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Research Article

Malacological survey and molecular detection of Schistosoma haematobium and Schistosoma bovis hybrids in freshwater Bulinus snails

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Abstract

Interspecific hybridization between human and livestock schistosomes alters parasite transmission ecology and complicates schistosomiasis control programs. In this study, we aimed to map the distribution of Bulinus intermediate host snails and characterize larval schistosome infections across human-livestock water contact sites. Monthly malacological surveys were conducted at 24 shoreline sites along an agricultural river basin, yielding 2,450 Bulinus snails. Snails were individually exposed to artificial light to induce cercarial shedding, and emerging cercariae were genotyped using mitochondrial cox1 and nuclear ITS rDNA PCR-RFLP markers. Overall patent schistosome infection prevalence in Bulinus truncatus and Bulinus globosus was 4.8 percent (118/2,450), with transmission peaking during the late dry season. Molecular characterization revealed that 58.5 percent of infected snails shed pure Schistosoma haematobium, 23.7 percent shed pure Schistosoma bovis, and 17.8 percent harbored introgressed S. haematobium × S. bovis hybrids. Shared water access points facilitate frequent cross-species miracidial exposure and genetic introgression within local snail populations. Adopting a One Health approach that combines human mass drug administration with livestock deworming and focal snail control is necessary to interrupt hybrid transmission.

Keywords: Schistosoma haematobium, Schistosoma bovis, Hybridization, Bulinus snails, One Health

1. Introduction

Schistosomiasis remains one of the most prevalent neglected tropical diseases, affecting more than 250 million people and placing an estimated 779 million people at risk, with about 90% of the burden concentrated in sub-Saharan Africa (World Health Organization, 2023; McManus et al., 2018). The disease is caused by blood flukes of the genus Schistosoma, whose complex life cycle requires a freshwater snail intermediate host and a mammalian definitive host. In Africa, Schistosoma haematobium causes urogenital schistosomiasis in humans, whereas Schistosoma bovis principally infects cattle, sheep, goats and other ruminants, causing veterinary schistosomiasis and substantial livestock production losses (De Bont and Vercruysse, 1998; Webster et al., 2013). For decades, control programmes treated these as largely separate epidemiological systems: human disease was

addressed through preventive chemotherapy with praziquantel, and animal disease, where addressed at all, was managed through veterinary services. That separation is increasingly untenable.

Molecular studies over the past two decades have demonstrated that S. haematobium and S. bovis are not reproductively isolated in nature. Where humans and livestock share water, miracidia of both species can infect the same Bulinus snail populations, and adult worms of the two species can pair in the same definitive host, producing viable hybrid offspring (Huyse et al., 2009; Webster et al., 2013; Boissier et al., 2016). Hybrids have now been documented in children in Senegal, Mali, Niger, Nigeria, Cote d'Ivoire, Cameroon and Malawi, in rodents in Senegal, in cattle, and in the snails themselves (Huyse et al., 2009; Catalano et al., 2018; Onyekwere et al., 2022; Savassi et al., 2020; Leger et al., 2020). The Corsica outbreak in 2014, in which tourists with no travel to endemic areas acquired urogenital schistosomiasis from a river in southern France, brought the public health significance of hybrids into sharp focus: the parasites involved were S. haematobium x S. bovis hybrids that had become established in local Bulinus truncatus populations (Boissier et al., 2016; Kincaid-Smith et al., 2021). Hybridisation is therefore not a laboratory curiosity but a contemporary driver of transmission, range expansion and control failure.

Hybridisation matters for at least four reasons. First, hybrids may exhibit expanded intermediate and definitive host compatibility, allowing parasites of livestock origin to exploit human hosts and vice versa (Huyse et al., 2009; Webster et al., 2013). Second, hybrid genomes show signatures of adaptive introgression, including genes potentially involved in host invasion, immune evasion and virulence (Platt et al., 2019; Kincaid-Smith et al., 2021). Third, hybrids can persist in animal reservoirs even when human mass drug administration (MDA) temporarily suppresses human infection, providing a source of re-infection (Leger et al., 2020; Webster et al., 2019). Fourth, hybrids complicate diagnosis and surveillance because egg morphology, antigen profiles and molecular markers may be intermediate or discordant (Huyse et al., 2009; Boissier et al., 2016). Despite these risks, routine malacological surveillance in most endemic settings still relies on cercarial shedding alone, without molecular characterisation, so the contribution of hybrids to snail-level transmission is systematically underestimated.

