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 biological status of the individuals, which we put in perspective with the annual phenology of 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 rearing (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 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 new 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 cohabit together by hundreds or 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). They are exposed to resources extraction (minerals, guano, etc.) or recreational activities (caving, tourism, etc.) (Okonkwo et al., 2017; Simons, 1998). In return, these case dwelling bats create through the resource they produce (e.g., live and dead-bats, guano) niches for cave-dwelling communities (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 temporal 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 bring observer bias (Forsyth et al., 2006; Koger et al., 2023; Westcott & McKeown, 2004).

The development of new technologies have 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. Yet, no application of this method was published 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 more or less important patches of tropical forest.

Boundou and Mont Belo caves, are 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.

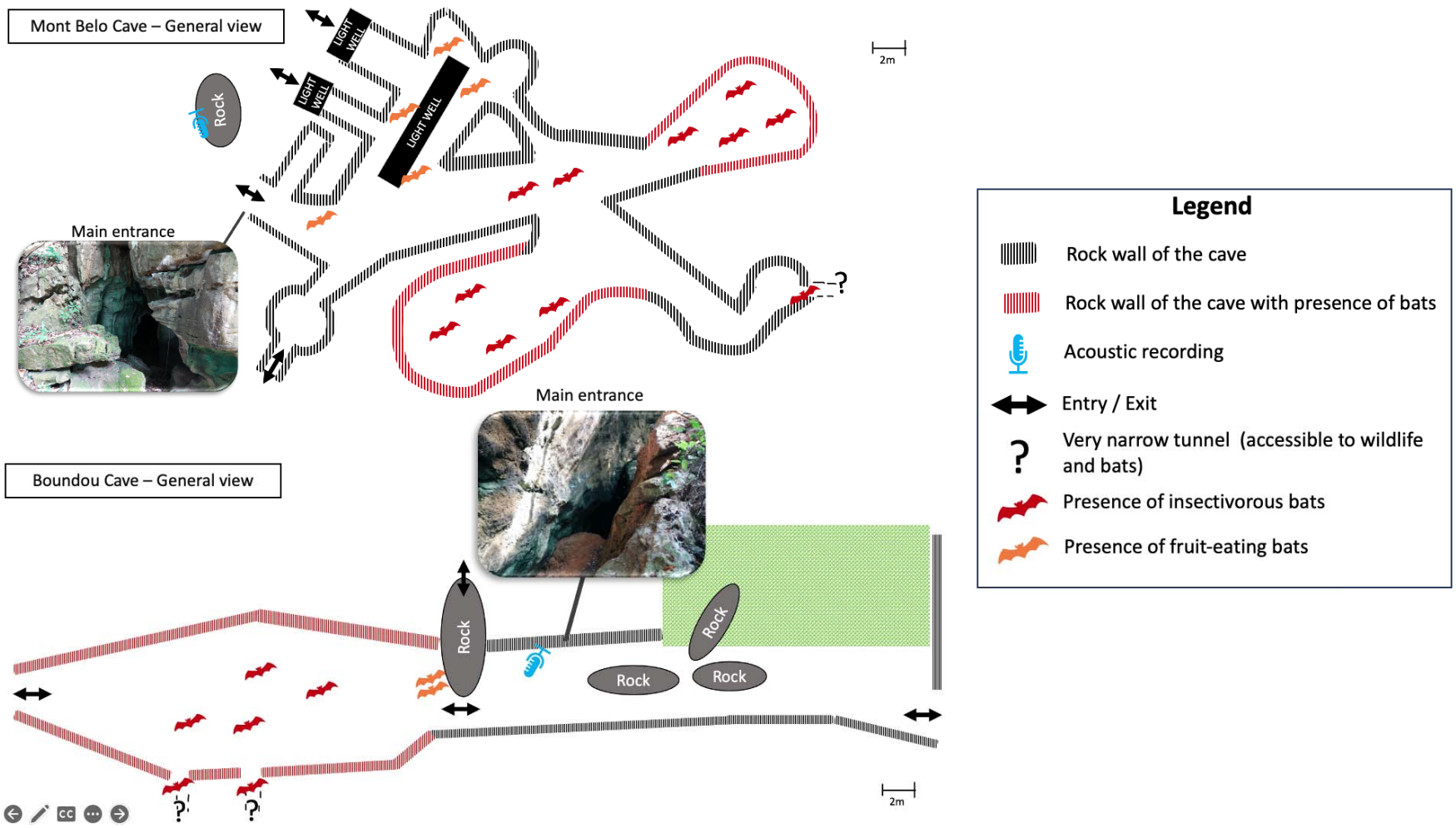


Figure 1 - General diagram of the configuration of the Boundou and Mont Belo Cave, the location of the acoustic recorder and the bat roosting sites.

