



Article

Diversity and Conservation of Cave-Dwelling Bats in the Brunca Region of Costa Rica

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Abstract: The Brunca region in Costa Rica contains the largest number of caves in the country, yet the diversity and distribution of bat species within those caves is currently unknown. Without this information, it is not possible to assess changes in populations and assemblages that may indicate severe damages to these critical roosting habitats, and to take evidence-based conservation actions. We present the first study to describe the diversity of cave-dwelling bat species in the Brunca region of Costa Rica in a large number of caves. We collected data of bat species diversity by direct observation and capturing bats inside roosts. Bats were observed in 38 of the 44 surveyed caves, representing 20 species from 4 families, with colony sizes ranging from a few individuals to >7500. In addition, we collected information about the human activities carried out in and around the roosts to assess potential threats that these sites face. Data indicate that caves suffer mostly from unregulated tourist visitation and that one of the most visited caves is also the one with the most species-rich bat assemblages. Our study determined the most important and vulnerable bat roosts in the region and shows the need for urgent conservation actions to protect them.

Keywords: bats; Brunca region; caves; conservation; Costa Rica; diversity

1. Introduction

Caves are broadly defined as natural openings in solid rock [1], and as such, they serve as the “windows” in which we glance into the underground. Caves have been attracting people’s interest from prehistoric times by serving as shelters, sacred places, or sources of artistic expression [2], but present a significant challenge for scientific research because they are largely hidden from view and hardly accessible for exploration. Most caves do not appear on topographic maps or satellite images and are neglected by mainstream scientists, making cave research a priority for only a small number of highly dedicated individuals [3]. Their unique features, the complete absence of light, almost constant temperature, and high air humidity make caves a suitable habitat for a large variety of highly specialized organisms such as cave crickets [1,4], and some vertebrates including the blind salamander and angel fish [1,5]. These organisms are so well adapted to the specific conditions in caves that they would not survive in a surface habitat.

Caves are dependent on energy sources brought by several organisms that forage at the surface and which use caves as shelter, such as oilbirds, swiftlets, and bats [1,2,6]. Bats, in fact, are so tightly associated with caves and are often so abundant that they can significantly modify these ecosystems by altering their microclimatic conditions and providing significant amounts of guano, the essential food source and base of the food chain in most caves [2,7]. In turn, caves provide bats a refuge from predators and inclement weather, and a critical venue for social interactions [8–10]. Caves are so important for bats worldwide that the majority of species, including many that are vulnerable and rare, are either specialized cave-dwellers or use caves temporarily [11]. Also, the largest aggregations of

bats are found in caves, with numbers reaching several millions of individuals [12–14], which makes them critical roosts for species that form such large colonies.

Costa Rica is a bat diversity hotspot with 114 species, most of which are well represented in the southwestern Brunca region [15,16]. The Brunca region has the largest karst region (185 km²) and the largest number of caves ($n = 156$) in the country [17]. While many of the species that inhabit the region are known to roost in caves in other parts of their range [15,18,19], there is still no baseline information about the populations of cave-dwelling bats in this region. Cave-dwelling bats are extremely important for the local ecosystems, playing the role of pollinators, seed-dispersers, and pest-suppressors [20]. Cave-related tourism activities are also becoming popular in the Brunca region [17], which makes the caves potential sources of local income, but also endangers cave-dwelling bats, which are often vulnerable to disturbance. Other threats that bats are facing include habitat loss and direct killing at their roosts. To the best of our knowledge, there is no information on distribution and the ecology of cave-dwelling bats in this region, nor information about which roosts contain large colonies or rare species of bats that need to be considered a conservation priority [18], or even the types of threats these roosts are facing. This study is the first to assess the diversity and distribution of cave-dwelling bats species in a large number of the caves in the country. Our study provides valuable information about underground roosts of conservation importance.

Monitoring cave roosts is a highly accurate method for estimating colony size, species composition, and seasonal changes in the populations of cave-dwelling bats [21,22], and in the temperate zones, it is a widely distributed activity with well-established traditions [23–25]. The regular monitoring of bat roosts is of particular importance to assess population decline in vulnerable species and for the identification of potential threats (e.g., disturbance or dangerous diseases) [26,27]. Roost monitoring is, however, uncommon in Costa Rica, where most of the research on bat diversity and distribution is conducted around research stations and with the method of mist-netting [28–30], and most recently also with acoustic monitoring at feeding or commuting sites. Our efforts are aimed at establishing roosts of national monitoring priority, which will help us assess population trends and serve as a base for conservation activities in the future.

Cave-dwelling bats are facing threats worldwide such as habitat loss, pollution, disturbance, quarrying and mining, guano extraction, and vandalism [31–33]. Bats that roost in caves are particularly vulnerable to human activities due to their tendency to aggregate in large colonies in a single roost, as a single disturbance event could lead to the eradication of an entire colony [10]. In the Neotropics, cave-dwelling bats face additional threats due to direct killing, as local residents attempt to eradicate species that are considered pests, specifically vampire bats (*Desmodus rotundus*) [34]. These bats are chased by cattle farmers and killed inside the caves where they roost, leading to the decline of other species as well [35]. The efforts against vampire bats threaten all of the cave-roosting bats, as people aiming to kill vampire bats do not distinguish the different species and often destroy all bats in a single roost [36]. It is crucial to obtain information about the distribution of cave-dwelling bats in Costa Rica, so we can take conservation actions before important bat colonies are lost.