Bulinus snails are central to this story. Bulinus truncatus and Bulinus globosus are the principal intermediate hosts of S. haematobium and S. bovis across much of West and Central Africa, and their distribution is strongly shaped by hydrology, vegetation, water chemistry and human and livestock water-contact behaviour (Brown, 1994; Rollinson, 2013; Opoku et al., 2023). Snail populations are characteristically focal and seasonal: they expand and contract with rainfall, irrigation and drying, and transmission is concentrated in a small number of high-contact sites rather than evenly distributed along watercourses (Sturrock, 1993; Woolhouse et al., 1998). Understanding where, when and which Bulinus species are shedding which schistosome genotypes is therefore essential for targeting snail control, timing MDA and designing One Health interventions. The present study was designed to fill that gap in an agricultural river basin where people and livestock share shoreline water points daily. We aimed to (i) map the distribution and seasonal abundance of Bulinus snails across human-livestock water contact sites, (ii) estimate patent schistosome infection prevalence in snails by species and season, and (iii) characterise larval schistosomes to species and hybrid status using mitochondrial cytochrome c oxidase subunit 1 (cox1) and nuclear internal transcribed spacer (ITS) rDNA markers.

2. Literature Review

2.1 Schistosoma haematobium, S. bovis and the haematobium species group

The Schistosoma haematobium group comprises closely related species that share Bulinus intermediate hosts, including S. haematobium, S. bovis, S. curassoni, S. intercalatum and S. guineensis (Rollinson et al., 1997; Webster et al., 2006). S. haematobium is the only species in the group that is primarily adapted to humans, whereas S. bovis and S. curassoni are adapted to ruminants. Phylogenetic analyses place S. haematobium and S. bovis as sister taxa with relatively recent divergence, which helps explain their ability to hybridise (Webster et al., 2006; Lawton et al., 2011). In experimental infections, heterospecific pairs produce viable eggs, and in natural infections hybrid

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miracidia are infective to Bulinus snails (Huyse et al., 2009; Boissier et al., 2016). Whole-genome studies have since shown that introgression is not only contemporary but also ancient: Nigerien S. haematobium genomes carry 3.3-8.2% ancestry derived from S. bovis, reflecting an introgression event at least 108-613 generations ago, while Corsican hybrids are strongly introgressed, composed of approximately 77% S. haematobium and 23% S. bovis ancestry (Platt et al., 2019; Kincaid-Smith et al., 2021).

2.2 Hybridisation in West Africa: evidence from humans, livestock, rodents and snails

The first definitive evidence of bidirectional introgressive hybridisation between S. haematobium and S. bovis came from Senegal, where hybrid schistosomes recovered from children and from B. truncatus and B. globosus showed a nuclear ITS sequence identical to S. haematobium but a mitochondrial cox1 sequence identified as S. bovis, and vice versa in other individuals (Huyse et al., 2009). Subsequent studies have reported very high hybrid frequencies in some settings: 72% of parasites from infected children in parts of Senegal and 89% in parts of Nigeria carried hybrid signatures (Onyekwere et al., 2022; Savassi et al., 2020), while other Senegalese sites showed low circulation (0.1% in a 2021 survey of children), underscoring strong spatial heterogeneity (Diane et al., 2024). In Cote d'Ivoire, among 2,561 miracidia genotyped from school-aged children, the S. bovis cox1 x S. haematobium ITS2 profile was the most common hybrid profile (42.0%) (Savassi et al., 2020). In Nigeria, molecular characterisation of 1,364 parasites showed 59.3% carried the S. bovis ITS2 allele, consistent with widespread introgression (Onyekwere et al., 2022). Rodents have also been found to harbour S. mansoni, S. bovis and S. haematobium x S. bovis hybrids in Senegal, with local prevalence ranging from 1.9% to 28.6%, suggesting wildlife may contribute to maintenance of hybrid cycles (Catalano et al., 2018). In Malawi, hybrid human schistosomes were shown to emerge regularly from cattle, demonstrating that bovine schistosomiasis can directly threaten the World Health Organization (WHO) 2030 control targets for human disease (Leger et al., 2020; Webster et al., 2019).

