Listen, who is it? A novel method for studying the nightly and annual phenologies of cave bat communities in data deficient areas of the world.

Morgane Labadie*[1,2], Serge Morand[3,4,5], Alexandre Caron[1,2,6], Helene Marie De Nys[1,2,7], Fabien Roch Niama[8], Franel Nguilili[9], N'Kaya Tobi[9], Mathieu Bourgarel[1,2,6], Yves Bas[10,11], Charlotte Roemer[10,11]

[1] CIRAD, UMR ASTRE, F-34398 Montpellier, France,

[2] ASTRE, CIRAD, INRAE, Univ Montpellier, Montpellier, France

[3] IRL HealthDEEP CNRS – Kasetsart University – Mahidol University, Bangkok, Thailand

[4] Faculty of Veterinary Technology, Kasetsart University, Bangkok, Thailand

[5] Department of Social and Environmental medicine, Faculty of Tropical Medicine, Mahidol University, Bangkok, Thailand

[6] Faculdade de Veterinaria, Universidade Eduardo Mondlane, Maputo, Mozambique

[7] CIRAD, UMR ASTRE, Harare, Zimbabwe

[8] Laboratoire National de Santé Publique, Brazzaville, République du Congo

[9] Direction Générale de l'Élevage (Service vétérinaire), Ministère de l'Agriculture, de l'élevage et de la pêche, Brazzaville, République du Congo

[10] Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France

[11] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

*Corresponding author
Correspondence: morgane.labadie@gmail.com

ABSTRACT

Context: Bats are the only mammals who have conquered the skies (Gunnell & Simmons, 2005; Thewissen & Babcock, 1992) and the leading mammals in terms of total biomass (Greenspoon et al., 2023) with the exception of domestic mammals. However, the ecology of bats is still a mystery, especially in poorly sampled regions such as Central Africa.

Aims: We present a new method for studying the nocturnal and annual phenologies of cave bat communities in data deficient regions.

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 an acoustic monitoring protocol (PAM) over a period of 19 months. In both caves, we collected a total of 2,375,956 acoustic files. We detected the presence of five distinct bat groups or species.

Key results: Our results showed bimodal activity throughout the year, except during the long rainy season, when tri- or quadri-modal activity was detected. Activity distributed throughout the night is related to the period of juvenile rearing (gestation, parturition and lactation). For all acoustic groups, we also observed high activity from October to March (long rainy season, short dry season and short rainy season) and low activity during the long dry season (June, July, August). 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 demonstrated the great variability of activity in five acoustic groups of cave-dwelling insectivorous bats, while at the same time gathering valuable information on bat species in the Congo. These variations are strongly linked to the season and/or the biological cycle of these species. This information is relevant to understanding the mechanisms by which colonies of cave bats can merge and fission.

Implications: The use of this technique can provide essential information to estimate insectivorous bat populations in habitats that have been poorly sampled using this passive acoustic monitoring protocol.

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). 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 1,470 recognised bat species worldwide, 34% are cave-dwelling species (IUCN, 2023; Simmons & Cirranello, 2023), 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). However, there is little information about bat populations and the animal community they interact with in these habitats, especially in African countries.

In order to meet its three primary needs (feeding, reproduction or rest), an organism will adopt activity patterns located in spatial and temporal dimensions (Alcock, 2013; Appel et al., 2019; Jones & Rydell, 1994). For example, at the end of gestation, female bats will reduce their foraging rate due to the increase in their body weight (Rydell, 1993). During the parturition and lactation periods, female bats may reduce their flight distance in search for food while increasing their activity due to the energy costs associated with milk production. (Cumming & Bernard, 1997; Henry et al., 2002; Kurta et al., 1989; Rydell, 1993). The temporal phenology of the activity of a species is also an indicator of its function in the ecosystem (i.e. niche sharing (Schoener, 1971), predator-prey dynamics (Flynn & Wolkovich, 2018; Forrest & Miller-Rushing, 2010; Tambling et al., 2015; Violle et al., 2017). Any alteration in this phenology could indicate an adaptation to an environmental change (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). This technique exploits the physiological characteristic of more than 70% of the world's bats (Browning et al., 2017; Gibb et al., 2019) (except Pteropodidae) which use echolocation to move and forage. Recording these sounds, which are often specific to a species, makes it possible to make a quantitative monitoring of a 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 of counting bat populations as they leave caves.

Our goal was to describe the activity patterns of communities of cave-dwelling bats using a novel method (counting bat pass during emergence and entry period) in bioacoustics and discuss these patterns in the light of their biological status assessed with capture data. Our study was implemented in an area in which no species classifier was developed, and thus we tested a new method using a sonotype classifier (Labadie et al., 2025). Firstly, we described the nightly phenology of the five acoustic groups identified in these caves and compare it across the different months of the year. Secondly, we looked at their annual phenology for each site. We assumed that nightly and annual phenologies are linked to bat life-cycle. Thus, we expected acoustic groups to be more active during periods when the species are breeding and rearing their young (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 and Fig. 2.

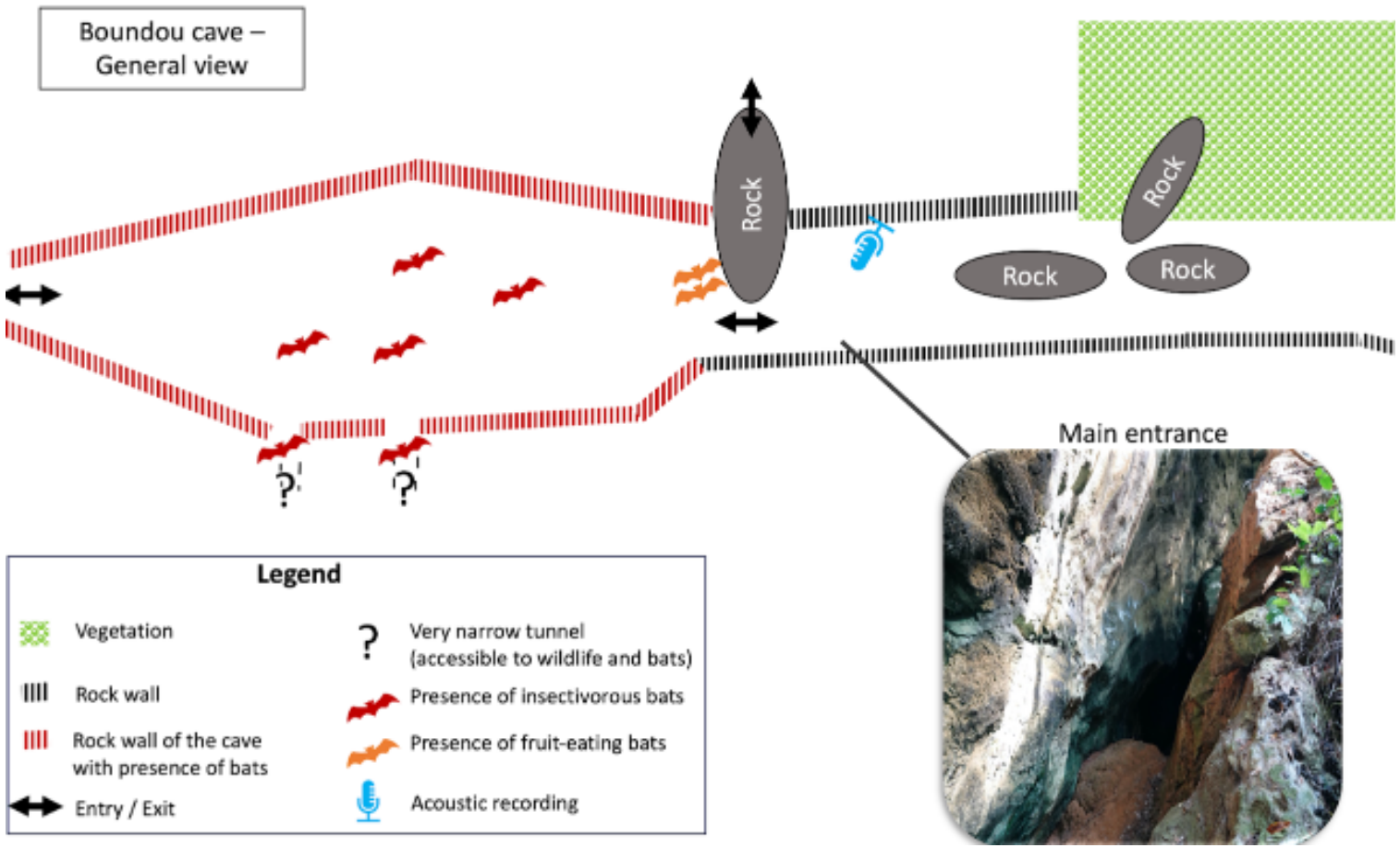


Figure 1 - General diagram of the configuration of the Boundou Cave, the location of the camera trap and the bat roosting sites.