2. Materials and Methods

2.1. Study Region

We investigated caves and artificial tunnels in the Southwestern (Brunca) region of Costa Rica (N 9.23643, W 82.84233) at sites ranging in altitude from 0 to 520 masl. The Brunca region contains the largest karst area of the country, with 185 km² of karst surface and 156 caves [17]. The region has an average annual temperature of 26.2 °C and an average annual rainfall of 4398 mm [37]. The dominant habitat of the region is evergreen moist lowland forest, including large areas of well-preserved rainforests in the Corcovado and Amistad national parks [38]. For a better visual portrayal of the field sites, we roughly divided them into 5 areas (Figure 1): area A—Ballena, area B—Boruca, area C—Osa, area D—Rio Claro, and area E—Corredores. We do not provide the exact locations of the field sites to

protect them from further disturbance; however, these data are available upon request from the digital repository Figshare (https://figshare.com/projects/Diversity_and_conservation_of_cave-dwelling_bats_in_the_Brunca_region_of_Costa_Rica/34415).

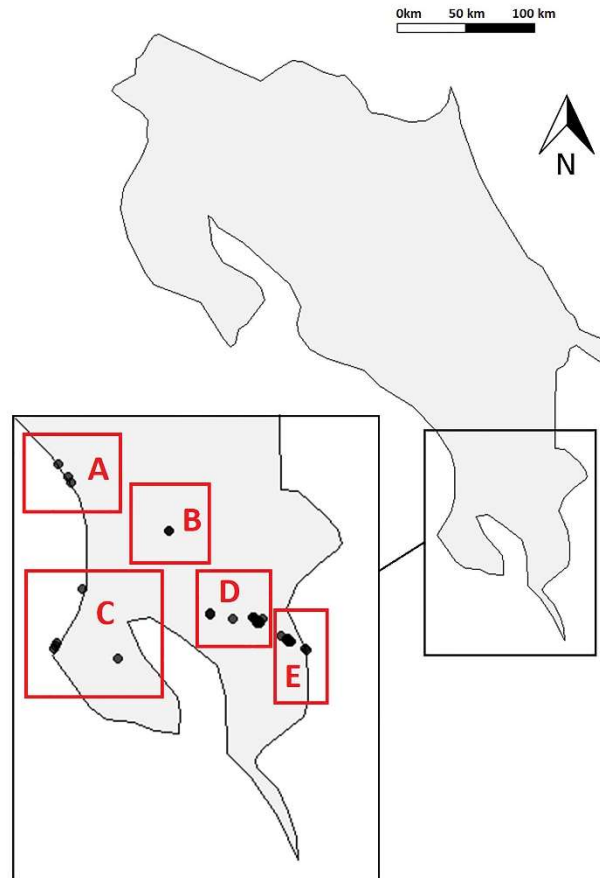


Figure 1. The Brunca region on the map of Costa Rica and the general location of the field work sites (marked by black dots), divided into 5 areas: (A) Ballena, (B) Boruca, (C) Osa, (D) Rio Claro, and (E) Corredores.

2.2. Cave Surveys

We obtained information about the existing caves in the Brunca region by consulting with the members of the only caving organization in Costa Rica—Anthros Speleological Group. The organization manages a national cave database, containing maps and descriptions of more than 340 caves in the country [39], which we used to select caves for research. Our selection of caves for this study was based on their size (in favor of greater length and depth) and available information about the presence of bat colonies in expedition reports [40]. We selected for research 14 caves from the national database and searched for additional caves by interviewing local people and performing transects in karst areas.

Our research took place during the periods from December 2015–May 2016, October 2016–May 2017, and December 2017–February 2018. We recorded the location and altitude of each cave using a GPS unit (Garmin, KS, USA). We entered the caves during daylight hours in groups ranging from two to four people using standard caving equipment (i.e., helmet, two independent light sources, and protective clothing). To survey the caves with vertical passages we used technical equipment and followed the approach of the single-rope technique [41]. We used the available cave maps to aid our movement inside the caves and to facilitate our bat surveys. If maps were not available, we created them using standard cave survey methods [42]. The number of visits varied between 1 and 4 times, depending on the complexity of the roost and the presence of bats during our first visit (Appendix A,

Table A1, column D). If we observed only a few (<30) bats and low species richness (1 or 2 species), we visited the roost only once. When a large number of individuals or indirect traces of presence (e.g., guano, food remains) was observed during our first visit, we performed additional monitoring and tried to obtain data in both the rainy and dry seasons if possible. Due to high water levels and technical difficulties, some caves were inaccessible during the rainy season, so we visited them in the intermediate period between seasons (December–January and May–June).

In addition to the field surveys, we interviewed local people about the activities conducted in caves. We included questions about visitation, hunting, other uses of the caves, and awareness about bat populations. We focused on farmers and landowners living near the locations of the caves. We also used direct observations in and around roosts to assess additional anthropogenic activities. For example, we recorded evidence of graffiti, waste, broken speleothems, footprints, entrance blocking or traces of resource extraction inside the roosts. In proximity to the roosts (radius of 1 km), we recorded the land use activities (agriculture, deforestation, quarrying). Depending on the dimension of the activities, we evaluated them on a scale from 1 to 4, 1 being the highest and 4 the lowest disturbance.

