

Mortality in three species of bats of the genus *Pteronotus* Gray, 1838 (Mammalia, Chiroptera, Mormoopidae) due to overpopulation, and harassment by blaberid cockroaches, in a Venezuelan cave

Mortalidad en tres especies de murciélagos del género *Pteronotus* Gray, 1838 (Mammalia, Chiroptera, Mormoopidae) debida a sobrepoblación, y hostigamiento por cucarachas blabéridas, en una cueva venezolana

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ABSTRACT

Nearly half of the world's bat species roosts in caves. Despite the availability of caves being thought to limit their abundance, roost overpopulation has not been listed as a cause of mass mortality in cavernicolous bats, suggesting that predation and other factors will normally prevent them from surpassing the carrying capacity of caves. We report mortality likely due to roost overpopulation in three species of insectivorous bats inhabiting a small cave located in a non-karstic outcrop in the Venezuelan Llanos. Outside the cave, abundant bat remains were found washed away by rainwater. At the entrance of the cave, bats were roosting exposed to sunlight (a highly unusual behavior for the species involved), which thus risked dehydration, and detection by diurnal predators. Inside the cave, the ceiling, walls, and part of the floor were densely packed with bats. On the floor, bats were resting in quadrupedal position and interacted agonistically with large guanophilic cockroaches. Most of the bats had skin lesions apparently caused by cockroach bites. We attribute these findings to roost overpopulation, and suggest that, owing to the orography, lithology and high primary production in the region, caves used as roosts by insectivorous bats are in much shorter supply than insect prey.

Keywords: Blaberidae, Blattodea, Dictyoptera, guano invertebrates, interspecific aggression, predation, *Pteronotus davyi*, *Pteronotus gymnonotus*, *Pteronotus personatus*, Venezuelan Llanos.

RESUMEN

Casi la mitad de las especies de murciélagos del mundo se refugia en cuevas. Pese a que se cree que la disponibilidad de cuevas limita su abundancia, la sobrepoblación de refugios no ha sido listada como una causa de mortalidad en masa de murciélagos cavernícolas, lo cual sugiere que la depredación y otros factores normalmente les impiden superar la capacidad de carga de las cuevas. Reportamos mortalidad probablemente debida a sobrepoblación del refugio en tres especies de murciélagos insectívoros que habitan una pequeña cueva ubicada en un afloramiento no kárstico en los Llanos venezolanos. Fuera de la cueva se encontraron abundantes restos de murciélagos arrastrados por el agua de lluvia. En la entrada de la cueva, los murciélagos dormían expuestos a la luz solar (un comportamiento altamente inusual para la especie involucrada), corriendo el riesgo de deshidratarse y ser detectados por depredadores diurnos. Dentro de la cueva, el techo, las paredes y

parte del suelo estaban densamente cubiertos por murciélagos. En el suelo, los murciélagos estaban descansando en posición cuadrúpeda e interactuaban de forma agonística con grandes cucarachas guanófilas. La mayoría de los murciélagos tenían lesiones en la piel aparentemente causadas por mordeduras de cucarachas. Atribuimos estos hallazgos a la sobrepoblación de refugios y sugerimos que, debido a la orografía, la litología y la elevada producción primaria en la región, las cuevas utilizadas como refugio por murciélagos insectívoros son escasas relativamente a la abundancia de insectos presa.

Palabras clave: agresión interespecífica, Blaberidae, Blattodea, depredación, Dictyoptera, invertebrados del guano, Llanos venezolanos, *Pteronotus davyi*, *Pteronotus gymnonotus*, *Pteronotus personatus*.

INTRODUCTION

With 1,475 currently recognized species, bats (Chiroptera) are the second most diverse order of living mammals (ASM 2024). Almost all bat species are exclusively nocturnal (Speakman 1995), and about 48.5% of them are dependent on caves as diurnal retreats (Tanalgo *et al.* 2022). Cavernicolous bats form the largest aggregations of vertebrates, ranging from tens of thousands to millions of individuals (Kunz 1982, Russell & McCracken 2006, Furey & Racey 2016). Some bat species are found only in few caves (*e.g.*, the Paraguana Common Mustached Bat, *Pteronotus paraguayensis* Linares & Ojasti, 1974 in Paraguana Peninsula, Venezuela; Gutiérrez & Molinari 2008), or even in just one (*e.g.*, the Cuban Greater Funnel-eared Bat, *Natalus primus* Anthony, 1919, in Guanahacabibes Peninsula, Cuba; Tejedor 2011).

