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Using Acoustic Monitoring to Assess Insectivorous Bat Richness and Activity in a Sub-Tropical Savanna

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ABSTRACT

Understanding insectivorous bat diversity and activity is crucial for conservation efforts, particularly in under-researched regions like sub-tropical savannas. Our study assessed bat species richness and seasonal activity (i.e., number of passes) in MalaMala Game Reserve, located within the south-western region of the Greater Kruger National Park (KNP), South Africa, a hitherto unsampled site. We conducted acoustic monitoring using ultrasonic detectors over two distinct seasons: the wet season (January to March) and the dry season (June to August) in 2022. Our findings revealed 16 species from six families, representing 40% of the bat species known in KNP. The Molossidae family was the most dominant, followed by Vespertilionidae, while the Hipposideridae family recorded the fewest calls, likely due to their high-frequency echolocation calls, which attenuate rapidly, or possibly because these bats were less active in our study area, or a combination of both factors. Seasonal variations in bat activity were observed, with significantly higher activity during the wet season, likely due to increased insect abundance and reduced thermoregulatory costs. By targeting a previously unsurveyed region and incorporating seasonal comparisons, our study addresses a critical spatial and temporal knowledge gap and provides a valuable foundation for the development of long-term, standardized bat monitoring across the Greater KNP landscape.

1 | Introduction

Bats, of which there are over 1400 species comprising approximately 20% of the world's extant mammals (Simmons and Cirranello 2020), play essential roles in ecosystems worldwide (Linden et al. 2019; Rocha et al. 2021). Insectivorous bats, which make up around 70% of all bat species (Rydell 2006), contribute important ecosystem functions such as regulating insect populations and serving as bioindicators of environmental change (Jones et al. 2009; Mtsetfwa et al. 2018; Roeleke et al. 2020). Their nocturnal foraging behavior is closely tied to insect activity, which is influenced by ambient temperature and seasonal variation (Mellanby 1939; Ciechanowski et al. 2007; Rydell et al. 1996). These traits make insectivorous bats particularly sensitive to environmental change and important indicators of ecosystem health.

Insectivorous bats can be classified into three major functional foraging groups: open-air, clutter-edge, and clutter foragers. Each group has distinct echolocation call patterns and wing morphology adapted to their specific foraging strategies (Barclay 1985; Denzinger and Schnitzler 2013; Jacobs 2016; Mtsetfwa et al. 2018). Open-air foragers hunt in open spaces and generally fly above any vegetation, possessing narrowband and low-duty cycle echolocation calls (Denzinger and Schnitzler 2013). They have small, pointed wings with

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high aspect ratios, which allow them to reach high speeds (Norberg and Rayner 1987; Denzinger and Schnitzler 2013; Jacobs 2016). Clutter-edge foragers, on the other hand, hunt near and along vegetation edges. They navigate along the edges to avoid collisions and can distinguish insect echoes from vegetation echoes (Barclay 1985; Jacobs 2016). Clutter-edge foraging bats use mixed search signal echolocation calls, which include a shallow modulated narrowband followed by a broadband, steeply downward frequency modulated component (Denzinger and Schnitzler 2013). Their wings have average aspect ratios and wing loadings, with rounded tips adapted for slower flight in the presence of background objects (Norberg and Rayner 1987; Denzinger and Schnitzler 2013). Clutter foragers search and capture insects in highly cluttered environments (Barclay 1985; Jacobs 2016). They have constant frequency calls and emit short frequency modulated calls of low-duty cycle to navigate and capture insect prey in these cluttered environments (Falk et al. 2014). Clutter foragers have short, broad wings for enhanced maneuverability (Barclay 1985; Norberg and Rayner 1987). Given these varied foraging strategies, acoustic analysis of echolocation calls provides a non-invasive method for surveying bat communities and is increasingly used in bat conservation studies (Brinkley et al. 2021; de Jong et al. 2025; Castro-Fernandes et al. 2025).

