



Unexplored Diversity and Conservation Potential of Neotropical Hot Caves

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Abstract: *The term hot cave is used to describe some subterranean chambers in the Neotropics that are characterized by constantly high ambient temperatures generated by the body heat of high densities of certain bat species. Many of these species have limited geographic ranges, and some occur only in the hot-cave environment. In addition to the bats, the stable microclimate and abundant bat guano provides refuge and food for a high diversity of invertebrates. Hot caves have so far been described in the Caribbean and in a few isolated locations from Mexico to Brazil, although there is some evidence that similar caves may be present throughout the tropics. The existing literature suggests these poorly known ecosystems, with their unique combination of geomorphology and bat-generated microclimate, are particularly sensitive to disturbance and face multiple threats from urbanization, agricultural development, mining, and tourism.*

Keywords: arthropods, bats, Brazil, species discovery

Diversidad No Explorada y Potencial de Conservación de Cuevas Neotropicales Calientes

Resumen: *El término cueva caliente es utilizado para describir algunas cámaras subterráneas en el Neotrópico que se caracterizan por temperaturas ambientales elevadas generadas por el calor corporal de densidades altas de ciertas especies de murciélagos. Muchas de estas especies tienen rangos de distribución geográfica limitados, y algunas solo ocurren en el ambiente de cueva caliente. Adicionalmente a los murciélagos, el microclima estable y la abundancia de guano de murciélago proporcionan refugio y alimento a una alta diversidad de invertebrados. A la fecha, se han descrito cuevas calientes en el Caribe y en unas cuantas localidades aisladas entre México y Brasil, aunque hay evidencia de que puede haber cuevas similares en los trópicos. La literatura existente sugiere que estos ecosistemas poco conocidos, con su combinación única de microclima generado por la geomorfología y los murciélagos, son particularmente sensibles a la perturbación y enfrentan múltiples amenazas por la urbanización, el desarrollo agrícola, la minería y el turismo.*

Palabras Clave: Artrópodos, Brasil, descubrimiento de especies, murciélagos

Attributes of Hot Caves

It has long been known that some chambers within caves in the Neotropics can reach very high temperatures (approximately 40 °C) due to the body heat emanating from high densities of certain bat species (Juberthie 2000). In one of the first descriptions of this

phenomenon, Dalquest and Hall (1949) describe a visit to a cave in the Tuxtla Mountains, Veracruz, Mexico, inhabited by thousands of Wagner's mustached bat (*Pteronotus personatus*) and Davy's naked-backed bat (*Pteronotus davyi*) (both Mormoopidae). They recount that "it was impossible to remain long in the upper rooms because the temperature was high, probably more than

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95 °F [35 °C], and the stench was almost unbearable” (p. 426).

Hot caves have distinct physical and biological characteristics. They usually have a single relatively small entrance, low air circulation, a high (typically tens to hundreds of thousands of individuals) density of bats, constant year-round ambient temperatures of 28–40 °C, and relative humidity >90% (Silva Taboada 1979; De La Cruz 1992). There appears to be a lower size limit for the formation of hot caves because the distinct microclimate depends on the maintenance of a sufficiently dense bat population (Rodríguez-Durán 2009). More recently, Rodríguez-Durán (2009) categorized Caribbean hot caves as “hot chamber foyers” (23–28 °C) or “hot main chambers” (29–40 °C). This dichotomy is useful for classification, but is not absolute, and large cave systems may have chambers with a wide range of temperatures that create opportunities for segregation of species on the basis of thermal associations (Rodríguez-Durán & Soto-Centeno 2003; Rodríguez-Durán 2009).

Although caves are common geological features worldwide, only a small proportion have the geomorphology to become hot caves: medium to large fluviokarst caves, over 1 km in total length, a single small entrance, and poorly ventilated chambers (Rodríguez-Durán 2009). It has been estimated that as many as 8% (approximately 160) of caves in Puerto Rico could be classified as hot caves and provide roosts for diverse bat communities (Rodríguez-Durán 1998), although the proportion could be higher in other countries, where geomorphological features facilitate the formation of caverns with poor air flow (Mancina et al. 2007).

