Revealing year-round activity of cave-dwelling insectivorous bats with a sonotype classifier in data-deficient areas.

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ABSTRACT

Context: Bats are the only mammals who have conquered the skies and the leading mammals in terms of total biomass with the exception of humans and domestic mammals. However, the ecology of many bat species is still unknown, especially in poorly sampled regions such as Central Africa.

Aims: We present the first application of an acoustic method for studying the nocturnal activity patterns and annual phenology of bat activity of cave bat communities in regions where no bat acoustic classifier exists.

Methods: In two caves (Mont Belo and Boundou) in the Republic of Congo, which are home to several species of insectivorous bats throughout the year, we set up a passive acoustic monitoring (PAM) over a period of 19 months. To identify the massive recordings collected, we used a sonotype classifier. To assign a species name or species group to the different sonotypes identified by the classifier, we collected local reference calls by capturing bats at the cave entrances. This enabled us to identify two bat groups and three species despite the absence of local call libraries. The capture sessions also allowed us to collect information about the reproductive condition of the individuals, which we interpreted in relation to the annual phenology of bat activity. To quantify bat activity, we defined the activity of each acoustic group as the number of bat passes, where a bat pass corresponds to the detection of one or several echolocation calls within a five-second interval. This standardized measure allowed us to quantify nightly and seasonal variations in activity.

Key results: The nightly activity displayed strong peaks in the evening and the morning, except during the long rainy season, when a tri- or quadri-modal activity was detected. This more evenly distributed activity throughout the night is related to the period of juvenile (gestation, parturition and lactation). For all acoustic groups, we also observed a higher activity during the rainy seasons and the short dry season, compared to the long dry season. This high activity is linked to the lactation period, the weaning and increasing independence of young bats, and potentially the mating period. Finally, the reproductive activity of insectivorous bat species is synchronized with the period of high resource availability.

Conclusion : This study represents the first long-term acoustic monitoring of cave bats in the Republic of Congo. This was allowed by the use of a classifier built without any pre-existing regional call data, highlighting a practical pathway for studying bat activity in other data-deficient regions.

Implications : Information about the biological status of individuals captured at the monitored caves in association with the cave annual activity phenology produced with this method are key to progress in the understanding of the ecology and the conservation issues of cave bat communities, which are particularly threatened globally.

Keywords *:* PAM, Tadarida, activity pattern, abundance, bats phenology, Congo

Introduction

Human activities are currently triggering a massive loss of biodiversity, with rates of species decline or extinction unprecedented for several millennia (Barnosky et al., 2011; Ceballos et al., 2015; IPBES, 2019). However, the scale of this crisis is probably still concealed by the lack of data on the populations of many species around the world (Hughes, 2017). Chiropterans are one of these taxa, as information on their populations is still poor despite the many threats they face (Furey & Racey, 2016; Mickleburgh et al., 2002).

Of the 1,500 recognised bat species worldwide, 38% are cave-dwelling species (IUCN, 2023; Simmons & Cirranello, 2025, Tanalgo et al., 2022), living in caves or natural or man-made underground cavities (e.g. mines or tunnels). These habitats are crucial for bats, which use them to reproduce, raise their young, rest on a daily or temporary basis and hibernate (Barros et al., 2020; Keeley & Tuttle, 1999; Kunz, 1982; Kunz et al., 2003; Lewis, 1995; Mering & Chambers, 2014; Ormsbee et al., 2007; Russo & Ancillotto, 2015; Struebig et al., 2009; The Protection of Bat Roost Guidelines Subcommittee et al., 1992). In tropical environments, most cave-dwelling species use caves as permanent roosts, and several species can co-occur in groups of hundreds or even thousands (Kunz, 1982; Monadjem et al., 2020). However, despite their ecological importance, these fragile environments are threatened and still poorly protected on a global scale (Balogh et al., 2020; Medellin et al., 2017; Neuhuber et al., 2020). Threats include resources extraction (minerals, guano, etc.) or recreational activities (caving, tourism, etc.) (Okonkwo et al., 2017; Simons, 1998). In turn, cave-dwelling bats generate ecological niches for diverse cave communities through the resources they produce (e.g., live and dead-bats, guano) (Labadie et al. 2025a).

Deleva et al. (2023) highlight the need to identify and protect key underground roosts. Broader global syntheses emphasize that effective conservation of bats roosting underground requires coordinated protection, monitoring, and policy measures (Meierhofer et al., 2024). Recent tools, such as the bat cave vulnerability index, provide integrative frameworks for assessing and ranking cave vulnerability at multiple scales (Tanalgo & Hughes, 2024). Unfortunately, due to largescale underfunding for bat research and conservation, the ecological information available on cave-dwelling bats is often too limited to inform these tools. In particular, data on bat populations and annual phenology of the occupation of caves is lacking, especially in African countries (Moutaouakil et al., 2024; Pretorius et al., 2021). Understanding when and how bats use caves throughout the year is therefore fundamental to assigning appropriate conservation value to each site. For example, a cave that hosts colonies during key reproductive periods (e.g. parturition or lactation) contributes critically to population persistence and should thus receive a higher conservation rank than a site used only for transient or non-reproductive activities.

The annual phenology of species at a given site is the result of the adaptation of its activity patterns to meet three primary needs: feeding, reproduction or rest (Alcock, 2013; Appel et al., 2019; Jones & Rydell, 1994). The phenology of bat activity in tropical caves reflects reproductive cycles adapted to local environmental conditions. In African regions, the timing of parturition in cave-dwelling insectivorous bats is closely linked to rainfall and subsequent insect availability (Cumming & Bernard, 1997). Insect abundance peaks about a month after peak rainfall, while births occur earlier to ensure weaning before maximum prey availability (Cumming & Bernard, 1997; Happold & Happold, 1990). This synchrony, though variable among species, highlights strong selective pressures imposed by seasonal food dynamics. Such cave-associated activity patterns are especially critical during maternity, when energetic demands are highest, and their

alteration may signal adaptation to changing microclimatic or trophic conditions (Nkoana, 2020; Wolkovich et al., 2014).

Historically, bat communities have been studied using both invasive and non-invasive methods. Invasive methods, such as bat capture, remain often necessary to make an exhaustive species inventory, verify individual reproductive status and collect biometric data or samples (Appel et al., 2021; Barnhart & Gillam, 2014; Flaquer et al., 2007). Direct observation of individuals in their roost (e.g., cave, tree) or when they emerge to forage have also provided information on their behavior, abundance and movements (Thomas & West, 1989). Visual counts are sometimes difficult because of the large number of bats or the difficulty accessing the roosting sites. In addition, human observations are time-consuming and observer bias (Forsyth et al., 2006; Koger et al., 2023; Westcott & McKeown, 2004).

The development of new technologies has made it possible to set up precise counts of individuals in caves using digital image analysis, thermal cameras (Azmy et al., 2012; Sabol & Hudson, 1995) or bioacoustics (Sugai et al., 2020; Whiting et al., 2021). Passive acoustic monitoring (PAM) has a number of advantages: it is non-invasive, applicable in all environments (even the most remote ones), can collect a large amount of information such as abundance proxies, and the analysis can be automated (Hill et al., 2019). PAM exploits the use of echolocation to move and forage by more than 70% of the world's bats (Browning et al., 2017; Gibb et al., 2019), Pteropodidae excluded. Recording these often species-specific sounds makes it possible to make a quantitative monitoring of bat species and/or communities. In recent years, several protocols, including that of Revilla-Martin et al (2020), have demonstrated the reliability of this technique compared to other methods for counting bat populations as they leave caves. Recent work by Appel et al. (2025) demonstrated that combining active and passive monitoring and optimally placing recorders at cave entrances maximizes species detection and comparability across sites and seasons.

However, PAM also faces limitations, such as the difficulty to distinguish between overlapping calls. This issue is compounded by the lack of reference call libraries in many regions, especially in Central Africa, and thus the impossibility to identify species in massive recordings. Sonotype classifiers were recently developped to counter this issue (Roemer et al., 2019) and opened the possibility to classify bat sounds in shapes and frequency groups where no species classifier is available. Labadie et al. (2025b) proposed a method to apply a sonotype classifier in association with local reference calls collected at cave entrances to obtain sound identification at the species level, or acoustic group, in massive recordings in the Republic of Congo. However, no application of this method has been reported so far.

The aim of this study was to demonstrate the possibility to conduct quantitative studies of cave-dwelling bat communities using acoustics in data-deficient areas. The Republic of Congo has very limited information on the acoustic repertoire of bats (Bates et al., 2013). Over a period of 19 months, we set up a PAM to describe the annual phenology of bat activity in two caves. We used the Tadarida sonotype classifier to classify bat vocalizations. To associate each sonotype with a species, we performed captures to obtain a species list and record reference calls, following the approach of Labadie et al. (2025b, c). To progress in the understanding of the biology and the ecology of bats in Central Africa, we compared seasonal variation in activity with the reproductive

status of bats assessed from capture data. We expected species to show higher activity during periods of breeding and juvenile rearing (Catto et al., 1995; Dietz & Kalko, 2006).

Methods

Study area

Our study took place in the Republic of Congo, in a highly karstic region favouring the presence of numerous caves and/or cavities of various sizes in a rolling habitat of herbaceous savannah with patches of tropical forest. We selected two caves for the study: Boundou and Mont Belo, located in the Bouenza and Niari departments, about 50 km apart. Both caves are close to Dolisie, one of the three most important towns in the Republic of Congo on the southbound Brazzaville - Pointe Noire route. In this region, the seasons are divided into four: the short dry season (January to February), the short rainy season (March to May), the long dry season (June to mid-September) and the long rainy season (mid-September to December).

