ARTICLE

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Guardians of the Mayan temples: microclimatic conditions of archaeological sites used as roosts by *Chrotopterus auritus* in Southeastern Mexico

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Resumen

El falso vampiro lanudo, *Chrotopterus auritus*, es un murciélago carnívoro con una amplia distribución en América. Además de refugiarse en árboles huecos y cuevas, este murciélago utiliza sitios arqueológicos mayas en la península de Yucatán, donde se encuentra amenazado. Comprender qué condiciones microclimáticas le permiten a esta especie utilizar estos refugios es importante en el contexto de cambio antropogénico en la región, incluyendo el cambio de uso de suelo y la instalación de infraestructura turística en los sitios arqueológicos. Se utilizaron *data loggers* de temperatura y humedad relativa para medir la temperatura interna, la humedad relativa interna y la temperatura externa de tres refugios en templos mayas en Calakmul, Campeche, esperando que las condiciones internas fueran, en promedio, cercanas a la zona termoneutral reportada para la especie (~27-34 °C). Registramos datos de 54,7 días de temperatura y 42,5 días de humedad relativa en cuatro meses distintos del año. La temperatura interna promedio anual de los refugios fue de 24,6 °C (DE=2,03), mientras que la humedad relativa interna promedio anual fue del 79,4 % (DE=8,3), con diferencias significativas entre refugios y entre meses de muestreo. *Chrotopterus auritus* tolera condiciones energéticamente subóptimas y potencialmente prioriza otros factores en la selección de refugios.

Palabras clave: falso vampiro lanudo, humedad relativa, microclima, ecología de los refugios, temperatura.

Abstract

The woolly false- vampire bat, *Chrotopterus auritus,* is a large carnivorous bat with a wide distribution in the Americas. Besides roosting in hollow trees and caves, this bat makes use of Mayan archaeological sites in the Yucatan Peninsula, where it is threatened. Understanding the microclimatic conditions that allow this species to exploit these roosts is important in the face of increasing anthropogenic change in the region, such as land development and tourist accommodations in archaeological sites, which could threaten their suitability. We used temperature and relative humidity data loggers to record the internal temperature and relative humidity and external temperature of three Mayan temple roosts in Calakmul, Campeche, expecting internal conditions to be, on average, close to the reported thermoneutral zone of the species (~27-34 °C). We recorded 54,7 days of temperature data and 42,5 days of relative humidity data in four different months of the year. The yearly average internal temperature of the roosts was 24,6 °C (SD=2,03), while yearly average internal relative humidity was 79,4 % (SD=8,3), with significant differences between roosts and between sampling months. *Chrotopterus auritus* tolerates energetically suboptimal conditions, potentially prioritising other factors in its selection of roosts.

Key words: woolly false-vampire bat, relative humidity, roost microclimate, roosting ecology, temperature.

1. INTRODUCTION

Selecting a suitable roost provides multiple advantages to bats, including protection from predators and the elements, cheaper thermoregulation, reduced commuting distance to foraging sites, and increased opportunities for social interactions (Altringham 2011). Temperature is the most important factor influencing roost selection in bats (Ávila-Flores & Medellín 2004). Bats that use caves, mines, and rock crevices as roosts benefit from their relative permanency and thermal stability; however, these roosts may be patchily distributed (Kunz & Lumsden 2005) and thus a limiting factor, so human structures that resemble natural caves have become an important substitute for many species (Voigt et al. 2016). Although phyllostomid bats play a key role in Neotropical ecosystems, their roosting behaviour remains less studied compared to temperate-dwelling bat families' (Fleming & Rodríguez-Durán 2020).

One example of a neotropical bat species with particular roosting preferences is the woolly false vampire bat, *Chrotopterus auritus* (Phyllostomidae, Chiroptera), which is a large bat found from Northern Argentina to Southeastern Mexico (Solari et al. 2019). It is listed as threatened by Mexican law (SEMARNAT 2019). It is carnivorous and its roosts include caves, abandoned buildings and mines, hollowed-out termite nests, and hollow trees and dead trunks (Gual-Suárez & Medellín 2021), exhibiting high roost fidelity and group stability (Medellín 1988). Individuals spend on average only five hours per night outside of their roost (Vleut et al. 2019). It maintains a body temperature of 37,2°C, and its thermoneutral zone ranges from 27 to 34°C (McNab 1969). The internal conditions of four roosts in Brazil were recorded as 14-22°C with 77-93 % relative humidity (%RH) (McNab 1969), while a cave roost in Bolivia had an internal temperature of 26,7 °C and an average %RH of 68.4 %RH (Lizarro et al. 2020).

