

DISTRIBUTION PATTERNS AND CERCARIAL SHEDDING OF *BULINUS NASUTUS* AND OTHER SNAILS IN THE MSAMBWENI AREA, COAST PROVINCE, KENYA

H. CURTIS KARIUKI, JULIE A. CLENNON, MELINDA S. BRADY, URIEL KITRON, ROBERT F. STURROCK, JOHN H. OUMA, SAIDI TOSHA MALICK NDZOVU, PETER MUNGAI, ORIT HOFFMAN, JOSEPH HAMBURGER, CARA PELLEGRINI, ERIC M. MUCHIRI, AND CHARLES H. KING

Division of Vector Borne Diseases, Ministry of Health, Nairobi, Kenya; Division of Epidemiology and Preventive Medicine, Department of Veterinary Pathobiology, University of Illinois, Urbana, Illinois; London School of Hygiene and Tropical Medicine, London, United Kingdom; Kenya Medical Research Institute, Nairobi, Kenya; Helminthology Unit, Hadassah Medical School, Hebrew University of Jerusalem, Israel; University of Pennsylvania School of Medicine, Philadelphia, Pennsylvania; Center for Global Health and Diseases, Case Western Reserve University School of Medicine, Cleveland, Ohio

Abstract. In the Msambweni area of the Kwale District in Kenya, an area endemic for *Schistosoma haematobium*, potential intermediate-host snails were systematically surveyed in water bodies associated with human contact that were previously surveyed in the 1980s. *Bulinus (africanus) nasutus*, which accounted for 67% of the snails collected, was the only snail shedding *S. haematobium* cercariae. *Lanistes purpureus* was the second most common snail (25%); lower numbers of *Bulinus forskalii* and *Melanoides tuberculata* were also recovered. Infection with non-*S. haematobium* trematodes was found among all snail species. Rainfall was significantly associated with the temporal distribution of all snail species: high numbers of *Bulinus nasutus* developed after extensive rainfall, followed, in turn, by increased *S. haematobium* shedding. Spatial distribution of snails was significantly clustered over a range of up to 1 km, with peak clustering observed at a distance of 400 meters. Water lily (*Nymphaea* spp.) and several aquatic grass species appeared necessary for local colonization by *B. nasutus* or *L. purpureus*.

INTRODUCTION

Urinary schistosomiasis due to *Schistosoma haematobium* is common in most areas of Coast Province, Kenya, where infection prevalence ranges from 25% to more than 90% (Muchiri EM, unpublished data, Clennon JA and others, unpublished data).^{1–4} Prevalence among schoolchildren in the Kwale District is typically 57–90%, with prevalence in the present study area, the Msambweni Division, of up to 78%.⁵ In contrast, there is no transmission of *S. mansoni* in Msambweni, and the intestinal form of schistosomiasis is absent from a region extending 100 km inland from the coast. The absence of *S. mansoni* is attributable to the absence of the *Biomphalaria* spp. intermediate-host snails from most of Coast Province, apart from the inland district of Taita-Taveta.^{6,7} Sturrock⁸ has suggested that high constant temperatures, among other limiting factors,⁹ may account for the failure for *Biomphalaria* to establish in this area. However, the *S. haematobium* intermediate hosts of the *Bulinus (africanus)* group species, which are more tolerant of high temperatures, are well represented here.

In Kenya, the *B. africanus* group of snails is represented by *B. (africanus) globosus*, *B. (a.) africanus*, *B. (a.) nasutus*, and *B. (a.) ugandae*. All, apart from *B. (a.) ugandae*, are important hosts of *S. haematobium* in Kenya.^{10,11} The distribution of *B. (a.) globosus* and *B. (a.) nasutus* overlaps in Coastal Kenya and in the Lake Victoria area. *Bulinus (a.) africanus* is commonly found in higher altitude areas of eastern and central Kenya. *Bulinus (a.) ugandae* is distributed in limited foci in the Lake Victoria area.¹² In the Coast Province of Kenya, *B. globosus* and *B. nasutus* can be found occupying a wide diversity of habitats such as quarry pits, streams, drainage canals, dams, and seasonal pools.¹³ In the Msambweni area, the focus of the present study, transmission of *S. haematobium* occurs most frequently in small freshwater impoundments, which may dry for varying periods, depending on rainfall. Remarkably, in contrast to the high human prevalence of *S. haematobium* infection in Msambweni, the proportion of

snails shedding *S. haematobium* cercariae has been previously detected to be only 0.5–1.2%.¹⁴

To understand how an area with such a low percentage of snails shedding *S. haematobium* cercariae could coincide with high human infection prevalence, we characterized the snail population patterns within the area and examined their overlap with human infection patterns. Because snail populations are highly variable temporally, it was also essential to consider both seasonal and spatial trends for factors associated with the presence and density of *S. haematobium* intermediate-host species, and the snail species that compete with them.¹⁵ This report describes the distribution and seasonal fluctuation of the intermediate host snail (*B. nasutus*) and other snails sharing the same aquatic habitats in Msambweni area. (Similar snail studies were performed some 20 years ago in this same area,¹⁴ allowing comparison with the present study.) The spatial and temporal patterns were analyzed and associated with rainfall and environmental determinants as part of a comprehensive study of transmission of *S. haematobium* in 10 villages. With a companion paper,¹⁶ we apply novel mapping and statistical tools to analyze the patterns of local snail and human infection.