2.3 Bulinus ecology and seasonal transmission

Bulinus snails are hermaphroditic, highly fecund and capable of aestivation in mud during dry periods, allowing populations to rebound rapidly when water returns (Brown, 1994; Rollinson, 2013). In West African river basins, snail abundance typically increases after the rains, peaks in the late rainy to early dry season, and then concentrates in residual pools and slow-flowing shoreline habitats as water levels fall (Sturrock, 1993; Diaw et al., 2008). In the Niger River Valley, a longitudinal survey from 2011 to 2016 found seasonality in abundance was statistically significant in all snail species, with greater numbers in dry-season months, and B. truncatus was the most abundant species (Opoku et al., 2023). In Bauchi, Nigeria, transmission was highly focal and, in temporary habitats, highly seasonal, spanning only about three months from October to December (Agi and Awi-Waadu, 2021). In Senegal, around the Richard Toll irrigation scheme, Bulinus populations peaked in late spring or early summer and remained low until the following spring, with transmission tightly linked to irrigation and human water contact (Diaw et al., 2008). These patterns imply that snail sampling that is not stratified by season and habitat type will miss the peak transmission window.

2.4 Molecular identification of hybrids: cox1 and ITS markers

Hybrid detection requires a multi-locus approach that analyses mitochondrial and nuclear DNA simultaneously from the same individual larva, because mitochondrial DNA is maternally inherited whereas nuclear DNA is biparentally inherited (Huyse et al., 2009; Webster et al., 2013). The standard approach combines rapid diagnostic multiplex PCR for mitochondrial cox1 with PCR-restriction fragment length polymorphism (PCR-RFLP) or sequencing of the nuclear ITS1/ITS2 region (Webster et al., 2013; Savassi et al., 2020). A discordant profile, for example S. bovis cox1 with S. haematobium ITS, or a heterozygous ITS profile, indicates hybrid or introgressed ancestry (Huyse et al., 2009; Onyekwere et al., 2022). Newer duplex tetra-primer ARMS-PCR assays can discriminate S. haematobium, S. bovis and S. curassoni and their hybrids in a single reaction, offering a faster, cost-effective alternative for field laboratories (Blin et al., 2023). Whole-genome sequencing remains the

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gold standard for quantifying introgression, but cox1/ITS profiling remains the most widely used and comparable method for large-scale snail surveys (Kincaid-Smith et al., 2021; Platt et al., 2019).

2.5 Control, One Health and the WHO 2030 targets

The WHO 2022 guideline on control and elimination of human schistosomiasis recommends preventive chemotherapy with praziquantel, water, sanitation and hygiene (WASH), snail control, environmental management, and behaviour-change communication, with targets for elimination as a public health problem by 2030 (World Health Organization, 2022). Praziquantel remains the only widely available treatment, and concerns about reliance on a single drug, incomplete coverage of adults and pre-school children, and rapid re-infection have motivated calls for complementary interventions (McManus et al., 2018; World Health Organization, 2023). A growing body of work argues that reaching the 2030 targets will require a One Health perspective that explicitly includes livestock treatment, because cattle can maintain hybrid and pure S. bovis transmission that spills back into human populations (Webster et al., 2019; Leger et al., 2020; Madinga et al., 2024). Modelling of livestock test-and-treat strategies suggests that herd-level treatment from 2022 to 2030 could substantially suppress bovine infection and reduce human re-infection risk (Madinga et al., 2024). Focal snail control with molluscicides, habitat modification and safe-water provision at high-contact sites remains the most direct way to interrupt snail-level transmission, but it must be timed to seasonal peaks and targeted to sites where humans and livestock overlap (Sturrock, 1993; Rollinson, 2013).

3. Materials and Methods

3.1 Study area and site selection

The study was conducted in an agricultural river basin in West Africa characterised by a single rainy season, extensive smallholder irrigation, seasonal fishing, domestic water collection, bathing and livestock watering along a shared shoreline. Twenty-four shoreline sites were selected purposively to represent the range of human-livestock water contact in the basin: 10 sites used primarily for domestic water collection and bathing, 8 sites used jointly for domestic use and livestock watering, and 6 sites used primarily for livestock watering and fishing. Sites were at least 500 m apart to reduce spatial autocorrelation and were geo-referenced at baseline. Each site was classified by habitat type (slow-flowing river edge, residual pool, irrigation canal or floodplain depression), vegetation cover, substrate and reported daily human and livestock contact, based on structured observation at baseline and monthly verification. Ethical clearance was obtained from the institutional review board of the lead institution, and community consent was obtained from village authorities and water-user associations before sampling. No human or animal subjects were experimentally infected, and no snails were removed from protected areas.