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, eleven capture sessions using a harp trap were set up at the main entrance of each cave, in order to identify the different bat species. 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 the study site.

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

Post-sorting of the Tadarida output which represents the raw results of the acoustic classifier after analyzing all recorded files. 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 have eight different models (see Appendix 1, p23). 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

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 2, 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 was at the beginning of the night around 6pm (after sunset) and another peak between 3am and 4am, depending on the species (Fig. 3 and Fig. 4).

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 species-specific patterns predictions

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 2, 4, 5 and 6 for entry activity prediction). The annual phenology of activity varied according to the acoustic group and the month (Appendix 2 and 3). 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 5 and 6).

For the *Miniopterus* group, in both caves, predicted activity (including emergence and entry) showed an increase in activity during the short dry season (Jan, Feb; of which January is a copulation period) and the short rainy season (March, April, May; with March a period for rearing young). For this group, we observed a decline in activity during the long dry season (June, July, August; June was a period for copulation and rearing young, depending on the individual) and the long rainy season (September, October, November, December; period for rearing young) (Figure 5 and Appendix 7).

For *Hipposideros caffer*, in both caves we observed an increase in activity during the short dry season (January, February) and the short rainy season (March, April, May). In this group, these two periods are linked to the mating activity by certain individuals and the rearing of young. Secondly, *Hipposideros caffer* showed a sharp drop-in predicted activity during the long dry season, which stabilized during the long rainy season (end of the year and period of juvenile rearing) (Figure 5 and Appendix 7).

For Mont Belo cave, the predicted activity for *Rhinolophus landeri-alcyone* showed an increase in activity during the short dry season and the short rainy season. Then, during the long dry season, we observed a sharp drop-in activity, which rose again during the long rainy season

(the period when females are pregnant, give birth and nurse their young) (Figure 5 and Appendix 7).

For Boundou cave, the *Rhinolophus denti* showed a strong increase in predicted activity during the long rainy season and the start of the short dry season (end of the year and start of the new one; period of rearing young), and low activity during two seasons: the short rainy season and the long dry season (no individuals captured with individuals rearing young or mating) (Figure 5 and Appendix 7).

Finally, in Boundou cave, we observed a predictive activity for the *Rhinolophus* Macro Tria group that increased during the short dry and rainy seasons (Jan, Feb, Mar, Apr) and decreased during the long dry and rainy seasons (Figure 5 and Appendix 7).