Several Mayan temple roosts of this species are known in the Yucatan Peninsula (Brigham et al. 2018; Vleut et al. 2019). Three such roosts are located just a few dozen kilometres apart in Calakmul, Campeche, with 5-7 bats each but with contrasting structures. We recorded the internal and external temperature, as well as internal %RH, at various times of the year in these roosts. We expected the internal temperature of the roosts located in this area to be, on average, close to the species' thermoneutral zone, but that the distinct characteristics of the temples would result in variations in how the internal temperature of each roost fluctuates in relation to external temperature and throughout the year.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in three Mayan temple roosts located in the Calakmul municipality of the State of Campeche, Yucatan Peninsula, Mexico (18.5082, -89.3948, 250 m a.s.l.; Figure 1). The mean annual temperature in the area is 26°C and the mean annual precipitation is 1.350 mm/year, and the region is predominantly covered by tropical semideciduous forest interspersed with patches of secondary vegetation, shaped by seasonal rainfall patterns (Pennington & Sarukhán 2005; Vleut et al. 2019). This area is near the northern edge of this species' distribution. It has two seasons: the dry season, spanning November through April, and the rainy season, from May to October (Vidal Zepeda 2005); the rainiest month (September) receives about nine times as much rain as the driest month (March) (Márdero et al. 2012)

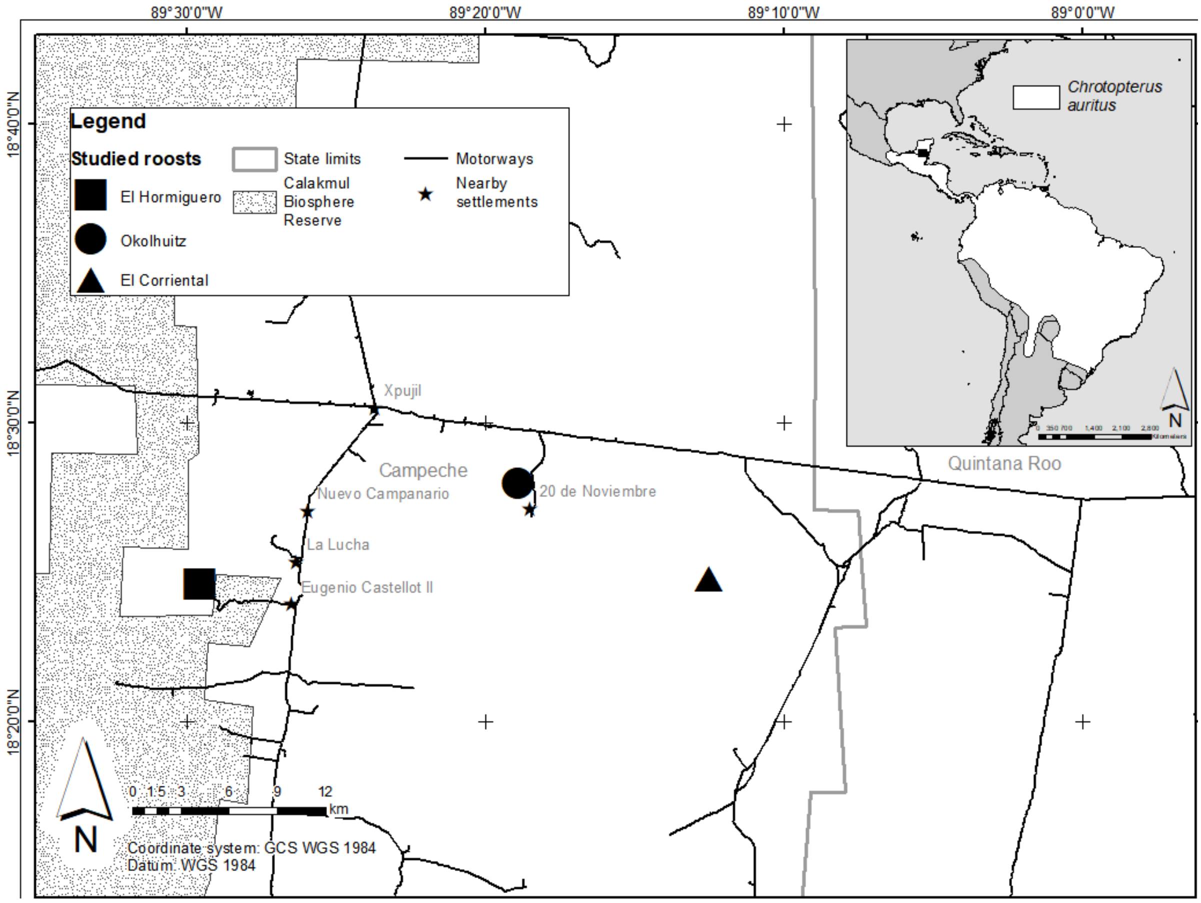

FIGURE 1. Study area, with the location of the Mayan temple in the Calakmul municipality of the State of Campeche, Yucatan Peninsula, Mexico. *C. auritus* roosts featured in this study. Distribution data based on Solari *et al.* (2019).

