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Bat species diversity at Rugezi Marsh, northern Rwanda, as a basis for wetland conservation

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Abstract. East African marshlands are critical natural resources, but information on wildlife species richness and abundance is lacking. Rwanda is characterised by its hilly terrain, with marshes and other wetlands accounting for approximately 8% of the nation's area. Marshlands, which serve as roosting and foraging sites, are expected to harbour a greater diversity of bat species than adjacent open farms and eucalypt-dominated hills. A survey of bats was conducted at Rugezi Marsh, northern Rwanda, in 2023, across two distinct seasons, June to July and November to December. Roost searches, traditional capture methods, acoustic monitoring, and DNA barcoding were used to gather data. Twenty-two bat species across six families were recorded, including an undetermined *Pipistrellus* that may represent a new species based on molecular data and therefore warrants further examination. Remarkably, more than forty per cent of Rwanda's bat biodiversity is found here; nonetheless, many species appear to be rare, such as the threatened Harrison's giant mastiff bat (*Otomops harrisoni*), which is designated as Vulnerable on the IUCN Red List. Strong grounds exist for the protection of this wetland because of the exceptionally high bat species richness, including one threatened species. The baseline data on bat biodiversity offer a unique opportunity for tracking changes with the potential restoration of this special wetland.

Keywords: wetland, conservation, bat species richness, northern Rwanda, Rugezi marsh.

Resumen. Los humedales de África Oriental constituyen recursos naturales fundamentales, pero se carece de información sobre la riqueza y abundancia de especies de fauna silvestre. Ruanda se caracteriza por su relieve accidentado, donde los pantanos y otros humedales representan aproximadamente el 8% de la superficie del país. Se prevé que estos humedales, que sirven como zonas de refugio y alimentación, alberguen una mayor diversidad de especies de murciélagos que las tierras agrícolas abiertas y las colinas dominadas por eucaliptos adyacentes. En 2023 se llevó a cabo un estudio sobre murciélagos en el humedal de Rugezi, en el norte de Ruanda, abarcando dos temporadas distintas: de junio a julio y de noviembre a diciembre. Para la recopilación de datos se emplearon técnicas de búsqueda de refugios, métodos tradicionales de captura, monitoreo acústico y códigos de barras de ADN. Se registraron veintidós especies de murciélagos pertenecientes a seis familias, incluida una especie indeterminada del género *Pipistrellus* que, según datos moleculares, podría constituir una nueva especie y, por tanto, requiere un análisis más exhaustivo. Cabe destacar que aquí se encuentra más del cuarenta por ciento de la biodiversidad de murciélagos de Ruanda; no obstante, muchas especies parecen ser escasas, como el amenazado murciélago gigante de Harrison (*Otomops harrisoni*), clasificado como Vulnerable en la Lista Roja de la UICN. Existen razones de peso para proteger este humedal dada su excepcional riqueza de especies de murciélagos, que incluye una especie amenazada. Los datos de referencia sobre la biodiversidad de murciélagos ofrecen una oportunidad única para monitorear los cambios que podrían derivarse de una eventual restauración de este singular humedal.

Palabras clave: conservación, riqueza de especies de murciélagos, norte de Ruanda, pantano de Rugezi, humedal.

INTRODUCTION

Africa exhibits significant ecological diversity, hosting over 325 recognised bat species (Mammalia: Chiroptera) across the Afrotropical (sub-Saharan Africa) and Malagasy regions (Madagascar and adjacent islands) (Monadjem *et al.* 2024a; Mammal Diversity Database 2026), representing approximately 22% of global bat diversity (Burgin *et al.* 2018; Simmons and Cirranello 2026). However, researchers greatly underestimate the diversity of African bat species because large areas of sub-Saharan Africa are either un-surveyed or inadequately sampled (Herkt *et al.* 2016; Montauban *et al.* 2026). Bats are often the most diverse group of mammals in Africa at a local scale, particularly in savanna and woodland ecosystems at altitudes below 1500 m above sea level (Monadjem *et al.* 2024b).

Bats serve as a valuable indicator group for research on the effects of habitat disruption due to their remarkable versatility, sensitivity to alterations in habitat quality, and vital roles in plant pollination, seed dispersal, and insect pest control (Kunz *et al.* 2011; Aziz *et al.* 2021; Tuneu-Corral *et al.* 2023). However, despite their ecological and economic significance, bats are largely understudied and often persecuted (Frick *et al.* 2020; Rocha *et al.* 2021). A significant disparity exists in bat surveys across Africa (Montauban *et al.* 2026), with southern Africa being comprehensively sampled (Monadjem *et al.* 2020), but numerous regions in tropical Africa remain substantially under-represented (Monadjem *et al.* 2024a). For instance, the Albertine Rift, which is recognised as one of Africa's biodiversity hotspots (Plumptre *et al.* 2007), has yet to be systematically surveyed (Montauban *et al.* 2026). The region features an exceptionally high concentration of bat species diversity and localised endemism, attributable to its intricate topography, steep elevational gradients, and varied habitats ranging from dense montane forests to savannahs. Targeted surveys in underexplored regions of the Albertine Rift, including the Misotschi-Kabogo highlands and Kahuzi-Biega National Park in the Democratic Republic of Congo (DRC), consistently uncover previously undescribed small mammal species (e.g., Kerbis Peterhans *et al.* 2013a, 2013b) and underscore the urgency for conservation planning. The region is a significant hub of endemism, exhibiting remarkable ecological and geological diversity, with deep freshwater lakes, active volcanoes, and some of Africa's highest mountain ranges. Specialised species, notably the horseshoe bats (family Rhinolophidae), comprise several endemic and highly restricted species (e.g., *Rhinolophus hilli*, *R. ruwenzorii*, and *R. willardi*), particularly within the isolated Afromontane and Afroalpine forests of the rift, which straddle the borders of five central and eastern African countries: Burundi, the DRC, Rwanda, Tanzania, and Uganda.

Given that the most recent synopsis is 42 years old (Baeten *et al.* 1984), our understanding of the bat fauna

of Rwanda is particularly inadequate. However, Van Cakenberghe and colleagues published a monograph on the bats of the DRC, Rwanda, and Burundi (Van Cakenberghe *et al.* 2017). Zarek S. Cockar published a compendium of Rwandan mammals, which included bats (Cockar 2022). Rwanda is home to 51 documented bat species (Patterson and Webala 2012; Cockar 2022), which is notably high for its small area of 26,338 km² (<https://www.gov.rw/about>); however, a systematic survey has yet to be conducted across the country.

Recent bat surveys in Rwanda, namely in Nyungwe National Park, have concentrated on identifying rare species, notably the critically endangered Hill's horseshoe bat (*Rhinolophus hilli*), which was successfully rediscovered in 2019 after being presumed extinct for 40 years (Flanders *et al.* 2022). These surveys documented over 10 species, including the inaugural sightings of the Damara woolly bat (*Kerivoula argentata*) in Rwanda and Lander's horseshoe bat (*Rhinolophus landeri*) at Nyungwe National Park. Nevertheless, aside from a limited number of expedited surveys (e.g., Nziza *et al.* 2019) and a catalogue of Rwandan bats (Cockar 2022), bat communities remain unexamined in a systematic and thorough manner within other notable protected areas — such as Volcanoes National Park, Akagera National Park, and Gishwati-Mukura National Park — and, crucially, in wetland ecosystems that serve as vital natural resources for both humans and wildlife.

