Methods

Figure 1 could be improved to show a more zoomed in map of where the caves are. A base map showing different vegetation biomes/types, nearby water sources and human settlements etc. would be interesting and relevant.

I suggest compiling other figures to include: I recommend drawing up a basic map of the caves showing their structures, the locations of the camera traps and the approximate area covered by the camera traps. I'm wondering how much of the cave was covered by traps and if there is any overlap in their line of sight. Also, show the locations of temporary / permanent bat roosting sites relative to the camera positions to understand how close animals and humans are to bats in physical proximity. I also recommend creating a figure showing the time periods (on a timeline) for which of the nine cameras were functional and when they were not. The numbering system of the cameras in this figure should link to that of the cave map for readers to more easily visualise when and which cameras were operational.

Line 217: Spiders are not insects and should be removed from the 'other insects' group and counted as their own group - arachnids.

Line 237 – 240: Please explain the logic of cataloguing moving and 'other' behaviours separately? The animals may be 'moving' in the video to sit and observe in another part of the cave. Also, does the foraging behaviour imply that the animals are finding food within the cave or have brought food into the cave from the outside? For the interspecific interactions – did you only include eating and hunting? And not that different species may be in close proximity to one another or within the cave at the same time? We know infectious diseases may be spread via aerosols without the need for physical contact. I recommend adding a figure / table to quantify the number and types of interspecific interactions (and between which species) to better assess the contact, transmission, competition and predation as mentioned in the introduction.

Line 265: What is the reasoning for using three species richness indices? What value does it add to the manuscript to use three? Why not rather calculate species diversity?

After reading the methods, I am left wondering why you selected these two caves specifically. Please include a rationale or reasoning for monitoring these caves.

Results

There is an important oversight of the description of bats in this manuscript Which species of bats are present in the caves and at what abundance during which months of the year? Is this a maternal colony or just a roosting site?

Line 300 – It is not clear what was used as the input data for number of samples and why it is maximum of 15 for the 4 plots? Shouldn't the x-axis be camera trap sampling effort? The outside curves don't plateau, so it seems not all species were captured – this needs to be stated in the manuscript.

Figure 3 – this plot would show the trends better if the y-axes are comparable between all of the taxa classes. Consider transforming the axes or compiling a stacked chart rather to make the trends more easily noticeable.

Line 303: It isn't clear whether the results in Table 1 are for the differences between seasons compared per cave or between the two caves. It would make most sense to me to compare detections between different seasons for each cave separately as figure is showing clear seasonal differences. It would be interesting to understand the difference in seasonal activity between inside and outside for each cave as this helps readers to how connected the cave ecosystem is to the outside ecosystem.

Table 3 – Why did the authors decide to combine the species richness estimates for both caves? I am of the opinion they should be estimated for inside and outside of the two caves separately. Again, I think this manuscript would benefit from using just one species richness estimate and including diversity metrics.

Figure 4 – This figure can be improved by stacking the bars for easier comparison. I would combine the four categories (two caves and inside/outside) into one plot – should make it easier to see differences in classes.

Line 334 – It hasn't been stated in the manuscript why the correlations were run for a select group of taxa only.

Line 377 – 390: It isn't mentioned in the manuscript whether the observations from in and outside of the cave were grouped for the activity overlap analysis. Also, it seems these estimates were calculated for both caves combined. Why did the authors make the decision to calculate for both caves together and for inside and outside. I suspect the activity would differ between the caves and whether it is inside and outside.

Considering the introduction is framed in the light of species interactions to understand disease spillover, I'm not sure it is of much interest to understand the overlap in activity of bats/rodents with insects. Why did the authors not investigate the overlap between bats and rodents?

Discussion

Why are the bat hunting human activities in Mont Belo occurring only at the beginning of the observation years (March 2022 and Jan 2023)? Does this correspond with migrations of large bat species into the cave or general abundance of bats? Lack of other protein sources for people at that time of the year? It is important to understand this as this is a high risk for pathogen spillover between humans and bats.

Line 405 – "identifies mechanisms of potential transmission routes (trophic chain, bridge hosts, etc.) of different micro-organisms". This was not done in this study so the claim should be removed.

Lastly and most importantly, the discussion lacks sections talking to the aims and hypotheses posed in the introduction.

Habitat sharing and interspecies interactions in bat caves in the Republic of Congo

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Abstract

Bats play key roles in ecosystem functions and provide services and disservices to human populations. The study of the interface between bats and other animals, including humans, is of importance to protect bats and to mitigate the risks associated with pathogen spillover. Caves are key habitats for many bat species, which use them as roosting and breeding sites. Caves, bats and their guano also attract many other animals along trophic chains which might favor direct or indirect interspecies interactions creating a potential pathway for infectious agents' transmission. Two caves hosting colonies of insectivorous bats have been investigated in the Republic of Congo to characterize habitat sharing and interactions between bats, humans and animals. We implemented a camera-trap monitoring protocol for nineteen months at the entrance of and within each cave. Our results demonstrated the richness and complexity of the species interactions around and within these caves. We identified and/or quantified mainly rodents, but also numerous species of insects, birds, reptiles and carnivores using the caves. We investigated the temporal variation in the use of caves and the potential interactions between humans, wild animals and bat colonies. Our study provides some of the first quantified insights of the trophic chains and interfaces between communities, including humans, associated with caves. Our study may help investigating putative transmission pathways between cave-dwelling bats, bridge hosts and humans which could guide disease surveillance and control at the bat-human interface.

