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Dietary variation in a family group of the woolly false vampire Bat (*Chrotopterus auritus*, Phyllostomidae) at the north of its distribution

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Abstract
Carnivorous bats are species that feed on terrestrial vertebrates year-round or seasonally, a food habit observed in four families. Within Phyllostomidae, *Chrotopterus auritus* is one of the largest Neotropical bat species with a diet mainly consisting of small vertebrates. Few studies have detailed the diet of carnivorous bats throughout the year. Here, we recorded the diet of a family group of *C. auritus* weekly during a year in the northernmost location of its distribution, in the Los Tuxtlas region (Mexico). Dietary items were collected from guano in a cave roost. The food items were separated and classified [mammal, bird, insects and unidentified soft-tissue], dried and weighed, and identified to the lowest possible taxonomic level based on morphological characteristics. We recorded each item as a single incidence to calculate frequency and abundance. We estimated prey category diversity using morphospecies richness. Prey morphospecies diversity did not differ between the dry and windy seasons, but both had higher diversity than the rainy season. Mammal remains had the highest biomass (62.41% of sample weight) and were consumed especially during the rainy season, as well as bird remains. Insects peaked in the windy season but were found all year. We found that this group of *C. auritus* preys on vertebrates during its reproductive season and pup-rearing period, while relying on insects as a year-round food source.

Keywords Carnivory · Insects · Birds · Small mammals · Los Tuxtlas

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Introduction

In Chiroptera, carnivory is a feeding habit in which a bat species consumes terrestrial vertebrates year-round or seasonally as the main component of its diet (Wilson 1979; Hill and Smith 1984; Gual-Suárez and Medellín 2021). The families in which carnivorous habits are observed include Phyllostomidae, Megadermatidae, Nycteridae, and Vespertilionidae (Gardner 1977; Wilson 1979; Hill and Smith 1984). Within the Phyllostomidae family, five Mexican species (out of 61 species in the family for the country; Simmons and Cirranello 2025) have vertebrates as significant components of their diets (˃75% of their diet): the Greater False Vampire Bat (*Vampyrum spectrum),* the Woolly False Vampire Bat, (*Chrotopterus auritus*), the Keenan's Hairy-nosed Bat (*Gardnerycteris keenani)*, the Cozumelan Golden Bat (*Mimon cozumelae)*, and Coffin's Bat (*Trachops coffini*) (Gual-Suárez and Medellín 2021).

Chrotopterus auritus, is one of the largest bat species in the Neotropics, with a forearm between 77–83 mm. In comparison, *Vampyrum spectrum's* is between 98–110 mm and *Phyllostomus hastatus* 80–93 mm (Navarro and Wilson 1982; Santos et al. 2003). *Chrotopterus auritus* ranges from southern Mexico to northern Argentina and Paraguay (Barquez et al. 2015). This species typically occurs in small groups composed of a reproductive couple and one or two pups (Medellín 1989; Linares 1998; Ochoa et al. 2005). It occupies a variety of roosting sites, including caves, termite nests, hollow trees, dead trunks and abandoned human structures (Gual-Suárez and Medellín 2021), with roosts reaching up to 30 °C and high humidity levels (Gual-Suárez et al. 2025). The maximum recorded flight distance is 2.06 km, with a total of up to 5.3 km traveled per night (Vleut et al. 2019). Individuals spend approximately five hours outside the roost each night (Vleut et al. 2019). Studies show that its diet primarily consists of small mammals, representing more than 70% of the biomass consumed, and may even include other bat species (Bonato et al. 2004; Nogueira et al. 2007), with no significant dietary differences between sexes (Bonato et al. 2004), it is also categorized as a gleaning animalivorous species (de Oliveira et al. 2017).

Among the species known to be consumed by *C. auritus* are various vertebrates, including rodents (Oryzomyinae; *Ototylomys phyllotis, Heteromys goldmani*, *Reithrodontomys mexicanus*, *Peromyscus oaxacensis*, *P. guatemalensis*, and *Nyctomys sumichrasti*), mouse opossums (*Marmosa* sp.), shrews (*Sorex* spp.), doves (*Columbigallina talpacoti)*, *Knipolegus cabanisi*; geckos (*Thecadactylus rapicaudus*), anurans (possibly Hylidae) (Medellín 1988). There are also reports of *C. auritus* preying on other bats, such as *Glossophaga soricina* (Acosta-Lara 1951), *Carollia perspicillata* (Bordignon 2005; Nogueira et al. 2007), *Peropteryx macrotis* (Bordignon 2005), *Tadarida brasiliensis* (Brito et al. 2010), and *Myotis* sp. (Witt and Fabián 2010). However, most information on the diet of *C. auritus* has been obtained from the stomach contents of isolated specimens (Medellín 1988) and is limited to the southernmost part of its distribution. This suggests that diet components may vary in a study conducted in the northern portion of the species' range, such as the present study, since *C. auritus* may not encounter the same prey species. Moreover, diet plays a key role in the macroecological dynamics of phyllostomid bats due to its relationship with habitat heterogeneity (Carballo-Morales et al. 2024). Bat species with more specialized diets are also more likely to be of conservation concern (Boyles and Storm 2007).

Although carnivorous bats consume both vertebrates and invertebrates (Wilson 1979; Hill and Smith 1984), few studies have detailed their diets, including how the proportions of different animal taxa vary throughout the year. This study presents, for the first time, the annual variation in the diet of *C. auritus*, which is an endangered species in Mexico (SEMARNAT 2010), in the northernmost portion of its range, specifically in the Los Tuxtlas region of Veracruz, Mexico. We monitored a small group of *C. auritus* and documented their diet over the course of a year. We expect that the diet would consist mainly of vertebrates and would be more diverse during the rainy season or during the species' reproductive period. By identifying the food items consumed by this species, we gain insights into its ecological niche (Carvalho et al. 2020) and its vulnerability to habitat transformation, especially in a context where prey for carnivorous bats may vary both geographically and seasonally.

