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Longitudinal malacological surveys reveal local drivers of persistent intestinal schistosomiasis transmission in Lakes Albert and Victoria, Uganda

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Abstract

Background: Despite decades of mass treatment of Ugandan communities in the Lake Victoria (LV) and Lake Albert (LA) basins with praziquantel, transmission of intestinal schistosomiasis continues. To better understand local drivers of persistent transmission, we conducted a longitudinal study to investigate intermediate-host snail population and infection dynamics, seasonal lacustrine environmental changes, and human activities to guide more effective control.

Methods: Snail sampling was conducted at ten human-water contact sites of each lake zone for eighteen months, collected snails identified by morphology and examined for schistosome cercarial shedding. We observed human activities, environmental changes, and counted spots of open defaecation (OD) at each site. Kruskal-Wallis test was performed to compare schistosome infection in snails between sites with Spearman's correlation and logistic regression assessing associations with local factors.

Results: A total of 11,329 *Biomphalaria* species snails from LV and 6,626 from LA were collected. Schistosome cercariae shedding rate by the snails ranged from 0% to 8.1%, with significant heterogeneity by site ($\chi^2(18) = 5.9 \times 10^{11}$, $p < 0.01$). Snail infection rate was insignificantly higher, during the wet than dry season on LA (OR = 1.23, 95% CI: 0.40–3.8, $p = 0.7$) and LV (OR = 1.80, 95% CI: 0.68–4.76, $p = 0.233$). The mean daily number of visitors arriving at lake shore villages of LA from other endemic areas was 1307 and 689 on LV. Sites in villages with higher influx of people had more spots of OD, and the high OD status positively correlated with greater snail infection rates (Spearman's $\rho = 0.521$, $p = 0.0196$, $n = 20$). Local village residents in LA and LV communities usually collected water for domestic use from the Lakes. Floating vegetation aided the dispersal of infected snails during the flooding period.

Conclusion: Continuous contact of residents with schistosome-infested water, human defaecation on the Lake shores, population influx from other endemic areas, and seasonal heterogeneity of *Biomphalaria* species appear to be the local drivers of persistent transmission of

schistosomiasis. Sanitation improvements, behaviour change communication, treatment of mobile populations, and targeted control of intermediate host snails are needed to mitigate the disease transmission.

Key words: *Biomphalaria* spp snail, open-defecation, population-influx, environmental drivers, persistent schistosomiasis transmission, Uganda

Background: Schistosomiasis, commonly known as Bilharzia, is a neglected tropical disease (NTD) caused by trematode worms of the genus *Schistosoma*, transmitted by freshwater snails. The two forms of this disease are the intestinal and urogenital schistosomiasis, caused by *Schistosoma mansoni* and *Schistosoma haematobium*, respectively (1). The intermediate host for intestinal schistosomiasis are *Biomphalaria* snails while the *Bulinus* species transmit the urogenital type (1,2). Schistosomiasis is the second most prevalent parasitic disease with 779 million people at risk and 260 million infected globally, of which 90% of the cases are localised in Africa (2–4) The disease causes devastating chronic morbidity leading to permanent disability and often death if not treated (1). Several interconnected factors are generally known to support *S. mansoni* transmission in African communities, including tropical climate, ignorance of masses, poor sanitation , lack of safe water and myths around schistosomiasis morbidity (5–7), but understanding peculiar local drivers for particular communities is imperative to guide specifically appropriate interventions which can make impact. Although the 2030 NTD Road Map guidelines (8) provide a comprehensive tool box of interventions for eventual elimination of schistosomiasis (2,3,9), most Sub-Saharan African countries have majorly relied on mass treatment of endemic communities, without implementation of community-specific holistic approaches (10,11). With many communities in developing countries trapped in poverty in face of current and future predicted climate change effects (12) achieving targets of the global Neglected Tropical diseases roadmap 2030 may not be possible. Therefore, making progress in achieving the sustainable development goals (SDG) will definitely stop transmission of poverty driven diseases in countries

(13,14)

The geographical location of Uganda in the great lakes region of Africa makes the country one of the global foci with a huge population at risk of schistosomiasis infections (5). About 11.2 million people, approximately 25.3% of 44.3 million Ugandans living in about 70% of the districts in the country are affected (15). The initial large scale mass treatment of Ugandan endemic communities with praziquantel from 2003-2010 achieved reduction of schistosomiasis prevalence (16), but the gains were rapidly eroded with evidence of persistent hot spots of high prevalence and morbidity of schistosomiasis, causing severe morbidity in communities on the shores of Lake Albert and Victoria (17–20).

Previous malacology studies have reported *B. stanleyi*, *B. sudanica* and *B. pfeifferi* on Lake Albert (21–24) while on Lake Victoria *B. sudanica*, *B. choanomphala* and *B. pfeifferi* as the major intermediate hosts (24–28). The *S. mansoni* prevalence in intermediate hosts has been reported to be higher in Lake Albert than Victoria, purportedly indicating a higher transmission of intestinal schistosomiasis in the Albertine region (25,27). Poverty is generally the major risk factor of schistosomiasis transmission in Uganda (29), but also, varying environmental parameters on the lake shores including seasonal changes, intermediate host snail species dynamics, anthropogenic activities (25,27,29,30). determine focal transmission of the disease at different sites of the Lakes. In addition, population mobility, settlement patterns on the shoreline, latrine coverage and social-cultural factors of resident communities are key in promoting or preventing *S. mansoni* transmission (6,7,29). Lacustrine environmental changes including flooding of shores and drought, have been predicted by modelling to determine snail species seasonal variation and schistosome infection rates (31,32). All these factors influence intermediate host snail survival and infection rates. Snail surveillance, integrated with real time environmental and anthropogenic activity observations have been proven to be cost effective approaches to identify and monitor

drivers of persistent schistosomiasis transmission (33,34).

Understanding local environmental factors, human activities and the seasonal variation of snail species and infection rates are critical aspects in identifying communities that should be prioritised while planning interventions. In this study, we aimed to investigate seasonal abundance of *Biomphalaria* species and their natural schistosome cercaria shedding rate and describe local drivers that need to be addressed to control *S. mansoni* transmission. We report findings of a longitudinal malacological study to describe local human activities and environmental drivers of persistent schistosomiasis transmission in communities of Lake Albert and Victoria ecological zones of Uganda.

Methods and materials

Study area and design: The study was conducted in Kikuube district for Lake Albert (LA) and Namayingo District for Lake Victoria (LV) ecosystems, shown in Figure 1.