MATERIAL AND METHODS

Study area. Msambweni Division is situated in the Kwale District of Coast Province, approximately 50 km south of Mombasa, Kenya. The 25-km² research area is centered at the geographic coordinates 4.46°S and 39.45°E (Figure 1) and has been previously described in detail.^{5,14,17} The area has a monsoon-type climate, with the period of January to April–May being hot and dry. The mean monthly temperature varies from 26.3°C to 26.6°C, with lows of 23.5°C (July) to 26.9°C (March–April) and highs from 26.7°C (August) to 36.3°C (February). Annual precipitation varies from 900 mm to 1,500 mm, with large yearly and monthly fluctuations. There are usually two rainy seasons, the long rains starting around March and continuing until July, and the short rains beginning in October and lasting through November. Monthly rainfall records for the study period were obtained from the di-

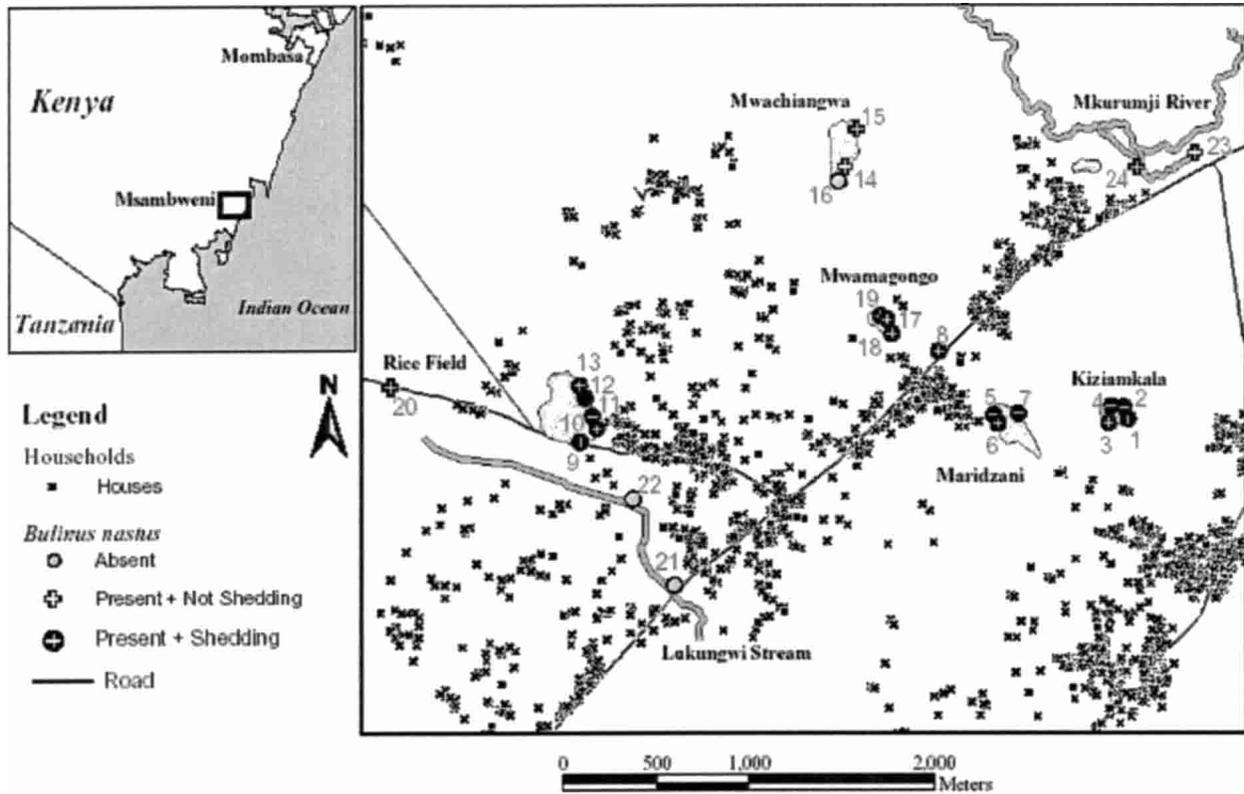


FIGURE 1. Snail collection sites, presence of *Bulinus nasutus*, and shedding of *Schistosoma haematobium* cercariae in Msambweni, Kenya, 2001–2003. The inset shows the location of study area in coastal Kenya.

visional agriculture offices situated near the Msambweni hospital.

A perennial river (the Mkwangwa River) and a seasonal stream (the Lukungwi Stream), flow through the area.¹⁴ Several rain-filled ponds are located in proximity to the 10 villages included in this study, but most of the pools dry out completely during periods of prolonged drought. When they contain water, these pools harbor various snail species, including *B. nasutus*, one of the intermediate hosts of *S. haematobium* in Kenya.¹⁴ Subsistence rice cultivation close to the water bodies is widely carried out. Maize, cassava, sweet potatoes, and other crops are planted in the general area for domestic consumption. Livestock (cattle and goats) is also kept.