The Mont Belo Cave has several chambers (a main chamber and two secondary chambers). The Boundou Cave, on the other hand, is a smaller cavity integrated into a rocky complex, with a main chamber and an annex chamber that is very difficult for humans to access, and houses a small internal lake. Details of the configuration of the two caves in this study are presented in Fig. 1.

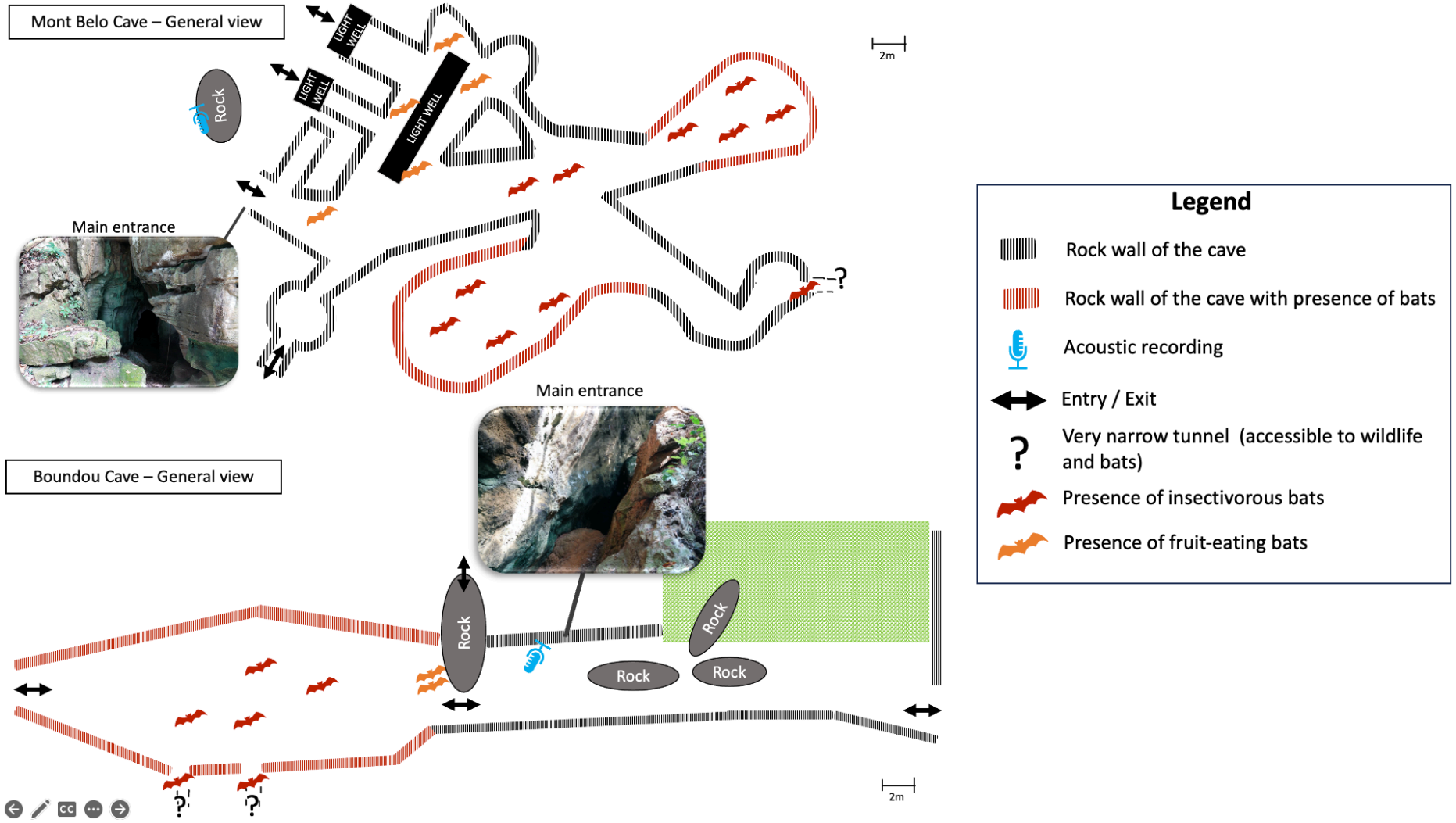


Figure 1 - General diagram of the configuration of the Boundou and Mont Belo Cave, the location of the acoustic recorder and the bat roosting sites.

Ethic statements

The protocols presented below have all been validated by the Ethics Committee of the Ministry of Scientific Research and Technological Innovation and by the Ministry of Forest Economy of the Republic of Congo (N°212/MRSIT/IRSSA/CERSSA and N°687/MEF/CAB/DGEF-DFAP). This work was also carried out with the agreement and participation of the authorities in the Niari and Bouenza departments, as well as the communities and landowners close to our study sites.

Capturing bats

During the 19 months of data collection (September 2021 – March 2023), we conducted eleven capture sessions at the main entrance of each cave using a harp trap (© Ecotone) between 5:00 and 10:00 pm. The sessions were distributed across different months and seasons to capture temporal variation in activity and reproductive condition. During the first session at Mont Belo in September 2021, no bats were captured, likely due to a nearby crop fire that may have forced bats to temporarily abandon the cave. In total, 672 bats were captured, including 344 individuals at Boundou Cave and 328 at Mont Belo Cave (Appendix 1). During these capture sessions, a wide range of information was collected, including the time of capture, the family and species identified in the field, sex, age and reproductive status. The reproductive status of individuals was determined by assessing females for pregnancy (abdominal palpation) and lactation (mammary gland size, absence of fur, presence of milk at the nipple). Males were assessed for sexual activity based on testes size and epididymal coloration. At the beginning of the study, in order to confirm the genera and species of bats present in the caves, we collected genetic samples, acoustic recordings and specimens for reference purposes.

Passive acoustic monitoring (PAM)

At each main entrance of the two caves, at a maximum distance of five meters, we placed an SM4BAT acoustic recorder with a U1 microphone (Wildlife acoustics, Maynard, MA, USA). Each microphone was placed on a pole or tree and oriented to best record the acoustic calls of bats emerging and re-entering through the main entrance. These recorders ran continuously several weeks per month for a period of 19 months (September 2021 to first day of March 2023). The SM4BATs were set up according to the stationary points protocol of Vigie-chiro, a citizen science programme for the acoustic monitoring of bat populations in France (French Museum of Natural History (see Mariton et al., 2023) starting 30 minutes before sunset and 30 minutes after sunrise. Figure 1 show the location of the acoustic recorder in relation to the configuration of each cave.

Processing acoustic data

Recordings were cut in durations of five seconds maximum. In order to process all the acoustic files collected during this study in the two caves, we used the automatic sonotype classifier published in Roemer et al., (2021) and modified in Labadie et al. (2025b) to identify the presence of different sonotypes inside each file. The classifier returns a table in which each line corresponds to a group of calls with similar call shape and frequency, associated with information about their acoustic parameters (e.g., frequency, duration). Because of an overlap in the shape and frequency of certain acoustic calls from bat species of the same family, we decided to group the species at each study site using a posteriori classification (detail for the different acoustic groups in Labadie et al., 2025b). The Boundou cave has four distinct groups: (1) the *Miniopterus* group (*Miniopterus cf minor*/ *Miniopterus cf. inflatus*), (2) *Hipposideros caffer* (*Hipposideros cf. caffer)*, (3)

Rhinolophus denti (*Rhinolophus cf. denti*) and (4) the *Rhinolophus* - Macro - Tria group (*R. cf. landeri-alcyone* /*Macronycteris gigas*/*Triaenops cf. afer*) (Fig. 2). The Mont Belo cave also has four distinct groups: (1) the *Miniopterus* group (*M. cf minor*/ *M. cf. inflatus*), (2) *Hipposideros caffer* (*Hipposideros cf. caffer*), (3) *Rhinolophus denti* (*Rhinolophus cf. denti)* and (4) *Rhinolophus landeri-alcyone (Rhinolophus cf. landeri-alcyone*) (Fig. 2). For more details on the automatic classification and on a posteriori sorting of acoustic groups, please respectively refer to Roemer et al. (2021) and Labadie et al. (2025b).

Statistical analysis

After analyzing all recorded files, the Tadarida acoustic classifier produced raw results, which were then organized in the post-sorting output. All the statistical analyses presented below were carried out using R software v. 4.3.1 (R Core Team, 2023). The graphics were produced using ggplot2 (Wickham, 2016) or ggradar (Bion, 2023).

Bat counting techniques and acoustics analyses

Bats may emerge from and enter a cave at any time during the night; nonetheless, most of them emerge after sunset and enter before sunrise (Erkert, 1982). In order to assess the activity of the five groups of bats during emergence and their entry at each cave during the 19 months, we decided to standardise our methodology based on the protocol of Mariton et al. (2023). As in other acoustic studies (Millon et al., 2015), we defined the activity of the different groups of bats as the number of bat passes. A bat pass is the occurrence of a single or several calls detected during a five seconds interval.

As our study took place in the tropics and in two caves that are geographically close, the characterisation of the diel activity of groups of bats can be based on a time scale (on sunrise and sunset). To begin with, we defined the time of sunset and sunrise based on the geographical coordinates and using the getSunlightTimes function in the suncalc package (Thieurmel et al., 2022). We then quantified the number of bat passes, over two specific time periods: (a) the period of emergence, from 30 minutes before sunset to two hours after sunset, and (b) the period of entry into the cave, from two hours before sunrise to 30 minutes after sunrise. This calculation was carried out for each species, each site and each day on which a complete night was recorded by the SM4BATs.

Distribution of activity during the night

To calculate the distribution of the activity of acoustic groups of bats throughout the night, we estimated the activity density using the density function in the R package. This calculation was done for the twelve months of the year (some months were sampled repetitively during different years) for each species and each study site.