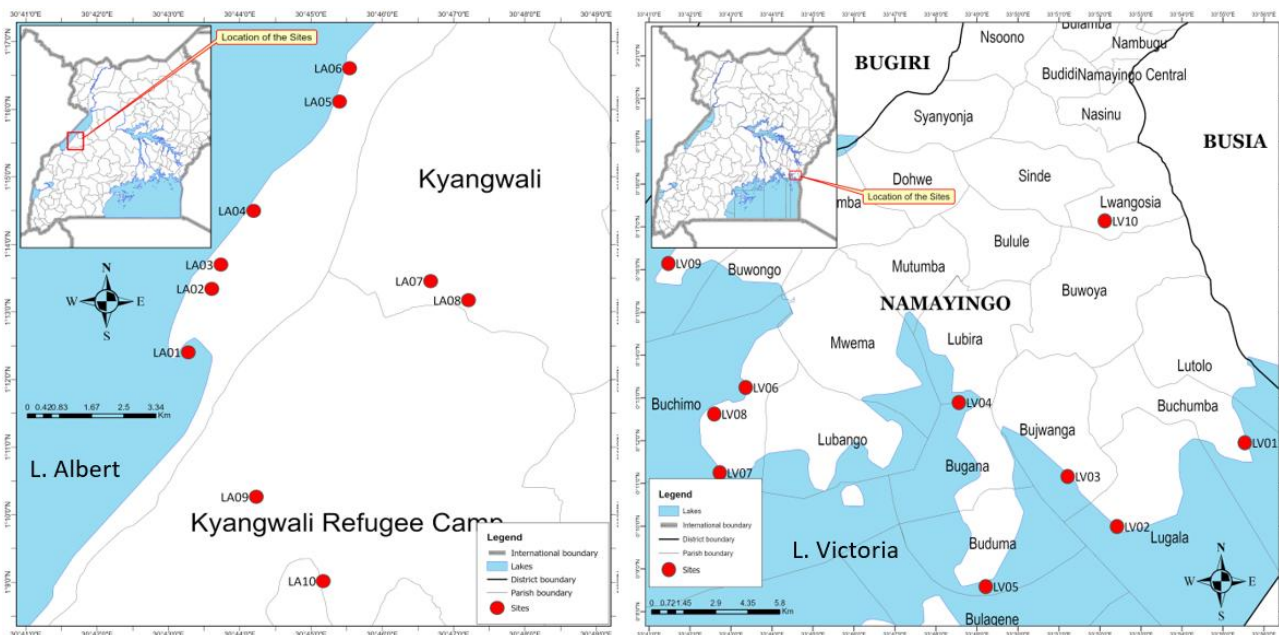


Figure 1. Maps showing snail monitoring sites in Kikuube, Lake Albert and Namayingo, Lake

Victoria.

We collected snails from ten sites of each lake zone every two months, from June 2023 to November 2024, to determine seasonal patterns of snail populations and natural infection rates with schistosomes in relation to observed environmental changes and human activities at the Lake shores and swamps. Lake Albert is a rift valley lake with a fairly linear shoreline in Buhuka area. Six sites, Kiina (LA01), Sunzu Bay (LA02), Sunzu Beach (LA03), Songa (LA04), Kabalendu (LA05) and Nyalebe (LA06) are human water contact sites on the Lake shore while four sites, Ngoma (LA07), Nyakatehe puddle (LA08), Nyampindu (LA09) and Kigoma (LA10) are swamps. The Kabalendu and Nyalebe sites are located in Kyakapere village. The Albertine zone of Uganda has a rapidly developing petroleum industry which attracts influx of people from neighbouring districts and the Democratic Republic of Congo (DRC) to seek casual employment. Some come as displaced persons from intertribal conflict zones of Ituri province in the DRC. To note, people on either side of the Lake in DRC and Uganda are related by culture and language, hence they usually cross the porous borders without any immigration visa control. The cross border movements in both study areas were not officially documented, but visitor records were only available from village leaders during a security operation period of 2024.

For Lake Victoria, the shoreline is characterised by bays and peninsulas. Seven sites; Lugala (LV01), Buyundo (LV02), Busiro (LV03), Buduma (LV05) Bumeru A (LV07) Bumeru B (LV08) and Maruba (LV09) are human water contact sites on the shoreline. Simase (LV04) and Buchimo (LV06) were marshy points at the edge of the Lake while Namutaba (LV10) was an upland site at the swamp edge. Namayingo district Borders Kenya and serves as the gateway from Sigulu islands.

Snail monitoring: Snails were collected from 10 sites per lake zone once every 8 weeks over a period of 18 months. Global positioning system (GPS) coordinates of each site were taken using a Garmin set (e-trex, Garmin, Othale, USA). A snail sampling site on the Lake shore covered a

stretch of entire human water contact area for small sites while for wide sites a length of at least 50 meters. Snails were collected using standard two-meter handle scoops with a 2.0 mm mesh. The sampling was semi-quantified, with two collectors, each searching for snails at a site for 30 minutes and collecting all *Biomphalaria species* snails found. The collected snails were identified using a morphological identification key (35).

Screening *Biomphalaria* species for schistosome cercarial shedding

Each snail was placed in cell culture plate well shedding tray containing 2.0 ml of water and exposed to indirect sunlight for intervals of 2-4 hours. The snails were examined for schistosome and other trematode cercariae shedding under a dissecting microscope (27,36,37). The cercaria were identified by morphology using a key described by expert malacologists (36).

Environmental observations: We observed and noted environmental parameters such as vegetation and human water contact activities on a site monitoring form. We inspected the area within 10 metres around each site and physically counted visible spots of open defaecation (OD) with presence of fresh human faeces and took photographs. Prevailing weather conditions, wave action, shoreline water level changes at the time of snail collection were recorded. Aquatic vegetation at snail collection sites were identified and any new landing rafts of floating vegetation were recorded using methods described earlier (38).

Human activities and population influx: In each snail sampling site village, we observed and noted human water contact activities on a field observation form every other month for 18 months. We interviewed village administrative chairpersons about their local population, the number of public latrines, and reviewed the available records of visitors to estimate the average number of people arriving every day from other areas. The counting of visitors in landing boats had taken place for only one month during the local security operations on L. Albert and L. Victoria.

Data analysis: The data sets were entered in Excel. Statistical analysis was conducted using

Stata 19 (StataCorp. 2025). Comparison of *Biomphalaria* species population and infection rates across sites and seasons was performed using the Kruskal-Wallis test. A zero-inflated negative binomial model, which takes into account over dispersion, zero inflation, and clustering, was used to test whether snail counts differed between Lake Albert and Lake Victoria while accounting for site-level and monthly variation. Binomial logistic regression was used to analyse the association of different environmental factors and human activities with snail infection rates. Spearman's rank correlation was used to analyse the relationship between number of faecal spots and snail infection rate. We categorised the number of faecal spots equal or less than the median as low and greater than the median as high OD intensities.

Results

Intermediate snail host abundance: We collected a total of 11,329 *Biomphalaria* snails from the ten sites of Lake Victoria and 6,626 from the sites of Lake Albert. The shallow water snails, *B. sudanica* and *B. pfeifferi*, inhabit both lake zones, but each lake had a different deep water species, *B. stanleyi* in Lake Albert and *B. choanomphala* in L. Victoria. *Biomphalaria sudanica* was the most abundant species on both lakes, constituting 75.5% in LV and 52% in LA (Table 1).