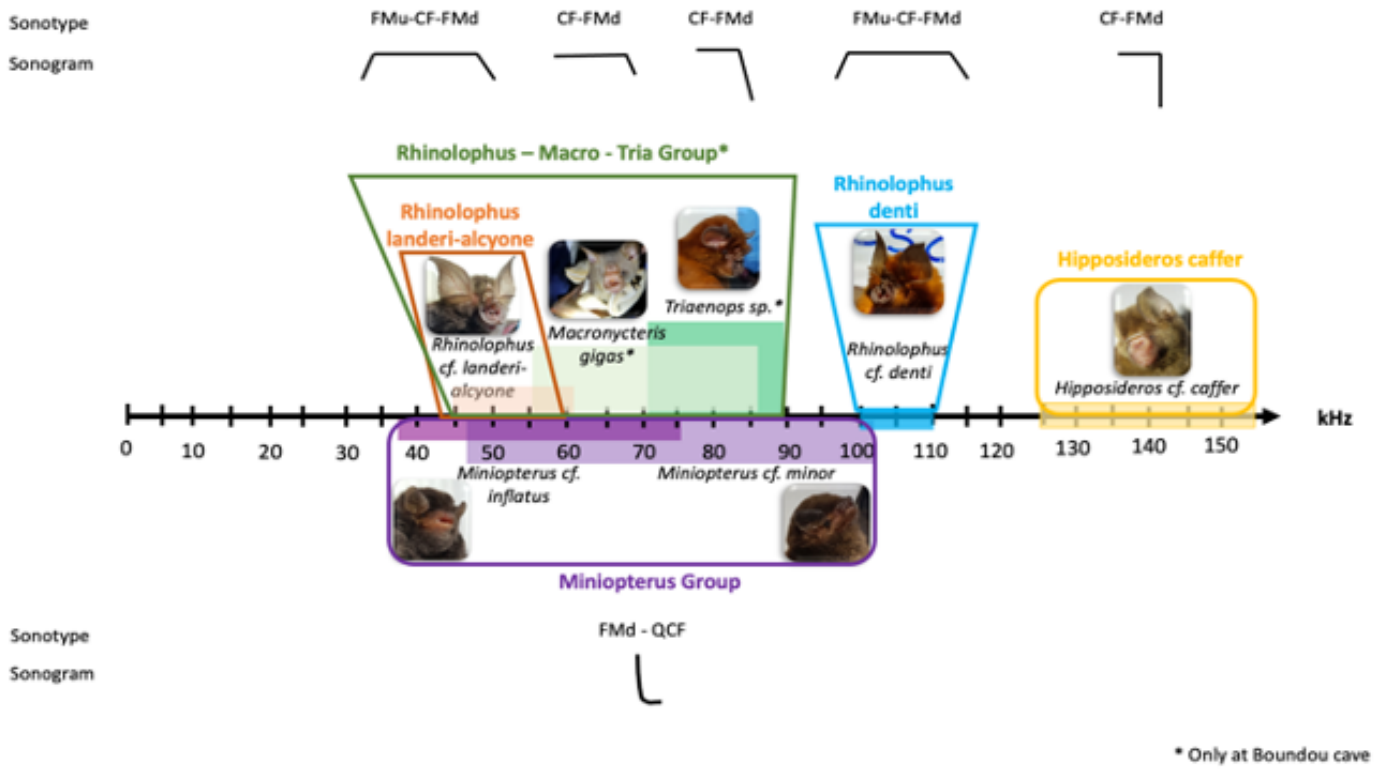


Figure 2 - Acoustic characteristics for the different bat species captured at the two study sites and categorization into different acoustic groups or species. Detail of sonotype, sonogram and acoustic frequency recorded or listed in reference works for each bat genus and species captured in the two 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).

