

# Therya

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AMMAC

La portada

Murciélago vampiro de patas peludas (*Diphylla eucaudata*) se localiza principalmente en la vertiente del Golfo de México hasta Sudamérica. Se considera que se alimenta principalmente de la sangre que extrae de diferentes tipos de aves. Dentro de las especies de vampiros no se considera la más abundante de las tres existentes (foto de Sergio Ticul Álvarez-Castañeda).

Nuestro logo "Ozomatli"

El nombre de "Ozomatli" proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimer en la cosmogonía mexicana. "Ozomatli" es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. " Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo."

# Therya

Volumen 12, número 3

septiembre 2021

## Contenido

### EDITORIAL

#### Divulgación de la mastozoología

Alina Gabriela Monroy-Gamboa 389

### ARTICLES

#### A new species of *Eptesicus* (Mammalia: Chiroptera: Vespertilionidae), from the sub-Andean Forest of Santa Cruz, Bolivia

Luis H. Acosta S., José Luis Poma-Urey, Paula A. Ossa-López, Fredy A. Rivera-Páez, and Héctor E. Ramírez-Chaves 391

#### Mitochondrial DNA indicate paraphyletic relationships and resolve disjunct distributions in the *Neotoma mexicana* species group

Giovani Hernández-Canchola, Livia León-Paniagua, and Jacob A. Esselstyn 411

#### Relative abundance and habitat selection of the montane guinea pig *Cavia tschudii* in a wetland at coastal desert with comments on its predators

Manuel Quispe-López, Sue Barreda, Diego Marcelo-Carranza, Víctor Pacheco, Héctor Aponte, and Dámaso W. Ramírez 423

#### Characterization of assemblages in neotropical cave dwelling bats based on their diet, wing morphology, and flight performance

Fernando Salgado-Mejía, Ricardo López-Wilchis, Luis M. Guevara-Chumacero, Pedro L. Valverde-Padilla, Pablo Corcuera Martínez del Río, Sergio L. Porto-Ramírez, Ixchel Rojas-Mertínez, and Gihovani A. Samano-Barbosa 435

#### The Big Naked-backed Bat, *Pteronotus gymnotus*, Chiroptera, Mormoopidae, in its northernmost geographic distribution range

Ricardo Lopez-Wilchis, Aline Méndez-Rodríguez, Javier Juste, Juan Luís García-Mudarra, Fernando Salgado-Mejía, and Luis Manuel Guevara-Chumacero 449

#### Mammals of the Natural National Park Selva de Florencia, Caldas, Colombia

Héctor E. Ramírez-Chaves, Daniela Velásquez-Guarín, Juan D. Ocampo-Velásquez, Ingrith Yuliany Mejía-Fontecha, Amilvia E. Acosta, Javier E. Colmenares-Pinzón, John Harold Castaño, and Néstor Roncancio Duque 461

<b>The ghost mammals from Mexico and their implications</b>	477
Alina Gabriela Monroy-Gamboa	
<b>Habitat heterogeneity facilitates coexistence of two syntopic species of <i>Peromyscus</i> in a temperate forest of Central México</b>	487
Ivan M. De-la-Cruz, Alondra Castro-Campillo, and Arturo Salame-Méndez	
<b>Identification keys to murid rodents of Argentina</b>	501
Pablo Teta, and J. Pablo Jayat	
<b>Coexistence of three mephitids in Tehuacán-Cuicatlán Biosphere Reserve, México</b>	527
Verónica Farías-González, and Karen Haydee Hernández-Mendoza	
<b>Mammal species richness and new records in protected natural areas of the northern part of the metropolitan area of the Valley of México</b>	537
Yolanda Hortelano-Moncada, Asela Samari Barragán-Saldaña, Jesús R. Fernández-Reyes, Fernando A. Cervantes, Leonardo Barragán Guerrero, and M. Vianey Gómez-Naranjo	
<b>Spatial ecological interactions between coyote and gray fox in a temperate forest</b>	553
César R. Rodríguez-Luna, Jorge Servin, David Valenzuela-Galván, and Rurik List	
<b>Relationship between age-sex classes and prevalence of <i>Giardia</i> spp. and <i>Blastocystis</i> spp. in black and gold howler monkeys inhabiting fragmented forests</b>	563
Rumesilda Eliana Alegre, María Sol Gennuso, Francisca Milano, and Martin Kowalewski	
<b>Use of distribution models in the conservation of a Mexican endemic lagomorph</b>	571
Luis José Aguirre-López, and Tania Escalante	
<b>Ethological studies of native Mexican mammals: A review</b>	583
Elaine Mariana Méndez-Muñiz, Michael Jowers, Samer Angelone, and Luis Manuel Guevara-Chumacero	
<b>Use of mineral licks by mammals in areas of the Amazonia with no hunting pressure</b>	599
Patricio Macas-Pogo, and María Cristina Osorio Sánchez	
<b>THERYA y AMMAC</b>	
<b>Corrigendum: Morphological differentiation of <i>Peromyscus leucopus</i> and <i>P. maniculatus</i> in East Texas</b>	609
Jessica E. Light, Leila Siciliano-Martina, Emma G. Dohnalik, Grace Vielleux, David J. Hafner, A. Michelle Lawing, and Ira F. Greenbaum	

fascículo 36 <http://www.revistas-conacyt.unam.mx/therya/index.php/THERYA/issue/view/39>

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## Divulgación de la mastozoología

Es común que se confunda la divulgación y la difusión o que se usen de manera indiferente, pero en realidad existe una gran diferencia que vale la pena aclarar. La difusión es dispersar o esparcir la información. Mientras que la divulgación científica consiste hacer llegar el conocimiento de una manera sencilla y concisa a la población en general. De manera que la divulgación lleva implícita la difusión, pero la difusión no siempre es divulgada, porque se puede difundir información en lenguaje muy técnico que la gente no especializada en el tema no siempre va a entender, como ejemplo son los artículos científicos que contiene esta revista.

La divulgación de la ciencia es una actividad relativamente nueva, en el país su mayor auge comenzó en la década de los 80s. En 1986 se crea la Sociedad Mexicana para la Divulgación la Ciencia y la Técnica, A. C. (Somedicyt) y comienzan a abrir más y nuevos espacios. Se tienen diferentes maneras de divulgar. La manera oral fue la original debido a que el conocimiento se fue transmitiendo de boca en boca, así la gente puede aprender a hacer ciertas cosas, como puede ser una receta sencilla o a germinar una semilla. Otros modos de divulgación oral son por medio de programas de radio o televisión, conferencias, pláticas o entrevistas a una audiencia no especializada. Hoy en día los videos publicados en diversas plataformas de internet o redes sociales han incrementado la divulgación. Los museos son el mejor ejemplo de divulgación científica, en ellos los visitantes aprenden sobre temas diversos y muy complejos, pero al brindar los contenidos de manera sencilla, toda la gente que acude puede aprender algo. Los medios que más influyen y ayudan a tener una mayor difusión son los escritos, originalmente como impresos (boletines, libros, periódicos, revistas, trípticos, entre otros) y en la actualidad digitales (blogs, infografías, libros digitales y revistas).

La explosión de los medios digitales se ha incrementado en la actualidad, lo que ha provocado que exista una gran cantidad de información científica disponible sobre diversos temas, pero no siempre tienen un contenido fundamentado o científico. Los contenidos se pueden difundir masivamente, lo que provoca que la gente pueda tener mayor cantidad de información, pero muchas veces puede ser errónea. Los niños y jóvenes, consultan con frecuencia el internet para hacer sus tareas, incluso durante las clases presenciales y con la posibilidad de poder ir a una biblioteca, prefieren hacer sus consultas por internet, debido a la rapidez, facilidad de búsqueda y gran cantidad de contenido. El problema, es que no buscan las fuentes originales o fuentes fidedignas (revisadas por expertos), entonces asumen como verdad toda la información que encuentran.

Otro problema, es que en ocasiones los que desarrollan los contenidos, no son expertos en el tema, debido a que a los científicos en ocasiones les resulta complicado comunicar los resultados y descubrimientos de sus investigaciones o explicar en lenguaje sencillo y no técnico sus conocimientos, para que estén al "alcance" de la población en general. Adicionalmente, esta actividad es poco valorada, no siempre es evaluada en los sistemas institucionales y en consecuencia siempre hay un déficit presupuestal para poder realizarla y los expertos pierden el interés en realizarla.

Es importante que el conocimiento llegue a la mayor cantidad de gente posible, pero siempre se debe tener claridad desde un inicio a quién estará dirigido el contenido de la información, porque en ese tenor será el lenguaje usado. El divulgador tiene que conocer ampliamente el tema, para que pueda expresar correctamente y de manera simple los conocimientos a una diversidad de público receptor. Las principales características de los contenidos de divulgación científica es que la información debe ser de lectura agradable, puntual, concisa, explicada en pocas palabras para no perder la atención de quienes están recibiendo la información, de este modo el aprendizaje resulta más sencillo y eficiente. En el caso de la divulgación científica escrita, no se debe dejar de lado la formalidad de una buena escritura (consultar fuentes científicas, tener buena ortografía y puntuación, estructura, no ser redundante en las ideas que se plasman, etc.).

En México una de las revistas más representativas de la divulgación científica y además fue de las primeras en surgir, fue el Boletín de la Sociedad Mexicana de Física, que después de algunos cambios de nombre en 1969, se convierte en la revista "Naturaleza" que se publicó durante 15 años. Actualmente, existe el Índice de Revistas Mexicanas de Divulgación Científica y Tecnológica, administrado por la Comisión Nacional de Ciencia y Tecnología (Conacyt), en el que aparecen 18 revistas, con temas de ciencia en general o multidisciplinarias, solamente tres de ellas son de temas especializados (ciencias sociales y humanidades, inteligencia artificial y robótica y psicología). Existen pocas opciones de medios consolida-

dos y serios para que los investigadores divulguen sus conocimientos y muchas menos opciones cuando se trata de temas especializados como lo es la mastozoología. No existe en el país una revista específica sobre ciencias naturales y menos de mamíferos que contribuya a que la población en general, niños y jóvenes puedan consultar y aprender sobre ellos.

Sería de gran utilidad a la sociedad en general, que académicos y estudiantes en formación contaran con un medio digital donde pudieran divulgar sus conocimientos, descubrimientos y aportaciones en el área de los estudios relacionados con los mamíferos. Es por ello que se debe de contar con una revista formal que impulse la divulgación de las ciencias con una fuerte base científica y de difusión internacional.

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# A new species of *Eptesicus* (Mammalia: Chiroptera: Vespertilionidae), from the sub-Andean Forest of Santa Cruz, Bolivia

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Bats of genus *Eptesicus* are represented in South America by nine species of short-eared taxa (subgenus *Eptesicus*), and 10 species of long-eared species (subgenus *Histiotus*). Here we describe a new species of short-eared *Eptesicus* based on 19 specimens collected in the sub-Andean Bolivian-Tucumani forest of Santa Cruz, between 1800-2020 masl. For this, we include morphological, morphometric, and molecular comparisons; we use principal component, discriminant function and mitochondrial genes (cytochrome-*b*, cytochrome *c* oxidase subunit I, and nicotinamide adenine dinucleotide dehydrogenase) to compare the new species with other taxa of the subgenus *Eptesicus* from South America. The new species is distinguished from its congeners by cranial shape, body measurements, and genetic distances. Furthermore, the new species is similar in cranial morphology to *Eptesicus andinus* but presents a highly developed frontal preorbital process, poorly developed in other related species (*i. e.*, *E. andinus*, *E. furinalis*, and *E. brasiliensis*). All males were consistently darker than females in the new species. This taxon increases to 10 the number of species of bats of the subgenus *Eptesicus* in South America.

Los murciélagos del género *Eptesicus* en Sudamérica están representados por nueve especies de murciélagos de orejas cortas (subgénero *Eptesicus*) y 10 especies de orejas largas (subgénero *Histiotus*). Describimos una nueva especie de *Eptesicus* de orejas cortas, con base en 19 especímenes, que fueron colectados en el Bosque Boliviano-Tucumano del subandino de Santa Cruz, entre los 1800-2020 msnm. Para esto, incluimos comparaciones morfológicas, morfométricas y moleculares; utilizamos los análisis de componente principal, función discriminante y genes mitocondriales (citocromo-*b*, citocromo *c* oxidasa subunidad I y nicotinamida adenina dinucleótido deshidrogenasa) para comparar la nueva especie con otros taxones del subgénero *Eptesicus* de Sudamérica. La nueva especie se distingue de sus congéneres por su forma craneal, medidas corporales, dicromatismo sexual notable y las distancias genéticas. Además, la nueva especie es similar en la morfología craneal con *Eptesicus andinus*, pero esta presenta un proceso preorbital frontal muy desarrollado el cual es pobremente desarrollado en las especies relacionadas (*i. e.*, *E. andinus*, *E. furinalis* y *E. brasiliensis*). Todos los machos en la nueva especie fueron evidentemente más oscuros que las hembras. Este nuevo taxón aumenta a 10 el número de las especies del subgénero *Eptesicus* en Sudamérica.

**Keywords:** Andes; cryptic diversity; *cyt-b*; COI; *Histiotus*; morphology; ND1.

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## Introduction

The genus *Eptesicus* Rafinesque, 1820 in South America comprises 19 species. These 19 species are grouped into two subgenera. The subgenus *Eptesicus* includes nine species and several subspecies (Miranda *et al.* 2006; Davis and Gardner 2008; Díaz *et al.* 2016; Sánchez *et al.* 2019): *Eptesicus andinus* Allen, 1914 (monotypic), *Eptesicus brasiliensis* (Desmarest, 1819; with four subspecies), *Eptesicus chiriquinus* Thomas, 1920 (monotypic), *Eptesicus diminutus* Osgood, 1915 (with two subspecies), *Eptesicus furinalis* (d'Orbigny and Gervais, 1847; with two subspecies), *Eptesicus fuscus* (Palisot de Beauvois, 1796; one subspecies), *Eptesicus innoxius* (P. Gervais, 1841; monotypic), *Eptesicus taddeii* Miranda, Bernardi and Passos 2006 (monotypic), and *Eptesicus ulapeensis* Sánchez, Montani, Tomasco, Díaz and Barquez 2019

(monotypic). The subgenus *Histiotus* endemic to South America includes the other 10 species (Rodríguez-Posada *et al.* 2021). *Histiotus* has been considered by some authors as a subgenus of *Eptesicus* (Hooper and Van Den Bussche 2003; Giménez *et al.* 2019; Simmons and Cirranello 2020), but this suggestion has not been followed by other authors (see Burgin *et al.* 2018; Moratelli *et al.* 2019; Barquez and Díaz 2020). Historically, Neotropical bats of the subgenus *Eptesicus* have been defined as species complexes based on fur variability. For example, Davis (1966) identified three long-haired species: *E. andinus* with two subspecies (*E. inca* and *E. chiriquinus*), *E. montosus* with two subspecies (*E. montosus* and *E. chiralensis*), and *E. fuscus* (monotypic). However, Simmons and Voss (1998) reviewed the holotypes of *E. andinus* and *E. chiralensis* and topotypic

specimens of *E. inca* and *E. chiriquinus*, concluding that *E. chiralensis* and *E. andinus* are conspecifics and similarly, *E. inca* and *E. chiriquinus* are also conspecific with *E. chiriquinus* having priority over *E. inca*. [Simmons and Voss \(1998\)](#) suggested that *E. andinus* and *E. chiriquinus* can be differentiated by skull shape and the arrangement of the sagittal and nuchal ridges, as well as differences in size (*E. chiriquinus* tends to be larger than *E. andinus*).

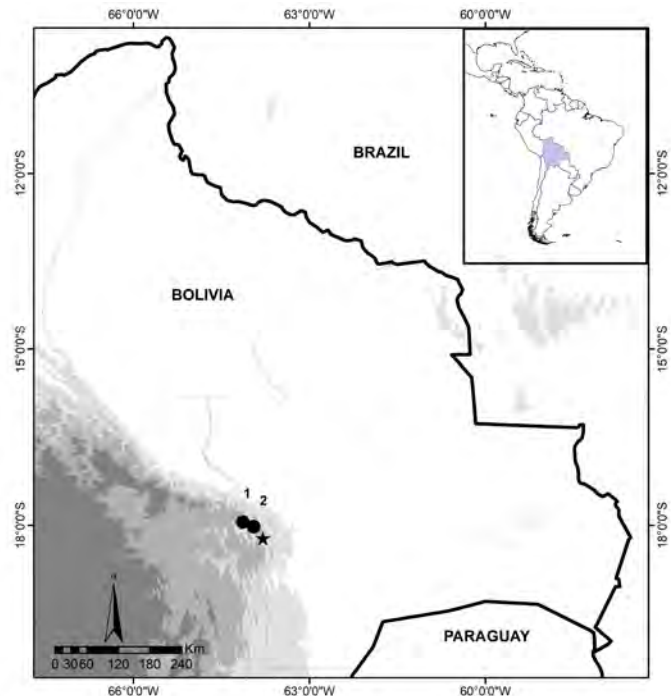
Five species of the subgenus *Eptesicus* currently occur in Bolivia: *E. andinus*, *E. brasiliensis*, *E. chiriquinus*, *E. diminutus*, and *E. furinalis* ([Anderson 1997](#); [Siles 2007](#); [Vargas-Espinoza 2007](#); [Aguirre et al. 2010, 2019](#); [Poma-Urey et al. 2019](#)); being one of the countries with the highest diversity of the subgenus in South America. Despite that, there are several, information gaps related to the distribution and richness of the genus remain ([Poma-Urey et al. 2019](#)). Here, we describe a new species of the subgenus *Eptesicus* based on 19 specimens collected in the sub-Andean Bolivian-Tucumanian forest of Santa Cruz, and by comparisons with specimens from other localities of South America. The new species is morphologically similar to *E. andinus* but can be differentiated from *E. andinus* and its congeners by genetic distances, discrete morphological and morphometric traits.

## Material and Methods

A total of 19 specimens of bats of subgenus *Eptesicus* were collected during field trips between 2007 and 2013 in two localities in the Province of Florida, Santa Cruz Department, Bolivia (Figure 1). To assess their specific identity, 131 specimens belonging to five species of *Eptesicus* with confirmed presence in Bolivia were also examined: *E. andinus* ( $n = 39$ ), *E. brasiliensis* ( $n = 5$ ), *E. chiriquinus* ( $n = 21$ ), *E. diminutus* ( $n = 10$ ), and *Eptesicus furinalis* ( $n = 56$ ). The specimens reviewed are housed at the following institutions: American Museum of Natural History, New York, USA (AMNH); British Museum Natural History, London, England (BMNH); Colección de Mamíferos Lillo, Tucumán, Argentina (CML); The Field Museum of Natural History, Chicago, USA (FMNH); the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (ICN); Noel Kempff Mercado Natural History Museum, Santa Cruz, Bolivia (MHNNKM); Museo de Historia Natural Universidad del Cauca, Popayán, Colombia (MHNUC); Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia (MHN-UCa); Museo Universidad Distrital Francisco José de Caldas, Bogotá, Colombia (MUD); Colección Teriológica Universidad de Antioquia, Medellín, Colombia (CTUA); Colección Mastozoológica Universidad del Valle, Cali, Colombia (UV), and the National Museum of Natural History, Washington, DC., USA (USNM; Appendix 1).

Several external, and cranial characters described in the literature ([Simmons and Voss 1998](#); [Davis and Gardner 2008](#); [Díaz et al. 2016](#)) were analysed in all the specimens reviewed, including the development of the sagittal and lambdoidal ridges, and the length and colour of the coat hairs (according to [Ridgway 1912](#)), and compared with the information provided in the literature (e. g., [Davis 1966](#)).

**Morphometric analysis.** Nineteen cranio-dental measurements from 149 specimens were explored. These measurements included: greatest length of the skull (GLS), condylo-canine length (CCL), basicranial length (BL), palatal length (PAL), postorbital constriction (POC), braincase height (BCH), braincase breadth (BCB), mastoid breadth (MB), zygomatic breadth (ZB), interorbital breadth (IOB), breadth across canines (C-C), breadth across upper molars (M3-M3), maxillary toothrow length (C-M3), incisive length-M3 (I-M3), upper molariforms length (P-M3), lower canine-m3 length (c-m3), lower molariforms length (p-m3), mandibular length (MAL), mandibular height (MH; [Simmons and Voss 1998](#); [Ramírez-Chaves 2008](#)). We also took seven external measurements (the first two from labels) including: total length (LT), length of tail (TL), length of hind foot (LF), length of ear (EL), length of forearm (FA), and two from the hairs: length of dorsal hair (PD) and length of ventral hair (PV). The cranio-dental measurements were taken with a 0.01 precision digital calliper, and then Log transformed for further normalization and analyses. To show the main measurements that separate the species into different groups, the data of the first two principal main components (PCA) were selected. To define the variability between the groups provided by the first two main components, a Discriminant Function Analysis (DFA; [Brown and Wicker 2000](#)) was performed, considering the first two DFAs. For both the PCA and DFA analyses, due to completeness only 14 cranio-dental measurements were used (GLS, BCH, BL, PAL, P-M3, MB, M3-M3, C-C, I-M3, C-M3, CCL, IOB, POC, BCB), and the analyses were calculated using the software PAST ver-



**Figure 1.** Collecting sites for *Eptesicus langeri* sp. nov. in South America. Municipalities of Samaipata and Pampagrande, Province of Florida, Department of Santa Cruz, Bolivia. Agua Rica Type locality (star), Reserve Municipal El Chape (circle 1) and Agua Clarita (circle 2).

sion 2.17c for Windows platform (Hammer et al. 2001). The PCA and DFA included four similar-sized species of *Eptesicus* (*E. andinus*, *E. brasiliensis*, *E. chiriquinus*, and *E. furinalis*), the holotypes of *E. montosus* Thomas, 1920, and *E. chiralensis* Anthony, 1926 (considered both junior synonyms of *E. andinus*), one smaller species (*E. diminutus*), and the 19 specimens of the Province of Florida in Bolivia. We also calculated the cranial index (CRI =  $((\text{POC} + \text{BCB}) \times \text{GLS})/2$ ) and the maxillary index (MXI =  $((\text{C-C} + \text{M3-M3}) \times \text{C-M3})/2$ ) (Baud and Menu 1993).

**Molecular analyses.** We extracted genomic DNA from muscle tissues preserved in 96 % ethanol from five specimens of *Eptesicus* collected in the sub-Andean Bolivian-Tucumanian forest of Bolivia, and two *E. andinus*, one *E. chiriquinus*, and one *E. furinalis* from Colombia. DNA were extracted using Wizard® Genomic DNA Purification kit (Promega Corporation) following the manufacturer's protocol. Amplification of three mitochondrial genes was done as follows: the amplification of cytochrome-b (*cyt-b*) gene was performed using two pairs of primers. First pair of primers L14816: 5'-CCATCCAACATCTCAGCATGATGAAA-3' and H15173: 5'-CCCCTCAGAATGATATTTGTCCTCA-3' which amplifies a  $\approx 358$  bp fragment (Parson et al. 2000), and the other pair of primers LGL765F: 5'-GAAAAACCAAYCGTTGT-WATTCAACT-3' (Bickham et al. 1995) and LGL766R 5'-GTT-TAATTAGAATYTYAGCTTTGGG-3', targeting a  $\approx 1140$  bp fragment (Bickham et al. 2004). Amplification of nicotinamide adenine dinucleotide dehydrogenase (ND1) gene using primers ND1-Forward 5'-CGCCATTATATGATCAGGAT-GAGCC-3' and ND1-Reverse 5'-GTWGAGATRAATCATAT-TAT-3' which amplifies a  $\approx 293$ -295 bp fragment (Hamilton et al. 2015). The cytochrome c oxidase subunit I (COI) gene was amplified using the primer pair MCOIF 5'-CTGTA-CTAGATTTACAGTCTAATGCC-3' and MCOIR 5'-CCAAAGC-CAGGCAAATTAATAATA-3', which amplify a fragment of approximately 657 bp (Sánchez et al. 2019). The final amplification reaction volume was 30  $\mu\text{L}$ , which contained 16.84  $\mu\text{L}$  ultrapure water, 6  $\mu\text{L}$  5X buffer, 1.8  $\mu\text{L}$   $\text{MgCl}_2$  (25 mM), 2.4  $\mu\text{L}$  dNTP mix (10 mM), 0.36  $\mu\text{L}$  of each primer (25  $\mu\text{M}$ ), 1.2 U of GoTaq Flexi DNA Polymerase (Promega), and 2  $\mu\text{L}$  DNA (approximately 100–150 ng of DNA).

The amplifications were performed on a Techne TCPLUS thermocycler, according to the following conditions for the *cyt-b* and ND1 genes: initial denaturation of 3 min at 94 °C, followed by 35 cycles of 30 s of denaturation at 94 °C, 30 s of annealing at variable temperature depending on markers (between 46 °C and 50 °C) and 30 s of extension at 72 °C, and a final extension of 5 min at 72 °C. Initial denaturation at 95 °C for 5 min, followed by 5 cycles at 94 °C for 5 min, 46 °C for 1 min 30 s, and 72 °C for 1 min 30 s, followed by 35 cycles at 94 °C for 1 min, 53 °C for 1 min, and 72 °C for 1 min, completing the reaction with a final extension cycle at 72 °C for 5 min, for the COI gene. The PCR products were quantified by fluorometry using a Quantus Fluorometer™ (Promega®) with the QuantiFluor® dsDNA System (Promega®), according to the manufacturer's protocol. PCR products were sent

to Macrogen Inc. (South Korea) for purification and DNA sequencing. The sequenced fragments were evaluated and edited using Geneious Trial v8.14 (Drummond et al. 2009). To further compare sequence divergence, we downloaded sequences of closely related taxa of the subgenera *Eptesicus* and *Histiotus* available in GenBank (Appendix 1 and 7). As outgroup, we used *Myotis riparius* and *Neoromicia guineensis* (Appendix 1 A and B).

The sequences for each gene were aligned using ClustalW (Thompson et al. 1997), included in the program MEGA X (Kumar et al. 2018). Intraspecific and interspecific nucleotide divergences were estimated with the program MEGA X, using the Kimura 2-Parameter distance model (K2P; Kimura 1980) and 1,000 bootstrap replications. For single and concatenated sets of mitochondrial genes we selected the best-fitting models of sequence evolution, using the Akaike Information Criterion (AIC) calculated with ModelFinder (Kalyaanamoorthy et al. 2017) in PhyloSuite (Zhang et al. 2020). For the concatenated analysis, and the *cyt-b* gene (Appendix 1) we selected the GTR+F+I+G4 substitution model. Bayesian Inference (BI) analysis was conducted with MrBayes 3.2.6 (Ronquist et al. 2012), with four parallel runs, 2,000,000 generations, in which the initial 25 % of sampled data were discarded as burn-in.

Phylogenetic analyses for the ND1 and COI genes were inferred by using the Maximum Likelihood (ML) method with different evolutionary models (GTR+F+G4 for ND1, and TVM+F+R2 for COI). The ML analysis was conducted with IQ-TREE (Nguyen et al. 2015), 5,000 ultrafast bootstraps (Minh et al. 2013); as well as Shimodaira–Hasegawa-like approximate likelihood-ratio test (SH-like aLRT) for branches with 1,000 replicates (Guindon et al. 2010), all included in PhyloSuite platform (Zhang et al. 2020). Finally, we used the graphical viewer of phylogenetic trees FigTree v.1.4.3 (Rambaut 2007).

## Results

Based on the review of 131 specimens of *Eptesicus andinus*, *E. brasiliensis*, *E. chiriquinus*, *E. diminutus* and *E. furinalis*, the 19 individuals from the Province of Florida, were assigned to the *andinus* group based on cranial morphology, *E. andinus* being the most morphological similar taxon. However, the specimens from Florida (Bolivia) showed a combination of discrete morphological characteristics that were not observed in any other *Eptesicus* known in South America. Among these, the presence of a well-developed frontal pre-orbital process allowed us to separate the specimens from Florida from specimens of *E. andinus*. The first two components of the PCA and DFA (Figure 2) account for 84.9 % and 84.7 % of the variation in the dataset, respectively (Table 1). PCA 1 accounted for 78.9 % of the variation, with all positive values, the highest values were given by the variables: GLS, CCL, I-M3 and C-M3. The second PCA explained 6.1 % of the variation; POC, BCB were among the variables with higher positive values, while the negative values were obtained for IOB, MB and PAL (Table 1).

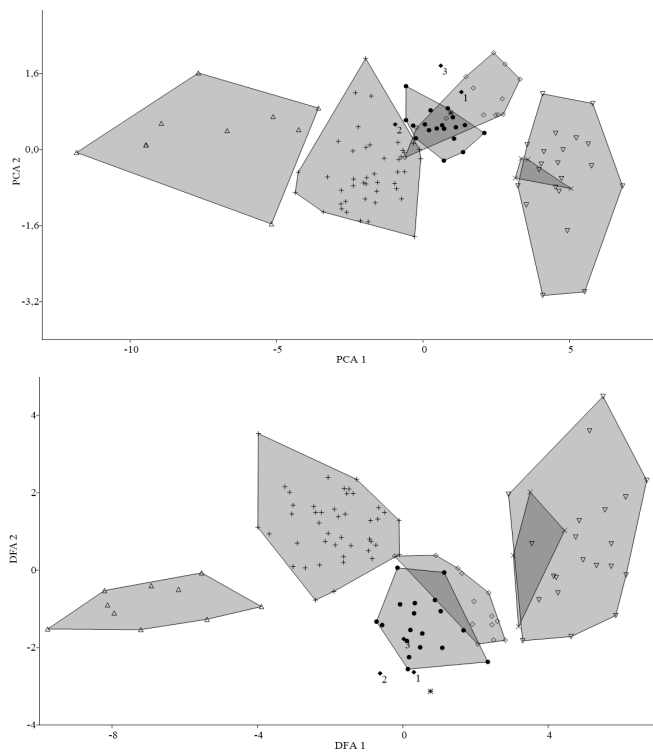
The DFA shows that specimens from Province of Florida are part of the medium-sized *Eptesicus* along with *E. furinalis* and *E. andinus* (Figure 2). Although these species tend to overlap in cranial measurements, the variation observed in DFA 1 is positively influenced by the CCL, I-M3 and C-M3, while those that intervene negatively are BCB and C-C. For the DFA 2, the highest positive values are provided by MB, GLS, and I-M3, while the negative variables were IOB and M3-M3 (Table 1).

We obtained four *cyt-b* (GenBank accession numbers MW488942-MW488945), two COI (MW490595; MW490596), and four ND1 [MW488933-MW488936] individual sequences of specimens from the Bolivian-Tucumanean forest of Bolivia. A BLAST (Basic Local Alignment Search Tool) search of these *cyt-b* and ND1 sequences showed a range between 94.5 % and 92.9 % of identity with *E. furinalis* and *E. diminutus*. The specimens from Province of Florida, Bolivia, showed high *cyt-b* distances (Table 2) when compared with the *cyt-b* sequences of *E. chiriquinus* from Colombia (11 %), *E. andinus* (9.4 to 9.8 %), and *E. furinalis* (7.5 to 7.8 %). For the ND1 gene, the distances from *Eptesicus* from Bolivia were 8.7 to 8.8 % with *E. chiriquinus* (MHN-UCa 1951), 11.2 % with *E. andinus*, and 6.3 to 6.5 % with *E. furinalis* (Table 2). Similarly, the COI distances were between 9.7 to 12.7 % with *E. andinus*, and over 7.0 % with *E. chiriquinus* and *E. furinalis* (see Appendix 2). In addition, the Bayesian Inference and Maximum Likelihood consensus trees for the single and concatenated sets of mitochondrial genes show

a monophyletic group conformed by the sequences of the Bolivian-Tucumanean forest of Bolivia specimens (Figure 3 and Appendix 1 to 3). Based on the results of the molecular and morphological analyses we described the Bolivian-Tucumanean forest specimens as a new species of *Eptesicus*.

### Discussion

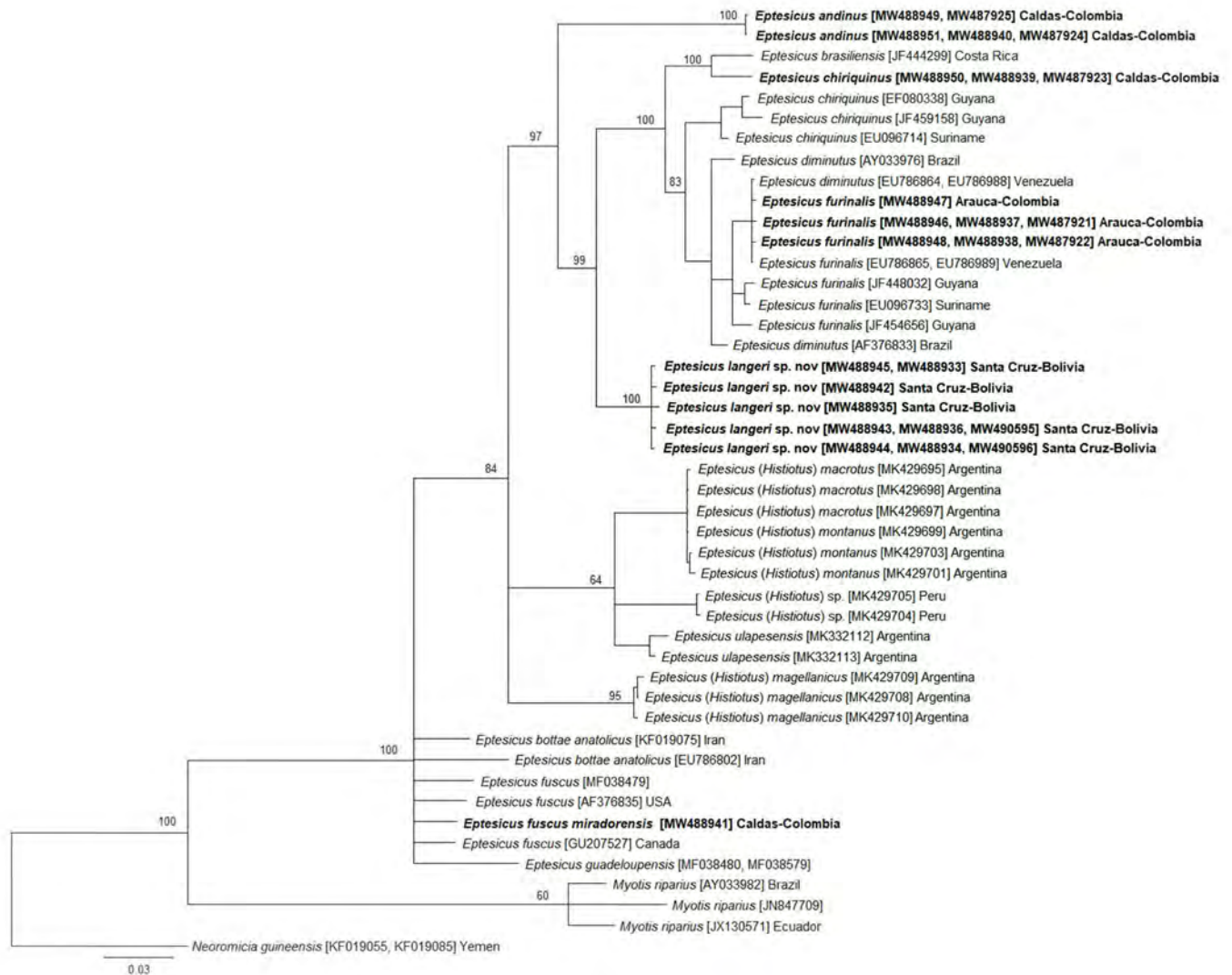
Our results show that, morphologically the Bolivian-Tucumanean forest specimens described here as *Eptesicus langeri* sp. nov. are part of the long-haired species of the subgenus *Eptesicus* that include high elevation Andean species such as *E. andinus* and *E. chiriquinus*, and cranially is similar to *E. andinus* rather to any other *Eptesicus* taxa. Most of the Neotropical *Eptesicus* have connected sagittal and nuchal ridges (in *E. brasiliensis*, *E. chiriquinus*, *E. furinalis*, *E. innoxius*, and *E. taddeii*), being *E. andinus* the exception, as this presents poorly developed ridges, creating a flattened and triangular space in dorsal view (Simmons and Voss 1998; Miranda et al. 2006; Tirira 2007; Ramírez-Chaves 2008). In addition, Neotropical *Eptesicus* have been grouped by hair length (Davis and Gardner 2008; Díaz et al. 2016; Sánchez et al. 2019), in short (less than 8.0 mm: *E. brasiliensis*, *E. furinalis*, *E. taddeii* and *E. ulapesensis*) and long-haired species (larger than 8.0 mm: *E. andinus* and *E. chiriquinus*). In contrast, some authors (e. g., García-García et al. 2007; Gregorin and Loureiro 2011), provided longer hair measurements for *E. brasiliensis* (9 to 10 mm), overlapping mainly with *E. chiriquinus* (Simmons and Voss 1998).



**Figure 2.** PCA (top) and DFA (bottom) graphs of 14 cranial and external measurements of six *Eptesicus* species: triangle *E. diminutus* (n = 10); cross, *E. furinalis* (n = 44); circle full, *E. langeri* (n = 19); diamond, *E. andinus* (n = 13); triangle invert, *E. chiriquinus* (n = 21); X, *E. brasiliensis* (n = 4). Holotype of *E. langeri* (asterisk); holotype of *E. andinus* (filled diamond 1); *E. chiralensis* (filled diamond 2); *E. montosus* (filled diamond 3).

**Table 1.** PCA and DFA results for 14 cranial variables of 138 specimens belonging to five *Eptesicus* species.

Variable	Principal Component Analysis		Discriminant Function Analysis	
	PCA 1	PCA 2	DFA 1	DFA 2
GLS	0.966	-0.094	-28.789	47.078
BCH	0.824	0.081	3.874	-33.086
BL	0.940	-0.173	-14.950	3.470
PAL	0.931	-0.041	8.328	17.541
P-M3	0.932	-0.127	12.880	5.316
MB	0.896	-0.001	8.694	60.880
M3-M3	0.926	-0.050	5.516	-4.856
C-C	0.866	-0.060	-6.571	-15.323
I-M3	0.955	-0.147	25.194	29.397
C-M3	0.955	-0.138	23.414	-26.821
CCL	0.964	-0.075	45.083	-32.240
IOB	0.855	-0.001	6.330	-1.828
POC	0.608	0.711	8.475	-24.852
BCB	0.740	0.479	-1.940	-26.743
Eigenvalue	11.039	0.850	9.330	11.490
% variance	78.9	6.1	73.0	11.7
% variance accumulated	78.9	84.9	73.0	84.7



**Figure 3.** Phylogenetic tree inferred from the concatenation of *cyt-b*, ND1 and COI genes partial sequences of bats specimens collected in the present study (in bold) and sequences from GenBank accession numbers in brackets (*cyt-b*, ND1 and COI respectively) using Bayesian inference (BI) with the GTR+I+G4 evolutionary model, and *Neoromicia guineensis* and *Myotis riparius* were used as outgroup. Bayesian posterior probabilities (%) are indicated in the nodes.

Despite the suggested morphological groups, our phylogenetic analyses show that these characters are not related to monophyletic clades, as shown by the position of *E. langeri*, *E. chiriquinus* and *E. andinus* in the phylogenetic trees (Figure 3 and Appendix 1 to 2).

The lack of genetic data for *E. andinus* in previous phylogenetic analyses or species descriptions (Giménez et al. 2019; Sánchez et al. 2019), limited the assessment of the morphological and phylogenetic association within the Neotropical *Eptesicus*. In this way, our work is also filling these gaps by including and analysing the phylogenetic position of *E. andinus* for first time. In addition, our work showed that the diversity of Neotropical *Eptesicus* has been underestimated as suggested by newly proposed species (Sánchez et al. 2019). Finally, the systematics of *Eptesicus* and *Histiotus* is not deeply understood, and integral revisions of both taxa are needed (Giménez et al. 2019; Sánchez et al. 2019), therefore, the information that we provide here can be useful for additional integrative analyses at continental scale.

## Taxonomy

Family Vespertilionidae Gray 1821

Genus *Eptesicus* Rafinesque, 1820

Subgenus *Eptesicus* Rafinesque, 1820

*Eptesicus langeri* sp. nov.

**Holotype:** The holotype is an adult lactating female, preserved as skin and skull, and deposited in the mammal collection of the Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia, with catalogue number MNKM-5584. Collected on December 01, 2013 by Luis H. Acosta, field number L. Acosta 732, at an elevation of 2,020 masl, in a fern grove of the Bolivian-Tucumani forest surveyed during a biological diagnosis of the locality El Cedral-Agua Rica.

**Type locality:** El Cedral-Agua Rica, 15 km from the Municipality of Samaipata, Province of Florida, Department of Santa Cruz, Bolivia (-18° 13' 10.55" S, -63° 47' 49.74" W; 2,020 masl (Figure 1).

**Table 2.** Distances based on Kimura two parameters for the mtDNA Cyt-*b* gene (intraspecific on the diagonal and interspecific below the diagonal), and for the mtDNA nicotinamide adenine dinucleotide dehydrogenase (ND1) gene (in bold, above the diagonal).

Species	1	2	3	4	5	6	7	8	9	10	11	12
1 <i>Eptesicus</i> sp. nov (Bolivia)	0.000/0.000	<b>0.112</b>	<b>0.068-0.072</b>	<b>0.082-0.084</b>	<b>0.205-0.213</b>		0.167-0.170	0.061-0.072				
2 <i>E. andinus</i>	0.094-0.098	0.00	<b>0.093</b>	<b>0.101</b>	<b>0.187</b>		0.137	0.093-0.101				
3 <i>E. furinalis</i>	0.076-0.079	0.116-0.135	0.000	<b>0.053-0.056</b>	<b>0.191-0.219</b>		0.165-0.176	0.000-0.048				
4 <i>E. chiriquinus</i>	0.111-0.117	0.107-0.111	0.078-0.093	-	<b>0.236</b>		0.152	0.053-0.060				
5 <i>E. bottae anatolicus</i>	0.202-0.208	0.194-0.205	0.205-0.218	0.232	-		0.182	0.183-0.193				
6 <i>E. guadeloupensis</i>	0.118-0.140	0.191-0.203	0.135-0.176	0.180	0.202	-						
7 <i>E. fuscus</i>	0.114-0.136	0.164-0.183	0.120-0.149	0.149-0.152	0.170-0.191	0.078-0.093	0.080	<b>0.160-0.169</b>				
8 <i>E. diminutus</i>	0.072-0.079	0.124-0.134	0.000-0.031	0.063-0.078	0.208-0.214	0.163-0.176	0.137-0.149	0.027				
9 <i>E. (Histiotus) montanus</i>	0.128-0.143	0.131-0.142	0.133-0.161	0.144-0.145	0.196-0.199	0.171-0.172	0.151-0.159	0.128-0.134	0.001-0.003			
10 <i>E. (Histiotus) magellanicus</i>	0.093-0.103	0.124-0.136	0.120-0.132	0.139-0.143	0.181-0.183	0.159-0.160	0.134-0.154	0.132-0.145	0.132-0.137	0.002-0.004		
11 <i>E. (Histiotus) sp.</i>	0.128-0.134	0.138-0.147	0.155-0.172	0.149-0.152	0.195-0.196	0.176-0.178	0.158-0.176	0.139-0.155	0.072-0.073	0.125-0.130	0.001	
12 <i>E. (Histiotus) macrotus</i>	0.128-0.138	0.131-0.143	0.133-0.156	0.144-0.145	0.196	0.171-0.172	0.151-0.159	0.127-0.136	0.000-0.004	0.132-0.135	0.072-0.074	0.000-0.001

**Paratypes:** 18 individuals, six females (MNKM 4436, 5088, 5117, 5585, 5587, 5588) and seven males (MNKM 4678, 4679, 5126, 5590, 5591, 5592, 5692) from the type locality; four females (MNKM 5586, 5589, 5636, 5676) from Agua Clarita (-17° 56' 47.71" S, -64° 08' 0.28" W, 1,578 masl); and one female (MNKM 5697) from Reserva Municipal El Chape (-18° 01' 21.46" S, -63° 56' 50.23" W, 2,054 masl). External and cranial measurements are provided in Appendix 3 to 5.

**Distribution:** *Eptesicus langeri* sp. nov. is known from three localities: i) El Cedral-Agua Rica, ii) Agua Clarita, and iii) the Reserva Municipal El Chape, all three in the Province of Florida, Department of Santa Cruz, Bolivia (Figure 1).

**Nomenclatural statement:** A life science identifier (LSID) number was obtained for new species described herein: urn:lsid:zoobank.org:act:3723D032-6800-401F-ACEE-0326F1AE72B1.

**Etymology:** The epithet *langeri* is in honour of Fray Andrés Ma Langer o.p., a Dominican parish priest who made important contributions to the mammalogy of the inter-Andean valleys of Bolivia, especially in the Province of Florida of the Department of Santa Cruz. Several specimens collected by Fray Andrés Ma Langer are deposited and catalogued at the Museo de Historia Natural Noel Kempff Mercado.

**Diagnosis:** *Eptesicus langeri* is a medium-sized bat (forearm length 40 to 44 mm), with dorsal fur that is long (~ 8 mm), dark brown or orange-brown in females and dark brown in males (Figure 4). The skull has developed sagittal and lambdoidal ridges, that do not reach the posterior region of the skull (Figure 5). A developed preorbital process between the smallest width of the interorbital and postorbital (Figure 6). Coronoid process tall (Figure 5).

**Description:** *Eptesicus langeri* is a medium-sized bat, similar in size to *E. furinalis* and *E. andinus* (Table 3). The dorsal and ventral fur is bicoloured with dark bases and light tips (dark brown to dark orange, near one quarter hair length; Figure 4). Both sexes present the dorsal fur longer between the shoulders (7 to 9 mm) and shorter in the middle part

of the body (~ 6 mm), the ventral region hairs differ from the back by being lighter. Males have a longer dark brown dorsal fur between the shoulders (~ 9 mm) and shorter in the middle of the back (~ 7 mm). Pregnant and lactating females have dorsal fur coloured "orange-brown".

The skull is long, with developed sagittal and lambdoidal ridges. The sagittal crest gives the skull an elevated appearance that is more evident in the middle part of the cranial vault, while the lambdoidal or nuchal crest is developed at the edges of the occipitoparietal suture. Both ridges do not come into contact in the posterior region of the skull, leaving a gap between them (Figure 5).



**Figure 4.** Dorsal and ventral view of the coat colour pattern. From left to right: A. female (MNKM-5584 holotype) and B. male (MNKM-5592 paratype) of *E. langeri* sp. nov. and C. *E. andinus* (MNKM-5598).



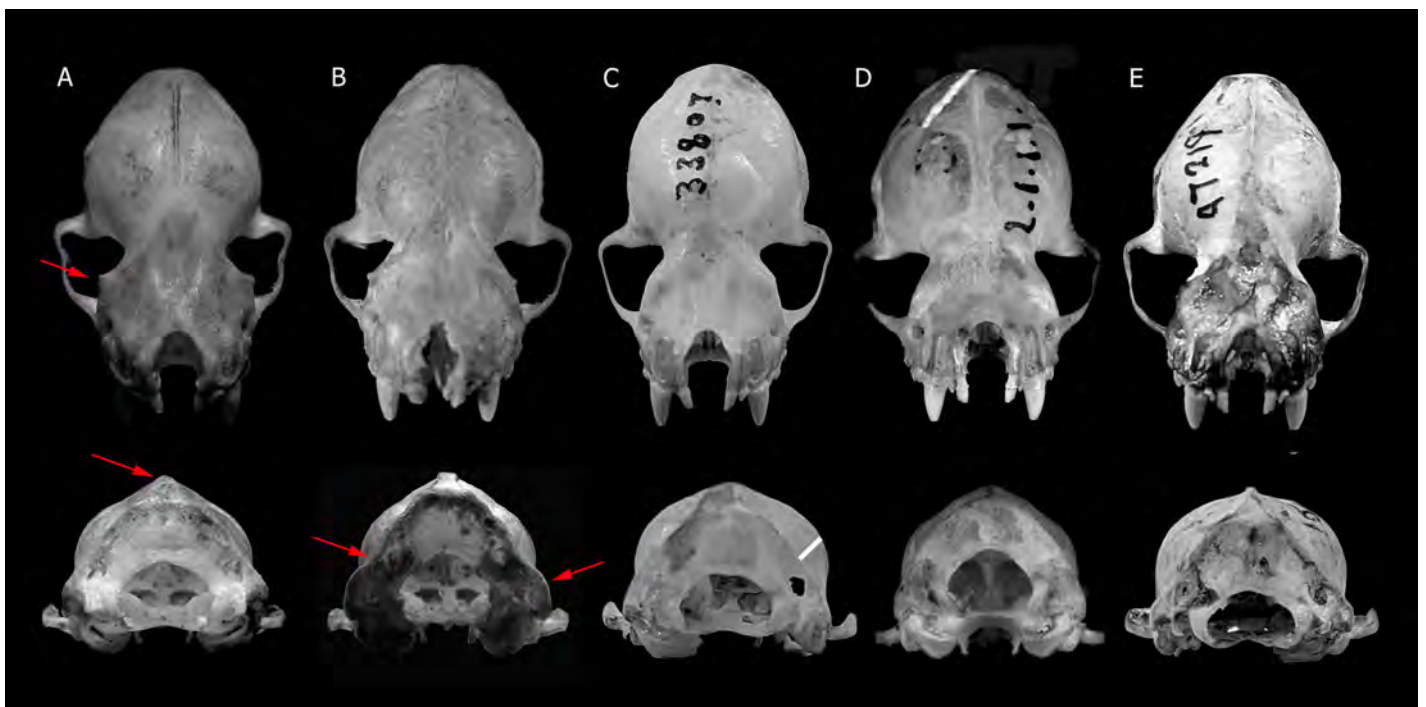


**Figure 5.** Dorsal (A), ventral (B) and lateral (C) views of the skull of the holotype of *Eptesicus langeri* sp. nov. (MNKM-5584).

*Eptesicus langeri* presents a well-developed frontal pre-orbital processes (Figure 6). In adult females these processes are more developed than in adult males. The upper internal incisors are larger than the external incisors. There is a small diastema between the upper external incisors and canine. The canine is attached to the premolar. First and second upper molars are similar, and the occlusal surfaces are W-shaped. The third upper molar is smaller than the rest of the molars and posteriorly extends beyond the anterior insertion of the zygomatic arches. The lower external incisors are in contact with the canines. The lower canine is slightly inclined towards the back, and in contact with first lower premolar which is approximately half the height of the canine; second lower premolar is higher than the first and in contact with first lower molar.

The mandible has a triangular and slightly curved coronoid process. The anterior part of the dentary has a straight oblique mandibular line; the mandibular process is slightly curved with a rounded end. A semi-circular mandibular incisure is located between the coronoid process and the anterior part of the dentary; the angular process is dorsally curved, and the mandibular ramus has a central depression (Figure 5).

**Comparisons:** *Eptesicus langeri* is a medium-sized bat (FA: 40.09 to 44.1 mm; GLS: 14.75 to 16.15 mm) with a dorsal and ventral fur length between 6.0 to 10.0 mm. It can be easily distinguished of other South American *Eptesicus* based on the forearm length, *E. diminutus* < 37.0 mm, *E. innoxius* < 39.0 mm, *E. furinalis* < 41.0 mm, *E. taddeii* > 44.1 mm and *E. fuscus miradorensis* > 49.0 mm. *E. langeri* is smaller than *E.*



**Figure 6.** Top: Frontal-dorsal view of the crania of the frontal pre-orbital process: A, B. *Eptesicus langeri* (MNKM-5564, Holotype female, MNKM-5592, Paratype male). C. *E. andinus* (AMNH 33807, Holotype). D. *E. montosus* (BMNH 2.1.1.1, Holotype). E. *E. chiralensis* (AMNH 47219, Holotype). Bottom: Space between sagittal and lambdoidal crest; notch and base of lambdoidal crest (red arrows); space between lambdoidal ridges and the parietal (white line).

*brasiliensis*, *E. chiriquinus*, *E. taddeii* and *E. ulapesensis*, especially in the GLS (Table 3), and discrete characters of the skull and skin (Appendix 9). *Eptesicus langeri* is characterized by a highly developed preorbital process, which is poorly developed in *E. andinus*, *E. furinalis* (Figure 6), *E. brasiliensis*, *E. fuscus miradorensis*, *E. innoxius*, and *E. taddeii*, whereas in *E. chiriquinus* this process is evident but not well-developed. Based on dorsal fur length, *E. langeri* can be differentiated of *E. furinalis* (< 7.0 mm) and *E. ulapesensis* (~ 6.0 mm). In *E. taddeii* the coat is reddish and 7.0 mm long (Miranda et al. 2006).

Comparison with holotypes of *Eptesicus andinus* (AMNH 33807), *E. chiralensis* (AMNH 47219), and *E. montosus* (BMNH 2.1.1.1): *Eptesicus langeri* can be differentiated from *E. andinus* and two of its junior synonyms (*E. chiralensis* and *E. montosus*) by cranial characteristics including: a) lambdaoidal crest developed in the lateral region of the interparietal in *E. langeri*, vs. poorly developed in *E. andinus*, *E. chiralensis*, and *E. montosus* (Figures 6 to 8). B) base of the lambdaoidal crest, broad in posterior view and with a smooth notch in the middle region in *E. langeri*, vs. lacking a notch and almost straight in *E. andinus*, *E. chiralensis*, and *E. montosus* (Figure 6). C) Frontal preorbital process present in *E. langeri* vs. poorly developed in *E. andinus*, *E. chiralensis*, and *E. montosus* (Figures 6 to 7). D) circular appearance in the nasal-premaxillary region in *E. langeri*, vs. rectangular in *E. andinus*, *E. chiralensis* and *E. montosus* (Figure 8). E) angular process of the mandible with a robust tip in *E. langeri*, vs. delicate in *E. andinus*, *E. chiralensis* and *E. montosus* (Figure 8). F) ascending ramus of the coronoid process lacking a steep slope in *E. langeri* (31°), *E. andinus* (30°) and *E. chi-*

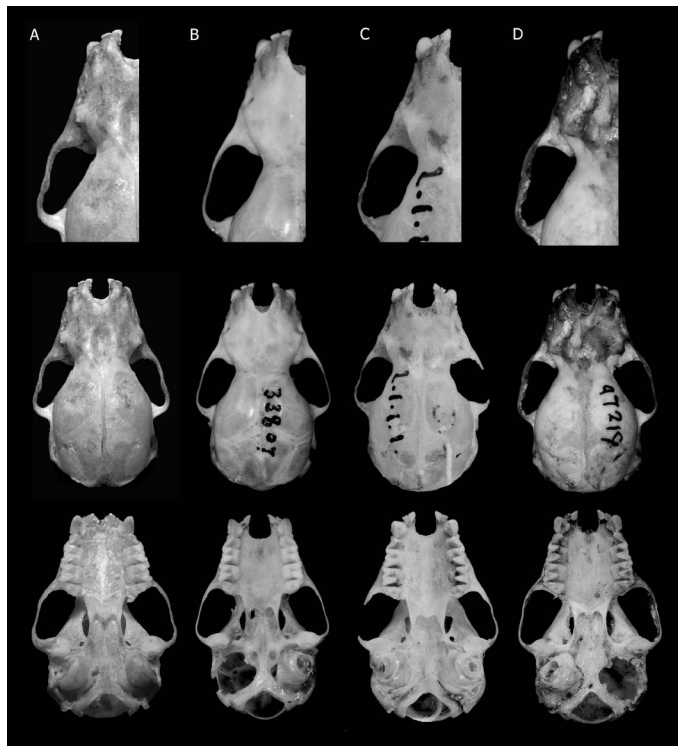
*ralensis* (35°), vs. with steep slope in *E. montosus* (40°; Figure 8). G) ramus of ventral mandible curved in *E. langeri*, vs. smoothly curve in *E. andinus* and *E. montosus*, and straight in *E. chiralensis* (Figure 8). *Eptesicus langeri* overlaps in some external and cranial measurements with *Eptesicus andinus*, *E. chiralensis*, and *E. montosus* although *E. langeri* can be separated when the postorbital width and cranial index are plotted (Appendix 6).

**Ecology:** The type locality is part of the Bolivian-Tucumani forest, characterized by Chari (*Parapiptadenia excelsa*) and Tipa (*Tipuana tipu*) trees, and connected to the Andean vegetation of the Peruvian-Bolivian Yungas (Navarro 2011). Specimens of the type locality were collected from 19:24 to 23:30 h. Most specimens were collected using mist nets installed at a height of 5 to 8 m above ground in forest clearings (newly opened road) of a secondary road. Lactating females and males with testicles in scrotal position have been recorded from November to January. Specimens from Agua Clarita were collected inside a hollow of a standing tree. Other bat species reported at the type locality are *Anoura geoffroyi*, *Sturnira lilium*, *S. oporophilum*, *Chrotopterus auritus*, *Desmodus rotundus*, *Platyrrhinus masu*, *Myotis nigricans*, and *M. keaysi*.

We suggest that discreet dental skull characters should be used together with some measurements for an accurate identification of *E. langeri*. Thus, we propose the following identification key for some South American *Eptesicus* (sensu Davis and Gardner 2008), with emphasis on some cranial variables:

*Taxonomic key*

1. Ears longer than 20.0 mm, extending well beyond muzzle .....subgenus *Histiotus*
- 1a. Ears normal, less than 20.0 mm, not extending beyond muzzle .....subgenus *Eptesicus*
2. Skull longer than 16.3 mm; upper toothrow > 6.3 mm ....3
- 2a. Skull less than 16.3 mm; upper toothrow less than 6.3 mm .....7
3. Forearm greater than 49.0 mm .....*Eptesicus fuscus miradorensis*
- 3a. Forearm less than 49.0 mm .....4
4. U-shaped nasal opening .....*Eptesicus brasiliensis*
- 4a. V-shaped nasal opening .....5
5. Dorsal fur longer than 12.0 mm .....*Eptesicus chiriquinus*
- 5a. Dorsal fur less than 12.0 mm .....6
6. Skull length between 17.3 to 18.4 mm .....*Eptesicus taddeii*
- 6a. Skull length between 15.9 to 17.0 mm .....*Eptesicus ulapesensis*
7. Skull less than 13.6 mm; upper toothrow less than 5.0 mm .....*Eptesicus diminutus*
- 7a. Skull longer than 13.6 mm; upper toothrow longer than 5.0 mm .....8
8. Sagittal and lambdaoidal crests connected .....9



**Figure 7.** Dorsal, and ventral, view of skulls (left to right) of A. *Eptesicus langeri* sp. nov (MNKM-5592, Paratype). B. *E. andinus* (AMNH 33807, Holotype). C. *E. montosus* (BMNH 2.1.1.1, Holotype). D. *E. chiralensis* (AMNH 47219, Holotype).



**Figure 8.** Lateral view of the skull, the white lines show the shape of the rostrum and skull: A. *Eptesicus langeri* sp. Nov (MNKM-5592, Paratype). B. *E. andinus* (AMNH 33807, Holotype). C. *E. montosus* (BMNH 2.1.1.1, Holotype). D. *E. chiralensis* (AMNH 47219, Holotype “inversed”), scale 10mm. Lateral view of the mandible of: E. *Eptesicus langeri* sp. nov (MNKM-5592, Paratype). F. *E. andinus* (AMNH 33807, Holotype). G. *E. montosus* (BMNH 2.1.1.1, Holotype). H. *E. chiralensis* (AMNH 47219, Holotype), scale 5mm.

- 8a. Skull with separate sagittal and lambdoidal ridges forming a triangular flat bone .....10  
 9. Pale greyish brown hair colour .....*Eptesicus innoxius*  
 9a. Dark brown to blackish brown hair colour .....  
 .....*Eptesicus furinalis*  
 10. Skull with very poorly developed/absent sagittal and lambdoidal ridges, poorly developed preorbital process .....*Eptesicus andinus*  
 10a. Skull with evident/developed sagittal and lambdoidal crests, preorbital process present .....*Eptesicus langeri*

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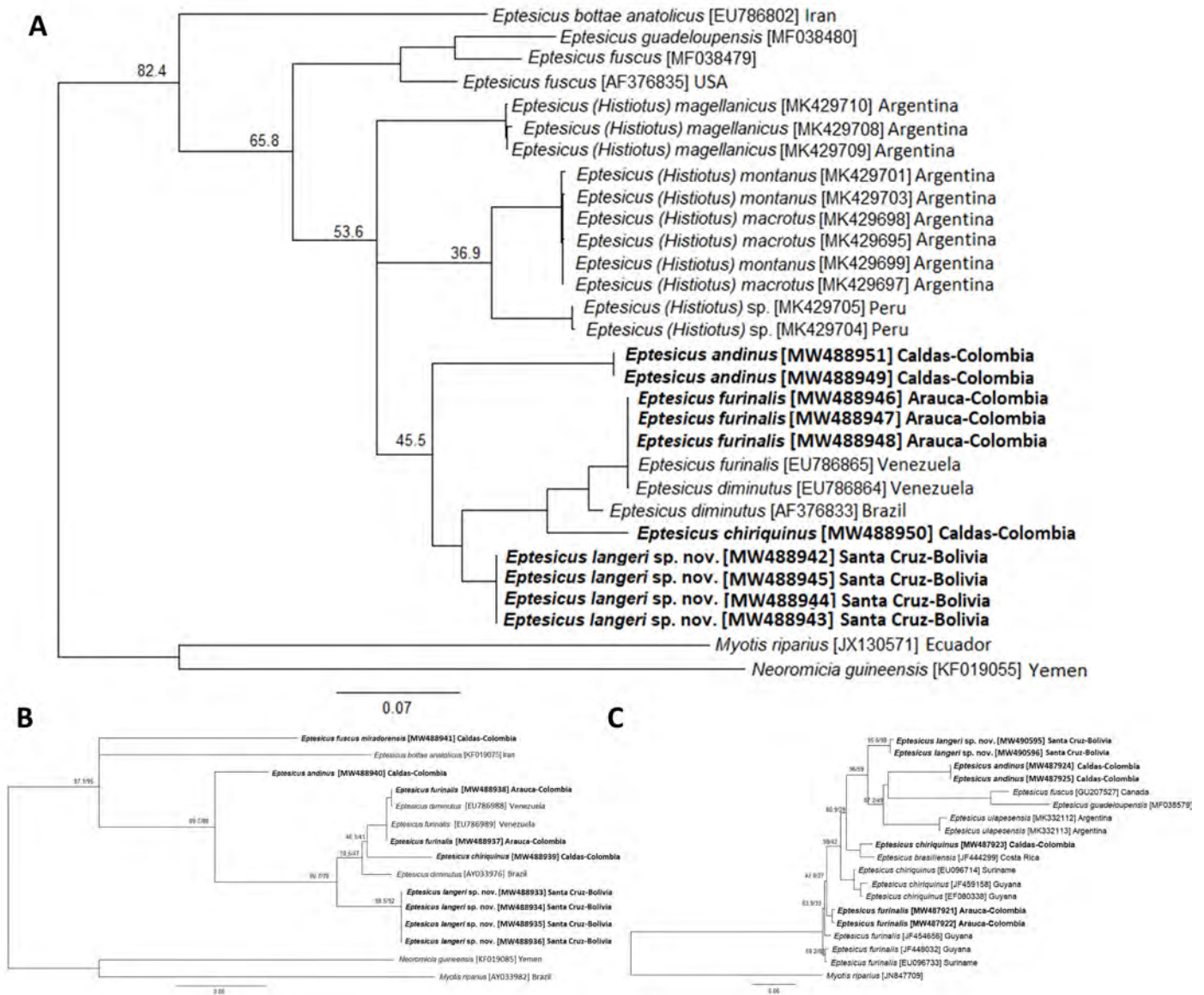
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## Appendix 1

A) Tree of the mitochondrial *cyt-b* gene partial sequences of bats specimens collected in the present study (in bold) and sequences from GenBank (accession numbers in brackets), obtained by Bayesian inference (BI) by the evolutionary model GTR+F+I+G4, and *Neoromicia guineensis* and *Myotis riparius* were used as outgroup. Bayesian posterior probabilities (%) are indicated in the nodes. B) Tree of the mitochondrial ND1 gene partial sequences of bats specimens collected in the present study (in bold) and sequences from GenBank (accession numbers in brackets), using Maximum Likelihood (ML) method and GTR+F+G4 model. Numbers at nodes are above-selected branch support analysis from left to right: ultrafast bootstraps values, and Shimodaira–Hasegawa–like approximate likelihood-ratio test (SH-like aLRT). The sequence of *Neoromicia guineensis* and *Myotis riparius* were used as outgroup. C) Tree of the mitochondrial COI gene partial sequences of bats specimens collected in the present study (in bold) and sequences from GenBank (accession numbers in brackets), using Maximum Likelihood (ML) method with the TVM+F+R2 evolution model. Numbers at nodes are above-selected branch support analysis from left to right: ultrafast bootstraps values, and Shimodaira–Hasegawa–like approximate likelihood-ratio test (SH-like aLRT). The sequence of *Myotis riparius* was used as outgroup.



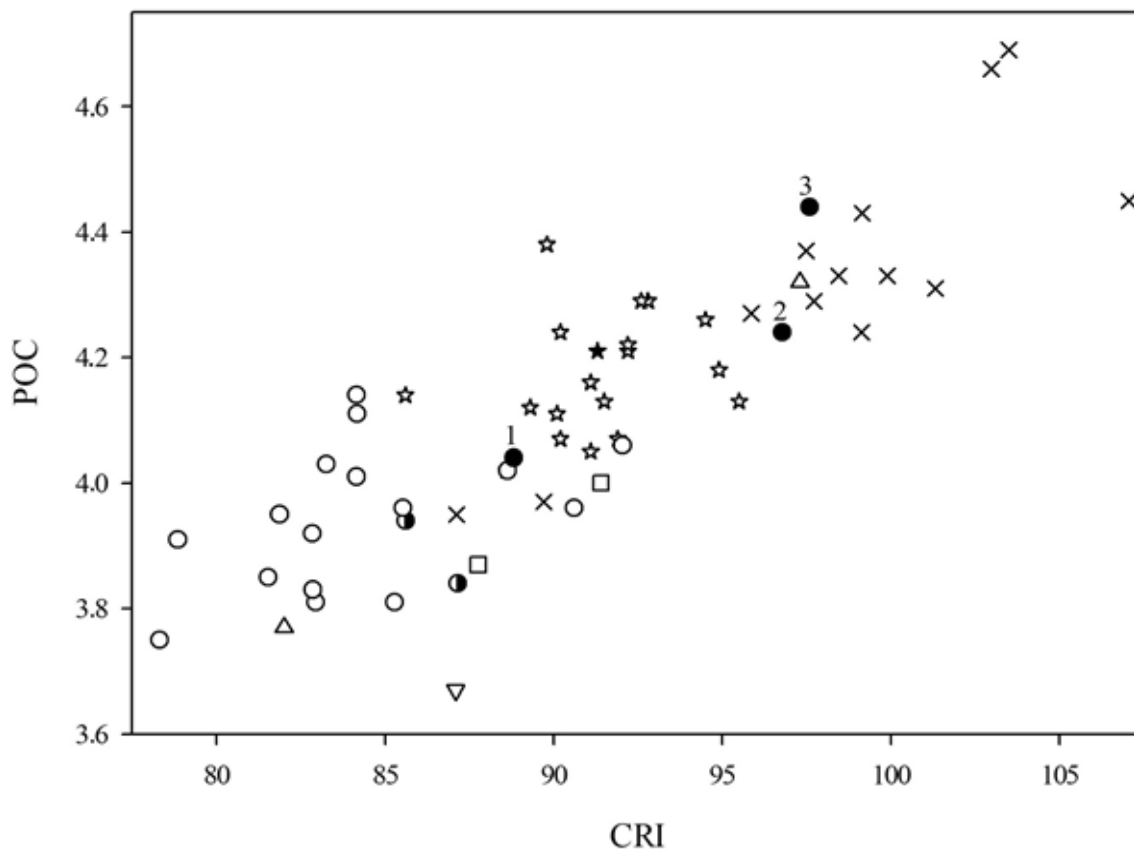
## Appendix 2

Average intraspecific (on the diagonal) and interspecific (below the diagonal) distances based on Kimura two parameters for the mtDNA cytochrome c oxidase subunit I (COI) gene.

Species	1	2	3	4	5	6	7	8	9
1 <i>Eptesicus</i> sp. (Bolivia)	0.005								
2 <i>E. furinalis</i>	0.085-0.094	0.006-0.025							
3 <i>E. chiriquinus</i>	0.077-0.079	0.037-0.067	0.011-0.074						
4 <i>E. andinus</i>	0.097-0.127	0.137-0.168	0.119-0.138	0.000					
5 <i>E. ulapesensis</i>	0.116-0.129	0.135-0.160	0.129-0.146	0.148-0.154	0.011				
6 <i>E. brasiliensis</i>	0.091	0.069-0.071	0.035-0.065	0.124-0.137	0.134-0.140	-			
7 <i>E. fuscus</i>	0.170-0.172	0.169-0.191	0.183-0.202	0.206-0.220	0.188-0.194	0.194	-		
8 <i>E. guadeloupensis</i>	0.207-0.214	0.178-0.204	0.190-0.215	0.243-0.245	0.212-0.223	0.206	0.101	-	
9 <i>Myotis riparius</i>	0.277-0.283	0.258-0.292	0.279-0.304	0.330-0.353	0.304-0.313	0.290	0.312	0.320	-

## Appendix 3

Morphometric comparison of two cranial variables of *Eptesicus andinus* from: Bolivia (square), Brazil (inverted triangle), Colombia (X), Ecuador (black and white circle), Peru (triangle) and Venezuela (circle); *E. langeri* (star), holotype (star full); holotypes from *E. andinus* (circle full 2), *E. chiralensis* (circle full 1) and *E. montosus* (circle full 3).



## Appendix 4

Comparison of measurements (mm) of *E. langeri* with other Neotropical *Eptesicus* species. Average, minimum and maximum (parentheses), number of specimens examined.

Variable	<i>E. diminutus</i>	<i>E. furinalis</i>	<i>E. andinus</i>	<i>E. langeri</i> sp. nov.	<i>E. ulapesensis</i> (Sánchez et al. 2019)	<i>E. brasiliensis</i>	<i>E. chiriquinus</i>	<i>E. taddeii</i> (Miranda et al. 2006)
GLS	13.7 (12.5–14.7) 10	15.2 (14.4–16.1) 44	15.4 (14.2–16.7) 38	15.6 (14.8–16.2) 19	16.5 (15.9–17.0) 9	17.0 (16.7–17.4) 5	17.0 (16.5–17.8) 21	17.9 (17.3–18.4) 24
CCL	12.8 (11.9–13.6) 10	14.1 (13.3–14.9) 44	15.3 (14.3–15.9) 13	14.5 (13.7–14.9) 19	15.8 (15.6–16.1) 9	15.8 (15.6–16.4) 5	16.0 (15.6–16.5) 21	16.8 (16–17.4) 24
BL	11.4 (10.2–13.7) 10	12.7 (12.0–13.5) 44	13.4 (12.9–14.1) 13	13.1 (12.6–13.6) 19	–	–	14.3 (13.8–14.8) 21	–
PAL	5.8 (5.1–6.4) 10	6.7 (6.2–7.1) 44	7.3 (6.9–7.5) 13	7.2 (6.5–7.7) 19	6.7 (6.0–7.6) 6	7.6 (7.5–8.0) 5	7.8 (6.9–8.8) 21	–
POC	3.7 (3.4–4.0) 10	3.8 (3.5–4.9) 44	4.1 (3.7–4.7) 38	4.2 (4.0–4.4) 19	3.9 (3.8–4.1) 9	4.0 (3.8–4.1) 5	4.2 (3.8–4.6) 21	4.1 (3.9–4.4) 24
BCH	5.1 (4.7–6.1) 10	5.7 (4.9–6.2) 44	5.9 (5.7–6.3) 13	6.4 (5.9–6.8) 19	–	–	6.5 (5.8–7.6) 21	–
BCB	6.9 (6.5–7.6) 10	7.3 (6.8–7.7) 44	7.6 (7.1–8.4) 38	7.5 (7.4–7.7) 19	8.3 (8.1–8.6) 9	7.7 (7.5–8.1) 5	7.8 (6.3–8.3) 21	8.1 (7.7–8.5) 24
MB	7.4 (6.8–8.2) 10	8.3 (7.7–9.3) 44	8.3 (7.8–8.8) 36	8.4 (8.1–8.6) 19	8.8 (8.2–9.2) 9	9.1 (8.7–9.5) 5	8.9 (8.5–9.3) 21	–
ZB	9.3 (8.6–10.3) 6	10.3 (9.7–10.8) 35	10.7 (10.1–11.2) 12	10.7 (10.4–11.0) 19	11.1 (10.6–11.6) 9	12.0 (12.0–12.1) 2	11.5 (10.7–12.0)	12.2 (11.7–12.9)
IOB	4.6 (4.1–4.9) 10	4.9 (3.8–5.5) 44	5.4 (4.9–5.8) 13	5.2 (4.9–5.4) 19	–	6.4 (5.9–7.2) 5	5.8 (5.4–6.4) 21	–
C–C	4.3 (3.9–4.7) 10	4.8 (4.3–5.1) 44	5.1 (4.6–5.4) 13	4.9 (4.7–5.3) 19	5.1 (4.8–5.4) 9	5.5 (5.3–5.7) 5	5.3 (4.9–5.6) 21	5.7 (5.5–6.1) 24
M3–M3	6.1 (5.5–6.6) 10	6.7 (6.0–6.9) 44	6.7 (6.3–7.4) 38	6.9 (6.4–7.2) 19	6.7 (6.2–7.2) 9	7.3 (7.1–7.6) 5	7.4 (7.0–7.8) 21	7.5 (7.0–7.8) 24
C–M3	4.9 (4.6–5.4) 10	5.7 (5.1–6.0) 44	5.9 (5.5–6.2) 38	6.0 (5.8–6.3) 19	6.2 (5.9–6.5) 9	6.4 (6.2–6.7) 5	6.6 (6.4–6.9) 21	6.8 (6.4–7.1) 24
I–M3	5.8 (5.4–6.2) 10	6.5 (6.2–6.8) 44	6.9 (6.7–7.3) 13	6.8 (6.6–7.0) 19	–	–	7.6 (7.2–8.1) 21	–
c–m3	5.4 (5.0–5.8) 10	6.2 (5.5–6.5) 44	6.6 (6.4–6.8) 13	6.4 (6.3–6.8) 19	6.8 (6.4–7.3) 9	6.8 (6.7–7.0) 5	7.2 (6.9–7.5) 21	7.3 (7.1–7.7) 24
P–M3	3.9 (3.6–4.2) 10	4.5 (4.1–4.9) 44	4.8 (4.6–5.1) 13	4.8 (4.6–5.0) 19	–	–	5.2 (4.3–5.6) 21	–
p–m3	4.7 (4.3–5.2) 7	5.5 (5.2–6.2) 44	5.7 (5.4–5.9) 13	5.6 (5.4–5.9) 19	–	–	6.2 (5.7–6.6) 21	–
MAL	10.1 (9.5–11.0) 10	11.7 (11.0–12.4) 44	12.5 (11.3–13.0) 13	12.1 (11.2–12.6) 19	12.2 (11.8–12.8) 9	13.1 (12.9–13.5) 5	13.7 (13.1–14.4) 21	13.5 (13.0–13.7) 24
MH	3.9 (3.4–4.6) 10	4.6 (4.1–5.2) 44	4.6 (4.2–5.2) 13	4.5 (4.2–4.8) 19	–	–	5.2 (4.9–5.7) 21	–
LT	84.8 (80–91) 8	95.4 (84–107) 38	97.1 (83–116) 35	96.4 (90–106) 19	103.6 (93–115) 9	108.8 (101–117) 6	104.6 (92–114) 17	108.6 (99–117) 24
TL	34.6 (27–39) 8	40.7 (35–48) 38	40.2 (31–52) 35	42.1 (39–46) 19	44.7 (36–49) 9	43.8 (37–49) 6	43.4 (36–48) 21	47.9 (43–53) 24
EL	13.4 (12–15) 7	14.6 (10–19) 38	14.6 (8–19) 30	14.8 (12.5–17) 19	15.3 (13–19) 9	16.8 (16–18) 6	14.2 (10–17) 21	15.6 (14–17) 24
LF	7.8 (7–10) 8	8.6 (7–10) 38	9.7 (7–13) 37	8.6 (7–10) 19	8.6 (7–10) 9	9.1 (8–11) 6	10.3 (8.6–11.24) 21	–
Weight	6.3 (5–7.5) 4	8.0 (5–11.5) 36	9.7 (7–13) 13	9.6 (8–12) 17	10.7 (9–14) 9	5.9 (4.9–6.5) 5	11.6 (10–14) 14	–
PD	6.3 (5–8) 3	6.8 (6–8) 13	9.5 (8–12) 12	7.7 (6–9.5) 16	~ 6	–	9.3 (7–11) 18	~ 7
PV	(7) 1	6.1 (5–7) 13	7.9 (7–9) 12	6.8 (6–8) 14	–	–	7.7 (7–9) 17	–
FA	33.8 (31.2–35.9) 9	40.1 (36.4–43.4) 44	41.4 (37.2–47.0) 38	42.2 (40.1–44.1) 19	42.8 (41.0–44.6) 9	42.0 (40.5–45.0) 5	45.9 (43.6–47.6) 21	46.5 (44.1–48.7) 24
CRI	73.1 (62–83) 10	84.1 (76–92) 44	90.3 (78–107) 38	91.3 (86–96) 19	100.9 (98–106) 9	–	116 (92–108) 21	–
MXI	25.9 (22–29) 10	32.1 (27–36) 44	36.3 (33–39) 13	35.5 (33–39) 19	36.5 (34–41) 9	–	41.9 (40–45) 21	44.8 (41–49) 24



## Appendix 5

Cranio-dental and external measurements of male and female and holotype of *Eptesicus langeri*, compared with the holotypes of *E. montosus* and *E. chiralensis* (junior synonyms of *E. andinus*), and *E. andinus*.

Variables	<i>montosus</i>	<i>chiralensis</i>	<i>andinus</i>	<i>langeri</i>	<i>langeri</i>	<i>langeri</i>
	BMNH	AMNH	AMNH	MNKM		
	2.1.1.1	47219	33807	5584	n=7	n=12
	Bolivia	Ecuador	Colombia	Bolivia	Bolivia	Bolivia
Sex	Male	Male	Male	Female	Male	Female
GLS	15.79	15.22	16.01	15.44	14.75-15.98	15.26-16.15
CCL	14.80	14.68	15.13	14.64	13.77-14.78	14.29-14.93
BL	12.73	12.6	13.47	12.69	12.55-13.27	12.69-13.57
PAL	6.92	6.66	6.87	7.09	6.85-7.37	6.51-7.69
POC	4.44	4.04	4.24	4.21	4.05-4.38	4.02-4.29
BCH	5.97	6.00	5.98	6.43	6.30-6.63	5.95-6.83
BCB	7.92	7.63	7.85	7.62	7.43-7.70	7.43-7.70
MB	8.64	8.10	8.40	8.39	8.06-8.48	8.13-8.64
ZB	10.35	10.34	10.55	10.68	10.35-10.86	10.49-11
IOB	5.23	5.15	5.30	5.24	4.92-5.30	4.97-5.39
C-C	5.14	4.94	5.28	5.33	4.67-5.03	4.83-5.33
M3-M3	6.76	6.69	6.62	7.07	6.37-6.92	6.73-7.15
C-M3	5.94	5.83	6.07	6.08	5.86-6.15	5.83-6.30
I-M3	6.76	6.47	6.74	6.72	6.59-6.93	6.68-7.01
c-m3	6.30	6.26	6.40	6.41	6.25-6.53	6.26-6.75
P-M3	4.50	4.48	4.81	4.76	4.67-4.94	4.6-5.04
p-m3	-	5.05	5.67	5.54	5.42-5.73	5.39-5.92
MAL	10.90	11.49	12.21	12.39	11.16-12.32	11.64-12.6
MH	-	4.44	4.49	4.77	4.22-4.84	4.29-4.77
LT	98.00	97.00	100	94	90.00-106.00	90.00-100.00
TAIL	43.00	38.00	35.00	42.5	38.50-43.00	40.00-46.00
EAR	18.00	-	-	16.5	12.50-15.60	13.00-17.00
HF	10.04	10.00	8.00	9	7.00-9.00	7.00-10.00
FA	42.79	41.10	43.60	43.02	40.09-43.11	40.64-44.10
PD	9.00	7.00	9.00	7	8.00-10.00	6.00-10.00
PV	-	7.00	8.00	5	6.00-8.00	5.00-7.00
CRI	97.60	88.80	96.80	91.3	85.60-94.90	88.60-95.50
MXI	35.30	33.90	36.10	37.7	32.60-36.40	34.20-38.40

## Appendix 6

Morphometry of *E. langeri* sp. nov. from Bolivia, \* holotype.

	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM	MNKM
	5584 *	5117	5585	4436	5586	5587	5588	5589	5676	5636	5088	5697	4679	5592	5126	4678	5692	5590	5591
Sex	female	female	female	female	female	female	female	female	female	female	female	female	male	male	male	male	male	male	male
GLS	15.44	15.79	15.39	15.48	15.26	15.64	15.45	16.15	15.40	15.74	15.58	16.02	15.09	15.76	14.75	15.80	15.77	15.70	15.98
CCL	14.64	14.88	14.41	14.53	14.29	14.51	14.46	14.93	14.30	14.38	14.60	14.80	13.90	14.78	13.77	14.57	14.50	14.44	14.75
BL	12.69	13.46	12.80	13.27	13.07	12.98	12.83	13.57	13.15	13.33	13.14	13.24	12.55	13.12	13.13	13.27	12.88	13.2	12.73
PAL	7.09	7.69	6.51	7.38	6.99	7.36	7.01	7.43	6.93	7.29	7.06	7.34	6.87	7.22	6.85	7.36	7.16	7.37	7.10
POC	4.21	4.13	4.12	4.02	4.24	4.16	4.07	4.13	4.11	4.21	4.29	4.26	4.38	4.07	4.14	4.29	4.05	4.22	4.18
BCH	6.43	6.44	6.38	6.33	6.30	6.39	6.19	6.83	5.95	6.32	6.20	6.68	6.40	6.63	6.35	6.40	6.44	6.30	6.49
BCB	7.62	7.46	7.49	7.43	7.58	7.49	7.61	7.70	7.59	7.50	7.62	7.54	7.52	7.59	7.47	7.43	7.50	7.52	7.70
MB	8.39	8.22	8.13	8.44	8.43	8.35	8.34	8.64	8.37	8.62	8.60	8.29	8.27	8.48	8.40	8.38	8.17	8.06	8.31
ZB	10.68	10.49	10.69	10.59	10.58	10.69	10.62	11.00	10.73	10.72	10.76	10.69	10.86	10.85	10.53	10.84	10.35	10.39	10.66
IOB	5.24	5.16	5.18	4.97	5.19	5.02	5.23	5.19	5.19	5.05	5.37	5.39	4.93	5.14	5.14	5.25	4.92	5.17	5.30
C-C	5.33	4.85	4.83	4.96	4.93	4.99	5.04	4.94	5.06	4.97	4.88	5.22	4.71	5.03	4.67	4.96	4.75	4.92	5.03
M3-M3	7.07	7.10	6.74	6.74	6.78	6.80	6.90	6.84	6.92	6.73	6.99	7.15	6.75	6.84	6.78	6.87	6.37	6.92	6.87
C-M3	6.08	6.30	5.92	6.09	6.03	6.07	5.83	5.96	5.99	5.99	5.89	6.22	5.90	6.09	5.86	6.12	5.88	6.15	6.03
I-M3	6.72	7.01	6.80	6.98	6.77	6.68	6.71	6.76	6.77	6.83	6.71	6.97	6.63	6.85	6.59	6.93	6.70	6.86	6.84
c-m3	6.41	6.66	6.29	6.63	6.37	6.41	6.26	6.50	6.47	6.44	6.51	6.75	6.38	6.34	6.25	6.53	6.45	6.39	6.42
P-M3	4.76	4.69	4.77	4.83	4.66	4.72	4.63	4.67	4.60	4.66	4.82	5.04	4.67	4.93	4.79	4.82	4.84	4.87	4.94
p-m3	5.54	5.88	5.62	5.64	5.59	5.92	5.39	5.65	5.49	5.58	5.48	5.85	5.46	5.72	5.42	5.73	5.53	5.59	5.73
MAL	12.39	12.60	12.26	12.54	12.45	12.48	12.15	12.13	11.64	11.70	11.97	11.98	11.16	12.32	11.87	11.90	11.44	12.23	12.30
MH	4.77	4.57	4.69	4.75	4.49	4.72	4.40	4.72	4.29	4.34	4.5	4.46	4.38	4.37	4.22	4.84	4.46	4.36	4.47
LT	94	100	98	97	95	96	97	100	90	92	94.5	97	90	106	97	98.5	90	100	100
TL	42.5	40	43	43	46	44.5	44.5	44	38.5	40.5	41	44	38.5	43	39	41	41	40	40
EL	16.5	14	16	13.5	13	17	15	13.5	14	14	15.5	15	15	15	12.5	15.6	15.5	15	14
HF	9	10	8	10	8.5	10	8	9.5	8	9	7	8	9	8	8.5	9	8.5	9	7
FA	43.02	41.52	41.54	42.95	43.2	43.25	43.76	44.1	41.15	43.35	40.64	42.77	41.58	41.85	42.66	43.11	41.15	40.09	40.54
PD	7	-	7	7	6	10	8	-	7	7	8	-	10	8	9	9	10	8	8
PV	5	-	6	6	6	7	6	-	-	-	6	-	7	7	7	8	8	6	7
CRI	91.30	91.50	89.30	88.60	90.20	91.10	90.20	95.50	90.10	92.20	92.80	94.50	89.80	91.90	85.60	92.60	91.10	92.20	94.90
MXI	37.70	37.60	34.20	35.60	35.30	35.70	34.80	35.10	35.90	35.00	34.90	38.40	33.80	36.10	33.50	36.20	32.60	36.40	35.90

## Appendix 7

GenBank accession numbers for sequences generated in this study are indicated in **boldface type**; all others were published previously. Cyt-*b* = cytochrome b; ND1 = nicotinamide adenine dinucleotide dehydrogenase; COI = cytochrome oxidase subunit I.

Taxon	Cyt-b	ND1	COI
<i>Eptesicus andinus</i>	<b>MW488951, MW488949</b>	<b>MW488940</b>	<b>MW487924, MW487925</b>
<i>Eptesicus brasiliensis</i>			JF444299
<i>Eptesicus bottae anatolicus</i>	EU786802	KF019075	
<i>Eptesicus chiriquinus</i>	<b>MW488950</b>	<b>MW488939</b>	JF459158, EU096714, EF080338, <b>MW487923</b>
<i>Eptesicus diminutus</i>	EU786864, AF376833	EU786988, AY033976	
<i>Eptesicus furinalis</i>	EU786865, <b>MW488946-MW488948</b>	EU786989, <b>MW488937, MW488938</b>	EU096733, JF448032, JF454656, <b>MW487921, MW487922</b>
<i>Eptesicus fuscus</i>	AF376835, MF038479		GU207527
<i>Eptesicus fuscus miradorensis</i>		MW488941	
<i>Eptesicus guadeloupensis</i>	MF038480		MF038579
<i>Eptesicus langeri</i>	<b>MW488942-MW488945</b>	<b>MW488933-MW488936</b>	<b>MW490595; MW490596</b>
<i>Eptesicus ulapesensis</i>			MK332112, MK332113
<i>Eptesicus (Histiotus) montanus</i>	MK429701, MK429703, MK429699		
<i>Eptesicus (Histiotus) magellanicus</i>	MK429710, MK429709, MK429708		
<i>Eptesicus (Histiotus) macrotus</i>	MK429698, MK429697, MK429695		
<i>Eptesicus (Histiotus) sp.</i>	MK429705, MK429704		
<i>Myotis riparius</i>	JX130571	AY033982	JN847709
<i>Neoromicia guineensis</i>	KF019055	KF019085	

## Appendix 8

### Revised Specimens:

*Eptesicus andinus* ( $n = 39$ ). BOLIVIA. Beni: Lago Largo-Comunidad Maravilla (MNKM 5598). Cochabamba: Corani (AMNH 268653). Choro (BMNH 2.1.1.1 "Holotype *E. montosus*"). La Paz: PN ANMI Madidi (MNKM 5599). BRASIL. Goiás (AMNH 134910). COLOMBIA. Cauca: Municipio de Páez (Belalcázar); Parque Nacional Natural, (P.N.N.) Nevado del Huila, Irlanda, Estación Inderena, 2800 m (ICN 7637-40). Caldas: Aranzazu, vereda El Diamante, 3420 m (MHN-UCa-M 2633-2634). Huila: Valle de las Papas (AMNH 33807 "Holotype *E. andinus*"). Quindío: municipio de Salento; 3250 m (UV 3358-59). Reserva Natural Cañón Quindío, frente de reforestación "La Montaña", 2900 m (ICN 12449). Frente de reforestación "La Romelia", 2630 m, (ICN 12450). Frente de reforestación "La Picota", 2730 m (ICN 12451-2). El Roble (AMNH 32802). Risaralda: Pereira, vereda La Pastora, Parque Regional Natural Ucumarí, 2470 m (ICN 11270). ECUADOR. El Oro: El Chiral (AMNH 47218, 47219 "Holotype *E. chiralensis*", 47220). PERÚ. Chanchamayo (BMNH 76152). Junín, Tarma, San Ramón (AMNH 23780). Cuzco, Pillahuata (FMNH 123953). VENEZUELA. Caracas: Los Venados (USNM 370935-37, 370943-44, 370949-53, 370955, 370962-63). Maracaibo: Falcon Cerro Sapoco (USNM 441764). Montalbán: La Copa (USNM 441755).

*Eptesicus brasiliensis* ( $n = 4$ ). ARGENTINA. Corrientes, Goya (BMNH 98345, 98346). BOLIVIA. Santa Cruz: Comarapa (AMNH 260257). COLOMBIA. Meta (UV 7725). ECUADOR. Oriente, Canelos (BMNH 54373).

*Eptesicus chiriquinus* ( $n = 21$ ). COLOMBIA. Quindío: municipio Finlandia; vereda El Roble, Reserva Forestal Bremen-La Popa, 1950 m, (ICN 12483). Antioquia: San Luis; San Pablo, quebrada San Antonio, 810 m (ICN 9881-82). Yarumal; El Cedro, Media Luna (CTUA 11083). El Cedro, El Sombrero (CTUA 10965). Cauca (JVS-254, 269, MHNUC 1497); municipio de Cajibío: vereda El Cofre, finca La Herencia 1700 m (UV 13178). Cundinamarca: municipio de Paima, vereda El Carmen, Inspección de Policía Cuatro Caminos, 1400 m (MUD 116, 125, 138, 139). Santander: municipio Los Santos, vereda Mesitas de San Javier, bosque de Los Alpes, 1550 m (ICN 16653). Encino, Vereda Río Negro, sitio Cachalú, finca La Desdichada, 2000 m (ICN 17623). Valle Del Cauca: municipio La Victoria; hacienda El Chaquiral (UV 4055). Pance: río Pance, estación Pueblo Pance 1460 m (UV 3551, 3889, 4363). Municipio El Cairo, Estación Cerro del Inglés 2000 m (UV 13094). Valle Del Cauca: Buenaventura; vía Buenaventura-Zaragoza, 180 m (MHNUC, colector number HERC-502).

*Eptesicus diminutus* ( $n = 7$ ). ARGENTINA. Río Negro, Balneario Las Cañas (CML 1859). Buenos Aires: Delta, Canal 6 y P. Palmas (CML 1820). Jujuy: Laguna La Brea 25km al W de Palma Sola (CML 3086). Salta Dept. General San Martín; 11 km intersección ruta 34 camino a Acambuco, (CML 6139). Anta Arroyo La Sala Centro Administrativo Parque Nacional El Rey (CML 6050). Corrientes (BMNH 24664). Santa Fe, Esperanza (BMNH 1241). BOLÍVIA. SANTA CRUZ, Ñuflo de

Chávez (MNKM 4527). Florida (MNKM 5658). PARAGUAY. Villa Rica (BMNH 1811).

*Eptesicus furinalis* ( $n = 56$ ). ARGENTINA. Chaco: Almirante Brown (CML 3220, 3221, 3225, 3226, 3850, 3854). Güemes (CML 5397). Córdoba: Cruz del Eje (BMNH 2251). Corrientes: Ituzaingó, San Borgita (BMNH 691246). Formosa: Bermejo (CML 3855-56). Pilcomayo (CML 4670); Río Bermejo (CML 5311). Estero Poi, Pto. Algarrobo (CML 4572). Jujuy: Laguna La Brea (CML 3085). Doctor Manuel Belgrano (CML 4312-13). Río Ledesma (CML 5223). Río de Sora (CML 5224). La Rioja: San Blas de los Sauces (CML5445). Misiones: Guaraní (CML 3857). Salta: Piquirenda Viejo (CML 5220, 522). Río Itiyuro (CML 5372). Oran: Santa María (CML 5221), Oran (CML 4331, 5142-45). Tucumán: Arroyo Aguas Chiquitas (CML 5225-27), Concepción (BMNH 25311). Río chico: Reserva Provincial Santa Ana (CML 5430). BOLIVIA. Beni: Reserva de la Paraba Barba Azul (MNKM 4982). Santa Cruz: Parque Kaa Iya, Cerro Cortado (MNKM 3440). Agua Rica (MNKM 4677-5692). Lajas (MNKM 4999). Pampa Grande (MNKM 5594). Buena Vista (BMNH 2612421). Estancia San Miguelito (MNKM 4546-47). San José de Chiquitos TCO Turubó Este (MNKM 4957-58-59). San Miguel (MNKM 4888-47). Parque Noel Kempff Mercado (MNKM 5565-95-96). Tarija: Parque Aguara Güe (MNKM 5597). COLOMBIA. Cundinamarca: Bogotá, Santa Fe De Bogotá (BMNH 711368). Cueva del Ermitaño (BMNH 991142). Tolima: Santana, Near Honda (BMNH 109238). Valle Del Cauca: Villa Carmelo (ICN 6298). Risaralda: Pueblo Rico, camino a la bocatomía (ICN 11519). GUYANA. Georgetown: Demerara (BMNH 51111).

*Eptesicus langeri* sp. nov. ( $n = 19$ ). BOLIVIA. Santa Cruz: Agua Rica (MNKM 5584 holotype, MNKM 5117, 5585, 4436, 5587, 5588, 5088, 5590, 5591, 4679, 5592, 5126, 4678, 5692 paratypes). Agua Clarita (MNKM 5586, 5589, 5676, 5636 paratypes). Reserva Municipal El Chape (MNKM 5697 paratype).

## Appendix 9

Comparison of diagnostic traits among six species of the genus *Eptesicus*.

Characters	<i>E. furinalis</i>	<i>E. andinus</i>	<i>E. langeri</i> sp. nov.	<i>E. chiriquinus</i>	<i>E. brasiliensis</i>	<i>E. ulapesensis</i>
Sagittal and nuchal crests	Joined	Separated	Separated	Joined	Joined	Joined
Development of sagittal and nuchal crests	Developed	Poorly developed	Developed	Well developed	Well developed	Well developed
Dorsal coloration	Dark or pale brown	Dark brown	Dark brown	Dark brown – oily black	Dark brown	Yellowish-brown
Dorsal fur length	< 7 mm	~ 9 mm	~ 8 mm	> 8 mm	< 9 mm	~ 6 mm
Bands of dorsal hair	Base almost black, tips light Brown, can change geographically	Dark Brown with lighter tips	Slightly bi-colored, dark base with lighter tips	Blackish, homogeneous	Base dark Brown with lighter tips	Base dark brown with tips brownish or goldish-yellowish
Bands of ventral hair	Base dark Brown, almost black, with yellowish tips	Strongly bi-colored, base dark and lighter tips “tanny color”	Base dark with lighter tips	Base dark Brown with lighter tips	Base dark Brown with paler tips (yellowish)	Base dark Brown with whitish tips
Preorbital process	Poorly developed	Poorly developed	Well developed	Moderately developed	Poorly developed	Poorly developed
Braincase	Straight and flattened	Enlarged and rounded	Elevated and rounded	High and developed due to the presence of cranial crests	Straight and flattened	Domed
Rostrum	Flattened and robust	Delicate and slender	Robust and inflated	Delicate and slender	Robust and inflated	Slightly flattened and robust



# Mitochondrial DNA indicates paraphyletic relationships of disjunct populations in the *Neotoma mexicana* species group

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Woodrats (genus *Neotoma*) comprise 24 species found primarily in the United States and México. The *Neotoma mexicana* species group reaches its southernmost distribution in the highlands of southern México and Central America. Previous research suggested that *N. mexicana* has a discontinuous distribution, whereas *N. ferruginea* and *N. picta* have allopatric distributions around the lowlands of the Isthmus of Tehuantepec. However, these hypotheses were suggested with incomplete subspecific sampling near the isthmus. We used samples of *N. m. parvidens* from the Sierra Sur de Oaxaca and *N. m. tropicalis* from the Sierra Norte de Oaxaca to assess their taxonomic affinity. Our phylogenetic analyses of the mitochondrial cytochrome-b gene place both subspecies in *N. ferruginea*. Therefore, we suggest that *N. mexicana* is continuously distributed from the United States to the Transmexican Volcanic Belt, *N. picta* inhabits the Guerreran Sierra Madre del Sur, and *N. ferruginea* ranges from the Oaxacan Sierra Madre del Sur to Central America. Our findings also indicate that the Isthmus of Tehuantepec did not promote speciation in these woodrats.

Las ratas de campo (género *Neotoma*) incluyen 24 especies que principalmente habitan en Estados Unidos de América y México. El grupo de especies *Neotoma mexicana* alcanza su distribución más sureña en las zonas montañosas del sureste de México y Centro América. Previas investigaciones sugirieron que *N. mexicana* presenta una distribución discontinua, mientras que *N. ferruginea* y *N. picta* tienen distribuciones alopatricas alrededor de las tierras bajas del Istmo de Tehuantepec. Sin embargo, estas hipótesis fueron sugeridas con un muestreo sub-específico incompleto cerca del istmo. Utilizamos muestras de *N. m. parvidens* de la Sierra Sur de Oaxaca y *N. m. tropicalis* de la Sierra Norte de Oaxaca para evaluar su afinidad taxonómica. Nuestros análisis filogenéticos del gen mitocondrial citocromo b revelaron que ambas subespecies pertenecen a *N. ferruginea*. Por lo tanto, sugerimos que *N. mexicana* se distribuye de manera continua desde Estados Unidos hasta la Faja Volcánica Transmexicana, *N. picta* habita en la Sierra Madre del Sur en Guerrero, y *N. ferruginea* se distribuye desde la Sierra Madre del Sur en Oaxaca hasta Centro América. Nuestros resultados también indican que el Istmo de Tehuantepec no promovió procesos de especiación en estas ratas de campo.

**Keywords:** Cytochrome b; Isthmus of Tehuantepec; molecular phylogeny; *Neotoma ferruginea*; Sierra Madre del Sur.

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## Introduction

The heterogenous topography of southern México, and Pleistocene climatic changes, generated complex biogeographic patterns and high species diversity in vertebrates (León-Paniagua and Morrone 2009; Morrone 2017), especially in small mammals (Vallejo and González-Cózatl 2012; Guevara and Cervantes 2014; León-Paniagua and Guevara 2019). Many of the region's mammals possess conservative morphologies; therefore, the number of species and their phylogenetic relationships are not entirely understood (Sullivan et al. 1997; Ordóñez-Garza et al. 2014; Pérez-Consuegra and Vázquez-Domínguez 2017). Without an adequate taxonomy, it is impossible to understand fundamental aspects of the processes that generate and maintain biodiversity (Upham et al. 2019).

Woodrats of the genus *Neotoma* comprise at least 24 species, distributed across portions of southern Canada and most of the continental United States and México, reaching Central America (Edwards and Bradley 2002a; Longhofer and Bradley 2006; Pardiñas et al. 2017). Although *Neotoma*

has been studied for almost 200 years, phylogenetic relationships and species limits are not entirely resolved (Edwards and Bradley 2002a; Longhofer and Bradley 2006; Matocq et al. 2007; Ordóñez-Garza et al. 2014) because some species and subspecies are rare and/or have restricted distributions that are poorly sampled (Rogers et al. 2011; Fernández 2014).

Taxonomic revisions (Merriam 1894; Goldman 1910) divided woodrats into several species groups, with only the *N. mexicana* species group reaching southern México and Central America (Pardiñas et al. 2017). The *N. mexicana* species group, as defined by Goldman (1910), included eight species: *N. chrysomelas*, *N. distincta*, *N. ferruginea* (with subspecies *N. f. ferruginea*, *N. f. chamula*, *N. f. isthmica*, *N. f. ochracea*, *N. f. picta*, *N. f. solitaria*, and *N. f. tenuicauda*), *N. mexicana* (subspecies *N. m. mexicana*, *N. m. bullata*, *N. m. fallax*, *N. m. madrensis*, *N. m. pinetorum*, and *N. m. sinaloae*), *N. navus*, *N. parvidens*, *N. torquata*, and *N. tropicalis*. Subsequently, *N. f. griseoverter* Dalquest, 1951; *N. f. vulcani* Sanborn, 1935; *N. m. atrata* Burt, 1939; *N. m. eremita* Hall, 1955;

*N. m. inopinta* Goldman, 1933; *N. m. inornata* Goldman, 1938; and *N. m. scopulorum* Finley, 1953 were also described. However, all species and subspecies in the *N. mexicana* species group, except *N. chrysomelas*, were relegated to subspecific status within *N. mexicana* by [Hall \(1955\)](#), and later, [Anderson \(1972\)](#) synonymized the subspecies *N. m. madrensis* with *N. m. mexicana*. As defined by these revisions, the *N. mexicana* species group inhabits montane areas from northern Colorado throughout much of New México and western Arizona south to western Nicaragua ([Edwards and Bradley 2002b](#); [Ordóñez-Garza et al. 2014](#)).