Freshwater marshes, especially the large peatlands of Rwanda, such as the Rugezi Marsh, are among the most productive ecosystems globally, frequently demonstrating high net primary production rates (Cherry 2011; Rodal *et al.* 2025). Consequently, they support a high species richness of various organisms, including aquatic plants, fish, migratory birds, amphibians, and microorganisms (Prasad and Sharma 2025). Rwanda's wetlands sustain ecosystems by operating as natural sponges that manage flooding, filter contaminants, and guarantee a consistent water supply (Björkqvist and Kennell 2025; Ma *et al.* 2023). They constitute carbon sinks that moderate climate change (Balwan and Kour 2021), and ensure economic stability associated with fishing, papyrus harvesting, agriculture, and other human economies (Dawson and Martin 2015; Damm 2022). Unsurprisingly, despite their immense importance, human activities place enormous pressure on wetlands on a global scale (Shine and De Klemm 1999; O'Connell 2003), leading to habitat degradation and loss (Bjerstedt 2011).

The drainage and conversion of wetland habitats significantly affect biodiversity in a disproportionate manner. Wetlands in Rwanda comprise roughly 8% of the country's surface area (GBIF 2019; CBD 2020) and serve as significant biodiversity hotspots (ARCOS Biodiversity Information System: <http://arbims.arcosnetwork.org/out.biodiversitydata.php>). Notable examples comprise the Akanyaru, Nyabarongo, and Rugezi complex, acknowledged for their diverse avian species, akin to those present

at Akagera National Park (GBIF 2019; CBD 2020). These wetlands and others in Rwanda provide essential habitats for diverse plant and animal species. However, the wetlands face threats, including illegal agriculture and deforestation. They are under considerable pressure from the rapidly growing human population, leading to unsustainable practices such as illegal farming and deforestation (Butler 2004).

Our study sought to generate baseline data on bats in the vicinity of Rugezi Marsh. The Marsh is a significant wetland in northern Rwanda, serving as a natural watershed for the Twin Lakes, Burera and Ruhondo. It serves as a principal water source for hydroelectric plants in the area. The marsh controls, holds, and filters the water that flows into these lakes, making sure that communities have a steady supply of water and that hydroelectric power can be generated. The marsh serves significant ecological, hydrological, socioeconomic, historical, and recreational functions for a significant human population and diverse, mainly undocumented species (Gashakamba 2026). The marsh serves as an important bird area (IBA), recognized as a sanctuary for various rare and threatened bird species, notably the iconic grey crowned crane (*Balearica regulorum*), which breeds in this area. It is also a breeding ground for other rare species, such as the Grauer's swamp warbler (*Bradypterus graueri*) and sitatunga (*Tragelaphus spekii*), the latter of which is thought to be locally extinct (Fishpool and Evans 2001). Although there is a substantial dearth of information regarding bat communities at Rugezi Marsh, previous surveys conducted at the Musanze Caves and Volcanoes National Park, both of which are located in northern Rwanda, have identified a range of species, such as *Epomophorus labiatus*, *Rousettus aegyptiacus*, *Stenonycteris lanosa*, *Rhinolophus acrotis*, *R. eloquens*, *Mops condylurus*, *M. pumilus*, *Otomops harrisoni*, *Nyctinomus aegyptiacus*, and *Miniopterus* spp., among others (Nziza *et al.* 2019; P. W. Webala, unpublished data).

The study examined bat activity and species richness within a broader initiative led by the Rwanda Wildlife Conservation Association (RWCA) aimed at gathering comprehensive data on biodiversity at Rugezi Marsh. We focused on characterizing bat species richness, distribution status, and relative abundance. Specifically, surveys were carried out during the dry season (June–July) and the wet season (November–December) of 2023. We hypothesised that 1) the combined use of acoustic monitoring, roost searches, and standard capture methods yields a significantly higher total species count than relying on any single method; 2) mean nightly bat activity (quantified by the number of acoustic bat passes per night) is significantly greater in the wet season compared to the dry season due to a corresponding increase in insect abundance and foraging opportunities; and 3) species richness and overall activity levels increase significantly during the wet season compared to the dry season, likely driven by climatic variables and resource availability.

MATERIAL AND METHODS

Study area

Bat surveys were conducted at Rugezi Marsh, which is located in the Northern Province of Rwanda, spanning Gicumbi and Burera Districts (Fig. 1). The marsh lies between 1°21'30" and 1°36'11"S and 29°49'59" and 29°59'50"E. Perched at an elevation of 2050 m a.s.l., this highland peat bog's spatial configuration resembles a homogeneous unity of marshes and peat bogs (Hategekimana 2005).

The Rugezi Marsh extends over a surface of 67.35 km² and its catchment reaches approximately 190.70 km² (de Dieu Nizeyimbabazi and Maniragaba 2023). The annual mean rainfall on the hillsides is 1200 mm/year at 'Rwerere-Colline' site whereas at the marsh surface it is 1050 mm/year at Rwerere-Maraïs site. The hillsides are very steep and many of them have a slope greater than 35%. Formerly, this swamp originated from the trapping of runoff in a synclinal depression behind a quartzitic ridge that led to the formation of a vast waterlogged valley (Hategekimana 2005). Peat formation would have resulted from the build-up of water and alluvia, as well as the sphagnum vegetation's colonization of the valley. From a hydrological perspective, precipitation and small streams in the catchment contribute to the marsh's inflow. Nonetheless, the outflow includes runoff from the Rusumo stream.

Field methods

Two phases of the bat survey were carried out at Rugezi Marsh in 2023: the first phase took place in June and July, during the dry season, and the second phase took place in November and December, during the wet season. Following best practices (Kunz and Parsons 2009; Collins 2023), we applied three sets of complementary techniques to survey for bats: 1) inquiring about the presence of bats and searching for roosts; 2) capturing bats using hand nets at roosts, mist nets, and a single harp trap; and 3) conducting static acoustic surveys. Mist nets are useful for catching frugivorous and insectivorous species that have less agile flight and produce lower-frequency calls (e.g., Flaquer *et al.* 2007; Pech-Canche *et al.* 2011). Harp traps can be used in more restricted settings, like dense vegetation, and counteract mist net biases by capturing the more sophisticated, slower-flying, and highly manoeuvrable echolocating bats that regularly detect and elude nets (Kingston 2013; Tanshi *et al.* 2021). To sample hard-to-capture species (O'Farrell and Gannon 1999), we employed ultrasonic detectors. We selected 14 sites for bat sampling to span the breadth and diversity of Rugezi Marsh and to target the most important habitats, but five roost sites were identified and also sampled (Fig. 1, Table 1, and Supplementary Fig. S1).

Roost surveys

In order to locate known roosts or fruit-bat colonies within the study area, we queried local communities about the presence of bats or bat roosts. Once located, we captured a few from accessible sites (e.g., caves) using hand nets for identification and recorded reference echolocation calls from hand-released insectivorous bat species.

Bat captures

We selected sites for bat captures (harp trap, mist nets) with the aim of covering the project area as much as possible within patches of native woodlands or forests, forest trails, or water points or trails, as they maximize bat captures (Kunz *et al.* 2009). At each sampling site, we deployed four mist nets (6×2.5 m or 9×2.5 m, denier 75/2, mesh 16×16 mm, five shelves — Ecotone, Inc., Poland) and a single harp trap (two-bank 4.2 m² — Austbat Research Equipment, Victoria, Australia), spaced ~ 50 m apart at ground level along trails, around trees or shrubs, along edges, and other potential flyways. Nets were left open for approximately 3.5 h, from 18:30 h (± 30 min) until 22:00 h, and were checked regularly.