While noting that bats are the only major vertebrate group that continuously and extensively uses caves as shelter, Jepsen (1970) suggested that ancestral bats took advantage of their capacity for echolocation to become cavernicolous, which in turn allowed them to evade avian predators, and to conserve energy and body water when not foraging. Humphrey (1975) proposed roosts, especially caves, to be more important than the growing season and insect diversity as determinants of the distribution and abundance of temperate bats. Caves and artificial cave-like structures such as tunnels and abandoned buildings are deemed fundamental for the conservation of bats worldwide (Arita 1993, Furey & Racey 2016, Medellín *et al.* 2017, Tanalgo *et al.* 2022, Guixé *et al.* 2024, Meierhofer *et al.* 2024), and the construction of artificial caves has been proposed to protect some bat species (Lavoie & Northup 2009, Gulickx *et al.* 2011, Slider & Kurta 2011, Molinari *et al.* 2012, Albayrak 2013, Gibbons 2013, Mering & Chambers 2014).

By bringing huge amounts of nutrients into caves in the form of guano and their own carcasses, bats have created the conditions for the evolution and survival of unique and highly diverse communities of cavernicolous organisms, ranging from bacteria and yeasts to arthropods and

vertebrates (Ferreira & Martins 1999, Gnaschini & Trajano 2000, Fenolio *et al.* 2006, Biswas & Shrotriya 2010, Cunha *et al.* 2020, Pimentel *et al.* 2022, Lundberg & McFarlane 2024). Cavernicolous bats provide major ecosystem services outside caves, including pollination, seed dispersal, and control of insect populations (Jones *et al.* 2009, Kunz *et al.* 2011, Ghanem & Voigt 2012, Medellín *et al.* 2017, Ramírez-Fráncel *et al.* 2021).

Bats congregating in caves are affected by higher levels of parasitism and are exposed to a greater risk of epidemics than solitary and foliage-roosting bats (Patterson *et al.* 2007, O'Shea *et al.* 2016, Hoyt *et al.* 2021). Within and around caves, bats serve as prey for cockroaches (Rice 1957, Wilson 1971, Braack 1989, Bell *et al.* 2007, López-Wilchis *et al.* 2023), mealworms (Hermanson & Wilkins 1986), spiders (Nyffeler & Knörnschild 2013, Dias *et al.* 2015, Leivers *et al.* 2021), and centipedes (Molinari *et al.* 2005); and for predatory vertebrates, including fish and amphibians (Yager & Williams 1988, Mikula 2015), lizards and snakes (Herreid 1962, Hammer & Arlettaz 1998, Esbérard & Vrcibradic 2007, Barti *et al.* 2019, Clarkson & Massyn 2020, Tanalgo *et al.* 2020), raptors and other birds (Twente 1954, Harden 1972, Looney 1972, Barclay *et al.* 1982, Fenton *et al.* 1994, Lenoble *et al.* 2014, Spitzenberger *et al.* 2014, Mikula *et al.* 2016, Sieradzki & Mikkola 2020), and mammals (Urbanczyk 1981, Kokurewicz 2004, Rodríguez-Durán *et al.* 2010, McAlpine *et al.* 2011, Mas *et al.* 2015, Haarsma & Kaal 2016, Cichocki *et al.* 2021). The latter include both specialized and opportunistically carnivorous bat species (Fischer *et al.* 1997, Bordignon 2005, Oprea *et al.* 2006, Rodríguez-Durán & Rosa 2020). Remarkably, there is a record of diurnal birds entering caves to catch and eat hibernating bats (Estók *et al.* 2010).