Although several studies have investigated the phylogenetic relationships among *Neotoma* species ([Edwards and Bradley 2002a](#); [Longhofer and Bradley 2006](#); [Matocq et al. 2007](#)), only two have focused on the *N. mexicana* species group ([Edwards and Bradley 2002b](#); [Ordóñez-Garza et al. 2014](#)). Using mitochondrial cytochrome b (*cyt-b*) sequences, [Edwards and Bradley \(2002b\)](#), and [Ordóñez-Garza et al. \(2014\)](#) concluded that this species group includes at least the species *N. mexicana* from the United States through northern and central México and south of the Transmexican Volcanic Belt in southeastern México and Central America, *N. picta* in the Sierra Madre del Sur from Guerrero, *N. ferruginea* from western portions of the Isthmus of Tehuantepec south to El Salvador, and *Neotoma chrysomelas*, which inhabits parts of Honduras and Nicaragua ([Pardiñas et al. 2017](#)). After these taxonomic changes, 19 subspecies of *N. mexicana* and four subspecies of *N. ferruginea* are recognized, whereas *N. picta* and *N. chrysomelas* are monotypic ([Pardiñas et al. 2017](#)).

Despite the progress on the systematics and phylogenetic relationships in the *N. mexicana* species group, no samples of some subspecies have been analyzed with genetic data. These include *N. m. parvidens*, *N. m. tropicalis* from Oaxaca, or *N. m. solitaria* from Central America, and these three subspecies, with disjunct geographic ranges, have remained in *N. mexicana* ([Edwards and Bradley 2002b](#); [Ordóñez-Garza et al. 2014](#); [Pardiñas et al. 2017](#); Figure 1). Nevertheless, [Edwards and Bradley \(2002b\)](#) suggested that individuals from southeastern Oaxaca and east of the Isthmus of Tehuantepec (possibly including *N. m. solitaria* from Guatemala and Honduras) are *N. ferruginea*, specimens from the Sierra Madre del Sur in Guerrero (and possibly including *N. m. parvidens* from the Sierra Sur de Oaxaca) are *N. picta*, and all samples in northern Oaxaca (possibly including *N. m. tropicalis* from Sierra Norte de Oaxaca and hills near the Chiapas border) represent *N. mexicana*. These taxonomic hypotheses, which placed the boundaries among the ranges of *N. mexicana*, *N. ferruginea*, and *N. picta* near the Isthmus of Tehuantepec, relied on the biogeographic recognition of this lowland area as an essential barrier that has promoted speciation in many other highland mammals species ([Woodman and Timm 1999](#); [Arellano et al. 2005](#); [León-Paniagua et al. 2007](#); [Ordóñez-Garza et al. 2010](#)).

Herein, we use samples of *N. m. parvidens* and *N. m. tropicalis* from the western Isthmus of Tehuantepec (Figure 1)

to test the taxonomic affinity of these subspecies. *Neotoma m. parvidens* and *N. m. tropicalis* are geographically isolated from other populations of *N. mexicana* (Figure 1). The type locality of *N. m. parvidens* is “Juquila, Oaxaca, México” and the *N. m. parvidens* sample (MZFC 11029) is from the same location: La Yerbabuena, Santa Catarina Juquila, Oaxaca (Figure 1). The type locality of *N. m. tropicalis* is the north-eastern Oaxacan mountains ([Goldman 1910](#)) in Totontepec ([Goldman 1904](#)). This subspecies only occurs in the Sierra Norte de Oaxaca and hills near the Chiapas border, and no other *Neotoma* inhabit this area ([Ordóñez-Garza et al. 2014](#); [Pardiñas et al. 2017](#)). The *N. m. tropicalis* sample (MZFC 8088) is from Xiacaba, 6.5 km ESE de Santa María Yavesía, Santa María Yavesía, Oaxaca, in the Sierra Norte de Oaxaca, around 36 km west of the type locality (Figure 1).

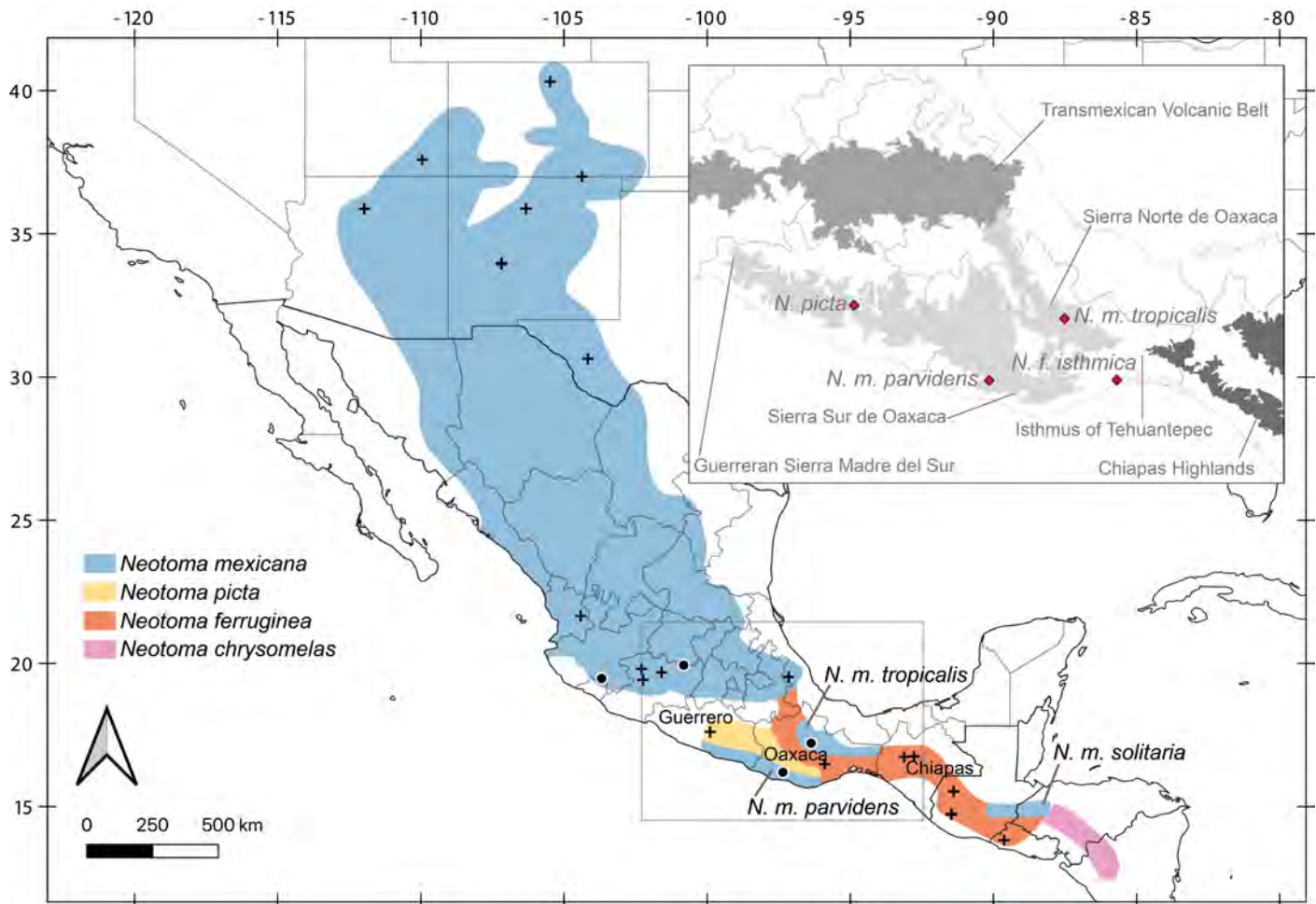
We sequenced the mitochondrial *cyt-b* because of its availability from a broad range of *N. mexicana* samples ([Edwards and Bradley 2002b](#); [Ordóñez-Garza et al. 2014](#)), and its proven utility to clarify relationships in *Neotoma* ([Edwards and Bradley 2002a](#)) and closely related genera ([Amman and Bradley 2004](#); [Arellano et al. 2005](#); [Bradley et al. 2007](#); [León-Tapia 2013](#); [Rogers et al. 2007](#); [Vallejo and González-Cózatl 2012](#)).

## Materials and methods

We sequenced 1,143 base pairs of the mitochondrial *cyt-b* in specimens of *N. m. parvidens* ( $n = 1$ ), *N. m. tropicalis* ( $n = 1$ ), *N. m. tenuicauda* ( $n = 2$ ), and *N. leucodon* ( $n = 1$ ). We examined the external and cranial morphology of these specimens to confirm their taxonomic identity ([Goldman 1904, 1910](#)). Voucher specimens are deposited in the mammal collection of the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México (MZFC; Appendix I). We also downloaded twenty-five sequences from GenBank: *N. mexicana* ( $n = 15$ ), *N. picta* ( $n = 2$ ), *N. ferruginea* ( $n = 7$ ), and *N. stephensi* ( $n = 1$ ; Appendix I; [Edwards and Bradley 2002b](#); [Ordóñez-Garza et al. 2014](#)).

**Molecular protocols.** We extracted whole genomic DNA using a Qiagen DNEasy Blood and Tissue kit (Qiagen, Germantown, Maryland), following the manufacturer’s recommended protocols. Through polymerase chain reaction (PCR), we amplified the complete *cyt-b* using the primers MVZ05 ([Smith and Patton 1993](#)) and H15915 ([Irwin et al. 1991](#)). Each PCR had a final reaction volume of 13  $\mu$ L and contained 6.25  $\mu$ L of GoTaq Green Master Mix (Promega, Madison, WI, USA), 4.75  $\mu$ L of H<sub>2</sub>O, 0.5  $\mu$ L of each primer [10 $\mu$ M], and 1  $\mu$ L of DNA stock. The PCR thermal profile included 2 minutes of initial denaturation at 95°C, followed by 38 cycles of 30 seconds of denaturation at 95°C, 30 seconds of annealing at 50°C, and 68 seconds for the extension at 72°C. We included a 5-minute final extension step at 72°C. We visualized 3  $\mu$ L of each PCR product using electrophoresis in 1% agarose gels, stained with SYBR Safe DNA Gel Stain (Life Technologies, Carlsbad, CA, USA). Each PCR product was then cleaned with 1  $\mu$ L of a 20 % dilution





**Figure 1.** Specimens analyzed in this study. Black circles represent samples sequenced in this work, whereas black crosses indicate previously published sequences. Map colors show previously suggested geographic ranges for the *N. mexicana* species group (Edwards and Bradley 2002b; Pardiñas et al. 2017). The inset shows all type localities from Guerrero and Oaxaca (red diamonds) and the main biogeographic regions. Localities of samples included in this work: *N. m. parvidens*, México: Oaxaca; Santa Catarina Juquila, La Yerbabuena (MZFC 11029); *N. m. tenuicauda*, México: Colima; Comala, La Yerbabuena (MZFC 11989); Michoacán; Zinapécuaro, Araró, Campo Alegre (MZFC 12327); *N. m. tropicalis*, México: Oaxaca; Santa María Yavesía, Xiacaaba, 6.5 km ESE de Santa María Yavesía (MZFC 8088).

of ExoSAP-IT (GE Healthcare Bio-Sciences Corp. Piscataway, NJ, USA) incubated for 30 minutes at 37°C followed by 15 minutes at 80°C. Samples were cycle-sequenced using 6.1 µL of H<sub>2</sub>O, 1.5 µL of 5x buffer, 1 µL of 10µM primer, 0.4 µL of ABI PRISM Big Dye v. 3.1 (Applied Biosystems, Foster City, CA, USA), and 1 µL of the cleaned template. The cycle-sequencing profile included 1 minute of initial denaturation at 96°C, followed by 25 cycles of 10 seconds for denaturation at 96°C, 5 seconds for annealing at 50°C, and 4 minutes for the extension at 60°C. Cycle sequencing products were purified using an EtOH-EDTA precipitation protocol and were read with an ABI 3130xl genetic analyzer (Applied Biosystems, Foster City, CA, USA). DNA sequences were edited, aligned, and visually inspected using MEGA X (Kumar et al. 2018) and FINCHTV 1.4 (Patterson et al. 2004).

**Phylogenetic relationships.** We used maximum likelihood (ML) and Bayesian inference (BI) to estimate the *N. mexicana* species group's phylogenetic relationships. We analyzed a total of 28 individuals in the *N. mexicana* species group with *N. leucodon* and *N. stephensi* as outgroups. We used both external groups because it is not clear if *N. stephensi*, or the clade that includes the species groups *N. floridana* + *N. lepida* + *N. micropus* (that includes *N. leucodon*),

is sister to the *N. mexicana* species group (Matocq et al. 2007). In PARTITIONFINDER 2 (Lanfear et al. 2016), we selected the best model and partition scheme (maximally divided by codon position) among all available models in MRBAYES 3.2 (Ronquist et al. 2012), using the Bayesian Information Criterion (BIC). We used this result for both ML and BI. In IQ-TREE 1.6.12 (Nguyen et al. 2015), we estimated the ML gene tree, with branch support estimated by 1,000 replicates of nonparametric bootstrap. In MRBAYES 3.2 we used three hot chains and one cold chain in two independent runs of 10 million generations, sampling data every 1,000 iterations. We checked for convergence of MCMC results by examining trace plots and sample sizes in TRACER 1.7 (Rambaut et al. 2018). The final topology was obtained using a majority rule consensus tree and considering a burn-in of 25 % (with effective sample sizes > 200).

To test whether our inferred best topologies are statistically superior to past taxonomic hypotheses, we constrained topologies to fit taxonomy (forcing the monophyly of *N. m. parvidens* or *N. m. tropicalis* and all other *N. mexicana* samples) and analyzed these in MRBAYES 3.2 (same settings as above). To compare the unconstrained BI and the constrained topologies, we used the Shimodaira-Hasegawa

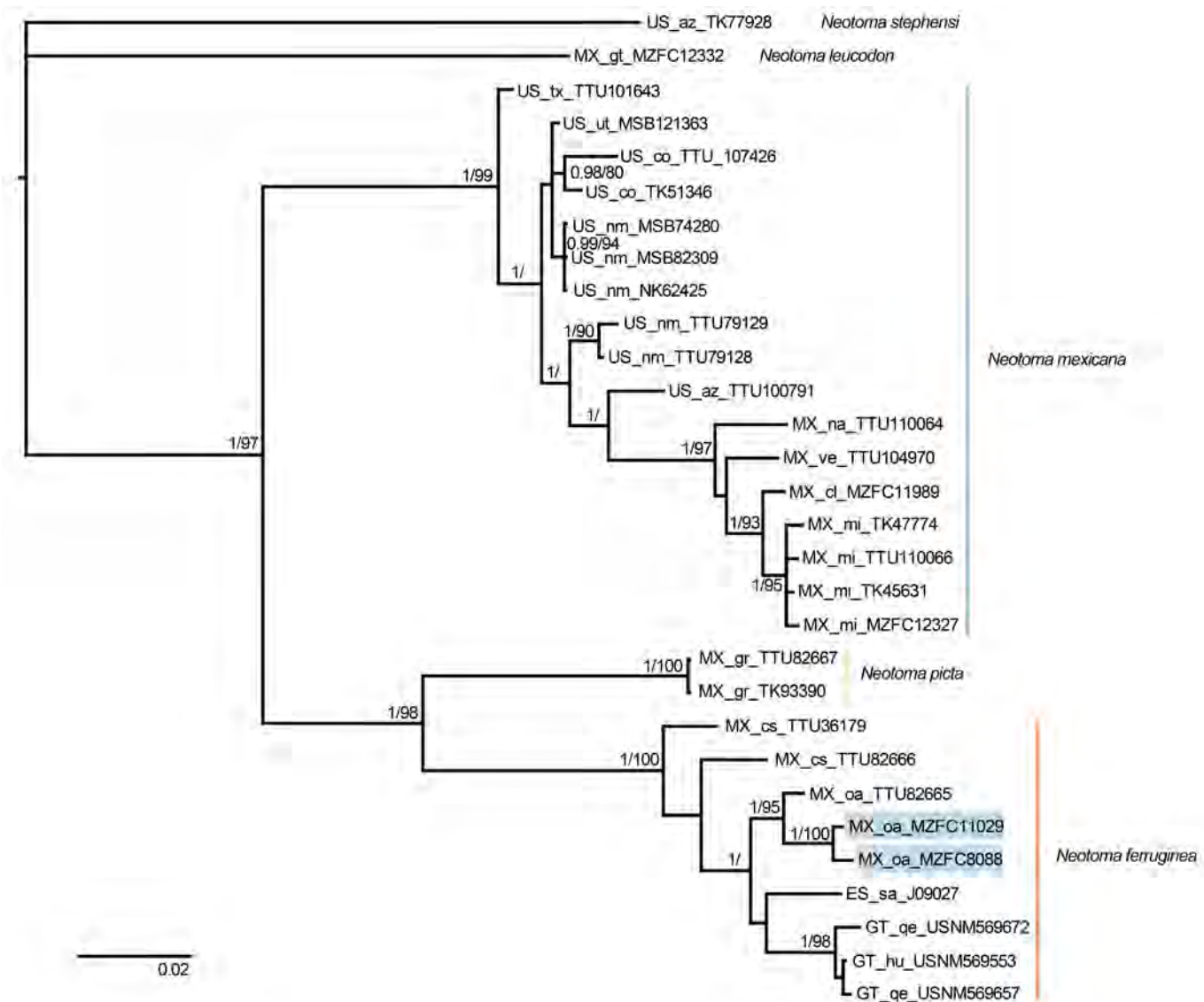
test (Shimodaira and Hasegawa 1999) as implemented in the package PHANGORN 2.5.5 (Schliep 2011) for R 3.6.2 (R Core Team 2014). We compared the likelihood fits assuming an HKY+G substitution model and 10,000 bootstrap replicates. We performed analyses with and without optimizing the rate matrices and base frequencies.

*Genetic differentiation and genetic diversity.* To evaluate differentiation levels among members of the *N. mexicana* species group, we calculated p-distances in MEGA X, using the pairwise deletion option and the Kimura 2-parameter model (Kimura 19804). These settings were chosen to facilitate comparisons with previous works (Bradley and Baker 2001; Baker and Bradley 2006; Ordóñez-Garza et al. 2014). To clarify whether intraspecific variation was correlated with geography, we performed a Mantel test on genetic distances (previously calculated in MEGA) and Euclidean geographic distances in the R package ADEGENET 2.1.3 (Jombart

2008; Jombart and Ahmed 2011). The Mantel test's significance was assessed using 99,999 permutations, and plots were colored by 2-dimensional kernel density estimation in the R package MASS 7.3-51.4 (Venables and Ripley 2002). To further characterize genetic diversity, we used DNASP 5.10 (Librado and Rozas 2009) to calculate the number of segregating sites, the number of haplotypes, haplotype diversity (*Hd*), and nucleotide diversity ( $\pi$ ) for each species.

### Results

Our alignment covered 100 % in > 97 % of positions, contained 290 variable characters, and 196 parsimony-informative characters. The best evolutionary model scheme was K80+G, HKY+I, and GTR+I applied to the first, second, and third codon positions, respectively. Topologies from ML and BI trees were similar (Figure 2), revealing well-supported sister relationships between *N. picta* (from the Guerreran Sierra



**Figure 2.** Majority rule consensus tree of the *Neotoma mexicana* species group, obtained from Bayesian analysis of cytochrome b sequences. Support values are shown as posterior probabilities followed by bootstrap values from a maximum likelihood analysis. Support values < 0.8/80 are not shown. Samples of *N. m. parvidens* (MZFC 11029) and *N. m. tropicalis* (MZFC 8088) are denoted with blue boxes within *N. ferruginea*. Tip labels show country (ES = El Salvador, GT = Guatemala, MX = México, US = the United States), states/provinces (sa = Santa Ana; hu = Huehuetenango, qe = Quetzaltenango; cl = Colima, cs = Chiapas, gr = Guerrero, gt = Guanajuato, mi = Michoacán, na = Nayarit, oa = Oaxaca, ve = Veracruz; az = Arizona, co = Colorado, nm = New Mexico, tx = Texas, ut = Utah), and catalog number.

Madre del Sur) and *N. ferruginea* (Oaxaca to Central America; ML and BI), with this clade sister to *N. mexicana* (from the United States to the Transmexican Volcanic Belt in central México; BI only). Our samples of *N. m. parvidens* (MZFC 11029) and *N. m. tropicalis* (MZFC 8088) were closely related to *N. ferruginea* rather than *N. mexicana*. The constrained analyses, which forced these subspecies to be members of *N. mexicana*, produced significantly worse likelihoods in both cases, with the optimized ( $P < 0.001$  for each subspecies) and not optimized ( $P < 0.001$  for each subspecies) data. Hence, the Shimodaira-Hasegawa test strongly rejected the placement of *N. m. parvidens* and *N. m. tropicalis* in *N. mexicana* (Table 1). In the following analyses, we included both specimens (MZFC 11029 and 8088) in *N. ferruginea*.

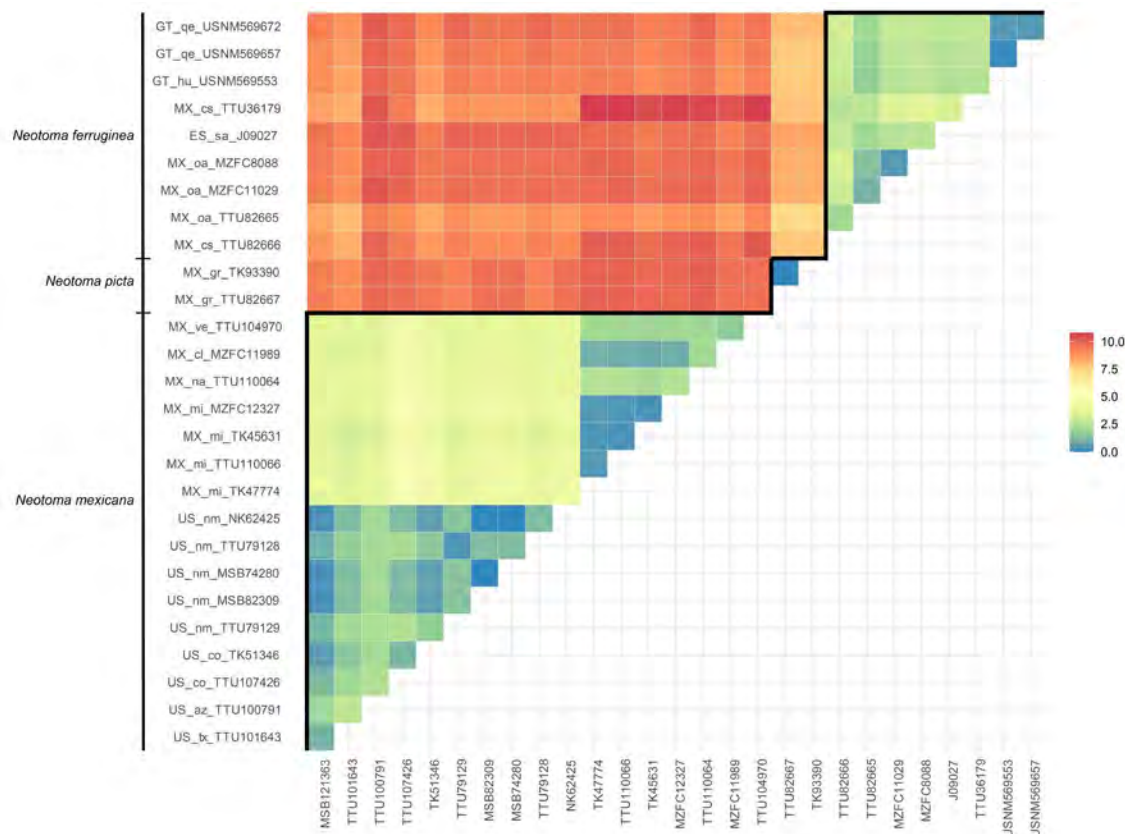
**Table 1.** Results of Shimodaira-Hasegawa tests of alternative phylogenetic hypotheses (unconstrained = obtained in this work from BI, constrained = monophyly of *N. m. parvidens* or *N. m. tropicalis* forced with all other *N. mexicana* samples), with and without optimizing the rate matrices and base frequencies. Asterisks indicate statistical rejection of topological equivalence ( $\alpha = 0.05$ ).

	No optimization			Optimization		
	In L	$\Delta$ L	P	In L	$\Delta$ L	P
Unconstrained	-4568.9	0.000	0.4965	-4089.1	0.000	0.4967
Constrained ( <i>N. m. parvidens</i> )	-4684.6	115.665	0.0000*	-4137.5	48.405	0.0000*
Constrained ( <i>N. m. tropicalis</i> )	-4683.2	114.291	0.0000*	-4136.8	47.736	0.0001*

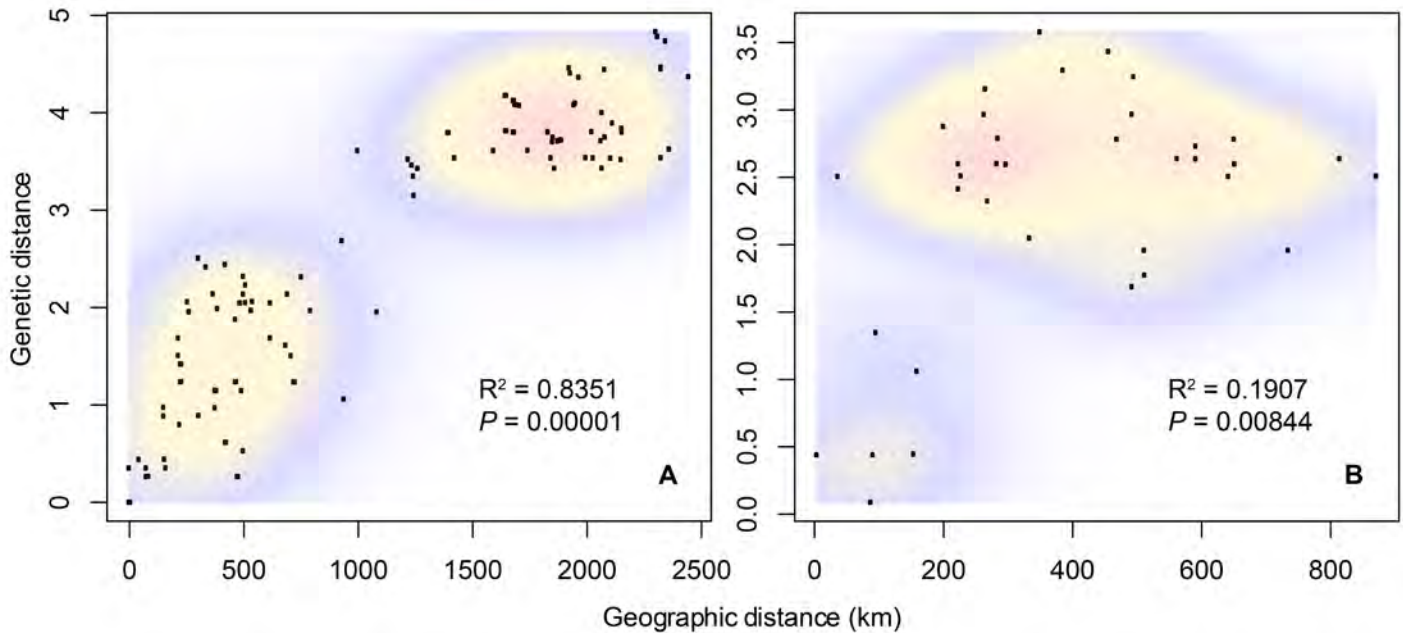
**Table 2.** Genetic diversity summary statistics for species in the *Neotoma mexicana* species group. n = sample size, S = number of segregating sites, h = number of haplotypes, Hd = haplotype diversity,  $\pi$  = nucleotide diversity, SD = standard deviation.

	n	S	h	Hd	SD (Hd)	$\pi$	SD ( $\pi$ )
<i>Neotoma mexicana</i>	17	99	15	0.978	0.031	0.025	0.002
<i>Neotoma picta</i>	2	0	1	0	0	0.000	0.000
<i>Neotoma ferruginea</i>	9	72	9	1	0.052	0.023	0.003

The average mitochondrial distance between *N. mexicana* and *N. picta* was 9.68 % (range = 8.97 to 10.1), between *N. mexicana* and *N. ferruginea* was 9.46 % (range = 8.02 to 10.81), and between *N. picta* and *N. ferruginea* was 7.94 % (range = 7.79 to 7.98). Within species, the average genetic distance between the Chiapan and all other samples in *N. ferruginea* was 2.91% (range = 2.05 to 3.3), and between the Mexican and the United States *N. mexicana* samples was 3.86 % (range = 3.15 to 4.83; Figure 3). The Mantel tests revealed significant isolation by distance among *N. mexicana* ( $P = 0.00001$ ,  $R^2 = 0.8351$ ) and *N. ferruginea* ( $P = 0.00844$ ,  $R^2 = 0.1907$ ; Figure 4). Finally, in *N. mexicana* and *N. ferruginea* we found high haplotype diversity values ( $Hd = 0.978$  and 1, respectively), but within each species, all haplotypes were similar ( $\pi = 0.025$  and 0.023, segregating sites = 99 and 72, respectively). In *N. picta* the two analyzed specimens had the same haplotype (Table 2).



**Figure 3.** Heat map showing Kimura 2-parameter genetic distances in the *N. mexicana* species group. Interspecific and intraspecific comparisons are shown above and below the black line, respectively. Geographic information is shown on the y-axis (ES = El Salvador, GT = Guatemala, MX = México, US = the United States; sa = Santa Ana, hu = Huehuetenango, qe = Quetzaltenango; ci = Colima, cs = Chiapas, gr = Guerrero, gt = Guanajuato, mi = Michoacán, na = Nayarit, oa = Oaxaca, ve = Veracruz; az = Arizona, co = Colorado, nm = New Mexico, tx = Texas, ut = Utah).



**Figure 4.** Bi-variate plots of geographic and genetic distances of A) *Neotoma mexicana*, and B) *Neotoma ferruginea*. Warmer colors indicate higher point densities. Mantel test results are shown.

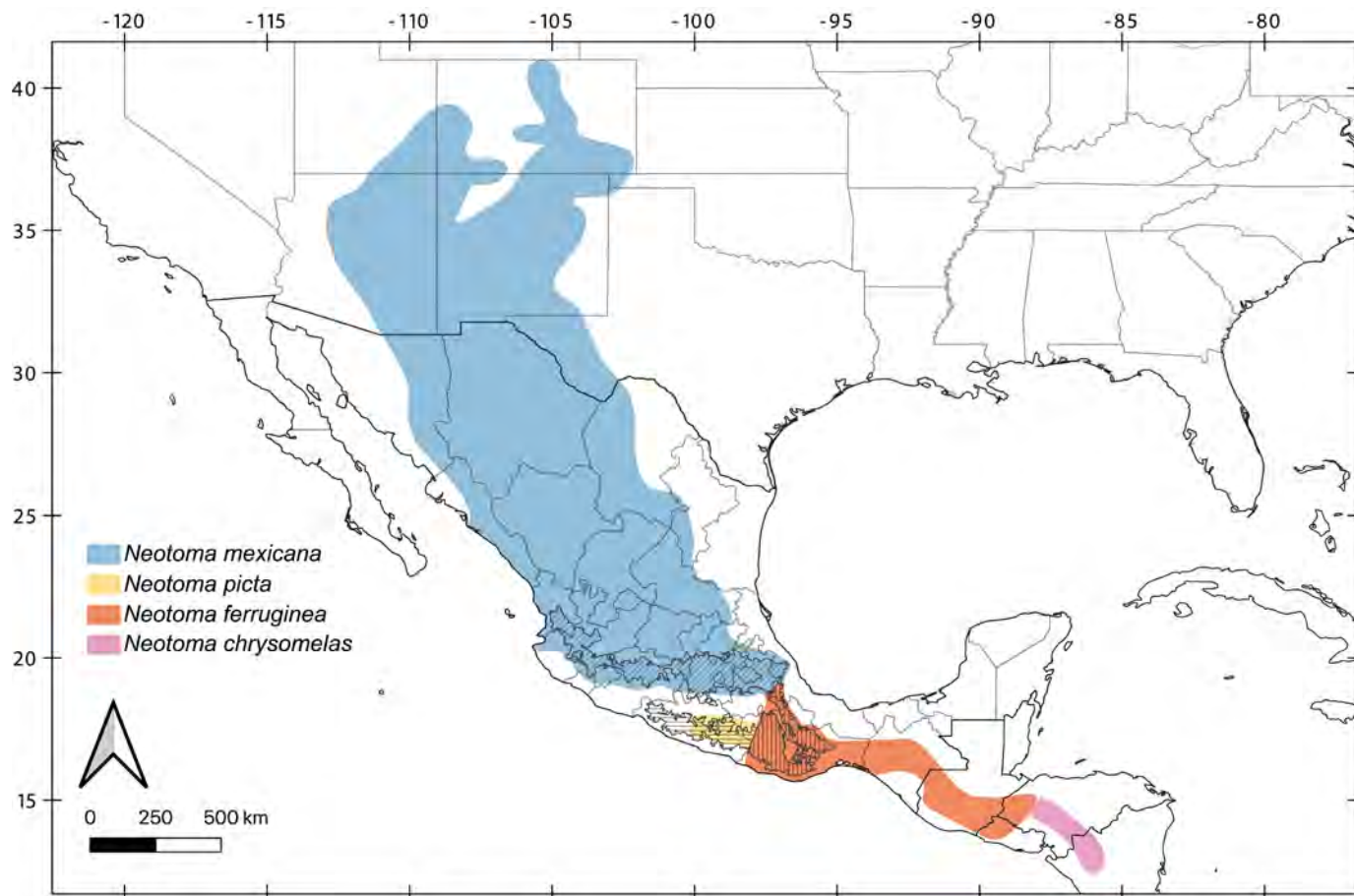
## Discussion

Although woodrats are regionally typical, taxa in the *N. mexicana* group are poorly known regarding their systematics and ecology (Edwards and Bradley 2002b). Previous analyses pointed out the possibility that the Isthmus of Tehuantepec promoted diversification in this species group because individuals from the eastern Isthmus were assigned to *N. ferruginea*, those from the Guerreran Sierra Madre del Sur and, possibly from Sierra Sur the Oaxaca, were referred to *N. picta*, and individuals from northern Oaxaca were designated *N. mexicana* (Edwards and Bradley 2002b). However, our results reject these taxonomic hypotheses. We found that *N. ferruginea* is paraphyletic, both *N. m. parvidens* from the Sierra Sur de Oaxaca and *N. m. tropicalis* from Sierra Norte de Oaxaca are related to *N. ferruginea* rather than *N. mexicana* or *N. picta*. For taxonomy to reflect evolutionary history, the parvidens and tropicalis subspecies should be considered populations of *N. ferruginea*. With these taxonomic modifications, species boundaries in the *N. mexicana* species group no longer lie near the Isthmus of Tehuantepec, and *N. ferruginea* spans this biogeographic barrier. As such, we find no evidence that the isthmus promoted speciation or maintains long-term geographic isolation in this species group. Our conclusions are based on high levels of mitochondrial DNA divergence and backed by morphological evidence (see below), but should be further tested in future works using independently sorting nuclear loci.

Our placement of parvidens and tropicalis in *N. ferruginea* (Figures 2, 3, 4, Table 1) is consistent with Goldman's (1910) conclusions. Although *N. f. parvidens* and *N. f. tropicalis* were considered independent species in his monograph, he described both taxa as members of the "ferruginea section" inhabiting mountain slopes of southwestern and northeast Oaxaca, respectively (Goldman 1910). The geographic ranges we suggest herein eliminate some of

the previously proposed geographic disjunctions, and they align well with some common biogeographic boundaries. Firstly, the southern geographic limit of *N. mexicana* is located in the Transmexican Volcanic Belt (Figure 5), a biogeographic barrier to many other Nearctic species (Morrone 2019). We detected intraspecific genetic variation consistent with isolation by distance (Figures 3 and 4A). Secondly, in southern México, *Neotoma picta*, *N. f. parvidens*, and *N. f. tropicalis* inhabit the eastern Sierra Madre del Sur sub-province, because the Sierra Sur de Oaxaca and the Sierra Norte de Oaxaca are also part of the eastern Sierra Madre del Sur. A recent biogeographical study of the eastern Sierra Madre del Sur suggested that it comprises two areas, the Guerreran and the Oaxacan Highlands districts, each one supported by many local endemic taxa (Santiago-Alvarado et al. 2016; Morrone 2017). We suggest that *N. picta* inhabits the Guerreran district of the Eastern Sierra Madre del Sur sub-province, whereas *N. ferruginea* inhabits a large area from the Oaxacan highlands district across the Isthmus of Tehuantepec to Central America (Figure 5).

A previous dated phylogenetic analysis inferred Late Pleistocene diversification in the *N. mexicana* group and suggested that habitat expansion and contraction promoted diversification (Ordóñez-Garza et al. 2014). We detected low levels of nucleotide diversity but high levels of haplotype diversity (Table 2), a pattern consistent with recent demographic expansions (Hedrick 2011), so the hypothesized effect of Pleistocene habitat cycles on this species group is consistent with our results. Additionally, we found intraspecific genetic differentiation from 1.68 to 3.58 % in *N. ferruginea* across the Isthmus of Tehuantepec. These lowlands are a minimally 200-km-wide valley at approximately 250 meters above sea level (Barrier et al. 1998), representing a significant barrier for many montane species (Peterson et al. 1999). However, the Isthmus of Tehuantepec did not



**Figure 5.** Revised geographic ranges within the *N. mexicana* species group. Guerreroan Sierra Madre del Sur district is shown as horizontal hashes, Oaxacan highlands district as vertical hashes, and Transmexican Volcanic Belt with diagonal hashes (Morrone 2017).

promote speciation in these woodrats because its genetic differentiation seems more related to geographic distances rather than geographic barriers (Figure 4B), there is not a clear and supported geographic structure in the phylogenetic inferences (Figure 2), and because the most different individuals were detected in Chiapas and not between eastern and westernmost populations (Figure 3). Interestingly, a Chiapan Pleistocene refugium has been suggested in other mammal studies (Guevara-Chumacero et al. 2010; Gutiérrez-García and Vázquez-Domínguez 2012). Future phylogeographic studies on *N. ferruginea* could test for signals of a Pleistocene refuge in the highlands of Chiapas, which could have served as a source for the Oaxacan and Central American populations.

Finally, *N. m. solitaria* from Guatemala and Honduras's uncertain placement, as a subspecies of *N. mexicana* or *N. ferruginea* has been previously mentioned (Ordóñez-Garza et al. 2014; Pardiñas et al. 2017). *Neotoma m. solitaria* was initially described as a subspecies of *N. ferruginea* with a small body size, and short, bright fur (Goldman 1905), but it was relegated to subspecific status within *N. mexicana* by Hall (1955) without a formal analysis. Subsequent revisions on the *N. mexicana* species group showed that the lumping of its members obscured the real diversity and evolutionary history of these woodrats (Edwards and Bradley 2002b; Ordóñez-Garza et al. 2014). Although we did not analyze

samples of *N. m. solitaria*, previous morphological descriptions (Goldman 1910), and the geographic ranges of the *N. mexicana* species group members (Figure 5) suggest the best available option is to re-assign *N. m. solitaria* to *N. ferruginea*.

Although our results rely on a small data set, the inclusion of novel samples from type localities improved resolution of the evolutionary history and geographic limits of *N. mexicana* species group members. The species ranges we propose are geographically coherent and separated by standard biogeographic boundaries. A continued sampling of wild populations is needed to provide a rigorous understanding of southern Mexican mammals' diversity and endemism.

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## Appendix I

### Specimens analyzed in this work

Taxon	GenBank	Catalog #	Tissue #	Country	State/Province	Lat	Long
<i>Neotoma leucodon</i>	MW419110	MZFC 12332	3814	México	Guanajuato	21.583	-100.993
<i>Neotoma stephensi</i>	AF308867	TTU 78505	TK 77928	US	Arizona	34.737	-110.043
<i>Neotoma mexicana inopinata</i>	AF298841	MSB 121363	NK 36282	US	Utah	37.592	-109.955
<i>Neotoma mexicana mexicana</i>	AF294346	TTU 101643	TK 90038	US	Texas	30.639	-104.166
<i>Neotoma mexicana pinetorum</i>	FJ716222	TTU 100791		US	Arizona	35.874	-111.972
<i>Neotoma mexicana scopulorum</i>	FJ716223	TTU 107426		US	Colorado	40.321	-105.484
<i>Neotoma mexicana scopulorum</i>	AF186821	DMNH 8577	TK 51346	US	Colorado	37.002	-104.369
<i>Neotoma mexicana scopulorum</i>	AF294345	TTU 79129	TK 78350	US	New Mexico	35.883	-106.324
<i>Neotoma mexicana scopulorum</i>	AF298848	MSB 74280	NK 62439	US	New Mexico	33.990	-107.181
<i>Neotoma mexicana scopulorum</i>	AF298849	TTU 79128	TK 78349	US	New Mexico	35.883	-106.324
<i>Neotoma mexicana scopulorum</i>	AF298846	MSB 82309	NK 62415	US	New Mexico	33.944	-107.187
<i>Neotoma mexicana scopulorum</i>	AF298847		NK 62425	US	New Mexico	33.943	-107.186
<i>Neotoma mexicana tenuicauda</i>	MW419114	MZFC 11989	4442	México	Colima	19.478	-103.683
<i>Neotoma mexicana tenuicauda</i>	AF298843		TK 47774	México	Michoacán	19.809	-102.290
<i>Neotoma mexicana tenuicauda</i>	KF772877	TTU 110066		México	Michoacán	19.427	-102.244
<i>Neotoma mexicana tenuicauda</i>	AF298842		TK45631	México	Michoacán	19.689	-101.591
<i>Neotoma mexicana tenuicauda</i>	MW419113	MZFC 12327	4581	México	Michoacán	19.942	-100.820
<i>Neotoma mexicana tenuicauda</i>	KF772878	TTU 110064		México	Nayarit	21.660	-104.421
<i>Neotoma mexicana torquata</i>	KF801364	TTU 104970		México	Veracruz	19.527	-97.156
<i>Neotoma picta</i>	AF305568	TTU 82667	TK93384	México	Guerrero	17.612	-99.896
<i>Neotoma picta</i>	AF305569		TK 93390	México	Guerrero	17.612	-99.896
<i>Neotoma ferruginea chamula</i>	AF305567	TTU 82666	TK 93296	México	Chiapas	16.755	-92.773
<i>Neotoma ferruginea chamula</i>	KF772876	USNM 569553		Guatemala	Huehuetenango	15.535	-91.393
<i>Neotoma ferruginea ferruginea</i>	KF772873	JGO 9027		El Salvador	Santa Ana	13.827	-89.625
<i>Neotoma ferruginea isthmica</i>	AF298840	TTU 36179	TK 20551	México	Chiapas	16.738	-93.117
<i>Neotoma ferruginea isthmica</i>	AF329079	TTU 82665	TK 93257	México	Oaxaca	16.486	-95.893
<i>Neotoma ferruginea parvidens</i>	MW419111	MZFC 11029	4123	México	Oaxaca	16.203	-97.355
<i>Neotoma ferruginea tropicalis</i>	MW419112	MZFC 8088	2604	México	Oaxaca	17.216	-96.367
<i>Neotoma ferruginea vulcani</i>	KF772874	USNM 569657		Guatemala	Quetzaltenango	14.752	-91.463
<i>Neotoma ferruginea vulcani</i>	KF772875	USNM 569672		Guatemala	Quetzaltenango	14.721	-91.481



# Relative abundance and habitat selection of the montane guinea pig *Cavia tschudii* in a wetland at coastal desert with comments on its predators

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*Cavia tschudii* inhabits coastal and Andean wetlands where it is important prey for medium carnivores, but its habitat selection and its role in the wetlands are unknown. In order to reduce this lack of knowledge, we evaluated changes in the abundance for two seasons and the habitat selection of *C. tschudii* in a wetland on the central coast of Peru. Additionally, we report information on their movement distances and provide comments on their predators. We carried out six evaluations during the autumn and spring of 2019, with nine grids in three plant communities: grassland, bulrush community, and cattail community. Each captured individual was marked with a numbered ear tag. We compared the relative abundance between seasons using the Mann-Whitney U test, and calculated the relative abundance per evaluated month and carried out regressions to model its behavior. The use/availability of habitat was evaluated with the Chi-square test together with Bonferroni confidence intervals to show habitat selection. Finally, we estimate the mean maximum distance moved (MMDM) of recaptured individuals. The results show significant differences between the seasons, with higher relative abundance in autumn. The relative abundance showed a peak in April, from which the values decrease. Likewise, we found significant differences in habitat selection, showing positive selection for the cattail community, neutral selection for the bulrush community, and negative selection for the grassland. The MMDM was  $36.5 \pm 15.7$  m. We report a decrease in the relative abundance of *C. tschudii*, possibly related to seasonal changes in habitat quality or to the presence of predators. The peak of abundance in mid-autumn and the apparent decrease in the population until late spring resembles the annual dynamics reported for *C. aperea*. It is also confirmed that *C. tschudii*, like other *Cavia*, select environments with greater plant coverage, possibly as an anti-predation strategy. We report dogs predating *C. tschudii* and provide a list of other potential predators. This study increases the information on *C. tschudii* in coastal wetlands and gives a first approach to the necessary knowledge for its management and conservation within these fragile ecosystems.

*Cavia tschudii* habita humedales costeros y andinos donde es presa importante de carnívoros medianos, pero su selección de hábitat y su rol en los humedales son desconocidos. Con el fin de disminuir estos vacíos de información, evaluamos cambios en la abundancia de *C. tschudii* durante dos estaciones del año y su selección de hábitat en un humedal de la costa central del Perú. Adicionalmente, reportamos información sobre sus movimientos y ofrecemos comentarios sobre sus depredadores. Realizamos seis evaluaciones durante el otoño y primavera de 2019; con nueve cuadrantes en tres comunidades vegetales: gramadal, juncal y totoral. Cada individuo capturado fue marcado con un arete numerado. Comparamos las abundancias relativas entre estaciones mediante la prueba de U de Mann-Whitney. Además, calculamos las abundancias relativas por mes evaluado y realizamos regresiones para modelar su comportamiento. Evaluamos el uso/disponibilidad del hábitat con la prueba Chi-cuadrado junto con intervalos de confianza de Bonferroni para evidenciar selección de hábitat. Además, estimamos el promedio de distancias máximas de movimiento (MMDM). Los resultados muestran diferencias significativas entre las estaciones, siendo la abundancia relativa mayor en otoño. La abundancia relativa mostró un pico en abril, a partir del cual los valores descienden. Asimismo, encontramos diferencias significativas en la selección de hábitat, mostrando selección positiva por el totoral, selección neutra por el juncal y selección negativa por el gramadal. El MMDM fue de  $36.5 \pm 15.7$  m. Reportamos una disminución en la abundancia relativa de *C. tschudii*, posiblemente relacionados a cambios estacionales en la calidad de hábitat o en la presencia de depredadores. El pico de abundancia a mediados de otoño y el aparente decrecimiento de la población hasta fines de la primavera, se asemeja a dinámicas anuales reportadas en *C. aperea*. Confirmamos también que *C. tschudii*, similar a otros *Cavia*, prefiere ambientes con mayor cobertura vegetal; posiblemente como una estrategia anti-depredación. Reportamos perros depredando *C. tschudii* y proveemos una lista de otros depredadores potenciales. Este estudio incrementa la información sobre *C. tschudii* en humedales costeros y da un primer acercamiento al conocimiento necesario para su manejo y conservación dentro de estos ecosistemas frágiles.

**Keywords:** Habitat selection; movement distance; Ramsar wetland; relative abundance; small mammal.

## Introducción

*Cavia tschudii* es la especie de cuy silvestre que originó a su doméstico *C. porcellus* (Dunnum y Salazar-Bravo 2010). Esta especie se distribuye principalmente en los Andes del Perú, Bolivia, Chile y Argentina, con un rango desde los 0 a 4500 msnm. Habita humedales costeros, andinos y pastizales donde es una importante presa de carnívoros medianos (Dunnum 2015). A nivel internacional, su estado de conservación es Preocupación Menor de acuerdo a la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN; Dunnum y Teta 2016); sin embargo, el conocimiento sobre las poblaciones de esta especie es escaso. Al límite sur de su distribución, en Argentina y Chile, ha sido categorizado como una especie con Datos Insuficientes (Cirignoli 2019) y Rara (Ministerio de Agricultura 1998, 2015) respectivamente por los escasos registros, desconocimiento general sobre el estado de sus poblaciones y de las amenazas que pueden afectar a las poblaciones que habitan el territorio de cada país. En Bolivia, Tarifa et al. (2010) evidencian la falta de información sobre su ecología; especialmente sobre la abundancia y densidad poblacional de *C. tschudii*.

En Perú, se conoce su presencia en las ecorregiones de serranía esteparia, puna y desierto costero (Pacheco et al. 2009). En esta última ecorregión, los cuyes silvestres habitan los humedales costeros, ecosistemas que son considerados de acuerdo con la legislación peruana como ecosistemas frágiles de conservación prioritaria (Congreso de la República 2005). A pesar de ello, estos ecosistemas son continuamente afectados principalmente por la agricultura y la ganadería (Aponte y Ramirez 2011), así como por otros procesos antropogénicos como la urbanización, cambio de uso de suelo e incendios (Aponte et al. 2015; Gonzales et al. 2019; Flores et al. 2020). Particularmente en este tipo de ambientes la información es escasa; los estudios publicados solo abordan registros de presencia de la especie (Zeballos 2010; Pacheco et al. 2015), un reporte de amenaza por incendios (Ramirez et al. 2018) y un caso de albinismo (Ramirez et al. 2019).

El Refugio de Vida Silvestre Los Pantanos de Villa (Pantanos de Villa) es un Área Natural Protegida (ANP) amenazada por la creciente presión urbana (SERNANP 2016) y el único humedal costero del departamento de Lima donde se ha reportado la especie (Pacheco et al. 2015). Este humedal es importante por su belleza paisajística, la gran diversidad biológica que alberga y por ser un lugar esencial en el recorrido migratorio para numerosas especies de aves a lo largo de la región Neotropical. Por ello, los estudios en esta ANP se han enfocado principalmente en su vegetación y sus aves (Cano et al. 1993; Wust et al. 1994; Ramirez y Cano 2010; Pulido 2018; Flores et al. 2020).

En este sentido, con el fin de aumentar el conocimiento sobre las poblaciones de *C. tschudii* en los humedales costeros, nos planteamos dos objetivos: evaluar cambios en la abundancia de *C. tschudii* en el humedal Pantanos de Villa durante otoño y primavera del 2019 y su selección de hábitat dentro de este humedal costero. Adicionalmente,

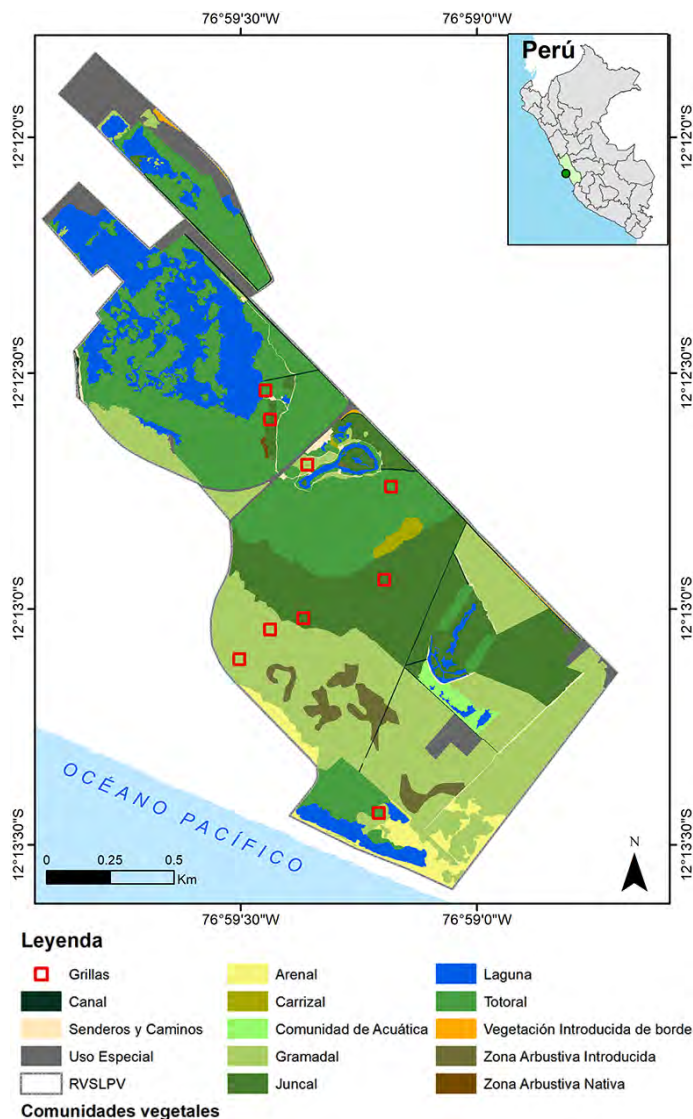
proveemos comentarios sobre depredadores potenciales y confirmados de *C. tschudii* en el área de estudio y reportamos información sobre el movimiento de sus individuos.

## Materiales y métodos

Área de estudio. Pantanos de Villa se ubica en el departamento y provincia de Lima (Perú), en el distrito de Chorrillos, entre los kilómetros 18 y 21 de la antigua carretera panamericana sur ( $-12^{\circ} 11' 42''$ ,  $-12^{\circ} 13' 18''$  S,  $-76^{\circ} 58' 42''$ ,  $-76^{\circ} 59' 42''$  W; Figure 1). El área se encuentra rodeada de zonas urbanas, clubes campestres, un club hípico y una universidad. El ecosistema comprende una superficie de 263 ha (Ministerio de Agricultura 2006). Debido a que el humedal es un refugio de aves migratorias, fue reconocido internacionalmente a partir del 20 de febrero de 1997 como un humedal de importancia internacional o sitio RAMSAR. En el 2006 fue recategorizado a nivel nacional como Refugio de Vida Silvestre. El ecosistema está conformado por seis espejos de agua de diferentes tamaños (Laguna Mayor, Laguna Génesis, Laguna ANAP, Laguna Marvilla, Laguna Las Garzas y Laguna La Pampa), dos canales principales que abastecen de agua a todo el humedal, un afloramiento y zonas pantanosas con abundante materia orgánica de origen vegetal y terrenos calcáreos-arenosos (Ramirez et al. 2018).

El clima se caracteriza por una estación húmeda durante los meses de julio y septiembre (temperatura media: 15 a 17 °C) y una estación seca entre diciembre y abril (temperatura media: 23 a 25 °C). La ausencia de lluvias en la costa central peruana es casi constante, oscilando entre 0 y 5.5 mm de precipitación total mensual promedio (Ministerio del Ambiente 2015; Pulido 2018). Con el fin de comparar este estudio con otros estudios poblacionales del género *Cavia*, consideramos las estaciones de otoño y primavera, comprendiendo el otoño los meses antes de la época húmeda (de marzo a junio) y la primavera los meses posteriores a la época húmeda (de septiembre a diciembre). El otoño se caracteriza por ser una transición entre la época seca y húmeda, donde las temperaturas medias van descendiendo según avanzan los meses (de los 23 °C a los 19 °C). Por el contrario, en la primavera las temperaturas van aumentando con el avance de los meses (de 17 °C a 22 °C; CORPAC S. A. 2020; SENAMHI 2020).

La vegetación predominante es de tipo herbácea y está representada por comunidades vegetales como totorales (66.1 ha), juncales (52.2 ha), gramadales (73.4 ha), zonas arbustivas (5.8 ha) y acuáticas (1.8 ha; Cano y Young 1998; Aponte et al. 2018). En el presente estudio evaluamos tres tipos de vegetación: 1) gramadal; vegetación típicamente dominada por *Distichlis spicata* y menos frecuente por *Sporobolus virginicus* "grama salada", especies que alcanzan alturas de 50 a 70 cm y presentan coberturas cercanas al 60 a 80 %; en algunos sectores puntuales del humedal el gramadal es dominado por *Paspalum vaginatum* "grama dulce" con presencia de un suelo más húmedo y terroso (Figure 2a). 2) juncal; comunidad vegetal dominada por *Schoenoplectus americanus* "junco" que alcanza alturas de



**Figura 1.** Ubicación del Refugio de Vida Silvestre Los Pantanos de Villa (Lima, Perú), comunidades vegetales que lo componen y distribución de grillas de muestreo dentro del área de estudio.

1.0 a 1.5 m y presenta coberturas cercanas al 100 %; en algunos juncuales se puede observar una codominancia con *D. spicata*; el sustrato donde se desarrolla esta comunidad se encuentra húmedo a saturado y depende de la dinámica del agua subterránea para su distribución en el humedal (Figure 2b). 3) totoral; comunidad vegetal dominada por *Typha domingensis* "totora" de 2.0 a 2.5 m de altura, la especie puede cubrir rápidamente los espacios libres en los bordes de los cuerpos de agua y presenta coberturas cercanas al 80 a 100 %; el sustrato de esta comunidad se caracteriza por estar siempre saturado o inundado; la vegetación se desarrolla principalmente en los bordes de las lagunas o cubriendo canales de escorrentía lenta (Figure 2c). No evaluamos las zonas arbustivas por su poca extensión y por no hallar indicios de la presencia del cuy silvestre (Aponte et al. 2018; Quispe-López obs. pers.).

**Diseño de muestreo.** Realizamos evaluaciones mensuales durante seis meses, abarcando el otoño (de marzo a mayo) y la primavera (de septiembre a diciembre) del 2019. En cada

evaluación establecimos nueve cuadrantes, colocando tres por cada comunidad vegetal (totoral, juncal, gramadal; Figure 1); excepto por el gramadal en las dos primeras evaluaciones, donde contó sólo con una grilla en la primera evaluación y con dos en la segunda. Los cuadrantes estuvieron activos cinco días continuos por evaluación. Cada cuadrante consistió en un arreglo de 3 x 4 trampas Tomahawk abarcando un área de 30 x 40 m<sup>2</sup>. Cada trampa fue cebada con una mezcla de hojas de alfalfa y conejina humedecida (alimento balanceado para conejo), y cubierta con la vegetación circundante para reducir el estrés en los individuos capturados.

La distancia entre cuadrantes continuos fue 310 ± 222 m (promedio ± SD) (distancia mínima 113 m, distancia máxima 804 m). Buscamos distanciar los cuadrantes al menos 125 m por ser la longitud máxima de área de acción registrada para *C. aerea* (Asher et al. 2004). Sin embargo, por lo relativamente pequeña del área de estudio dos cuadrantes se distanciaron 113 m. Al respecto, utilizando el marcaje de individuos durante este estudio, obtuvimos el valor promedio de distancias máximas de movimiento (mean maximum distance moved, MMDM) y lo consideramos un proxy del área de acción (Wilson y Anderson 1985; Karanth y Nichols 1998); basados en ello, confirmamos que el distanciamiento mínimo entre cuadrantes fue suficiente para este estudio (ver resultados). Calculamos el esfuerzo de muestreo multiplicando el número de trampas activas por el número de noches que las trampas estuvieron activas, obteniendo la cantidad de trampas/noche (T/N; Grinnell 1914; Lim y Pacheco 2016).

**Captura de individuos.** Cada individuo capturado fue marcado con un arete de código único (ear tag 1005-1, National Band & Tag Co., Kentucky, Estados Unidos) y liberado en el mismo punto de captura (Figure 2d), permitiéndonos distinguir las recapturas. El estrés observado en los animales capturados fue reducido cubriendo las trampas antes de cada manipulación. Durante las recapturas no observamos daños causados por los aretes. Los métodos descritos fueron previamente aprobados por la autoridad nacional SERNANP (RJ-RVSLPV N°005-2019-SERNANP-JEF), la autoridad municipal PROHVILLA (carta de consentimiento, 04-04-2019) y por el comité ético de la Universidad Científica del Sur (constancia N° 38-CIEI-AB-CIENTIFICA-2019). Asimismo, seguimos los lineamientos de la American Society of Mammalogists para el uso de mamíferos silvestres en investigación y educación (Sikes et al. 2016).

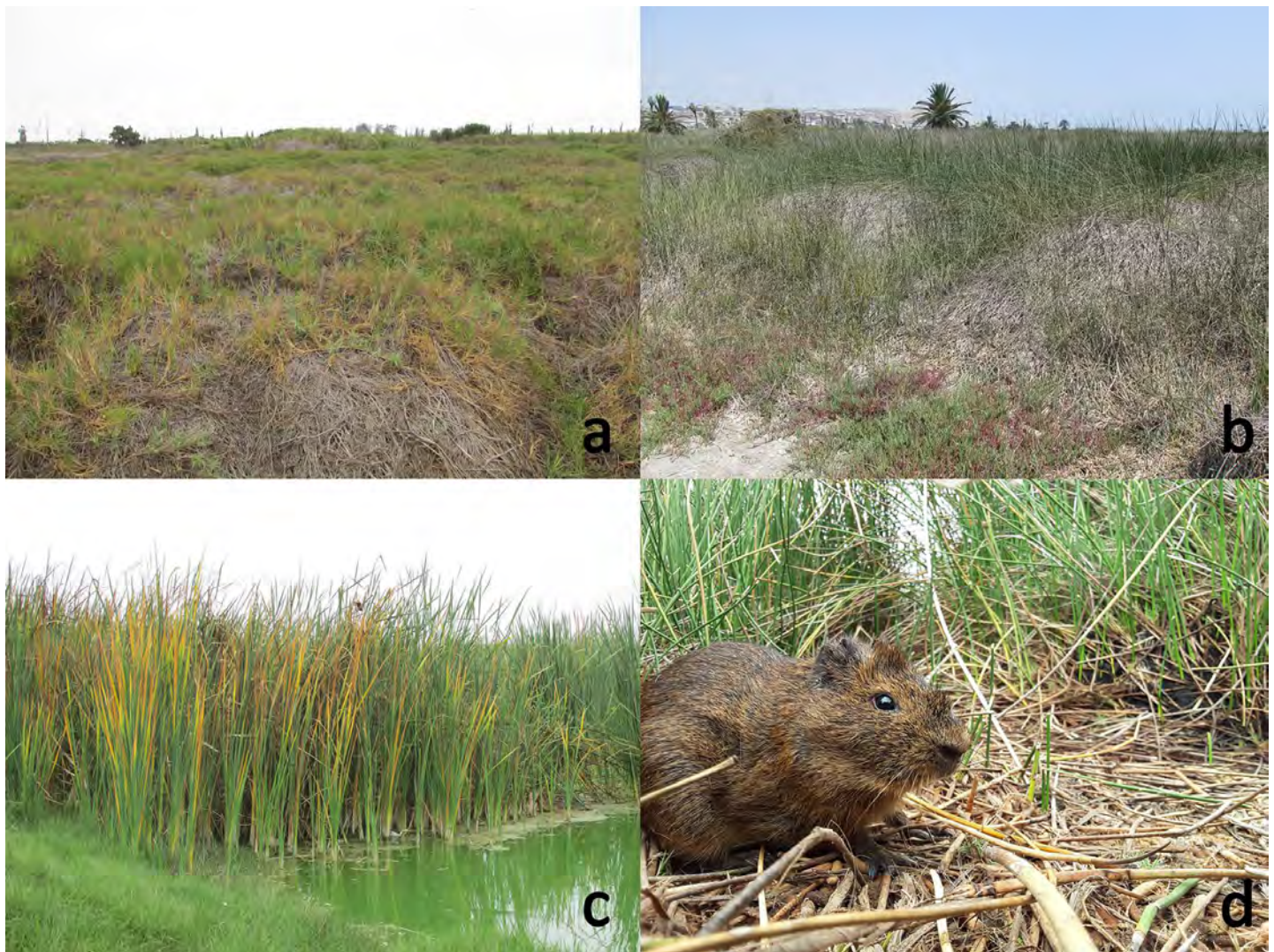
**Cambios en la abundancia.** Para evaluar cambios en la abundancia de *C. tschudii* comparamos las abundancias relativas entre las estaciones de otoño y primavera. Calculamos las abundancias relativas con el índice de capturabilidad (W; Pucek 1981). Dicho índice estandariza el esfuerzo de muestreo expresando la abundancia relativa como el número de individuos capturados por cada 100 trampas-noche (Pacheco et al. 2007; Salas et al. 2013). Las comparaciones las hicimos por cada comunidad vegetal y agrupando las tres comunidades vegetales; obtuvimos la significancia mediante la prueba estadística U de Mann-Whitney en el software Minitab 17 (2010).

Para evaluar los cambios mensuales graficamos y modelamos el comportamiento de la muestra de población que obtuvimos durante el periodo de estudio realizando múltiples regresiones no polinómicas seguidas de un proceso de selección de modelos; las variables utilizadas fueron la abundancia relativa y el tiempo (en meses, se consideró el primer mes de muestreo como el mes 1); para ello, se utilizó el coeficiente de correlación ( $r$ ), el coeficiente de determinación ( $R^2$ ) y el Criterio de Información de Akaike (AIC). El mejor modelo fue aquel que tuvo un AIC más bajo (que representa un modelo de mejor calidad) y un  $R^2$  y  $r$  más cercano a la unidad (que nos indica que ese modelo representa mejor la distribución de la data evaluada). Todo este procedimiento fue realizado mediante la función Curve finder del programa Curve Expert Professional 2.6.5 (Hyams 1996).

**Selección de hábitat.** Consideramos el hábitat como un ambiente delimitado por las asociaciones vegetales (Hall et al. 1997), las capturas como un indicador de uso de hábitat y la disponibilidad como el área de las comunidades vegetales estudiadas. La existencia de selección negativa o rechazo, y selección positiva de *C. tschudii* hacia alguna

comunidad vegetal fue evaluada determinando las diferencias entre los valores del uso y la disponibilidad de hábitat con la prueba de Chi-cuadrado de bondad de ajuste donde los datos observados son las capturas por hábitat y los datos esperados son calculados con la multiplicación entre el área relativa del tipo de hábitat y el número total de individuos (Byers et al. 1984). Las áreas de cada comunidad vegetal fueron tomadas del mapa de vegetación del humedal (Aponte et al. 2018). Cuando estas diferencias fueron estadísticamente significativas, se calcularon los intervalos simultáneos de Bonferroni al 95 % de confianza a partir del número de individuos observados y el área relativa de cada comunidad vegetal (Neu et al. 1974; Byers et al. 1984).

**Promedio de distancias máximas de movimiento (MMDM).** Calculamos el MMDM de *C. tschudii* para ambas temporadas y por cada temporada por separado. Para ello utilizamos la siguiente fórmula (Williams et al. 2002):  $\bar{d} = \sum_{i=1}^m d_i / m$ . Donde  $\bar{d}$  = Promedio de distancias máximas de movimiento,  $m$  = número de individuos capturados al menos dos veces,  $d_i$  = distancia máxima entre lugares de captura de cada individuo  $i$  capturado al menos dos veces.



**Figura 2.** Comunidades vegetales evaluadas en el Refugio de Vida Silvestre los Pantanos de Villa y ejemplar de *Cavia tschudii*. a. Gramadal. b. Juncal. c. Totoral. d. *C. tschudii* liberado en su punto de captura.

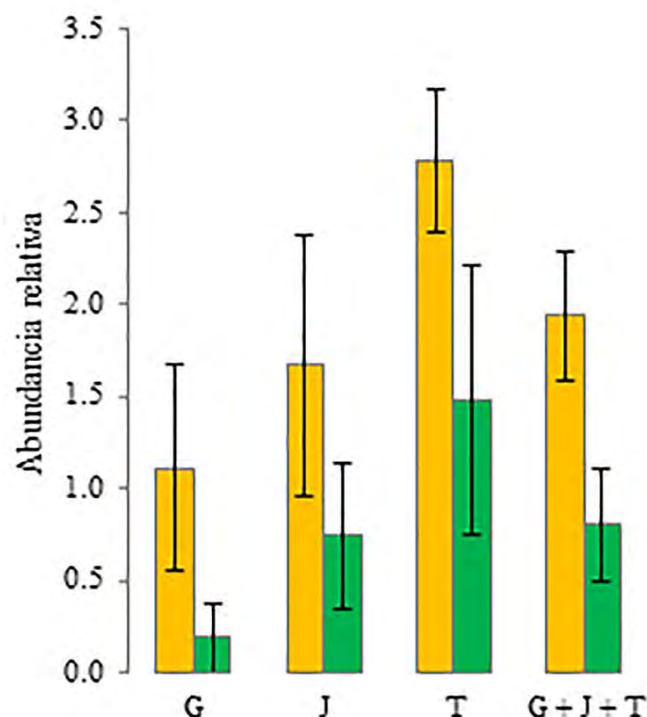
**Comentarios sobre depredadores.** Reportamos evidencias de depredación observadas durante el trabajo de campo. Asimismo, revisamos la literatura publicada sobre rapaces presentes en Pantanos de Villa (Pulido 2018) y elaboramos un cuadro (Apéndice 1) señalando los potenciales depredadores de *C. tschudii* en base a reportes de consumo de especies del género *Cavia* en otros lugares, o consumo de otros roedores.

### Resultados

Con un esfuerzo de muestreo total de 3,060 trampas/noche (T/N) obtuvimos 43 capturas de 33 individuos; incluyendo 15 machos, 15 hembras y 3 indeterminados. Veinticinco individuos fueron capturados durante el otoño (1,440 T/N) y 11 durante la primavera (1,620 T/N; Tabla 1). Seis individuos fueron recapturados a lo largo del estudio, tres fueron recapturados una vez, dos recapturados dos veces, y sólo un individuo fue recapturado tres veces.

**Cambios en la abundancia.** Al comparar el otoño y la primavera en cada comunidad vegetal las abundancias relativas promedio siempre fueron mayores en otoño (Figure 3). Sin embargo, el test de Mann-Whitney no soportó estas diferencias (gramadal  $P = 0.11$ ; juncal  $P = 0.282$ ; totoral  $P = 0.107$ ). Por otro lado, al agrupar los datos de las tres comunidades vegetales y compararlos entre las dos estaciones, se hallaron diferencias significativas ( $P < 0.01$ ) siendo la abundancia relativa mayor en otoño (Figure 3).

Durante los meses evaluados registramos un pico de abundancia relativa en abril a partir del cual los valores descendieron (Figure 4). Por otro lado, el proceso de selección de modelos brindó la puntuación más alta a tres modelos: el modelo de DR-Hill, el modelo Morgan-Mercer-Flodin (MMF), y el modelo de Weibull. Dichos modelos mostraron los mismos valores de  $r$  (0.96),  $R^2$  (0.93) y AIC (-3.34) que les brindan confianza matemática. Las tres ecuaciones muestran la disminución de la población en el período de estudio. Por la menor complejidad de la ecuación escogimos describir el modelo MMF (Figure 4); la ecuación obtenida es la siguiente:  $y = ab + cx^d / b + x^d$ . Donde  $x$  = es el tiempo en meses;  $y$  = la abundancia relativa;  $a = 8.02$ ;  $b = 9.35$ ;  $c = -2.22$  y  $d = -1.9$ .



**Figura 3.** Abundancias relativas (promedio ± IC) de *Cavia tschudii* en Pantanos de Villa durante otoño y primavera del 2019. Comparaciones por cada comunidad vegetal y considerando las tres comunidades juntas. Las abreviaciones son: G, gramadal; J, juncal; T, totoral. Otoño (de marzo a mayo; naranja); Primavera (de septiembre a diciembre, verde).

acción escogimos describir el modelo MMF (Figure 4); la ecuación obtenida es la siguiente:  $y = ab + cx^d / b + x^d$ . Donde  $x$  = es el tiempo en meses;  $y$  = la abundancia relativa;  $a = 8.02$ ;  $b = 9.35$ ;  $c = -2.22$  y  $d = -1.9$ .

**Selección de hábitat.** El valor obtenido de Chi-cuadrado ( $X^2$ ) fue de 14.10 ( $n = 43$ ;  $P < 0.01$ ;  $g. l. = 2$ ). Un análisis de los datos obtenidos encuentra que el totoral fue el hábitat más usado de lo esperado, evidenciando selección positiva. Por el contrario, el gramadal fue la comunidad vegetal donde *C. tschudii* tuvo una proporción de uso menor a lo esperado, mostrando una selección negativa. El juncal no presentó diferencias significativas entre su disponibilidad y el uso de los cuyes silvestres (Tabla 2).

**Promedio de distancias máximas de movimiento.** Considerando ambas temporadas obtuvimos un MMDM de  $36.5 \pm 15.7$  m (promedio ± SD), siendo la mayor distancia máxima de movimiento registrados para un mismo individuo de 54.8 m en los totorales. El MMDM en otoño fue de  $27.2 \pm 14.9$  m y en primavera  $34.8 \pm 8.8$  m. La distancia máxima de movimiento de un mismo individuo en otoño fue 43.6 m y en primavera 44 m. Teniendo en cuenta que ningún individuo capturado en una grilla fue recapturado en otra grilla distinta, confirmamos que el distanciamiento mínimo establecido entre grillas fue suficiente para este estudio.

**Comentarios sobre depredadores.** Durante el trabajo de campo observamos evidencias que señalarían a los perros como uno de los principales depredadores de cuyes silvestres dentro de Pantanos de Villa. Observamos al menos 10 perros distintos formando grupos que recorrían el área de estudio revisando senderos y madrigueras de *C. tschudii*.

**Tabla 1.** Número de individuos capturados de *Cavia tschudii* en tres comunidades vegetales de Pantanos de Villa durante otoño y primavera del 2019.

Mes	Comunidad vegetal			Sexo		Total
	Gramadal	Juncal	Totoral	♂	♀	
<b>Otoño</b>						
Marzo	2	2	5	2	5	9*
Abril	1	4	6	3	7	11*
Mayo	1	3	4	3	5	8
<b>Primavera</b>						
Septiembre	0	2	2	2	2	4
Noviembre	1	2	3	5	1	6
Diciembre	0	0	3	2	1	3
Total	5	13	15	15	15	33

\*Contando individuos de sexo indeterminado.

**Tabla 2.** Resultados del uso y disponibilidad de hábitat de *Cavia tschudii* en 3 comunidades vegetales diferentes. Los signos de uso significan: (+) selección positiva, (-) rechazo o selección negativa y (n.s.) no hay selección.

Comunidad vegetal	Área total (ha) <sup>1</sup>	Uso observado	Uso esperado	Proporción de uso observado (p <sub>i</sub> )	Proporción de uso esperado	Intervalos de Bonferroni
Gramadal	73.4	5	16	0.116	<b>0.383 (-)</b>	0.00 ≤ p <sub>i</sub> ≤ 0.23
Juncal	52.2	14	11	0.326	0.272 (n.s.)	0.16 ≤ p <sub>i</sub> ≤ 0.50
Totoral	66.12	24	15	0.558	<b>0.345 (+)</b>	0.38 ≤ p <sub>i</sub> ≤ 0.74

<sup>1</sup>Tomado de Aponte *et al.* (2018).

Asimismo, dentro de los totorales hallamos un refugio con cachorros de perros y carcasas de cuyes silvestres; y en una ocasión pudimos observar directamente perros cazando un cuy silvestre.

Entre las rapaces presentes resaltan *Tyto alba* y *Parabuteo unicinctus* por ser residentes de la zona y tener reportes donde especies del género *Cavia* han sido la presa principal en cuanto a biomasa consumida (Vargas *et al.* 2002; Aliaga-Rossel y Tarifa 2005; Salvador 2012; Gómez y Lires 2015).

## Discusión

**Cambios en la abundancia.** Nuestros resultados muestran una disminución en la población de *C. tschudii* a nivel de las tres comunidades vegetales juntas, donde la mayor abundancia fue durante el otoño. Al no haber otros estudios sobre variación en poblaciones de *C. tschudii*, no es posible complementar estos resultados para la especie. No obstante, existen estudios de este tipo en otras especies del mismo género las cuales muestran que algunas de sus especies siguen un patrón estacional. Galante y Cassini (1994) y Bilenca *et al.* (1995) encontraron fluctuaciones estacionales en las densidades de poblaciones de *C. aperea* en Argentina. Los picos de densidad más altos ocurrieron a finales de otoño e inicios de invierno, declinaron durante el invierno y alcanzaron sus niveles más bajos en primavera o verano; a partir del cual, los valores de densidad volvieron a incrementar hasta llegar a un nuevo pico en otoño. Nuestros resultados sugieren un patrón parecido: la abundancia relativa tuvo sus valores más altos durante el otoño (marzo y abril), empezó a descender a finales de esta temporada (mayo), y alcanzaría sus valores más bajos durante el invierno y primavera (de junio a diciembre; Figure 4). De cumplirse este patrón, las abundancias relativas empezarían a aumentar durante el verano, alcanzando nuevamente sus valores más altos durante el otoño. Sin embargo, para poder confirmar un patrón estacional, son necesarios estudios que abarquen todo el año durante más años.

Las dinámicas estacionales en especies del género *Cavia* son principalmente atribuidas a la disminución de la calidad de hábitat (Galante y Cassini 1994; Bilenca *et al.* 1995) o a la presión por depredación (Kraus y Rödel 2004). Respecto a la disminución de calidad de hábitat, las especies vegetales dominantes en humedales como Pantanos de Villa sufren una disminución de biomasa durante las épocas secas (Mitsch *et al.* 2009; López-Rosas y Moreno-Casasola 2012). Este cambio puede interpretarse como una disminución en la calidad de hábitat para *C. tschudii* pues disminuiría la calidad de alimento y la cobertura vegetal que los protege de

depredadores, incrementando la mortalidad y disminuyendo el número de individuos. Por otro lado, respecto a cambios en la presión por depredación, se ha reportado que *C. magna* presenta estacionalidad en su abundancia debido a cambios estacionales en la presencia de *Galictis cuja* (Kraus y Rödel 2004). Una dinámica parecida podría estar ocurriendo en Pantanos de Villa, donde algunas de las aves rapaces siguen hábitos migratorios (Pulido y Bermúdez 2018). El cambio estacional en la presencia de estas aves rapaces podría propiciar cambios estacionales en la abundancia de *C. tschudii*.

**Selección de hábitat.** Este trabajo es el primer estudio realizado sobre selección de hábitat de *C. tschudii*, por lo que resulta complejo mostrar semejanzas con otras investigaciones. Sin embargo, muchos estudios muestran que otras especies del género *Cavia* también seleccionan hábitats caracterizados por su densa cobertura. Asher *et al.* (2004) evidenciaron selección positiva de *C. aperea* para una vegetación densa de largas cañas de más de 3 m de longitud, crecidas en áreas húmedas como las orillas de un lago o pequeños arroyos en Brasil. En Argentina, Guichón y Cassini (1998) no encontraron diferencias significativas sobre el uso de hábitat por *C. aperea* respecto a la disponibilidad de plantas que consumen, pero sí a los ambientes con cobertura vegetal de más de 1.5 m de longitud. Asimismo, las otras especies de roedores que habitan Pantanos de Villa, también fueron más abundantes en los totorales, aunque no se evaluó selección de hábitat (Pacheco *et al.* 2015). Este patrón de comportamiento podría deberse a una estrategia anti-depredación. Ebensperger y Hurtado (2005) explican que el animal que selecciona un ambiente con cobertura vertical busca protección frente a los depredadores aéreos a costa de su visibilidad lateral, facilidades en el escape y la detección de depredadores terrestres.

La selección negativa de *C. tschudii* por los gramadales, puede deberse también a la presencia de potenciales depredadores. Pulido *et al.* (2020) analizaron la selección de hábitat de las aves residentes y migratorias del ANP, evidenciando el siguiente comportamiento de las aves rapaces: todas las especies de la familia Accipitridae y de los ordenes Falconiformes y Strigiformes estaban presentes en los gramadales; todos los falcónidos y cinco de los seis accipitriformes fueron encontrados en la vega de ciperáceas (entendida como juncales para el presente estudio) y no hubo registros de ningún falcónido, accipitriforme o strigiforme en los totorales. Por otro lado, durante el trabajo en campo observamos evidencias de depredación de cuyes silvestres por parte de perros en los tres hábitats eval-



uados, siendo más recurrente su presencia en los gramadales. [Amaro y Goyoneche \(2017\)](#) atribuyeron que la disminución de nidos de aves en Pantanos de Villa se debe a la presencia de especies introducidas como perros, caballos y actividades humanas. Sin embargo, se necesitan estudios que evidencien dicho impacto en la selección de hábitat y población del cuy silvestre.

Dentro de los juncales y gramadales, hemos observado que *C. tschudii* mostraría otras estrategias para disminuir el riesgo de exposición a depredadores como el uso de madrigueras, las cuales no fueron vistas en los totorales. Asimismo, en el humedal de Caucato (Ica, Perú), se ha observado a *C. tschudii* realizar actividades de forrajeo en grupo a cortas distancias desde la zona con mayor cobertura vegetal (V. Pacheco obs. pers.). Ambos comportamientos también fueron reportados en *C. aperea* ([Asher et al. 2004](#); [Cassini 1991](#)).

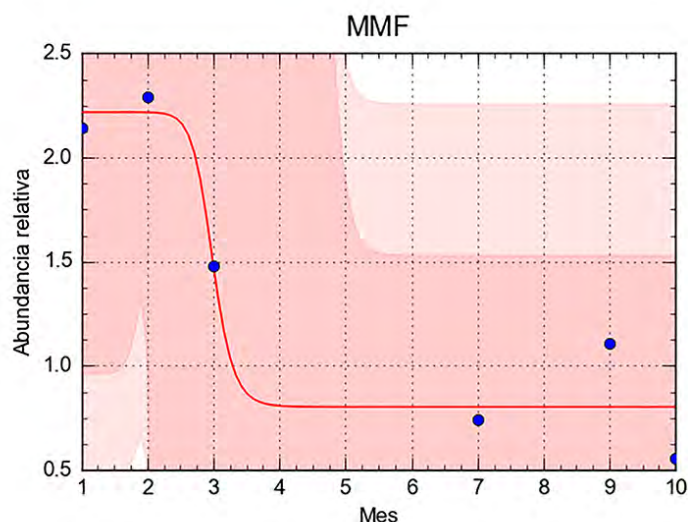
Desde el punto de vista de la conservación, se destaca que *C. tschudii* muestre un mayor uso de hábitat en totorales y juncales, pues ambas comunidades vegetales se han visto afectadas por amenazas como la fragmentación de su hábitat e incendios antrópicos ([Pulido 2018](#); [Ramirez et al. 2018](#)). En este contexto, recomendamos fortalecer el plan de manejo de estas comunidades vegetales para evitar su degradación, pues probablemente son hábitats fuente y de gran calidad para *C. tschudii*. Adicionalmente, es resaltante que el hábitat seleccionado por *C. tschudii* sea un ambiente con suelos frecuentemente saturados de agua o inundados. A la fecha no hay estudios que documenten alguna adaptación de *C. tschudii* que le permita minimizar la pérdida de calor al mojarse, un problema al que son susceptibles los mamíferos pequeños por su limitada capacidad de termorregulación ([Hull 1973](#)).

**Promedio de distancias máximas de movimiento.** Al no haber reportes del MMDM para otros *Cavia* no fue posible comparar adecuadamente el valor obtenido en este estudio para *C. tschudii*, aun así, mencionaremos algunos estudios que reportan información de movimiento en *Cavia*. [Rood \(1972\)](#) reporta para *C. aperea* el promedio de longitud de rango observado (la distancia entre los cuadrantes más exteriores en los que fue observado un mismo individuo), alcanzando  $48 \pm 7$  m para machos y  $47 \pm 8$  m para hembras. Dicho valor es cercano a lo registrado en este estudio, sin embargo, por corresponder a una metodología distinta, no se puede señalar si el movimiento de *C. aperea* fue mayor o menor que el de *C. tschudii*. En estudios con telemetría, [Asher \(2004\)](#) reporta áreas de acción para *C. aperea* con distancias máximas de alrededor de 125 m, siendo mucho mayor a lo reportado aquí para *C. tschudii*; sin embargo, estos *C. aperea* habitaban parches de vegetación alargados que bordeaban un lago, explicando la gran diferencia de valores. Es posible que los *C. tschudii* en Pantanos de Villa tengan áreas de acción más circulares debido a lo extenso de las comunidades vegetales que habitan. Por otro lado, el MMDM y la distancia máxima de movimiento fueron mayores en primavera, esto podría estar relacionado con una mayor escasez de recursos, correspondiendo también con el descenso de la abundancia

reportado en este estudio. Sin embargo, son necesarios estudios de telemetría para poder esclarecer los distintos aspectos de sus áreas de acción.

**Comentarios sobre depredadores.** Los perros observados durante el estudio probablemente se traten de individuos cimarrones debido a la presencia de cachorros dentro del área natural ([Silva et al. 2018](#)). [Kraus y Rödel \(2004\)](#) sostienen que los principales depredadores de *C. magna* son otros mamíferos. Del mismo modo, los perros podrían estar ocupando este rol con *C. tschudii* en nuestra área de estudio, pues dentro del área no se han reportado mamíferos silvestres que los puedan depredar ([Pacheco et al. 2015](#)).

En este estudio encontramos una disminución en la abundancia relativa de *C. tschudii* durante el periodo de evaluación y sugerimos que este cambio puede ser parte de una dinámica estacional donde la abundancia estaría respondiendo a cambios estacionales de la calidad de hábitat o de la presión por depredación, como ha sido observado en otras especies del género *Cavia*. Sin embargo, son necesarios estudios a largo plazo para entender la dinámica de la población, pues también pueden ser ciclos normales de la especie. Por otro lado, identificamos una selección positiva por los ambientes con mayor cobertura vegetal y altura como los totorales, mientras que en ambientes menos protectores como los gramadales y juncales *C. tschudii* podría estar usando otras estrategias anti-depredación como el uso de madrigueras y actividades de forrajeo en grupo. Asimismo, reportamos perros, probablemente cimarrones, como depredadores de *C. tschudii* y presentamos una lista de aves rapaces como potenciales depredadores de esta especie. En este sentido, este estudio contribuye a la escasa información actual sobre *C. tschudii*, brindando un primer acercamiento al conocimiento necesario para el manejo y conservación de esta especie dentro de ecosistemas frágiles como los humedales costeros.



**Figura 4.** Modelo de regresión Morgan-Mercer-Flodin (MMF) ajustado a la abundancia relativa de *Cavia tschudii* por mes evaluado durante el 2019 en Pantanos de Villa (mes 1: marzo; mes 10: diciembre; meses 4, 5, 6 y 8 no evaluados).

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## Apéndice 1

Lista de depredadores potenciales de *Cavia tschudii* presentes en los Pantanos de Villa y el tipo de presa reportada en la literatura.

	<i>C. tschudii</i>	<i>Cavia</i> spp.	Otros roedores
<i>Canis lupus familiaris</i>	Este estudio		
<i>Asio flammeus</i>		Jaksic y Simontetti 1987	
<i>Athene cucularia</i>		Sánchez et al. 2008	
<i>Buteo platypterus</i>			Fitch 1974
<i>Buteo polyosoma</i>			Bó et al. 2007
<i>Buteogallus meridionalis</i>			Mader 1982
<i>Caracara plancus</i>		Idoeta y Roesler 2012	
<i>Circus cinereus</i>		Baladrón et al. 2012	
<i>Falco femoralis</i>			Bó et al. 2007
<i>Falco peregrinus</i>			Bó et al. 2007
<i>Falco sparverius</i>			Bó et al. 2007
<i>Geranoaetus melanoleucus</i>		Pinto et al. 2002	
<i>Glaucidium peruanum</i>			Cadena-Ortiz et al. 2013
<i>Milvago chimachima</i>			De La Ossa et al. 2018
<i>Parabuteo unicinctus</i>		Gómez y Lires 2015	
<i>Tyto alba</i>		Aliaga-Rossel y Tarifa 2005	



# Characterization of assemblages in neotropical cave dwelling bats based on their diet, wing morphology, and flight performance

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Bats have a great variety of wing morphologies that determines the bat's flight performance, and this in turn conditions the forage aerosphere and the food it can obtain. Several studies have shown differences in wing morphology, flight performance, and forage aerospheres among species from different trophic guilds. However, for species that share a guild this is not entirely clear. It is possible that these species have differences in their diet and show changes in wing morphology that modify their flight performance and forage areas. Determining this will allow a better understanding of spatial segregation among species that share a trophic guild. These studies allow the identification of species assemblages based on wing morphological differences and flight performance that would not be distinguished only by guild membership. Our goal was to define the species assemblages that make up a community of Neotropical cave dwelling bats based on their trophic guild, flight performance, and forage zone. A community of Neotropical cave dwelling bats from a cave in Veracruz, Mexico was analyzed. The diet of each species was determined by means of their stomach contents and bibliographic review. In addition, aspect ratio, wing loading and tip index were calculated. Based on the wing characteristics and diet, multivariate groupings and orders were performed, as well as to define the assemblages present. According to the wing characteristics and the dietary composition, four groups of species were found that represent four different flight characteristics in terms of agility and maneuverability. There was agreement between diet and wing characteristics, and the four trophic groups were identified through canonical correspondence analysis. Correlating wing morphology, diet and forage area allows us to adequately define the assemblages of a community of bats. Regarding the hypothesis, it was found that species that share a food guild show differences in the composition of their food and wing morphology, which generate differences in flight performance and forage areas. Four assemblages differing in forage aerospheres among three trophic guilds are described: understory and facultative arthropodivorous, semi-clearing hematophages, and facultative nectarivores. Finally, spatial segregation between the species of the families Mormoopidae and Natalidae was recognized.

Los murciélagos presentan gran variedad de morfologías alares que determina el desempeño de vuelo del murciélago y condiciona la aerósfera de forraje y alimento que puede conseguir. Varios estudios han demostrado diferencias en morfología alar, desempeños de vuelo y aerósferas de forraje entre especies de diferentes gremios tróficos. Sin embargo, para especies que comparten un gremio esto no es del todo claro. Es posible que estas especies tengan diferencias en su dieta a pesar de pertenecer al mismo gremio trófico, y manifiesten cambios en la morfología alar, desempeño de vuelo y zonas de forraje. Analizar esto permiten entender la segregación espacial entre especies que comparten un gremio trófico, además de identificar ensambles de especies con base en diferencias morfológicas alares y desempeño de vuelo. Nuestro objetivo fue definir los ensambles de especies que integran una comunidad de murciélagos cavernícolas neotropicales con base en su gremio trófico, desempeño de vuelo y zona de forraje. Se analizó una comunidad de murciélagos cavernícolas neotropicales en Veracruz, México. La dieta de cada especie se determinó por medio de sus contenidos estomacales y revisión bibliográfica. Además, se calculó relación de aspecto, carga alar e índice de punta. Con base en las características alares y la dieta, se realizaron ordenaciones multivariadas para definir los ensambles presentes. Se encontraron cuatro grupos de especies que representan cuatro desempeños de vuelo distintos en cuanto a agilidad y maniobrabilidad. Hubo concordancia entre la dieta y las características alares en el análisis canónico de correspondencia. Correlacionar morfología alar, dieta y zona de forraje permite definir adecuadamente los ensambles de una comunidad de murciélagos. Con respecto a la hipótesis, se encontró que especies que comparten un gremio alimenticio muestran diferencias en la composición de sus alimentos y morfología alar, lo que genera diferencias en desempeños de vuelo y zonas de forraje. Se describen cuatro ensambles que difieren en aerósferas de forraje entre tres gremios tróficos: artropódvoros de sotobosque y facultativos, hematófagos de zonas semidespejadas y nectarívoros facultativos. Por último, se reconoció la segregación espacial entre las especies de las familias Mormoopidae y Natalidae.

**Keywords:** Chiroptera; coexistnce; Mormoopidae; Natalidae; trophic guild.

## Introducción

Los murciélagos son el segundo orden de mamíferos más diverso en el mundo con más de 1,400 especies ([Burgin et al. 2018](#) y [American Society of Mammalogists 2020](#)). Este orden se compone de seis familias con distribución exclusivamente neotropical: Phyllostomidae, Mormoopidae, Nocilionidae, Thyropteridae, Natalidae y Furipteridae ([Clare et al. 2011](#)). En México se pueden encontrar las primeras cinco familias distribuidas a lo largo de las vertientes del Golfo, el Pacífico y la Península de Yucatán ([Medellín et al. 2008](#)). Habitan principalmente en matorrales xerófilos y selvas bajas, medianas y altas ([Ortega y Arita 1998](#)). Entre las características generales de los murciélagos neotropicales se destaca que son de hábitos nocturnos, tienen sistema de ecolocalización, pesan entre 5 y 65 g ([Tirira 1998](#)), y algunas especies, como las que integran las familias Mormoopidae y Natalidae, son cavernícolas estrictos ([Rodríguez-Durán 2009](#)). Los murciélagos cavernícolas neotropicales tienen gran impacto en los ecosistemas, donde proveen servicios ecosistémicos como dispersores de semillas, controladores de plagas y polinizadores de flores ([Kunz et al. 2011](#)). Por otra parte, la comunidad de murciélagos cavernícolas es de gran interés para la investigación ecológica, ya que estas especies tienen características de simpatria y coexistencia a lo largo de su distribución, condiciones importantes para analizar y entender la estructura y composición de las comunidades.

Los estudios sobre la diversidad de murciélagos se han centrado en definir los factores que determinan la estructura y composición de sus comunidades ([Moreno y Halfpeter 2000](#); [Kalko y Handley 2001](#); [Stevens et al. 2004](#); [Stoner 2005](#); [Stevens y Amarilla-Stevens 2012](#)). Uno de los principales ejes de análisis consiste en tratar de explicar la coexistencia de especies en escenarios de simpatria con base en la competencia ([Arlettaz 1999](#); [Ashrafi et al. 2011](#); [Salsamendi et al. 2012](#); [Emrich et al. 2014](#)), donde se postula que la coexistencia se logra al evitar la competencia mediante la diferenciación del nicho realizado ([Hutchinson 1959](#); [MacArthur y Levins 1967](#)).

El nicho realizado se ha diferenciado entre especies del orden Chiroptera en gran medida por la especialización de sus dietas en el eje trófico, donde podemos identificar diferentes gremios alimenticios (*i. e.*, artropodívoros, frugívoros, nectarívoros, hematófagos y carnívoros; [Denzinger y Hans-Ulrich 2013](#)). Esta diferenciación del nicho trófico se manifiesta en la especialización de las estructuras alares, cuya variabilidad en forma y tamaño proporciona diferentes capacidades de vuelo entre especies ([Norberg y Rayner 1987](#); [Norberg et al. 1993](#); [Mancina et al. 2012](#)). Las variaciones en la estructura alar y el desempeño de vuelo están relacionadas con la especialización del alimento, lo que hace evidente la relación entre la morfología alar de las especies que pertenecen a diferentes nichos tróficos ([Norberg et al. 1993](#); [Norberg y Norberg 2012](#); [Marinello y Bernard 2014](#); [Furey y Racey 2016](#)). Se ha observado que murciélagos con alas pequeñas y redondeadas generalmente son del gre-

mio artropodívoro; aquellos con alas pequeñas y puntiagudas por lo general se asocian con el gremio nectarívoro, y las alas grandes y redondeadas a menudo corresponden a murciélagos frugívoros ([Norberg y Rayner 1987](#); [Norberg y Norberg 2012](#)). Por otra parte, la masa y tamaño corporal de los murciélagos tiene un gran efecto en el desempeño de vuelo y selección de dieta. Murciélagos de talla grande y mayor peso se asocian a la selección de presas grandes, así como, a desempeños de vuelo poco maniobrables y ágiles ([Barclay y Brigham 1991](#)), y murciélagos con talla pequeña y masa corporal menor se asocian a selección de presas pequeñas y desempeños de vuelo ágiles y maniobrables ([Aldridge y Rautenbach 1987](#); [O'Neill y Taylor 1989](#)).

Aunque la diferenciación morfológica alar entre especies que pertenecen a diferentes gremios alimenticios está bien establecida ([Norberg y Rayner 1987](#); [Moreno et al. 2006](#); [Carvalho et al. 2013](#); [Marinello y Bernard 2014](#)), esta no se ha estudiado entre las especies que tienen tallas similares y comparten el mismo gremio alimenticio, como en el caso de las especies insectívoras de la comunidad de murciélagos cavernícolas neotropicales que pertenecen a las familias Mormoopidae y Natalidae. Podría suceder que, entre especies que comparten gremio alimenticio existan pocas o muy sutiles diferencias en la selección de alimento, y que debido a esto, no puedan ser relacionadas con la morfología alar. Sin embargo, es posible que la diferenciación en la selección de alimento entre especies que comparten un gremio alimenticio sea suficientemente distinta para ser relacionada con la morfología alar entre estas especies.

Por otra parte, las diferencias en la morfología alar proporcionan diferentes desempeños de vuelo ([Swartz et al. 2003](#); [Kalko et al. 2008](#); [Mancina et al. 2012](#)) y esta diferenciación separa las aerósferas de forraje entre las especies, ya que el espacio aéreo es un gradiente de complejidad estructural donde la morfología alar y el desempeño de vuelo de cada especie se ponen a prueba ([Kalko y Handley 2001](#); [Kalko et al. 2008](#); [Carvalho et al. 2013](#)). Sin embargo, este tipo de estudios aún son escasos para las especies neotropicales, y todavía más en especies neotropicales cavernícolas. Probablemente esto se deba a la dificultad para observar a estos individuos durante el vuelo en estas aerósferas estructuralmente complejas ([Carvalho et al. 2013](#); [Marinello y Bernard 2014](#)). Una solución es emplear la ecomorfología, una herramienta de análisis con la que se puede inferir el desempeño de vuelo de las especies sin tener que observar a los individuos durante el vuelo ([Norberg y Rayner 1987](#); [Norberg et al. 1993](#); [Norberg 2002](#)).

La ecomorfología investiga la relación causal que existe entre los diferentes diseños estructurales de los individuos con el comportamiento y desempeño que tienen estos para explotar su hábitat ([Norton 1995](#)). Esta ciencia estipula que de manera multifactorial la forma y tamaño de las estructuras anatómicas determinan el desempeño funcional del organismo ([Swartz 1991](#)). Sin embargo, también toma en cuenta que las interacciones ecológicas del individuo localmente pueden alterar su desempeño funcional, dependi-



endo de las características del hábitat, recursos disponibles y condiciones. El análisis ecomorfológico puede considerar estructuras particulares de un organismo, así como, una caracterización completa o exhaustiva de todo un sistema estructural anatómico que expliquen las funciones ecológicas del individuo (Swartz et al. 2003). Por lo tanto, en el caso de los murciélagos, analizar el tamaño y la forma de las alas permite describir la capacidad de vuelo (agilidad y maniobrabilidad) de cada especie (Norberg y Rayner 1987; Norberg et al. 1993; Mancina et al. 2012). La agilidad consiste en la velocidad a la que puede iniciarse un giro o cambio de dirección, mientras que la maniobrabilidad se define como el espacio en el que se puede dar un giro a una velocidad específica (Norberg y Rayner 1987). Para medir la agilidad y maniobrabilidad es necesario tomar en cuenta la teoría de giro en vuelo (Norberg y Norberg 1971) que menciona, que un individuo debe de mantener en equilibrio tres fuerzas para realizar un giro, la fuerza de inercia provocada por el peso del animal en movimiento, el empuje del individuo provocado por la velocidad en la que realiza el giro y la fuerza lateral que contrarresta las dos fuerzas anteriores mediante el batido de las alas. El tamaño y la forma alar del murciélago delimita la cantidad de fuerza lateral que puede desarrollar, características como baja carga alar provocan que el murciélago genere la mayor fuerza lateral permitiendo estabilizar el giro. Por otra parte, se considera que un individuo ágil y maniobrable presenta, área alar grande, envergadura pequeña y relación de aspecto bajo, que le permiten al individuo contrarrestar la fuerza lateral de giro, girar en espacios pequeños y mayor resistencia al viento en la punta del ala, respectivamente (Norberg y Rayner 1987). Por lo tanto, es posible medir la agilidad y maniobrabilidad de los murciélagos comparando los valores de carga alar, relación de aspecto e índice de punta entre individuos.

La maniobrabilidad y agilidad están íntimamente relacionadas con la actividad de forraje de dos formas: el desempeño de vuelo delimita la aerósfera en la que un murciélago puede volar para obtener su alimento y condiciona su éxito al conseguir el alimento (Kalko y Handley 2001; Kalko et al. 2008; Mancina et al. 2012). Por lo tanto, al describir la agilidad y la maniobrabilidad y correlacionarlas con la dieta de cada especie, se pueden inferir de forma teórica las aerósferas que utilizan (Swartz et al. 2003; Kalko et al. 2008; Mancina et al. 2012). Las aerósferas de forraje que describen Kalko et al. (1996) se describen a través de la complejidad estructural aérea mediante la observación y captura de especies. Ellos mencionan que los espacios aéreos que utilizan los murciélagos para forrajear tienen dos características principales: espacios aéreos despejados y espacios aéreos desordenados, estos últimos hacen referencia al sotobosque y el borde de la vegetación.

Describir ensambles de especies por características de vuelo, zona de forraje y tipo de dieta nos permite definir cómo se establecen las comunidades a escala local, al entender los mecanismos de segregación espacial y trófica entre especies que pertenecen a diferentes gremios

alimenticios (Marinello y Bernard 2014), y entre especies que pertenecen al mismo gremio alimenticio; por ejemplo, entre las especies de las familias Mormoopidae y Natalidae.

El objetivo de este trabajo es definir y proponer los ensambles de especies que integran una comunidad de murciélagos cavernícolas neotropicales con base en el desempeño de vuelo, la zona de forraje y el gremio alimenticio. Como hipótesis esperamos que existan diferentes ensambles dentro de la comunidad de murciélagos cavernícolas que se diferencien por sus desempeños de vuelo y dieta. Especies que dependen de vuelo activo para conseguir alimento como las especies artropodívoras, tendrán mayor desempeño de agilidad y maniobrabilidad durante el vuelo y explotarán aerósferas complejas. En contraparte, especies que no dependen del vuelo activo para conseguir alimento como las especies hematófagas o nectarívoras, tendrán desempeños de vuelo menos ágiles y maniobrables y explotarán aerósferas despejadas. Por último, esperaríamos que especies que comparten gremio alimenticio como los artropodívoros, tengan diferentes desempeños de vuelo debido a las preferencias en dieta y por lo tanto exploten distintas zonas de forraje.