Monthly pattern of the emergence and the entry activity at the roost

We used Generalised Linear Mixed Models (GLMM) to model the number of bat passes (proxy of activity) during their emergence and entry as a function of the month of the year in each cave and for each acoustic group. We added month and year as a random effect (1|month_year). In total, we fitted seven separate emergence models (see Appendix 2). Each model corresponds to a specific bat species or acoustic group at a given cave. This approach allows us to account for species-

specific emergence patterns at each site while controlling for temporal variation across months and years. We used the glmmTMB package (Brooks et al., 2017) to build our models. We used a lognormal distribution and checked the conditions and diagnostics using the DHARMa package (QQ plot residuals, Residuals vs predicted, dispersion, zero-inflation) (Hartig & Hartig, 2022). We used a Bonferroni correction to limit the type I error rate (false positive) when interpreting generalised linear models (Cabin & Mitchell, 2000).

Results

Species composition and reproductive phenology

In both caves, we captured a total of seven bat species. Five species were present at both sites: *Miniopterus cf. minor* (N = 99), *Miniopterus cf. inflatus* (N = 105), *Rhinolophus cf. landeri-alcyone* (N = 52), *Rhinolophus cf. denti* (N = 108), and *Hipposideros cf. caffer* (N = 204). *Triaenops cf. afer* (N = 100) and *Macronycteris cf. gigas* (N = 4) were recorded exclusively in the Boundou Cave. For each species, the number of captured individuals by sex and by site is summarized in Table 1, together with information on reproductive status.
Across species and sites, most bats exhibited a juvenile-rearing period (gestation, parturition, and lactation) during the long rainy season (October–December). Male sexual activity was mainly observed during the long dry season (June–mid-September), suggesting a seasonal separation between mating and juvenile rearing. Some taxa, particularly *Hipposideros cf. caffer*, showed evidence of two reproductive periods within the annual cycle.

Passive acoustic monitoring

In total, during nineteen months, we collected 2,375,956 acoustic files (five seconds duration) with 48.7% coming from Boundou and 51.3% from Mont Belo. The acoustic groups identified at each cave are shown in Figure 2 (Appendix 3, raw data for each group).

Nocturnal activity patterns

In both caves, for the five acoustic groups (*Hipposideros caffer, Miniopterus group, Rhinolophus denti, Rhinolophus landeri-alcyone, Rhinolophus Macro Tria group*), nocturnal activity patterns—specifically emergence and return activity— were generally bi-modal. More precisely, the first peak of activity occurred at the beginning of the night, around 6:00 pm (after sunset), and a second peak was observed between 5:00 and 6:00 am, depending on the species (Fig. 3 and Fig. 4). In contrast, *Rhinolophus cf. denti* showed an earlier onset of activity, beginning around 3:00 am in both caves.

In December, bat activity was more evenly distributed throughout the night than during the other months for all five acoustic groups and in both caves (Fig. 3 and Fig. 4). In addition, the Boundou cave activity was more spread-out during January and February (Fig. 3). In the Mont Belo cave, activity was also more spread out throughout the night in November and July (Fig. 4).

Annual phenology of bat activity and predicted species-specific patterns

Because analyses using emergence and entry activity produced similar annual phenology of bat activity, we decided to comment our results for the emergence activity only (Fig. 5) (Appendix 3, 4, 5 and 6 for entry activity prediction). The annual phenology of activity varied according to the acoustic group and the month (Appendix 3 and 4). For *Rhinolophus denti*, their low activity during emergence in Mont Belo cave meant that the model had no results (the model had too little data to run) (Appendix 6 and 7).

Hipposideros caffer

Predicted bat activity varied seasonally across species groups and caves (Figs. 4 and 5). For *Hipposideros caffer*, activity was generally moderate during the short dry (January–February) and short rainy seasons (March–May) in both caves. Nightly activity patterns (Fig. 4) were consistently bimodal, with distinct emergence and entry peaks. During the long dry season (June–August), activity declined, particularly at Boundou. Activity increased again toward the long rainy season (September–December), when nightly activity became more evenly distributed across the night, coinciding with the main juvenile-rearing period. According to Fig. 5 (Appendix 8), monthly predicted activity remained relatively stable at Mont Belo from January to April, while Boundou showed higher values during the same period. The highest predicted activity occurred at the end of the year in both caves.

Miniopterus group

The Miniopterus group showed the highest activity during the short dry and short rainy seasons in both caves (Fig. 4). During the long dry season, activity declined and nightly patterns became less structured. Activity remained lower during the long rainy season, despite the presence of juveniles, with reduced intensity of emergence and entry peaks. Fig. 5 (Appendix 8) indicates that predicted activity peaked between January and March at Mont Belo and remained high from January to May at Boundou. Minimum activity was observed during the long dry season, especially in July–August.

Rhinolophus landeri-alcyone

At Mont Belo, *Rhinolophus landeri–alcyone* exhibited low activity during the short dry season, followed by an increase during the short rainy season (Fig. 4). Activity decreased markedly during the long dry season, when nightly activity was minimal. An increase was observed again during the long rainy season, corresponding to pregnancy, parturition, and lactation, with more continuous nocturnal activity. As shown in Fig. 5 (Appendix 8), predicted activity reached its lowest values between July and September and increased again from October to December. The highest monthly values occurred during the late rainy season.

Rhinolophus denti

At Boundou, *Rhinolophus denti* showed low activity for most of the year, particularly from the short rainy season through the long dry season. A clear increase occurred during the long rainy season, with the highest activity at the end of the year (Fig. 4). Fig. 5 (Appendix 8) shows consistently low predicted activity from February to September, followed by a marked increase from October to December. The end of the year corresponds to the period of highest predicted bat passes.

Rhinolophus Macro-Tria group

Finally, the *Rhinolophus Macro–Tria group* at Boundou showed higher activity during the short dry and short rainy seasons (Fig. 4). Activity declined during the long dry season and remained generally low during the long rainy season, with reduced nightly structure. According to Fig. 5 (Appendix 8), predicted activity was highest in January–February and declined sharply during the long dry season. A secondary increase was observed at the end of the year.

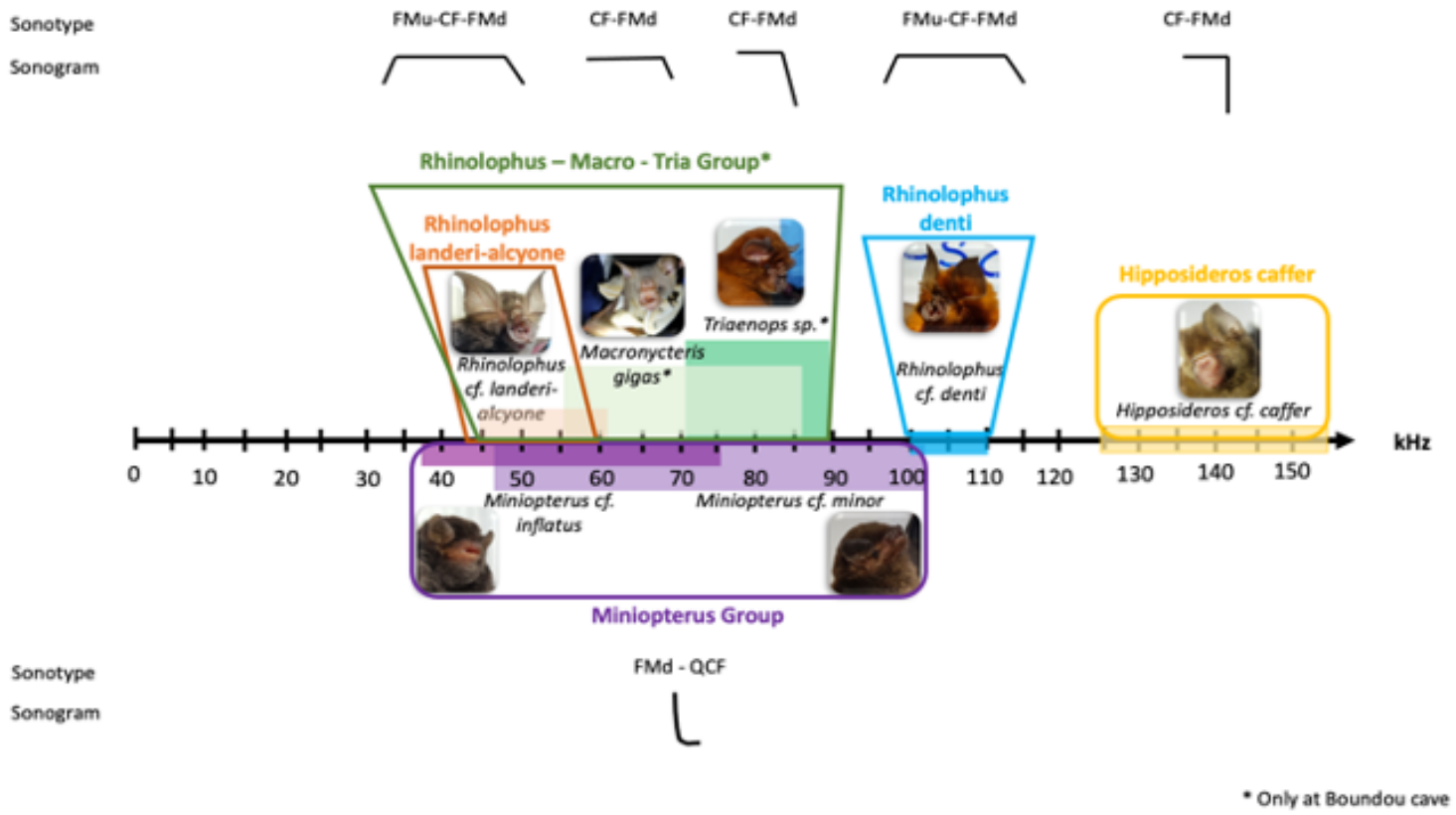


Figure 2 - Acoustic characteristics for the different bat species captured at the two study sites and categorization into different acoustic groups or species. Detail of sonotype, sonogram and acoustic frequency recorded or listed in reference works for each bat genus and species captured in the two caves (species with * are present only at Boundou). In the Boundou Cave, there are four acoustic groups (*Rhinolophus* – Macro – Tria group; *Rhinolophus denti*; *Hipposideros caffer* and *Miniopterus* group) and in the Mont Belo Cave there are four acoustic groups (*Rhinolophus landeri-alcyone*; *Rhinolophus denti*; *Hipposideros caffer* and *Miniopterus* group).