In caves, cockroaches are known to eat bat pups that have fallen on guano before the latter can climb to a safe place (Rice 1957, Wilson 1971, Bordon 1995, Bell *et al.* 2007). The bat genus *Pteronotus* Gray, 1838 is divided into three subgenera: *Pteronotus*; *Chilonycteris* Gray, 1839; and *Phyllodia* Gray, 1843 (Smith 1972). The subgenus *Pteronotus* includes three species of naked-backed bats,

whose wing membranes are attached to the midline of the dorsum and fully cover their backs, which thus appear to be hairless though they are not. There is a single report of possibly predatory behavior of cockroaches on adult bats (López-Wilchis *et al.* 2023). It involved a single individual of each species, namely the cockroach, *Nyctantonina azteca* (Saussure & Zehnter, 1893) (Dictyoptera, Blattodea, Nyctiboridae), and the Thomas's Naked-backed Bat, *Pteronotus fulvus* (Thomas, 1892) (Mammalia, Chiroptera, Mormoopidae) in a Mexican cave. A large *N. azteca* was found lodged in the interstice between the lower surface of the left-wing membrane and the back of the *P. fulvus*. Because both organisms had mutually caused injuries that were deemed not to be recent, the authors interpreted this interaction as a case of accidental ectoparasitism.

Venezuela is the country in which *Pteronotus* is most diverse. Seven species of this bat genus were included in the latest national list (Boher-Bentti *et al.* 2023): 1) the Davy's Naked-backed Bat, *Pteronotus* (*Pteronotus*) *davyi* Gray, 1838; 2) the Big Naked-backed Bat, *P. (Pt.) gymnonotus* (Wagner, 1843); 3) the Wagner's Lesser Mustached Bat, *P. (Chilonycteris) personatus* (Wagner, 1843); 4) the Allen's Common Mustached Bat, *P. (Phyllodia) fuscus* (J. A. Allen, 1911); 5) the Wagner's Common Mustached Bat, *P. (Ph.) rubiginosus* (Wagner, 1843); 6) *P. (Ph.) paraguayensis*; and 7) the Amazonian Common Mustached Bat, *P. (Ph.) alitonus* Pavan, Bobrowiec & Percequillo, 2018.

Species of the genus *Pteronotus* are dependent on caves and artificial cave-like structures as diurnal retreats (*e.g.*, Silva-Taboada 1979, Molinari *et al.* 2012, Soto-Centeno *et al.* 2015). Members of the subgenus *Phyllodia* show a tight dependence on forest (Gutiérrez & Molinari 2008, Oliveira *et al.* 2015, Martino *et al.* 2019), thus are largely absent from the savanna corridor (where caves are also scarce) of the Venezuelan Llanos region (Gutiérrez & Molinari 2008), which cover approximately 240,000 km² and are bounded to the west by the Andes, to the north by the Venezuelan Coast Range, and to the south by the Orinoco River (Huber *et al.* 2006).

Despite the availability of suitable caves being thought to limit their abundance (Humphrey 1975, Rodríguez-Durán 2009, Furey & Racey 2016, Vargas-Mena *et al.* 2020), roost overpopulation has not being listed as a cause of mass mortality in cavernicolous bats (O'Shea *et al.* 2016). This suggests other causes of mortality, the most important of which likely is predation by natural enemies (Mikula *et al.* 2024), to normally prevent the size of the colonies of cavernicolous bats from surpassing the carrying capacity of caves.

We report the first known case of multiple mortality in adult bats due to the carrying capacity of a cave being

surpassed, and to harassment by a dense population of cave-dwelling cockroaches. The observations involve three species of *Pteronotus* and were recorded in the Venezuelan Llanos.

