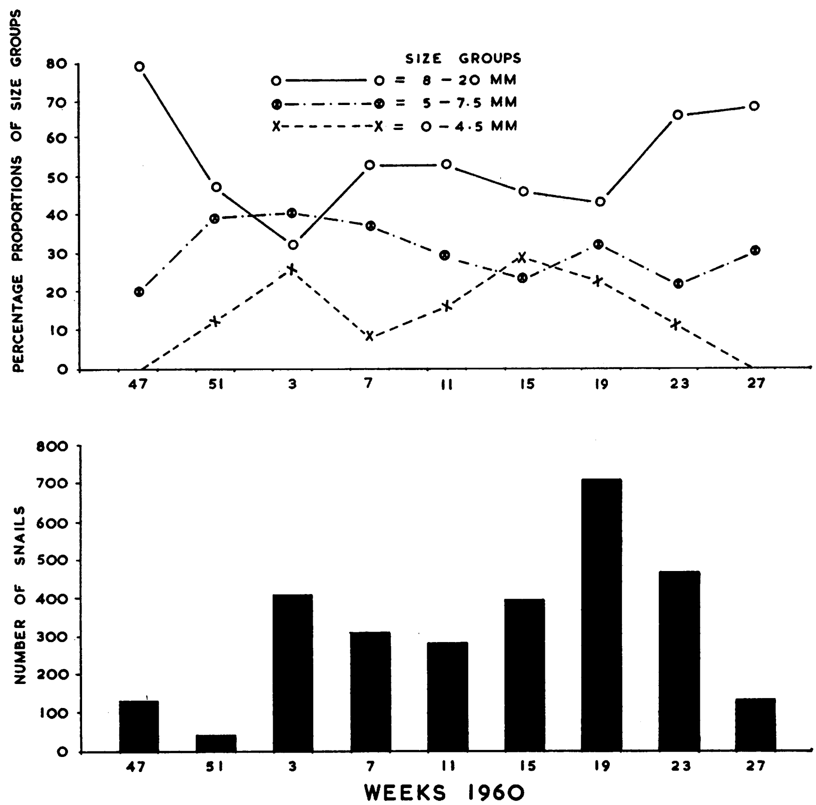


TABLE 5

PERCENTAGE PROPORTIONS OF SNAILS LESS THAN 5 MM (HEIGHT OF SHELL) AND CORRESPONDING DENSITY OF 3 POPULATIONS FOR 8 SAMPLINGS, APRIL TO JULY 1960

Weeks	Pond K		Pond I		Pond O	
	< 5 mm (%)	Density (No.)	< 5 mm (%)	Density (No.)	< 5 mm (%)	Density (No.)
13	62	101	33	45	0	73
15	3	30	28	50	36	113
17	23	141	25	39	51	105
19	12	119	48	212	22	45
21	7	77	42	201	50	182
23	1	73	33	102	6	118
25	0	32	7	113	0	115
27	0	26	13	115	0	110

51, " very young " snails were in evidence and the increase in the proportion of the " juvenile " group suggested that " very young " snails were present in the habitat on week 47, but probably still in the mud and therefore not revealed by sampling. On week 3 of 1960, an increase in the population density was apparent. A relatively high mortality of " old " snails occurred during this initial period. After week 3, the age composition of the population was reasonably stable until a decline began following week 19, with a corresponding increase in the proportion of " old " snails.

The age structures of these populations for the period examined show that they were changing in the same direction as far as the proportion of " very young " snails was concerned.

Pesigan et al. (1958), working in the Philippines, demonstrated that a relationship between mean density and proportion of young snails existed which provided a satisfactory explanation for differing densities within a population, but that this explanation did not hold when different populations were compared.