Structure II of the Hormiguero archaeological site (18,4100, -89,4929, Figure 2), it has two symmetrical chambers. These chambers, named Hormiguero Right (HR) and Hormiguero Left (HL), serve as a roost for a colony of *C. auritus* as roosts. The forest immediately surrounding the temple, up to approximately 20 metres away, was cleared decades ago to allow tourist visitation. This both increases the temperature of the area relative to the surrounding forest matrix and exposes the roosts to the occasional entry of tourists. Each chamber is accessible through a small rectangular opening perpendicular to a long, narrow corridor ending in a vertical shaft continuing to a second level room directly above the entrance level. Bats roost hanging from the ceiling of the upper levels, usually in the right-hand chamber.

The Okolhuitz archaeological site (18,4659, -89,3152, Figure 3) has a single chamber where bats roost. The area has not been recently cleared and is not easily accessible to the public. Access into the temple is through a small opening perpendicular to a long corridor in front of which a large section of the wall and ceiling is missing, exposing most of the chamber to the elements. Bats roost near the ceiling at the far end of the corridor, as far from the openings as possible.

El Corriental (18,3942, -89,2587, Figure 4) is an undisturbed archaeological site. It is a large (~15 m tall) structure covered by the forest matrix and closed to the public. The interior is accessible through a small rectangular opening leading to a narrow corridor that climbs steeply to a second level, where it is split in two perpendicularly and continues towards the back of the temple, where small rectangular openings at the canopy level. Bats roost in a depression of the ceiling near the lower opening.

