

# Bat functional diversity along the Chobe River floodplain, Botswana

Dan M. Parker<sup>1,2\*</sup> ()<sup>§</sup>, & Ric T.F. Bernard<sup>1,2</sup>

<sup>1</sup>Wildlife and Reserve Management Research Group, Department of Zoology and Entomology, Rhodes University, Makhanda, 6140 South Africa

<sup>2</sup>School of Biology and Environmental Sciences, University of Mpumalanga, Mbombela, 1200 South Africa

Received 19 January 2023. To authors for revision 27 March 2023. Accepted 1 June 2023

**Insectivorous bats are vital components of tropical and subtropical ecosystems in Africa.** However, they are not only threatened by habitat fragmentation, agriculture and urbanization but are also difficult animals to study. During 2014, we used acoustic monitoring to assess the activity and relative abundance of three functional guilds of insectivorous bats at eight sites along the Chobe River floodplain, Botswana. The activity of clutter and clutter-edge foragers was significantly higher in the dry season than in the wet season. By contrast, open-air foragers, which typically forage above or away from vegetation, were more active in the wet season than in the dry season. We believe that the availability of natural vegetation and the variability in the detection of the three bat functional guilds by our acoustic detectors likely explain our results. Although bats are volant animals, our study points towards the importance of conserving important structural vegetation elements along the Chobe River floodplain landscape. Large river systems in Africa, such as the Chobe River, are vital for insectivorous bat persistence, and the provision of the ecosystem services they provide. As such, conservation of riparian corridors along rivers is crucial for maintaining intact and diverse bat communities.

**Keywords:** riparian corridors, insectivores, acoustic sampling, savanna, chiroptera, foraging guilds.

## INTRODUCTION

Insectivorous bats provide important ecosystem services in tropical ecosystems, including pest insect suppression (Bohmann *et al.*, 2011; Boyles, Cryan, McCracken & Kunz, 2011; McCracken *et al.*, 2012; Rodríguez-San Pedro *et al.*, 2020; Taylor *et al.*, 2017), seed dispersal and pollination (Kunz, Braun de Torrez, Bauer, Lobova & Fleming, 2011). However, approximately a quarter of all bat species worldwide are threatened with extinction and most African bat species are poorly studied (Monadjem, Taylor, Cotterill & Schoeman, 2020). In addition, about 15% of all bat species in southern African are listed as data deficient by the International Union for the Conservation of Nature (IUCN) (Monadjem *et al.*, 2020). Due to their nocturnal behaviour, use of multiple (often difficult to access) roosts, and their variation in flight patterns, bats can also be difficult to survey despite being important components of the ecosystems they inhabit (Parker & Bernard, 2018).

Significantly, the fragmentation of natural habitats can negatively affect bats through the reduction of prey, the loss of suitable roosting sites, and reduced foraging areas (Frey-Ehrenbold, Bontadina, Arlettaz & Obrist, 2013; Kahlonitch, Lubin & Korine, 2018).

As the largest generalist, terrestrial herbivore, African elephants (*Loxodonta africana*) can decrease canopy cover and alter the structural integrity of vegetation in savanna habitats (Cumming *et al.*, 1997; Fenton *et al.*, 1998; Jones *et al.*, 2022; Kuiper & Parker, 2014). Reduced canopy cover, because of elephant and other herbivore browsing, may not necessarily affect the availability of insect prey for bats, but it can decrease the number of available roost sites for bats (Fenton *et al.*, 1998; Monadjem, Conenna, Taylor & Schoeman, 2018; Weier, Keith, Neef, Parker & Taylor, 2020). With a reduction in roost sites, larger insectivorous bat species may be excluded from the community (Fenton *et al.* 1998). For example, Fenton *et al.* (1998) captured significantly fewer *Scotophilus* spp. at sites browsed by elephants (87 individuals) in Zimbabwe compared to the number of individuals captured at intact

\*To whom correspondence should be addressed.  
E-mail: [daniel.parker@ump.ac.za](mailto:daniel.parker@ump.ac.za)



sites (129 individuals). However, the presence of elephants (and other large herbivores) in the environment can also be beneficial for bat communities (Laverty & Berger, 2022). Laverty & Berger (2022) demonstrated that the concentration of megaherbivores (including elephants) around waterholes in the Namib Desert during the dry season enhanced overall bat activity, likely due to abundant insects which were attracted to and emerged from the waterholes and fresh dung in the environment.

Africa has areas with some of the richest bat diversity in the world (Herkt, Barnikel, Skidmore & Fahr, 2016; Tanshi *et al.*, 2022). At any one location, the bat community will include species with different foraging strategies (Monadjem, Healy, Guillerme & Kane, 2023; Monadjem, Kane, *et al.*, 2018). These strategies, which are closely linked to flight ability and echolocation, include open-air foragers that fly high above the ground and catch flying insects; clutter-edge foragers that feed at the edges of vegetation; and clutter foragers that fly within cluttered spaces such as between and within the branches of trees and feed on prey that may be in flight or sedentary (Schnitzler & Kalko, 2001). Importantly, echolocation calls can be used to identify bat species, families, and their associated foraging strategies. Recent technological and analytical advances also mean that acoustic sampling can be used to estimate bat diversity and relative abundance in an area (Flaquer, Torre & Arrizabalaga, 2007; Monadjem, Shapiro, Mtsetfwa, Reside & McCleery, 2017; Parker, 2022; Parker & Bernard, 2018). However, it is important to be cognisant of the limitations of acoustic-only assessments of bat diversity (Russo, Ancillotto & Jones, 2018; Russo & Voigt 2016). Specifically, previous research has demonstrated that the development of site-specific call reference libraries are crucial (Monadjem *et al.*, 2017; Parker & Bernard, 2018) for disentangling local echolocation call variations/dialects due to habitat (Mutumi, Jacobs & Winker, 2016) and sex differences (Kearney, Keith, Markotter, Pretorius & Seemark, 2019).