STUDY AREA AND METHODS

The observations reported here were carried out in a small cave (Fig. 1) locally known as Cueva del Viejo [= Old Man's Cave], or Cueva del Ermitaño [= Hermit's Cave], which despite these names is not suitable for human habitation owing to its harsh interior environment. This cave is located at 8.98° N and 68.27° W, 2.7 km ENE El Baúl, Estado Cojedes, Venezuela, in El Baúl Massif, a complex of scattered hills composed of igneous, metamorphic and metasedimentary rocks of late Cambrian to early Permian age that emerges from beneath the mainly Quaternary alluvial deposits of the Venezuelan Llanos (Bucher 1952, Huber *et al.* 2006, Viscarret *et al.* 2012). It is at an elevation of 235 m, 500 m to the east of the road (Carretera Regional El Baúl-Las Galeras) and flat lowlands with elevations of 60–70 m. The climate of the region is characterized by a single rainy season (April-May to October) alternating with a dry season (November to April-May) (Huber *et al.* 2006).

At dawn on 19 January 2001, we ascended from the road to the cave following a rocky path. We stayed at the cave for 6 hours, capturing bats with a hand net and performing observations. The cave consists of a single chamber approximately 12 m long, 5 m wide, and 3 m high. The entrance (Fig. 1, top left) is its highest point, and the opposite end is its lowest point. Thus, the posterior of the cave functions as a cul-de-sac in which the layer of bat guano becomes progressively thicker, wetter, and more decomposed while going deeper. At the bottom of the cave, the concentration of ammonia made the air unbreathable for humans; thus, to observe the interaction between bats and cockroaches, we visited this portion of the cave multiple times while holding our breath. We had planned a subsequent visit with better equipment, but this was not possible, thus we decided to prepare this report.

RESULTS

As we ascended to the cave, at about 50 m from its entrance, we began to find on the ground disarticulated bones and whole skeletons belonging to the same bat species found in the cave, which were *Pteronotus davyi*, *P. gymnonotus*, and *P. personatus*. Of the three, the last species was the least abundant. No other bat species seemed to be present in the cave. The number of skeletons increased as



Figure 1. **Top left)** Entrance of the cave photographed from inside the cave. Note that the interior of the cave is lower than its entrance. The human silhouette is that of EEG. **Top right)** Bats roosting exposed to sunlight at the entrance of the cave, photographed from outside the cave. **Bottom)** Bats on the floor of the cave, which had started to escape when approached to obtain the photograph.

we were getting closer to the cave. We assumed that these remains were washed away by rainwater flowing along and around the path to the cave.

Upon reaching the cave, we discovered the likely source of the skeletons: numerous bats roosting at the entrance of the cave despite being exposed to sunlight (Fig. 1, top right). This was entirely unexpected, because species of *Pteronotus*, as other bats with small eyes, are normally

found only in the dark part of caves. Bats roosting at the entrance of caves can be exposed to diurnal predators and, if not adapted to roost outside caves, may lose body water. Bats dying inside the cave were unlikely to be the source of the skeletons because any water entering the cave would drain inwards together with the guano, since as mentioned above the cave decreases in height from entrance to bottom.

The ceiling and walls of the cave were densely packed with roosting bats. The guano on the floor of the cave and the low areas of the cave walls were covered by dense groups of cockroaches of an unidentified species (Dictyoptera, Blattodea, Blaberidae; Fig. 1, bottom), most of which were too large to be potential prey for these bats.

Another unexpected finding was an aggregation of bats resting in a quadrupedal position on the floor, deep in the cave (Fig. 1, bottom). They were tightly packed, and all had their heads pointing in the direction of the entrance of the cave, which is not evident in Fig. 1 because they started to fly whenever we approached them at a short distance (~1 m) to obtain photographs. We were able to observe the behavior of these bats by staying 2–3 m away. The aggregation covered a semicircular area of 5–6 m². Its curved edge was composed of bats with their hindquarters in contact with the posterior walls of the cave. Its straight edge was composed of bats arranged to form a sharp line limiting with cockroach-covered guano. The bats, especially those in the front edge, were alert (heads continually moving, mouths open) and agonistic (pouncing and retreating) towards the cockroaches. After a short while, the bats in the front edge would take flight and land on the backs of bats in the rear of the aggregation, thus were replaced by the bats that previously were just behind them, which in turn repeated this behavior. Thus, the aggregation functioned as a continuous track in which the treads were the bats. As the bats took flight, it was evident that they had cockroaches below them.