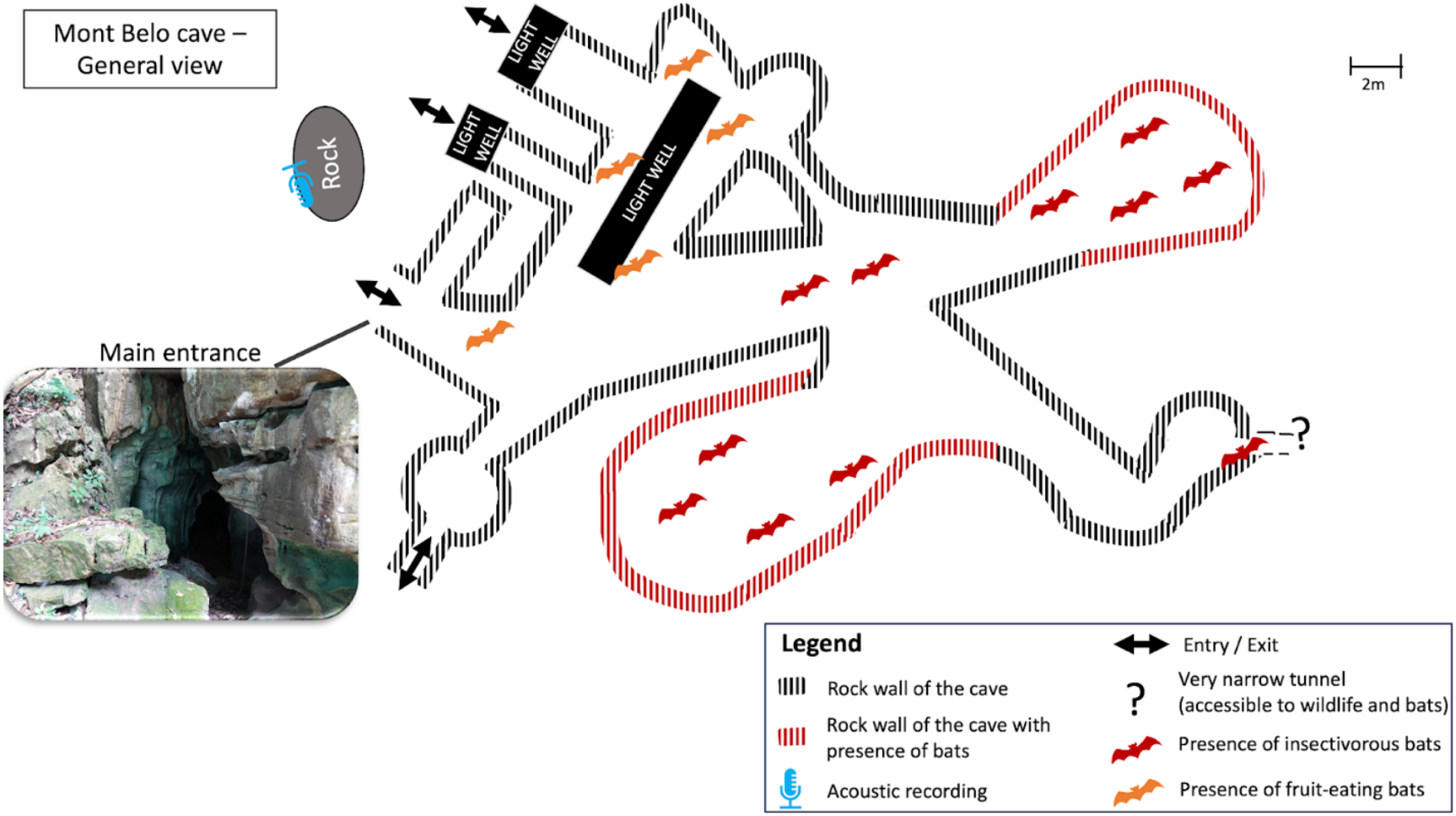


Figure 2 - General diagram of the configuration of the Mont Belo Cave, the location of the camera trap and the bat roosting sites.

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. 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. Figures 1 and 2 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. (2025) 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., 2025). The Boundou cave 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) the Rhinolophus - Macro - Tria group (R. cf. landeri-alcyone /M. gigas/Triaenops cf. afer). 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). 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. (2025).

Statistical analysis

Post-sorting of the Tadarida output and 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 phenology of the emergence and the entry 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 3 (Appendix 2, raw data for each group).

Nightly phenology

In both caves, for the five acoustic groups (Hipposideros caffer, Miniopterus group, Rhinolophus denti, Rhinolophus landeri-alcyone, Rhinolophus Macro Tria group), the patterns of emergence and entry activity in the caves 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. 4 and Fig. 5).

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. 4 and Fig. 5). In addition, the Boundou cave activity was more spread out during January and February (Fig. 4). In the Mont Belo cave, activity was also more spread out throughout the night in November and July (Fig. 5).

Annual phenology

Because analyses using emergence and entry activity produced similar annual phenologies, we decided to comment our results for the emergence activity only (Appendix 2, 4, 5 and 6). The activity at emergence 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 6 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 6 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 6 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 6 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 6 and Appendix 7).