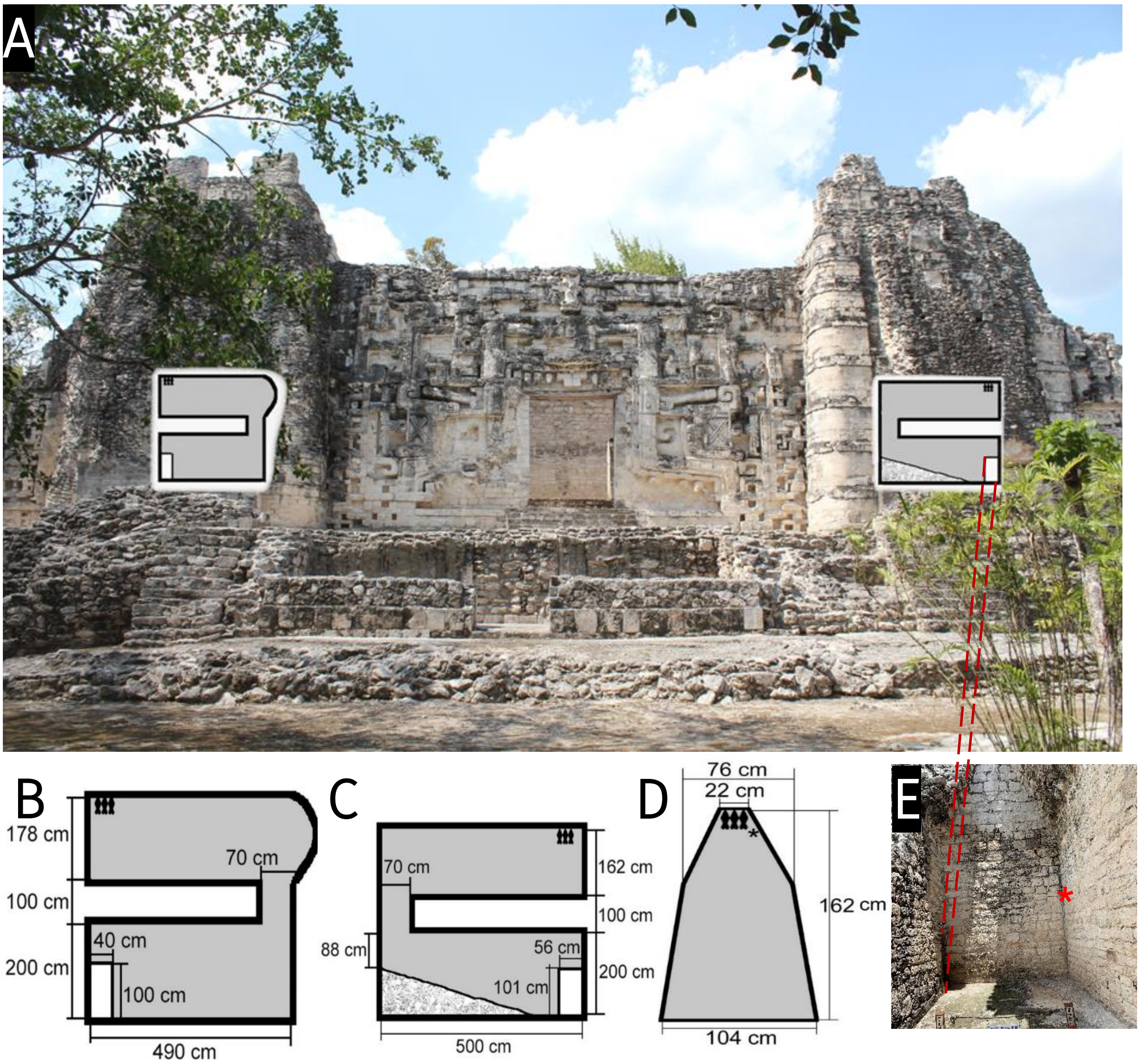

FIGURE 2. Schematic view of the Hormiguero roosts (A), showing Hormiguero Left (B) and Hormiguero Right (C) cavities on the left and right side of the structure, respectively, cross-section of the upper storey of these cavities (D), with the preferred roosting location of bats, and (E) entrance to the Hormiguero Right cavity behind the temple (lower left corner). The location of data loggers is marked with black (inside) and red (outside) asterisks. Photo of temple modified from original by Arian Zwegers: https://www.flickr.com/photos/azwegers/14179622808/in/photostream/, under a Creative Commons license. Photo of entrance: F. Gual Suárez. Diagrams: Mayra Ordóñez.

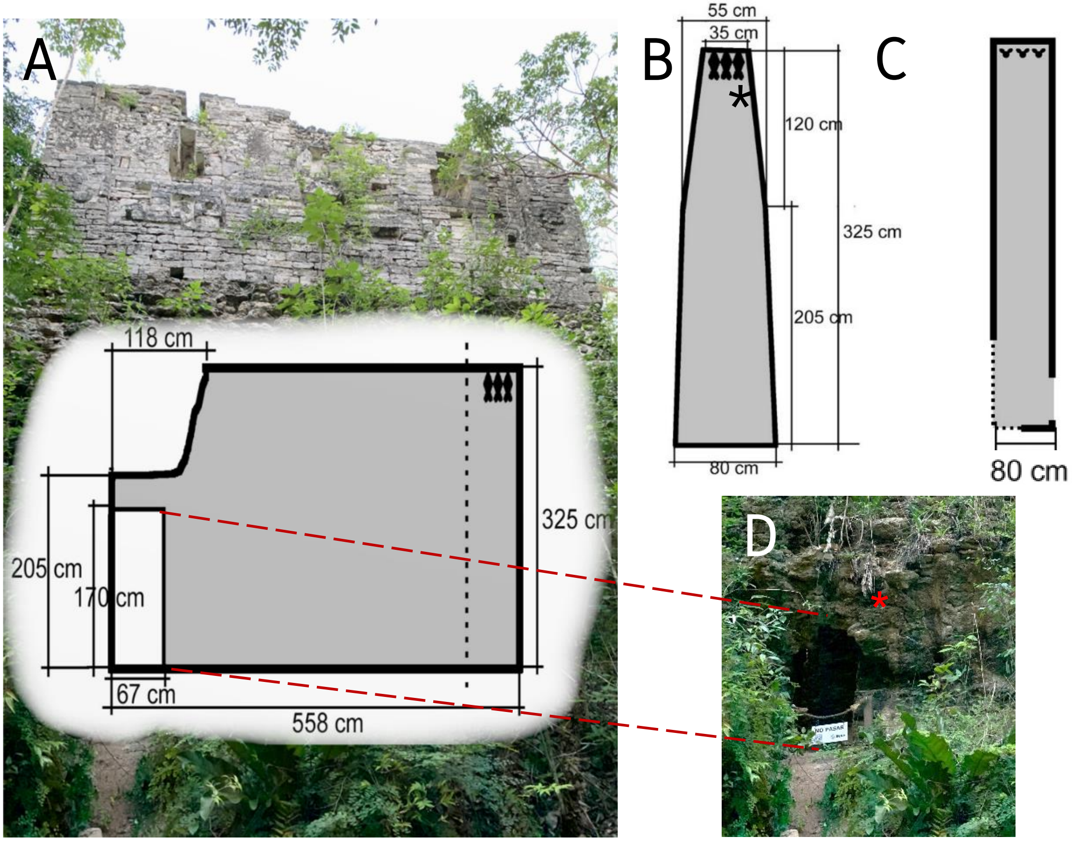

FIGURE 3. Schematic view of the lateral view (A), transverse view (B), top view (C) of the Okolhuitz roost, showing the preferred roosting site at the end of the corridor, and (D) entrance of the temple. Location of missing wall section shown as a dotted line in (C). The location of data loggers in the roost is marked with black (inside) and red (outside) asterisks. Photos: F. Gual Suárez. Diagrams: Mayra Ordóñez.