Table 1. Distribution of *Biomphalaria* species by Lake

Lake	Snail Species	Total Number of Snails	Abundance (%)
Albert	<i>B. pfeifferi</i>	1,752	26.4
	<i>B. stanleyi</i>	1,428	21.6
	<i>B. sudanica</i>	3,446	52.0
Subtotal		6,626	
Victoria	<i>B. choanomphala</i>	2,323	20.5
	<i>B. pfeifferi</i>	450	4.0
	<i>B. sudanica</i>	8,556	75.5

Subtotal	11,329
Grand Total	17,955

The *Biomphalaria* species composition and abundance differ significantly between Lake Albert and Lake Victoria ($p = 0.034$), suggesting almost complete species segregation between lakes, except for *B. sudanica* and *B. pfeifferi*, which are found in both water bodies. After adjusting for site type, snail species, and season, Lake Victoria sites showed significantly higher snail abundance compared to Lake Albert sites (adjusted IRR = 7.09, 95% CI: 1.15–43.73, $p = 0.035$). However, no significant difference was observed in the probability of structural zeros between lakes (adjusted OR = 0.31, 95% CI: 0.002–41.15, $p = 0.636$).

***Biomphalaria* snail population distribution by site:**

There were three forms of sites: the lake beach at the shoreline, marshes sheltered by vegetation from wave action and swamps on the upland areas. Some lake beach sites had both deep water and shallow water species depending on the vegetation. For sites in Lake Albert, there was a significant difference in the distribution of the number of *Biomphalaria* species snails across the 10 sites (χ^2 (9) with ties = 25.19, $p = 0.002$) (Table 2). The lake beach sites had significant differences in snail number (χ^2 (9) with ties = 12.7, $p = 0.03$) as well as the swamp sites (χ^2 (3) with ties = 11.61, $p = 0.01$).

Table 2. *Biomphalaria* species abundance in sites of L. Albert

Site		<i>B. sudanica</i>	<i>B. stanleyi</i>	<i>B. pfeifferi</i>	Total
Kiina	Lake beach	795	114	0	909
Sunzu Bay	Lake Beach	1200	333	0	1533
Sunzu Beach	Lake Beach	82	491	0	573
Songa	Lake Marsh	538	376	18	932
Kabalendu	Lake Beach	85	1	0	86
Nyalebe	Lake Marsh	345	113	0	458
Ngoma	Swamp	401	0	191	592

Puddle	Swamp	0	0	809	809
Nyampindu	Swamp	0	0	734	734
Kigoma	Swamp	0	0	0	0
Site Total		3446	1428	1752	6626
Relative abundance		52%	21.6%	26.4%	

In Lake Victoria sites, the number of *Biomphalaria* species snails was evenly distributed except for *B. choanomphala* which was only found at lake beach points where there was growth of *Vallisneria* grasses (Table 3).

Table 3. *Biomphalaria* species abundance in sites of L. Victoria

Site	Site type	<i>B. sudanica</i>	<i>B. choanomphala</i>	<i>B. pfeifferi</i>	Total
Lugala	Lake beach	1119	65	0	1184
Buyundo	Lake Beach	1235	24	0	1259
Busiro	Lake Beach	1736	30	0	1766
Simase	Lake Marsh	1502	0	0	1502
Buduma	Lake Beach	1026	0	0	1026
Buchimo	Lake Marsh	1173	0	0	1173
Bumeru A	Lake Beach	0	1745	0	1745
Bumeru B	Lake Beach	220	5	0	225
Maruba	Lake Beach	545	454	0	999
Namutaba	Swamp	0	0	450	450
Species total		8556	2323	450	11329
Relative abundance		75.5%	20%	4.5%	

There was no significant difference in the distribution of snails across the 10 sites (χ^2 (9) with ties = 5.68, $p = 0.771$). For the beach sites of Lake Victoria, there was no significant difference in the distribution of the number of snails (χ^2 (9) with ties = 5.60, p -value = 0.469 > 0.05).

Generally, among sites with snails, Lake Victoria exhibited a non-significant trend towards higher snail abundance compared to Lake Albert ($\beta = 0.26$, 95% CI: -0.10 to 0.62, $z =$

210 1.44, $p = 0.150$). However, the exponentiated coefficient indicates that Lake Victoria sites
211 had approximately 1.30 times the observed snail counts of Lake Albert sites (IRR = 1.30,
212 95% CI: 0.91-1.86), although this difference was not statistically significant.

213

214 **Seasonal *Biomphalaria* snail species dynamics:** During the 18 months of snail
215 collection we, noted two seasons, a short dry season from June to October 2023 and a
216 rainy season which caused flooding of Lake Albert and Lake Victoria shorelines. On Lake
217 Victoria, flooding stopped in June 2024 while on Lake Albert the flooding persisted for
218 several months after the rainy season. The unexpected rainy season and flooding
219 persisted throughout December 2023 to February 2024, the months which were usually
220 known to be dry in the Lake Albert and Victoria basins of Uganda.

221 There was switching of snail species at sites with the *Biomphalaria sudanica* colonising
222 the shoreline areas which used to support deep water snails on both LA and LV. There
223 was a sudden decline of *B. stanleyi* population at sites of LA and *B. choanomphala* on LV
224 after onset of flooding as shown in figures 2a and 2b.

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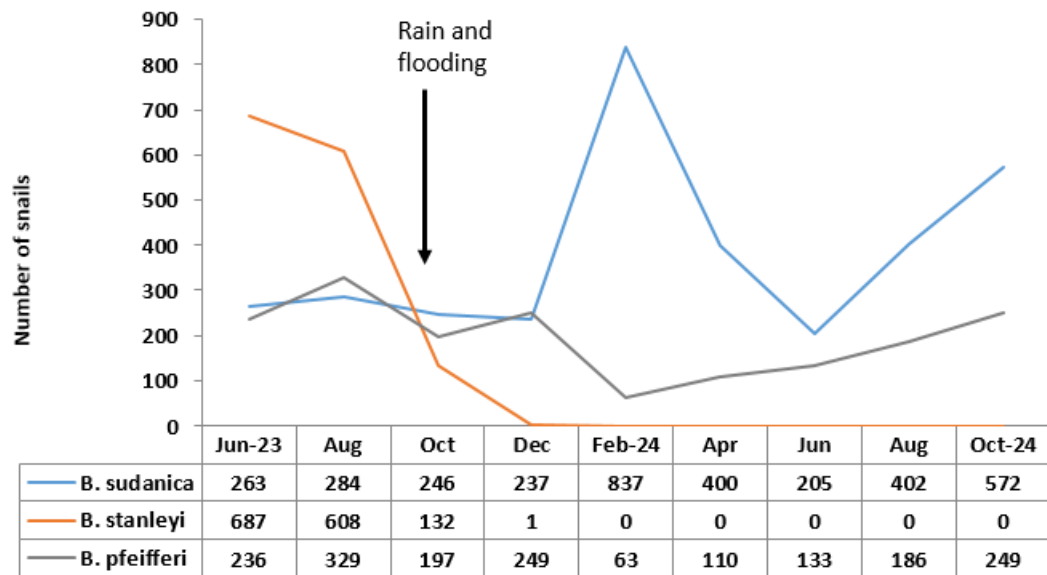