Table 1: Total number of individuals captured by species, cave, and sex, with observed reproductive periods based on eleven capture sessions (September 2021–March 2023). Juvenile-rearing periods include gestation, parturition, and lactation. Male sexual activity indicates reproductive activity inferred from testes size and epididymal coloration. '?' indicates insufficient data.

Group	Species	Cave	Males	Females	Total	Juvenile-rearing period(s)	Male sexual activity
Hipposideros caffer	*Hipposideros cf. caffer*	Mont Belo	62	17	79	Oct, Dec, Jan, Apr	Oct, Jan, Feb
	Hipposideros cf. caffer	Boundou	43	82	125	Sept – Dec, Feb, Jun	Sept – Nov, Jan, Mar, Jun
Miniopterus group	*Miniopterus cf. minor*	Boundou	41	26	67	Sept, Oct, Mar	Jan, Jun
	Miniopterus cf. minor	Mont Belo	14	18	32	Sept – Nov, Jun	Jan, Jun
	Miniopterus cf. inflatus	Boundou	2	1	3	Jun	?
	Miniopterus cf. inflatus	Mont Belo	77	25	102	Sept, Oct, Apr, Jun	Nov
Rhinolophus denti	*Rhinolophus cf. denti*	Boundou	4	2	6	Oct, Nov	?
	Rhinolophus cf. denti	Mont Belo	31	71	102	Sept – Jan, Apr, Jun	Nov, Feb
Rhinolophus landeri-alcyone	*Rhinolophus cf. landeri-alcyone*	Mont Belo	9	4	13	Oct, Nov, Jan	?
Rhinolophus Macro Tria Group	*Rhinolophus cf. landeri-alcyone*	Boundou	6	33	39	Oct, Nov	?
	*Triaenops cf. afer**	Boundou	42	58	100	Sept - Dec, Jan, Apr, Jun	Nov
	*Macronycteris cf. gigas**	Boundou	3	1	4	Nov	?

*Species found only in the Boundou cave

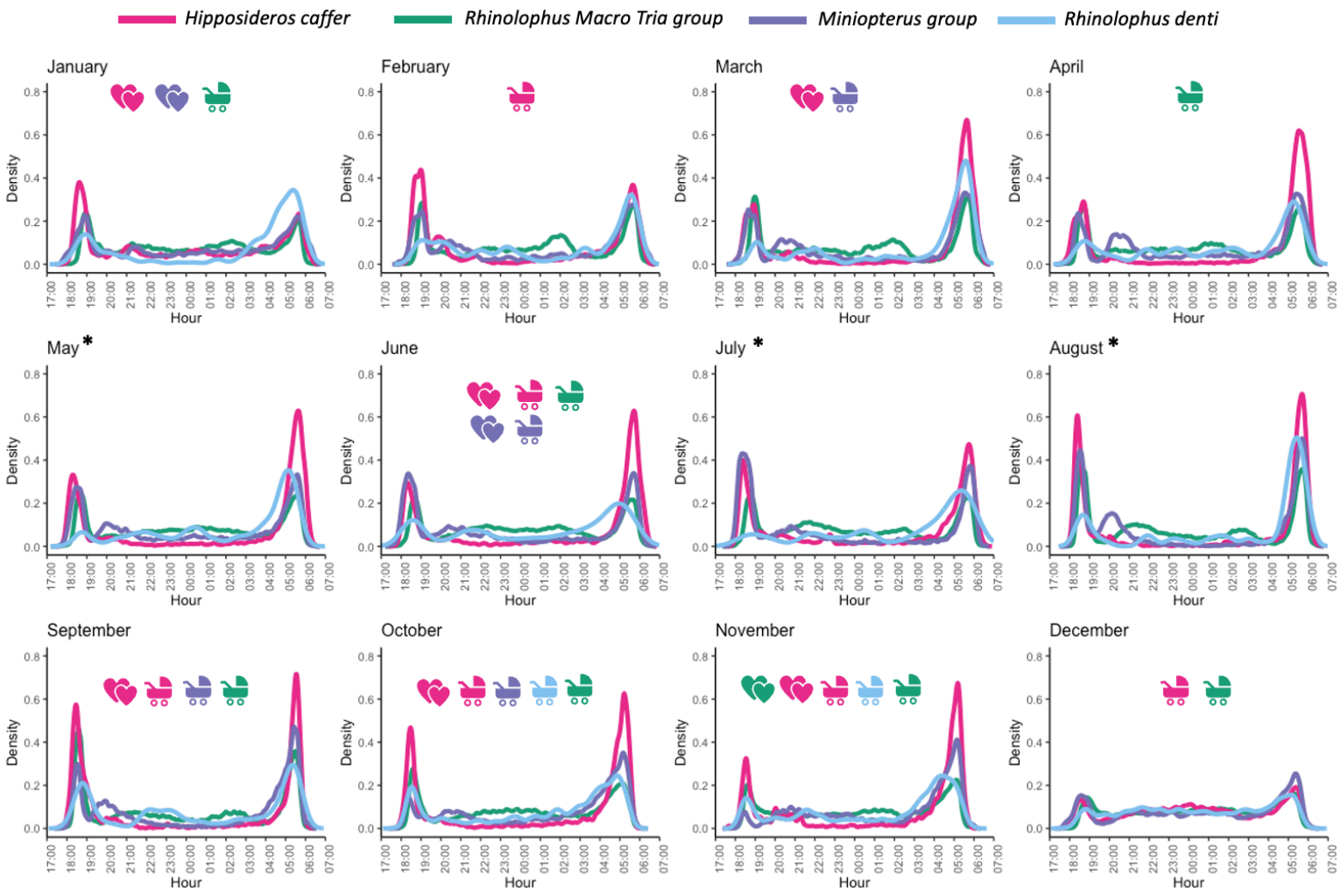


Figure 3 - Number of bat passes for each acoustic group according to month at Boundou Cave. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months of May, July and August, which have an *, are month when no captures were made, hence the absence of data on the reproductive status of the acoustic group.

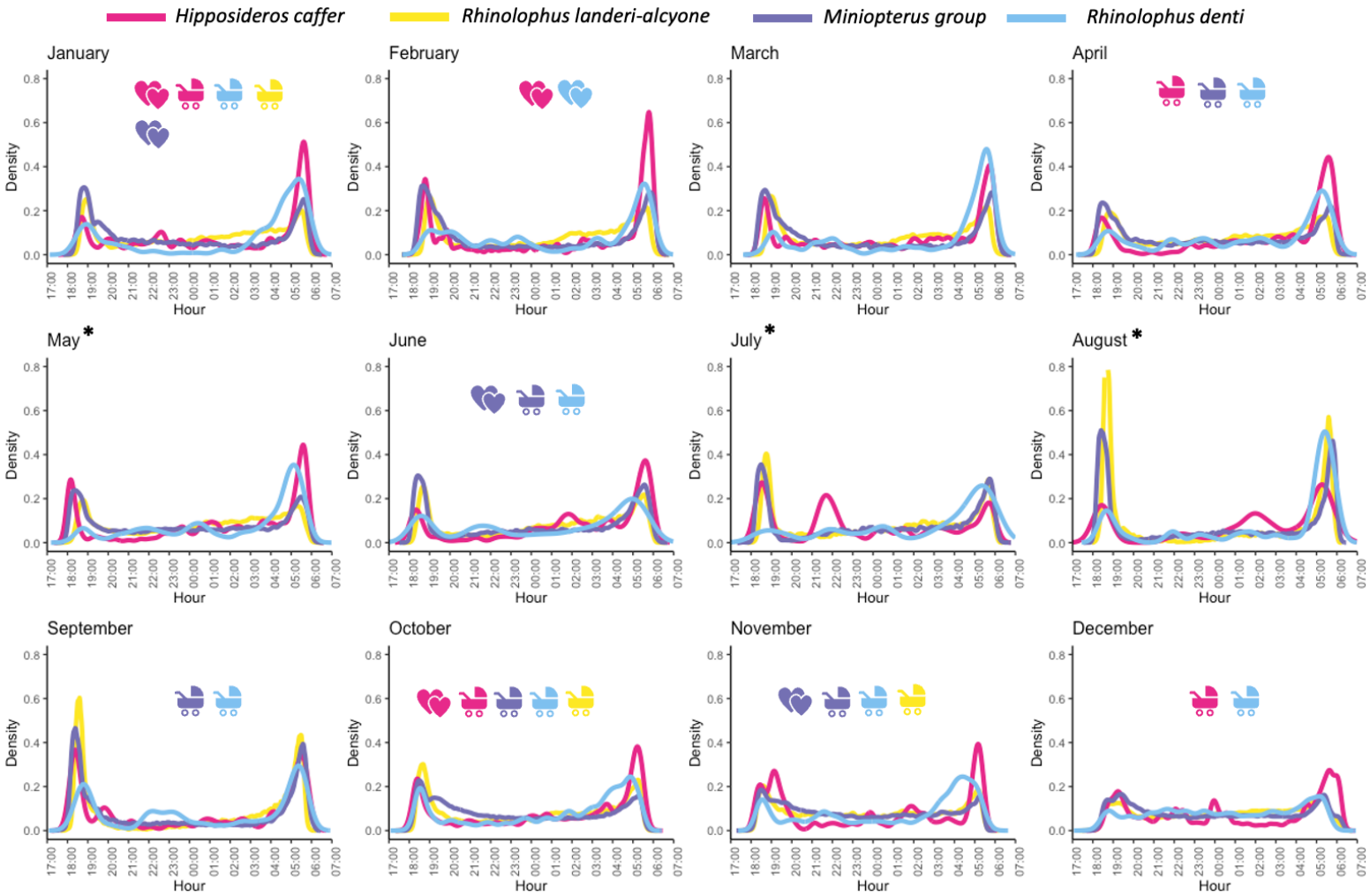


Figure 4 - Number of bat passes for each acoustic group according to month at Mont Belo Cave. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months of May, July and August, which have an *, are month when no captures were made, hence the absence of data on the reproductive status of the acoustic group.