The snail samples examined on weeks 17, 19 and 21 from Pond I, and on weeks 17, 19 and 21 from Pond O (Table 5), suggested that population density might be related to the proportion of " very young " snails. This was not always the case, however, and different population structures were maintained independently of density, as shown by the samples examined on weeks 17, 19, 21 and 23 from Pond K, on weeks 23, 25 and 27 from Pond I, and on weeks 23, 25 and 27 from Pond O.

These results show that differences in density from one snail population to another cannot be explained solely by differences in the proportion of " very young " snails. The occurrence of different population structures which are unrelated to density are probably consequent upon differences in survival rates for both young and old snails.

Mortality of adult snails

The adult daily mortality rates (Tables 6 and 7) show considerable differences among the populations studied for individual intervals between sampling. The average daily mortality rates of the different populations for the entire periods of sampling, however, were remarkably similar. The average daily mortality rate calculated for the 10 snail populations during the same period of sampling (March-June 1960) was 2.29%.

A knowledge of the adult mortality rate permits of calculation of the length of life of an average adult snail (i.e., the " half-life "), which in this case was 30.3 days. This relatively short average life under natural conditions may seem unreasonable in view of the appreciable numbers of " old " snails found in established populations. The method of sampling used, however, provided data on relative population density only, and not on total population numbers; and if one considers the exponential relationship of adult mortality to reduction of the population, the value for the average life is realistic, particularly under the field conditions in the area of observations.

TABLE 6

AVERAGE DAILY PERCENTAGE MORTALITY RATE FOR ADULT *BULINUS (P.) NASUTUS PRODUCTUS* IN 5 HABITATS FOR 11 INTERVALS BETWEEN SAMPLINGS, JANUARY TO JUNE 1960

Habitat	Weeks											Average
	1-3	3-5	5-7	7-9	9-11	11-13	13-15	15-17	17-19	19-21	21-23	
Pond L	1.30	0	3.64	0	2.90	0	0.01	0	3.21	5.52	6.26	2.08
Pond M	1.30	3.92	9.44	2.05	0	8.95	4.95	0.01	0	0	0	2.78
Pond N	7.64	0	0.68	8.59	0	2.90	4.95	0	0.01	0	0	2.25
Pond J	2.21	2.49	5.52	6.05	0	0	0.75	7.85	2.90	0	4.95	2.97
Pond Q	0	0	12.82	0	8.6	0	0	0	0	5.36	1.26	2.55
Average	2.49	1.28	6.42	3.34	2.30	2.37	2.13	1.57	1.22	2.18	2.49	2.53

TABLE 7

AVERAGE DAILY PERCENTAGE MORTALITY RATES FOR ADULT *BULINUS (P.) NASUTUS PRODUCTUS* IN 5 HABITATS FOR 8 INTERVALS BETWEEN SAMPLINGS, MARCH TO JUNE 1960

Habitat	Weeks								Average
	9-11	11-13	13-15	15-17	17-19	19-21	21-23	23-25	
Pond I	2.66	5.15	2.74	10.75	0	0	2.17	0	2.93
Pond K	2.79	4.07	0	0	0	4.16	0.49	6.18	2.21
Pond O	—	—	9.06	0	0	3.8	0	1.68	2.42
Pond T	3.5	0.87	2.4	0	1.45	2.13	1.34	8.9	2.57
Dam 4	0.59	0	4.65	0	0.33	1.42	0.87	5.94	1.73
Average	2.39	2.52	3.77	2.15	0.36	2.30	0.97	4.54	2.38

Reproduction index

In calculating the reproduction index it was necessary to take a minimum interval of four weeks between the samplings and different intervals for the two groups of populations investigated, because of the small numbers of "very young" snails recognizable as offspring which were collected for shorter intervals.

The results, which are set out in Tables 8 and 9, show that the reproduction indices of the different populations varied considerably for individual intervals between samplings, but the average daily reproduction indices of different populations for the entire periods of sampling were broadly similar, with the exception of the populations in Pond T and Dam 4. In the majority of the populations sharp bursts of breeding activity occurred between week 7 and week 21 of 1960 (March-May).