Figure 2a. Seasonal *Biomphalaria* species population dynamics by month on LA

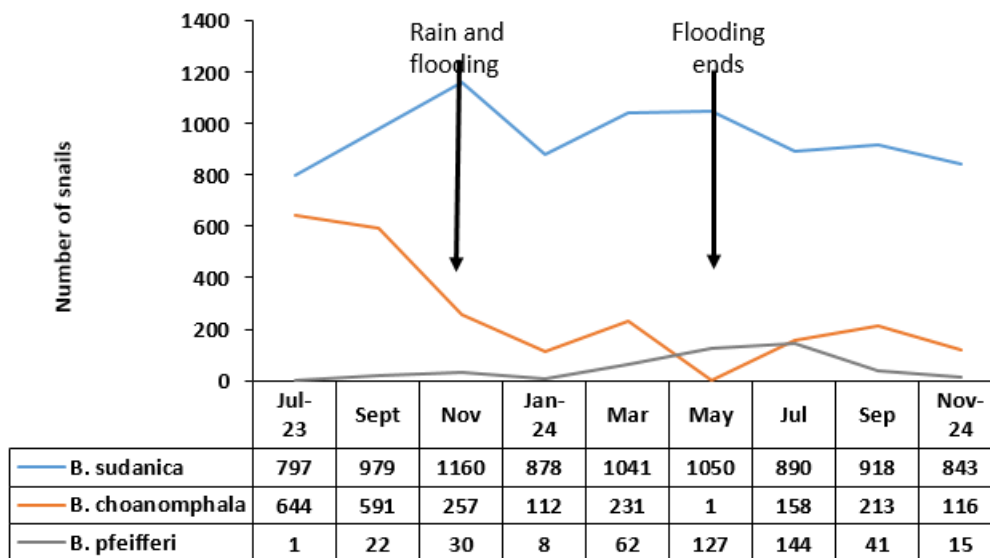


Figure 2b. Seasonal *Biomphalaria* species population dynamics by Month on LV

Schistosome cercaria shedding by site: The prevalence of *Biomphalaria* snails

236 shedding schistosome cercariae varied by site. Human water contact sites with large
237 populations and commercial activities had more infected snails than those with few
238 people. On Lake Albert, this was observed at Nyalebe, Songa and Kabalendu, while on
239 Lake Victoria, Busiro, Maruba, Buyundo, and Buduma were the highest risk sites for
240 schistosomiasis infection (Table 4)

241

242 **Table 4.** Proportion of Infected *Biomphalaria* snails by site in LA and LV

Lake	Site	Total Snails	No. Shedding Cercaria	Infected (%)
Albert	Kabalendu	86	7	8.14
	Kigoma	0	0	0.00
	Kiina	909	6	0.66
	Ngoma	592	0	0.00
	Nyalebe	458	17	3.71
	Nyampindu	734	1	0.13
	Puddle	809	10	1.23
	Songa	932	14	1.50
	Sunzu Bay	1,533	4	0.26
	Sunzu Beach	573	1	0.17
Total Lake Albert		6,626	60	0.91
Victoria	Buchimo	1,173	1	0.09
	Buduma	1,026	7	0.68
	Bumeru A	1,745	2	0.11
	Bumeru B	225	4	1.78
	Busiro	1,766	19	1.08
	Buyundo	1,259	6	0.48
	Lugala	1,184	6	0.50
	Maruba	999	11	1.10
	Namutaba	450	2	0.44
	Simase	1,502	2	0.13
Total Lake Victoria		11,329	60	0.53
Total Both Lakes		17,955	120	0.67

243

244 *Biomphalaria* snails shedding schistosome cercaria on both lakes ranged from 0% to

245 8.1%. Binomial regression, accounting for differences in the number of snails across sites,

246 showed significant heterogeneity in infection proportions ($\chi^2(18) = 5.9 \times 10^{11}$, $p < 0.0001$).

247 There was no significant difference in snail infection rates between Lake Albert and Lake

248 Victoria (OR = 0.58, 95% CI: 0.24–1.40, $p = 0.228$), despite a 1.7-fold difference in pooled

rates (Albert: 0.91% [(60/6,626) *100 snails]; Victoria: 0.53% [(60/11,329) *100 snails]).

Table 5. Distribution of infected *Biomphalaria* by species in LA and LV

Lake	Species	No. Snails	Shedding	% of shedding per species	% of total shedding
Albert	<i>B. pfeifferi</i>	1,752	14	0.80	23.3
	<i>B. stanleyi</i>	1,428	17	1.19	28.3
	<i>B. sudanica</i>	3,446	29	0.84	48.4
	Total	6,626	60		
Victoria	<i>B. pfeifferi</i>	450	2	0.44	3.3
	<i>B. choanomphala</i>	2,323	7	0.30	11.7
	<i>B. sudanica</i>	8,556	51	0.60	85.0
	Total	11,329	60		
Overall total		17,955	120		

In L. Victoria, *B. sudanica* had the highest infection rate (**0.60%**). In LA, no statistically significant differences in species infections were detected ($p > 0.05$). In Lake Victoria, *sudanica* exhibited a marginally higher infection rate compared to *B. choanomphala* ($p = 0.09$). However, when data from both lakes were combined, *pfeifferi* ($p = 0.035$), *B. stanleyi* ($p = 0.002$), and *B. sudanica* ($p = 0.043$) had significantly higher odds of infection ($p < 0.05$).

Seasonal schistosome transmission by *Biomphalaria* snails

Seasonal analysis revealed no significant differences in snail infection rates during dry and wet seasons (Figure 3). In Lake Albert, the odds of infection during the wet season were 23% higher than during the dry season, but this difference was not statistically

significant (OR = 1.23, 95% CI: 0.40–3.76, $p = 0.716$). Lake Victoria exhibited a larger but non-significant trend toward higher wet-season infection (OR = 1.80, 95% CI: 0.68–4.76, $p = 0.233$). Overall analysis combining both lakes confirmed no significant seasonal association (OR = 1.43, 95% CI: 0.67–3.03, $p = 0.357$). All models showed substantial over dispersion (Pearson $\chi^2/df = 2.35\text{--}7.81$), indicating that site-specific factors contributed more to infection variation than seasonal patterns.