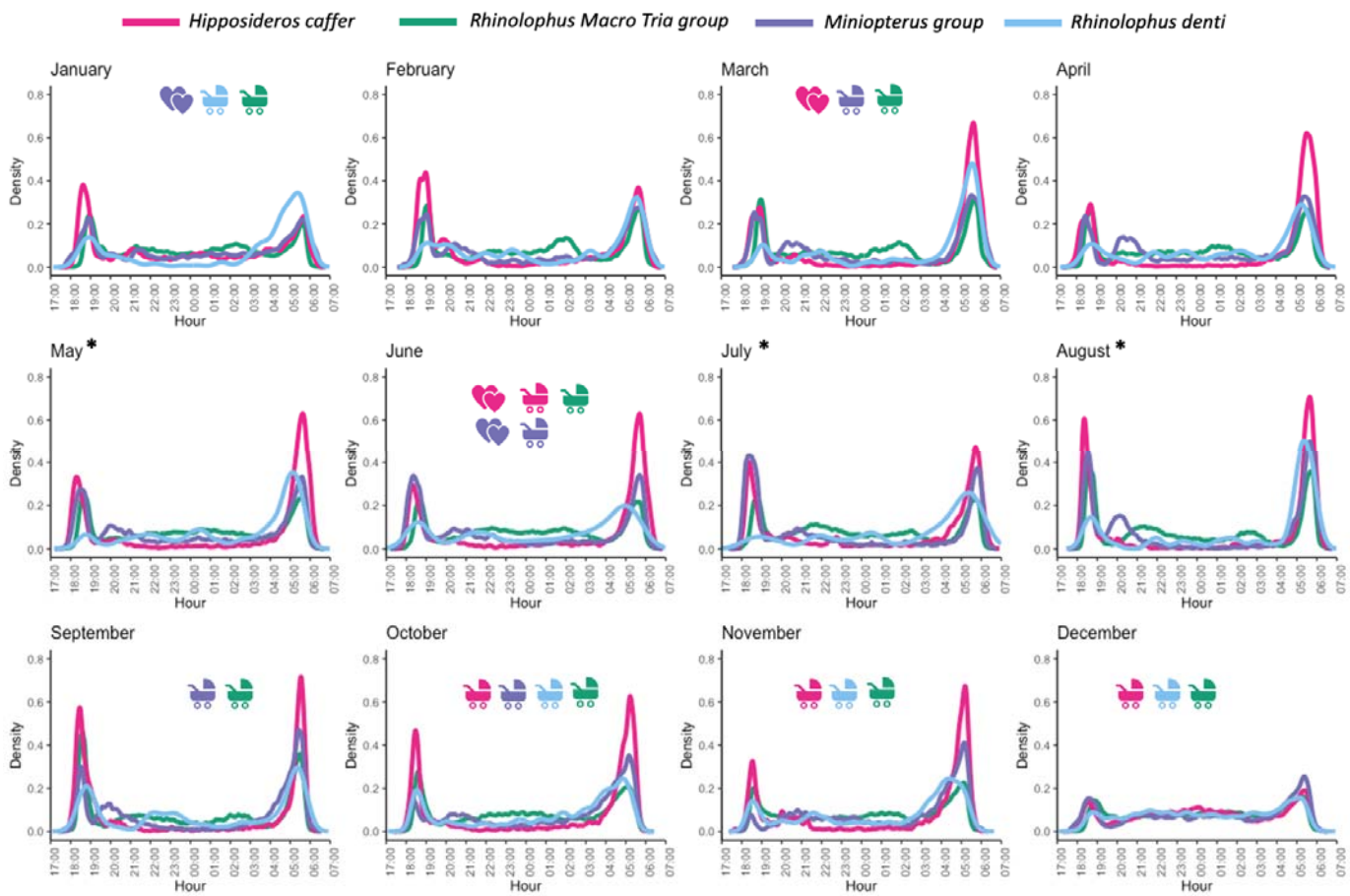


Figure 3 - Number of bat passes for each acoustic group according to month at Boundou Cave. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months 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.