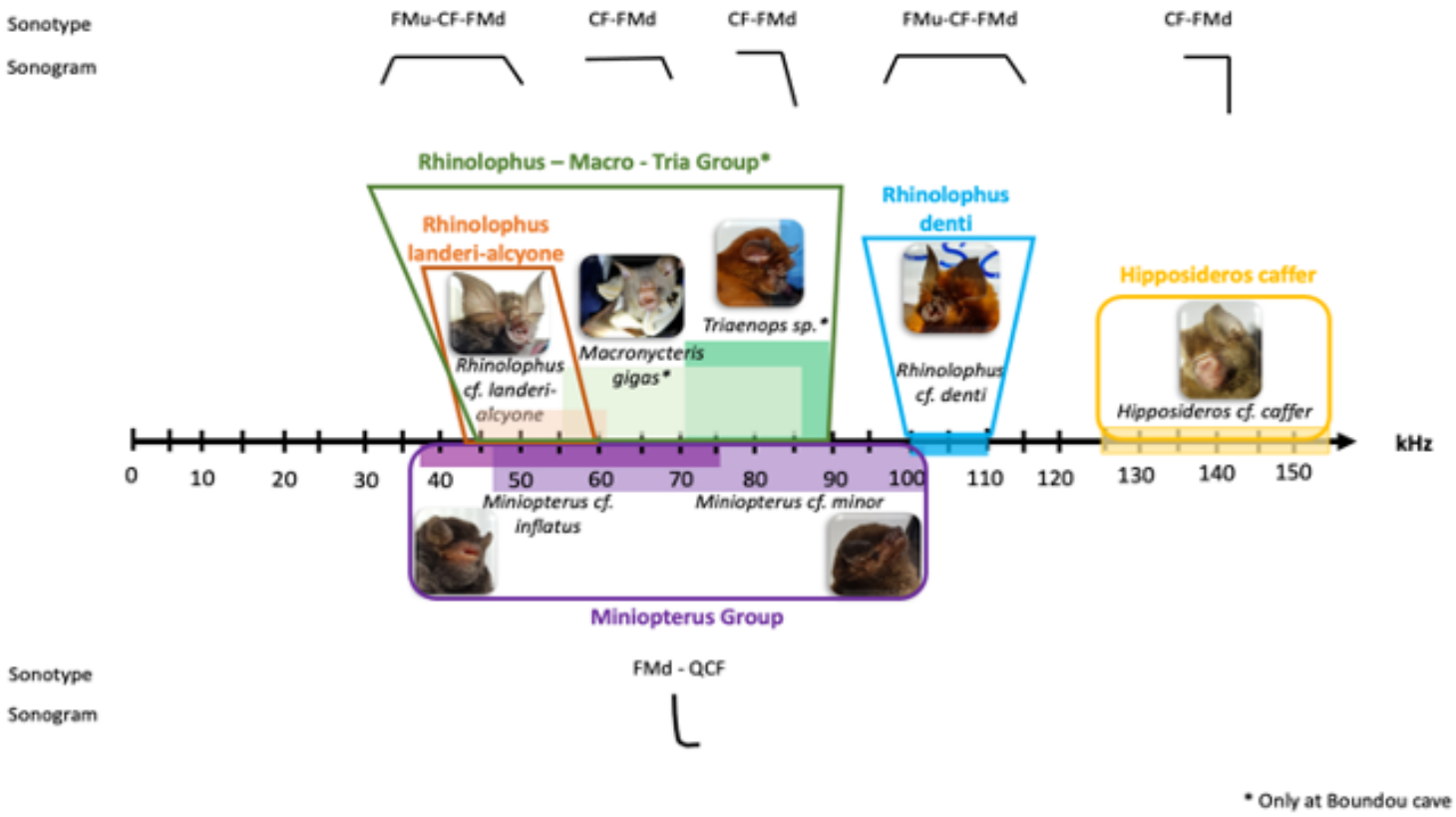


Figure 3 - Acoustic characteristics for the different bat species captured at the two study sites and categorization into different acoustic groups or species. Detail of sonotype, sonogram and acoustic frequency recorded or listed in reference works for each bat genus and species captured in the two 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).

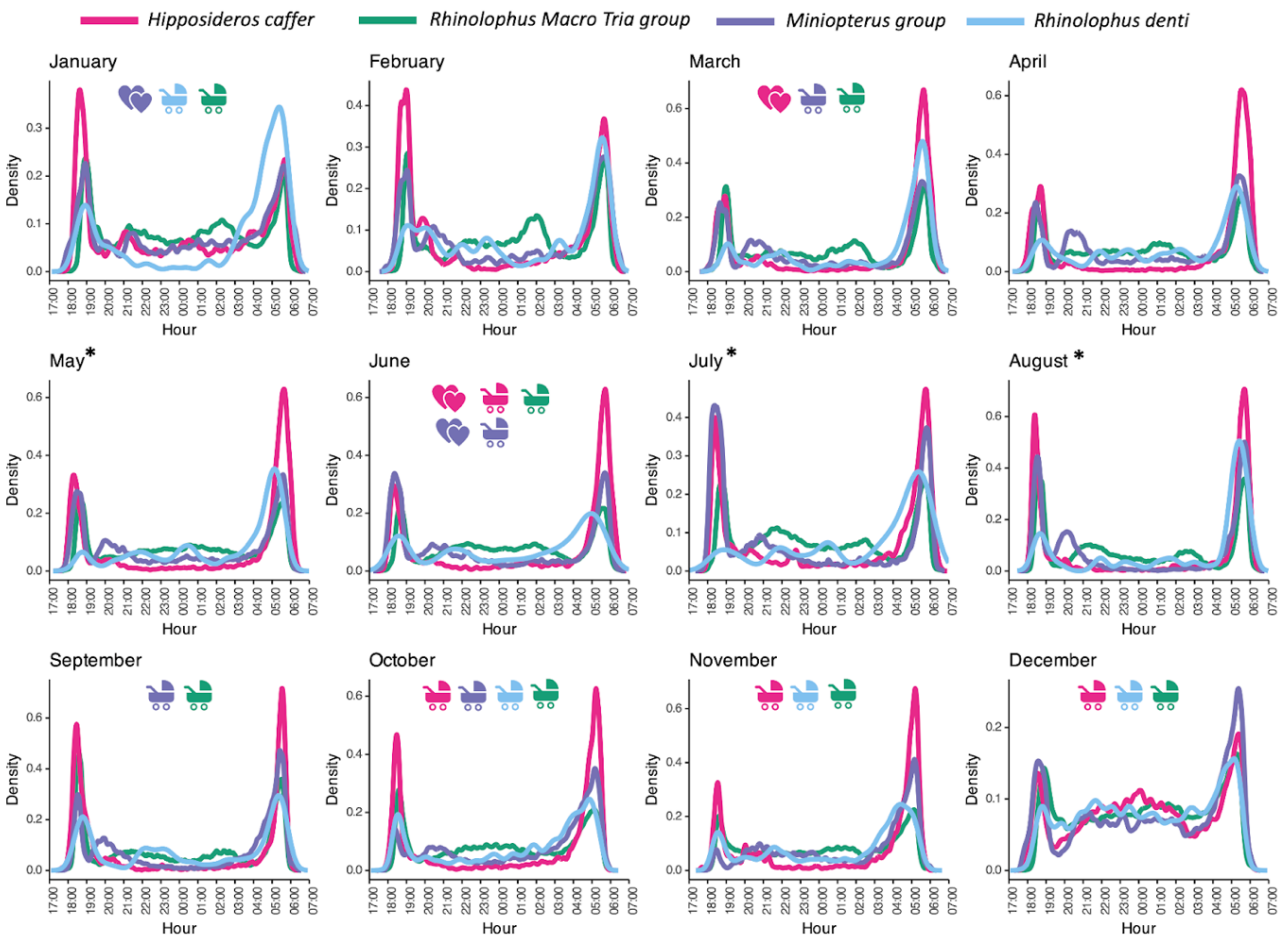


Figure 4 - Number of bat passes for each acoustic group according to month at Boundou Cave. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months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