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Introduction

Bats are notorious for their relationships with emerging infectious diseases, yet they are also key species in our ecosystems. They provide important ecological systems functions such as helping to pollinate and disperse the seeds of over 549 plant species, and regulating arthropod and insect pest populations, thereby limiting economic losses for many farmers worldwide (Kunz et al. 2011; Ramírez-Fráncel et al. 2022; Ghanem and Voigt 2012; Castillo-Figueroa 2020). Bats are threatened by numerous human activities (destruction of their habitat, pesticides, hunting) (Almeida et al. 2021; Furey and Racey 2016), but they are also victims of bad reputation due to their role in the transmission of zoonotic pathogens (Afelt et al. 2018; Banerjee et al. 2019; Calisher et al. 2006; López-Baucells, Rocha, and Fernández-Llamazares 2018; MacFarlane and Rocha 2020). It is therefore important to understand and protect bats, while monitoring and managing the potential health risk to human populations, especially in human-bat interface habitats.

Caves offer very specific light, humidity and temperature conditions that create ecological niches that benefit the many cave-dwelling species of animals, plants and micro-organisms (Gabriel and Northup 2013; Kosznik-Kwaśnicka et al. 2022; Kovác 2018; Tomczyk-Żak and Zielenkiewicz 2016; Pacheco et al. 2020). The presence of caves in an ecosystem therefore influences local biodiversity through their contribution of specialized cave-dwelling species, but also attracts non-cavernicolous species through the feeding, foraging or hunting opportunities they provide. Caves are key habitats for many bat species, which use them as resting and refuge places as well as breeding and parturition sites (Barros, Bernard, and Ferreira 2020; Ormsbee, Kiser, and Perlmeter 2007; Struebig et al. 2009). Caves can host a high diversity of bat species. In addition, some bat species can gather in caves by hundreds or thousands (Kunz 1982; Monadjem, Taylor, and Schoeman 2020). This habitat can also be important for many other animal species (e.g., insects, birds) that use them for different purposes (e.g., refuges, breeding, foraging). In a cave populated by bats, many direct and indirect interactions can occur between bats, animals (wild or domestic) and humans (Furey and Racey 2016; McCracken 1989). From time immemorial, humans have been using caves as places of refuge and/or worship (Bonsall and Tolan-Smith 1997; Moyes 2012; Straus 1979). More recently, humans have been exploiting these habitats to extract minerals and guano, or as tourist attractions (Okonkwo, Afoma, and Martha 2017; Simons 1998). Wild animals take advantage of the presence of bat colonies as a food source, with numerous examples of predation by birds, small mammals or snakes, but also insects, e.g., centipedes (Mallick, Hossain, and Raut 2021; Mas, López-Baucells, and Arrizabalaga 2015; Molinari et al. 2005; Ridley 1898; Scrimgeour, Beath, and Swanney 2012; Tanalgo et al. 2019). Domestic pets, cats and dogs can also be major predators of these bat colonies (Costa-Pinto 2020; Merz et al. 2022; Oedin et al. 2021). Salinas-Ramos et al. (2021) emphasized the danger that cat predation poses for pathogen transmission in human populations. Caves represent therefore specific habitats for the interface between bat and other animals.

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Recent studies have suggested an increased risk of zoonotic transmission in highly disturbed environments characterized by a rise in the frequency and the intensity of wildlife-humans interactions (Afelt et al. 2018; Allen et al. 2017; Becker et al. 2018; Johnson et al. 2020; Plowright et al. 2021; Rulli et al. 2017; Wilkinson et al. 2018). However, studies on bat-animal interfaces (including humans) are still rare. Yet, events involving the transmission of pathogenic micro-organisms (fungi, viruses, bacteria or parasites) between cave bats and animals, including human, have been recognized (Agustin et al. 2019; Federici et al. 2022; Jurado et al. 2010; Karunarathna et al. 2023). Transmission may be due to direct contact with bats (i.e., bites, consumption). Other routes of transmission of micro-organisms are indirect via (1) aerosols present in the air, such as histoplasmosis (Amona et al. 2021; Gugnani and Denning 2023; Jülg et al. 2008), (2) body fluids present in the habitat and (3) via a bridge host which may then interact with other animals and/or human. For example, many parasites can be transmitted between different bat species, but also to other animals that may come into contact with humans, such as dogs and cats (Obame-Nkoghe et al. 2016; Obame-Nkoghe, Leroy, and Paupy 2017; Stevens et al. 2014). However, the mechanisms of transmission of bat pathogens to a bridge host that can transmit micro-organisms to humans are far from being understood. Studying the animal-human interface to identify interactions and potential pathogen transmission routes is essential (Caron et al. 2021; de Garine-Wichatitsky et al. 2021). The emergence of many zoonotic pathogens from bats has highlighted the need to study the interfaces between bats and humans, as well as the interactions that bats may have with other wild or domestic animals that could create potential transmission routes to humans, is becoming increasingly necessary. This approach is not only important for the field of health ecology, but will also help to understand bat ecology, their importance in the trophic chain, and promote their conservation.