## Materiales y Métodos

**Área de estudio.** Se estudió la comunidad de murciélagos de la cueva "El Vado de la Chachalaca" (19° 21' 12.09" N; -96° 39' 30.27" W, 449 msnm), localizada cerca de la población Villa de Emiliano Zapata, en el municipio de Emiliano Zapata, Veracruz, México (Figura 1). El tipo de vegetación original de la zona es el bosque tropical caducifolio (Rzedowski 2006); sin embargo, actualmente es un mosaico de vegetación compuesto por fragmentos de bosque secundario, relictos de bosque tropical caducifolio y áreas de actividad ganadera y agrícola. La vegetación circundante a la cueva corresponde principalmente a relictos de bosque tropical caducifolio (Figura 1). La temperatura y la precipitación anual promedio en la zona es de 25.2 °C y 2,779 mm, respectivamente. Las lluvias se registran de junio a septiembre con un período prolongado de secas en los meses restantes.

**Captura de murciélagos y nota nomenclatural.** Se realizaron colectas de una noche por mes durante un período de un año, desde el mes de marzo del 2016 a marzo del 2017. Para la captura de murciélagos se utilizaron trampas de arpa colocadas en la entrada de la cueva. Se estableció un tiempo de captura de tres horas a partir del ocaso. Durante la colecta, se contaron e identificaron todos los murciélagos capturados. La identificación se realizó mediante la clave de Medellín et al. (2008) para el uso de *P. mesoamericanus* seguimos a Pavan y Marroig (2016, 2017).

**Gremios alimenticios.** La descripción de la dieta de *Mormoops megalophylla* y *Pteronotus mesoamericanus* se realizó por análisis de contenidos estomacales. Se sacrificaron 15 hembras y 15 machos adultos de cada especie. A estos individuos se les extrajo el contenido estomacal e intestinal, los cuales fueron transportados al laboratorio inmersos

en una capa de hielo. En el laboratorio se analizaron los contenidos estomacales de *M. megalophylla* y *P. mesoamericanus* por separado. Los insectos presentes en el contenido estomacal se identificaron hasta el nivel de orden mediante los métodos de [Whitaker et al. \(1996, 2003\)](#).

Para definir la dieta de *Natalus mexicanus* se emplearon las identificaciones de insectos del contenido estomacal de 30 individuos adultos colectados por el grupo de investigación de marzo del 2003 a marzo del 2005. Los contenidos estomacales fueron extraídos y analizados en el laboratorio mediante el método antes descrito. Los individuos y contenidos estomacales pertenecen a una población de *N. mexicanus* localizada en el Estado de Colima, México ([Torres-Flores y López Wilchis 2018](#)).

*Diphylla ecaudata* y *Desmodus rotundus* se categorizaron en cuanto a su dieta como murciélagos hematófagos de aves y mamíferos, respectivamente, con base en información publicada por [Ruschi \(1951\)](#), [Goodwin y Greenhall \(1961\)](#), [Estefano et al. \(2015\)](#) e [Ito et al. \(2016\)](#). A *Glossophaga soricina* se le definió como una especie con dieta necrívora según los datos de [Sánchez y Álvarez \(2000\)](#).

Para determinar los grupos de especies con mayor similitud entre sus dietas de acuerdo con la descripción de la dieta

obtenida para cada especie, se realizó un análisis de similitud Bray-Curtis con el programa Past 3 ([Hammer y Harper 2006](#)).

**Morfometría alar.** Para calcular el área alar del antebrazo y la punta alar, así como el área total del ala ([Gager et al. 2016](#)), se realizó lo siguiente. Los individuos fueron inmovilizados de forma mecánica sobre una hoja de papel milimétrico donde se dibujó el contorno del ala. Posteriormente, se recortó cada porción alar en la hoja de papel y se calculó el área con base en el método para determinar áreas de polígonos irregulares de [Jonckhere et al. \(2004\)](#). Cada porción de papel milimétrico se pesó con una báscula electrónica digital (SCALE modelo 100g/0.01g); además, se pesó un área definida de 10 cm<sup>2</sup> de la misma hoja de papel milimétrico. Por último, los valores de peso obtenidos en la báscula se usaron en la siguiente ecuación para calcular cada área  $AP = Pa \times Am/Pam$ . Donde: *AP* es el área de la porción, *Pa* es el peso del área alar recortada, *Am* es el área conocida (10 cm<sup>2</sup>) y *Pam* es el peso del área conocida.

De igual manera, se midió la longitud del quinto dedo del ala derecha con un vernier, se pesó al individuo con una báscula electrónica (SCALE modelo 100g/0.01g) y con un escalímetro se midió la envergadura alar. Con los datos antes mencionados y las áreas de cada porción alar, se calculó la relación de aspecto, carga alar e índice de punta,

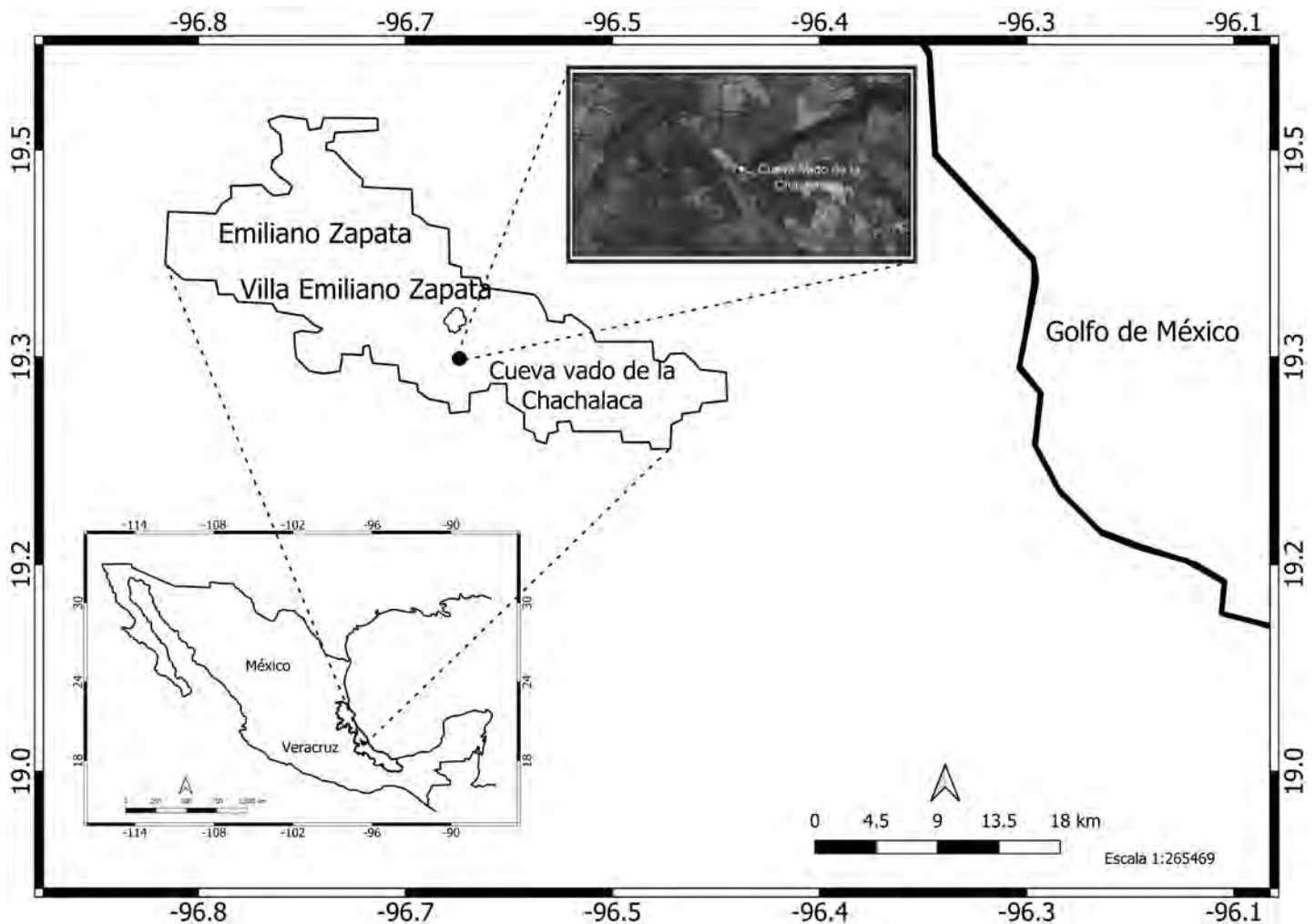


Figura 1. Mapa de ubicación de la cueva "Vado de la Chachalaca".

siguiendo las ecuaciones propuestas por [Moreno et al. \(2006\)](#) y [Gager et al. \(2016\)](#).

Con los datos obtenidos se realizaron comparaciones estadísticas con pruebas de hipótesis de *t* de Student con las variables de relación de aspecto y carga alar entre la comunidad aquí analizada y dos comunidades más, la primera de ellas compuesta de especies estrictamente cavernícolas ([Torres-Flores y López-Wilchis 2018](#)) y la segunda con especies principalmente insectívoras, pero no estrictamente cavernícolas ([Furey y Racey 2016](#)). Con estas comparaciones pretendemos identificar si es posible caracterizar la comunidad de murciélagos cavernícolas con respecto a sus características alares. Por otra parte, al considerar la hipótesis de que las especies son más ágiles y tienen mejor maniobrabilidad cuando presentan valores bajos en relación de aspecto y carga alar ([Norberg y Rayner 1987](#)), se decidió hacer una escala para cuantificar y clasificar los valores como bajos, medios y altos en función de estas variables. El intervalo estadístico de carga alar y la relación de aspecto de todas las especies encontradas en este estudio se dividieron en tres categorías. Con respecto a la carga alar, se consideró un valor alto cuando era mayor o igual al percentil 75 de la distribución,  $x \geq 8.931$  (Mg/S/Nm<sup>2</sup>); un valor medio corresponde a la media estadística,  $5.265 < x < 8.931$  (Mg/S/Nm<sup>2</sup>); y un valor bajo corresponde a valores iguales o menores al percentil 25,  $x \leq 5.265$  (Mg/S/Nm<sup>2</sup>). Para la relación de aspecto se siguió la misma metodología, los valores, de alto a bajo, fueron los siguientes:  $A \geq 6.496$ ,  $5.189 < A < 6.496$  y  $A \leq 5.189$ . Con base en este mismo criterio, se asignaron los valores altos, medios y bajos de relación de aspecto y carga alar entre los grupos de especies resultantes en el análisis de similitud por tipo de dieta y de forma inversamente proporcional, asignamos las categorías de agilidad y maniobrabilidad (baja, media y alta) para cada grupo.

**Ensamblés.** Se realizó una ordenación multivariada mediante el método de análisis de correspondencia canónico (CCA, *canonical correspondence analysis*) con el programa Past 3 ([Hammer y Harper 2006](#)). Las variables categóricas fueron el tipo de dieta y las características alares de envergadura, índice de punta, carga alar y relación de aspecto. Con respecto a los datos de dieta se realizó lo siguiente. Para las especies *M. megalophylla*, *N. mexicanus* y *P. mesoamericanus* se usaron datos cuantitativos que representan partes de insectos en el contenido estoma-

cal. Sin embargo, los datos cualitativos de dieta obtenidos por bibliografía para las especies *D. rotundus*, *D. ecaudata* y *G. soricina* fueron transformados a datos cuantitativos de la siguiente manera. A cada individuo se le asignó un valor aleatorio entre 1 y 10 dentro de su gremio alimenticio, sangre de mamíferos para *D. rotundus*, sangre de aves para *D. ecaudata* y néctar para *G. soricina*. El valor obtenido por individuo fuera de su gremio alimenticio fue igual a 0.1. Por último, para normalizar los datos de partes de insectos y los valores atribuidos a los gremios hematófagos y nectarívoros, se transformaron los datos a escala logarítmica natural y se sumaron tres unidades para evitar números negativos, estos datos son los que se usaron para el análisis CCA. Los grupos resultantes del CCA son los ensambles que se proponen en esta investigación. Estos ensambles fueron nombrados de la siguiente forma: 1) nombre de la comunidad a la que pertenecen “murciélagos neotropicales cavernícolas”, 2) nombre del gremio alimenticio al que pertenecen (*i. e.*, “artropodívoros”) y 3) aerósfera en la que desarrollan la actividad de forraje, (*i. e.*, “sotobosque”).

Para el sacrificio de los murciélagos se emplearon las recomendaciones de [Sikes et al. \(2016\)](#) y se tomaron en cuenta los lineamientos éticos de la División de Ciencias Biológicas y de la Salud de la Universidad Autónoma Metropolitana-Iztapalapa ([Anónimo 2010](#)). Los permisos federales que avalan esta colecta son SGPA/DGVS Nos. 09131/14, 05853/13 y CC 08450/92.

## Resultados

Se analizaron un total de 109 individuos que representan seis especies residentes permanentes en la cueva: *Diphylla ecaudata* ( $n = 9$ ), *Desmodus rotundus* ( $n = 5$ ), *Glossophaga soricina* ( $n = 5$ ), *Mormoops megalophylla* ( $n = 30$ ), *Natalus mexicanus* ( $n = 30$ ) y *Pteronotus mesoamericanus* ( $n = 30$ ). La proporción de gremios en la comunidad analizada es de 82.6 % de especies artropodívoras, 12.8 % de especies hematófagas y 4.6 % de especies nectarívoras. Las características alares para cada especie se observan en la Tabla 1.

Con respecto al tipo de dieta de los murciélagos presentes en la comunidad, detectamos cuatro grupos bien definidos (Figura 2) por el método de Bray Curtis ([Bray y Curtis 1957](#)), los cuales fueron discriminados principalmente por gremio alimenticio, como era de esperarse, diferenciando a los hematófagos (*D. rotundus* y *D. ecaudata*), nectarívoros (*G. soricina*) y artropodívoros (*N. mexicanus*, *M. megalophylla* y *P.*

**Tabla 1.** Características alares por especies, valores promedio y error estándar.

Especie	Envergadura (S/m)	Área alar total (S/m <sup>2</sup> )	Relación de aspecto (A)	Carga alar (Mg/S/Nm <sup>2</sup> )	índice de punta (I)	N
<i>Diphylla ecaudata</i>	0.373 ± 0.003	0.0010 ± 0.00004	5.927 ± 0.250	17.189 ± 0.511	0.7011 ± 0.031	9
<i>Desmodus rotundus</i>	0.365 ± 0.006	0.0011 ± 0.00006	6.210 ± 0.146	19.380 ± 1.001	0.784 ± 0.129	5
<i>Glossophaga soricina</i>	0.248 ± 0.005	0.0005 ± 0.00002	6.530 ± 0.224	11.968 ± 0.951	0.756 ± 0.275	5
<i>Mormoops megalophylla</i>	0.325 ± 0.003	0.0010 ± 0.00002	5.677 ± 0.209	7.438 ± 0.256	0.453 ± 0.035	30
<i>Natalus mexicanus</i>	0.263 ± 0.002	0.0006 ± 0.00002	5.998 ± 0.216	4.330 ± 0.185	0.203 ± 0.014	30
<i>Pteronotus mesoamericanus</i>	0.351 ± 0.002	0.0011 ± 0.00003	5.784 ± 0.193	7.146 ± 0.251	0.164 ± 0.008	30

*mesoamericanus*). Sin embargo, en el gremio artropodívoro encontramos dos grupos definidos. El primer grupo lo componen únicamente individuos de *N. mexicanus* (Figura 2), el cual se denominó “Murciélagos con dieta de artrópodos no voladores”, ya que su principal fuente de alimento son opiliones, aunque también consumen insectos voladores como lepidópteros (Tabla 2). El segundo grupo, compuesto por *M. megalophylla* y *P. mesoamericanus*, se denominó “Murciélagos con dieta de artrópodos voladores”, ya que la principal fuente de alimento son lepidópteros, dípteros, tricópteros y hemípteros (Tabla 2). Los resultados de los contenidos estomacales analizados y la clasificación de alimento por especie se observa en la Tabla 2.

Sobre la caracterización morfométrica alar de la comunidad de murciélagos cavernícolas neotropicales encontramos que, al comparar las características de relación de

aspecto y carga alar promedios de la comunidad analizada en este estudio respecto a una comunidad de murciélagos cavernícolas ubicada en el estado de Colima al oeste de México (Torres-Flores y López Wilchis 2018), no se encontraron diferencias significativas en los promedios de relación de aspecto ( $\bar{X} = 5.88 A$ ;  $t_{11} = -2.002$ ;  $p = 0.071$ ), y carga alar ( $\bar{X} = 8.06 \text{ Mg/S/Nm}^{-2}$ ;  $t_{11} = -1.990$ ;  $p = 0.072$ ). Cabe destacar que ambas comunidades son de murciélagos cavernícolas neotropicales; sin embargo, la composición de especies es diferente. Torres-Flores y López Wilchis (2018) reportan la presencia de *P. davyi*, *P. personatus* y *Macrotus waterhousii*, así como, la ausencia de *D. rotundus* y *D. ecaudata*. Por otra parte, observamos que no existen diferencias significativas para ambas variables relación de aspecto ( $t_7 = -2.21$ ;  $p = 0.077$ ) y carga alar ( $t_7 = -0.766$ ;  $p = 0.477$ ) al comparar nuestros datos con una comunidad dominada por organismos artropodívoros no estrictamente cavernícolas (Furey y Racey 2016). Con base en estas observaciones, podría decirse que las especies que integran la comunidad de murciélagos cavernícolas neotropicales tienen alas con forma y tamaño similar, probablemente dominadas por características alares de individuos artropodívoros. Las alas de las especies presentes en la comunidad de murciélagos cavernícolas neotropicales presentan valores promedio de relación de aspecto y carga alar de  $5.99 \pm 0.21 A$  y  $7.28 \pm 0.90 \text{ Mg/S/Nm}^{-2}$ , respectivamente.

Respecto al desempeño de vuelo de los cuatro grupos resultantes por selección de alimento en la comunidad se encontró lo siguiente. El primer grupo lo conforman individuos de las especies *D. rotundus* y *D. ecaudata*. Estas especies tienen el desempeño más bajo de agilidad y maniobrabilidad, ya que los promedios en relación de aspecto y carga alar de estas especies son los más altos entre todas las especies analizadas (Tabla 3). El segundo grupo está compuesto por individuos de *N. mexicanus*, que representan la especie con el mejor desempeño en maniobrabilidad y agilidad, al tener los valores más bajos en promedio de relación de aspecto y carga alar (Tabla 3). El tercer grupo lo componen individuos de las especies *P. mesoamericanus* y *M. megalophylla*, el promedio obtenido para los valores de relación de aspecto y carga alar (Tabla 3) representan un desempeño de agilidad y maniobrabilidad media de vuelo en comparación con los otros grupos. El último grupo lo conforman individuos de *G. soricina*, estos individuos comparten valores altos de carga alar con el grupo uno ( $11.968 \text{ Mg/S/Nm}^{-2}$ ) y valores medios de relación de aspecto con el grupo tres ( $6.530 A$ ), debido a esto los categorizamos como murciélagos con agilidad y maniobrabilidad media-baja (Tabla 3).

Con el CCA se forman cuatro grupos definidos (Figura 3). Los primeros dos ejes del análisis explican el 99.89 % de la variación total. El eje 1 está definido por diferentes variables, dentro de tipo de alimento lo definen, araneae, hemiptera e hymenoptera y dentro de variables morfométricas los definen, carga alar, relación de aspecto e índice de punta. El eje 2 está definido por las variables de dieta, hemiptera, araneae y ephemeroptera y por la variable mor-

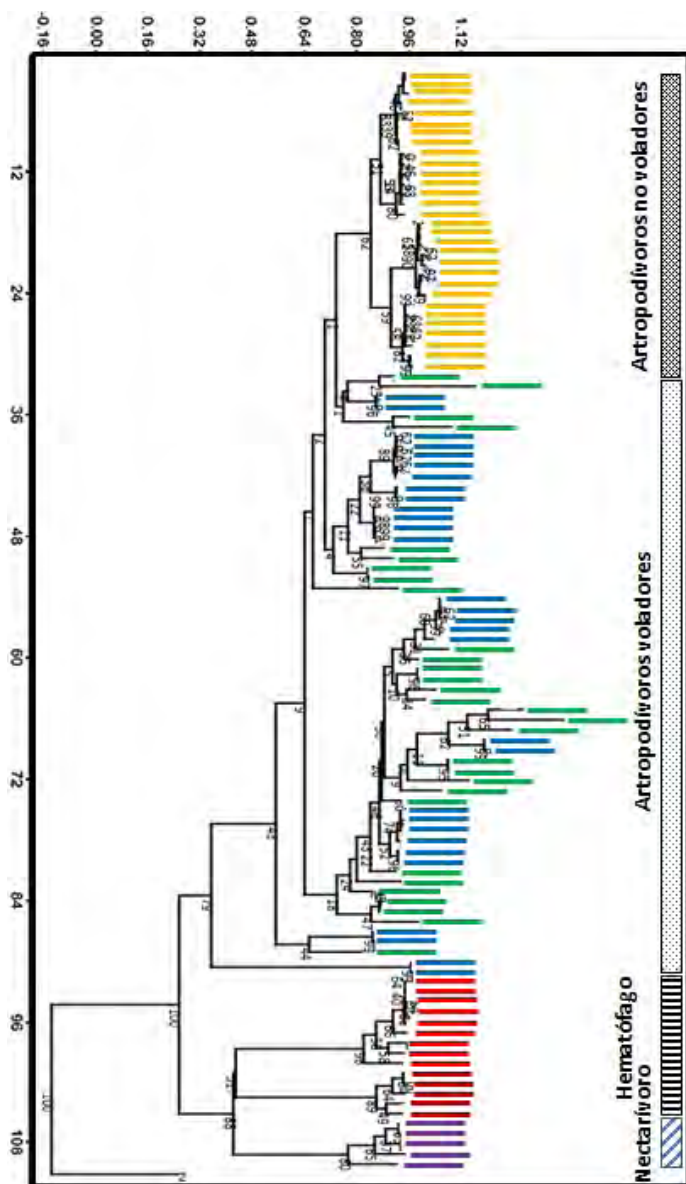


Figura 2. Agrupamiento de individuos por tipo de alimento mediante el método de Bray-Curtis. Código de colores: Amarillo *N. mexicanus*, verde *M. megalophylla*, azul *P. mesoamericanus*, rojo claro *D. ecaudata*, rojo intenso *D. rotundus* y Morado *G. soricina*.

**Tabla 2.** Dieta por especie. Para especies insectívoras, los números representan la cantidad de partes de insectos encontradas. Los círculos indican el orden de mayor a menor cantidad de partes de insectos encontradas; los cuatro círculos son el orden más consumido. NP = no presente y P = presente.

	<i>Dyphylla ecaudata</i>	<i>Desmodus rotundus</i>	<i>Glossophaga soricina</i>	<i>Mormoops megalophylla</i>	<i>Natalus mexicanus</i>	<i>Pteronotus mesoamericanus</i>
Lepidoptera	NP	NP	NP	1515 <sup>oooo</sup>	940 <sup>ooo</sup>	869 <sup>oooo</sup>
Coleoptera	NP	NP	NP	369 <sup>ooo</sup>	580	281 <sup>ooo</sup>
Trichoptera	NP	NP	NP	142 <sup>o</sup>	NP	187 <sup>oo</sup>
Diptera	NP	NP	NP	151 <sup>oo</sup>	630 <sup>oo</sup>	111
Hemiptera	NP	NP	NP	103	NP	127 <sup>o</sup>
Ephemeroptera	NP	NP	NP	26	NP	118
Hymenoptera	NP	NP	NP	6	30 <sup>o</sup>	12
Aranae	NP	NP	NP	NP	970 <sup>oooo</sup>	NP
Sangre mamíferos	NP	P	NP	NP	NP	NP
Sangre aves	P	NP	NP	NP	NP	NP
Néctar	NP	NP	P	NP	NP	NP

fométrica envergadura. Existe concordancia entre el tipo de dieta de los individuos con respecto a las características alares. Los individuos hematófagos (*D. rotundus* y *D. ecaudata*) están asociados principalmente con una alta carga alar (Figura 3). Por el contrario, los individuos artrópodos con predilección por artrópodos no voladores (*N. mexicanus*) son mayormente asociados con una baja carga alar (Figura 3). Los murciélagos que tienen mayor área total alar (*M. megalophylla* y *P. mesoamericanus*) se asocian con dietas artrópodívoras con predilección por el consumo de lepidópteros, dípteros, tricópteros y hemípteros (Figura 3). Por último, los individuos con alta carga alar y media relación de aspecto se asocian con individuos nectarívoros (*G. soricina*; Figura 3). También se observan los cuatro grupos que representan los ensambles que se proponen en este trabajo, los cuales componen a la comunidad de murciélagos cavernícolas neotropicales (Figura 3).

## Discusión

**Composición de especies.** Se han registrado aproximadamente 20 especies de murciélagos neotropicales en el área de estudio pertenecientes a familias Phyllostomidae, Natalidae y Mormoopidae (Moreno et al. 2006). Seis de estas especies son residentes permanentes en la cueva que se estudió. La diferencia entre el número de especies encontradas en la cueva respecto al total de especies registradas en el área se debe a que no todos los murciélagos del área son estrictamente cavernícolas. De las especies cavernícolas reportadas para esta zona por Moreno et al. (2006) no se registraron en la cueva a *P. personatus* y *P. davyi*. Una posible explicación es que hay más cavernas en la zona que albergan murciélagos donde se pueden refugiar estas especies. Por lo tanto, las seis especies que registramos representan una fracción de la comunidad de murciélagos cavernícolas presentes en el área de estudio.

La proporción de gremios alimenticios encontrada en este estudio difiere con lo reportado por García et al. (2015) para una comunidad de murciélagos neotropicales

cavernícolas en Venezuela. Ellos reportan 16.6 % de artrópodívoros, 16.6 % de hematófagos y 66.0 % de frugívoros. Por otra parte, en una comunidad de murciélagos cavernícolas neotropicales que se localiza en el estado de Colima, México, se reportó una proporción de gremios de 71.0 % de artrópodívoros, 14.2 % nectarívoros y 14.2 % frugívoros (Torres-Flores y López-Wilchis 2018), que también difiere a lo encontrado en este estudio. Sin embargo, es importante destacar que el gremio artrópodívoro es el predominante en la comunidad de murciélagos cavernícolas, y es representado principalmente por las especies de las familias Mormoopidae y Natalidae a lo largo de la región neotropical en México y en algunas zonas de Centroamérica (García et al. 2015; Torres-Flores y López-Wilchis 2018; Rodríguez-Durán 2020).

**Características de vuelo de las especies neotropicales cavernícolas.** Según los datos reportados por Norberg y Rayner (1987), el intervalo de dispersión estadístico de relación de aspecto y de carga alar en murciélagos abarca de 5.4 A a 11.1 A y de 4.1 Mg/S/Nm<sup>2</sup> a 35.7 Mg/S/Nm<sup>2</sup>, respectivamente. Al comparar los promedios de relación de aspecto y carga alar obtenidos en la comunidad de murciélagos cavernícolas aquí analizada (Tabla 1) contra el intervalo de dispersión obtenido por Norberg y Rayner (1987), se observa que la comunidad de murciélagos cavernícolas neotropicales se ubica por debajo de la media en cada una de las variables. Se sabe que los valores bajos de relación de aspecto y carga alar generan mayor agilidad y maniobrabilidad en el vuelo y que se relacionan con vuelos en zonas estructuralmente complejas (Norberg y Rayner 1987; Norberg 2002; Mancina et al. 2012; Marinello y Bernard 2014). Por lo tanto, podemos decir que, las características alares que encontramos en las especies que componen la comunidad de murciélagos neotropicales cavernícolas en general son alas redondeadas y con baja carga alar, que favorecen un forraje activo durante el vuelo y su desarrollo en aerósferas estructuralmente complejas (Norberg y Norberg 2012), posiblemente estas características podrían

estar determinadas en su mayoría por las características alares de las especies insectívoras, que como ya habíamos mencionado son el gremio predominante.

**Definición de ensambles por características de vuelo, dieta y zona de forraje.** En las características alares del cuarto grupo integrado por individuos de la especie *G. soricina* (Figura 3), se observa que tienen carga alar alta, lo que indica que necesitan bastante fuerza de sustentación para mantener el vuelo. Esto condiciona el vuelo a velocidades bajas, ya que, al disminuir la velocidad, se pierde fuerza de sustentación (Mancina et al. 2012). Por otra parte, presentan alta relación de aspecto, lo que indica que no pueden hacer cambios de dirección dentro de espacios reducidos (Findley et al. 1972), pues al intentarlo tendrían que disminuir la velocidad y, por lo tanto, perder la sustentación de vuelo. Además, debido a los valores de relación de aspecto e índice de punta que presentan, pueden volar con rapidez con poco desgaste energético, gracias a que tienen un menor arrastre del viento (Hedenströ y Johansson 2015).

Con base en las características alares antes mencionadas, se considera que este grupo de individuos tiene agilidad y maniobrabilidad media-baja en comparación con los otros grupos (Tabla 3; Figura 3). Teóricamente, los individuos de *G. soricina* debería evitar vuelos en aerósferas estructuralmente complejas que requieran giros o maniobras frecuentes y repentinas, por ejemplo, al interior del sotobosque. Sin embargo, esta especie se ha encontrado de forma natural en aerósferas estructuralmente complejas. Kalko et al. (2008) clasifican a *G. soricina* como un murciélago que vuela principalmente en espacios estrechos haciendo referencia a la aerósfera dentro del sotobosque. Por otra parte, Carvalho et al. (2013) lo describen como un murciélago que vuela principalmente alrededor del dosel. Tomando en cuenta el desempeño de vuelo que presenta esta especie, se podría decir que los espacios aéreos despejados le son más favorables, aunque tienen la facultad de desarrollar su vuelo en el interior del sotobosque, así como alrededor del dosel.

Con respecto a la dieta de *G. soricina*, Sánchez y Álvarez (2000) mencionan que cerca del 80 % de su dieta se compone del néctar producido por *Mastichodendron* sp., *Cordia alliodora*, *Ceiba pentandra*, *Crescentia alata*, *Pseudobombax ellipticum*, *Ipomoea* sp., *Mucuna* sp., *Combretum farino-*

*sum*, *Agave* sp. y *Stenocereus* sp., plantas que forman parte de dos estratos arbóreos: el sotobosque y el dosel. Por lo anterior, se puede deducir que el desempeño de vuelo de esta especie se favorece en aerósferas estructuralmente no complejas, aunque acostumbra volar entre estos dos estratos arbóreos, uno de ellos complejo, para conseguir su alimento (Norberg et al. 1993; Marinello y Bernard 2014). Por último, se ha reportado que *G. soricina* puede introducir en su dieta algunos insectos como lepidópteros, dípteros y coleópteros cuando escasea la producción de néctar, efecto que sucede principalmente en ecosistemas estacionales (Howell 1974; Clare et al. 2011). Esta conducta alterna entre nectarívoro y artrópodívoro en la dieta de *G. soricina* puede explicar que ocupe de forma alterna las aerósferas de sotobosque y dosel, concordando con su desempeño de vuelo y características alares.

Tomando en consideración las características de vuelo, zona de forraje y dieta de este grupo, representado por *G. soricina*, se propone el ensamble denominado “Murciélagos neotropicales cavernícolas nectarívoros de vuelo facultativo” (Figura 3). Algunas especies que podrían agregarse a este ensamble, y que no encontramos en la comunidad que se analizó, son aquellas que pertenecen a la subfamilia Glossophaginae y el género *Leptonycteris*.

El grupo uno integra las características alares y de desempeño de vuelo de los individuos de *Desmodus rotundus* y *Diphylla ecaudata*. Este grupo tiene el valor más alto de carga alar y el segundo valor más alto en relación de aspecto de entre todos los demás grupos (Tabla 3; Figura 3), lo que indica que necesitan mucha fuerza de sustentación para sostener el vuelo y, además, no pueden girar a alta velocidad ni en espacios reducidos. Sin embargo, estas especies son las que tienen menos arrastre del viento, lo que les permite volar distancias más grandes en áreas despejadas (Hedenströ y Johansson 2015). Tomando en cuenta estas características, son las especies menos ágiles y maniobrables en comparación con el resto de las especies de la comunidad. Estas especies teóricamente deberían de volar en aerósferas con poca complejidad estructural, espacios que están relacionados con la periferia del dosel y senderos despejados a través de la vegetación. Sin embargo, Kalko et al. (2008) y Carvalho et al. (2013) coinciden en que *D. rotundus* vuela dentro del sotobosque, lo que no es compat-

Tabla 3. Promedio y error estándar de las características alares por grupo.

Grupo	Especie	Envergadura	Área alar total	Relación de aspecto	Carga alar	Índice de punta	Agilidad y maniobrabilidad
1	<i>D. rotundus</i> y <i>D. ecaudata</i>	0.370 ± 0.003	0.001 ± 0.00004	6.027 ± 0.169	17.971 ± 0.546	0.730±0.048	Baja
2	<i>N. mexicanus</i>	0.263 ± 0.001	0.001 ± 0.00002	5.736 ± 0.216	4.378 ± 0.185	0.392±0.030	Alta
3	<i>M. megalophylla</i> y <i>P. mesoamericanus</i>	0.340 ± 0.003	0.001 ± 0.00001	5.628 ± 0.141	6.989 ± 0.179	0.546±0.054	Media
4	<i>G. soricina</i>	0.248 ± 0.005	0.001 ± 0.00002	6.530 ± 0.224	11.968 ± 0.951	0.756 ± 0.275	Media-Baja

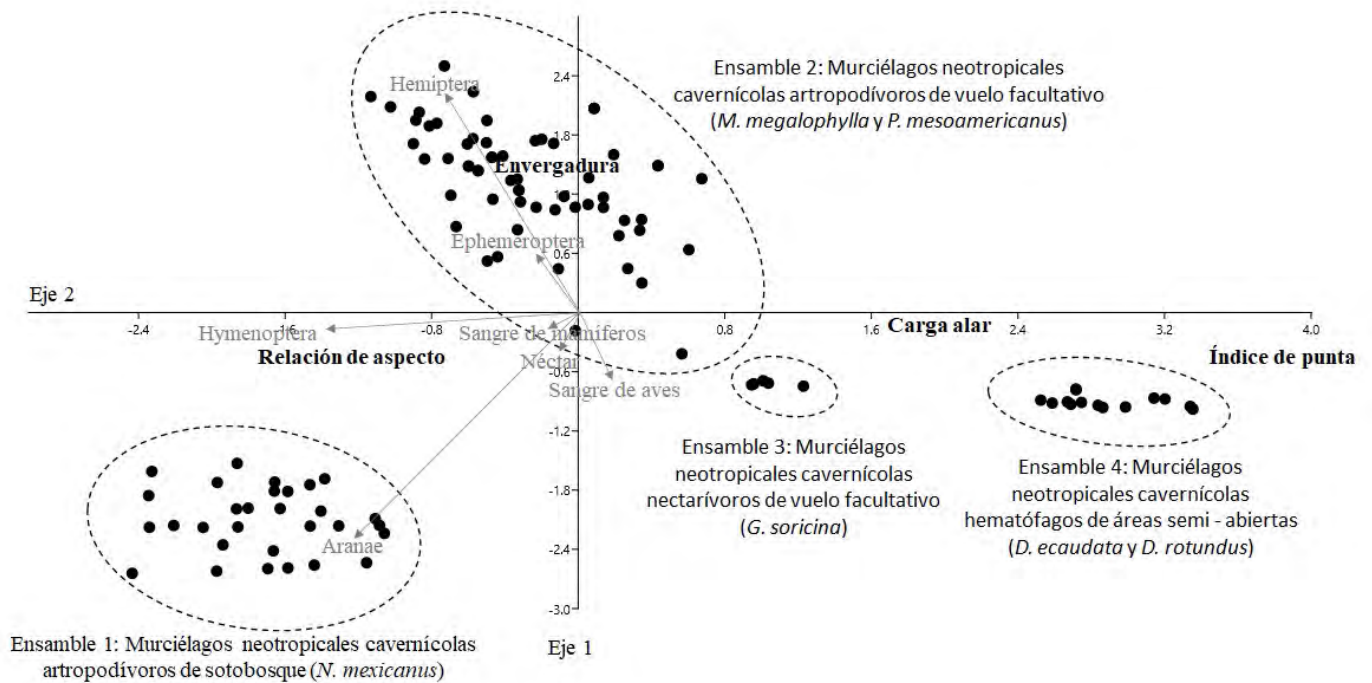


Figura 3. Análisis canónico de correspondencia entre las características alares y los contenidos estomacales de las especies de murciélagos analizadas.

ible con la inferencia teórica del desempeño de vuelo que nosotros describimos. Por otra parte, [Carvalho et al. \(2013\)](#) registraron que *D. ecaudata* vuela a la altura del dosel, lo que concuerda con lo que se describe en este estudio. A pesar de que las características alares de estos murciélagos, en teoría, favorecen el vuelo en aerósferas estructuralmente no complejas según los datos de este estudio, estas especies suelen volar dentro del espacio aéreo del sotobosque. Una posible explicación a esta contradicción es que estas especies vuelan en el espacio aéreo del sotobosque por resguardo o protección de depredadores ([Sánchez-Hernández et al. 2006](#)). Otro aspecto a considerar es que las capacidades de vuelo de ambas especies no están altamente relacionadas con la actividad de forraje, ya que consumen su alimento posados en su presa.

Con respecto a la dieta de estas especies, *D. ecaudata* tiene un tipo de alimentación especialista, consume principalmente sangre fresca proveniente de aves ([Uieda 1996](#); [Ito et al. 2016](#)). Cuando hay escasez de este alimento, se pueden alimentar ocasionalmente de sangre fresca de mamíferos como porcinos, ovinos, equinos e incluso de humanos ([Ruschi 1951](#); [Ito et al. 2016](#)). Por otra parte, *D. rotundus* no es especialista en su dieta y se puede alimentar de sangre de reptiles, mamíferos y aves ([Goodwin y Greenhall 1961](#); [Estefano et al. 2015](#)). Por lo tanto, en la actualidad, los recursos alimenticios de estas especies están principalmente confinados a corrales o encierros ([Estefano et al. 2015](#)), y las conductas de vuelo están más relacionadas con el desplazamiento hacia estos encierros y no para el forraje activo durante el vuelo. Por lo anterior, se sugiere que las características alares que presentan son más favorables para desplazarse distancias grandes con poco desgaste

energético ([Sánchez-Hernández et al. 2006](#)) en lugares semiabiertos, y así llegar a presas silvestres o a los encierros donde están las principales fuentes de alimento.

Tomando en consideración las características de vuelo, zona de forraje y dieta de este grupo, el cual es representado por las características de los individuos de *D. rotundus* y *D. ecaudata*, se propone el ensamble "Murciélagos neotropicales cavernícolas hematófagos de áreas semiabiertas" (Figura 3). Se optó por el término semiabierto porque a pesar de que este grupo de individuos es el más apto para volar en lugares abiertos con poca complejidad estructural, aún pertenecen a la comunidad de murciélagos cavernícolas neotropicales que, como ya se habíamos mencionado, son especies que se desarrollan en sotobosque, dosel y subdosel. La única especie que podría incluirse en este ensamble es *D. youngi*.

El grupo tres que integra las características alares y desempeño de vuelo de los individuos de *M. megalophylla* y *P. mesoamericanus* presenta carga alar media y relación de aspecto alto en comparación con las demás especies de la comunidad (Tabla 3). La relación de aspecto alta no les permite hacer cambios de dirección dentro de espacios pequeños a velocidades altas. Sin embargo, sí pueden realizar giros en espacios reducidos, ya que los valores medios de carga alar les permiten disminuir la velocidad sin perder sustentación, de tal forma que logran hacer giros al reducir su velocidad ([Mancina et al. 2012](#)). Por otra parte, en comparación con los dos primeros grupos definidos en esta investigación, estos son individuos que no pueden recorrer grandes distancias, ya que tienen mayor arrastre con el viento, lo que generaría mayor desgaste energético ([Hedenström y Johansson 2015](#)). Esta misma condición hace

que tengan menor velocidad de vuelo en comparación con los dos grupos antes descritos (Hopkins *et al.* 2003). Este grupo de individuos se clasificó con maniobrabilidad y agilidad media. En teoría, deberían evitar lugares que demanden alta agilidad y maniobrabilidad (Marinello y Bernard 2014). Sin embargo, pueden disminuir su velocidad y girar en espacios pequeños lo que les permite volar en aerósferas medianamente complejas. Según los datos de este trabajo, se podría inferir que las zonas de vuelo de estos individuos están relacionadas con bordes de vegetación, lugares semiabiertos e, inclusive, el interior del sotobosque. Esto concuerda con lo reportado por Kalko *et al.* (2008) y Queiroz de Oliveira *et al.* (2015) quienes registraron que *P. mesoamericanus* vuela alrededor e interior del sotobosque. También coincide con lo reportado para *M. megalophylla* que se encuentra principalmente volando por encima de arroyos y cuerpos de agua ubicados entre la vegetación (Rezsutek y Cameron 1993).

Con respecto a la dieta, los resultados indican que *P. mesoamericanus* consume principalmente lepidópteros, coleópteros y dípteros (Tabla 2). Esta composición de alimento se ha observado a lo largo de la distribución de *P. mesoamericanus* (Emrich *et al.* 2014; Salinas-Ramos *et al.* 2015). Por otra parte, también se observó que *M. megalophylla* presenta una dieta muy similar a la de *P. mesoamericanus*, al alimentarse principalmente de lepidópteros, coleópteros y dípteros (Tabla 2). Esta composición concuerda con lo reportado por Rezsutek y Cameron (1999) y Boada *et al.* (2003), con la diferencia de que ellos reportan el orden dermóptera, que no se identificó en este estudio. Sin embargo, se encontró que *M. megalophylla* también se puede alimentar de hemípteros, himenópteros y efemerópteros (Tabla 2).

Se observó que entre *M. megalophylla* y *P. mesoamericanus* existe una amplia sobreposición de nicho trófico. En la revisión bibliográfica no se encontró este patrón descrito para estas dos especies; sin embargo, se ha reportado sobreposición de nicho trófico entre *M. blainvilliei* y *P. quadridens*, especies filogenéticamente emparentadas con *M. megalophylla* y *P. mesoamericanus*, respectivamente (Rolfe y Kurta 2012; Rolfe *et al.* 2014), además de que la composición de alimento que ellos reportan es muy similar con lo encontrado en nuestros resultados. Se puede decir que entre *M. megalophylla* y *P. mesoamericanus* muy probablemente no exista diferenciación de nicho trófico. Los principales componentes de la dieta de *M. megalophylla* y *P. mesoamericanus* se encuentran en áreas de pastizales, sotobosque y áreas cercanas a cuerpos de agua (MacSwiney *et al.* 2009). Por lo tanto, el requerimiento alimenticio de ambas especies se ubica dentro y alrededor del sotobosque, donde su desempeño de vuelo es óptimo.

Tomando en consideración las características de vuelo, zona de forraje y dieta de este grupo, representado por las características de *P. mesoamericanus* y *M. megalophylla*, proponemos el ensamble denominado "Murciélagos neotropicales cavernícolas artropodívoros de vuelo facultativo"

(Figura 3). Se optó por el término "facultativo" porque estas especies pueden volar entre aerósferas complejas, como el sotobosque, y aerósferas semidespejadas, como el dosel o los senderos. La facultad de volar entre el sotobosque y el dosel para conseguir el alimento podría permitir la sobreposición de su nicho trófico al disminuir la competencia entre ambas especies de forma espacial; mientras que una puede realizar su actividad de forraje en el dosel, la otra lo realiza en el sotobosque o viceversa. Este fenómeno ya se ha reportado para otras especies de murciélagos del género *Myotis* (Krüger *et al.* 2014). Algunas especies que podrían pertenecer a este ensamble por sus requerimientos alimenticios y características alares son *P. davyi*, *P. gymnonotus*, *P. personatus*, *P. quadridens* y *M. blainvilliei*.

El grupo dos, formado por las características alares y desempeño de vuelo de los individuos que representan a la especie *N. mexicanus*, tiene carga alar media y relación de aspecto bajo (Tabla 3). Esta especie necesita la menor fuerza de sustentación en comparación con las especies anteriores. La baja carga alar le permite reducir la velocidad sin perder sustentación durante el vuelo, y la relación de aspecto medio le permite hacer giros o variaciones de dirección en espacios pequeños sin tener que reducir la velocidad (Mancina *et al.* 2012). Estas características permiten considerar a *N. mexicanus* como un murciélago muy ágil y maniobrable en comparación con las demás especies de esta comunidad. Sin embargo, es la especie que genera el mayor arrastre de viento, lo que le impide volar distancias grandes, así como a velocidades altas (Hedenström y Johansson 2015). Las características alares de esta especie sugieren que puede volar en lugares donde se requieran cambios de dirección, giros y alteraciones de velocidad frecuentes, características relacionadas con aerósferas estructuralmente complejas; por ejemplo, al interior del sotobosque (Kalko y Handley 2001; Kalko *et al.* 2008).

Con respecto a la dieta de *N. mexicanus*, según los datos, el 32 % de lo que consume son organismos del orden Araneae (Tabla 2). Es posible que también utilice lepidópteros como segunda fuente de alimento, que representa 30 % de la dieta, y dípteros, coleópteros e himenópteros, que en conjunto representan cerca del 38 % restante de su dieta (Tabla 3). Esto discrepa de lo encontrado por Torres-Flores y López Wilchis (2018), quienes reportan que el 70 % de la dieta de *N. mexicanus* se compone de organismos del género Araneae, y el 30 % restante son lepidópteros y dípteros. Sin embargo, es evidente que la principal fuente de alimento son los organismos del orden Opiliones.

El área de forraje de *N. mexicanus* está delimitada por la localización de su principal fuente de alimento: los opiliónidos, que se localizan generalmente entre rocas, hojas, ramas y suelo dentro del sotobosque (Acosta *et al.* 2007). Podría decirse que tanto las características alares del murciélago como la distribución de su principal alimento delimitan la zona de forraje de *N. mexicanus* al interior del sotobosque de forma exclusiva.



Tomando en consideración las características de vuelo, zona de forraje y dieta de este grupo, el cual es representado por las características de los individuos de *N. mexicanus*, se propone el ensamble denominado "Murciélagos neotropicales cavernícolas artropodívoros de sotobosque" (Figura 3). Dentro del listado de características alares de [Norberg y Rayner \(1987\)](#) no existe otro murciélago neotropical con estas características; sin embargo, pueden integrar este ensamble otras especies de la familia Natalidae que se distribuyen en el centro y sur de América como *Natalus major*, *N. primus*, *N. stramineus*, *N. tumidirostris* y *N. brevimanus*.

Mediante la descripción de estos ensamblajes es posible decir que la coexistencia entre las especies de las familias Natalidae y Mormoopidae está mayormente relacionada con la diferenciación de la zona de forraje más que con la diferenciación de nicho trófico (Figura 3). Estas especies podrían disminuir la competencia al realizar las actividades de forraje en dos aerósferas distintas. *N. mexicanus* comparte recursos alimenticios con *P. mesoamericanus* y *M. megalophylla*. Sin embargo, *N. mexicanus* realiza sus actividades de forraje principalmente en aerósferas complejas como el sotobosque, mientras que *P. mesoamericanus* y *M. megalophylla* pueden buscar su alimento tanto en el sotobosque como en zonas semidespejadas o a la altura del dosel. Diferenciar el área de forraje puede disminuir la competencia a escala local y permitir la coexistencia entre estas familias.

La comunidad de murciélagos cavernícolas neotropicales se puede caracterizar por tener valores de relación de aspecto y carga alar bajos, los cuales hacen que estas especies tengan capacidades para volar en aerósferas que demandan alta maniobrabilidad y agilidad de vuelo, en comparación con otras especies del orden Chiroptera. Estas características parecen estar relacionadas con murciélagos con hábitos artropodívoros más que con la composición de especies de la comunidad, esto puede ser debido a que el gremio predominante en la comunidad es el gremio artropodívoro.

Correlacionar las características alares, composición alimenticia y zona de forraje permite definir de forma óptima ensamblajes dentro de una comunidad de murciélagos. Además, con respecto a nuestra hipótesis, se encontró que especies que comparten un gremio alimenticio aún tienen diferencias en la composición de alimento, las cuales se manifiestan en las estructuras alares, generando diferentes desempeños de vuelo, y por lo tanto entre estas especies se pueden observar diferencias en las aerósferas de forraje. Dentro de la comunidad de murciélagos neotropicales cavernícolas se lograron definir cuatro ensamblajes que distinguen las aerósferas que emplean los murciélagos para la actividad de forraje en tres zonas diferentes dentro y alrededor del sotobosque. La primera corresponde al interior del sotobosque, la segunda se compone de murciélagos que pueden volar de forma facultativa entre el sotobosque y lugares semiabierto, y, por último, murciélagos que vuelan en lugares semiabierto, ya sea alrededor del dosel o en senderos. Existen otras especies que pueden

pertener a estos ensamblajes o existir ensamblajes que no se pudieron identificar debido a la cantidad de especies que se analizan en este trabajo. Sin embargo, se abre la puerta a nuevas investigaciones para identificar nuevos ensamblajes o identificar otras especies dentro de los ensamblajes aquí propuestos.

Por último, se logró reconocer la diferenciación que existe en las zonas de forraje entre las especies que representan a las familias Mormoopidae y Natalidae, que podría ser el mecanismo que utilizan estas especies para disminuir la competencia que produce la superposición de nicho trófico a escala local.

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# The Big Naked-backed Bat, *Pteronotus gymnonotus*, Chiroptera, Mormoopidae, in its northernmost geographic distribution range

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The Big Naked-backed Bat, *Pteronotus gymnonotus*, is one of the 15 species currently recognized of this genus, with relatively few specimens in scientific collections, besides being poorly studied. It has a geographical distribution spanning from México through Central America and reaching Perú and Brazil, in which it occupies a variety of habitats from desert to tropical forests below 400 meters above sea level. Here, we report the records that demonstrate its presence, and data about its natural history in southeastern México, the northernmost part of its geographic distribution range. Between June 2002 and July 2018, we captured specimens in 44 bat roosts located in southeastern México, including the Parque Estatal Agua Blanca, Macuspana, Tabasco; Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca; and in Cueva de Villa Luz, Tapijulapa, Tabasco. In the three locations mentioned, we recorded the occurrence of *P. gymnonotus* individuals, whose taxonomic identification at species level was corroborated by both morphological data and genetic analyses. Previously, the only records of *P. gymnonotus* in México were from only four specimens scattered across time, so these new recorded locations confirm the presence of this species in the country. In addition to this, in Agua Blanca State Park and Villa Luz Cave we found a reproductive resident population. The record from Grutas de Martínez de la Torre is located in the middle of the Tehuantepec Isthmus, a well known biogeographical barrier for many taxa in the transitional area to the Pacific lowland's region. We suggest that the occurrence of *P. gymnonotus* in México is also associated with large remnants of evergreen and gallery forests, located in the lowland areas along the Gulf of México and in the north and east of the Tehuantepec Isthmus.

El gran murciélago de espalda desnuda, *Pteronotus gymnonotus*, es una de las 15 especies actualmente reconocidas del género, de la cual existen pocos registros en colecciones científicas, además de ser poco estudiada. Tiene una distribución geográfica que se expande desde México a lo largo de América Central hasta el Perú y el Brasil, ocupando una variedad de hábitats desde el desierto hasta las selvas tropicales por debajo de los 400 metros sobre el nivel del mar. Se reportan los registros que atestiguan su presencia y datos sobre su historia natural, en el sureste de México, la parte más septentrional de su intervalo de distribución geográfica. Entre junio de 2002 y julio de 2018 capturamos murciélagos en 44 refugios localizados en el sureste de México. Encontramos individuos de *P. gymnonotus* en tres localidades: el Parque Estatal Agua Blanca, Macuspana, Tabasco; Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca y en la Cueva de Villa Luz, Tapijulapa, Tabasco. La identificación a nivel de especie fue corroborada con datos morfológicos y análisis genéticos. Anteriormente, los registros de *P. gymnonotus* en México correspondían sólo a cuatro ejemplares dispersos en el tiempo, por lo que su registro para estas nuevas localidades confirma definitivamente la presencia de esta especie en el país. Además, en el Parque Estatal de Agua Blanca y en la Cueva de Villa Luz encontramos una población residente reproductivamente activa. El registro correspondiente a las Grutas de Martínez de la Torre se encuentra en el centro del Istmo de Tehuantepec, zona que es bien conocida por ser una barrera biogeográfica para muchos taxones y en la zona de transición a la región de las tierras bajas del Pacífico. Sugerimos que la presencia de *P. gymnonotus* en México también está asociada a grandes remanentes de bosques siempre verdes y de galería, situados en las zonas bajas a lo largo del Golfo de México y en el norte y el este del Istmo de Tehuantepec.

**Keywords:** Biogeography; geographic distribution; Isthmus of Tehuantepec; México; Mormoopid bats.

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## Introduction

The Big Naked-backed Bat, *Pteronotus gymnonotus*, is a rare and poorly studied species belonging to the Family Mormoopidae. It is one of the 15 currently recognized species of *Pteronotus* (Pavan and Marroig 2017; Pavan and Tavares 2020). *P. gymnonotus* is relatively large and heavy, with a forearm length usually measuring 50 to 56 mm. and a body mass between 9.8 to 17.2 gr. The rostrum is conspicuously short and broad. It is mainly characterized by its naked back, resulting from its wing membranes meeting on the dorsal midline. The naked-looking rump is covered with

very short fur and appears velvety when examined closely. The overall coloration of the upper parts is dark brown, rarely orange, with generally paler underparts; membranes are blackish brown (Smith 1972; Smith 1977; Pavan and Tavares 2020).

Very little is known about its biology and natural history (Pavan and Tavares 2020). *P. gymnonotus* is an aerial insectivorous bat that roosts exclusively in caves. Generally, this bat occurs at altitudes below 400 m, inhabiting a variety of habitats from deserts, dry and semi-deciduous forests, to savannas and tropical wet forests (Handley 1966;

[Emmons and Feer 1997](#); [Eisenberg and Redford 1999](#); [LaVal and Rodríguez-Herrera 2002](#); [Reid 2009](#); [Pavan and Tavares 2020](#)). In México, it is associated with tropical evergreen high forest ([Álvarez-Castañeda and Álvarez 1991a](#)), tropical deciduous forests ([Guzmán-Soriano et al. 2013](#)), water bodies and riparian vegetation ([Davis et al. 1964](#); [Ibáñez et al. 2000](#)).

It is widely distributed in the Neotropical region, with records from southern México (Veracruz) throughout Central America, and south to Perú, Colombia and Venezuela, northeast and central Brazil, Bolivia, and Guyana ([Smith 1972](#); [Simmons 2005](#); [Reid 2009](#); [Pavan and Tavares 2020](#)). Although it can be locally abundant in the southern part of its continental distribution, it becomes less abundant and even rare northwards ([Smith 1972](#); [Simmons and Conway 2001](#); [Solari 2019](#); [Pavan and Tavares 2020](#)).

Despite its wide geographical range, this species is relatively poorly represented in scientific collections, with only 618 voucher specimens from Central America (Costa Rica, El Salvador, Honduras, Nicaragua, and Panama) and 388 from South America (Brazil, Colombia, Peru, Suriname, and Venezuela) collected between 1901 and 2016 ([GBIF 2020](#)). It is categorized as “subject to special protection” by SEMARNAT in México ([NOM-059 SEMARNAT-2010](#)) but overall considered as ‘Least Concern’ according to the IUCN ([Solari 2019](#)).

Most of the records for *P. gymnonotus* in México refer to only single specimens scattered across time. In fact, this species is considered rare not only in México, but also in most of its geographical distribution ([Pavan and Tavares 2020](#)). [Davis et al. \(1964\)](#) provided the first record of *P. gymnonotus* for México based on a single male collected in Cueva Laguna Encantada, Los Tuxtlas, Veracruz. This is its northernmost geographical record, but the species was not recorded again for more than 50 years in spite of subsequent searches made by other authors ([Villa-R. 1966](#); [Estrada et al. 1993](#)), including three made by us in March 2005, April 2011 and July 2018. Likewise, [Álvarez-Castañeda and Álvarez \(1991a\)](#) reported one male from Yaxchilan, Chiapas; but its presence in this area could not be confirmed despite the collecting efforts made by [Medellín et al. \(1986\)](#), [McCarthy \(1987\)](#) and [Medellín \(1993\)](#). The species was reported in Tabasco by [Ibáñez et al. \(2000\)](#), but prior to that was not found during the intensive field efforts made by [Sánchez-Hernández and Romero \(1995\)](#) and [Castro-Luna \(1999\)](#) in the area, nor later by [Castro-Luna et al. \(2007\)](#). [Ibáñez et al. \(2000\)](#) reported the capture of two specimens, a female and a male, from Cueva de Villa Luz, Tapijulapa, Tabasco. Because the female was pregnant, these authors suggested the presence of an undetected reproductive population of *P. gymnonotus* in southeastern México. Finally, the most recent published record of *P. gymnonotus* in México is a single male from El Volcán de los Murciélagos, Calakmul, Campeche, captured in November 2010 ([Guzmán-Soriano et al. 2013](#)).

The main objectives for this study were: to report the records that demonstrate the presence of this species in southeastern México. To report two new localities in México, one from the state of Tabasco and the first from the state of

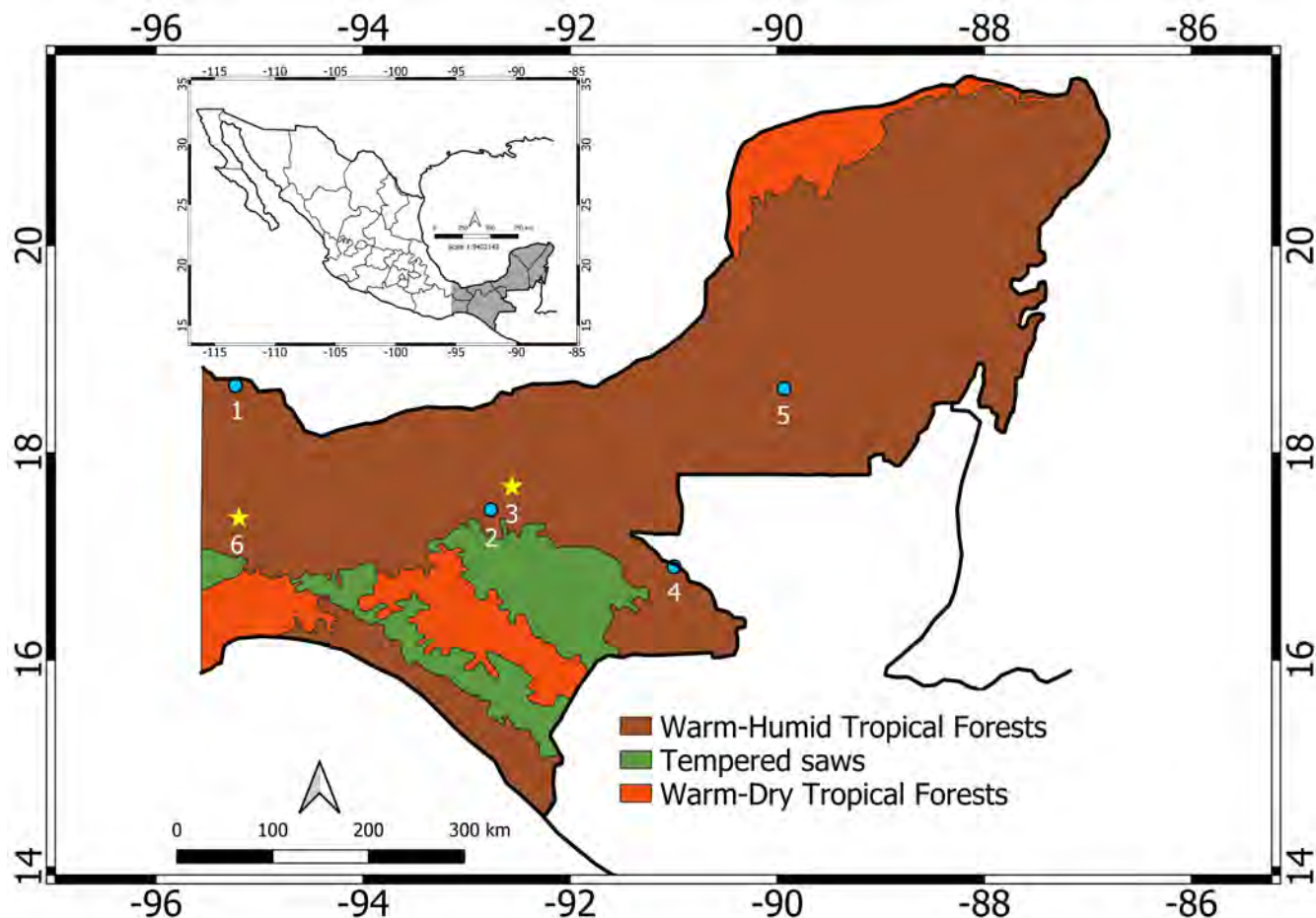
Oaxaca, and to present data about the natural history of this species in the northernmost extent of its distribution.

## Methods and Materials

**Study area.** We explored caves and some artificial roosts located in Southern México, a region including the states of Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, Veracruz, and Yucatan, a low-lying and generally flat region except for the presence of the mountains and hills that make up the Sierra Atravesada, whose highest point “el paso de Chivela” rises to about 250 masl. The area is characterized by a variety of environments with tropical climates which can be humid, sub-humid or semi-dry determined by the presence and amount of rainfall varying from 500 to 4500 mm and with high temperature variation that oscillates between 15 to 34 °C ([García 1988](#); [Vidal et al. 2007](#); [INEGI 2008](#)). In general, the rains fall with a marked seasonality, clearly distinguishing a dry season from November to April, and a rainy season from May to October ([Cavazos and Hastenrath 1990](#); [Santos-Moreno and Ruiz-Velásquez 2007](#); [Lorenzo et al. 2011](#)). The heterogeneity of the landscape includes seven types of vegetation: the upper evergreen and sub-evergreen forest predominate, followed by medium forest (with two variants, sub-deciduous and sub-evergreen) with small areas of low deciduous forest, savannas, aquatic and underwater vegetations, forest gallery, thorny scrub, and xerophilous scrub ([IGGUNAM 2007](#); [INEGI 2008](#)).

We prioritized sampling of bats inside and near the Tehuantepec Isthmus region, an area located between the -94° and -96° W meridians, which encompasses the states of Chiapas, Oaxaca, Tabasco and Veracruz (Figure 1). It consists of the narrowest land strip that separates the Pacific Ocean from the Gulf of México, spanning only 203 km (North to South), connecting the North American continent with Central America. This area is characterized by warm and humid climates, a rainy season in the summer, an annual average temperature of around 24 to 27 °C, and precipitation ranging from 1,100 to 2,600 mm ([García-Romero 2003](#); [Vidal and Matias 2003](#); [Barragan et al. 2010](#)).

**Field trips and sampling.** Thirteen field trips were undertaken between June 2002 and July 2018 in search of moroopid bats. Surveys were conducted during both the dry and rainy seasons, with a mean coverage of three to five nights in each locality. We used mist-nets (Avinet Nylon 30 mm mesh) and/or harp-traps (standard 4.2 m<sup>2</sup> model). The number of harp-traps and mist-nets varied according to the characteristics of each site, but most times we used two of each one. The nets were set before sunset as determined by the expected bat flight routes, or trying to cover cave entrances ([Kunz et al. 2009](#)) and remained open for 5 to 7 hours. Every night, we took all captured bats regardless of the species, but when a single species had more of 25 individuals, only a representative portion was collected (approximately 10 to 20 specimens) and the rest were immediately released. Those animals were kept separately in soft cot-



**Figure 1.** Map with all records known to date for *Pteronotus gymnonotus* in México 1) Cueva Laguna Encantada. 2) Cueva de Villa Luz. 3) Parque Estatal Agua Blanca. 4) Ruinas de Yaxchilan. 5) El Volcán de los murciélagos. 6) Grutas de Martínez de la Torre. Blue dots indicate previously reported localities, yellow stars the new ones described in this work. The depicted ecoregions were obtained from Atlas de Biodiversidad (CCA, CONABIO, INEGI, INE. 2010).

ton bags for a maximum of three hours and released after recording sex, weight, forearm measurements, and obtaining a biopsy from wing membranes using 3.0 mm biopsy punches (Fray Products Corp., Buffalo, NY). Tissue samples were stored at  $-20^{\circ}\text{C}$  in 70 % ethanol and deposited in the tissue collection of the Laboratorio de Biología y Ecología de Mamíferos de la Universidad Autónoma Metropolitana-Iztapalapa (LBEM-UAMI).

**Morphological identifications.** *Pteronotus gymnonotus* is easily distinguishable from other species of *Pteronotus* by its overall size (forearm length of 50 to 56 mm) and its naked back formed by its fused wing membranes in the dorsal midline, which are diagnostic characters (Medellín et al. 2008; Álvarez-Catañeda et al. 2017). Within its distribution range in México, *P. fulvus* is the only other bat species that could be confused with *P. gymnonotus*, but the former is smaller (forearm length between 41 to 49 mm) and much lighter (5 to 10 g; Figure 2).

**Genetic identification.** Species identification was confirmed using molecular techniques. We performed DNA extraction and amplification of a 607 bp fragment of the gene Cytochrome Oxidase Subunit I (COI) following López-Barrero et al. (2008) and using primers VF1d and VR1d, according to Ivanova et al. (2006). The amplifications

were sequenced 3'-5' in an ABI PRISM 370xl sequencer. Sequences were edited and aligned in Geneious v. 5.6.4 using the Clustal W algorithm (Kearse et al. 2012) and deposited in GenBank (MK883711, MK883712, MT863621, MT863628). A Bayesian Inference analysis using Mr. Bayes v 3.2 program (Ronquist et al. 2012) was constructed including previously available sequences for *P. gymnonotus* from Guatemala and Panama, as well as sequences for the phylogenetically closest species *P. fulvus* and *P. davyi*. Sequences of *P. macleayii* and *P. quadridens* were used as the external group using the optimal evolutionary model estimated with jModeltest v 2.1.6 considering the Akaike information criterion (Posada 2008). In addition, using the program MEGA v. 5.0.5 (Tamura et al. 2011) and the Kimura 2 Parameters (K2P) model, genetic distances between the sequences of individuals of *P. gymnonotus*, *P. fulvus*, and *P. davyi* were estimated.

**Statement of ethics.** All bats were collected and handled following the procedures described by the American Society of Mammalogists (Sikes et al. 2016) and our institutional ethical guidelines (Anonymous 2010). Permits to capture and handle the bat species were provided by the Mexican government (SGPA/ DGVS Nos. 05853/13, 09131/14, 003061/18, 9377/19 and CC 08450/92).

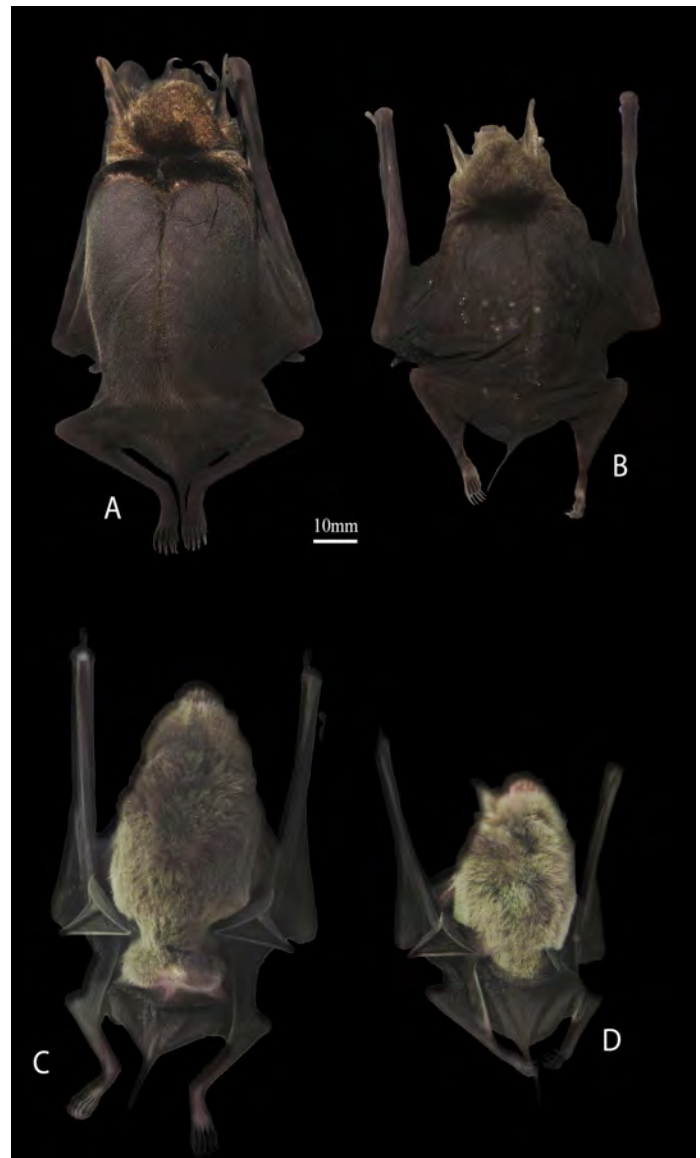
## Results

During the study period, we visited 44 bat roosts (caves, abandoned buildings and sewers, etc.; Table 1). *P. gymnonotus* was encountered only in three of the explored caves. We recorded *P. gymnonotus* in Parque Estatal Agua Blanca, Macuspana, Tabasco (17° 37.20' N, -92° 28.34' W, 100 masl; Figure 1). This area has a system of caves measuring 5,200m in length (Castro-Luna *et al.* 2007). The climate in this area is humid warm, with a mean annual temperature of 26.8 °C, with rains all year round, and average annual precipitation of 2,614 mm (Vargas 2012). We visited this locality in March 2005, April 2011, December 2014, and May 2016. During these visits, we captured a total of three males and twenty-eight females. Tissue samples (biopsy) were taken and stored at the LBEM-UAMI with the following registration numbers: 050305Pgy383, 050305Pgy384, 070411Pg1 to 070411Pg7, 20141201Pgym1 to 20141201Pgym16, 20160508PgyH1 to 20160508PgyH4, and 20160508Pgym1, 20160508Pgym2. The individuals of *P. gymnonotus* were captured late in the night, most of them between 21:00 to 0:30 hrs. Other bat species captured were *Balantiopteryx io*, *Carollia brevicauda*, *Lonchorhina aurita*, *Mormoops megalophylla*, *Natalus mexicanus*, *Pteronotus fulvus*, *P. mexicanus* and *P. psilotis*.

In July 2018, we captured two specimens of *P. gymnonotus* in Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca (17° 22.26' N, -95° 11.98' W; 50 masl; Figure 1). This site is located in northeastern Oaxaca state. It is a cave system surrounded by tropical evergreen forest with warm and humid climate, rainy season in summer and with annual precipitation ranging from <2,000 to 2,500 mm (INEGI 2008). The riparian vegetation is very abundant because a stream emerges from the cave, which joins the Jaltepec River 350 m away. Tissue samples (biopsy) were obtained and deposited in the (LBEM-UAMI), with the registration numbers Pgy23072018m1 and Pgy23072018m2. The bats were two adult males with scrotal testes, and both were collected in a mist net inside the cave at nearly 50 m from the entrance. They were captured late at night (22:00 and 23:30), with more than one hour difference between them. Other bat species captured were *Balantiopteryx plicata*, *M. megalophylla*, *P. fulvus*, *P. mexicanus*, *P. psilotis*, and *N. mexicanus*.

The other locality in which we captured *P. gymnotus* was the Cueva de Villa Luz, Tapijulapa, Tabasco (17° 27.58' N, -92° 46.75' W; 80 masl; Figure 1). This cave is also known as Cueva del Azufre or Cueva de las Sardinias, it includes a main corridor of about 2 km long and more than 20 short side passages formed by the dissolving action of the stream current. The cave has at least 24 skylights, mostly vertical shafts with dissolution features. It has several chambers, some with vaults up to 15m high. However, the passages between the chambers are low. A cave map was published by Hose y Pisarowicz (1999). Its atmosphere contains dangerous concentrations of hydrogen sulfide, carbon monoxide, carbon dioxide, and other harmful gases, in addition

to low levels of oxygen; the levels measured exceed the concentrations reported to be toxic for humans. The water, especially that which drips from organic masses known as snottites, is very acidic as well as some springs and streams that are inside the cave. It is a very active ecosystem, based on bacteria that synthesize sulfur and that, contrary to what is expected, allows the existence of a community of several thousand bats (Hose and Pisarowicz 1999; Plath *et al.* 2006; Guzman-Cornejo *et al.* 2012). Until now, no study has been carried out to understand how bats can fight against the high concentrations of toxic gases and acid fumes present in the atmosphere. The vegetation of the area corresponds to remnants of a high perennial forest, degraded by the clearings for crop and livestock areas. Riparian vegetation is abundant thanks to the large number of streams. Floristic lists of the cave surroundings area are in Gamboa and Ku (1998) and Moreno-Jiménez (2019).



**Figure 2.** Dorsal and ventral views of an adult female of *Pteronotus gymnonotus* (A, C) and an adult female of *P. fulvus* (B, D). Both specimens were captured in Parque Estatal Agua Blanca, Tabasco, México on December 01, 2014.



**Table 1.** Localities sampled in the southeast of México between 2002 and 2018 with their coordinates and arranged in alphabetical order according to the Mexican state, the name of the town and the dates they were visited.

Localities	Coordinates	Dates (dd,mm,year)
Campeche		
Grutas de Xtacumbilxunáhn, Bolonchén	19° 59.42' N, -89° 45.83' W	01/03/2005; 30/07/2013
Volcán de los Murciélagos, Calakmul	18° 31.37' N, -89° 49.42' W	21/02/2005; 19/07/2013
Chiapas		
Cueva de Cerro Hueco, Tuxtla Gutiérrez	16° 73.33' N, -93° 08.33' W	07/06/2002; 10/05/2013
Cueva de El Aguacero, Ocozocoatlá	16° 04.46' N, -93° 31.52' W	31/03/2014
Cueva de Galicia (El Fresnal), Chicomosuelo	15° 43.83' N, -92° 22.71' W	11/06/2002
Cueva de Nueva Alianza, Mapastepec	15° 25.29' N, -92° 43.98' W	07/04/2014
Cueva Lázaro Cárdenas, Tuxtla Gutiérrez	16° 53.91' N, -93° 44.44' W	10/06/2002
Cueva Los Laguitos, Tuxtla Gutiérrez	16° 49.32' N, -93° 09.12' W	07/06/2002; 11/11/2007; 11/05/2013
Finca la Esmeralda, Huixtla	15° 19.14' N, -92° 30.84' W	24/03/2009
Grutas de Arcoton, Ejido Artículo 27	16° 16.69' N, -91° 49.96' W	03/04/2014
Grutas de San Francisco, La Trinitaria	16° 05.89' N, -92° 02.75' W	08/06/2002; 04/04/2014
Grutas de Teopisca, Teopisca	16° 38.84' N, -92° 29.63' W	02/04/2014
Piedra de Huixtla, Huixtla	15° 11.90' N, -92° 28.49' W	06/04/2014
Oaxaca		
Alcantarilla, Presa Benito Juárez, Tehuantepec	18° 15.49' N, -89° 02.23' W	29/07/2007
Cerro Huatulco, Santa María Huatulco	15° 50.59' N, -96° 21.07' W	18/01/2018
Colonia Cuauhtemoc, Matías Romero	17° 05.04' N, -94° 52.44' W	26/03/2009
Cueva La Mata, Matías Romero	16° 36.82' N, -94° 57.14' W	23/07/2007
Grutas de Lázaro Cárdenas, Sto. Domingo Petapa	16° 55.40' N, -95° 15.21' W	10/06/2002; 27/07/2007
Grutas de Martínez de la Torre	17° 22.26' N, -95° 11.98' W	23/07/2018
Guiengola, Tehuantepec	16° 19.73' N, -95° 15.28' W	30/07/2007
Ojo de Agua, Tolistoque	16° 35.19' N, -94° 52.42' W	16/07/2013; 09/04/2014
San Sebastian de las Grutas, Ayoquezco de Aldama	16° 37.83' N, -96° 58.40' W	28/03/2009
2km al NW Tapanatepec, Tapanatepec	16° 22.16' N, -94° 11.67' W	24/07/2007
Quintana roo		
Alcantarilla, Tres Garantías, Othón P. Blanco	18° 15.49' N, -89° 02.23' W	24/02/2005
Cueva de Kantemó, Dziuché	19° 55.84' N, -88° 47.46' W	26/02/2005; 21/07/2013
Cueva Ejido Pedro A. de los Santos	18° 57.55' N, -88° 12.35' W	25/02/2005
Grutas de Aktun Chen, Akumal	20° 21.64' N, -87° 20.50' W	25/07/2013
Pueblo Chiclero, Chacchoben	19° 10.49' N, -88° 15.20' W	25/02/2005
Tabasco		
Campus Colegio de Posgraduados, Cárdenas	17° 57.27' N, -93° 22.54' W	02/03/2005; 19/07/2018
Cueva de Los Vientos, Tapijulapa	17° 27.50' N, -92° 46.40' W	03/03/2005
Cueva de Villa Luz, Tapijulapa	17° 27.58' N, -92° 46.75' W	05/06/2002; 05/05/2016; 20/07/2018
Grutas de Coconá, Teapa	17° 33.52' N, -92° 56.07' W	03/03/2005
Grutas de Cuesta Chica, Tapijulapa	17° 26.49' N, -92° 45.54' W	04/03/2005
Parque Estatal Agua Blanca, Macuspana	17° 37.20' N, -92° 28.34' W	05/03/2005; 06/04/2011; 01/12/2014; 08/05/2016
Veracruz		
Cueva Arroyo del Bellaco, Pachuquilla	19° 13.32' N, -96° 38.34' W	01/06/2002
Cueva Boca del Cántaro, Pachuquilla	19° 13.78' N, -96° 38.24' W	12/04/2011
Cueva Cerro Colorado, Apazapan	19° 21.21' N, -96° 41.77' W	15/05/2014
Cueva del Vado de la Chachalaca, Apazapan	19° 20.25' N, -96° 39.28' W	07/03/2005; 08/12/2014
Cueva Huichapan, Apazapan	19° 21.35' N, -96° 41.97' W	16/05/2014
Cueva Laguna Encantada, San Andrés Tuxtla	18° 27.71' N, -95° 11.18' W	07/03/2005; 09/04/2011; 18/07/2018
Cueva Sala Seca, Cuitlahuac	18° 50.00' N, -96° 93.50' W	02/06/2002
Roca del Zopilote, Juchique de Ferrer	19° 47.88' N, -96° 40.02' W	06/06/2014
Yucatan		
Cenote Hochtún, Hochtún	20° 51.37' N, -89° 11.70' W	27/07/2013
Grutas de Calcehtok, Calcehtok	20° 33.03' N, -89° 54.73' W	28/02/2005; 28/07/2013

We visited this locality in Jun 2002, May 2016, and June 2018 and during this visits we captured six females and 14 males. Tissue samples were deposited in the LBEM-UAMI with the following registration numbers: 020605PGY1- 020605PGY3; 050516PGY1- 050516PGY10; 200718PGY1- 200718PGY7. Specimens were captured individually between 22:00 and 24:30 hrs. Eight species of bats representing four different families were identified in this cave: two Emballonuridae (*B. plicata*, *Saccopteryx bilineata*), five Mormoopidae (*M. megalophylla*, *P. davyi*, *P. gymnonotus*, *P. parnellii* and *P. personatus*), and one Vespertilionidae (*M. californicus*).

In the three localities, the momoopid species *P. fulvus* was particularly abundant, and although the characteristics of the caves did not allow us to determine the size of their populations, we observed that in each case there were thousands of individuals. In the study area *P. gymnonotus* and *P. fulvus* are quite similar to each other (Figure 2),

but their differences in size, as well as the forearm values and weight allow their correct separation easily (Table 2). Our genetic analyses also confirmed the identifications made based on morphometric characteristics, and genetic distances obtained (Table 3), as well as the phylogenetic reconstruction (Figure 3), clearly separate *P. fulvus* from *P. gymnonotus*. Due to the rarity of the *P. gymnonotus*, we highlight the presence of pregnant females in May 2016 in the Cueva de Villa Luz and in the Agua Blanca State Park.

**Discussion**

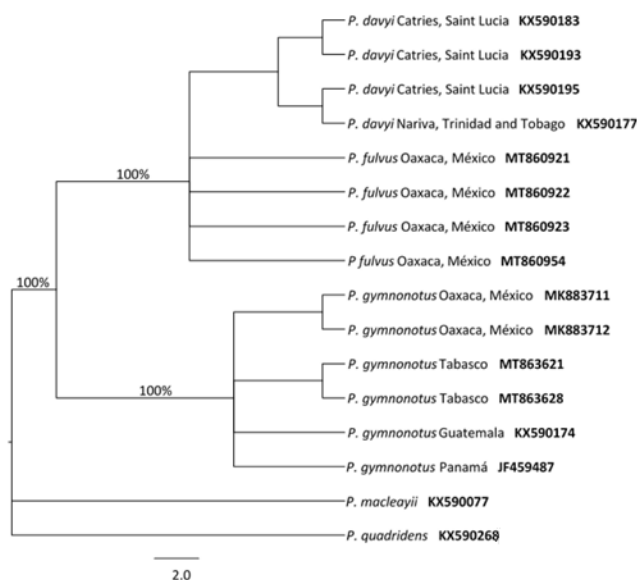
The presence of *P. gymnonotus* in México, the northernmost part of its geographical distribution, was supported only by scattered records in over fifty years (Davis et al. 1964; Álvarez-Castañeda and Álvarez 1991a; Ibañez et al. 2000; Guzmán-Soriano et al. 2013). The three locations reported here, in which we found *P. gymnonotus*, definitely reaffirm the presence of this species in the country.

**Table 2.** Weight and forearm values (mean, standard deviation, minimum and maximum) for females and males of *Pteronotus gymnonotus* and *P. fulvus* in four locations in the northernmost part of the distribution of *P. gymnonotus*.

	<i>Pteronotus gymnonotus</i>				<i>Pteronotus fulvus</i>			
	Mean	D.S.	Min	Max	Mean	D.S.	Min	Max
Cueva de Villa Luz, Tapijulapa, Tabasco								
Females (n = 6)*					Females (n = 14)*			
Weight	15.16	0.93	14.3	17.2	8.53	0.75	7	9.5
Forearm	52.61	1.26	50	53.8	44.48	0.72	43.4	46
Males (n = 14)					Males (n = 20)			
Weight	14.02	1.25	12.2	15.9	7.46	0.59	5.8	8.7
Forearm	52.4	0.57	51.3	53.2	44.13	1.29	42.1	53.2
Parque Estatal Agua Blanca, Macuspana, Tabasco								
Females (n = 20)					Females (n = 20)			
Weight	13.39	1.13	9.8	14.8	7.16	0.68	6	8.1
Forearm	53.8	1.19	52.2	55.8	44.67	0.82	43.7	46.3
Males (n = 5)					Males (n = 20)			
Weight	14.18	1.3	12.8	15.6	7.46	1.2	6	10
Forearm	53.16	1.28	51.3	54.9	44.29	0.96	42.2	46.3
Grutas de Martínez de la Torre, Matías Romero Avendaño, Oaxaca								
Females (n = 0)					Females (n = 1)			
Weight					7.4		7.4	7.4
Forearm					42.6		42.6	42.6
Males (n = 2)					Males (n = 2)			
Weight	15.3	0.07	15.3	15.4	7.55	0.35	7.3	7.8
Forearm	52.1	0.85	51.5	52.7	43.7	1.2	42.9	44.6
El Volcán de los murciélagos, Calakmul, Campeche								
Females (n = 0)					Females (n = 1)			
Weight					6.18	0.33	5.8	6.5
Forearm					44.5	0.6	43.2	45
Males (n = 1)**					Males (n = 16)			
Weight	14.5		14.5	14.5	6.11	0.28	5.7	6.6
Forearm	54.1		54.1	54.1	44.2	1.06	43.2	46,7

\* = Hembras preñadas.

\*\* Datos obtenidos de Guzmán-Soriano et al. (2013).



**Figure 3.** Phylogenetic reconstruction of mitochondrial data (COI) to confirm the identification of bats from Martínez de La Torre, Oaxaca (Genbank: MK883711 and MK883712) and Agua Blanca, Tabasco (Genbank: MT863621 and MT863628) as *Pteronotus gymnonotus*. Sequences of *P. gymnonotus* from Guatemala and Panamá (Genbank: KX590174 and JF459487), *P. fulvus* from Oaxaca (Genbank: MT860921, MT860922, MT860923 and MT860954) and *P. davyi* from Saint Lucia and Trinidad and Tobago (Genbank: KX590183, KX590193, KX590197) were included for comparison. Sequences of *P. macleayii* and *P. quadridens* (Genbank: KX590077 and KX590268) were used as an external group. Values in branches indicate Bayesian posterior probabilities.

Parque Estatal Agua Blanca has been until now the locality with the largest number of specimens collected in México and most of Central America; only [Deleva and Chaverri \(2018\)](#) report a bigger roost for this species in Costa Rica. This locality is a protected natural area of 2,025 ha with tropical evergreen forest as the dominant vegetation type ([Castro-Luna et al. 2007](#); [Vargas 2012](#)). According our observations *P. gymnonotus* seems to prefer to move and forage inside the gallery forest, a vegetation type that is also abundant in the area.

Our capture records at Grutas de Martínez de La Torre are important because this cave complex is located near the center of the Isthmus of Tehuantepec, 105 km South from the Gulf of México Coast and 134 km North from the Mexican Pacific Coast. This is an area that is well known for being a biogeographic barrier for many taxa ([Mulcahy et al. 2006](#)). In it, medium and low deciduous forests predominate, the kind of habitat in which [Reid \(1999\)](#) mentions the presence of *P. gymnonotus* in South America. The closest previous record corresponds to the Laguna Encantada, Veracruz, located 110 km to the North and we suggest that the Isthmus of Tehuantepec may have played an important role in allowing the expansion of *P. gymnonotus* northward until reaching the area of Los Tuxtlas, Veracruz. The absence of recent records in this area is probably related to the almost total loss of tall evergreen forests that the region has experienced in recent times ([García-Romero et al. 2004](#); [Taubert et al. 2018](#)), and to the intensive use of the cave by the local population for ritual ceremonies ([Münch 2012](#)). This location is in the transitional area to the Pacific

lowlands, a region in which individuals considerably larger than typical specimens of *P. fulvus*, and whose measures are very near to those of *P. gymnonotus*, have been occasionally recorded ([Goodwin 1958, 1969](#); [Smith 1972](#); [Álvarez and Álvarez-Castañeda 1991b](#)) suggesting possible hybridization between those species.

At Cueva de Villa Luz, [Gordon and Rosen \(1962\)](#) reported the presence of at least three large bat colonies, consisting mainly of bats from the Family Mormoopidae. The largest of these colonies is located approximately 150 m from the main entrance, a site with 32.3 °C and a relative humidity of 85 %. In 2018, using a hand net, we captured two specimens of *P. gymnonotus* among thousands of *P. fulvus* individuals in this site.

Mormoopid bats are commonly found living syntopically with other members of the same family, as well as with species from other families ([Smith 1972](#); [Emmons and Feer 1997](#)). *P. gymnonotus*, living in the northernmost part of its geographic range, is not the exception. Five families and thirteen species of bats have been recorded associated with this species: three emballonurids (*B. io*, *B. plicata*, and *S. bilineata*), three phyllostomids (*C. brevicauda*, *D. rotundus*, and *L. aurita*), five mormoopids (*M. megalophylla*, *P. fulvus*, *P. mexicanus*, *P. personatus*, and *P. psilotis*), one natalid (*N. mexicanus*) and one vespertilionid (*M. californicus*; [Gordon and Rosen 1962](#); [Palacios Vargas 2009](#); [Guzman-Cornejo et al. 2012](#); this paper).

In the caves visited by us, we always found *P. gymnonotus* associated with *P. davyi*. [Pavan and Tavares \(2020\)](#) observed that *P. gymnonotus* is rarely found syntopically with other species of naked-backed bats, with only a few sparse records of this situation. However, in the northernmost part of its geographic range, this species usually has been reported to co-occur with *P. fulvus* ([Davis et al. 1964](#); [Ibáñez et al. 2000](#); this paper).

Our data are indicative of the presence of a reproductive population of *P. gymnonotus* in the southeast of México. We found pregnant females in May 2016 in the Cueva de Villa Luz and in the Agua Blanca State Park. These females may belong to the same reproductive population, since both places are only 38 km apart. This population seems to be a resident one, because regardless of the year, our samples have covered the months of March to July, plus one in December, and we have always registered the presence of *P. gymnonotus* in the area.

**Table 3.** Genetic distance data between COI sequences of individuals of *P. gymnonotus* (Pgy), *P. fulvus* (Pfu) and *P. davyi* (Pda). Oaxaca (O), Tabasco (T), Guatemala (G), Antillas Menores (A). Data was obtained using the Kimura 2 Parameters (K2P) model.

	Pgy-O	Pgy-T	Pgy-G	Pfu-O	Pda-A
Pgy-O	-				
Pgy-T	1.1	-			
Pgy-G	0.7	0.3	-		
Pfu-O	8.6	8.1	7.8	-	
Pda-A	9.0	8.6	8.2	0.05	-

Beside this, all other *P. gymnonotus* specimens captured in our field trips were adults, without an evident reproductive status and only one juvenile male was registered in July for Cueva de Villa Luz. This suggests that *P. gymnonotus* in its northernmost geographic distribution has a monestral reproductive cycle, probably with births between late June - early July, data that are in agreement with the report of pregnant females in the same month in Nicaragua, El Salvador and México (Jones *et al.* 1971; Hayssen *et al.* 1993; Ibañez *et al.* 2000).

*Pteronotus gymnonotus* is an obligate cave-dweller bat. In Costa Rica colonies have been reported with more than 500 individuals in several karstic caves (Deleva and Chaverri 2018); also large assemblages of many thousands of individuals have been observed in karstic localities in northeastern Brazil (Rocha *et al.* 2011; Feijó and Rocha 2017; Vargas-Mena *et al.* 2018). In México, this species is not abundant, with only very few specimens collected in karstic caves in the Parque Estatal Agua Blanca, El Volcán de los Murciélagos and in the Grutas de Martínez de la Torre (Guzmán-Soriano *et al.* 2013; this paper). It is noteworthy that in México some records are from two non-karstic caves, Laguna Encantada and Villa Luz, both of volcanic origin.

There are studies mentioning that *P. gymnonotus* is more abundant in dry and semi-open environments (Pavan and Tavares 2020), but in México this species has been recorded in the ecoregion called warm-humid tropical forest located in the low areas along the Gulf of México and in the North and East of the Isthmus of Tehuantepec. Two earlier reports (Álvarez-Castañeda and Álvarez 1991a; Guzmán-Soriano *et al.* 2013) recorded this species in moist tropical deciduous forests and we found it associated with large remnants of tropical evergreen forest and especially in gallery forests. Finding *P. gymnonotus* in this type of environment is probably due to the fact that insectivorous bats often use riparian forests as feeding refuges due to the high availability of insects and the facilities they offer for flight and echolocation (Grindal *et al.* 1999; Robinson *et al.* 2002; Hagen and Sabo 2011).

During the last fifty years the processes of deforestation and habitat fragmentation have been very important in southeastern México, the northernmost geographic distribution range for *P. gymnonotus*. In México, the warm-humid tropical forests include the high and medium evergreen and sub-evergreen forests, which are found almost exclusively in the plains of the Gulf of México, the South and East of the Yucatán Peninsula and the East of Chiapas. It is estimated that these forests have been reduced by more than 80 % in recent years (Challenger and Soberón 2008) at an annual rate of deforestation between 1993 and 2007 of 0.83 %, although this deforestation rate tends to decrease in the area (Kolb and Galicia 2012). Currently these types of forests are only found in the most rugged terrain, but they also continue to be affected by factors such as selective timber extraction, firewood collection, grazing or man-induced fires. Bats have a high tolerance to landscape modification due to their ability to fly and the

ease with which they can cross open areas (Medellín *et al.* 2000; Castro-Luna *et al.* 2007). In this context, we highlight the need for more precise information about the distribution, conservation status, and ecology of this species.

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# Mammals of the Natural National Park Selva de Florencia, Caldas, Colombia

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The Department of Caldas, Central Andes of Colombia, has two National Natural Parks protecting strategic Andean ecosystems. However, the available information on mammals in these protected areas has not been compiled or updated recently. Here, we present an updated inventory of the mammals present in the Selva de Florencia National Natural Park. To construct the inventory, we used historical (museum vouchers) and recent records obtained during field activities over the last 20 years. We used several trapping methods including Sherman and Tomahawk traps, mist nets, and camera traps. We documented 81 mammal species belonging to nine orders, 25 families and 59 genera. Bats (Chiroptera: 30 spp.), rodents (Rodentia: 17 spp.), and carnivores (Carnivora: 13 spp.) were the most diverse groups, representing 73.2 % of recorded species. We also recorded orders such as Didelphimorphia (8 species), Primates (5), Pilosa (3), Artiodactyla (2), Cingulata (2), and Eulipotyphla (1). Also, we recorded two endemic species (*Marmosops chucha* and *Cryptotis colombianus*) and two new species for the Department of Caldas (*Bassaricyon neblina* and *Heteromys* aff. *anomalus*). These species constitute elements of the Andean region and the Nor-Andean and Chocó-Magdalena biogeographic provinces. We highlight the presence of four endangered primates (*Aotus lemurinus*, *Ateles hybridus*, *Cebus versicolor*, and *Saguinus leucopus*), two of which are endemic to Colombia: *S. leucopus* and *C. versicolor*. This work is the baseline to update the management plan of the protected area, from the review of its conservation targets, the definition of the specific management goals, to its effective monitoring.

El departamento de Caldas, Andes Centrales de Colombia, posee dos Parques Nacionales Naturales, que protegen ecosistemas estratégicos de la zona andina. Sin embargo, la información disponible sobre los mamíferos de estas áreas protegidas no ha sido compilada ni actualizada recientemente. Aquí presentamos un inventario actualizado de los mamíferos presentes en el Parque Nacional Natural Selva de Florencia. Para construir el inventario empleamos registros históricos (especímenes en museos) y registros recientes obtenidos en campo en los últimos 20 años. Empleamos varios métodos de trapeos que incluyen trampas Sherman y Tomahawk, redes de niebla, y trampas cámara. Registramos 81 especies de mamíferos pertenecientes a nueve órdenes, 25 familias y 59 géneros. Los murciélagos (Chiroptera: 30 spp.), roedores (Rodentia: 17 spp.) y carnívoros (Carnivora: 13 spp.) representan el 73.2 % de las especies registradas. Otros órdenes registrados son Didelphimorphia (8 especies), Primates (5), Pilosa (3), Cingulata (2), Artiodactyla (2) y Eulipotyphla (1). Además, registramos dos especies endémicas (*Marmosops chucha* y *Cryptotis colombianus*) y dos nuevas especies para el departamento de Caldas (*Bassaricyon neblina* y *Heteromys* aff. *anomalus*). Las especies registradas constituyen elementos de la región andina y de las provincias biogeográficas Norandina y Chocó-Magdalena. Destacamos la presencia de cuatro especies de primates amenazadas (*Aotus lemurinus*, *Ateles hybridus*, *Cebus versicolor* y *Saguinus leucopus*), de las cuales dos son endémicas de Colombia: *S. leucopus* y *C. versicolor*. Este trabajo es la base para la actualización del plan de manejo del área protegida desde la revisión de sus valores objeto de conservación, la definición de objetivos específicos de manejo hasta su monitoreo efectivo.

**Keywords:** Mist nets; monitoring; photo-trapping; Sherman and Tomahawk traps.

## Introduction

The research efforts on mammals of Colombia have increased in recent years, and currently the country ranks sixth in number of species on a global scale (Ramírez-Chaves *et al.* 2016; 2018). In the last 20 years, almost 100 mammal species have been added to the checklist of mammals of the country (see Alberico *et al.* 2000; Ramírez-Chaves *et al.* 2020a). This trend has been driven in part by the increase of taxonomic reviews and updates on South American mammals (Gardner 2008; Patton *et al.* 2015), by the participation of public and private institutions of Colombia, and by the exploration of previously inaccessible areas (Solari *et al.* 2013). Despite the significant advances made on various research topics, there are still knowledge gaps related to the taxonomy and systematics of several groups, and the ecology and conservation of endemic and endangered species for some regions across the country (see Solari *et al.* 2013; Noguera-Urbano *et al.* 2019).

The information gaps are particularly accentuated in protected areas of the country, as most of them lack complete faunal inventories despite mammals being key elements for research and conservation (Roncancio-Duque and Vélez-Vanegas 2019). Mammal's inventories in protected areas have increased in the last decade, especially in large areas such as National Natural Parks (e. g., Mantilla-Meluk *et al.* 2018). In general, there is available information for Natural Parks located in the Amazon region (e. g., Polanco-Ochoa *et al.* 2000; Mantilla-Meluk *et al.* 2018), and specific works on charismatic large mammals such as the cougar (*Puma concolor*) and the Andean bear (*Tremarctos ornatus*) in the Andean region of Colombia (e. g., Hernández-Guzmán *et al.* 2011; Cáceres-Martínez *et al.* 2020).

At the regional level, the Department of Caldas, located in the Andean region of the country (eastern slope of the Western Cordillera and both slopes of the Central Cordillera), 167 mammal species have been registered (Castaño Salazar 2012; Ramírez-Chaves *et al.* 2020b). This number includes limited information on records in protected areas like the National Natural Park (NNP) Selva de Florencia, and NNP Los Nevados (Castaño *et al.* 2003). For example, in the NNP Selva de Florencia, which protects Andean and sub-Andean ecosystems, around 40 species of mammals have been recorded (Castaño *et al.* 2003; Roncancio Duque 2012; Acosta Castañeda *et al.* 2014). This number is likely underestimated, and updated evaluations plus field validations are needed to contribute to the protection of these species and the ecosystems where they are found.

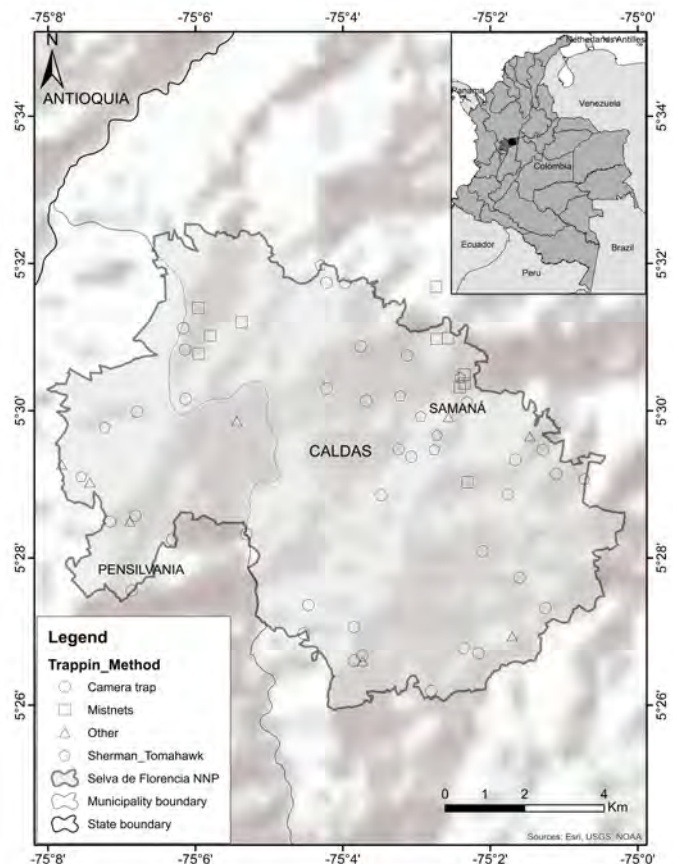
Here, we present the available information on the mammals that inhabit the NNP Selva de Florencia, Central Andes of Colombia. We aim to provide a taxonomic list of mammal species found in the study area and notes on natural history, the methods employed to register them, the localities, elevations, and number of records. This information will serve as baseline for the future research and monitoring plans, as well as to focus more cost-effectively the con-

servation efforts of the mammals of this protected area and the landscape in which it is immersed.

## Materials and methods

**Study area.** The NNP Selva de Florencia is located on the eastern slope of the Central Cordillera, in the municipalities of Pensilvania and Samaná, east of the Department of Caldas, Colombia. The NNP comprises 10,019 ha with an altitudinal gradient between 850 and 2,400 m, and an average annual rainfall of 6,270 mm. This area includes the last Andean rainforest remnants of the current Colombian Coffee Region (Paiba-Alzate *et al.* 2010), that are part of the Magdalena River Basin (Gómez *et al.* 2020), and the Magdalena-Urabá Moist Forests and the Magdalena Valley Montane Forests ecoregions (Olson *et al.* 2001). We sampled localities near the Hondo and San Antonio river basins, and the sectors of the Las Mercedes, Chupaderos I and La Selva microbasins (Figure 1, Table 1).

**Data collection.** To assess the diversity of mammals in the study area, we conducted sampling efforts in four periods across 2000 and 2018 years: A) October and November 2000. B) April 2001. C) October 2017, and D) February and April 2018. In addition, we implemented 26 sampling points where 30 camera traps (sampling effort: 9,540 camera-days) were randomly located between March 2017 and August 2018. To have a broad taxonomic coverage,



**Figure 1.** Study area at the Selva de Florencia National Natural Park, Central Andes of the Department of Caldas, Colombia.

we implemented several trapping methods, including Sherman and Tomahawk<sup>®</sup> traps for small non-flying mammals, and mist nets for bats, for 64 effective days. The traps installed were baited with roasted and ground peanuts with bacon and salt, in addition to banana or with canned sardines, chicken bones and a mixture of rolled oats, bananas, banana or vanilla essences, and peanut butter (e. g., [Voss and Emmons 1996](#)). For capturing bats, five mist nets (12m long x 6m wide) were installed in four sampling points, between 18:00 and 23:00 hours. To complement the information, we included incidental captures, observations in the field, search for tracks and occasional interviews with park rangers and inhabitants near the NNP Selva de Florencia. In addition, we reviewed vouchers from the NNP Selva de Florencia or its surroundings deposited at the mammal collection of the Natural History Museum of the University of Caldas (MHN-UCa), Manizales, the Instituto Alexander von Humboldt (IAvH), Villa de Leyva, Colombia, and the Field Museum of Natural History (FMNH), Chicago, USA.