Despite growing interest in bat conservation globally, large gaps in ecological knowledge remain in many parts of the world, particularly in Africa (Frick et al. 2020). Compared to their North and South American and European counterparts, African bat species are poorly studied, limiting efforts to develop effective conservation and monitoring strategies (Meyer et al. 2016; Walters et al. 2012). This issue is especially problematic in ecologically important but under-surveyed biomes such as African savannas, which dominate much of the continent and comprise ~54% of southern Africa's vegetation cover (Rutherford et al. 2006). These dynamic systems support a diverse community of insectivorous bats due to their varied vegetation structure, roosting opportunities, and abundant prey—especially in warmer regions (Shapiro et al. 2020). However, savannas are increasingly threatened by land conversion, bush encroachment, and altered fire regimes, making them a conservation priority (Parr et al. 2014; Laurance et al. 2014).

Bats in these landscapes are particularly vulnerable to such changes due to their life-history traits (i.e., low reproductive output, long lifespans, and elevated metabolic rates) which constrain their capacity to recover from environmental disturbances (Voigt and Kingston 2016). In addition to habitat loss and fragmentation, bats across Africa face direct threats including hunting for bushmeat, persecution, and use in traditional medicine (Voigt and Kingston 2016). These pressures are contributing to local and regional population declines, highlighting the need for robust, spatially explicit monitoring across different habitats and seasons.

In southern Africa, bat diversity follows a biogeographic gradient, decreasing from the wetter north-eastern regions toward the more arid west, where suitable roosting and foraging habitats become increasingly scarce (Schoeman and Monadjem 2018). Within this context, the Kruger National Park (KNP) is particularly important, offering a range of savanna habitats that support high bat diversity. The Pafuri region in the northern KNP, for example, has the highest recorded bat species richness in South Africa (Rautenbach et al. 1985). However, recent studies suggest a possible reduction in richness in this region, potentially due to environmental change, survey effort, or methodological differences (Brinkley et al. 2021). In contrast, the southern and south-western regions of the Greater KNP remain largely unsurveyed, creating a critical spatial knowledge gap in national bat monitoring efforts.

We conducted seasonal acoustic monitoring to evaluate insectivorous bat species richness and activity in a sub-tropical savanna ecosystem in the south-western Greater KNP; a region that remains ecologically important yet under-sampled. By establishing the first contemporary acoustic baseline in this area, we address a critical regional knowledge gap in bat ecology. Specifically, we aimed to characterize both species richness and seasonal variation in bat activity because activity patterns offer insights into resource availability, habitat use, and functional responses to environmental conditions. Understanding these seasonal dynamics is essential for interpreting how insectivorous bats respond to habitat heterogeneity and climate-driven changes (key factors shaping conservation strategies in savanna systems). Although some studies from the northern KNP suggest potential declines in bat richness, methodological differences limit direct comparison. Rather than evaluating historical change, our study provides a robust reference point for future long-term monitoring and biodiversity assessment across the Greater KNP landscape. We hypothesized that bat activity and species richness would peak in the warm, wet season due to increased insect abundance and lower thermoregulatory costs (Pretorius et al. 2020), and that open-air foragers would dominate acoustic detections due to the greater detectability of their call structures (Monadjem et al. 2020).

2 | Methods

2.1 | Study Site

We conducted our study in MalaMala Game Reserve (MMGR; 13,300 ha), South Africa, which is part of the Sabi Sands Nature Reserve–MalaMala–Sabi Game Reserve Complex. MMGR forms part of the Greater KNP protected area network, encompassing over 20,000 km^2, and shares an unfenced border with KNP to the east (see Figure 1). The reserve holds the protection status of a private game reserve and supports conservation-focused tourism. The region receives an average annual rainfall of about 620 mm (Schulze 2008), with the wet season (October to March) receiving most of the rainfall (~514 mm) and the dry season (April to September) being relatively dry (~114 mm; Fick and Hijmans 2017). Wet season average monthly maximum temperatures range from 29°C to 32°C, while minimum temperatures range from 16°C to 21°C. In contrast, dry season average monthly maximum temperatures range from 24°C to 28°C, and minimum temperatures range from 8°C to 16°C. The natural vegetation at our study site is predominantly a mixed Combretum/Terminalia woodland (Gertenbach 1983).