We used acoustic sampling to determine functional bat diversity along the Chobe River floodplain in Botswana. Elephants and other large herbivores have previously been demonstrated to have a significant negative effect on the structural integrity of the vegetation of the Chobe River floodplain (Skarpe *et al.*, 2004). However, like other major rivers in Africa, the Chobe River likely provides an important resource and habitat

corridor for bats (Monadjem & Reside, 2008; Taylor, Nelufule, Parker, Toussaint & Weier, 2020). In this context, understanding bat functional diversity along the Chobe River is an important research priority. We aimed to determine seasonal bat activity along the Chobe River floodplain as a first step towards understanding the role played by this important river, and its associated large herbivore communities, in influencing insectivorous bat communities.

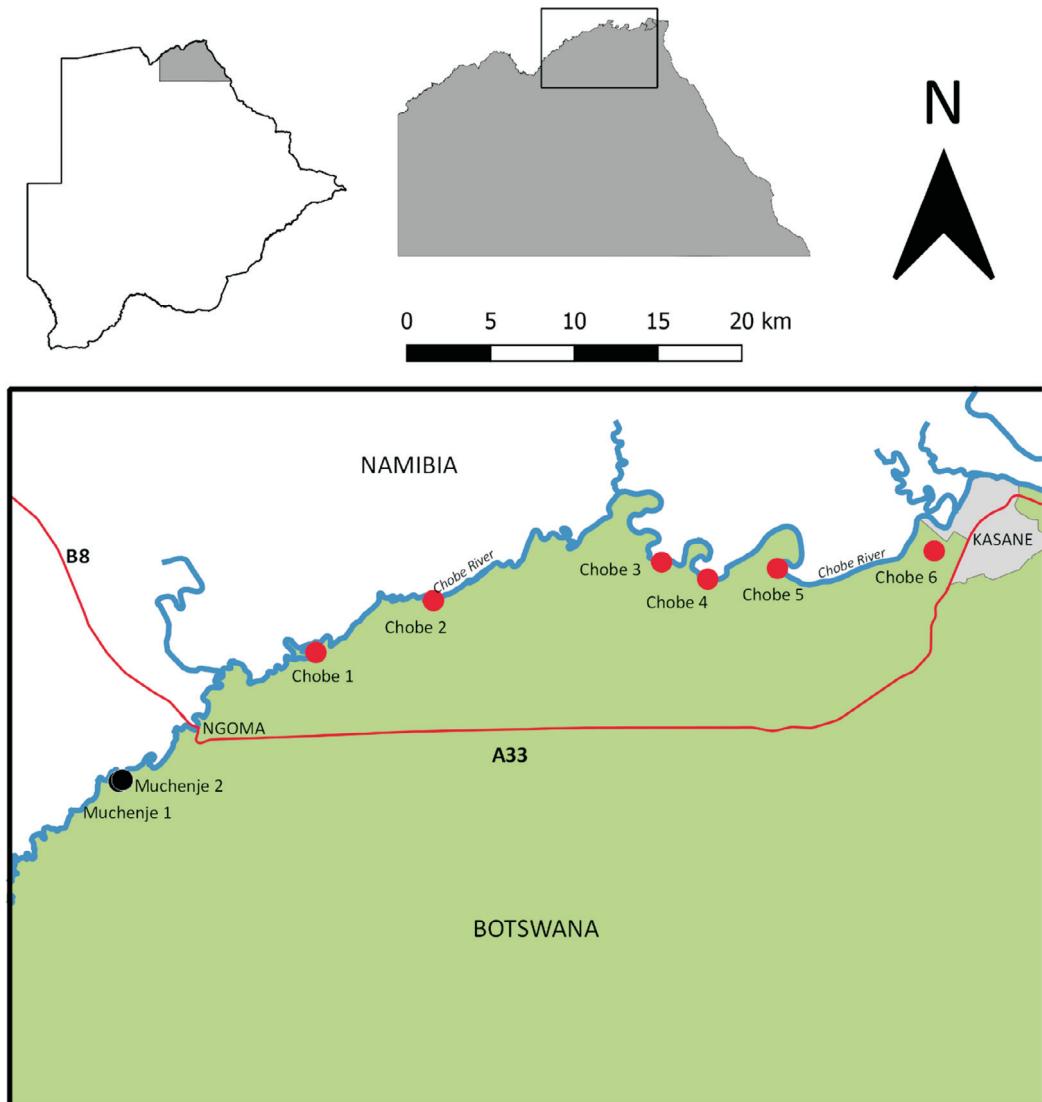
## MATERIAL AND METHODS

### Study area

Our study took place near the Chobe Enclave and within the Chobe National Park in Botswana, between the town of Kasane in the East and the village of Legothwana in the West (Lat. 17°51' 29"S; Long. 24°57'53"E) (Fig. 1). The area in which we surveyed falls within the Kalahari basin and consists of sandy soils (Vittoz *et al.*, 2020). Although eight distinct plant communities have been described for our broader study area (Vittoz *et al.*, 2020), our bat survey sites were located within *Croton megalobotrys*-*Setaria verticillata* forest along the Chobe River floodplain. Dominant tree species of this plant community include *Berchemia discolor*, *Vachellia tortilis* and *Croton megalobotrys* (Vittoz *et al.*, 2020). The study area receives approximately 650 mm of rain per annum and is characterized by a wet season between November and March (maximum daily temperatures 30–40°C) and a dry season between April and October which is cooler (Vittoz *et al.*, 2020). Agriculture, in the form of small-scale maize production and some livestock pastoralism, is the dominant land-use outside of the protected Chobe National Park. Chobe National Park is home to a high diversity of wildlife species, including elephants (Skarpe *et al.*, 2004; Vittoz *et al.*, 2020)

### Sampling sites

Six sampling sites were situated along the Chobe River floodplain within the Chobe National Park (Fig. 1). Two sampling sites were located within the fenced Muchenje campsites and cottages compound, also along the Chobe River floodplain (Fig. 1) and with the same vegetation present as the Chobe National Park sampling sites. Since the Muchenje compound is surrounded by a 2 m electrified fence and excluded elephants and all other large herbivores, we initially



**Fig. 1.** Sample locations along the Chobe River in northern Botswana (grey block in top insets). The eight bat sampling sites are denoted by red (where elephants had access) and black circles (where elephants did not have access). The red line indicates the position of the A33 (Botswana) and B8 (Namibia) highway.