We collected vouchers for taxonomic determination in the laboratory, and prepared them as skin and skull, or in fluid (alcohol) with tissues preserved at 96 % ethanol. All the collected specimens were deposited at the MHN-UCa mammal collection (see [Ramírez-Chaves et al. 2020b](#)). We took cranial and external measurements following to [Simmons and Voss \(1998\)](#) and [Voss et al. \(2001\)](#). Measurements included for selected specimens (Appendix 1): length of head-and-body (HBL); length of tail (LT); length of hindfoot (HF); length of ear (LE); weight (Wt) in grams (g); greatest length of skull (GLS); condylobasal length (CBL); braincase breadth (BB); maxillary toothrow (MTR); molar length (LM); palatal breadth (PB); palatal length (PL); nasal breadth (NB); Least interorbital breadth (LIB); least postorbital breadth (LPB); zygomatic breadth (ZB); breadth of the zygomatic plate (BZP); rostral breadth (BR); length of diastema (LD); breadth of the first maxillary molar (BM1); length of one incisive foramen (LIF); breadth across both incisive foramina (BIF); interparietal breadth (IPB). For bats we also took the forearm length (FL); condylocanine length (CCL); condyloincisive length (CIL); lacrimal breadth (LB); mastoid breadth (MB); breadth across canines (BC-C), and width across upper molars (BM-M). Taxonomic identification was done using specialized literature and taxonomic keys mainly for marsupials ([Gardner 2008](#); [Voss et al. 2018, 2020](#); [Giarla and Voss 2020](#)), bats ([Gardner 2008](#); [Díaz et al. 2016](#)), rodents ([Patton et al. 2015](#)), and carnivores ([Suárez-Castro and Ramírez-Chaves 2015](#)). For marsupials, we include one species as *Marmosa* sp. which is morphologically similar to *M. meridae* but a molecular confirmation is needed.

As additional support for taxonomic identification of some rodents collected between 2017 and 2018, we implemented a *Cytb*-based (Cytochrome B) molecular approach. This marker has been traditionally used for studying mammalian alpha-taxonomy because of its strength to detect cryptic diversity, especially in widely distributed and morphologically homogeneous taxa. Thus, species selected

for *Cytb* characterization have broad geographic ranges or have been pointed out as including undocumented taxonomic variation ([Patton et al. 2015](#)): *Coendou quichua*, *Neacomys tenuipes*, *Heteromys* aff. *anomalus*, and *Sigmodontomys alfari*. DNA was extracted from fresh tissues of these species with a GeneJet Genomic DNA Purification Kit (Thermo Fisher Scientific), following the manufacturer's instructions. Resulting sequences were verified to represent endogenous DNA of *Coendou*, *Neacomys*, *Heteromys*, and *Sigmodontomys* by performing independent searches with the Basic Alignment Search Tool (BLAST; [Altschul et al. 1990](#)). Matches with identities above 95 % were considered as good candidate species to our samples, according to the genetic species concept ([Bradley and Baker 2001](#)). We generated a total of six *Cytb* sequences: a) One 1,140 base pairs sequence from *Coendou quichua* (MT822488). b) Two sequences of 688 bp and 703 bp of *Heteromys* aff. *anomalus* (Acr1 and Acr2, respectively). c) Three sequences of 872-775 bp sequence from the specimens of *Neacomys tenuipes* (MT536169-MT536171). d) One 866 bp sequence from *Sigmodontomys alfari*. We assessed potential cryptic diversity with a close comparison of our sequences with all the sequences of *N. tenuipes*, *H. anomalus*, *H. australis*, and *S. alfari*, available in GenBank. Finally, the conservation status of the species, especially endemic and threatened, was evaluated with the context of current legislation ([MADS 2017](#)), and the International Union for the Conservation of Nature (IUCN 2019). For the endemic species, we include the ecoregions where they inhabit (sensu [Olson et al. 2001](#)).

## Results

We recorded a total of 81 mammal species at the NNP Selva de Florencia. The mammals registered belong to 9 orders, 25 families and 59 genera (Table 1). Bats (Chiroptera: 30 spp.), rodents (Rodentia: 17 spp.), and carnivores (Carnivora: 13 spp.) represent 71.4 % of the recorded species. Other orders registered are Didelphimorphia (8 spp.), Primates (5 spp.), Pilosa (3 spp.), Artiodactyla (2 spp.), Cingulata (2 spp.), and Eulipotyphla (1 spp.). We recorded 43 species during 2000 and 2001, and 34 during 2017 and 2018 (Figure 1). Using trapping methods, we captured 330 specimens of bats (mist nets), 24 rodents (Sherman), and 4 marsupials (Tomahawk; Figure 2). The taxa recorded by camera traps include six orders (Didelphimorphia, Cingulata, Pilosa, Carnivora, Artiodactyla and Rodentia) and 16 species (Figure 3). In addition, we recorded 28 species through manual captures, observations, and other indirect records.

*Didelphimorphia*. We recorded a total of eight species of seven genera in the study area (Table 2), using Tomahawk traps (four species) and direct observations (one species). The review of collections contributed with three additional species (Table 2). In camera traps, only four records of *Didelphis marsupialis* were obtained in August and December 2017, in two localities at elevations of 1,078 and 1,571 m, respectively. We highlight the presence two species of the genus *Marmosa* (*Marmosa* sp., and the short-furred woolly

**Table 1.** Sampled localities and dates (day, month, year) at the Selva de Florencia National Natural Park, Department of Caldas, Central Andes of Colombia

	Code / Locality	Latitude	Longitude	Elevation (masl)	Date
Municipality of Pensilvania, "Corregimiento" Pueblo Nuevo					
1	Vereda El Paraíso	5° 29' 51.7" N	-75° 05' 26.3" W	2,224	19.03.2019
2	Vereda Las Colonias	5° 29' 06.6" N	-75° 07' 32.9" W	1,733	26.10.2015
	Vereda Las Colonias	5° 29' 16.0" N	-75° 07' 48.9" W	1,530	26.10.2015
	Vereda Las Colonias	5° 29' 01.5" N	-75° 07' 25.9" W	1,752	26.10.2015
3	Vereda Buenos Aires, sector Montebello, predio Segundo Zuluaga	5° 28' 29.9" N	-75° 06' 53.3" W	2,088	March-July 2016
	Buenos Aires, sector Montebello	5° 28' 34.4" N	-75° 06' 48.9" W	2,082	26.10.2016 - 05.12.2016
	Buenos Aires, sector Montebello	5° 28' 29.7" N	-75° 07' 09.4" W	2,167	26.10.2016 - 05.12.2016
4	Vereda El Silencio	5° 29' 46.7" N	-75° 07' 13.8" W	1,620	Feb.-May 2014
5	Vereda Miraflores, sector Cuchilla de Miraflores	5° 30' 09.7" N	-75° 06' 07.9" W	1,980	26.07.2016 - 28.09.2016
	Vereda Miraflores, sector Cuchilla de Miraflores	5° 30' 49.8" N	-75° 06' 08.4" W	1,986	28.10.2016 - 06.12.2016
	Vereda Miraflores, Reserva La Italia	5° 31' 07.3" N	-75° 06' 09.9" W	1,951	12.07.2018 - 30.08.2018
6	Vereda San Francisco, sector Boquerón	5° 27' 33.6" N	-75° 06' 51.8" W	1,920	08.11.2017 - 11.12.2017
	Vereda San Francisco, sector Boquerón	5° 28' 15.2" N	-75° 06' 18.8" W	1,999	02.05.2018 - 05.06.2018
7	Vereda Las Mercedes	5° 29' 59.2" N	-75° 06' 47.3" W	1,818	11.04.2018 - 15.05.2018
Municipality of Samaná, "Corregimiento" de Florencia					
8	Vereda San Antonio	5° 30' 22" N	-75° 02' 21.0" W	1,300	07.10.2017
	Vereda San Antonio, Microcuenca Las Mercedes	5° 30' 27.1" N	-75° 02' 24.5" W	1,227	
	Microcuenca Las Mercedes	5° 30' 07.7" N	-75° 02' 18.8" W	1,066	
	Microcuenca Las Mercedes	5° 30' 29.5" N	-75° 02' 21.2" W	1,275	
	Microcuenca Las Mercedes	5° 30' 19.3" N	-75° 02' 24.7" W	1,259	20.02.2018-24.02.2018
	Sector El Hoyo, cráter volcán El Escondido	5° 30' 58.5" N	-75° 02' 43.7" W	2,224	27.08.2018
9	Vereda La Cabaña	5° 31' 41.4" N	-75° 02' 44.3" W	1,200	05.01.2001
	Vereda La Cabaña	5° 29' 28.2" N	-75° 01' 17.3" W	1,382	29.01.2018 - 08.03.2018
	Sector La Vega	5° 29' 01.7" N	-75° 02' 18.4" W	1,450	March-June 2014
	Sector La Vega	5° 28' 52.0" N	-75° 01' 45.7" W	1,375	16.08.2017 - 16.09.2017
	Sector La Vega	5° 29' 20.0" N	-75° 01' 39.7" W	1,078	27.11.2017 - 17.01.2018
	Predio San Antonio	5° 29' 39.1" N	-75° 01' 27.9" W	1,458	06.04.2016 - 05.05.2016
10	Vereda San Vicente, Finca Jose Luis Orozco	5° 31' 59.0" N	-75° 04' 18.1" W	1,700	12.12.2001
11	Vereda San Lucas, cinco minutos abajo casa Miguel Molano, quebrada San Lucas	5° 30' 12.4" N	-75° 03' 13.2" W	1,285	10.07.2001
	Microcuenca La Selva, cráter volcán El Escondido, sector Coliadero	5° 30' 59.1" N	-75° 02' 34.5" W	1,478	18.10.2017-20.10.2017
	Transecto altitudinal en el sector Coliadero	5° 30' 00.0" N	-75° 03' 00.0" W	1,536-1,809	18.10.2017-20.10.2017
	Microcuenca Chupaderos 1	5° 29' 55.7" N	-75° 02' 56.5" W	1,309	21.04.2018-23.04.2018
	Microcuenca Chupaderos 1	5° 29' 28.6" N	-75° 02' 45.6" W	1,423	
	Microcuenca Chupaderos 1	5° 29' 40.3" N	-75° 02' 43.4" W	1,438	21.04.2018-23.04.2018
	Río San Antonio	5° 29' 54.9" N	-75° 02' 34.0" W	1,330	04.2018
	San Lucas	5° 30' 45.0" N	-75° 03' 07.8" W	1,636	21.03.2017 - 14.04.2017;
	San Lucas	5° 30' 08.2" N	-75° 03' 41.0" W	1,482	28.06.2017 - 30.07.2017
	San Lucas	5° 29' 28.6" N	-75° 03' 14.6" W	1,290	29.06.2017 - 30.07.2017
	San Lucas	5° 29' 22.6" N	-75° 03' 04.3" W	1,463	29.06.2017 - 30.07.2017
	San Lucas	5° 28' 51.1" N	-75° 03' 28.9" W	1,581	29.08.2017 - 13.10.2017
	San Lucas	5° 30' 18.1" N	-75° 04' 13.1" W	1,719	30.08.2017 - 14.10.2017
	Sector Sierra Morena	5° 30' 52.3" N	-75° 03' 45.5" W	2,034	26.04.2017 - 15.06.2017
12	Vereda La Abundancia, cuenca del Río Hondo	5° 31' 01.2" N	-75° 05' 47.9" W	1,538	23.08.2017 - 03.10.2017
	Cuchilla del Dulce	5° 31' 1.34" N	-75° 04' 53.0" W	1,470-1,800	19.11.2000 - 21.11.2000
	Mina La Concha, cabecera del riachuelo	5° 30' 46.5" N	-75° 05' 57.4" W	1,980	16.04.2001
	Quebrada Seca, 40 minutos aguas arriba vía Florencia-Pueblo Nuevo	5° 31' 23.9" N	-75° 05' 57.7" W	1,800	05.07.2001
	Caño Las Agüitas	5° 31' 12.1" N	-75° 05' 22.4" W	1,573	
13	Vereda Río Claro, sector Bocatomas	5° 30' 22.0" N	-75° 02' 21" W	1,300	07.10.2017
14	Vereda La Bretaña	5° 31' 44.3" N	-75° 03' 58.1" W	1,819	10.06.2017 - 13.07.2017
	Vereda La Bretaña	5° 31' 44.4" N	-75° 04' 13.4" W	1,783	17.05.2017 - 21.06.2017

Table 1. Continuation...

	Code / Locality	Latitude	Longitude	Elevation (masl)	Date
15	Vereda Las Encimadas	5° 29' 04.7" N	-75° 00' 43.5" W	1,008	05.07.2017 - 09.08.2017
	Vereda Las Encimadas	5° 29' 08.6" N	-75° 01' 06.5" W	1,361	25.10.2017 - 26.11.2017
Municipality of Samaná, "Corregimiento" Encimadas,					
16	Vereda Yarumalito, sector cuchilla El Micay	5° 26' 35.8" N	-75° 03' 43.8" W	1,856	23.05.2016 - 01.06.2016
	Vereda Yarumalito, sector cuchilla El Micay	5° 26' 40.6" N	-75° 03' 44.2" W	1,873	
	Vereda Yarumalito, sector cuchilla El Micay	5° 26' 36.5" N	-75° 03' 50.9" W	2,306	19.07.2017 - 22.08.2017
17	Vereda El Quindío	5° 26' 42.5" N	-75° 02' 09.6" W	1,513	20.06.2017 - 21.07.2017
	Vereda El Quindío	5° 26' 11.6" N	-75° 02' 48.0" W	1,744	20.10.2017 - 22.11.2017
	Vereda El Quindío	5° 26' 46.6" N	-75° 02' 21.8" W	1,409	31.07.2018 - 04.09.2018
	Sector Los Planes	5° 26' 56.0" N	-75° 01' 42.2" W	1,471	21.06.2016 - 21.07.2016
18	Vereda El Diamante	5° 28' 05.5" N	-75° 02' 06.1" W	1,552	22.06.2017 - 25.07.2017
	Vereda El Diamante	5° 27' 19.1" N	-75° 01' 15.2" W	1,374	21.06.2017 - 26.07.2017
	Predio El Retiro	5° 27' 44.0" N	-75° 01' 36.3" W	1,384	23.06.2017 - 25.07.2017
19	Vereda Santa Isabel	5° 27' 21.7" N	-75° 04' 28.1" W	1,917	04.07.2017 - 09.08.2017
	Vereda Santa Isabel	5° 26' 58.4" N	-75° 04' 31.8" W	1,861	03.07.2017 - 07.08.2017
	Río Tenerife	5° 28' 19.6" N	-75° 05' 18.4" W	1,559	25.09.2017 - 26.10.2017
	Sector La Gruta	5° 27' 03.8" N	-75° 03' 51.1" W	1,870	19.06.2018 - 24.07.2018

mouse opossum, *Marmosa regina*, the latter considered a senior synonym of *M. isthmica* by [Giarla and Voss 2020](#) which are differentiated based on size (Appendix 1), tail and coat coloration, and skull morphology.

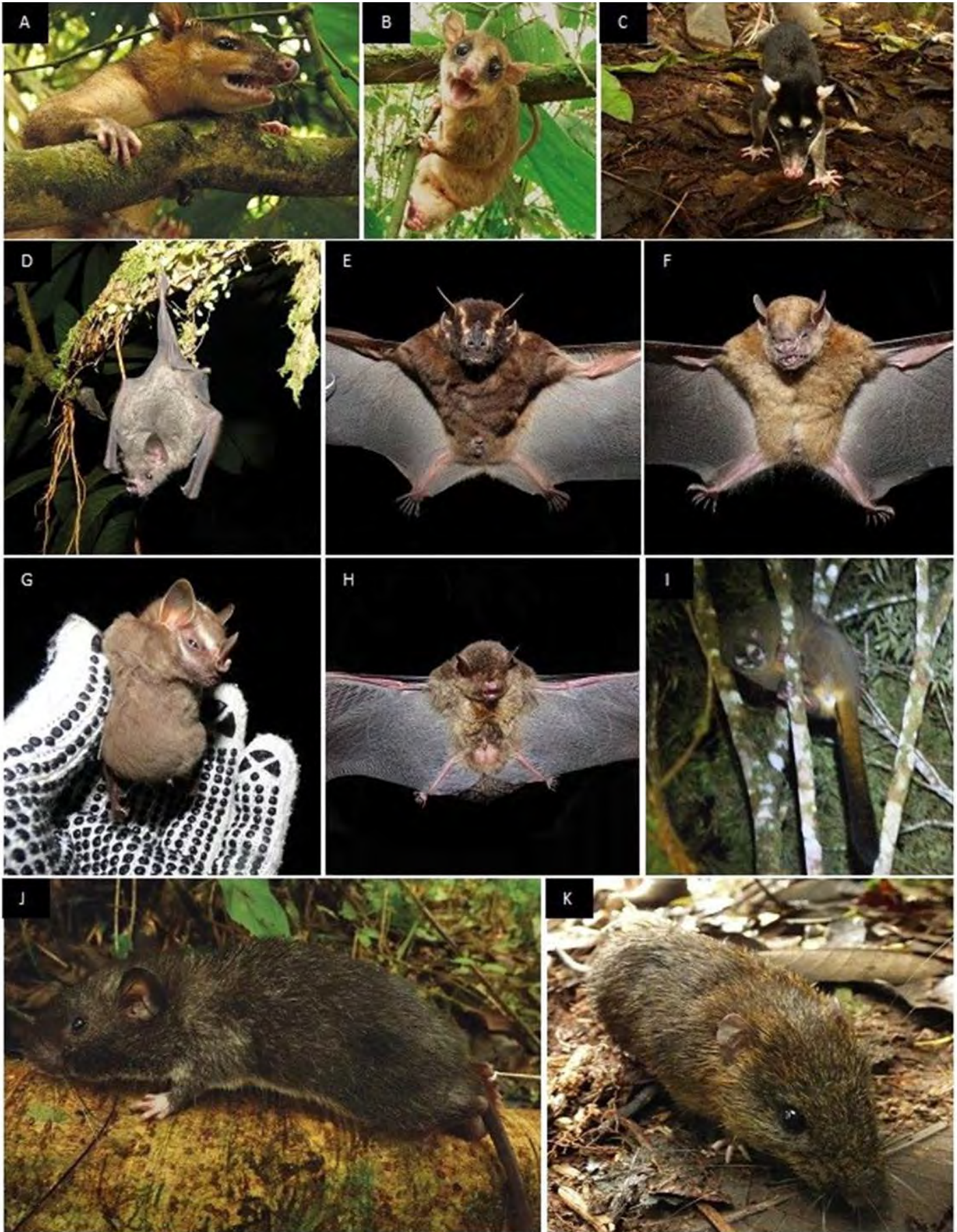
*Eulipotyphla*. We recorded only one species (*Cryptotis colombianus*), based on a male specimen (MHN-UCa 193: skin and skull) collected in the San Vicente village, 1,700 m (28 December 2001). External measurements are: TL: 96, HB: 69, Tail: 27, feet: 12, W: 7 g. LT/HB: 39.13 %. Cranio-dental skull measurements are: condylobasal length: 19.68, cranial amplitude: 9.53, zygomatic plate width: 3.91, interorbital width: 40.8, length of unicuspid teeth row: 3.78, mandibular length: 7.50, mandibular tooth row length: 5.38, width between upper second molars: 6.00 mm. One additional specimen of *Cryptotis* was captured but not collected in 2014 and the specific identity is uncertain.

*Cingulata and Pilosa*. We registered five species in the study area. One species of Cingulata (*Dasyus novemcinctus*) and two of Pilosa (*Choloepus hoffmanni* and *Tamandua mexicana*) were documented using direct observations and indirect records (bones). *Cyclopes dorsalis* was photographed in 2012 near to a farm in the study area. Based on camera traps, we obtained seven records of *Cabassous centralis* in June, October, and November 2017, in three locations at of 1,361, 1,744 and 1,783 masl. Similarly, we obtained a total of 17 records for *D. novemcinctus* during June to September and December 2017 and in February and May 2018, in 11 locations located at elevations between 1,078 and 1,999 m. For Pilosa, we obtained eight records of *T. mexicana* between July and October 2017 in six locations with elevations between 1,008 and 1,719 m.

*Chiroptera*. We registered a total of 30 species of two families (Phyllostomidae and Vespertilionidae; Table 2). Bats were the best represented group in terms of richness

with 12 (152 captured individuals) and 16 species (179 individuals captured), during 2000 to 2001 and 2017 to 2018, respectively. The most abundant species was *Carollia brevicauda* with 17 (2000 to 2001) and 100 (2017 to 2018) captured individuals. We highlight the presence of three species of small *Artibeus* (*anderseni*, *bogotensis*, and *glauca*) (Appendix 1), which are differentiated based on the number of lower molars (two or three), and skull morphology.

*Carnivora*. We registered a total of 13 species of Canidae, Felidae, Mustelidae, and Procyonidae (Table 1). During 2000 and 2001, we recorded nine species based on indirect records. During 2017 to 2018 we registered four species based on indirect records and observations, one of them (*Bassaricyon neblina*) had no previous records at the NNP or for the Department of Caldas. The specimen was identified as *N. neblina* based on the long dorsal hair coat, dense and of rufous coloration with black tips, the fur of the belly pale yellowish; the face has a medium and pointed muzzle of dark-gray coloration, eyes are big and brown, ears are rounded with hairs, and the tail is proportionately short (412 mm), bushier and straight becoming darker at the tip. In camera traps, we obtained total of 19 records of individuals of the four families. Among these, four records of *Eira barbara* (Mustelidae) in July, October, and December 2017 and May 2018, in four locations located at elevations between 1,692 and 1,599 m. For Procyonidae, we obtained five records of *Nasua nasua* between June and September 2017, and May 2018 in five localities between 1,463 and 1,999 m. In addition, a record of *Procyon cancrivorus* in July 2017 at 1,917 m elevation. For Felidae, we recorded *Herpailurus yagouaroundi* in September 2017 in a locality at 1,375 m; six records of *Leopardus pardalis* between June and September 2017, and February 2018, in five localities at elevations between 1,382 and 2,306 m. In addition, four



**Figure 2.** Small mammal species captured and observed in 2017 and 2018: Didelphimorphia: A) *Metachirus myosuros*. B) *Marmosa regina/isthmica*. C) *Philander melanurus*. Chiroptera: D) *Carollia brevicauda*. E) *Enchisthenes hartii*. F) *Sturnira parvidens*. G) *Vampyressa thylene*. H) *Myotis keaysi*. Primates: I) *Aotus lemurinus*. Rodentia: J) *Heteromys aff. anomalus*. K) *Neacomys tenuipes*.

records of *L. wiedii* in August and September 2017, and April 2018, in three localities with elevations between 1,719 and 2,306 m. Finally, in May and June 2017, we reported *L. tigrinus* twice in different locations at 1,374 and 1,738 m elevation. Cranial measurements of three specimens from the study area are shown in Appendix 1.

**Artiodactyla.** We confirmed the presence of two families (Cervidae and Tayassuidae) and two species. *Dicotyles tajacu* (Tayassuidae) was registered based on indirect records and by camera traps (16 events) in July, September, October, and November 2017, and in February, March, and May 2018 at elevations between 1,382 and 1,999 m. The dwarf brocket deer, *Mazama rufina* (Cervidae) was recorded based on incidental records and observations.

**Primates.** We reported five species (*Aotus lemurinus*, *Alouatta seniculus*, *Ateles hybridus*, *Cebus versicolor* and *Saguinus leucopus*) of three families (Atelidae, Cebidae, and Callitrichidae) by direct observation. A predation event by an unidentified eagle on an individual of *Aotus lemurinus* was registered by the local community in March 2020.

**Rodentia.** We registered 16 species from seven families at the NNP Selva de Florencia (Table 1; Appendix 1). During 2000 and 2001, we reported seven species, five captured individuals and three species, based on dead specimens or bone fragments. During 2017 to 2018, rodents contributed with five species (19 captured individuals and two species recorded by dead specimens or bone fragments), with *Heteromys* aff. *anomalus* as the most abundant with 13 captures. We reported two species of *Nephelomys* which are differentiated based on the frequency of ventral white patches, the size of the posterolateral palatal pits and the shape of the palatal fossae. Using camera traps, we found that *Dasyprocta punctata* and *Cuniculus paca* were the species with the highest number of records (125 and 56, respectively). In addition, we obtained 14 records of *Syntheosciurus granatensis* plus 133 of unidentified rodents.

The BLAST query with our sequence of *Coendou quichua* recovered two sequences from GenBank (accessions and KC863881) with percentages of identity of 98.86 % and 95.87 %. The first (KC463882) was obtained from another Colombian specimen (Department of Cesar), whereas the second corresponds to an Ecuadorian specimen. This result unequivocally supports that the specimen we collected in the NNP Selva de Florencia belongs to this species.

Our sequences of *H. aff. anomalus* obtained identity values of 90.18 % and 90.04 % with sequences of *H. australis* (GU646927 and GU646928) from Panama, and 90.18 % with sequences of *H. anomalus* from Venezuela (DQ168468). This result suggests that specimens from the Selva de Florencia Natural Park identified morphologically as *H. aff. anomalus*, cannot be assigned to this species on basis on molecular data. The percentages of identity below 95 % with respect to all *Cytb* sequences of the genus even indicate they are not assignable to any of the known species

(at least those genetically characterized for this marker). The name *Heteromys (Heteromys) anomalus hershkovitzi* Hernández-Camacho, 1956 was suggested for populations of this genus from the Magdalena River basin in Colombia, and it is an available name for this taxon. The assignation and revalidation of this name to the populations of Selva de Florencia identified as *H. aff. anomalus* is needed.

For *Neacomys tenuipes*, our two sequences are 100 % identical. The highest genetic score (93.02 %) was obtained with a sequence of *N. rosalingae* (KY859763) from Peru. The only sequence of *N. tenuipes* available in GenBank (also from Colombia) was not recovered in the queries, probably due to its short length (only 177 bp). Thus, with identities below 95 % with respect to other *Neacomys Cytb* sequences in Genbank, and without larger sequences of *N. tenuipes* available to compare, specimens of the NNP Selva de Florencia cannot be molecularly assigned to any species in the genus. However, considering these specimens present all the morphological diagnostic character for *N. tenuipes*, sequences generated here can be considered the most complete publicly available. Finally, for our sequence of *S. alfari*, four matches with highest percentages of identity were of the same species: 96.88 % compared to an Ecuadorian specimen (EU340016), and three with the same value of 95.61 % from specimens collected in Panama (KY754155, GU126548, EU074635).

**Threatened categories and endemic species.** We identified eight species listed in threatened categories according to the national legislation (MADS 2017), and in the Red List of the International Union for the Conservation of Nature and Natural Resources (IUCN 2019). The most threatened species include the primates *Ateles hybridus* (Critically Endangered - CR), *Aotus lemurinus* (Vulnerable - VU), *Cebus versicolor* and *Saguinus leucopus* (Endangered - EN), the latter is considered Vulnerable according to Colombian legislation (MADS 2017). Other species in a threaten category include the carnivores *Leopardus tigrinus* and *Lontra longicaudis*, the dwarf brocket deer *Mazama rufina* (all listed globally as VU), and the pacarana *Dinomys branickii* listed as VU in Colombia (MADS 2017). The endemic species registered are: *Cryptotis colombianus* distributed in one ecoregion (the Magdalena Valley Montane Forest), *Saguinus leucopus* distributed in two ecoregions (Magdalena-Urabá Moist Forests, and *Nephelomys pectoralis* in two (Cauca Valley Montane Forests, and Northwest Andean Montane Forests), *Nephelomys childi* in three (Cauca Valley Montane Forests, Cordillera Oriental Montane Forests, and Northwest Andean Montane Forests), *Marmosops chucha*, distributed in four ecoregions (Cauca Valley Dry Forests, Magdalena-Urabá Moist Forests, Northwest Andean Montane Forests, and Magdalena Valley Montane Forests), and *Cebus versicolor* in five ecoregions (Guajira-Barranquilla Xeric Scrub, Magdalena-Urabá Moist Forests, Magdalena Valley Dry Forests, Magdalena Valley Montane Forests, and Sinú Valley dry Forests).

**Table 2.** List of mammals reported at the Parque Nacional Natural, Selva de Florencia. For bats, the number of captured individuals is included. Abbreviations are, CT: Camera trap records, Ob: Observation, To: Tomahawk, Sh: Sherman, Ind: indirect record (bones or tracks). For Carnivora, A: 2012. Obs. NNP Rangers (Weimar Hincapie – Uriel Quiceno): sector La Vega. B: Obs. 2013 (Weimar Hincapie) at quebrada Las Mercedes, Near río San Antonio, Vereda San Lucas, Florencia. C: 2019. Obs. (Hugo Ballesteros and Rigoberto Lancheros), two individuals at vereda La Abundancia. NPL: the locality is Río Hondo (a river inside the Park), but not precise locality is available. \*Endemic species. Localities are explained in Table 1. Voucher specimens are housed at the MNH-UCa unless otherwise specified.

Taxon	Year		Vouchers or type of record	Localities
	2000-2001	2017-2018		
<b>DIDELPHIMORPHIA</b>				
<i>Chironectes minimus</i>	1 Ob		218	12
<i>Didelphis marsupialis</i>	1 To, 2 Ob		208, 2427-2428	11
<i>Marmosa regina/isthmica</i>		1 Sh	1612, FMNH 70978	8, NPL
<i>Marmosa</i> sp.			876	2
<i>Marmosops chucha</i> *			FMNH 70925	NPL
<i>Metachirus myosuroides</i>		1 Sh	1613, 3165	8
<i>Monodelphis adusta</i>			227 (lost); 263	NPL
<i>Philander melanurus</i>		1 Sh	1614	8
<b>EULIPOTYPHIA</b>				
<i>Cryptotis colombianus</i>	1		193	10
<b>CINGULATA</b>				
<i>Cabassous centralis</i>			4 CT	14, 15, 17
<i>Dasypus novemcinctus</i>			201, 1800, 2430, (18 CT)	6, 8, 9, 11, 14, 17, 18, 19
<b>PILOSA</b>				
<i>Cyclopes dorsalis</i>			Photographs	NPL
<i>Choloepus hoffmanni</i>		1 obs	197, 1615, 2424-2425, 3160-3163	11, 13
<i>Tamandua mexicana</i>			2426, (8 CT)	1, 9, 11, 14, 15, 18
<b>CHIROPTERA</b>				
<b>Phyllostomidae</b>				
<i>Carollia brevicauda</i>	1	100	019-032, 035, 037, 043, 048, 055, 062, 065, 069-074, 076, 083, 088, 095, 097, 099-100, 166-168, 175, 236, 239, 243, 1603, 1634, 1635, 1638	3, 8, 11, 12
<i>Carollia castanea</i>		18	1636; 1637; 1673	3, NPL
<i>Carollia perspicillata</i>		9	22, 91, 1672	3, NPL
<i>Desmodus rotundus</i>	1		Interviews	
<i>Anoura cultrata</i>	2		94, 171	2, 10
<i>Anoura fistulata</i>	1		44	3
<i>Anoura caudifer</i>	4		58, 59, 60, 78	12
<i>Anoura geoffroyi</i>	1			NPL
<i>Micronycteris megalotis</i>		1	1632	8
<i>Artibeus lituratus</i>		6	1639, 1640, 1678	11, NPL
<i>Artibeus anderseni</i>		5	1641	11
<i>Artibeus bogotensis</i>		3	1642	11
<i>Artibeus glaucus</i>	1		0172	10
<i>Chiroderma salvini</i>	2		0067, 0081	12
<i>Enchisthenes hartii</i>	1	1	66, 77, 237, 240, 259, 1633	11, 12
<i>Phyllostomus discolor</i>	1		0089	11
<i>Platyrrhinus albericoi</i>		3	1644, 1645	11
<i>Platyrrhinus dorsalis</i>	1		0034, 0082, 0087, 0090	11, 12
<i>Platyrrhinus helleri</i>	1	7	0045, 1643, 1663	11
<i>Platyrrhinus ismaeli</i>	1		0038, 0063, 0085, 0170	10, 11, 12
<i>Sturnira bogotensis</i>		5	0042, 0047, 0084, 0093, 1056, 1652, 1654	11, 12, NPL
<i>Sturnira erythromos</i>			0080, 0084, 0234	12
<i>Sturnira parvidens</i>	1	6	24-25, 29, 39-41, 49, 51, 53-54, 64, 68, 1649, 1651, 1678	8, 11, 12
<i>Sturnira oporophilum</i>	1	8	0061	12
<i>Vampyressa thyone</i>		5	0073, 1646, 1647, 1676	8, 11, 12



Table 2. Continuation...

Taxon	Year		Vouchers or type of record	Localities
	2000-2001	2017-2018		
<b>VESPERTILIONIDAE</b>				
<i>Eptesicus chiriquinus</i>	1		147	12
<i>Myotis caucensis</i>	1		50, 152	12
<i>Myotis riparius</i>		2	1657, 1658	11
<i>Myotis keaysi</i>		1	1659	11
<b>CARNIVORA</b>				
<i>Leopardus pardalis</i>		1	(8 CT), Ind.	6, 9, 14, 17, 18
<i>Leopardus tigrinus</i>			205, (2 CT)	9, 14, 18
<i>Leopardus wiedii</i>			4 CT, photographs	6, 11, 14
<i>Herpailurus yagouaroundi</i>			1 CT, photographs	9
<i>Puma concolor</i>			Skull, FMNH 70567	NPL
<i>Cerdocyon thous</i>	1		Skull, 0200	NPL
<i>Eira barbara</i>			(6 CT)	5, 6, 7, 14, 18
<i>Bassaricyon neblina</i>		1	1631	13
<i>Nasua nasua</i>	1994	1	(6 CT), IAvH 7318	6, 11, 14, 17, 19, NPL
<i>Potos flavus</i>	1	1	3164, Obs, video	10
<i>Procyon cancrivorus</i>			(1 CT), photographs	19
<i>Lontra longicaudis</i>			A, B, C.	12
<i>Mustela frenata</i>		1	Obs.	2
<b>ARTIODACTYLA</b>				
<i>Mazama rufina</i>		1	Obs.	3
<i>Pecari tajacu</i>			1668, (17 CT)	5, 6, 7, 9, 11, 14, 18
<b>PRIMATES</b>				
<i>Alouatta seniculus</i>		1- 9 ind	3159, Obs.	4, 6, 7, 8, 9, 11, 12, 15, 17, 18, 19, NPL
<i>Ateles hybridus</i>		3 ind	Obs.	4, 9, 16
<i>Aotus lemurinus</i>		3 ind	Obs.	11, 16
<i>Cebus versicolor*</i>		1 - 15 ind	Obs.	6, 11, 12, 17, 18
<i>Saguinus leucopus*</i>		1 - 14 ind	Obs.	2, 8, 9, 15, 16, 17, 19
<b>RODENTIA</b>				
<i>Syntheosciurus granatensis</i>	1	Obs	16 CT	5, 7, 9, 11, 14, 17, 18, 19
<i>Leptosciurus pucheranii</i>		1	Photographs	1, 2, 5, 16, 18
<i>Heteromys australis</i>	1		FMNH 71185-71190	NPL
<i>Heteromys aff. anomalus</i>		13 Sh	1617, 1618, 1619, 1620	11
<i>Handleyomys alfaroi</i>			FMNH 72062, 72073-72075, 72077-72080	NPL
<i>Melanomys caliginosus</i>			FMNH 71816-71822	NPL
<i>Neacomys tenuipes</i>		5 Sh, 1 ma	1627, 1628, 1692	8, NPL
<i>Nephelomys childi*</i>	1		771, 772	12
<i>Nephelomys pectoralis*</i>			185, 188, 189, 190	12
<i>Sigmodontomys alfari</i>		1 Sh	1630	8
<i>Tylomys mirae</i>			FMNH 71215	NPL
<i>Transandinomys talamancae</i>			FMNH 72063, 72066	NPL
<i>Rhipidomys latimanus</i>	1		1690-1691	7
<i>Coendou quichua</i>		2 ind	1616, 2422-2423, (1 CT)	11
<i>Cuniculus paca</i>	1		1811-1812, (58 CT)	5, 9, 11, 14, 17, 18, 19, NPL
<i>Dasyprocta punctata</i>	1	1 ind	1607, (136 CT)	7, 9, 11, 14, 15, 17, 18, 19
<i>Dinomys branickii</i>			216-217, 883, (1 CT), 1 Photograph, IAvH 19984	10, 17, NPL

## Discussion

To our knowledge, the inventory of mammalian species at the NNP Selva de Florencia is one of the most complete for a protected area in the Colombian Andes. This information complements previous inventories for this sector of the country (Castaño *et al.* 2003; Castaño Salazar 2012; Acosta Castañeda *et al.* 2014) and becomes a base tool for the formulation of new mammal research and conservation strategies on a regional scale. Furthermore, the genetic characterization performed here for some of the species constitutes a valuable approach to explore mammal richness in Colombia, and particularly within protected areas.

Despite the mammal richness documented for the NNP Selva de Florencia is high (16.30 % of the terrestrial mammals from Colombia; Ramírez-Chaves *et al.* 2020a), many of the small mammal species registered probably require further assessments of their variation, and therefore, of its taxonomic status and distributional limits. For example, both species of genus *Nephelomys* recorded in this study are likely out of the distributional ranges suggested in a recent study based on morphometric and limited genetic data (Cárdenas 2017). Cárdenas (2017) mentioned that for Colombia, *N. childi* is restricted to the Eastern Cordillera, *N. pectoralis* is distributed in the Western Cordillera, and specimens from the Central Cordillera belong to an undescribed



**Figure 3.** Medium and large mammals registered using camera traps and direct observations in Selva de Florencia. Cingulata: A) *Dasyops novemcinctus*. Pilosa: B) *Tamandua mexicana*. Carnivora: C) *Herpailurus yagouaroundi*. D) *Leopardus pardalis*. E) *Leopardus tigrinus*. F) *Eira barbara*. G) *Nasua nasua*. Artiodactyla: H) *Pecari tajacu*. Rodentia: I) *Syntheosciurus granatensis*. J) *Cuniculus paca*. K) *Dasyprocta punctata*. L) *Dinomys branickii*.

taxon (*Nephelomys* sp.). In contrast, [Percequillo \(2015\)](#) considered that *N. childi* is present in the three Colombian Cordilleras. Therefore, the inclusion of more specimens from both mountain ranges and the north of the Department of Caldas is required to clarify the species inhabiting in this area of Colombia. This implies conducting additional field expeditions, collecting new individuals, and performing a complete molecular characterization. Molecular data (*Cytb*) of some of the species characterized here reflect higher divergence values (ca. 4 %) than those that have traditionally been used to separate sister species in mammals ([Bradley and Baker 2001](#)). This might reflect that a large portion of this diversity surely represents hidden or cryptic diversity (see [Bickford et al. 2007](#)), and in most cases only molecular information (even from a single marker, as Cytochrome b or Cytochrome C Oxidase Subunit 1) might offer enough resolution to detect it ([Bradley and Baker 2001](#)).

In some groups especially, such as rodents, shrews, marsupials, and bats, taxonomy has changed dramatically in recent years with the introduction of molecular data in revisionary works, allowing multiple species to be discriminated from what was once considered a single species (e. g., [Basantes et al. 2020](#); [Voss et al. 2020](#)). Despite that, there are few examples including material from Colombia ([Díaz-Nieto et al. 2016](#); [Franco-Sierra and Díaz-Nieto 2020](#); [Voss et al. 2020](#)), which reflects a delay in the implementation of modern methods for studying mammals in the country. Even though in this work we obtained *Cytb* sequences of common and widely distributed rodent species ([Patton et al. 2015](#)), most of them have been poorly characterized at the genetical level. For instance, our sequence of *C. quichua* is the fourth for the species (second from Colombia) showing intraspecific divergences reaching the range observed between species ([Voss et al. 2013](#)). Similarly, the sequences of *N. tenuipes* are between the first for the species ([Colmenares-Pinzón 2021](#)), and that of *Sigmodontomys alfari* is the fifth for the species (first for Colombia). For *Heteromys* aff. *anomalus* the sequences are the first molecular data from Colombian populations that will be publicly available, and the genetic distances are larger than most of the interspecific values ([Rogers and González 2010](#)). In contrast, for *Sigmodontomys* the distances are within the intraspecific ranges observed for other cricetids (e. g., *Melanomys*; [Hanson and Bradley 2008](#)). In addition, the taxonomy of the rodent species characterized here for the *Cytb* (all rodents) has relied principally on morphology and has remained stable, and none of them have included material collected in protected areas (see [Patton et al. 2015](#)). These efforts must also be replicated for other species of small mammals such as marsupials and shrews, for which cryptic diversity has been observed in Colombia ([Díaz-Nieto et al. 2016](#); [Noguera-Urbano et al. 2019](#)).

The endemic species registered at the NNP Selva de Florencia are typical elements of the Andean region and its inter-Andean valleys and ecoregions (Nor-Andean and Chocó-Magdalena Biogeographic Provinces; [Hernández Camacho](#)

[et al. 1992](#)). Other species documented are more widely distributed in the country and are within the elevational ranges known for the country (see [Solari et al. 2013](#); [Patton et al. 2015](#)). Although the species of mammals recorded in this work were expected at the NNP Selva de Florencia, we highlight the records of the olinguito (*Bassaricyon neblina*), and the Caribbean spiny pocket mouse (*Heteromys* aff. *anomalus*), that were not previously registered for the Department of Caldas ([Castaño Salazar 2012](#)). Of these, the olinguito has been included as the species of Procyonidae with the highest priority and need for research in Colombia ([Andrade-Ponce et al. 2016](#)). In addition, the presence of species in different threaten categories is highlighted, among which, primates have covered the greatest research efforts ([Castaño et al. 2003](#); [Roncancio Duque 2012](#)). Other charismatic and endangered species include felines such as the jaguar (*Panthera onca*) for which its presence has been suggested in the park ([Escobar-Lasso et al. 2014](#)). Finally, for the endemic species, additional analyses integrating biogeographic aspects, molecular information and monitoring plans inside the protected areas are needed due to the limited information available for these taxa ([Noguera-Urbano et al. 2019](#); [Ramírez-Chaves et al. 2020c](#)).

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## Appendix 1

Cranial and external measurements (in mm) of the mammals registered in the Selva de Florencia National Natural Park (see materials and methods for the acronyms of the measures we take). M: male; F: female

### Didelphimorphia:

***Marmosa regina/isthmica*** (MHN-UCa 1612 M Ad): HBL: 410; LT: 220; HF: 27; LE: 32; Wt: 159; CBL: 44.95; MTR: 17.07; LM: 8.50; PB: 14.32; PL: 24.93; NB: 5.52; LIB: 7.93; LPB: 6.74; ZB: 25.20.

***Marmosa sp.*** (MHN-UCa 876 M Ad): HBL: 462; LT: 255; HF: 25.25; LE: 20.17; Wt: -; CBL: 47.89; MTR: 18.67; LM: 9.13; PB: 12.29; PL: 25.41; NB: 6.85; LIB: 8.7; LPB: 7.48; ZB: 26.81.

***Philander melanurus*** (MHN-UCa 1614 M Ad): HBL: 600; LT: 300; HF: 50; LE: 33; Wt: -; CBL: 71.24; MTR: 29.95; LM: 14.18; PB: 21.51; PL: 42.18; NB: 9.66; LIB: 13.86; LPB: 9.53; ZB: 38.90.

***Didelphis marsupialis*** (MHN-UCa 208 juvenile): HBL: -; LT: -; HF: -; LE: -; Wt: -; CBL: 85.12; MTR: 35.31; LM: 14.93; PB: 26.98; PL: 52.12; NB: 13.46; LIB: 17.53; LPB: 11.40; ZB: 45.77.

***Monodelphis adusta*** (MHN-UCa 263 F Ad): HBL: 100; LT: 37; HF: 12; LE: 10; Wt: 6; CBL: -; MTR: -; LM: -; PB: -; PL: -; NB: -; LIB: -; LPB: -; ZB: -.

***Metachirus myosuroides*** (MHN-UCa 1613M Ad): HBL: 617; LT: 315; HF: 47; LE: 35; Wt: 307; CBL: 59.77; MTR: 24.31; LM: 11.75; PB: 15.42; PL: 32.55; NB: 10.13; LIB: 13.74; LPB: 9.85; ZB: 31.91.

### Chiroptera:

***Artibeus anderseni*** (MHN-UCa 1641M): HBL: 45; LT: 0; HF: 8.8; LE: 15.5; FL: 37.6; Wt: 10; GLS: 18.39; CIL: 16.5; CCL: 15.89; LB: 6.05; PB: 4.05; ZB: 10.83; BB: 8.32; MB: 9.53; MTR: 5.9; BM-M: 7.91; BC-C: 5.18.

***Artibeus glaucus*** (MHN-UCa 0172F): HBL: 57; LT: 0; HF: 9; LE: 16; FL: 40; Wt: 15; GLS: 20.08; CIL: 18.07; CCL: 17.31; LB: 5.58; PB: 4.71; ZB: 11.52; BB: 8.89; MB: 10.45; MTR: 6.55; BM-M: 8.18; BC-C: 5.55.

***Artibeus bogotensis*** (MHN-UCa 1642 F): HBL: 52; LT: 0; HF: 7.4; LE: 16.5; FL: 41.8; Wt: 17.5; GLS: 20.69; CIL: 19.93; CCL: 18.16; LB: 6.13; PB: 5.28; ZB: 12.02; BB: 9.28; MB: 10.75; MTR: 6.86; BM-M: 8.74; BC-C: 5.45

***Eptesicus andinus*** (MHN-UCa 0914 F): HBL: 112; LT: 47.3; HF: 9.4; LE: 17; FL: 43.2; Wt: 10; GLS: 16.94; CIL: 16.1; CCL: 15.17; LB: 6.53; PB: 4.29; ZB: 18.82; BB: 7.99; MB: 8.46; MTR: 6.35; BM\_M: 6.92; BC-C: 5.03.

***Eptesicus chiriquinus*** (MHN-UCa 0147 F): HBL: 109; LT: 48; HF: 11.4; LE: 15.6; FL: 46.4; Wt: 14; GLS: -; CIL: -; CCL: 15.77; LB: PB: 4.31; ZB: -; BB: -; MB: 9.25; MTR: 6.93; BM\_M: 7.65; BC-C: 5.29.

***Myotis caucensis*** (MHN-UCa 0050 M): HBL: 81.7; LT: 40.2; HF: 7.3; LE: 13; FL: 37.3; Wt: 5; GLS: 14.29; CIL: 13.73; CCL: 12.79; LB: 3.88; PB: 3.72; ZB: -; BB: 6.55; MB: 7.15; MTR: 5.7; BM\_M: 6.15; BC-C: 3.85.

***Myotis keasyi*** (MHN-UCa 1659 F): HBL: 85; LT: 38; HF: 6; LE: 12; FL: 38.9; Wt: 6; GLS: 14.01; CIL: 13.47; CCL: 12.62; LB: 4.19; PB: 3.64; ZB: 9.23; BB: 6.51; MB: 7.26; MTR: 5.43; BM\_M: 5.69; BC-C: 3.72.

***Myotis riparius*** (MHN-UCa 1658 F): HBL: 83; LT: 38; HF: 8; LE: 15; FL: 36; Wt: 5; GLS: 13.49; CIL: 13.17; CCL: 12.03; LB: 3.92; PB: 3.62; ZB: 8.62; BB: 6.97; MB: 7.03; MTR: 5.13; BM\_M: 5.75; BC-C: 3.83. (MHN-UCa 1657 M): HBL: 84; LT: 43; HF: 6.8; LE: 14; FL: 39.1; Wt: 6; GLS: 13.98; CIL: 13.76; CCL: 12.61; LB: 3.53; PB: 3.36; ZB: 8.61; BB: 6.33; MB: 7.03; MTR: 6.16; BM\_M: 5.79; BC-C: 3.81.

### Carnivora:

***Cerdocyon thous*** (MHN-UCa 200): CBL: 126.13; BB: 45.33; LIB: 24.14; LPB: 32.15; BR: 20.69; ZB: 69.4.

***Leopardus tigrinus*** (MHN-UCa 205): CBL: 85.24; BB: 37.56; LIB: 15.5; LPB: 23.15; BR: 19.99; ZB: 51.6.

***Bassaricyon neblina*** (MHN-UCa 1631 F): CBL: 74.39; BB: 34.68; LIB: 15.93; LPB: 17.4; BR: 16.1; ZB: 46.05.

**Rodentia:** Values are the observed range (in parentheses) and the mean.

***Handleyomys alfaroi*** (n= 2 M): HBL: (212-244) 228; LT: (106-127) 116.5; HF: (25-28) 26.5; LE: 17 -; CIL: (23.14-26.7) 24.92; LD: (6.43-7.82) 7.13; LM: (3.58-4.1) 3.84; BM1: (1.15-1.24) 1.195; LIF: (4.56-5.18) 4.87; BIF: (2.08-2.72) 2.4; PB: (2.61-3.48) 3.05; BZP: (2.65-3.09) 2.87; ZB: (12.74-15.39) 14.07; LIB: (4.8-5.43) 5.12; NL: (10.39-11.62) 11.01; IPB: (10.63-11.25) 10.94.

***Handleyomys alfaroi*** (n= 5 F): HBL: (215-230) 220.6; LT: (105-119) 111; HF: (25-28) 26; LE: (16-18) 17; CIL: (23.03-25.12) 24.26; LD: (6.26-7.09) 6.7; LM: (3.74-3.87) 3.83; BM1: (1.07-1.19) 1.15; LIF: (4.18-4.9) 4.5; BIF: (2.13-2.39) 2.29; PB: (2.71-2.93) 2.81; BZP: (2.66-3.07) 2.86; ZB: (13.14-13.69) 13.46; LIB: (4.9-5.53) 5.12; NL: (10.73-11.78) 11.16; IPB: (10.48-11.11) 10.92.

***Transandinomys talamancae*** (n= 2 M): HBL: (184-264) 224; LT: (94-127) 110.5; HF: (26-29) 27.5; LE: 17; CIL: 23.18; LD: (6.37-8.27) 7.32; LM: (4.49-4.58) 4.535; BM1: 1.33; LIF: (3.49-4.43) 3.96; BIF: (1.83-1.88) 1.855; PB: (2.5-3.14) 2.82; BZP: (2.58-3.43) 3.01; ZB: 13.26; LIB: (5.08-5.34) 5.21; NL: (10.01-11.99) 11; IPB: 11.12.

***Melanomys caliginosus*** (n= 4 F): HBL: (197-243) 217.5; LT: (85-108) 93.75; HF: (26-28) 27; LE: (16-15) 15.75; CIL: (24.51-28.02) 26.27; LD: (6.41-7.62) 7.095; LM: (3.97-4.81) 4.6; BM1: (1.18-1.51) 1.36; LIF: (3.85-4.6) 4.375; BIF: (1.78-2.25) 1.97; PB: (2.87-3.21) 3.01; BZP: (2.55-3.12) 2.86; ZB: (13.68-16.14) 15.25; LIB: (4.82-6.23) 5.74; NL: (10.2- 12.12) 11.56; IPB: (11.48-12)

21.77. (n= 3 M): HBL: (200-216) 206.6; LT: (85-95) 88.67; HF: (26-27) 26.33; LE: (15-16) 15.67; CIL: (24.23-27.44) 25.93; LD: (6.39-7.46) 6.926; LM: (4.52-4.77) 4.58; BM1: (1.39-1.44) 1.41; LIF: (3.5-4.68) 4.26; BIF: (1.63-1.83) 1.74; PB: (2.5-2.87) 2.65; BZP: (2.31-2.83) 2.65; ZB: (14.57-15.78) 15.19; LIB: (5.93-6.12) 6.02; NL: (10.70-10.74) 10.60; IPB: (11.61-12.1) 11.87.

***Tylomys mirae*** (FMNH 71215 M): HBL: 477; LT: 229; HF: 40; LE: 29; CIL: 47.54; LD: 14.04; LM: 8.73; BM1: 2.23; LIF: 8.82; BIF: 3.76; PB: 4.61; BZP: 8.23; ZB: 26.14; LIB: 10.90; NL: 17.0; IPB: 17.33.

***Nectomys magdalenae*** (MHN-UCa 1448 M): HBL: 500; LT: 242; HF: 48; LE: 15.87; CIL: 42.62; LD: 12.38; LM: 7.08; BM1: 2.13; LIF: 6.74; BIF: 3.43; PB: 4.97; BZP: 5.26; ZB: 24.57; LIB: 7.44; NL: 18.59; IPB: 8.91.

***Neacomys tenuipes*** (MHN-UCa 1627, 1628, 1692 F) HBL: 157; LT: 85; HF: 18; LE: 14; CIL: 18.42; LD: 5.16; LM: 2.68; BM1: 0.79; LIF: 2.47; BIF: 1.62; PB: 2.41; BZP: 1.73; ZB: 10.06; LIB: 4.17; NL: 8.6; IPB: 7.79. (2n= M) HBL: (160-166.22) 163.11; LT: (87-91.3) 89.15; HF: (20.3-21) 20.65; LE: 15.6; CIL: (18.17-19.58) 18.88; LD: (5.2-5.89) 5.545; LM: (2.268-2.85) 2.56; BM1: (0.91-0.92) 0.92; LIF: (2.41-2.47) 2.44; BIF: (1.61-1.48) 1.55; PB: (2.34-2.63) 2.49; BZP: (1.68-1.86) 1.77; ZB: 11.33; LIB: (4.26-4.41) 4.36; NL: (8.7-8.87) 8.79; IPB: (8.03-8.37) 8.20.

***Sigmodontomys alfari*** (MHN\_UCa 1630 M): HBL: 280; LT: 155; HF: 31; LE: 17; CIL: 31.58; LD: 9.59; LM: 5.52; BM1: 1.85; LIF: 4.9; BIF: 2.32; PB: 3.09; BZP: 4.23; ZB: 17.64; LIB: 6; NL: 14.43; IPB: 7.73.

***Heteromys aff. anomalus*** (n= 4 M): HBL: (196-265) 232.25; LT: (110-145) 132.50; HF: (28.6-33) 30.20; LE: (13.5-19) 16.13; CIL: (23.25-29.02) 26.59; LD: (7.11-9.06) 8.18; LM: (4.08-5.07) 4.71; BM1: (1.4-1.72) 1.52; LIF: (1.6-1.9) 1.76; BIF: (0.91-0.95) 0.93; PB: (1.67-2.62) 2.18; BZP: (3.29-3.72) 3.45; ZB: (15.13-16.79) 15.86; LIB: (7.27-9.07) 8.47; NL: (12.65-13.97) 13.29; IPB: (7.63-8.49) 8.12. (F): HBL: 242; LT: 147; HF: 33.1; LE: 17; CIL: 27.66; LD: 8.45; LM: 4.69; BM1: 1.59; LIF: 1.63; BIF: 0.93; PB: 2.61; BZP: 3.46; ZB: 15.02; LIB: 8.96; NL: 13.52; IPB: 7.75.

***Nephelomys pectoralis*** (MHN-UCa 185 F, 190 F): HBL: (300-335) 317.5; LT: (162-190) 117.6; HF: (34.3-36.7) 35.5; LE: (21-22.4) 21.7; CIL: (32.65-35.53) 34.09; LD: (9.78-10.48) 10.13; LM: (5.29-5.84) 5.57; BM1: (1.63-1.67) 1.65; LIF: (6.27-6.77) 6.52; BIF: (2.97-2.98) 2.98; PB: (3.82-3.85) 3.84; BZP: (3.87-3.96) 3.92; ZB: (17.22-19.63) 18.43; LIB: (4.97-5.36) 5.17; NL: (13.25-14.64) 13.95; IPB: (9.4-10.78) 10.09. (MHN-UCa 188 M): HBL: 300; LT: 160; HF: 33.1; LE: 21.1; CIL: 31.01; LD: 9.12; LM: 5.54; BM1: 1.57; LIF: 6.4; BIF: 2.99; PB: 3.69; BZP: 3.77; ZB: 17.12; LIB: 5; NL: 11.94; IPB: 9.25.

***Nephelomys childi*** (MHN-UCa 772 M): HBL: 290.7; LT: 140; HF: 33.45; LE: 21.95; CIL: 31.49; LD: 9.44; LM: 5.33; BM1: 1.51; LIF: 5.37; BIF: 2.56; PB: 3.71; BZP: 3.7; ZB: 17.27; LIB: 5.57; NL: 12.29; IPB: 9.61.





# The ghost mammals from Mexico and their implications

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The species records are key to determine their distribution. In México, there are records located up to more 200 km outside the known range of *Ateles geoffroyi*, *Cryptotis mayensis*, *Pteronotus davyi* and *Tlacuatzin sinaloae*. Other species were captured in their type locality but have not been recorded again over up to 100 years: *Dipodomys gravipes*, *Oryzomys peninsulae*, *Peromyscus mekisturus*, *P. pembertoni*, *Sorex sclateri*, *S. stizodon*, *Tylomys bullaris* and *T. tumbalensis*. This study analyzes these mammalian species records, their information gaps related with their known range, and discusses the likely implications for conservation. A survey of the literature and databases of scientific collections available on the Internet were conducted. A geographic information system was used for the spatial analysis of the records obtained. Records outside the limit of the known range of these species are due to misidentification of specimens, accidental introduction and lack of field corroboration. Some of the species captured only in their type locality can be deemed extinct while others require field and laboratory work. Geographic records of the species are valuable inputs to define the distribution range of species and advance our current knowledge about the Mexican. The use of records with errors or that should no longer be considered have an impact on the risk categorization of species and the development of conservation strategies.

Los registros de especies son importantes para conocer su distribución geográfica. En México, hay especies con registros fuera de su área de distribución conocida hasta por más de 200 km: *Ateles geoffroyi*, *Cryptotis mayensis*, *Pteronotus davyi* y *Tlacuatzin sinaloae*. Otras se capturaron en su localidad tipo y no se han vuelto a registrar hasta por 100 años: *Dipodomys gravipes*, *Oryzomys peninsulae*, *Peromyscus mekisturus*, *P. pembertoni*, *Sorex sclateri*, *S. stizodon*, *Tylomys bullaris* y *T. tumbalensis*. El objetivo de este trabajo es analizar los registros de estas especies de mamíferos, sus vacíos de información en relación con su área de distribución conocida, así como las posibles implicaciones que conllevan para la conservación. Se realizó una consulta bibliográfica y de bases de datos de colecciones científicas disponibles en internet. Se usó un sistema de información geográfica para el análisis espacial de los registros obtenidos. Los registros encontrados muy fuera del límite de la distribución conocida de estas especies, se deben a identificación errónea de los ejemplares, introducción accidental y falta de corroboración en campo. Mientras que las especies que solo se han capturado en su localidad tipo, algunas pueden considerarse extintas y otras más requieren trabajo de campo y laboratorio. Los registros geográficos de las especies son información importante para definir la distribución de las especies y de esta manera robustecer el conocimiento que se tiene sobre la biodiversidad mexicana. El uso de registros, con errores no deben ser considerados, debido a que repercuten en la categorización riesgo de las especies y por ende las estrategias de conservación.

**Keywords:** Conservation; extinction; geographic distribution range; records; systematics; taxonomy.

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## Introduction

Records of wild species are essential to determine their geographic distribution through the reconstruction of biodiversity from historical times (fossil records) to the present. These records can be consulted by searching literature reports or databases of scientific collections, many of them are already digitalized and are available at Internet in many platforms. Some of these platforms are fed by records from citizen observations, and experts validate the identifications of the species, like Naturalista (<https://www.naturalista.mx/>), but sometimes the photographs do not show accurate characteristics in order to identify them correctly. Today, the use of scientific collection databases is increasingly common in research because of the convenience and low cost of obtaining these data. By combining them with environmental variables, known distribution ranges, and ecological and evolutionary aspects of species, they can be used for the management, use, and conservation of species and their ecosystems (Graham et al. 2004; Funk 2018; Cook and Light 2019).

In México, several mammal species were collected once at a certain time and place and were never observed or collected again, it means they are unique records. This can be potentially caused by two scenarios: records outside the known range of the species and unique records from type localities that have not been recorded again over up to 100 years. The first involves species with a broad range that have any record on the literature or in scientific collections databases completely outside their known range, with large areas between them. This is the case of the Spider monkey (*Ateles geoffroyi*), recorded 10 km NNW of Cihuatlán, Jalisco and 25 km NNW of Ciudad Victoria, Tamaulipas (Villa 1958). Yucatán small-eared shrew (*Cryptotis mayensis*), family Soricidae, collected at Cueva del Cañón del Zopilote, Guerrero (Choate 1970). Davy's naked-backed bat (*Pteronotus davyi*), family Mormoopidae, collected at Cueva de los Mártires, Sierra La Laguna, Southern Baja California Sur (Woloszyn and Woloszyn 1982). The grayish mouse opossum (*Marmosa* sp. [*Tlacuatzin sinaloae* sic]), family Didelphidae, collected at Misión de San Ignacio, Baja California Sur (López-Forment and Urbano 1977).

The second regards endemic species with restricted distribution that were collected in the type locality when they were described but have not been recorded again for more than 100 years. This is the case of San Quintín kangaroo rat (*Dipodomys gravipes*) from San Quintín, Baja California; Lower California rice rat (*Oryzomys peninsulae*) from Santa Anita, Baja California Sur; Puebla deer mouse (*Peromyscus mekisturus*) from Ciudad Serdán, Puebla; San Pedro Nolasco deer mouse (*Peromyscus pembertoni*) from San Pedro Nolasco island, Sonora; Sclater's shrew (*Sorex sclateri*) and San Cristóbal shrew (*Sorex stizodon*) from San Cristóbal de las Casas, Chiapas. Chiapan climbing rat (*Tylomys bullaris*) from Tuxtla Gutiérrez, Chiapas; and Tumbalá climbing rat (*Tylomys tumbalensis*) from Tumbalá, Chiapas. Of these, *P. pembertoni* and *O. peninsulae* are considered extinct ([Álvarez-Castañeda et al. 2017](#); [DOF 2019](#)).

The species records mentioned here, are used to produce lists of species for particular geographic areas, and also, their biological richness. Furthermore, the records are used to know the potential distribution of the species in a given area; in turn, this is a meaningful variable in determining the risk status of species as reflected in national and international regulations and laws (NOM-059-SEMAR-NAT-2010, Red List of the International Union for Conservation of Nature and the Endangered Species Act for the United States and Canada). Altogether, the species listings and proposed distribution have potential implications for the conservation, as well as for the creation and regulation of conservation, management, and utilization policies for the species from a given geographic area. If the information taken as input is incorrect, this will affect the whole approach proposed; so, it highlights the importance of the curatorship of scientific collections and the deposit of the specimens in them, in order to contribute for the verification of the records.

The analysis of the mammals of México commonly uses historical records of these species, although each of these records has been mentioned in recent publications and referencing the original work with no critical perspective on the relevance of these records or the permanence of the species.

This warrants a critical review of the 12 mammal species mentioned above, aiming to contribute to solve the questions regarding the knowledge of their distribution, ecology, biology and conservation. The objective of this study is to analyze the records, their information gaps related with the known range of these mammal species, and discuss the potential implications for the conservation of the geographic their area involved; even though they are records outside the known distribution range and unique records.

## Materials and Methods

Literature references and databases of scientific collections were surveyed through VertNet (<https://vertnet.org/>), GBIF (<https://www.gbif.org/>), IBdata (<https://www.ibdata.ib.unam.mx/web/>), in addition to the Mammal Collection of Centro de Investigaciones Biológicas del Noroeste, S.C., to

locate specimens collected in areas near the records of the localities of the species concerned: *Ateles geoffroyi* (Jalisco and Tamaulipas), *Cryptotis mayensis* (Guerrero), *Pteronotus davyi* (Baja California Sur) and *Tlacuatzin sinaloae* (Baja California Sur). The records were projected into the geographic space for measurements of distances between the outside of the known distribution range records and analyze them by a geographic information system with the software QGIS v.3.8.3 ([QGIS 2018](#)).

Also considered were species known only from the type locality, with a very limited number of specimens collected at least 100 years ago and for which no additional specimens have been recorded again after the original date of collection. For the above reason, information on ecology and biology is virtually unknown.

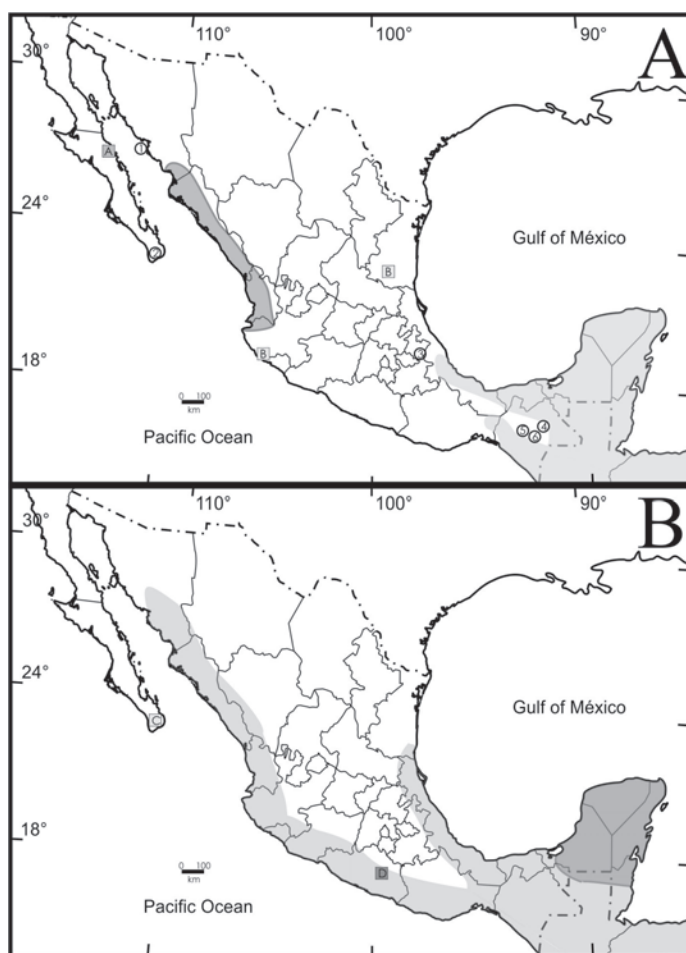
## Results

*Records outside the known distribution.* *Ateles geoffroyi* was reported by sightings in two states outside its known distribution. In the state of Jalisco, a group of five individuals was observed on the road to Bahía de Navidad (currently Barra de Navidad; Figure 1A) in a tropical forest with *Ficus* sp. vegetation ([Villa 1958](#)). [Villa \(1958:346\)](#) states "I immediately got the idea that these animals may have escaped from the captivity of some transhumant circus or from the possession of local people; but the fact that they were found in an area of very small human population and that the few ranchers interviewed were not surprised by their presence, makes me think that they have been endemic in the region. I certainly do not know since when these animals have prowled the contours and I fear they will not persist for much longer". The closest confirmed record on the Pacific coast is located in Oaxaca at 1,045 km to the south, and on the Gulf of México slope, 781 km away in Veracruz (Table 1; [GBIF 2021](#)).

There are indications of the possible presence of Spider monkeys in Acapulco, Guerrero ([Kellogg and Goldman 1944](#)); in addition, this species was frequently used as pet in the 1960s, and there are accounts that monkeys were captured near Acapulco. Therefore, it is highly likely that some troops would have survived until that time (Juan Pablo Gallo-Reynoso, pers. comm.). The Spider monkey is also depicted in pre-Columbian representations such as vessels and stone engravings; there was even a ruler named "Gran Mono" (Great Monkey) in 1393. This suggests that the species inhabited localities of the state of Guerrero, such as La Sabana and Palma Sola in Acapulco, from pre-Columbian times to the colonial period, when it was recorded by Humboldt ([Reyes-Álvarez and Guerrero-Gómez 2014](#)). Its presence in these localities was not confirmed from records in scientific collections. There is a single record (1895613809 [GBIF 2021](#)) with geographic coordinates between the localities mentioned in Acapulco, but all other data correspond to a record of [Goodwin \(1969\)](#) in the state of Oaxaca; this case highlights the need to always review the complete set of data instead of

only considering the species and geographic coordinates reported, as the error may lie in how the locality was georeferenced.

In case the Spider monkey is considered to be present in Acapulco, the Jalisco record is still 567 km away (Table 1). Two additional factors are key for ruling out the presence of *Ateles geoffroyi* in the state of Jalisco. The first is the Balsas basin and river, which is an insurmountable barrier for Spider monkeys because of their ethology of aversion of open areas; the second is the lack of continuous vegetation that would allow the survival of this species throughout the year (González-Zamora et al. 2009). It results feasible that the Spider monkey population referred to Jalisco (Villa 1958) in fact, was a circus or pet release, when people can not maintain the animals anymore, they release them in a place that they think is optimal for their subsistence.



**Figure 1.** Map showing the distribution of species known only by the type locality. A. *Dipodomys gravipes* (1), *Peromyscus pembertoni* (2), *Oryzomys peninsulae* (3), *Peromyscus mekisturus* (4), *Tylomys tumbalensis* and *Sorex stizodon* (5), *Tylomys bullaris* (6) and *Sorex sclateri* (7). The current distribution of *Ateles geoffroyi* is shown in light gray; the boxes with the letter A, B and C mark the records outside its known range, the letter D marks a possible distribution and the letters E and F show records from the known range. The current distribution of *Tlacuatzin sinaloae* is shown in dark gray; the box with the letter L marks the record outside its known range and the letter M shows a record from the known range. B. The current distribution of *Cryptotis mayensis* is shown in dark gray; the boxes with the letter G marks the record outside its known range and the letters H and I show records from the known range. The current distribution of *Pteronotus dayi* is shown in light grey; the box with the letter J marks the record outside its known range and the letter K show a record from the known range.

*Ateles geoffroyi* was also recorded in the vicinity of Ciudad Victoria, Tamaulipas (Villa 1958). In this record, Villa (1958) refers to it from a talk with Dr. Málaga Alba: “He informed me of another similar encounter, but in the highest portion of Barranca de Caballeros, approximately 25 km in straight line NNW of Ciudad Victoria, Tamaulipas, in 1954” (Villa 1958:347). However, this claim was never confirmed by the author, nor he was physically in the area to determine whether the type of habitat was appropriate for the presence of the species. Villa (1958) considered this account as valid based on the suggestion by Kellogg and Goldman (1944) that *A. geoffroyi* may inhabit the tropical forest in the southern region of the state, because in 1898, the northern limit of its distribution was San Luis Potosí, but these authors did not confirm this distribution. Subsequently, Álvarez (1963) mentioned that in addition to the account by Villa (1958) and the suggestion of Kellogg and Goldman (1944), no additional records are available, not even after having conducted fieldwork in the area.

Currently, the records available in the collection databases are those referred to in the literature (Villa 1958; Álvarez 1963). The linear distance between the Tamaulipas record to the nearest known record in the locality of Teocelo, Veracruz, is 781 km (Table 1).

There is another atypical record of *Ateles geoffroyi* in Ciudad Juárez, Chihuahua, corresponding to a male that was found dead in a waste lot; the skin and skull are deposited in the collection of the University of Texas at El Paso (UTEP 7964). This record most likely corresponds to a discarded corpse of a dead pet since the closest record of its known distribution is in Teocelo, Veracruz, at 1,657 km (Table 1).

The analysis of the three records of *A. geoffroyi* mentioned above coincides in that they are not located within the distribution range of the species and its habitat is also discontinuous; besides, individuals of this species are commonly kept as pets. Based on this, we consider that these records should not be used. *Ateles geoffroyi* is listed as Endangered in NOM-059-SEMARNAT-2010 (DOF 2019) and as Endangered category (A4cd: Population decline to observed levels of 30 % or lower over ten years due to the decline in the distribution area, potential range, habitat quality, and actual exploitation levels) by IUCN (Cortes-Ortiz et al. 2021).

*Cryptotis mayensis* were recorded from remains (parts of skulls and mandibles) found in pellets of *T. alba* collected on 9 September 1969 (López-Forment and Urbano 1977; Figure 1B), deposited in the Colección Nacional de Mamíferos of the Instituto de Biología at Universidad Nacional Autónoma de México (CNMA 11031-11043 and 12666-12692; Choate 1970; Ramírez-Pulido and Sánchez-Hernández 1972; Carraway 2007). The survey in VertNet and IBData yielded no records of *C. mayensis* in the state of Guerrero, with La Tuxpeña, Campeche, being the nearest locality at 1,013 km in a straight line (Table 1); however, this implies transiting through habitats that are not typical of the species. Should the species had dispersed through the

**Table 1.** Distances between the mammal species records outside their known distribution range and the closest records inside their known distribution range. Localities are in referencences to Figure 1

Species	Type of record	Georeference	Locality	Distance (km)	Reference	
<i>Ateles geoffroyi</i>	A	Out range	31.7020, -106.4670	Ciudad Juárez, Chihuahua	A/E = 1,657	GBIF 2021
	B	Out range	23.7361, -99.1461	Barranca de Caballeros, Ciudad Victoria, Tamaulipas	B/E = 512	Villa 1958
	C	Out range	19.2255, -104.6501	Cihuatlán, Jalisco	C/F = 1,045	Villa 1958
	D	Possible range	16.8668, -99.8206	Acapulco, Guerrero	C/D = 567	Reyes-Álvarez and Guerrero-Gómez 2014
	E	In range	19.3916, -96.9750	Teocelo, Veracruz		GBIF 2021
	F	In range	16.3226, -95.2423	Tehuantepec, Oaxaca		Hall 1981
<i>Cryptotis mayensis</i>	G	Out range	17.1327, -99.6013	Cañón del Zopilote, Guerrero	G/H = 1,013	Ramírez-Pulido and Sánchez Hernández 1972
	H	In range	18.4494, -90.1144	La Tuxpeña, Campeche		GBIF 2021
	I	In range	17.3936, -89.6336	Uaxactún, Guatemala	G/I = 1,206	GBIF 2021
<i>Pteronotus davyi</i>	J	Out range	23.6533, -109.6908	Cueva de los Mártires, BCS	J/K = 232	Woloszyn and Woloszyn 1982
	K	In range	24.9319, -107.8738	La Chinacatera, Sinaloa		GBIF 2021
<i>Tlacuatzin sinaloae</i>	L	Out range	27.2839, -112.8839	Misión de San Ignacio, BCS	L/M = 393	López-Forment and Urbano 1977
	M	In range	27.0233, -108.9322	Álamos, Sonora		GBIF 2021

inhabits considered by the species records implies a dispersion through the Isthmus of Tehuantepec, coast of Chiapas, Oaxaca and Guerrero of approximately 1,206 km to reach the nearest locality by this route in Uaxactún, Petén in Guatemala (Table 1).

Choate (1970:270-277) analyzed the referred specimens and states that these may not belong to *mayensis*, at that time belonging to *C. nigriscens*, although they show certain morphological dental characteristics suggesting a potential association. Hall (1981:63) still considered the record at Cañón del Zopilote, Guerrero as belonging to *C. nigriscens mayensis*. The analysis of the database shows that the only species of *Cryptotis* distributed in the state of Guerrero is *C. goldmani* ( $n = 35$ ). Cañón del Zopilote is 30 km in a straight line from Omiltemi, the type locality of *C. goldmani* (Choate 1970). It is highly likely that the records classified as *C. mayensis* actually belong to *C. goldmani*, although confirmatory genetic analyses are required. *Cryptotis mayensis* is listed under the Special Protection category in NOM-059-SEMARNAT-2010 (DOF 2019) and as Least Concern by IUCN (Cuarón et al. 2016).

The record of *Pteronotus davyi* in Baja California Sur is based on a single female (Woloszyn and Woloszyn 1982), but it could not be located in any of the four possible scientific collections where it might have been deposited: Universidad Autónoma de Baja California Sur, Centro de Investigaciones Biológicas del Noroeste, Colección Nacional de Mamíferos of the Instituto de Biología at Universidad Nacional Autónoma de México, and Zoological Collection of the Mammal Research Institute at the Polish Academy of Sciences (<https://ibs.bialowieza.pl/en/scientific-collection/>). The lack of records and the reference in the book by Woloszyn and Woloszyn (1982) describing that most of the organisms captured were released *in situ* suggest that this is the case of this specimen (Woloszyn and Woloszyn 1982; Jones 1983), thus making it impossible to confirm its correct identification. The analysis of specimens deposited in

collections yielded 5,274 records from the databases of 37 national and international scientific collections corresponding to the genus *Pteronotus* from across its distribution; no other record for the Baja California peninsula of any of the four species of the genus distributed in México was found. The record of *Pteronotus davyi* that is closest to Baja California Sur is La Chinacatera, Sinaloa, located on the other side of the Gulf of California in the continental portion of México located 232 km away in a straight line (Figure 1B; Table 1). In the state of Sinaloa, 289 specimens of *Pteronotus* have been recorded. Bats have been collected across this region over 30 years, surveying more than 30 mines with bat colonies. In some cases, monthly follow-up of the colonies has been conducted in some mines (Segura-Trujillo 2014), and other research groups have carried out field surveys, with no records of the species in any such cases (Arnaud et al. 2012; Vanderplanck et al. 2016). The unique Mormoopid species present and abundant in the area is *Mormoops megalophylla* (Cortés-Calva et al. 2016).

Possible explanations are that *P. davyi* may have been misidentified as *Mormoops*; this seems rather unlikely given the dissimilar morphology; another scenario is that the specimen was captured across the Gulf of California by a hurricane. The data analysis shows no evidence or a valid record to confirm the presence of *P. davyi* in the Baja California peninsula, so this area should not be considered within the distribution range of this species. *P. davyi* is listed as Least Concern by the IUCN (Solari and Dávalos 2019).

The record of *Marmosa* sp. (López-Forment and Urbano 1977) can be assigned to *Tlacuatzin sinaloae* (Arcangeli et al. 2018) based on species with closest distribution. The record is based on the finding of a mandible fragment found in a pellet of a barn owl (*Tyto alba*), that is not deposited in any scientific collection. López-Forment and Urbano (1977:240) state that "It is impossible to accurately determine the species because it is the only fragment in our material is a mandible. If it were not for this circumstance, we would be

inclined to believe that it belongs to *Marmosa canescens*, considering that this species reaches its northernmost distribution on the western coast." According to the distribution, the only species in the *Marmosa* complex is *T. sinaloe*, distributed along the Pacific coast from its border of Jalisco with Nayarit to Álamos, Sonora (Figure 1A). Álamos is the known locality of *Tlacuatzin* that is closest in straight-line to the Baja California Sur record, 393 km apart (Table 1), on the other side of the Gulf of California, which at this point has a width of 220 km. This is a species of exclusively terrestrial habits; thus, if it had dispersed, it would have moved along the coast northward through the coast of Sonora and then south through the Baja California peninsula. The covering a distance between both localities is 1,149 km and crossing the Altar Desert — one of the most inhospitable landscapes in North America. This displacement may have occurred during the Pliocene, some 4 to 5 million years ago (Gastil *et al.* 1975) when the peninsula was still united to the continent. There is a record of a fossil marsupial (*Pedionomys* sp.) in El Rosario, Baja California, which is common to localities in the central-western United States during the Mesozoic-Cretaceous period (Ferrusquía-Villafranca and Torres-Roldán 1980; Ferrusquía-Villafranca *et al.* 2010). The review of literature references and databases of 30 national and international museum collections shows that this is the only record of the Northern Grayish mouse opossum corresponding to the Baja California peninsula. In contrast, 123 records were found in Sinaloa and seven in Álamos, Sonora.

The likely logic explanation is that the Northern Grayish mouse opossum was predated and eaten by a Barn owl in Sinaloa, which then flew to the Baja California peninsula, regurgitated its mandible and been found into the pellet. When migrating, *Tyto alba* can travel between 20 and 1,000 km, flying over the South Atlantic Ocean (Santillán *et al.* 2011; Audubon 2021). It has also been suggested that the Northern Grayish mouse opossum may have been carried in a box of fruit from the mainland and was subsequently consumed by *T. alba* once in the Baja California peninsula (Gardner and Cortés-Calva 1999). The incidentally introduction of a species is a common event in aquatic species, insects, and plants (Ramírez-Albores and Badano 2013; Mendoza-Alfaro and Koleff 2014). The previous explanations lead to consider that the Northern Gray mouse opossum is not currently distributed in the Baja California peninsula. *Tlacuatzin sinaloe* is listed (as *T. canescens*) under Least Concern category on the IUCN Red List (Martin 2017). Its recent taxonomic changes warrant a reassessment of its conservation status.

*Type-locality records.* *Dipodomys gravipes* was described from a locality 3 km west of Misión de Santo Domingo, Baja California (Huey 1925; Figure 1A) and is known only from the San Telmo plains to El Rosario de San Quintín, in the eastern portion of the Baja California peninsula, associated with desert coastal shrub vegetation in relatively flat areas with deep soils (Best 1983; Best and Lackey 1985; Patton and Álvarez-Castañeda 1999). When Huey (1925) collected

the original specimen, there were two large colonies in the collection area and these were considered abundant until 1972, when the area started to be cleared for agriculture (Best 1983; Best and Lackey 1985). The last record dates back to 1986, although Tremor *et al.* (2019) possibly captured an individual of the species, but it is not confirmed. In addition, an analysis of the remaining optimal habitat for *D. gravipes* was conducted, where a small population may still exist in the wild (Cab-Sulub and Álvarez-Castañeda 2020). *Dipodomys gravipes* is listed as Extinct by NOM-059-SEMARNAT-2010 (DOF 2019) and as Critically Endangered (possibly extinct, D: Number of mature individuals lower than 1,000) by IUCN (Álvarez-Castañeda and Lacher 2018).

*Oryzomys peninsulae* is described from six specimens from Santa Anita, Baja California Sur (Thomas 1897; Figure 1A); it was last recorded in 1906 by Goldman (1951) in Santa Anita and San José del Cabo, Baja California Sur. Nelson (1922) considers that it is an introduced species that should be considered as *O. couesi*. Later, Carleton and Arroyo-Cabrales (2009) reviewed the status of this species and considered it to be valid.

At the beginning of the 1990s, Álvarez-Castañeda (1994) searched for the species and determined that tourist development in the Los Cabos region led to the drying-up of the Santa Anita stream, causing the loss of habitat for *Oryzomys*, and thus declared it as potentially extinct. *Oryzomys peninsulae* is listed as Extinct by NOM-059-SEMARNAT-2010 (DOF 2019) and as a Least Concern (as a subspecies of *O. couesi*) by IUCN (Linzey *et al.* 2016), if is validated *O. peninsulae* as a full species, it could change its risk category.

*Peromyscus mekisturus* has its type locality in Ciudad Serdán (Chalchicomula), Puebla, documented by Merriam (1898; Figure 1A) from a single specimen. Later, another specimen collected at Tehuacán, Puebla was identified as *P. mekisturus* (Hooper 1947); however, this second specimen may instead correspond to *P. melanophrys*, according to the analysis of Castañeda-Rico *et al.* (2014), where it is mentioned that this specimen was previously considered a member of the *melanophrys* species group (Hooper 1968; Hall 1981; Carleton 1989). Chalchicomula is surrounded by oat, barley, and chickpea crop fields and uncultivated land where pastures, agave, cacti, small oak trees, and thorny shrubs grow (Goldman 1951:237). Castro-Campillo *et al.* (2014) and Bradley *et al.* (2017) described this species as occupying a pine-oak forest microhabitat based on Goldman (1951). The Chalchicomula specimen was not collected by Goldman but was donated by a local inhabitant, so no reliable geographic record is available. *P. mekisturus* is listed a Threatened in NOM-059-SEMARNAT-2010 (DOF 2019) and as Critically Endangered in the IUCN Red List (possibly extinct) (B1ab (iii): distribution less than 100 km<sup>2</sup> highly fragmented and with still declining populations (Álvarez-Castañeda 2018).

*Peromyscus pembertoni* collected in the San Pedro Nolasco Island, Sonora, was reported along with *P. boylii glasselli*, which was captured in a similar amount (Burt

1932; Figure 1A). Subsequently, [Lawlor \(1983\)](#) sampled the island and captured *P. boylii glasselli* organisms but no *P. pembertoni*. Although collection efforts on the island have continued, no other *P. pembertoni* organisms have been captured ([Álvarez-Castañeda and Cortés-Calva 1999](#); [Álvarez-Castañeda and Ortega-Rubio 2003](#); Sergio Ticul Alvarez-Castañeda, pers. comm.). The presence of *P. boylii* and the absence of *P. pembertoni* suggest that *P. boylii* probably replaced *P. pembertoni* due to strong island and interspecific competition ([Lawlor 1971](#)). *P. pembertoni* is listed as Extinct in both NOM-059-SEMARNAT-2010 ([DOF 2019](#)) and the IUCN Red List ([Álvarez-Castañeda et al. 2017](#)).

The type locality of the shrew *Sorex sclateri* in Tumbalá and San Antonio Buenavista, Chiapas, is known only from the specimens used in their original description ([Merriam 1897](#); [Carraway 2007](#); Figure 1A). *S. sclateri* is a unique species due to its large size relative to species of the genus *Sorex*, so it is easy to distinguish by a specialist. To note, the only record of the species dates back to approximately 125 years ago, and the area where it was recorded is today heavily deforested ([Cruz 2017](#)). Shrews are hard-to collect species; in fact, *Cryptotis lacandonensis* was recently described ([Guevara et al. 2014b](#)). However, specimens from this species were already collected four years before being described, and their distribution range was expanded ([Lorenzo et al. 2019](#); [Pérez et al. 2019](#)). The circumstances around its collection and the reference of the presence of other Soricidae in tropical regions suggests that *S. sclateri* as currently extinct. *S. sclateri* is listed as Threatened in NOM-059-SEMARNAT-2010 ([DOF 2019](#)) and as Critically Endangered (B1ab (iii): Current range less than 5,000 km<sup>2</sup> severely fragmented and continuously declining) by IUCN ([Cuarón and de Grammont 2018](#)).

*Sorex stizodon* is described from a specimen collected in what is now the Huitepec Ecological Reserve, Chiapas, located on the outskirts of the city of San Cristobal de las Casas (Figure 1A). *S. cristobalensis* is also found within the range of *S. stizodon* ([Jackson 1925](#); [Matson and Ordóñez-Garza 2017](#)). Most of the soricidae species are very difficult to identify, but in this case, *S. stizodon* distinguishes easily because it has a unique character within the genus, i.e., the second unicuspid tooth is much larger than the first ([Merriam 1895](#)). *S. cristobalensis* was recently collected near its type locality, very close to the reference locality of *S. stizodon* ([Guevara et al. 2014a](#)). This confirms the presence of species of the genus *Sorex* in the region and the absence of *S. stizodon*, which can therefore be considered extinct. *S. stizodon* is listed as Threatened in NOM-059-SEMARNAT-2010 ([DOF 2019](#)) and as Critically Endangered (B1ab (iii): current range less than 5,000 km<sup>2</sup>, severely fragmented and continuously declining) by IUCN ([Cuarón et al. 2018](#)).

*Tylomys bullaris* is known from a single specimen collected at the Tuxtla Gutiérrez region, Chiapas ([Merriam 1901](#); Figure 1A). Some authors have considered that this specimen is actually a juvenile of *T. nudicaudus* ([Hall 1981](#); [Espinoza and Martínez 2009](#)), although it has very enlarged audi-

tory bullae that allow its easy differentiation. The distribution range has rough physiography, so there are still areas with optimum habitats; however, the difficult access to this area, also affected by constant social conflicts ([Castro 2007](#)), hinders the study of the fauna. This set of variables produces an unclear picture of the status of the species, despite the lack of collection records in over 120 years. *Tylomys bullaris* is listed as Threatened in NOM-059-SEMARNAT-2010 ([DOF 2019](#)) and as Critically Endangered (Possibly Extinct; B1ab (i, ii, iii, iv, v) + 2ab (i, ii, iii, iv, v): distribution area less than 100 km<sup>2</sup>; severely fragmented; continuous decline of the area of occurrence and habitat occupation and quality; number of localities less than 50 km<sup>2</sup> in a continuous decline in the area of occurrence and habitat occupation and quality) by IUCN ([Álvarez-Castañeda and Castro-Arellano 2019a](#)).

*Tylomys tumbalensis* has been recorded only from Tumbalá, Chiapas, with a single specimen that is a sub-adult male ([Merriam 1901](#); Figure 1A). Some authors have considered that this specimen is actually a juvenile of *T. nudicaudus* ([Hall 1981](#); [Espinoza and Martínez 2009](#)). *T. tumbalensis* has been recorded in areas outside its type locality, but no specimens supporting these identifications are available in these cases ([Espinoza et al. 1998](#); [1999a](#); [1999b](#); [Goodwin \(1955\)](#)). Based on reviews of specimens of both species from collections and the literature, they are considered to have distinguishing characteristics, such as the length of the maxillary tooththrow ([Monroy-Gamboa et al. in press](#)). For its part, [Goodwin \(1955\)](#) recorded a specimen collected in La Primavera, Guatemala, that is larger but shows the dental trait that characterizes the species, so that it could be the second locality of *T. tumbalensis*. The locality in Guatemala implies a distribution broader than the known range and the possible validity and permanence of the species. It is worth highlighting that the species of the genus *Tylomys* are strictly arboreal, making the collection method highly complicated; consequently, this genus is scarcely represented in scientific collections. The natural vegetation in the Tumbalá region has been cleared or transformed across large areas ([Cruz 2017](#)), thus reducing the habitat of *Tylomys*. Hence, the record of [Goodwin \(1955\)](#) is important for expanding the range of this genus, which may be present in other localities of Chiapas and Guatemala. It is currently listed as Special Protection in NOM-059-SEMARNAT-2010 ([DOF 2019](#)) and as Critically Endangered (Possibly Extinct; B1ab (iii, v): area of occurrence less than 100 km<sup>2</sup>, severely fragmented, area and number of mature individuals under continuous decline) by IUCN ([Álvarez-Castañeda and Castro-Arellano 2019b](#)).

## Discussion

The erroneous location and misidentification of species individuals affect the species knowledge because they are assigned biological, ecological, and climatic habits to which the species are not actually linked. This results in the distortion of the environmental parameters to which these species are associated.

Any records that are geographically separated from the known and confirmed distribution range lead to erroneous associations between species and parameters. This type of uncertainty modifies some of the parameters used to propose the potential areas of distribution of the species, leading to errors because they can significantly increase the range considering habitats that are not viable for the species (Morrone and Escalante 2016). As a result, these errors impact the risk classification of species because they may affect their geographic projection of species distribution when models are developed (Teta and D'Elia 2019). In the case studies outlined in the present study, the mentioned records show locations outside the known range of the species, over 200 km away, (e. g. *Tlacuatzin sinaloae*, López-Forment and Urbano 1977; Arcangeli et al. 2018), with intermediate areas and off-limit records showing climatic variables and vegetation types different from those of the habitat associated with the species.

The use of records without following due care can have a direct effect on the knowledge of Mexican biodiversity. This study showed that at least three of the species analyzed can be considered as extinct, directly affecting the number of species recorded in the country and, in at least four species, influencing to modify the biodiversity estimators at regional and state scales.

The absence of specimens in collections does not allow the revision of the material to clarify doubts. This highlights the curatorial importance of the data and the support of this information through the deposit of specimens in scientific collections, because they serve as a reference and help to resolve some identification discrepancies that may have been committed, through the reexamination and morphological measurement of the species and even be used with molecular techniques to clarify doubts such as the case of *P. mekisturus* (Castañeda-Rico et al. 2020).

The global analysis of data for these 12 species has several implications. The first regards aspects of taxonomy. In the case of the two species of *Tylomys*, their taxonomic validity is questionable (Hall 1981; Espinoza and Martínez 2009; Monroy-Gamboa et al. in press). In both cases, the type specimens are the only ones known and do not involve adult organisms, nor take into account the wide intraspecific morphological variation in the genus *Tylomys* (Monroy-Gamboa et al. in press); therefore, the possibility that these species are synonymous with *T. nudicaudus* cannot be ruled out. Must be realized genetic studies to confirm and validate them.

The extinction of species is the second one. Currently, *Oryzomys peninsulae* (Álvarez-Castañeda 1994) and *Peromyscus pembertonii* (Álvarez-Castañeda et al. 2017) are deemed extinct. The status of *Dipomys gravipes* is indeterminate because it is listed as Extinct in NOM-059-SEMAR-NAT-2010 (DOF 2019), but there is a recent record (Tremor et al. 2019), which has not been corroborated with museum material or genetic data from samples (Cab-Sulub and

Álvarez-Castañeda 2020); therefore, more detailed studies should be conducted on these species in particular to achieve a related conclusion and a correct risk categorization thereof. This study revealed that three species — *Peromyscus mekisturus*, *Sorex sclateri* and *Sorex stizodon* — have not been recorded over at least 100 years of biological exploration trips in México; we even know that some of them have been surveyed through systematic sampling approaches with no positive findings (Susette S. Castañeda-Rico, pers. comm. for *P. mekisturus*). This fact, together with the modification of the original areas from which these species were recorded, supports the assumption that these three species have an high probability to be currently extinct.

The third fact is that there are between seven and nine mammal species recently described for México. These species are known to have restricted distribution areas, i.e., they are habitat specialists, thus increasing the possibility of extinction associated with changes in their habitat from natural phenomena such as fires or anthropic issues such as changes in land use and deforestation.

*Implications for mammal conservation in México.* The above considerations are sufficient to produce an impact at local, regional, and national levels because strong arguments are presented to modify the current known range of *Ateles geoffroyi*, *Cryptotis mayensis*, *Pteronotus davyi* and *Tlacuatzin sinaloae*, in addition to the likely extinction of the other group of species. One or several species are found within protected areas and thus included in the respective management plans; therefore, it is considered that some adaptations are necessary to reflect the current situation facing the probability that they do not occur in that regions.

*Tylomys bullaris* and *T. nudicaudus* have been considered present in other areas in addition to their known range. The current and available data are insufficient to confirm their presence. However, the possibility of their presence in habitats differing from their common range cannot be ruled out, for being species with unique requirements, little-known features that restrain our current understanding of their biology and ecology (Monroy-Gamboa et al. in press). It is recommended to carry out systematized surveys for the species of arboreal habits, using *ad hoc* field methodologies that allow to know their biology and thus determine their distribution and current risk status.

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# Habitat heterogeneity facilitates coexistence of two syntopic species of *Peromyscus* in a temperate forest of Central México

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An essential topic in ecology is to understand how the structure of the habitat and its changes in space and time (*i. e.*, habitat heterogeneity) affect the frequency and interactions between cohabiting species. Here, we assessed the effect of the biotic and abiotic components that configure the microhabitat heterogeneity and its temporal shifts (dry and rainy seasons), on the frequency (total and by sex) of two congeneric species, *Peromyscus difficilis* and *P. melanotis*, that co-occurs in a temperate forest of Central Mexico. To address this, an experimental plot composed of 120 sampling stations was placed within a temperate forest in the National Park Desierto de los Leones, Mexico City. In each sampling station, we set Sherman traps to capture mice of two syntopic *Peromyscus*, and we also evaluated six variables related to the spatial heterogeneity of the habitat during two rainy seasons. Our results revealed differential effects of habitat heterogeneity on the frequency of each species. Moreover, habitat heterogeneity also had a different effect on male and female frequencies of each *Peromyscus* species. While *P. difficilis* was captured more frequently in sampling stations with high presence and coverage of logs in the soil, *P. melanotis* was regularly captured in sampling stations with high vegetation cover and plant species richness. Thus, it seems that the different requirements and habitat preferences of these two *Peromyscus* species facilitate their spatial and temporal coexistence in this mid-latitude temperate forest. In general, we provide evidence of the importance of studying the heterogeneity of the habitat to better understand the interactions between syntopic species, offering new insights into the spatial and temporal mechanisms that could determine its coexistence at local scale.

Un tema fundamental en ecología, es comprender cómo la estructura del hábitat y sus cambios en el espacio y tiempo (*i. e.*, heterogeneidad del hábitat) afectan la frecuencia y las interacciones entre especies que cohabitan. En este estudio, evaluamos el efecto de los componentes bióticos y abióticos que configuran la heterogeneidad del microhábitat y sus cambios temporales (temporada seca y lluviosa), sobre la frecuencia (total y por sexo) de dos especies congénicas, *Peromyscus difficilis* y *P. melanotis*, que ocurren en un bosque templado del centro de México. Para este fin, una parcela experimental compuesta por 120 estaciones de muestreo fue colocada dentro un bosque templado en el Parque Nacional Desierto de los Leones, Ciudad de México. En cada estación de muestreo, colocamos trampas Sherman para capturar ratones de los dos *Peromyscus* sintópicos, y también evaluamos seis variables relacionadas a la heterogeneidad espacial del hábitat durante dos temporadas lluviosas. Nuestros resultados revelaron efectos diferenciales de la heterogeneidad de hábitat sobre la frecuencia de cada especie. Más aún, la heterogeneidad del hábitat también tuvo un efecto diferente sobre las frecuencias de machos y hembras de cada especie de *Peromyscus*. Mientras que *P. difficilis* fue capturado con mayor frecuencia en estaciones de muestreo con alta presencia y cobertura de troncos en el suelo, *P. melanotis* fue capturado con mayor regularidad en estaciones de muestreo con alta cobertura vegetal y riqueza de especies de plantas. Por lo tanto, parece que los diferentes requerimientos y preferencias de hábitat que tienen estas dos especies de *Peromyscus*, facilitan su coexistencia espacial y temporal en este bosque templado de latitud media. En general, demostramos la importancia de estudiar la heterogeneidad del hábitat para comprender mejor las interacciones entre especies sintópicas, ofreciendo nuevos conocimientos sobre los mecanismos espaciales y temporales que podrían determinar su coexistencia a escala local.

**Keywords:** Desierto de los Leones; habitat preferences; microhabitat; niche partitioning; small mammals' conservation; species interactions.

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## Introduction

Co-occurrence processes between different species depend on the spatial scale at which they perceive the habitat (Morris 1987; Barrio and Hik 2013). For instance, it has been proposed that small mammals possibly perceive the habitat structure/heterogeneity at smaller scales than medium-sized or large mammals (*i. e.*, microhabitat; Morris 1984, 1987; Chesson 2000; Whittaker *et al.* 2001). This is relevant since spatial scale may alter species assemblage's patterns perception and the order of importance of the explanatory variables of these patterns (Morris 1987; Whittaker *et*

*al.* 2001). Likewise, coexistence requires species to be different in the way they affect and are affected by competitors and available resources, resulting in niche differences or average fitness differences between species (Chesson 2000; Chen *et al.* 2020). Indeed, differences in the ecological niches occupied by the species within a community act to stabilize the system, with larger differences promoting coexistence (Chen *et al.* 2020). Therefore, determination of the mechanisms for coexistence among several species within a community is of basic ecological interest.

Habitat heterogeneity (*i. e.*, different biotic and abiotic components that shape the habitat architecture) is expected to increase species coexistence of small mammals, as they increase the number of microhabitats that may be occupied by species with different environmental requirements (Rosenzweig and Winakur 1969; Cramer and Willig 2002; Corbalán and Ojeda 2004; Schreiber and Kilingback 2013; Novillo *et al.* 2017). Likewise, more available microhabitats offer more shelters for mice to hide from predators, and also provide more diversity of food resources (Corbalán and Ojeda 2004; Traba *et al.* 2010; Novillo *et al.* 2017). However, temporal changes in the habitat structure have also a substantial impact on species coexistence (Valladares *et al.* 2015). For example, changes in the availability of food resources and refuges for species through space and time, affect its population size and how they interact (Valladares *et al.* 2015). Indeed, temporal variation in habitat heterogeneity should increase available niche spaces, allowing more species to coexist (Currie 1991). It has been reported that temporal fluctuations in habitat structure can stabilize species coexistence via the “storage effect” (Chesson 2000), when inter and intra-annual variation in climate or resource availability favors one group of species over others (Zavaleta *et al.* 2003). Similarly, it has reported that the sex of individuals could contribute to the coexistence of two competitive species (Chesson 2000). For instance, it has found a positive effect on coexistence when differences in competitive ability among conspecific individuals (*e. g.*, competition for resources between males vs. males or males vs. females of the same species) can break down competitive hierarchies of species, such that intraspecific competition is stronger than interspecific competition (Chesson 2000; Hubbell 2005; Fridley *et al.* 2007; Uriarte and Menge 2018).

In this study, we focus on whether different microhabitat elements and their spatial and temporal changes shape the frequency of two syntopic (animals that may use the same habitat; Hart *et al.* 2018) and congeneric species of deer mice (*P. difficilis* and *P. melanotis*). These two model systems were selected for several reasons. First, these two congenics co-occur in similar habitats and environmental conditions along its distribution (Álvarez-Castañeda 2005; Fernández *et al.* 2010). In the Transmexican Neovolcanic Belt, they cohabit in the understory of mixed and coniferous temperate forests, such as in the Desierto de los Leones National Park (DLNP; Castro-Campillo *et al.* 2008), where this study was conducted. Second, since the DLNP is located at the edge of an ever-growing megalopolis (Mexico City), it is important to understand what elements of the habitat shape the frequency and coexistence of these kind of species to elaborate better strategies to reduce the human impact on natural areas and their wild inhabitants. Urban growth produces fragmentation of natural microhabitats that are important to small mammals, which in turn play a fundamental role in the dispersal of seeds and as habitat architects within the forest.

Third, these two congeneric species have different body sizes (*P. difficilis* is larger than *P. melanotis* (see Álvarez-Castañeda 2005; Fernández *et al.* 2010)). This morphological differentiation represents an opportunity to compare their different requirements in relation to their respective ecological niche. Fourth, the reproductive season of *P. difficilis* occurs mainly during the dry season, while that of *P. melanotis* occurs in the rainy season (Castro-Campillo *et al.* 2012; De-la-Cruz *et al.* 2019; Salame-Méndez *et al.* 2018, 2019, 2020). Thus, it is possible that spatial and temporal variation in habitat heterogeneity, such as availability of food resources and shelters, could be related to the different reproductive seasons, relaxing its interspecific competition and promoting its coexistence (Kaufman and Kaufman 1989; Chesson 2000). Nevertheless, while several studies have quantified variation in resource use (*e. g.*, food, shelters, water) in heterogeneous environments among mice from the same genus (Kaufman and Kaufman 1989; Kalcounis-Rüppell and Millar 2002; Villanueva-Hernández *et al.* 2017), there is still a lack of information about how temporal changes in the habitat structure/heterogeneity affect the frequency of congeneric mice species inhabiting at the same place (but see Kalcounis-Rüppell and Millar 2002; Hart *et al.* 2018). Here, we measured different variables that compose the structure of the microhabitat and their changes during two rainy seasons (dry and rains), and we related this information with total and sex frequencies of two species of small mammals, *P. difficilis* and *P. melanotis*, that co-occurs in a temperate forest of Central Mexico.