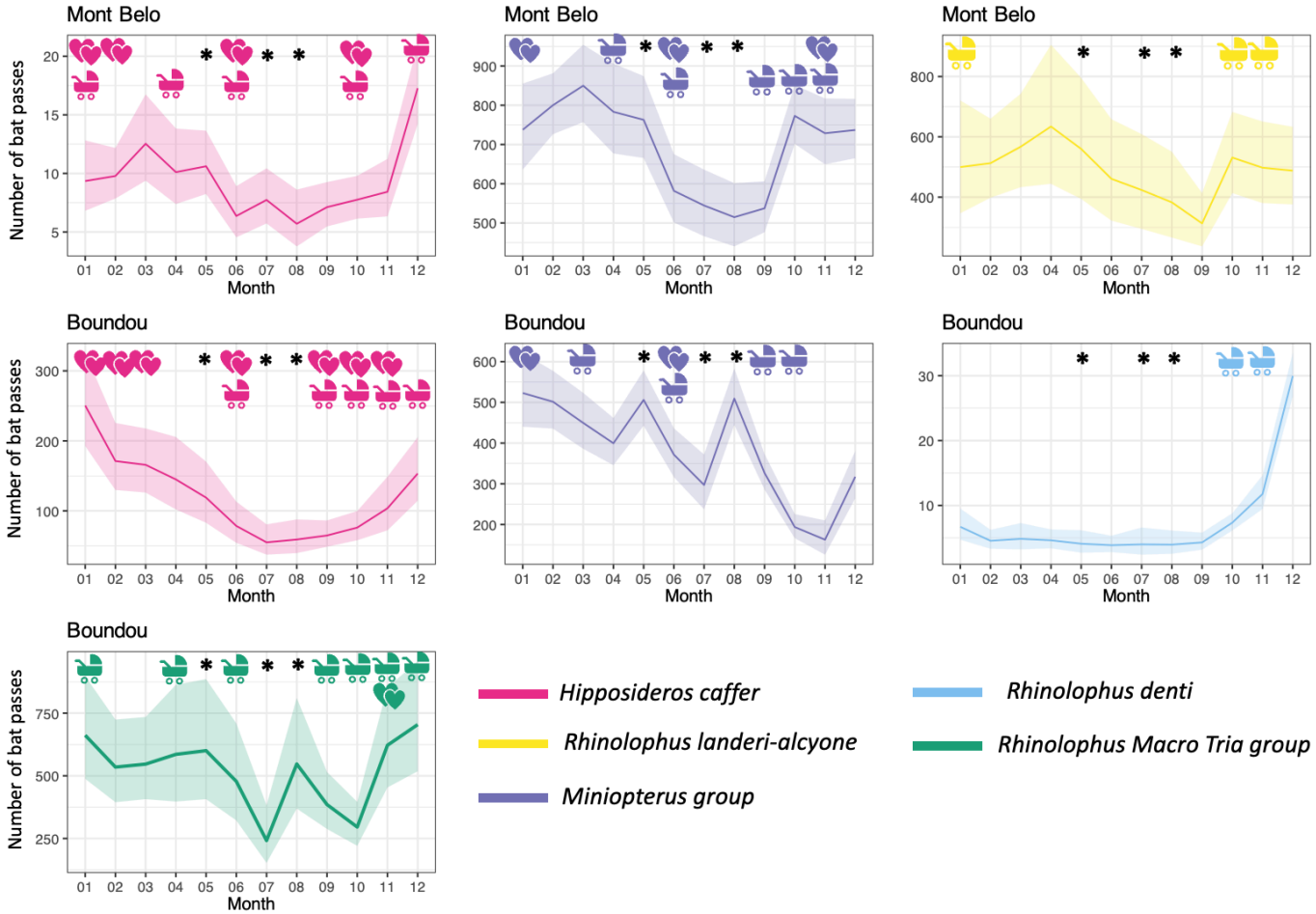


Figure 5 - Prediction of acoustic group emergence activity (estimated based on the number of bat passes) with 95% confidence interval as a function of months and study sites (Boundou and Mont Belo Cave). The *Rhinolophus denti* group at Mont Belo has not been represented here due to lack of data. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months of May, July and August, which have an *, are month when no captures were made, hence the absence of data on the reproductive status of the acoustic group.

Discussion

We used passive acoustic monitoring to characterize bat communities and their phenologies at the entrances of caves in the Republic of Congo, addressing key challenges in cave-dwelling bat research in datadeficient countries. A global sonotype classifier augmented with locally recorded reference calls allowed to overcome the main challenges of bat research in these contexts: the absence of pre-existing reference acoustic libraries; the difficulty of monitoring nocturnal and cryptic species in remote places; and the absence of standardized frameworks for quantifying bat activity. In two caves, we quantified the activity of five acoustic groups of bats and described their nightly and annual phenologies. This methodological adaptation, combining sonotypes with on-site reference recordings, offers a framework that can be replicated in other regions lacking acoustic data, potentially across different biomes and bat communities.

Nocturnal activity patterns

Five acoustic groups were detected in both caves: *Hipposideros caffer*, the *Miniopterus* group, *Rhinolophus denti*, *Rhinolophus landeri-alcyone*, and the *Rhinolophus Macro Tria group*. Overall, their emergence and entry patterns showed similar dynamics, with two bi-modal nocturnal activity patterns (a period of emergence and a period of entry into the cave) for most months in both caves. In several months, however, nocturnal activity patterns was more evenly distributed throughout the night—particularly in December for all groups, in January–February at Boundou, and in November and July at Mont Belo. When outside the cave, the large number of individuals observed are hypothesized to go hunting before returning to the cave. Some individuals may move to another resting place or return later.

Nightly observations revealed patterns consistent with known ecological behaviors. With a few exceptions, bats emerged from their daytime roosts at dusk—around 6 p.m.—to fly to feeding sites, as expected (Bullock et al., 1987). The time of this nocturnal emergence was correlated with the time of sunset (Erkert, 1982). A second peak of nocturnal activity generally occurred during the early morning hours, around 5–6 a.m., corresponding to their return to the caves. Central African countries such as Congo have little variation in sunrise and sunset throughout the year (average sunrise: about 05:50 – 06:02 am local time; average sunset: about 05:55 – 06:05 pm local time) (WorldData, 2024), leading to little variation in emergence time across the year. In our study, we also observed “burst activity” patterns during emergence, where several bats exited the cave in rapid succession followed by short periods of reduced activity, a behavior previously described in other bat colonies (Swift, 1980). However, between October and January, nocturnal activity was less concentrated around the initial emergence period and instead occurred more evenly across the night. This shift is evidenced by a flatter distribution of detections among hourly intervals, indicating sustained activity rather than a pronounced early-night peak. These nocturnal activity patterns provide the detailed temporal resolution necessary to interpret the annual phenology of bat activity, which is strongly shaped by reproductive cycles and resource availability.

Annual phenology of bat activity and reproductive period

Building on nocturnal activity patterns, we examined the annual phenology of bat activity across the year to understand seasonal trends. In our study, activity peaks during the main rainy season (October–December) coincided with maternity colony formation (gestation, birth, and beginning of lactation). In December and January, nocturnal activity was not restricted to the initial emergence

peak but extended across the entire night. Such patterns have previously been interpreted as reflecting lactating females alternating between foraging and nursing their young (Catto et al., 1995 ; Dietz & Kalko, 2006 ; Maier, 1992 ; Swift, 1980, 1997). Field observations and the ecological knownledge of these species support this interpretation. We therefore hypothesise that activity spread throughout the night corresponds to females making repeated trips between the cave and foraging sites to alternately nurse their offspring and feed. This pattern is consistent with Henry et al. (2002), who showed that *Myotis lucifugus* females reduced their foraging range and returned to the roost one to two times per night. Such repeated returns created secondary and/or tertiary nocturnal activity patterns several hours after the initial emergence observed in our data.

As young bats begin to fly and forage independently, overall activity can increase and become less strictly tied to maternal commuting behavior. For example, young *Hipposideros caffer* become independent between three and three and a half months after birth (Wright, 2009). However, the young are not carried by their mother throughout this period, and may begin to fly one month after birth, staying in the roost with other individuals of the same generation when their mothers forage out of the cave (Wright, 2009). This transition could contribute to some seasonal variation observed in activity levels during certain months following gestation and lactation.

Some acoustic groups in our study showed two reproductive periods within the year. For example, the *Miniopterus* group (two species) exhibited peaks of reproductive activity in March–April and again from September to December, while *Rhinolophus Macro Tria group* (three species) showed similar patterns between September–January and March–June. These patterns likely reflect the presence of multiple species within each acoustic group. Each species may have distinct reproductive cycles. In the case of *Hipposideros caffer*, the dual activity could be explained by the presence of a cryptic species complex within this acoustic group, as suggested in previous studies (Wright, 2009). Alternatively, the observed extended annual phenology of bat activity could reflect some flexibility in reproductive timing. Although individual females may start reproduction at slightly different times, parturition generally occurs during the peak of insect availability in the rainy season. This partial synchrony allows offspring to benefit from abundant food resources while maintaining flexibility in reproductive timing, which can maximize survival (Racey & Entwistle, 2000; McWilliam, 1988). This flexible reproductive timing likely aligns annual phenology of bat activity with seasonal resource peaks.