In the Republic of Congo, a camera trapping protocol was used in two caves hosting bat colonies to characterize the interfaces between cave bats, other animals and humans. Firstly, we described the communities exploiting the inside and outside of the cave using a richness index. We hypothesize that different caves constitute different microhabitats and are therefore occupied or used differently. Inside the cave, cave-dwelling species should be the most represented, while at the cave entrance, outside the cave, species exploiting the cave interior, as well as other species not entering the cave, should be present. Secondly, the overlap in activity patterns, on a daily basis, between non-bat species and bats was characterized in order to identify times of day conducive to contact, transmission, competition or predation. We hypothesize that species with strong interactions will have overlapping activity. Finally, using a non-parametric test, we verified whether the species richness of taxa varied over time. We hypothesize that seasonal variations may have an impact on species richness in both caves due to variations in food resources.

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Materials & Methods

Ethic statements

All protocol was carried out with the permission from the Ministry of Forest Economy and Ethics Committee of the Ministry of Scientific Research and Technological Innovation in the Republic of Congo (N°212/MRSIT/IRSSA/CERSSA and N°687/MEF/CAB/DGEF-DFAP).

Study Area

Our study took place between 2021 to 2023 in two different caves situated in the Niari and Bouenza Department, about 50 km away from each other, near the town Dolisie, in the South of the Republic of Congo (Fig. 1). This region is subject to four seasons: the short dry season (January and February), the short-rainy season (March to May), the long-dry season (June to August), and the long-rainy season (September to December) (Samba, Maloba Makanga, and Mbayi 1999).

The landscape is mountainous and calcareous, favoring the presence of numerous caves and cavities. It is mainly composed of grassy savannah with patches of secondary forests and a patchwork of crops close to villages. The first cave, Mont Belo, consists of several chambers with a main entrance. The cave is surrounded by a small patch of secondary forest, followed after by large variety of food crops (peanuts, cassava, tomatoes, etc.) located at almost five km from the village. The second cave, named Boundou, is a tunnel-shaped cave in the rock face, with a main entrance and a small exit at the end on the other side. This cave is also surrounded by a small secondary forest surrounded by a large grassy savannah. The nearest village is more than 5 km away, and human activity is much lower. Both caves are considered sacred by the local population. Mont Belo cave attracts many pilgrims and members of the local population for religious rites. Boundou cave, despite its sacred nature, is seldom visited by the local population, and to our knowledge there are no regular religious activities or pilgrimages.

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Camera trap data collection

The camera traps survey was conducted between September 2021 and March 2023. We used nine Moultrie M50 cameras (Moultrie, Birmingham, USA) deployed inside and outside the two caves. We installed at least one camera trap in front of the main entrance of the cave (i.e. "outside"), another inside the cave in the main chamber, and additional cameras at the other entrances/exits which serve as passages for wild animals. In both caves, we did not cover the aerial exits (exit wells) which lead to the top of the caves, due to technical and safety constraints. In total, four camera traps were installed in Mont Belo cave (including one inside and three entrances – outside camera) and five cameras traps in Boundou cave (including one inside and four entrances – outside camera) over nineteen months. The cameras were programmed to trigger automatically (high-sensitivity detector) by taking a picture followed immediately by a 30s video, and to re-trigger after a 5-minute delay. This configuration enabled us to limit repeated triggering by the same individual and to visualize their behavior through a video. Over the nineteen months study period, we encountered technical problems with certain camera traps

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(camera shutdown due to technical problems, presence of insects or dirt obstructing the camera lens, over exposure). During December 2021 and January 2022, the cameras inside the caves (one of the two cameras at Mont Belo and the single camera inside Boundou) experienced technical problems, resulting in unusable data (black images and videos). Other cameras suffered other technical problems and were replaced and re-started as soon as the problem was detected. During our field activities (approximately every two months, defined in this article as research activities), we restarted the cameras after our visit with new batteries and SD cards. For the other months when we were not present, a local guide was trained to come and restart the cameras at the beginning of the month (between the 2nd and 10th of the month) with new batteries and SD cards. In total, the camera traps at both sites operated for 159 months (19 months x 9 cameras = 171 minus 12 months of malfunction = 159 months).