## Materials and methods

**Study area.** The study area (19°18'17"N, 99°19'14"W at 2,289 masl) is located in a mixed temperate forest of coniferous and broad-leaved trees at Desierto de los Leones National Park (DLNP) in Mexico City (CONANP 2006). This forest is part of the Trans-Mexican Neovolcanic Belt (CONANP 2006). The rainy season occurs from summer through early fall (June to October) with a monthly average precipitation of  $252.92 \pm 28.01$  mm, and an average monthly temperature of  $11.72 \pm 0.53$  °C (CONANP 2006). In contrast, the dry season occurs from fall through winter (October to February); the monthly average precipitation is  $13.2 \pm 3.11$  mm, and the average monthly temperature is  $8.97 \pm 0.68$  (CONANP 2006).

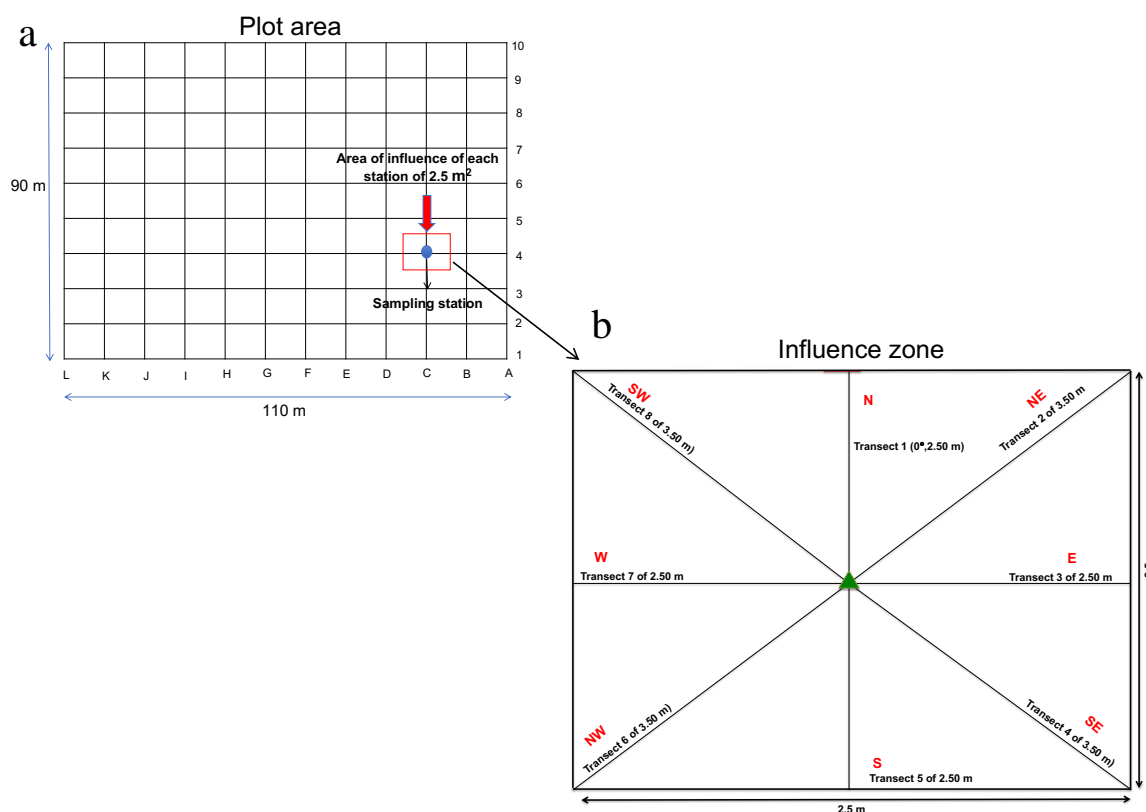
**Habitat heterogeneity during dry and rainy seasons.** To assess how temporal changes in the habitat heterogeneity affect the frequency of capture of each *Peromyscus* species, we set a plot of 9,900 m<sup>2</sup> (110 x 90 m; Figures 1a, b). Within this plot, we placed 120 sampling stations every ten meters, along 12 columns (A to L) and ten rows (1 to 10; Figure 1a). Each sampling station was marked with buried wooden stakes. In each sampling station, we delimited an “influence zone” of 2.5 m<sup>2</sup> (Figure 1b). Within these influence zones of every sampling station, eight fixed transects were set in a clockwise conformation to measure seven variables that qualify as components of the vertical and horizontal struc-

ture of the habitat (Morris 1984; Jorgensen 2004; Villanueva-Hernández et al. 2017). These variables are indicators of possible shelters from predators, spaces for resting and mating, and food resources (Jorgensen 2004). We applied the Canfield's Line Intercept (CLI) method (Canfield 1941) in each transect of the influence zone to measure the percentage of vegetation coverage at three different heights (10, 35, and 100 cm; VC10, VC35, and VC100, respectively). We also counted the number of all herbaceous plants (H) and the number of all woody plants (W). Likewise, plant species richness (SR) was registered as the number of different plant species found within each influence zone (Figure 1b). The percentage of logs (Logs) covering the ground surface (fallen trees) more than one meter long and ten centimeters in diameter was also registered using Canfield's method. The CLI method is based on the measurement of all plants and objects intercepted by a transect, and the length/coverage of each plant or object that is touched by the line is registered. All habitat features were sampled once during the most representative months of the rainy (July 2017) and dry seasons (February 2018; CONANP 2006).

**Mice trapping.** The *Peromyscus* mice were captured alive for ten months to include data for the dry (October 2017 to February 2018) and rainy (March 2018 to July 2018) seasons. We set a single live trap (H. B. Sherman, Inc., Tallahassee, FL 32303, USA), baited with oat flakes and vanilla extract at each sampling station of the plot ( $n = 120$ ). Traps were set for two consecutive nights each month with a total of 20 capture events (10 months x 2 nights; 2,400 night/traps). Mice were

marked in their abdomen with gentian violet to avoid overestimation of capture frequencies. Despite this temporal mark did not allow us to identify the mice at individual level (e. g., as with an id code to trace the movements or range home of a certain individual), it turned out to be a practical way to calculate mice abundance accurately by pulling out the recaptured individuals. At the end of the samplings, we could have an estimate of the mice abundance for the dry and rainy seasons. In addition, to avoid recurrence behavior (e. g., mice returning to the traps for bait) or shyness (e. g., mice avoiding traps due to other mice odors), all the traps were thoroughly cleaned and randomly oriented within each sampling station in each capture event. Handling of the mice was following the guidelines of the American Society of Mammalogists (Sikes 2016). To prevent hypothermia during capture, we placed 3 to 5 cotton balls inside the trap and put the traps inside open plastic bags. We recorded the species and sex of every mouse (De-la-Cruz et al. 2019). If a mouse died overnight while being trapped ( $n = 3$ ), it was skinned and prepared as a study specimen, and incorporated as voucher specimen in the Mammal Collection of the Universidad Autónoma Metropolitana-Iztapalapa. A scientific collecting permit, SEMARNAT-08-049-B, was issued to Alondra Castro-Campillo (ACC) by DGVS, SGPA-09712/13, SEMARNAT, MEXICO.

**Statistical analysis.** All statistical analyses were performed using the JMP statistical package (v. 14.0; SAS Institute). Plotting was made using ggplot2 (Wickham 2016) in RStudio version 1.1.463 (R Core Team 2020).



**Figure 1.** a) Location of the sampling plot in a temperate mixed forest at the Desierto de los Leones National Park, Mexico City. b) Configuration of the experimental plot area (grid) where 120 sampling stations were set with its corresponding influence zone of 2.5 m<sup>2</sup>. Within each influence zone, eight fixed transects were set in a clockwise conformation (North to Southwest) to measure the variables related to the habitat heterogeneity. Green triangle = center of the sampling station where each Sherman trap was also set.

*Differentiation of habitat heterogeneity between dry and rainy seasons.* Prior to analyses, all variables (habitat elements and mice captures) were log-transformed ( $\log n + 1$ ) to meet normality assumptions. A Student's *t*-test was used to evaluate mean differences between the rainy and dry seasons for each of the seven variables of the habitat heterogeneity (see above).

*Relationship between habitat heterogeneity and frequency of each Peromyscus species during the dry and rainy seasons.* Prior to analyses, variables representing the habitat's heterogeneity and structure were standardized to a mean of zero and a standard deviation of one ( $X^{\wedge} = 0$ ,  $SD = 1$ ). Generalized linear models (GLMs) were used to evaluate the relationships between habitat heterogeneity and the capture frequency of each *Peromyscus* species. All GLMs were performed with 1,000 iterations of the maximum likelihood method. The GLMs described hereafter were selected based on the statistical significance of the model and the lowest corrected AIC values, that is, models that best explained the relationship between the variables (Akaike 1974).

To evaluate the relationship between the habitat heterogeneity and the frequency of each *Peromyscus*, two GLMs (link = logarithmic, distribution = Poisson) were constructed using the respective abundances of *P. difficilis* and *P. melanotis* as response variables, whereas the vegetation coverage at 10 and 100 cm (VC10 and VC100, respectively), the number of all herbaceous plants (H), the number of all woody plants (W), plant species richness (SR), the percentage of logs (Logs), season, and their interaction were used as predictors. Adding the interaction between season and the covariates in the models, allowed us to assess whether the effect of the habitat heterogeneity or structure differed depending on the season of testing (cf. Zar 1999). A similar GLM was carried out using the abundance of females or males of each *Peromyscus* as response variables.

Since habitat heterogeneity depends on the interaction between different biotic and abiotic elements of the habitat, we also carried out principal component analyses (PCA) for each season, using the seven habitat indicators (variables) to produce new functions that could explain the microhabitat heterogeneity in a more detailed way. Likewise, the PCAs also helped to reduce data dimensionality. One PCA was performed for each season. Since in the dry season, the first two components explained 61.23 % of the variance and in the rainy season, the two first components explained 73.88 % of the variance, we used only these two principal components for subsequent analyses (see below).

A GLM (link = logarithmic, distribution = Poisson) was constructed where the response variable was the abundance of *P. difficilis* and/or *P. melanotis* and the two principal components, season and their interaction as covariate effects. A similar GLM was carried out using the abundance of females or males in each *Peromyscus* species as response variables. The generalized linear coefficients (viz.  $\beta_i$ ; Lande and Arnold 1983) obtained from the GLMs represent the

strength and direction of the relationships acting directly on the frequency of the species in comparable units (standard deviations).

## Results

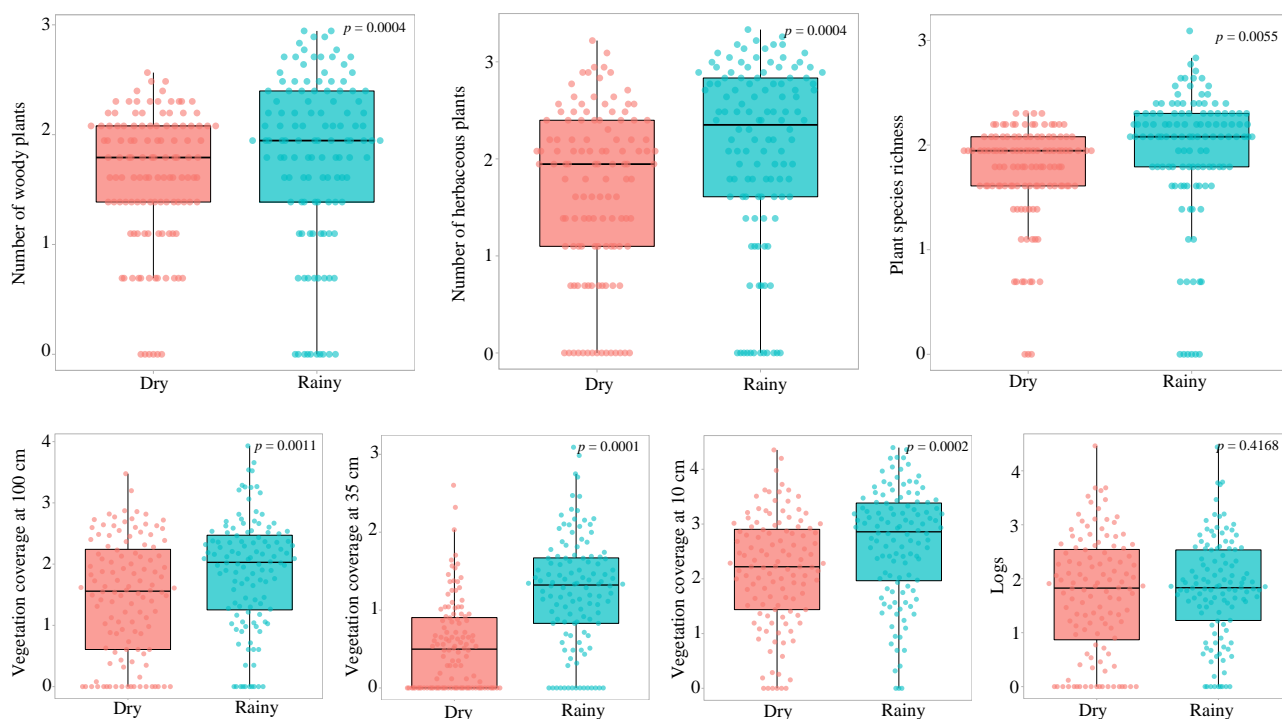
*Frequency of captures.* We captured a total of 516 mice of both *Peromyscus* species for all the study. During the dry season, the total number of captured individuals was 312: 174 individuals for *P. difficilis* (120 males and 54 females) and 138 *P. melanotis* individuals (66, 72). During the rainy season, the total number of captures was 204; 114 individuals of *P. difficilis* (80, 34), and 92 individuals of *P. melanotis* (58, 34).

*Changes in habitat structure between the dry and rainy season.* The mean difference between seasons was significant for most of the habitat features (Table 1). The mean of almost all habitat variables was higher in the rainy season. Only the coverage of wood logs on the ground surface between seasons did not change (Table 1, Figure 2).

*Relationships between frequency of capture for the Peromyscus species and the seven variables of habitat heterogeneity/structure.* The GLM between the seven variables that describe the microhabitat heterogeneity/structure and the frequency of *P. difficilis* was significant (*L-R* chi-square<sub>15</sub> = 37.16, *AICc* = 451.30, *P* = 0.0012, Table 2, Appendix 1). However, only the percentage of logs on the ground (positive effect) and season (positive effect) as predictors were significant. The GLM between the seven habitat variables and *P. difficilis* females' frequency was not significant (*L-R* chi-square<sub>15</sub> = 15.56, *AICc* = 263.26, *P* = 0.4118, Appendix 1, 2). In this model, the percentage of herbaceous plants (H) showed a significant negative effect on the frequency of females of *P. difficilis*. However, this result must be interpreted with caution. In contrast, the effect of the seven habitat variables on the frequency of males of *P. difficilis* was significant (*L-R* chi-square<sub>15</sub> = 44, *AICc* = 365.51, *P* = 0.0001, Appendix 1, 2), being percentage of logs covering the ground and the interaction season × woody plants significant predictors (positive effects).

**Table 1.** Mean (se, standard error) differences in seven elements of microhabitat structure between seasons. VC10 = vegetation coverage at 10 cm, VC35 = vegetation coverage at 35 cm, VC100 = vegetation coverage at 100 cm, H = number of herbaceous plants, W = number of woody plants, SR = plant species richness. d.f. = degrees of freedom. *p* = *p*-values (significant *p*-values are in bold).

Habitat feature	N	Mean (se)		<i>t</i>	<i>df</i>	<i>p</i>
		Dry season	Rainy season			
VC10	240	12.28 (1.17)	20.10 (1.59)	3.75	238	<b>0.0002</b>
VC35	240	1.09 (0.15)	3.44 (0.32)	8.25	238	<b>0.0001</b>
VC100	240	5.42 (0.15)	8.28 (0.32)	3.29	238	<b>0.0011</b>
Logs	240	8.48 (1.03)	8.37 (0.98)	0.81	238	0.4168
H	240	6.12 (0.47)	9.98 (0.65)	3.60	238	<b>0.0004</b>
W	240	4.80 (0.26)	6.55 (0.41)	3.60	238	<b>0.0004</b>
SR	240	5.19 (0.19)	7.02 (0.32)	2.80	238	<b>0.0055</b>



**Figure 2.** Median differentiation of the seven variables that describe the habitat heterogeneity between dry and rainy seasons. Dots represent each sampling station. Y-axis is in log scale.

The GLM between the seven variables and the frequency of *P. melanotis* was significant ( $L-R$  chi-square<sub>15</sub> = 36.37,  $AICc$  = 401.37,  $P$  = 0.0016, Table 2, Appendix 1). Significant effects included the season and plant species richness. Both effects were positively related to the frequency of *P. melanotis*. The GLM between the seven habitat variables and the frequency of *P. melanotis* females was nearly significant ( $L-R$  chi-square<sub>15</sub> = 24.93,  $AICc$  = 277.54,  $P$  = 0.0508, Appendix 1, 2). In this model, only the season was significant. The effect of the seven habitat variables on the frequency of *P. melanotis* males was significant ( $L-R$  chi-square<sub>15</sub> = 34.59,  $AICc$  = 295.11,  $P$  = 0.0028, Appendix 1, 2). In this GLM, the effect of the species richness and the interaction between season and species richness were significant and positively related to *P. melanotis* males. On the other hand, the number of woody plants was significant and negatively related to *P. melanotis* males.

**Relationships between capture frequency and principal components.** Principal component analysis for the dry season showed that the first two components explained almost all the variance (61.23 %). The highest loadings in the first component (PC1) were variables related to vegetation including plant species richness. Hence, this new function describes those sampling stations with high vegetation coverage and species richness. In contrast, the principal component two (PC2) was only related to the coverage of logs on the ground, representing the fixed and stable elements of the habitat. In the rainy season, the first two principal components explained 73.88 % of the variance. As in the dry season, PC1 was related to vegetation and species richness and PC2 with logs' coverage (Appendix 3).

The GLM between the frequency of *P. difficilis* and the principal components was significant ( $L-R$  chi-square<sub>5</sub> = 30.01,  $AICc$  = 436.37;  $P$  = 0.0001; Table 3, Figure 3 a, b). However, significant predictors only included the PC2, indicating a positive relationship between the frequency of *P. difficilis* and logs' coverage during the two rainy seasons. The GLM between the frequency of *P. difficilis* females and the principal components was not significant ( $L-R$  chi-square<sub>5</sub> = 3.15,  $AICc$  = 253.60;  $P$  = 0.6767) (Appendix 2). The effect of the principal components on the frequency of *P. difficilis* males was significant ( $L-R$  chi-square<sub>5</sub> = 36.28,  $AICc$  = 351.15;  $P$  = 0.0001). However, the only significant and positive effect was the PC2 (logs on the ground; Appendix 2).

The GLM between the abundance of *P. melanotis* and the principal components was significant ( $L-R$  chi-square<sub>5</sub> = 22.46,  $AICc$  = 393.20;  $P$  = 0.0004) (Table 3, Figure 3 c, d). The significant and positive predictors were the PC1 (vegetation) and season in this model. The GLM between the frequency of *P. melanotis* females and the principal components was significant ( $L-R$  chi-square<sub>5</sub> = 12.93,  $AICc$  = 267.46;  $P$  = 0.0240; Appendix 2). The significant effects also included the PC1 and season (positive effects). The GLM between the frequency of *P. melanotis* males and the principal components was also significant ( $L-R$  chi-square<sub>5</sub> = 17.92,  $AICc$  = 289.70;  $P$  = 0.0030; Appendix 2). The significant effects included the PC1 (positive effect) and PC2 (negative effect).

## Discussion

Our results revealed different relationships between the habitat heterogeneity and the frequency of both *Peromyscus* species. Likewise, the habitat heterogeneity/structure

**Table 2.** Effect of the seven microhabitat variables, season (dry, rainy) and their interaction on the frequency of capture of (a) *Peromyscus difficilis* and (b) *Peromyscus melanotis*. d. f. = degrees of freedom,  $\beta_i$  = linear coefficient from the GLM, se = standard error,  $p$  =  $p$ -value. Significant  $p$ -values are in bold. VC10 = vegetation coverage at 10 cm, VC35 = vegetation coverage at 35 cm, VC100 = vegetation coverage at 100 cm, H = number of herbaceous plants, W = number of woody plants, SR = plant species richness.

Response variable (Frequency)	Effects	N	d.f.	$\beta_i$	se	L-R ChiSquare	$p$
<i>Peromyscus difficilis</i>	VC10	240	15	0.02	0.16	0.02	0.8696
	VC35	240	15	0.19	0.11	2.91	0.0876
	VC100	240	15	-0.06	0.13	0.23	0.6262
	H	240	15	-0.26	0.17	2.21	0.1363
	W	240	15	0.08	0.15	0.28	0.5909
	SR	240	15	0.10	0.17	0.36	0.5452
	Logs	240	15	0.24	0.05	13.07	<b>0.0003</b>
	Season	240	15	0.23	0.11	4.37	<b>0.0364</b>
	Season × VC10	240	15	-0.20	0.16	1.63	0.2012
	Season × VC35	240	15	0.00	0.11	0.00	0.9389
	Season × VC100	240	15	0.09	0.13	0.52	0.4693
	Season × H	240	15	0.19	0.17	1.17	0.2786
	Season × W	240	15	0.27	0.15	3.42	0.0641
	Season × SR	240	15	-0.12	0.17	0.50	0.4768
	Season × Logs	240	15	0.01	0.05	0.04	0.8276
<i>Peromyscus melanotis</i>	VC10	240	15	-0.21	0.17	1.63	0.2013
	VC35	240	15	0.12	0.13	0.83	0.3612
	VC100	240	15	0.15	0.10	1.86	0.1715
	H	240	15	-0.04	0.18	0.05	0.8202
	W	240	15	-0.21	0.16	1.76	0.1844
	SR	240	15	0.53	0.19	7.94	<b>0.0048</b>
	Logs	240	15	-0.23	0.14	3.15	0.0758
	Season	240	15	0.40	0.13	9.03	<b>0.0026</b>
	Season × VC10	240	15	0.23	0.17	1.89	0.1687
	Season × VC35	240	15	0.03	0.13	0.05	0.8126
	Season × VC100	240	15	-0.07	0.10	0.46	0.4931
	Season × H	240	15	-0.31	0.18	2.92	0.0870
	Season × W	240	15	0.01	0.16	0.01	0.9128
	Season × SR	240	15	0.22	0.19	1.34	0.2467
	Season × Logs	240	15	-0.24	0.14	2.73	0.0981

had a different effect on male and female frequencies of both species of *Peromyscus*. First, while *P. difficilis* was more frequently captured in sampling stations with high presence and coverage of logs on the ground, individuals of *P. melanotis* were usually captured in sampling stations with high vegetation coverage and plant species richness. It has been found that spatial heterogeneity in habitat quality reverses the competition between two sympatric species (Chen *et al.* 2020). Thus, it seems that both *Peromyscus* species have different habitat requirements and preferences that could be facilitating their coexistence in the study zone (Pianka 1973; Chen *et al.* 2020).

Why *P. difficilis* had a higher association in places with a high presence of logs? Logs on the ground surface represent small patches of microhabitat with food sources, burrows and refuges for mice (Bellows *et al.* 2001; Bowman *et al.* 2015; Grelle 2003; Dalmagro and Vieira 2005). Individuals of *P. dif-*

*ficilis* could also use the large fallen logs as safe pathways for fast and straight locomotion within the forest (Bellows *et al.* 2001; Grelle 2003; Dalmagro and Vieira 2005). Indeed, fallen logs promote the structural heterogeneity of forests and may enhance positive interactions among species of small mammals (Bowman *et al.* 2015). The relationship between *P. difficilis* and microhabitats with a higher number and cover of logs could also be related with the morphology and climbing habits of this species (Fernández *et al.* 2010). For instance, the long tail of *P. difficilis* enables it to rush and climb along shrubs, trees, or logs (Bowman *et al.* 2015), hence, increasing its preference for habitats with fixed elements (*e. g.*, fallen logs), where mice can escape from predators or use holes in logs as burrows (Bowman *et al.* 2015). In contrast, it is possible that *P. melanotis* - the species with smaller body size and more cursorial locomotion - prefers zones with higher vegetation coverage and plant species richness as strategy to



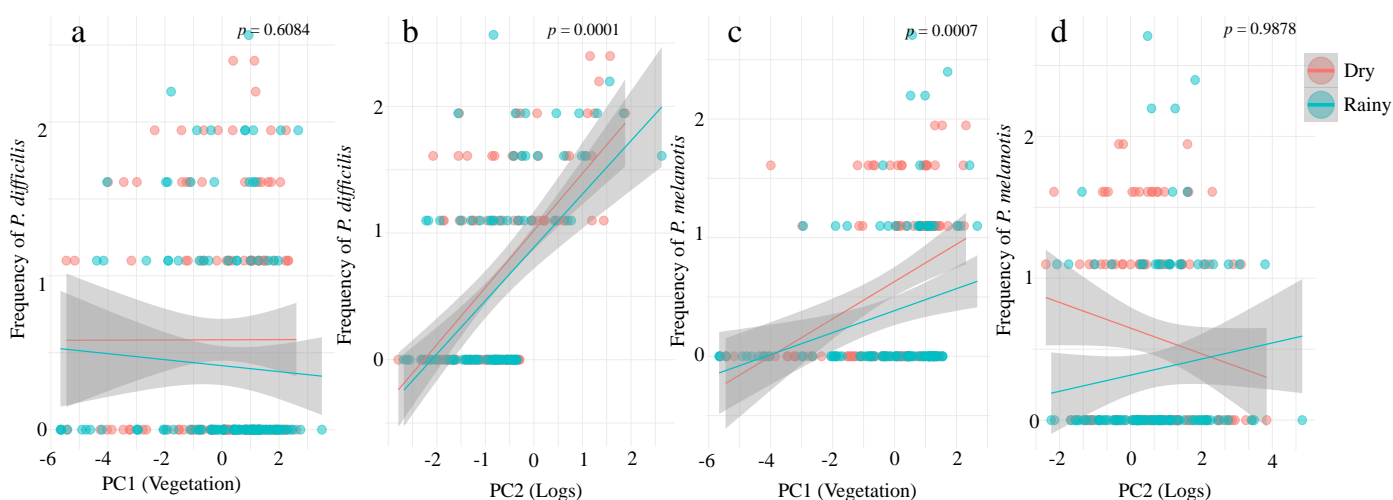
**Table 3.** Effect of the principal components (PC1-2) as new functions of habitat heterogeneity (see methods), season (dry and rainy) and their interaction on the frequency of capture of (a) *Peromyscus difficilis* and (b) *Peromyscus melanotis*. d. f. = degrees of freedom,  $\beta_i$  = linear coefficient from the GLM, se = standard error,  $p$  =  $p$ -value. Significant  $p$ -values are highlighted in bold. VC10 = vegetation coverage at 10 cm, VC35 = vegetation coverage at 35 cm, VC100 = vegetation coverage at 100 cm, H = number of herbaceous plants, W = number of woody plants, SR = plant species richness.

Response variable (Frequency)	Effects	N	d.f.	$\beta_i$	se	L-R ChiSquare	$p$
<i>Peromyscus difficilis</i>	PC1 (Vegetation)	240	5	-0.02	0.04	0.26	0.6084
	PC2 (Logs)	240	5	0.46	0.09	25.65	<b>0.0001</b>
	Season	240	5	0.17	0.10	2.97	0.0848
	Season $\times$ PC1	240	5	0.02	0.04	0.21	0.6401
	Season $\times$ PC2	240	5	-0.00	0.09	0.00	0.9672
<i>Peromyscus melanotis</i>	PC1 (Vegetation)	240	5	0.21	0.06	11.54	<b>0.0007</b>
	PC2 (Logs)	240	5	-0.00	0.10	0.00	0.9878
	Season	240	5	0.27	0.11	6.05	<b>0.0139</b>
	Season $\times$ PC1	240	5	0.00	0.06	0.00	0.9821
	Season $\times$ PC2	240	5	-0.19	0.10	3.56	0.0592

avoid predation by aerial hunters or other predators, as well as to obtain food resources more quickly, since seeds may be concentrated under shrub canopies (Bowman et al. 2015; Grelle 2003; Dalmagro and Vieira 2005). Likewise, we have found evidence that *P. melanotis* has a higher intermediate metabolism rate than *P. difficilis* (Salame-Méndez and Castro-Campillo, unpublished results). Thus, it is possible that due to its higher metabolic requirements, *P. melanotis* needs to disperse more frequently in search for food resources richer in sugar in areas with higher diversity and richness of plants (such as we observed in this study) that supply its higher metabolic requirements and promoting its ecological niche differentiation (Suarez and Welch 2017; Chen et al. 2020).

Our results also revealed that temporal changes in the habitat heterogeneity only seem to affect the frequency of males of both *Peromyscus* species in the study zone, the sex more frequently related to territorial endeavors in mammals (Ostfeld 1990). For instance, males of *P. difficilis* were positively associated with woody plants in the dry and rainy seasons. However, this association was stronger during the

dry season. In contrast, males of *P. melanotis* were negatively associated with woody plants in the dry season and positively associated with plant species richness in both seasons, but the association was also stronger during the rainy season. Thus, it seems that there is a different microhabitat use by males of both *Peromyscus* species. Likewise, it is possible that the stronger association between woody plants and males of *P. difficilis* during the dry season could be related to the breeding season of this species. It has been reported that the breeding of *P. difficilis* occurs primarily during the dry season (De-la-Cruz et al. 2019; Salame-Mendez et al. 2020). Hence, since males could be searching for females to breed during the dry season, it is possible that they are more easily captured than the females or that the density of males in the area increased due to breeding season. This same pattern could also explain the stronger association between males of *P. melanotis* and plant species richness or areas with higher vegetation coverage during the rainy season, where the breeding of *P. melanotis* occurs (De-la-Cruz et al. 2019; Salame-Mendez et al. 2020).



**Figure 3.** Relationships between the abundance of *Peromyscus difficilis* or *Peromyscus melanotis* with the principal components.  $p$ -values are showed in the plots.

Our findings also revealed that females of both *Peromyscus* species did not show a significant association with the microhabitat variables. One explanation is that females may be associated with other habitat variables not measured in this study. Likewise, it is possible that females spend more time in their burrows than males, and they only go out to obtain food and water for short periods, being more cautious and not necessarily associated with a specific habitat component. Indeed, it has been reported for several small mammal species that females have shorter home ranges than males (e. g. [Ribble et al. 2002](#); [Flores-Manzanero et al. 2019](#)). Nevertheless, the lack of a significant association between females and habitat variables could also be related to a statistical bias ([Zar 1999](#)), since we captured more males than females during both seasons, except for *P. melanotis* in the dry season where we captured six more females than males of this species.

Finally, this study provides evidence of how two congeneric mice species are affected by the habitat heterogeneity. Interestingly, although these two coexisting *Peromyscus* species can move along different microhabitats (i. e., logs, vegetation coverage), the fact that each one was associated with a different habitat component, suggests a different microhabitat use and selection ([Chesson 2000](#)). Habitat partitioning is considered an important mechanism for coexistence among small mammal species ([Schoener 1974](#); [Stevens and Tello 2009](#)). Therefore, partitioning of some of the available resources (e. g. space, food, refuges, and time) could be enhancing the coexistence of these two syntopic *Peromyscus* species with similar environmental requirements ([Shenbrot 1992](#); [Chesson 2000](#); [Novillo et al. 2017](#)). Overall, we demonstrate the importance of the study of habitat heterogeneity on the interaction of two syntopic species, offering some new insights into the mechanisms of spatial and temporal coexistence of two mice species at local scale.

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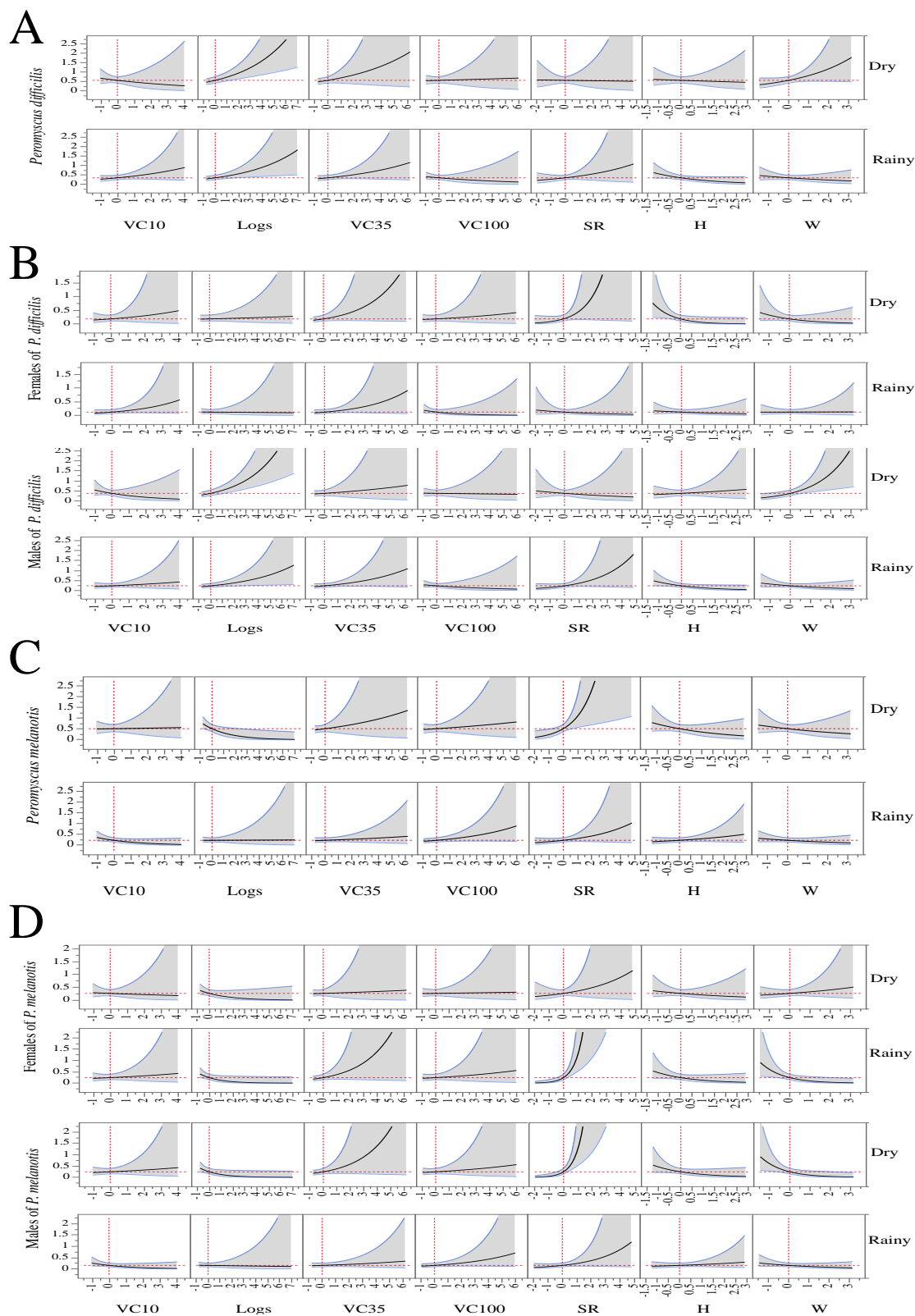
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## Appendix 1

Profilers of the generalized linear models (GLMs) testing the effect of the seven habitat variables on A) total frequency; B) males and females of *Peromyscus difficilis*, and C) total frequency; D) males and females of *P. melanotis* during the dry and rainy seasons. VC10 = vegetation coverage at 10 cm. VC35 = vegetation coverage at 35 cm. VC100 = vegetation coverage at 100 cm. H = number of herbaceous plants. W = number of woody plants. SR = plant species richness. Logs = percentage of logs covering the ground.



## Appendix 2

Effect of the seven microhabitat variables, seasonality and their interaction on the frequency of (a) females and (b) males of *P. difficilis* and (c) females and (d) males of *P. melanotis*. Effect of the principal components (PC1-2) as new functions of habitat heterogeneity (see methods), season (dry and rainy) and their interaction on the frequency of capture of (e) females *Peromyscus difficilis*, (f) males *P. difficilis*, (g) females *P. melanotis* and (h) males *P. melanotis*. d. f. = degrees of freedom,  $\beta_i$  = linear coefficient from the GLM, se = standard error,  $p = p$ -values. Significant  $p$ -values are in bold. VC10 = vegetation coverage at 10 cm. VC35 = vegetation coverage at 35 cm. VC100 = vegetation coverage at 100 cm. H = number of herbaceous plants. W = number of woody plants. SR = plant species richness. Logs = percentage of logs covering the ground.

Response variable (Frequency)	Effects	n	d.f.	$\beta_i$	se	L-R Chi-Square	p
Females of <i>Peromyscus difficilis</i>	VC10	240	15	0.30	0.24	1.44	0.2297
	VC35	240	15	0.36	0.17	3.58	0.0584
	VC100	240	15	-0.15	0.24	0.46	0.4940
	H	240	15	-0.70	0.34	4.66	<b>0.0307</b>
	W	240	15	-0.27	0.28	0.96	0.3257
	SR	240	15	0.30	0.32	0.85	0.3561
	Logs	240	15	0.01	0.15	0.00	0.9351
	Season	240	15	0.20	0.20	0.98	0.3200
	Season × VC10	240	15	-0.07	0.24	0.08	0.7698
	Season × VC35	240	15	0.03	0.17	0.05	0.8203
	Season × VC100	240	15	0.29	0.24	1.60	0.2045
	Season × H	240	15	-0.44	0.34	1.76	0.1842
	Season × W	240	15	-0.28	0.28	1.04	0.3068
	Season × SR	240	15	0.53	0.32	2.80	0.0941
	Season × Logs	240	15	0.04	0.15	0.08	0.7691
Males of <i>Peromyscus difficilis</i>	VC10	240	15	-0.10	0.20	0.27	0.5969
	VC35	240	15	0.18	0.13	1.67	0.1954
	VC100	240	15	-0.11	0.16	0.50	0.4793
	H	240	15	-0.21	0.21	1.06	0.3016
	W	240	15	0.16	0.18	0.81	0.3677
	SR	240	15	0.14	0.20	0.48	0.4856
	Logs	240	15	0.28	0.06	14.25	<b>0.0002</b>
	Season	240	15	0.23	0.14	2.79	0.0948
	Season × VC10	240	15	-0.25	0.20	1.59	0.2064
	Season × VC35	240	15	-0.06	0.13	0.24	0.6220
	Season × VC100	240	15	0.09	0.16	0.31	0.5757
	Season × H	240	15	0.36	0.21	2.94	0.0863
	Season × W	240	15	0.47	0.18	7.24	<b>0.0071</b>
	Season × SR	240	15	-0.28	0.20	1.89	0.1687
	Season × Logs	240	15	0.04	0.06	0.56	0.4524
Females of <i>Peromyscus melanotis</i>	VC10	240	15	-0.40	0.28	2.37	0.1233
	VC35	240	15	0.05	0.18	0.09	0.7627
	VC100	240	15	0.17	0.13	1.46	0.2254
	H	240	15	0.15	0.26	0.34	0.5565
	W	240	15	0.04	0.21	0.04	0.8265
	SR	240	15	0.20	0.26	0.59	0.4395
	Logs	240	15	-0.18	0.19	0.97	0.3235
	Season	240	15	0.56	0.21	7.65	<b>0.0057</b>
	Season × VC10	240	15	0.31	0.28	1.22	0.2680
	Season × VC35	240	15	0.00	0.18	0.00	0.9883
	Season × VC100	240	15	-0.14	0.13	1.17	0.2785
	Season × H	240	15	-0.42	0.26	2.55	0.1102

## Appendix 2

## Continuation

Response variable (Frequency)	Effects	n	d.f.	$\beta_i$	se	L-R Chi-Square	p
Males of <i>Peromyscus melanotis</i>	Season × W	240	15	0.15	0.21	0.53	0.4652
	Season × SR	240	15	0.10	0.26	0.15	0.6908
	Season × Logs	240	15	-0.27	0.19	1.73	0.1879
	VC10	240	15	-0.17	0.21	0.72	0.3956
	VC35	240	15	0.28	0.16	2.47	0.1160
	VC100	240	15	0.19	0.14	1.63	0.2016
	H	240	15	-0.21	0.24	0.76	0.3822
	W	240	15	-0.63	0.24	7.44	<b>0.0064</b>
	SR	240	15	1.03	0.27	15.07	<b>0.0001</b>
	Logs	240	15	-0.35	0.20	3.66	0.0556
	Season	240	15	0.21	0.17	1.38	0.2390
	Season × VC10	240	15	0.31	0.21	2.19	0.1381
	Season × VC35	240	15	0.15	0.16	0.83	0.362
	Season × VC100	240	15	-0.05	0.14	0.14	0.7046
	Females of <i>Peromyscus difficilis</i>	Season × H	240	15	-0.43	0.24	3.23
Season × W		240	15	-0.27	0.24	1.31	0.2523
Season × SR		240	15	0.61	0.27	5.12	<b>0.0235</b>
Season × Logs		240	15	-0.30	0.20	2.17	0.1405
PC1		240	5	-0.01	0.07	0.02	0.8694
PC2		240	5	0.13	0.15	0.82	0.3629
Season		240	5	0.18	0.15	1.48	0.2226
Season × PC1		240	5	0.01	0.07	0.01	0.8926
Season × PC2		240	5	0.08	0.15	0.31	0.5772
Males of <i>Peromyscus difficilis</i>		PC1	240	5	-0.04	0.05	0.58
	PC2	240	5	0.60	0.10	31.59	<b>0.0001</b>
	Season	240	5	0.18	0.12	2.16	0.1414
	Season × PC1	240	5	0.02	0.05	0.24	0.6180
	Season × PC2	240	5	0.01	0.10	0.01	0.9113
Females of <i>Peromyscus melanotis</i>	PC1	240	5	0.19	0.10	4.60	<b>0.0320</b>
	PC2	240	5	0.06	0.15	0.20	0.6525
	Season	240	5	0.45	0.17	7.89	<b>0.0049</b>
	Season × PC1	240	5	-0.06	0.10	0.48	0.4877
	Season × PC2	240	5	-0.17	0.15	1.28	0.2577
Males of <i>Peromyscus melanotis</i>	PC1	240	5	0.29	0.09	11.56	<b>0.0007</b>
	PC2	240	5	-0.13	0.13	0.98	0.3200
	Season	240	5	0.04	0.15	0.07	0.7886
	Season × PC1	240	5	0.07	0.09	0.66	0.4150
	Season × PC2	240	5	-0.26	0.13	3.99	<b>0.0456</b>

### Appendix 3

Loadings of the principal components analyses for the dry and rainy season. The highest loadings are marked in red. VC10 = vegetation coverage at 10 cm. VC35 = vegetation coverage at 35 cm. VC100 = vegetation coverage at 100 cm. H = number of herbaceous plants. W = number of woody plants. SR = plant species richness. Logs = percentage of logs covering the ground. % of Variance = percentage of total variance explained by each component.

Dry season	PC1	PC2	PC3	PC4	PC5	PC6	PC7
% of Variance	46.8	14.4	12.9	12.0	8.4	3.9	1.6
VC10	0.47	-0.12	0.28	0.20	0.00	0.66	-0.44
VC35	0.25	0.20	-0.76	0.42	0.36	0.01	-0.05
VC100	0.32	0.13	0.07	-0.68	0.63	0.00	0.05
H	0.44	-0.13	0.35	0.40	0.14	-0.18	0.65
W	0.39	0.24	-0.31	-0.34	-0.61	0.25	0.36
SR	0.49	-0.00	0.04	-0.03	-0.25	-0.67	-0.47
Logs	-0.07	0.92	0.33	0.18	0.00	-0.00	-0.06
Rainy season	PC1	PC2	PC3	PC4	PC5	PC6	PC7
% of Variance	59.3	14.6	10.0	6.8	5.1	3.0	1.2
VC10	0.41	-0.10	0.05	0.59	0.05	-0.67	0.03
VC35	0.36	0.05	0.62	-0.22	-0.64	0.01	0.04
VC100	0.39	0.01	0.34	-0.44	0.70	-0.07	-0.16
H	0.43	-0.14	0.00	0.36	0.15	0.65	0.44
W	0.36	0.33	-0.54	-0.41	-0.11	-0.22	0.46
SR	0.43	0.19	-0.35	0.09	-0.16	0.24	-0.74
Logs	-0.14	0.90	0.24	0.28	0.13	0.05	0.06



# Identification keys to murid rodents of Argentina

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Muroid rodents are the most species-rich superfamily of rodents occurring in Argentina. Increased fieldwork with these mammals depicts the need of adequate keys to identify species on the base of external characters. In this contribution we provide three keys (one for families and subfamilies, and another two for Sigmodontinae and Muridae, respectively) for all known species of Cricetidae and Muridae distributed in Argentina (42 genera and 110 species). In addition to the dichotomous keys, and as a way to facilitate the identification, we include for each species a brief description of its distribution and the main habitats where it occurs.

Los roedores muroideos constituyen la superfamilia de roedores con más especies en Argentina. El creciente interés en el trabajo de campo con estos mamíferos ha puesto en evidencia la necesidad de contar con claves para identificar sus especies a partir de características externas. En esta contribución se proporcionan tres claves (una para familias y subfamilias y otras dos para Sigmodontinae y Muridae) para todas las especies conocidas de Cricetidae y Muridae que se distribuyen en Argentina (42 géneros y 110 especies). Además de las claves dicotómicas, y como una forma de facilitar la identificación, para cada especie incluimos una breve descripción de su distribución y de los principales hábitats en donde ocurre.

**Keywords:** Cricetidae, integument, Muridae, Sigmodontinae, taxonomic identification.

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## Introducción

La superfamilia Muroidea constituye el grupo de roedores con más especies en el Nuevo Mundo. En Argentina están representados por dos familias, Cricetidae y Muridae (introducida); la primera incluyendo dos subfamilias, Arvicolinae (introducida) y Sigmodontinae (nativa). Su diversidad abarca desde formas anfibias hasta arborícolas, cursoriales o semifosoriales (e. g., [Voss 1988](#); [Carrizo et al. 2014](#)), con hábitos tróficos que van desde la herbivoría más o menos estricta hasta la omnivoría y animalivoría (e. g., [Voss 1988](#); [Maestri et al. 2016](#); [Verde Arregoitia y D'Elía 2020](#)). Al igual que otros pequeños mamíferos, los muroideos desempeñan un papel fundamental en las redes tróficas, donde actúan como presas de otros vertebrados, contribuyendo al flujo de energía y nutrientes ([Lacher et al. 2017](#)). Muchas especies ocupan nichos ecológicos especializados y proporcionan funciones importantes a los ecosistemas, como la remoción de suelos y la dispersión de semillas ([Lacher et al. 2017](#)). A su vez, algunas de ellas también son vectores de zoonosis, algunas de elevada mortalidad, como el virus Hanta, y plagas de muchos cultivos ([Pardiñas et al. 2017](#)). Por todo esto, su importancia para los seres humanos no ha pasado desapercibida, transformándose en uno de los grupos más estudiados en cuanto a distintos aspectos de su taxonomía e historia natural.

Si bien existen diferencias, por regla general, las características externas de los muroideos responden a un plan

corporal generalizado ([Carrizo et al. 2014](#); [Maestri et al. 2016](#)). Esta situación dificulta la identificación específica de especímenes sobre la base de rasgos externos fácilmente observables, práctica común en distintos trabajos en el campo. Al mismo tiempo, parte importante de la literatura que contiene datos morfológicos relevantes para la identificación de estos animales se encuentra dispersa y en publicaciones muchas veces antiguas y/o en la llamada literatura gris (e. g., [Gyldenstolpe 1932](#); [Yepes 1935a, 1935b](#); [Massoia 1964, 1971, 1973a, 1973b, 1974, 1976, 1979](#); [Massoia y Fornes 1964, 1965a, 1965b, 1967a, 1967b](#); [Massoia et al. 1968](#)), la que no siempre es de fácil acceso, al menos para cierto tipo de público (estudiantes, guardaparques, personal técnico de apoyo a la investigación, entre otros).

Independientemente de las dificultades que plantea la identificación de las especies de muroideos a partir de caracteres externos (sobre todo para quienes tienen poco entrenamiento) en la actualidad existe un número considerable de investigadores que de todos modos debe lidiar con esta problemática. En este contexto, la confección de una clave de identificación constituye una herramienta necesaria, y hasta ahora no disponible para los muroideos de Argentina, para el desarrollo de un conjunto importante de investigaciones en distintos campos de aplicación en nuestro país.

El objetivo de este trabajo es ofrecer una serie de claves para la identificación de los roedores muroideos de Argentina a partir de sus características externas. Una de

las claves se centra en familias y subfamilias de Muroidea, otra en Sigmodontinae y la restante en Muridae. Se pretende que éstas sean una herramienta fácil de utilizar en el campo y el laboratorio, para que investigadores, personal técnico, o cualquier otro tipo de usuario no familiarizado con las especies del grupo, pueda determinar a nivel de especie ejemplares capturados en cualquier región geográfica de Argentina. Estas claves incluyen todas las especies de muroideos vivientes conocidas para Argentina, un conjunto que abarca 42 géneros y 110 especies (Teta *et al.* 2018, con modificaciones; *e. g.*, Abreu *et al.* 2021; Prado *et al.* 2021; Teta *et al.* 2021).

## Materiales y métodos

El formato de las claves sigue una estructura dicotómica, donde se han privilegiado las posibilidades de identificación antes que el ordenamiento taxonómico y las relaciones de parentesco entre las especies. Muchas especies de roedores muroideos son externamente muy similares entre sí, por lo cual es probable que el uso exitoso de la clave, al menos para los principiantes, demande de la ayuda de algunas herramientas adicionales (*e. g.*, lecturas sobre terminología anatómica; Figuras 1 y 2) y cierta práctica o experiencia acumulada (*e. g.*, en observación de animales en el campo y pieles de museos). A los fines de superar parcialmente esta situación, para cada taxón se incluye una enumeración de sus rasgos morfológicos diagnósticos y un párrafo con sus medidas externas, datos de distribución y hábitat. Además, intercaladas en las claves, se agregan una serie de notas taxonómicas, comparaciones entre especies similares y figuras, para que sirvan de ayuda en la identificación.

En la preparación de las claves sólo se han considerado caracteres externos, por ser los que pueden observarse más fácilmente en el campo. Para algunos géneros y especies seguramente no alcance sólo con esos datos, ya que una identificación inequívoca podría requerir del estudio de la anatomía craneana y dentaria, cariotipos o análisis de ADN (situación que se indica en cada caso). Los caracteres utilizados en las claves fueron tomados de la bibliografía (*e. g.*, Gyldenstolpe 1932; Yebes 1935a; Pearson 1958; Massoia 1964, 1973a, 1973b, 1974, 1976, 1979; Massoia y Fornes 1964, 1965a, 1965b, 1967a, 1967b; Massoia *et al.* 1968; Myers 1989; Pearson 1995; Weksler *et al.* 2006; Bonvicino *et al.* 2008; Mares *et al.* 2008; Jayat *et al.* 2010; Teta *et al.* 2017) y contrastados, siempre que fue posible, con material de referencia, principalmente de la Colección Nacional de Mastozoología del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Ciudad Autónoma de Buenos Aires, Argentina) y la Colección de Mamíferos del Centro Nacional Patagónico (Puerto Madryn, Chubut). También hemos aprovechado nuestra experiencia de campo con las especies del grupo, utilizando información morfológica recopilada a lo largo de más de 20 años de trampeos.

La terminología anatómica corresponde a la discutida por Stepan (1995), Pacheco (2003), Weksler (2006) y Teta

*et al.* (2017). En la construcción de las claves se privilegiaron los caracteres discretos y menos ambiguos (*e. g.*, la longitud comparativa entre los dedos de las patas, el largo de las vibrisas, el tamaño y forma de las garras, la presencia de membranas interdigitales o de espinas, etc.), por sobre aquellos de valoración más subjetiva (*e. g.*, la coloración del pelaje), siempre que fue posible. Cuando se considera, en la descripción de la coloración externa se ha privilegiado el aspecto general, sin entrar en detalles sobre la coloración de distintos tipos de pelos. La mayoría de los caracteres seleccionados pueden verse a ojo desnudo, aunque en algunos casos su correcta visualización pueda requerir de una lupa común (*e. g.*, los surcos en la cara anterior de los incisivos). En algunos casos se hace referencia al efecto agutí, que está dado por pelos que incluyen bandas claras y oscuras alternadas (lo que les otorga a esos animales una apariencia como "salpicada"). Los caracteres que consideramos más relevantes para la identificación fueron **resaltados en negrita**; no obstante, en todas las especies se anotan varios caracteres adicionales que pretenden ayudar con las identificaciones.

Las claves están mayormente pensadas para la identificación de ejemplares adultos, con alguna mención a los juveniles cuando correspondiese. Hay que tener en cuenta que con cierta frecuencia los individuos jóvenes de distintos géneros (*e. g.*, *Akodon* con *Oxymycterus*, *Rattus* con *Sooretamys*) o incluso los adultos (*Abrothrix* con *Akodon*) pueden prestarse a confusión, aún entre formas filogenéticamente distantes. En general, una coloración más oscura o grisácea, un pelaje más corto y fino y la proporción de algunas partes corporales (usualmente cabeza y patas grandes en relación con el tamaño del cuerpo) son rasgos típicos de los ejemplares que aún no han alcanzado la adultez.

Las medidas externas fueron tomadas de la literatura (*e. g.*, Massoia 1964, 1974, 1976; Massoia y Fornes 1964, 1965a, 1965b; Massoia *et al.* 1968; Pardiñas *et al.* 2017) y de datos propios de los autores. En la mayoría de los casos se expresan como rango (mínimo y máximo), pero en unos pocos se indican valores medios. Todos los valores están expresados en milímetros. Para cada especie, se indican algunas de las siguientes medidas externas: LT = largo total, medido en línea recta vertebral desde el extremo del hocico hasta el extremo de la cola, sin incluir el pincel; CC = longitud cabeza-cuerpo, medida en línea recta vertebral desde el extremo del hocico hasta la base de la cola (usualmente se obtiene restando la longitud de la cola del largo total [LT]); C = longitud de la cola, medida desde su punto de inserción en el cuerpo hasta el extremo distal, sin incluir el pincel (si lo hubiese); P = longitud de la pata trasera, medida desde el borde posterior del talón hasta el extremo (incluyendo la uña) del dedo más largo; O = longitud de la oreja, medida desde la escotadura basal hasta el borde externo del pabellón auricular (Figura 1A). En forma orientativa, se han considerado 4 grupos de tamaño, según el largo CC: pequeño (hasta 100 mm), mediano (entre 101 y 150 mm), grande (151-230 mm) y muy grande (>231 mm).

Para todas las especies se anotan datos de hábitat y una breve descripción de su distribución. Este punto no pretende ser exhaustivo y debe ser tomado con cautela, pues para muchas especies no hay información precisa sobre hábitat. La información distribucional también se utilizó para las claves en el caso de especies muy similares, pero con poblaciones geográficamente disyuntas (e. g., aquellas del género *Bibimys*). Mapas detallados de la distribución de todas las especies y fotografías adicionales se pueden consultar en <https://cma.sarem.org.ar/>. No obstante, téngase en cuenta que con frecuencia pueden producirse registros por fuera del área reconocida para una especie dada, ya que los límites de distribución no son estáticos, ni tenemos un conocimiento detallado de los mismos para todas las especies.

A modo de recomendación general, se sugiere que los usuarios de este trabajo lean y consideren todas las combinaciones de caracteres que se plantean en cada una de las entradas dobles antes de hacer una determinación y seguir avanzando en las claves.

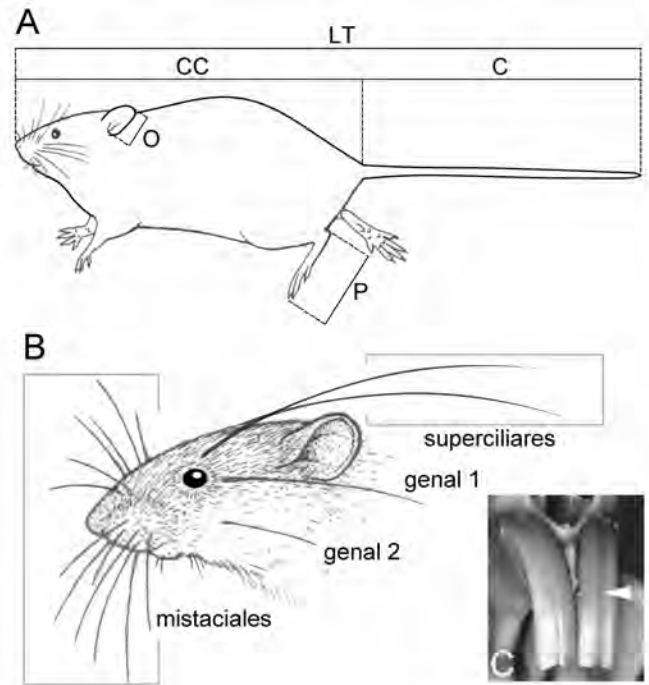
## Resultados

### Clave A. Familias y subfamilias

1. Tamaño muy **grande** (CC = 230-320 mm; C = 180-300 mm); patas traseras robustas y oscuras, con los dedos II-IV unidos por una membrana interdigital y garras bien desarrolladas de color blanco rosáceo; **cola escamosa y desnuda, achatada lateralmente en toda su longitud**, semejando un remo (humedales y cuerpos de agua en Tierra del Fuego).....Cricetidae, Arvicolinae (introducida, un solo género y especie, *Ondatra zibethicus*; Figura 22A)
  - 1a. Tamaño pequeño a grande, la **longitud CC < 230 mm; cola de sección redondeada a ovalada y generalmente menor que 200 mm**.....2
  2. Cola con escamado dérmico visible o no, escasamente a densamente cubierta de pelos; generalmente en áreas naturales.....Cricetidae, subfamilia Sigmodontinae (clave B; Figuras 1-21)
    - 2a. **Cola mayormente desnuda, con escamado dérmico bien visible; generalmente de hábitos peridomicilia-rios**..... familia Muridae (clave C. Figura 22B-D)

### Clave B. Subfamilia Sigmodontinae

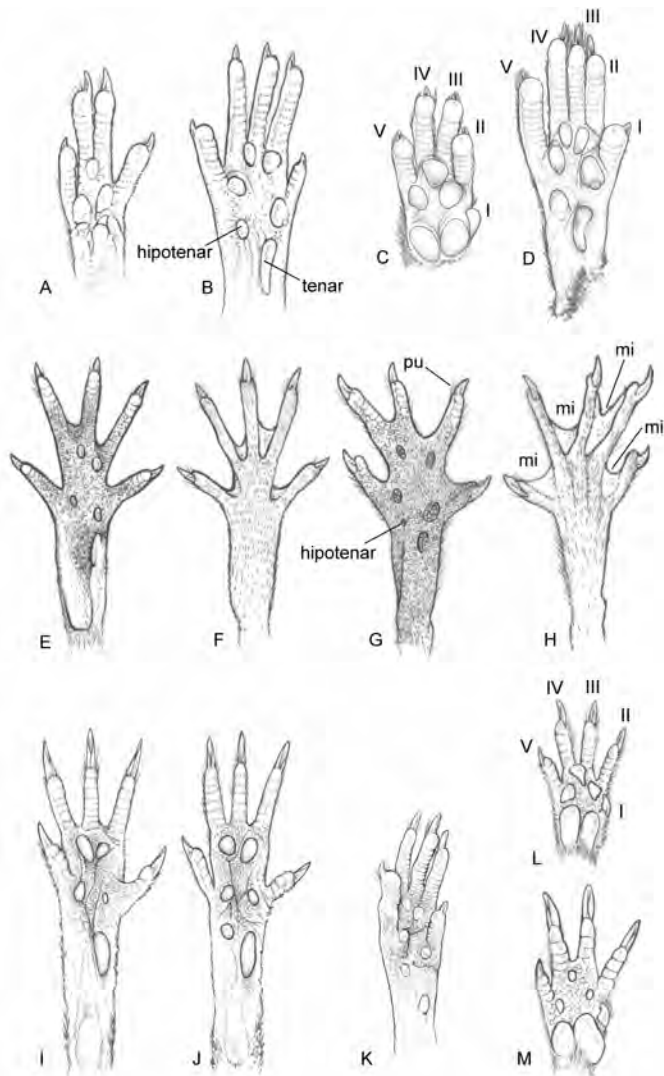
1. Tamaño mediano (CC = 105-120; C = 112-133; P = 28-29; O = 17); **pelos del dorso y flancos modificados en forma de espinas achatadas** (~11 mm de longitud), transparentes o blanquecinas en su porción proximal y distalmente marrones; cabeza robusta; orejas medianas y redondeadas; coloración dorsal marrón grisácea, con marcado efecto agutí; cola marrón oscuro, más larga que la longitud conjunta de la cabeza más el cuerpo y terminada en un pincel de pelos marrón oscuro; manos con los dos dedos centrales muy alargados (Figura 2A); patas traseras alargadas y dorsalmente cubiertas por



**Figura 1.** A) Medidas somáticas estándar para mamíferos: CC, largo cabeza-cuerpo; C, largo de la cola; LT, largo total; O, largo de la oreja; P, largo de la pata trasera. B) vibrissas faciales (sólo se anotan las mencionadas en el texto). C) cara anterior de los incisivos en *Euneomys mordax* (la flecha muestra la posición del surco longitudinal).

pelitos oscuros (Figura 2B) (selvas primarias y secundarias en Misiones).....*Abrawayaomys ruschii* (Figura 3A)

- 1a. Sin pelos modificados en forma de espinas.....2
2. Los dedos de las patas traseras están unidos por una membrana cutánea.....3
  - 2a. Los dedos de las patas traseras no están unidos por una membrana cutánea.....7
3. Tamaño grande (CC = 165-258; C = 151-287; P = 47-59; O = 23-25); **cuerpo rollizo**; cola gruesa y escamosa, igual de larga que la longitud cabeza-cuerpo; pelaje fino y suave, dorsalmente **castaño oscuro brillante**, con pelos negros más largos entremezclados; flancos lavados de amarillento; vientre blanquecino a grisáceo, lavado de ocre; cabeza grande, con ojos y orejas medianos; vibrissas mistaciales (Figura 1B) oscuras y brillantes, las más largas alcanzan la mitad de la oreja; patas alargadas, dorsalmente cubiertas por pelitos blancos; borde del pie cubierto por un peine de pelos blancos; **plantas amplias, desnudas y escamadas hasta el talón**; almohadilla hipotenar pequeña; **la membrana cutánea de los dedos II-IV de la pata posterior se extiende por delante de la segunda articulación interfalangeana** (Figura 2G-H) (cursos de agua en selvas de Misiones) .....*Nectomys squamipes* (Figura 3E)
  - 3a. **La membrana cutánea en los dedos II-IV se extiende hasta la primera articulación interfalangeana o menos** (Figura 2E-F).....4
  4. Tamaño mediano (CC = 99-127; C = 102-133; P = 27-31; O = 13-19); **cola igual de larga que la longitud conjunta de la cabeza más el cuerpo**; pelaje largo y suave; colo-



**Figura 2.** Esquemas de las manos en vista palmar (A, C, L, M) y patas en vista dorsal (F, H) y plantar (B, D, E, G, I, J, K) de *Abrawayaoomys ruschi* (A, B), *Juliomys pictipes* (C, D), *Holochilus brasiliensis* (E, F), *Nectomys squamipes* (G, H), *Gyldenstolpia fronto* (I), *Scaptomys aquaticus* (J), *Oligoryzomys nigripes* (K), *Bucepattersonius iheringi* (L) y *Oxymycterus rufus* (M) (redibujados de varias fuentes). Los números romanos corresponden a los que identifican a cada dedo. Abreviaturas: mi, membrana interdigital; pu, pelos ungueales. Las figuras no están en escala.

**ración dorsal marrón olivácea, con efecto agutí, más clara hacia los flancos; vientre blanco amarillento, poco contrastado con el color del dorso; orejas medianas; patas posteriores estrechas, cubiertas por pelitos blanco-grisáceos por arriba y con los dedos II-IV reunidos en sus bases por una membrana cutánea rudimentaria; pelos ungueales blancos y cortos, raramente extendidos por delante de las uñas; cola bicolor, oscura por arriba y más clara por debajo, con las escamas visibles; 4 pares de mamas (pastizales, palmares y humedales, desde el este de Formosa hasta el norte de Santa Fe).....**  
 ..... *Pseudoryzomys simplex* (Figura 3B)

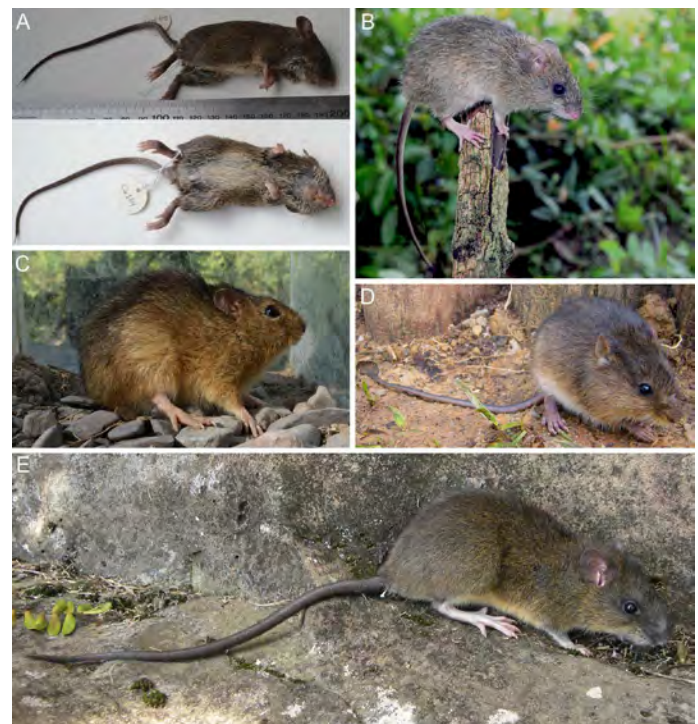
4a. Tamaño grande; cuerpo rollizo con cola mediana a larga, gruesa, fuerte y escamosa; cabeza grande, con hocico obtuso (romo o que no termina en punta); ojos y orejas medianos; vibrisas cortas y poco abundantes, que

no alcanzan la base de la oreja; **pelaje dorsal con tonos rojizos o castaños, más oscuro hacia la línea media y anaranjado hacia los flancos; manos y patas muy desarrollados, dorsalmente cubiertos por pelitos blancos; dedos de las patas traseras reunidos por una membrana cutánea rudimentaria; pelos ungueales cortos y escasos; palmas y plantas desnudas, con escamación entre las almohadillas interdigitales y la tenar; almohadilla hipotenar ausente o muy reducida (Figura 2E-F); 4 o 5 pares de mamas.....***Holochilus* (Figura 3C-D)

5. Tamaño grande (CC = 185-238; C = 200-238; P = 47-55; O = 21-26); pelaje largo, denso y suave; coloración dorsal castaño anaranjada a rojiza, con pelos más largos de color negro entremezclados; **vientre de color blanco puro, a veces con una faja transversal ocre-anaranjada, castaña o grisácea y con parches blancos en el mentón y el área inguinal; longitud de la cola mayor que la longitud CC (humedales y cursos de agua en el noreste y centro-este de Argentina, hasta el sur de Buenos Aires).....***Holochilus brasiliensis* (Figura 3D)

5a. Longitud de la **cola menor que la longitud CC.....**6

6. Tamaño grande (CC = 140-195; C = 148-183; P = 38-46; O = 17-20); coloración dorsal castaño anaranjada a rojiza, con pelos más largos de color negro entremezclados; **pelaje ventral blanco puro o blanco grisáceo u ocráceo, pero con el mentón y región inguinal siempre de color blanco puro (humedales y cursos de agua desde Salta y Jujuy hasta Santa Fe y el norte de Buenos Aires).....**  
 ..... *Holochilus chacarius* (Figura 3C)



**Figura 3.** Aspecto externo de *Abrawayaoomys ruschi* (A), *Pseudoryzomys simplex* (B), *Holochilus chacarius* (C), *Holochilus brasiliensis* (D) y *Nectomys squamipes* (E). Las fotos no están en escala.

- 6a. Tamaño grande (CC = no disponible; C ~136; P = 46; O = no disponible); coloración dorsal rojiza, más oscura en la línea media y anaranjada hacia los flancos; **vientre grisáceo, con una banda pectoral anaranjada entre las patas delanteras y parches de pelos completamente blancos en el mentón, garganta y el área inguinal** (humedales y cursos de agua en Mendoza; posiblemente extinta).....*Holochilus lagigliai*
7. **Cara anterior de los incisivos superiores con un surco longitudinal**, de posición medial o lateral, visible a ojo desnudo o mediante lupa (Figura 1C).....8
- 7a. Cara anterior de los incisivos superiores sin surco longitudinal..... 15
8. Tamaño mediano (CC = 108-130; C = 162-196; P = 28-32; O = 17); pelaje fino y suave, de color marrón acanelado o marrón grisáceo en el dorso y blanco-grisáceo, a veces lavado de canela, en el vientre; orejas medianas y muy oscuras, a veces con un parche de pelos blancos en la base; ojos grandes, rodeados por un anillo de pelos oscuros; patas traseras alargadas y dorsalmente cubiertas por pelitos blancos; **cola moderadamente gruesa y mucho más larga que la longitud conjunta de la cabeza más el cuerpo**, negruzca dorsalmente y apenas más clara por debajo (bosques y matorrales ecotonales, desde el oeste de Neuquén hasta el sudoeste de Chubut).....*Irenomys tarsalis* (Figura 4A)
- 8a. Cola menor que el 65% de la longitud conjunta de la cabeza más el cuerpo ..... 9
9. **Con aspecto general de conejo**; cuerpo robusto y rechoncho; cabeza grande, con el perfil dorsal convexo; ojos redondos y grandes; orejas redondeadas y prominentes; pelaje largo, denso y suave, con parches de pelos más claros en la base de las orejas y alrededor de los ojos; miembros anteriores cortos y posteriores más largos; manos y patas cubiertas por pelitos blancos; dedos provistos de garras cortas; **el extremo distal de los dedos I y V en las patas traseras no alcanza la base de los dedos III-IV**; cola bicolor y moderadamente peluda; 4 pares de mamas.....*Reithrodon* 10
- 9a. **Sin aspecto general de conejo**; orejas medianas o grandes; sin parche de pelos claros en la base de las orejas; **el extremo distal del dedo V de la pata trasera sobrepasa la base del IV**.....12
10. Tamaño mediano (CC =128-160; C = 65-100; P = 30-34; O = 23-25); coloración dorsal variable, desde marrón hasta gris, más oscura en la línea media y lavada de amarillento hacia los flancos; vientre blanquecino a grisáceo, usualmente lavado de amarillento o canela; **plantas de las patas mayormente cubiertas por pelos, dedos con pelos ungueales largos y abundantes** (pastizales y estepas arbustivas y herbáceas desde Buenos Aires, La Pampa y sudoeste de Mendoza hasta Tierra del Fuego; también en pastizales de altura en Córdoba).....*Reithrodon auritus* (Figura 4D)
- 10a. Tamaño mediano; **plantas de las patas mayormente desnudas, dedos con pelos ungueales largos pero poco abundantes**.....11
11. Tamaño mediano (CC = 127-149; C = 94-99; P = 30.5-34.5; O = 24-28); coloración dorsal castaño-ocrácea, más oscura hacia la línea media y la parte superior de la cabeza y amarillenta hacia los flancos; **vientre blanquecino, sin lavado amarillento o castaño (pastizales de altura por encima de los 2,000 msnm en Catamarca, Jujuy y Tucumán)**..... *Reithrodon caurinus*
- 11a. Tamaño mediano (CC = 139-152; C = 90-94; P = 27-31; O = 22-27); coloración dorsal castaño clara a marrón, más oscura hacia la línea media y la parte superior de la cabeza y amarillenta hacia los flancos; **vientre blanquecino a grisáceo, lavado de amarillento. (pastizales en Corrientes y Entre Ríos)**.....*Reithrodon typicus*
12. Tamaño mediano (CC = 98-125; C = 52-69; P = 21-25; O = 20-24); pelaje largo, laxo y suave; coloración dorsal grisácea, lavada de amarillento en el dorso y de anaranjado hacia los flancos y grupa; vientre grisáceo teñido de ocre, bien separado del dorso; **orejas grandes y de contorno ovalado; parche postauricular de pelos ocre; mejillas gris ocráceas; vibrisas largas, pero que no sobrepasan el borde externo de la oreja; orejas marrón oscuro, cubiertas por pelitos dispersos anaranjados; cola blanco grisácea, excepto por una fina línea dorsal oscura; incisivos superiores blancos o amarillo pálidos, con un surco poco profundo y visible bajo lupa**; patas robustas, dorsalmente cubiertas por pelitos blanco grisáceos; palmas y plantas desnudas; pelos ungueales largos, que cubren parcialmente las uñas; cola blanco grisácea, excepto por una fina línea dorsal oscura, proporcionalmente muy corta, algo gruesa y peluda (pastizales, matorrales y roquedales de la **Puna y Altos Andes**, por encima de 3,200 msnm en Jujuy y Salta)..... *Auliscomys sublimis* (Figura 5B)
- 12a. **Sin parche postauricular; orejas medianas y de contorno casi circular; incisivos anaranjados**.....13
13. Tamaño grande (CC = 160-180; C = 60-85; P = 23-25; O = 18-19); cuerpo robusto y miembros cortos; **hocico castaño rojizo brillante**; pelaje largo y espeso, dorso marrón grisáceo; vientre blanco grisáceo; faja pectoral de pelos ocre variablemente presente; cabeza grande, con vibrisas abundantes y orejas medianas, redondeadas y bien cubiertas de pelos; **grupa teñida de castaño rojizo**; manos y patas cubiertos por pelitos grises a ocre; palmas y plantas desnudas; cola peluda y bicolor; **incisivos superiores anchos**, con un surco longitudinal de posición lateral; 4 pares de mamas (pastizales húmedos asociados a vegas y cursos de agua por encima de los 2,600 msnm, **desde Jujuy hasta el norte de San Juan**) ....  
..... *Neotomys ebriosus* (Figura 4E)
- 13a. **Hocico y grupa sin castaño rojizo**; cuerpo robusto y miembros cortos; pelaje suave y denso; cabeza grande, con orejas redondas y medianas; vibrisas largas, algu-

nas claras y otras oscuras, alcanzando posteriormente el pabellón auditivo; sin faja pectoral; palmas y plantas desnudas, cubiertas por almohadillas amplias; 4 pares de mamas (**desde el sur de San Juan hasta Tierra del Fuego**).....*Euneomys* (Figura 4B-C) 14

14. Tamaño mediano (CC = 97-156; C = 46-81; P = 22-32; O = 19-24); coloración dorsal marrón, lavada de amarillento o gris, más oscura hacia la línea media; vientre blanco-grisáceo, a veces lavado de amarillento; cola bicolor, con la mitad dorsal oscura y formando una banda ancha todo a lo largo; **manos, pies, borde del hocico y labios blancos; cara anterior de los incisivos con un surco longitudinal, de posición lateral** (roquedales y peladares desde el sur de San Juan hasta Tierra del Fuego).....*Euneomys chinchilloides* (Figura 4B)

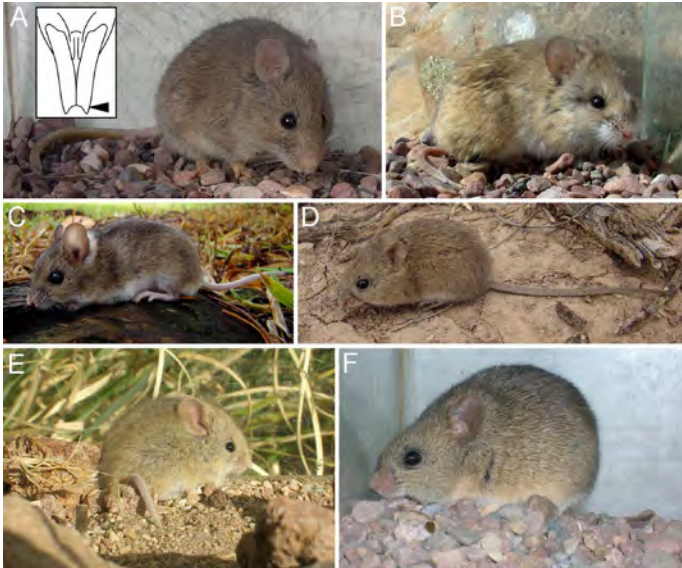
14a. Tamaño mediano (CC = 145-149; C = 78-85; P = 28-32; O = 24-27); coloración dorsal marrón grisácea, más clara hacia los flancos y el vientre, que es gris; cola bicolor, con la mitad dorsal oscura y formando una banda fina todo a lo largo; **sin blanco en hocico y labios; cara anterior de los incisivos con un surco longitudinal, de posición central** (pastizales húmedos, praderas herbáceas de altura y matorrales en el sudoeste de Mendoza y oeste de Neuquén, por encima de los 1600 msnm).....*Euneomys fossor* (Figura 4C)

15. Tamaño pequeño (CC < 100 mm); cola aproximadamente igual o levemente más larga que la longitud conjunta de la cabeza más el cuerpo; cabeza proporcionalmente grande, con rostro corto y perfil abovedado; pelaje largo, sedoso y suave, usualmente marrón amarillento, que contrasta con el vientre blanco; orejas medianas, cubiertas por pelos cortos amarillentos a marrones; área alrededor de la nariz y boca cubierta por pelos blancos; miembros anteriores cortos y posteriores bien desarrollados; manos y patas cubiertos dorsalmente por pelos blanquecinos; **plantas de las patas con las tres almohadillas interdigitales centrales fusionadas en un tubérculo único, cubierto de pelos**; hipotenar ausente; dedo V del pie largo, con el extremo (sin la garra) alcanzando o sobrepasando el extremo distal de la primer falange del dedo IV; almohadillas palmares variablemente fusionadas e igualmente peludas (Figura 6D); 4 pares de mamas (estepas arbustivas y herbáceas en áreas abiertas, normalmente asociadas con ambientes de suelo predominantemente arenoso).....*Eligmodontia* (Figura 6A-D) 16

Nota 1: la identificación de las especies del género *Eligmodontia* es difícil de realizar sólo sobre la base de caracteres externos, requiriendo usualmente de estudios de morfología cráneo-dentaria, cariotípicos y de ADN.



Figura 4. Aspecto externo de *Irenomys tarsalis* (A), *Euneomys chinchilloides* (B), *Euneomys fossor* (C), *Reithrodon auritus* (D) y *Neotomys ebriosus* (E). Las fotos no están en escala.



**Figura 5.** Aspecto externo de *Andinomys edax* (A; en el recuadro interno se ilustra la cara anterior de los incisivos; la flecha destaca el borde biselado de estos dientes en su extremo distal), *Auliscomys sublimis* (B), *Calomys laucha* (C), *Calomys musculus* (D), *Calomys lepidus* (E) y *Calomys fecundus* (F). Las fotos no están en escala.

- 15a. Almohadillas interdigitales no fusionadas.....20
16. Plantas de las patas densamente peludas; **largo de la cola ~90-93% de la longitud conjunta de la cabeza más el cuerpo**.....17
- 16a. Plantas de las patas escasamente peludas; **largo de la cola ~110-130% de la longitud conjunta de la cabeza más el cuerpo**.....18
17. Tamaño pequeño (CC = 75-100; C = 69-90; P = 21-25; O = 14-19); coloración dorsal marrón claro, lavada de dorado en los flancos; vientre y pecho blancos, que contrastan notoriamente con el color del dorso (**estepas arbustivas en el sudoeste de Mendoza y la Patagonia**).....*Eligmodontia morgani* (Figura 6B y D)
- 17' Tamaño pequeño (CC = 65-105; C = 67-97; P = 21-25; O = 15-22); coloración dorsal marrón grisáceo a marrón claro, bien separada del vientre por una línea anaranjada que se extiende desde las mejillas hasta las ancas; cola levemente bicolor a unicolor, sin pincel de pelos (**estepas arbustivas altoandinas y de la puna de Jujuy, Salta y Catamarca, por encima de los 3,500 msnm**) .....*Eligmodontia puerulus*
18. Tamaño pequeño (CC = 60-90; C = 84-106; P = 19-23; O = 16-20); dorso marrón amarillento, separado del vientre por una línea ocrácea; **vientre blanco, con la base de los pelos generalmente gris**; cola bicolor (estepas arbustivas y medanales desde el sur de Catamarca hasta el noreste de Santa Cruz) .....*Eligmodontia typus* (Figura 6C)
- 18a. **Vientre blanco puro, base de los pelos completamente blanca**.....19
19. Tamaño pequeño (CC = 73-94; C = 74-105; P = 21-26; O = 15-19); dorso marrón amarillento pálido; **cola completamente blanquecina, sin pincel de pelos conspicuo**

(estepas arbustivas en el sur de Salta y este de Catamarca) .....*Eligmodontia bolsonensis* (Figura 6A)

- 19a. Tamaño pequeño (CC = 80-99; C = 99-121; P = 23-26; O = 18-26); **cola bicolor y terminada en un pincel de pelos (~5 mm)**. Similar a *E. bolsonensis*, pero más grande y con el dorso menos amarillento, el área alrededor de los ojos más pálida y las orejas más oscuras (estepas arbustivas; **desde Catamarca, por el oeste, hasta el sur de Mendoza**) ..... *Eligmodontia moreni*
20. Longitud de la cola igual o más larga que la longitud conjunta de la cabeza más el cuerpo; vibrisas mistaciales medianas a largas, que extendidas hacia atrás sobre las mejillas suelen sobrepasar el borde externo de la oreja.....21
- 20a. Longitud de la cola más corta que la longitud conjunta de la cabeza más el cuerpo; vibrisas mistaciales cortas a medianas, que extendidas hacia atrás sobre las mejillas no suelen sobrepasar el borde externo de la oreja.....47
- Nota 2: en *Andinomys edax* la longitud de la cola varía entre el 75 (más corta) y 95% (casi igual) de la longitud combinada de la cabeza más el cuerpo. Si se llega a este punto de la clave, conviene repasar los rasgos que definen a esa especie, los cuales se anotan en la entrada 61.
21. Tamaño mediano (CC = 117-135; C = 100-145; P = 27-32; O = 16-20); cuerpo alargado; coloración dorsal gris amarillenta, más oscura hacia la línea media, **con o sin una línea negra longitudinal marcada desde la nuca hasta la base de la cola**; **vientre grisáceo, bien contrastado con el dorso**; hocico agudo y orejas largas, mayormente desnudas y redondeadas; pelaje dorsal corto y espeso;



**Figura 6.** Aspecto externo de *Eligmodontia bolsonensis* (A), *Eligmodontia morgani* (B y D; en D se muestra un detalle de la superficie plantar de la pata trasera, en donde se destacan las almohadillas interdigitales centrales fusionadas), *Eligmodontia typus* (C), *Andalgalomys olrogii* (E) y *Salinomys delicatus* (F). Las fotos no están en escala.

patas angostas, con la garra del dedo I extendida hasta la mitad de la falange del dedo II y la garra del dedo V hasta ca. la segunda articulación interfalangeana del dedo IV; **plantas desnudas, con almohadillas grandes y carnosas**, y escamación evidente sólo en la parte distal del metatarso; pelos ungueales blanco plateados, que cubren parcialmente las uñas; cola bicolor, con escamado dérmico evidente y aproximadamente igual de larga que la longitud conjunta de la cabeza más el cuerpo; 3 o 4 pares de mamas (selvas en Misiones) .....  
 ..... *Delomys dorsalis* (Figura 7A)

21a. Combinación de caracteres no como en la opción anterior.....22

22. Tamaño pequeño (CC = 85-110; C = 82-97; P = 19-21; O = 12-15); **coloración general castaño rojiza, más brillante y anaranjada en el hocico, grupa, y muslos; vientre blanco-amarillento, bien separado del dorso y lavado de naranja en la región inguinal** y la base de la cola; orejas pequeñas y cubiertas dorsalmente por pelos marrones; vibrisas largas, con algunas que sobrepasan el borde posterior de las orejas; **patas cortas, pero anchas, dorsalmente cubiertas por pelitos anaranjados**, con almohadillas plantares prominentes; **almohadilla hipotenar en forma de coma**, con el borde anterior en la misma línea que el borde posterior de la tenar (Figura 2C-D); dedos blancos, con pelos ungueales abundantes y más largos que las uñas; cola bicolor, excepto por la porción terminal que es oscura todo alrededor y aproximadamente igual de larga que la longitud conjunta de la cabeza más el cuerpo; 4 pares de mamas (selvas en Misiones) .....*Juliomys pictipes* (Figura 7B)

Nota 3: *Juliomys* puede confundirse con *Oligoryzomys* spp., pero se diferencia por tener la cabeza y los ojos proporcionalmente más grandes, las patas más anchas y la cola más corta.

22a. Combinación de caracteres no como en la opción anterior..... 23

23. Longitud CC usualmente menor que 120 mm.....24

23a. Longitud CC usualmente mayor que 120 mm.....31

Nota 4: la separación entre un grupo de especies con longitudes de CC mayores o menores de 120 mm es orientativa; frente a esta disyuntiva, lo más conveniente es que el usuario de la clave evalúe alternativamente las distintas opciones posibles.

24. **Sin manchas blancas alrededor de la nariz y la boca;** pelaje fino y suave, dorsalmente castaño rojizo a castaño amarillento; flancos y mejillas más claros, a veces con tonalidades anaranjadas formando una línea; límite entre dorso y vientre moderadamente a bien definido; **vientre blanco grisáceo o amarillento, con pelos individuales de base gris;** ojos grandes; orejas medianas y redondeadas; vibrisas largas, que extendidas hacia atrás sobre las mejillas alcanzan o sobrepasan el borde externo de las orejas; patas largas y finas, con dedos largos (especialmente el primero), cubiertas por pelitos



Figura 7. Aspecto externo de *Delomys dorsalis* (A), *Juliomys pictipes* (B), *Euryoryzomys russatus* (C) y *Euryoryzomys legatus* (D). Las fotos no están en escala.

claros (Figura 2K); cola fina, bicolor, poco peluda y comparativamente larga; 4 pares de mamas.....  
 .....*Oligoryzomys* (Figura 8A-E) 25

Nota 5: la identificación de las especies del género *Oligoryzomys* es difícil de realizar sólo sobre la base de caracteres externos, requiriendo usualmente de estudios de morfología cráneo-dentaria, cariotípicos y de ADN.

24a. **Con manchas blancas alrededor de la nariz y la boca y parches post y subauriculares del mismo color; pelos del vientre de color blanco puro**..... 29

25. Tamaño pequeño a mediano (CC = 80-110; C = 101-146; P = 18-30; O = 13-19); dorso marrón anaranjado (parecido al color de un ladrillo), con línea lateral indistinta o apenas anaranjada; vientre blanquecino contrastado fuertemente con el dorso, lavado de amarillento en algunos casos, pero siempre con **mentón y garganta completamente blancos; orejas cubiertas por pelitos anaranjados, con un parche de pelos anaranjados por delante;** cola moderadamente bicolor (pastizales, pajonales, matorrales del Chaco y bosques de transición con las Yungas, desde Formosa, Jujuy y Salta hasta el norte de Santiago del Estero, casi siempre por debajo de los 900 msnm).....*Oligoryzomys chacoensis* (Figura 8A)

Nota 6: *O. chacoensis* se diferencia de *O. flavescens*-*O. fornesi* por su mayor tamaño y vientre más blanco, y de *O. nigripes* por su coloración más pálida y amarillenta, ausencia de faja pectoral y vientre más blanco.

25a. Coloración, medidas y/o distribución no como en la opción anterior.....26

26. Tamaño pequeño a mediano (CC = 83-105; C = 108-135; P = 26-29; O = 15-18); pelaje más largo, suave y oscuro que en otras especies del género; **dorsalmente marrón, lavado de amarillo o anaranjado hacia los flancos;** vientre blanco grisáceo; orejas cubiertas por pelitos ocres; patas dorsalmente blanquecinas (pastizales, pajonales, matorrales y áreas forestadas en el **Monte y la Patagonia**, desde el sur de Buenos Aires, La Pampa y



Mendoza hasta Tierra del Fuego) .....  
 .....*Oligoryzomys longicaudatus* (Figura 8C)

26a. Coloración, medidas y/o distribución no como en la opción anterior.....27

27. Tamaño pequeño a mediano (CC = 70-130; C = 96-155; P = 21-29; O = 14-20); dorso marrón anaranjado a marrón grisáceo, con el **vientre blanco grisáceo a gris claro (nunca ocráceo); faja pectoral anaranjada** usualmente presente, extendiéndose **entre las patas delanteras; cola bicolor; orejas cubiertas por pelitos grises** (selvas y matorrales desde Misiones y Formosa hasta el nordeste de Buenos Aires).....

.....*Oligoryzomys nigripes* (Figura 8B)

Nota 7: *O. nigripes* se diferencia de *O. flavescens*-*O. fornesi* por su mayor tamaño y el color más oscuro de sus orejas.

27a. Coloración, medidas y/o distribución no como en la opción anterior..... 28

28. Tamaño pequeño (CC = 69-109; C = 94-155; P = 22-29; O = 14-20); **dorso castaño anaranjado**, más **grisáceo hacia la cabeza** y lavado de amarillento hacia los flancos; vientre blanco grisáceo a gris amarillento o anaranjado; **orejas oscuras, cubiertas por pelitos marrones** (áreas forestadas, principalmente de las Yungas, pero también en algunas zonas del Chaco Serrano, pastizales y matorrales, desde Jujuy y Salta hasta La Rioja).....

.....*Oligoryzomys brendae* (Figura 8E)

Nota 8: *O. brendae* se diferencia de *O. flavescens*-*O. fornesi* por su mayor tamaño y orejas más oscuras y de *O. chacoensis* por su mayor tamaño, coloración dorsal menos anaranjada, ausencia de pelos completamente blancos en mentón y garganta y de parches anaranjados por delante de las orejas.

28a. **Tamaño pequeño** (CC = 60-100; C = 94-137; P = 22-27; O = 12-16); dorso castaño anaranjado a castaño grisáceo, con el vientre blanquecino, variablemente lavado de gris o amarillo; flancos anaranjados o no; cola bicolor; **orejas cubiertas por pelitos ocreos o castaños**. (bosques, pastizales, pajonales, matorrales y bordes de campos cultivados; también en baldíos, basurales, bordes de arroyos y terraplenes de ferrocarril en áreas urbanas y suburbanas, desde el norte de Argentina hasta Mendoza, La Pampa y Buenos Aires) .....

.....*Oligoryzomys flavescens* (incluyendo *O. f. occidentalis*)-*O. fornesi* (Figura 8D)

Nota 9: las especies en este grupo son difíciles de diferenciar entre sí, pero se distinguen de otras simpátricas como *O. brendae*, *O. chacoensis* y *O. nigripes* por su menor tamaño y sus orejas más claras.

29. Tamaño pequeño (CC = 68-83; C = 94-117; P = 20-23; O = 16-19); pelaje largo y suave, dorsalmente marrón grisáceo a oliváceo, bien separado del vientre; una **mancha alrededor de la nariz y boca, de color blanco**, se extiende casi hasta el ojo; **parche de pelos blanquecinos arriba y debajo de cada ojo**; orejas muy grandes, con **parches**

**postauriculares conspicuos de color blanco; cola muy larga (140-160% de la longitud conjunta de la cabeza más el cuerpo)**, moderadamente peluda, apenas bicolor y **terminada en un pincel de pelos de 8-10 mm**; manos y patas cubiertas por pelitos blancos; patas alargadas, con las plantas desnudas (medanales, arbustales y algarrobales en bordes de salares del centro-oeste de Argentina, desde La Rioja hasta San Luis).....*Salinomys delicatus* (Figura 6F)

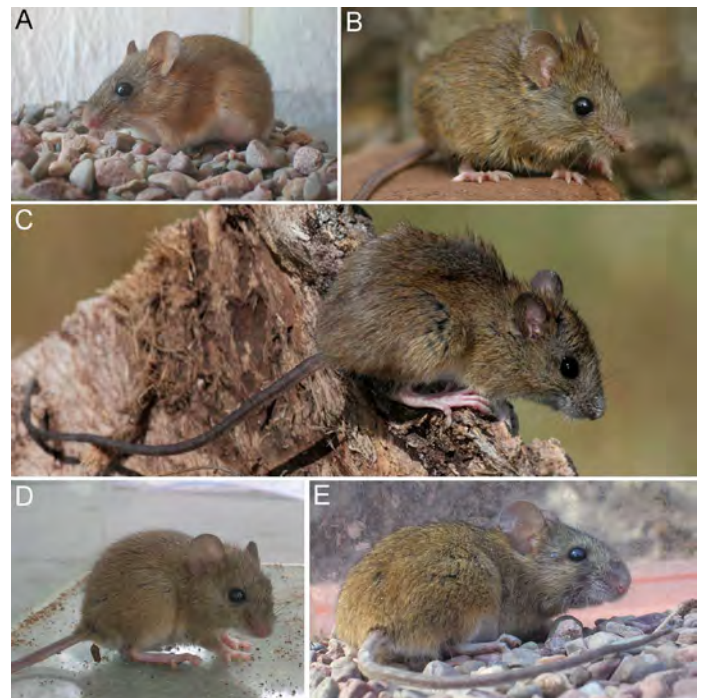
29a. Pelaje largo y laxo; coloración dorsal marrón grisácea a anaranjada, más pálida hacia los flancos, pero bien contrastada con el vientre, que es de color blanco puro; **parches postauriculares y subauriculares blancos**, igual que el extremo de la nariz y área alrededor de la boca; orejas grandes y poco peludas; **cola casi tan larga o apenas más larga que la longitud conjunta de la cabeza más el cuerpo**, bicolor y más oscura hacia la punta, terminada o no en un pequeño pincel de pelos (3-9 mm); manos y patas cubiertas por pelitos blancos; plantas desnudas..... *Andalgalomys* 30

30. Tamaño pequeño (CC = 80-119; C = 92-127; P = 22-25; O = 18-20); **pelaje dorsal marrón rojizo; cola sin pincel de pelos evidente** (matorrales en el Chaco Seco en Salta y Santiago del Estero).....*Andalgalomys pearsoni*

30a. Tamaño pequeño (CC = 75-113; C = 85-126; P = 21-25; O = 17-23); **pelaje dorsal marrón amarillento a marrón grisáceo; cola terminada en un pincel de pelos moderado** (áreas arbustivas abiertas del Chaco Seco y Monte, desde Catamarca hasta el norte de Mendoza y San Luis) .....

.....*Andalgalomys olrogi* (Figura 6E)

31. Tamaño grande (CC = 140-172; C = 165-195; P = 28-34; O = 23-29); **pelaje denso y suave, dorsalmente castaño**



**Figura 8.** Aspecto externo de *Oligoryzomys chacoensis* (A), *Oligoryzomys nigripes* (B), *Oligoryzomys longicaudatus* (C), *Oligoryzomys flavescens occidentalis* (D) y *Oligoryzomys brendae* (E). Las fotos no están en escala.

**anaranjado, contrastando con el vientre, que es blanquecino a crema; garganta completamente blanca; ojos grandes; orejas largas, ovaladas y de color marrón; vibrisas mistaciales y superciliares largas**, que extendidas hacia atrás sobre las mejillas sobrepasan el borde externo de la oreja y en algunos casos **alcanzan el hombro; patas** proporcionalmente **cortas y anchas, con una mancha oscura dorsal**; dedos cubiertos por pelos grises o blancos; palmas y plantas desnudas, con almohadillas grandes y planas; pelos ungueales claros; garras cortas y recurvadas, **cola gruesa, más larga que la longitud conjunta de la cabeza más el cuerpo (110-135%)**, unicolorreada, con escamado dérmico evidente **y terminada en un pincel de pelos** de hasta 10 mm; 6 pares de mamas (áreas forestadas de Yungas en Jujuy y Salta) .....  
 .....*Rhipidomys austrinus* (Figura 9A)

- 31a. Combinación de caracteres no como en la opción anterior..... 32
- 32. Coloración dorsal con tonos castaño amarillentos a marrón rojizos; si es marrón grisáceo entonces tiene el rinario y las orejas teñidos de rojizo; cola escasamente cubierta de pelos, con escamado dérmico visible y no terminada en un pincel de pelos. Mayormente restringidos a áreas forestadas subtropicales en el norte de Argentina.....33
- 32a. Coloración dorsal marrón grisácea a marrón oscura, variablemente lavada de oliváceo o amarillo; cola moderadamente a densamente cubierta de pelos, con escamado dérmico mayormente oculto y usualmente terminada en un pincel de pelos más oscuros. Principalmente en estepas arbustivas y herbáceas, roquedales y bosques xerófilos.....36
- 33. Tamaño mediano (CC = 139-151; C = 166-176; P = 28-30; O = 20-22); pelaje suave y abundante, dorsalmente marrón grisáceo, más pálido hacia los flancos; vientre blanquecino lavado de amarillo, bien contrastado con el color del dorso; **parches de pelos completamente blancos en garganta y pecho; abdomen, porción interna de las patas, áreas inguinal y perianal con tonos anaranjados; rinario y orejas teñidos de rojizo; orejas** relativamente largas y ovaladas; vibrisa genal 2 presente; cola unicolor, marrón clara, con escamado epidérmico evidente; **patas cortas y anchas**, cubiertas dorsalmente por pelos marrones; pelos ungueales largos y abundantes; garras cortas; plantas desnudas, con almohadillas grandes y redondeadas (Figura 9D); 4 pares de.....*Oecomys franciscorum* (Figura 9C)
- 33a. Combinación de caracteres no como en la opción anterior.....34
- 34. **Tamaño grande** (CC = 164-194; C = 191-230; P = 35-41; O = 22-26); pelaje dorsal marrón rojizo, más o menos lavado de gris o amarillento según los individuos; vientre blancuzco o amarillento, bien separado del dorso; **orejas pequeñas, que dobladas hacia delante no cubren los ojos; dorso de las manos y patas cubiertos por pelitos**

marrones; plantas desnudas, pero densamente escuteladas (cubiertas de escamas); garra del dedo I de la pata trasera extendida hasta la mitad de la primer falange del dedo II; garra del dedo V extendida hasta o apenas por detrás de la primera articulación interfalangeana del dedo IV; **cola muy larga y unicolor**; 4 pares de mamas (selvas y bosques en galería desde Misiones y Formosa hasta Entre Ríos).....*Sooretamys angouya* (Figura 9B)

- 34a. **Tamaño mediano**; pelaje dorsal de color marrón lavado de amarillento o rojizo, según las especies; vientre blanco-grisáceo, bien contrastante respecto del dorso; **orejas grandes, que dobladas hacia delante alcanzan los ojos**; manos y patas cubiertos por pelitos color blanquecino o crema; plantas desnudas, pero escuteladas; garra del dedo I de la pata trasera extendida apenas por delante de la base de la primer falange del dedo II; garra del dedo V extendida hasta la mitad de la primer falange del dedo IV; cola apenas más larga que la longitud conjunta de la cabeza más el cuerpo y bicolor; 4 pares de mamas.....*Euryoryzomys* 35
- 35. Tamaño mediano (CC = 87-185; C = 118-161; P = 30-37; O = 21-27); **coloración dorsal marrón rojiza**, lavada de anaranjado hacia los flancos (pudiendo formar una línea brillante desde las mejillas a la cola) (selvas y bosques de Yungas en **Salta y Jujuy**).....  
 .....*Euryoryzomys legatus* (Figura 7D)
- 35a. Tamaño mediano (CC = 118-146; C = 114-156; P = 29-33; O = 20-23); **coloración dorsal castaño oscura**, lavada de anaranjado hacia los flancos (selvas en **Misiones**) .....  
 .....*Euryoryzomys russatus* (Figura 7C)
- 36. Pelaje denso y suave; vientre grisáceo, con o sin faja pectoral; línea lateral ocrácea más o menos definida; vibrisas largas, pero que no alcanzan a sobrepasar el borde posterior de la oreja; orejas marrones; manos



**Figura 9.** Aspecto externo de *Rhipidomys austrinus* (A), *Sooretamys angouya* (B) y *Oecomys franciscorum* (C y D); en D se muestra la pata trasera en vista dorsal [izquierda] y plantar [derecha]. Las fotos no están en escala.