Materials and methods

Study area

Samples were collected in Ejido Adolfo Ruiz Cortines (18° 32′ 40.04″ N, 95° 09′ 2.20″ W, 1082 m), located within the Los Tuxtlas Biosphere Reserve, on the southeastern slope of the San Martín Tuxtla volcano (municipality of San Andrés, Tuxtla) from January 2019 to December 2019. The mean annual temperature in this area is 18 °C, and the mean annual precipitation is approximately 4000 mm (Soto 2004). The study area experiences three seasons; rainy season (June to October); windy season (November to February); and dry season (March to May; Soto 2004; Nogueira et al. 2007). The original vegetation was montane cloud forest, now largely reduced to remnants surrounded by a matrix of secondary vegetation, crops, and cattle pastures (Castillo-Campos and Laborde 2004).

Prey remains collection

Dietary items were collected from guano and prey remains left in a cave roost occupied by a group of specimens of *Chrotopterus auritus,* consisting of a reproductive pair and one or two juveniles, which is typical for this species (Araujo and Machado 2012). No more individuals of this species were registered in any inspection of the cave (or in nearby caves), even during our mist-netting sampling at the three entrances of the cave prior to this study (more than 20 sampling nights over three years before this study). Other bats inhabiting this cave include Mormoopidae (*Mormoops megalophylla, Pteronotus mesoamericanus, Pteronotus fulvus*), Phyllostomidae; (*Artibeus jamaicensis, Artibeus toltecus, Glossophaga mutica, Desmodus rotundus*), Vespertilionidae (*Myotis extremus* and *Myotis elegans*), none of which are carnivorous bat species. Since vertebrate-eating bats tend to leave prey remains (Medellín 1988; Jordan 2005; Felix et al. 2013), we conducted preliminary daytime inspections to locate individual roosting sites within the cave where the *C. auritus* group rested. We identified areas containing food remains and guano directly below perching bats-hereafter referred to as "feeding sites". Over the months leading up to sample collection, we established four feeding sites within the cave, used consistently by *C. auritus* individuals during feeding, where prey remains accumulated beneath them.

We inspected these areas weekly for prey remains and guano containing partially consumed items. At each feeding site, we cleared a 1 m^2 section of the substrate and placed a plastic sheet over it to collect additional material (Whitaker et al. 1981, 2009; Martínez-Fonseca et al. 2022). Two people examined the plastic sheets each week, manually collecting remains and guano using tweezers. Samples were stored in resealable plastic bags containing 70% ethanol (one bag per week) and refrigerated until further analysis (Gardner 1977; McAney et al. 1991; Martínez-Fonseca et al. 2022).

We also recorded field observations when bats were seen perching above the feeding sites, noting the number of individuals, their relative size, and fur coloration to identify juveniles or pups. Sample collection was completed in under five minutes per site using dim red light, minimizing disturbance to roosting bats. Unless directly illuminated by a headlamp, bats rarely responded to the researchers' presence. The most frequent behavior observed was adult individuals "hugging" the juveniles.

Laboratory work

In the laboratory, each bag was cleaned and processed. Ethanol was poured out, and the contents were transferred to Petri dishes and rinsed with distilled water to remove any debris. Food remains were manually separated using tweezers and classified as mammal remains (bones and hair), bird remains (hollow bones and feathers), arthropod exoskeleton parts (Bonato et al. 2004) or unidentified soft tissues. The remains, including soft tissues, were placed in waxed paper bags to dry with silica gel desiccant (Hansson 1970), then weighed using a digital scale (Ohaus Mod. PA214). Samples containing soft tissue were also cleaned with distilled water, weighed, and preserved in 70% ethanol (Whitaker et al. 2009). Due to the fragmented condition of the remains, most items were identified only to morphospecies, limiting taxonomic resolution.

Putative mammal bones, skull fragments, and hair were examined using a stereoscopic microscope and taxonomic guides (Hall and Kelson 1959; Altenbach 1979; Huckaby 1980; Reid 2009; Gardner 2008; Ceballos and Oliva 2002). We compared them with specimens from the Mammal Collection at Universidad Veracruzana to determine the lowest possible taxonomic category. Cusp morphology was measured on the upper and lower teeth, jaws, and palates, and compared with corresponding structures in local mammal specimens. This process was also used to identify other bones, including bat forearms, humeri (evaluating humeral head and epicondyle shape and size), sternum, ribs and vertebrae. Leg and tail remains (with soft tissue, nails and hair attached) were measured, photographed, and compared with taxidermized specimens from the collection, then verified with taxonomic keys. Rodent taxonomy followed Álvarez et al. (2015), while Choate (1973) and Woodman (2018) were used for shrews and bats, with names validated by Díaz et al. (2021) and Da Silva Fonseca et al. (2024). Additionally, several bone clusters were found in fur clumps, suggesting each clump represents an individual. Unclassifiable tissue remains were cleaned, photographed, and stored in vials with 70% alcohol.

Feathers were identified by cross-referencing with the local bird species list, considering features such as the rachis size and shape, tip shape, and plumage color, following Slud (1964), Howell and Webb (1995), Baptista et al. (1997), Johnsgard (1997), Schodde and Manson (1997), Peterson and Chalif (1989), and Howell (2002). Identification guides, including The Taxonomy of Avibase (1766), Cory (1918), and Bernis et al. (1998), were used for scientific naming. Some feathers were identified as juvenile due to their clustering, with bones found within the clumps, suggesting they may belong to the same individual.

Chitinous insect remains (elytra, legs, etc.) were mounted on a 1 cm^2 piece of sulfated cardboard using entomological glue and sorted by morphotype (Whitaker et al. 2009). Identification was performed using morphological characteristics and taxonomic keys (White 1983; Arnett et al. 2002; Leschen et al. 2010).

Data analysis

Weekly samples were weighed and analyzed per season to identify which category had the highest biomass (Kunz et al. 1995; Whitaker et al. 2009; Borloti et al. 2019). In addition, we recorded each observed item (feathers, bones, wings, nails, etc.) as a single occurrence in each category: mammals, birds, insects (i.e., two different feathers were counted as 2 for the "bird" category). These counts were summed per season to determine seasonal abundance (Jordan 2005; Whitaker et al. 2009). We also calculated relative frequency, defined as the number of items of a given taxon divided by the total number of items. Both biomass and frequency data were presented due to the nature of the samples-fragmented remains mixed with fur and feathers- and the inability to separate individual prey items. Frequency-based proportions are indicative rather than precise representations of diet (Jordan 2005).