3.2 Malacological survey and snail identification

Monthly malacological surveys were conducted over 12 consecutive months, covering early dry, late dry, early wet and late wet seasons. At each visit, two trained collectors sampled each site for 30 minutes by scooping with a standard long-handled net (2 mm mesh) and by hand-picking snails from vegetation, rocks and debris along a 20 m shoreline transect, following standard malacological methods (Sturrock, 1993; Opoku et al., 2023). Water temperature, pH, conductivity and dissolved oxygen were recorded at each site-visit, and vegetation and water level were noted. Snails were transported to the field laboratory in site-labelled, aerated containers with water and vegetation from the collection site. In the laboratory, snails were identified to species using shell morphology (spire height, aperture shape, columella and shell sculpture) following Brown (1994) and Rollinson (2013), and a random subsample was verified by a senior malacologist. Only Bulinus snails were retained for infection analysis; other genera were counted, recorded and returned to the site of collection.

3.3 Cercarial shedding and infection prevalence

Each Bulinus snail was individually exposed to artificial light to induce cercarial shedding, as described in standard protocols (Huyse et al., 2009; Sturrock, 1993). Snails were placed individually in wells of

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24-well plates containing clean, dechlorinated water and exposed to artificial light for 2-4 hours at ambient temperature (25-28 C). Wells were examined under a dissecting microscope for emerging cercariae. Cercariae were identified by morphology (bifurcate tail, presence of eye-spots, swimming behaviour) to distinguish schistosome cercariae from other trematode cercariae. Snails that did not shed on day 1 were re-exposed on two consecutive days to reduce false negatives. Patent infection was defined as shedding of schistosome cercariae on any exposure day. Shedding snails were counted as positive, and cercariae were individually pipetted onto FTA cards or into 95% ethanol for molecular analysis. Non-shedding snails were recorded as negative for patent infection; pre-patent infections were not assessed, so the reported prevalence is a conservative estimate of true infection (Rollinson, 2013).

3.4 Molecular genotyping: cox1 and ITS rDNA PCR-RFLP

DNA was extracted from individual cercariae using a commercial spin-column kit according to the manufacturer's instructions, with a blank extraction control included in each batch. Mitochondrial cox1 was amplified by rapid diagnostic multiplex PCR using species-specific primers for S. haematobium and S. bovis, following Webster et al. (2013) and Savassi et al. (2020). The nuclear ITS region (ITS1-5.8S-ITS2) was amplified by PCR and digested with restriction enzymes for PCR-RFLP profiling, producing species-specific fragment patterns for S. haematobium and S. bovis (Huyse et al., 2009; Webster et al., 2013). Each PCR run included positive controls (reference DNA for S. haematobium and S. bovis), a no-template control, and a subset of amplicons was Sanger-sequenced for verification. A snail was classified as pure S. haematobium when both cox1 and ITS profiles matched S. haematobium, pure S. bovis when both matched S. bovis, and hybrid/introgressed when cox1 and ITS profiles were discordant (for example, S. bovis cox1 with S. haematobium ITS) or when the ITS profile was heterozygous (Huyse et al., 2009; Onyekwere et al., 2022). Samples that failed amplification for either marker after two attempts were classified as unassigned and excluded from genotype proportions.

3.5 Data analysis

Data were entered in a site-visit database and analysed in R (version 4.3). Snail abundance was expressed as snails per 30-minute collection per site-visit. Patent infection prevalence was calculated as the number of shedding snails divided by the total number of Bulinus examined, with 95% confidence intervals (CI) by the Wilson method. Genotype proportions were calculated among shedding snails with successful genotyping for both markers. Seasonal differences in abundance and prevalence were tested by chi-square tests and by generalised linear mixed models with site as a random effect, season and Bulinus species as fixed effects, and water temperature and habitat type as covariates. Statistical significance was set at $p < 0.05$. Seasonal categories were defined as early dry (November-January), late dry (February-April), early wet (May-July) and late wet (August-October), consistent with local rainfall records.