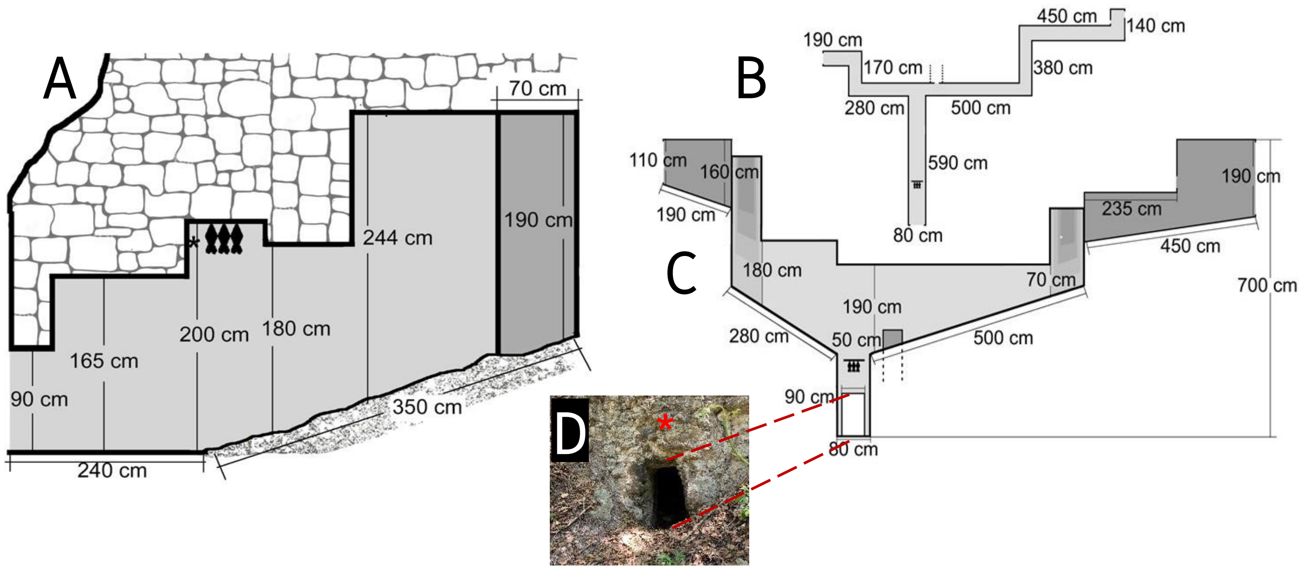

FIGURE 4. Schematic view of the lateral (A), top (B), front (C) views of the El Corriental roost, showing the preferred roosting site in a hollow on the ceiling near the lower entrance, and (D) bottom entrance of the temple. The location of data loggers in the roost is marked with black (inside) and red (outside) asterisks; darker colours represent depth. The site appears as a large mound completely covered by vegetation and is thus difficult to photograph. Photo: F. Gual Suárez. Diagrams: Mayra Ordóñez.

2.2. Methods

The sites were visited during April, July, and November-December 2019 as well as February 2020. A Hygrochron (DS1923) iButton (Maxim Integrated, USA) was used to collect temperature and humidity data inside the roosts. A Thermochron (DS1921G-F5) iButton (Maxim Integrated, USA) collected temperature data from outside the roost simultaneously. Data points were recorded every 10 minutes with a resolution of 0,5 °C and 0,6 %RH. Devices were placed on small rock ledges inside the chambers within 30 cm of the bats' preferred roosting area in each temple to measure inner microclimatic conditions (Figure 2-4) and on crevices near the entrance of each roost where they were exposed to outside air temperature but shielded from sunlight. At Hormiguero, the device was placed in whichever roost the bats were occupying upon our arrival at the site.

For each month, we estimated the average, maximum, and minimum internal and external temperatures; average internal/external temperature difference; and average, maximum, and minimum internal %RH. Kruskal-Wallis tests and Multiple Pairwise Comparisons (Bonferroni correction) were executed in R 4.1.0 (R Core Team 2021) to determine if differences in internal temperature and humidity between sites and between months were significant. Linear models were used to determine the relationship between external and internal temperature in each roost each month, where:

$$T\ internal = m(T\ external) + b$$

3. RESULTS

The average internal temperature across all Mayan temple roosts studied was 24,6 °C (SD=2,03, n=7.877, 54,7 day/night cycles), and ranged from 17,1 °C (El Corriental in December) to 30,6°C (Okolhuitz in July). Internal %RH was on average 79,4 % (SD=8,3, n=6.120, 42,5 day/night cycles), and ranged from 40,6 % (Okolhuitz in April) to 96,8 % (Hormiguero HL, in April). The Hormiguero roosts tended to maintain internal temperatures slightly cooler than outside temperatures while El Corriental and Okolhuitz maintained warmer temperatures relative to the outside; across all sites, the temperature was only 0,25 °C warmer than external conditions (Figure 5 A, Total). At Hormiguero, bats were consistently found in the HR roost, so temperature data was collected from the HL chamber only briefly in April and in February and was found to be on average 0,3 °C cooler than HR. Average internal temperature and %RH, external temperature, and the differences between internal and external temperatures are shown in Supplementary Material 1.

The internal temperature within roosts differed significantly (Kruskal-Wallis χ^2=815,2, df=3, $p<2{,}2\times10^{-16}$, Pairwise comparisons yielded $p<2\times10^{-16}$ for all comparisons except Hormiguero HL-Hormiguero HR, $p=4.4\times10^{-16}$ and Hormiguero HL-Okolhuitz, $p=1.6\times10^{-7}$), as well as %RH (Kruskal-Wallis χ^2=3181,6, df=3, $p<2{,}2\times10^{-16}$, Pairwise comparisons yielded $p<2\times10^{-16}$ for all comparisons). Significant differences were also found between sampling months in the internal temperature (Kruskal-Wallis χ^2=4.757,5, df=3, $p<2.2\times10^{-16}$, Pairwise comparisons yielded $p<2\times10^{-16}$ for all comparisons) and %RH (Kruskal-Wallis χ^2=1.498,1, df=3, $p<2{,}2\times10^{-16}$, Pairwise comparisons yielded $p<2\times10^{-16}$ for all comparisons except July-April, p=0,00012).