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Data preparation

All videos and images were integrated into Timelapse (S Greenberg 2023; Saul Greenberg and Godin 2015) to extract metadata and standardize the extraction of data from photos and videos. We used Megadetector (Beery, Morris, and Yang 2019; Fennell, Beirne, and Burton 2022), an artificial intelligence tool, to make an initial screening of visual material regarding the detection of animals. This software only works on photos, and indicates animal presence with a blue square, and human presence with a red square. Megadetector results can be integrated into Timelapse.

We defined one event of “detection” of a specific species or animal category as the presence of this species or animal category on a photo. One detection can be the presence of several individuals at the same time, for example a detection of two humans at the same time on an image.

A comparison of detections between Megadetector and manual analysis of the photos by an observer was carried out on all photos recorded over the first 6 months of the study. Megadetector proved its effectiveness in detecting all presences (except insects and bats), despite a few detection errors (false detection on a landscape element, absence of detection for fast-moving bats). Hence, we decided to use Megadetector to reduce the time of treatment of the last thirteen months. The videos linked to the pictures on which animals or humans were detected by Megadetector were viewed manually in order to verify the number of individuals and to describe the behavior of animals. When the number of individuals of a species or animal category varied between the photo and corresponding video, we retained the highest count of individuals for our analysis. As Megadetector can only be used on photos and not on videos, and is not parameterized to specifically identify bats and insects, we estimated that the detection of these two specific taxa was under-represented. Moreover, counting the number of insects and bats on video is not feasible. To avoid bias and to standardize our analysis, we decided to note the presence of insects and bats, but not to count the number of individuals.

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Species identification

Species on pictures and videos were identified using zoological taxonomic guides (Kingdon et al. 2013; Sinclair and Ryan 2003), or with the help of experts. If identification at species level was not possible due to poor image or video quality, identification was made at class or order level. As rodents were difficult to identify at species level, we classified them into three categories: small rodents (< 60 cm without tail), large rodents (> 60 cm without tail) including mainly Giant pouched rat (*Cricetomys emini*) and porcupines. We also grouped birds according to their size: small (from 2 to 20 cm in length) or medium (from 21 to 60 cm in length), and categorized owl and hawk species as raptors. To simplify the presentation of our results, we also categorized insects into two groups: (1) flying insects, which include midges, butterflies and bees, and (2) other crawling insects such as cave beetles, crickets and spiders.
Our results are presented using common names for species or the categories mentioned above.

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Categorizing human activities

During the course of our study, we had the opportunity to interview local people, landowners, village chiefs and local guides (non-standardized informal interviews) on several subjects of interest to our study, such as cave used and the wildlife species consumed by the local population.
Due to the high level of human activity at Mont Belo, it was decided with the local population to cover the cameras if necessary to avoid disturbing religious practices. In some cases, the presence of a human followed by the recording of a "black photo" for a certain period of time could indicate the presence of prayer activity. We viewed the 30s videos in order to identify and categorize the human behaviors detected in our study caves. We defined five distinct categories: (1) guano collection inside the caves, (2) hunting activity on bats present in the caves (we saw nets being laid inside the cave), (3) praying activity or religious rites, (4) our research activities such as changing cameras, capturing bats or collecting guano and (5) others, for all undefined activities (e.g., people who apparently just visited the cave), encompassing activities that couldn't be clearly categorized.

Categorizing animal species behaviors

The behavior of the animal was classified into five different categories: (1) moving, (2) foraging behavior excluding the action of hunting, (3) interspecific interaction (i.e., hunting, feeding on another animal), (4) other behavior (i.e., defecating, grooming, sitting, observing) and (5) intraspecific interaction (i.e., chasing each other, fighting or mating). We did not categorize the behavior of insects, bats or unidentified animals or when the videos were of poor quality.

Statistics analysis

Selection of data

We identified detection events as independent if the detected species or animal category on simultaneous pictures or videos was different for each camera trap and if the detection interval between the previous and next detection was greater than or equal to 30 minutes (O'Brien, Kinnaird, and Wibisono 2003; Sollmann 2018). All analyses were performed using the number of independent detections except for the graphs on animal and human behavior, where we used the exact number of individuals detected per independent event.

Analysis and graph

All graphs presented in this study were produced using ggplot2 (Wickham 2016), patchwork (Pedersen 2023) and cowplot (Wilke 2020) packages implemented in R software (R Core Team 2023).

We presented the results as a function of the number of camera days, i.e., the number of detections divided by the sum of the number of days each camera was in operation per site, multiplied by one hundred (Rovero et al. 2013; Yasuda 2004).

To quantify the temporal activities between the species or categories and the extent of temporal overlap, we used camtrapR package (Niedballa et al. 2016). The "activityOverlap" function was used to estimate the kernel density (non-parametric method), which calculates the probability density function of a detection distribution (Meredith and Ridout 2014). The overlap coefficient (Dhat1) can vary between zero and one (no overlap = 0 and total overlap =1) (Linkie and Ridout 2011).