One of the key features of hot caves is that the high temperatures are caused by heat radiating from the bodies of the high densities of bats that occupy the chambers and from decomposing guano (Peck et al. 1998). Thus, they are qualitatively different from caves that are hotter than ambient due to the effects of geothermal heating (Bell et al. 1986) through the convection of hot air into the cave (Rodríguez-Durán 2009). Rather, hot caves represent a form of ecosystem engineering in which the exceedingly stable microclimate and the abundant guano strongly affect the space where other organisms (e.g., arthropods, gastropods, microbes) live (Hastings et al. 2007).

Bat-engineered hot caves are best known from the Caribbean, especially the islands of the Greater Antilles (De La Cruz 1992). They have been most extensively studied in Cuba (Sampedro Marin et al. 1977; Tejedor et al. 2005; Mancina et al. 2007) and Puerto Rico (Rodríguez-Durán 1995, 1998; Rivera-Marchand & Rodríguez-Durán 2001). Continental hot caves have been described in Mexico (Dalquest & Hall 1949), Venezuela (De La Cruz 1992; Arends et al. 1995), and, most recently, northeastern Brazil (J.V.L.F., unpublished data). Fossil evidence from the Pleistocene suggests that hot caves may have

once existed as far south as the Brazilian state of Bahia (Czaplewski & Cartelle 1998) and as far north as Florida in the United States (Morgan 1987). However, the scattered reports of hot caves in the scientific literature almost certainly underestimate their frequency because, even when surveyed, they may not have been recognized, classified, or labeled as such.

Although not referred to as hot caves, there is evidence that similar bat-generated microclimates may exist in other parts of the tropics. Churchill (1991) describes cave roosts of the orange horseshoe-bat (*Rhinonycteris aurantius*) in tropical Australia of up to 25,000 individuals that maintain a constant cave temperature of 28–32 °C and 85–100% relative humidity. However, it is not clear to what extent, if any, this species contributes to the stability of the microclimate, and the cave is occupied by bats for only part of the year. Another likely location of hot caves is the extensive karst landscapes of Southeast Asia, which occupy an area of approximately 400,000 km² (Day & Ulrich 2000). A diverse and abundant bat fauna inhabits these landscapes. Some cave systems in the Mulu karsts, Sarawak, contain more than a million individual wrinkle-lipped bats (*Chaerephon plicata*) (Clements et al. 2006).

Fauna of Hot Caves

The most prominent fauna of hot caves are the bat species that contribute to the characteristic microclimate. In the Neotropics, the family Mormoopidae is the main taxon associated with hot caves, although they frequently share roosts with species in the families Phyllostomidae and Natalidae. All Antillean endemics in the family Mormoopidae and most Natalidae are either restricted to hot caves year round or during parturition. The same pattern exists for the range-restricted phyllostomid genera *Monophyllus*, *Erophylla*, and *Phyllonycteris* (Silva Taboada 1979; Rodríguez-Durán 1995; Gannon et al. 2005). Moreover, hot caves often have a limited number of characteristic bat species assemblages (Rodríguez-Durán 1998).

One of the most notable differences between the bat fauna of hot caves and other caves is in the density of bats: the former are typically occupied by roosts of thousands or even hundreds of thousands of individuals, whereas the latter typically have much lower abundances (Rodríguez-Durán 2009). Rodríguez-Durán and Lewis (1987) estimated that one cave in Puerto Rico contained approximately 141,000 individuals of the sooty mustached bat (*Pteronotus quadridens*), a hot-cave specialist.

The stable microclimatic conditions and high humidity produced by the high density of bats also support a large number of other animals (Juberthie 2000), especially arthropods that feed on the abundant bat guano and the decomposing remains of bats and other cave

inhabitants (e.g., Vandel 1965; Barr 1968; Howarth 1983; Trajano 2012). Most of these species are facultative cave-inhabiting species as opposed to troglobites, which are generally found deeper in cave systems and are not typically associated with guano. In contrast to the relatively well-studied bat communities, the cave-dwelling arthropod fauna of Neotropical caves in general, and hot caves in particular, is poorly known (Peck et al. 1998).

Probably the best known arthropods that are closely associated with hot caves are the ectoparasites. For example, De La Cruz and Estrada-Peña (1995) described 4 new species of ticks (genus *Antricola*) collected in bat guano from hot caves in Cuba and Curacao. Likewise, in a recent survey of mormoopid bat ectoparasites from a hot cave in Puerto Rico, researchers found a large number of new host-parasite associations (new host records) and one new subspecies of mite (Kurta et al. 2007). The discovery of new ectoparasitic taxa or associations on these islands is not surprising because, again, hot caves are occupied by many bat species endemic to single islands or that have small geographic regions (Rodríguez-Durán 1998; Tejedor et al. 2005).