Each site was sampled for a single night before moving the traps to the next site. The harp trap was operational between 18:30 h and 06:00 h at each site and was checked at 30-minute intervals after dark until 22:00 h and again at 06:00 h the next day. Nights with rain and immediately before, during, and after the full moon were not sampled to minimise potential bias (Saldaña-Vázquez and Munguía-Rosas 2013). All captured bats were measured, photographed, and released at the point of capture. Recorded data for each captured bat included the species, sex, reproductive status, age, forearm length, and body mass (Supplementary Table S1). We measured the forearm length of each captured bat with a digital calliper to the nearest 0.1 mm and body mass with a Pesola scale to the nearest 0.1 g. Bat identifications and nomenclature followed several recent works (e.g., Patterson and Webala 2012; Monadjem *et al.* 2020, 2021b; Mammal Diversity Database 2026). No voucher specimens were collected during this survey because the study prioritised non-lethal sampling; however, tissue samples (wing biopsies) and photographic records were retained to support species identification. We acknowledge the importance of voucher collections for resolving African bat taxonomy and will consider limited voucher collection in future surveys where appropriate permits

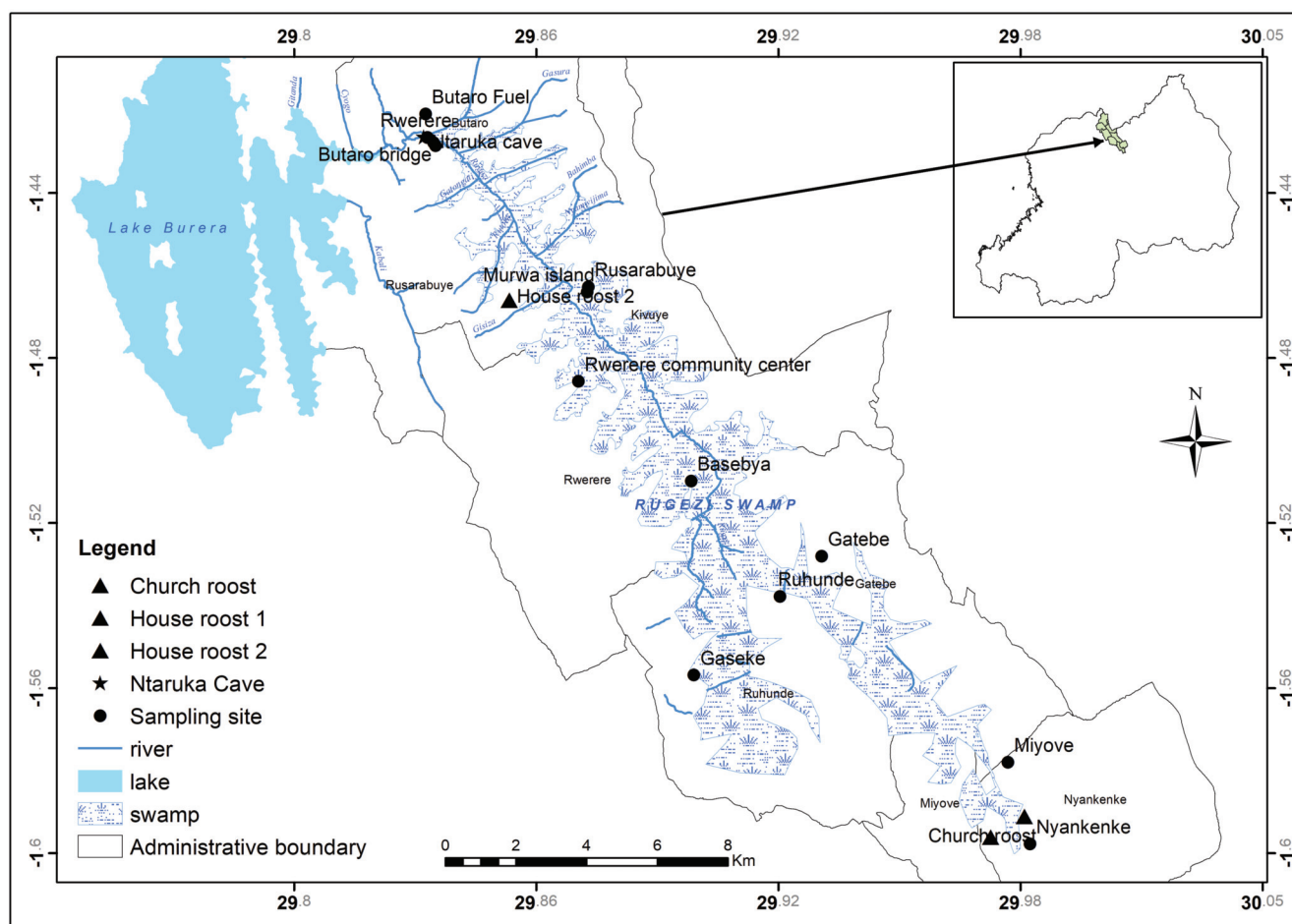


Figure 1. Map showing the spatial arrangement of 14 sampled sites and five bat-roosting sites in Rugezi Marsh during the dry (June–July) and wet (November–December) seasons of 2023. Inset shows the study area location in Rwanda.

Table 1. Summary description of bat sampling locations at Rugezi Marsh, June–December 2023

Site	Latitude	Longitude	Habitat	Type of survey
1. Basebya	-1.50910	29.90039	Island under restoration with indigenous tree species (e.g., <i>Croton</i> , <i>Prunus</i> , <i>Olea</i> , <i>Vachellia</i>)	Netting, Acoustic, Roost searches
2. Butaro Bridge	-1.42162	29.83333	Incomplete bridge with a water reservoir nearby for Burera Hydropower Project	Netting, Acoustic, Roost searches
3. Butaro Fuel Station	-1.41700	29.84167	A small city's suburbs with a shallow river and elevated human activity of locals harvesting grass	Netting, Acoustic
4. Gaseke	-1.55851	29.90112	A well-vegetated buffer section of the wetland with big <i>Alnus acuminata</i> trees and tall reeds	Netting, Acoustic
5. Gatebe	-1.53339	29.94968	A hanging rocky cliff covered with vegetation attached to the roots of a <i>Ficus climber</i>	Netting, Acoustic, Roost searches
6. Miyove	-1.58070	29.98107	A narrow belt of <i>Alnus acuminata</i> woodland	Netting, Acoustic
7. Miyove Ranger's Post	-1.42162	29.83333	A narrow belt of <i>A. acuminata</i> plantation	Netting, Acoustic
8. Murwa Island	-1.46095	29.87392	The island is undergoing restoration and features a mix of indigenous trees along with fruit trees, including avocado (<i>Persea americana</i>) and guava (<i>Psidium guajava</i>)	Netting, Acoustic, Roost searches
9. Nyankenke	-1.585179	29.9780	<i>Alnus acuminata</i> and <i>Eucalyptus</i> woodland with scattered <i>P. guajava</i>	Netting, Acoustic
10. Nyankenke Miyove	-1.42291	29.83481	A narrow belt of <i>A. acuminata</i> plantation	Netting, Acoustic
11. Ruhunde	-1.53849	29.92302	A degraded buffer zone with many cut stumps of <i>Alnus acuminata</i>	Netting, Acoustic
12. Rusarabuye Ranger's Post	-1.45966	29.87424	A narrow belt of <i>A. acuminata</i> plantation	Acoustic, Roost searches
13. Rwerere	-1.294568	29.525738	A buffer of <i>A. acuminata</i> trees with patches of <i>Eucalyptus</i> plantation	Acoustic, Roost searches
14. Rwerere Community Centre	-1.350336	29.58435	A community education centre with patches of <i>Alnus acuminata</i> , banana farms and some avocado (<i>P. americana</i>)	Netting, Acoustic, Roost searches

and ethical approvals allow. To identify captured individuals in subsequent sample sessions, adult bats were fitted with coloured and numbered plastic forearm bands, following the ageing criteria established by Anthony (1988) and the marking methods described by Handley *et al.* (1991). Reference calls from hand-released insectivorous bats were recorded to create a local reference call library to help with acoustic identification.