Internal temperature showed varying degrees of correlation with external conditions in different roosts (Figure 6). El Corriental showed the strongest correlation (R2=0,89), followed by Okolhuitz (R^2=0,83), while the temperature inside HR remained stable despite external daily variation (R^2=0,19). Limited data on HL indicates similar conditions. Internal roost temperature closely tracked external temperature at El Corriental and Okolhuitz during December. Temperature and %RH graphs for each month can be found in Supplementary Material 2.

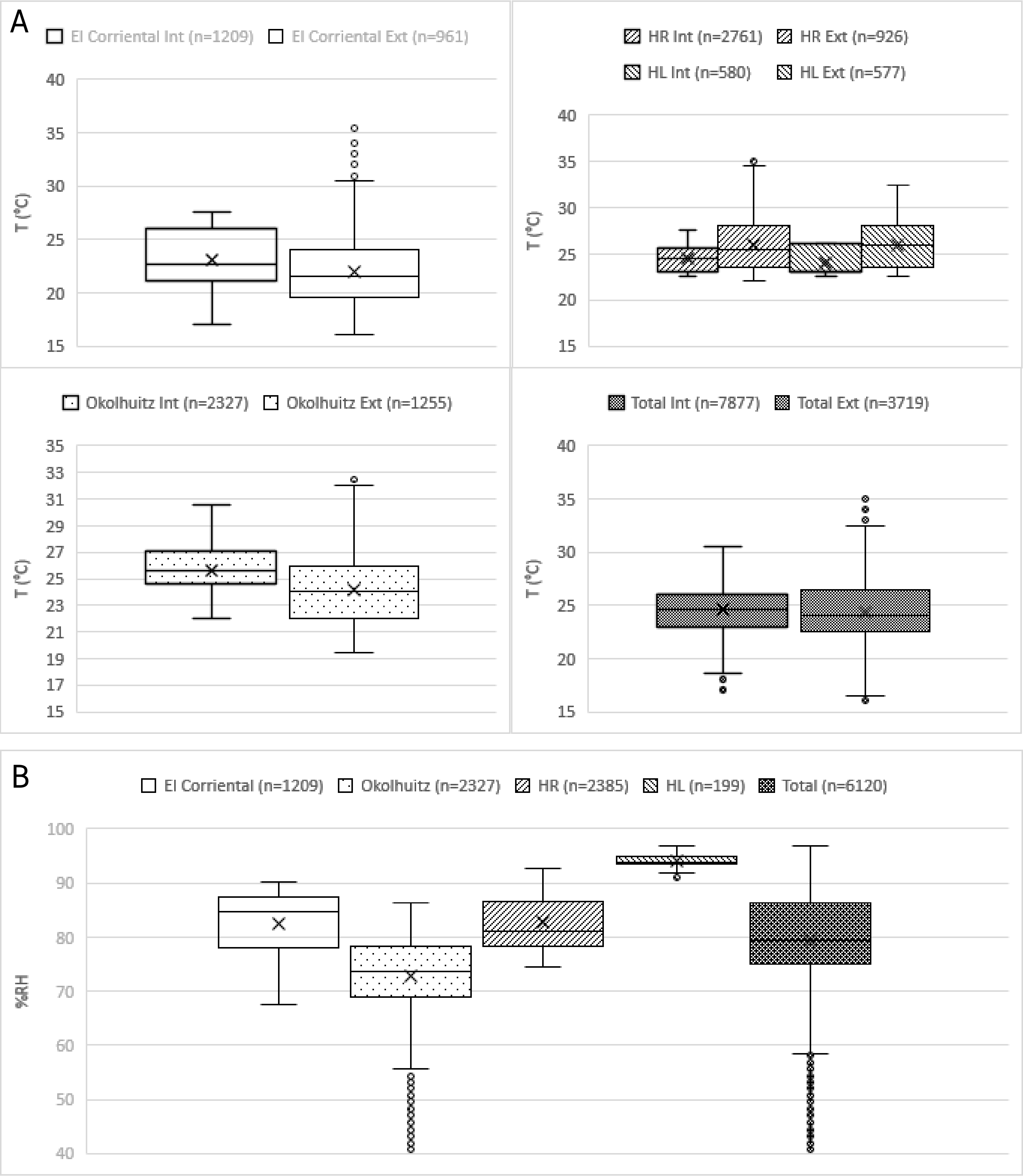

FIGURE 5. Accumulated internal and external temperature (A) and relative humidity (B) data for three Mayan temples used as roosts by *C. auritus* through the year, × depicts the yearly mean for each site. Int: internal, Ext: external. n: data points.