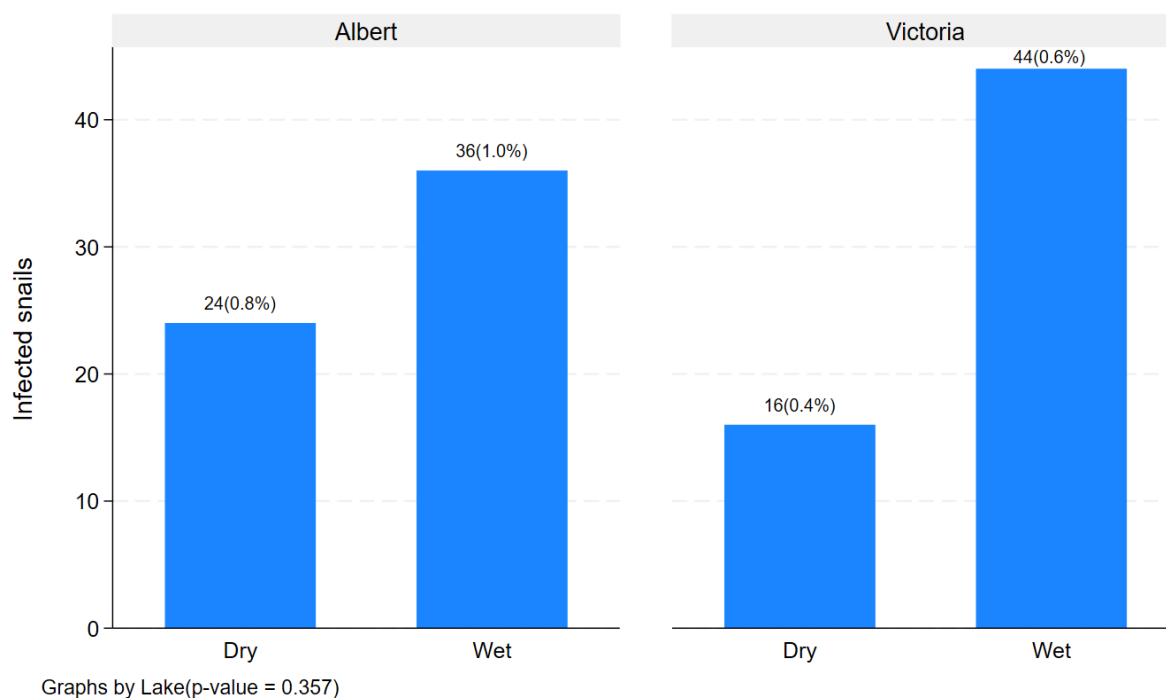


Figure 3. Seasonal *Biomphalaria* infection rate on LA and LV

Temporal pattern of schistosome cercaria shedding by *Biomphalaria* species:

On Lake Albert the highest cercaria shedding rate by *B. stanleyi* was 2.2% in June 2023, but the snails disappeared from accessible lake shore sites as soon as rains and flooding ensued in October 2023 until November 2024. *B. sudanica* population survived throughout the flooding season and maintained schistosomiasis transmission throughout the year with a peak of cercaria shedding in October 2024. However, on the upland sites of Lake Albert, *B. pfeifferi* was the major transmitter in the swamps (Figure 4a)

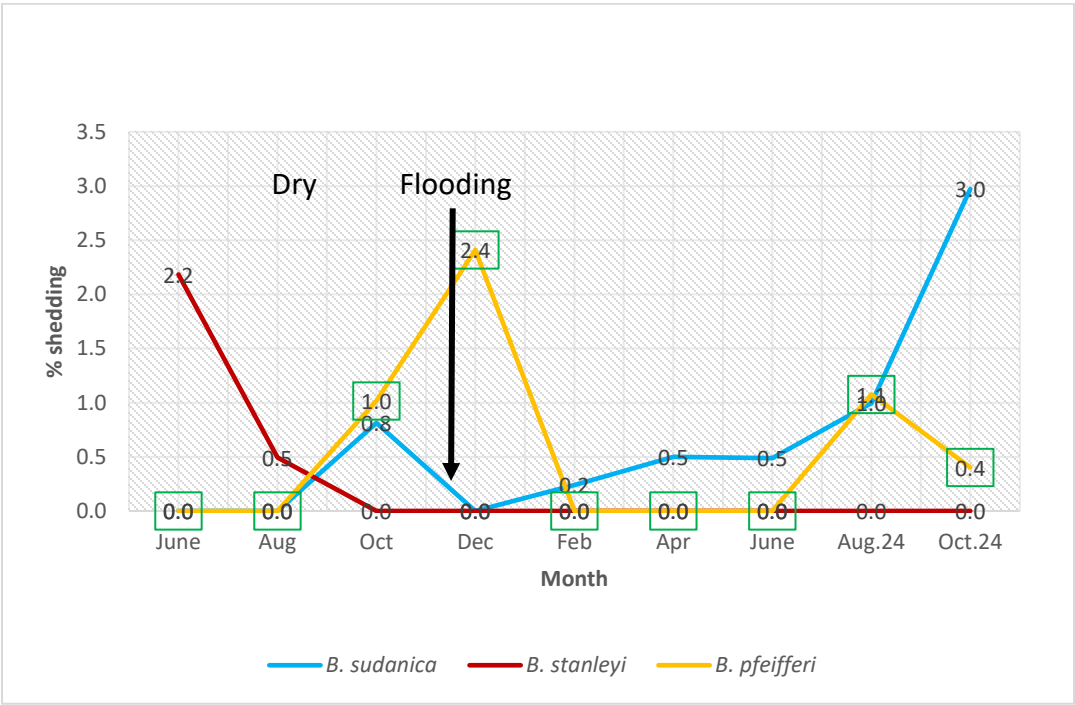


Figure 4a, Seasonal Schistosome cercaria shedding pattern by *Biomphalaria* species in LA.

On Lake Victoria, infected *B. choanomphala* snails contributed to schistosomiasis transmission during a dry season at a few sites where they thrived, but their population declined after the onset of rains and flooding. *Biomphalaria sudanica* colonized and

survived at all sites during both flooding and dry seasons, maintaining transmission throughout the sampling period, with a peak in May 2024 (Figure 4b). At the upland site 10, Namutaba, *B. pfeifferi* survived in small numbers and continued schistosome transmission.