wished to compare bat activity and community composition between sites 'with' and 'without' elephants. However, the Muchenje compound had only excluded elephants and other large herbivores for two years prior to our study and we did not measure the vegetation in any way at any of our sites to be certain of any 'elephant effect' on the bat communities. In addition, the distance between the two sampling sites in Muchenje was 225 m because of the limited size (5 ha) of the fenced area. As such, we elected to combine our bat acoustic data from all sites to assess bat

activity along the Chobe River floodplain. The distance between the Muchenje compound and the Chobe National Park boundary is 5.2 km. The average distance between the six sampling sites in Chobe National Park was 7.7 km (range = 3.0–13.8 km). The maximum detection range of the ultrasonic microphones used in our study (see below) was 30 m (Darras *et al.*, 2020). We recognize that this distance (and the distance between the two sites used at Muchenje) is well within the nightly flight distances of many of the bat species likely present in our study area (Monadjem *et al.*,

2020). However, since our assessment of bat communities was at the functional guild level and did not include absolute abundance estimates (see below), we do not believe that such an approach confounded our data collection or interpretation.

#### Bat sampling

Bat echolocation calls were recorded using two SM2BAT+ bat detectors (Wildlife Acoustics, U.S.A.), which were systematically deployed across eight sampling sites during three separate field trips in 2014 (Table 1). The first field trip took place between 27 February and 2 March 2014 ( $n = 4$  nights of acoustic sampling at two sites). The second field trip took place between 4 and 10 July 2014 ( $n = 10$  nights of acoustic sampling at four sites). The final field trip took place between 4 and 10 November 2014 ( $n = 10$  nights of acoustic sampling at four sites). The detectors were programmed to passively record echolocation calls for 12 hours from sunset each night (Kunz & Parsons, 2009; Parker, 2022; Parker & Bernard, 2018). Detectors were attached to suitable trees or structures 2–4 m above ground with the microphone angled at 45° to reduce the recording of echoes (Parker, 2022). Each detector was equipped with a new, omnidirectional, and waterproof SMX-US microphone connected directly to a waterproof unit, which included four interchangeable flashcards for storing recordings. The units were programmed to record at a 384 kHz sampling frequency with 16-bit sample resolution and to only record sounds above 12 dB, with a trigger frequency of 8 KHz.

#### Analysis

Kaleidoscope Pro software version 5 (Wildlife Acoustics, Concord, MA, U.S.A.) was used to analyse and identify each bat call series (a minimum of three individual bat calls in one .wav file) (Brinkley, Weier, Parker & Taylor, 2021). Kaleidoscope Pro can automatically cluster recordings based on the characteristics of each call series using either a built-in or customized classifier tool (Brinkley *et al.*, 2021). Since the customized classifier built by Brinkley *et al.* (2021) was for the species-rich northern Kruger National Park of South Africa which harbours many of the same species as northern Botswana (Monadjem *et al.*, 2020), it was used for our analysis. Based on the recorded call characteristics, all bat call recordings (wet season = 11 854 call series; dry season =

**Table 1.** The eight acoustic sampling sites used, and the number of nights sampled during each of three field trips during 2014 along the Chobe River floodplain, Botswana.

Site	Feb./Mar. 2014	July 2014	Nov. 2014
Muchenje 1	2	3	–
Muchenje 2	2	3	–
Chobe 1	–	2	–
Chobe 2	–	2	–
Chobe 3	–	–	2
Chobe 4	–	–	4
Chobe 5	–	–	2
Chobe 6	–	–	2
Total	4	10	10

12 409 call series) from the 24 nights of acoustic sampling were run through the classifier tool (Brinkley *et al.*, 2021; Parker, 2022). Call characteristics used by the software to cluster the data included the total duration of the call (Dur) measured in milliseconds, the characteristic frequency (Fc) measured in KHz, the minimum call frequency (Fmin), and the maximum call frequency (Fmax) (Monadjem *et al.*, 2020). The classifier tool identified each call series (.wav file with at least three individual calls present) to a putative species. However, since the classifier was originally developed for the northern Kruger National Park, South Africa, we elected to assign each putative species to its respective foraging category (Monadjem *et al.*, 2020) and analyse our data at the functional guild level. We recognized three foraging categories; open-air foragers, clutter foragers and clutter-edge foragers based on the putative species identifications of the cluster tool (Monadjem *et al.*, 2020). To assess the appropriateness of our cluster tool identifications and assignments, we cross-referenced the species and functional guild classifications of our classifier tool by manually identifying the bat species recorded during the first field trip (February/March 2014). Our approach for the manual species identifications followed Parker & Bernard (2018) and the results of the comparison are provided in Appendix 1. To assess whether there was any association between season and our bat functional guilds, we used a Chi-square test of independence in R (R Core Team, 2021).

## RESULTS

We manually identified 15 putative species from six families during our first field trip (Appendix 1).