2.3. Bat Surveys

We used flashlights and binoculars to search visually for roosting bats or indirect traces of their presence (i.e., skulls, guano or food remains) [43]. Small clusters of bats (up to 50 individuals) were counted directly at the cave. We photographed larger groups of bats using a digital DSLR camera (D3200, Nikon, Tokyo, Japan) and used ImageJ software [44] to estimate the number of individuals. We determined the species of observed bats using the available literature [15,16,45] as a reference. To confirm species identification and obtain biometric data, we used a custom-made hand-held 2 m mist net to capture a few individuals within the roost. We measured forearm length, sex, age, and reproductive status of the captured bats [21]. In one vertical cave, we used a harp trap at the entrance to capture bats during their evening emerge. After taking biometric data, we released all individuals without further disturbance. No voucher specimens were collected during this study. We operated under the research permit INV-ACOSA-018-16.

2.4. Assessing Conservation Priority

We evaluated the conservation priority of each cave using the Bat Cave Vulnerability Index (BCVI), based on the bat species diversity and presence of human-induced threats in the caves [46]. The index is a novel approach for conservation prioritization of bat caves and it was developed with a focus on tropical regions. It contains two components: Biotic Potential Index (BP) and Biotic Vulnerability Index (BV). The Biotic Potential Index includes several species diversity and rarity measurements, including species richness, abundance, relative abundance, endemism, conservation status [47], and rarity index. The BP index has a value between 1 and 4, with level 1 being the highest and 4 the lowest biotic potential. The Biotic Vulnerability Index includes information on cave accessibility, morphology, visitation, and land use in adjacent areas. The BV index has a value of A, B, C, and D, with A being the highest vulnerability to disturbance and D no disturbance. We classified all roosts based on the combined values of BP and BV. The roosts with indicated values of 1A and 1B were considered of highest conservation priority. The roosts with values between 1C and 3D were considered as medium conservation priority, and the roosts in category 4 of low priority.

3. Results

In the study period we visited 44 underground roosts, including 40 caves, 2 artificial tunnels, and 2 abandoned gold mines. From the researched caves, 30 were described for the first time during this study and included in the National Cave Database, and named after geographical or morphological features in their respective locations (Appendix A, Table A1). From all caves, 22 were horizontal and 22 were vertical (Appendix A, Figure A1). We observed bats in 38 of the 44 roosts. We identified 20 species of bats from the families Phyllostomidae, Emballonuridae, Natalidae and Mormoopidae

(Table 1, Figure 2). The most frequently observed species was *Carollia perspicillata*, which occurred in 25 roosts. Other common species were *Peropteryx kappleri* (found in 18 roosts) and *Saccopteryx bilineata* (14 roosts). We observed relatively large ($n > 100$ ind.) colonies of bats (*Anoura* sp., *Artibeus jamaicensis*, *C. perspicillata*, *Desmodus rotundus*, *Natalus mexicanus*, *Pteronotus gymnonotus*, *Pteronotus parnellii*, and *Pteronotus personatus*) in 11 caves and very large (>500 ind.) (*C. perspicillata*, *P. gymnonotus*, *P. parnellii*, and *P. personatus*) in 6 caves (Appendix A, Table A1). The largest colony of bats was observed in the Campanario cave, estimated at around 7600 individuals, and included three species of the genus *Pteronotus* (Appendix A, Table A1). Other large colonies are those found in the Laguna Perdida (ca. 2000 individuals) and Corredores (ca. 1500 individuals) caves. The roost with the greater species richness was Corredores, with 8 species, followed by Emus and Laguna Perdida with 7 species (Appendix A, Table A1). Three caves were inhabited by mixed colonies of *Pteronotus* spp.: Tortuga, Campanario, and Corredores; the first two are considered maternity colonies since we observed hundreds of pups. Both Tortuga and Campanario are very similar littoral caves, which have a single entrance, leading to a simple chamber, and are partially filled with sea water during high tides. In the Campanario cave, we observed a third species of *Pteronotus*, *P. personatus*, which is so far the only known location of the species during this study. A single bat species occurred in 14 caves, specifically the greater dog-like bat (*Peropteryx kappleri*) and Seba's short-tailed bat (*C. perspicillata*), observed in 6 roosts each.

Table 1. Observed species of bats and their respective locations.

Family	Species	Roosts
	<i>Anoura</i> sp.	Laguna Perdida, Piedras Blancas 2
	<i>Artibeus jamaicensis</i>	Arelis, Carma, Corredores, Gran Galería, Túnel ICE 2, San Pedrillo
	<i>Carollia perspicillata</i>	Afrodiziaco Pozo, Alma, Árbol Caido, Bananal, Bombasa, Buena Cueva, Caballo Muerto, Cinco Millones, Corredores, Dos Brazos, Emús, Final 7 Pozo, Gran Galería, Gran Madre, Túnel ICE 1, Túnel ICE 2, San Josecito, Laguna Perdida, Los Sueños, Miramar Pozo, San Pedrillo, Sapo Gordo Pozo, Titi Mono, Tortuga
	<i>Carollia sowelli</i>	Miramar
Phyllostomidae	<i>Chrotopterus auritus</i>	Corredores
	<i>Desmodus rotundus</i>	Alma, Bombasa, Buena Cueva, Cinco Millones, Emús, Gran Madre, Túnel ICE 2, San Josecito, Laguna Perdida, Los Sueños, Miramar
	<i>Glossophaga soricina</i>	Alma, Bombasa, Corredores, Dos Brazos
	<i>Lonchophylla concava</i>	San Josecito, Miramar Pozo, San Pedrillo
	<i>Lonchophylla robusta</i>	Bombasa, Laguna Perdida
	<i>Lonchorhina aurita</i>	Gran Madre, Miramar
	<i>Phyllostomus discolor</i>	Arelis
	<i>Phyllostomus hastatus</i>	Laguna Perdida
	<i>Trachops cirrhosus</i>	Bombasa, San Pedrillo
	Emballonuridae	<i>Peropteryx kappleri</i>
<i>Peropteryx macrotis</i>		Emús, Gran Galería
<i>Saccopteryx bilineata</i>		Alma, Arelis, Bamboo Pozo, Cinco Millones, Corredores, Emús, Gran Galería, Gran Madre, Túnel ICE 2, Laguna Perdida, Los Sueños, Monteadores, Rectángulo, San Pedrillo
Natalidae	<i>Natalus mexicanus</i>	Corredores, Emus
	<i>Pteronotus gymnonotus</i>	Campanario, Corredores, Tortuga
Mormoopidae	<i>Pteronotus parnellii</i>	Bombasa, Campanario, Corredores, Emus, Túnel ICE 2, Laguna Perdida, Los Sueños, Tortuga
	<i>Pteronotus personatus</i>	Campanario