- y patas cubiertas por pelitos blancos, **mancha de pelos más oscuros sobre el dorso de la pata presente o ausente**; pelos ungueales blancos, que cubren parcialmente las garras; cola bicolor y moderadamente peluda .....*Tapecomys* 37
- Nota 10: las especies de *Tapecomys* pueden ser difíciles de diferenciar externamente de *Phyllotis* y *Graomys*, de las que se distinguen por su coloración sin tintes anaranjados.
- 36a. Similar al anterior, pero con la coloración más brillante, usualmente teñida de anaranjado o amarillo hacia los flancos y con las patas sin manchas oscuras; vientre grisáceo o completamente blanco .....38
37. Tamaño mediano (CC = 124-139-; C = 136-143; P = 29-34; O = 25-28); coloración dorsal marrón, más oscura hacia la línea media y amarillenta hacia los flancos; **una mancha de pelos marrones en el dorso de la pata, cercana a la base de los dedos** (áreas forestadas de Yungas en Jujuy).....*Tapecomys primus*
- 37a. Tamaño mediano (CC = 122-134-; C = 121-145; P = 26-28; O = 24-25); coloración dorsal castaño grisácea, más pálida y amarillenta hacia los flancos y gris hacia los lados de la cabeza; vientre gris; hocico amarillento (**conocido para una sola localidad en Salta, en pastizales de altura de Yungas a 2100 msnm**).....*Tapecomys wolffsohni*
38. Pelaje moderadamente largo y suave; orejas medianas a grandes, poco peludas y ovaladas; ojos grandes; **talones sin pelos**; pelos ungueales abundantes y blancos, que cubren parcialmente las garras; cola generalmente bicolor y poco peluda, usualmente terminada en un pincel de pelos oscuros; 4 pares de mamas; **comportamiento generalmente agresivo**; bordes supraorbitarios del cráneo posteriormente divergentes y bien marcados, palpables externamente .....*Graomys* 39
- 38a. Pelaje moderadamente largo y suave; orejas medianas a grandes, poco peludas y ovaladas; cabeza y ojos grandes; faja pectoral (Figura 11) de pelos anaranjados presente (e. g., *P. caprinus*, algunas poblaciones de *P. tucumanus* y de *P. xanthopygus*) o ausente (*P. alisosensis*, *P. anitae*, *P. bonariensis*); **talones cubiertos de pelos**; pelos ungueales abundantes y blancos, que cubren parcialmente las garras; cola generalmente bicolor y poco peluda, con o sin pincel terminal de pelos. **Comportamiento no agresivo**; bordes supraorbitarios del cráneo no palpables externamente .....*Phyllotis* 42
39. **Tamaño pequeño** (CC = 108; C = 127; P = 25; O = 20); **LT ~235 mm**; sin línea amarillenta sobre los flancos y con pincel de pelos en la cola menos notable (conocido únicamente de la localidad tipo y cercanías, en el extremo sur de la **Sierra de Ambato**, Catamarca, **entre 400 y 3,000 msnm**) .....*Graomys edithae*
- 39a. **Tamaño mediano (LT >260 mm)**, usualmente con una línea amarillenta o anaranjada brillante sobre los flancos y con pincel de pelos en la cola más notable .....40
40. Tamaño mediano (CC = 131-161; C = 149-184; P = 30-35; O = 25-27); coloración dorsal castaña, lavada de ocre hacia los flancos; **vientre blanco grisáceo, lavado de amarillento o crema, con pelos completamente blancos en la garganta**; orejas marrones; cola bicolor, terminada en un pincel de pelos poco evidente; patas blanquecinas (**zonas de transición entre bosques pedemontanos de Yungas y bosques chaqueños en Jujuy, Salta y Tucumán**) .....*Graomys domorum* (Figura 10B)
- 40a. Coloración dorsal marrón amarillento a marrón grisáceo, lavado de amarillo o anaranjado hacia los flancos; **vientre completamente blanco o con pelos individuales de base gris y punta blanca, pero siempre bien contrastante con el dorso**; patas dorsalmente blancas, con las plantas oscuras; cola bicolor, con pincel terminal de pelos conspicuo.....41
41. Tamaño mediano (CC = 111-165; C = 114-185; P = 26-33; O = 20-25), pero en general más pequeño que *G. griseoflavus*; coloración más brillante, menos ocrácea y con el vientre siempre blanco (**áreas boscosas y arbustivas del Chaco Seco y Húmedo y Espinal**).....*Graomys chacoensis* (Figura 10C)
- 41a. Tamaño mediano (CC = 118-169; C = 134-171; P = 27-31; O = 23-25), pero en general más grande que *G. chacoensis* y con la coloración menos brillante; vientre completamente blanco o con pelos de base gris y punta blanca (**áreas boscosas y arbustivas en el oeste y sur de Argentina, principalmente en el Monte y Estepa Patagónica, aunque también en el Espinal, desde Salta hasta Santa Cruz**).....*Graomys griseoflavus* (Figura 10D)
42. Tamaño pequeño a mediano (CC = 82-144; C = 89-139; P = 27-31; O = 18-24); coloración general marrón oscura a casi negra; **vientre ocre o acanelado, que no contrasta fuertemente con el dorso**; orejas oscuras y poco cubiertas de pelo; manos y patas cubiertas por pelitos blancos; cola bicolor (áreas ecotonales entre pastizales de altura y bosques montanos de Yungas, por encima de los 1,200 msnm en Tucumán)..... *Phyllotis anitae*
- 42a. Coloración general comparativamente más clara, marrón grisáceo, a veces lavada de amarillento; **vientre blanco grisáceo, que contrasta más notablemente con el dorso**.....43
43. Tamaño mediano (CC = 127-151; C = 110-147; P = 25-28; O = 23-25); dorso marrón amarillento, más pálido hacia los flancos, pero bien separado del vientre; región ventral gris blanquecino, a veces lavada de amarillento; faja pectoral ausente o muy poco definida; manos y patas cubiertos dorsalmente por pelitos blanco sucio; cola bicolor y poco peluda (**roquedales en Sierra de la Ventana, sudoeste de Buenos Aires**).....*Phyllotis bonaeriensis*
- 43a. Distribución distinta de la opción anterior.....44
44. Tamaño mediano (CC = 102-140; C = 116-151; P = 21-23; O = 19-24); **coloración dorsal marrón grisácea lavada de amarillento, más brillante hacia los flancos y mej-**

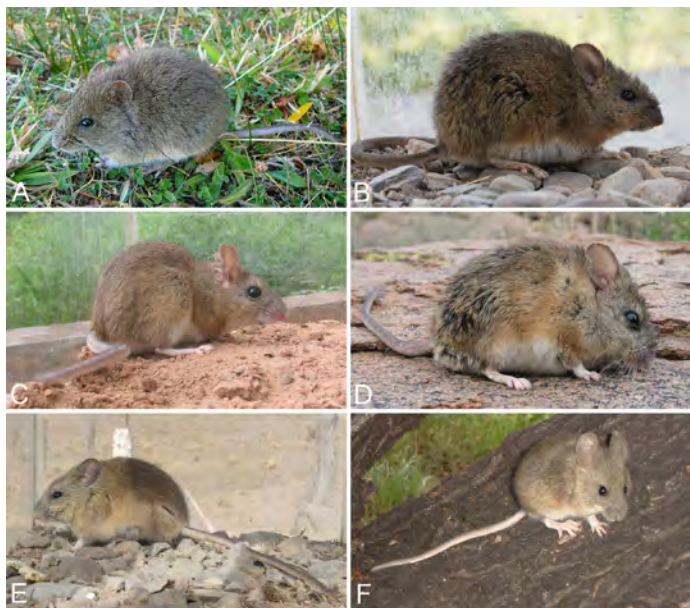


Figura 10. Aspecto externo de *Loxodontomys micropus* (A), *Graomys domorum* (B), *Graomys chacoensis* (C), *Graomys griseoflavus* (D), *Phyllotis tucumanus* (E) y *Phyllotis xanthopygus* (F). Las fotos no están en escala.

llas, que están teñidos de anaranjado; vientre blanco-grisáceo (áreas arbustivas y de pastizales asociadas a roquedales en la Prepuna y Puna, por encima de los 2,000 msnm, en Jujuy) .....*Phyllotis caprinus*

Nota 11: *P. caprinus* es simpátrica con *P. xanthopygus* en Jujuy, pero se distingue por su mayor tamaño, sus orejas comparativamente más pequeñas, la cola más gruesa y menos peluda y por presentar usualmente una faja pectoral anaranjada.

44a. Coloración, medidas y/o distribución no como en la opción anterior.....45

45. Tamaño mediano (CC = 104-142; C = 107-145; P = 24-30; O = 22-29); coloración dorsal marrón clara o grisácea, lavada de amarillento, más brillante hacia los flancos y mejillas, que pueden o no estar teñidos de anaranjado; vientre blanco-grisáceo, a veces lavado de amarillento; **faja pectoral mayormente ausente; orejas generalmente mayores de 24 mm**; cola bicolor, sin escamado visible y terminada en un pincel de pelos oscuros (Figura 11); manos y patas cubiertos por pelitos blanco sucio (**roquedales** en áreas altoandinas y puneñas, pastizales de altura en el Monte y el Chaco Seco, y en estepas de la Patagonia, desde Salta y Jujuy hasta Santa Cruz).....*Phyllotis xanthopygus* (Figura 10F)

Nota 12: evidencias genéticas y morfológicas sugieren que el actual concepto de *P. xanthopygus* se corresponde con un complejo de especies. En Argentina, este complejo estaría representado por al menos 5 entidades morfológicamente crípticas, con diferencias cualitativas y cuantitativas sutiles.

45a. Dorso marrón grisáceo, lavado de amarillento; flancos y mejillas teñidos de anaranjado; vientre blanco grisáceo; **faja pectoral casi constantemente presente**; cola menos peluda y casi sin pincel; **orejas proporcional-**

**mente más cortas (usualmente <24 mm) y más oscuras** (especialmente hacia el borde) que en *P. xanthopygus* (Figura 11) (**selvas de Yungas y pastizales húmedos asociados a Yungas y Monte**, en el noroeste de Argentina) .....46

46. Tamaño mediano (CC = 118-137; C = 125-137; P = 32-33; O = 22-24); **muy difícil de distinguir de *P. tucumanus*, de la que apenas se diferencia por su tamaño algo mayor, su pelaje más largo, oscuro y de tonalidades más intensas, la presencia de un anillo periocular más contrastante, los flancos más anaranjados y el vientre más ocráceo (selvas y bosques de Yungas hasta el ecotono con pastizales montañosos en el centro y sur de la Sierra de Zenta, entre 1,200 y 3,100 msnm, en Jujuy y Salta) ....** .....*Phyllotis nogalaris*

46a. Tamaño mediano (CC = 95-129; C = 108-132; P = 27-32; O = 21-23); coloración general más clara y de tonos menos intensos que en *P. nogalaris* (**pastizales montañosos húmedos desde Jujuy y Salta hasta Catamarca**) ... .....*Phyllotis tucumanus* (Figura 10E)

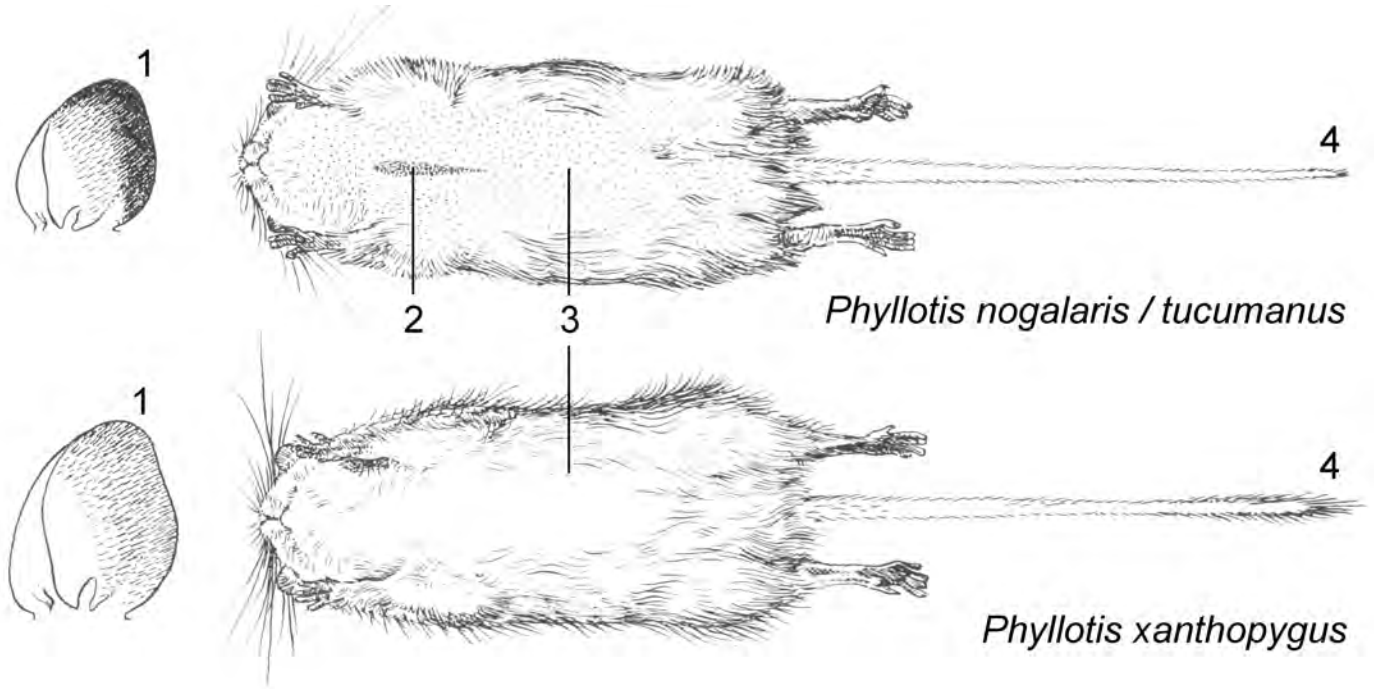
47. Tamaño pequeño, cuerpo robusto, cola corta y **hocico corto, pero abultado y de tono rosado intenso; márgenes de la boca cubiertos por pelitos cortos y rígidos de color blanco**; pelaje suave, dorsalmente castaño oscuro, con efecto agutí fino pero visible; línea media dorsal casi negra; laterales castaño-amarillento y vientre gris claro; orejas medianas; ojos pequeños; cola bicolor, gris oscura por arriba y blanquecina por debajo, con anillado epidérmico notorio; manos y patas cubiertos por pelitos grises, pero que dejan ver la piel rosada por debajo; uñas medianamente desarrolladas ... .....*Bibimys* (Figura 12C) 48

47a. Hocico no abultado, ni rosado intenso.....49

48. Tamaño pequeño (CC = 94-107; C = 70-75; P = 21-22,5; O = 14-17); indistinguible de *B. torresi*, excepto por su distribución (**pastizales periselváticos del Chaco Húmedo y sur de Misiones**).....*Bibimys chacoensis* (Figura 12C)

48a. Tamaño pequeño (CC = 84-97; C = 65-78; P = 22-23; O = 15-17); indistinguible de *B. chacoensis*, excepto por su distribución (bosques ribereños, pastizales, espadañales y pajonales en terrenos inundables de la **porción media e inferior del Delta del Paraná**).....*Bibimys torresi*

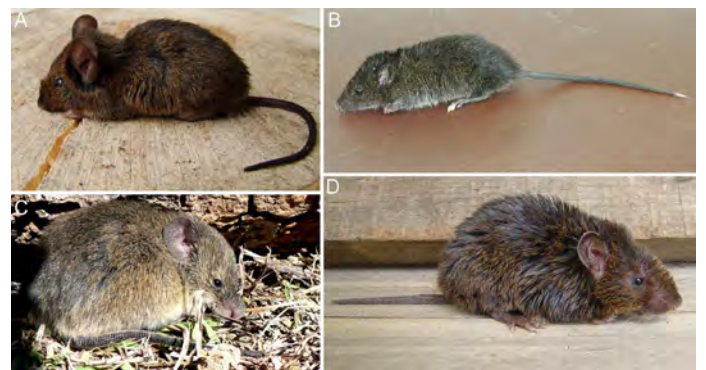
49. **Tamaño pequeño** (CC = 78-92; C = 35-46; P = 17-21; O = 6-8); pelaje corto y sedoso, dorsalmente marrón amarillento, con tintes anaranjados hacia los flancos y netamente separado del blanquecino del vientre; **rinario conspicuo y rosado**, con los **lados del hocico de color anaranjado**; **orejas rudimentarias, completamente cubiertas por el pelo de la cabeza y apenas indicadas externamente por un penacho de pelitos blancos**; ojos medianos; manos y patas cubiertos por pelitos anaranjados; dedos blancos; manos con **garras muy desarrolladas (~4-5 mm)**, transversalmente comprimidas y con una quilla que se extiende desde la base hasta ca.



**Figura 11.** Caracteres distintivos entre *Phyllotis nogalaris / tucumanus* y *Phyllotis xanthopygus* (redibujado de Hershkovitz 1962); el complejo *nogalaris / tucumanus* se diferencia de *xanthopygus* por tener sus orejas proporcionalmente más pequeñas y con el borde más oscuro (1), la presencia de una faja pectoral anaranjada (2), la coloración ventral apenas más oscura (3), y la cola sin pincel de pelos (4). Las figuras no están en escala.

- la mitad de cada uña; **patas con un fleco o peine de pelos blancos sobre cada lado; cola muy corta y blanquecina**, apenas más oscura por encima y cubierta de pelos en la base (estepas arbustivas y herbáceas de Patagonia, desde Río Negro hasta Santa Cruz) .....  
 .....*Notiomys edwardsii* (Figura 13G)
- 49a. **Orejas** desde muy pequeñas a grandes, pero **no rudimentarias** (siempre visibles externamente) y sin penacho de pelos .....50
50. **Tamaño pequeño**, con **aspecto general de musaraña; hocico moderadamente aguzado; ojos y orejas pequeños, mayormente ocultos entre los pelos de la cabeza; cola muy corta (<50% de la longitud conjunta de la cabeza más el cuerpo)**; pelaje corto, de aspecto aterciopelado; coloración general oscura, marrón a negruzca; garras de las manos bien desarrolladas, casi tan largas o más que el dedo correspondiente.....51
- 50a. Sin aspecto de musaraña.....53
51. **Tamaño pequeño** (CC = 99-116; C = 30-52; P = 16-21; O = 8-10); **pelaje corto, hispido y brillante**; coloración general negruzca a castaño oscuro, apenas más clara en el vientre; **extremo del hocico generalmente blanquecino**; cola negra, cubierta por pelitos cortos, pero con las escamas visibles; manos y patas cubiertos por pelitos castaños; palmas y plantas escamadas, con almohadillas plantares pequeñas (**selvas en Misiones**) .....  
 .....*Blarinomys breviceps* (Figura 14)
- 51a. **Tamaño pequeño; pelaje corto, fino y denso**; coloración dorsal marrón o negruzca, a veces lavada de castaño o de oliva, poco o moderadamente contrastada con el vientre, que suele ser de color grisáceo; cola corta,

- robusta y densamente cubierta de pelos, ocultando las escamas; manos y pies proporcionalmente cortos y anchos; garras bien desarrolladas, transversalmente comprimidas y con una quilla que se extiende desde la base hasta ca. la mitad de cada uña (**bosques y estepas ecotonales de la Patagonia**).....*Geoxus* (Figura 14) 52
52. **Tamaño pequeño** (CC = 100-110; C = 39-51; P = 20-22; O = 10-12); coloración **dorsal marrón, con tintes oliváceos o amarillentos; vientre gris, bien separado del dorso (matorrales ecotonales en Santa Cruz)** .....  
 .....*Geoxus michaelsoni*
- 52a. **Tamaño pequeño** (CC = 95-100; C = 30-44; P = 18-20; O = 10-12); **coloración general marrón oscura a casi negra**, a veces lavada de castaño en el dorso, más clara hacia el vientre (**bosques y matorrales ecotonales desde el centro-oeste de Neuquén hasta por lo menos el sudoeste de Chubut**).....*Geoxus valdivianus*



**Figura 12.** Aspecto externo de *Castoria angustidens* (A), *Deltamys kempi* (B), *Bibimys chacoensis* (C) y *Thaptomys nigrita* (D). Las fotos no están en escala.

53. Tamaño **mediano** (CC = 100-130; C = 47-59; P = 23-27; O = 11-17); **contextura robusta**; pelaje corto y suave, dorsalmente marrón amarillento a marrón muy oscuro, con el vientre gris o blanco grisáceo; **orejas pequeñas y redondeadas**; ojos medianos; manos con **garras muy desarrolladas (>4 mm)**, transversalmente comprimidas y con una quilla que se extiende desde la base hasta ca. la mitad de cada uña; patas anchas y robustas, con las palmas y las plantas desnudas, cubiertas por seis almohadillas grandes, redondeadas y prominentes; **borde externo de la pata con un peine de pelos evidente** (estepas herbáceas y arbustivas, matorrales y bosques; principalmente en áreas cordilleranas y pedemontanas, desde el centro de Mendoza, por el oeste, hasta el sur de Santa Cruz).....*Paynomys macronyx* (Figura 13H)

53a. Combinación de caracteres no como en la opción anterior..... 54

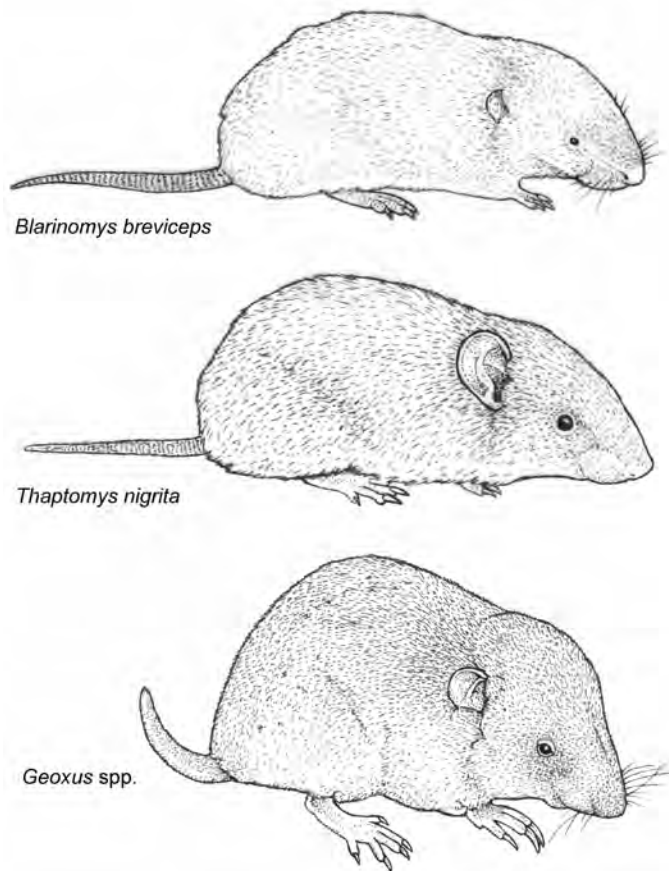
54. **Hocico característicamente alargado** (aunque no siempre de forma evidente en los ejemplares juveniles); garras de las manos bien desarrolladas..... 55

54a. Hocico nada o apenas alargado; garras de las manos poco o bien desarrolladas.....59

55. **Tamaño pequeño** (CC = 93-113; C = 83-90; P = 23-25; O = 16-19); pelaje dorsal fino y suave, castaño a gris; vientre grisáceo o marrón, lavado de amarillento; orejas medianas; **ojos pequeños, mayormente ocultos en el pelaje de la cabeza**; en algunos ejemplares los pelos



**Figura 13.** Aspecto externo de *Akodon albiventer* (A), *Abrothrix jelskii* (B), *Abrothrix hirta* (C), *Abrothrix illutea* (D), *Abrothrix olivacea* (E y F; en E se destaca la coloración típica de los ejemplares de estepa y en F la de los bosques), *Notiomys edwardsii* (G) y *Paynomys macronyx* (H). Las fotos no están en escala.

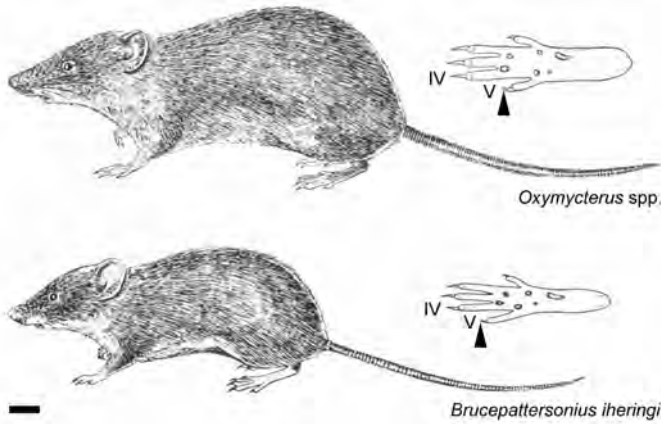


**Figura 14.** Aspecto externo de tres roedores sigmodontinos semifosoriales; nótese las diferencias en el tamaño de los ojos, orejas y garras de las patas delanteras.

de la punta de la nariz y barbilla son blancos o amarillentos; manos y patas cubiertas por pelitos blanquecinos, marrones o grises; uñas de las manos alargadas y curvas (2.3-2.6 mm) (Figura 2L); **dedo V del pie largo, su extremo sobrepasa el punto de inserción de los dedos II-IV** (Figura 15); cola bicolor o marrón uniforme, poco pilosa y con el anillado epidérmico notorio; 3 pares de mamas (selvas en Misiones) .....  
.....*Bucepattersonius iheringi* (Figura 16E)

Nota 13: las especies de *Bucepattersonius* se suelen confundir con las formas selváticas del género *Akodon* (i. e., *A. montensis* y *A. paranaensis*), pero se diferencian de aquellas por su menor tamaño y sus ojos conspicuamente más pequeños y ocultos entre los pelos de la cabeza.

55a. **Tamaño mediano a grande**; cola relativamente gruesa; orejas cortas y redondeadas; coloración general marrón o incluso negra en algunas especies, con tonalidades rojizas y en algunos casos anaranjada, más clara en el vientre, con las bases de los pelos siempre grises; cola cubierta por escamas anulares grandes y escasamente peluda; patas robustas; **dedo V del pie más corto, su extremo no sobrepasa el punto de inserción de los dedos II-IV** (Figura 15); en la mano, la uña del dedo III es casi tan larga como el mismo dedo; la uña del dedo V se extiende hasta la base del dedo IV y la del dedo



**Figura 15.** Aspecto externo en *Oxymycterus* spp. y *Brucepattersonius iheringi* (redibujado de Massoia 1969); se destaca la distinta longitud del dedo V con respecto al dedo IV (flecha) en las patas traseras de ambos taxones. La escala es igual a 10 mm.

- I apenas alcanza los carpales** (Figura 2M); 4 pares de mamas.....*Oxymycterus* (Figura 16A-C) 56
56. Tamaño mediano (CC = 114-145; C = 70-97; P = 28-32; O = 17-21); **coloración general negruzca, lavada de ocre o rojizo**; el dorso de las patas traseras y la cara interna de las orejas están cubiertas por pelitos negros; cola casi negra, apenas más clara por debajo; **en la barbilla y a veces en la garganta hay una característica mancha blanca**; **garras de las patas anteriores notablemente desarrolladas (largas y robustas)** (selvas y Bosques Montanos del extremo sur de Yungas y su ecotono con pastizales de altura, entre 800 y 3,000 msnm, en el sur de Salta, Catamarca y Tucumán).....*Oxymycterus wayku*
- 56a. **Coloración general marrón rojiza** ..... 57
57. Longitud CC >160 (CC = 170-180; C = 110-120; P = 27-40; O = 19-22); coloración general marrón rojiza, con tintes metálicos sobre la línea media; flancos anaranjados o marrón-amarillentos; vientre gris, lavado de ocre; cola y orejas marrón oscuras (selvas en Misiones) .....  
.....*Oxymycterus quaestor* (Figura 16A)
- 57a. Longitud CC <160 mm..... 58
58. Tamaño mediano (CC = 105-153; C = 66-115; P = 25-35; O = 18-22); coloración dorsal marrón olivácea a negruzca (en algunos ejemplares de Jujuy), con pelos negros entremezclados y lavada de rojizo hacia las ancas; vientre gris amarillento; usualmente con una **mancha oscura por encima del rinario** (selvas y bosques montanos de Yungas, y áreas de ecotono con pastizales de altura, en **Jujuy, Salta y el extremo norte de Tucumán**) .....  
.....*Oxymycterus paramensis* (Figura 16C)
- 58a. Tamaño mediano (CC = 134-150; C = 81-10; P = 27-32; O = 15-19); coloración general fuertemente rojiza, con pelos negros entremezclados; vientre anaranjado a castaño; cola y orejas marrón oscuras (pastizales y pajonales densos, especialmente en áreas cercanas a cuerpos de agua, permanentes o temporarios, **desde Misiones y Corrientes hasta el sur de Santa Fe y norte, este y sur de Buenos Aires**; también en pastizales de **ambientes serranos de Córdoba y San Luis**) .....  
.....*Oxymycterus rufus* (Figura 16B)
59. Tamaño grande, CC generalmente > 150 mm.....60
- 59a. Tamaño mediano a pequeño, CC generalmente <150 mm) ..... 62
60. Tamaño grande (CC = 135-185; C = 102-164; P = 22-37; O = 22-34); **pelaje fino, largo y suave, de color gris amarillado en el dorso**, más oscuro hacia la línea media y lavado de ocre hacia los flancos; **vientre gris blanquecino**, a veces con tintes amarillentos; orejas medianas y redondeadas, de color marrón oscuro; **cola bicolor**, marrón oscuro por arriba y blanquecina por debajo (a veces con una línea media ventral fina y oscura que corre desde la base hasta cerca del ápice); manos y patas cubiertas por pelitos blanquecinos; palmas y plantas desnudas, con almohadillas grandes, redondeadas y prominentes; **garras delanteras muy cortas**; 4 pares de mamas; **en vista frontal, el extremo distal de los incisivos superiores tiene forma de bisel (pastizales y matorrales en ambientes Altoandinos y de la Puna, Selvas y pastizales húmedos de Yungas, entre 500 y 4800 msnm, en Jujuy, Salta, Tucumán y Catamarca)** .....  
.....*Andinomys edax* (Figura 5A)
- 60a. **Garras delanteras casi tan largas como el dedo correspondiente y apenas recurvadas** .....61
61. Tamaño grande (CC = 152-198; C = 132-159; P = 34-38; O = 19-24); **pelaje fino, suave y brillante**; coloración dorsal **marrón oscura a negra**; **vientre blanco grisáceo, con la línea que lo separa del dorso moderadamente delimitada**; orejas comparativamente pequeñas, redondeadas y densamente cubiertas de pelos oscuros; manos y patas cubiertas dorsalmente por pelitos blanquecinos; pelos ungueales cortos, pero abundantes; **almohadilla hipotenar vestigial o ausente** (Figura 2J); **cola corta (entre 65% y 90% de la longitud conjunta de la cabeza más el cuerpo)** y unicolor, cubierta por pelos oscuros, cortos por arriba y más largos por debajo; 4 pares de mamas (terrenos anegadizos con pajonales densos, desde Formosa y Corrientes hasta el norte y este de Buenos Aires).....*Scapteromys aquaticus* (Figura 16D)
- 61a. Tamaño grande (CC = 225; C = 110; P = 43; O = no disponible); **pelaje largo y algo hispido**, dorsalmente marrón, con brillo metálico, dorado a verde, a la luz incida; **vientre grisáceo, con la línea que lo separa del dorso no bien delimitada**; orejas redondeadas y pequeñas, densamente cubiertas por pelitos cortos de color marrón; **cola corta (~55% de la longitud conjunta de la cabeza más el cuerpo)** y unicolor, negruzca todo alrededor; los pelos que recubren la cola son más largos abajo y a los lados; manos y patas marrón grisáceas, con algunos pelitos plateados; palmas y plantas desnudas, pero con escutelado dérmico notorio; **almohadilla hipotenar vestigial** (Figura 2I) (especie sólo conocida por un ejemplar, coleccionado a finales del siglo XIX en el noreste del Chaco y probablemente extinta; se desconocen sus



Figura 16. Aspecto externo de *Oxymycterus quaestor* (A), *Oxymycterus rufus* (B), *Oxymycterus paramensis* (C), *Scapteromys aquaticus* (D) y *Brucepattersonius iheringi* (E). Las fotos no están en escala.

- hábitos, aunque es posible que habitase en pastizales inundables).....*Gyldenstolpia fronto*
62. Tamaño mediano (CC = 99-144; C = 80-112; P = 25-32; O = 15-23); **aspecto robusto; pelaje espeso, laxo y suave; dorso marrón**, a veces lavado de gris u ocre en el dorso, más claro en los flancos y gris o plumizo, con tintes ocre, en el vientre; orejas medianas de color marrón; **cola (~75% de la longitud conjunta de la cabeza más el cuerpo)** cubierta por pelos ralos y dispersos, marrones sobre la línea media dorsal y más claros hacia los lados y por debajo; patas delgadas, con las palmas y las plantas desnudas; éstas últimas cubiertas por seis almohadillas bajas y grandes; el dedo V del pie es largo y alcanza el extremo distal de la primer falange del dedo IV (bosques, pastizales húmedos y áreas arbustivas de Cordillera hasta 3,000 msnm y pedemonte, **desde el sur de Mendoza hasta Santa Cruz**) .....*Loxodontomys micropus* (Figura 10A)
- Nota 14: *Loxodontomys* se puede confundir con *Phyllotis xanthopygus*, del que se diferencia por su cola y orejas más cortas y con *Reithrodon* y *Euneomys*, de los que se distingue por su cola más larga y por los incisivos sin surcos anteriores.
- 62a. Combinación de caracteres no como en la opción anterior.....63
63. Tamaño pequeño; miembros cortos y orejas medianas (<20 mm); **coloración dorsal y ventral usualmente bien diferenciadas, con el vientre blanco a blanco grisáceo**; ojos saltones; **parches postauriculares blancos**, poco o bien definidos; **patas pequeñas**, siempre < 23 mm y dorsalmente **cubiertas por pelitos blancos**, excepto en los talones que están desnudos; pelos ungueales largos, que sobrepasan pero no ocultan las uñas; cola propor-

cionalmente corta, bicoloreada, bien cubierta de pelos, fina y sin pincel terminal; 4 a 7 pares de mamas.....*Calomys* (Figura 5C-F) 64

- 63a. Combinación de caracteres no como en la opción anterior.....68
64. Tamaño pequeño a mediano (CC = 92-119; C = 65-87; P = 18-22; O = 16-19); coloración dorsal grisácea, lavada de amarillento hacia los flancos; **vientre blanco grisáceo, con la línea que lo separa del dorso poco definida; orejas medianas, generalmente >16 mm**, redondeadas y oscuras, con parches postauriculares indistintos; 5 a 7 pares de mamas.....*Calomys* spp. (Fig 5F)
- Nota 15: en este grupo se incluyen cuatro especies grandes del género *Calomys*, difíciles de diferenciar en el campo: *C. fecundus* (Yungas y su ecotono con el Chaco Seco, entre 600 y 2,700 msnm, en toda la región noroeste de Argentina), *C. callidus* (pastizales en el Chaco Húmedo y Mesopotamia), *C. callosus* (pastizales y pajonales en ambientes chaqueños, desde el este de Salta y Santiago del Estero hasta Formosa y Chaco) y *C. venustus* (pastizales y campos cultivados en Córdoba, San Luis, Santa Fe y Santiago del Estero).
- 64a. **Orejas generalmente <16 mm**.....65
65. Tamaño pequeño (CC = 73-79; C = 40-45; P = 14-20; O = 16-17); pelaje denso, suave, largo y sedoso; coloración dorsal marrón grisácea, más oscura hacia la línea media y con **aspecto marmolado; vientre blanco**; orejas cubiertas por pelitos marrón claro, con parches postauriculares notorios; **cola blanquecina y muy corta**, apenas amarillenta por encima; plantas desnudas, excepto el talón y su mitad proximal; 4 o 5 pares de mamas. (**pastizales de altura de Yungas, Puna y Altos Andes, por encima de los 2,800 msnm, en Jujuy, Salta, Catamarca, y Tucumán**) .....*Calomys lepidus* (Figura 5E)
- 65a. Sin aspecto marmolado y con la cola proporcionalmente más larga.....66
66. Tamaño pequeño (CC = 69-108; C = 77-91; P = 17-22; O = 13-17); coloración dorsal marrón amarillenta a grisácea, más pálida hacia los flancos, con una línea lateral ocrácea en algunas poblaciones; **vientre blanco grisáceo, que contrasta con el dorso, pero sin formar una línea de separación definida**; en algunos ejemplares los pelos de la garganta son completamente blancos; orejas medianas, marrón amarillentas; cola corta, **~50% de la longitud conjunta de la cabeza más el cuerpo**; 5 o 6 pares de mamas (pastizales, campos cultivados, roquedales y estepas arbustivas desde Jujuy hasta Santa Cruz, desde el nivel del mar hasta 3,900 msnm).....*Calomys musculinus* (Figura 5D)
- Nota 16: esta especie se diferencia de *C. laucha*, con la cual convive en un extenso sector del centro y norte de Argentina, por su pelaje más ralo, coloración más clara y menos contrastada entre el dorso y vientre y orejas y cola más largas (Figura 17); *C. lepidus* es más pequeña, con los parches postauriculares menos definidos y tiene



la cara interna de las orejas cubierta por pelitos amarillentos (grisáceos en *C. musculus*).

- 66a. Tamaño pequeño; **coloración dorsal y ventral bien contrastada**; cola ~44% de la longitud conjunta de la cabeza más el cuerpo.....67
67. Tamaño pequeño (CC = 57-76; C = 42-54; P = 13-15; O = 12-14); **coloración dorsal gris ocrácea a gris pardusca**, más oscura hacia la línea media; **vientre blanco, bien separado del dorso**; garganta y mentón cubiertos a veces por pelos completamente blancos; con **parches postauriculares blancos conspicuos**; a veces con un mechón de pelos ocre preauriculares; 4 a 5 pares de mamas (pastizales y campos cultivados en el **norte y centro de Argentina, normalmente por debajo de los 1,000 msnm**).....*Calomys laucha* (Figura 5C)
- 67a. Tamaño pequeño (CC = 74-88; C = 38-77; P = 13-15; O = 12-14); **coloración dorsal amarillenta a marrón oscura, a veces lavada de rojizo o castaño**; **vientre gris claro, bien separado del dorso**; en algunos especímenes el mentón es completamente blanco; anillo periorcular marcado o no; parches postauriculares pálidos (pastizales y campos cultivados en **Misiones**).....*Calomys tener*
68. Tamaño pequeño (CC = 81-111; C = 39-55; P = 14-21; O = 9-13); pelaje corto, dorsalmente **castaño oscuro a marrón oliváceo oscuro (a veces con cierto brillo metálico)**, más claro hacia el vientre; **coloración dorsal y ventral poco diferenciadas**; **ojos reducidos**; **orejas pequeñas y redondeadas**; **manos y patas cubiertas por pelitos castaño oscuro**; garras de las manos largas y finas; **cola menor que el 50% de la longitud conjunta de la cabeza más cuerpo**, oscura, poco pilosa y con el escamado dérmico visible; 4 pares de mamas (selvas en Misiones).....*Thaptomys nigrita* (Figuras 12D, 14)
- Nota 17: *Thaptomys* se diferencia de las especies selváticas de *Akodon* (i. e., *A. montensis*, *A. paranaensis*) por su

coloración más oscura, ojos y orejas más pequeños y su cola proporcionalmente más corta.

- 68a. Cola mayor que el 50% de la longitud cabeza-cuerpo ..... 69
69. Tamaño pequeño (CC = 89-108; C = 74-87; P = 20-22; O = 12-14); pelaje espeso, fino y suave, con **aspecto aterciopelado**; **coloración dorsal marrón oscura**, con tintes oliváceos a ocre en la cabeza y flancos; **vientre gris oscuro**; patas cubiertas por pelitos gris oscuro; cola marrón oscura, apenas más clara por debajo y cubierta por pelitos finos que no esconden el escamado epidérmico; **ojos pequeños**; **orejas cortas y ovaladas**, cubiertas por pelitos oscuros y moderadamente escondidas en el pelaje de la cabeza; algunos ejemplares presentan una mancha blanca en el mentón (pajonales en terrenos anegadizos, pastizales periselváticos y bosques ribereños en el **noreste de Buenos Aires y sur de Entre Ríos**) ...  
..... *Deltamys kempi* (Figura 12B)
- Nota 18: *D. kempi* se puede confundir con *A. azarae*, con la cual convive en el noreste de Buenos Aires y sur de entre Ríos, y del que se diferencia por su cuerpo más redondeado y grácil, la cola proporcionalmente más larga y sus orejas más ovaladas y oscuras (Figura 18).
- 69a. Sin aspecto aterciopelado, con las orejas más redondeadas.....70
70. Tamaño pequeño a mediano; textura robusta; anillo periorcular más o menos evidente según la especie; cabeza ancha y hocico corto; orejas cortas y redondeadas; cola proporcionalmente corta, bicolor y moderadamente peluda, aunque con el escamado dérmico notorio; patas robustas cubiertas por pelitos grises o marrones; **la garra del dedo V de la pata trasera se extiende hasta 1/2 a 1/3 de la falange proximal del dedo IV** (Figura 20B); pelos ungueales claros, cubriendo parcialmente las garras; garras de manos y patas largas y

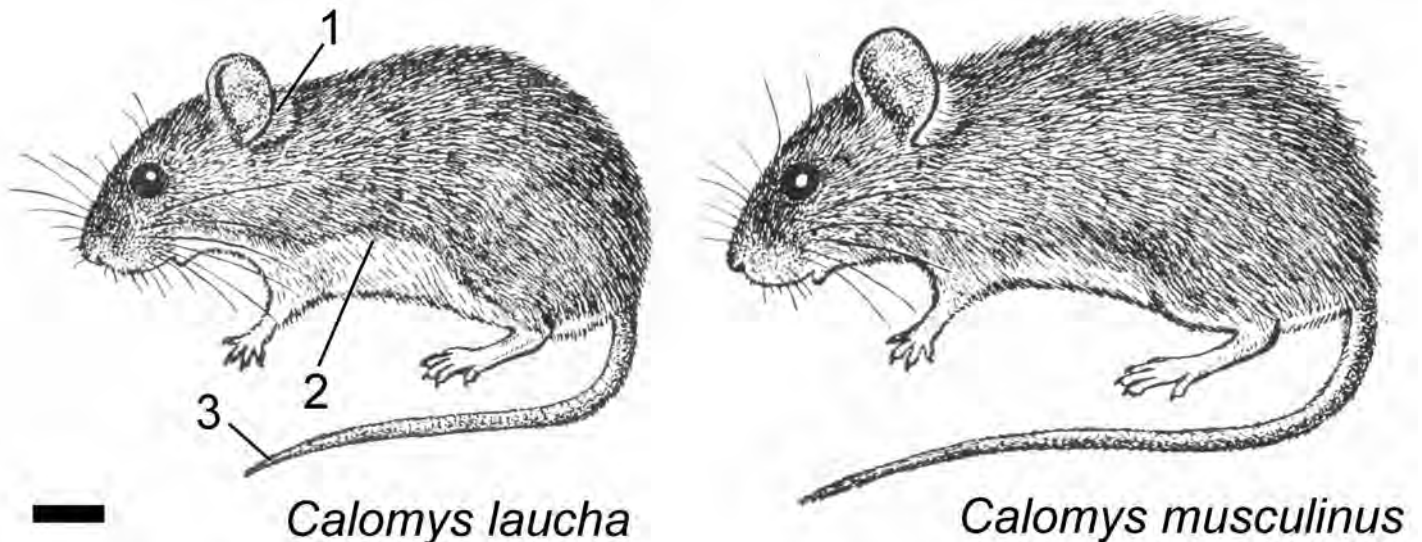


Figura 17. Caracteres distintivos entre *Calomys laucha* y *Calomys musculus* (redibujado de Massoia et al. 1968); la primera se diferencia de la segunda por sus orejas más pequeñas, con parches postauriculares mejor definidos (1), la separación bien definida entre las coloraciones dorsal y ventral (2) y la cola proporcionalmente más corta (3). La escala es igual a 10 mm.

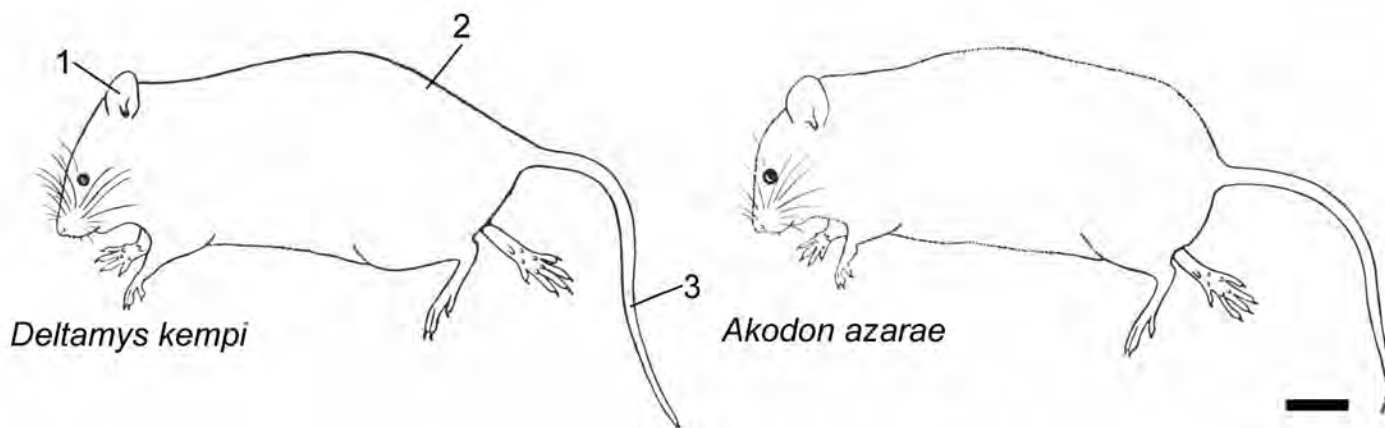


Figura 18. Caracteres distintivos entre *Deltamys kempii* y *Akodon azarae* (redibujado de Massoia 1964); el primero se diferencia del segundo por sus orejas más ovaladas (1), su cuerpo más grácil (2) y su cola proporcionalmente más larga (3). La escala es igual a 10 mm.

- curvadas, con la garra del dedo III de la mano mayor que el 50% del largo del mismo dedo y con una quilla corta en la base.....*Necromys* (Figura 19A-F) 71
- 70a. La garra del dedo V de la pata trasera se extiende por delante de la primera articulación interfalangeana del dedo IV (Figura 20A).....75
71. Tamaño pequeño (CC = 95-103; C = 63-79; P = 20-23; O = 12-14); **coloración dorsal marrón amarillenta**, teñida de ocre hacia los flancos y definiendo una línea que a veces puede estar bien marcada; **vientre blancuzco, bien contrastado con el color del dorso**; mentón y garganta a veces completamente blancos; **anillo periorcular amarillento bien marcado**; **manos y patas cubiertas por pelitos ocre (áreas andinas de altura, por encima de los 3,500 msnm en la provincia de Salta y probablemente de Jujuy)**.....*Necromys amoenus* (Figura 19C)
- 71a. Coloración no como en la opción anterior.....72
72. Tamaño mediano (CC = 98-124; C = 63-89; P = 23-29; O = 11-17); **coloración dorsal marrón oscura**, con efecto agutí más evidente hacia los flancos; **vientre acanelado**; mancha blanca en barbilla y/o garganta; con un anillo periorcular amarillento bien marcado en algunos especímenes (mayormente restringido a **pastizales de altura por encima de las Yungas**, entre 1,500 y 3,000 msnm)....  
..... *Necromys lactens* (Figura 19A)
- 72a. Coloración no como en la opción anterior .....73
73. Tamaño mediano (CC = 101-120; C = 53-71; P = 21-23; O = 15-16); **coloración dorsal castaño oscura brillante a negruzca, con los flancos y mejillas teñidos de ocre o naranja**; **vientre grisáceo, lavado de amarillo o anaranjado**; a veces con una mancha blanca en la barbilla (pastizales y áreas serranas en el **sudeste de Buenos Aires**)...  
..... *Necromys obscurus* (Figura 19B)
- 73a. Coloración no como en la opción anterior.....74
74. Tamaño mediano (CC = 105-128; C = 66-96; P = 20-26; O = 13-18); **coloración dorsal marrón olivácea**, con **efecto agutí marcado**, variablemente lavada de amarillento y más pálida hacia los flancos; **vientre grisáceo a blanquecino a gris lavado de ocre**; con anillo periorcular amarillento y poco marcado (pastizales, pajonales, estepas herbáceas y arbustivas y bordes de campos cultivados; desde el norte de Argentina hasta Buenos Aires y La Pampa).....*Necromys lasiurus* (Figura 19E-F)
- 74a. Tamaño mediano (CC = 98-113; C = 70-77; P = 24-26; O = 15-17); **coloración dorsal marrón amarillenta, con efecto agutí marcado**; vientre gris, lavado de amarillento y poco diferenciado del dorso; una mancha blanca en el mentón; con anillo periorcular poco marcado; manos y patas cubiertos por pelitos gris claro (**pastizales del Chaco serrano en Tucumán**) .....  
.....*Necromys lilloi* (Figura 19D)
75. Tamaño pequeño o mediano; **vibrisa genal 1 ausente**; pelaje largo y suave; **coloración dorsal variable**, desde muy oscura a marrón grisáceo pálida, **usualmente bien diferenciada del vientre**, que es más claro; a veces con marcas brillantes rojizas o anaranjadas en hocico, patas y cola; hocico alargado, más perceptible en unas especies (*hirta*, *lanosa*, *manni*) que en otras (*andina*, *illutea*, *jelski*, *olivacea*); orejas medianas, con o sin parches postauriculares conspicuos; vibrisas abundantes, garras de la mano cortas a moderadamente desarrolladas y sin quilla ventral; dedos de las patas traseras con pelos ungueales largos, que sobrepasan el extremo anterior de las uñas; cola moderadamente peluda y bicolor, con el escamado epidérmico visible o no; 3 o 4 pares de mamas.....*Abrothrix* (Figura 13B-F) 76
- 75a. Tamaño pequeño o mediano; **vibrisa genal 1 presente**; **coloración dorsal y ventral usualmente poco contrastadas (con excepciones, como es el caso de *Akodon albiventer*)**, generalmente en tonos grises y marrones; vibrisas cortas e inconspicuas; manos y patas provistos de garras usualmente cortas; cola moderadamente peluda y bicolor, con el escamado epidérmico visible o no; 4 pares de mamas .....82
76. Tamaño pequeño (CC = 97-102; C = 74-79; P = 24-25; O = 18); **coloración muy contrastada**; **mitad dorsal**



**Figura 19.** Aspecto externo de *Necromys lactens* (A), *Necromys obscurus* (B), *Necromys amoenus* (C), *Necromys lilloi* (D) y *Necromys lasiurus* (E y F). Las fotos no están en escala.

- marrón grisácea, netamente separada de la mitad ventral, que es blanca; hocico, orejas, periorcular y dorso de las patas y cola rojizo-anaranjado; dedos de la pata blancos; almohadillas palmares y plantares grandes y bulbosas; patas delanteras con garras moderadamente desarrolladas (pastizales y roquedales altoandinos, por encima de 3,400 msnm en Jujuy y Salta) .....  
.....*Abrothrix jelskii* (Figura 13B)**
- 76a. Coloración no como en la opción anterior ..... 77
77. Tamaño pequeño (CC = 110; C = 72; P = 24; O = 15); coloración general **marrón muy oscuro, casi negro, apenas más claro en el vientre**; algunos ejemplares presentan una faja de pelos más rojizos sobre la línea media del dorso (un solo registro en Argentina, en un área boscosa del centro-oeste de Neuquén) .....*Abrothrix manni*
- 77a. Coloración no como en la opción anterior ..... 78
78. Tamaño mediano (CC = 110-130; C = 80-91; P = 26-30; O = 19-22); pelaje dorsal suave, lanoso y denso; **coloración general marrón grisáceo oscuro**, levemente más clara hacia el vientre; **a veces con una mancha blanca en el mentón; la mayoría de los ejemplares presentan el extremo del hocico de color levemente ocráceo**; área interna de la oreja cubierta por pelos finos (Bosque Montano y Selva Montana del extremo sur de Yungas entre 700 y 3,000 msnm en el sur de Salta, Catamarca y Tucumán) .....*Abrothrix illutea* (Figura 13D)
- 78a. Coloración, distribución y hábitat no como en la opción anterior .....79
79. Tamaño mediano (CC = 100-120; C = 60-84; P = 22-25; O = 15-18); **coloración dorsal marrón grisácea a gris, con una faja de pelos castaño-rojizos hacia la línea media;**

vientre blanquecino a gris; **hocico alargado**, manos y patas cubiertos por pelitos blancos a grises (bosques, matorrales y estepas arbustivas y herbáceas desde el sudoeste de Mendoza hasta Tierra del Fuego) .....  
.....*Abrothrix hirta* (Figura 13C)

- 79a. Coloración no como en la opción anterior, **sin faja dorsal castaño rojiza** .....80
80. Tamaño pequeño (CC = 79-111; C = 51-70; P = 20-23; O = 11-13); **coloración dorsal olivácea oscura; vientre grisáceo**; orejas pequeñas y redondeadas, cubiertas por pelitos ocre; manos y pies cubiertos por pelitos blancos (bosques, matorrales y turberas en Santa Cruz y Tierra del Fuego) .....*Abrothrix lanosa*
- Nota 19: *A. lanosa* se diferencia de *A. olivacea*, con la que convive en el sur de Argentina, por sus orejas más cortas, su coloración dorsal con efecto agutí más marcado, contraste menos notorio entre las tonalidades del dorso y vientre y patas cubiertas por pelitos blancos.
- 80a. Coloración no como en la opción anterior .....81
81. Tamaño pequeño (CC = 92-98; C = 52-65; P = 20-22; O = 13-15); **coloración general marrón olivácea, a veces lavada de marrón rojizo en el dorso** (sobre todo la zona de las ancas) y de gris en los flancos; vientre blanco grisáceo; **parches postauriculares blancos**; cola marrón en el dorso y blancuzca por debajo (**pastizales y arbustales altoandinos (>2,500 msnm), desde Jujuy hasta el centro de Mendoza**) .....*Abrothrix andina*
- 81a. Tamaño pequeño (CC = 70-100; C = 45-80; P = 18-22; O = 10-17); **coloración dorsal variable, entre gris-oliváceo a marrón oliváceo oscuro**; en los ejemplares de áreas forestadas el vientre es de color gris oscuro; **en áreas de estepa, los individuos presentan el hocico, el dorso y laterales de la cola y la superficie dorsal de las patas cubiertos por pelitos anaranjados** (bosques, matorrales y estepas arbustivas y herbáceas desde el sudoeste de Mendoza hasta Tierra del Fuego) .....  
.....*Abrothrix olivacea*-*A. xanthorhina* (Figura 13E-F)
- Nota 20: la distinción entre *A. olivacea*, de distribución continental, y *A. xanthorhina*, restringida a Tierra del Fuego e islas adyacentes, sustentada fundamentalmente en diferencias en el ADN mitocondrial, requiere ser evaluada con el estudio de otros caracteres y el análisis de más especímenes.
82. Tamaño pequeño (CC = 85-105; C = 70-85; P = 23-25; O = 17-18); pelaje largo y suave; dorsalmente **marrón, lavado de anaranjado, más pálido hacia los flancos y poco diferenciado del vientre**, que es gris lavado de ocre; **área anal y mejillas anaranjadas**; orejas medianas, marrón oscuras; manos y patas cubiertas por pelitos marrón oscuro; **cola casi desnuda, bicolorada y con escamado epidérmico notable** (selvas en Misiones) .....  
.....*Castoria angustidens* (Figura 12A)
- Nota 21: *Castoria* es externamente muy similar a *A. montensis* y *A. paranensis*, de las que se distingue por sus garras delanteras más cortas y por su coloración general

más oscura, lavada de anaranjado, especialmente en las mejillas y alrededor del ano.

82a. Coloración no como en la opción anterior, **sin manchas anaranjadas en el área anal o mejillas** .....  
 .....*Akodon* 83 (Figuras 13A, 20 y 21)

83. Tamaño pequeño (CC = 93-109; C = 62-77; P = 20-23; O = 12-14); pelaje corto y lanoso; dorsalmente **marrón grisáceo, con efecto agutí fino; vientre blanco a blanco grisáceo, bien contrastado con el dorso; anillo periocular blanquecino; orejas pequeñas, con parches postauriculares blancos indistintos; manos y patas dorsalmente cubiertos por pelitos blancos; cola peluda y bicolor (pastizales y matorrales altoandinos y de la Puna, por encima de los 2300 msnm, en Jujuy y Salta)** .....  
 .....*Akodon albiventer* (Figura 13A)

83a. Coloración no contrastada como en la opción anterior .....84

84. Tamaño pequeño (CC = 90-114; C = 60-76; P = 21-25; O = 14-16); pelaje denso y suave; **coloración dorsal marrón claro, lavada de oliváceo; vientre teñido de ocráceo, moderadamente contrastado con el color del dorso; mentón con un mechón de pelos blancos; cola bicolor (pastizales serranos en Córdoba y San Luis por encima de 1,500 msnm)** .....*Akodon polopi* (Figura 20F)

84a. Distribución no como en la opción anterior (excepto por *A. dolores*, de la que se diferencia por su menor tamaño) ..... 85

85. Tamaño pequeño (CC = 75-114; C = 68-90; P = 21-25; O = 14-17); **dorso marrón oscuro a marrón oliváceo, lavado de amarillento hacia los flancos y mejillas, con efecto agutí poco evidente; vientre gris a gris pardusco, a veces lavado de amarillento; orejas marrones; cola bicolor, con anillos poco marcados; patas dorsalmente cubiertas por pelitos castaños y grisáceos (pastizales, pajonales, bordes de campos cultivados y estepas arbustivas; también en baldíos, basurales, bordes de arroyos y terraplenes de ferrocarril en áreas urbanas y suburbanas, desde Formosa y Corrientes hasta La Pampa y Buenos Aires)** .....*Akodon azarae* (Figura 20G)

[Nota 22: *A. azarae* es simpátrica con *A. dolores* y *A. toba*, de las que se diferencia por su menor tamaño; se distingue de *A. iniscatus* por su cola y patas proporcionalmente más largas y su coloración menos grisácea].

85a. Coloración, medidas y/o distribución no como en la opción anterior .....86

86. Mayormente en ambientes áridos a semiáridos del Chaco Seco, Monte y Patagonia .....87

86a. Distribución no como en la opción anterior .....89

87. Tamaño pequeño (CC = 80-110; C = 50-80; P = 17-23; O = 11-14); **coloración dorsal marrón oliváceo uniforme, con efecto agutí fino; vientre gris y moderadamente demarcado del dorso; un mechón de pelos blancos en el mentón; cola bien cubierta de pelos y bicolor (pastizales, estepas arbustivas y herbáceas del Monte**

**y Patagonia, desde La Pampa y sudoeste de Buenos Aires hasta Santa Cruz)** .....*Akodon iniscatus*

Nota 23: *A. iniscatus* es ampliamente simpátrido con *A. dolores* en el centro-sur de Argentina, del que se diferencia por su tamaño más pequeño y orejas más cortas.

87a. Tamaño mediano, **orejas >16 mm** .....88

88. Tamaño mediano (CC = 100-120; C = 78-89; P = 22-24; O = 16-19); **pelaje largo y denso; coloración dorsal marrón olivácea pálida a gris olivácea, lavado de amarillo; vientre blanco grisáceo, moderadamente contrastado con el dorso, pero sin línea de separación definida; anillo periocular pálido; orejas marrones; manos y patas cubiertos por pelitos blanco grisáceos; cola bicolor y bien cubierta de pelos (pastizales, pajonales, estepas arbustivas y bosques xerófilos en el Espinal, Chaco Seco (en el NOA) y Monte, desde Tucumán y Santiago del Estero, por el oeste, hasta el sur de Buenos Aires y noroeste de Chubut)** ..... *Akodon dolores* (Figura 21B)

Nota 24: *A. dolores* es simpátrida con *A. azarae* y *A. iniscatus* en una zona amplia del centro y centro-sur de Argentina, de las que se diferencia por su mayor tamaño; evidencias cariotípicas, moleculares y morfológicas sugieren su conespecificidad con *A. toba*.

88a. **Tamaño mediano (CC = 91-126; C = 67-87; P = 24-27; O = 16-20); coloración dorsal marrón olivácea, lavada de gris, con efecto agutí fino; vientre gris, escarchado de blanco, moderadamente contrastado con el dorso; anillo periocular poco marcado; en algunos especímenes hay una mancha blanca poco conspicua en el mentón; manos y patas cubiertos por pelitos blanco grisáceos;**



Figura 20. Vistas plantares de las patas traseras de *Akodon azarae* (A) y *Necromys lasiurus* (B) (compárese la longitud del dedo V con respecto al IV) y aspecto externo de *Akodon fumeus* (C), *Akodon spegazzini* (D), *Akodon boliviensis* (E), *Akodon polopi* (F) y *Akodon azarae* (G). Las fotos no están en escala.

- cola bicolor y bien cubierta de pelos (**pastizales, pajonales y matorrales en el Chaco Seco**, desde Salta y Formosa hasta Santiago del Estero) .....  
 .....*Akodon toba* (Figura 21A)
- Nota 25: *A. toba* se diferencia de *A. simulator* por su pelaje con efecto agutí más fino y por la ausencia de tonalidades dorsales castaño amarillentas a rojizas (especialmente hacia las ancas) y de *A. azarae* por su mayor tamaño; *A. montensis* posee el vientre con tonos castaños o grisáceo amarillentos.
89. Nordeste de Argentina (Corrientes, Misiones, este de Chaco y Formosa) .....90
- 89a. Noroeste y oeste de Argentina (desde Jujuy y Salta, por el oeste, hasta Mendoza) .....91
90. **Tamaño pequeño** (CC = 70-109; C = 47-69; P = 17-19; O = 11-12); coloración dorsal marrón grisácea oscura, con efecto agutí fino; vientre gris, poco diferenciado del dorso; manos y patas cubiertos por pelitos blancos; cola cubierta por pelitos marrones, pero con escamado epidérmico igualmente visible (**pastizales en el sur de Misiones**)..... *Akodon philipmyersi*
- 90a. **Tamaño mediano** (CC = 88-125; C = 60-98; P = 22-25; O = 15-19); **coloración dorsal marrón olivácea**, poco contrastada con el **vientre**, que es de **color castaño o gris amarillento**; manos y patas cubiertos por pelos marrón grisáceos; pelos ungueales blancos y largos, que se extienden por delante de las uñas; cola bicolor, con el escamado dérmico claramente visible (*A. montensis* ocupa **selvas y bosques en galería** en Misiones, norte de Corrientes y este de Chaco y Formosa, mientras que *A. paranaensis* tiene un solo registro para un área forestada en el centro-norte de Misiones) .....  
 .....*Akodon montensis-A. paranaensis* (Figura 21D)
- Nota 26: *A. montensis* y *A. paranaensis* se diferencian mayormente por rasgos cariotípicos y morfométricos; *A. montensis* se diferencia de *A. toba*, con la que coexiste en el este de Chaco y Formosa, por su coloración ventral castaño o gris amarillenta (blanco grisáceo en *A. toba*).
91. Tamaño pequeño a mediano (CC = 83-114; C = 65-89; P = 21-27; O = 14-21); **coloración dorsal marrón olivácea**, finamente salpicada de negro y generalmente **poco contrastada con el vientre**; orejas del mismo color que el dorso; anillo periocular ausente o poco definido; mancha blanca en el mentón poco definida; cola apenas bicoloreada (**yungas y pastizales de altura en el sudeste de Jujuy (Sierra de Santa Bárbara y áreas adyacentes), entre 700 y 2,500 msnm**) .....*Akodon sylvanus*
- 91a. Coloración y medidas distintos de la opción anterior ....  
 .....92
92. Longitud CC generalmente >100 mm .....93
- 92a. Longitud CC generalmente <100 mm .....94
- Nota 27: la separación entre un grupo de especies con longitudes de CC mayores o menores de 100 mm es orientativa; frente a esta disyuntiva, lo más conveniente es que el usuario de la clave evalúe alternativamente las distintas opciones. Muchas de las especies de *Akodon* en el NOA son difíciles de distinguir externamente entre sí, requiriendo de otras evidencias (cráneos, secuencias de ADN), para una identificación precisa.
93. Tamaño mediano (CC = 93-126; C = 52-99; P = 22-29; O = 12-22); dorso marrón oliváceo, finamente salpicado con pelos negros; vientre levemente más pálido, con una **mancha de pelos blancos en el mentón y a veces la garganta**; cola bicolor (pisos superiores de las Yungas **en Jujuy y Salta, entre 1,000 y 3,000 msnm**) .....  
 .....*Akodon budini*
- 93a. Tamaño mediano (CC = 92-135; C = 59-105; P = 20-29; O = 15-22); **coloración dorsal marrón grisácea, lavada de amarillo o rojizo (especialmente en la grupa), más o menos oscura o pálida según los individuos o las poblaciones**; flancos y vientre gris blanquecinos, a veces lavados de ocre, bien delimitados del color del dorso; anillo periocular amarillento evidente; mancha blanca en el mentón y garganta de desarrollo variable, pero siempre presente; cola bicolor; patas y manos cubiertas por pelitos blanquecinos (**ambientes forestados en las Yungas y en el ecotono con pastizales de altura y con ambientes chaqueños**, desde Jujuy hasta La Rioja y Santiago del Estero) ..... *Akodon simulator* (Figura 21C)
- Nota 28: *A. simulator* se diferencia de *A. toba* por su pelaje con efecto agutí más marcado y la grupa más rojiza.
94. Tamaño pequeño a mediano (CC = 63-117; C = 70-90; P = 20-26; O = 12-19); **pelaje dorsal marrón oliváceo oscuro, a veces con tonos rojizos, más pálido hacia el vientre**; anillo periocular pálido; cola escasamente peluda y bicolor; **patas cubiertas por pelitos bicoloreados, blancos y marrones** (bosques de Yungas **en Salta y Jujuy**) .....*Akodon fumeus* (Figura 20C)
- 94a. Coloración no como en la opción anterior; **patas cubiertas por pelitos completamente blanquecinos** ....  
 .....95
95. Tamaño pequeño (CC = 85-101; C = 48-87; P = 20-25; O = 11-16); coloración dorsal marrón rojiza (estepas arbus-tivas y pastizales en **San Juan y Mendoza**) .....  
 .....*Akodon oenos*
- 95a. Desde La Rioja hacia el norte ..... 96
96. Tamaño pequeño (CC = 86-103; C = 57-83; P = 18-23; O = 13-15); **dorso y flancos marrón oliváceos; vientre más pálido, lavado de ocre; área inguinal más oscura, a veces rojiza; anillo periocular amarillento**; cola bicolor y bien cubierta de pelos (**pastizales de altura de Yungas, Altoandinos y de la Puna por encima de los 2500 msnm en Jujuy y Salta**) ... *Akodon boliviensis* (Figura 20E)
- 96a. Coloración no como en la opción anterior .....97
97. Tamaño pequeño (CC = 78-94; C = 46-75; P = 20-26; O = 12-15); **coloración dorsal variable**, que oscila entre

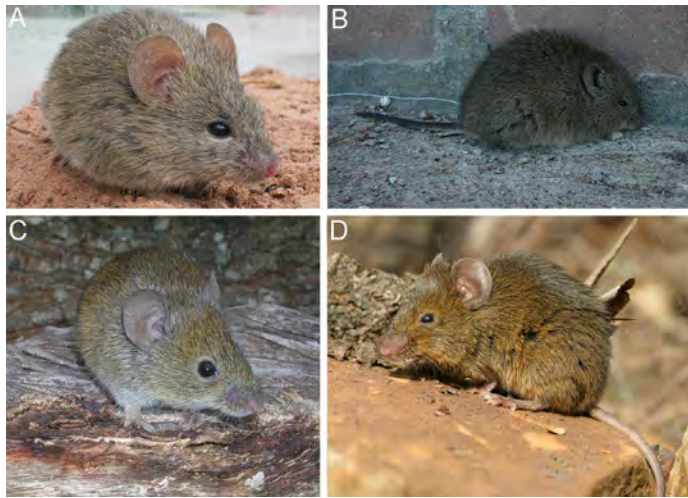


Figura 21. Aspecto externo de *Akodon toba* (A), *Akodon dolores* (B), *Akodon simulador* (C) y *Akodon montensis* (D). Las fotos no están en escala.

el marrón amarillento, marrón rojizo o marrón oliváceo; vientre gris blanquecino, gris amarillento o canela, bien contrastado con el dorso; a veces con unos pocos pelos blancos en el mentón, pero sin formar un parche conspicuo; cola fuertemente bicolor (yungas y pastizales de altura, entre 400 y 3,500 msnm, en Jujuy, Salta, Tucumán y Catamarca) .....  
*Akodon caenosus*

97a. Tamaño pequeño a mediano (CC = 68-120; C = 45-84; P = 17-25; O = 10-21); coloración similar a *A. caenosus*, de la que se diferencia por su tamaño algo mayor. (Yungas y pastizales de altura, entre 400 y 3,500 msnm, desde el centro de Salta hasta La Rioja) .....  
.....*Akodon spegazzini* (Figura 20D)

Clave C. Familia Muridae

1. Tamaño pequeño (CC = 74-98; C = 69-89; P = 16-24; O = 11-19); longitud CC < 100 mm pelaje muy corto, suave y lustroso; dorsalmente variable, entre gris claro y marrón, más pálido hacia el vientre; cola de longitud mayor que la longitud conjunta de la cabeza más el cuerpo; orejas grandes, casi desnudas y membranosas; patas estrechas; 5 pares de mamas. En todo el país, mayormente peridoméstica, pero también en áreas naturales .....*Mus musculus* (Figura 22B)

1a. Tamaño grande; longitud CC > 150 mm ..... *Rattus 2*

2. Tamaño grande (CC = 150-270; C = 105-240; P = 30-44; O = 14-22); cuerpo robusto y hocico obtuso; pelaje hispido, dorsalmente marrón amarillento o grisáceo, con el vientre marrón grisáceo claro o gris; cola con anillos marcados, apenas más corta que la longitud conjunta de la cabeza más el cuerpo; orejas pequeñas y redondeadas, casi desnudas, que dobladas hacia adelante no alcanzan el borde posterior del ojo; ojos pequeños; 6 pares de mamas. En todo el país, mayormente peridoméstica, pero también en áreas naturales .....*Rattus norvegicus* (Figura 22C)

2a. Tamaño grande (CC = 157-184; C = 163-229; P = 31-38; O = 20-26); cuerpo alargado y hocico proporcionalmente aguzado; se reconocen tres variantes de coloración: a) dorsalmente gris plumizo oscuro, con el vientre gris claro; b) dorso marrón amarillento, más claro hacia el vientre; c) dorso gris perla, con el vientre blanco puro; cola con anillos marcados, apenas más larga que la longitud conjunta de la cabeza más el cuerpo; orejas grandes, ovaladas y casi desnudas, que dobladas hacia delante alcanzan el borde posterior del ojo; ojos grandes; 5 a 6 pares de mamas. En todo el país, mayormente peridoméstica, pero también en áreas naturales .....*Rattus rattus* (Figura 22D)

Discusión

Las claves para la identificación de especies son una herramienta útil para la investigación biológica en general. En muchas ocasiones, constituyen el punto de partida para el entrenamiento de investigadores que desean conocer la diversidad de los grupos taxonómicos que constituyen el foco de su interés. En otras instancias, las claves son un insumo imprescindible para llevar a cabo estudios en terreno, incluyendo inventarios y monitoreos de biodiversidad (Bonvicino et al. 2008; Godínez y Guerrero 2014). En algunos casos, como en el de los roedores muroideos, la necesidad de contar con claves de identificación tiene un sentido particularmente destacado. Este grupo normalmente constituye la mayor fracción de la diversidad de los ensamblajes locales de mamíferos, lo cual impone un reto a la hora de individualizar sus especies. Pero más importante aún, esta diversidad tiene un correlato directo con múltiples funciones ecosistémicas, e impactos económicos (muchas especies constituyen plagas de cultivos) y sanitarios (algunas son vectores de enfermedades zoonóticas potencialmente letales para el hombre), destacando la relevancia que tiene la identificación taxonómica precisa de sus

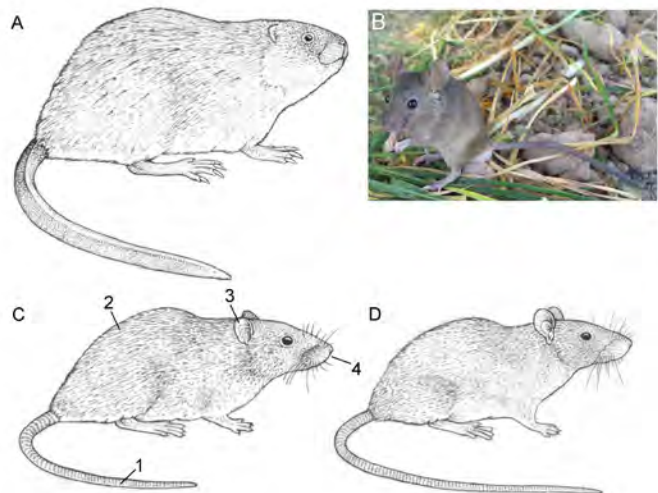


Figura 22. Aspecto externo de *Ondatra zibethicus* (A), *Mus musculus* (B), *Rattus norvegicus* (C) y *Rattus rattus* (D). En C y D se destacan los caracteres distintivos entre ambas especies de *Rattus*; en *R. norvegicus* la cola (1) es más corta que la longitud conjunta de la cabeza más el cuerpo (vs. más larga en *R. rattus*), el cuerpo (2) más compacto (vs. más estilizado), las orejas (3) más cortas (vs. más largas) y el hocico más corto (vs. más puntiagudo).

especies en las investigaciones ([Patton et al. 2015](#) y la literatura allí anotada).

La mayoría de las claves elaboradas para roedores incluyen caracteres de la morfología externa y cráneo-dentaria (e. g., [Massoia y Fornes 1967a, 1969](#); [Patton et al. 2015](#)). Sin embargo, muchos estudios deben realizarse en el campo en circunstancias de investigación o manejo en las cuales la colecta de ejemplares no es una opción viable y por lo tanto no se accede a material óseo. En este sentido, creemos que las claves basadas en caracteres externos constituyen un primer paso hacia la solución de este problema. La similitud en el plan morfológico general entre las especies de roedores muroideos constituyó un reto importante a la hora de elaborar las claves. A pesar de estas limitaciones, nuestra experiencia en el manejo de las claves y su puesta a prueba con personas no entrenadas en la determinación de roedores, indica que la identificación de la gran mayoría de los taxones tratados no presenta grandes inconvenientes.

Si bien existen algunos antecedentes generales ([Yepes 1935b](#); [Olrog y Lucero 1981](#)) y regionales (e. g., [Barquez et al. 1991](#); [Díaz y Barquez 2002](#); [Gómez Villafaña et al. 2005](#); [Chebez et al. 2014](#)) de contribuciones elaboradas para la identificación de roedores a partir de caracteres externos, ninguno de esos trabajos fue diseñado con el formato de una clave dicotómica y con el alcance taxonómico y geográfico que aquí se propone. Las claves elaboradas por [Massoia y Fornes \(1967a, 1969\)](#) son destacables por el especial cuidado que el autor puso en la descripción de los caracteres externos de los muroideos, correspondiéndole el crédito de haber diferenciado taxones externamente muy similares, cuyas diferencias habían pasado desapercibidas para otros investigadores (e. g., *Calomys*, véase [Hershkovitz 1962](#) y [Massoia et al. 1968](#)). Sin embargo, sus claves fueron pensadas con un alcance regional y elaboradas sobre un esquema taxonómico que con el tiempo ha quedado desactualizado.

Aunque creemos que las claves presentadas en este trabajo constituirán una ayuda para la identificación de la mayoría de las especies de muroideos de Argentina, las mismas no pretenden reemplazar a otras herramientas y aproximaciones que también son necesarias en el proceso de identificación. Antes bien, su objetivo es el de ser una guía con la cual disminuir el margen de error en las identificaciones, tarea de por sí poco sencilla y que debe complementarse con otras evidencias. Si bien muchos taxones poseen características lo suficientemente distintivas para una identificación certera, sea a nivel genérico (e. g., los tubérculos interdigitales fusionados en *Eligmodontia*, las patas traseras con membranas interdigitales en *Holochilus*, *Nectomys* o *Pseudoryzomys*) o específico (e. g., el pelaje espinoso de *Abrawayaomys ruschi*), muchos otros (e. g., las especies de *Akodon*, *Calomys*, *Oligoryzomys*) son ciertamente difíciles de identificar si no se tiene cierta experiencia de campo, un conocimiento básico sobre las distribuciones geográficas y preferencias de hábitat, o se cuenta con la ayuda de otras fuentes de evidencias (e. g., cráneos, cariotipos, secuencias de ADN). Aun así, ninguna identificación está exenta de

errores o de la posibilidad de ser corregida sobre la base de nuevas evidencias. Del mismo modo, siempre existe la posibilidad de encontrarse con ejemplares que se aparten de las características generales de su especie (e. g., individuos muy viejos o con alteraciones de color) o incluso de hallar especies nuevas para la ciencia o previamente no citadas para Argentina.

Para algunos taxones, los datos de distribución y ambientes que se ofrecen en las claves pueden facilitar la identificación. Por ejemplo, *Akodon spegazzini* y *A. oenos* son externamente muy similares, pero sus distribuciones aparentemente no se solapan ([Jayat et al. 2020](#)). Lo mismo sucede entre *A. boliviensis* y *A. spegazzini* ([Jayat et al. 2010](#)) o *Geoxus michaelsoni* y *G. valdivianus* ([Teta y D'Elía 2017](#)). El hábitat también puede ser orientativo, tal es el caso de algunas especies del género *Phyllotis* que están muy vinculadas a la presencia de afloramientos rocosos ([Pearson 1958](#)). Aun así, tanto la distribución como el hábitat deben ser cuidadosamente sopesados, pues nuestro conocimiento sobre estos aspectos es aún incompleto y no es infrecuente encontrar especies fuera de su área de distribución conocida o en ambientes novedosos (e. g., [Jayat et al. 2018](#)).

En última instancia, debe entenderse que toda determinación realizada mediante estas claves debe considerarse como tentativa, sujeta al estudio de otros conjuntos de caracteres y la revisión de la literatura. Mas en general, se sugiere estar siempre en contacto con especialistas y coleccionar, en todos los casos en los que sea posible, ejemplares de referencia para resolver los interrogantes que puedan plantearse durante el proceso de identificación. Por ejemplo, en los estudios ecológicos que requieran de la captura y recaptura de ejemplares, se deberían establecer algunas líneas de trampas por separado que permitan la colección de especímenes completos para su posterior estudio ([Pearson 1995](#)). En este sentido, debe quedar claro que la colección de ejemplares y su depósito en colecciones biológicas resulta una actividad irremplazable y el único camino para obtener determinaciones sólidas y repetibles en el tiempo ([Patterson 2002](#)).

*Nota final.* Por todo lo expresado previamente, resulta evidente que un trabajo como el que aquí se propone es factible de ser perfeccionado, ya sea a partir de nuevos estudios o por la experiencia de otros investigadores con la identificación de especies. Por este motivo, invitamos a todos aquellos que estén interesados a contactarse con los autores para señalar potenciales errores y/o sugerir modificaciones, en un esfuerzo por mejorar colectivamente la utilidad de esta clave como herramienta.

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# Coexistence of three mephitids in Tehuacán-Cuicatlán Biosphere Reserve, México

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Three species of mephitids coexist in the Tehuacán-Cuicatlán biosphere reserve (TCBR) and belong to a guild of mammalian carnivores that feed mainly on invertebrates. To infer the interspecific interactions that allow coexistence, we aimed to compare activity patterns and abundance of hog-nosed skunk (*Conepatus leuconotus*), hooded skunk (*Mephitis macroura*), and southern spotted skunk (*Spilogale angustifrons*) in a tropical dry forest with ecological integrity. We analyzed activity patterns and overlap, and compared the relative abundance index (IAR) of mephitids, between rainy and dry seasons and among species, and used 235 records for *C. leuconotus*, 39 for *M. macroura*, and 42 for *S. angustifrons* from 15 camera-trap stations in Mount Tepetroja, Puebla, from May 1<sup>st</sup>, 2013 to April 30<sup>th</sup>, 2020. The three mephitids were active mainly during the nocturnal period, although *C. leuconotus* showed a unimodal pattern with activity peak around midnight, *M. macroura* had a bimodal pattern with activity peaks during the crepuscular hours at sunset and sunrise, and *S. angustifrons* had a unimodal pattern with activity peak around 2:00 a.m. Mean activity of *C. leuconotus* ( $\mu \pm SE = 00:42 \pm 00:12$  h) and *M. macroura* (01:02  $\pm$  00:33 h) were similar ( $P = 0.32$ ), and differed from the mean activity of *S. angustifrons* (01:49  $\pm$  00:23 h,  $P = 0.02$ ). *C. leuconotus* had the highest IAR (2.53 to 7.90) and differed from *M. macroura* (0.44 to 1.21) and *S. angustifrons* (0.83 to 0.96) in both seasons ( $P < 0.01$ ). *C. leuconotus* and *M. macroura* showed higher IAR during the rainy season, in contrast with *S. angustifrons* that had no differences in IAR between seasons. The mephitids presented temporal segregation and variability in seasonal abundance as coexistence mechanisms. *S. angustifrons* showed the most restricted circadian activity and avoided the other two mephitids' activity peaks. *C. leuconotus* was the most abundant species; thus, we inferred that the hog-nosed skunk determined the dynamics of intraguild interactions among mephitids in the tropical dry forest in the TCBR.

Tres especies de mefitidos coexisten en la reserva de la biosfera Tehuacán-Cuicatlán (RBTC) y pertenecen a un gremio de mamíferos carnívoros que se alimentan principalmente de invertebrados. Para inferir sobre las interacciones interespecíficas que permiten la coexistencia, nuestros objetivos fueron comparar la actividad circadiana y la abundancia del zorrillo de espalda blanca (*Conepatus leuconotus*), zorrillo rayado sureño (*Mephitis macroura*) y zorrillo manchado del sur (*Spilogale angustifrons*) en selva baja caducifolia con integridad ecológica. Analizamos los patrones de actividad y su superposición, y comparamos el índice de abundancia relativa (IAR) de los mefitidos entre la temporada de lluvia y la temporada seca, y entre especies, a partir de 235 registros de *C. leuconotus*, 39 de *M. macroura* y 42 de *S. angustifrons* de 15 estaciones de fototrampeo en el Cerro Tepetroja, Puebla, del 1 de mayo de 2013 al 30 de abril de 2020. Los tres mefitidos presentaron actividad principalmente durante el periodo nocturno, aunque *C. leuconotus* mostró un patrón unimodal con el pico de actividad alrededor de la media noche, *M. macroura* presentó un patrón bimodal con picos de actividad durante las horas crepusculares del atardecer y amanecer, y *S. angustifrons* tuvo un patrón unimodal con el pico de actividad alrededor de las 2:00 a.m. La actividad promedio de *C. leuconotus* ( $\mu \pm SE = 00:42 \pm 00:12$  h) y *M. macroura* (01:02  $\pm$  00:33 h) fueron similares ( $P = 0.32$ ), y difirieron de la actividad promedio de *S. angustifrons* (01:49  $\pm$  00:23 h,  $P = 0.02$ ). *C. leuconotus* presentó los mayores IAR (2.53 a 7.90) y difirió de *M. macroura* (0.44 a 1.21) y de *S. angustifrons* (0.83 a 0.96) en las dos temporadas del año ( $P < 0.01$ ). *C. leuconotus* y *M. macroura* mostraron mayores IAR durante la temporada de lluvia, en contraste con *S. angustifrons* que no tuvo diferencias en los IAR entre temporadas. Los mefitidos presentaron segregación temporal y variaciones estacionales en la abundancia como mecanismos de coexistencia. *S. angustifrons* presentó la actividad circadiana más restringida y evitó los picos de actividad de los otros dos mefitidos. *C. leuconotus* fue el más abundante, por lo que inferimos que el zorrillo espalda blanca determinó la dinámica de las interacciones intragremiales entre mefitidos en la selva baja caducifolia de la RBTC.

**Keywords:** Abundance; circadian activity; interspecific interactions; Mephitidae; photo-capture; skunk ecology; temporal segregation; tropical dry forest.

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## Introducción

En el centro de México habitan tres especies de zorrillos o mofetas (Carnívora: Mephitidae) que explotan la misma clase de recursos, se alimentan principalmente de invertebrados adultos, sus larvas y de pequeños vertebrados (Root 1967; Cuarón et al. 2016; Helgen 2016; Helgen et al. 2016). Los tres mefitidos presentan pelaje con coloración aposemática en blanco y negro, y es posible reconocer a cada especie mediante características morfológicas, patrones de franjas, manchas en el pelaje y tamaño corporal

(Kinlaw 1995; Hwang y Larivière 2001; Dragoo y Sheffield 2009; Mills y Patterson 2009). El zorrillo de espalda blanca (*Conepatus leuconotus*) es el de mayor tamaño (1.1 a 4.5 kg); posee un cojinete largo y sin pelo cubriendo la nariz, una franja dorsal amplia de color blanco desde la cabeza hasta la punta de la cola, cola blanca y corta, con longitud generalmente menor a la mitad de la longitud corporal, la frente sin franja ni mancha blanca y garras largas para excavar (Reid 1997; Dragoo y Sheffield 2009; Helgen 2016).

El zorrillo rayado sureño (*Mephitis macroura*) presenta tamaño intermedio (0.6 a 2.7 kg). Se caracteriza por su delicada nariz, una delgada franja blanca vertical en la frente y una cola muy larga y esponjada en comparación con *C. leuconotus* (Reid 1997; Hwang y Larivière 2001; Cuarón et al. 2016). También presenta variabilidad en la coloración blanca dorsal, debido a que pueden tener una a dos franjas, delgadas o gruesas, pequeñas o grandes, y estar presente en los costados, dorso y cola (Hwang y Larivière 2001; Aranda-Sánchez 2012). El zorrillo manchado del sur (*Spilogale angustifrons*) es el segundo más pequeño en México (0.2 a 0.8 kg). Se caracteriza por poseer bandas y manchas blancas en todo el cuerpo y una mancha blanca en la frente (Aranda-Sánchez 2012; Helgen et al. 2016). Las tres especies de zorritos coexisten en la Reserva de la Biosfera Tehuacán-Cuicatlán (RBTC) reconocida por su valiosa biodiversidad, elevado número de endemismos y alta riqueza específica de mamíferos (Rzedowski 1978; Arriaga et al. 2000; Briones-Salas 2000; Dávila et al. 2002; Téllez-Valdés et al. 2010). La selva baja caducifolia es el tipo de vegetación con mayor extensión (38%), seguida del matorral xerófilo (25%; Dávila et al. 2002; SEMARNAT 2013). La integridad en la complejidad ecológica se mantiene en sitios con vegetación nativa en buen estado de conservación y complejidad estructural, lo que permite la abundancia y diversidad de las presas de los depredadores alfa nativos (i. e., *Puma concolor*) y la diversidad de mesodepredadores, como es el caso de los mefitidos (Estes et al. 2011; Berruecos-Pérez 2015; Cruz-Jácome et al. 2015; Farías et al. 2015; Farías-González y Vega-Flores 2019; Pérez-Irineo et al. 2020). La integridad ecológica permite la continuidad de las interacciones bióticas entre las diferentes especies dentro de la RBTC (Estes et al. 2011; Farías-González y Vega-Flores 2019; Pérez-Irineo et al. 2020).

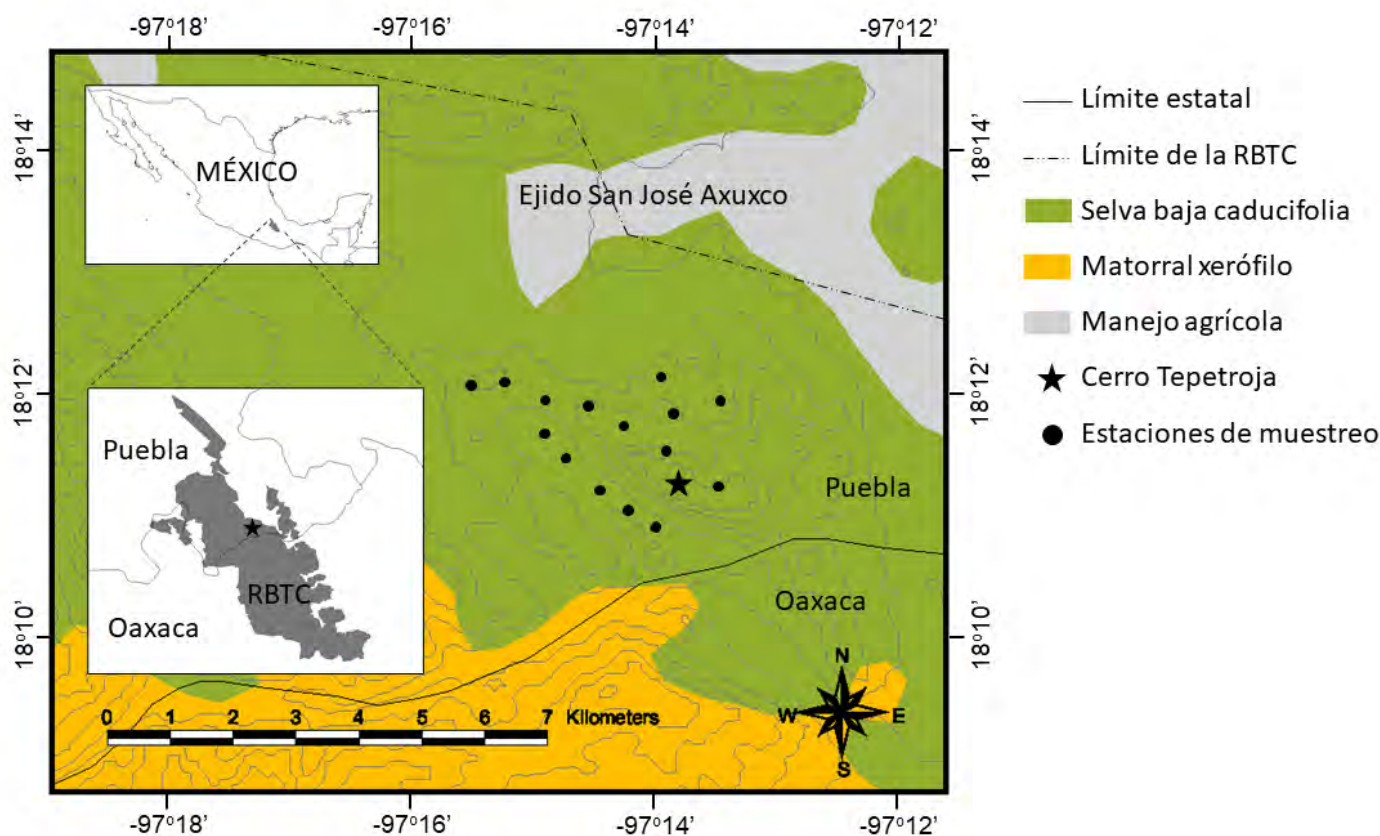
La coexistencia entre los mamíferos del orden Carnivora es posible principalmente por las diferencias en el tamaño corporal de las especies competidoras, debido a que la especie más grande es generalmente dominante (Simberloff y Dayan 1991; Holt y Polis 1997). Además, mediante la segregación en actividad circadiana, microhábitat y dieta, las especies subordinadas pueden prevenir o atenuar las desventajas de la competencia (Simberloff y Dayan 1991; Doty y Dowler 2006; Davies et al. 2007). Las especies de mayor tamaño tienen el potencial de determinar la dirección y fuerza de la dinámica intragremial y ser capaces de excluir a otros carnívoros o limitar su acceso a los recursos (Polis et al. 1989; Palomares y Caro 1999; Donadio y Buskirk 2006; Hunter y Caro 2008). Las interacciones intragremiales juegan un papel importante en la formación de comunidades ecológicas, incluso se ha sugerido que estas interacciones pueden haber sido factores determinantes en la adaptación evolutiva a estratos específicos del hábitat y también los patrones de actividad de las especies, ya que la segregación temporal es común entre mamíferos carnívoros como mecanismo de coexistencia (Van Valkenburgh 1985; Marti et al. 1993; Kronfeld-Schor y Dayan 2003). La forma en que un animal distribuye sus actividades dentro

del periodo circadiano es una dimensión importante del nicho ecológico. Estos patrones son una adaptación conductual a las variaciones diarias y estacionales de los factores ambientales, así como a la presencia de presas, competidores y depredadores (Aschoff 1966; Nielsene 1983; Gerber et al. 2012; Lesmeister et al. 2015; Karanth et al. 2017). Al reducir la superposición en los periodos de mayor actividad entre las especies de un gremio, la competencia y el riesgo de interacciones agonísticas pueden atenuarse (Schoener 1974; Carothers y Jaksic 1984; Polis et al. 1989). Los estudios previos sobre coexistencia de mefitidos permiten suponer que existe segregación en alguna dimensión del nicho ecológico. Por ejemplo, en México, *C. leuconotus* fue registrado con más frecuencia que *M. macroura* y *S. angustifrons* en selva baja caducifolia y matorral xerófilo en Oaxaca (Cortés-Marcial y Briones-Salas 2014; Cruz-Jácome et al. 2015; Pérez-Irineo et al. 2020). En contraparte, *M. macroura* presentó más registros que *C. leuconotus* en selva baja caducifolia deteriorada, pastizal inducido y cultivos para la Sierra de Nanchititla, Estado de México (Monroy-Vilchis et al. 2011). Mientras que, *S. gracilis* fue más activo durante los periodos de menor actividad de *M. mephitis* en Texas (Neiswenter et al. 2010).

Para inferir las interacciones intragremiales que permiten la coexistencia de los mefitidos en un ecosistema con integridad ecológica, los objetivos de este estudio fueron determinar los patrones de actividad y estimar la abundancia relativa de *C. leuconotus*, *M. macroura* y *S. angustifrons* en la selva baja caducifolia dentro de la RBTC. De acuerdo con el tamaño corporal, categorizamos a *C. leuconotus* como grande, a *M. macroura* como mediano y a *S. angustifrons* como pequeño. Se plantean dos hipótesis, partiendo del supuesto que los mefitidos presentan actividad principalmente durante el periodo nocturno. Nuestra primera hipótesis fue que, de existir una segregación temporal, la especie de menor tamaño tendrá menos actividad durante los periodos de más actividad de la especie de mayor tamaño. La segunda planteó que, si la abundancia de las poblaciones de los mefitidos está determinada por sus interacciones interespecíficas, entonces la especie de mayor tamaño presentará mayor abundancia relativa.

## Métodos

**Área de estudio.** El área de estudio se ubicó en el Ejido de San José Axuxco, Municipio de San José Miahuatlán, al sureste del estado de Puebla. Colinda con el estado de Oaxaca al sur. El fototrampeo se llevó a cabo en el Cerro Tepetroja con cima en las coordenadas geográficas 18.231167° N, - 97.207306° O, y una altitud entre 900 a 1,400 msnm (Figura 1). El Cerro Tepetroja se encuentra dentro de la RBTC y las autoridades civiles del Ejido controlan el acceso y realizan constantemente recorridos de vigilancia para prevenir la caza ilegal de fauna nativa y la extracción ilegal de flora nativa. El clima es semiárido con lluvias en verano de mayo a octubre, precipitación promedio anual de 300 mm y temperatura media anual



**Figura 1.** Localización geográfica de las 15 estaciones de muestreo en el Cerro Tepetroja, Ejido San José Axuxco, Puebla. El Cerro Tepetroja se encuentra dentro de la reserva de la biosfera Tehuacán-Cuicatlán (RBTC), México.

de 22 °C (Dávila et al. 2002). La vegetación en el Cerro Tepetroja es selva baja caducifolia con cactáceas columnares de los géneros *Cephalocereus*, *Myrtillocactus*, *Neobuxbaumia* y *Pachycereus* como principales dominantes fisonómicos y árboles de copas extendidas y arbustos principalmente de los géneros *Bursera*, *Castela*, *Ceiba*, *Ficus*, *Fouquieria*, *Parkinsonia* y *Ziziphus* (Rzedowski 1978; Valiente-Banuet et al. 2000).

**Fototrampeo.** Las unidades de muestreo fueron 15 estaciones con una cámara trampa digital (LTL Acorn 6210, Little Acorn Outdoors, Green Bay, Wisconsin, U. S. A.) separadas por una distancia lineal de 500 m a lo largo de la cima y de una cañada del Cerro Tepetroja (Figura 1). La distancia entre cámaras trampa fue determinada con base en el tamaño mínimo reportado para el ámbito hogareño y la densidad de las especies bajo estudio, ya que al menos una cámara trampa debe estar incluida dentro del ámbito hogareño de los individuos residentes que habitan en las inmediaciones de cada estación de fototrampeo (Karanth 1995; Gilbert et al. 2020). El promedio del ámbito hogareño registrado para *C. leuconotus* fue de  $1.94 \pm 0.62$  (SD) km<sup>2</sup> para 15 machos y  $0.64 \pm 0.24$  km<sup>2</sup> para 14 hembras en Texas, EE. UU. (Brashear et al. 2015) y se estimó la densidad en 0.6 a 1.3 indiv/km<sup>2</sup> en el istmo de Tehuantepec, México (Cervantes et al. 2002). El ámbito hogareño de *M. macroura* ha sido registrado registrado entre 2.8 a 5.0 km<sup>2</sup> en Jalisco

(Ceballos y Miranda 1986) y la densidad en 1.2 a 1.7 indiv/km<sup>2</sup> en Oaxaca (Cervantes et al. 2002). El ámbito hogareño de *S. angustifrons* no ha sido estimado, pero para *S. putorius* se reportó 0.54 a 0.87 km<sup>2</sup> (Lesmeister et al. 2009) y la densidad de *S. angustifrons* se estimó en 0.5 indiv/km<sup>2</sup> en Oaxaca (Cervantes et al. 2002).

Las cámaras se colocaron en la intersección de dos o tres senderos de fauna silvestre donde se localizaron huellas o excrementos de mamíferos. Se sujetaron a la base de cactáceas columnares a una altura de 20 a 40 cm del suelo y se programaron para registrar una fotografía de 12 megapíxeles y un video de 15 s de 1080 megapíxeles con un periodo de inactividad de 30 s entre cada detección, imprimir el ID de la estación, la fecha y la hora de acuerdo al horario natural, y no fue utilizado el horario de verano (Fariás-González y Vega-Flores 2019). No se utilizaron atrayentes ni cebos. Las cámaras se activaron con un sensor infrarrojo al detectar la presencia de algún animal y operaron las 24 h del día. Se revisaron las estaciones cada 5 a 8 semanas para cambiar las baterías AA y las tarjetas de memoria digital (SDHC de 8 GB). Durante el periodo de muestreo, del 1 de mayo de 2013 al 30 de abril de 2020, entre 8 y 15 cámaras fueron funcionales y la variación se debió a que en 2013 iniciamos el fototrampeo con 8 cámaras y añadimos más estaciones en los años siguientes. En ocasiones algunas cámaras dejaron de funcionar durante periodos cortos por descomposturas

(Farías-González y Vega-Flores 2019). El esfuerzo de muestreo ( $EM$ ) se estimó sumando todos los días (1 día = 24 h) que cada cámara permaneció activa durante el periodo de muestreo; las unidades fueron los días-trampa (Meek et al. 2014; Farías et al. 2015).

**Registros de mefítidos.** Las especies de mefítidos se identificaron siguiendo literatura especializada (Kinlaw 1995; Hwang y Larivière 2001; Dragoo y Sheffield 2009; Aranda-Sánchez 2012). Se comparó el tamaño y robustez corporal, el tamaño, forma, coloración y porte de la cola, las franjas y manchas blancas sobre el pelaje negro del cuerpo, forma de la nariz y la presencia de franjas o manchas en el rostro (Theimer et al. 2017). Los registros de cada especie se agruparon por hora del día. El esfuerzo de muestreo fue de 31,386 días trampa. Los registros se categorizaron de acuerdo a la temporada de lluvia (mayo a octubre) y la temporada seca (noviembre a abril).

Las detecciones múltiples de individuos de la misma especie que no pueden ser distinguidos por sus características morfológicas pueden tratarse de un individuo residente que repite sus incursiones en el área de detección de la cámara, o pueden ser incursiones de dos o más individuos parecidos (Gilbert et al. 2020). Sin embargo, todos nuestros registros de la misma especie estuvieron separados por periodos >2 h, con la excepción de un video de *C. leuconotus* en el que se pudo identificar la presencia simultánea de dos individuos diferentes, en cuyo caso se tomó como un registro independiente a cada individuo.

**Patrones de actividad.** Para determinar los patrones de actividad las 24 h se contaron a partir de las 12:00 h hasta las 11:59 h del día siguiente. La actividad circadiana se analizó utilizando el software Oriana 4 versión demo (Kovach Computing Services, Pentraeth, Isle of Anglesey, Wales, U. K.) que nos permitió graficar diagramas de rosa que representaron la hora solar (0 a 24 h del día) como ángulos (0 a 360 grados) y la frecuencia de registros en cada hora, estimar el vector promedio ( $\mu$ ) que representa el pico de mayor actividad, el error estándar ( $SE$ ) de  $\mu$ , la longitud ( $r$ ) de  $\mu$  que es la medida de dispersión de las observaciones, el parámetro de concentración ( $k$ ) para una distribución uniforme en un círculo, y el intervalo de confianza (95 %  $CI$ ) de  $\mu$ . La superposición de los patrones de actividad entre especies se analizó con el software R versión 4.0.3 (RStudio Team 2020) con el paquete overlap versión 0.3.3 (Meredith y Ridout 2020), lo que permitió graficar la actividad circadiana como una distribución de densidad kernel que representó la hora solar como radianes (0 -  $2\pi$ ) y la frecuencia de registros como la densidad bajo la curva kernel, así como el coeficiente de superposición entre los patrones de actividad. Se realizó la prueba de Mardia-Watson-Wheeler ( $W$ ; Fisher 1995; Zar 1999) para determinar diferencias significativas entre la temporada de lluvia y la temporada seca en los patrones de actividad de cada especie y entre especies.

**Abundancia relativa.** El índice de abundancia relativa ( $IAR$ ) se estimó con la fórmula propuesta por Maffei et al. (2002) y adaptada para su uso con el método de fototram-

peo por Lira-Torres y Briones-Salas (2012) donde  $IAR = (C/EM) \times 100$ .  $C$  es el número de registros,  $EM$  es el esfuerzo de muestreo (días-trampa) y 100 es el factor de corrección estándar. Comparamos el  $IAR$  de la temporada de lluvia vs. la temporada seca. La determinación de si existieron diferencias estadísticamente significativas se realizó mediante la prueba de ANOVA de Friedman con el programa InfoStat versión 2017 (Di Rienzo et al. 2017).