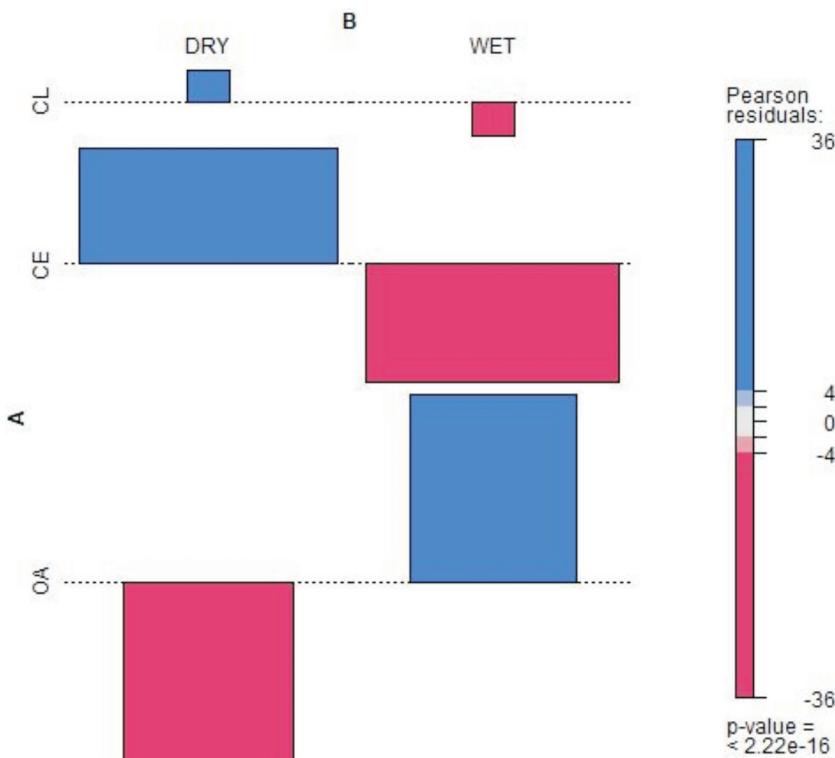
By comparison, the cluster tool identified 17 putative species from the same six families (Appendix 1). Five species (23%) were only identified during the manual identification process, seven species (32%) were only identified using the cluster tool, and 10 (45%) species were identified by both (Appendix 1). Crucially, however, all the species identified manually potentially overlapped with the call characteristics of the species identified by our cluster tool and vice versa (Appendix 1). Moreover, irrespective of species assignment, the assignment to foraging category was not compromised by using the cluster tool (Appendix 1). As such, all remaining analyses at the functional guild level utilized the call series identified by our cluster tool.

During our 2014 study (sampling nights = 24), a total of 264 hours of acoustic data were recorded across the eight sampling sites. Over the course of the three field trips, 24 263 bat call series were identified. Overall, calls were predominantly from clutter-edge foragers ( $n = 16\ 676$ ), followed by

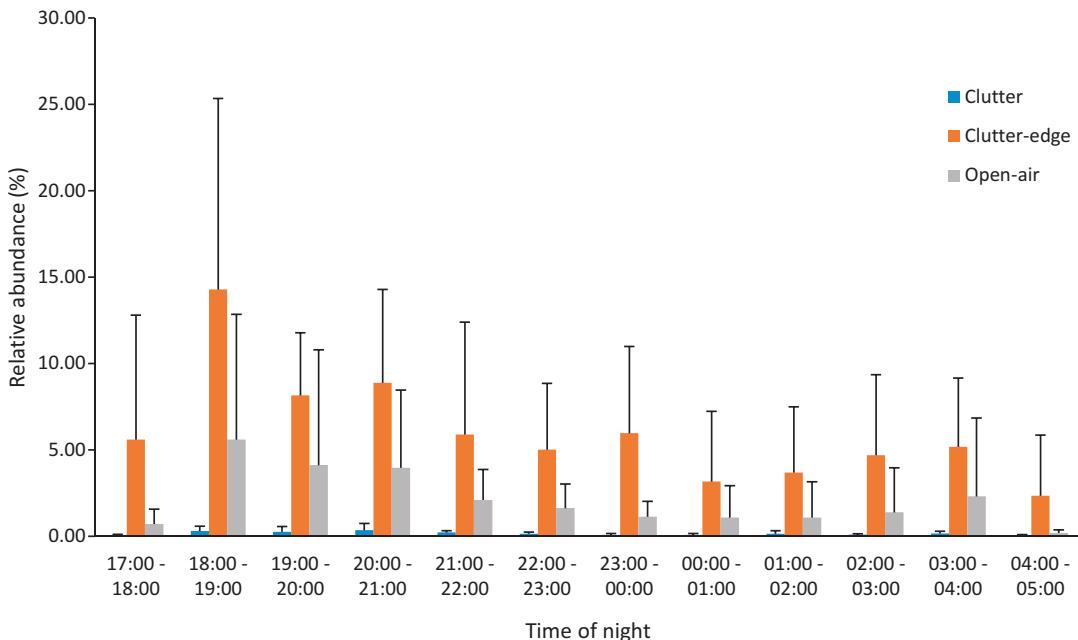
**Table 2.** Mean ( $\pm$  S.D.) number of bat call series for each identified foraging guild across all eight sampling sites in the wet and dry season of 2014 along the Chobe River floodplain, Botswana.

Season	Foraging guild	No. call series ( $\pm$ S.D.)
Dry	Clutter	32.40 $\pm$ 22.57
	Clutter-edge	1059 $\pm$ 782.48
	Open-air	150.5 $\pm$ 179.94
Wet	Clutter	12.30 $\pm$ 12.94
	Clutter-edge	608.30 $\pm$ 608.30
	Open-air	564.80 $\pm$ 730.64

open-air foragers ( $n = 7\ 153$ ) and clutter foragers ( $n = 447$ ). Clutter-edge and clutter foragers were significantly more active (*i.e.* based on number of call series recorded) in the dry season than in the wet season ( $\chi^2 = 3\ 692.9$ , d.f. = 2,  $P < 0.0001$ ; Table 2; Fig. 2). By contrast, open-air foragers were significantly more active in the wet season, than in the dry season ( $\chi^2 = 3\ 692.9$ , d.f. = 2,  $P < 0.0001$ ; Table 2; Fig. 2).



**Fig. 2.** Pearson residuals (the difference between the observed and expected values) for each variable using a Chi-square test of independence. Residuals in blue show positive associations between variables whereas residuals in red show negative associations between variables. The A-axis depicts the three foraging guilds (CL = Clutter; CE = Clutter-edge; OA = Open-air) and the B-axis depicts the dry and wet seasons.



**Fig. 3.** Mean ( $\pm$  S.D.) relative abundance (% of total no. of call series) of each of the three bat functional guilds (see text for details) over the course of the night (for all sampling nights) along the Chobe River floodplain, Botswana.

### Nightly activity

The relative abundance (*i.e.* the proportion of call series per hour of the night) of clutter foragers was low but appeared to be highest between 20:00 and 21:00 (Fig. 3). By contrast, clutter-edge and open-air foragers showed more sustained nightly activity (Fig. 3). However, both foraging groups showed early evening peaks in activity which then declined over the course of the night.