Acoustic surveys

We sampled insectivorous bat assemblages in the project area using acoustic monitoring to assess bat habitat use and derive measures of relative abundance and species richness. Acoustic monitoring serves to detect the insectivorous bat community and provides an index of bat activity (number of bat passes) for each site. A bat pass is defined as “a sequence of greater than two echo-location calls made as a single bat fly past the microphone” (Fenton 1970). For analysis, two or more bat calls in a continuous sequence were considered, up to five seconds in duration. Sound files longer than five seconds were split using Kaleidoscope software (<https://www.wildlifeacoustics.com/products/kaleidoscope-pro>). For every detector position at every point, we added up the activity for every species as well as the total activity for all species combined. While these data do not provide exact species abundance estimates, they do allow relative abundance to be determined by comparing data across habitats and seasons.

At each of the 14 sampling sites, two bat acoustic monitoring passive recorders (Song Meter SM4BAT FS and ZC Bat Detectors: Wildlife Acoustics, Inc., Massachusetts, USA) were deployed, totalling 56 independent static bat detector stations across the dry and wet sampling seasons. Detectors were deployed along potential bat flyways (e.g., woodland trails, along edges, or at water points). The detectors were programmed to begin recording 30 minutes before dusk and to stop recording 30 minutes after sunrise using an automated trigger.

To identify bat calls, we need to establish a reference library of bat calls for Rugezi and Rwanda as a whole. Therefore, from our capture effort, we recorded the calls of all insectivorous bats at the time of release to create a preliminary reference library for acoustic monitoring. From the vocalizations of the few released bats, whose identities are known, we were able to identify the calls of free-flying bats through manual comparisons in the Kaleidoscope software. Additionally, bats were identified by comparing recorded calls to those of known species from a library of bat vocalizations developed by the PI for most bat species in Kenya and Rwanda, and a few from other countries in the region (Ethiopia, the DRC, and Djibouti). A caveat here is that it is often only possible to identify the genus from which bat calls are recorded because certain species, like those in the genera *Myotis* and *Nycteris* (e.g., Taylor-Boyd *et al.* 2025), may not be reliably identified acoustically.

Genetic identification of bat species

DNA extraction was performed from tissue samples (wing biopsies) preserved in Zymo 1× or 1 ml of 100% ethanol. For digestion and DNA purification, the Quick-DNA/RNA™ Viral MagBead kit (Zymo Research) was used according to manufacturer guidelines. For digestion, 200 µl of Zymo 1× plus the tissue sample were transferred into a 1.5 ml tube and 15 µl of Proteinase K were added and incubated at 55°C overnight or until the tissue was completely digested (samples were vortexed slowly periodically to enhance tissue disruption). Samples that were stored in 95% ethanol were treated the same way after discarding the ethanol.

Where possible, two genes were amplified using previously published primer sequences for common mitochondrial markers cytochrome oxidase I (*COI*) and cytochrome *b* (*Cyt b*). All custom DNA oligo primers were ordered from Integrated DNA Technologies (IDT) with universal overhangs added to the 5' ends, which are useful for downstream sequence analysis (Supplementary Table S2 — Watsa *et al.* 2024). For *COI*, we used a mammal-specific primer cocktail (C_VFILFt1 and C_VRLRt1, 10 µM each) following the protocol described by Kress and Erickson (2012). The PCR protocol included Promega GoTaq® Green Master Mix (1×) with 0.725 µM of each *COI* primer cocktail, 2 µL of template DNA, and nuclease-free water to a final volume of 15 µL – the thermal cycling profile consisted of initial denaturation at 94°C for 2 minutes, followed by 5 cycles of denaturation at 94°C for 30 seconds, annealing at 50°C for 40 seconds, and extension at 72°C for 1 minute; then 35 additional cycles of denaturation at 94°C for 30 seconds, annealing at 50°C for 40 seconds, and extension at 72°C for 1 minute; and a final extension at 72°C for 10 minutes. For *Cyt b*, we used mammal-specific primers MVZ05 and MVZ16 following the protocol described by Smith and Patton (1993). The PCR mix was the same as previously stated, and the thermal cycling profile was as follows: an initial denaturation at 94.5°C for 3 minutes, followed by 36 cycles of denaturation at 94°C for 45 seconds, annealing at 45°C for 45 seconds, and extension at 72°C for 1 minute, and a final extension at 72°C for 10 minutes. Amplifications were checked on 1.2% Agarose gel and products were stored at -20°C for downstream processes.

For sequencing library preparation on the Oxford Nanopore platform, amplicons were diluted in water 1:20 and indexed by PCR with custom oligo barcodes ordered from IDT. Indexing PCR products (corresponding to the custom barcodes) were pooled together according to gel electrophoresis band intensity, cleaned with 1× SPRI beads, and then prepped for sequencing using Nanopore's Native Barcoding Kit (NBD-SQK114.24). Multiplex sample sequencing was performed on an Mk1b device with R10 Minion and Flongle flow cells. The full sample indexing strategy is available on protocols.io (Watsa *et al.* 2024).

Sequence data analysis consisted of high-accuracy base calling using Dorado (v1.0.0), sample demultiplexing with Guppy (v6.3.5), consensus sequence generation and polishing with NGSpeciesID, and comparison with GenBank records using the NCBI-blast toolkit — full details are available on protocols.io (Erkenswick *et al.* 2024). All software, except for Dorado, were accessed through publicly available docker images (insitublab/jungleogenomics and genomicpariscentre/guppy). *COI* sequences were also compared with the BOLD System. If a sequence was more than 95% similar to a reference sequence, it was identified as the species represented by that reference. If it was less than 95%, the genetic identification was retained, but the sample was considered either a potential new species or the first recorded sequence for that species. These results were compared with the morphological identifications made in the field. When the genetic and morphological IDs did not match, we evaluated whether this was due to the absence of an available reference sequence or a potential field misidentification.