To compare prey category diversity across seasons, we estimated diversity using Hill numbers: 0D (species richness), 1D (effective number of common prey categories), and 2D (effective number of abundant prey categories) across the three seasons studied (dry, rainy, and windy). These calculations were based on proportional prey category abundances. First, to guarantee a fair comparison among data sets, we assessed sample coverage for each season using the Chao non-parametric estimator (Chao et al. 2014). If 100% sample coverage was not achieved, even with doubled sample extrapolation, we applied standardized sample coverage (Chao et al. 2014). We then estimated 84% confidence intervals from 1000 bootstrap iterations, as they better approximate a 0.05 significance test than 95% intervals (MacGregor and Payton 2013). All calculations were conducted in R using the *iNEXT* package (Hsieh et al. 2020; R Development Core Team 2022).

Results

The composition of the family group of *Chrotopterus auritus* changed throughout the year. Most of the year, a pair of reproductive individuals cohabited with a subadult. However, by the end of the dry season, we observed the presence of a younger pup, bringing the group to four individuals (two reproductive adults, the previous year´s subadult, and the pup; Fig. 1, Video S1). A total of 44 samples were collected (208 food items; Tables 1 and 2), with weekly samples over a year, except in October when no remains were found. Mammals contributed the highest biomass, totaling 26.19 g (62.41% of sample weight), followed by birds with 12.32 g (29.35%), insects with 3.26 g (7.76%), and unidentified remains with 0.42 g (0.42%; Table 1). However, insects (Cerambycidae, Passalidae and Orthoptera) accounted for *ca.* 64% of the total items found (Table 2). Unidentified remains mostly consisted of soft tissues, especially digestive organs (i.e., stomach, intestines and gizzards), along with some hard parts (not bony structures) that were difficult to assign to any specific category. Insect remains included legs and wings, while mammal remains mostly comprised incomplete jaws, palates, worn teeth (Álvarez et al. 2015) and unidentifiable hair. Feathers, although abundant throughout the year, were mostly unidentifiable juvenile feathers.

Mammalian remains identified belonged to the families Soricidae (e.g., Nelson's Small-eared Shrew [*Cryptotis nelsoni*]), Cricetidae (*Nyctomys* sp. [Vesper Rat], *Oryzomys alfaroi* [Alfaro's Rice Rat], *Peromyscus mexicanus* [Mexican Deer Mouse], and *P. leucopus* [White-footed Mouse]), Phyllostomidae (*Artibeus jamaicensis* [Jamaican Fruit Bat], *Desmodus rotundus* [Common Vampire Bat]), and the Mormoopidae family (leaf-chinned bats), which were observed only in September (Figs. 2 and 3; Table 2). Bird feathers from the families Columbidae (pigeons and doves) (determined as *Columbina* sp.), Thraupidae (tanagers) (*Cyanerpes cyaneus*) and Trochilidae (hummingbirds) were also identified (Fig. 4), the former being found across seasons (Table 2). Insect remains included two orders, Coleoptera (beetles) (five families identified) and Orthoptera (no family identification). Orthoptera (crickets and grasshoppers; Fig. 5) were found in seven months, while Coleoptera appeared in eight months (Table 2). Cerambycidae, Passalidae and Orthoptera were present throughout all seasons. The "Other" category contained unclassifiable samples, mostly soft tissues (primarily viscera).

Mammals were consumed throughout the year, with the highest occurrence of mammalian remains in September, coinciding with the rainy season and a decrease in March (Fig. 1). Bird remains were more common in the rainy season, while insect remains peaked in the windy season. Notably, insect consumption spiked in December during the windy season, which overlaps with the mating season (January-August), while insect consumption was absent in August and November (Fig. 1).

Sample coverage during the dry season did not reach 100%, even with doubled sample size extrapolation, so we standardized coverage to 79% across seasons. Prey category richness (0D) was similar between the dry and windy seasons, but both were higher than in the rainy season (Fig. 6). Effective diversity (1D) and dominance (2D) were higher in the windy season compared to the rainy season,