The reproduction indices appeared to be related to the average daily mortality rates, though not always to density. This relationship (Fig. 11) was not apparent in the population in Pond T, but in Dam 4 there was a low average adult mortality to compensate for the low average reproduction index.

In the snail populations in Ponds J, L, M, N and Q (Fig. 12), rainfall appeared to increase adult mortality and to stimulate reproduction. Reproduction lagged behind mortality and fell sharply when habi-

TABLE 8

MEAN DAILY REPRODUCTION INDEX (× 1 000) FOR 5 HABITATS FOR 4 INTERVALS BETWEEN SAMPLINGS, JANUARY TO JUNE 1960

Habitat	Weeks				Average
	1-7	7-13	13-19	19-25	
Pond L	61.0	110.0	0	0	56.0
Pond M	0	66.0	60.0	16.0	47.25
Pond N	0	15.4	150.0	11.0	42.7
Pond J	12.0	0	150.0	62.0	35.5
Pond Q	38.0	151.0	0	0	44.1
Average	22.2	68.5	72.0	17.8	45.1

TABLE 9

MEAN DAILY REPRODUCTION INDEX (× 1 000) FOR 5 HABITATS FOR 5 INTERVALS BETWEEN SAMPLINGS, FEBRUARY TO JUNE 1960

Habitat	Weeks					Average
	5-9	9-13	13-17	17-21	21-25	
Pond I	0	1.0	2.0	250.0	13.0	53.2
Pond K	0	71.0	100.0	4.2	0	35.0
Pond O	0	0	58.0	150.0	4.8	42.6
Pond T	0.34	1.5	25.0	13.0	2.0	8.4
Dam 4	0	0	0	0.24	0.21	0.09
Average	0.07	14.7	37.0	83.5	4.0	27.9

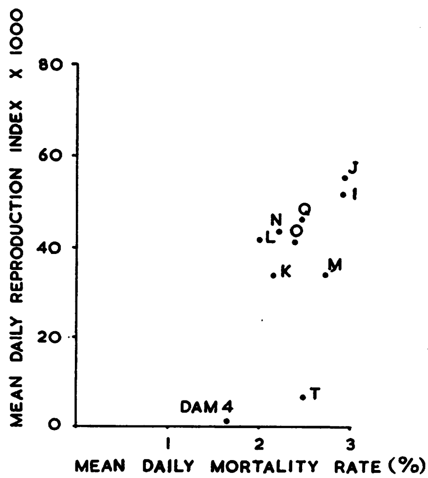
tats began to dry out, a corresponding increase in mortality being apparent. The same picture of reproduction indices and mortality rates in relation to rainfall was reflected by the populations in Ponds I, K, O, T and Dam 4.

DISCUSSION

Barlow & Muench (1951), working in Egypt, studied the life-span and monthly mortality rates of *Bulinus truncatus* and *Planorbis boissyi* and found that the mortality was very high among young snails, very much reduced during mid-life and high again among adult snails. McCullough (1957), working in Ghana, found that the density patterns of *Bulinus (P.) globosus* belonging to broadly different age-groups did not necessarily coincide with the density curve of the entire population or, indeed, with one another, and concluded that snails of different ages appeared to have different optimal requirements for survival. Pesigan et al. (1958) concluded that the maintenance of different population structures independently of density must depend upon different survival rates for both young and adult snails, and that both must be involved since equal survival rates for adults and different rates for young, or *vice versa*, would result in a direct relationship between population structure and density, which did clearly not obtain.