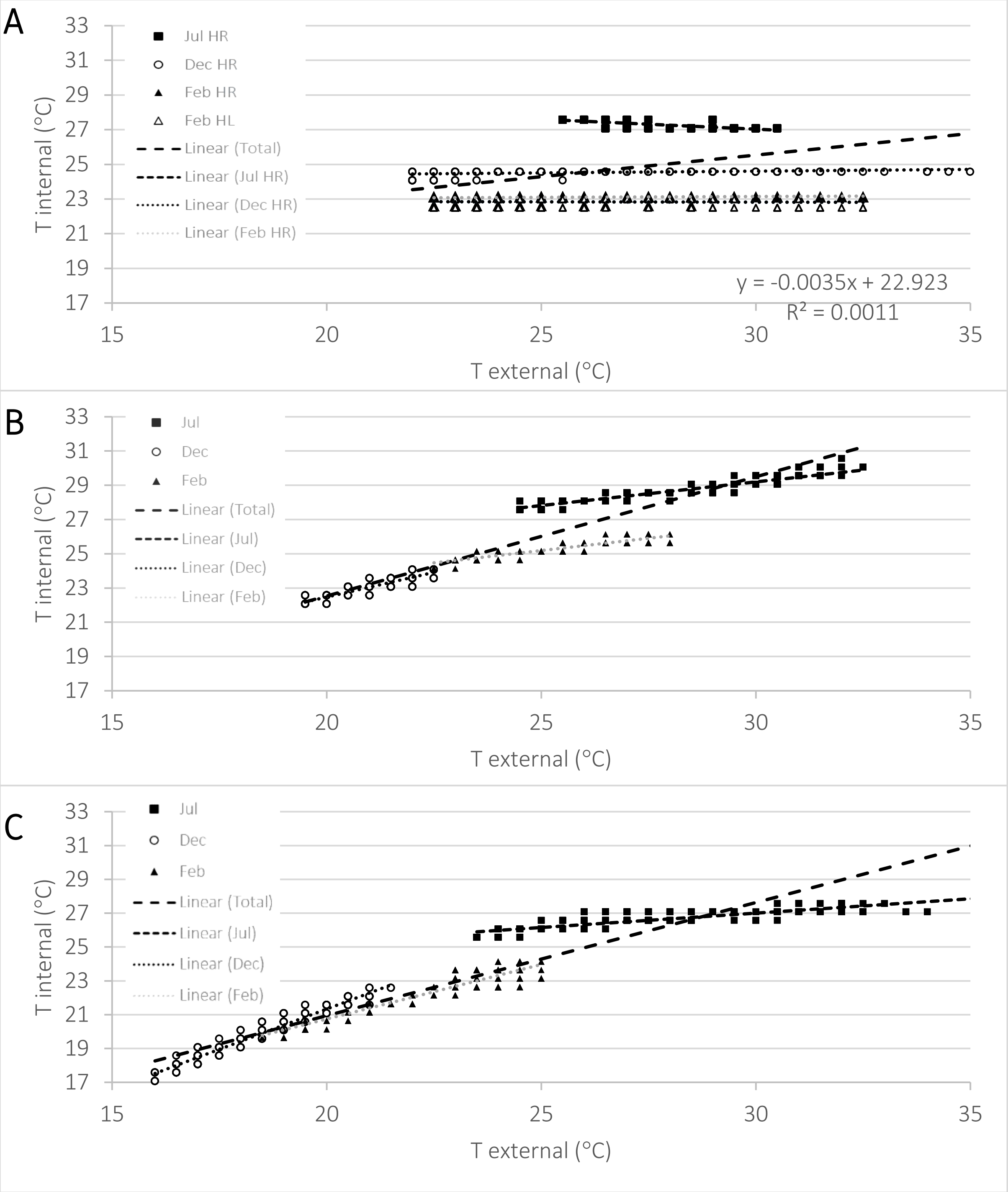

FIGURE 6 Linear models for external vs internal temperatures in three *Chrotopterus auritus* Mayan temple roosts in Calakmul, Mexico. (A) Hormiguero (Jul HR: $y=-0,1143x+30,458$, $R^2=0,5936$; Dec HR: $y=0,0201x+24,003$, $R^2=0,1466$; Feb HR: $y=0,0095x+22,859$, $R^2=0,0255$; Feb HL: $y=-0.0035x+22.923$, $R^2=0.0011$; Total: $y=0,2495x+18,048$, $R^2=0,1889$). (B) Okolhuitz (Jul: $y=0,2762x+20,913$, $R^2=0,8851$; Dec: $y=0,5779x+10,913$, $R^2=0,8656$; Feb: $y=0,2868x+18,018$, $R^2=0,8417$; Total: $y=0,6962x+8,6094$, $R^2=0,8303$). (C) El Corriental (Jul: $y=0,1699x+21,906$, $R^2=0,7017$; Dec: $y=0,952x+2,2921$, $R^2=0,9616$; Feb: $y=0,6448x+7,8451$, $R^2=0,8212$; Total: $y=0,6689x+7,5632$, $R^2=0,894$). The linear regression equation for each month is plotted. Data for Hormiguero HL excluded from Total equation in (A).