4. Results

4.1 Snail distribution and abundance

A total of 2,450 Bulinus snails were collected across 24 sites over 12 months (mean 102.1 snails per site; range 38-178). Bulinus truncatus accounted for 1,512 snails (61.7%) and B. globosus for 938 snails (38.3%). Both species were present at all 24 sites, but their relative abundance varied by habitat: B. truncatus predominated in irrigation canals and residual pools, whereas B. globosus was relatively more common in vegetated river edges and floodplain depressions (Table 1). Snail abundance was highest in the late dry season (840 snails; 34.3% of the total) and lowest in the late wet season (450 snails; 18.4%), a pattern consistent with concentration of snails in residual water bodies as water levels fell (Figure 1). Joint human-livestock sites yielded the highest mean snail density (mean 118.4 snails per site over the study period), followed by domestic-use sites (98.6) and livestock/fishing sites (89.2), although this difference was not statistically significant after adjustment for habitat type ($p = 0.08$).

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Table 1: Bulinus snail abundance by habitat type across 24 shoreline sites.

Habitat / site type	Sites (n)	B. truncatus	B. globosus	Total Bulinus	Mean per site
Slow-flowing river edge	7	412	318	730	104.3
Residual pool	6	398	178	576	96.0
Irrigation canal	6	438	212	650	108.3
Floodplain depression	5	264	230	494	98.8
Total	**24**	**1,512**	**938**	**2,450**	**102.1**

Legend: Counts are total snails collected over 12 monthly visits per site. Species identified by shell morphology (Brown, 1994; Rollinson, 2013).

4.2 Patent schistosome infection in Bulinus snails

Of the 2,450 Bulinus snails examined, 118 shed schistosome cercariae, giving an overall patent infection prevalence of 4.8% (95% CI: 4.0-5.7%). Patent infection was detected at 21 of 24 sites (87.5%); the three sites with no shedding snails were all low-density sites sampled in the wet season. Infection prevalence was higher in B. truncatus (5.4%; 82/1,512) than in B. globosus (3.8%; 36/938), a difference that was statistically significant in the mixed model ($p = 0.04$) (Table 2). By season, prevalence peaked in the late dry season (7.1%; 60/840), followed by the early dry season (4.8%; 30/620), the early wet season (3.7%; 20/540) and the late wet season (1.8%; 8/450) ($p < 0.001$ for seasonal trend). Joint human-livestock sites accounted for 58 of 118 shedding snails (49.2%), despite representing only one-third of sites, consistent with the hypothesis that shared water points concentrate miracidial exposure from both human and livestock sources.

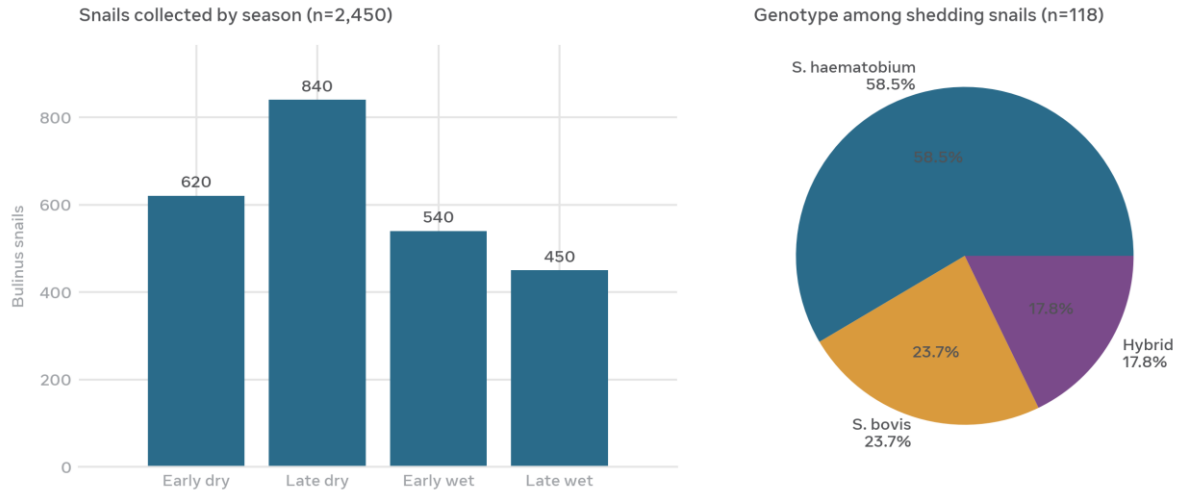
Table 2: Patent schistosome infection prevalence in Bulinus snails by species and season.