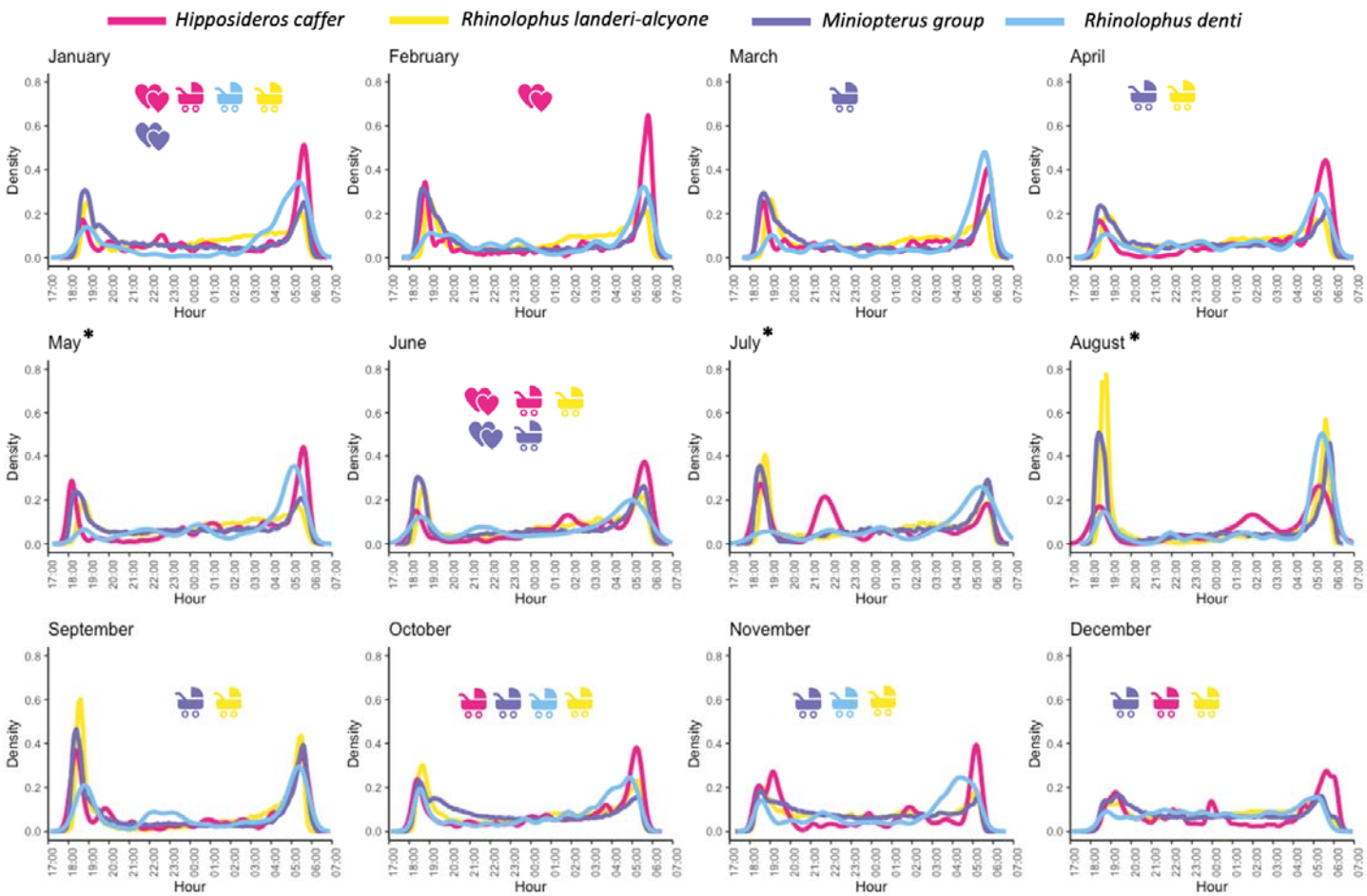


Figure 4 - Number of bat passes for each acoustic group according to month at Mont Belo Cave. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months 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.