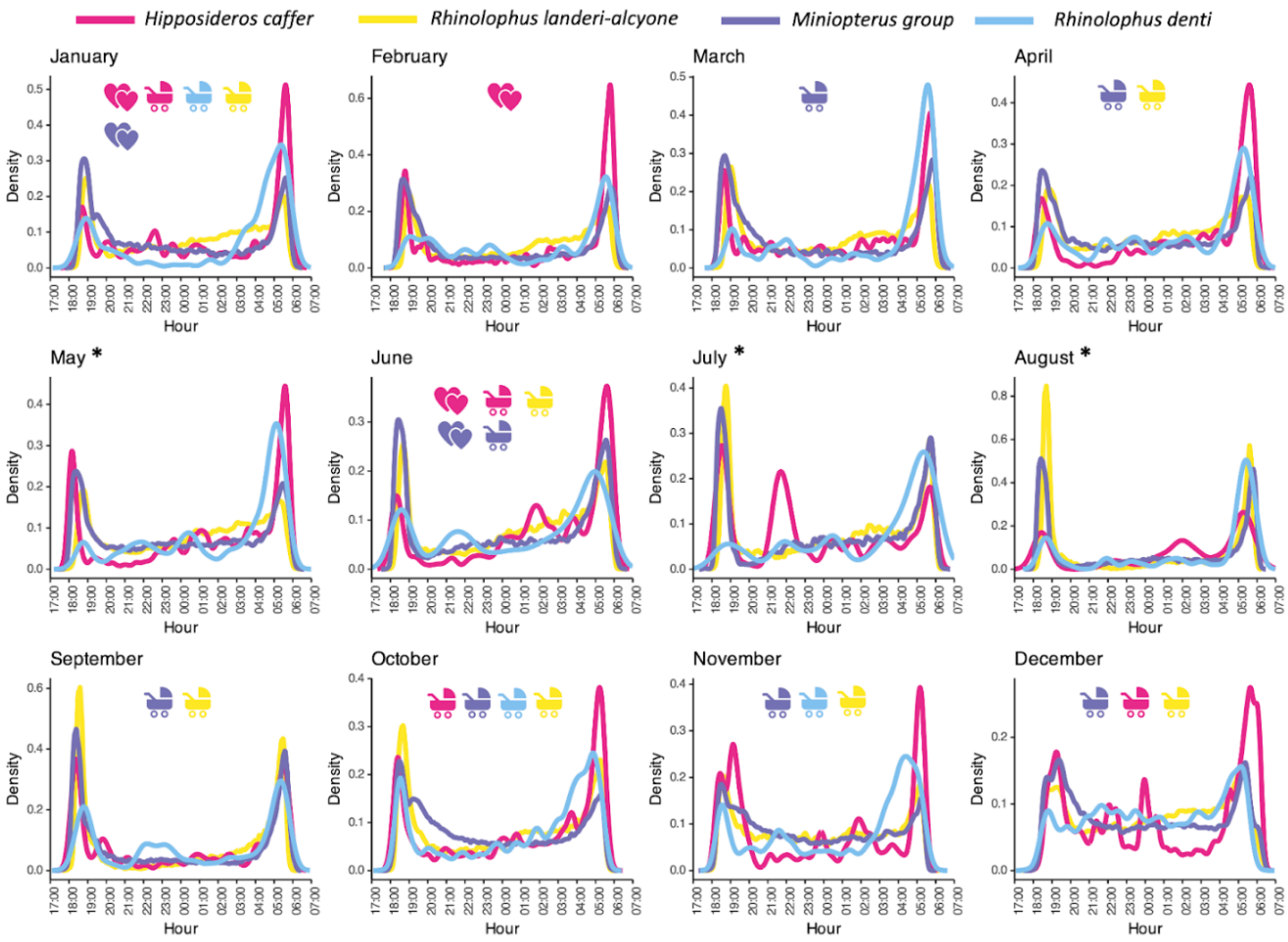


Figure 5 - Number of bat passes for each acoustic group according to month at Mont Belo Cave. The reproductive status of the species or acoustic group is indicated by two pictograms with the color of the acoustics groups: young rearing (lactation, pregnant) and : mating period/male activity. The months 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.

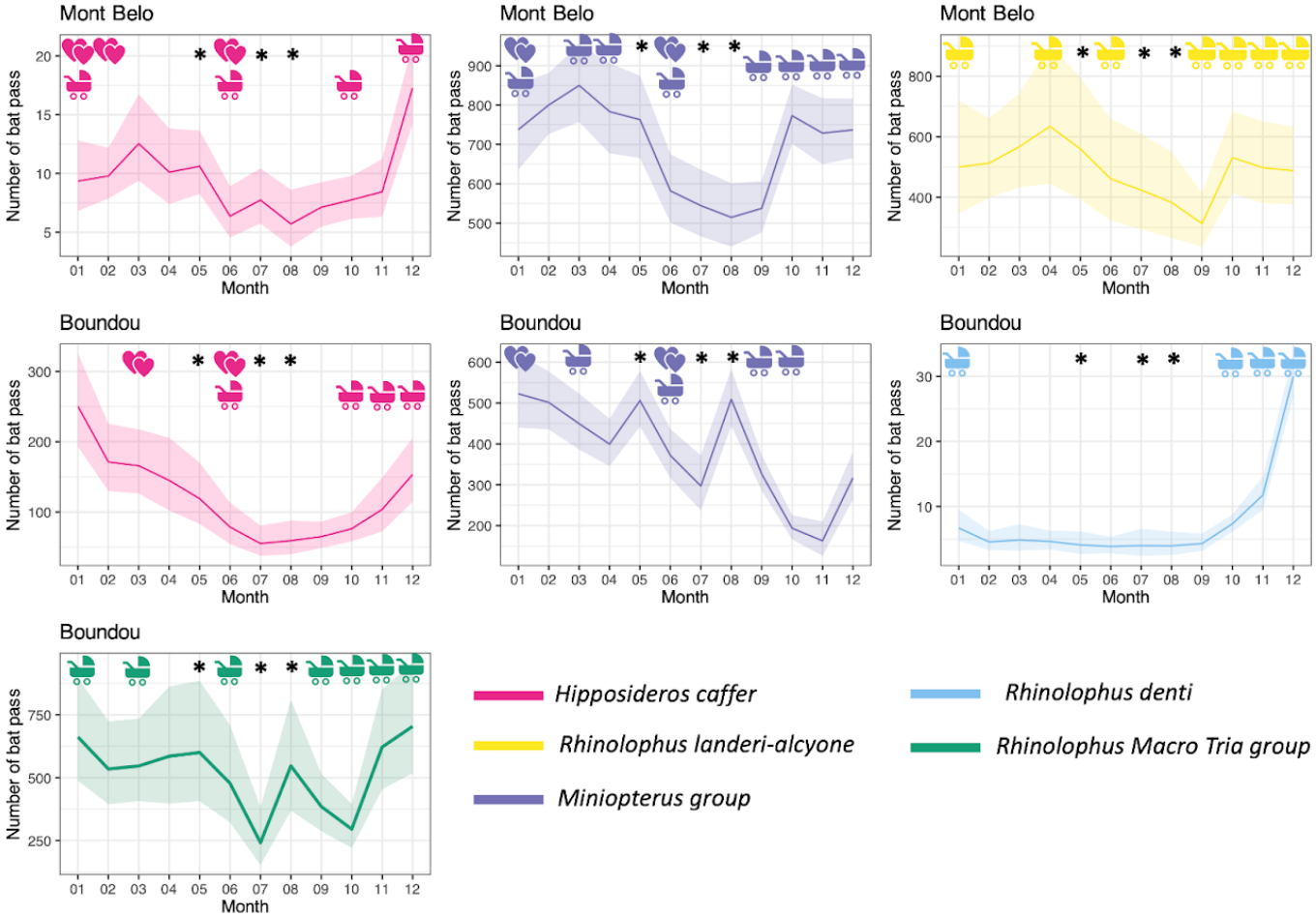


Figure 6 - Prediction of acoustic group emergence activity with 95% confidence interval as a function of months and study sites (Boundou and Mont Belo Cave). The Rhinolophus denti group at Mont Belo has not been represented here due to lack of data. The reproductive status of the species or acoustic 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

This study is the first to use passive acoustic monitoring at the entrances of caves in a country without a classifier designed for the local species, to quantify the activity (proxy of abundance, (Revilla-Martín et al., 2020) of five acoustic groups of bats and to describe their nightly and annual phenologies. Our results characterized the variation in activity of acoustic groups in relation to season and linked to their breeding status.

Description of nightly and annual phenologies

With a few exceptions, bats emerged from their daytime roosts at dusk to fly to feeding sites (Bullock et al., 1987). The time of this nocturnal emergence was correlated with the time of sunset (Erkert, 1982). Unlike northern countries, Central African countries such as Congo have little variation in sunrise and sunset throughout the year (no more than half an hour) (WorldData, 2024). Furthermore, in many bat colonies, bat emergence is characterised by "burst activity", where several bats emerge in rapid succession, interspersed with periods during which few bats emerge (Swift, 1980). Jones et Rydell (1994) that bats exit from the roost to forage for most of the night before returning to rest at the end of the night to rest. Our study confirmed these results by showing the presence of strong bi-modal activity (a period of emergence and a period of entry into the cave) for most months in both caves. Thus, when they are absent from the site, we could hypothesise that a large number of individuals go hunting before returning to the cave. The other individuals may move to another resting place or return later.