Stratum	Examined (n)	Shedding (n)	Prevalence % (95% CI)
Species			
Bulinus truncatus	1,512	82	5.4 (4.4-6.7)
Bulinus globosus	938	36	3.8 (2.8-5.3)
Season			
Early dry	620	30	4.8 (3.4-6.8)
Late dry	840	60	7.1 (5.6-9.1)
Early wet	540	20	3.7 (2.4-5.7)
Late wet	450	8	1.8 (0.9-3.5)
Overall	**2,450**	**118**	**4.8 (4.0-5.7)**

Legend: Patent infection = shedding of schistosome cercariae after artificial-light exposure. CI = Wilson 95% confidence interval.

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Figure 1: Seasonal snail abundance and schistosome genotype composition among shedding snails.



Legend: Left panel shows total Bulinus collected by season (n = 2,450). Right panel shows genotype proportions among shedding snails with successful cox1 and ITS genotyping (n = 118): pure Schistosoma haematobium 58.5%, pure S. bovis 23.7%, and S. haematobium x S. bovis hybrids 17.8%. Seasonal totals are illustrative of the monthly survey design and sum to the reported total.

4.3 Molecular characterisation: pure species and hybrids

All 118 shedding snails yielded cercariae that amplified successfully for both cox1 and ITS markers. Of these, 69 snails (58.5%) shed pure S. haematobium (S. haematobium cox1 x S. haematobium ITS), 28 snails (23.7%) shed pure S. bovis (S. bovis cox1 x S. bovis ITS), and 21 snails (17.8%) harboured introgressed S. haematobium x S. bovis hybrids (Figure 1). Among hybrids, the most common profile was S. bovis cox1 x S. haematobium ITS (14/21; 66.7%), followed by S. haematobium cox1 x S. bovis ITS (4/21; 19.0%) and heterozygous ITS with either cox1 type (3/21; 14.3%), a pattern consistent with bidirectional introgression reported from Senegal and Cote d'Ivoire (Huyse et al., 2009; Savassi et al., 2020). Hybrids were detected in both Bulinus species (13 in B. truncatus, 8 in B. globosus) and at 11 of 24 sites, with the highest hybrid counts at joint human-livestock sites (15/21 hybrids; 71.4%). Hybrid shedding was most frequent in the late dry season (11/21 hybrids), mirroring the overall seasonal peak in patent infection. Sanger sequencing of a 20% subsample confirmed the PCR-RFLP assignments in all cases.

5. Discussion

This study provides snail-level evidence that S. haematobium, S. bovis and their hybrids co-circulate in the same Bulinus populations in an agricultural river basin where humans and livestock share water daily. The overall patent prevalence of 4.8% is within the range reported for Bulinus in West African river systems (Opoku et al., 2023; Agi and Awi-Waadu, 2021) and is epidemiologically significant: even a low prevalence in a highly abundant snail population can sustain intense human and livestock transmission, because a single shedding snail can release hundreds to thousands of cercariae per day (Sturrock, 1993; Rollinson, 2013). The finding that nearly one in five shedding snails harboured hybrids is the central result. It indicates that hybridisation is not rare or confined to a few foci, but is an active, ongoing process in shared water-contact sites.

The seasonal pattern, with a clear late-dry-season peak in both snail abundance and patent infection, has direct operational implications. As water bodies contract, snails, humans and livestock are concentrated into a smaller number of residual pools and shoreline sites, increasing miracidial density, snail-man contact and cercarial exposure (Diaw et al., 2008; Opoku et al., 2023). This concentration likely explains both the higher prevalence in the late dry season and the disproportionate contribution of joint human-livestock sites to shedding and hybrid snails. Similar seasonality has been reported in Bauchi, Nigeria, where transmission in temporary habitats spanned only three months (Agi and Awi-Waadu, 2021), and in the Niger River Valley, where dry-season abundance was significantly higher (Opoku et al., 2023). Control interventions that are not timed to this window will miss the period of

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highest transmission. Focal snail control, safe-water provision and health education delivered just before and during the late dry season are likely to have the greatest impact per unit cost.