### DISCUSSION

Most of the bat calls we recorded during our study were from clutter-edge foragers, followed by open-air foragers, and, finally, clutter foragers. In addition, clutter-edge and clutter foragers were significantly more active in the dry season than in the wet season. Open-air foragers showed the opposite trend and were significantly more active in the wet season than in the dry season.

Vegetation provides key structural elements that are important for clutter and clutter-edge foragers as the bats forage around vegetation edges and within the natural vegetation, likely explaining the prevalence of clutter-edge foragers, especially in the dry season (Shapiro, Monadjem, Röder & McCleery, 2020). Open-air foragers search for insects above vegetation (sometimes up to several kilometres in the air) rather than along its edges

(Monadjem *et al.*, 2020). By foraging higher-up, in open spaces, these bats may have also been beyond the recording range of the detectors in the dry season (Monadjem *et al.*, 2017; Müller *et al.*, 2013). Clutter foragers had the lowest activity of the three guilds in our study. This foraging guild typically has short and broad wings, ideal for high maneuverability for foraging in dense, cluttered vegetation (Monadjem *et al.*, 2020; Shapiro *et al.*, 2020). Clutter foragers also have short detection ranges with bat detectors (Monadjem *et al.*, 2017). Thus, a true indication of their activity may have been elusive because we used an acoustic-only sampling design (Kerbiriou *et al.*, 2019; Parker & Bernard, 2018). Moreover, the activity of clutter foragers could also be low because some members of the guild typically roost in small groups and generally have lower population numbers than bats in other guilds (Monadjem *et al.*, 2020). Nevertheless, Jung & Threlfall (2016) suggest that clutter foragers are the most sensitive to structural changes in their environment. As such, we recommend that future research concentrates on both the live-capture and acoustic recording of bats from this guild where large herbivores are present to disentangle the potential effects of elephants and other forms of browsing on this indicator group.

Our study showed some seasonal patterns in bat activity, commonly observed for tropical savannas in southern Africa (Monadjem & Reside, 2008; Mtsetfwa *et al.*, 2018; Weier *et al.*, 2018), and elsewhere (Mendes, Fonseca, Marques, Maia & Ramos Pereira, 2017). The temporal change in bat activity (generally lower in the dry season) suggests that bat activity is likely related to insect prey availability which decreases in the dry season (Heim *et al.*, 2017; Pluciński, Zmihorski & Pluciński, 2015; Weier *et al.*, 2018). In addition, the positive influence of the Chobe River on bat richness and activity may have decreased during the dry season, similar to the findings of Taylor *et al.* (2020) along the Limpopo River in South Africa. However, we did not formally assess prey availability in our study, making this an important future research avenue.

Vegetation cover is vital for retaining a stable bat community (Fuentes-Montemayor, Goulson, Cavin, Wallace & Park, 2013; Rodríguez-San Pedro *et al.*, 2020). In addition, riparian areas and river valleys, with their associated vegetation, have been shown to be important corridors for bats to commute between roosting and foraging habitats (Akasaka, Akasaka & Nakamura, 2012; Furmarkiewicz & Kucharska, 2009; Monadjem & Reside, 2008). Moreover, river systems in semi-arid savanna habitats in Africa are vital for promoting bat richness, diversity, activity and community structure (Taylor *et al.*, 2020). We believe that our study provides important information on the potential role of natural vegetation along a key riparian corridor for bats. If the vegetation along the Chobe River floodplain were to become homogenized by, for example, heavy browsing by elephants and/or other large herbivores, it is possible that the regional diversity of insectivorous bats may be threatened (Underwood, Viers, Klausmeyer, Cox & Shaw, 2009). However, because bats are volant animals, capable of commuting between suitable foraging and roosting sites in the landscape, it may be feasible to implement conservation management strategies that enhance bat populations and assemblages. Such efforts could include the preservation of intact vegetation patches within protected areas like the Chobe National Park and perhaps the introduction of new elements such as indigenous trees (Frey-Ehrenbold *et al.*, 2013) outside the protected area to allow for habitat connectivity and additional roosting opportunities.

## ACKNOWLEDGEMENTS

We thank the Director of Wildlife and National Parks in Botswana for permission to conduct this research (Permit No.: EWT/8/36/4XXV(52)). Funding was provided by Rhodes University, and we thank Gareth Nuttall-Smith for designing the map used in Fig. 1.

## COMPETING INTERESTS

The authors declare no conflict of interests.

---

### <sup>§</sup>ORCID iD

D.M. Parker  0000-0001-7555-5674

## REFERENCES

- Akasaka, T., Akasaka, M. & Nakamura, F. (2012). Scale-independent significance of river and riparian zones on three sympatric *Myotis* species in an agricultural landscape. *Biological Conservation*, 145(1), 15–23.  
<https://doi.org/10.1016/j.biocon.2011.08.017>
- Bohmann, K., Monadjem, A., Lehmkuhl Noer, C., Rasmussen, M., Zeale, M.R.K., Clare, E., Jones, G., Willemsen, E. & Gilbert, M.T.P. (2011). Molecular diet analysis of two African free-tailed bats (Molossidae) using high throughput sequencing. *PLOS ONE*, 6(6), e21441.  
<https://doi.org/10.1371/journal.pone.0021441>
- Boyles, J.G., Cryan, P.M., McCracken, G.F. & Kunz, T.H. (2011). Economic importance of bats in agriculture. *Science*, 332(6025), 41–42.  
<https://doi.org/10.1126/science.1201366>
- Brinkley, E.R., Weier, S.M., Parker, D.M. & Taylor, P.J. (2021). Three decades later in the northern Kruger National Park: multiple acoustic and capture surveys may underestimate the true local richness of bats based on historical collections. *Hystrix the Italian Journal of Mammalogy*, 32(2), 0.  
<https://doi.org/10.4404/hystrix-00319-2020>
- Cumming, D.H.M., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, A.G.P., Hovorka, M.D., Johnston, D.S., Kalcounis, M.C., Mahlangu, Z. & Portfors, C.V. (1997). Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science*, 93, 231–236.
- Darras, K.F.A., Deppe, F., Fabian, Y., Kartono, A.P., Angulo, A., Kolbrek, B., Mulyani, Y.A. & Prawiradilaga, D.M. (2020). High microphone signal-to-noise ratio enhances acoustic sampling of wildlife. *PeerJ*, 8, e9955.  
<https://doi.org/10.7717/peerj.9955>
- Fenton, M.B., Cumming, D.H.M., Rautenbach, I.L., Cumming, G.S., Cumming, M.S., Ford, G., Taylor, R.D., Dunlop, J., Hovorka, M.D., Johnston, D.S., Portfors, C.V., Kalcounis, M.C. & Mahlangu, Z. (1998). Bats and the loss of tree canopy in African woodlands. *Conservation Biology*, 12(2), 399–407.  
<https://doi.org/10.1111/j.1523-1739.1998.96376.x>
- Flaquer, C., Torre, I. & Arrizabalaga, A. (2007). Comparison of sampling methods for inventory of bat communities. *Journal of Mammalogy*, 88(2), 526–533.  
<https://doi.org/10.1644/06-MAMM-A-135R1.1>

- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R. & Obrist, M.K. (2013). Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology*, 50(1), 252–261.  
<https://doi.org/10.1111/j.1365-2664.12034>
- Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M. & Park, K.J. (2013). Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment*, 172, 6–15.  
<https://doi.org/10.1016/j.agee.2013.03.019>
- Furmankiewicz, J. & Kucharska, M. (2009). Migration of bats along a large river valley in southwestern Poland. *Journal of Mammalogy*, 90(6), 1310–1317.  
<https://doi.org/10.1644/09-MAMM-S-099R1.1>
- Heim, O., Lorenz, L., Kramer-Schadt, S., Jung, K., Voigt, C.C. & Eccard, J.A. (2017). Landscape and scale-dependent spatial niches of bats foraging above intensively used arable fields. *Ecological Processes*, 6(1), 24.  
<https://doi.org/10.1186/s13717-017-0091-7>
- Herkt, K.M.B., Barnikel, G., Skidmore, A.K. & Fahr, J. (2016). A high-resolution model of bat diversity and endemism for continental Africa. *Ecological Modelling*, 320, 9–28.
- Jones, M.M., Fletcher Jr, R., Kruger, L., Monadjem, A., Simelane, P. & McCleery, R. (2022). Drought limits large trees in African savannas with or without elephants. *Austral Ecology*, 47(8), 1668–1684.
- Jung, K. & Threlfall, C.G. (2016). Urbanisation and its effects on bats—A global meta-analysis. In C.C. Voigt & T. Kingston (Eds), *Bats in the anthropocene: conservation of bats in a changing world* (pp. 13–33). Springer International Publishing.  
[https://doi.org/10.1007/978-3-319-25220-9\\_2](https://doi.org/10.1007/978-3-319-25220-9_2)
- Kahnonitch, I., Lubin, Y. & Korine, C. (2018). Insectivorous bats in semi-arid agroecosystems – effects on foraging activity and implications for insect pest control. *Agriculture, Ecosystems & Environment*, 261, 80–92.  
<https://doi.org/10.1016/j.agee.2017.11.003>
- Kearney, T.C., Keith, M., Markotter, W., Pretorius, M. & Seemark, E.C.J. (2019). Bat species (Mammalia: Chiroptera) occurring at Telperion Nature Reserve. *Annals of the Ditsong National Museum of Natural History*, 8(1), 30–42.
- Kerbiriou, C., Bas, Y., Le Viol, I., Lorrillière, R., Mougnot, J. & Julian, J.-F. (2019). Bat pass duration measurement: an indirect measure of distance of detection. *Diversity*, 11(3), 47.
- Kuiper, T.R. & Parker, D.M. (2014). Elephants in Africa: big, grey biodiversity thieves? *South African Journal of Science*, 110(3/4), 1–3.  
<https://doi.org/10.1590/sajs.2014/a0058>
- Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T. & Fleming, T.H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, 1223(1), 1–38.  
<https://doi.org/10.1111/j.1749-6632.2011.06004.x>
- Kunz, T.H. & Parsons, S. (2009). *Ecological and behavioral methods for the study of bats*. Baltimore, U.S.A.: Johns Hopkins University Press.
- Laverty, T.M. & Berger, J. (2022). Indirect effects of Afri- can megaherbivore conservation on bat diversity in the world's oldest desert. *Conservation Biology*, 36(2).  
<https://doi.org/10.1111/cobi.13780>
- McCracken, G.F., Westbrook, J.K., Brown, V.A., Eldridge, M., Federico, P. & Kunz, T.H. (2012). Bats track and exploit changes in insect pest populations. *PLOS ONE*, 7(8), e43839.  
<https://doi.org/10.1371/journal.pone.0043839>
- Mendes, E.S., Fonseca, C., Marques, S.F., Maia, D. & Ramos Pereira, M.J. (2017). Bat richness and activity in heterogeneous landscapes: guild-specific and scale-dependent? *Landscape Ecology*, 32(2), 295–311.  
<https://doi.org/10.1007/s10980-016-0444-0>
- Monadjem, A., Conenna, I., Taylor, P.J. & Schoeman, M.C. (2018). Species richness patterns and functional traits of the bat fauna of arid southern Africa. *Journal of Mammalogy*, 29(1):19–24.  
<https://doi.org/10.4404/hystrix-00016-2017>
- Monadjem, A., Healy, K., Guillerme, T. & Kane, A. (2023). Dispersal ability is associated with contrasting patterns of beta diversity in African small mammal communities. *Journal of Biogeography*, 50(3), 539–550.
- Monadjem, A., Kane, A., Taylor, P., Richards, L.R., Hall, G. & Woodborne, S. (2018). Morphology and stable isotope analysis demonstrate different structuring of bat communities in rainforest and savannah habitats. *Royal Society Open Science*, 5(12), 180849.
- Monadjem, A. & Reside, A. (2008). The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. *Acta Chiropterologica*, 10(2), 339–348.  
<https://doi.org/10.3161/150811008X414917>
- Monadjem, A., Shapiro, J.T., Mtsetfwa, F., Reside, A.E. & McCleery, R.A. (2017). Acoustic call library and detection distances for bats of Swaziland. *Acta Chiropterologica*, 19(1), 175–187.  
<https://doi.org/10.3161/15081109ACC2017.19.1.014>
- Monadjem, A., Taylor, P.J., Cotterill, F.P.D. & Schoeman, M.C. (2020). *Bats of southern and central Africa: a biogeographic and taxonomic synthesis* (2nd edn). Johannesburg, South Africa: Wits University Press.
- Mtsetfwa, F., McCleery, R.A. & Monadjem, A. (2018). Changes in bat community composition and activity across a conservation-agriculture boundary. *African Zoology*, 53(3), 99–106.  
<https://doi.org/10.1080/15627020.2018.1531726>
- Müller, J., Brandl, R., Buchner, J., Pretzsch, H., Seifert, S., Strätz, C., Veith, M. & Fenton, B. (2013). From ground to above canopy—Bat activity in mature forests is driven by vegetation density and height. *Forest Ecology and Management*, 306, 179–184.  
<https://doi.org/10.1016/j.foreco.2013.06.043>
- Mutumi, G.L., Jacobs, D.S. & Winker, H. (2016). Sensory drive mediated by climatic gradients partially explains divergence in acoustic signals in two horseshoe bat species, *Rhinolophus swinnyi* and *Rhinolophus simulator*. *PLOS ONE*, 11(1), e0148053.
- Parker, D.M. (2022). Three new insectivorous bat species records for the Mountain Zebra National Park, South Africa. *African Journal of Wildlife Research*, 52, 17–22.  
<https://doi.org/10.3957/056.052.00017>