FIG. 11

RELATION BETWEEN REPRODUCTION INDEX AND ADULT MORTALITY IN 10 SNAIL POPULATIONS [a]

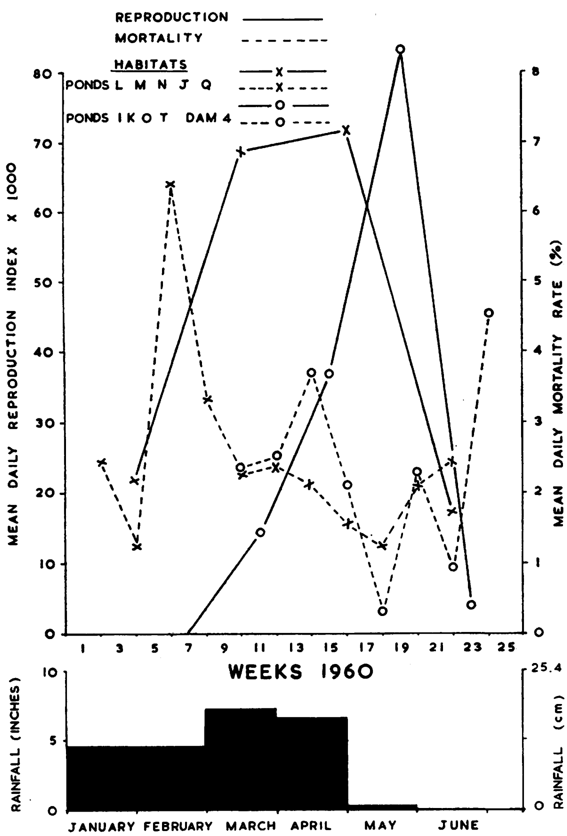


[a] Letters refer to the respective ponds.

The present results show that populations were changing in the same direction as far as the proportion of "very young" snails was concerned and that population structures, like density, varied from place to place, with quite large changes occurring from time to time. The appreciable differences in the mortality rates of adult snails among the populations studied were large enough to affect the considerable changes in population density and structure which were apparent at different times.

FIG. 12

CHANGES IN AVERAGE ADULT MORTALITY RATES AND IN AVERAGE REPRODUCTION INDICES OF TWO GROUPS OF SNAIL POPULATIONS IN RELATION TO RAINFALL



The relationship which appears to exist between adult mortality and reproduction in most of the populations studied provides a reasonable explanation for the fact that different populations failed to show a relationship between structure and density.

Rainfall appeared to increase mortality initially, and then to stimulate reproduction. In different populations the balance between these factors must vary and so cause the differences in density and population structure which were demonstrated.

It has been shown in the second part of this paper that the extrinsic factors, rainfall and temperature, altered the environment and caused seasonal crises in the life of snails with corresponding fluctuations in *S. haematobium* infection rates as populations expanded or declined. The results suggested that infection rates rose as population densities increased and as their age structures changed. Further, the period during which most snails were present in an aquatic environment, and therefore actively breeding and growing, was relatively short, and any attempt to limit their growth and thereby reduce transmission of *S. haematobium* should be based on this information.

Few, if any, available methods involving the use of chemicals are likely to result in the complete eradication of snails, and their high intrinsic rate of natural increase is likely to result in the rapid restoration of damaged populations, while the reintroduction of individuals from surrounding uncontrolled areas must also be considered. The influence of density upon survival rates may be judged to some extent by the repopulation of habitats after periods of desiccation, when rapid population build-up was frequently observed from relatively small numbers of survivors. Under conditions of low population density, therefore, a few scattered survivors of a chemical treatment may repopulate an area rapidly, since survival rates under suitable environmental conditions are probably high.

Chemical treatment might, however, be so timed as to cause the maximum damage to a population just before the dry season, and so drastically reduce numbers of snails before aestivation begins. A second treatment might then be made soon after habitats are refilled by rainfall in order to reduce yet further the number of snails which have survived chemical treatment and dry conditions. The evidence presented in the second part of this paper suggests that the "juvenile" and "middle-aged" snails present in a population at the end of one wet season are most likely to become infected during the following season. The measures outlined above might, therefore, result in a reduction of transmission by lowering population density and by altering the age structure of populations which have survived chemical treatment and a period of desiccation.