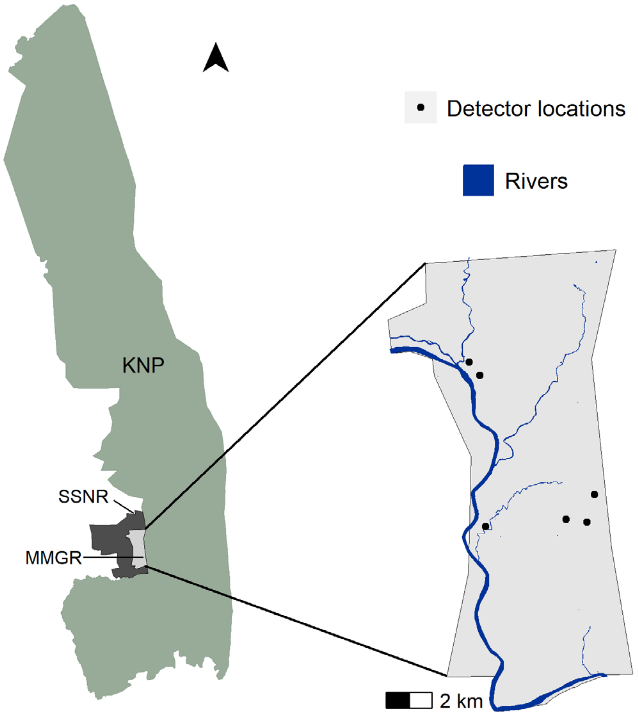

FIGURE 1 | Location of our study site, MalaMala Game Reserve (MMGR), South Africa, which lies between the Sabi Sands Nature Reserve (SSNR) and the Greater Kruger National Park (KNP). The inset shows our study site with the black dots representing the location of each acoustic detector. Three detectors were located close to permanent water (< 500 m) and three were located far (> 3.5 km) from permanent water. The Sand River (bold blue line) represents permanent water at our study site.

2.2 | Data Collection

We conducted data collection during the wet (January to March) and dry (June to August) seasons of 2022. Additional bat species richness data were recorded in the wet season (March) of 2021 to assess sampling completeness (see below). We selected six sampling sites to reflect the dominant mixed Combretum/Terminalia woodland of the region (Gertenbach 1983). Each site was monitored for five consecutive nights in each season (see below for rarefaction information), specifically during periods of minimal lunar illumination (Mushabati et al. 2022), resulting in 30 sampling nights per season. Given that bat activity and species richness are strongly influenced by insect activity and proximity to water (Fukui et al. 2006; Hagen and Sabo 2011, 2014; de Oliveira et al. 2015), we intentionally placed three acoustic detectors close to water (< 500 m) and three detectors far (> 3.5 km) from water (Figure 1) to increase our ability to capture as many potential bat calls (and species) as possible.

2.2.1 | Acoustic Bat Monitoring

We used SM4BAT FS song meter detectors (Wildlife Acoustics, Concord, MA, USA) to record insectivorous bat echolocation calls. The detectors were housed in waterproof cases and equipped with SMM-UI highly sensitive, low-noise ultrasonic and weatherproof microphones. We set each detector to record ultrasound with a sampling rate of up to 384 kHz, a sampling frequency of 16-bit sample resolution, and to only record sounds above 12 dB with a trigger frequency of 8 kHz (Parker 2022). We mounted detectors ~1.5 m above the ground with the microphones connected (Parker and Bernard 2018) and programmed them to record from sunset until dawn (Parker 2022).