Our study showed that the activity of the different species of insectivorous bats in these two caves was mainly bi-modal throughout the year, with the exception of December and January. These two months correspond to a period during which females suckle their young or finish raising them. This hypothesis is based on field observations and the ecology of these species. We therefore hypothesise that this activity spread throughout the night corresponded to females coming back and forth to the cave to alternatively suckle their young and forage. These results are in accordance with several studies which have shown that the relationship between activity patterns in bat foraging habitats is influenced by the reproductive status of the individuals (Catto et al., 1995; Dietz & Kalko, 2006; Maier, 1992; Swift, 1980, 1997). In addition, the study by Henry et al (2002) showed that Myotis lucifugus decreased its flight distance by 35% and its home range by 51% between its gestation and lactation periods. In this study, lactating females returned to the roost between one and two times per night, imposing a distance constraint on foraging activity and observing an increase in roost activity three hours after the initial emergence time.

During the main rainy season (October, November, December), bat activity showed a sharp increase in terms of numbers of individuals. This sharp increase in activity can be explained by the formation of maternity colonies by the females for the period when they are rearing their young. (gestation, parturition and lactation, represented by a stroller in the figures) which forces them to change their behavior. During the short dry season (Jan, Feb; just after the main rainy season) and during the short rainy season (Mar, Apr, May), we observed a strong peak in activity in all of the acoustic groups in our study. This high

activity may indicate (i) the beginning of juvenile independence and (ii) the beginning of a reproductive cycle for certain species such as Hipposideros caffer or the Miniopterus group.

The time when youngs 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 (Wright, 2009). In fact, the two reproduction periods of the insectivorous species in our study could be explained by two hypotheses. The first is that the two reproductive cycles identified during the captures confirm the presence of two groups of species (as is the case for the Miniopterus group and the Rhino Macro Tria group). Or, we could have the presence of a cryptic complex (as for the Hipposideros) (Wright, 2009).

Finally, for most of the species present, our results showed relatively low activity during the long dry season (June, July, August) compared with the other seasons. We hypothesize that since this is not the period when young are reared, activity decreases drastically and/or that bat species do not congregate in large numbers in these habitats during this period, which is not very favourable in terms of resources (Barclay & Kurta, 2007; Patriquin & Ratcliffe, 2016; Patterson et al., 2007; Postawa & Gas, 2009). The most favourable period in terms of resources is the long rainy season (Oct, Nov, Dec) and the short rainy season (March, April, 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). Indeed, species tend to synchronize their period of reproduction with periods of high resource availability (Cumming & Bernard, 1997). In mammals, including bats, this synchronization may be all the more important because of the high energy expenditure by females when suckling their young (Racey & Entwistle, 2000). In addition, the aggregation of individuals can be an advantage, as females cooperate with each other to raise their young. This also enables individuals, including young, to group together to share their body heat, thus reducing the cost of thermoregulation (Boyles et al., 2008; Carter & Wilkinson, 2013; Willis & Brigham, 2007).

Scattered activity was observed throughout the night during the long dry season (June, July and August). Unfortunately, we did not capture in July and August, and could not assess the reproductive status of the individuals. However, the observation of a gestation period from late September to early December in the females of all the acoustic groups would tend to place the copulation period towards the end of summer during the long dry season (June, July). This hypothesis is fairly consistent with other studies of bat copulation behaviour in other countries (Günther et al., 2016). For example, according to several studies concerning Hipposideros caffer, the copulation period occurs at the end of the first rainy season (June-July) and calving in the middle of the second rainy season (October-November) (Bernard, 1982; Brosset, 1968).

The only exception to this drop-in activity was the Minioptera group in Boundou cave, which was 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.

Variation in roost use by month and species

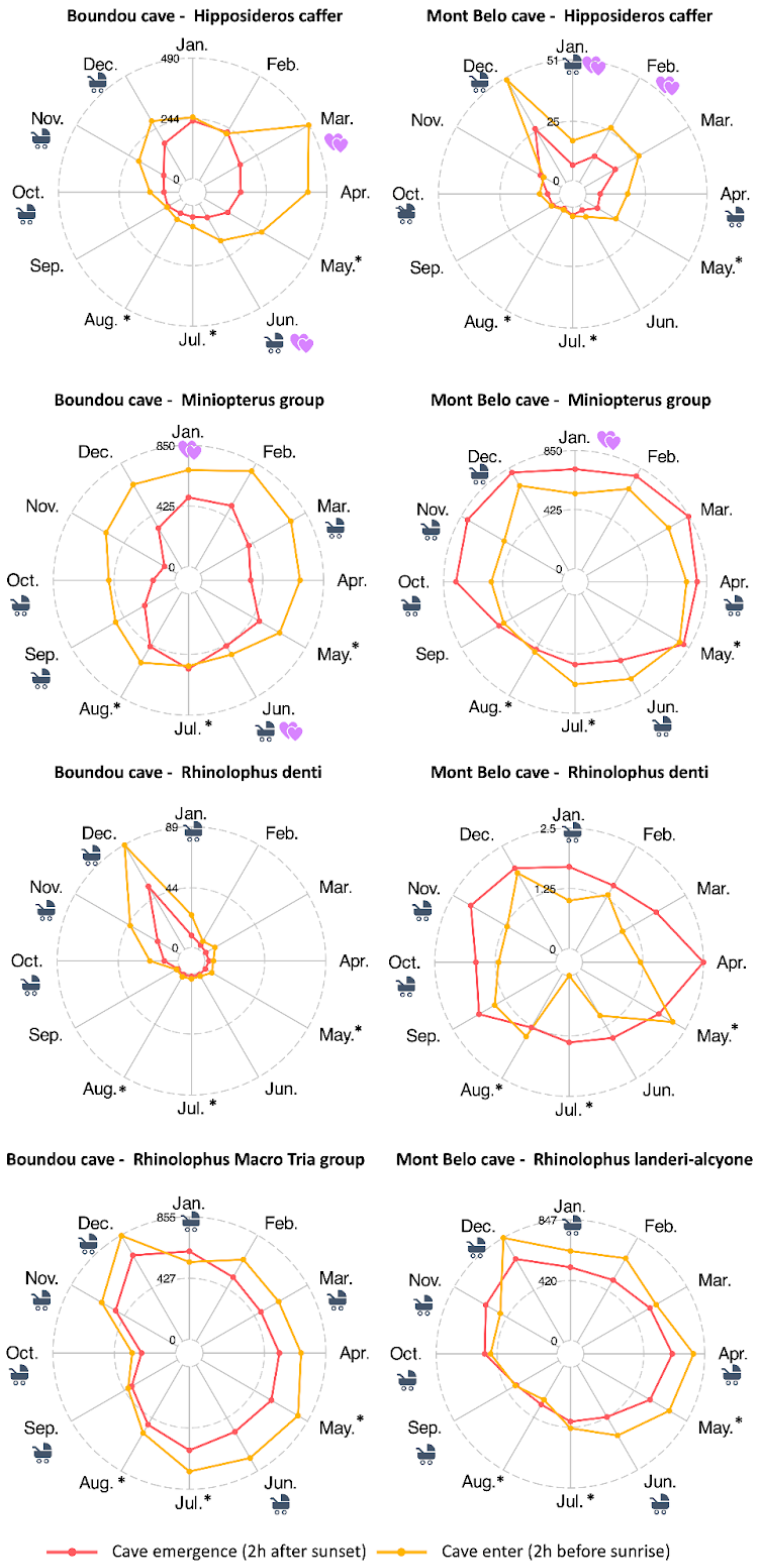
Our study showed a difference in species use of the two caves over the time scale; for example, Rhinolophus denti seemed to use both caves only for rearing young, not for mating. Conversely, Hipposideros caffer used both caves for mating and rearing young. We can note that for Hipposideros caffer, the mating period seemed to vary from cave to 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 inside this study (Labadie et al., in prep.).