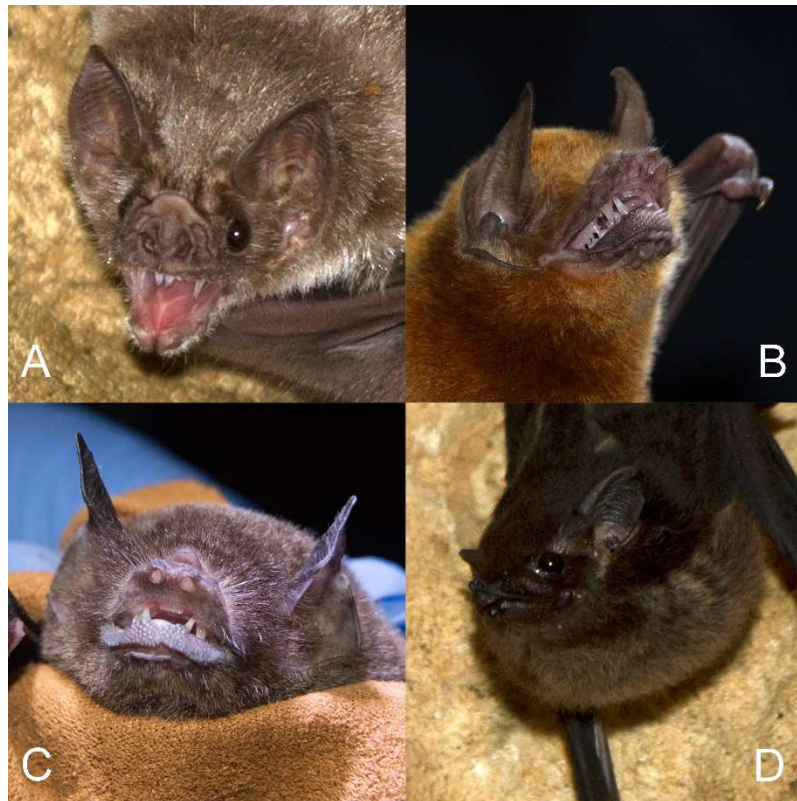


Figure 2. Some of the species, observed during our study: (A) Common vampire bat (*D. rotundus*), (B) Big naked-backed bat (*P. gymnotus*), (C) Parnell's mustached bat (*P. parnellii*), and (D) Greater sac-winged bat (*S. bilineata*) (photos: S. Deleva).

We interviewed 10 groups of people, mainly farmers and landowners around the locations of the field sites. There were reports of hunting activities in two of the caves, in both of which we observed blocked entrances. Most of the farmers were not interested in the caves on their land and were not visiting them, but in two cases the owners were collecting entrance fees for their caves without offering other services, such as a guided tour or providing safety equipment. During our visits, six of the landowners showed us new caves and assisted in the explorations. From our observations inside the roosts, we recorded traces of uncontrolled visitation (footprints and waste) in 16 of the 44 roosts, vandalism (broken speleothems and graffiti) in two caves, and disposal of large quantities of household waste in one cave. The activities observed around the caves included small-scale agriculture and deforestation. Only three caves were located in a relatively undisturbed habitat (rainforest without agriculture activities in a 1 km radius around the cave entrance). We evaluated the morphological features of the roosts, difficulty of approach (distance to urbanized areas), cave use (tourism, hunting, littering, etc.), and the land-use activities around the roosts to calculate the Biotic Vulnerability Index (BV). According to the BV index, three caves had the highest level of vulnerability (Level A), and 13 caves showed high vulnerability (Level B). The rest of the caves ($n = 27$) had a lower level of vulnerability (Level C). Only one cave showed no disturbance (Level D) (Table 2).

Based on the Biotic Potential Index (BP), 11 caves had high diversity with large bat populations and high species richness, including rare species (Level 1). Only one cave was classified as Level 2, with relatively large bat populations, and three caves were classified as level 3, with few species, mainly common, widespread, and small populations of bats. The other 29 caves were classified as level 4, as they showed very low species richness, represented by only a few individuals (Table 2).

We combined the two indexes to determine the roosts with the highest conservation priority (Bat Cave Vulnerability Index). Our results showed that nine caves have the highest conservation

priority. The Tortuga cave received the highest BCVI (1A) due to the large bat colony and vulnerability. In addition, eight other caves (i.e., Arelis, Bombasa, Corredores, Dos Brazos, Emus, Túnel Ice 2, Laguna Perdida, and San Pedrillo) had a BCVI result of 1B—highest species diversity and very high vulnerability. Medium conservation priority caves were evaluated with BCVI values between 1C (High diversity and low vulnerability) and 3B (low diversity and high disturbance). The roosts with category 4A, 4B, and 4C were evaluated as low conservation priority due to their low bat diversity (Table 2).