We hand-netted ~120 bats within the cave. To complement material from this location already in museums, we selected 33 specimens as vouchers and released the rest. Most of the bats (>70%) that we handled had erosive wounds (1–5 mm wide) on their wing and tail membranes that may have been caused by cockroach gnawing.

DISCUSSION

Numerous instances of three species of *Pteronotus* inhabiting the same diurnal roost have been reported throughout the Neotropics: 1) The Macleay's Mustached Bat, *P. (Ch.) macleayi* (Gray, 1839), the Sooty Mustached Bat, *P. (Ch.) quadridens* (Gundlach, 1840), and the Parnell's Common Mustached Bat, *P. (Ph.) parnellii* (Gray, 1843) in 15 Cuban and two Jamaican caves (Silva-Taboada 1979, Genoways *et al.* 2005, Tejedor *et al.* 2005); 2) *P. (Pt.) fulvus*, the Dobson's Lesser Mustached Bat, *P. (Ch.) psilotis*, and the Mexican Common Mustached Bat, *P. (Ph.) mexicanus* in five caves and one abandoned mine in Mexico (Bateman & Vaughan 1974, Torres-Flores *et al.* 2012, Ayala-Téllez *et al.* 2018); 3) *P. gymnonotus*, *P. per-*

sonatus, and the Mesoamerican Common Mustached Bat, *P. (Ph.) mesoamericanus* in a Costa Rican cave (Deleval & Chaverri 2018); and 4) *P. gymnonotus*, *P. personatus*, and *P. rubiginosus* in two Brazilian caves (Zortéa *et al.* 2015, Barros & Bernard 2023). In Venezuela, the only reports of roost co-occurrence between species of *Pteronotus* involve *P. davyi* and *P. paraguayensis* (the latter misidentified as '*P. personatus*': Bonaccorso *et al.* 1992, de La Torre & Medellín 2010) in the three main caves of Paraguaná Peninsula (Molinari *et al.* 2012). The Cueva del Viejo (Fig. 1, top left) is smaller than all those caves and mines, and differs from many of them in not being a hot cave (Silva-Taboada 1979, Rodríguez-Durán 2009). The non-karstic lithology of El Baúl Massif (Viscarret *et al.* 2012) may limit the number, size and suitability of caves available to bats of the genus *Pteronotus*.

Savannas represent ~17% of the area and contribute ~30% of the primary production of the Earth's terrestrial vegetation (Grace *et al.* 2006). As in other biomes (Borer *et al.* 2012, Cusens *et al.* 2012), in grasslands primary production determines the abundance of phytophagous insects (Prather & Kaspari 2019, Welti *et al.* 2020, Delabye *et al.* 2022). These arthropods are the dominant herbivores in terms of biomass in savannas worldwide (Andersen & Lonsdale 1990, Lewinsohn & Price 1996). Consequently, in savanna regions like those of the Venezuelan Llanos, owing to the combined effect of orography (in our case also the non-karstic lithology) and primary production, caves used as roosts by insectivorous bats can be in much shorter supply (relatively to the needs of the bats) than insect prey. We believe that this is the situation that applies to the species of *Pteronotus* at our study site, where three clear signs of overpopulation were evident: first, abundant remains of these species were found outside the cave; second, bats had to roost at the entrance of the cave, thus were exposed to death by dehydration and diurnal predators; and third, bats also had to roost on the floor of the cave, thus were suffering harassment by guanophilic cockroaches resulting in metabolic energy loss, and skin lesions apparently caused by the bites of these insects.