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)

415 :

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		

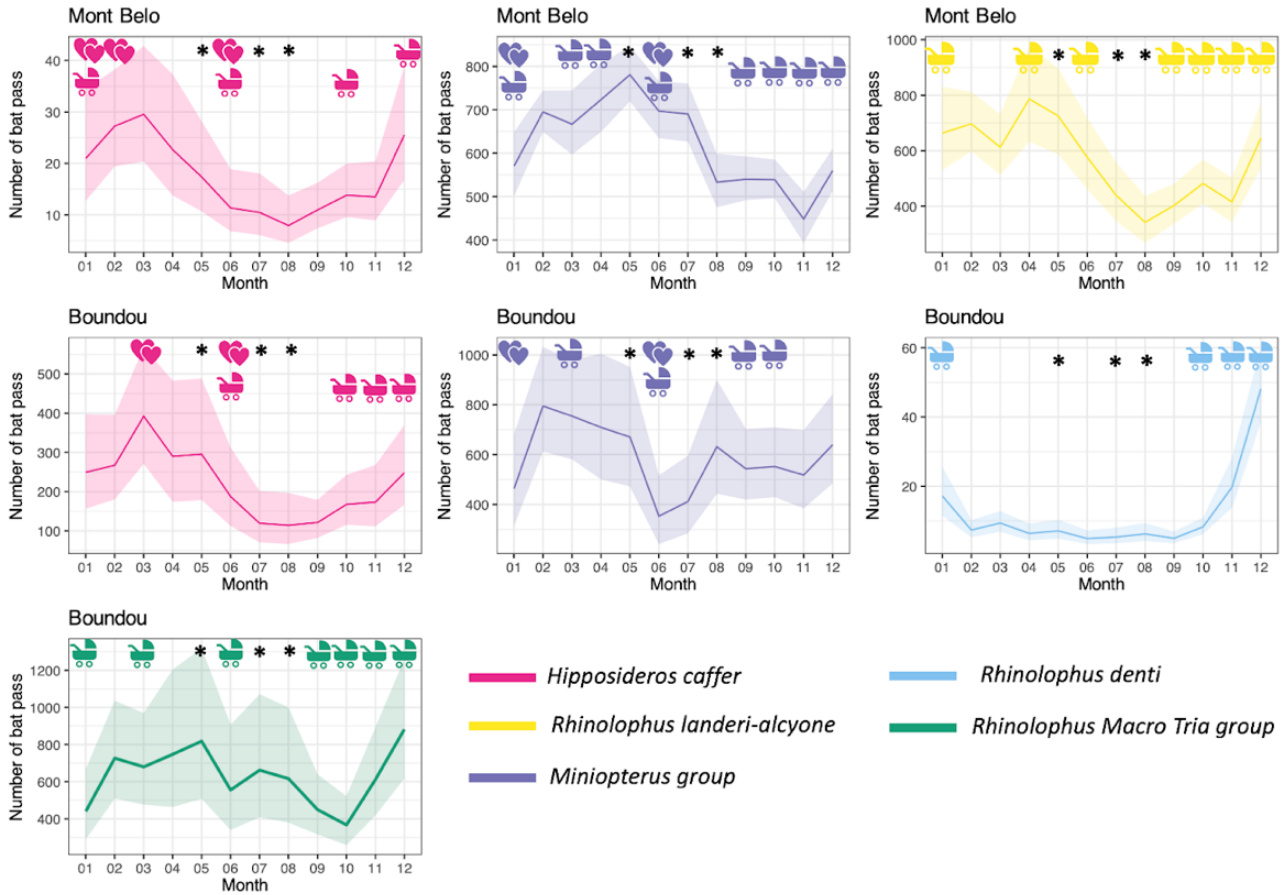
** p<0.05 ** p<0.01 *** p<0.001*

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.



Acknowledgements

I would also like to extend my 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 species summary file and the scripts for making the figures can be made available on request from the author or via a link on a download platform.

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.

References

Alcock, J. (2013). Animal Behavior: An Evolutionary Approach (10th edition). Sinauer Associates.

Appel, G., Capaverde, U. D., De Oliveira, L. Q., do Amaral Pereira, L. G., da Cunha Tavares, V., López-Baucells, A., Magnusson, W. E., Baccaro, F. B., & Bobrowiec, P. E. (2021). Use of complementary methods to sample bats in the Amazon. Acta Chiropterologica, 23(2), 499–511. https://doi.org/10.3161/15081109ACC2021.23.2.017

Appel, G., López-Baucells, A., Magnusson, W. E., & Bobrowiec, P. E. D. (2019). Temperature, rainfall, and moonlight intensity effects on activity of tropical insectivorous bats. Journal of Mammalogy, 100(6), 1889–1900. https://doi.org/10.1093/jmammal/gyz140

Azmy, S. N., Sah, S. A. M., Shafie, N. J., Ariffin, A., Majid, Z., Ismail, M. N. A., & Shamsir, M. S. (2012). Counting in the dark: Non-intrusive laser scanning for population counting and identifying roosting bats. Scientific Reports, 2(1), 1–4.https://doi.org/10.1038/srep00524

Balogh, A., Ngo, L., Zigler, K. S., & Dixon, G. (2020). Population genomics in two cave-obligate invertebrates confirms extremely limited dispersal between caves. Scientific Reports, 10(1), 17554.https://doi.org/10.1038/s41598-020-74508-9

Barclay, R. M., & Kurta, A. (2007). Ecology and behavior of bats roosting in tree cavities and under bark. Bats in Forests: Conservation and Management (MJ Lacki, JP Hayes, and A. Kurta Eds.). Johns Hopkins University Press, Baltimore, Maryland, 352, 17–59.

Barnhart, P. R., & Gillam, E. H. (2014). The impact of sampling method on maximum entropy species distribution modeling for bats. Acta Chiropterologica, 16(1), 241–248.https://doi.org/10.3161/150811014X683435

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? Nature, 471(7336), 51–57. https://doi.org/10.1038/nature09678

Barros, J. D. S., Bernard, E., & Ferreira, R. L. (2020). Ecological preferences of neotropical cave bats in roost site selection and their implications for conservation. Basic and Applied Ecology, 45, 31–41. https://doi.org/10.1016/j.baae.2020.03.007

Bernard, R. & Meester, J. A. J. (1982). Female reproduction and the female reproductive cycle of Hipposideros caffer caffer (Sundevall, 1846) in Natal, South Africa. Annals of the Transvaal Museum, 33(8), 131–144.

Bion, R. (2023). ggradar: Create radar charts using ggplot2. R Package Version 0.2.

Boyles, J., Storm, J., & Brack Jr, V. (2008). Thermal benefits of clustering during hibernation: A field test of competing hypotheses on Myotis sodalis. Functional Ecology, 632–636. https://doi.org/10.1111/j.1365-2435.2008.01423.x

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal, 9(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Brosset, A. (1968). La Permutation du Cycle sexuel saisonnier chez le chiroptère Hipposideros caffer, au voisinage de l'Équateur.