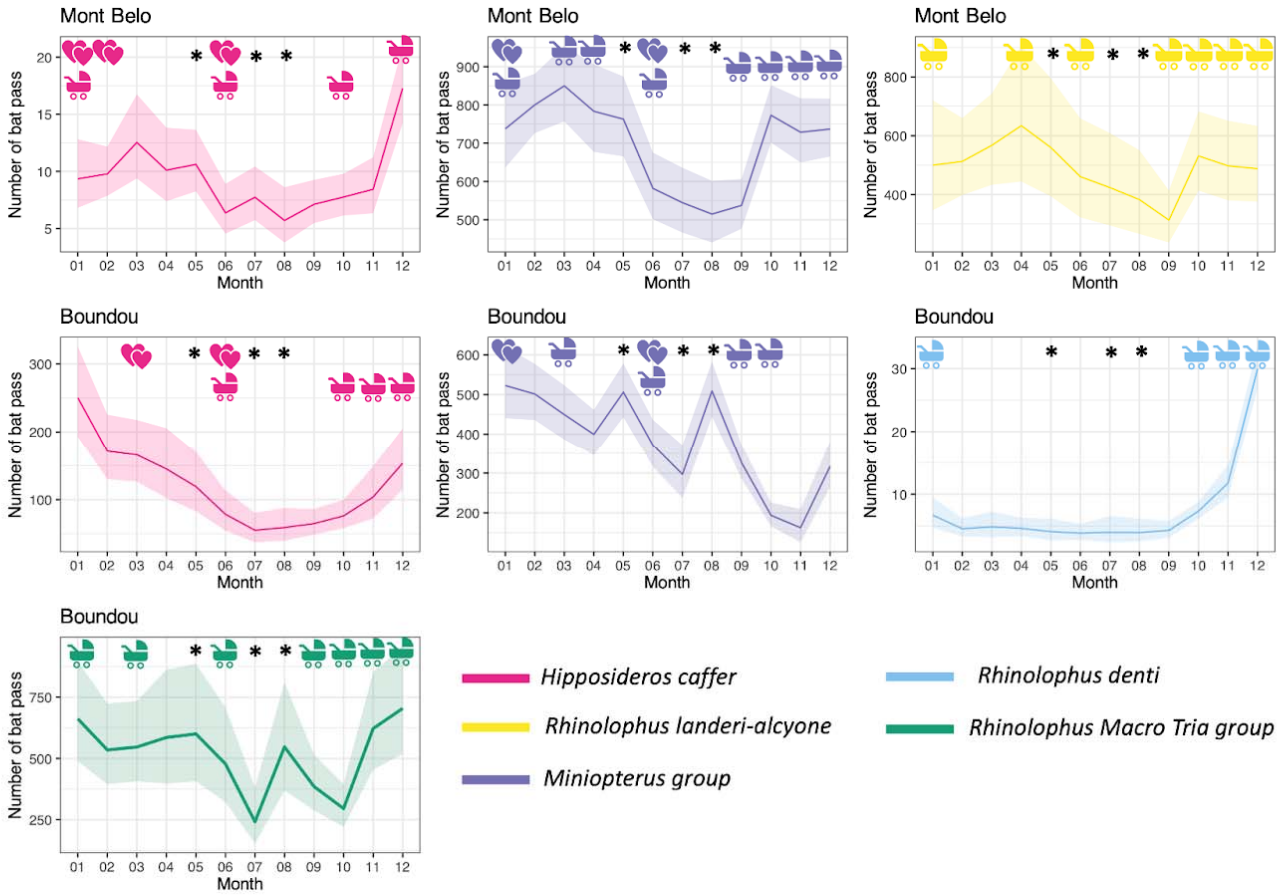


Figure 5 - Prediction of acoustic group emergence activity with 95% confidence interval as a function of months and study sites (Boundou and Mont Belo Cave). The *Rhinolophus denti* group at Mont Belo has not been represented here due to lack of data. The reproductive status of the species or acoustic 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 data_deficient 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 pattern

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 3–4 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 (no more than half an hour) (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, during some months (October – January), nightly activity patterns was more evenly distributed across the night, reflecting changes in foraging and maternal behavior. 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) coinciding with maternity colony formation (gestation, birth, and beginning of lactation). In December and January, emergence nocturnal activity was spread throughout the

night likely reflecting females alternating between foraging and suckling their young, as reported in previous studies (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 the 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* 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.

Our results also show peaks during the short rainy season (March–May), likely reflecting the independence of juveniles. The period when young reach their independence can vary according to bat species. 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).

Finally, based on capture observations, we hypothesise that the annual phenology of bat activity peaks observed during the dry season (January–February) correspond to the initiation of reproductive cycles for certain species, such as *Hipposideros caffer* and the *Miniopterus group*.

Some acoustic groups in our study showed two reproductive periods within the year. For example, the *Miniopterus* group exhibited peaks of reproductive activity in March–April and again from September to December, while *Rhino Macro Tria group* 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 a somewhat flexible reproductive period. 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.

This methodological framework can thus link nocturnal activity patterns with ecological drivers such as resource availability and rainfall cycle. The most favorable period in terms of resources is the long rainy season (October - December) and the short rainy season (March - May) for insectivorous bats (Fenton and Thomas, 1980). These wet periods favour the presence of a great diversity and abundance of insects (Jenber & Wili, 2021; Wolda, 1988). In mammals, including bats, this synchronization is important because of the high energy expenditure by lactating females (Racey & Entwistle, 2000). In addition, the aggregation of individuals can be an advantage, as females cooperate with each other to raise their young.

The long dry season (June–August) showed reduced nocturnal activity patterns compared with the other seasons. This suggests that bats congregate less in these habitats due to limited resources, a pattern that aligns with previous studies (Barclay & Kurta, 2007; Patriquin &

Ratcliffe, 2016; Patterson et al., 2007; Postawa & Gas, 2009). Scattered nocturnal activity patterns were observed throughout the night during the long dry season (June - August). Unfortunately, we did not capture in the months of July and August, and could not assess the reproductive status of the individuals. However, the gestation period observed from late September to early December in all acoustic groups suggests that copulation likely occurs towards the end of the long dry season (June–July). This timing aligns with swarming behavior and is consistent with observations from other countries. 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 only exception to the general drop-in nocturnal activity patterns was the *Miniopterus* group in Boundou cave, which remained very active in August (long dry season). The females of this species may use the cave to gather in a maternity colony before giving birth in September and October (obs. per ML). 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 and cave highlights the complexity of bat ecology in these systems. *Rhinolophus denti* appeared to use caves solely for rearing young, not for mating. Conversely, *Hipposideros caffer* used both caves for mating and rearing young. It is noteworthy that the mating period of *Hipposideros caffer* seemed to vary between cave (January, February, June in Mont Belo Cave and March and June in Boundou Cave). This variation in breeding months could potentially be explained by the presence of two cryptic species of Hipposideros in this study (obs. per ML).