Bats of the genus *Pteronotus* have a highly manoeuvrable flight and forage in background-cluttered space: those of the subgenera *Pteronotus* and *Chilonycteris* hunt arthropod prey in proximity to but not within vegetation, whereas those of the subgenus *Phyllodia* do so within dense vegetation (Jennings *et al.* 2004, Mancina *et al.* 2012, Oliveira *et al.* 2015, Martino *et al.* 2019, personal observation). For this reason, species of the first two subgenera, such as *P. davyi*, *P. gymnonotus*, and *P. personatus*, have the potential to act as insect pest controllers at a low height above agricultural land, even gleaning flightless pests directly from

the vegetative organs of crop plants. Because in the Venezuelan Llanos the scarcity of caves likely limits their populations, it should be feasible to construct artificial caves to increase the local densities of these bats, thus boosting their effect as natural pest controllers. Such caves should be positioned near farms and be designed to contain hot chambers, thus making them ideal for mormoopids and unsuitable for vampire bats, and to facilitate the harvest of guano to be used as a fertilizer (Molinari *et al.* 2012).

Cockroaches are related to praying mantises, with which they form the superorder Dictyoptera (Evangelista *et al.* 2019, Ma *et al.* 2023). In the Mesozoic, the superorder included several lineages of cockroach-like predatory species, possessing mantis-like forelegs (Dittmann 2015, Vrsanský & Bechly 2015, Liang *et al.* 2018). The mandibular apparatus of cockroaches allows them to chew all sorts of materials (Weihmann *et al.* 2015). Accordingly, extant cockroach taxa are scavengers or detritivores, but there are reports of them preying on other insects, and they can be cannibalistic (Roth & Willis 1960, Bordon 1995, Persad & Hoy 2004, Bell *et al.* 2007, Pfannenstiel *et al.* 2008). Cockroaches are known to feed on corpses, and to bite sleeping persons, carving significant skin lesions (Roth & Willis 1957, Denic *et al.* 1997, Uieda & Haddad 2014, Viero *et al.* 2019). A dead mouse placed into a dense cockroach culture was skeletonized overnight, suggesting that cockroaches might be used to clean osteological material (Bell *et al.* 2007).

Cockroaches can be superabundant in caves, where they feed on guano, but also on dead and live invertebrates and vertebrates, including bats (Rice 1957, Roth & Willis 1960, Wilson 1971, Schal *et al.* 1984, Braack 1989, Bordon 1995, Bell *et al.* 2007, López-Wilchis *et al.* 2023). Cockroaches cause mortality in the cave swiftlets of tropical Asia by eating their nests, which are largely composed of the birds' salivary proteins (Cruz *et al.* 2008, Manchi & Sankaran 2009). In the caves of Paraguaná Peninsula, we have witnessed the American cockroach, *Periplaneta americana* (Linnaeus, 1758), quickly taking away (or tearing them apart when two or more cockroaches were competing for the victim) wounded conspecifics. Bordon (1995) provided an impressive account of the behavior of cockroaches feeding on dead bats in a Venezuelan cave. An abridged translation follows: '*Near the entrance some bats were collected (Artibeus and Phyllostomus), which were left on the ground in individual plastic bags to later obtain ectoparasites. Then we entered the area of complete darkness. After returning to the entrance, we noticed that the bags with the bats had disappeared. A little further away we saw something like large self-propelled balls that moved irregularly from one place to another. They were hundreds of giant*

wingless cockroaches (probably Megaloblatta) which, after having broken the plastic bags, fiercely and frantically fought over what was left of the bats; there were manifestations of cannibalism'. Therefore, under propitious circumstances, such as those that we witnessed (Fig. 1), cave-dwelling cockroaches can be expected to bite adult bats.

Similarly to López-Wilchis *et al.* (2023), we have difficulties to characterize the interaction between bats and cockroaches at our study site. Because according to their observations the cockroach had been living in symbiosis with the bat for some time, they concluded that it was an unusual case of accidental parasitism rather than predation. Based on our observations, we conclude that the cave was overcrowded with bats, which thus were forced to come into close contact with the cockroaches on the guano. The agonistic behavior of the bats towards the cockroaches suggests that their skin lesions were caused by these insects. Given that there was no symbiosis between both kinds of organisms, if the assumption is made that the cockroaches were biting the bats to opportunistically feed on them, their behavior could be classified as accidentally predatory. Although cockroaches cannot kill active adult bats, if present in huge numbers as observed in this cave, they could harass them, thus contributing to bat mortality.

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