For genetic identification, *COI* and *Cyt b* sequences were evaluated using percent identity $\geq 95\%$ together with phylogenetic placement relative to reference sequences. For some taxa, including *Nycteris* and *Epomophorus*, maximum-likelihood phylogenetic trees were constructed. Reference sequences and outgroups were selected from BOLD and GenBank following systematic studies for each focal family: Pteropodidae (Almeida *et al.* 2011; Hassanin 2014; Hassanin *et al.* 2020), Nycteridae (Demos *et al.* 2019), Molossidae (Goodman *et al.* 2010; Lamb *et al.* 2011; Gregorin and Cirranello 2016; Naidoo *et al.* 2016; Torrent *et al.* 2025), and Vespertilionidae (Monadjem *et al.* 2021a). For each dataset, sequences were aligned in MAFFT (<https://mafft.cbrc.jp/alignment/server/index.html>; Katoh *et al.* 2019) with default parameters; the alignments were inspected in Geneious ver. 7.1.3 to verify the reading frame and avoid potential artificial stop codons. Maximum-likelihood trees were inferred using the IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at/>; Trifinopoulos *et al.* 2016) with 1,000 ultrafast bootstrap replicates (UFBoot) (Minh *et al.* 2013). Trees were visualized in FigTree ver. 1.4.4, and final figures were edited in Inkscape.

Data analyses

A smoothed species accumulation curve (using the ‘Mao Tau’ function) was generated for bats recorded at Rugezi in the program EstimateS, ver. 7.5 (Colwell 2005). This accumulation curve allows one to observe the rate at which additional species were added (accumulated) during the study, and hence one can determine how completely a particular fauna was surveyed. Ideally, the accumulation curve will reach an asymptote — i.e., it will stop climbing vertically and flatten out horizontally, indicating that most of the species inhabiting a particular location have been recorded.

The open wetland area and the narrow buffer zone belt precluded any statistical analysis of the habitat types. A generalised linear model (GLM) with a negative binomial error distribution and a log link function examined seasonal bat activity, measured as bat passes. The explanatory variable was dry and wet seasons. A generalised linear mixed model (GLMM) with sampling site as a random effect was initially assessed, but the estimated random-effect variance was negligible. The simpler GLM, with a lower AIC and comparable fit, was therefore selected for further inference.

To compare species between seasons, species diversity for all the sites sampled was computed using the modified inverse of Simpson-Yule diversity of concentration, C , for equally abundant species (Dunstan and Fox 1996):

$$D = 1/(\sum p_i^2)$$

where p_i is the proportional abundance of the i^{th} species, given by $p_i = n_i/N$, $i = 1, 2, 3, S \dots$. S = species richness, which equals the total number of species in a community. As an index, S is easily conceptualised and compared across habitats or seasons. N is the total number of individuals. The Simpson’s index was preferred in this study because it is weighted more towards the abundance of the common species (emphasises evenness) than providing a measure of species richness. Evenness values were derived from the Shannon-Wiener (H') index of diversity. Evenness values were derived from the expression $E_1 = H'/\ln S$, where $\ln S$ is the natural logarithm of the number of species. Evenness values indicate how the species are distributed in a community. When the evenness is high, the mammal fauna is diverse and the species are equally abundant (Magurran 2013).

RESULTS

A cumulative effort of 392 mist-net hours, 336 harp-trap hours, and 672 detector recording hours resulted in the identification of 22 bat species from six families during the surveys conducted at Rugezi Marsh, northern Rwanda, in 2023, across two distinct seasons: June to July and November to December. The documented species belonged to the families Pteropodidae, Rhinolophidae, Nycteridae, Molossidae, Miniopteridae, and Vespertilionidae (Table 2; Supplementary Material S1). The highest number of species was recorded through acoustic surveys ($n = 18$), followed by captures ($n = 7$) and roost searches ($n = 3$ — Tables 2 and 3).

Species detection: morphological and genetic data

A total of 49 bats were captured, comprising 26 individuals from mist nets, 16 from hand nets at roosts, and seven from the harp trap. In this study, in addition

Table 2. Bat species recorded in the Rugezi Marsh project area using roost searches, capture surveys, and passive acoustic monitoring. Check marks indicate the survey methods by which each species was detected. Molecular identifications are provided where genetic material was available; ambiguous or incomplete identifications are reported at the genus level or as the closest matching species. IUCN Red List categories are abbreviated as LC, Least Concern, and VU, Vulnerable.

Species	Genetic identification	IUCN status	Sampling method		
			Roost search	Captures	Passive acoustic sampling
Little epauletted fruit bat <i>Epomophorus labiatus</i>	<i>Epomophorus labiatus</i>	LC		✓	
Egyptian rousette <i>Rousettus aegyptiacus</i>	<i>Rousettus aegyptiacus</i>	LC	✓	✓	
Long-haired rousette <i>Stenonycteris lanosa</i>	<i>Stenonycteris lanosa</i>	LC		✓	
Heuglin's horseshoe bat <i>Rhinolophus acrotis</i>		LC			✓
Eloquent horseshoe bat <i>Rhinolophus eloquens</i>		LC			✓
Horseshoe bat <i>Rhinolophus</i> spp.					✓
Mauritian tomb bat <i>Taphozous mauritanus</i>					✓
Slit-faced bat <i>Nycteris</i> spp. 1	<i>Nycteris aurita/hispida</i>	LC	✓	✓	✓
Slit-faced bat <i>Nycteris</i> spp. 2	<i>Nycteris macrotis</i>	LC		✓	
Angolan free-tailed bat <i>Mops condylurus</i>		LC			✓
Little free-tailed bat <i>Mops pumilus</i>	<i>Mops pumilus</i>	LC	✓		✓
Harrison's giant mastiff bat <i>Otomops harrisoni</i>		VU			✓
Egyptian free-tailed bat <i>Nyctinomus aegyptiacus</i>		LC			✓
Free-tailed bat <i>Tadarida</i> spp.					✓
Greater long-fingered bat <i>Miniopterus</i> spp.					✓
Banana serotine <i>Afronycteris nanus</i>	<i>Afronycteris nanus</i>	LC		✓	✓
Pipistrelle bat <i>Pipistrellus</i> spp.	<i>Pipistrellus</i> sp. indet. 'Rwanda'	LC	✓	✓	✓
Myotis <i>Myotis</i> spp.					✓
Somali pipistrelle <i>Neoromicia somalica</i>		LC			✓
Dusk pipistrelle <i>Pipistrellus hesperidus</i>		LC			✓
Dark-winged lesser house bat <i>Scotoecus hirundo</i>		LC			✓
Andrew Rebori's house bat <i>Scotophilus andrewreborii</i>		LC			✓
Total			4	7	18

to capture and acoustic sampling, we conducted roost searches. We concentrated our roost-search efforts to find potential bat roosting and/or breeding habitats in the vicinity of the wetland, particularly in areas with reasonably dense remnants of the *Alnus acuminata* forest buffer. Nevertheless, no roost locations were found close to the wetland. Rather, four bat roosts were identified approximately 700 m from the wetland edge, with two located in houses and two in churches within the surrounding community settlement areas. Church roosts were occupied by *Pipistrellus* spp. and *Mops pumilus*, while house roosts contained *Nycteris aurita*/*N. hispida* and *Nycteris macrotis*. An additional large cave roost, located more than five km north of Rugezi Marsh, supported a colony of *Rousettus aegyptiacus*.

A total of 32 tissue samples were processed for genetic identification using the *COI* and *Cyt b* genes, leading to the identification of eight species (Supplementary Table S3). The closest matches in BOLD and GenBank supported the field identification for six species ($\geq 95\%$ identity), and these samples clustered with reference sequences in the maximum-likelihood tree (Table 2 and Supplementary Material S1: Supplementary Figs. S2.3b,

S2.6, S2.7, and S2.9). In contrast, samples tentatively identified as *N. macrotis* did not meet that threshold, as well as samples assigned to *Pipistrellus* that may represent an undescribed species; both cases are discussed further in the species accounts (Supplementary Material S1: Supplementary Figs. S2.5 and S2.10).