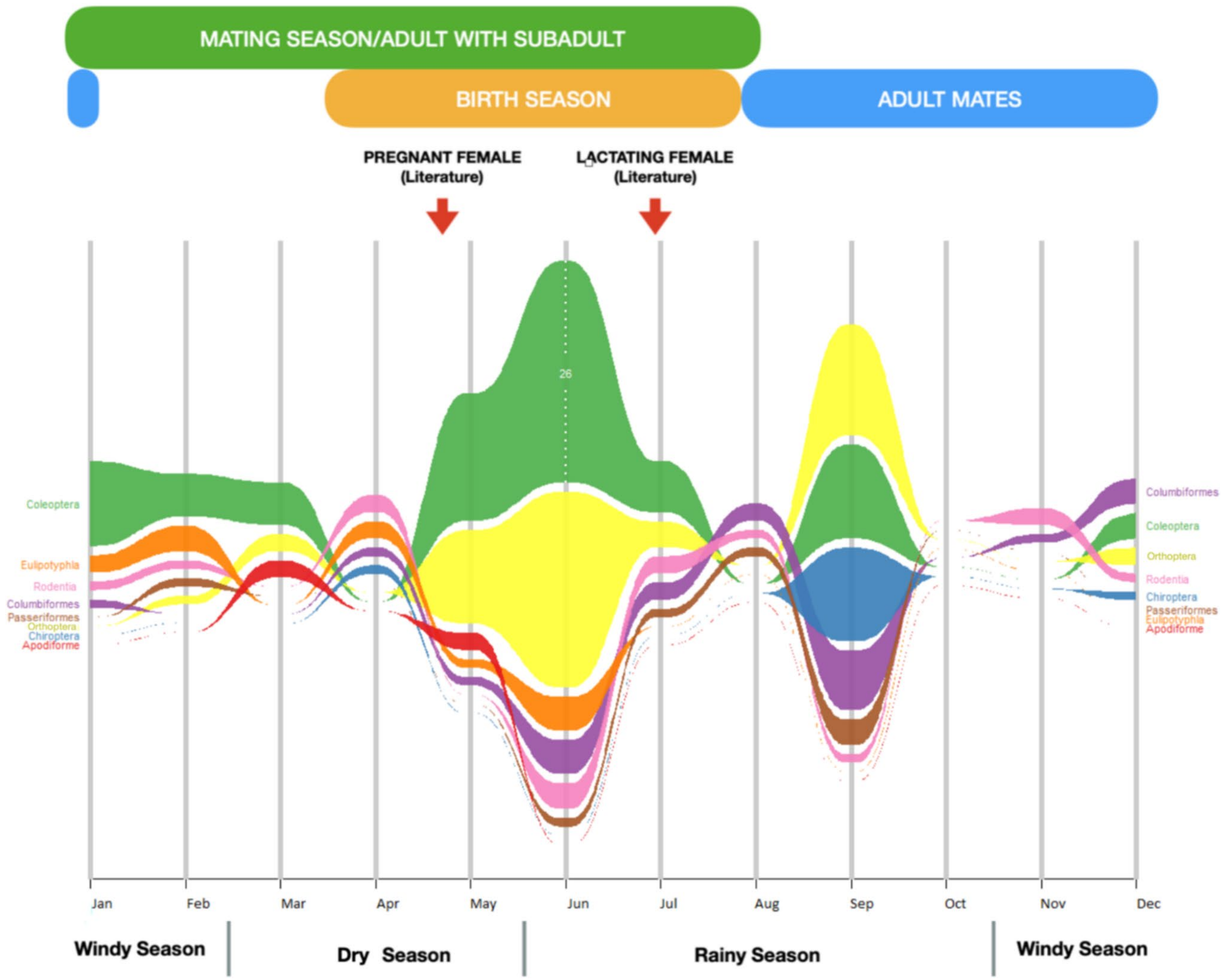


Fig. 1 Alluvial diagram showing the occurrence of prey items in the diet of a group of *Chrotopterus auritus* through a year. Each color represents an order and its occurrence in the diet (each time a prey item in such category was found), by month. The line thickness increases with higher incidence. The figure also depicts the three climatic seasons and the life stages of *C. auritus*, based on our observations and consulted literature (e.g., Wilson 1979; Álvarez et al. 2015)

Table 1 Mean biomass (in g) and error data of the four categories of remains consumed by a family of *Chrotopterus auritus,* categorized by climatic season throughout the year

Item Category	Windy Season	Dry Season	Rainy Season
Mammals	0.40 ± 0.28	0.72 ± 0.51	5.62 ± 5.95
Birds	0.13 ± 0.08	0.42 ± 0.34	2.63 ± 1.97
Insects	0.27 ± 0.32	0.10 ± 0.08	0.47 ± 0.45
Others*	0.02 ± 0.02	0.01 ± 0.01	0.02 ± 0.04

but not significantly different from the dry season. Overall, the diversity analysis indicates that the rainy season has lower values than the dry and windy seasons (Fig. 6).

Discussion

Prey remains found in the refuge of *Chrotopterus auritus* suggest that the diet of the studied group consists mainly of small vertebrates, accounting for nearly 80% of the total dry weight (including hair, feathers, and bones). This aligns with the expectations for a carnivorous bat (Gual-Suárez and Medellín 2021) and with prior reports on *C. auritus* as a predator that primarily consumes vertebrates of various sizes, supplementing its diet with insects year-round (de Oliveira et al. 2017).

Medellin (1989) described *C. auritus* as primarily carnivorous and insectivorous. Reported prey includes lizards, birds (e.g., *Columbina* spp.), small mammals like mouse opossums (*Marmosa* spp.), shrews (*Sorex* spp.), and mice

Table 2 Abundance (number of items in a given category), richness (number of taxa in the season) and relative frequency (percentage of a given taxon in the samples) of the taxa found in the samples and carcasses left by a group of *Chrotopterus auritus* over one year

Item Category	Family	Taxon*	Seasonal abundance of each taxon			Abundance per taxon (relative frequency %)**
			Windy Season	Dry Season	Rainy Season	
Mammals	Phyllostomidae	*Desmodus rotundus* **a,c,d**	1		8	9 (4.33)
		Artibeus jamaicensis **a,b,c,d**	–	–	1	1 (0.48)
	Mormoopidae	Mormoopidae sp. 1 **a,d**	–	–	1	1 (0.48)
	Soricidae	Soricidae spp. **a,b,d**	–	1	1	2 (0.96)
		Cryptotis spp. **a,b,d**	3	1	1	5 (2.40)
		Cryptotis nelson **a,b,d**	2	1	2	5 (2.40)
	Cricetidae	*Rodentia* sp. **a,b**	3	1	1	5 (2.40)
		Peromyscus mexicanus **a,b,c,d**	1	–	2	3 (1.44)
		Peromyscus leucopus **a,b,c,d**	–	–	1	1 (0.48)
		Peromyscus sp. **a,b,c,d**	–	–	1	1 (0.48)
		Nyctomys sp. 1 **a,b,c,d**	1	–	1	2 (0.96)
		Oryzomys alfaroi **a,b,c,d**	–	1	1	2 (0.96)
Birds	Columbidae	Columbidae sp. 1 **a,e**	2	1	9	12 (5.77)
		Columbina sp. **a,e**	4	1	6	11 (5.29)
	Thraupidae	*Cyanerpes cyaneus* **e**	–	–	6	6 (2.89)
	Trochilidae	Trochilidae sp. 1 **e**	1	1	2	4 (1.92)
Insects	Cerambycidae	Cerambycidae sp. 1 **f**	8	9	22	39 (18.75)
	Chrysomelidae	Chrysomelidae sp. 1 **f**	1	–	–	1 (0.48)
	Passalidae	Passalidae sp. 1 **f**	9	10	20	39 (18.75)
	Scarabaeidae	Scarabaeidae sp. 1 **f**	–	–	1	1 (0.48)
	Staphylinidae	Staphylinidae sp. 1 **f**	–	1	–	1 (0.48)
		Orthoptera sp 1 **f**	3	13	39	55 (26.44)
Abundance/season			**39**	**41**	**126**	**208**

*Type of remains used for identification (as bold superindexes): a) bones (mandibles, radius, etc.), b) teeth, c) hair, d) whole body parts (head, limbs, tails), e) feathers, f) exoskeleton pieces (mainly legs) and arthropod wings