The present study was conducted between March 1984 and July 1987, in addition to February 2001 and May 2003, around nine water bodies: six rain-filled ponds, one rice field, two sites along the banks of the Mkwangwa River, and two sites on the seasonal Lukungwi Stream (Figure 1). A total of 24 sites were monitored with up to five snail sampling sites selected per pond based on human water contact activity. The water bodies studied were Kiziakala pond, with four sites (1–4); Maridzani pond, with three sites (5–7); Bovo pond (site number 8); Nimbodze pond, with five sites (9–13); Mkwangwa pond, with three sites (14–16); Mwamagongo pond, with three sites (17–19); a rice field, (site 20); Mkwangwa River, with two sites (21 and 22) and Lukungwi Stream, with two sites (23 and 24) (Figure 1).

The major water contact activities included doing laundry, bathing, and swimming, and for young children fishing and

playing. Although some alternative water sources (wells, boreholes, piped water stands, and water kiosks) are available, residents appeared to prefer the customary water contact points at the pools where, due to the hot weather conditions for most of the year, they can also bathe and/or swim (Clennon JA and others, unpublished data).¹⁷

Ethical oversight. After obtaining informed consent from area residents (or for children from their parents), human infection status and water use activities were monitored under human investigations protocols reviewed and approved by the Ethical Review Board of the Kenya Medical Research Institute (Nairobi, Kenya) and by the Human Investigations Review Board of University Hospitals of Cleveland, Ohio.

Snail sampling. Snail sampling was conducted by one man searching each site for five minutes using a standard flat wire-mesh scoop with a mesh size of 2 mm.¹⁸ Snails were taken to the laboratory at Msambweni Hospital, separated by species, and tested for cercarial shedding. Species confirmation for *B. nasutus* was carried out by genetic mapping¹⁹ at the Natural History Museum (London, London, United Kingdom) and at Hebrew University (Jerusalem, Israel) (Hamburger J, Hoffman O, unpublished data). The snails were placed individually in flat-bottomed glass vials (height = 7.5 cm, Diameter = 2.5 cm) containing clear, filtered, pond water and exposed to indirect sunlight for a maximum duration of four hours. Snails that did not shed cercariae on the first exposure were re-exposed on the second day. Cercariae were categorized either as those of *S. haematobium* or those of other trematodes (non-*S. haematobium* cercariae), as described by Frandsen and Christensen.²⁰

Other parameters recorded at each site during every snail collection were water temperature (at a depth of 15 cm), water pH and conductivity (Oakton portable meters; Fisher Scientific, Pittsburgh, PA), turbidity (visual scale), site condition (dry or having water), water level, and the presence or absence of vegetation such as water lilies (*Nymphaea* spp.), sedge (*Cyperus exaltatus* Retz). or various species of grass.

Mapping and statistical analysis. All snail collection sites were located using a global positioning system (GPS) (GeoExplorer II; Trimble, Sunnyvale, CA) and identified on an Ikonos (Space Imaging, Atlanta, GA) satellite image acquired on March 4, 2001 at 7:45 AM. The 25-km² study area is centered around 4.464°S and 39.449°E.

The image and GPS readings were imported into ArcView version 3.3 and ArcGIS version 8.3 (Environmental Systems Research Institute, Redlands, CA). Statistical spatial analyses were conducted using point pattern analysis.²¹ Specifically, we used a weighted K-function (second-order analysis) to detect global clustering,^{22,23} and the Getis and Ord²⁴ Gi*(d) statistic to detect local clustering of snails and cercarial shedding. (For details on the mapping and spatial statistic analysis, see Clennon and others.¹⁶)

Correlation, homogeneity chi-square (continuity adjusted), analysis of variance, and linear regression analyses were conducted using SPSS version 11.5.0 (SPSS, Inc., Chicago, IL).

RESULTS

Diversity and spatial distribution of snails. Three species of snails, *B. nasutus*, *Lanistes purpureus*, and *B. forskalii*, were common in the study area, and were found in eight, seven, and six of the nine water bodies, respectively. Two other snail species were also recovered: *Melanoides tuberculata* was found in two water bodies, and *Pila ovata* was found only occasionally at the rice field and in the connected Lukungwi Stream (Table 1). *Bulinus nasutus*, the intermediate host for *S. haematobium* in this study area, was the most common snail, accounting for more than two-thirds of all snails collected, with *L. purpureus* accounting for most of the rest (25%) of all snails.

Bulinus nasutus was found in all water bodies except the Mkurumji River; although it was rare in Mwachiangwa pond, it was common in Nimbodze, Mwamagongo, Maridzani, and Kiziamkala ponds. *Lanistes purpureus* was found in all water bodies, except for the Mkurumji River and Kiziamkala pond,

and was most common in Mwamagongo, Nimbodze, and Bovo ponds. *Bulinus forskalii* was most common in Kiziamkala and Maridzani (Table 1). Only at Maridzani was there complete species overlap (i.e., more than a single specimen of each of the four common snail species found). In the Mkurumji River, only *M. tuberculata* was found.