Species detection: acoustic detection

In total, 20,754 bat passes were recorded from 19 species at 56 static acoustic detector survey points during the dry (June–July) and wet (November–December) seasons of 2023 (Table 3). Three species — the banana serotine (*Afronycteris nanus*; Supplementary Fig. S2.9), cape serotine (*Laeophotis capensis*), and an unidentified free-tailed bat (*Tadarida* spp.) — were the most frequently recorded and widespread, with 63% of the bat passes being recorded from the three species (Table 3). Additionally, about 99% of bat passes were from species that forage in open spaces. In general, however, most bat species, including the threatened Harrison's giant mastiff bat (*Otomops harrisoni*), which is classified as Vulnerable (VU) on the IUCN Red List, had extremely low bat activity.

Table 3. The activity of different bat species from static acoustic surveys during dry (June–July) and wet (November–December) seasons, 2023. Names of sampling sites are as indicated on Table 1.

Species	Bat sampling sites														Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Rhinolophidae — horseshoe bats															
<i>Rhinolophus acrotis</i>	0	1	0	0	6	0	1	0	0	0	4	0	0	0	12
<i>Rhinolophus eloquens</i>	0	0	0	0	0	0	2	0	0	1	1	0	0	0	4
<i>Rhinolophus</i> spp.	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2
Emballonuridae — sheath-tailed bats															
<i>Taphozous mauritanus</i>	0	2	150	0	0	0	0	36	0	0	0	0	0	0	188
Nycteridae — slit-faced bats															
<i>Nycteris</i> spp.	1	11	2	3	0	0	1	0	0	70	0	1	1	2	92
Molossidae — free-tailed bats															
<i>Mops condylurus</i>	0	10	0	0	0	0	0	0	0	3	2	11	0	0	26
<i>Mops pumilus</i>	130	613	239	476	307	1	189	24	22	518	188	200	163	231	3,301
<i>Otomops harrisoni</i>	370	168	202	18	33	0	13	17	5	40	5	32	216	220	1,339
<i>Nyctinomus aegyptiacus</i>	1	59	1	21	9	0	8	7	7	15	5	13	15	55	216
<i>Tadarida</i> spp.	58	2,158	326	2,028	214	73	242	0	23	244	71	408	76	68	5,989
Miniopteridae — long-fingered bats															
<i>Miniopterus</i> spp.	8	36	5	103	246	9	28	1	5	9	109	9	32	5	609
Vespertilionidae — vesper bats															
<i>Afronycteris nanus</i>	20	56	88	380	178	1	722	10	184	607	868	82	508	27	3,731
<i>Myotis</i> spp.	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
<i>Neoromicia somalica</i>	1	11	3	0	245	6	2	0	0	0	3	0	0	5	276
<i>Pipistrellus hesperidus</i>	8	8	0	0	9	0	4	1	4	40	1	0	0	5	80
<i>Pipistrellus</i> sp. indet.	8	240	40	236	1,035	2	199	17	64	350	910	58	106	91	3,356
<i>Scotoecus hirundo</i>	0	164	15	151	64	0	74	10	0	20	39	23	0	5	565
<i>Scotophilus andrewreborii</i>	0	75	23	66	6	0	97	3	190	265	162	23	33	27	970
Total	605	3,612	1,094	3,482	2,352	92	1,583	126	504	1,849	2,368	861	1,150	741	20,754
Bat passes per night	302.5	1,806	547	1,741	1,176	46	792	63	252	924.5	1,184	431	575	371	370.6
Species richness (S)	10	15	12	10	12	6	15	10	9	12	15	10	10	12	19

Species composition by season from acoustic surveys

The wet season yielded the highest number of bat passes of 11,371 from 16 species, whereas we recorded a slightly lower number of bat passes of 9,383 from 17 species in the dry season. Bat activity did not differ significantly between dry and wet seasons ($\beta = 0.192 \pm 0.597$ SE, $z = 0.322$, $p = 0.748$). Similarly, the Type III Wald χ^2 test showed no significant seasonal effect on bat activity ($\chi^2 = 0.104$, $d.f. = 1$, $p = 0.748$). The estimated incidence rate ratio (IRR = 1.21; 95% CI: 0.38–3.90) suggests that bat activity was 21% higher during the wet season than the dry season, but the confidence interval was one, indicating that this increase was not statistically significant.

The overall species accumulation curve for bat activity approached an asymptote after approximately half of the total bat passes had been recorded, indicating adequate sampling effort (Fig. 2). Across 28 survey nights, no additional species were detected beyond the 14th sampling night, further suggesting that species richness had been sufficiently characterised (Fig. 2).

The activity of bats at Rugezi Marsh was bimodal. During the dry season, activity peaked three hours after sunset and again at 04:00 h. In contrast, bat activity peaked two hours post-sunset during the wet season, with the subsequent peak occurring one hour later than in the dry season (Fig. 3).

DISCUSSION

This is the first study to document bat species at Rugezi Marsh, northern Rwanda, using conventional methods and DNA barcoding. The survey revealed 22 bat species, which is more than 43% of the number of bat species known from Rwanda (Patterson and Webala 2012; Cockar 2022). We also recorded a potentially new species within the genus *Pipistrellus* that requires formal

taxonomic assessment. Our results, therefore, highlight the Rugezi Marsh as an important site for bat species diversity and future systematic work.

The elevated species richness of Rugezi Marsh may be attributed to the combination of the high net primary productivity of tropical wetlands (Rodal *et al.* 2025) and the many habitats present within and next to the wetland, encompassing marshland, remnants of vegetation, valleys, and nearby hills. Habitat complexity is a crucial determinant of the assembly of biotic groups and the functioning of ecosystems (Tews *et al.* 2004; Fischer and Lindenmayer 2007). The habitat heterogeneity of Rugezi Marsh probably offers various roosting sites and foraging areas for multiple bat species. Furthermore, due to their ability for active flight, bats can traverse extensive distances and navigate various habitats that serve as daily roosts, breeding sites, commuting routes, drinking areas, and foraging grounds; thus, they can sustain considerably larger home ranges than non-volant small mammals of comparable body size (Flaquer *et al.* 2009). Consequently, despite significant human-induced alterations at Rugezi Marsh, bat assemblages may endure owing to their adaptability in selecting roosting and foraging sites. Nevertheless, our project documented a higher number of species suited to exploit open environments than those adapted to navigate cluttered spaces at Rugezi Marsh (Table 3 — Jung *et al.* 2014). These open-space foraging species generally emit narrowband, low-frequency echolocation calls for long-range detection (Schnitzler *et al.* 2003; Denzinger and Schnitzler 2013). In contrast, clutter-tolerant species, like the Rhinolophidae and Nycteridae families, which were documented in fewer numbers, forage in proximity to obstacles and clutter, possessing short and broad wings.