2.2.2 | Acoustic Data Identification

To analyze and identify bat calls, we used Kaleidoscope Pro Software (Wildlife Acoustics, Concord, MA, USA), which is designed for bat call identification (Parker and Bernard 2018). The software utilizes built-in classifiers tailored to different global regions to automatically identify recordings. However, we used a KNP-specific classifier developed by Brinkley et al. (2021), which applied to our study due to its location within the same broad eco-region. Kaleidoscope uses an unsupervised machine learning algorithm to group similar echolocation recordings based on their acoustic features (viz.: call duration (Dur), characteristic frequency/frequency of maximum energy (F_c), minimum call frequency (F_{min}), maximum frequency (F_{max}), and the frequency slope of the call (F_k)) and to generate putative sonotypes (Guerrero et al. 2023). Brinkley et al. (2021) manually verified and identified each sonotype for northern KNP and trained the algorithm to produce a custom classifier.

While the custom classifier efficiently filters and accelerates the classification of unknown bat calls, it is not infallible (Rydell et al. 2017). To improve accuracy, we also manually reviewed each call series/pass following initial classification using our custom classifier. In other words, the classifier tool was used primarily to cluster calls based on their shared acoustic characteristics. These clusters were then further subjected to a structured manual identification process (Brinkley et al. 2021; Parker and Bernard 2018; Parker 2022).

Each call series/pass within these clusters was examined by the same observer (LG) and assigned to species using a reference call library and published call parameters for southern African bats (Monadjem et al. 2020; Brinkley et al. 2021; Parker 2022). A call series or bat pass was defined as three or more pulses per individual trigger event (Castro-Fernandes et al. 2025). Species-level identification was also only attempted when at least three pulses were present in the call series, reducing the likelihood of misclassification due to background noise, social calls, or partial call sequences (Brinkley et al. 2021). Series/passes that could not be confidently identified were excluded.

To minimize Type I errors (i.e., false positives), manual identification followed a three-phase process (Parker 2022). In the first phase, we made preliminary identifications using the minimum frequency (F_{min}) ranges of known species. In the second phase, these identifications were cross-validated using either characteristic frequency/frequency of maximum energy (F_c) or maximum frequency (F_{max}) values. Only calls that met the criteria in both phases advanced to the final phase, where species-level assignments were confirmed using known F_c or

$F_{\max}$ ranges, depending on which provided greater diagnostic clarity.

2.3 | Data Analysis

2.3.1 | Rarefaction Curve

Prior to deploying the detectors for the seasonal surveys, we deployed a SM4 detector at two of the six sites to assess sampling completeness. We deployed these two detectors for 10 nights in March 2021 and used the data to construct a rarefaction curve to provide a meaningful interpretation of the species richness found at our study site and set the minimum necessary number of sampling nights for our study (Gotelli and Colwell 2001; Colwell et al. 2012). We used the *fossil* package in R version 4.4.1. (R Development Core Team 2024), which stems from the EstimateS programme, to calculate species richness and various species richness estimators (Vavrek 2022). This package computes a mean and variance for species richness by randomly selecting a sample size from the total data sample to generate a S(obs), an Incidence Coverage-based Estimator (ICE), and an Abundance Coverage-based Estimator (ACE; Gotelli and Colwell 2001). S(obs) is the calculated species richness from the observed data, while ICE, derived from incidence data, and ACE, derived from abundance data, estimate the sampling efficiency to infer species richness within the study area (Chao et al. 2000; Gotelli and Colwell 2001). When an asymptote across the two estimators and S(obs) is reached, sufficient sampling is achieved (Colwell et al. 2012).

2.3.2 | Bat Species Richness and Activity

Prior to data analyses, we log transformed bat activity (i.e., number of passes per night per site) to meet the assumptions of normality and homogeneity of variance. We used the formula:

$$\log(x + 1)$$

where x is the number of passes per night per site.