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 annual phenology of bat activity 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 distinct biannual reproductive peaks (especially for Miniopterus and R. landeri–alcyone), whereas Boundou displays more evenly distributed activity and possibly more stable year-round occupation (notably for *Hipposideros caffer* and the *Rhinolohus* Macro Tria group). These patterns suggest functional complementarity between the two caves — Mont Belo cave likely serving as a breeding and maternity site, and Boundou cave as a multi-species roost used across seasons. These observations underscore the potential of PAM combined with acoustic classification to study reproductive behavior in wild populations, a novel application in Central African caves.

Our study demonstrates that quantitative bat monitoring is possible even in data-deficient areas. This approach offers a valuable tool for cave conservation, as it enables the identification of critical periods of bat activity, reproductive timing, and species-specific cave use. This information is essential for prioritizing protection and managing disturbance of cave bats (Tanalgo & Hughes, 2024). 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.

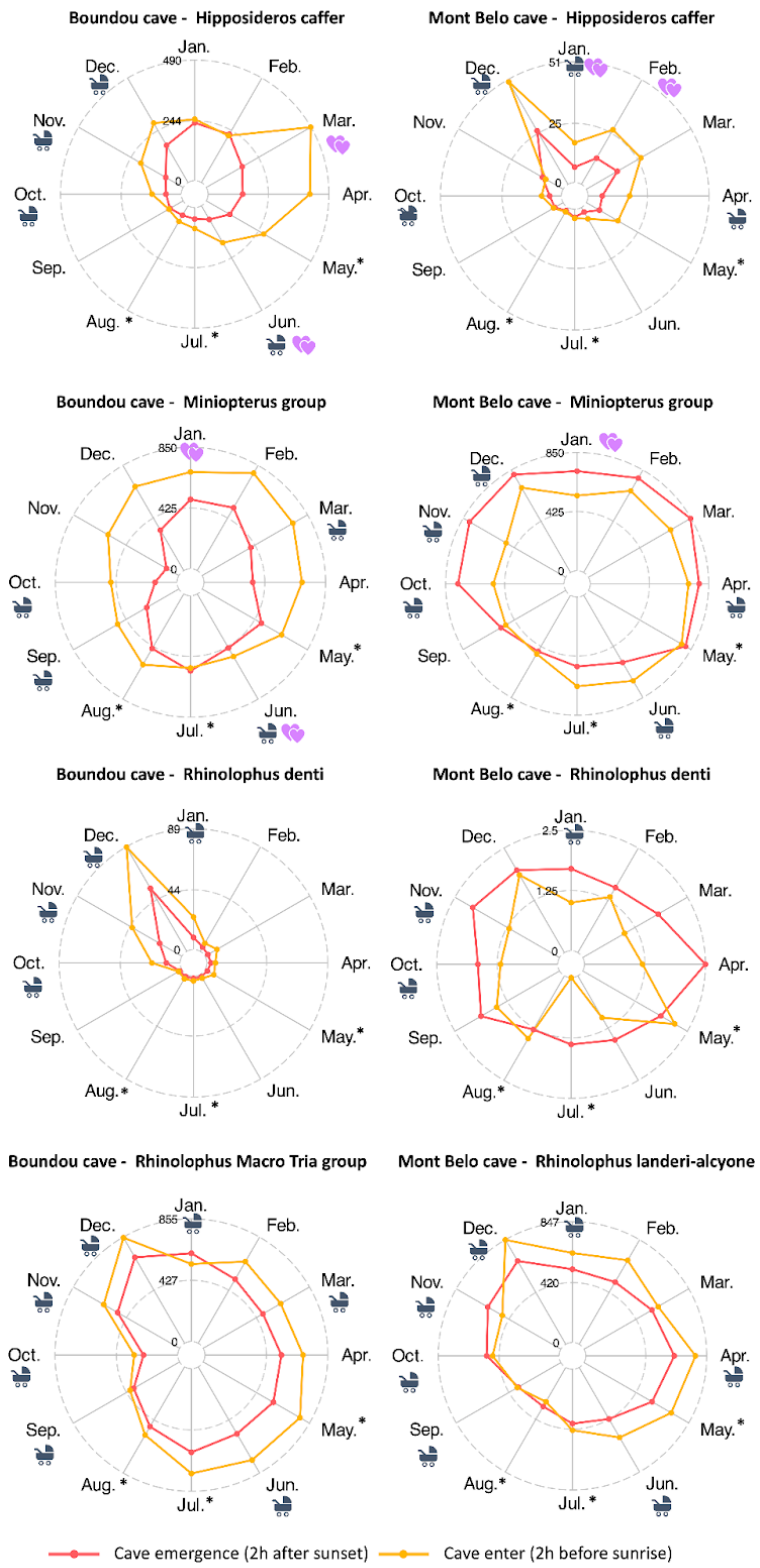
Future improvements could include non-invasive hormonal monitoring by collecting bat urine to analyze stress levels and reproductive hormones, allowing identification of mating and lactation periods without capturing bats (Greville et al., 2022; Kumar & Umapathy, 2019; Voigt & Schwarzenberger, 2008; 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- Summary table of eight 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 denti re-enter Mont Belo Cave	Nb_batpass ~ Month + (1|month-year)
Model Rhinolophus Macro Tria emergence Boundou Cave	Nb_batpass ~ Month + (1|month-year)