- Parker, D.M. & Bernard, R.T.F. (2018). The use of acoustic detectors for assessing bat species richness and functional activity in a South African National Park. *Mammalia*, 83(1), 53–63.  
<https://doi.org/10.1515/mammalia-2017-0055>
- Pluciński, T., Źmihorski, M. & Pluciński, P. (2015). Impact of night-time crop harvesting on bat activity in agricultural landscape. *Zoology and Ecology*, 25, 1–7.  
<https://doi.org/10.1080/21658005.2014.999501>
- R Core Team (2021). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.  
<https://www.R-project.org/>
- Rodríguez-San Pedro, A., Allendes, J. L., Beltrán, C.A., Chaperon, P.N., Saldarriaga-Córdoba, M.M., Silva, A.X. & Grez, A.A. (2020). Quantifying ecological and economic value of pest control services provided by bats in a vineyard landscape of central Chile. *Agriculture, Ecosystems & Environment*, 302, 107063.  
<https://doi.org/10.1016/j.agee.2020.107063>
- Russo, D., Ancillotto, L. & Jones, G. (2018). Bats are still not birds in the digital era: echolocation call variation and why it matters for bat species identification. *Canadian Journal of Zoology*, 96(2), 63–78.
- Russo, D. & Voigt, C.C. (2016). The use of automated identification of bat echolocation calls in acoustic monitoring: a cautionary note for a sound analysis. *Ecological Indicators*, 66, 598–602.
- Schnitzler, H-U. & Kalko, E.K. (2001). Echolocation by insect-eating bats: we define four distinct functional groups of bats and find differences in signal structure that correlate with the typical echolocation tasks faced by each group. *Bioscience*, 51(7), 557–569.
- Shapiro, J.T., Monadjem, A., Röder, T. & McCleery, R.A. (2020). Response of bat activity to land cover and land use in savannas is scale-, season-, and guild-specific. *Biological Conservation*, 241, 108245.  
<https://doi.org/10.1016/j.biocon.2019.108245>
- Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., du Toit, J.T., Halley, D.J., Hytteborn, H., Makhabu, S., Mari, M., Marokane, W., Masunga, G., Modise, D., Moe, S.R., Mojaphoko, R., Mosugelo, D., Mtsumi, S., Neo-Mahupeleng, G., Ramotadima, M., Wegge, P. (2004). The return of the giants: ecological effects of an increasing elephant population. *AMBIO: A Journal of the Human Environment*, 33(6), 276–282.  
<https://doi.org/10.1579/0044-7447-33.6.276>
- Tanshi, I., Obitte, B.C., Monadjem, A., Rossiter, S.J., Fisher-Phelps, M. & Kingston, T. (2022). Multiple dimensions of biodiversity in paleotropical hotspots reveal comparable bat diversity. *Biotropica*, 54(5), 1205–1216.
- Taylor, P.J., Matamba, E., Steyn, J.N., Nangammbi, T., Zepeda-Mendoza, M.L. & Bohmann, K. (2017). Diet determined by next generation sequencing reveals pest consumption and opportunistic foraging by bats in macadamia orchards in South Africa. *Acta Chiropterologica*, 19(2), 239–254.  
<https://doi.org/10.3161/15081109ACC2017.19.2.003>
- Taylor, P.J., Nelufule, M., Parker, D.M., Toussaint, D.C. & Weier, S.M. (2020). The Limpopo River exerts a powerful but spatially limited effect on bat communities in a semi-arid region of South Africa. *Acta Chiropterologica*, 22(1), 75.  
<https://doi.org/10.3161/15081109ACC2020.22.1.007>
- Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L. & Shaw, M.R. (2009). Threats and biodiversity in the mediterranean biome. *Diversity and Distributions*, 15(2), 188–197.  
<https://doi.org/10.1111/j.1472-4642.2008.00518.x>
- Vittoz, P., Pellacani, F., Romanens, R., Mainga, A., Verrecchia, E.P. & Fynn, R.W.S. (2020). Plant community diversity in the Chobe Enclave, Botswana: insights for functional habitat heterogeneity for herbivores. *KOEDOE - African Protected Area Conservation and Science*, 62(1).  
<https://doi.org/10.4102/koedoe.v62i1.1604>
- Weier, S.M., Grass, I., Linden, V.M.G., Tscharntke, T. & Taylor, P.J. (2018). Natural vegetation and bug abundance promote insectivorous bat activity in macadamia orchards, South Africa. *Biological Conservation*, 226, 16–23.  
<https://doi.org/10.1016/j.biocon.2018.07.017>
- Weier, S.M., Keith, M., Neef, G.G., Parker, D.M. & Taylor, P.J. (2020). Bat species richness and community composition along a mega-transect in the Okavango River Basin. *Diversity*, 12(5), 188.  
<https://doi.org/10.3390/d12050188>