Table 2. Bat Cave Vulnerability Index (BCVI) as the combination of the Biotic Potential Index (BP) and the Biotic Vulnerability Index (BV), description of each observed category and the roosts.

BCVI		Priority	Description *	Roosts
BP	BV			
1	A	High	Large population, highest site accessibility, highly prone to disturbance.	Tortuga
1	B	High	Large population, high species diversity, high site accessibility, highly prone to disturbance.	Arelis, Bombasa, Corredores, Dos Brazos, Emus, Túnel Ice 2, Laguna Perdida, San Pedrillo
1	C	Medium	Large population, high species diversity, low site accessibility and less prone to disturbance.	Campanario, Miramar
2	C	Medium	Relatively high population, low species diversity, low site accessibility and less prone to disturbance.	Carma
3	B	Medium	Small populations, relatively high species diversity, high site accessibility, highly prone to disturbance.	Alma, Gran Galeria
3	D	Medium	Relatively large population, low species diversity, rare species present, low site accessibility, not prone to disturbance.	Piedras Blancas 2
4	A	Low	No bats present, highest site accessibility, highly prone to disturbance.	Arco, Ventana
4	B	Low	Small populations, relatively high species diversity, high site accessibility.	San Jocesito Cataratas, Los Sueños, Gran Madre
4	C	Low	Very small population, low species diversity, lower site accessibility and less prone to disturbance.	Afrodiziaco, Aprendizaje, Arbol Caido, Bamboo, Bananal, Banano Quemado, Buena Cueva, Caballo Muerto, Castillo Real, Cinco millones, Cueva 1, Cueva 3, Cueva 5, Cueva cerca Corredores., Final 7, Túnel ICE 2, La Troja, Lagrima, Metros 12, Monteadores, Rectangulo, Sapo Gordo, Serpiente Dormida, Titi Mono.

* Based on Tanalgo et al. 2018 [46].

4. Discussion

This study represents the first significant effort to characterize bat diversity in a large number of caves in Costa Rica. We provide new data on some additional roosting resources that are available to many bat species in the region, and our study will serve as a baseline for further research on the cave-dwelling bats in the Brunca region and in the country (Appendix A, Table A1). With our results, we have identified caves with a large number of species that potentially may require strong initiatives to protect, such as the Corredores and Laguna Perdida caves [46]. We have also identified colonies of a few species that are extremely rare and were only found in one or two caves, including Corredores and Emus (*N. mexicanus* in both, *C. auritus* in the former, and *Peropteryx macrotis* in the latter), Miramar (*L. aurita*), and Campanario (*P. personatus*), which points to the need for establishing strict visitation controls for all visitors (including speleologists) to secure the persistence of these colonies, as some of these species may be considered of high extinction risk [48]. These caves were not categorized as high-priority by the BCVI given that they do not suffer, yet, from human disturbance, as the caves are fairly inaccessible. Furthermore, we have also identified two maternity colonies that harbor large

numbers of individuals from three species of the genus *Pteronotus*, primarily in the Campanario cave, but also in Tortuga (Figure 3). To secure the long-term persistence of these populations, visitation of these sites should never be allowed during lactation (February—May) as during this period, a single event of disturbance could lead to the detachment and fall (and possibly death) of hundreds of pups [25].

From the 44 studied caves, 38 (86.36%) were occupied by bats, which represents a higher occupation rate than similar studies reported in other countries in Latin America. In Puerto Rico, for example, only 31% of the caves in the National Speleology database are used as roosts [49]. A similar study in Brazil shows that only about half of the observed caves had bats [50]. We also found that in combination, all caves harbor a total of 20 species. However, we know that at least 46 species in the Brunca region of Costa Rica are considered cave-dwellers [15], and therefore, wonder why none of these other species were recorded in our study (Appendix A, Table A2). One possibility is that other roosting resources are more readily available to bats that are not cave-specialists, such as several species within the tribe Micronycterini (e.g., *Micronycteris microtis* and *Lampronnycteris brachyotis*), which may often roost in hollow trees [51], and *Artibeus lituratus*, which is typically found roosting under foliage [52]. Alternatively, more vulnerable and rare species, such as the carnivorous bat *Vampyrum spectrum* and *Macrophyllum macrophyllum* [53–55], may have already disappeared from the area where the majority of study caves were located, as surrounding natural habitats face severe loss and/or significant degradation [38]. However, we hope that some of these other species will be recorded as we continue to monitor the same and additional cave roosts with a combination of other research techniques, including captures at the cave entrance and the use of ultrasound detectors [56].



Figure 3. A nursery colony of *Pteronotus* spp. in the Tortuga cave (photo: S. Deleva).

From the 44 caves we visited, only two (i.e., Laguna Perdida and Piedras Blancas 2) are under some level of protection, as they are located in the Piedras Blancas National Park. There is no law protecting caves in Costa Rica, and most are located on private properties, which makes their protection a decision of the landowners. From the 114 species of bats in Costa Rica, at least 48 are cave-dwellers and depend on caves as roosts in one degree or another [15,57]. This makes the protection of caves and other underground roosts such as artificial tunnels and gold mines a matter of the highest priority. The most effective way to preserve the caves is to propose the roosts categorized as of high conservation priority as important sites for the conservation of bats (Sitio Importante para la Conservación de los Murciélagos), based on the documentation of the Latin American Bat Conservation Network [58]. Two of the caves with the highest conservation priority, Corredores and Emus, are also the most heavily affected by anthropogenic activities, such as uncontrolled visitation and vandalism, and both

are readily accessible. Due to the frequent disturbance, the bat colonies in these caves are facing a dire future unless conservation groups, tour guides, and landowners join forces to set limits to visitation rates and enforce proper visitation guidelines [59].