**Percentage (in parenthesis, rounded to the upper unit)

(*Heteromys goldmani, Peromyscus oaxacensis, Nyctomys sumichrasti*, and *Ototylomys phyllotis*). Insects consumed include families from the Coleoptera order. Vleut et al. (2019) noted a similar diet, however, this species also consumes some fruits (Uieda et al. 2007; Lintulaakso et al. 2023; Carballo-Morales et al. 2024). Our findings also identified mammals such as *Peromyscus, Oryzomys, Nyctomys*, and *Desmodus* as part of the diet, with insects as the main food category year-round, and birds, particularly chicks. No direct evidence of plant consumption was found. The absence of lizards or larger mammals may be due to differences in species availability between our study and those done in the south of the country (i.e., Calakmul in Campeche and El Triunfo in Chiapas, both with similar vegetation and climate to Los Tuxtlas, but less fragmented forests).

Due to the scattered, incomplete remains found at the roost, we classified most prey at the morphospecies level. The reported biomass reflects only identifiable remains, such as the discarded or rejected parts, including faces, skulls, beaks, bones, limbs, and long feathers. Viscera are also frequently discarded, as reported by Medellín (1989) in his study. Insect remains were mostly legs and wings, while mammal remains were typically fragmented jaws or palates with worn-out teeth, as stated by Álvarez et al. (2015). Feathers were abundant but mostly unidentifiable juvenile feathers. Among the mammal remains, rodent species such as *Oryzomys* and *Peromyscus* were prevalent, consistent with Witt and Fabian's (2010) observations in Brazil, where Rodentia made up 47.61% of the total sample. *Cryptotis nelsoni,* a shrew species endemic to Los Tuxtlas, was found in the diet, marking a new dietary record for *C. auritus.*

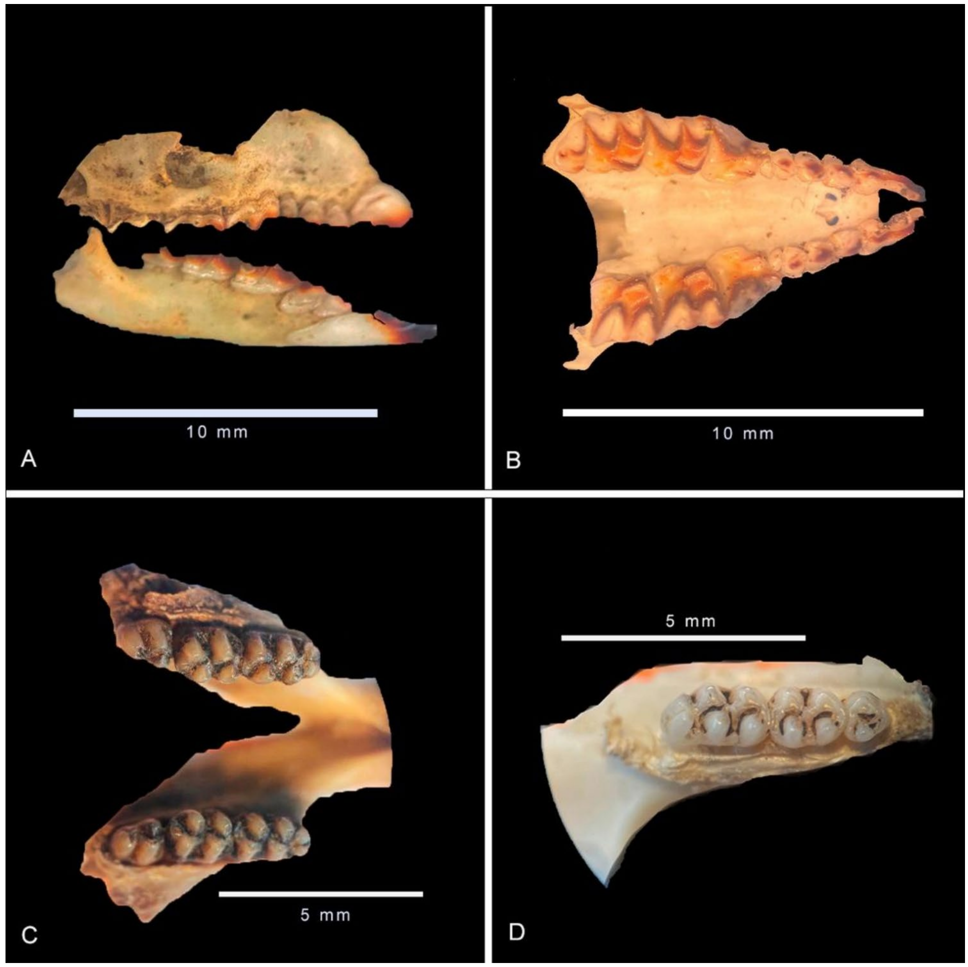


Fig. 2 Cranium remains found among the items preyed upon by the studied *C. auritus* group over one year: **A**) Palate and jaw of *Cryptotis* sp.; **B**) Palate of *Cryptotis* sp.; **C**) Palate of *Peromyscus leucopus*; **D**) Mollar teeth of *Peromyscus mexicanus*

Previously documented prey species included *Glossophaga soricina, Carollia perspicillata*, *Peropteryx macrotis*, *Tadarida brasiliensis*, and *Myotis* sp. (Acosta 1951; Arita and Vargas 1995; Bonato et al. 2004; Bordignon 2005). In this study, we identified a mormoopid bat (likely *Pteronotus mesoamericanus*), *Artibeus jamaicensis*, and *Desmodus rotundus,* all of which share roost with this *C. auritus* group. This supports the idea of *C. auritus* as an opportunistic predator, potentially preying on roost-mates (at least in September).