Appendix 2 - 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)

:

Appendix 3 - 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 4 - 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 5 - 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		

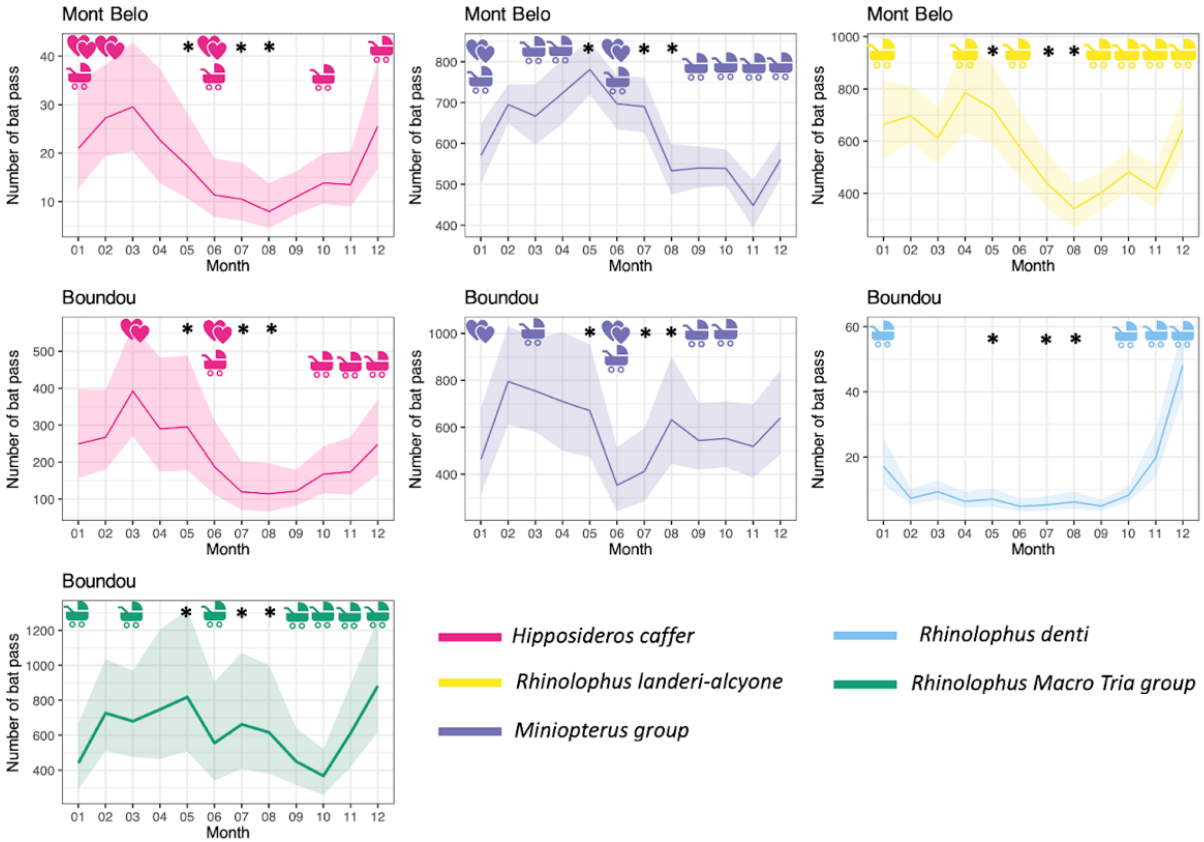
** p<0.05 ** p<0.01 *** p<0.001*

Appendix 6 - 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 7: 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.



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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.

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