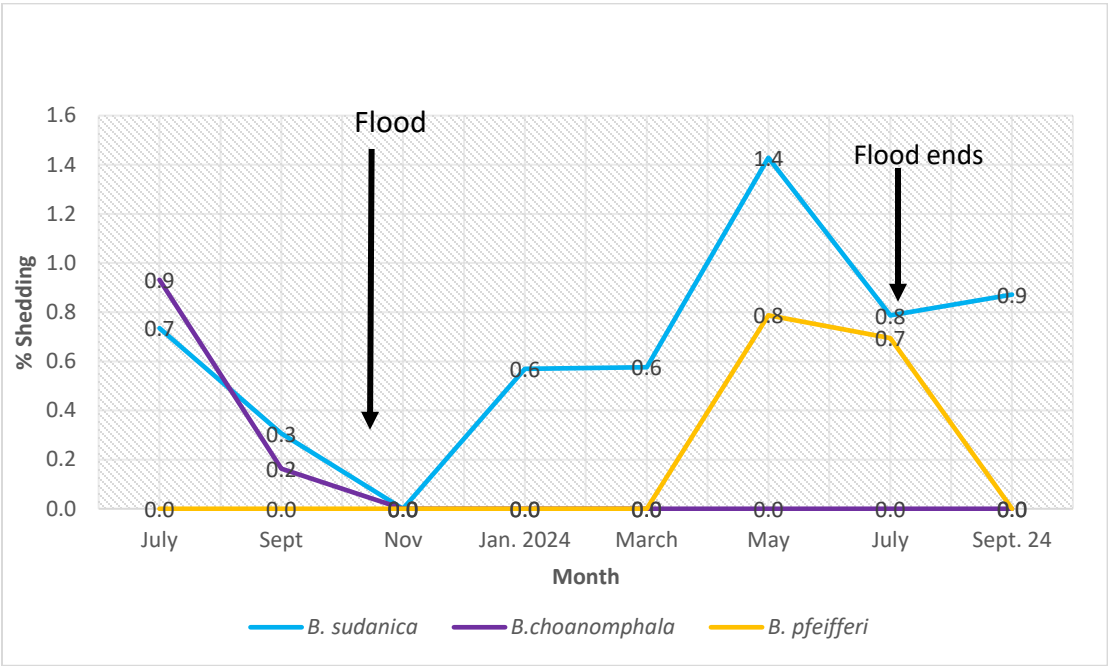


Figure 4b. Seasonal Schistosome cercarial shedding pattern by *Biomphalaria* species on LV

Local drivers of schistosome transmission: We observed habitual disposal of human faeces on the shorelines through open defaecation, dispersal of infective snails by floating vegetation during flooding months, continuous human-water contact, and population influx to villages from other endemic areas as potential local drivers of persistent transmission of schistosomiasis on LA and LV. We counted a total 421 open defaecation (OD) spots around the sites of LA and 406 on LV. High intensity of OD was found at most sites on the shores of both Lakes, but it was low in the swamps and marshy sites (Tables 6a and 6b). Sites which had influx of many people from other areas had more OD spots.

302 **Table 6a.** Number of open defaecation spots at snail collection sites of Lake Albert

Site	Type	2023				2024					Total	OD Intensity
		Jun	Aug	Oct	Dec	Feb	Apr	Jun	Aug	Oct		
Kiina	Lake shore	6	4	7	11	8	6	9	10	5	66	High
Sunzu Bay	Lake shore	3	2	4	6	4	3	4	5	3	34	High
Sunzu Beach	Lake shore	5	4	6	5	8	4	6	5	7	50	High
Songa	Lake shore	8	6	9	7	6	5	7	10	6	64	High
Kabalendu	Lake shore	5	7	4	8	6	8	12	8	7	65	High
Nyalebe	Lake shore	15	12	8	10	8	8	16	10	9	96	High
Ngoma	Swamp	1	1	0	1	0	1	1	0	1	6	Low
Puddle	Swamp	2	0	1	2	0	1	2	1	0	9	Low
Nyampindu	Swamp	2	1	1	3	0	1	3	2	3	16	Low
Kigoma	Swamp	2	3	1	2	0	1	2	0	4	15	Low

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304

305 **Table 6b.** Number of open defaecation spots at snail collection sites of Lake Victoria

Site	Type	2023					2024				Total	OD Intensity
		Jul	Sep	Nov	Jan	Mar	May	Jul	Sep	Nov		
Lugala	Lake shore	4	3	2	1	2	3	2	4	2	23	Low
Buyundo	Lake shore	3	5	2	3	6	5	6	4	7	41	High
Busiro	Lake shore	14	10	12	9	15	17	8	13	9	107	High
Buduma	Lake shore	7	9	6	9	8	5	6	7	8	65	High
Simase	Lake Marsh	1	0	0	1	0	1	3	0	0	6	Low
Buchimo	Lake Marsh	1	0	0	1	1	0	1	0	0	4	Low
Bumeru A	Lake shore	9	7	6	11	8	7	9	5	6	68	High
Bumeru B	Lake shore	3	2	5	2	4	2	1	3	2	24	Low
Maruba	Lake shore	7	9	11	6	8	5	8	6	5	65	High
Namutaba	Swamp	0	0	1	0	1	0	0	1	0	3	Low

306

307 Binomial regression analysis showed that sites with low OD intensity were associated
 308 with significantly lower odds of snail infection compared to high OD sites (OR = 0.39, 95%
 309 CI: 0.19–0.81, $p = 0.012$). In Lake Albert, there was a strong positive correlation between
 310 the number of fecal spots and the proportion of infected snails (Spearman's $\rho = 0.71$, $p =$
 311 0.024). In contrast, in Lake Victoria, although the correlation was positive, it was moderate
 312 and not statistically significant (Spearman's $\rho = 0.42$, $p = 0.224$).

313

314 **Population influx from other endemic areas:** There was daily arrival of people from
315 other endemic areas on both LA and LV. Lake Albert shore villages in Kikuube district
316 received approximately 1,307 visitors every day of which 47% were from Democratic
317 Republic of Congo and 53% from the neighbouring districts of Nebbi, Pakwach and
318 Buliisa (Table 7a). The visitors from the mentioned endemic areas usually came to
319 transact business at the lake shore village markets, seek employment in the petroleum
320 industry construction, carry out fishing activities or transit to other destinations including
321 the Kyangwali refugee camp. Due to lack of adequate public latrines, open defaecation
322 was common around shore line bushes, sand and in the Lake as illustrated in Figure 5.
323 For Lake Victoria, population influx to shoreline villages of Namayingo was majorly from
324 the Sigulu Islands (36%), the fishing villages of Kenya 13% and the rest from upland
325 locations (Table 7b).

326

327

Table 7a. Population of Lake Albert villages and daily number of visitors from other endemic areas.

Village	Local popn	Public latrines	Daily arrivals from other areas				Total
			DRC	Nebbi	Pakwach	Buliisa	
Nsonga A	984	1	140	88	70	35	333
Sunzu A	1940	1	8	6	20	3	37
Kyabasambo	640	1	18	10	4	9	41
Kyakapere	3160	1	211	80	57	84	432
Kiina	767	1	79	8	2	18	107
Nsonga B	4032	1	40	15	50	30	135
Sunzu B	1400	1	120	50	37	15	222
Total	12923	7	616	257	240	194	1307
% arrivals from other areas			47	20	18	15	

Table 7b. Population of Lake Victoria snail sampling villages and the daily number of visitors from other endemic areas.