The Bat Cave Vulnerability Index (BCVI) has further allowed us to identify roosts with high species diversity that are currently subject to anthropogenic pressure, thus urgent actions are needed to prevent further disturbance. Some roosts with high bat diversity are excluded from the list due to their difficult approach, which makes them less vulnerable to anthropogenic pressure. Others, which are highly vulnerable or already affected by anthropogenic activities, were excluded from the list due to low species diversity. We propose that if limited resources are available, we should focus our conservation efforts on the roosts of category 1A and 1B, but the other categories need further monitoring, as new visits can detect new bat species or new threats that could be prevented before extensive damage is caused to the colonies [46].

5. Conclusions

With this study, we now have the tools to develop conservation strategies to protect the most important and vulnerable roosts and baseline information to start long-term monitoring programs of the bat colonies that inhabit these caves. Previous data of cave-dwelling bats in the Brunca region are available from a few expedition reports made in 1993, conducted mainly by non-specialists, that present general information about the presence of just a few bat species without information on their abundance [40]. As such, this report does not provide reliable baseline data to gauge changes in bat colony size and species assemblages that might allow us to determine if caves are suffering from human activities conducted in them, most notably uncontrolled visitation.

Our data confirm that caves in the Brunca region of Costa Rica are inhabited by a rich bat fauna and we must take urgent conservation efforts to protect them. Many of the bats in Costa Rica are of the lowest conservation priority (least concern) because of their wide distribution, but some species may be locally rare or declining. We propose cave surveys be included in the national priorities for bat research and an annual monitoring scheme for roosts to be set up. In this way, we will be able to trace the change in populations and to take actions if certain species are declining.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. All field sites in the Brunca region, their location (see Figure 1), visit dates, the Bat Cave Vulnerability Index (BCVI), and the Number of individuals of each species.

Cave	Area	Visits/mm/yy	BCVI	No of Species	A sp. **	A jam	C per	C sow	C aur	D rot	G sor	L con	L rob	L aur	N mex	P kap	P mac	P dis	P has	P gym	P par	P per	S bil	T cir
AFRODIZIACO POZO *	D	03/16	4 C	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ALMA	E	02/16, 05/16, 02/17, 12/17	3 B	5	0	0	10	0	0	6	3	0	0	0	0	59	0	0	0	0	0	0	15	0
APRENDIZAJE POZO *	D	03/16	4 C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ARBOL CAIDO *	D	03/16	4 C	2	0	0	14	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0
ARCO *	A	02/16, 05/16	4 A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ARELIS *	D	01/16; 04/16	1 B	4	0	22	0	0	0	0	0	0	0	0	45	0	36	0	0	0	0	0	55	0
BAMBOO POZO *	D	03/17	4 C	2	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	14	0
BANANAL	E	01/17	4 C	1	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BANANO QUEMADO	E	03/16	4 C	2	0	0	0	3	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
BOMBASA *	C	02/18	1 B	6	0	0	350	0	0	1	40	0	20	0	0	0	0	0	0	0	100	0	0	1
BUENA CUEVA *	D	03/16	4 C	2	0	0	74	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CABALLO MUERTO *	D	01/16, 03/16	4 C	2	0	0	3	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
CAMPANARIO *	C	05/17, 02/18	1 C	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2000	5000	600	0	0	0
CARMA	E	02/16	2 C	1	0	179	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CASTILLO REAL	E	04/16	4 C	1	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0
CINCO MILLONES *	D	03/16	4 C	4	0	0	15	0	0	4	0	0	0	0	26	0	0	0	0	0	0	0	20	0
CORREDORES	E	01/16, 03/16, 02/16, 12/17	1 B	8	0	14	49	0	1	0	1	0	0	0	235	0	0	0	0	500	700	0	8	0
CUEVA 1 NO NAME *	D	01/16	4 C	1	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0
CUEVA 3 NO NAME *	D	01/16	4 C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUEVA 5 NO NAME *	D	01/16	4 C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUEVA CERCA COR	E	02/16	4 C	1	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0
DOS BRAZOS *	C	03/17, 02/18	1 B	2	0	0	663	0	0	0	90	0	0	0	0	0	0	0	0	0	0	0	0	0
EMUS	D	01/16, 04/16, 12/17	1 B	7	0	0	813	0	0	44	0	0	0	0	10	9	2	0	0	0	200	0	26	0
FINAL 7 POZO *	D	03/16	4 C	1	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GRAN GALERIA	E	03/16, 10/16, 12/17	3 B	5	0	49	60	0	0	0	0	0	0	0	15	1	0	0	0	0	0	0	24	0
GRAN MADRE *	D	03/16, 03/16	4 C	5	0	0	16	0	0	4	0	0	1	0	62	0	0	0	0	0	0	0	31	0
ICE 1 TUNNEL	B	02/17	4 C	1	0	0	200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ICE 2 TUNNEL	B	02/17, 12/17	1 B	5	0	320	70	0	0	39	0	0	0	0	0	0	0	0	0	0	150	0	12	0
LA TROJA	E	04/16	4 C	1	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0
LAGRIMA POZO *	D	03/16	4 C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LAGUNA PERDIDA *	D	10/16, 10/16, 12/17	1 B	7	100	0	1239	0	0	176	0	0	118	0	0	0	0	57	0	350	0	1	0	0
LOS SUEÑOS *	D	11/16, 02/18	4 B	4	0	0	250	0	0	25	0	0	0	0	0	0	0	0	0	4	0	65	0	0
METROS 12 NO NAME *	D	01/16	4 C	1	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
MIRAMAR POZO *	E	12/15, 01/16	1 C	5	0	0	134	1	0	1	0	11	0	108	0	0	0	0	0	0	0	0	0	0
MONTEADORES *	E	01/16	4 C	2	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	2	0	0
PIEDRAS BLANCAS 2 *	D	10/17	3 D	1	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RECTANGULO	E	04/16	4 C	2	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	4	0	0
SAN JOSECITO *	C	05/17, 02/18	4 B	3	0	0	35	0	0	19	0	4	0	0	0	0	0	0	0	0	0	0	0	0
SAN PEDRILLO *	C	05/17	1 B	5	0	34	5	0	0	0	0	50	0	0	0	0	0	0	0	0	0	1	1	1
SAPO GORDO POZO *	D	03/16	4 C	1	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SERPIENTE DORMIDA	E	03/17	4 C	1	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0
TITI MONO *	D	03/16	4 C	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TORTUGA *	A	05/16, 10/16, 02/17	1 A	3	0	0	6	0	0	0	0	0	0	0	0	0	0	0	427	400	0	0	0	0
VENTANA *	A	05/16	4 A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* New caves, according to the National Cave database. ** Species abbreviations: *Anoura sp.*, *Artibeus jamaicensis*, *Carollia perspicillata*, *Carollia sowelli*, *Chrotopterus auritus*, *Desmodus rotundus*, *Glossophaga soricina*, *Lonchophylla concava*, *Lonchophylla robusta*, *Lonchorhina aurita*, *Natalus mexicanus*, *Peropteryx kappleri*, *Peropteryx macrotis*, *Phyllostomus discolor*, *Phyllostomus hastatus*, *Pteronotus gymnotus*, *Pteronotus parnellii*, *Pteronotus personatus*, *Saccopteryx bilineata*, *Trachops cirrhosus*.