We ran a two-sample *t*-test to assess the effect of season on bat activity. The data were back-transformed ($y = \exp(x) - 1$) for graphical representation. No transformation of the data on bat species richness per night per site allowed these data to meet the assumptions required for parametric analyses. As such, we used a non-parametric Mann–Whitney *U*-test to quantify the effect of season on bat species richness. All significance levels were set to $\alpha = 0.05$.

3 | Results

3.1 | Rarefaction Curve Analysis

The interpolated species richness, ACE and ICE values for our initial sampling during the wet season of 2021 are shown in Figure 2. The 95% confidence intervals (error bars) of the observed species richness S(obs) and the two estimators overlapped after replicate two, with an asymptote clearly reached between S(obs) and the two estimators after replicate four. As a result, sampling was deemed adequate after five nights (Figure 2; Robinson et al. 2007).

3.2 | Bat Species Richness and Activity

A total of 18,669 identifiable echolocation call sequences/passes were recorded during wet and dry seasons in MalaMala Game Reserve in 2022 (Table 1). These calls were attributed to six bat families: Molossidae (68.09%), Vespertilionidae (23.75%), Emballonuridae (2.96%), Rhinolophidae (2.72%), Miniopteridae (2.49%), and Hipposideridae (0.01%; Table 1).

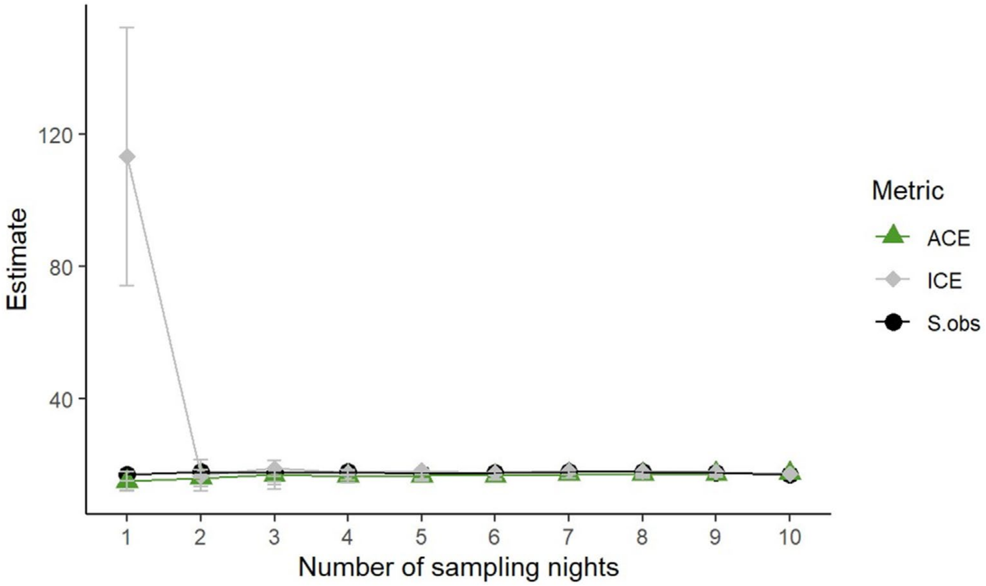

FIGURE 2 | Species accumulation curve for the bat acoustic data collection in March 2021 from MalaMala Game Reserve, South Africa. S(obs) is the observed data, and ACE (Abundance Coverage Estimator), and ICE (Incidence Coverage Estimator) are the two species richness estimators; error bars represent 95% confidence intervals.

TABLE 1 | Putative bat species, their associated family and foraging category (Ce, clutter-edge; Cl, clutter; Oa, open-air) recorded during dry and wet seasons of 2022 at MalaMala Game Reserve, South Africa. Detections represent number of echolocation call sequences/passes.