The long dry season (June–August) generally showed reduced nocturnal activity patterns compared with the other seasons. This likely reflects lower use of these habitats due to limited resource availability, here meaning a lower abundance of insects, the main food source for these species (Barclay & Kurta, 2007; Patriquin & Ratcliffe, 2016; Patterson et al., 2007; Postawa & Gas, 2009). However, the dry season also included some of the highest activity levels of the year for certain species, particularly in August. This was especially evident for *Rhinolophus landeri alcyone* (Mont Belo cave) and *Miniopterus group* (Boundou cave). Scattered nocturnal activity was observed throughout the night during this period, which may reflect swarming behaviour and increased movements around roosts. Although we did not capture bats in July and August and could not directly assess reproductive status, the gestation period observed from late September to early December suggests that copulation likely occurs toward the end of the long dry season (June–August). Such mating activity may increase flight activity and the frequency of returns to the cave, potentially explaining some of the observed activity peaks. This timing is consistent with reports from other regions. For example, *Hipposideros caffer* typically mates at the end of the first rainy

season (June–July) and gives birth during the middle of the second rainy season (October–November) (Bernard, 1982; Brosset, 1968; Günther et al., 2016).

The females of the species in our study, with the exception of *Macronycteris gigas*, use the cave to gather in a maternity colony before giving birth in September and October (ML personal observation). This would support Cumming and Bernard (1997) who mentioned that many bat species give birth to their young about a month before the peak in resource availability.

Finally, variation in roost use by species highlights the complexity of bat ecology in these systems. It is noteworthy that the mating period of *Hipposideros caffer* seemed to vary between cave (January, February, September, October in Mont Belo Cave;January, March, June and September - November in Boundou Cave). This variation in breeding months could potentially be explained by the presence of two cryptic species of *Hipposideros* in this study (ML personal observation).

Conservation implications for the caves and application in other biomes

By describing nocturnal activity patterns and annual phenology of bat activity, our results also highlight the ecological and conservation significance of these caves. Although this study did not aim to formally calculate the Bat Cave Vulnerability Index (BCVI) (from Tanalgo & Hughes, 2024), a quick assessment of standard criteria suggests differing vulnerability between the two caves. Mont Belo hosts more species and several maternity colonies. It therefore has the highest biotic value. Its vulnerability score must then be assessed by considering the different threats affecting the site (Labadie et al., 2025a). Boundou shows lower vulnerability, with fewer disturbances and only occasional predation (Labadie et al., 2025a).

Limitation of this study

Information on reproductive status cannot be obtained from acoustic monitoring, it requires the capture of individuals. We were not able to capture during the long dry season (June–August), which hampers our understanding of the reproduction status of the different species. Moreover, we did not have the opportunity to validate our acoustic monitoring method with manual counts, video monitoring, or infrared cameras to verify the number of individuals in each cave per month due to logistical constraints. These complementary methods would have provided direct estimates of colony size and temporal fluctuations in bat abundance. Such information would have allowed us to link nocturnal activity patterns more precisely to actual population dynamics and to better distinguish between changes in the number of individuals. Acoustic activity is, however, generally correlated with colony size in caves (Revilla-Martín et al., 2020). Still, variations in flight behavior—such as increased vocal activity during social interactions or reduced calling during certain foraging strategies—may lead to an over- or underestimation of this correlation.

Conclusion

We characterized the variation in activity of acoustic groups in relation to season and breeding status, providing insights into temporal use of roosts and potential sensitivity to disturbance. While both caves host similar species groups and share general seasonal trends, Mont Belo shows more pronunced biannual peaks in acoustic activity (especially *R. landeri–alcyone*), whereas Boundou displays more evenly distributed activity and possibly more stable year-round occupation (notably for *Hipposideros caffer* and the *Rhinolophus Macro Tria group*). Because overall activity levels differ substantially between sites, these comparisons should be

interpreted cautiously and are intended to describe relative temporal patterns within each cave rather than absolute differences between caves.

Taken together, these patterns suggest differences in seasonal use between caves, with Mont Belo potentially experiencing stronger seasonal concentrations of activity, while Boundou appears to support more continuous multi-species use throughout the year. Rather than indicating strict functional specialization, these results point to complementary patterns of cave use across seasons, which may reflect differences in roost structure, microclimate, or local landscape context.

These observations highlight the potential of passive acoustic monitoring (PAM), combined with automated acoustic classification, to explore seasonal and reproductive-associated changes in bat activity, an application that remains limited for Central African cave systems. While quantitative acoustic monitoring has been successfully applied in other data-poor tropical and subtropical regions, our study provides the first standardized acoustic baseline for cave-roosting bat assemblages in this region, contributing new information for poorly documented taxa and sites.

This approach offers a valuable tool for cave conservation by enabling the identification of periods of increased bat activity and species-specific patterns of cave use, which are relevant for minimizing disturbance (Tanalgo & Hughes, 2024), although direct inference of reproductive timing requires complementary data. A major strength of this study lies in its non-invasive approach, applicable across multiple caves and species, while obtaining both nocturnal activity patterns and annual phenology of bat activity.

Future improvements could include non-invasive hormonal monitoring by collecting bat urine to analyze stress levels and reproductive hormones, allowing identification of mating and lactation periods without capturing bats (Greville et al., 2022; Kumar & Umapathy, 2019; Voigt & Schwarzenberger, 2008; Wilkinson et al., 2024). Given the importance of bats for the health of the environment across the world, this study provides new avenues to produce knowledge in data-deficient and remote areas in order to adapt bat conservation and management.

Appendices

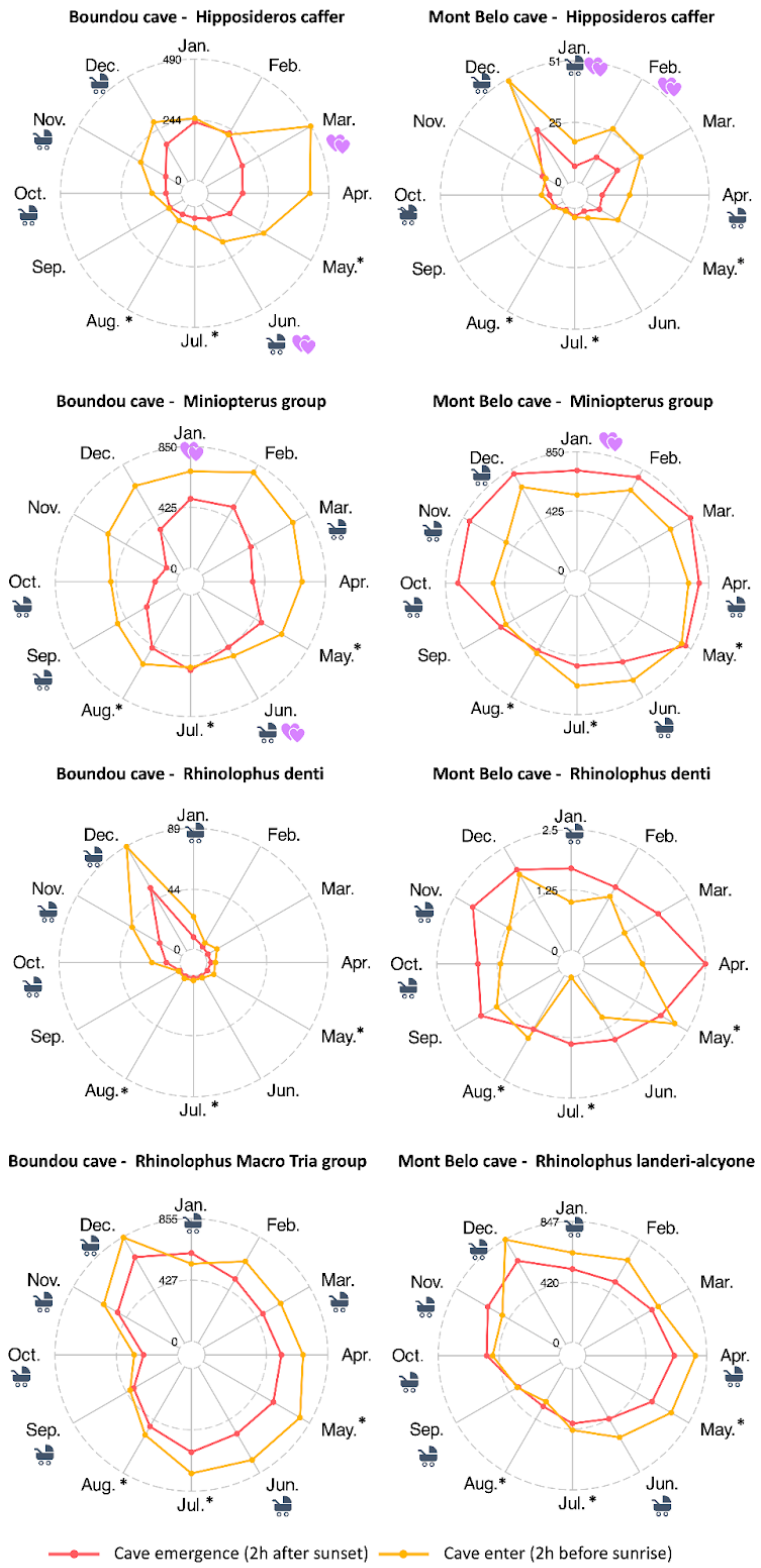
Appendix 1 - Morphometric Data of Insectivorous Bat Communities in Two Caves of The Republic of Congo

CIRAD Dataverse. https://doi.org/doi:10.18167/DVN1/M2J0TY.