Spatial statistical analysis of the distribution of *B. nasutus* in the study area, using a weighted K-function, demonstrated significant clustering of snails through distances of less than 1 km, with peak clustering at a distance of 400 meters. This is less than the distance between any two ponds, indicating that the clustering effect is in force around individual ponds. The global statistical result was supported by the subsequent application of Gi*(d) testing to detect local clustering. Gi*(d) was > 3.0 ($P < 0.01$) for all Nimbodze pond sites, but not significant for any other sites. This implies that the observed global clustering effect noted for *B. nasutus* snails was primarily due to the high numbers of snails found in the five collection sites of Nimbodze pond.

Cercarial shedding. Only *B. nasutus* snails were found to shed *S. haematobium* cercariae, and the percentage of shedding snails within the ponds ranged from 0.2% in Bovo pond to 2.5% in Nimbodze pond (Table 2). Overall, 1.2% of the *B. nasutus* recovered in the Msambweni area shed *S. haematobium* cercariae. Nimbodze pond accounted for 73 (60%) of the 122 *S. haematobium* cercariae shedders. In contrast, 9.1% of *B. nasutus*, 0.7% of *L. purpureus*, 3.9% of *B. forskalii*, and 9.5% of *M. tuberculata* shed other, non-*S. haematobium* cercariae, with *B. nasutus* accounting for more than 90% of non-*S. haematobium* cercariae shedders within all ponds (Table 2). As for the shedding of *S. haematobium* cercariae, most of the snails shedding non-*S. haematobium* cercariae were collected from Nimbodze pond.

Snail density did not vary from site to site within individual ponds ($F < 1.7$, $P > 0.16$ for all ponds). The two running-water bodies, the Lukungwi Stream and the Mkurumji River, also showed no significant site-to-site variation in snail numbers ($t = 0.23$, $P > 0.5$ and $t = -0.24$, $P > 0.5$, respectively). Shedding prevalence for *S. haematobium* cercariae did not significantly differ among the different collection sites at Maridzani pond ($P > 0.5$, by Fisher's exact test) or at Nimbodze pond ($P > 0.4$, by Fisher's exact test). At Kiziamkala pond, *B. nasutus* shedding *S. haematobium* cercariae were primarily collected at site 1 ($P < 0.05$, by Fisher's exact test). Data from Mwamagongo pond showed a strong difference between collection sites in terms of shedding prevalence: 86% of the *S. haematobium*

TABLE 1

Distribution of snails among water bodies in Msambweni, Kenya, February 2001–May 2003

Water body	<i>Bulinus nasutus</i>	<i>Lanistes purpureus</i>	<i>Bulinus forskalii</i>	<i>Melanoides tuberculata</i>	Total
Kiziamkala	1,697	0	389	0	2,086
Maridzani	1,750	186	491	198	2,625
Bovo	1,127	833	0	0	1,960
Nimbodze	2,929	1,153	96	0	4,178
Mwachiamangwa	2	117	28	1	148
Mwamagongo	2,752	1,568	10	0	4,330
Rice field	684	92	1	0	776
Mkurumji	0	0	0	79	79
Lukungwi	59	95	1	1	156
Total	11,000	4,044	1,016	279	16,339

TABLE 2

Number (percent) of snails per pool shedding *Schistosoma haematobium* cercariae and non-*S. haematobium* cercariae in ponds in Msambweni, Kenya, February 2001–May 2003

Water body	<i>S. haematobium</i> cercariae	Non- <i>S. haematobium</i> cercariae			
	<i>Bulinus nasutus</i>	<i>Bulinus nasutus</i>	<i>Lanistes purpureus</i>	<i>Bulinus forskalii</i>	<i>Melanoides tuberculata</i>
Kiziamkala	16 (0.9)	74 (4.4)	0	15 (3.9)	0
Maridzani	9 (0.5)	124 (7.1)	4 (2.3)	16 (3.3)	19 (9.6)
Bovo	2 (0.2)	30 (2.7)	0	0	0
Nimbodze	73 (2.5)	552 (18.8)	24 (2.1)	9 (9.4)	0
Mwamagongo	22 (0.8)	151 (5.5)	0	0	0
Total	122 (1.2)	931 (9.1)	28 (0.7)	40 (3.9)	19 (9.5)

cercariae shedders in this pond were collected at site 17 ($P < 0.001$, by Fisher's exact test). In fact, site 17 showed anomalous high numbers of *S. haematobium* shedders in general (Table 3); only Nimbodze pond was comparable in terms of overall numbers of *B. nasutus* shedding *S. haematobium* cercariae. Analysis of environmental variables, including pH, water temperature, and water conductivity, indicated no obvious differences between site 17 and the two other sites at Mwamagongo that would explain this difference in shedding prevalence for *S. haematobium* cercariae. However, our observations did show that site 17 was the most intensely used human water contact site of the three Mwamagongo locations (Clennon JA and others, unpublished data).