Three species richness indices with standard error were calculated for each study site and location (inside or outside the cave) using the vegan package (Oksanen et al. 2022). The first, the Chao estimator, calculates an estimate of the total number of species, taking into account "rare" species. The second estimator, Jackknife, gives an overview of potential bias and variability by systematically removing samples, and the third estimator, bootstrap, will assess uncertainty by simulating sampling while providing a confidence interval and standard error (Chiu et al. 2014; O'Hara 2005; Smith and Belle 1984).

We used a non-parametric Friedman test to test the effect of season and study location (inside and outside each cave) on the number of detections for each taxonomic class. We also tested the existence of associations between the different species in each study site using a Pearson's product-moment correlation. Our data being tied, we were unable to use a non-parametric Spearman's test.

Results

Dataset

In total, we collected 88,231 observations (including photos, videos and duplicate of one detection of different species) over a nineteen month period, of which 45,670 (51.8 %) came from Boundou and 42,561 (48.2 %) from Mont Belo. We detected the presence of animals or humans in 24% of observations (21,123 observations) with 12,001 (56.8 %) detections from Boundou cave and 9,122 (43.2 %) detections from Mont Belo cave. Of these 21,123 detections, 8,836 (41.8 %) were bat detections, 8,218 (38.9 %) were detections of other taxa, including humans and 4,069 (19.3 %) were insect detections. Following selection of independent detections (>30 min interval), the dataset contained 11,581 detections, including 4,443 bats,

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2,899 insects, 263 humans and 3,840 detections of others vertebrates. The number of days of functional cameras varied between months, with an average of 16.4 days per month for camera traps at Boundou cave and 11.5 days for camera traps at Mont Belo cave (Fig. 2). Cameras inside the caves generally performed better than those outside (14.5 days vs 12.2 days) (Fig. 2).

Presence of vertebrates and invertebrates in the two caves

In both caves, we mostly observed the presence of mammals (72.7 % of all detections) including humans (2.3% of all mammalian detection), followed by insects (25 % of all detections), birds and reptiles (Fig. 3A, 3B, 3C and 3D). Species richness was higher outside for both caves compared to inside (Table 2). Richness accumulation curves for each study site (inside and outside) are presented in supplementary material 5. All taxonomic classes showed some variation of number of detections over the different seasons and the two study sites (Fig. 3A, 3B, 3C and 3D), but none was significant (p value > 0.05; Table 1). We observed greater species richness inside the Mont Belo cave than in the Boundou cave and the opposite for the outside of the caves (Table 2). Outside the two caves, species richness was highest during the main rainy season, followed by the main dry season and the two short seasons (wet and dry) (Table 3). Conversely, inside the caves, species richness was slightly higher during the long dry season (Table 3). The long rainy season was the season with the highest number of detections of any class. During the long and short rainy seasons, Boundou cave recorded a higher number of bird detections than Mont Belo cave (Fig. 3A). During the short rainy season, mammals and reptiles were in higher numbers in Boundou cave than in Mont Belo cave (Fig. 3B and 3C). Insects were detected in greater numbers in Boundou cave during the short dry and short rainy seasons, but the opposite trend was observed for the other two seasons, long dry and long rainy seasons (Fig. 3D) in Mont Belo. During the short dry season, birds were not detected at Mont Belo (Fig. 3A). Reptiles were absent at Boundou during the long dry and short dry seasons (Fig. 3C).

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More specifically, inside the Mont Belo cave (MB), we mostly detected small rodents (62.2 % of detection inside MB), followed by bats (18.3 % of detection inside MB), other insects (crickets, spiders) (10.5 % of detection inside MB), large rodents (2.3 % of detection inside MB) and flying insects (2.1 % of detection inside MB) (Fig. 4A). Inside Boundou cave (BD), bats were most often detected (40 % of detection inside BD), followed by other insects (cave beetles, crickets) (35 % of detection inside BD), genet (14.3 % of detection inside BD) and flying insects (5.9 % of detection inside BD) (Fig. 4A). In Boundou cave, the genet, identified as the rusty-spotted genet (*Genetta maculata*) was one of the most frequently observed species both inside and outside the cave (Fig. 4A and 4B). However, at Mont Belo cave, the genet, identified as the servaline genet (*Genetta servalina*) was not observed inside the cave, but only six times outside this cave (Fig 4A and 4B).

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Outside both caves, we identified the presence of species already detected inside the caves such as small rodents, genet, other insects, large rodents, but also the presence of other species such as birds of different sizes (raptors), monkeys, pangolins and nile monitors (Fig. 4B). We also had a high level of detection of flying insects compared to inside the caves (14. 4 % of detection inside BD and 17.7 % of detection inside MB) (Fig 4A and 4B). Inside and outside both caves we also detected the presence of humans (Fig 4A and 4B).