The abundant guano and stable microclimate provides ideal conditions for many ground-dwelling invertebrates. For example, in Cuba researchers identified 26 species of beetle, 17 (59%) of which were endemic to Cuba, that can complete their entire life cycle within caves and another 3 that regularly use caves (Peck et al. 1998). Although none of these species are strictly limited to hot caves, the high humidity and abundant food (guano) in hot caves support high population densities, and the stability of the microclimate may provide a refuge when climate conditions elsewhere in the cave system are unfavorable. Moreover, Neotropical invertebrate communities associated with bat guano are thought to be particularly species rich due to the diversity of bat feeding strategies (Trajano 2012); some species of invertebrates to specialize on guano from particular species of bats (Gnaspini-Netto 1989, 1992).

Adaptations

Some bat species appear to be adapted to the biophysical condition of hot caves; for example, they have physiological adaptations such as relatively low basal metabolic rates (Rodríguez-Durán 1995) and morphologies that conserve water. Puerto Rican mormoopid species that roost in hot caves have relatively larger kidney medulla than species that roost in cooler microclimates (Rivera-Marchand & Rodríguez-Durán 2001). This apparent adaptation of hot-cave species, whose wing membranes are easily dehydrated (Silva Taboada 1979), may reduce water loss when they are foraging outside the humid microclimate of the cave. Although the tropics are commonly thought of as warm, temperatures may fall below the

thermoneutral temperature of bats on a daily basis in many locations (McNab 1969). These relatively low temperatures are not trivial for small bats, which respond through behaviors such as clustering and roost modification. The benign conditions within hot-cave chambers facilitate the conservation of energy, allowing individuals to reduce energy expenditure on thermoregulation without becoming torpid (Rodríguez-Durán 1995).

Temperature is also an important physical variable that affects roost selection in bats (Avila-Flores & Medellín 2004). Behavioral choice experiments demonstrate that species associated with hot caves have strong preferences for these microclimates. In laboratory experiments, sooty mustached bat (Mormoopidae) chose temperatures equivalent to the hot caves in which it is found, whereas the sympatric phyllostomid species, the brown flower bat (*Erophylla bombifrons*), preferred cooler roosts (Rodríguez-Durán & Soto-Centeno 2003). Under natural conditions, the brown flower bat roosts in the cooler hot-chamber foyers (Rodríguez-Durán 2009), whereas sooty mustached bat roosts inside the main hot chamber. Such species-specific temperature preferences and associated adaptations may be one of the drivers of multispecies coexistence and structure of bat assemblages in tropical cave-dwelling species (Rodríguez-Durán & Soto-Centeno 2003).

There have been few studies of the physiological adaptations of invertebrates to the high temperature and humidity of hot caves. Peck et al. (1998) observed that the majority of Cuban cave dwelling beetles are present in caves if abundant food (guano) is available and the humidity is sufficiently high (95–98%), whatever the temperature. More generally, early researchers observed few troglobitic invertebrate species that exhibit ecological-morphological adaptations (e.g., loss of pigment, eyes) to cave life in the Neotropics, possibly due to the abundance and stability of the food supply, lessens the selection pressure for troglobitic adaptations that economize energy (Vandel 1965; Mitchell 1969). Results of recent research indicate there may be considerably more Neotropical troglobites than previously recognized (Peck et al. 1998), although the cave faunas of the Neotropics remain terra incognita compared with many other regions where caves occur.

There have been few studies of the microbial communities associated with bat guano that accumulates in caves (Chroňáková et al. 2009), and none, to the best of our knowledge, of microbial communities in hot caves. However, the stable microclimate and diverse bat communities of hot caves provide an ideal environment for microbial production.

Threats to Hot Caves

Cave ecosystems throughout the world are threatened by human activities (Vermeulen & Whitten 1999). In the

Neotropics, caves are under particular threat from increasing numbers of visitors who damage or modify the structure of the caves by mining for construction material or through extraction of guano for fertilizer (Mancina et al. 2007). The karst landscapes of the Caribbean, where most hot caves have been documented, are quarried for building materials, mined for bauxite, used as a source of groundwater, and are affected by urbanization, agricultural development, and tourism (Day 2007). Major human uses of hot caves are limestone quarrying for construction, especially cement production (Day 2010). According to the U.S. Geological Survey, in the Caribbean islands more than 8 million t of cement are produced per year (4 million t from the Dominican Republic alone), and over 2 million t of limestone are extracted from the region annually (USGS 2009).