Neither Kiziamkala pond nor Nimbodze pond showed any significant site-to-site variation in non-*S. haematobium* cercarial shedding ($\chi^2 = 5.43$, $P > 0.1$ and $\chi^2 = 7.83$, $P > 0.1$, respectively). However, site 7 at Maridzani had two months of high shedding prevalence in June and July of 2001, making its overall prevalence significantly higher than that of the other Maridzani sites ($\chi^2 = 15.9$, $P < 0.01$). At Mwamagongo, site 17 had significantly fewer non-*S. haematobium* cercariae ($\chi^2 = 15.9$, $P < 0.0001$). However, when examined more closely, this pattern resulted from very high numbers of uninfected *B. nasutus* collected at the site during July–August 2001. When the data from September 2001 were analyzed, the time when most non-*S. haematobium* cercariae from Mwamagongo were collected, no significant relationship between the Mwamagongo site and number of non-*S. haematobium* shedders was found ($\chi^2 = 1.86$, $P > 0.3$).

Seasonal patterns of snail density. For our study sites, variation in snail density over time followed the changes in water level due to seasonal and inter-annual rainfall fluctuation (Figure 2). The highest snail density was observed between July and November, with a peak in September–October 2001, but since February 2002, snail populations have remained low.

Since these rain-filled pools are the main snail habitats, rainfall was a major contributing factor in the distribution and occurrence of snails. During the long rainy season in 2001, 366 mm of rainfall were recorded in April, followed by 568 mm in May. The short rains expected in October–November failed, resulting in the drying up of most habitats. Subsequently, the long rains in 2002 did not fall with the same intensity as in 2001; the highest peak in April was only 274 mm. This rainfall amount was not sufficient to fill the ponds.

In 2001, all study ponds contained water throughout the year, except for Bovo and Mwamagongo, which were dry from February to April and again from November to December. However, in 2002, with the lack of rains, most ponds dried out. Maridzani pond was the only pond that contained

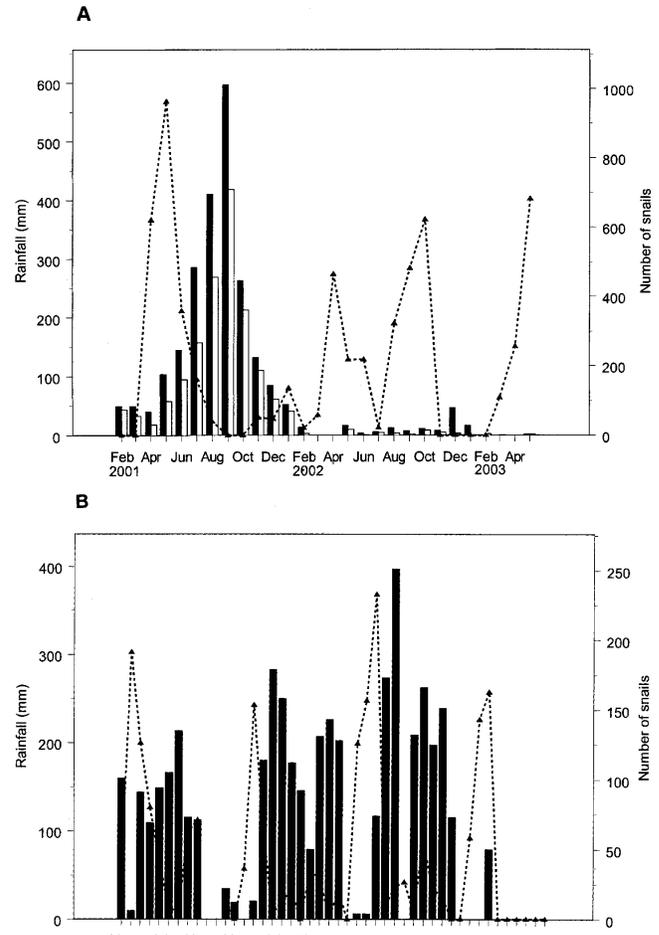


FIGURE 2. Rainfall and weekly averages for the number of snails overall, and for *Bulinus nasutus* only, for all collection sites in the Msambweni, Kenya study area. **A**, February 2001–May 2003. **B**, March 1984–July 1987 (*B. nasutus* only).¹⁴ **Solid bars** = all snails; **open bars** = *B. nasutus*; **▲** = rainfall.

water at least at one site throughout the two-year duration of this study. As of May 2003, Mwamagongo has been dry since November 2001 (19 months), Nimbodze since March 2002 (15 months), Kiziamkala since October 2002 (7 months), and Mwachiangwa since November 2002 (6 months). In comparison, for a period with more consistent rainfall, the data for *B. nasutus* and rainfall in Msambweni during 1984–1987¹⁴ are shown in Figure 2B.

Overall, no significant relationship between rainfall and snail numbers was found when the complete 2001–2003 data were used. This result is not surprising since most of the sites experienced significant periods of complete dryness between March 2002 and May 2003, and no snails were recovered at these sites during this period. However, for the initial 2001–2002 period alone, when rainfall was correlated with snail density, a significant four-month lag in the snail population response to rainfall was found. Factoring in the four-month lag produced a significant relationship between total snail numbers and total rainfall ($r = 0.90$, $P < 0.0001$). In comparison, data collected in the same area between 1984 and 1987¹⁴ showed a significant relationship between snail density and total rainfall with only a two-month lag ($r = 0.43$,

TABLE 3

Snail collection totals for sites in Nimbodze and Mwamagongo, Kenya ponds for the period July–October 2001

	Nimbodze sites					Mwamagongo sites		
	9	10	11	12	13	17	18	19
July	37	61	153	82	102	546	127	35
August	50	67	141	65	90	670	300	138
September	128	152	269	160	244	731	1,044	602
October	74	102	200	184	199	5	5	13

$P < 0.01$). This discrepancy between the two time-lag periods is likely due to the more consistent level of rainfall that the region experienced during the mid-1980s, and indicates that longer-term precipitation patterns affect the relationship between the peak rainfall and peak snail populations in any given year.