In the Mont Belo cave, we observed a significant association between bats and flying insects ($p < 0.01$) as well as between small rodents and other insects ($p < 0.01$) (Table 4). In the Boundou cave, we observed a significant association between bats and both types of insects (flying insects: $p < 0.01$ and other insects: $p < 0.01$), and between both types of insects ($p < 0.01$) (Table 5).

Supplementary material 2 provides a detailed list of all the identified animals and number of individuals per site. Some examples of images recorded for different species are also shown in Figure 5.

Animal behavior inside the two caves - viewing video recordings

For 34% of the detected vertebrates (with the exclusion of bats, insects, humans and unidentified animals; N = 7,742 detections), usable videos (i.e., enabling the action to be seen clearly, N = 500 detections) were analyzed to characterize their main behavior. For vertebrates counted in both caves (N = 1,146), we observed in ascending order: moving behavior (70.1 % of all behavior observed), followed by foraging behavior (20.6 %), interspecific interactions (5.7 %), other behaviors (2.2 %) and intraspecific interactions (1.3 %) (Fig. 6).

Some pictures of Giant pouched rat show one or more individuals that appear to have swollen jowls (Supplementary Material 3) and this event may underline the use of the cave as a food storage site by this species. In the case of small rodents, we observed a few videos which shows predatory behavior on the insects present in the cave.

The rusty-spotted genet regularly visited the inside of the Boundou cave and showed strong foraging, predation and potential scavenging behavior inside the cave towards bats, rodents and insects (Labadie et al. 2023). The servaline genet, on the other hand, was not recorded entering into the Boundou cave.

In the bird class, we observed the presence of the African wood owl (Strix woodfordii) at the entrance of the Mont Belo cave on ten occasions over a two-year period. Videos showed that the individuals positioned themselves on a rocky promontory, close to the cave entrance, at around 18:00 to 19:00, a period of high bat flying activities at the entrance of the cave. In one of these videos, we were able to observe the hunting behavior of this owl as it dived towards the bats flying out from the Mont Belo cave.

Human activities in the two caves

Local people informed us that Mont Belo cave was used for prayer rites, while no human activities were reported in Boundou cave. Local people acknowledged performing bat hunting (mainly large bat species- frugivores) and guano harvesting but rarely in the two studied caves. We observed more human activities in Mont Belo cave (n= 59.2 % of the number of humans detected) than in Boundou cave (n=40.8 % of the number of humans detected). In Mont Belo cave, we detected in descending order: prayer activities (n = 38.8 %), research activities (27 %), other activities (i.e., undefined human activities) (22.8 %), bat hunting (6.7 %) and guano collection (4.7 %) (Fig 7A). The human presence at Boundou cave was observed for only two categories: our research activities (88.7 %) followed by other undefined activities (11.4 %) (Fig. 7B).

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Activity patterns of vertebrates of interest

We focused our analyses on the pattern of daily activity for vertebrates with the highest detection rates (> 950 detections at both sites), with the exception of humans.

Genet exhibited a bimodal pattern of activities which peaked mainly at sunset (18:00) and to a lesser extent at night until sunrise (between 03:00 and 06:00) (Fig. 8A). Bats and insects also showed a bimodal activity pattern, with a main peak of activities at sunset (around 18:00) and another peak before sunrise (between 04:00 and 06:00) (Fig. 8A and 8B). Small rodents showed a main peak of activities at sunset (around 18:00) and their activities remained fairly constant throughout the night, decreasing at sunrise (Fig. 8C). The highest activity overlap coefficient was observed between small rodents and other insects (ground insects) (Dhat1= 0.86), followed by genet and bats (Dhat1= 0.84) and flying insects and bats (Dhat1= 0.71) (Fig. 8A, 8B and 8C).

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The daily pattern of human activity was observed to be unimodal, almost exclusively during the day (Fig. 9). Only prayer activities inside the cave showed activity with several peaks, including one at night (Fig. 9D and Fig. 9E).

Discussion

This is, to our knowledge, the first comprehensive study of cave-dwelling communities characterizing the bat-animals, including human, interactions. Implemented in a region prone to land transformation, biodiversity conservation and emerging infectious disease issues, this study feeds the field of the ecology of the interfaces between wild and domestic animals, including humans (Caron et al. 2021; de Garine-Wichatitsky et al. 2021). This field is growing and important in order to address the complex nature of health issues at the nexus Biodiversity – Health – Agriculture.