Responsible Editor: L.W. Traill

**Appendix 1.** Summary table of the putative bat species, family, and foraging category (Cl = Clutter; Ce = Clutter-edge; Oa = Open-air) which were identified manually and using a Kaleidoscope cluster tool at two sites along the Chobe River floodplain, Botswana during February/March 2014. Reference call characteristics are shown and are based on published data (Brinkley *et al.*, 2021; Monadjem *et al.*, 2020; Parker & Bernard, 2018) and unpublished release call data held by the authors. Data are means  $\pm$  S.D. Fc = the characteristic frequency - the flattest portion of the call (kHz); Fmax = maximum frequency (kHz); Fmin = minimum frequency (kHz); Foraging category and potential overlap species (*i.e.* some or all echolocation call characteristics are shared with one or more species) following Monadjem *et al.* (2020).

Species	Potential overlap species	Foraging category	Manual Classifier	Reference call characteristics		
				Fc	Fmax	Fmin
<b>HIPPOSIDERIDAE</b>						
<i>Hipposideros caffer</i>	–	Cl	X	X	143.00 $\pm$ 1.64	143.28 $\pm$ 1.63
<i>Hipposideros vittatus</i>	–	Cl	X		63.30 $\pm$ 1.40	64.40 $\pm$ 1.60
<b>RHINOLOPHIDAE</b>						
<i>Rhinolophus smithersi</i>	–	Cl		X	47.23 $\pm$ 1.62	47.47 $\pm$ 1.50
<i>Rhinolophus fumigatus</i>	–	Cl		X	54.70 $\pm$ 0.60	55.80 $\pm$ 0.90
<b>EMBALLONURIDAE</b>						
<i>Taphozous mauritianus</i>	<i>C. pumilus</i> / <i>M. welwitschii</i>	Oa		X	27.90 $\pm$ 2.50	33.20 $\pm$ 8.00
<b>MOLOSSIDAE</b>						
<i>Chaerephon ansorgei</i>	<i>T. ventralis</i> / <i>C. nigeriae</i> / <i>T. fulminans</i>	Oa	X	X	18.21 $\pm$ 1.01	20.92 $\pm$ 3.39
<i>Chaerephon pumilus</i>	<i>T. aegyptiaca</i> / <i>M. condylurus</i> / <i>T. mauritianus</i>	Oa	X	X	26.65 $\pm$ 2.53	34.87 $\pm$ 5.75
<i>Mops condylurus</i>	<i>C. pumilus</i> / <i>T. aegyptiaca</i> / <i>T. perforatus</i>	Oa		X	29.12 $\pm$ 0.70	30.72 $\pm$ 1.52
<i>Tadarida aegyptiaca</i>	<i>T. mauritianus</i> / <i>C. pumilus</i>	Oa	X	X	23.68 $\pm$ 1.51	29.23 $\pm$ 5.77
<b>MINIOPTERIDAE</b>						
<i>Miniopterus natalensis</i>	<i>P. rusticus</i>	Ce	X	X	49.91 $\pm$ 0.95	67.84 $\pm$ 4.75
<i>Miniopterus fraterculus</i> *	<i>N. nana</i>	Ce	X		62.30 $\pm$ 1.90	–
<b>VESPERTILIONIDAE</b>						
<i>Eptesicus hottentotus</i>	<i>L. botswanae</i> / <i>M. tricolor</i> / <i>M. welwitschii</i> / <i>S. dingani</i>	Ce		X	33.50 $\pm$ 2.50	55.90 $\pm$ 9.0
<i>Laephotis botswanae</i>	<i>S. dingani</i> / <i>M. welwitschii</i> / <i>E. hottentotus</i>	Ce	X		31.46 $\pm$ 1.47	53.20 $\pm$ 7.20
<i>Myotis tricolor</i>	<i>M. bocagei</i>	Ce	X	X	42.68 $\pm$ 0.70	70.40 $\pm$ 3.85
<i>Neoromicia capensis</i>	<i>S. viridis</i> / <i>N. schlieffenii</i>	Ce	X	X	39.54 $\pm$ 1.17	63.06 $\pm$ 5.75
<i>Neoromicia nana</i>	<i>N. thebaica</i>	Ce	X	X	68.53 $\pm$ 2.10	85.09 $\pm$ 10.70
						67.61 $\pm$ 2.57

*Continued on p. 55*

**Appendix 1** (continued)

Species	Potential overlap species	Foraging category	Manual	Classifier	Reference call characteristics		
					Fc	Fmax	Fmin
<i>Neoromicia zuluensis</i>	<i>P. hesperidus</i> / <i>P. rusticus</i>	Ce	X	X	48.11 ± 1.17	63.23 ± 4.44	47.70 ± 1.36
<i>Nycticeinops schlieffeni</i>	<i>M. tricolor</i> / <i>N. capensis</i> / <i>P. hesperidus</i>	Ce		X	42.10 ± 0.30	42.80 ± 1.30	40.10 ± 1.50
<i>Pipistrellus hesperidus</i>	<i>M. natalensis</i> / <i>M. tricolor</i> / <i>N. capensis</i> / <i>N. zuluensis</i> / <i>P. rusticus</i>	Ce	X		45.30 ± 1.60	63.00 ± 11.1	44.60 ± 1.60
<i>Pipistrellus rusticus</i>	<i>M. natalensis</i> / <i>H. anchietae</i>	Ce	X	X	55.20 ± 0.92	64.41 ± 3.75	54.00 ± 1.05
<i>Scotophilus dinganii</i>	<i>E. hottentotus</i> / <i>L. botswanae</i> / <i>M. tricolor</i> / <i>M. welwitschii</i>	Ce		X	33.00 ± 1.20	53.60 ± 8.10	32.30 ± 1.10
Unknown vespertilionid (36 kHz)	<i>L. botswanae</i> / <i>S. dinganii</i> / <i>E. hottentotus</i>	Ce	X		36.36 ± 1.02	57.92 ± 7.02	35.43 ± 1.47

\*Identification made based solely on Monadjem *et al.* (2020).