			Seasonal detections		
Family	**Species**	**Foraging category**	**Dry**	**Wet**	**Total detections**
Emballonuridae	*Taphozous mauritianus*	Oa	45	507	552
Hipposideridae	*Hipposideros caffer*	Cl	—	1	1
Miniopteridae	*Miniopterus natalensis*	Ce	73	391	464
Molossidae	*Chaerephon ansorgei*	Oa	696	782	1478
	Mops condylurus	Oa	371	4300	4671
	Mops midas	Oa	584	702	1286
	Tadarida aegyptiaca	Oa	703	4573	5276
Rhinolophidae	*Rhinolophus darlingi*	Cl	—	5	5
	Rhinolophus smithersi	Cl	131	361	492
	Rhinolophus simulator	Cl	—	9	9
	Rhinolophus clivosus	Cl	—	1	1
Vespertilionidae	*Myotis tricolor*	Ce	—	2	2
	Laephotis capensis	Ce	260	2337	2597
	Neoromicia zuluensis	Ce	275	1275	1550
	Pipistrellus rusticus	Ce	—	2	2
	Scotophilus dinganii	Ce	57	226	283
	Total	—	3195	15,474	18,669
	Number of species	—	10	16	16

Note: See Appendix S1 for species call characteristics.

Within these families, 16 putative bat species were identified (Table 1). Four species from the family Molossidae dominated the calls recorded (i.e., *Chaerephon ansorgei*, *Mops condylurus*, *M. midas*, and *Tadarida aegyptiaca*.). The majority of echolocation calls were from open-air foraging bats (13,233 calls), primarily within the Molossidae (12,711 calls) and Emballonuridae (552 calls) families. Clutter-edge foraging bats, represented by Vespertilionidae (4434 calls) and Miniopteridae (464 calls), contributed a smaller proportion of the recordings. In contrast, clutter-foraging bats including Rhinolophidae (507 calls) and Hipposideridae (1 call) were the least frequently recorded families (Table 1).

We found that the wet season had significantly higher bat activity ($t_{(58)} = -5.64$, $p < 0.001$) and species richness ($W = 254.5$, $p = 0.003$) per night per site compared to the dry season (Figure 3). In the dry season, bat species richness per night per site averaged 8.2 ± 0.3 (mean ± SE), and bat activity was 110 ± 19.70 (mean ± SE) passes per night per site (Figure 3). By contrast, during the wet season, species richness averaged 9.6 ± 0.22 (mean ± SE) per night per site, and bat activity was 513 ± 89.9 (mean ± SE) passes per night per site (Figure 3). Moreover, we observed species turnover between the wet and dry season. For example, *Hipposideros caffer*, *Rhinolophus clivosus*, *R. simulator*, *R. darlingi*, *Pipistrellus rusticus*, and *Myotis tricolor* were only recorded during the wet season, but no new species were recorded during the dry season (Table 1).

4 | Discussion

Our study revealed clear seasonal variation in bat activity, with significantly greater species abundance and acoustic activity recorded during the wet season (January to March) compared to the dry season (June to August). This seasonal pattern is consistent with other studies across savanna systems and likely reflects increased insect abundance and reduced thermoregulatory constraints during the warmer, wetter months (Parker and Bernard 2018; Taylor et al. 2013; Mtsetfwa et al. 2018). Elevated prey availability during the wet season likely reduces landscape-level constraints, allowing bat activity to increase; whereas drier periods may force bats to adjust their foraging behavior in response to resource scarcity (Fukui et al. 2006; Hagen and Sabo 2011; Salsamendi et al. 2012; Geluso and Geluso 2012; Rainho and Palmeirim 2011; Voigt and Kingston 2016).