Notwithstanding generic threats to landscapes that contain hot caves, it is currently difficult to assess the potential level of threat to species and populations that inhabit hot caves, especially in continental South America, where hot caves are poorly documented. Globally, the lack of ecological studies makes it difficult to develop conservation measures for troglobites, especially in tropical regions (Howarth 1983).

Even with limited data there are several reasons to suspect that communities of organisms in hot caves, especially bats, may be sensitive to disturbance. First, the distinct geomorphology of hot caves could be quickly and irreversibly altered by natural or human-assisted erosion. This could increase air flow and decrease temperatures and lead to specialized bat species abandoning the roost. Results of research in the Caribbean indicate that 80% of caves with fossilized remains of hot-cave bat communities are currently well ventilated and may no longer support (a cave cannot create a microclimate) a hot-cave microclimate even if the appropriate bat species were present in the chamber (Tejedor et al. 2004). Guano extraction may also affect the microclimate by reducing the warming effect of guano decay. In Cuba, De La Cruz (1992) observed that 7 of 9 hot-cave chambers where guano extraction was permitted had lower temperatures than equivalent chambers where extraction was not permitted.

Second, bat species that are adapted to hot caves may have a potentially high risk of extirpation when roosts with geomorphology characteristic of hot caves are scarce. This may be particularly relevant for taxa with relatively low dispersal ability such as the natalids. For example, the relatively low dispersal potential and association with hot caves of the rare natalid, the Hispaniolan greater funnel-eared bat (*Natalus major*), led Tejedor et al. (2004) to suggest that this species has “a relatively high extinction potential” in Cuba (Tejedor et al. 2004). Hispaniolan greater funnel-eared bat is only known from a single permanent roost on the island, and many large roosts of this species in Cuba have already disappeared due to disturbance by increasing numbers

of visitors (Silva Taboada 1979). More generally, there are at least 7 species of Cuban bats that are predominantly found in hot caves and are considered to be at risk of decline due to microclimate modifications (Mancina et al. 2007).

Third, the relatively higher risk of extinction, compared with other bats, of species that predominantly occupy hot caves is also supported by patterns of recent extinctions. Among the 27 species of Antillean bats that became extinct in the late quaternary, 63% (17 species) were hot-cave specialists in the families Mormoopidae, Natalidae, and Phyllostomidae (Morgan 2001). All 8 recognized species in the Mormoopid genera *Mormoops* and *Pteronotus* in the Caribbean have either become extinct or have had numerous local extinctions, especially from smaller islands (Morgan 2001).

Fourth, the formation of hot caves requires a minimum number of individuals to create the characteristic microclimate. Consequently, a decrease in bat abundance below the critical minimum number for a given chamber could threaten the viability of the colony. Various natural and anthropogenic factors could cause a reduction in colony size, although the loss of foraging grounds through deforestation is likely to be one of the most widespread and substantial drivers.

Opportunities for Conservation

There are a number of range-restricted bat species that are predominantly found in hot caves, and there is clear potential to discover new species of invertebrates. However, with a few notable exceptions (Puerto Rico, Cuba), hot caves have been poorly surveyed and the development of protection measures would benefit from better knowledge of their geographic distribution. The recent discovery of a hot cave in Brazil (Estrada-Peña et al. 2004) suggests there may be many more undiscovered hot caves in South America and possibly in other tropical regions.

Improved knowledge may also come about by increasing awareness of hot caves among the international research community. The literature is currently scattered and the term *hot caves* (*cuevas calientes*) has been predominantly used by the Latin American scientific community. Better labeling of this phenomenon might increase interest in research.

Most critically, data are required on resilience of hot caves to factors such as human activities, changes in the surrounding land cover, and climate change. Research on community dynamics and biophysical processes within hot caves needs to be explicitly multidisciplinary, ranging from better characterization of the suite of geomorphological features that promote the formation of hot caves to research on microclimate and community ecology (including microbial communities) in these fascinating ecosystems.

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