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Even if the known events are rare, caves are favorable habitats for the transmission of micro-organisms (fungus, virus, parasites, bacteria) through cohabitation in closed chambers (favorable to indirect transmission by aerosols and droppings) or direct contact (hunting, etc.). This study therefore provides information on the use of these particular and complex habitats (Fenolio et al. 2006; Gnaspini 2012; Simon 2012) by species and identifies mechanisms of potential transmission routes (trophic chain, bridge hosts, etc.) of different micro-organisms. It illustrates this complexity by describing the presence, of these four major taxonomic classes inside/or outside the caves, as well as their behavior and interactions. We detected greater species richness outside of both caves compared to inside, particularly during the long rainy season and the dry season. We also observed a greater richness inside Mont Belo cave than in Boundou cave and a

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greater richness outside Boundou cave than outside Mont Belo cave (Table 2 and 3). This difference in species richness between the two caves in our study could be explained by the unique microhabitat of each cave (Gabriel and Northup 2013; Gnaspini 2012; Kosznik-Kwaśnicka et al. 2022). Indeed, each cave has its own unique configuration (entrance shape, number of chambers, humidity, temperature, species present), external habitat (forest, savannah, presence of crops) and its own human frequentation.

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However, we did not detect any significant effect of season on the presence of the different taxonomic classes (Table 2). During the rainy season, cave-dwelling insectivorous bats are known to be more numerous in caves, as many species synchronize their denning and young-rearing activity with the period of high food resource availability (Arlettaz et al. 2001; Nurul-Ain, Rosli, and Kingston 2017; Paksuz, Özkan, and Postawa 2008). However, we were unable to confirm the high detection of bats due to the difficulty of accurately counting the quantity of insects and bats with camera traps. A specific protocol to count bats when they were flying out the cave was envisaged but it would have biased the presence and activities of species outside the caves.

Our results showed an overlap between bat activity and flying insects inside the study caves (Fig. 7B). We also observed an association of bats with flying insects in the Mont Belo cave, and with both types of insects in the Boundou cave (Table 3 and Table 4). These results may reflect an increased presence/activity of insects in the habitat at specific time such as dusk. Our result suggests a common period of their activities in both types of insects (flying and otherwise) and the microhabitat of cave. Nonetheless, we cannot overlook the existing link between the detection of mammals (potentially bats) and the observation of insects once the camera has been triggered with our methodology (use of Megadetector and its poor performance in detecting bats and insects).

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Species identified and behavior

Four major groups of mammals are significantly represented: bats, rodents (small and big), genets and humans. As both our study caves are home to bat colonies, our camera traps detected a high level of bat presence and activity. The periods of flying activity of bats corresponded with emergence at dusk and then return to the cave at dawn.

The high density of bats in a given area can favor the predatory behavior of certain species such as snakes, various carnivorous mammals and birds (Ridley 1898; Tanalgo et al. 2019). For example, at the entrance of Mont Belo cave, we observed the presence of the African wood owl on ten occasions. This species was most probably predating on bats exiting the cave, as it has been observed previously flying for hunting even if never seen catching a bat (Kemp and Calburn 1987).

The frequent detection of rodents (multiple time during a day), especially inside Mont Belo cave, could be explained by the presence of food resources (i.e., insects) and the use of the cave by individuals as a refuge or for reproduction. Inside Mont Belo cave, we observed a high presence of several insect species that seemed to exploit the bat guano such as crickets and cave beetles

(Gnaspini 2012; Sakoui et al. 2020). These insects could be a food resource for some of the small rodents. We put forward this hypothesis following few records showing rodents hunting insects and information gathered during one of our rodent capture sessions carried out in the cave. We identified a species of small insectivorous rodent (pers. obs.; awaiting genetic confirmation of the species). The results of daily overlap activities of small rodents and other insects using the litter in the caves also showed a strong relationship (Fig. 7C). In the Mont Belo cave, we also detected a strong association between small rodents and other insects (Table 3). However, our photo-trap protocol only allowed us to indirectly measure the presence of insects inside and outside the caves through the frequency of detection. To obtain an accurate measure of insect abundance and the types of insects present according to the season, it is necessary to set up an insect collection protocol.

We identified a Giant pouched rat (*Cricetomys emini*) which seems to use the Mont Belo cave as a food storage site. This result is in accordance with existing literature: this species is known to store its food in specific locations (Skinner and Chimimba 2005; Tosso et al. 2018). The daily activity of Giant pouched rat is not the same as the other small rodents. It regularly frequents but shows irregular activity patterns (Supplementary Material 4), which could also support the hypothesis of food storage in the cave. The Giant pouched rat would come into the cave either to retrieve food already stored in the cave or to store food found outside the cave.

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Another mammal frequently detected in the caves was the rusty-spotted genet (*Genetta maculata*) in Boundou cave (both inside and outside the cave) and the servaline genet (*Genetta servalina*) outside of Mont Belo cave. Our results showed that rusty-spotted genets regularly visited the inside of the Boundou cave in search of food by predating on bats, rodents or insects, or by scavenging on bats (Labadie et al. 2023). We also detected strong overlap of daily activity between genets and bats, validating the opportunistic foraging behavior of genets in the Boundou cave and possibly to increase their hunting success rate on bats (Fig 7A). However, we did not detect a significant association between small rodents and genets (Table 4).