The Molossidae and Vespertilionidae families were the most commonly detected families across both seasons, aligning with findings from other savanna landscapes in southern Africa (Parker and Bernard 2018; Shapiro et al. 2020). Vespertilionids—which are largely clutter-edge foragers—were especially well represented, likely due to the structurally heterogeneous nature of the savanna woodland matrix in our study area (Parker et al. 2023; Schmitt et al. 2022). In contrast, the Hipposideridae, which forage in denser vegetation and produce high-frequency

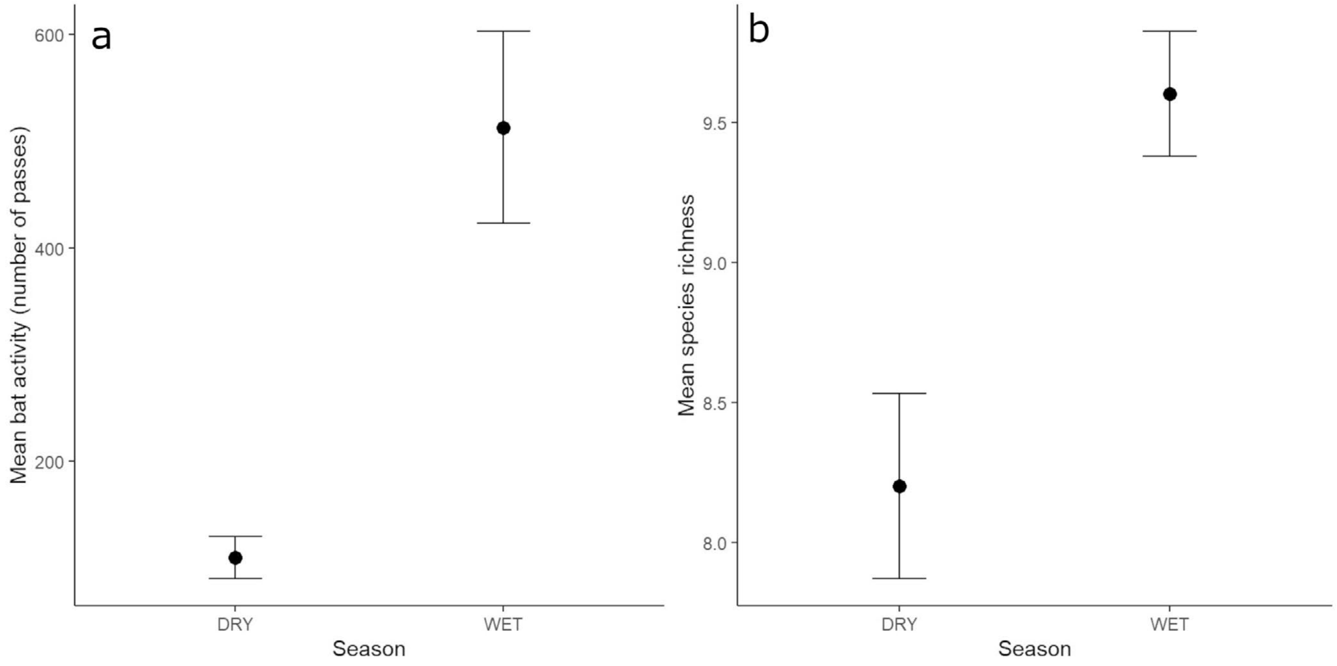

FIGURE 3 | The effects of season (wet and dry) on (a) mean (±SE) insectivorous bat activity (i.e., number of passes per night per site) and (b) mean (±SE) species richness per night per site (b) at MalaMala Game Reserve, South Africa.

echolocation calls, were poorly detected. This underrepresentation is likely due to a combination of their foraging ecology, lower abundance, and reduced acoustic detectability due to rapid call attenuation over distance (Thiagavel et al. 2017; Monadjem et al. 2007).

Across our six survey sites, we identified 16 species from six families, representing approximately 40% of the bat species documented in the KNP (Monadjem et al. 2020). Although lower than the 27 species recently recorded in northern KNP (Brinkley et al. 2021), this finding cannot yet be interpreted as a regional decline given the lack of standardized, long-term data across the region. However, the disparity does underscore the knowledge gap in the southern Greater KNP region and the importance of expanding survey coverage. Our results establish a valuable ecological benchmark for this understudied region and form the foundation for future efforts to assess spatial and temporal trends in bat richness and activity across the Greater KNP.