Overall, the high bat activity and species richness at Rugezi conform to other wetland studies of bat activity elsewhere (e.g., Grindal *et al.* 1999; Franc 2008). This is probably because of the presence of open water sources, which are more important as foraging and drinking grounds for bats (Korine *et al.* 2016). Additionally, vegetation structures around water sources may provide habitat for insects, which are food resources for insectivorous bats (Almeida *et al.* 2014; Cruz *et al.* 2019). The riparian vegetation also provides roosting resources, and shelter from wind and predators, and bats use the vegetation as flyways during foraging activities (Rydell *et al.* 1996; Estrada and Coates-Estrada 2002; Law and Chidel 2002), reducing the distance that they need to travel from and to their refuges (Daniel *et al.* 2008).

For some functional groups, only a few species were detected. Despite intensive capture efforts, only three of the 18 fruit bat species (Family Pteropodidae) reported in Africa (Monadjem *et al.* 2020) and 10 from Rwanda (Patterson and Webala 2012) were recorded at Rugezi Marsh. Since frugivorous bats are easily caught using standard capture techniques (e.g., Meyer *et al.* 2011), the lower species richness of fruit bats at Rugezi may reflect: (i) limited food resources, because few native fruiting trees occur in the degraded landscape and most of them

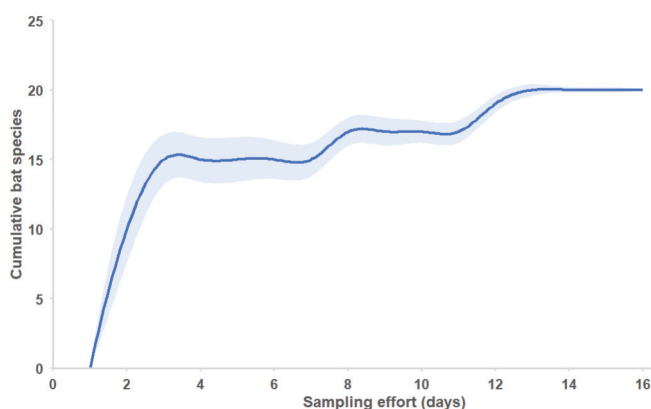


Figure 2. Species accumulation curve for insectivorous bat activity at Rugezi Marsh showing the progressive increase in species richness with sampling effort across survey nights. Note the curve flattens off after the 14th sampling night.

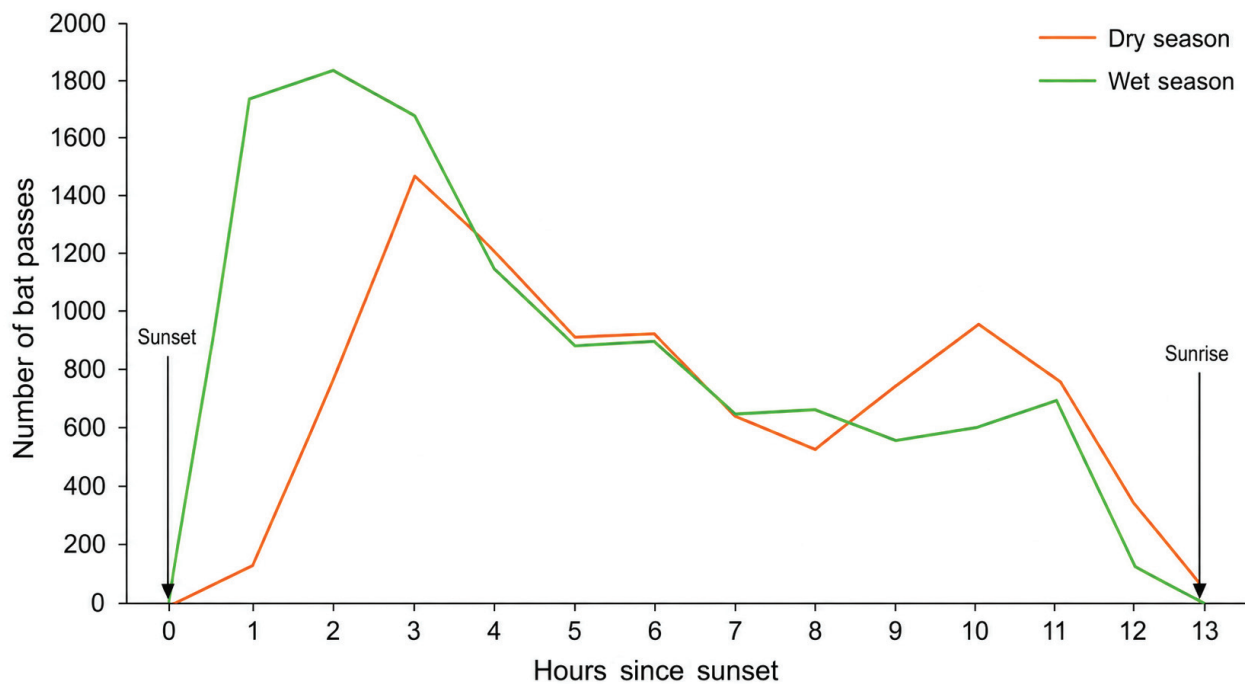


Figure 3. Nightly bat activity at Rugezi Marsh across dry (June–July) and wet (November–December) seasons in 2023.

have been replaced by exotic species, especially *Eucalyptus*, forming a narrow buffer belt along the wetland, and (ii) limited roost availability, because the scarcity of dense forest/woodland reduces nearby tree-roosting opportunities for taxa such as *Epomophorus* spp.

Among insectivorous bat species, a few species were dominant (e.g., *A. nanus* — Table 3), whereas most of them were recorded infrequently and showed low acoustic activity. This pattern could reflect low local occurrence at Rugezi Marsh, potentially consistent with a degraded and highly disturbed landscape facing threats such as water extraction, fires, human settlements, and exotic tree plantations. However, low activity may also reflect detectability biases inherent to the acoustic technique: species that produce low-intensity calls that rapidly attenuate, like *Nycteris* spp. (Neuweiler 1989). Additionally, some species (e.g., *Clootis percivali* and *Hipposideros caffer*) emit higher-frequency calls (> 130 kHz), which also attenuate more rapidly and are not detected at great distances from detector microphones. Since detector-based surveys of this kind typically show low representation of these species (e.g., Barclay 1999), we advise caution on drawing inferences about the overall abundance of these species from our acoustic survey results.

Roost searches revealed two insectivorous bat species — *M. pumilus* and *Pipistrellus* spp. — within active human residences. In landscapes like Rugezi Marsh, where natural roosting sites such as trees or caves are limited, artificial constructions like houses offer critical alternative roosting habitats that augment the diversity and abundance of local bat populations (Suominen *et al.* 2023). This effect is particularly significant in urbanized or agricultural areas where the natural ecosystem has been modified. The absence of appropriate roost sites

frequently limits bat populations. Buildings effectively mimic certain characteristics of natural roosting habitats by offering several places for bats to roost, including attics, wall voids, and cracks beneath siding or eaves. This enhances the habitat for several bat species (Voigt *et al.* 2016; Suominen *et al.* 2023). Our findings indicate that these alternative roosts are critical for bat species and must be safeguarded within the broader landscape of a possible protected area, such as Rugezi Marsh, and included in land-use planning.