Three bird groups were identified in the study: Passeriformes (*Cyanerpes cyaneus*), Apodiformes (Trochilidae), and Columbiformes (Columbidae). Medellin (1989) recorded a preference in *C. auritus* for Passeriformes, whereas *Vampyrum spectrum* favors larger bird species. In the studied family group, however, larger bird species were preferred. The most common bird remains were juvenile feathers, suggesting that chicks of various species were included in the diet of this *C. auritus* group, as large clumps of juvenile feathers accounted for 20.18% of the dry weight. In the Los Tuxtlas region, 17 species of columbids have been recorded (Monterrubio et al. 2016), 13 of which are residents (Schaldach and Escalante-Pliego 1997). Feathers found across all three seasons likely belong to one of the 13 resident species in the region. In general, we found an increase in bird occurrence from March to August, mainly coinciding with the mating season of many birds in the study area (P.A. A.-R. pers. Obs.), suggesting that *C. auritus* may be taking advantage of the abundance of young birds. For example, *Cyanerpes cyaneus´* breeding season varies depending on its geographical distribution (Peterson and Chalif 1989; Howell and Webb 1995; Herverth et al. 2016; Hilty 2018). In this study, feathers from this species were observed only during the rainy season (June to October), coinciding with the breeding season of the species reported for Mexico.

Of the 17 Trochilidae species in Los Tuxtlas (Wetmore 1943; Andrle 1967), Toledo (1975) identified 11 as permanent or occasional inhabitants of the study area, with four typically residing within the forest interior. Given that *C. auritus* is linked to conserved areas (Vleut et al. 2019) and may avoid disturbed regions (but still tolerant to habitat perturbation; see Gamboa Alurralde and Díaz 2021), the hummingbirds in its diet are likely *Phaethornis*

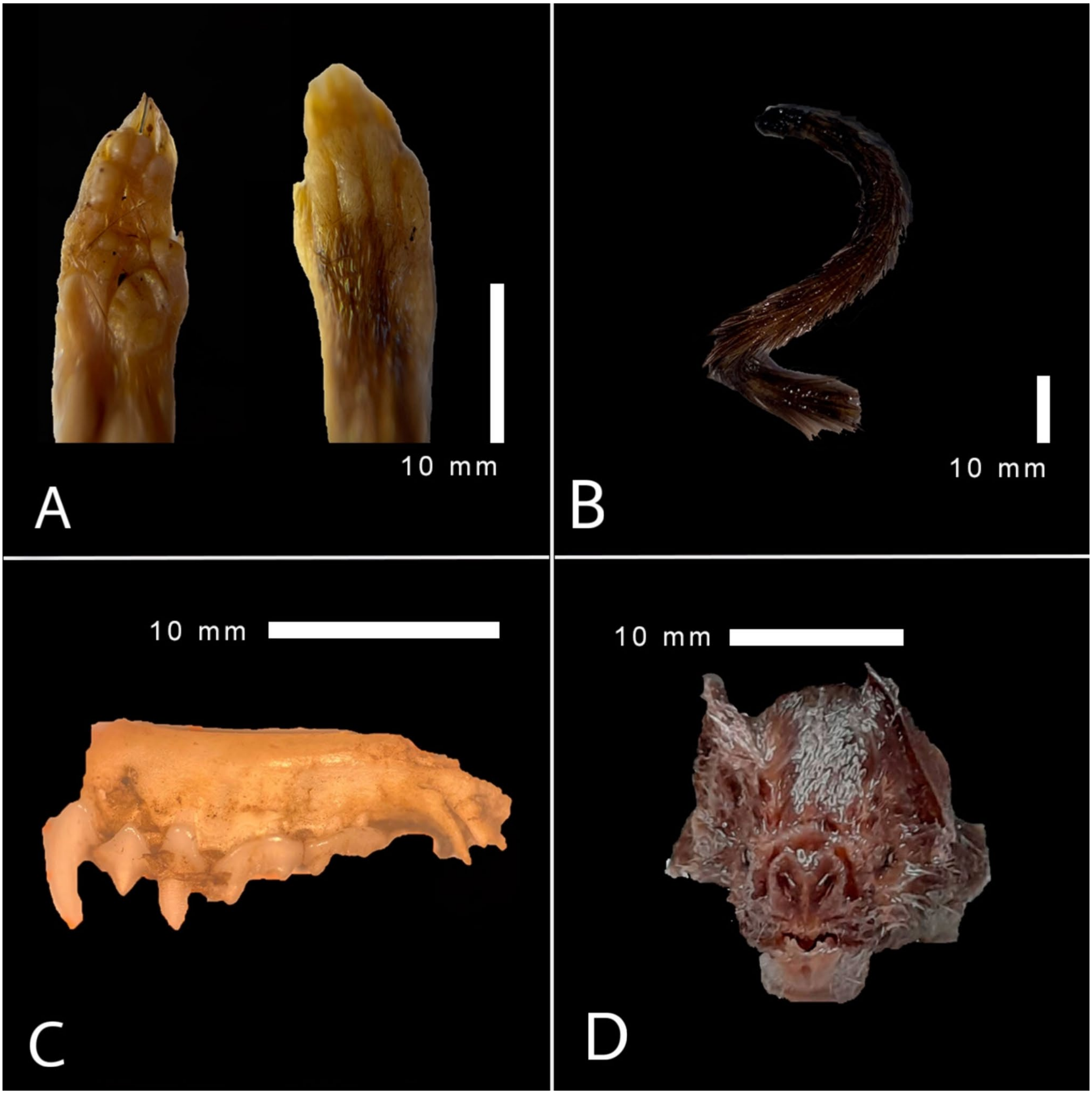


Fig. 3 Mammalian remains found among the prey of a *C. auritus* group: **A**) Dorsal (right) and ventral (left) views of a foot of *Oryzomys alfaroi*; **B**) Severed tail of *Nyctomys* sp.; **C**) Superior teeth of *Artibeus jamaicensis*; **D**) Frontal view of a severed head of *Desmodus rotundus*

superciliosus, Campylopterus, Amazilia tzacat, or *Campylopterus curvipennis.*

Comparing the diet of *C. auritus* with its relative *Vampyrum spectrum*, prey sizes for the latter range from 20 to 150 g (Vehrencamp et al. 1977), overlapping with the *C. auritus* range of 10 to 35 g, and up to 70 g (Medellín 1988). *V. spectrum* typically captures larger avian prey and some bats (McCarthy 1987), while *C. auritus* primarily consumes rodents and small birds, rarely preying on bats (Medellin 1989). This study reflects this pattern, with bat remains found only in September.