Table A2. Bat species in the Brunca region, their conservation status, population trend [51], presence in caves, and cave dependence [11,15,51].

Common Name	Latin Name	IUCN Status	Population Trend	Cave-Dwelling	Cave-Dependent
Handley's tailless bat	<i>Anoura cultrata</i>	LC	decreasing	Yes	No
Geoffroy's tailless bat	<i>Anoura geoffroyi</i>	LC	stable	Yes	No
Jamaican fruit bat	<i>Artibeus jamaicensis</i>	LC	stable	Yes	No
Great fruit-eating bat	<i>Artibeus lituratus</i>	LC	stable	Yes	No
Chestnut short-tailed bat	<i>Carollia castanea</i>	LC	stable	Yes	No
Seba's short-tailed bat	<i>Carollia perspicillata</i>	LC	stable	Yes	No
Sowell's short-tailed bat	<i>Carollia sowelli</i>	LC	stable	Yes	No
Shaggy bat	<i>Centronycteris centralis</i>	LC	unknown	No	No
Wrinkle-faced bat	<i>Centurio senex</i>	LC	stable	No	No
Salvin's big-eyed bat	<i>Chiroderma salvini</i>	LC	stable	No data	No
Hairy big-eyed bat	<i>Chiroderma villosum</i>	LC	stable	No	No
Godman's long-tailed bat	<i>Choeroniscus godmani</i>	LC	unknown	No data	No data
Big-eared wooly bat	<i>Chrotopterus auritus</i>	LC	stable	Yes	No
Wagner's sac-winged bat	<i>Cormura brevirostris</i>	LC	unknown	No	No
Aztec fruit-eating bat	<i>Dermanura azteca</i>	LC	unknown	Yes	No
Toltec fruit-eating bat	<i>Dermanura tolteca</i>	LC	unknown	Yes	No
Thomas' fruit eating bat	<i>Dermanura watsoni</i>	LC	stable	No	No
Common vampire bat	<i>Desmodus rotundus</i>	LC	stable	Yes	No
White-winged vampire bat	<i>Diaemus youngi</i>	LC	unknown	Yes	No
Northern ghost bat	<i>Diclidurus albus</i>	LC	unknown	No	No
Hairy-legged vampire bat	<i>Diphylla ecaudata</i>	LC	stable	Yes	No
Velvety fruit-eating bat	<i>Enchisthenes hartii</i>	LC	unknown	No data	No data
Brazilian brown bat	<i>Eptesicus brasiliensis</i>	LC	unknown	No	No
Chirqui brown bat	<i>Eptesicus chiriquinus</i>	LC	unknown	No	No
Argentine brown bat	<i>Eptesicus furinalis</i>	LC	unknown	Yes	No
Big brown bat	<i>Eptesicus fuscus</i>	LC	increasing	Yes	No
Black bonneted bat	<i>Eumops auripendulus</i>	LC	unknown	No	No
Sanborn's bonneted bat	<i>Eumops hansae</i>	LC	unknown	No data	No data
Commissaris's long-tongued bat	<i>Glossophaga commissarisi</i>	LC	stable	Yes	No
Pallas's long-tongued bat	<i>Glossophaga soricina</i>	LC	stable	Yes	No
Underwood's long-tongued bat	<i>Hylonycteris underwoodi</i>	LC	stable	Yes	Yes
Yellow-throated big-eared bat	<i>Lampronnycteris brachyotis</i>	LC	stable	Yes	No
Desert red bat	<i>Lasiurus blossevillii</i>	LC	unknown	No	No
Southern yellow bat	<i>Lasiurus ega</i>	LC	unknown	No	No
Dark long-tongued bat	<i>Lichonycteris obscura</i>	LC	unknown	No data	No data
Goldman's nectar bat	<i>Lonchophylla concava</i>	LC	unknown	Yes	No data
Orange nectar bat	<i>Lonchophylla robusta</i>	LC	unknown	Yes	Yes
Tomes's sword-nosed bat	<i>Lonchorhina aurita</i>	LC	stable	Yes	Yes
Pygmy round-eared bat	<i>Lophostoma brasiliense</i>	LC	stable	No	No
White-throated round-eared bat	<i>Lophostoma silvicolom</i>	LC	unknown	No	No
Long-legged bat	<i>Macrophyllum macrophyllum</i>	LC	unknown	Yes	No data
Hairy big-eared bat	<i>Micronycteris hirsuta</i>	LC	unknown	No	No