Village	Local popn	Public latrines	Daily arrivals from other areas			Total
			Kenya	Island	Upland	
Busiro beach	2968	1	30	120	80	230
Buyundo	1932	1	50	70	90	210
Bumeru A	3428	2	3	50	40	93
Bumeru B	2761	2	3	2	74	79
Maruba	1583	0	4	5	68	77
Total	12672	6	90	247	352	689
% arrivals from other areas			13	36	51	

Flooding of Lake shores

Water levels on LA and LV increased and submerged shores, creating new shallow water pools suitable for breeding of *B. sudanica* (Figure 5). The village residents usually walked across the cercaria infested shallow water pools to access the Lake, hence increasing the risk of schistosomiasis transmission.

341

342 **Dispersal of infected *Biomphalaria* snails from other areas:** Dispersal of Infected
343 snails on floating rafts of vegetation introduced intermediate host snails and
344 schistosomiasis transmission from place to place. At Kabalendu site on LA, where
345 *Biomphalaria* had been absent for one year, the landing of a huge raft of floating
346 vegetation suddenly brought along infected snails in October 2024 (Figures 4a and 5).
347 Dislodgement of huge masses of vegetation in the lakes occurred due to flooding of the
348 shorelines as illustrated in Figure 5.



Figure 5: Pictures illustrating observed local drivers of persistent *S. mansoni* transmission; **a.** Nyalebe shore in dry season, **b.** Nyalebe shore during wet- flooding season, **c&d** Human faeces at shores of Lake Albert and **e,** human faeces in water at Nyalebe shore, **f.** Rafts of floating vegetation driven by wind on Lake Albert, **g.** huge raft

of floating vegetation landed at Sunzu beach and introduced *B. sudanica* from other locations, h. human water contact activities on LA

Continuous exposure of residents to schistosome-infested water: Each of the snail monitoring sites was a human water contact point. For the Lake shore sites of both Lakes, the most common activities were fetching water for domestic use, washing clothes, fishing, swimming, snail shell harvesting and sand mining. For the swamp and marsh sites fetching water for domestic use, washing clothes, farming and papyrus harvesting were the major human exposure activities.

Discussion

This malacological study aimed to identify and describe local environmental and human activities that act as drivers of persistent transmission of intestinal schistosomiasis in the Lake Albert and L. Victoria zones of Uganda. The results show that *Biomphalaria* snails thrive at all lake shores, with greater abundancy in L. Victoria sites than in Lake Albert. The data show seasonal switching of *Biomphalaria* species at sites to maintain focal transmission throughout the year. The deep water snails, *B. stanleyi* in Lake Albert and *B. choanomphala* in Lake Victoria, highly contribute to schistosomiasis transmission during dry season, but decline in population and temporarily disappear from shorelines during wet and flooding months. *Biomphalaria sudanica* snails multiply rapidly in flood water and take over the schistosomiasis transmission role in all seasons. Large masses of onshore vegetation harbouring snails were dislodged by flooding to form rafts of floating vegetation driven by wind, aiding dispersal of infected *Biomphalaria* snails from place to place. Influx of populations from other endemic areas coupled with open defaecation on shores likely maintain *S. mansoni* transmission on both Lakes.

378

379 During the period of the study, we noted a seasonal change with onset of unexpected
380 rainfall and flooding from October 2023 to February 2024. These are usually dry months,
381 in the Albertine region (39), but due to global climate change trends, the seasons are
382 often difficult to predict correctly. In 2006, Kazibwe and others (23)

383 observed a high population of *B. stanleyi* on the Lake during months of January to May
384 in 2003, but, our study found no snails due heavy rains and flooding in the same months
385 in 2023 and 2024. This suggests that climate change is advancing in the region and might
386 become a major factor driving transmission dynamics of intestinal schistosomiasis as
387 predicted in a recent model (40) and Borrhani, et al (12) . Despite the fact that rains
388 stopped in April 2024, Lake Albert continued to have increased flooding of the Lakeshores
389 favouring *B. sudanica* snail multiplication. This could have been caused by high-volume
390 water flow of rivers into the Lake from the western escarpment in DRC and the Nile. Our
391 observation is consistent with the ecological studies of (41), which explained that local
392 rainfall had no influence on the water levels of Lake Albert. During rainy and flooding
393 season *B. stanleyi* on LA and *B. choanomphala* on L. Victoria were not found at
394 accessible deep water sites. These snails are vulnerable to debris washed into the Lake
395 by flood rain water. The debris burry *Vallisneria* plants at the lake bed and deny them
396 sufficient light for photosynthesis resulting in mortality of the snails inhabiting the grasses
397 near the shoreline. However, we found few snails 50 metres away from the shoreline,
398 implying *B. stanleyi* snails in deeper water, far from the shoreline have chances to survive
399 the bad season and later disperse to points near the shoreline when the dry season sets
400 in and supports growth of *Vallisneria*. Flooding covers wide areas of the lakeshores with

shallow water, creating more suitable breeding environment for *B. sudanica*. Whereas the deep water snails disappeared during flooding season, *B. sudanica* inhabited the same human water contact sites and assumed the transmission role. We found *B. sudanica* surviving under varying vegetation types in shallow waters with temperature up to 30° C. Subsequent rains seemed to cause some mortality of *B. sudanica*, but the population quickly recovered probably when survivors got adapted to the new environment. The resilience of *B. sudanica* to survive varying environmental changes and maintain high population makes it the most important species playing a major role in *S. mansoni* transmission on LA and LV. Although *B. stanleyi* and *B. choanomphala* are known to be more compatible with *S. mansoni* in lab experiments (42), they are vulnerable in the natural environment and only support transmission during dry season when their survival is best favoured. With, the observed effects of environmental change including unpredictable flooding on both Lakes, *B. sudanica* continues to be the major transmitter throughout the year. This switching of species at sites during different seasons ensured schistosomiasis transmission throughout the year. The seasonal changes we observed agree with the previous work described by Nuwagira and others (43).