## Resultados

**Patrones de actividad.** Se obtuvieron 235 registros de actividad para *C. leuconotus*, 39 para *M. macroura* y 42 para *S. angustifrons* (Figura 2). Las tres especies presentaron la mayor parte de su actividad durante el periodo nocturno (20:00 a 4:00 h) y cierta actividad en los periodos crepusculares, atardecer y amanecer. No se detectaron diferencias estadísticamente significativas entre la actividad circadiana durante la temporada de lluvia y la seca para ninguno de las tres especies ( $P > 0.32$ ). Por lo tanto, los patrones de actividad se analizaron combinando los datos de ambas temporadas por cada especie (Figuras 3 y 4). *C. leuconotus* y *S. angustifrons* presentaron patrones de actividad unimodales, en comparación con el *M. macroura* que tuvo un patrón bimodal, con los picos de actividad durante los periodos crepusculares (Figura 4). El pico de actividad de *C. leuconotus* ocurrió alrededor de las 0:00 h y se antecedió al pico de actividad de *S. angustifrons* que ocurrió alrededor de las 2:00 h (Figuras 3 y 4b). Los vectores de actividad promedio ( $\mu \pm SE$ ) de *C. leuconotus* (0:42  $\pm$  0:12 h) y *M. macroura* (1:02  $\pm$  0:33 h) no presentaron diferencias estadísticamente significativas ( $W = 2.31, P = 0.32$ ). El coeficiente de superposición tuvo un valor alto ( $\Delta = 0.89$ , Figura 4a). La actividad promedio de los mefítidos grande y mediano difirió por 20 min y el intervalo de confianza (95 %  $CI$ ) de *C. leuconotus* (0:18 - 1:06 h) quedó incluido en el intervalo de confianza de *M. macroura* (23:56 - 2:08 h). En contraste, el vector de actividad promedio de *S. angustifrons* (1:49  $\pm$  0:23 h) resultó estadísticamente diferente al de *C. leuconotus* ( $W = 7.56, P = 0.02$ ) y al de *M. macroura* ( $W = 7.57, P = 0.02$ ). El zorrillo manchado del sur presentó un coeficiente de superposición ligeramente más alto con *C. leuconotus* (0.81) en comparación con *M. macroura* (0.77, Figuras 4b y c). La longitud del vector promedio ( $r$ ) y la concentración de las observaciones ( $k$ ) fueron similares para los mefítidos grande y mediano, *C. leuconotus* ( $r = 0.72, k = 2.1$ ) y *M. macroura* ( $r = 0.66, k = 1.8$ ), y *S. angustifrons* presentó el patrón de actividad más restringido de las tres especies con la mayor  $r$  (0.80), y la mayor  $k$  (2.9).

**Abundancia relativa.** *C. leuconotus* y *M. macroura* presentaron mayor frecuencia de registros durante la temporada de lluvia, en comparación con *S. angustifrons* que mantuvo un número similar de registros al comparar las dos temporadas (Figura 5). Los meses con mayor frecuencia de registros presentaron superposición, y fueron: julio y agosto para *M. macroura*, agosto y septiembre para *C. leuconotus* y septiembre y noviembre para *S. angustifrons* (Figura 5).



**Figura 2.** (a, b) Zorrillo espalda blanca (*Conepatus leuconotus*), (c) zorrillo rayado sureño (*Mephitis macroura*) y (d) zorrillo manchado del sur (*Spilogale angustifrons*) foto-capturados en la selva baja caducifolia, Cerro Tepetroja, Ejido de San José Axuxco, Puebla.

Se detectaron diferencias significativas al comparar los IAR promedio de *C. leuconotus* (IAR lluvia = 7.90 vs. IAR seca = 2.53), y de *M. macroura* (lluvia = 1.21 vs. seca = 0.44) entre temporadas ( $P < .01$ ). En cambio, *S. angustifrons* (lluvia = 0.83 vs. seca = 0.96) no presentó diferencias en sus IAR promedio entre temporadas ( $P > 0.4$ ). *C. leuconotus* presentó mayor abundancia relativa con los mayores IAR promedio en ambas temporadas y significativamente diferentes en comparación con *M. macroura* y *S. angustifrons*.

Los tres meffítidos estuvieron presentes durante los 12 meses del año, con la excepción de que *S. angustifrons* no presentó registros en agosto (Figura 5). *C. leuconotus* y *M. macroura* se detectaron en las 15 estaciones de fototrampapeo y *S. angustifrons* se registró en 10 de las 15 estaciones.

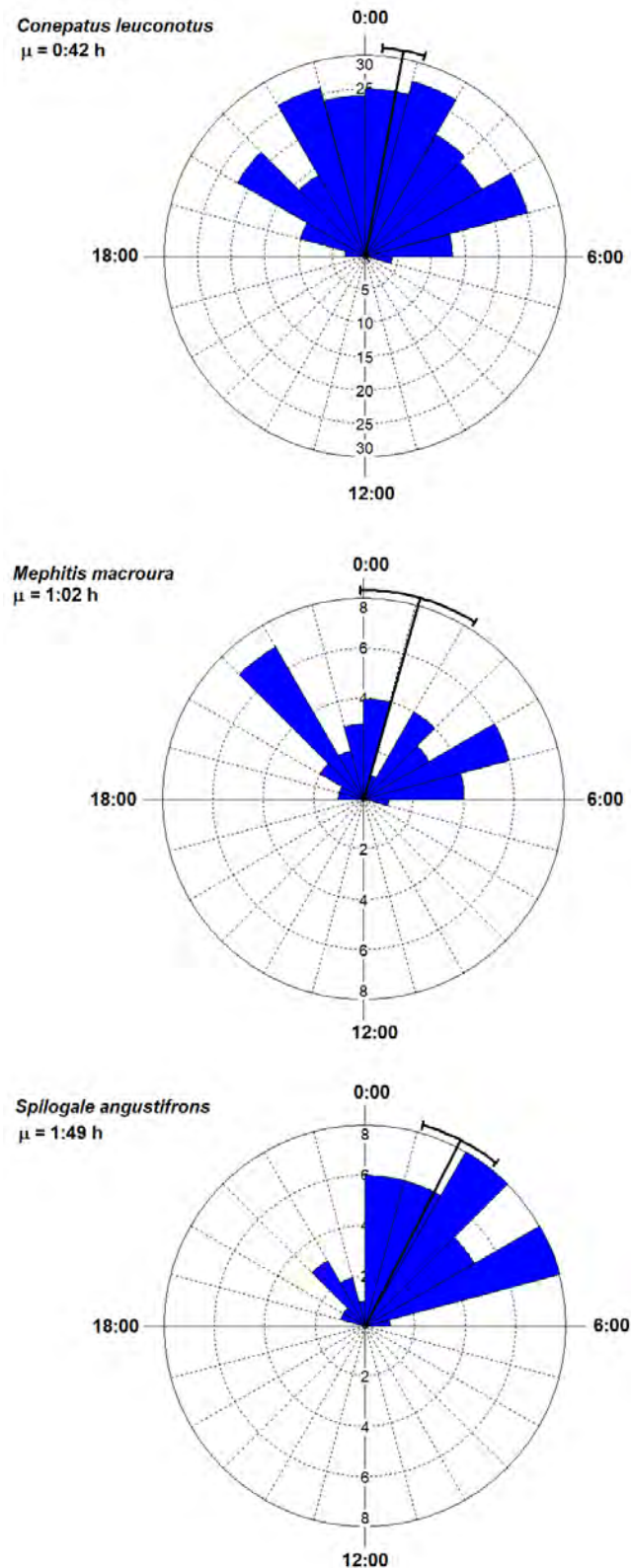
## Discusión

Los estudios sobre coexistencia de meffítidos son escasos y una parte del conocimiento sobre la ecología de las especies ha sido un subproducto del estudio de otras especies de mamíferos carnívoros (Fuller y Khuen 1985; Fuller et al.

1987; Neiswenter y Dowler 2007; Dragoo y Sheffield 2009). La información sobre actividad sincrónica y abundancia de las especies de *Conepatus*, *Mephitis* y *Spilogale* es limitada, aun cuando son simpátricos en gran parte de su distribución (Wade-Smith y Verts 1982; Rosatte y Larivière 2003). Los resultados de nuestra investigación representan la dinámica intragremial, contribuyen al conocimiento de la ecología, y mostraron que la segregación temporal y las diferencias en la abundancia relativa estacional entre las especies funcionaron como mecanismos para la coexistencia.

La primera hipótesis se cumplió debido a que el meffítido pequeño (*S. angustifrons*) presentó la actividad circadiana más restringida y el pico de actividad más concentrado, por lo que inferimos que evitó los periodos de mayor actividad de las especies grandes (Figura 4). También la especie más grande presentó el patrón y el pico de actividad más amplios de las tres especies. Además, es notable mencionar que aún cuando *C. leuconotus* y *M. macroura* no presentaron diferencias significativas en su actividad promedio ( $\mu \pm 95\% \text{ CI}$ ), los picos de actividad de *M. macroura* ocurrieron

durante los periodos crepusculares, en comparación con el pico de actividad de *C. leuconotus* que ocurrió alrededor de la media noche (Figura 4). Se infiere que la especie mediana también evitó los periodos de mayor actividad de la grande.



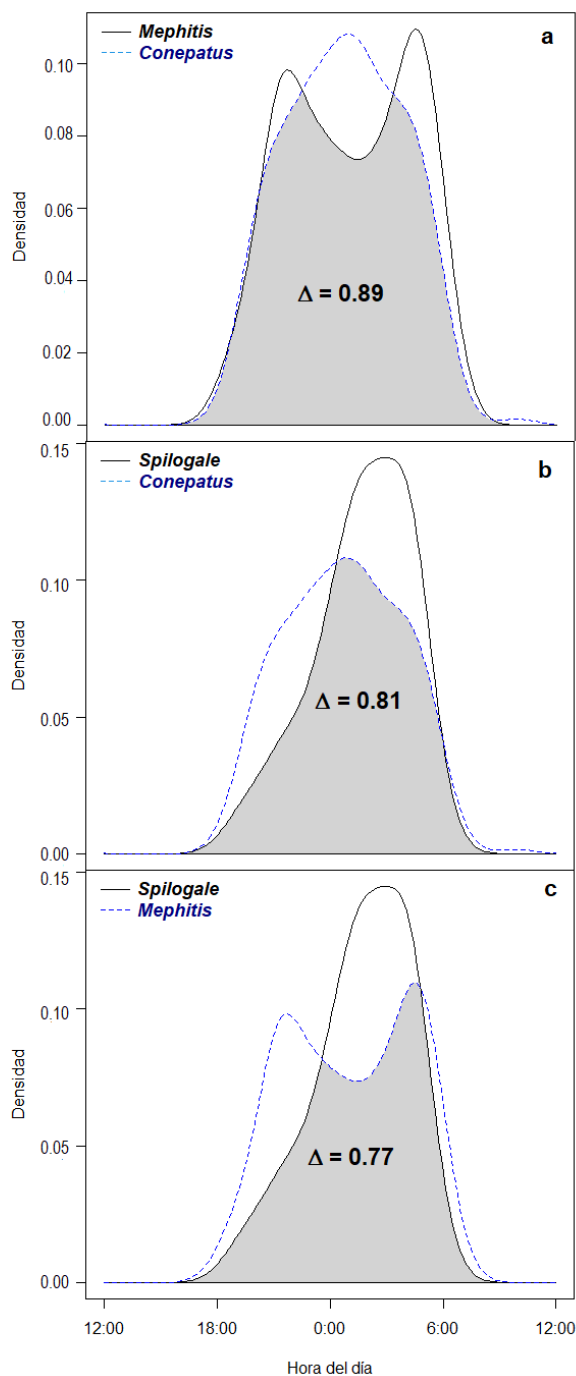
**Figura 3.** Actividad circadiana de tres mefítidos en el Cerro Tepetroja, reserva de la biosfera Tehuacán-Cuicatlán, del 1 de mayo del 2013 al 30 de abril del 2020. El vector promedio ( $\mu$ ) y su intervalo de confianza (95% *C*) están representados con líneas negras.

Nuestros resultados fueron congruentes con el estudio que comparó la actividad de *S. gracilis* y *M. mephitis* en Texas, EE. UU. donde hubo diferencias en primavera, verano, otoño e invierno, en el que la especie pequeña evitó encuentros con la grande (Neiswenter et al. 2010). El comportamiento de segregación temporal como mecanismo de coexistencia entre mamíferos carnívoros ha sido ampliamente estudiado en otras familias como los cánidos y los felinos (Harmsen et al. 2009; Lucherini et al. 2009; Farías et al. 2012; Lesmeister et al. 2015; Karanth et al. 2017). Es el caso de especies de tamaño corporal y hábitos alimentarios similares como dos cánidos (*Lycalopex gymnocercus* y *Cerdocyon thous*; Di Bitteti et al. 2009) o hasta seis especies de felinos neotropicales de diferentes tamaños corporales que coexistieron por partición temporal en Sudamérica (Di Bitteti et al. 2010).

La segunda hipótesis se cumplió debido a que la especie grande fue más abundante en relación con las otras dos, lo que permite inferir que *C. leuconotus* determinó la dinámica de las interacciones interespecíficas en la selva baja caducifolia de la RBTC. Los resultados coincidieron con un estudio reciente que sumó información de cuatro localidades de la RBTC y *C. leuconotus* fue la especie con mayor frecuencia de registros (Pérez-Irineo et al. 2020). Es posible que la mayor abundancia relativa de *C. leuconotus* se haya debido al buen estado de conservación de la vegetación en el Cerro Tepetroja en nuestra área de estudio, y a que *C. leuconotus* está mejor adaptado a zonas áridas y semiáridas en comparación con *M. macroura*. Las especies de los géneros *Conepatus* y *Spilogale* requieren vegetación arbustiva con cobertura densa y complejidad estructural y evitan áreas abiertas deterioradas y campos de cultivo (Patton 1974; Kinlaw 1995; Cervantes et al. 2002; Doty y Dowler 2006; Dragoo y Sheffield 2009; Lesmeister et al. 2009). En comparación, las especies del género *Mephitis* pueden ser abundantes en áreas abiertas y perturbadas tales como hábitat nativo deteriorado o rodeado de campos de cultivo o zonas residenciales suburbanas (Wade-Smith y Verts 1982; Reid 1997; Hwang y Larivière 2001; Cervantes et al. 2002; Neiswenter y Dowler 2007; Monroy-Vilchis et al. 2011). *C. leuconotus* tiene adaptaciones a las zonas áridas tales como ser capaz de obtener suficiente agua de su alimento, en comparación con las especies de *Mephitis* (Patton 1974; Hwang y Larivière 2001; Dragoo y Sheffield 2009). La evidencia fósil indica que *Conepatus* y *Mephitis* son géneros que se originaron durante el Plioceno en América; *Conepatus* se diversificó en el centro de México y *Mephitis* en una latitud mayor, en Kansas, EE. UU., y por ello *Mephitis* está mejor adaptado a tolerar los climas templados y fríos (Wang y Carranza-Castañeda 2008; Wang et al. 2014). Por estos motivos, la simpatria de *Conepatus*, *Mephitis* y *Spilogale* con una menor abundancia relativa de *Mephitis* bien podría entenderse como un indicador de la integridad ecológica en zonas áridas (Larivière y Messier 1998; Neiswenter y Dowler 2007; Estes et al. 2011).

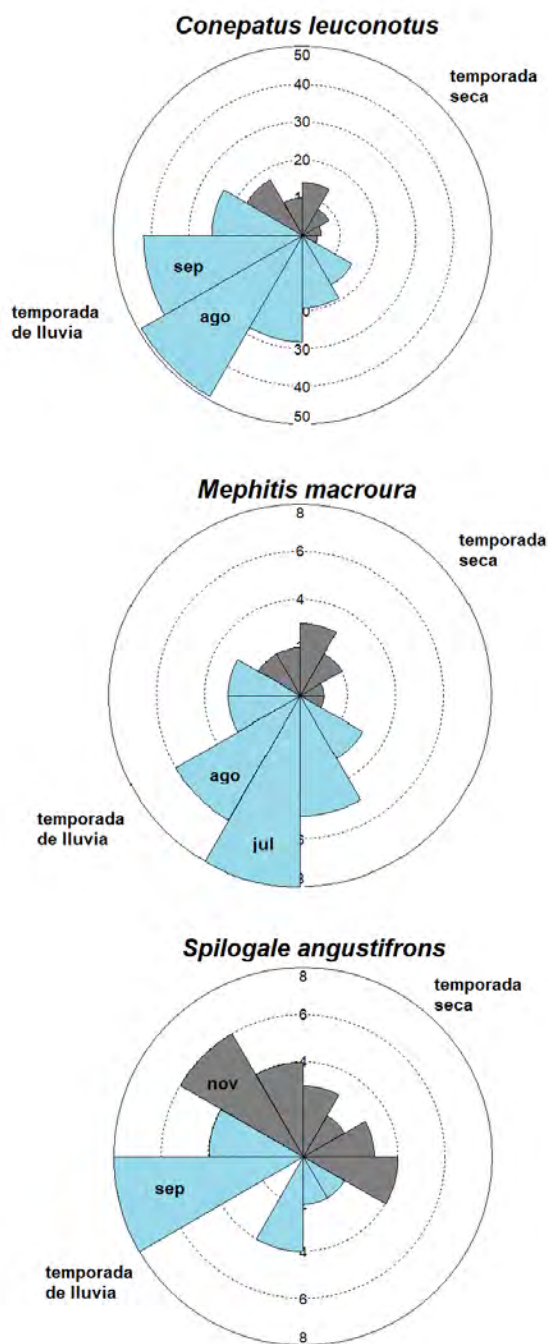
Además de demostrar una mayor abundancia relativa de *C. leuconotus* en el Cerro Tepetroja, RBTC, los resultados mostraron que *C. leuconotus* y *M. macroura* fueron más abundantes durante la temporada de lluvia y *S. angustifrons*





**Figura 4.** Actividad circadiana y coeficientes de superposición ( $\Delta$ ) de los meffitidos *Conepatus leuconotus*, *Mephitis macroura* y *Spilogale angustifrons* en el Cerro Tepetroja, reserva de la biosfera Tehuacán-Cuicatlán, del 1 de mayo del 2013 al 30 de abril del 2020.

no mostró diferencias estacionales, lo cual puede explicarse en relación a la información científica sobre la segregación del nicho en la dimensión trófica de los meffitidos. *C. leuconotus* es principalmente insectívoro, es la especie más insectívora entre los meffitidos y sus presas principales son los coleópteros, pero cuando los insectos escasean puede consumir frutas y vertebrados pequeños (Patton 1974; Dragoo y Sheffield 2009). Las garras y extremidades anteriores son muy fuertes y están adaptadas para excavar, el sentido del olfato es muy sensible y capaz de detectar a sus presas enterradas (Dragoo y Sheffield 2009). Este comportamiento



**Figura 5.** Frecuencia mensual de registros de tres meffitidos en el Cerro Tepetroja, reserva de la biosfera Tehuacán-Cuicatlán, del 1 de mayo del 2013 al 30 de abril del 2020. La temporada de lluvia es de mayo a octubre (azul) y la temporada seca de noviembre a abril (gris).

fue detectado entre nuestros registros mediante videos de individuos de *C. leuconotus* excavando en los meses de marzo, junio, julio y noviembre. En Texas, EE. UU. los insectos representaron del 50 - 90 % de la dieta de especies de *Conepatus* y los escarabajos principalmente en estado larvario constituyeron el 66% (Davis 1945; Taylor 1953; Patton 1974; Rosatte y Larivière 2003; Meaney et al. 2006). En comparación, las especies de *Mephitis* presentan una dieta oportunista y más diversa: consumen coleópteros, ortópteros, larvas de lepidópteros, vertebrados pequeños, frutos, y huevos de aves (Larivière y Messier 1998; Hwang y Larivière

2001). En nuestro estudio, probablemente *C. leuconotus* y *M. macroura* tuvieron mayor número de registros durante la temporada de lluvia debido a que la disponibilidad de sus recursos alimentarios principales, como los coleópteros, sea mayor durante los meses con mayor precipitación pluvial (Skipper *et al.* 2020). Los resultados concuerdan con lo descrito para *C. chinga* que prefirió el pastizal nativo debido a la mayor abundancia de coleópteros adultos en las Pampas, Argentina (Castillo *et al.* 2012). Finalmente, las especies de *Spilogale*, son las más carnívoras en comparación con *Conepatus* y *Mephitis*, y consumen mamíferos pequeños en mayor proporción (Kinlaw 1995; Neiswenter *et al.* 2010). Los tres géneros son capaces de trepar a los árboles, pero *Spilogale* es más ágil y hábil como escalador y puede explotar una gama diferente de recursos en comparación con *Conepatus* y *Mephitis* (Wade-Smith y Verts 1982; Kinlaw 1995; Reid 1997; Rosatte y Larivière 2003). No fue posible comparar los resultados de abundancia relativa y sus diferencias estacionales con información de otras poblaciones de meffítidos en México, ya que se limitan a documentar que *C. leuconotus* y *M. macroura* pueden estar en proximidad y alimentarse en cercanía física, y a reportar densidades poblacionales bajas (List y MacDonald 1998; Cervantes *et al.* 2002; Monroy-Vilchis *et al.* 2011; Elizalde-Arellano *et al.* 2014). En México, el estado de conservación de las poblaciones de meffítidos simpátricos es incierto. El presente trabajo es una contribución para el conocimiento sobre las tres especies que coexisten en selva baja caducifolia en un área natural protegida del centro del país.

## Agradecimientos

Se agradece y reconoce la colaboración del Ejido de San José Axuxco, Municipio de San José Miahuatlán, Puebla. La Comisión Nacional de Áreas Naturales Protegidas (CONANP) a través de las autoridades de la RBTC otorgó las facilidades y el permiso para realizar este estudio. La Comisión Nacional Forestal (CONAFOR) brindó apoyo a las autoridades civiles de San José Axuxco a través del pago de servicios ambientales para realizar recorridos de vigilancia. Agradecemos a tres revisores por sus valiosas contribuciones al trabajo. Investigación realizada gracias al Programa UNAM-DGAPA-PAPIIT Proyecto IA200812 y UNAM-DGAPA-PAPIIT Proyecto IN221814.

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# Mammal species richness and new records in protected natural areas of the northern part of the metropolitan area of the Valley of México

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Sierra de Guadalupe is the only mountain range in the northern part of the Valley of Mexico metropolitan area. The accelerated urban expansion over the past decades has turned Sierra de Guadalupe into an isolated natural area immersed within the urban matrix. This study aimed to gather a documented inventory of the mammals of Sierra de Guadalupe as such information is useful to improve the management, restoration, and conservation of this important natural area of the basin of Mexico. Mammal collection records were extensively surveyed in the literature, collection databases, web pages, and scientific collections; field surveys were also conducted. A taxonomic list of the mammal species and their conservation status in the four Protected Natural Areas of Sierra de Guadalupe was compiled. A species-accumulation curve was constructed using the Chao 1 model and a map showing the distribution of collection records was produced. This work reveals that the mammals of Sierra de Guadalupe include 29 species, 23 genera, 15 families, and six orders. Six species are endemic to Mexico; two of them, *Choeronycteris mexicana* and *Cratogeomys fumosus*, are listed as threatened and one, *Leptonycteris yerbabuena*, as under special protection. Collection records were gathered from 62 different localities. The largest number of species records and collections were made between 2009 and 2020. The species-accumulation curve projects a total of 36 mammal species. This is the first documented inventory ever compiled of the wild mammals of Sierra de Guadalupe. The species richness observed in this area is remarkable, considering its extension and environmental stressors; in addition, it harbors species endemic to Mexico, some of which are threatened. This is the first time that the species *Sorex saussurei*, *Choeronycteris mexicana*, *Leptonycteris yerbabuena*, *Cratogeomys merriami*, *Neotomodon alstoni*, and *Peromyscus melanophrys* have been recorded in this area. The species-accumulation curve indicates that our inventory provides a good representation of the local species assemblage. This information can support the formulation of action plans for the conservation and restoration of the biological diversity of these important Protected Natural Areas and the last significant natural area remaining in the northern part of the Valley of Mexico Metropolitan Area.

La Sierra de Guadalupe es la única cadena montañosa en la parte norte de la Zona Metropolitana del Valle de México. Debido a la expansión acelerada de las áreas urbanas, en las últimas 40 décadas, la Sierra de Guadalupe se ha convertido en un espacio natural aislado e inmerso en esta matriz urbana. El objetivo de este trabajo fue realizar un inventario documentado de los mamíferos de la Sierra de Guadalupe y que la información generada contribuya al manejo, recuperación y conservación de este importante pulmón ubicado en la Cuenca de México. Se hizo la búsqueda de registros en la literatura, bases de datos, portales electrónicos, colecciones biológicas y se realizaron colectas de campo. Se elaboró un listado taxonómico de las cuatro áreas naturales protegidas de la Sierra de Guadalupe, incluyendo su estado de conservación. Se obtuvo la curva de acumulación de especies utilizando el modelo de Chao 1 y se generó un mapa de distribución de localidades. La composición taxonómica para la Sierra de Guadalupe fue de 29 especies, seis órdenes, 15 familias y 23 géneros. Seis especies son endémicas de México, dos en categoría de Amenazadas *Choeronycteris mexicana* y *Cratogeomys fumosus* y una en Protección especial *Leptonycteris yerbabuena*. Las colectas corresponden a 62 localidades. La mayor riqueza y abundancia se observó entre los años 2009 a 2020. La curva de acumulación de especies predijo un total de 36 especies. Este es el primer inventario documentado de la fauna de mamíferos silvestres para la Sierra de Guadalupe, la cual presenta una riqueza notable considerando su extensión y su problemática. Alberga especies endémicas de México y en estado de conservación. Se registran por primera vez en el área a las especies *Sorex saussurei*, *Choeronycteris mexicana*, *Leptonycteris yerbabuena*, *Cratogeomys merriami*, *Neotomodon alstoni* y *Peromyscus melanophrys*. La curva de acumulación de especies indica que se tiene una buena representación de las especies. La información que se aporta es valiosa para establecer acciones de conservación y recuperación de la diversidad biológica de estas importantes ANP y último reducto de área natural ubicado al norte del Área Metropolitana de la Ciudad de México.

**Keywords:** Basin of Mexico; biodiversity; conservation; endemic; inventory; Protected Natural Areas, Trans-Mexican Volcanic Belt.

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## Introduction

The Sierra de Guadalupe mountain range is an isolated natural area in the northern part of the Valley of Mexico Metropolitan Area, bordering the southern end of the extensive arid zones of northern Mexico. Sierra de Guadalupe is the largest remnant of natural vegetation north of Mexico City (CDMX); it harbors a high species richness and supplies environmental services to the inhabitants of this vast urban area. It comprises one federal and three state-level Protected Natural Areas (PNA): Parque Nacional El Tepeyac (PNT), Parque Estatal Sierra de Guadalupe (PESG), Zona Sujeta a Conservación Ecológica Sierra de Guadalupe (ZSCESG), and Zona de Conservación Ecológica La Armella (ZCELA). The PESG is entirely located in the Estado de México (EDOMEX) jurisdiction, whereas the other three are in CDMX. Except for the Parque Nacional El Tepeyac, the other PNA are managed according to an official management program ([Periódico oficial 1999](#); [GOCDMX 2016a, b](#)). The term Sierra de Guadalupe is used herein to refer to the four PNA, as they are contiguous to each other and share similar morphological, geological, and ecological characteristics.

Very few scientific studies on the Sierra de Guadalupe have been published, mainly focused on invertebrates ([Velázquez 2014](#); [Stanford-Camargo et al. 2016](#); [Medina-Reyes et al. 2019](#)), flora ([Márquez et al.](#) undated), soil ([Vela-Correa and Flores-Román 2004](#)), geomorphology ([Lugo-Hubp and Salinas-Montes 1996](#); [Martínez-Yáñez et al. 2009](#)), land-use planning ([Villavicencio 2007](#)), hydrology ([Vázquez 2016](#)), and conservation status ([Cedillo et al. 2007, 2008](#); [Paniagua 2016](#)). Information on vertebrates is almost nil, with only two publications on avifauna ([Contreras 1999](#); [Salazar et al. 2018](#)) and three on herpetofauna ([Méndez de la Cruz et al. 1992](#); [Martínez 2017](#); [Arias 2018](#)). No scientific publications focused on the mammals of the area are currently available; there is only one study that includes some collection records ([Hortelano-Moncada et al. 2016](#)) and several general technical reports ([GEM.SE.CGCE 2002](#); [GODF 2006](#); [Cedillo et al. 2008](#); [PAOT 2009](#); [CEPANAF 2015](#); [GOCD 2016a, b](#)).

The knowledge and conservation of the biodiversity of Sierra de Guadalupe face several challenges that should be addressed. Its location within one of the most populous cities of the world puts an enormous pressure on its natural resources, soil, water, flora and fauna. The main threats to Sierra de Guadalupe include irregular settlements, wildfires, changes of land use for agricultural and livestock ranching activities, feral fauna, solid waste dumping in the surroundings or within the area that facilitates the proliferation of harmful fauna, and pollution of soil, groundwater, and air ([Periódico oficial 1999](#); [Paniagua 2016](#)). This mountain range lies in between areas dedicated to urban, industrial, or mineral exploitation uses, as well as deforested areas; thus, it functions as a natural barrier against pollution and environmental degradation, in addition to supplying environmental services. Its morphological, geological, and eco-

logical features make it one of the most important biotic reserves in the basin of Mexico ([Cedillo et al. 2007, 2008](#)).

This study aimed to compile a properly documented inventory of the diversity of wild mammals of the four Protected Natural Areas in Sierra de Guadalupe. This information would contribute to the better management, restoration, and conservation of this important natural area of the northern part of the Valley of Mexico metropolitan area.

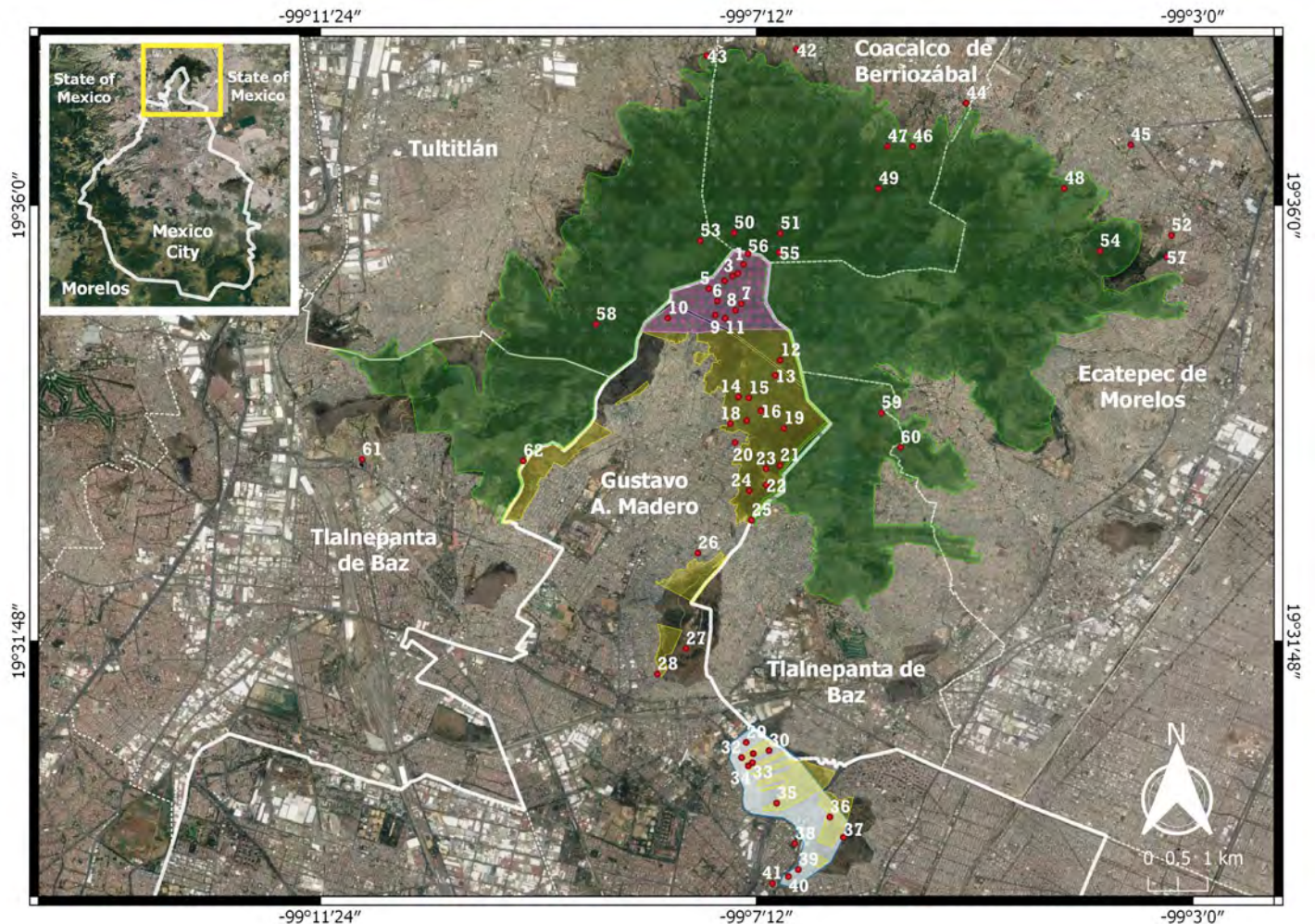
## Materials and Methods

**Study Area.** Sierra de Guadalupe is located at  $-19^{\circ} 37' 00''$ ,  $-19^{\circ} 29' 09''$  N and  $99^{\circ} 11' 20''$ ,  $99^{\circ} 03' 00''$  W and comprises a total area of 8,649 ha (Figure 1). Some 82 % of this mountain range is located in the State of Mexico and the remaining 18 % in the Gustavo A. Madero municipality, in the northern part of Mexico City ([PAOT 2009](#)). It is part of the Trans-Mexican Volcanic Belt physiographic province, corresponding to the Alto Río Pánuco hydrological region in the drainage basin of the Moctezuma river.

Sierra de Guadalupe includes some of the highest peaks in the basin of Mexico: Picacho Moctezuma, with an elevation of 3,055 m; Cerro del Sombrero y Pico Tres Padres, 3,010 m; Cerro del Chiquihuite, 2,730 m; Zacatenco, 2,500 m; El Guerrero, 2,440 m; Los Gachupines, 2,330 m, and El Tepeyac, 2,270 m ([SPC 2014](#)). The native vegetation cover includes xeric shrubland and oak forest, but the latter can now be found only in hard-to-access areas or as scattered patches. Induced or cultivated vegetation includes pastures, thorny shrubland, and tree plantations of eucalyptus, casuarina, acacia and, less frequently, Peruvian pepper, cypress, pine, ash, oak, and several types of fruit trees such as Mexican hawthorn, peach, quince, guava, pear, and black cherry ([Rzedowski 1979, 1986](#); [Periódico oficial 1999](#); [GOCDMX 2016a](#)). A network of seasonal streams and intermittent creeks crisscrosses the area, carrying little surface water but supplying a high infiltration into the water table ([GODF 2006](#); [Cedillo et al. 2008](#); [GOCDMX 2016a](#)).

The Parque Estatal Sierra de Guadalupe (PESG) was decreed in 1976 and currently comprises 6,322 ha; it includes parts of the municipalities of Coacalco de Berriozábal, Ecatepec de Morelos, Tlalnepantla de Baz, and Tultitlán, in the Estado de México (Periódico oficial 1976; [CEPANAF 2015](#)). The other three Protected Natural Areas are located in the Gustavo A. Madero municipality in Mexico City. The Zona Sujeta a Conservación Ecológica Sierra de Guadalupe (ZSCESG) was decreed in 1990 ([DOF 1990a, b](#)) with 633.68 ha ([GOCDMX 2016a](#)). The zona de Conservación Ecológica La Armella (ZCELA) was decreed in 2006 with a total area of 93.38 ha ([GODF 2006](#)). The federal Protected Natural Area, Parque Nacional El Tepeyac (PNT) was decreed in 1937 with an area of approximately 1,500 ha; it comprises El Tepeyac, Gachupines, Guerrero, and Zacatenco mountains (Figure 1b; [DOF 1937](#); [PAOT 2009](#)).

**Gathering of Collection Records.** The relevant literature was thoroughly reviewed to gather all mammal collection records made in Sierra de Guadalupe: [Villa-Ramírez 1953](#),



**Figure 1.** Location of the four Sierra de Guadalupe protected natural areas: Parque Estatal Sierra de Guadalupe (PESG, green polygon), Zona de Conservación Ecológica Sierra de Guadalupe (ZCESG, yellow polygon), Zona Sujeta a Conservación Ecológica Sierra de Guadalupe (ZSECSG; purple polygon), and Parque Nacional El Tepeyac (PNT; blue polygon). PESG is located in the Coacalco de Berriozábal, Ecatepec de Morelos, Tlalnepantla de Baz, and Tultitlán municipalities in the State of Mexico; the three other protected natural areas are located in the Gustavo A. Madero municipality, Mexico City. Numbered red dots = Collection localities.

Hall 1982, Chávez and Ceballos 1998, Villa-Ramírez and Cervantes 2003, Chávez et al. 2009, Hortelano-Moncada and Cervantes 2011, Guevara et al. 2016, Hortelano-Moncada et al. 2016, Ramírez-Pulido et al. 2017. Databases and image collections available in the following web pages were also reviewed: Sistema Nacional de Información sobre la Biodiversidad de México (SNIB 2019; <https://www.snib.mx/ejemplares/mamiferos.201904.csv.zip>), Global Biodiversity Information Facility (GBIF 2019; <https://doi.org/10.15468/dl.7fc2rw>; <https://doi.org/10.15468/dl.k4k7dr>), iNaturalist (<https://www.naturalista.mx/>), and IREKANI (<https://unibio.unam.mx/irekani/>).

The databases of four institutional scientific collections were also reviewed, and some of their specimens were examined to retrieve supplementary data: Instituto de Biología, Universidad Nacional Autónoma de México (CNMA), Escuela Nacional de Ciencias Biológicas (ENCB), Universidad Autónoma Metropolitana Iztapalapa (UAMI), and Museo de Zoología “Alfonso L. Herrera”, Facultad de Ciencias, Universidad Nacional Autónoma de México (FCMM). The database of the Biodiversity Institute and Natural History Museum (KU) was also reviewed. The names

and acronyms of these collections are as listed in the directory of mammal collections of the Western Hemisphere (Dunnun et al. 2018).

In addition, six field trips were carried out in the Zona Sujeta a Conservación Ecológica Sierra de Guadalupe and Zona de Conservación Ecológica La Armella as part of a wildlife monitoring program: 12-13 March, 20-21 and 27-28 May, 12-14 June, and 2-3 September 2019, and 23 September, 2020. Only one-night monitoring was carried out in five of the six field surveys due to security concerns and logistic restrictions; a two-night monitoring was conducted only during the June 2019 survey.

The field surveys allowed capturing specimens, recovering material, and containing specimens in the field. A total of 30 collapsible Sherman traps measuring 8×9×23-cm were used to capture small terrestrial mammals; with a separation of approximately 5 m between adjacent traps. These were baited with a mixture of oatmeal and vanilla and set in operation from 17:00 h until the morning of the following day. Bats were captured with three 6×2 m mist nets set within the vegetation, on roads, water bodies, and potential shelters, where they were left open for four hours

starting at dusk and then checked every 30 minutes. Morphometric measurements, weight, sex, and reproductive status of each specimen were recorded; some specimens were prepared by taxidermy for further study following the guidelines issued by [Sikes \(2016\)](#).

Medium-sized mammals were captured with four Tomahawk traps; the traps were placed near trails, water sources, and latrines, baited with sardine and fruit (orange, tangerine, and apple), and left in operation for 12 consecutive hours. The specimens captured were photographed, their ectoparasites sampled, and then released at the same capture site.

Two motion-activated camera traps were used for recording medium- and large-sized mammals; simple photo-trapping stations baited with sardine were placed at strategic sites such as near burrows, water sources, roads, and trails that showed footprints or excreta. These camera traps were set at 17:00 h, left in operation overnight, and deactivated on the following morning, for an approximate sampling intensity of 13 h per night per camera. The name and geographic coordinates of the location of each photograph were recorded, along with the name of the person who set the camera-trap, date and time of the event, and surrounding vegetation type. In addition, excreta and pellets were collected, where available, and their contents (hair, bone material) were examined to add to the mammal record.

The specimens and derived materials were identified ([Álvarez-Castañeda et al. 2015](#)) and then deposited into the CNMA collection; the photographic material was uploaded onto the CNMA image collection (Irekani repository: ([https://unibio.unam.mx/irekani/handle/123456789/186/browse?proyecto=Irekani&type=title&submit\\_browse=Title&collec=only](https://unibio.unam.mx/irekani/handle/123456789/186/browse?proyecto=Irekani&type=title&submit_browse=Title&collec=only))).

The specimens and derived material for this study were collected under collection permit 09/k5-144/06/19 issued by the Subsecretaría de Gestión para la Protección Ambiental, Dirección General de Vida Silvestre, Secretaría de Medio Ambiente y Recursos Naturales, México.

*Taxonomic List, Geographic Distribution, and Analysis.* The biological, taxonomic, and geographic data recorded for each specimen were systematized in an *ad hoc* database. A taxonomic list of the mammal species recorded in Sierra de Guadalupe was prepared following [Ramírez-Pulido et al. \(2014\)](#); the nomenclature was updated, as needed, based on more recent studies ([Burgin et al. 2018](#); [Greenbaum et al. 2019](#)).

All the collection localities were georeferenced on Google Earth and the species collection records were mapped using the Geographic Information System QGIS v 3.14. A species-accumulation curve was constructed to evaluate the completeness of our sampling. The data were first subjected to a smoothing process using the program Estimates S v 9.1.0 ([Colwell 2013](#)). The species-accumulation curve was then constructed in the program Excel using the Chao 1 model; this method is recommended for studying

individual abundances in a single sample ([Escalante 2003](#)). Species-accumulation models use site and species richness data to analyze the accumulation of species as the number of sampling sites increases and thus estimate the number of unrecorded species in the area ([Oksanen 2020](#)). Pivot tables and dynamic graphs were used for a historical analysis and visualization of how the records evolved over time.

## Results

A total of 178 collection records were compiled; of these, 149 correspond to specimens deposited in five scientific collections: 65 in CNMA, 78 in ENCB, one in UAMI, one in FCMM, and four in KU. The other 29 records were found in virtual galleries: 11 in IREKANI and 18 in iNaturalist. These records were made in 62 different localities, 41 in CDMX and 21 in EDOMEX; 21 records were made in the PESG, 11 in ZCELA, 21 in the ZSCESG, and nine in the PNT (Figure 1, Appendix 1).

*Taxonomic List, Geographic Distribution, and Conservation Status.* The taxonomic list of the mammals of Sierra de Guadalupe compiled in this work includes 29 different species in 23 genera, 14 families, and 6 orders (Table 1). Six of these species are new records for Sierra de Guadalupe: *Saussure's shrew*, *Sorex saussurei*; Mexican long-tongued bat, *Choeronycteris Mexicana*; lesser long-nosed bat, *Leptonycteris yerbabuena*; Merriam's pocket gopher, *Cratogeomys merriami*, Mexican volcano mouse, *Neotomodon alstoni*; and plateau mouse, *Peromyscus melanophrys*.

The species distribution across the PNA was as follows: 20 species in PESG, eight in ZCELA, 17 in ZSCESG, and seven in PNT. Thirteen species were recorded in more than one PA: *Baiomys taylori*, *Bassariscus astutus*, *Didelphis virginiana*, *Nyctinomops macrotis*, *Otospermophilus variegatus*, *Peromyscus difficilis*, *P. gratus*, *P. labecula*, *Sciurus aureogaster*, *Sigmodon toltecus*, *Spilogale angustifrons*, *Syvilagus floridanus*, and *Urocyon cinereoargenteus*. Sixteen species were found in only one PA: *Canis latrans*, *C. fumosus*, *Heteromys irroratus*, *Microtus mexicanus*, *Mustela frenata*, *Myotis velifer*, *Reithrodontomys fulvescens*, *S. saussurei*, *Tadarida brasiliensis* were recorded only in the PESG; *Aeorestes cinereus*, *C. mexicana*, *L. yerbabuena*, and *P. melanophrys* were recorded only in ZSCESG; *C. merriami* and *N. alstoni* in ZCELA; and *M. occultus* in PNT (Figure 2).

Overall for the Sierra de Guadalupe, rodents are the group best represented with 14 species (48.3 %), followed by bats with seven species (24.1 %), carnivores with five species (17.2 %), and marsupials, shrews, and rabbits represented by a single species each (*D. virginiana*, *S. saussurei*, and *S. floridanus*, respectively), which together account for 10.4 % of all the mammal species recorded in Sierra de Guadalupe.

The Rodentia species belong to four different families: Cricetidae (nine species), Sciuridae (two), Geomyidae (two), and Heteromyidae (one) and ten genera. The species most frequently recorded was *P. gratus* with 33 specimens,





**Figure 2.** Some mammals inhabiting Sierra de Guadalupe. a) Gray fox, *Urocyon cinereoargenteus*, b) Mexican gray squirrel, *Sciurus aureogaster*, c) eastern cottontail, *Sylvilagus floridanus*, d) lesser long-nosed bat, *Leptonycteris yerbabuena*, e) Mexican long-tongued bat, *Choeronycteris mexicana*, f) Merriam's piñon mouse, *Peromyscus gratus*, g) Virginia opossum, *Didelphis virginiana*. (Photos: Rafael Alvarado (a), Diego Alvarado (b, c, d); Asela Barragán (e); Jesús Fernández (f, g).

followed by the Zacatecan deer mouse, *P. difficilis*, with 27 specimens, and the fulvous harvest mouse, *R. fulvescens*, with 11. The Chiroptera species belong to three different families: Vespertilionidae (three species), Molossidae (two), and Phyllostomidae (two), and seven genera; the species most frequently recorded was *M. velifer*, with seven specimens.

Three species are listed in the Official Mexican Standard NOM-059 (SEMARNAT 2019): *C. mexicana* and *C. fumosus* are threatened species, and *L. yerbabuena* is under special protection. The International Union for the Conservation of Nature (IUCN 2019) lists *C. mexicana* as near-threatened (NT), *L. yerbabuena* as vulnerable (VU), and the other species as of least concern. None of these species has been listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Six species inhabiting the Sierra de Guadalupe are endemic to Mexico (Table 1).

**Specimens Collected, Species, and Collection Periods.** The collection records compiled were used to analyze how the number of specimens collected and species recorded evolved over time. Three time periods were defined for this analysis: a historical period (1937 to 1980), an intermediate period (1981 to 2008) when little collection activity took place, and the recent period (2009 to 2020) when renewed collection activity and new findings are observed.

A total of 100 specimens, representing 14 different species, were collected during the historical period. One new species was recorded in each of the years 1947 (seven specimens collected), 1949 (eight specimens), 1952 (four),

and 1967 (25); two additional species were recorded in 1937 (seven specimens) and 1948 (two specimens); and three new species in each of 1964 (16 specimens) and 1980 (three). Although 1965 and 1967 were the years when most collections were made, no new species were recorded in the area. Only two specimens were collected during the second 27-year period (1981–2008), in 1988 and 1997, with no new species recorded in the area.

The collection of mammal specimens in Sierra de Guadalupe resumed in the recent period (2009–2020). Two species, the hoary bat, *A. cinereus*, and the Mexican volcano mouse, *N. alstoni*, were first recorded in the area in 2009. One new species was recorded in each of the years 2012, 2013, 2015, 2017, and 2018; these included the Virginia opossum, *D. virginiana*; the ringtail, *B. astutus*; the Saussure's shrew, *S. saussurei*; the gray fox, *U. cinereoargenteus*; and the Mexican gray squirrel, *S. aureogaster*. The smoky pocket gopher, *C. fumosus*, and the coyote, *C. latrans*, were first recorded in 2014. The largest number (36) of specimens was collected in 2019, finding two previously unrecorded species: the Mexican long-tongued bat, *C. mexicana*, and the plateau mouse *P. melanophrys*. An additional species, the lesser long-nosed bat, *L. yerbabuena*, was first recorded in 2020. A total of 76 specimens were collected and 14 previously unrecorded species were found during this period (Figure 3).

A total of 24 data points was used to construct the species-accumulation curve. This analysis included only those

**Table 1.** Mammal species recorded in the four Sierra de Guadalupe protected natural areas. En = species endemic to Mexico. NOM = listed in the official Mexican standard NOM-059-SEMARNAT-2019 (A = Threatened, Pr = under special protection). IUCN = International Union for Conservation of Nature (VU = Vulnerable, NT = Near Threatened, LC = Least Concern). TR = type of record (C = collected specimen, F = photograph, E = excreta, H = footprint). ANP = Protected Natural Areas (PESG = Parque Estatal Sierra de Guadalupe; ZCELA = Zona de Conservación Ecológica La Armella; ZSCESG = Zona Sujeta a Conservación Ecológica Sierra de Guadalupe; PNT = Parque Nacional El Tepeyac).

Especie	En	NOM	IUCN	TR	ANP
Orden Didelphimorphia					
Familia Didelphidae					
<b><i>Didelphis virginiana</i></b>			LC		
<i>Didelphis virginiana californica</i>				C,F	PESG, ZCELA, ZSCESG
Orden Eulipotyphla					
Familia Soricidae					
<b><i>Sorex saussurei</i></b>			LC	C	PESG
Orden Chiroptera					
Familia Phyllostomidae					
<b><i>Choeronycteris mexicana</i></b>	A		NT	C	ZSCESG
<b><i>Leptonycteris yerbabuenae</i></b>	Pr		VU	C	ZSCESG
Familia Molossidae					
<b><i>Tadarida brasiliensis</i></b>			LC		
<i>Tadarida brasiliensis mexicana</i>				C	PESG
<i>Nyctinomops macrotis</i>			LC	C	PESG, ZSCESG, PNT
Familia Vespertilionidae					
<i>Aeorestes cinereus</i>			LC		ZSCESG
<i>Myotis occultus</i>			LC	C	PNT
<b><i>Myotis velifer</i></b>			LC		
<i>Myotis velifer velifer</i>				C	PESG
Orden Lagomorpha					
Familia Leporidae					
<i>Sylvilagus floridanus</i>			LC		
<i>Sylvilagus floridanus orizabae</i>				C,H	PESG, ZCELA, ZSCESG
Orden Rodentia					
Familia Sciuridae					
<i>Otospermophilus variegatus</i>			LC		
<i>Otospermophilus variegatus variegatus</i>				C,F	PESG, ZCELA, ZSCESG
<i>Sciurus aureogaster</i>			LC		
<i>Sciurus aureogaster aureogaster</i>				F	PESG, ZSCESG
Familia Geomyidae					
<i>Cratogeomys fumosus</i>	En	A	LC		
<i>Cratogeomys fumosus tylorhinus</i>				C	PESG
<i>Cratogeomys merriami</i>	En		LC	C	ZCELA
Familia Heteromyidae					
<i>Heteromys irroratus</i>			LC		

Especie	En	NOM	IUCN	TR	ANP
<i>Heteromys irroratus alleni</i>				C	PESG
Familia Cricetidae					
<i>Microtus mexicanus</i>			LC		
<i>Microtus mexicanus mexicanus</i>				C	PESG
<i>Baiomys taylori</i>			LC		
<i>Baiomys taylori analogus</i>				C	PESG, ZSCESG, PNT
<i>Neotomodon alstoni</i>	En		LC	C	
<i>Neotomodon alstoni alstoni</i>					ZCELA
<i>Peromyscus difficilis</i>	En		LC		
<i>Peromyscus difficilis felipensis</i>			LC	C	PESG, ZCELA, ZSCESG, PNT
<i>Peromyscus gratus</i>			LC		
<i>Peromyscus gratus gratus</i>				C	PESG, ZCELA, ZSCESG, PNT
<i>Peromyscus labecula</i>			LC		
<i>Peromyscus labecula fulvus</i>				C	ZSCESG
<i>Peromyscus labecula labecula</i>				C	PNT
<i>Peromyscus melanophrys</i>	En		LC		
<i>Peromyscus melanophrys melanophrys</i>				C	ZSCESG
<i>Reithrodontomys fulvescens</i>	En		LC		
<i>Reithrodontomys fulvescens toltecus</i>				LC	C
<i>Sigmodon toltecus</i>			LC		PESG, ZSCESG, PNT
Orden Carnivora					
Familia Canidae					
<i>Canis latrans</i>			LC		
<i>Canis latrans cagottis</i>				C	PESG
<i>Urocyon cinereoargenteus</i>			LC		
<i>Urocyon cinereoargenteus nigrirostris</i>				F	PESG, ZCELA
Familia Mephitidae					
<i>Spilogale angustifrons</i>			LC		
<i>Spilogale angustifrons angustifrons</i>				C,F	ZSCESG, PNT
Familia Mustelidae					
<i>Mustela frenata</i>			LC		
<i>Mustela frenata frenata</i>				C	PESG
Familia Procyonidae					
<i>Bassariscus astutus</i>			LC		
<i>Bassariscus astutus astutus</i>				C,F,E	PESG, ZSCESG

years for which the number of specimens collected could be accurately determined (namely, years 1936, 1937, 1947, 1948, 1949, 1950, 1952, 1956, 1964, 1965, 1967, 1969, 1980, 1988, 1997, 2009, 2012, 2013, 2014, 2015, 2017, 2018, 2019, and 2020). The results of the Chao 1 model projected a total of 36 (35.95) mammal species in Sierra de Guadalupe, with a completeness index (probability of finding new species) of 0.81; this means that, given the relationship between

the number of sites sampled and the number of species recorded, seven additional species may be expected.

### Discussion

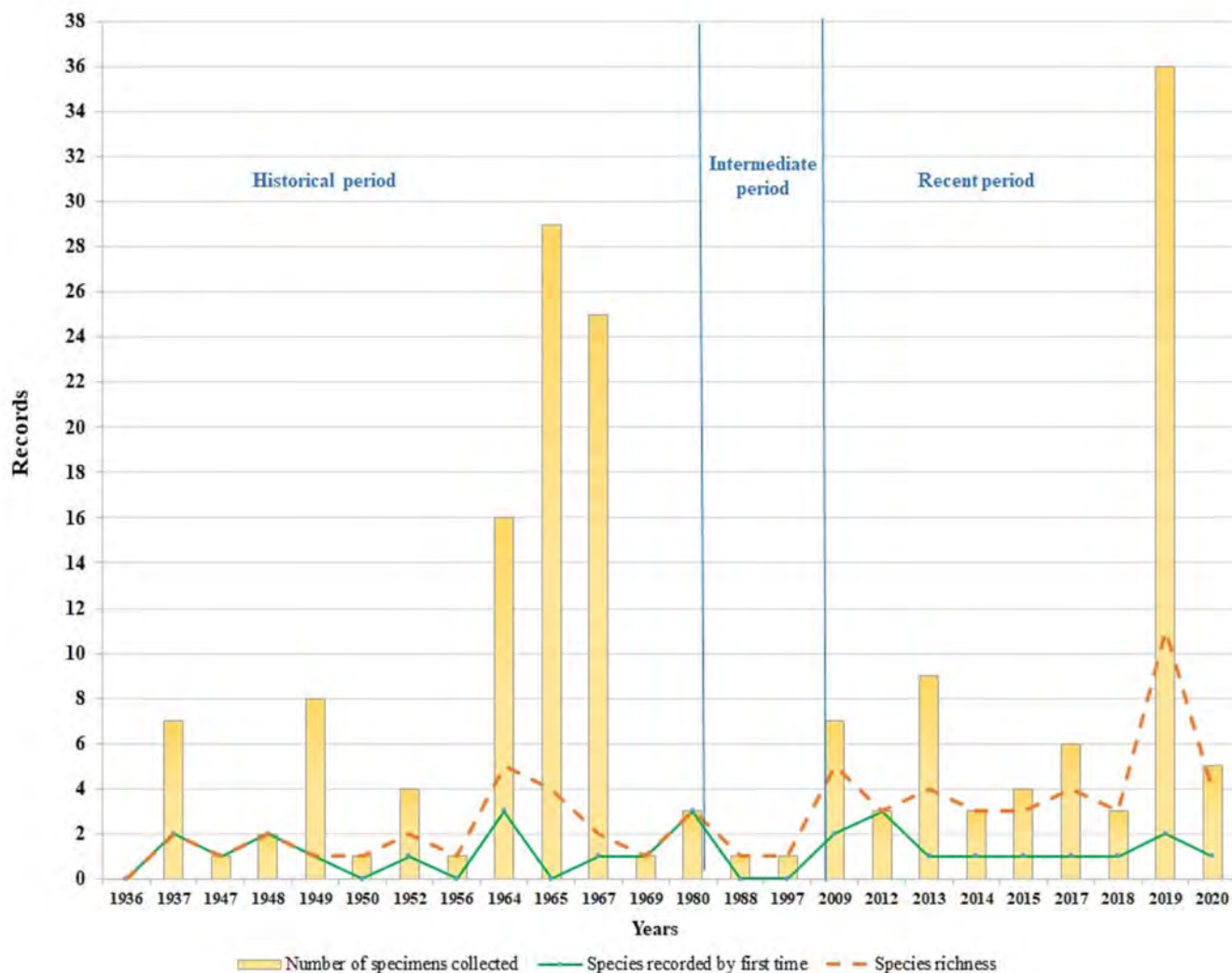
Our inventory of the wild mammals of Sierra de Guadalupe includes a total of 29 different species. Prior to this study, the presence of only four species had been properly documented: *N. macrotis*, *S. toltecus*, *M. occultus* ([Hortelano-](#)

Moncada et al. 2016), and *P. gratus* (IREKANI-CFB-2366). No peer-reviewed scientific publications on the wild mammals of Sierra de Guadalupe could be found; various technical reports and the management plans of the PNA of the area mention some species. Nineteen species were reported by GEM.SE.CGCE (2002), six species by GODF (2006), seven by Cedillo et al. (2008), six by PAOT (2009), six by CEPANAF (2015), twenty nine by GOCDMX (2016a), and twenty seven by GOCDMX (2016a b). In most of those cases, the source of such information and the existence of specimens supporting such claims are unknown.

The cumulative list of mammals reported by those sources includes 29 different species. The presence of 21 of those species was corroborated by our study; the remaining eight species, which are not included in our inventory, are the Mexican ground squirrel, *Ictidomys mexicanus*; the nine-banded armadillo, *Dasybus novemcinctus*; Mexican long-tailed shrew, *S. oreopolus*; nimble-footed mouse, *P. levipes*; Western harvest mouse, *R. megalotis*; bobcat, *Lynx rufus*; American hog-nosed skunk, *Conepatus leuconotus*; and hooded skunk, *Mephitis macroura*. In contrast, we documented the presence of eight species that had not been

previously reported for the area. Six of these species are new records for Sierra de Guadalupe: the Saussure's shrew, *S. saussurei*; Mexican long-tongued bat, *C. mexicana*; lesser long-nosed bat, *L. yerbabuena*; Merriam's pocket gopher, *C. merriami*; Mexican volcano mouse, *N. alstoni*; and plateau mouse, *P. melanophrys*. The other two species are the recently recorded *N. macrotis* and *S. toltecus* (Hortelano-Moncada et al. 2016).

The criteria adopted for including species in our inventory were that their presence in the area is properly documented through a formal record with correct taxonomic identification, and that the collection site is located within the boundaries of Sierra de Guadalupe. Thus, three species the Mexican ground squirrel, *I. mexicanus* (CNMA-7908); Mexican least shrew, *Cryptotis soricinus* (CNMA-1963); and silky pocket mouse, *Perognathus flavus* (ENCB 2268-2269) were not included in our inventory because they have been recorded near Sierra de Guadalupe but not within its boundaries. If the latter two species ever occurred in Sierra de Guadalupe, they are unlikely to be found now as records of them from other areas of CDMX are old and scarce (Hortelano-Moncada and Cervantes 2016). The Mexican



**Figure 3.** Number of specimens collected per year (yellow bars) and per period, number of species recorded per year (solid green line), and total species richness (dashed orange line) in Sierra de Guadalupe.

ground squirrel has been recently recorded in other parts of CDMX in habitats with shrubby herbaceous vegetation and can also occupy suburban green spaces. Thus, natural conditions suitable for its occurrence do exist in Sierra de Guadalupe ([Linzey et al. 2016](#)).

There are informal reports of the presence of the bobcat, *L. rufus*, in Sierra de Guadalupe and, in fact, we obtained a photographic record of what seems to be *L. rufus* excreta within the boundaries of Sierra de Guadalupe; however, since this could not be ascertained, we did not include this species in our inventory; this aspect deserves further surveys in the best preserved areas of Sierra de Guadalupe. In contrast, the lesser long-nosed bat, *L. yerbabuena*, had not been initially included in our inventory as only one recent photographic record (iNaturalist\_15353123) from within the area was found, but its poor resolution did not warrant its taxonomic determination. However, we were able to properly document the presence of this species in 2020 (specimen CNMA-49828).

Our data search found three records of the wrinkle-faced bat, *Centurio senex*, from areas near Sierra de Guadalupe. The first is a 2014 photographic record (iNaturalist-581022) from the Gustavo A. Madero municipality; the record entry states that the specimen had been collected and deposited in a scientific collection, but this could not be confirmed. A second specimen (ENCB\_4322) was collected in 2002 in the same municipality, and the third was mentioned by [Ramírez \(2012\)](#) as recorded in the Tlalnepantla municipality, State of Mexico, without reporting the collection locality. In the absence of further supporting evidence and based on the conclusions reached by [Sánchez et al. \(1989\)](#) and [Uhart and López-Vidal \(2008\)](#), who regard those records as the product of incidental dispersal, we believe that the distribution range of this species does not include the Sierra de Guadalupe, CDMX, or EDOMEX. Although [Ceballos et al. \(2006\)](#) include Mexico City and the State of Mexico within the potential distribution of this species, the nearest properly documented record comes from the Sierra de Huautla Biosphere Reserve, State of Morelos, where the dominant vegetation is deciduous tropical forest ([Orozco-Lugo et al. 2014](#)).

The most species-rich PNA within Sierra de Guadalupe is the Parque Estatal Sierra de Guadalupe (PESG) with 20 species, followed by the Zona Sujeta a Conservación Ecológica Sierra de Guadalupe (ZSCESG) with 17, the Zona de Conservación Ecológica La Armella (ZCELA) with eight, and the Parque Nacional El Tepeyac (PNT) with only seven species. These results seem consistent given that the PESG covers 82 % of the area of this mountain range, it is better preserved than the other PNA, its vegetation cover is mainly oak forest and xeric shrubland, and it includes the highest elevations of Sierra de Guadalupe ([Cedillo et al. 2007](#); [CEP-ANAF 2015](#)).

The historical analysis of the number of collections made and species recorded shows that 14 species (48.3 % of the total number of known species) were first documented in Sierra de Guadalupe between 2009 and 2020. This figure

contrasts with the 43-year historical period (1937–1980) when only 15 species were recorded. Only two specimens were collected, and no new species were recorded during the 27-year period between 1981 and 2008). This might be related, on the one hand, to the restrictions on the collection of wild specimens imposed with the decree of these areas as Protected Natural Areas. The portion of the Sierra de Guadalupe mountain range located in the State of Mexico was officially decreed as the Sierra de Guadalupe State Park in 1976. The portion located in CDMX was decreed as the Sierra de Guadalupe Ecological Conservation Area by the federal government in 1990 aimed at containing urban expansion; the gradual invasion of irregular settlements was causing serious damage to this area of great ecological value and adversely affecting the wildlife. Moreover, in an attempt to protect the Sierra de Guadalupe, a perimeter fence was built in the mid-1990s in the area corresponding to CDMX; this led to social conflicts that increased insecurity in the area and perhaps also contributed to the lack of field studies therein.

The study reported herein, which started in 2019, has recorded the largest number of specimens and species collected, with 36 specimens and 11 species, respectively. This highlights the importance of carrying out systematic and scheduled samplings using various data collection methods, including direct and indirect evidence (excreta, pellets, and photographic material) in addition to collecting specimens. On the other hand, the support of and collaboration with staff of the Dirección General de Sistemas de Áreas Naturales Protegidas y Áreas de Valor Ambiental Sierra de Guadalupe DGSANPAVA) office at the Secretaría del Medio Ambiente (SEDEMA) of the Mexico City government was extremely valuable. They provided biological material that they had collected while implementing the management programs; this material was properly documented and deposited in the Colección Nacional de Mamíferos of Instituto de Biología of Universidad Nacional Autónoma de México. Another valuable source of historical information was the specimens deposited in various scientific collections; this highlights the importance of such collections for a range of studies, including biological inventories, as they keep the specimens and their supplementary information available now and in the future ([Hortelano-Moncada and Cervantes 2011](#); [León-Tapia et al. 2020](#)).

The species-accumulation curve showed that the data gathered provide a reasonably good representation of the mammal species inhabiting Sierra de Guadalupe. The possibility of finding additional species such as bats, particularly in the PA located in EDOMEX, cannot be ruled out. At the same time, some of the species listed in our inventory might no longer be found in Sierra de Guadalupe due to the reduction and alterations of the original habitat in this area ([Cedillo et al. 2007, 2008](#); [Villavicencio 2007](#)). This might be the case of *H.s irroratus* (last recorded in 1964 and 1967), *M. mexicanus* (1949), *P. maniculatus* (1948, 1956), and *R. fulvescens* (1956, 1964). Additional collection efforts may

be required to confirm the continued presence of other species such as *N. macrotis* (last recorded in 1980, 1988, and 1997), *M. occultus* (1969), *M. velifer* (1937, 1950, 1956), and *C. merriami* (1980).

The number of wild mammal species reported herein for Sierra de Guadalupe accounts for 35.8 % of all the species recorded for CDMX (Hortelano-Moncada et al. 2016) and 23.2 % of the species for EDOMEX (Chávez et al. 2009). A total of 21 species (considering the three PNA) were recorded in the CDMX portion of Sierra de Guadalupe, while 20 species were recorded in the area located in EDOMEX, representing 72.4 and 68.9 %, respectively, of the total diversity of mammals of Sierra de Guadalupe. Our field work was mainly carried out in the PNA of CDMX due to security concerns and logistic considerations. However, if additional collection efforts are carried out, the number of species in the PESG (EDOMEX) would be expected to increase, as this PNA is almost three times the size of the PNA located in CDMX and has a larger well-preserved area (GEM.SE.CGCE 2002).

Eleven species (38 %) are shared by CDMX and EDOMEX; these include highly vagile species such as *B. astutus*, *D. virginiana*, *N. macrotis*, *O. variegatus*, *S. aureogaster*, *S. floridanus*, and *U. cinereoargenteus*, as well as other less vagile but widespread species such as *B. taylori*, *P. difficilis*, *P. gratus*, and *S. toltecus*. Nine species (31 %) are unique to either CDMX or EDOMEX; these are rare species that use sites of Sierra de Guadalupe as a refuge, habitat, or perch during their migration, and others that are difficult to capture. The species recorded in Mexico City but not in EDOMEX are *A. cinereus*, *C. mexicana*, *C. merriami*, *L. yerbabuena*, *M. occultus*, *N. alstoni*, *P. labecula*, *P. melanophrys*, and *S. angustifrons*. The species unique to the State of Mexico are *C. latrans*, *C. fumosus*, *H. irroratus*, *M. mexicanus*, *M. frenata*, *M. velifer*, *R. fulvescens*, *S. saussurei*, and *T. brasiliensis*.

Of the 118 Protected Natural Areas in EDOMEX and the 24 in CDMX, studies with documented records of mammals have been conducted only in 11: five protected natural areas of EDOMEX (Monroy-Vilchis and Velázquez 2002; Monroy-Vilchis et al. 2011; Sánchez-Jasso et al. 2013; Aranda et al. 2014; Espinosa-Graciano and García-Collazo 2017) and six in CDMX (Villa-Ramírez 1953; Aranda et al. 1980; Mandujano and Hernández 1990; Castro-Campillo et al. 1992; Ramírez-Pulido et al. 2004; Bárcenas and Medellín 2007; Navarro-Frías et al. 2007; Castro-Campillo et al. 2008; Hortelano-Moncada et al. 2016). These are disturbing figures as, even including the four PNA studied in the present work, it means that documented records of mammals only exist for 12.7 % of the PNA of both states.

Considering its extent, the species richness of Sierra de Guadalupe is remarkable; for instance, only 11 species have been reported for the similarly sized (9768.2 ha) Sierra de Tepozotlán State Park (Espinosa-Graciano and García-Collazo 2017). Sierra de Guadalupe is also species-richer than the Desierto de los Leones National Park where 22 species have been recorded (Aranda et al. 1980; Mandujano

and Hernández 1990; Ramírez-Pulido et al. 2004; Castro-Campillo et al. 2008), although this protected natural area is about half the size of Sierra de Guadalupe. Thus, the Desierto de los Leones is proportionately more diverse per unit area, but Sierra de Guadalupe is richer in terms of the total number of species. Moreover, Desierto de los Leones is better preserved than Sierra de Guadalupe and has drawn greater scientific interest. Separately, there are fewer mammal species in Sierra de Guadalupe than in the urban reserve Reserva Ecológica del Pedregal de San Ángel, where 33 mammal species have been recorded in only 237.3 ha. We attribute this difference to the great scientific interest that Pedregal de San Ángel has drawn for many years, which has led to a large number of collection records and species findings (Hortelano-Moncada et al. 2009).

The conservation of Sierra de Guadalupe is fundamental as it harbors three Mexican mammal species (*C. mexicana*, *L. yerbabuena*, and *C. fumosus*) that are listed under some level of threat by the Official Mexican Standard (NOM-059-SEMARNAT-2019), and the first two are also listed by IUCN (2020). Sierra de Guadalupe harbors six rodent species (*C. fumosus*, *C. merriami*, *N. alstoni*, *P. difficilis*, *P. melanophrys*, and *R. fulvescens*) that are endemic to Mexico. Although all the species living in this mountain range have been also recorded in other parts of CDMX and EDOMEX, they have probably become isolated in these PNA that are surrounded by urban areas.

Sierra de Guadalupe is the last significant natural area remaining in the northern part of Mexico City. This is the first documented inventory of the wild mammals occurring in that area and one of the few detailed inventories addressing the protected natural areas of CDMX and EDOMEX. Anthropogenic alterations and impacts including formal and irregular human settlements, introduced fauna and flora, illegal trade of native fauna, logging and timber extraction, pollution, agricultural activities, induced pastures for sheep and cattle ranching, and wildfires altogether pose enormous pressures on the area and jeopardize its preservation (Cedillo et al. 2007; Villavicencio 2007; SPC 2014).

Our study highlights the importance of nature reserves for wildlife conservation in urbanized landscapes. Knowledge of the native mammal fauna helps the local population to better appreciate the natural environment and perceive its benefits; it can also inform the formulation and implementation of governmental actions for the preservation and restoration of the natural resources of this area, which has endured high disturbance rates driven by increasing population density (SPC 2014). It is also expected to help improve the coordination between the two states that have jurisdiction over the Sierra de Guadalupe in the implementation of management plans.

A total of 29 wild mammal species was found in the Sierra de Guadalupe PA; this is a significant number compared to other smaller PNA. Three of those species have been listed under some level of threat by the Mexican government and two of those are also listed in an international

standard; six other species are endemic to Mexico. These facts are important, particularly considering that this area is located in one of the most populated areas of the world, under enormous pressures caused by urban expansion, pollution, wildfires, introduction of exotic fauna, and vandalism, among others.

Our study contributes to better appreciate the importance of the wild fauna thriving in the last significant natural area remaining in the northern part of Mexico City, where resources are limited and the demands of a growing population make conservation actions difficult to implement and maintain. The updated taxonomic list of mammals sets the grounds to initiate actions for the conservation and restoration of biodiversity in this area.

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## Appendix 1

Specimens examined (n) of the species that are distributed in the Sierra de Guadalupe. Catalog number and biological collections or web pages where the specimens are deposited (CNMA = Colección Nacional de Mamíferos del Instituto de Biología de la Universidad Nacional Autónoma de México; ENCB = Colección de Mamíferos de la Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional; UAMI = Colección Mastozoológica de la Universidad Autónoma Metropolitana, Unidad Iztapalapa; FCMM = Colección de Mamíferos del Museo de Zoología "Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México; KU = Biodiversity Institute and Natural History Museum; IR = IREKANI e iN = iNaturalist). Collection location: number, geographical description, coordinates (location in Figure 1). ZCELA = Zona de Conservación Ecológica "La Armella"; ZSCESG = Zona Sujeta a Conservación Ecológica "Sierra de Guadalupe"

***Didelphis virginiana*** (n = 14). **Mexico City:** Locality 1: ZCELA, 1.76 km NNE Malacates, 2,471 m (19° 35' 25.70", -99° 07' 19.66"; 49450 CNMA); Locality 5: Paraje La Cruz, 1.13 km NNE Malacates, 2,590 m (19°35'11.78", -99°07'39.59"; 49448 CNMA); Locality 8: ZCELA, 1.03 km NE Malacates, 2,585 m (19°34'59.27", -99°07'24.17"; 9508175 iN); Locality 12: ZSCESG, 1.51 km E Malacates, 2,414 m (19°34'30.42", -99°06'58.34"; 7635574 iN); Locality 14: Caballerizas, 0.58 km ENE La Forestal 1, 2,359 (19°34'09.28", -99°07'22.55"; 12659 IR); Locality 15: Barranca La Mora, 0.77 km ENE La Forestal, 2,431 m (19°34'08.57", -99°07'16.62"; 49447, 49449 CNMA); Locality 18: La Mora 0.49 km ESE La Forestal 1, 2,380 m (19°33'53.70", -99°07'27.18"; 48826 CNMA); Locality 21: Torre de Joya, 0.88 km ENE La Casilda, 2,508 m (19°33'29.58", -99°06'58.57"; 12656 IR); Locality 23: Torre de Joya, 0.64 km ENE La Casilda, 2,563 m (19°33'27.62", -99°07'06.60"; 49822-49825 CNMA). **State of Mexico:** Locality 52: 0.15 km NW Amp. Izcalli, Ecatepec de Morelos, 2,294 m (19°35'42.61", -99°03'12.43"; 38032568 iN).

***Sorex saussurei***. (n = 2). **State of Mexico:** Locality 51: 3.25 km SEE Amp. San Mateo, Tultitlán, 2,375 m (19°35'43.73", -99°06'58.31"; 49452 CNMA); Locality 55, 3.90 km ESE Solidaridad 3ra Secc., Tultitlán, 2,285 m (19°35'32.70", -99°06'58.95"; 49451 CNMA).

***Choeronycteris mexicana***. (n = 1). **Mexico City:** Locality 33: Cerro Zacatenco, 0.55 Km NNW San Pedro Zacatenco, 2,259 m (19°30'37.73", 99°07'14.47"; 49827 CNMA).

***Leptonycteris yerbabuena***. (n = 1). **Mexico City:** Locality 33: Cerro Zacatenco, 0.55 Km NNW San Pedro Zacatenco, 2,259 m (19°30'37.73", 99°07'14.47"; 49828 CNMA).

***Tadarida brasiliensis***. (n = 3). **State of Mexico:** Locality 47: 0.67 km SW Bosques de Coacalco, Coacalco de Berriozábal, 2,384 m (19°36'33.99", -99°05'56.40"; 5177-5178 ENCB); Locality 49: 1.40 km SSW Bosques de Coacalco, Coacalco de Berriozábal, 2,472 m (19°36'09.59", -99°06'01.67"; 49453 CNMA).

***Nyctinomops macrotis***. (n = 4). **Mexico City:** Locality 26: 0.38 km S Cerro del Chiquihuite, 2,274 m (19°32'39.00", -99°07'46.00"; 3160 UAMI); Locality 31: Cerro Zacatenco 0.50 km

E Zacatenco Lindavista, 2,248 m (19°30'42.99", -99°07'14.00"; 30502 ENCB); Locality 41: Cerro Los Gachupines, 0.83 km SSW Santa Isabel Tola, 2,240 m (19°29'28.00", -99°07'03.00"; 6684 FCMM). **State of Mexico:** Locality 42: 1.05 km WSW San Francisco Coacalco, Coacalco de Berriozábal, 2,253 m (19°37'56.74", -99°06'49.07"; 37309396 iN).

***Aeorestes cinereus***. (n = 1). **Mexico City:** Locality 32: ZSCESG, 0.75 km SSE La Casilda, 2,445 m (19°32'57.95", -99° 07'15.44"; 49454 CNMA).

***Myotis occultus***. (n = 1). **Mexico City:** Locality 39: Cerro de la Villa, 0.49 km S Santa Isabel Tola, 2,255 m (19°29'36.00", -99°06'48.00"; 4238 ENCB).

***Myotis velifer***. (n = 7). **State of Mexico:** Locality 45: 0.72 km E Vista Hermosa, Ecatepec de Morelos, 2,392 m (19°36'35.00", -99°03'36.00"; 5167 CNMA); Locality 47: 0.67 km SO Bosques de Coacalco, Coacalco de Berriozábal, 2,384 m (19°36'33.99", -99°05'56.40"; 5170-5175 ENCB).

***Sylvilagus floridanus***. (n = 8). **Mexico City:** Locality 9: ZCELA, 0.75 km NE Malacates, 2,533 m (19°34'56.64", -99°07'36.12"; 7620962, 7689594 iN); Locality 10: ZCELA, 0.69 km NW Malacates, 2,463 m (19°34'54.77", -99°08'03.40"; 49829 CNMA); Locality 16: ZSCESG, 0.94 km E La Forestal 1, 2,460 m (19°34'01.30", -99°07'09.69"; 7689602 iN); Locality 19: ZSCESG, 1.24 km ENE Arboledas de Cuauhtepic, 2,465 m (19°33'51.03", -99°06'56.34"; 12696 IR); Locality 5: ZCELA, 1.22 km NNE Malacates, 2,599 m (19°35'13.85", -99°07'36.45"; 12696 IR). **State of Mexico:** Locality 45: 0.72 km E Vista Hermosa, Ecatepec de Morelos, 2,392 m (19°36'35.00", -99°03'36.00"; 1055 CNMA); Locality 52: 0.15 km NW Amp. Izcalli, Ecatepec de Morelos, 2,294 m (19°35'42.61", -99°03'12.43"; 48488674 iN); Locality 54: 1.30 km W Amp. Izcalli, Ecatepec de Morelos, 2,376 m (19°35'33.55", -99°03'53.79"; 10492020 iN).

***Otospermophilus variegatus***. (n = 4). **Mexico City:** Locality 6: ZCELA, 0.98 km NNE Malacates, 2,511 m (19°35'04.62", -99°07'34.80"; 7635584 iN); Locality 27: Cerro Chiquihuite, 0.48 km E La Pastora, 2,473 m (19°31'43.68", -99°07'52.91"; 49456 CNMA). **State of Mexico:** Locality 52: 0.15 km NW Amp. Izcalli, Ecatepec de Morelos, 2,294 m (19°35'42.61", -99°03'12.43"; 48488763 iN); Locality 57: 0.31 km SSW Amp. Izcalli, Ecatepec de Morelos, 2,284 m (19°35'30.17", -99°03'15.25"; 23814129 iN).

***Sciurus aureogaster***. (n = 3). **Mexico City:** Locality 23: Torre de Joya, 0.64 km ENE La Casilda, 2,563 m (19°33'27.62", -99°07'06.60"; 12691 IR). **State of Mexico:** Locality 52: 0.15 km NW Amp. Izcalli, Ecatepec de Morelos, 2,294 m (19°35'42.61", -99°03'12.43"; 12692 IR, 19493033 iN).

***Cratogeomys fumosus***. (n = 1). **State of Mexico:** Locality 43: 0.39 km ESE Santa María Cuauhtepic, Tultitlán, 2,333 m (19°37'26.49", -99°07'41.40"; 49457 CNMA).

***Cratogeomys merriami***. (n = 1). **Mexico City:** Locality 4: ZCELA, 1.36 km NNE Malacates, 2,600 m (19°35'16.30", -99°07'30.57"; 27176 CNMA).

***Heteromys irroratus***. (n = 4). **State of Mexico:** Locality 61: 0.75 km W Amp. Independencia, Tlalnepantla de Baz, 2,257 m (19°33'33.01", -99°10'59.99"; 1164 ENCB); Locality 46: 0.47

km S Bosques de Coacalco, Coacalco de Berriozábal, 2,392 m (19°36'33.99", -99°05'42.00"; 3387-3389 ENCB).

**Microtus mexicanus.** ( $n = 8$ ). **State of Mexico:** Locality 60: 0.42 km NNE Loma Linda, Tlalnepantla de Baz, 2,361 m (19°33'40.01", -99°05'48.99"; 850-857 CNMA).

**Baiomys taylori.** ( $n = 4$ ). **Mexico City:** Locality 30: Cerro Zacatenco 0.78 km ENE Zacatenco Lindavista, 2,262 m (19°30'44.76", -99°07'04.90"; 49830 CNMA); Locality 35: Cerro Zacatenco, 0.34 Km SE San Pedro Zacatenco, 2,252 m (19°30'15.71", -99°07'00.62"; 49831 CNMA). **State of Mexico:** Locality 61: 0.75 km W Amp. Independencia, Tlalnepantla de Baz, 2,257 m (19°33'33.01", -99°10'59.99"; 1179, 1255 ENCB).

**Neotomodon alstoni.** ( $n = 2$ ). **Mexico City:** Locality 11: ZCELA, 0.81 km NE Malacates, 2,443 m (19°34'54.70", -99°07'30.30"; 49661, 49662 CNMA).

**Peromyscus difficilis.** ( $n = 27$ ). **Mexico City:** Locality 2: ZCELA, 1.58 km NNE Malacates, 2,660 m (19°35'20.63", -99°07'22.85"; 49833, 49834 CNMA); Locality 4: ZCELA, 1.36 km NNE Malacates, 2,600 m (19°35'16.30", -99°07'30.57"; 49835 CNMA); Locality 22: Torre de Joya, 0.59 km E La Casilda, 2,561 m (19°33'18.36", -99°07'06.60"; 49832 CNMA); Locality 29: Cerro Zacatenco 0.39 km ENE Zacatenco Lindavista, 2,445 m (19°30'49.50", -99°07'18.08"; 49837 CNMA); Locality 37: Cerro Vicente Guerrero 0.81 km E Santa Isabel Tola, 2,262 m (19°29'54.64", -99°06'21.97"; 49458 CNMA). **State of Mexico:** Locality 46: 0.47 km S Bosques de Coacalco, Coacalco de Berriozábal, 2,392 m (19°36'33.99", -99°05'42.00"; 3390-3411 ENCB); Locality 53: 2.64 km ESE Solidaridad 3ra Secc., Tultitlán, 2,805 m (19°35'39.42", -99°07'44.62"; 49836 CNMA).

**Peromyscus gratus.** ( $n = 34$ ). **Mexico City:** Locality 7: ZCELA, 1.20 km NE Malacates, 2,610 m (19°35'03.06", -99°07'20.92"; 2366 IR-CFB); Locality 23: Torre de Joya, 0.64 km ENE La Casilda, 2,563 m (19°33'27.62", -99°07'06.60"; 49838 CNMA); Locality 24: ZSCESG, 0.33 km ESE La Casilda, 2,445 m (19°33'14.99", -99°07'16.40"; 49839 CNMA); Locality 37: Cerro Vicente Guerrero 0.81 km E Santa Isabel Tola, 2,262 m (19°29'54.64", -99°06'21.97"; 49459 CNMA); Locality 38: Cerro Vicente Guerrero 0.1 km E Santa Isabel Tola, 2,245 m (19°29'51.00", -99°06'50.00"; 686 CNMA). **State of Mexico:** Locality 44: 0.89 km ENE Bosques de Coacalco, Coacalco de Berriozábal, 2,358 m (19°36'59.00", -99°05'11.00"; 1216-1222, 2014, ENCB); Locality 53: 2.64 km ESE Solidaridad 3ra Secc., Tultitlán, 2,805 m (19°35'39.42", -99°07'44.62"; 49840 CNMA); Locality 61: 0.75 km W Amp. Independencia, Tlalnepantla de Baz, 2,257 m (19°33'33.01", -99°10'59.99"; 1168-1177, 1245-1254, 2013 ENCB).

**Peromyscus labecula fulvus.** ( $n = 2$ ). **Mexico City:** Locality 28: Cerro del Chiquihuite, 0.12 km NW Cuauhtémoc, 2,327 m (19°31'28.99", -99°08'09.37"; 49332-49333 KU).

**Peromyscus labecula labecula.** ( $n = 1$ ). **Mexico City:** Locality 38: Cerro Vicente Guerrero 0.1 km E Santa Isabel Tola, 2,245 m (19°29'51.00", -99°06'50.00"; 629 CNMA).

**Peromyscus melanophrys.** ( $n = 8$ ). **Mexico City:** Locality 14: Caballerizas, 0.58 km ENE La Forestal 1, 2,359 m (19°34'09.28", -99°07'22.55"; 49841-49848 CNMA).

**Reithrodontomys fulvescens.** ( $n = 12$ ). **Mexico City:** Locality 28: Cerro del Chiquihuite, 0.12 km NW Cuauhtémoc, 2,327 m (19°31'28.99", -99°08'09.37"; 49050-49051 KU). **State of Mexico:** Locality 44: 0.89 km ENE Bosques de Coacalco, Coacalco de Berriozábal, 2,358 m (19°36'59.00", -99°05'11.00"; 1165-1167 ENCB); Locality 61: 0.75 km W Amp. Independencia, Tlalnepantla de Baz, 2,257 m (19°33'33.01", -99°10'59.99"; 1209-1215 ENCB).

**Sigmodon toltecus.** ( $n = 5$ ). **Mexico City:** Locality 13: Barranca La Mora, 1.34 km ENE La Forestal 1, 2,373 m (19°34'21.64", -99°07'01.30"; 49460 CNMA); Locality 34: Cerro Zacatenco, 0.45 Km NNW San Pedro Zacatenco, 2,292 m (19°30'35.93", -99°07'16.88"; 49461 CNMA); Locality 41: Cerro Los Gachupines, 0.83km SSW Santa Isabel Tola, 2,240 m (19°29'28.00", -99°07'03.00"; 3425-3426 CNMA). **State of Mexico:** Locality 61: 0.75 km W Amp. Independencia, Tlalnepantla de Baz, 2,257 m (19°33'33.01", -99°10'59.99"; 1178 ENCB).

**Canis latrans.** ( $n = 1$ ). **State of Mexico:** Locality 58: 2.46 km E Buenavista 2da Secc., Tultitlán, 2,373 m (19°34'51.21", -99°08'44.82"; 49462 CNMA).

**Urocyon cinereoargenteus.** ( $n = 4$ ). **Mexico City:** Locality 3: ZCELA, 1.49 km NNE Malacates, 2,621 m (19°35'19.00", -99°07'26.00"; 12662 IR). **State of Mexico:** Locality 43: 0.39 km ESE Santa María Cuauhtémoc, Tultitlán, 2,333 m (19°37'26.49", -99°07'41.40"; 12693 IR); Locality 50: 3.46 km ESE Amp. San Mateo, Tultitlán, 2,321 m (19°35'44.05", -99°07'14.06"; 12694 IR); Locality 56: 3.45 km ESE Solidaridad 3ra Secc., Tultitlán, 2,270 m (19°35'32.00", -99°07'17.00"; 12659 IR).

**Spilogale angustifrons.** ( $n = 4$ ). **Mexico City:** Locality 25: ZSCESG, 0.75 km SSE La Casilda, 2,445 m (19°32'57.95", -99°07'15.44"; 49464-49465 CNMA); Locality 36: Cerro Vicente Guerrero 0.72 km NE Santa Isabel Tola, 2,241 m (19°30'06.39", -99°06'29.77"; 7714755 iN; Locality 40); Cerro Los Gachupines, 0.62 km S Santa Isabel Tola, 2,264 m (19°29'32.00"-99°06'53.70"; 49463 CNMA).

**Mustela frenata.** ( $n = 1$ ). **State of Mexico:** Locality 45: 0.72 km E Vista Hermosa, Ecatepec de Morelos, 2,392 m (19°36'35.00", -99°03'36.00"; 21581 CNMA).

**Bassariscus astutus.** ( $n = 7$ ). **Mexico City:** Locality 17: ZSCESG, 0.84 km NE Arboledas de Cuauhtémoc, 2,349 m (19°33'55.77", -99°07'17.81"; 7635408 iN); Locality 20: 0.40 km NE Arboledas de Cuauhtémoc, 2,377 m (19°33'42.80", -99°07'24.47"; 49849 CNMA); Locality 27: Cerro Chiquihuite, 0.48 km E La Pastora, 2,473 m (19°31'43.68", -99°07'52.91"; 49466 CNMA). **State of Mexico:** Locality 48: 0.83 km SSW Vista Hermosa, Ecatepec de Morelos, 2,371 m (19°36'09.66", -99°04'14.42"; 49874606 iN); Locality 55: 0.15 km NW Amp. Izcalli, Ecatepec de Morelos, 2,294 m (19°35'42.61", -99°03'12.43"; 24285898 iN); Locality 53: 2.64 km ESE Solidaridad 3ra Secc., Tultitlán, 2,805 m (19°35'39.42", -99°07'44.62"; 12654 IR); Locality 62: 1.11 km ENE Cuauhtémoc, Tlalnepantla de Baz, 2,404 m (19°33'32.25", -99°09'26.85"; 7635448 iN).



# Spatial ecological interactions between coyote and gray fox in a temperate forest

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Coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) are abundant and widely distributed in México, with no information currently available about their spatial interactions in the country. Our objectives were to evaluate the habitat use of these species and the environmental interactions between them throughout the overlapping areas of their home ranges in temperate forests of Durango, México. We expected that their coexistence would be facilitated by the spatial segregation of their ecological niche, exhibited by the low or nil overlap between their home ranges or by differentiated habitat use. Radio-collars (VHF) were attached to nine individuals — four coyotes (two males and two females) and five gray foxes (females) — that were radio-tracked from September 2017 to August 2019. We estimated their home ranges and the size of their core areas through the minimum convex polygon and determined the extent of overlap between them. Also, we evaluated third-order habitat selection and use based on habitat availability using Manly's habitat-selection ratios and simultaneous Bonferroni confidence intervals (95 %). The mean home range size for coyotes was larger ( $12.2 \pm 1.74 \text{ km}^2$ ) than for gray foxes ( $5.3 \pm 0.67 \text{ km}^2$ ); the interspecific mean overlap was 42 % (moderate). Of these two canids, just the gray fox showed a markedly selective habitat use. Our findings revealed a moderate overlap between the home ranges of both canids, so spatial segregation did not occur. Although a differential habitat use was observed, explaining the coexistence between these two canids in the areas where they thrive, they tend to avoid agonistic interactions.

El coyote (*Canis latrans*) y la zorra gris (*Urocyon cinereoargenteus*) son especies abundantes y de amplia distribución en México y con poca información acerca de sus interacciones espaciales. Nuestros objetivos fueron, evaluar sus interacciones ecológicas espaciales, a través de la superposición de sus ámbitos hogareños y del uso de hábitat en los bosques templados de Durango, México. Esperábamos que su coexistencia fuera facilitada por la segregación de su nicho ecológico a nivel espacial, exhibida por la baja o ausente superposición entre sus ámbitos hogareños y/o por un marcado uso diferenciado del hábitat. Se colocaron radio-collares (VHF) en nueve individuos, cuatro coyotes (dos machos y dos hembras) y cinco zorras grises (hembras), monitoreándolos entre septiembre de 2017 y agosto de 2019. Estimamos el tamaño de ámbito hogareño y zona núcleo de cada individuo mediante el método del mínimo polígono convexo y determinamos la proporción del área de superposición entre ellos. Además, evaluamos el uso y selección de hábitat de tercer orden con respecto a su disponibilidad mediante el coeficiente de selección de hábitat de Manly e intervalos de confianza de Bonferroni (95 %). El tamaño promedio del ámbito hogareño fue mayor para coyotes ( $12.2 \pm 1.74 \text{ km}^2$ ), que para las zorras grises ( $5.3 \pm 0.67 \text{ km}^2$ ); mientras que, el promedio de la superposición interespecífica fue de 42 % (intermedio). De los dos cánidos, sólo la zorra gris presentó un marcado uso selectivo del hábitat. Nuestros resultados mostraron que los ámbitos hogareños de ambos cánidos presentaron una superposición intermedia, por lo que no se presentó segregación espacial. Aunque si existió un uso diferencial del hábitat, que explica la coexistencia entre estos dos cánidos en los sitios donde ocurren, ya que tienden a evitar interacciones antagónicas.

**Keywords:** Biosphere reserve; *Canis latrans*; coexistence; Durango; habitat use; home range; overlap; radiotelemetry; segregation; *Urocyon cinereoargenteus*.

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## Introduction

The ecological interactions between sympatric species through competition (interference or exploitation) are key phenomena that contribute to shaping the structure of ecological communities, as they can influence the abundance, distribution, habitat selection, and behavior of species within communities (Case and Gilpin 1974; Holt and Polis 1997; Caro and Stoner 2003; Hunter and Caro 2008).

Interference competition is widely documented for mammals of the order Carnivora, being considered among

the main factors that shape intraguild relationships between predators (Polis *et al.* 1989; Palomares and Caro 1999; Linell and Strand 2000; Donadio and Buskirk 2006; Palomares *et al.* 2016). In fact, this type of competition between carnivores is generally higher when the species involved are morphologically similar and share similar diets (Morin 1999). The strategy of species to achieve coexistence consists of minimizing competition through niche segregation in one or several dimensions, mainly spatial, trophic, or temporal (MacArthur and Levins 1967;

[Pianka 1969](#); [Pianka 1973](#); [Schoener 1974](#)). Within this guild, the potential for competition between sympatric species that use similar resources is largely determined by the spatial overlap between them ([Kitchen et al. 1999](#); [Palomares and Caro 1999](#); [Grassel et al. 2015](#); [Palomares et al. 2016](#)). To minimize interference competition, subordinate species display a range of ecological strategies: avoidance of encounters with individuals of dominant species, separation of their home ranges, and differences in habitat use ([Case and Gilpin 1974](#); [Palomares and Caro 1999](#); [Linell and Strand 2000](#); [Hampton 2004](#); [Rosenheim 2004](#); [Donadio and Buskirk 2006](#); [Berger and Gese 2007](#); [Hunter and Caro 2008](#); [Chiang et al. 2012](#); [Viota et al. 2012](#); [Soto and Palomares 2015](#); [Xia et al. 2015](#); [Gompper et al. 2016](#); [Palomares et al. 2016](#)).

The quantification of the size and overlap of the home ranges of carnivores, as well as the description of habitat use and selection, are essential for understanding the dynamics of ecological communities, as well as for species conservation and management ([Bu et al. 2016](#)). However, these complex interactions between sympatric species are generally poorly known in the vast majority of the systems where they thrive ([Melville et al. 2015](#); [Gompper et al. 2016](#)).

In North America, the coyote (*Canis latrans*) and the gray fox (*Urocyon cinereoargenteus*) are mesocarnivorous species that are sympatric over large portions of their distribution ranges ([Bekoff 1977](#); [Fritzell and Haroldson 1982](#); [Fuller and Cypher 2004](#); [Servin et al. 2014a](#); [Servin and Chacón 2014](#)). The spatial interactions and the coexistence process between coyotes and various species of foxes in the Americas have been extensively studied in northern areas of their geographic range (United States of America and Canada). Research on spatial dynamics between coyotes and red foxes (*Vulpes vulpes*) has shown marked spatial segregation and differentiated use of the local habitat between these species ([Voigt and Earle 1983](#); [Sargeant et al. 1987](#); [Theberge and Wedeles 1989](#); [Harrison et al. 1989](#); [Sargeant and Allen 1989](#); [Gese et al. 1996](#); [Gosselink et al. 2003](#); [Mueller et al. 2018](#)). In turn, research on the spatial dimension between coyotes and kit foxes (*Vulpes macrotis*) has shown the absence of spatial segregation; instead, a differential habitat use has been observed ([White et al. 1994](#); [White et al. 1995](#); [Nelson et al. 2007](#); [Moehrensclager et al. 2007](#); [Kozłowski et al. 2008](#); [Kozłowski et al. 2012](#); [Andrade-Ponce et al. 2020](#)). Most information on spatial interactions between coyotes and gray foxes has been recorded in the United States of America, mainly in coastal shrubland and xeric shrubland areas at low altitudes (<1000 m asl). Some studies reported no spatial segregation between the two species ([Neale and Sacks 2001](#); [Chamberlain and Leopold 2005](#)), while others evidenced that gray foxes avoid spatial coexistence with coyotes to reduce the risk of predation ([Fedriani et al. 2000](#); [Farias et al. 2012](#)). This topic has been scarcely studied in areas within their distribution range in México, and the details about the spatial dynamics between these canid species in their natural distribution range in the country remain unknown.

For this reason, our objective was to evaluate the spatial ecological interactions between coyotes and gray foxes by analyzing the spatial segregation of the ecological niche under natural conditions in a temperate forest of the Sierra Madre Occidental, state of Durango, México. Our specific objectives were: 1) estimate the size and spatial overlap between the home ranges of both species and 2) evaluate habitat selection and use patterns to determine interspecific variations.

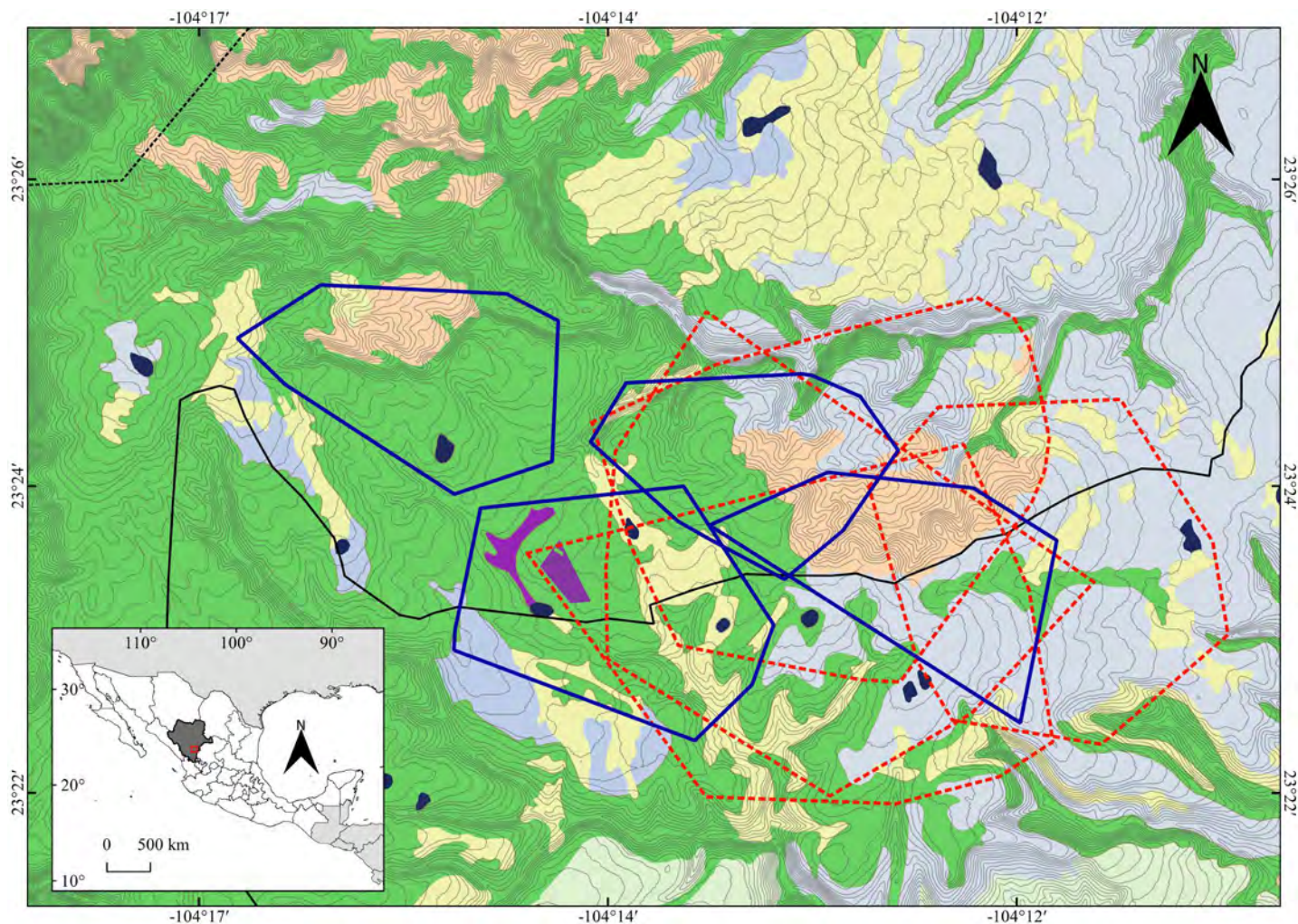
Our assumption was that the coexistence of these two species would be facilitated by the spatial segregation of their niches, exhibited by either a low or nil overlap of their home ranges or a pattern of differentiated habitat use. This is a case of an asymmetric interaction where coyotes display aggressive behavior against canids and other smaller species, which are displaced and even killed by coyotes, as reported for various fox species in North America ([Sargeant and Allen 1989](#); [Palomares and Caro 1999](#); [Moehrensclager and Sovada 2004](#); [Moehrensclager et al. 2007](#)). Thus, the gray fox (subordinate species) would be actively avoiding coyotes (dominant species) to reduce the risk of predation ([Polis et al. 1989](#); [Palomares and Caro 1999](#); [Fedriani et al. 2000](#); [Donadio and Buskirk 2006](#); [Temple et al. 2010](#); [Farias et al. 2012](#)).

## Materials and Methods

**Study area.** This study was conducted in the buffer zone of “La Michilía” Biosphere Reserve (RBM), located in the municipality of Suchil, Durango, México, between coordinates 23° 21’ to 23° 28’ N and -104° 09’ to -104° 21’ W (Figure 1). Physiographically, RBM is located in the transition zone between the Sierra Madre Occidental and the northern highlands of México ([Halffter 1978](#)); besides, it covers part of the transition zone between the Nearctic and Neotropical biogeographic regions ([Löwenberg-Neto 2014](#); [Morrone 2014](#); [Cuervo-Robayo et al. 2020](#)). Altitude in the study area ranges between 2,000 and 2,985 masl ([Gadsden and Reyes-Castillo 1991](#)). To the north of the RBM, the climate is temperate and semi-dry (BS1k); in the rest of the zone, the dominant climate is temperate sub-humid (CW; [García 2004](#)). The mean annual temperature is 12.6 °C, fluctuating between 2 °C (winter) and 22 °C (summer); the mean annual precipitation fluctuates between 600 and 900 mm ([INEGI 2017](#)).

The main vegetation types are conifer forest (*Pinus* spp.) and oak forest (*Quercus* spp.); also present are natural grassland (*Bouteloua* spp.) and xeric shrubland (*Arctostaphylos pungens*, *Acacia schaffneri*). There are also transition zones between these types of vegetation, where the dominant species vary according to altitude, geomorphology, and microclimatic conditions, resulting in 22 different types of vegetation ([González-Elizondo et al. 1993](#); [Servín et al. 2014b](#)).