Importantly, the decline in species richness observed by Brinkley et al. (2021) in the northern KNP—from 40 species during 1960–1990 to 27 species in the 2017–2018 survey—raises questions about broader patterns of bat community change in protected areas. While these differences may reflect variation in sampling methods and effort, they also highlight the importance of consistent and repeated monitoring. Our study contributes to this effort by providing the first seasonal acoustic survey in the south-western portion of the Greater KNP region, an area that has received little attention despite recent evidence of significant woody cover loss (Munyati and Sinthumule 2016). Given bats' sensitivity to habitat structure and resource availability, changes in vegetation cover could have cascading effects on species composition and foraging behavior (Fukui et al. 2001; Russo and Voigt 2016).

Bat species richness in southern Africa follows a broad east-to-west gradient, declining as vegetation cover and water availability decrease (Schoeman and Monadjem 2018). Bats in savanna landscapes are particularly at risk due to ongoing threats such as land-use conversion, fire suppression, and human-wildlife conflict (Voigt and Kingston 2016). These threats are compounded by the life-history traits of bats (i.e., long lifespans, low reproductive rates, and high metabolic demands), which limit their capacity to recover from disturbances (Voigt and Kingston 2016).

Methodologically, our study highlights both the value and the limitations of acoustic-only monitoring. Acoustic detectors allow for non-invasive, standardized sampling across seasons and sites, and are especially useful in environments where capture rates are low (Monadjem et al. 2020). However, acoustic classification is constrained by the accuracy of reference libraries and software tools. Several species in our study region exhibit overlapping call traits (e.g., *Laephotis capensis* and *Myotis tricolor*; *Chaerephon pumilus* and *Taphozous mauritianus*) (de Jong et al. 2025), which can result in misidentification. We attempted to minimize this risk by applying a conservative manual verification process using published frequency ranges and a vetted regional classifier (Brinkley et al. 2021; Reinhold et al. 2001). An alternative, and equally conservative approach, would be to merely characterize echolocation calls into sonotypes or phonic groups for species with similar call characteristics (Fenton and Bell 1981).

Nonetheless, our approach did not account for intraspecific or geographic variation in echolocation calls, which can further complicate acoustic classification. Recent findings by de Jong et al. (2025) demonstrated significant variation in call parameters across sexes and sites for several common savanna bats, including *Neoromicia zuluensis*, *Scotophilus dinganii*, and *Rhinolophus simulator*. These insights point to the need for regionally specific, sex-disaggregated call libraries to enhance acoustic classifier performance. Future studies in the Greater KNP region should consider integrating live-capture methods to refine acoustic reference datasets and improve species-level identification accuracy.

Our study provides the first seasonal acoustic assessment of insectivorous bats in the south-western Greater KNP region, an area that has historically been under-surveyed. Our results reveal strong seasonal shifts in bat activity and provide a current benchmark for assessing ecological responses to environmental change in savanna systems. Given the increasing threats facing African bats and the scarcity of long-term monitoring data, acoustic surveys such as ours offer a practical, scalable tool for conservation and research. Continued expansion of such efforts across the Greater KNP landscape is essential to detect biodiversity trends, guide adaptive management, and contribute to global understanding of bat responses to environmental pressures.

Author Contributions

Conceptualization: M.H.S., K.S., and D.M.P.; funding acquisition: M.H.S., K.S., and D.M.P.; investigation: L.G., M.H.S., and K.S.; supervision: M.H.S., K.S., and D.M.P; writing – original draft: L.G. and J.C.; writing – review and editing: L.G., J.C., M.H.S., K.S., and D.M.P.; visualization: K.S. and J.C.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All supporting data can be found at the following Zenodo repository https://doi.org/10.5281/zenodo.13787535 (Gumede et al. 2024).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Supporting Information.