Precise information on the probability of a miracidium infecting a standard density of snails is still lacking but the field evidence does suggest that a reduction in the cercarial infection rate may result if population density is reduced. Laboratory investigations at present in progress suggest that a reduction in the infection rate might also be effected if the number of miracidia available to inoculate a given density of snails were drastically reduced. This means that a combination of methods directed against two links in the schistosome life-cycle—the snail and the miracidium—through application of molluscicides and treatment of infected persons might be more efficacious than an attempt to reduce snail density and alter population structure only.

Quite apart from the shortcomings of known molluscicides and the inadequacy of available drugs, the practical difficulties likely to be encountered in an attempt to mount either or both forms of control would be formidable, but the possibility that a substantial reduction in transmission of *S. haematobium* might be effected does exist.

ACKNOWLEDGEMENTS

I wish to express my thanks to the Director of the East African Institute for Medical Research, Mwanza, Tanganyika, for the provision of facilities to carry out the work described in this paper, and to the African staff, who assisted me during the course of the observations.

I am also indebted to Dr G. Mandahl-Barth, Curator of the Danmarks Akvarium, Charlottenlund, Denmark, who kindly identified the snail material; to Professor G. Macdonald of the London School of Hygiene and Tropical Medicine for valuable advice in the course of the work; and to Dr N. G. Hairston, World Health Organization, for useful discussion.

This paper is published with the kind permission of the Chief Medical Officer of the Ministry of Health, Tanganyika.

RÉSUMÉ

Une enquête malacologique relative à l'écologie de différents mollusques vecteurs de *Schistosoma haematobium* a été poursuivie au Tanganyika (Province des Lacs) pendant deux années. Elle a montré, entre autres, qu'il n'existe pas de relation entre la microflore des habitats aquatiques et une espèce déterminée de mollusque. Dans cette région, *Bulinus (Physopsis) nasutus productus* est le vecteur principal; seul de son espèce, il prolifère dans les collections d'eau saisonnières, où il peut éventuellement résister à des températures diurnes élevées.

Bulinus (P.) nasutus productus a fait l'objet d'une étude méthodique qui portait notamment sur les points suivants: fluctuation de ses colonies et distribution par âge de sa population, résistance à la dessiccation, fécondité, degré d'infestation. La densité des colonies, liée aux modifications du milieu qui résultent de la pluie et de la température, augmente le taux d'infestation; ce dernier est maximum à l'âge de huit mois. Les pluies augmentent la mortalité des adultes et stimulent l'activité reproductrice de manière variable selon les populations.

Marqués au cobalt-60, les mollusques d'un habitat demeuré à sec pendant 130 jours ont été retrouvés vivants. Dans un autre habitat privé d'eau pendant 98 jours quelques spécimens libéraient des cercaires six jours après la venue des pluies. En général, c'est au début ou au milieu de leur vie que les mollusques présentent la résistance la plus élevée à la dessiccation. Mesurée sur dix échantillons, la létalité quotidienne moyenne était de 2,9% avec durée de vie moyenne de 30,3 jours pour les mollusques adultes.

Toutes ces caractéristiques biologiques sont d'un intérêt pratique direct pour les campagnes d'éradication, car les données recueillies laissent supposer que la transmission de *S. haematobium* pourrait être considérablement entravée par l'application de molluscicides qui réduiraient la densité des colonies avant le début de l'estivation. Un deuxième traitement chimique éliminerait ensuite les spécimens qui auraient échappé à la double action des molluscicides et de la dessiccation. Cependant, plutôt que de se borner à réduire le nombre des vecteurs ou à bouleverser les structures de leurs colonies, il serait sans doute plus judicieux et plus efficace d'associer au traitement des personnes infestées une attaque chimique dirigée contre le schistosome et visant à l'atteindre aux deux stades de son cycle, que sont la miracidie et sa vie parasitaire chez le mollusque.

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