Although snail density did not vary from site-to-site within individual ponds, there was significant variation between ponds in the timing and magnitude of peak snail populations (Table 3). Mwamagongo, which had the highest total number of snails, produced large numbers of snails only during July, August, and September 2001 before drying in October–November 2001. In contrast, Nimbodze, the pond with the next highest total, produced large numbers of snails from July 2001 through January 2002. Site 17 at Mwamagongo was particularly productive, with more than 500 snails collected at the site during each of its peak months. Most of the other ponds also had peak snail populations during the summer of 2001, although the duration of high snail populations varied for each water body: Kiziamkala, August to November; Bovo, only in August and September; and Maridzani, which appears to be more resistant to drying than the other sites, showing a slightly different pattern, a small peak in February–March of 2001 and then a longer period with high populations May to October. Interestingly, the population of *M. tuberculata* in Maridzani peaked from December 2001 to February 2002, long after the population peaks of *B. nasutus* and *L. purpureus*.

The cercarial shedding pattern followed the temporal changes in snail density (Figure 3); the correlation was positive and highly significant ($r = 0.64$, $P < 0.0001$, by log-transformed data). The pattern of non-*S. haematobium* cercariae shedding by *B. nasutus* also closely followed that of *S. haematobium* cercariae shedding over time (Figure 3).

Figure 4 shows a contour map of the numbers of *S. haematobium* cercariae-shedding snails by location over the first 13 months of observation, before most sites went dry. The observed patterns in the abundance of shedding snails indicates a strong pool-specific and seasonal variation in transmission

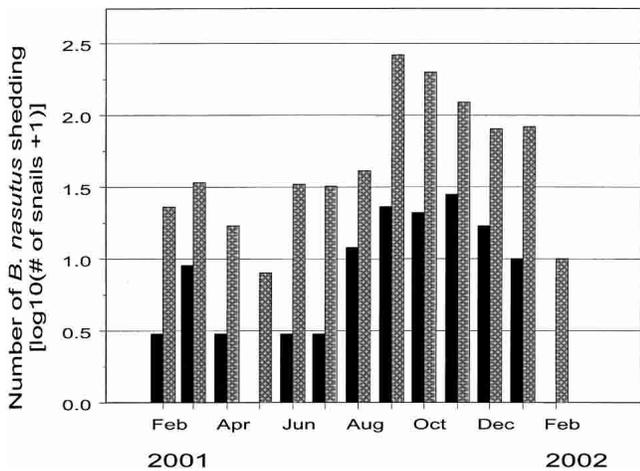


FIGURE 3. Number (log-transformed) of *Bulinus nasutus* snails shedding *Schistosoma haematobium* and non-*S. haematobium* cercariae each month in Msambweni, Kenya from February 2001–February 2002. **Hatched bars** = shedding non-*S. haematobium* cercariae; **solid bars** = shedding *S. haematobium* cercariae.

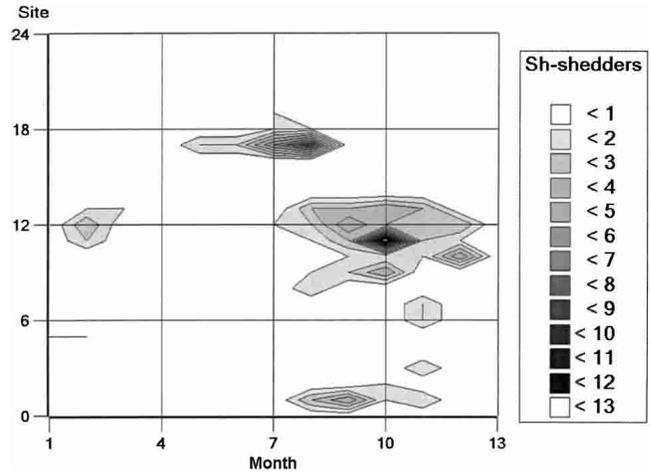


FIGURE 4. Contour plot of the number of *Schistosoma haematobium* (Sh)-shedding snails at individual study sites in the Msambweni, Kenya area (vertical axis with an arbitrary scale) during the first 13 months of the study (February 2001–March 2002). Contour lines indicate temporal and spatial clustering of positive sampling events, with each having more than a threshold number of *S. haematobium*-shedding snails either at the same time period at adjacent sampling points or at the same site over contiguous sampling times.

risk, with only a limited number of sites active overall, and only a few sites active at any given time.

Environmental associations. Changes in temperature, turbidity, and pH were not significantly associated with changes in snail numbers or the percentage of *S. haematobium* shedding snails.