Regarding seasonal variation, we observed the highest abundance of food items during rainy season (Table 2). Bats' diets may reflect prey availability (Burles et al. 2008), especially during rainy season (Bonaccorso 1979; Nurul-Ain et al. 2017). Additionally, previous studies show bats change their diet during pregnancy and lactation (Kunz 1974; Anthony and Kunz 1977; McLean and Speakman

Fig. 4 Some feathers found among the food remains in the studied *C. auritus* group: **A**) Feather of *Columbina* sp.; **B**) Feathers of Columbidae; **C**) Feathers of *Cyanerpes cyaneus;* **D**) Feather of Trochilidae

1999; Haarsma et al. 2023). Lactating females also require more calcium (Kovacs and Kronenberg 1997), and insects are poor sources of this mineral (Booher and Hood 2010).

Mammal intake remained consistent year-round in this study, while bird consumption rose during dry and rainy seasons, corresponding with pregnancy and lactation, and dropped in the windy season; this could also be due to the reproductive seasons of these bird species (Fig. 1). Insect remains were more abundant in the rainy season (higher dry weight) and more diverse in the windy season. Insectivorous bats consume more insects during the breeding season due to high energy demands (Arango-Diago et al. 2020), and this reasoning can be applied to *C. auritus's* breeding season. The species has a gestation period of approximately seven months (Taddei 1976), with mating estimated between August and September (the rainy season at the study site) (Álvarez et al. 2015, 2018) and births in April and May (dry season at the site) (Wilson 1979; Álvarez-Yax et al. 2018).

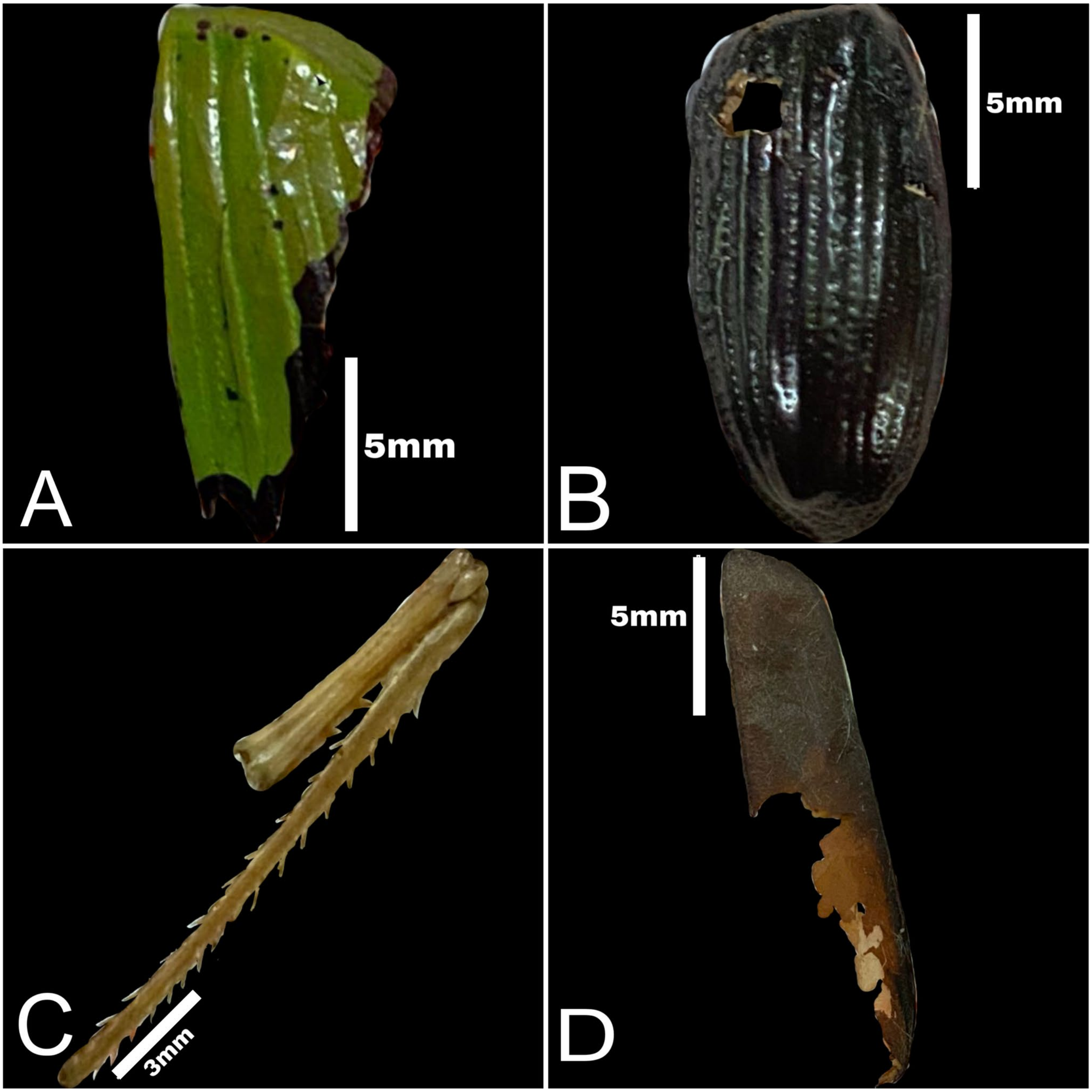
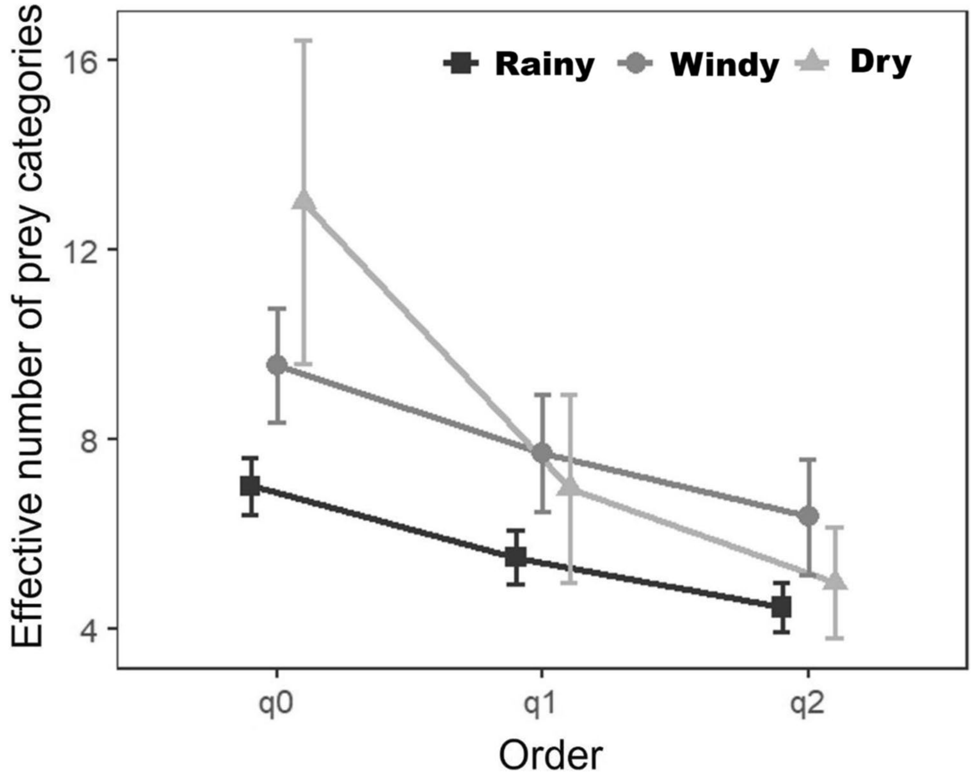