4. DISCUSSION

This study presents the first multiseasonal data on the temperature and humidity conditions inside Mayan temple roosts of *C. auritus* near the northern end of its range, where seasonal temperature variations can be significant. Mayan temple roosts of *C. auritus* reach temperatures of up to 30,6 °C and up to 96,8 %RH, which are the highest reported for roosts of this species. Internal temperatures in these Mayan temple roosts were considerably higher than the parameters reported by McNab (1969) for hollow tree and cave *C. auritus* roosts in Brazil and similar to Lizarro et al. (2020)'s in Bolivia, but still below the thermoneutral zone of the species. A high-energy diet and a larger body size may allow carnivorous bats to face challenging thermal environments more efficiently (Ávila-Flores & Medellín 2004), and more seasonal environments are correlated to larger body measurements in *C. auritus* (Stevens 2023). Therefore, bats may be able to choose roosts with temperatures below their thermoneutral zone with little cost, prioritising other attributes such as safety from predators or access to foraging areas. Alternatively, a shortage of more adequate roosting sites may force the choice of less suitable ones. Groups of bats in this study remained very stable and in their preferred roosts despite disturbance from other studies being carried out in parallel, potentially indicating these roosts are very adequate (in internal temperature and humidity conditions or some other parameter) in comparison to similar structures nearby where the bats could roost to avoid disturbance.

On average, Mayan temple roosts of *C. auritus* maintained a temperature only slightly higher than the average temperature of their surroundings. The average temperatures in all the roosts in this study during the warm months (April and July, 25,6-28,6°C) were very close to or within the species' thermoneutral zone, decreasing substantially during the cooler months (November and February, 19,8-25,3°C). Our observations on the diet of the bats in these roosts (Gual-Suárez 2023) suggest a higher proportion of energy dense vertebrate prey during the colder months, potentially helping them cope with lower internal roost temperatures.

The warm period when conditions inside the roosts are closest to the species' thermoneutral zone also coincides with the late stages of gestation, parturition, and lactation, the most energetically expensive stage in mammal females' reproductive cycles (Kunz & Hood 2000): most females were gravid in April, suckling pups could be found in all roosts by July, and they had been weaned by November. The effects of temperature variation on the reproduction of some bats include variations in embryonic growth rate and gestation length (Heideman 2000; Lewis 1993; Uchida et al. 1984), so this bat's reproductive cycle may align both with food availability and with favourable temperature conditions in their roosts.

The Hormiguero HR roost provided the most stable conditions with almost no variation during day/night cycles, no correlation to external temperature, and consistently high humidity. This may be due to the very small, single entrances to the roosts and their two-storey layout within a massive limestone structure, which trap warm air inside. The fact that these roosts had lower temperatures on average than their surroundings is probably due to the lack of forest cover around the temple, where daytime temperatures were noticeably warmer than in the surrounding forest. The abundance of discarded prey parts supports a very active community of decomposers and scavengers (Trujillo et al. 2021), potentially contributing significantly to the chambers' thermal balance and stability. The Okolhuitz roost had the highest internal temperature values and was consistently the driest roost, likely caused by the large opening at the back of the temple that allows both the wind and at certain times sunlight to enter the structure. However, some amount of trapped air or the thermal capacity of the exposed masonry maintained the temperature inside the roost 1,2-2,2 °C on average warmer than the outside during the night consistently through the cold season. El Corriental was consistently the coldest roost and depended the most on outside conditions, probably caused by its internal layout, which generates convection currents that constantly force cold air through the lower entrance and extract warm air through the upper openings. The bats' use of a depression in the roof as opposed to other locations in the corridors may be related to protection from these currents in a thermal trap.

Mayan temples in relatively well-preserved forest matrices are common throughout the study area, and our data shows these bats exploit roosts with diverse conditions. However, few of these temples are occupied by *C. auritus*. In Belize, another *C. auritus* roost was found inside a Mayan archaeological site despite being within an isolated 30 ha forest block (Brigham et al. 2018). This, and the fact that this species makes very little use of agricultural land (Vleut et al. 2019), suggests this species may be able to survive in a small area of well-preserved matrix as long as a suitable roost exists: therefore, care should be taken to preserve access to these matrices around archaeological sites when they are opened to tourist visitation. Future research could focus on comparing the characteristics of Mayan archaeological sites inhabited by this species to other potentially suitable sites where it is absent, as well as with other types of roosts of this species in the area such as caves; on the energetic needs of this bat in relation to its diet and different roosting conditions; and on the extent to which their presence, and the presence of discarded prey remains, may influence conditions inside roosts. These studies will help us better understand how *C. auritus* exploits these unique roosts and, in the context of its threatened status in the region, predict the impact of future habitat fragmentation and archaeological site modification for tourism on this remarkable species.

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