Appendix 2 - Summary table of seven emergence models for each cave (Boundou and Mont Belo) and each acoustics group tested in this study.

Model name	Description
Model *Hipposideros caffer* emergence Boundou Cave	Nb_batpass ~ Month + (1|month-year)
Model *Miniopterus group* emergence Boundou Cave	Nb_batpass ~ Month + (1|month-year)
Model *Rhinolophus denti* emergence Boundou Cave	Nb_batpass ~ Month + (1|month-year)
Model *Rhinolophus landeri-alcyone* emergence Boundou Cave	Nb_batpass ~ Month + (1|month-year)
Model *Hipposideros caffer* emergence Mont Belo Cave	Nb_batpass ~ Month + (1|month-year)
Model *Miniopterus group* emergence Mont Belo Cave	Nb_batpass ~ Month + (1|month-year)
Model *Rhinolophus Macro Tria* emergence Boundou Cave	Nb_batpass ~ Month + (1|month-year)

Appendix 3 - Number of bat passes for each acoustic group according to month and site (Boundou and Mont Belo Cave). The reproductive status of the species or acoustic group is indicated by two pictograms: young rearing (lactation, pregnant) and : mating period/male activity. The months of May, July and August, which have an *, are month when no captures were made, hence the absence of data on the reproductive status of the acoustic group.


Boundou cave - Hipposideros caffer
Mont Belo cave - Hipposideros caffer
Boundou cave - Miniopterus group
Mont Belo cave - Miniopterus group
Boundou cave - Rhinolophus denti
Mont Belo cave - Rhinolophus denti
Boundou cave - Rhinolophus Macro Tria group
Mont Belo cave - Rhinolophus landeri-alcyone
Jan.
Feb.
Mar.
Apr.
May.*
Jun.
Jul.*
Aug.*
Sep.
Oct.
Nov.
Dec.
Cave emergence (2h after sunset)
Cave enter (2h before sunrise)

527 :

Appendix 4 - Generalized linear mixed (GLM) with Bonferroni correction describing the relationship between activity and month for the four acoustic groups in the Boundou Cave during the emergence time of bats.

	Hipposideros caffer emergence Boundou			**Miniopterus group emergence Boundou**			**Rhinolophus denti emergence Boundou**			**Rhinolophus Macro Tria group emergence Boundou**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept Jan	250.45 ***	192.77 – 325.39	**<0.001**	522.93 ***	440.28 – 621.08	**<0.001**	6.71 ***	4.73 – 9.51	**<0.001**	661.78 ***	488.20 – 897.08	**<0.001**
Feb	0.68	0.47 – 1.00	0.593	0.96	0.77 – 1.19	1.000	0.68	0.43 – 1.06	1.000	0.81	0.53 – 1.24	1.000
Mar	0.66	0.45 – 0.96	0.382	0.86	0.69 – 1.08	1.000	0.72	0.43 – 1.21	1.000	0.83	0.54 – 1.26	1.000
Apr	0.58	0.37 – 0.89	0.166	0.76	0.61 – 0.95	0.191	0.69	0.44 – 1.07	1.000	0.88	0.54 – 1.45	1.000
May	0.47 *	0.30 – 0.74	**0.012**	0.97	0.78 – 1.20	1.000	0.61	0.36 – 1.03	0.750	0.91	0.55 – 1.48	1.000
Jun	0.31 ***	0.20 – 0.49	**<0.001**	0.71 *	0.57 – 0.89	**0.038**	0.58	0.37 – 0.91	0.203	0.72	0.44 – 1.19	1.000
Jul	0.22 ***	0.14 – 0.35	**<0.001**	0.57 ***	0.43 – 0.74	**<0.001**	0.60	0.33 – 1.08	1.000	0.37 **	0.21 – 0.63	**0.003**
Aug	0.24 ***	0.15 – 0.38	**<0.001**	0.97	0.79 – 1.21	1.000	0.59	0.34 – 1.01	0.671	0.83	0.50 – 1.36	1.000
Sep	0.26 ***	0.18 – 0.38	**<0.001**	0.62 ***	0.51 – 0.77	**<0.001**	0.64	0.41 – 0.99	0.557	0.58	0.38 – 0.89	0.137
Oct	0.30 ***	0.21 – 0.44	**<0.001**	0.37 ***	0.30 – 0.46	**<0.001**	1.10	0.76 – 1.58	1.000	0.45 **	0.29 – 0.68	**0.002**
Nov	0.41 **	0.27 – 0.64	**0.001**	0.31 ***	0.23 – 0.42	**<0.001**	1.75	1.19 – 2.59	0.056	0.94	0.61 – 1.46	1.000
Dec	0.61	0.41 – 0.90	0.166	0.61 ***	0.48 – 0.77	**0.001**	4.47 ***	3.13 – 6.38	**<0.001**	1.06	0.69 – 1.64	1.000
Random Effects												
σ^2	58.54			192.82			7.76			191.71		
τ_{00}	0.03_{month2}			0.00_{month2}			0.00_{month2}			0.04_{month2}		
ICC	0.00									0.00		
N	19_{month2}			19_{month2}			19_{month2}			19_{month2}		
Observations	275			275			182			275		
Marginal R^2 / Conditional R^2	0.003 / 0.004			0.001 / NA			0.047 / NA			0.001 / 0.001		
AICc	2867.068			3566.270			900.772			3695.560		

** p<0.05 ** p<0.01 *** p<0.001*

Appendix 5 - Generalized linear mixed (GLM) with Bonferroni correction describing the relationship between activity and month for the four acoustic groups in the Mont Belo Cave during the emergence time of bats.

	Hipposideros caffer emergence Mont Belo			**Miniopterus group emergence Mont Belo**			**Rhino landeri-alcyone emergence Mont Belo**			**Rhinolophus denti emergence Mont Belo**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept Jan	9.35 ***	6.82 – 12.82	**<0.001**	737.51 ***	636.15 – 855.01	**<0.001**	499.73 ***	346.52 – 720.68	**<0.001**	1.00	NaN – NaN	NaN
Feb	1.05	0.74 – 1.47	1.000	1.08	0.91 – 1.29	1.000	1.03	0.66 – 1.60	1.000			
Mar	1.34	0.91 – 1.98	1.000	1.15	0.96 – 1.39	1.000	1.14	0.72 – 1.79	1.000			
Apr	1.08	0.72 – 1.63	1.000	1.06	0.86 – 1.31	1.000	1.27	0.76 – 2.11	1.000			
May	1.14	0.79 – 1.64	1.000	1.03	0.85 – 1.26	1.000	1.12	0.68 – 1.86	1.000			
Jun	0.68	0.44 – 1.05	0.958	0.79	0.64 – 0.97	0.316	0.92	0.55 – 1.54	1.000			
Jul	0.83	0.55 – 1.24	1.000	0.74	0.60 – 0.91	0.064	0.85	0.51 – 1.42	1.000			
Aug	0.61	0.37 – 1.00	0.588	0.70 *	0.56 – 0.86	**0.012**	0.77	0.46 – 1.28	1.000			
Sep	0.76	0.52 – 1.11	1.000	0.73 *	0.60 – 0.88	**0.013**	0.63	0.40 – 0.99	0.542	1.00	NaN – NaN	NaN
Oct	0.83	0.58 – 1.18	1.000	1.05	0.88 – 1.25	1.000	1.06	0.68 – 1.65	1.000	1.00	NaN – NaN	NaN
Nov	0.90	0.61 – 1.33	1.000	0.99	0.82 – 1.19	1.000	1.00	0.63 – 1.57	1.000			
Dec	1.85 **	1.34 – 2.56	**0.003**	1.00	0.84 – 1.19	1.000	0.98	0.62 – 1.53	1.000			
Random Effects												
σ^2	13.88			152.17			169.52			0.00		
τ_{00}	0.00_{month2}			0.00_{month2}			0.03_{month2}			0.00_{month2}		
ICC				0.00			0.00					
N	18_{month2}			18_{month2}			18_{month2}			4_{month2}		
Observations	271			293			293			4		
Marginal R^2 / Conditional R^2	0.007 / NA			0.000 / 0.000			0.000 / 0.000			0.000 / NA		
AICc	1644.111			3796.908			3859.854			NA		

* *p<0.05* ** *p<0.01* *** *p<0.001*

Appendix 6 - Generalized linear mixed (GLM) with Bonferroni correction describing the relationship between activity and month for the four acoustic groups in the Boundou Cave during the enter time of bats.