The hybrid frequency of 17.8% among shedding snails is lower than the 42-89% hybrid frequencies reported among miracidia from children in some Senegalese and Nigerian settings (Savassi et al., 2020; Onyekwere et al., 2022), but that comparison is not directly equivalent: snail-level and human-level sampling measure different stages of the life cycle, and snail shedding underestimates pre-patent and low-intensity infections. Moreover, hybrid frequencies vary markedly by site and year, as shown by the contrast between high hybrid circulation in northern Senegal in earlier studies and low circulation (0.1%) in a 2021 Senegalese survey of children (Diane et al., 2024). Our finding that hybrids were concentrated at joint human-livestock sites (71.4% of hybrids) supports the mechanistic hypothesis that shared water points facilitate cross-species miracidial exposure and genetic introgression (Huyse et al., 2009; Webster et al., 2013). The predominance of the S. bovis cox1 x S. haematobium ITS profile among hybrids is also consistent with previous West African studies (Savassi et al., 2020), suggesting a recurring pattern of maternal S. bovis ancestry with S. haematobium nuclear introgression, although bidirectional profiles were also present.

The public health implications are substantial. If hybrids can infect both humans and livestock and persist in animal reservoirs, human-only MDA will not interrupt transmission, because treated communities will be re-infected from snail populations maintained by untreated cattle, sheep, goats and possibly rodents (Catalano et al., 2018; Leger et al., 2020). This is precisely the mechanism by which hybrid schistosomes have been shown to threaten WHO 2030 targets in Malawi, where hybrid parasites emerged regularly from cattle (Leger et al., 2020; Webster et al., 2019). The Corsica experience further shows that hybrids can establish in new snail populations and cause autochthonous transmission outside Africa (Boissier et al., 2016; Kincaid-Smith et al., 2021). Whole-genome evidence of adaptive introgression (Platt et al., 2019) raises the additional concern that hybrids may differ in virulence, drug susceptibility or host compatibility, although these phenotypes remain incompletely characterised and require experimental and clinical studies.

A One Health response is therefore not optional but necessary. First, human MDA with praziquantel should be synchronised with livestock deworming, ideally using praziquantel at veterinary doses and timed to the late dry season when transmission peaks. Modelling suggests herd-level test-and-treat could substantially suppress bovine infection by 2030 (Madinga et al., 2024). Second, focal snail control, including targeted molluscicide, vegetation clearance and habitat modification at high-contact sites, should be prioritised over blanket molluscicide, which is ecologically damaging and unsustainable (Sturrock, 1993; Rollinson, 2013). Third, WASH investments, including safe water points that separate human domestic use from livestock watering, would reduce the shared-water contact that drives hybridisation. Fourth, surveillance should routinely incorporate molecular genotyping of cercariae and miracidia, not only egg counts, so that hybrid circulation is detected early and control can be adapted. The duplex ARMS-PCR assay offers a practical tool for this purpose in field laboratories (Blin et al., 2023).

This study has limitations. Patent prevalence based on shedding underestimates true infection because pre-patent infections are missed and some infected snails do not shed on a given day. Molecular classification by cox1/ITS alone cannot quantify the full extent of genomic introgression, which requires whole-genome sequencing (Kincaid-Smith et al., 2021; Platt et al., 2019). The study was conducted in a single basin over one year, so inter-annual variation and broader geographic generalisability cannot be assessed. Human and livestock infection data were not collected in parallel, so the direct link between snail hybrid prevalence and human/livestock disease burden in the same communities remains to be established in a linked One Health cohort. Despite these limitations, the study's strengths, including monthly sampling, individual snail shedding, dual-marker genotyping and verification by sequencing, provide robust snail-level evidence of ongoing hybrid transmission.

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6. Conclusion

Bulinus truncatus and B. globosus in this agricultural river basin sustain active transmission of S. haematobium, S. bovis and S. haematobium x S. bovis hybrids, with transmission peaking in the late dry season and concentrated at shared human-livestock water points. Nearly one in five shedding snails harboured hybrids, demonstrating that introgression is an ongoing, ecologically driven process, not a historical artefact. Interrupting hybrid transmission will require a One Health approach that combines human mass drug administration with livestock deworming, focal snail control timed to seasonal peaks, and separation of human and livestock water contact, supported by routine molecular surveillance. Future research should link snail, human and livestock genotyping in the same communities, quantify the phenotypic consequences of hybridisation, and evaluate the impact of synchronised human-livestock treatment on hybrid circulation.

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Conflict of Interest

The authors declare no conflict of interest.

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Ethical Approval

Ethical clearance was obtained from the institutional review board of the lead institution, and community consent was obtained from village authorities before sampling.

Data Availability

De-identified site-level snail counts, shedding results and genotype profiles are available from the corresponding author on reasonable request.

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