Table A2. Cont.

Common Name	Latin Name	IUCN Status	Population Trend	Cave-Dwelling	Cave-Dependent
Common big-eared bat	<i>Micronycteris microtis</i>	LC	stable	Yes	No
White-bellied big-eared bat	<i>Micronycteris minuta</i>	LC	unknown	Yes	No
Schmidts' big-eared bat	<i>Micronycteris schmidtorum</i>	LC	stable	No	No
Striped hairy-nosed bat	<i>Mimon crenulatum</i>	LC	stable	No	No
Coiban Mastiff Bat	<i>Molossus coibensis</i>	LC	unknown	No	No
Velvety free-tailed bat	<i>Molossus molossus</i>	LC	unknown	No	No
Miller's mastiff bat	<i>Molossus pretiosus</i>	LC	unknown	Yes	No data
Black mastiff bat	<i>Molossus rufus</i>	LC	stable	No	No
Sinaloan mastiff bat	<i>Molossus sinaloae</i>	LC	stable	Yes	No
Silver-tipped myotis	<i>Myotis albescens</i>	LC	stable	Yes	No
Hairy-legged myotis	<i>Myotis keaysi</i>	LC	unknown	Yes	No
Black myotis	<i>Myotis nigricans</i>	LC	stable	Yes	No
Montane myotis	<i>Myotis oxyotus</i>	LC	unknown	No data	No data
Riparian myotis	<i>Myotis riparius</i>	LC	stable	No data	No data
Mexican funnel-eared bat	<i>Natalus mexicanus</i>	LC	unknown	Yes	Yes
Lesser bulldog bat	<i>Noctilio albiventris</i>	LC	stable	No	No
Greater bulldog bat	<i>Noctilio leporinus</i>	LC	unknown	Yes	No
Greater dog-like bat	<i>Peropteryx kappleri</i>	LC	unknown	Yes	No
Lesser doglike bat	<i>Peropteryx macrotis</i>	LC	stable	Yes	No
Pale spear-nosed bat	<i>Phyllostomus discolor</i>	LC	stable	Yes	No
Greater spear-nosed bat	<i>Phyllostomus hastatus</i>	LC	stable	Yes	No
Heller's broad-nosed bat	<i>Platyrrhinus helleri</i>	LC	stable	Yes	No
Greater broad-nosed bat	<i>Platyrrhinus vittatus</i>	LC	unknown	Yes	No data
Naked-backed bat	<i>Pteronotus davyi</i>	LC	stable	Yes	Yes
Big naked-backed bat	<i>Pteronotus gymnotus</i>	LC	stable	Yes	Yes
Parnell's mustached bat	<i>Pteronotus mesoamericanus</i>	LC	unknown	Yes	Yes
Wagner's mustached bat	<i>Pteronotus personatus</i>	LC	stable	Yes	Yes
Thomas' yellow bat	<i>Rhogeessa io</i>	LC	unknown	No	No
Proboscis bat	<i>Rhynchonycteris naso</i>	LC	unknown	No	No
Greater sac-winged bat	<i>Saccopteryx bilineata</i>	LC	unknown	Yes	No
Lesser sac-winged bat	<i>Saccopteryx leptura</i>	LC	unknown	No	No
Talamancan yellow-shouldered bat	<i>Sturnira mordax</i>	NT	stable	No data	No data
Mexican free-tailed bat	<i>Tadarida brasiliensis</i>	LC	stable	Yes	No
Spix's disk-winged bat	<i>Thyroptera tricolor</i>	LC	unknown	No	No
Stripe-headed round-eared bat	<i>Tonatia saurophila</i>	LC	stable	No	No
Fringe-lipped bat	<i>Trachops cirrhosus</i>	LC	stable	Yes	No
Niceforo's big-eared bat	<i>Trinycteris nicefori</i>	LC	unknown	No	No
Tent-making bat	<i>Uroderma bilobatum</i>	LC	stable	No	No
Striped yellow-eared bat	<i>Vampyriscus nymphaea</i>	LC	unknown	No	No
Northern little yellow-eared bat	<i>Vampyressa thuyone</i>	LC	unknown	No	No
Great stripe-faced bat	<i>Vampyrodes major</i>	LC	unknown	No	No
Spectral bat	<i>Vampyrum spectrum</i>	NT	decreasing	Yes	No



Figure A1. Some of the field work sites, mentioned in this study: (A) San Pedrillo cave, photo: S. Deleva; (B) Emus cave, photo: S. Trescott; (C) Bamboo cave, photo: C. Castillo Salazar; (D) Gran Madre cave, photo: S. Deleva.

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