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Human activities

Our results show that human activities in the two caves varies greatly between Mont Belo and Boundou. In the Mont Belo cave, over a two-year period, camera traps detected a high level of prayer activities, when Boundou cave is little or not used by the local population, as notified by the communities. In the Boundou cave, we also detected other human activities, including bat hunting and guano harvesting, or for unidentified purposes, which were not necessarily mentioned by local people for this cave during our discussions. At Mont Belo, local people collect the guano as natural fertilizer for crops (Sakoui et al. 2020). The hunting activity was not regular, probably due to the sacred nature of the cave and the almost exclusive presence of insectivorous bat species. However, in our study area, close to our caves, we were able to observe quite significant hunting pressure on colonies of frugivorous cave bats. In Africa, the consumption of bats by local populations as bushmeat is recognized and documented in the literature (Friant et al. 2020; Kamins et al. 2011; 2015; Mildenstein, Tanshi, and Racey 2015).

Cave communities can trigger micro-organisms emergence

In Central Africa, caves are teeming with mammals and insects creating a specific microbiome both inside and outside the cave. The presence of bats and their guano provides attractive food resources for other species in the cave. The daily emergence of bats attracts opportunistic predators such as birds of prey, genets or reptiles outside the cave. We characterized intra-specific interactions and actors involved in the trophic chain existing in the caves in the Rep of Congo. In the two caves, we described a trophic chain comprising the main bat-consuming species (inside and outside the cave) but also some other species that exploit the guano.

Our results suggest potential mechanisms of micro-organisms transmission between different species; some of which might act as bridge hosts between species known to carry numerous know pathogens (bats and rodents) and other at risk-species (humans, predators).

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At Mont Belo cave, three contact allowing a potential transmission of micro-organisms from bats to humans were identified through hunting and bat consumption, long presence inside the cave during prayer activities and guano collection without protection. The human activities inside caves increase the exposure of humans to various airborne pathogens, or create direct and indirect contacts with pathogen-carrying insects. Studies have shown the link between cave bats and several hematophagous arthropods that can transmit zoonotic diseases to vertebrates, including humans (Laroche, Raoult, and Parola 2018; Obame-Nkoghe et al. 2016).

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Indirect contacts linking humans to bats involves different mechanisms and bridge hosts species the genet sp. on one hand which eats bats or just infected by any aerosol, by entering regularly inside the cave and then consumed by humans and the Giant pouched rat on the other hand, which comes into direct and indirect contact with bats and guano and is then consumed by local populations. However, transmission of an infectious agent from its reservoir to humans depends on: (1) the distribution and density of the reservoir species, (2) the dynamics of the pathogen in the reservoir host, (3) the exposure of the human to the pathogen and (4) internal factors of the person in contact.

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Limitation of our study

During this study, we faced several limitations due to field constraints and the use of camera traps. Due to the rapid movement of the animals, the quality of the videos and the study environment (poor light and extreme humidity), it was very difficult to identify the rodents down to species level (Burns et al. 2017). One way of solving this problem would be to use cameras inside rodent traps (potentially with just a bait that releases the individual) to take a picture of the individual (Gracanin, Gracanin, and Mikac 2019). We used size categorization for rodents, but this depends on a number of factors. Indeed, the size of individuals may appear to vary according to the features of the camera field in which the individual was detected (near a rock, close to the camera or towards the back of the photo), its position in the photo or video (facing or from behind) and its behavior when the camera was triggered (e.g., running, sniffing or resting). Cameras placed inside caves also tended to operate for shorter periods due to the numbers of triggers caused by the movement of bats in the cave, as well as the presence of many insects. This problem may have limited the detection of some animals at certain periods. We also had to contend with a number of technical malfunctions due to the specificities of the cave environment (camera shutdowns, poor-quality photos and videos) which resulted in data loss. These various limitations have highlighted the improvements that could be made to this protocol to help increase data quality. This protocol could be improved by coupling it with two additional protocols. Firstly, by adding a protocol for collecting faeces from certain animals (rodents, genets, owls) in order to analyze their diet and confirm some of our hypotheses. Finally, we were unable to answer temporal questions (seasonal) due to the lack of data and the need to collect a large amount of data over many years.

Conclusions

This study is the first one to our knowledge that characterize the interactions between bats, wild animals and humans in two caves on central Africa. Our results enabled us to provide a preliminary description of the multi-species communities sharing cave habitats and pave the way for further and optimized similar studies based on our experience.

Bats need to be better protected as they are crucial to maintain ecosystem functions which translate into ecosystem services to humans. A better understanding of mechanisms of pathogen spillover from bats to humans can lead to improved risk mitigation and protection of cave habitats for its wild inhabitants and users, including humans. This work provides an avenue for more research at the wild/domestic/human interface in order to cope with hazards by managing risks and therefore to promote a better coexistence between living beings in social-ecological systems.

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