Fig. 5 Insect remains found among the items consumed by the studied *C. auritus* group: **A**) Elytra of Scarabaeidae; **B**) Wing of Passalidae; **C**) Leg of Orthoptera; **D**) Elytra of Cerambycidae

Results show an increase in dry-weight biomass during the rainy season (83.37% of the total sample), though this coincides with the lowest 0D diversity by category (i.e., fewer morphospecies). Additionally, the rainy season had the highest mammalian remains and coincided with observations of a lactating female in the group (May to July; Fig. 1), possibly reflecting increased intake to support the energy needs of lactation (Kunz et al. 1995). Prey items variability may also be related to the age and handling experience of juveniles. By our sampling design, we were unable to distinguish between preys consumed by adults and by juveniles, but Phyllostomid bats, including carnivorous species, learn prey selection and handling from their mothers (Vehrencamp et al. 1977; Patriquin and Ratcliffe 2023), and juveniles tend to consume smaller and easier-to-capture prey (Aldasoro et al. 2024). Bigger prey remains (like full heads and forearms from *Desmodus* and *Artibeus* bats) were present in the samples after the rearing of the small pup.

Fig. 6 Diversity of prey from *Chrotopterus auritus* in the three seasons for effective species in the orders: q0 (richness), q1 (abundant species) and q2 (very abundant species). Diversity of prey items peaks in the dry season, in all three components



This study, which examined a single-family group of up to four *C. auritus* individuals (a mating pair and two juveniles; Video S1), provides the first year-long analysis of dietary remains for this species. It also represents the northernmost diet report for *C. auritus*, documenting new food items not previously recorded in other areas, including *Cryptotis nelsoni*, endemic to the area. Furthermore, species such as *Peromyscus mexicanus, Peromyscus leucopus, Oryzomys alfaroi,* and *Cyanerpes cyaneus* were added to the known diet of *C. auritus*. Few studies address carnivorous bat diets across geographic areas, though some Phyllostomidae show dietary shifts across regions (e.g., species within *Trachops cirrhosus* complex and *Artibeus jamaicensis*; Tuttle and Ryan 1981; Kalko et al. 1996; Bonato and Facure 2000; Estrada et al. 1984; Ortega and Castro-Arellano 2001; Genoways et al. 2005; Lobova et al. 2009). Geographic variation in prey availability may also apply to *C. auritus,* as evidenced by prey differences within its distribution range, such as the predation of *C. nelsoni*, exclusively in Los Tuxtlas.

Our results confirm that *C. auritus* is a carnivorous bat in this region, relying on small vertebrates, mainly birds and mammals, for over 70% of its diet. Additionally, the diet of *C. auritus* varies throughout the year, likely reflecting the reproductive cycles and availability of its prey. These changes lead to increased consumption of certain organisms due to high energy demands and fluctuations in resource availability, aligning with previous studies on carnivorous bats and *C. auritus.* Unlike the southern populations of *C. auritus* in Mexico, where multiple roosts are known (Vleut et al. 2019; Gual-Suárez et al. 2025), this is the only known roost in Los Tuxtlas. Additional studies in other roosts and months, ideally incorporating DNA analysis from guano and prey remains, would help determine whether these dietary trends are consistent across the species´range.

It was expected that the rainy season would show the highest dietary diversity compared to the dry and windy seasons. However, this was not confirmed, as there was no significant difference in dietary diversity between the three seasons. Still, the rainy season did record the highest biomass in grams, indicating that during this season, *C. auritus* consumes a larger quantity of food but from a more limited range of species, suggesting a selective diet. For component q0, the most prevalent species appeared in the dry season; for q1 and q2, the most prevalent species were recorded during the windy and dry seasons. Overall, the rainy season had the lowest prevalence of certain species, suggesting that *C. auritus* consumes more common species in the rainy season, while in the dry and windy seasons, it may opportunistically consume rarer species when available.

Trophic guild and niche breadth reflect habitat heterogeneity and are related to extinction risk in Phyllostomidae (Carballo-Morales et al. 2024). Therefore, understanding diet is crucial for conservation, particularly in heavily deforested regions like Los Tuxtlas (Dirzo and García 1992; Von Thaden et al. 2018). This study also reflects the species´plasticity and its potential to persist in small patches of well-preserved forest matrix, provided suitable roosts (Vleut et al. 2019; Gual-Suárez et al. 2025) and prey are available (but see Shaw et al. 2013). The presence of *C. auritus*, a top-level predator, suggests the continued presence of its prey and indicates a functioning ecosystem.

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Data availability The data that supports the findings of this study is available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare that they have no conflict of interest.

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