	Hipposideros caffer enter Boundou			**Miniopterus group enter Boundou**			**Rhinolophus denti enter Boundou**			**Rhinolophus Macro Tria group enter Boundou**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept Jan	249.41 ***	156.62 – 397.20	**<0.001**	463.67 ***	314.74 – 683.07	**<0.001**	17.20 ***	11.53 – 25.65	**<0.001**	439.89 ***	289.90 – 667.50	**<0.001**
Feb	1.07	0.59 – 1.96	1.000	1.71	1.07 – 2.74	0.290	0.43 *	0.25 – 0.73	**0.020**	1.65	0.96 – 2.85	0.865
Mar	1.57	0.87 – 2.85	1.000	1.63	1.02 – 2.60	0.497	0.55	0.33 – 0.91	0.242	1.54	0.89 – 2.67	1.000
Apr	1.16	0.58 – 2.31	1.000	1.53	0.91 – 2.57	1.000	0.37 **	0.21 – 0.64	**0.005**	1.70	0.90 – 3.20	1.000
May	1.18	0.60 – 2.34	1.000	1.45	0.86 – 2.44	1.000	0.41 *	0.24 – 0.72	**0.021**	1.86	0.99 – 3.50	0.656
Jun	0.75	0.38 – 1.49	1.000	0.76	0.44 – 1.31	1.000	0.29 ***	0.16 – 0.50	**<0.001**	1.26	0.66 – 2.40	1.000
Jul	0.48	0.24 – 0.96	0.457	0.89	0.52 – 1.52	1.000	0.31 ***	0.17 – 0.55	**0.001**	1.50	0.80 – 2.84	1.000
Aug	0.46	0.22 – 0.93	0.377	1.36	0.81 – 2.30	1.000	0.36 **	0.20 – 0.65	**0.007**	1.40	0.74 – 2.65	1.000
Sep	0.49	0.27 – 0.89	0.229	1.17	0.74 – 1.87	1.000	0.29 ***	0.17 – 0.50	**<0.001**	1.02	0.59 – 1.76	1.000
Oct	0.67	0.37 – 1.21	1.000	1.19	0.75 – 1.89	1.000	0.48 *	0.30 – 0.77	**0.028**	0.83	0.48 – 1.44	1.000
Nov	0.69	0.37 – 1.31	1.000	1.12	0.68 – 1.83	1.000	1.15	0.72 – 1.82	1.000	1.39	0.79 – 2.44	1.000
Dec	1.00	0.54 – 1.84	1.000	1.38	0.85 – 2.23	1.000	2.80 ***	1.73 – 4.54	**<0.001**	2.01	1.16 – 3.47	0.154
Random Effects												
σ^2	155.58			202.81			9.54			229.51		
τ_{00}	0.06_{month2}			0.03_{month2}			0.02_{month2}			0.06_{month2}		
ICC	0.00			0.00			0.00			0.00		
N	19_{month2}			19_{month2}			19_{month2}			19_{month2}		
Observations	276			277			242			277		
Marginal R^2 / Conditional R^2	0.001 / 0.001			0.000 / 0.000			0.042 / 0.044			0.000 / 0.001		
AICc	3301.278			3769.686			1366.644			3790.904		

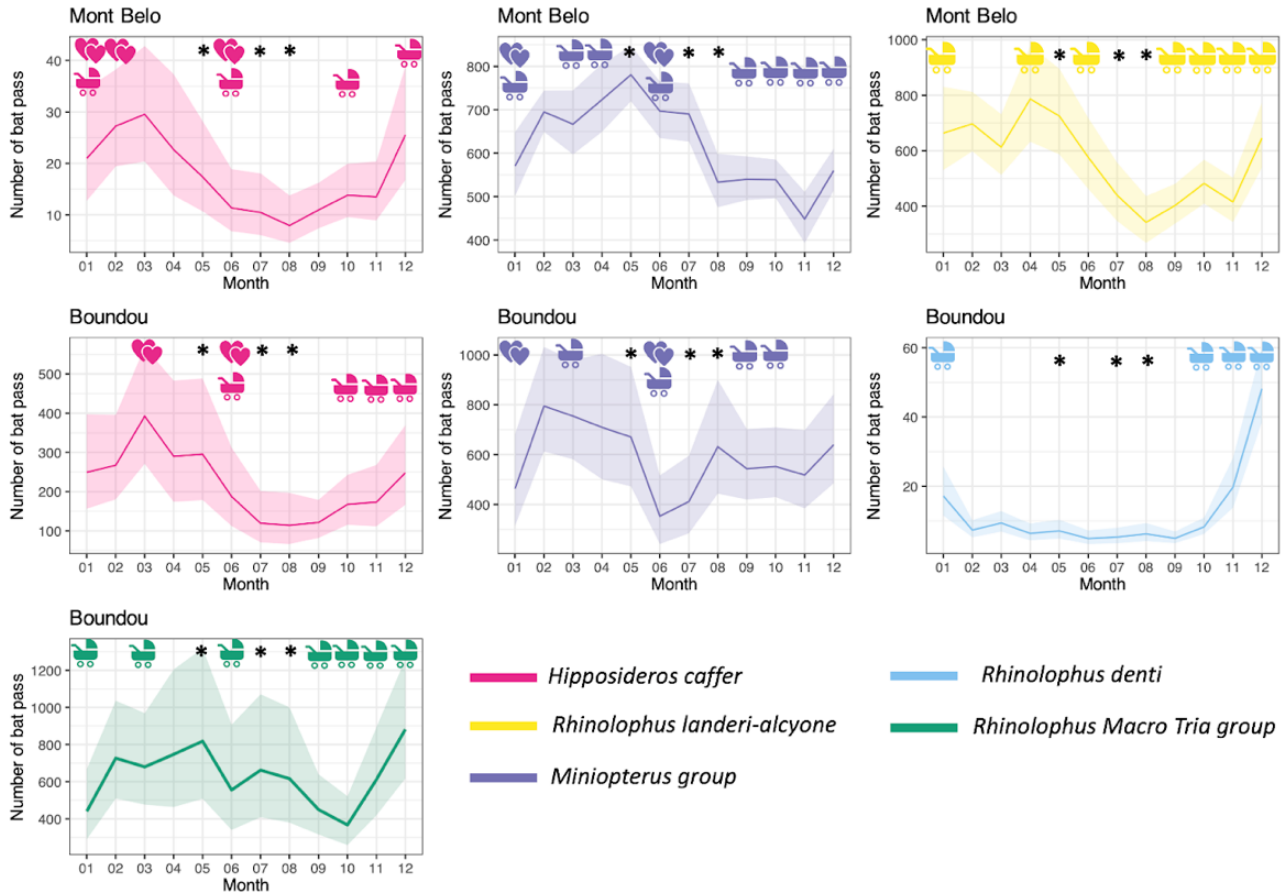
** p<0.05 ** p<0.01 *** p<0.001*

Appendix 7 - Generalized linear mixed (GLM) with Bonferroni correction describing the relationship between activity and month for the four acoustic groups in the Mont Belo Cave during the enter time of bats.

	Hipposideros caffer enter Mont Belo			**Miniopterus group enter Mont Belo**			**Rhino landeri-alcyone enter Mont Belo**			**Rhinolophus denti enter Mont Belo**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept Jan	20.98 ***	12.75 – 34.52	**<0.001**	570.35 ***	501.54 – 648.60	**<0.001**	663.65 ***	530.64 – 830.00	**<0.001**	1.17	0.47 – 2.93	1.000
Feb	1.30	0.72 – 2.33	1.000	1.22	1.05 – 1.41	0.086	1.05	0.80 – 1.38	1.000			
Mar	1.41	0.77 – 2.58	1.000	1.17	0.99 – 1.38	0.822	0.92	0.69 – 1.23	1.000			
Apr	1.08	0.54 – 2.15	1.000	1.27	1.07 – 1.50	0.063	1.19	0.87 – 1.62	1.000			
May	0.83	0.42 – 1.63	1.000	1.37 ***	1.18 – 1.59	**0.001**	1.09	0.80 – 1.49	1.000	1.00	0.32 – 3.13	1.000
Jun	0.54	0.27 – 1.08	0.988	1.22	1.04 – 1.43	0.153	0.87	0.64 – 1.19	1.000			
Jul	0.50	0.24 – 1.03	0.705	1.21	1.03 – 1.42	0.229	0.66	0.48 – 0.92	0.155			
Aug	0.38	0.18 – 0.78	0.103	0.94	0.79 – 1.11	1.000	0.52 ***	0.37 – 0.72	**0.001**			
Sep	0.52	0.28 – 0.96	0.453	0.95	0.81 – 1.11	1.000	0.61 **	0.46 – 0.81	**0.007**			
Oct	0.66	0.36 – 1.20	1.000	0.94	0.81 – 1.10	1.000	0.73	0.55 – 0.96	0.279			
Nov	0.64	0.34 – 1.20	1.000	0.79	0.66 – 0.94	0.110	0.63 *	0.47 – 0.84	**0.021**			
Dec	1.22	0.66 – 2.25	1.000	0.98	0.84 – 1.14	1.000	0.97	0.73 – 1.29	1.000	1.55	0.53 – 4.57	1.000
Random Effects												
σ^2	22.89			166.33			157.22					
τ_{00}	0.04_{month2}			0.00_{month2}			0.01_{month2}					
ICC	0.00						0.00					
N	18_{month2}			18_{month2}			18_{month2}			4_{month2}		
Observations	279			294			294			4		
Marginal R^2 / Conditional R^2	0.007 / 0.009			0.000 / NA			0.000 / 0.000			NA		
AICc	1995.258			3840.501			3818.869			-12.700		

** p<0.05 ** p<0.01 *** p<0.001*

Appendix 8 - Prediction of the activity of acoustic group entries with 95% confidence interval as a function of months and study sites (Boundou and Mont Belo Cave). The Rhinolophus denti group at Mont Belo has not been represented here due to lack of data. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months of May, July and August, which have an *, are month when no captures were made, hence the absence of data on the reproductive status of the acoustic group.



Acknowledgements

We would also like to extend our warmest thanks to Léa Mariton for her support and advice on the R scripts for the density of bat activity over time. Many thanks to our Congolese partners: the "Laboratoire National de Santé Publique de Brazzaville" (LNSP), the "Direction Générale de l'Elevage" (DGE) and "Ministère de l'économie forestière" for their support in this project, their help with the fieldwork and the applications for the capture and ethics permits. Thanks also to the bat field team who helped collect data: F. Nguilili, C. Bazola, N. Nguimbi (our wizard), R. Dimoukissi and R. Nguimbi. Finally, we would like to thank the local authorities in Dolisie and the local population for their help with this project.

Data, scripts, code, and supplementary information availability

The summary file of species and the scripts used to create the figures can be obtained by following this link: https://doi.org/10.5281/zenodo.15636144

Conflict of interest disclosure

The authors declare that they have no know competing financial interests or personal that could have appeared to influence the work reported in this paper.

Funding

This study and publication were supported by the European Union Delegation under the Agreement [FOOD/2016/379-660], signed between the EU and the WOAH for the implementation of the Action EBO-SURSY.

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