Browning, E., Gibb, R., Glover-Kapfer, P., & Jones, K. E. (2017). Passive acoustic monitoring in ecology and conservation. http://dx.doi.org/10.25607/OBP-876

Bullock, D., Combes, B., Eales, L., & Pritchard, J. (1987). Analysis of the timing and pattern of emergence of the pipistrelle bat (Pipistrellus pipistrettus). Journal of Zoology, 211(2), 267–274. https://doi.org/10.1111/j.1469-7998.1987.tb01533.x

Cabin, R. J., & Mitchell, R. (2000). To Bonferroni or not to Bonferroni: When and how are the questions. ESA Bulletin, 81, 246–248. 10.2307/20168454

Carter, G. G., & Wilkinson, G. S. (2013). Cooperation and Conflict in the Social Lives of Bats. In R. A. Adams & S. C. Pedersen (Eds.), Bat Evolution, Ecology, and Conservation (pp. 225–242). Springer. https://doi.org/10.1007/978-1-4614-7397-8_12

Catto, C., Racey, P., & Stephenson, P. (1995). Activity patterns of the serotine bat (Eptesicus serotinus) at a roost in southern England. Journal of Zoology, 235(4), 635–644. https://doi.org/10.1111/j.1469-7998.1995.tb01774.x

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances, 1(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Cumming, G., & Bernard, R. (1997). Rainfall, food abundance and timing of parturition in African bats. Oecologia, 111, 309–317. https://doi.org/10.1007/s004420050240

Cumming, G. S., & Bernard, R. T. F. (1997). Rainfall, food abundance and timing of parturition in African bats. Oecologia, 111(3), 309–317. https://doi.org/10.1007/s004420050240

Dietz, M., & Kalko, E. K. (2006). Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (Myotis daubentonii). Journal of Comparative Physiology B, 176, 223–231. https://doi.org/10.1007/s00360-005-0043-x

Erkert, H. G. (1982). Ecological Aspects of Bat Activity Rhythms. In T. H. Kunz (Ed.), Ecology of Bats (pp. 201–242). Springer US. https://doi.org/10.1007/978-1-4613-3421-7_5

Flaquer, C., Torre, I., & Arrizabalaga, A. (2007). Comparison of sampling methods for inventory of bat communities. Journal of Mammalogy, 88(2), 526–533. https://doi.org/10.1644/06-MAMM-A-135R1.1

Flynn, D., & Wolkovich, E. (2018). Temperature and photoperiod drive spring phenology across all species in a temperate forest community. New Phytologist, 219(4), 1353–1362. https://doi.org/10.1111/nph.1523

Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1555), 3101–3112. https://doi.org/10.1098/rstb.2010.0145

Forsyth, D. M., Scroggie, M. P., & McDonald-Madden, E. (2006). Accuracy and precision of grey-headed flying-fox (Pteropus poliocephalus) flyout counts. Wildlife Research, 33(1), 57–65. 10.1071/WR05029

Furey, N. M., & Racey, P. A. (2016). Conservation ecology of cave bats. In Bats in the Anthropocene: Conservation of Bats in a Changing World (pp. 463–500). Springer, Cham. https://doi.org/10.1007/978-3-319-25220-9_15

Gibb, R., Browning, E., Glover-Kapfer, P., & Jones, K. E. (2019). Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods in Ecology and Evolution, 10(2), 169–185. https://doi.org/10.1111/2041-210X.13101

Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Bar-On, Y. M., Moran, U., Antman, T., Meiri, S., Roll, U., Noor, E., & Milo, R. (2023). The global biomass of wild mammals. Proceedings of the National Academy of Sciences, 120(10), e2204892120. https://doi.org/10.1073/pnas.2204892120

Gunnell, G. F., & Simmons, N. B. (2005). Fossil Evidence and the Origin of Bats. Journal of Mammalian Evolution, 12(1–2), 209–246. https://doi.org/10.1007/s10914-005-6945-2

Günther, L., Lopez, M. D., Knörnschild, M., Reid, K., Nagy, M., & Mayer, F. (2016). From resource to female defence: The impact of roosting ecology on a bat's mating strategy. Royal Society Open Science, 3(11), 160503. https://doi.org/10.1098/rsos.160503

Hartig, F., & Hartig, M. (2022). Package 'DHARMa'. R Package. Available Online: Https://CRAN. R-Project. Org/Package= DHARMa (Accessed on 5 September 2022).

Henry, M., Thomas, D. W., Vaudry, R., & Carrier, M. (2002). Foraging Distances and Home Range of Pregnant and Lactating Little Brown Bats (Myotis Lucifugus). Journal of Mammalogy, 83(3), 767–774. https://doi.org/10.1644/1545-1542(2002)083<0767:FDAHRO>2.0.CO;2

Hill, A. P., Prince, P., Snaddon, J. L., Doncaster, C. P., & Rogers, A. (2019). AudioMoth: A low-cost acoustic device for monitoring biodiversity and the environment. HardwareX, 6, e00073. https://doi.org/10.1016/j.ohx.2019.e00073

Hughes, A. C. (2017). Understanding the drivers of Southeast Asian biodiversity loss. Ecosphere, 8(1), e01624. https://doi.org/10.1002/ecs2.1624

IUCN, N. and I. (International U. for C. of N. (2023). The IUCN Red List of Threatened Species. Version 2022-2. IUCN Red List of Threatened Species. https://www.iucnredlist.org/en

Jenber, A. J., & Wili, G. G. (2021). Insect diversity in wet and dry seasons at hursa forest, central Ethiopia. International Journal of Entomology Research, 6(4), 59–63.

Jones, G., & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 346(1318), 445–455. https://doi.org/10.1098/rstb.1994.0161

Keeley, B. W., & Tuttle, M. D. (1999). Bats in American bridges. Bat Conservation International Incorporated.

Koger, B., Hurme, E., Costelloe, B. R., O'Mara, M. T., Wikelski, M., Kays, R., & Dechmann, D. K. N. (2023). An automated approach for counting groups of flying animals applied to one of the world's largest bat colonies. Ecosphere, 14(6), e4590. https://doi.org/10.1002/ecs2.4590

Kunz, T. H. (1982). Roosting ecology of bats. In Ecology of bats (pp. 1–55). Springer.

Kunz, T. H., Lumsden, L. F., & Fenton, M. (2003). Ecology of cavity and foliage roosting bats. Bat Ecology, 1, 3–89. http://doi.org/10.5281

Kurta, A., Bell, G. P., Nagy, K. A., & Kunz, T. H. (1989). Energetics of pregnancy and lactation in freeranging little brown bats (Myotis lucifugus). Physiological Zoology, 62(3), 804–818. https://doi.org/10.1111/j.1469-7998.1992.tb04433.x

Labadie, M., Morand, S., Caron, A., De Nys, H. M., Niama, F. R., Nguilili, F., … Roemer, C. (2025). Passive acoustic monitoring of cave-dwelling bats with a sonotype classifier. Bioacoustics, 1–29. https://doi.org/10.1080/09524622.2024.2438600

Lewis, S. E. (1995). Roost Fidelity of Bats: A Review. Journal of Mammalogy, 76(2), 481–496. https://doi.org/10.2307/1382357

Maier, C. (1992). Activity patterns of pipistrelle bats (Pipistrellus pipistrellus) in Oxfordshire. Journal of Zoology, 228(1), 69–80.

Mariton, L., Le Viol, I., Bas, Y., & Kerbiriou, C. (2023). Characterising diel activity patterns to design conservation measures: Case study of European bat species. Biological Conservation, 277, 109852. https://doi.org/10.1016/j.biocon.2022.109852

Medellin, R. A., Wiederholt, R., & Lopez-Hoffman, L. (2017). Conservation relevance of bat caves for biodiversity and ecosystem services. Biological Conservation, 211, 45–50.