Vegetation. Vegetation type was significantly associated with presence of several snail species. Both *B. nasutus* and *L. purpureus* were positively associated with the presence of water lilies (*Nymphaea* spp.) ($\chi^2 = 57.1$ and 29.1 , respectively, $P < 0.001$), and negatively with a sedge (*Cyperus exaltatus*) ($\chi^2 = 5.4$, $P < 0.02$ and 12.4 , $P < 0.0001$, respectively). *Bulinus forskalii* was positively associated with sedge ($\chi^2 = 5.4$, $P < 0.02$) and *M. tuberculata* was negatively associated with grass ($\chi^2 = 4.3$, $P < 0.04$). These statistical associations, and particularly the positive association with the presence of lilies, was confirmed in the field by repeated observations of more snails resting on the underside of lily pads than in association with any other vegetation type.

Dissolved ions (conductivity). The highest levels of conductivity were recorded in Kiziamkala and Maridzani ponds; their high conductance was thought to be due to their proximity to the ocean. High conductivity was also recorded in the rice field, possibly due to application of agricultural fertilizers. Snail species differ in their tolerance to increasing ion concentrations: high conductivity was negatively correlated with *L. purpureus* ($r = -0.53$, $P < 0.0001$) while correlating positively with *B. forskalii* ($r = 0.18$, $P < 0.01$). For example, there were no *L. purpureus* in Kiziamkala pond and only relatively few occurring in the neighboring Maridzani pond (Table 1). However, *B. forskalii* appeared at these ponds in larger numbers than in all the other habitats. The observed high conductivity in these ponds did not appear to have a limiting effect on *B. nasutus*.

DISCUSSION

Our findings indicate that *B. nasutus* was the most common snail at the observed water contact sites, and that it was the only evident intermediate host for *S. haematobium* in the study area. At the sites where it was found, apart from Kiziamkala pond, *B. nasutus* was sympatric with the larger snail *Lanistes purpureus*. The spatial distribution of snails was clustered, with few ponds accounting for most of the snails.

In our study area, most *B. nasutus* snails, and particularly those shedding *S. haematobium* cercariae, were found in Nimbodze pond, the location that was most strongly associated also with clustering of human infection.¹⁷ Conversely, no *B. nasutus* snails were collected at Mwachiangwa pond, and only a few *Lanistes* were recovered there. It is likely that chemical, physical, and biologic factors determine the species diversity and snail density to be found in a particular water body at a given period of time. The ecologic conditions for transmission of schistosomiasis in favorable snail habitats can vary considerably from site to site and area to area, even within short distances.²⁵ To determine the environmental conditions that may inhibit snail survival or development, further investigations of water composition, e.g., measurements of specific dissolved ions,^{26,27} need to be carried out at these and comparison ponds. In other areas of the Coast Province of Kenya, abundance of *B. globosus* has been linked to water temperature, and rapid growth of *B. globosus* populations has been tied to unseasonable rains during the cooler months.¹⁴ In our study area, we did not find a significant link between snail abundance and water temperature, perhaps reflecting the narrow range of temperatures observed.¹⁰

One factor that was significantly associated with snail density was the presence of horizontal vegetation, namely water lilies (*Nymphaea* spp.). Most snails were observed resting on the underside of the lilies, areas probably rich in oxygen due to photosynthesis. The water lilies also provide egg-laying surfaces, shelter from the sun, and food for many species of snails. For food, the snails feed on the microflora and decaying plant matter of the water lily leaves.²⁸ Aquatic macrophytes may also protect snails from predators such as birds. A pitfall that may result in an overemphasis of the importance of water lily leaves is that they are much easier to sample than a dense stand of grass or sedges. For our study area, the presence of water lilies was an effective indicator for the presence of both *B. nasutus* and *L. purpureus*. This association deserves further study in other transmission areas. If validated, it is possible that aerial remote sensing, whether by satellite or by less expensive aerial photography, may offer effective means for detection of likely transmission sites.

During long periods of drought, temporary ponds dry up and the snails estivate.^{29,30} As the rains arrive and the ponds fill up, snails are triggered out of estivation and repopulate the water bodies.¹⁴ However, this effect of rainfall on snails depends on the intensity with which the rains fall; our experience suggests that heavy downpours over a short period of time will fill up snail habitats and have a marked influence on snail populations, while small amounts of rain over a long period of time, which has been the pattern in the study area since 2002, do not result in a sufficient amount of water to re-fill ponds that have dried. Published reports on the length of estivation period do not indicate survival of snails beyond 6–12 months.^{29–31} However, it appears that many of our

ponds, including Nimbodze pond (which had the greatest *B. nasutus* abundance and most frequent *S. haematobium* cercariae production), have been dry for periods that extend beyond the published survival records of aestivated *Bulinus* or other snails. While survival is likely to be extended in moist areas and under vegetation, the prolonged drought may have drastic long-term impacts on snail populations and cercariae shedding in our study area. This, in turn, may result in changes in human infection patterns and the age distribution of schistosomiasis.¹⁷