Open defecation on the shoreline was common at sites in fishing village with high busy local open field markets, high volume of boat landing and population influx from other areas. The reasons for population influx to shores of Lake Albert include seeking employment in the rapidly growing petroleum industry, frequent episodes of population displacement by insecurity in the neighbouring areas of DRC and cross border and inter-district trade in fish and general merchandise. On Lake Albert, Songa (LA04), Nyalebe

424 (LA06), Kabalendu (LA05) had the highest faecal contamination at the shore and the
425 greatest number of snails shedding cercariae. The strong correlation between open
426 defaecation spots and snail infection rates implies that most of the faeces on the shoreline
427 contain schistosome eggs which hatch into miracidia and infect snails when washed into
428 the lake. On Lake Victoria, similar observations were recorded at Busiro (LV03) beach,
429 Bumeru A (LV07) and Maruba (LV09). The huge number of people from DRC indicated
430 greater international human interactions and high rate of migration from Congo to Uganda
431 across L. Albert than from Kenya across Lake Victoria. Habitual open defaecation at the
432 Lake shores by a wide heterogeneity of people exacerbates continuous release of *S.*
433 *mansoni* eggs to sustain the disease transmission throughout the year. Without
434 addressing open defaecation, it might be extremely difficult to control the persistent
435 transmission of intestinal schistosomiasis on LA and LV. The ongoing strategy of annual
436 mass treatment of communities with praziquantel might help to control morbidity, but will
437 unlikely control the transmission as continuous influx of new people and local individuals
438 who miss treatment continue to introduce the parasite and maintain high reinfection rates
439 in communities as predicted by recent studies (12,40). The high population influx on the
440 Lakeshores suggests that there could be heterogeneous genotypes of *S. mansoni* in
441 lakeshore communities which need to be investigated by future studies to explain any
442 association with varying morbidity of individuals. Egypt is one of the model countries
443 which have successfully addressed environmental and anthropogenic related challenges
444 of schistosomiasis (44) and similar approaches could be applied in Uganda to mitigate
445 the ongoing persistent transmission. Therefore prioritising poverty reduction in line with
446 SDG 1, improvement of water, sanitation and Hygiene (WASH) coverage to achieve SDG

6 (13,14) and behavioural change communication (BCC) in shoreline communities of Uganda could reduce snail infection by miracidia from open disposal of faeces and minimise exposure of residents to schistosome infested water in the lakes as previous studies have also recommended (23,27,37)

On both Lakes, we observed movement and landing of huge rafts of floating vegetation with wide variety of plants including Papyrus, Water Hyacinth, Typha and other grasses at snail monitoring sites during the flooding period, bringing along *Biomphalaria* snails from other areas. The largest raft landed at Sunzu bay site covered approximately 10,000 m² area of the shore. These vegetation, were driven by wind from unknown places, but some could have come from the Lake Albert shores in Democratic Republic of Congo and other endemic districts. This observation provides further evidence of the future effects of climate change described by (43). At Kabalendu site where snails had been absent for 12 months due to unfavourable strong wave action, sudden landing of the floating vegetation sheltered the shoreline from strong waves, modified the site and introduced *B. sudanica* snails of which 8.14% shed schistosome cercariae. On Lake Victoria we found *B. sudanica* at the edge of a floating vegetation which landed at Buduma site. Change of seasons and excessive flooding which uproots shoreline vegetation to form huge rafts of floating vegetation, could be one of the effects of climate change Uganda is facing (43). Other than facilitating *Biomphalaria* dispersal and schistosomiasis transmission, the huge floating vegetation rafts also disrupt economic activities on LA, LV and River Nile as earlier reported (45).

In general, in the two Lake zones, differences in intermediate host snail species do not

470 seem to be a major factor for previously reported differences in *S. mansoni* transmission
471 because *B. sudanica* and *B. pfeifferi* inhabit both lakes, while the deep-water snail on
472 each lake is known to be highly efficient (27,46). The purported higher transmission on
473 Lake Albert (25,27) is most likely due to the observed greater intensity of open
474 defaecation on the shores, influx of people from endemic areas and daily human
475 exposure to infection. Also, the local communities on the Lake Albert shores depend
476 entirely on the Lake-derived resources (47) and therefore might get more frequently
477 exposed, compared to those of LV who carry out farming as an alternative economic
478 activity during rainy season (20). Human exposure activities we observed on LA and LV
479 are consistent with what a recent study (48) reported for urogenital schistosomiasis in
480 Tanzania.

481 As limitations of this study, we focused on public latrine availability only, because
482 assessing the latrine coverage in each household was beyond the study scope. We used
483 morphology to identify the *Biomphalaria* species. Due to the plasticity of shells some snail
484 species closely resemble and might not have been accurately identified, but this would
485 not change the schistosome cercaria shedding rates by site. Population influx numbers
486 relied on records of village leaders because there was no official immigration data. This
487 could have underestimated the population movement across Lake Albert to Buhuka area
488 landing sites.

489 **Conclusions:** Heterogeneity and seasonal switching of *Biomphalaria* intermediate host
490 species, habitual human defaecation the Lake shores, influx of people from endemic
491 areas, continuous contact of residents with schistosome-infested water and advancing
492 effects of environmental change appear to be the local drivers of persistent transmission

of intestinal schistosomiasis on LA and LV. All bionomics that exacerbate persistent schistosomiasis transmission exist in LA and LV communities. These findings highlight the importance of including environmental and human activity observations in malacology studies to enhance better understanding of peculiar local drivers of schistosomiasis transmission in different settings to guide most appropriate interventions. Improvement of WASH amenities, behaviour change communication in fishing communities, inclusion of immigrants in mass treatment, and targeted focal control of intermediate host snails should be considered by the Ministry of Health to mitigate the persistent transmission of intestinal schistosomiasis in Lakeshore communities.

List of abbreviations

OD: Open defaecation

LA: Lake Albert

LV: Lake Victoria

DRC: Democratic Republic of Congo

GPS: Geographical Positioning System

BCC: Behaviour change communication

SDG: Sustainable Development Goals

WASH: Water Sanitation and Hygiene

USMRC: Uganda Schistosomiasis Multidisciplinary Research Centre

MUST: Mbarara University of Science and Technology

Declarations

Ethics approval and consent to participate: This was a sub study of the Uganda

Schistosomiasis Multidisciplinary Research Centre project which obtained ethical approval from the Research Ethics Committees of the Uganda Virus Research Institute (GC/127/940), Mbarara University of Science and Technology (MUST-2024-1350), the Uganda National Council for Science and Technology (HS2568ES). Persons conducting snail sampling wore chest waders and heavy-duty gloves to prevent exposure to cercaria. The district health team and local leaders at every administrative level of the sampled sites were sensitized on the objectives and importance of the study to obtain permission to work in the area.

Consent for publication: We did not take photographs which can identify individuals.

Availability of data and materials

The data supporting the conclusions of this study are included in table and figures within the article body and its supplementary materials.

Competing interests

The authors declare that there is no competing interest.

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Authors' contributions: DOW was key in conceptualization, Field work administration, Methods, data collection curation and analysis, and writing the first draft, review and editing. NB, CUT, and JRS developed the research idea and framework. DOW, DK, BF, TD, JRS, and CUT designed the methods and conducted field work. DOW, DK, TD, analysed the data and interpreted the results. DOW, prepared the initial manuscript draft.

CUT, JRS, NB, AE and EMT critically reviewed the manuscript for intellectual content. CUT, JRS, TH, EMT, AE and NB provided oversight and guidance throughout the research process. CUT, JRS, AE, NB and EMT wrote the grant which obtained NIH funding to support this study.

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