Mering, E. D., & Chambers, C. L. (2014). Thinking outside the box: A review of artificial roosts for bats. Wildlife Society Bulletin, 38(4), 741–751. 10.1002/wsb.461

Mickleburgh, S. P., Hutson, A. M., & Racey, P. A. (2002). A review of the global conservation status of bats. Oryx, 36(1), 18–34. doi:10.1017/S0030605302000054

Millon, L., Julien, J.-F., Julliard, R., & Kerbiriou, C. (2015). Bat activity in intensively farmed landscapes with wind turbines and offset measures. Ecological Engineering, 75, 250–257. https://doi.org/10.1016/j.ecoleng.2014.11.050

Monadjem, A., Taylor, P. J., & Schoeman, M. C. (2020). Bats of southern and central Africa: A biogeographic and taxonomic synthesis. Wits University Press.

Neuhuber, S., Plan, L., Gier, S., Hintersberger, E., Lachner, J., Scholz, D., Lüthgens, C., Braumann, S., Bodenlenz, F., & Voit, K. (2020). Numerical age dating of cave sediments to quantify vertical movement at the Alpine-Carpathian transition in the Plio-and Pleistocene. Geologica Carpathica, 71(6), 539–557. https://doi.org/10.31577/GeolCarp.71.6.5

Okonkwo, E. E., Afoma, E., & Martha, I. W. (2017). Cave Tourism and its Implications to Tourism Development in Nigeria: A Case Study of Agu-Owuru Cave in Ezeagu. International Journal of Research, 3, 16–24. doi:dx.doi.org/10.20431/2455-0043.0303003

Ormsbee, P. C., Kiser, J. D., & Perlmeter, S. I. (2007). Importance of night roosts to the ecology of bats. Bats in Forests: Conservation and Management. Johns Hopkins University Press, Baltimore, MD, 129–151.

Patriquin, K. J., & Ratcliffe, J. M. (2016). Should I stay or should I go? Fission–fusion dynamics in bats. Sociality in Bats, 65–103. https://doi.org/10.1007/978-3-319-38953-0_4

Patterson, B. D., Dick, C. W., & Dittmar, K. (2007). Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). Journal of Tropical Ecology, 23(2), 177–189. doi:10.1017/S0266467406003816

Postawa, T., & Gas, A. (2009). Do the thermal conditions in maternity colony roost determine the size of young bats? Comparison of attic and cave colonies of Myotis myotis in Southern Poland. Folia Zoologica, 58(4), 396.

R Core Team. (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/

Racey, P. A., & Entwistle, A. C. (2000). Life-history and Reproductive Strategies of Bats. In Reproductive Biology of Bats (pp. 363–414). Elsevier. https://doi.org/10.1016/B978-012195670-7/50010-2

Revilla-Martín, N., Budinski, I., Puig-Montserrat, X., Flaquer, C., & López-Baucells, A. (2020). Monitoring cave-dwelling bats using remote passive acoustic detectors: A new approach for cave monitoring. Bioacoustics, 00(00), 1–16. https://doi.org/10.1080/09524622.2020.1816492

Roemer, C., Julien, J. F., & Bas, Y. (2021). An automatic classifier of bat sonotypes around the world. Methods in Ecology and Evolution, 12(12), 2432–2444. https://doi.org/10.1111/2041-210X.13721

Russo, D., & Ancillotto, L. (2015). Sensitivity of bats to urbanization: A review. Mammalian Biology, 80(3), 205–212. https://doi.org/10.1016/j.mambio.2014.10.003

Rydell, J. (1993). Variation in Foraging Activity of an Aerial Insectivorous Bat during Reproduction. Journal of Mammalogy, 74(2), 503–509. https://doi.org/10.2307/1382411

Sabol, B. M., & Hudson, M. K. (1995). Technique using thermal infrared-imaging for estimating populations of gray bats. Journal of Mammalogy, 76(4), 1242–1248. https://doi.org/10.2307/1382618

Schoener, T. W. (1971). Theory of Feeding Strategies. Annual Review of Ecology, Evolution, and Systematics, 2, 369–404. https://www.jstor.org/stable/2096934

Simmons, N. B., & Cirranello, A. L. (2023). Bat Species of the World: A taxonomic and geographic database. https://batnames.org/query.html

Simons, J. W. (1998). Guano mining in Kenyan lava tunnel caves. International Journal of Speleology, 27, 4. https://api.semanticscholar.org/CorpusID:56146083

Struebig, M. J., Kingston, T., Zubaid, A., Le Comber, S. C., Mohd-Adnan, A., Turner, A., Kelly, J., Bożek, M., & Rossiter, S. J. (2009). Conservation importance of limestone karst outcrops for Palaeotropical bats in a fragmented landscape. Biological Conservation, 142(10), 2089–2096. https://doi.org/10.1016/j.biocon.2009.04.005

Sugai, L. S. M., Desjonquères, C., Silva, T. S. F., & Llusia, D. (2020). A roadmap for survey designs in terrestrial acoustic monitoring. Remote Sensing in Ecology and Conservation, 6(3), 220–235. https://doi.org/10.1002/rse2.131

Swift, S. M. (1980). Activity patterns of pipistrelle bats (Pipistrellus pipistrellus) in north-east Scotland. Journal of Zoology, 190(3), 285–295. https://doi.org/10.1111/j.1469-7998.1980.tb01428.x

Swift, S. M. (1997). Roosting and foraging behaviour of Natterer's bats (Myotis nattereri) close to the northern border of their distribution. Journal of Zoology, 242(2), 375–384. https://doi.org/10.1111/j.1469-7998.1997.tb05809.x

Tambling, C. J., Minnie, L., Meyer, J., Freeman, E. W., Santymire, R. M., Adendorff, J., & Kerley, G. I. (2015). Temporal shifts in activity of prey following large predator reintroductions. Behavioral Ecology and Sociobiology, 69, 1153–1161. https://doi.org/10.1007/s00265-015-1929-6

Thewissen, J., & Babcock, S. (1992). The origin of flight in bats. BioScience, 42(5), 340–345. https://doi.org/10.2307/1311780

The Protection of Bat Roost Guidelines Subcommittee, Sheffield, S. R., Shaw, J. H., Heidt, G. A., & McClenaghan, L. R. (1992). Guidelines for the protection of bat roosts. Journal of Mammalogy, 707–710. https://doi.org/10.2307/1382051

Thieurmel, B., Elmarhraoui, A., & Thieurmel, M. B. (2022). Package 'suncalc'. R Package Version 0.5. https://cran.r-project.org/package=suncalc

Thomas, D. W., & West, S. D. (1989). Sampling methods for bats. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/pnw-gtr-243

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J., Cadotte, M. W., Livingstone, S. W., & Mouillot, D. (2017). Functional rarity: The ecology of outliers. Trends in Ecology & Evolution, 32(5), 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Westcott, D. A., & McKeown, A. (2004). Observer error in exit counts of flying-foxes (Pteropus spp.). Wildlife Research, 31(5), 551–558. 10.1071/WR03091

Whiting, J. C., Doering, B., Aho, K., & Rich, J. (2021). Long-term patterns of cave-exiting activity of hibernating bats in western North America. Scientific Reports, 11(1), 8175.

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org

Willis, C. K. R., & Brigham, R. M. (2007). Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. Behavioral Ecology and Sociobiology, 62(1), 97–108. https://doi.org/10.1007/s00265-007-0442-y

Wolda, H. (1988). Insect seasonality: Why? Annual Review of Ecology and Systematics, 19(1), 1–18. https://doi.org/10.1146/annurev.es.19.110188.000245

Wolkovich, E. M., Cook, B. I., McLauchlan, K. K., & Davies, T. J. (2014). Temporal ecology in the Anthropocene. Ecology Letters, 17(11), 1365–1379. https://doi.org/10.1111/ele.12353

WorldData. (2024). Worlddata—Republic of Congo. https://www.worlddata.info/africa/congo-brazzaville/sunset.php

Wright, G. S. (2009). Hipposideros caffer (Chiroptera: Hipposideridae). Mammalian Species, 845, 1–9. https://doi.org/10.1644/845.1.Key