The finding of a large number of snails shedding non-*S. haematobium* cercariae merits further study because it may be associated with infection of domestic livestock and possibly transmission to humans of zoonotic parasites. *Bulinus forskalii* is reported to be an intermediate host of *Paramphistomum phellerouxi*, an amphistome parasite of grazing animals, in Zambia,³² and is known to transmit *S. bovis*. *Bulinus globosus* has also been associated with transmission of *Calicophoron microbothrium*, another intestinal amphistome parasite of domestic animals, especially cattle.³³ A case of *Paragonimus*-like eggs in humans was reported in Natal Province of South Africa by Proctor and Gregory,³⁴ and similar eggs were obtained from cats in Durban area. They were thought to belong to *Paragonimus kellicotti*, which only rarely infects humans. In these South African studies, *M. tuberculata* was the only prosobranch snail found in the area, and was therefore suspected to be the intermediate host. *Lanistes carinatus* is reported to transmit the rat lung-worm *Angiostrongylus cantonensis* in Egypt.³⁵

In Msambweni, further studies will be needed to determine the role of sympatric non-host snails in controlling schistosomiasis transmission by local bulinid snails. The non-host snails may act as biologic control agents for the intermediate hosts by either competing for space and food or by acting as predators.¹⁵ *Marisa cornuarietis* has been reported to act as a predator for all stages of *Bulinus* and *Biomphalaria*, and has been used as part of schistosomiasis control measures in Puerto Rico and other Caribbean islands.³⁶ In addition, some of the non-host snails may protect the intermediate host snails from infection with schistosome miracidia by acting as decoys. Upatham, in a laboratory experiment in St. Lucia, found that two non-host snails, *Physa marmorata* and *Drepanotrema surinamensis* could prevent infection of susceptible *Biomphalaria glabrata* with *S. mansoni* miracidia to a certain degree.³⁷

The results of our combined human and snail mapping studies indicate that transmission patterns of urinary schistosomiasis are closely related to the abundance and spatial distribution of host snails, and that travel distance to transmission sites likely plays an important role in determining human risk for infection. For schistosomiasis control programs to be successful, an effective understanding of the spatial and temporal variations in snail densities will be important for determining both the location and timing of control interventions. The use of GIS to integrate remotely-sensed area data on climate and terrain³⁸ with other risk markers that can be readily determined at ground level (e.g., aquatic flora) has the potential to improve the effectiveness of site selection for control intervention. However, variability in rainfall patterns, compounded by the ability for the snail intermediate hosts to estivate for several months, complicates the design of predictive transmission models.^{39,40} Although snail abatement combined with population-based drug therapy has the potential to

strongly suppress transmission, it is likely that successful control of schistosomiasis at Msambweni (and other areas having similar transmission features) will need to be tailored according to the prevailing environmental and weather patterns.

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Authors' addresses: H. Curtis Kariuki and Eric M. Muchiri, Division of Vector Borne Diseases, Ministry of Health, PO Box 20750, Nairobi, Kenya, Telephone: 254-20-725-833, Fax: 254-20-720-030, E-mail: schisto@wananchi.com. Julie A. Clennon, Melinda S. Brady, and Uriel Kitron, Division of Epidemiology and Preventive Medicine, Department of Veterinary Pathobiology, University of Illinois, 2001 South Lincoln Avenue, Urbana, IL 61802, Telephone: 217-333-2449, Fax: 217-244-7421, E-mails: jaclenno@uiuc.edu, msbrady@uiuc.edu, and ukitron@uiuc.edu. Robert F. Sturrock, 92 Brennand Road, Dongara, Western Australia, 6525, Australia, Telephone: 61-8-9339-0560, E-mail: sturrock@iprimus.com.au. John H. Ouma, Kenya Medical Research Institute, Mbagathi Road, Nairobi, Kenya, Telephone: 254-20-722-541, Fax: 254-20-720-030. Saidi Tosha, Malick Ndzovhu, and Peter Mungai, c/o Case Western Reserve University/Division of Vector-Borne Diseases/Kenya Medical Research Institute Filariasis-Schistosomiasis Research Unit, PO Box 8, Msambweni, Kenya, Telephone: 254-40-52267, E-mail: dvbdcwru@wananchi.com. Orit Hoffman and Joseph Hamburger, Helminthology Unit, Hadassah Medical School, Hebrew University of Jerusalem, PO Box 12272, Jerusalem, 91120, Israel, Telephone: 972-2-675-8082, Fax: 972-2-6757425, E-mail: hambu@cc.huji.ac.il. Cara Pellegrini, Department of Medicine, Hospital of the University of Pennsylvania, 3400 Spruce Street, Philadelphia, PA 19104, Telephone: 215-62-2200, E-mail: drpelle3@yahoo.com. Charles H. King, Center for Global Health and Diseases, Wolstein Research Building, Room 4126, Case Western Reserve University School of Medicine, 10900 Euclid Avenue, Cleveland, OH 44106-7286, Telephone: 216-368-4818, Fax: 216-368-4825, E-mail: chk@po.cwru.edu.

Reprint requests: Charles H. King, Center for Global Health and Diseases, Wolstein Research Building, Room 4126, Case Western Reserve University School of Medicine, 10900 Euclid Avenue, Cleveland, OH 44106-7286.

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