Employing complementary capture methods, such as ground-level mist nets, hand nets at designated roosts, and the harp trap, facilitated the detection of a greater number of bat species compared to using a singular standard capture technique. Furthermore, the use of acoustic detectors contributed to the detection of additional species. Capture and acoustic approaches are complementary; hence, species difficult to detect using one method may be recorded by the other (e.g., Flaquer *et al.* 2007; Kunz and Parsons 2009; Meyer *et al.* 2011; Musila *et al.* 2020; Tanshi *et al.* 2021). The methods also enabled the detection of *Nycteris* spp., which are indistinguishable or not detectable from ultrasonic recordings. However, in the absence of canopy-level mist nets, ground-level trapping may have missed high-flying species (Meyer *et al.* 2011). In addition, acoustic detectors may detect bat species unequally (Barclay 1999), which may underrepresent certain species in surveys. While acoustic sampling identified species not easily captured by conventional capture methods, 13% of bat passes were unidentifiable, underscoring the likelihood that several species were overlooked in our study. Nevertheless, the acoustic sampling species accumulation plot reached an asymptote (i.e., levelled off; Fig. 2). All captured insectivorous bats were subsets of acoustically recorded bats. This suggests that Rugezi Marsh's bat

community has been well sampled and that future field-work will likely contribute few new species.

Nevertheless, the acoustic identification of African bats is exceedingly challenging, and this study may have missed or misidentified certain species. The challenges are a result of the overlapping echolocation frequencies employed by highly diverse sympatric species, pulse plasticity, a historical lack of comprehensive local reference libraries, and immense biodiversity (Monadjem *et al.* 2017; Barclay and Jacobs 2022; Taylor-Boyd *et al.* 2025). Many of these are members of morphologically cryptic species that emit echolocation frequencies that are nearly identical. This limitation is notably apparent in genera such as *Nycteris*, *Mops*, *Myotis*, and many vespertilionid bats, where it is frequently challenging to make a reliable distinction solely based on acoustic recordings. In this study, we analysed calls at a higher taxonomic level, specifically at the genus level, for some of these bats, where species-specific identification was impossible (e.g., *Miniopterus* spp.). Furthermore, we enhanced the confidence in our identification by integrating acoustic monitoring with mist netting, harp trapping, roost surveys, and unpublished regional reference call libraries. In the future, we recommend that to conduct comprehensive bat surveys in Africa, it is necessary to integrate passive acoustic monitoring, live capture/release, morphometrics, voucher specimen collection, and molecular DNA sequencing.

Our study used DNA barcoding (*COI* and *Cyt b*) as an ancillary method, which was effective in validating field identifications for the majority of captured taxa, especially in cases of missing voucher material or overlapping acoustic/field traits. Nevertheless, for several closely related lineages, mitochondrial markers failed to offer adequate resolution for unequivocal species identification, as exemplified by *Epomophorus*. Comparable limitations of mtDNA-based identification were recorded in African pteropodids (Hassanin *et al.* 2020). They demonstrated that mitochondrial data do not consistently differentiate between *E. gambianus* and *E. pusillus*, and other epauletted fruit bats, despite evident morphological differences. These patterns are anticipated as a result of inadequate lineage sorting and/or mitochondrial introgression, phenomena prevalent among animals that can compromise single-locus identifications (Funk and Omland 2003). Recent research indicates that mitochondrial divergence can forecast reproductive compatibility in mammalian hybrids; minimal mtDNA divergence correlates with enhanced hybrid fertility and gene flow, a situation where barcoding markers are also likely to exhibit limited discriminatory power among closely related taxa (Allen *et al.* 2020). Therefore, we recommend the sustained use of an integrative approach that merges mitochondrial barcodes with acoustics and morphological diagnoses and, in cases of ambiguity, employ independent nuclear markers or multilocus datasets to enhance species-level identification and more effectively delineate taxa within species complexes.

The bimodal pattern of bat activity at Rugezi Marsh (Fig. 3) is not unprecedented because insectivorous bats temporarily partition resources (Gehrt and Chelvig 2004), especially in tropical regions with high bat biodiversity (Emrich *et al.* 2014). Interspecific competition can lead to the temporal (and spatial) segregation of ecologically similar species. This phenomenon may have ecological and evolutionary ramifications because it creates a mechanism that permits species coexistence, which in turn affects the structure of biological communities (Kronfeld-Schor and Dayan 2003). In insectivorous bats, the majority of species take advantage of the high abundance of insects and other arthropods at the beginning and end of the night, which is why bat activity peaks a few hours after and before sunset and sunrise, respectively (Erkert 1982; Thompson and Withers 2003; LaVal and Lawton 2021). At Rugezi, overall bat activity in the wet season peaked earlier after sunset and later before sunrise compared to that of the dry season. Bats' seasonal fluctuations in peak activity at Rugezi Marsh are likely due to variations in energy levels during reproduction (Remmers *et al.* 2025) or fluctuations in food availability or foraging strategies (O'Donnell 2010; Vieira *et al.* 2017).

In summary, 22 species of bats from six families were recorded at Rugezi Marsh. For such a relatively small area, this represents more than 43% of all bat species in Rwanda, which makes it a 'hotspot' for bat biodiversity in the country. Of all the species recorded, one — Harrison's giant mastiff bat (*Otomops harrisoni* Ralph, Richards, Taylor, Napier, and Lamb, 2015) — is considered of conservation concern. The species is listed as Vulnerable on the IUCN Red List (Richards 2017). While *O. harrisoni* is fairly ubiquitous and widespread (Ralph *et al.* 2015), this area provides a critical foraging habitat because, not far south of Rugezi Marsh, a known roost for the species is located at Musanze Tourist Cave, where the other African *Otomops* species, *O. martiensseni*, also occurs (Patterson *et al.* 2018). Rugezi Marsh's exceptionally high bat species richness, in conjunction with the presence of this threatened species, provides a strong basis for its protection.

SUPPORTING INFORMATION

Contents: Supplementary Tables: Table S1. Range of external measurements of captured bats from Rugezi Marsh for both males and females: *n* = number of individuals captured; age: J = juvenile, A = adult; FA = forearm length in millimetres; M = body mass in grams; Table S2. Primers used for amplification and sequencing of the mitochondrial *COI* and *Cyt b* genes. Each locus-specific forward and reverse primer was ordered with the corresponding ONT forward or reverse overhang sequence added to its 5' end. The locus-specific primer sequences shown in the table exclude the ONT overhangs. Mix ratios are given for the components of the mammalian *COI* primer cocktails; Table S3. Species identified with genetic markers; *n* is the number of

specimens processed, whereas values in the *COI* and *Cyt b* columns are the numbers of sequences generated for each marker; Supplementary Fig. S1. Pictures of a few sampling sites: (A) Miyove, (B) Gaseke (C) Rwerere, (D) House roost 1, (E) Ruhunde, (F) Basebya, (G) Gatebe, and (H) Rwerere Community Centre; Supplementary Material S1. Species accounts, including illustrations of echolocation calls and mitochondrial-gene genealogies, for bat taxa recorded in the Rugezi Marsh region. Supplementary Information is available exclusively on BioOne.

AUTHOR CONTRIBUTIONS

PWW: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; SK: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, and final approval of the article; PI: collection and/or assembly of data, critical revision, and final approval of the article; PH: collection and/or assembly of data, and final approval of the article; PS-V: data analysis and interpretation, writing, critical revision, and final approval of the article; JJP: data analysis and interpretation, writing, critical revision, and final approval of the article; ZL: data analysis and interpretation, critical revision, and final approval of the article; RM: writing, critical revision, and final approval of the article; GE: data analysis and interpretation, writing, critical revision, and final approval of the article; ON: research concept and design, writing, critical revision, and final approval of the article.

COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose.

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