**Capture and Marking.** We used Tomahawk® live traps and jaw traps (Victor® Soft Catch No. 3) to capture five gray foxes (females) and five adult coyotes (two females, three males), respectively. The ten individuals captured were sedated by intramuscular injection with a mixture of xylazine (xylazine



**Figure 1.** Geographic location of the study area in the buffer zone of La Michilia Biosphere Reserve (RBM), Durango, México. Home ranges of radio-collared coyotes (dotted red lines) and gray foxes (solid blue lines), derived from the minimum convex polygon (95 %), and the overlap between them, as well as the habitat types in the study area: Sv, disturbed vegetation (purple); QF, oak forest (light blue); MF, mixed forests (green); F-MS, forests with manzanita shrubland (pale pink); G, grassland areas (pale yellow). Areas in dark blue represent water bodies; the solid black line marks the border of the RBM and the dotted black line, the core zone of the RBM; gray lines are level curves (15 m).

hydrochloride) and ketamine (ketamine hydrochloride). The composite dose to induce anesthesia was 4 mg/kg ketamine plus 2 mg/kg xylazine for coyotes and 3 mg/kg ketamine plus 20 mg/kg xylazine for gray foxes (Servin and Huxley 1992; Kreeger and Arnemo 2018).

While individuals were sedated, we recorded morphometrics, weight, and sex; age (pup, juvenile, and adult) was determined based on tooth wear. In individuals with weight and measurements of adult animals, we fitted a 150 MHz VHF radio transmitter collar (Telonics<sup>®</sup>), weighing 120 g (model 200) for gray foxes and 170 g (model 300) for coyotes. The net weight of these radio collars accounted for 1.49 % of the mean weight of the coyotes captured ( $W = 11,400 \pm 1418$  g) and 3.88 % of the mean weight of gray foxes captured ( $W = 3,094 \pm 205$  g). After the radio collar was fitted, each individual was released and at the capture site on the same day.

The handling and physical and chemical containment of individuals were performed according to the guidelines recommended by the American Society of Mammalogy (Sikes et al. 2016), under the scientific research collection

license number SGPA/DGVS/12685/18 granted to Jorge Servin, issued by the Ministry of Environment and Natural Resources of México.

**Radiotracking and Location Error.** We gathered radiotelemetry data between September 2017 and August 2019 (Table 1). We located individual animals at any time of the day or night using portable receivers (Telonics<sup>®</sup> Mod. TR-2) with “H”-type handheld antennas and fixed eight-element antennas known as zero-point systems (Wildlife Materials Inc.<sup>®</sup>). Animals fitted with radio collars were field-tracked using the “triangulation” method (Mech 1983). This method consists of determining the location involving at least two directions (bearings or azimuths) using a compass from two different sites of known location separated from one another by at least one kilometer. A straight line was projected from each site to the bearings obtained so that the site where these lines crossed marked the location of the animal at that time. For the laboratory analysis of these measurements, we considered only those pairs of readings that were taken within 5 minutes and with a difference greater than 20° and less than 160°. To note, read-

ings with differences less than 20° or greater than 160° produce triangles with very sharp vertices, which significantly increase location errors (White and Garrot 1990). Prior to the start of the monitoring period for radio-fitted animals, we estimated the location error using reference transmitters placed at known sites, yielding an error of ± 3° (White and Garrot 1990).

**Home Range and Overlap.** Using the location data recorded in the field, we constructed an Excel® database, which was loaded into the LOAS® program Location of a Signal, version 4.0.3.8 (ESS 2010a); this returned a cloud of points in space and a database containing the georeferences of the locations of each radio-collared individual. With this database, we used the program Biotas® version 2.0a 3.8 (ESS 2010b) to calculate the size of the home range of each radio-collared individual, using the minimum convex polygon method set at 95 % (MPC; Mech 1983; White and Garrot 1990), while 50 % of sites were used to determine the core zone (i. e., the area with a high priority of use; Powell 2000). We used the MPC for its simplicity (White and Garrot 1990) and to compare our results versus other studies addressing the species studied. To estimate the space shared between radio-collared animals, we measured the overlap of home ranges between pairs of individuals and then calculated the average of this overlap (Millspaugh and Marzluff 2001).

We compared the size of the home ranges between the two species through a Student’s *t*-test for independent samples; in the case of coyotes, we compared the size of the home ranges between sexes through a Student’s *t*-test for a single sample (Sokal and Rohlf 1987).

**Habitat Use and Selection.** We used a vegetation map of the RBM and its area of influence (1:50,000 scale) for the classification and assignment of habitat types according to the physiognomically dominant vegetation (sensu González-Elizondo et al. 1993), which was digitized by the Laboratory of Wildlife Ecology and Conservation at Univer-

sidad Autónoma Metropolitana, campus Xochimilco. This map grouped habitat types into five categories (Figure 1): disturbed vegetation and agricultural areas (Sv); oak forest (QF), dominated by *Quercus* spp.; mixed forests (MF), with *Pinus* and *Quercus* as dominant or subordinate species; forests (pine, oak, or mixed) including patches of *A. pungens* shrubland (F-MS); and grasslands (G), areas where *Bouteloua* spp. occur as dominant or subordinate species.

The locations of the radio-collared individuals of both species were superimposed to the resulting map to quantify the frequency with which each individual was located in each habitat type within the RBM. We calculated the habitat selection coefficient by species, individual, and habitat type, as the ratio between observed habitat use and habitat availability (Manly et al. 2004). The observed habitat use was determined from the radio-location points recorded for each individual by habitat type. Habitat availability was derived by multiplying the number of radio-location points of each individual in a particular habitat type by the observed proportion of that habitat type within its home range obtained through the MPC (Aebischer et al. 1993; Sankar et al. 2013). This comparison is analog to Johnson’s third-order selection (Johnson 1980). For each species, we calculated the habitat selection coefficient for the *j*-th individual and the *i*-th habitat type using the equation:  $\hat{w}_{ij} = u_{ij} / (\pi_i u_{+j})$ , where  $\hat{w}_{ij}$  is the selection coefficient of individual *j* in habitat *i*;  $u_{ij}$  is the number of radiolocation points of individual *j* in habitat *i*;  $\pi_i$  is the relative availability of habitat *i*; and  $u_{+j}$  is the total number of individual radio location points of individual *j* (Manly et al. 2004). We calculated a measure of the selection made by individuals of a given species as a group (taking into account the variation in the selection of habitats of each individual) with the following equation:  $\hat{w}_i = u_{i+} / (\pi_i u_{++})$ , where  $\hat{w}_i$  is the selection coefficient for habitat *i*;  $u_{i+}$  is the total number of radiolocation points in habitat *i*; and  $u_{++}$  is the total number of radiolocation points for all individuals (Manly et al. 2004). Under the assumption that

**Table 1.** Home range size (MPC 95 %) and locations (Loc.) of four coyotes and five gray foxes radio-collared in 2017–2019 in the buffer zone of La Michilia Biosphere Reserve (RBM), Durango, México.

Species	Sex	Individual	Follow-up		Loc.	Home Range (km <sup>2</sup> )	Core Zone (km <sup>2</sup> )
			Period	Days			
Coyote	F	H001	Sep 2017–Aug 2018	261	111	9.74	1.98
Coyote	M	M027	Sep 2017–Oct 2018	382	130	12.45	2.22
Coyote	M	M087	Apr 2018–Jun 2019	103	96	13.81	3.65
Coyote	M	M156	Sep 2017–Aug 2018	184	92	12.81	4.05
Average (SD)				232.5 (118)	107.25 (17)	12.20 (1.74)	2.97 (1.03)
Gray fox	F	H050	Apr 2018–Dec 2018	232	102	4.99	0.54
Gray fox	F	H060	Feb 2019–Aug 2019	157	67	4.40	1.63
Gray fox	F	H067	Apr 2018–Jan 2018	266	77	5.71	0.41
Gray fox	F	H077	Apr 2018–Jun 2019	429	184	6.09	1.21
Gray fox	F	H081	Sep 2017–Jun 2018	274	86	5.64	1.27
Average (SD)				271.6 (99)	103.2 (47)	5.37 (0.67)	1.01 (0.52)

The sex of individuals is denoted by: F for females and M for males.



individual  $j$  uses habitat type  $i$  randomly, the average value of the habitat selection coefficient is  $\hat{w}_i = 1$  (use according to availability); thus, coefficients with values  $\hat{w}_i > 1$  indicate a higher-than-expected use (*i.e.*, preference), while  $\hat{w}_i < 1$  indicate lower-than-expected use (*i.e.*, avoidance; Manly et al. 2004). To determine whether a value of habitat selection coefficient ( $\hat{w}_i$ ) was significantly different from 1, we generated and used the 95 % Bonferroni confidence intervals (*sensu* Manly et al. 2004). We used a G-test or two-step log-likelihood ratio to test the null hypothesis that habitat was used according to habitat availability (Sokal and Rohlf 1987). First, we performed the G-test for each individual; afterward, we added the values of the test statistics for all individuals of a given species to test the overall habitat selection of individuals (White and Garrot 1990; Manly et al. 2004).

We calculated the habitat selection coefficient with the `adehabitatHS` package (Calenge 2006) for R version 4.0.1 (R Core Team 2019). All statistical analyses were performed with this software, considering a significance level  $\alpha = 0.05$ . For those parameters that require so, we report the mean  $\pm$  standard deviation.

## Results

Although we captured and tracked ten individuals — five gray foxes and five coyotes —, a local inhabitant delivered one radio collar that we had fitted to a female coyote captured four weeks earlier, reporting that the collared coyote was found dead by gunshot. Therefore, below we report the data corresponding to nine individuals.

**Home Range and Overlap.** Between September 2017 and August 2019, we recorded a total of 945 radio location points, 429 corresponding to four coyotes ( $= 107.25 \pm 17$ ) and 516 to five gray foxes ( $= 103.20 \pm 47$ ; Table 1).

The average home range for coyotes was  $12.20 \pm 1.74$  km<sup>2</sup> ( $n = 4$ ; range 9.74–13.81 km<sup>2</sup>), with a mean core zone of  $2.97 \pm 1.03$  km<sup>2</sup> ( $n = 4$ ; range 1.98–4.05 km<sup>2</sup>); the home range of male coyotes ( $13.02 \pm 0.70$  km<sup>2</sup>;  $n = 3$ ) was significantly larger ( $t = 8.07$ ;  $d. f. = 2$ ;  $P = 0.01$ ) than the home range of the only female monitored (9.74 km<sup>2</sup>). The mean home range size for gray foxes was  $5.37 \pm 0.67$  km<sup>2</sup> ( $n = 5$ ; range 4.40–6.09 km<sup>2</sup>), with a mean core area of  $1.01 \pm 0.52$  km<sup>2</sup> ( $n = 5$ ; range 0.41–1.63 km<sup>2</sup>). A  $t$ -test showed that the mean home range size of coyote was significantly larger versus gray fox ( $t = 8.18$ ;  $d. f. = 7$ ;  $P = 0.001$ ).

The mean overlap of home ranges between coyotes (intraspecific overlap) was  $43.7 \pm 21$  % ( $n = 12$ ; range 18–77 %), whereas for gray foxes, the mean overlap was  $6.6 \pm 5$  % ( $n = 8$ ; range 1–14 %). The overlap of home ranges was significantly greater between coyotes than between gray foxes ( $t = 4.87$ ;  $d. f. = 18$ ;  $P = 0.001$ ). The mean overlap of home ranges between coyotes and gray foxes (interspecific overlap) was  $42.1 \pm 27$  % ( $n = 21$ ; range 13–98 %; Figure 1).

**Habitat Use and Selection.** We found that coyotes use the different habitat types according to their availability, both as a group ( $G = 18.36$ ;  $d. f. = 13$ ,  $P = 0.14$ ) and as individuals ( $P > 0.05$ ; Table 2), although the highest habitat selection coefficient was obtained for grassland areas ( $G$ ;  $\hat{w}_i = 1.17$ ) and the lowest for forests with *manzanita* shrubland (*Arctostaphylos pungens*; F-MS;  $\hat{w}_i = 0.77$ ; Table 2).

**Table 2.** G-test and habitat selection coefficients, per individual ( $\hat{w}_i$ ) and per group ( $\hat{w}_g$ ), of radio-collared individuals — four coyotes and five gray foxes — in the buffer zone of La Michilila Biosphere Reserve (RBM), Durango, México.

Species	Individual	G-test			Selection coefficient per individual ( $\hat{w}_i$ )				
		G-Value	d. f.	P-value	Sv	QF	MF	F-MS	G
Coyote	H001	5.40	3	0.145	NA	0.86	1.97	1.02	0.83
Coyote	M027	4.79	4	0.309	0.96	1.11	1.20	0.48	0.90
Coyote	M087	3.56	3	0.314	NA	0.76	0.89	1.13	1.65
Coyote	M156	4.62	3	0.202	NA	1.09	0.95	0.60	1.76
	By group	18.36	13	0.144					
	$\hat{w}_i \pm SD$				$0.96 \pm 0.0$	$0.94 \pm 0.08$	$1.12 \pm 0.13$	$0.77 \pm 0.15$	$1.17 \pm 0.22$
	95% CI				0.96–0.97	0.74–1.14	0.77–1.46	0.38–1.17	0.60–1.75
Gray fox	H050	47.22	3	< 0.001	NA	0.59	4.53	0.51	0.99
Gray fox	H060	7.64	3	0.054	NA	0.24	1.35	0.97	0.61
Gray fox	H067	15.23	3	0.002	NA	1.87	1.14	1.23	0.19
Gray fox	H077	37.92	3	< 0.001	0.17	1.36	1.41	NA	0.21
Gray fox	H081	5.93	2	0.301	NA	NA	1.18	0.47	0.20
	By group	113.9	14	< 0.001					
	$\hat{w}_i \pm SD$				$0.17 \pm 0.0$	$0.82 \pm 0.29$	$1.43 \pm 0.17$	$0.61 \pm 0.11$	$0.27 \pm 0.07$
	95% CI				0.16–0.17	0.19–1.57	1.01–1.86	0.33–0.89	0.10–0.44

Habitat types are denoted by: **Sv**, disturbed vegetation; **QF**, oak forest; **MF**, mixed forests; **F-MS**, forests (pine, oak or pine-oak) and *manzanita* shrubland; **G**, grassland areas.

The sex of individuals is denoted by F for females and M for males.

SD denotes standard deviation; *d. f.*, degrees of freedom; 95% CI, Bonferroni 95% confidence intervals.

On the other hand, although individual variations were observed, gray foxes showed selective habitat use as a group ( $G = 113.93$ ;  $d. f. = 14$ ;  $P < 0.001$ ; Table 2). The gray fox preferred mixed forests (MF;  $\hat{w}_i = 1.43 \pm 0.17$ ) and avoided disturbed vegetation (Sv;  $\hat{w}_i = 0.17 \pm 0.0$ ), grassland areas (G;  $\hat{w}_i = 0.27 \pm 0.07$ ), and forests with *manzanita* shrubland (F-MS;  $\hat{w}_i = 0.61 \pm 0.11$ ). Separately, selection coefficient values and their confidence intervals indicated that oak forest (QF;  $\hat{w}_i = 0.96$ ;  $CI_B = 0.17-1.74$ ) was used according to its availability (Table 2).

## Discussion

In a previous work carried out in the study area, Servin (2000) radio-tracked fifteen coyotes (eight males and seven females) over two years, reporting a mean home range size of  $C = 11.8 \pm 2.71 \text{ km}^2$  for coyotes in general,  $C_M = 13.1 \pm 2.5 \text{ km}^2$  for males, and  $C_H = 9.9 \pm 3.3 \text{ km}^2$  for females. These values are similar to the ones obtained in the present study. The home range size of coyotes is a highly dynamic variable influenced by climate, prey availability, and habitats suitable for reproduction, as well as by population density and mortality rate (Danner and Smith 1980; Laundré and Keller 1984; Gese et al. 1988; Servín and Huxley 1995; Servín et al. 2014b). While the home range size of a species varies geographically (Holzman et al. 1992; Chamberlain et al. 2000), our results indicate that home range size in the study area lies within the range of values reported for coyotes in different habitats across its range (Bekoff 1977; Andelt and Gipson 1979; Young et al. 2006), consistent with most of the studies carried out in temperate zones of North America (11.6–35.8  $\text{km}^2$ ; Servín and Huxley 1995; Servín 2000).

In the case of gray fox females, the mean home range size reported here was  $5.37 \pm 0.67 \text{ km}^2$ , an area 2.4 times larger than the one reported for females by Servin et al. (2014b), which was  $2.24 \text{ km}^2$ , in the same study area between 1991–1993. In this regard, some studies have reported that gray fox females tend to display a larger home range than males (Trapp and Hallberg 1975; Servín et al. 2014b) and that the home range size of this species may vary depending on habitat quality and resource availability (Fuller and Cypher 2004). Our results fall within the range of variation reported elsewhere for this species (Fritzell and Haroldson 1982; Fuller and Cypher 2004; Macdonald and Sillero-Zubiri 2004).

In the study area, the average spatial overlap between the home ranges of coyotes and gray foxes was moderate (42.1 %). However, one-third of the interspecific pairs (diads) analyzed ( $n = 21$ ) to derive this data showed high overlap values ( $> 60 \%$ ), as reported in other studies (Neale and Sacks 2001; Chamberlain and Leopold 2005). Our results suggested that, since there are no apparent patterns of spatial avoidance of the gray fox toward the coyote through spatial segregation of the ecological niche, the spatial dynamics between these species is not fully explained by interference competition, as reported for these canid species in other areas where they display a sympatric distribution (Fedriani et al. 2000; Farias et al. 2012).

Our results also suggest that the spatial coexistence dynamics between coyotes and gray foxes in the study area is governed by space-use mechanisms at a fine scale (Lonsinger et al. 2017) mediated by differential habitat use. The gray fox used oak forest (QF) according to its availability and showed preferences for mixed forests (MF), as already reported for this species in the study area (Servín et al. 2014b), as well as in other areas over its geographic range (Haroldson and Fritzell 1984; Chamberlain and Leopold 2000). These forests offer vast areas that provide protection and shelter for gray foxes (Servín et al. 2014b), being an important element within the home range of this species (Fritzell and Haroldson 1982). The complex architecture of mixed oak-pine and pine-oak forests in the study area provide natural structures that can be used as resting sites and shelters; at the same time, these forests serve as escape routes and, therefore, are useful to avoid the risk of predation, as gray foxes are able to climb trees and even jump between tree branches (Fritzell and Haroldson 1982; Fuller and Cypher 2004). In addition, foxes can use the tree stratum as a foraging zone, as its branches are habitats for potential prey that are part of their diet, such as passerine birds, squirrels (*Sciurus nayaritensis*, *Tamias bulleri*, and *T. durangae*), small rodents (*Peromyscus* spp. and *Reithrodontomys* spp.), lacertids (*Sceloporus* spp.) and insects. On the other hand, gray foxes avoided disturbed vegetation (Sv) and grassland areas (G). It has been shown that the risk of predation by coyotes can influence resource use by gray foxes (Fedriani et al. 2000; Chamberlain and Leopold 2005). Thus, foxes are likely to be avoiding these open areas as these are devoid of shelters, hence offering lower evasion opportunities against the potential chase by coyotes (which use these habitats according to their availability) to avoid intraguild predation (Temple et al. 2010).

In the case of coyotes, although no apparent preference for or avoidance of any particular habitat type was observed, a certain trend towards the preferential use of pasture areas (G) was noted since it attained the highest habitat selection coefficient ( $\hat{w}_i = 1.17$ ). This trend of preferential use is consistent with data reported for coyotes in the RBM, as this species forage and catch their main prey (rodents and lagomorphs) preferentially in areas with open vegetation, such as grasslands (P; Servín and Huxley 1991; Servín et al. 2003). These open vegetation areas in the RBM are also home to the checker bark juniper or *táscate* (*Juniperus deppeana*) with varying abundances in different areas (González-Elizondo et al. 1993). Juniper fruits are an important element in the diet of coyotes, being the plant food most frequently consumed by coyotes in the study area (Delibes et al. 1989; Servín and Huxley 1991); this food category is actively sought and consumed by coyotes in open and grassland areas.

An aspect worth highlighting is the role of forests with *manzanita* shrubland (F-MS) in habitat selection and use by both species. On the one hand, coyotes used this habitat as expected, while gray foxes avoided it. One potential

explanation lies in the different frequency of consumption of manzanita fruit by both species. These fruits represent a food resource highly consumed by coyotes, especially in the dry season (February-May; [Servin and Huxley 1991](#)), while it is consumed to a lesser extent by gray foxes ([Delibes et al. 1989](#)).

In the present study, we showed that the home ranges of coyotes and female gray foxes showed a moderate interspecific overlap, so no spatial segregation occurred. However, differential use of habitat was observed, which explains the coexistence of these canids in the same area because their antagonistic behavioral interactions decrease through a trend towards the differential use of resources ([MacArthur and Levins 1967](#); [Tilman 1982](#); [Holt 2001](#)). Our results are consistent with the theoretical hypothesis on intraguild predation ([Holt and Polis 1997](#); [Polis et al. 1989](#)), which suggests that the coexistence between species in the same guild sharing basic resources requires that the subordinated species (gray fox) be better at exploiting the resources shared with the dominant species (coyote).

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# Relationship between age-sex classes and prevalence of *Giardia* spp. and *Blastocystis* spp. in black and gold howler monkeys inhabiting fragmented forests

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Studies have shown that as age increases, parasitism could also be more frequent, on the other hand, the lack of immunity can increase the risk of infection in younger individuals. Regarding sex, there is a general tendency for males to be more parasitized than females, in the case of primates, this is related to the effort made by males into attaining and maintain a high rank, implying high levels of testosterone, a hormone with immunosuppressive effects. Immunosuppressive effects of stress hormones can also increase susceptibility in dominant or subordinate individuals, nevertheless, in a study, the level of exposure to parasites seems to be more important than the immunosuppressive effects of stress in explaining why dominant females have more infections from directly transmitted parasites. In this study, we investigated the relationship between the prevalence of *Giardia* spp. and *Blastocystis* spp. and the categories of age and sex in black and golden howler monkeys (*Alouatta caraya*) of Argentina. We analyzed 375 fecal samples from 27 individuals (juveniles and adults of both sexes), using microscopy and techniques of flotation and sedimentation. To analyze the relationship between age, sex, and infection prevalence, a Generalized Linear Mixed Model was used. In adults, the prevalence of infection was 78.5 % while in juveniles, all individuals (100 %) were infected with both protozoa. Males had a infection prevalence 84.6%, in females it was 92.8 %. When comparing infection prevalence between ages and between sexes, no significant differences were found ( $P > 0.05$ ). Research suggests that parasite infection rates may be influenced by specific form of transmission, in this sense, these protozoa, are transmitted through ingestion of cysts which are infectious immediately after defecation has occurred. On the other hand, all members of the group tend to defecate simultaneously, leaving all the members of the group exposed to infection. Therefore, we suggest that physiological or behavioral factors do not appear to be important in the risk of protozoan infection.

Algunos estudios han demostrado que a medida que aumenta la edad, el parasitismo también podría aumentar, por otro lado, la falta de inmunidad puede incrementar el riesgo de infección en individuos más jóvenes. En cuanto al sexo, existe una tendencia general a que los machos estén más parasitados que las hembras, en el caso de los primates, esto está relacionado al esfuerzo que realizan los machos para alcanzar y mantener un alto rango, implicando niveles elevados de testosterona, una hormona con efectos inmunosupresores. Efectos inmunosupresores de las hormonas del estrés también pueden incrementar la susceptibilidad en individuos dominantes o subordinados, sin embargo, en un estudio, el nivel de exposición a parásitos parece ser más importante que los efectos inmunosupresores del estrés para explicar por qué las hembras dominantes tienen más infecciones por parásito. En este estudio, investigamos la relación entre la prevalencia de *Giardia* spp. y *Blastocystis* spp. y las categorías de edad y sexo en monos aulladores negros y dorados (*Alouatta caraya*) de Argentina. Se analizaron 375 muestras fecales de 27 individuos (juveniles y adultos de ambos sexos), mediante microscopía y técnicas de flotación y sedimentación. Para analizar la relación entre edad, sexo y prevalencia de infección se utilizó un Modelo Lineal Generalizado Mixto. En adultos, la prevalencia de infección fue del 78.5 %, mientras que, en los juveniles, todos los individuos (100 %) estuvieron infectados con ambos protozoos. Los machos tuvieron una prevalencia de infección de 84.6 %, y las hembras 92.8 %. Al comparar la prevalencia de infección entre edades y entre sexos, no se encontraron diferencias significativas ( $P > 0.05$ ). Investigaciones sugieren que las tasas de infección parasitaria pueden ser afectadas por la forma de transmisión, en este sentido, estos protozoos, se transmiten a través de la ingestión de quistes, lo cuales son infecciosos inmediatamente después de la defecación. Por otro lado, todos los miembros del grupo tienden a defecar simultáneamente, contribuyendo a la presencia de áreas contaminadas con heces, dejando a todos los miembros del grupo expuestos a la infección. Por lo tanto, sugerimos que los factores fisiológicos o de comportamiento no parecen ser importantes en el riesgo de infección por protozoos.

**Keywords:** Endoparasites; intrinsic factors; non-human primates; prevalence of infection; protozoa.

## Introduction

Given that deforestation, habitat modification, and degree of human contact with wild animals are increasing exponentially in most parts of the world (Chapman *et al.* 2006), several studies have explored how these factors may impact on parasite infection risk in non-human primates (Clarke *et al.* 2002; Kowalewski and Gillespie 2009; Cristóbal-Azkarate *et al.* 2010). However, the studies focusing on the relationship between parasite prevalence and richness with life history variables such as individual age and sex in wild primates are scarce (MacIntosh *et al.* 2010; Friant *et al.* 2016).

The age of an individual has been reported to differentially affect rates of parasitic transmission in several vertebrate taxa including fish, birds, bats, rodents, and non-human and human primates (Krasnov *et al.* 2006; Plowright *et al.* 2008; MacIntosh *et al.* 2010). In the case of wild primates, studies have shown that when age increases, parasitism could also increase if, for example, larger-bodied individuals occupy more space, require more resources and have contact with contaminated foods and substrates disproportionately (Hudson and Dobson 1997). In fact, studies of non-human primates found that adults had higher helminth parasite infection rates than juveniles (*e. g.*, *Cebus capucinus*, Parr *et al.* 2013; *Alouatta pigra*, Eckert *et al.* 2006; *Mandrillus sphinx*, Setchell *et al.* 2007). On the other hand, lack of acquired immunity in younger individuals may increase risk of parasitism in juveniles (Hudson and Dobson 1997), given that younger individuals require constant exposure to pathogens to stimulate their immune system to develop antibodies to limit subsequent pathogenic infections during adulthood (Lloyd 1995). For example, a study in Mexico reported that juveniles *Alouatta palliata* showed a 1.6-fold higher helminth and protozoan parasite prevalence than adults (Stoner and González Di Piero 2006). However, other studies reported no differences between helminth and protozoa parasite infection and age classes (*e. g.*, *A. palliata*, Maldonado-López *et al.* 2014; *A. pigra*, Trejo-Macías and Estrada 2012; *Colobus vellerosus*, Teichroeb *et al.* 2009).

Regarding sex, parasitism tends to be more common in males than in females across vertebrate taxa, including humans (Klein 2004; Habig and Archie 2015). Males generally invest most of their effort into attaining and maintaining high rank and central positions in non-human primate species (Zuk and Stoehr 2002). In this regard testosterone facilitate the achievement of a high rank but there are a number of costs imposed by elevated levels of this hormone, such as immunosuppressive effects, increasing the risk of acquiring parasitic infections (tradeoffs hypothesis; Muehlenbein and Bribiescas 2005): This idea was tested in a study on adult male chimpanzees (*Pan troglodytes*) at Ngogo, Uganda, where high ranking males had higher testosterone levels and an increased intestinal helminth burden but not protozoan, when compared to lower male ranking animals (Muehlenbein and Watts 2010). In addi-

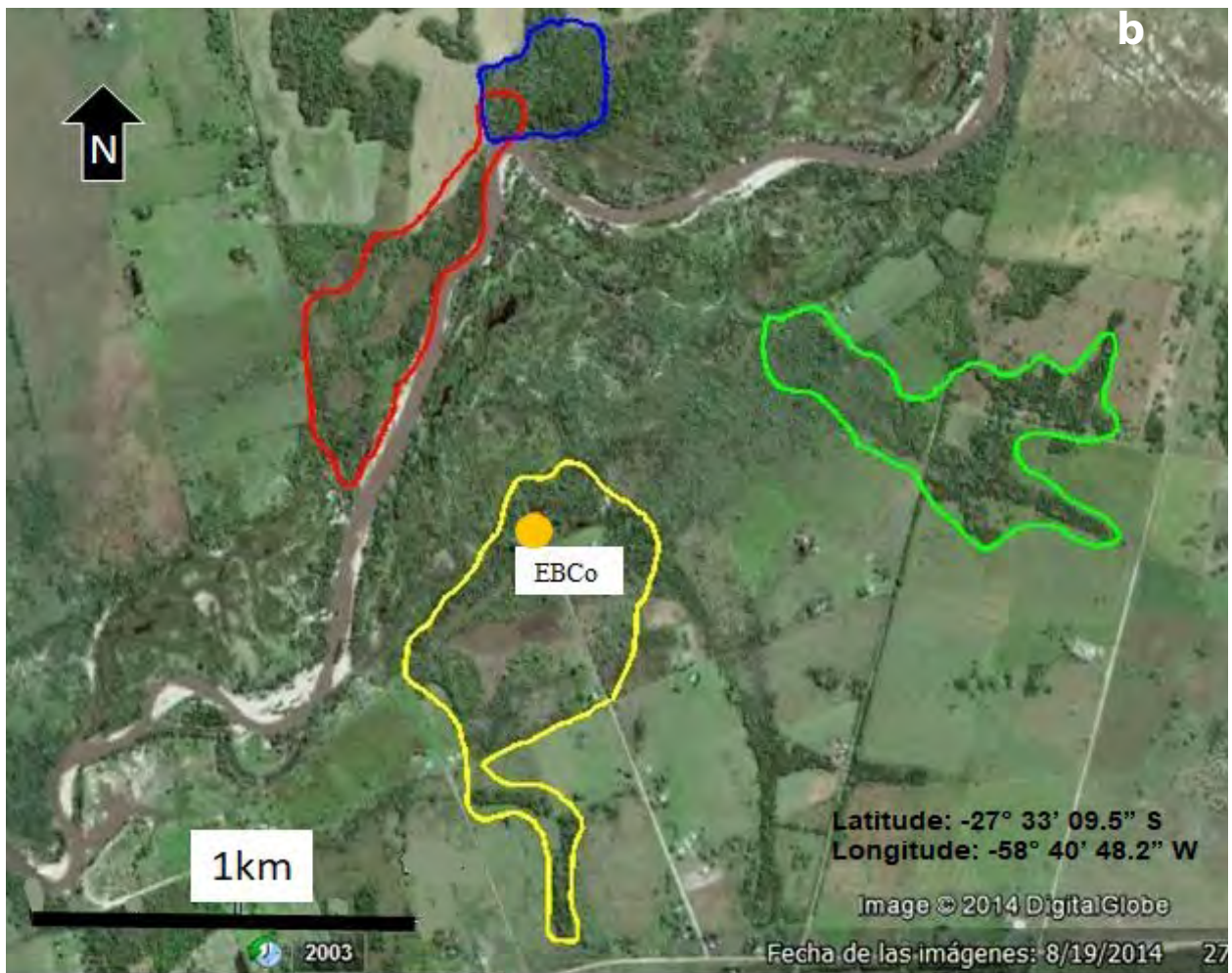
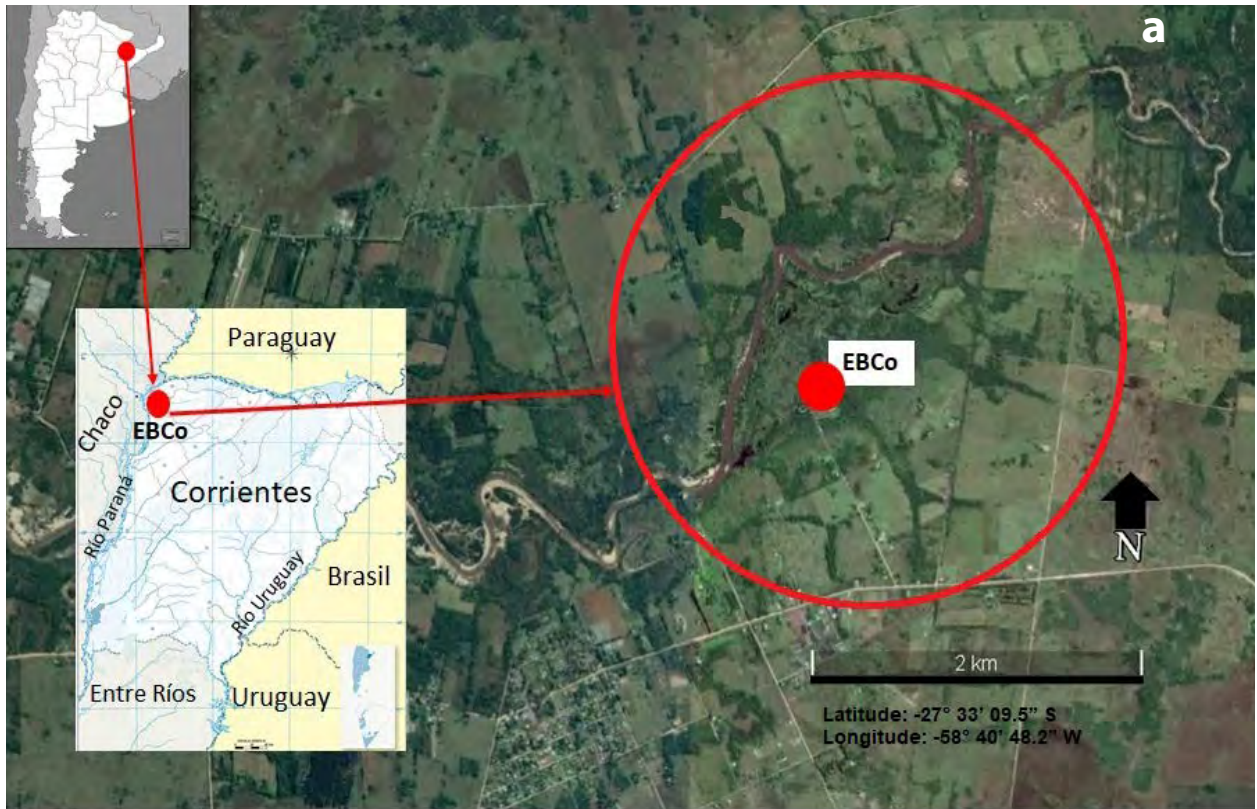
tion, studies in non-human primates, determined that immunosuppressive effects of stress hormones also could increase susceptibility in either dominant or subordinate individuals depending on species-typical dynamics and hierarchical stability (stress-response hypothesis; Cavigelli and Caruso 2015; Sapolsky 2005). Nevertheless, in Japanese macaques, *Macaca fuscata*, for example, socially mediated exposure seems to be more important than the immunosuppressive effects of stress in explaining why dominant females have more infections from directly transmitted parasites (MacIntosh *et al.* 2012). These studies, therefore, show that the relationship between infection patterns and intrinsic factors of the host need further research (Nunn and Altizer 2006) and consider that infection patterns largely depend on the level of exposure of the host to the infectious stages of the parasites, to the physiological factor, and the social dynamics of the group studied. For the first time, we investigated the relationship between *Giardia* spp. and *Blastocystis* spp. prevalence and age and sex categories in groups of black and gold howler monkeys (*Alouatta caraya*) that inhabit fragmented forests in Northern Argentina. Field studies conducted on wild populations of *A. caraya* in Argentina have shown that zoonotic protozoa as *Giardia* spp. and *Blastocystis* spp. are present and prevalent in wild black and gold howlers, therefore, these protozoa are a natural component of the howler parasite communities (Venturini *et al.* 2003; Kowalewski *et al.* 2011; Milozzi *et al.* 2012). These protozoa have a direct life cycle and are also the most commonly reported parasite in humans and both wild and domestic animals (dogs, cats, sheep, goats, cows, pigs, horses, among others), in both cases, transmission can occur through ingestion of infective stages (cysts), and human infection is associated with poor sanitary conditions, contact with animals and consumption of contaminated food or water (Godoy *et al.* 2004).

## Materials and Methods

**Study site and studied groups.** The *A. caraya* groups studied inhabit extensions of semideciduous gallery forests around the Estación Biológica Corrientes and San Cayetano Provincial Park (of 78 ha; -27° 33' 09.5" S, -58° 40' 48.2" W) in the northwest of Corrientes province in Argentina (Figure 1a). These forests have been strongly modified by logging, burning and the presence of livestock, and households are distributed throughout this rural site (Kowalewski *et al.* 2011). The climate is subtropical, with an average annual temperature of 21 °C and an average annual precipitation of 1,200 mm (Rumiz *et al.* 1986). Rains increase slightly towards the spring and summer seasons (September to December).

Fecal samples were collected from 27 individuals (13 juveniles and 14 adults) of both sexes (13 males and 14 females) belonging to four groups of howler monkeys. A subset of adult individuals was sampled, and all juvenile individuals. Figure 1b depicts the home range of the four study groups.





**Figure 1.** a) Location of area of study in Corrientes, Argentina and b) Area of action of the four studied groups. Blue (group 1), red (group 2), yellow (group 3), green (group 4).

We categorized juveniles in two age categories: category 1 (from 1 to 2.5 years of age) and category 2 (more than 2.5 to 4 years of age). The age-sex category composition of each of the study groups is in Table 1.

**Sample collection and examination.** Fecal samples were monthly collected during the morning between August 2014 and September 2015, immediately after defecation to minimize the risk of contamination. Only the central portion of the fecal sample was taken using disposable wooden spatulas. Samples were stored individually in 20 ml flasks with 10 % formalin and each flask was shaken to homogenize the sample with formalin (Gillespie 2006; Gillespie et al. 2008) and then labeled and stored with the date of collection, observer, location and identification of individuals.

Samples were examined in the Laboratorio de Biología de los Parásitos of the Facultad de Ciencias Exactas y Naturales y Agrimensura, during March-December 2017, using microscopy and techniques of flotation (Sheather's solution,  $D = 1.27$ ; Milozzi et al. 2012) and sedimentation (1g of feces), as per Gillespie (2006) to ensure the collection of cysts of both protozoa (Figure 2a, 2b). In each technique, slides (18 mm x 18 mm) were examined under a stereoscopic magnifying glass (Olympus CH30; x400 magnification), previously colored with a drop of Lugol's solution; all samples were examined in duplicate.

**Data analysis.** We described parasite infections in terms of prevalence of infection. Prevalence is the proportion of individuals hosts sampled infected with a particular parasite species (Stuart and Strier 1995; Bush et al. 1997; Gillespie 2006).

To analyze the relationship between age, sex and infection prevalence, a Generalized Linear Mixed Model (GLMM) was used with Gaussian family and link function "Identity", which considered prevalence ( $0.5 \pm 0.06$ ) as a variable response and age (with three levels: juvenile 1, juvenile 2, adult) and sex (with two levels: male, female) as fixed effects. Additionally, the individual nested in group was considered as a random effect. The adjustment of the model was evaluated using a maximum likelihood ratio test (LRT) where we compared models with variations in a fixed effect to take

**Table 1.** Distribution of the number of individuals according to sex and age category in each studied group in Corrientes, Argentina.

		Groups			
		1	2	3	4
Total (Individuals)		6	6	8	7
Adults	Males	1	2	2	1
	Females	2	2	2	2
Juveniles	Males category 1	-	1	2	1
	Males category 2	1	1	-	1
	Females category 1	1	-	1	1
	Females category 2	1	-	1	1



**Figure 2.** a) Cyst of *Giardia* spp. and b) Cyst of *Blastocystis* spp.

into account all the comparisons the random effects are the same (individual nested in group; Bolker et al. 2009). All statistical analyses were performed in R through the R-studio platform, version 3.2.1 (R Core Team 2016). Statistical significance was set at 0.05 for all interpretations.

## Results

A total of 375 samples were collected, with at least three samples (of different days) per individual per month from 27 individuals (13 juveniles and 14 adults), of both sexes (13 males and 14 females) belonging to four groups of howler monkeys.

Parasite prevalence for both protozoan taxa was 88.9 % (24/27). Of the 27 individuals analyzed, we found *Giardia* spp. infection prevalence to be 81.4 % (22/27) and *Blastocystis* spp. infection prevalence to be 77.7% (21/27).

In adults, infection prevalence was 78.5 % (11/14) while in juveniles, all individuals (juveniles 1 and juveniles 2; 100%) seemed to be infected with both protozoa. Males had a prevalence of general infection 84.6 % (11/13) and females had a 92.8 % (13/14; Table 2). No significant effects of age or sex on prevalence was found as the model selected by LRT was null ( $P > 0.05$  for sex and age; Figure 3a, 3b).

**Tabla 2.** Prevalence of infection according to sex/age categories in four groups of *A. caraya* in Corrientes, Argentina ( $n$  = number of Individuals analyzed).

Sex/age categories	n	Prevalence of Infection (%)			
		General	<i>Giardia</i> spp.	<i>Blastocystis</i> spp.	
Total	27	88.9	81.4	77.7	
Adults	Males	13	84.6	84.6	76.9
	Females	14	92.8	78.5	78.5
	Total	14	78.5	64.2	71.4
	Males	6	66.6	66.6	66.6
Juveniles	Females	8	87.7	62.5	75.0
	Total	13	100	100	84.6
	Males category 1	4	100	100	75.0
	Males category 2	3	100	100	66.6
	Females category 1	3	100	100	100
	Females category 2	3	100	100	100

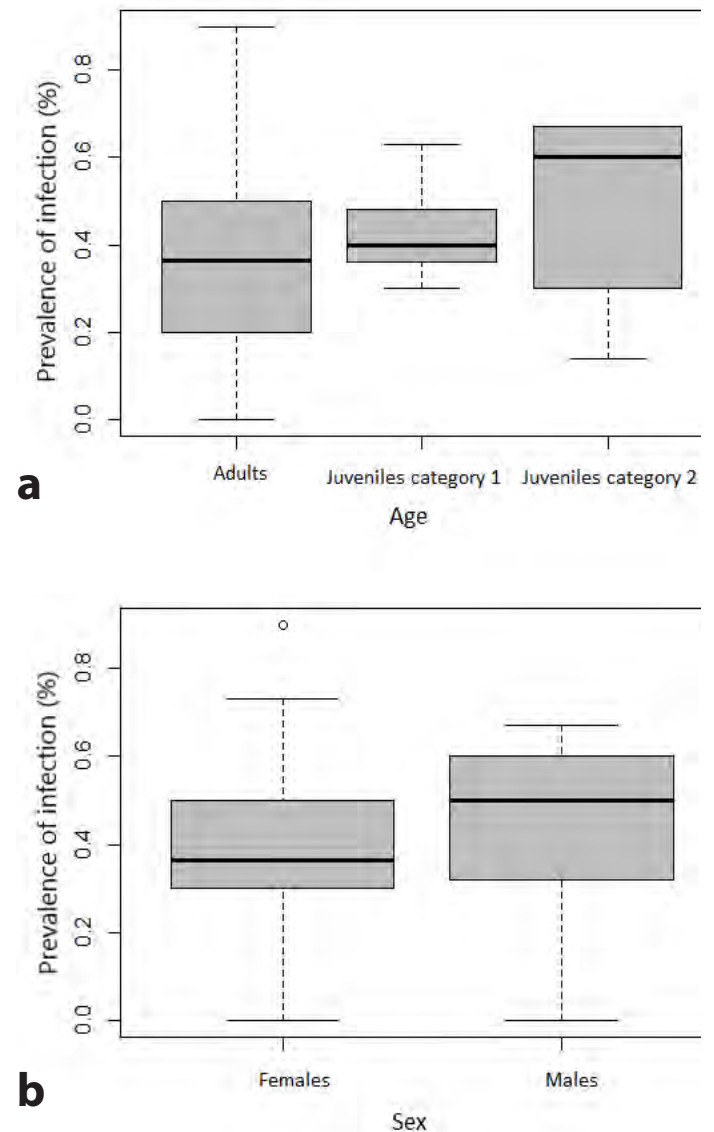
## Discussion

The goal of this research was to explore if *Giardia* spp. and *Blastocystis* spp. protozoa parasite infection rates (estimated through infection prevalence) were affected by sex-age in four groups of black and gold howler monkeys (*A. caraya*) living in forest fragments. Our results suggest that infection prevalence of these protozoans is not affected by these biological factors. These findings are consistent with other studies that also have examined whether host intrinsic traits (age-sex) affect infection gastrointestinal parasites in primates. For example, a study based on 982 stool specimens collected from adult and juvenile individuals from a multimale–multifemale social group of red-capped mangabeys (*Cercocebus torquatus*) in Nigeria, shows that the acquisition of protozoan infections did not vary according to host traits (Friant et al. 2016). Other studies, conducted over 6 to 7 months by Vitazkova and Wade (2007) and Trejo-Macías and Estrada (2012), based on < 200 fecal samples, did not find significant differences in helminth and protozoan parasite prevalence among adults, juveniles, and infants. On the other hand, Stoner and González Di Pierro (2006) reported that juveniles from three groups showed a 1.6-fold higher helminth and protozoan parasite prevalence than adult howler monkeys (*A. pigra*) in Montes Azules, México. In short, these set of studies indicate, that there is a general tendency for protozoa to be acquired in a uniform way in primate groups.

Recent research suggests that parasite infection rates may be influenced by specific form of transmission of different parasites (Día 2001; Nunn and Altizer 2006). Then, transmission of these protozoa may occur through ingestion of infective stages (cysts) that do not require develop in the external environment for days to months before they become infective like helminths (Freeland 1980), thus, they are immediately infective once defecation has occurred and can survive in the environment for weeks or months

(Godoy et al. 2004). Moreover, all members in social group tend to defecate simultaneously in their trees after periods of resting (Gilbert 1997; Kowalewski and Zunino 2005), this defecation pattern contributes to the presence of areas of vegetation (latrines) contaminated with clumped feces (potential sources of infection) within the home range of howler groups (Van Belle and Estrada 2006) leaving all members of the group exposed to infection. Therefore, we suggest that physiological or behavioral factors related to the risk of parasitic infection (*i. e.*, that tend to vary according to age and sex in primates) do not appear to be important in the risk of protozoan infection.

It is noteworthy that in our study a high general prevalence of infection was found (88.9 %), that is, 24 out of 27 individuals presented at least one or both protozoa. Our study area is under continued deforestation due to selective



**Figure 3.** Box plots showing infection prevalence according to age (a) and sex (b) in *Alouatta caraya*. Median (black line), interquartile ranges (rectangle) and minimum and maximum values (whiskers).

logging and cattle ranching, such levels of deforestation therefore, decrease habitat size, forcing all howler monkeys to descend to the ground and cross from fragment to fragment looking for supplemental food resources (Zunino *et al.* 2007) potentially increasing contact with parasites on the ground and in small water bodies (Kowalewski and Gillespie 2009). Additionally, cattle enter into the forest fragments opening trails and defecating along them, also, drink and defecate in streams where as well black and gold howlers drink water, thus increasing the chances of infection in the entire population (Kowalewski *et al.* 2011). These forest systems may explain our high infection rates for the study protozoans (Bublitz *et al.* 2015).

Although hypotheses are established that predict possible biases in wild primate populations in relation to intrinsic variables of the host such as sex and age, it is important to consider that host-parasite relationships are highly specific and vary among populations (Hudson and Dobson 1997). Therefore, we consider that studies designed to examine age-sex effects need to consider other potential infection risk factors, such as habitat disturbance (*e. g.*, logging rates, Gillespie and Chapman 2008), parasite life history and transmission, especially in non-human primate populations that are constantly subjected to the reduction of their habitats (Chapman *et al.* 2006).

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# Use of distribution models in the conservation of a Mexican endemic lagomorph

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The volcano rabbit (*Romerolagus diazi*), endemic to the central-eastern Transmexican Volcanic Belt, is one of the most threatened lagomorphs worldwide. Several factors threaten to decrease its geographical distribution, which is already restricted to the Pelado, Tláloc, Iztaccíhuatl, and Popocatepetl volcanoes. Our study aimed to propose priority areas for the conservation of this rabbit within Iztaccíhuatl-Popocatepetl National Park (IPNP) based on species distribution models. Volcano rabbit presence data were collected through different field sampling techniques and public and private databases. The environmental predictors used to model suitability were obtained from both open-access remote sensors and topographic information. The models' performance was adjusted by evaluating different sets of variables and data to improve the certainty of the results. We obtained an area of 132.5 km<sup>2</sup> within the IPNP potentially occupied by the volcano rabbit and a high suitability area of 7 km<sup>2</sup>. In addition, four priority conservation polygons for the volcano rabbit were identified within the National Park. We showed that the suitability and potential distribution are not uniform in the park, being the alpine meadow dominated by *Muhlenbergia* sp., the most suitable area for *R. diazi*. Therefore, the conservation strategies should focus on preserving these meadows in the prioritized polygons, avoiding tourist and unskilled personnel's access. This work represents a contribution to the conservation of the volcano rabbit and a theoretical and practical tool for use in the IPNP.

El conejo de los volcanes (*Romerolagus diazi*), endémico del centro-este de la Faja Volcánica Transmexicana, es uno de los lagomorfos más amenazados en todo el mundo. Muchos factores amenazan con disminuir su distribución geográfica, la cual ya está restringida a los volcanes Pelado, Tláloc, Iztaccíhuatl y Popocatepetl. El objetivo de nuestro estudio fue proponer áreas prioritarias para la conservación de este conejo en el Parque Nacional Iztaccíhuatl-Popocatepetl (PNIP), con base en modelos de distribución. Los datos de presencia del conejo de los volcanes fueron colectados a través de diferentes técnicas de muestreo en campo y bases de datos públicas y privadas. Los predictores ambientales usados para modelar idoneidad fueron obtenidos de sensores remotos e información topográfica, ambos de acceso libre. El desempeño de los modelos fue ajustado mediante la evaluación de diferentes conjuntos de variables y datos para mejorar la certeza de los resultados. Se obtuvo un área de 132.5 km<sup>2</sup> en el PNIP potencialmente ocupado por el conejo de los volcanes y un área de alta idoneidad de 7 km<sup>2</sup>. Además, se identificaron cuatro polígonos prioritarios para la conservación del conejo de los volcanes dentro del Parque Nacional. Aquí demostramos que la idoneidad y distribución potencial no son uniformes dentro del parque, siendo la pradera alpina dominada por *Muhlenbergia* sp., el área más idónea para *R. diazi*. Por lo tanto, las estrategias de conservación deberán enfocarse en preservar esas praderas en los polígonos prioritizados, evitando el acceso de turistas y personal no calificado. Este trabajo representa una contribución a la conservación del conejo de los volcanes y una herramienta teórica y práctica para su uso en el PNIP.

**Keywords:** Ecological niche modelling; MaxEnt; natural protected area; remote sensing; suitability; volcano rabbit.

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## Introduction

*Romerolagus diazi* (Ferrari-Pérez, 1893) is an endemic species of the central-eastern Trans-Mexican Volcanic Belt (TVB) biogeographic province (Barrera 1966; Velázquez et al. 1996), and it has been listed as endangered species with a decreasing estimated population of 7,000 individuals (Velázquez and Guerrero 2019). This rabbit is also known as the *zacatuche*, *teporingo*, or volcano rabbit; it is a monospecific and ancient genus with taxonomic, anatomical, and biogeographic features similar to *Pentalagus* and *Pronolagus* (Hoffman et al. 1994). The volcano rabbit is a gregarious species that form groups of two to five individuals, although the age and sex composition of these groups are unknown. To date, knowledge about home range or dispersal capacity is low (Rizo-Aguilar et al. 2014).

However, Galindo-Leal and Velázquez (1996) suggested low dispersal capacity than other lagomorphs, and Cervantes and Martínez-Vázquez (1996) proposed a home range of 2,500 m<sup>2</sup> based on their field research. In terms of reproduction, the gestation period is longer, and the litter size is smaller in these ancient rabbits compared to other rabbits (Cervantes 1982).

*Romerolagus diazi* faces intense human pressure due to agriculture expansion, poaching, and development for tourism and because its restricted distribution is surrounded by large cities, including Puebla, Toluca, and Mexico City. These situations modify, fragment, or destroy the specific habitat where *R. diazi* lives. All of these factors make this lagomorph species a priority conservation target. Also, its geographic distribution rarity increases its

vulnerability (Lawler *et al.* 2003). If the species is extirpated from its known geographic distribution, there is no other place in the world to find it.

The Iztaccíhuatl-Popocatepetl National Park (IPNP) is located in the Mexican states of Puebla, México and Morelos (19.2362° N, -98.6634° W), and it has an area of 39,819 ha and a human population of 244 people (Instituto Nacional de Estadística y Geografía (INEGI 2010); Comisión Nacional de Áreas Naturales Protegidas (CONANP 2013); Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT 2013). A large part of the geographic distribution of *R. diazi* (Martínez-Meyer 2005; Farías *et al.* 2015) is located within the natural protected area of IPNP (Figure 1), which includes pine forest, alpine meadows, rocks without vegetation and the Popocatepetl volcano. In the IPNP, Osuna *et al.* (2020) identified two of the four lineages of the *teporingo*, one at northern and the other at southern part.

The geographic distribution of a taxon depends on its ecological niche and dispersal ability (Soberón and Peterson 2005). Correlative methods link presence records of a taxon and its associated environmental variables, and therefore, they can be used to produce maps of potential distribution based on the theory of ecological niche (Soberón *et al.* 2017). In particular, species distribution models are representations in geographical space of the suitability of a place for a species' presence, where suitability is the mathematical or statistical relationship between the actual distribution and a set of predictor variables (Mateo *et al.* 2011).

We aimed to prioritize zones with high suitability for the volcano rabbit within Iztaccíhuatl-Popocatepetl National Park (IPNP), using data derived from satellite and fieldwork, relating the utility of correlative methods with helpful conservation strategies.

## Materials and Methods

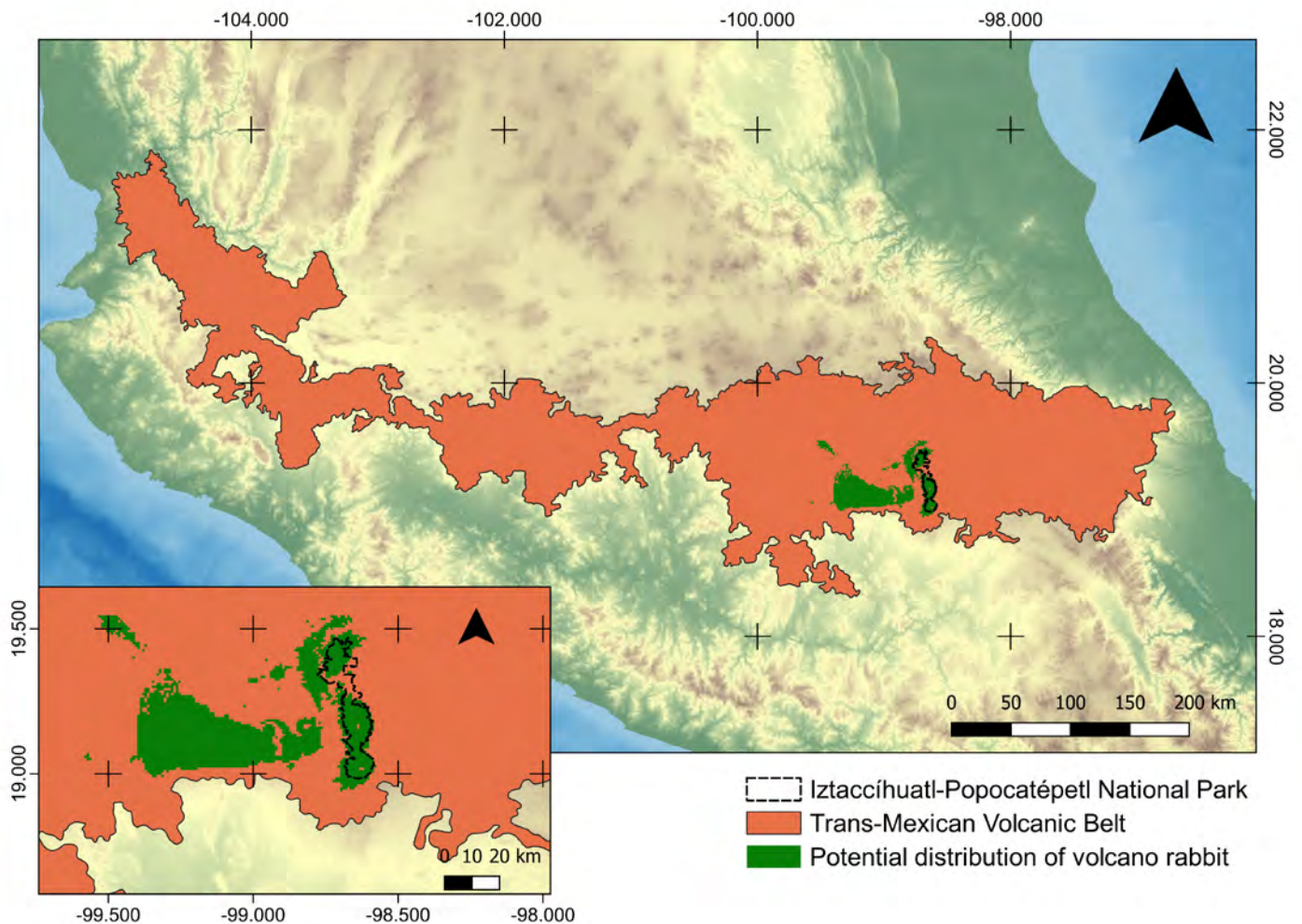
**Fieldwork.** The fieldwork aimed to obtain georeferenced presence records of *R. diazi*. Our study area for fieldwork was located on the southern part of the IPNP between the Popocatepetl and Iztaccíhuatl volcanos, a 74 km<sup>2</sup> site. Trap cameras were placed in the study area with a separation of 1 km between them. The cameras were installed 50 cm from the ground and were not impeded by vegetation. The cameras were operational from April 2018 through October 2018, with 2,138 camera days. Image processing was performed using Wild.ID 0.9.28 software (TEAM Network 2017). The following information was captured in the databases: project name, camera ID, geographic coordinates, date and time, type of photo, file name, taxonomic identification, number of animals, the person that identified, start date, end date, person who placed and removed the camera, camera model, and institution responsible. In addition to the camera images of volcano rabbits, their presence was recorded by direct and indirect observations. Throughout the study, transects were made to identify volcano rabbits and their latrines visually. The identification of latrines was based on a latrine surface area of approximately 20 cm x

20 cm, at least 20% fresh scat, a uniform discoid shape of feces, and a uniform 5 to 9 mm size of feces (Cervantes and Martínez-Vázquez 1996), with at least ten feces per latrine.

**Data analysis.** We performed different suitability models at a scale of 30 m to identify places with ideal conditions. To do this, we compiled the data obtained from our fieldwork into one database (model *a*) and in a separate database (model *b*) compiled data from fieldwork, GBIF data (biological collections or authors in Appendix 1), and data from the mammal database of the JM055 project funded by CONABIO (Escalante 2014). In both data sets, the locations were reviewed, and the points were filtered with a spatial resolution of 30 m. We used satellite images from November 7, 2017, January 10, 2018, and January 29, 2019, from Landsat 8 OLI/TIRS C1. United States Geological Survey (USGS 2019). First, we performed a radiometric calibration (conversion to reflectance with angular correction) of the Near Infrared (NIR), Red (R), and Shortwave Infrared 1 (SWIR1) bands (Ariza 2013; USGS 2013). Then, we used these calibrated bands to calculate the Normalized Difference Vegetation Index (NDVI; Rouse *et al.* 1973). To relate the NDVI values to specific vegetation types, six 50-m transects were performed in different areas and elevations of the IPNP. A 50-m rope was placed on the ground, and the vegetation under the rope was collected at one-m intervals. Plant species were identified *ex-situ* by César Miguel-Talonia (unpublished data). The NDVI values used for this vegetation characterization were from the satellite images from January 10, 2018, with the EPSG projection: 4326 – WGS84. The humidity was obtained using the Normalized Difference Moisture Index (NDMI; USGS 2013).

We estimated the surface temperature of the area using algorithms, as proposed by Wang *et al.* (2015) and Avdan and Jovanovska (2016). To do this, we first calculated the TOA (Top of Atmospheric Spectral Radiance; Barsi *et al.* 2014) from band 10 (TIR1) due to high uncertainty in the values of band 11 (TIR2; Wang *et al.* 2015). The value of  $O_{10}$  reported by Wang *et al.* (2015) is 0.29 (W·m<sup>-2</sup>·sr<sup>-1</sup>·μm<sup>-1</sup>), based on USGS files for dates before February 3, 2014. For later dates, as in our study, this value should not be included because the downloaded data is already processed, including this value (Wang *et al.* 2015). Secondly, we converted the reflectance to the brightness temperature (BT; USGS 2013), derived from an approximation of the Planck radiance function using the constants that appear in the product metadata. Third, we calculated the proportion of vegetation ( $P_v$ ) from the range of NDVI (maximum and minimum) depending on the area (Carlson and Ripley 1997; Sobrino *et al.* 2004; Dash *et al.* 2005). Sobrino and Raissouni (2000) proposed values of  $NDVI_s = 0.2$  and  $NDVI_v = 0.5$  for global conditions. For particular areas,  $NDVI_s$  and  $NDVI_v$  can be extracted from the NDVI histogram (Sobrino *et al.* 2008). Next, we calculated the emissivity of the Earth's surface (LSE, Land Surface Emissivity). In the wavelength range of Landsat 8 band 10, the emissivity can be calculated using the simplified threshold method for the NDVI ( $SNDVI_{THM}$ ;





**Figure 1.** Iztaccíhuatl-Popocatepetl National Park is located at the center east of the Transmexican Volcanic Belt. The potential distribution for *R. diazi* (Farias et al. 2015) is shown in the lower-left corner into the IPNP.

[Sobrino et al. 2008](#)). To calculate the emissivity, we used the values for general conditions proposed by [Sobrino and Raissouni \(2000\)](#). For NDVI values less than 0, the emissivity was assigned a value of 0.991; for NDVI values between 0 and 0.2, we considered that the surface is covered by soil and corresponds to an emissivity of 0.966; values between 0.2 and 0.5 corresponded with a mixture of soil and vegetation, while values above 0.5 were considered fully covered by vegetation, with an emissivity of 0.973 ([Wang et al. 2015](#)). We obtained the land surface temperature using the method of [Stathopoulou and Cartalis \(2007\)](#).

Finally, we used topography because it could affect species distributions. Therefore, we calculated the slope using the Continuous Mexican Elevation 3.0 ([INEGI 2013](#)). All layers obtained were projected to SCR: EPSG 4326 - WGS84.

For model calibration, and because our study is focused on the Iztaccíhuatl-Popocatepetl National Park, whose boundaries are based on natural factors ([CONANP 2013](#)), we considered the polygon of the park with a 2 km buffer as the accessible area. The environmental suitability was modeled using MaxEnt version 3.4.1 ([Phillips et al. 2006](#)). The model's parametrization strongly influences the final

results, and the output format has implications for its interpretation. Therefore, we used the cloglog transformation as the output format, derived from the interpretation of Max-Ent as a non-homogeneous Poisson process (IPP), producing a more robust theoretical justification than the logistic transformation ([Phillips et al. 2017](#)). Ecological theory suggests that response curves are unimodal for fundamental niches ([Austin 2007](#)), so quadratic features may be more appropriate.

On the other hand, linear features may be sufficient when the species' niche is cut on one side of the unimodal curve ([Merow et al. 2013](#)). For some authors, such as [Radosavljevic and Anderson \(2014\)](#), the regularization multiplier value must be greater than the default value (1) to achieve the model's optimal complexity. It is also advisable to eliminate highly correlated environmental layers since the features are already strongly correlated ([Merow et al. 2013](#)). In this work, to (a) have a unique criterion, (b) facilitate replication and (c) maximize the robustness of the resulting models, we used the 'kuenm' package ([Cobos et al. 2019](#)) in R Studio version 1.2.1k ([RStudio Team 2018](#)). We used the *kuenm\_cal* function to produce candidate models

combining all possible features (29 combinations) and the following values for the regularization multiplier: 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 5 and 6. To develop candidate models, we used different combinations of predictive variables: the first set with all the predictive layers, the second set only with the layers that did not show collinearity (based on a collinearity matrix and estimation of the VIF; R routine in Appendix 2), and the third group without topographic layers. The data partition for training and testing was done with the 'ENMeval' package (Muscarella *et al.* 2014) in RStudio version 1.2.1k (RStudio Team 2018) using the random k-fold method where 75 % of the data were selected for training and the remaining 25 % for testing. We evaluated each candidate model using the *kuenm\_ceval* function based on the statistical significance given by the partial ROC curve, the omission rate, and the complexity of the model, calculated with the Akaike information criterion corrected for small sample sizes (AICc; Akaike 1974; Burnham and Anderson 2002; Warren and Seifert 2011). The models that met the requirements were selected, and we generated the final models with the *kuenm\_mod* function using ten bootstrap replicates with a cloglog output format. Finally, we evaluated those final models with the *kuenm\_feval* function, based on an independent data set excluded before model calibration, and we selected the model with the best performance.

The conversion of the suitability model (with continuous values from 0 to 1) to a binary model (only absence and presence) was performed using the 'dismo' package (Hijmans *et al.* 2017) with an acceptable threshold of  $E = 10$  (Peterson *et al.* 2008). To establish a priority area for the conservation of *R. diazi* within the IPNP, the suitability model was converted to a distribution model reduced to an area of greater suitability with a threshold of  $E = 50$ , because some work such as Waltari and Guralnick (2008) suggests that a more stringent threshold provide high consensus presence and better refuge area. To obtain one unique distribution model for both thresholds, we summed all of the final binary models for each date and data set, and we selected the pixels where at least half of the models predicted presence.

*Polygons for conservation.* Finally, to obtain priority conservation polygons, we used the distribution model reduced to an area of greater suitability (threshold  $E = 50$ ) and a road map (Google Inc. 2019) from Google Maps Layer TMS (Tile Map Service) using the XYZ Tiles plug-in. We selected this distribution model's continuous areas that did not reach crossroads in QGIS 3.4.4 (QGIS Development Team 2019). Subsequently, we merged the chosen areas and produced four minimum convex polygons using the QGIS convex envelope function. We calculated the area and perimeter for each polygon, and to characterize them, their external vertices were extracted with their respective latitude-longitude coordinates. Furthermore, we obtained the elevational range for each polygon using the Continuous Mexican Elevation 3.0 (INEGI 2013) with a 90 m-resolution.

## Results

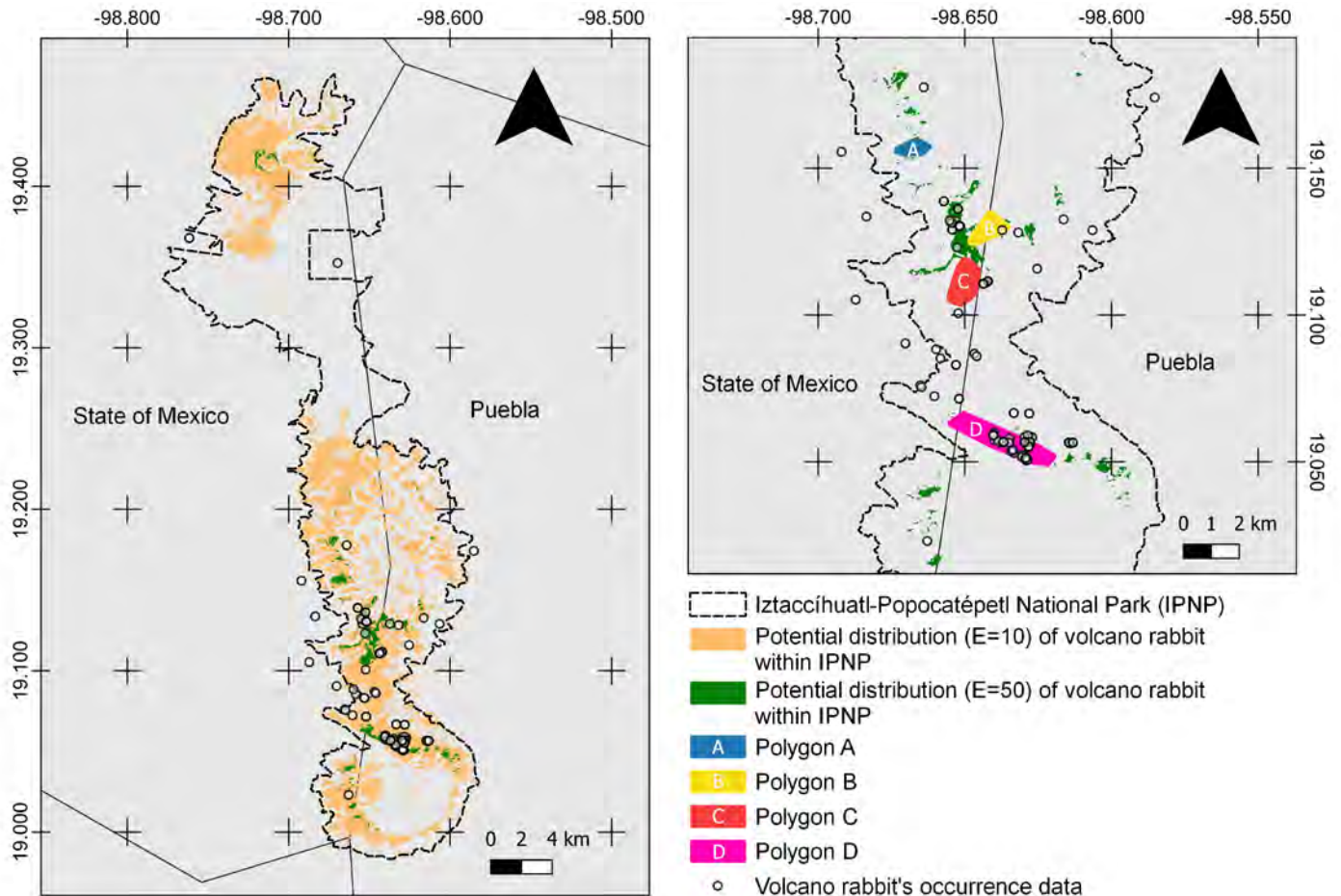
*Fieldwork.* In the camera traps, we obtained photos of 33 individuals of *R. diazi*. Adding the visual identification of latrines and direct observations of individuals, we obtained 82 occurrence records for the species. There were nine main plants recorded along the vegetation transects: *Pinus hartwegii*, *Lupinus montanus*, *Eryngium proteiflorum*, *Draba jorullensis*, *Senecio* sp., *Festuca tolucensis*, *Muhlenbergia* sp., *Trisetum* sp. and *Calamagrostis tolucensis*. We compared the NDVI value with the georeferenced transects and obtained a vegetation characterization, which we mapped. The results were the following: NDVI < 0, without vegetation; NDVI between 0 and 0.1, alpine meadow with *C. tolucensis* and bare soil and rock; NDVI between 0.1 and 0.2, meadow with *Muhlenbergia* sp. / *C. tolucensis*; NDVI between 0.2 and 0.3, meadow with *Muhlenbergia* sp.; NDVI between 0.3 and 0.4, meadow-forest ecotone; and NDVI > 0.4, pine forest.

*Suitability models.* For the model using only data from fieldwork (model *a*), we had 51 points for calibration (13 points used as testing data and 38 points as training data) and 17 points for independent evaluation. For the model with mixed data (model *b*; fieldwork, GBIF, and JM055 project), we had 66 points for calibration (50 points as training data and 16 points as testing data) and 22 independent points for final evaluation. Overall, 4,466 candidate models were evaluated (Table 1).

*Potential distribution model.* The area potentially occupied by the volcano rabbit, based on this final distribution model, reached 132.5 km<sup>2</sup> within the IPNP (Figure 2). Compared to the potential distribution (Martínez-Meyer 2005; Farías *et al.* 2015), the volcano rabbit's distribution was reduced to 33 % of the IPNP polygon.

*Potential distribution model reduced to a greater suitability area.* The more suitable area covered 7 km<sup>2</sup> (Figure 2). We overlapped this area with the vegetation characterization. We found that bare soil with sparse vegetation occupied 0.29 km<sup>2</sup> of this most suitable area, alpine meadow dominated by *Muhlenbergia* sp. and *C. tolucensis* covered 1 km<sup>2</sup>. The meadow dominated primarily by *Muhlenbergia* sp. occupied 4.6 km<sup>2</sup> of greatest suitability, being the most suitable vegetation for the volcano rabbit.

*Proposal of polygons for conservation.* We obtained four polygons as refuges for the conservation of *R. diazi* inside the IPNP (A, B, C & D; Figure 2). Polygon A had an area of 0.69 km<sup>2</sup> and a perimeter of 3.33 km, with an average altitude of 3,912 m, a minimum altitude of 3,848 m, and a maximum altitude of 4,029 m. Polygon B represented an area of 1.13 km<sup>2</sup> with a perimeter length of 4.39 km, and the mean altitude is 3,931 m with a minimum and maximum altitude of 3,835 m and 4,054 m, respectively. For Polygon C, the selected area had 1.61 km<sup>2</sup> and a perimeter of 4.92 km, where the mean altitude is 3,874 m. The minimum altitude is 3,780 m, and the highest value is 3,987 m. Finally, Polygon D had an area of 3.14 km<sup>2</sup> and a perimeter of 9.1 km, and its average altitude is 3,946 m with a minimum



**Figure 2.** The potential distribution model for *R. diazi* in the Iztaccihuatl-Popocatepetl National Park and potential distribution model with the area reduced to those with greater suitability. All the models obtained with the threshold  $E = 10$  or  $E = 50$  were added together, and the pixels where at least 50 % of the models predict presence were selected. On the right side, four polygons (A, B, C, and D) are shown based on the potential distribution model  $E = 50$  and Google Roads map.

value of 3,823 m and a maximum elevation of 4,066 m. The coordinates for each external vertex are shown in Appendix 3. The total proposed area to prioritize for the conservation of *R. diazi* within the IPNP occupies 6.57 km<sup>2</sup>.

## Discussion

Ecological niche modelling and its use as a hypothesis of potential or actual geographical distribution are helpful in prioritizing conservation areas (Sánchez-Cordero *et al.* 2004). The IPNP is a decreed conservation area; however, administration and management's decision-making should coincide under a theoretical-practical framework.

The information derived from satellite products is a powerful tool for generating models with better performance on detailed scales (e.g., Rödder *et al.* 2016; Vila-Viçosa *et al.* 2020). In this study, we included the NDVI as an abiotic predictor, although it can also be interpreted as a biotic predictor (He *et al.* 2015). Different plant species have different leaf anatomy that results in variations in the reflectance captured by remote sensing (He *et al.* 2009). Although it is possible to find areas with diverse vegetation where the NDVI calculated could be similar, the comparison between studies situated in other geographical regions should be

taken cautiously. Identifying georeferenced vegetation and its subsequent relationship with the NDVI values allows the replication of our research. For the future, the addition of NDVI values to flora catalogs, discriminating seasonally, altitudinally, and latitudinally, will facilitate sampling and knowledge of the vegetation of an area and its subsequent relationship with the geographical distribution of animals.

This study included different sets of variables from various data sources to obtain a broader spectrum of information. Because statistical methods controlled the evaluations, and we cannot be ensured that the results of the selected final models guarantee accurate geographic distribution, we decided to combine all the models and select only those pixels where at least half of them coincided with increasing the certainty of the results. Distribution models should be generated with high precision and strictly interpreted not to incur unhelpful or unproductive conservation practices that may put the target species at risk and other taxa. However, a potential distribution model from a suitability model is strongly influenced by the different existing configurations and settings. Thus, it is advisable to use methods that allow standardizing the calibration process of a model.

**Table 1.** Results of the evaluation of the final models (model a with fieldwork data only and model b with mixture data) for each date. P-value-pROC is the value of 'p' given in the Partial ROC analysis. OR is the omission rate. Features types: T = threshold, L = linear, Q = quadratic, P = product and H = hinge. AICc is the Akaike Information Criterion with a correction for small sample sizes. RM is the regularization multiplier.

Models date	pvalue-pROC	OR	AICc	Feature types	Variables	RM
Model 'a' dates						
Nov 7, 2017	0	0.08	1154.32	T	all	2
Jan 10, 2018	0	0.23	1147.74	L, Q, P, T	all	1.5
Jan 29, 2019	0	0.08	1161.14	T	no collinearity	1
Model 'b' dates						
Nov 7, 2017	0	0.06	1608.13	Q, T	all	4
Jan 10, 2018	0	0.13	1551.30	P, T	all	2.5
Jan 29, 2019	0	0.06	1636.80	L, Q, T, P, H	all	5

The distribution of *R. diazi* showed that the volcano rabbit's occupation could reach most of the IPNP surface (Martínez-Meyer 2005; Farías et al. 2015). However, this is uncertain, and the IPNP administration does not have the information required to determine the appropriate area for implementing a conservation strategy. For this reason, the search for a more realistic distribution area is necessary to provide that basic knowledge. At a 30-meter m scale, the potential distribution model significantly reduced volcano rabbit occupancy within the IPNP polygon to up to 33 % park's total area. This difference may be caused by the use of a different scale, but also by the use of different variables or the parameterization of the model, so comparisons should be made with caution.

On the other hand, the environmental predictors used corresponded only to the dry season in México. Therefore, the resulting models can be considered informative for the dry season. However, since *R. diazi* has a very small home range (Cervantes and Martínez-Vázquez 1996), the distribution of this rabbit will likely be very similar in the rainy season.

Several studies have been published about the volcano rabbit over the past few decades. Velázquez and Bocco (1994) considered agriculture one of the factors that most threatened this species on the Tláloc and Pelado volcanoes. They established areas with different degrees of suitability based on this risk factor. Rizo-Aguilar et al. (2015) showed that vegetation structure and altitudinal range are directly related to the abundance of *R. diazi*. Moreover, the percentage of meadow cover, short grass, and the scrub cover have a positive relationship with the abundance of the volcano rabbit.

In contrast, the closed forest, tall grass, cattle pasture, hunting, bare terrain, and slope have a negative relationship with its abundance (Hunter and Cresswell 2015). We demonstrated that the suitability and potential distribution are not uniform in the IPNP through modelling techniques and the cross-linking of information with data derived from satellite products. The alpine meadow dominated by *Muhlenbergia* sp. is the most suitable area for *R. diazi* in the IPNP, followed by the alpine meadow composed of *Muhlenbergia*

sp. and *Calamagrostis toluensis*, both belonging to the Poaceae family. The relationships between the volcano rabbit and plant communities were studied by Velázquez and Heil (1996) in the Pelado and Tláloc volcanoes, where the associations of *Festuca toluensis* and *Trisetum spicatum*–*Festuca toluensis* had the greatest abundance of *R. diazi*. While the floristic study of our work was not the main objective, the inclusion of the plants allowed us to corroborate the importance of alpine meadow without trees in the distribution of *R. diazi*. Conservation strategies should focus on preserving the alpine meadows in the prioritized polygons, avoiding tourist and unskilled personnel's access to those specific areas. Human activities in high-mountains ecosystems adversely affect animals (Peřsa and Ciach 2015). The speed of road traffic and the emission of noise in the surrounding areas should be controlled (Garriga et al. 2012), along with other practices to mitigate human impact, such as avoiding the discharge of inorganic and organic waste. In the coming years, scientific studies within the IPNP should be carried out jointly with the park administration and human communities to provide updated tools for decision makers.

Our conservation polygons for *R. diazi* are based on the most suitable areas and existing access roads in the IPNP because of the significant influx of tourists. Polygons were selected using a remote sensor from three specific dates, so we expected that the vegetation, humidity, and the land surface temperature would change at other times. Besides, our polygons have an average altitude upon 3,800 masl, so they could be helpful in a climate change scenario according to the ascent of the lowest altitudinal limit of the volcano rabbit's distribution (Anderson et al. 2009). Furthermore, the relative abundance of this rabbit is significantly higher in altitudes above 3,600 masl with abundant bunchgrass cover (Osuna et al. 2021). According to the significant evolutionary units proposed by Osuna et al. (2020), these polygons are located in the area of the Nevada south unit and can also be useful as a natural refugee for genetic management.

Global warming in the medium-long term could lead to changes in the distribution of the volcano rabbit since in the mountains there is an altitudinal temperature gradient that will likely lead species to move uphill (Gottfried

[et al. 2012](#)). This phenomenon may eventually result in an inability to reach optimal conditions, and the species may become extinct ([Colwell et al. 2008](#)). Therefore, we consider that the next step for conserving the teporingo could be selecting the most suitable areas within the IPNP under alternative climate change scenarios.

In addition to the proposed polygons, the most suitable areas identified by niche models should be used as a theoretical and practical basis to propose and execute any conservation strategy *in situ*. In particular, the vegetation within the reduced distribution of volcano rabbit should be conserved. The meadow with *Muhlenbergia* sp. is a priority area, and reforestation with pine in them is not advisable.

The boundaries of the IPNP were well designed to protect *R. diazi*. Although this park has recovered some of its forest covers and has a low amount of transformed area ([Aguilar-Tomasini et al. 2020](#)), the conservation of an area does not end with its declaration as a Natural Protected Area. Continuous updating is needed to provide precise conservation tools within protected areas. The abiotic and biotic conditions of the park polygon will vary. The methodological tools in the future will provide various techniques that will enable the rise of information about one of the most threatened and emblematic lagomorphs of México: the volcano rabbit.

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## Appendix 1

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## Appendix 2

```

#Correlations (Marco F. Ortiz and David Prieto-Torres)
library(sp)
library(raster)
library(rgeos)
library(maptools)
library(rgdal)
library(usdm)
library(foreign)
library(rJava)
library(spocc)
library(corrplot)
library(usdm)
rm(list=ls())
setwd("C:/Work_directory_with_climate_layers")
pca_path <- list.files(".",pattern = "*.asc$",full.names = T)
climatelayers<- stack(pca_path)
setwd("C:/Work_directory_with_presence_data")
data <- read.csv("species.csv")
plot(climatelayers[,1])
species<-data$species
lat<-data$y
lon<-data$x
Specie_estudied<-data.frame(species,lon,lat)
presences_climate <- data.frame(extract(climatelayers,
Specie_estudied[,2:3]))
presences_climate2<-data.frame(Specie_estudied,
presences_climate)
presences_climate3 <- na.omit(presences_climate2)
setwd("C:/Work_directory_presence_with_climate")
write.csv(presences_climate3[,1:3], file = "name.csv")
### Collinearity matrix and VIF estimation##
cormatriz <- cor(presences_climate3[,4:22]) ##bio1-
bio19##
setwd("C:/work_directory")
windows()
corrplot(cormatriz, outline = T, tl.col = "black", mar =
c(2,0,1,1.5), title = "title")
###VIF>10 [Montgomery and Peck (1992)]
vif(presences_climate2[,4:22])
no_corr <- vifstep(presences_climate2[,4:22], th=10)
no_corr

```

### Appendix 3

Geographic decimal coordinates of the proposed polygons for conservation of *Romerolagus diazi* within Iztaccíhuatl-Popocatepetl National Park.

Vortex	Longitude	Latitude	Vortex	Longitude	Latitude
Polygon A			14	-98.6444603	19.11589397
1	-98.670676	19.15410191	15	-98.6444603	19.11533619
2	-98.673186	19.15465969	16	-98.6455759	19.10724838
3	-98.6740227	19.15521747	17	-98.6461337	19.1066906
4	-98.6743016	19.15549636	18	-98.647807	19.10501726
5	-98.6743016	19.15577525	19	-98.6511537	19.10278614
6	-98.6740227	19.15689082	Polygon D		
7	-98.6737438	19.15716971	1	-98.6215913	19.04840257
8	-98.6729071	19.15772749	2	-98.6268903	19.04896035
9	-98.6723494	19.15800638	3	-98.6413925	19.05481705
10	-98.6664927	19.16079528	4	-98.6505959	19.05955818
11	-98.6662138	19.16079528	5	-98.6553371	19.06206819
12	-98.6617515	19.15828527	6	98.655616	19.06234708
13	-98.6611938	19.1574486	7	-98.6558948	19.06318375
14	-98.6611938	19.1571697	8	-98.6558948	19.06374153
15	-98.6637038	19.1546596	9	-98.6505959	19.0673671
16	-98.6642615	19.1543808	10	-98.650317	19.0673671
17	-98.6650982	19.1541019	11	-98.6254958	19.05649039
Polygon B			12	-98.6188024	19.05258592
1	-98.647807	19.12342401	13	-98.6188024	19.05147036
2	-98.6492015	19.12426068	14	-98.6213125	19.04840257
3	-98.6492015	19.12565513			
4	-98.6425081	19.13513739			
5	-98.6419503	19.13569517			
6	-98.6405559	19.13569517			
7	-98.6346992	19.13067515			
8	-98.6344203	19.13039626			
9	-98.6344203	19.12983848			
10	-98.6355359	19.12816514			
11	-98.6358147	19.12788625			
12	-98.6466915	19.12342401			
Polygon C					
1	-98.6514326	19.10278614			
2	-98.6547793	19.1039017			
3	-98.6553371	19.10418059			
4	-98.6558948	19.10473837			
5	-98.6561737	19.10529615			
6	-98.6561737	19.10585393			
7	-98.6558948	19.10780616			
8	-98.6533848	19.11589397			
9	-98.652827	19.11700953			
10	-98.6508748	19.11979843			
11	-98.6494804	19.11979843			
12	-98.6475281	19.11896176			
13	-98.6447392	19.11617286			

# Ethological studies of native Mexican mammals: A review

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The number of ethological studies based on Mexican mammals have increased in recent years compared to those from other Latin American countries. This study conducts an analytical review of the literature on ethological studies of native Mexican mammals. Specialized publications and electronic bibliographic databases were thoroughly searched to identify ethological studies of Mexican mammals published in scientific journals between 1900 and 2018. Information on the collection locality, state, first author nationality, country of origin of the journal, and taxa studied were recorded for each article. The articles were then classified into the 12 major ethological fields, and their data were grouped and summarized in five-year periods, and a map showing the geographic distribution of the studied localities was built using QGIS. A total of 160 studies were identified; three distinct periods could be recognized: the first (1900 to 1953) with a lack of publications, the second (1954 to 1995) with low production ( $n = 16$ ), and the third (1996 to 2018) with a notable increase in published articles ( $n = 144$ ); in general, there was a greater participation of Mexican authors (67.5 %). Most studies (> 70 %) focused on primates, rodents, bats, and carnivores. Veracruz is the entity with the most articles, while foraging, movement, nesting, rearing, and territorial behavior were the subjects most studied, followed by social behavior, cooperation, and kinship. The greater number of studies published in the past two decades is likely the result of an increased number of mammalogists and their engagement in national and international collaborative partnerships, mainly in areas such as ecology and taxonomy. Despite a relatively recent development of the field in México, an absence of studies on half of all terrestrial mammals orders, and few studies throughout northern parts of the country, mammalian ethology in México has already made significant contributions and is highly likely to continue its development and consolidation.

Los estudios de etología en mamíferos de México han repuntado en los últimos años con respecto a otros países latinoamericanos. El objetivo de este trabajo es elaborar un análisis bibliográfico de dichos estudios con enfoque etológico realizados con mamíferos nativos de México. Se obtuvo la bibliografía de estudios entre 1900 y 2018 sobre la etología de mamíferos de México con base en revistas periódicas, mediante la búsqueda en revistas especializadas y en bases de datos electrónicas. De cada artículo se registraron campos como: lugar de colecta, entidad federativa, nacionalidad del autor principal, origen de la revista y taxones trabajados, y se agruparon en uno de los doce temas etológicos principales. Con el programa QGIS se elaboró un mapa de las localidades de los estudios. Se registraron 160 trabajos que fueron distribuidos en tres periodos, el primero (1900 a 1953) con nula producción, el segundo (1954 a 1995) con baja producción ( $n = 16$ ) y el tercero (1996 a 2018) con un incremento notable en la publicación de artículos ( $n = 144$ ); en general, se presentó una mayor participación de autores nacionales (67.5 %). La mayoría de los trabajos (> 70 %) se han enfocado en el estudio de primates, roedores, quirópteros y carnívoros; Veracruz es la entidad federativa con más trabajos; mientras que, los temas más estudiados han sido sobre forrajeo, movimiento, anidación, crianza y territorialidad, así como comportamiento social, cooperación y parentesco. El incremento del número de publicaciones principalmente en las últimas dos décadas se puede deber al aumento de mastozoólogos y al establecimiento de colaboraciones nacionales e internacionales, principalmente en áreas como la ecología y la taxonomía. Aunque es una ciencia relativamente joven en México, y a pesar de la ausencia de estudios en la mitad de los órdenes de mamíferos terrestres y en la parte norte del país, el campo de la etología de mamíferos de México cuenta con un número importante de contribuciones y es muy probable que el desarrollo de esta área del conocimiento continúe en el proceso de crecimiento y consolidación.

**Keywords:** Behavior; ethology; land mammals; México.

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## Introduction

Traditionally, ethology has been defined as an approach to the study of animal behavior, derived from the discovery of instinctive movements ([Eibl-Eibesfeldt 1975](#); [Moreno and Muñoz-Delgado 2007](#); [Breed and Moore 2012](#)). This scientific discipline emerged from the interest in deepening the knowledge of animal behavior and understanding the variety of behaviors displayed by different species under dif-

ferent conditions ([Carranza 2010](#)). Ethology focuses on the study of behavior, understood as an exchange mechanism between the organism and its environment under natural conditions ([Díaz 1994](#); [Medawar and Medawar 1996](#)).

The earliest ethological studies conducted in México were carried out by ecologists and taxonomists interested in behavioral aspects of animals and their environment ([Herrera 1986](#)). Mammals exhibit a wide variety of life

histories that make them suitable models for conducting ethological studies (e. g., [Soares et al. 2016](#)). Eleven orders, 36 families, 169 genera, and 503 species of terrestrial mammals have been recorded in México ([Álvarez-Castañeda et al. 2015](#)). According to [Guevara-Chumacero et al. \(2001\)](#), very few studies on Mexican mammals have addressed behavior as the primary study field: only 0.6 % of the 1826 scientific articles published between 1890 and 1995 did so. The earliest clearly ethological studies on Mexican mammals addressed a diverse range of issues and taxa. For example, [Russell and Findley \(1954\)](#) described the swimming of a rodent of the genus *Onychomys* in the northern part of the country (State of Nuevo León), and [Packard \(1958\)](#) described carnivory behavior in the Mexican ground squirrel (*Ictidomys mexicanus*) in the State of Coahuila. [Wimsatt \(1969\)](#) described foraging and refuge selection by the common vampire bat (*Desmodus rotundus*) in the State of Tabasco, southern México, and [Greenhall et al. \(1971\)](#) documented the attack mode of this species on cattle in the State of Oaxaca. As these examples show, early ethological studies were observational and descriptive. These same study areas were explored in other Latin American countries prior to the adoption of experimental approaches ([Jaffe et al. 2020](#)). However, recent ethological studies from Latin America and other parts of the world (e. g., Europe and Australia) have used rigorous experimental methods based on hypothesis testing ([Hoffmann et al. 2018](#); [Morete et al. 2018](#); [Wierucka et al. 2018](#); [Mazza et al. 2020](#)).

The available data indicate that ethological studies have recently become more prominent in México and Brazil than in other Latin American countries. However, an increase in the number of ethological studies over time is evident throughout Latin America, as interest in the academic discipline of animal behavior has grown in recent years ([Jaffe et al. 2020](#)).

Although México has been an important contributor to ethological studies, the progress made to date and direction taken by this type of studies in Mexican mammalogy have not been documented. Therefore, this study conducts an analytical review of the literature on ethological studies of native Mexican mammals. The objective of the study is to assess the wealth of information gathered to date and the path followed by this scientific discipline in México and based on this, to identify study subjects that need to be addressed by future efforts.

## Materials and methods

**Data gathering.** An exhaustive search was conducted by consulting periodic journals on the bibliography concerning the ethology of mammals collected or observed in México between 1900 to 2018. We consulted the following websites: 1) Google Scholar (<https://scholar.google.com/>), 2) Clarivate Analytics - Web of science (<https://clarivate.com/webofsciencelibrary/>) and 3) databases in biodiversity (<https://bidi.uam.mx/bidi-ti/bases.html>), such as: Biological Abstract, BioOne Complete, Current Contents Connect,

EBSCO, Nature, ProQuest, Science, Scopus, and Scielo. The used search keywords were: mammals, México, behaviour, behavior, conduct, ethology, homeostasis, circadian cycles, learning, cognition, communication, movement, foraging, self-defense, mating systems, nesting, rearing, territoriality, social behavior, conservation and behavior; these words were also combined, and used in Spanish. Each article compiled was reviewed in detail to identify whether it had an ethological approach as its main objective.

**Processing of data.** The information contained in the references was reviewed and organized in a database using EndNote Plus v. X 7.5 (Niles & Associates, Inc). The fields used were: author, year, title, journal, volume, pages, language, nationality of the first author or corresponding author, federal entity, order, family, genus, species, location in geographical coordinates, state (wild, captive, semi-captive), subject of study, the Mexican institution affiliation of first or corresponding author, and the risk category according to the Mexican Official Standard ([SEMARNAT 2010](#)), the IUCN Red List of Threatened Species (Red List) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

**Study locations.** For each article, the locality/localities where the observations were performed or the place where the data of the individuals studied in captivity was collected, and were registered for the Mexican state and the geographic coordinates (in decimal degrees). When not included in the publications, the mentioned localities were georeferenced in Google Earth ([Lisle 2006](#)). Using open-source Geographic Information System QGIS 2018 v. 3.4.4, a map of the localities was prepared, using as a base layer the State Political Division (2018), available in the Geoportal of the National Commission for the Knowledge and Use of Biodiversity (CONABIO).

**Data analysis.** To view research trends in detail, the data was split into periods of five years (Lustrums), except for the last period that covers three years. When the corresponding author was absent, the main author was considered as first author. In addition, the authors were classified as national or foreign according to the country of origin. A grouping was also made according to the origin of the journal (national or foreign).

Each publication was grouped into one of the 12 main ethological fields (Table 1) following [Breed and Moore \(2012\)](#). In addition, the publications were grouped according to the Mexican state where each study was carried out. In this work we follow the taxonomic nomenclature proposed by [Álvarez-Castañeda \(2015\)](#).

## Results

One hundred and sixty-seven published scientific articles were registered between 1900 and 2018, with no productivity between 1900 to 1953, and a low productivity in the first forty years (1954 to 1995) with only 16 papers. On the other hand, in the period between 1996 to 2018, there was

**Table 1.** List of ethological studies according to Breed and Moore's categories (2012).

Fields	Subfields
Homeostasis and time budgets	Biological clock and circadian cycles, homeostatic regulation, time budgets and trade-offs.
Learning	Learning and memory, social learning, play, learning and development.
Cognition	Concept of self, thinking, predicting, and solving problems, intelligence and social cognition, personality and behavioral syndrome, impulse control, animal emotions.
Communication	Evolution of communication, types of communication, out-of-control sexual selection and signaling, deception and honest communication, game theory and communication, interspecific signaling.
Movement	Searching, homing (ability to return to a territory after leaving it), migration, dispersal.
Foraging	Diet and food choice, obtaining food, food disposal, prey handling, parasite cycles, foraging and optimization theory, optimal patch choice, prey choice.
Self-defense	Cryptic behavior and camouflage, surveillance and alarm, mimicry and deviance, evasion, predator deterrence and response to attack, pathogen avoidance, deterrence behavior and disease.
Mating systems	Sexual selection, variation in mating event, choice of male, hormones and sexual behavior, hormones territoriality and aggression, sperm competition, forced copulations, models of good genes for choosing a male.
Nesting, rearing, and territoriality	Nests and nesting, parental investment, parental care patterns, hormones and parental care, parenting, and conflict of interest, begging and weaning conflict, sibling conflict, infanticide, aggression, and territoriality.
Social behavior, cooperation, and kinship	Altruism and self-interest, herds and hordes, cooperation, eusociality, social recognition.
Comparative social behavior	To elucidate the differences of a specific behavior in different species.
Conservation and behavior	Integration of the other fields to obtain useful information for conservation.

a notable increase in published articles ( $n = 144$ ; 90 % of the total; Figure 1). In general, Mexican authors (108 articles, 67.5 %) had a more active participation than foreign authors (52, 32.5 %, respectively).

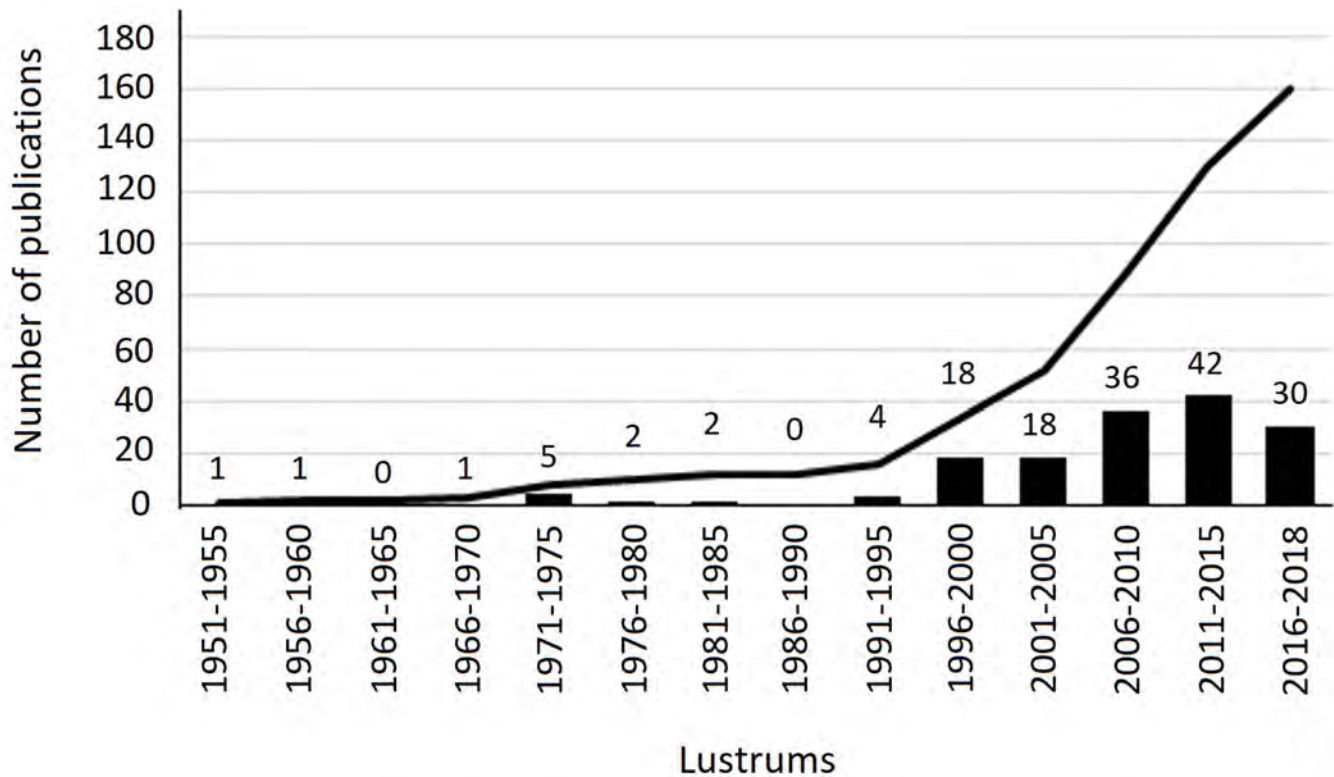
Studies were published in 51 different journals (40 included in the Journal Citation Reports 2018 of Institute for Scientific Information - ISI) from 14 countries, 7 of Mexican origin and 44 foreign (33 % corresponded to the United States). The journals with the highest number of publications were American Journal of Primatology ( $n = 16$ ), Journal of Mammalogy ( $n = 15$ ), and International Journal of Primatology ( $n = 14$ ). Among the Mexican journals, Acta Zoológica Mexicana (nueva serie) and Therya had the highest number of publications with 9 publications, each (Table 2).

In total the studies were based on 54 species from 16 families and 6 orders. The most studied species belonged to the order Primates and were *Ateles geoffroyi*, *Alouatta palliata* and *A. pigra*, with 43.6 % of the publications. Other orders were Rodentia (21.5 %), Chiroptera (15.4 %), Carnivora (15.4 %), Lagomorpha (2.1 %) and Cetartiodactyla (2.1 %; Table 3). Of the 54 species, 10 are endemic to México and 17 species have some category of risk at the national or international level.

Articles were recorded for 23 Mexican states, with Veracruz ( $n = 31$ ), Chiapas ( $n = 21$ ), Quintana Roo ( $n = 20$ ), totalling 43 % of all studies. States such as Aguascalientes, Nayarit, Sinaloa, Tlaxcala, among others, lack any studies (Figure 2). Sixty percent of the studies focused on foraging, movement, nesting, rearing and territoriality, social behavior, cooperation, and kinship, while only 2.4 % had as main objective the fields of learning and cognition (Figure 3).

## Discussion

The publication rate of ethological studies of Mexican mammals varied considerably over the study period (1900 to 2018). We are aware of the probability that some gray literature articles might have not been considered, although it should not affect the trends presented. No production was recorded between 1900 to 1953, while very few studies were published ( $n = 16$ ) between 1954 and 1995. This is consistent with the findings of [Guevara-Chumacero et al. \(2001\)](#) who found that only 0.6 % of the 1826 articles on Mexican terrestrial mammals that were published during the period from 1890 to 1995 dealt with behavioral studies. The number of publications increased noticeably since 1996 (Figure 1); one hundred and forty-four were published during 1996 to 2018. This increase, mostly in the last decade of the 20<sup>th</sup> century, is the result of increasing specialists in mammalogy and their engagement in interdisciplinary collaborations ([Ramírez-Pulido et al. 2017](#)), mainly in areas such as ecology and taxonomy ([Cordero 1994](#)) throughout México. In the second period, foreign authors had a more important role of participation than national authors. While in the third period, the national authors were the main authors of the studies (figure not shown). Institutions such as the Instituto de Neuroetología of the Universidad Veracruzana, Instituto Nacional de Psiquiatría Ramón de la Fuente Muñiz, El Colegio de la Frontera Sur-Campeche, as well as Facultad de Estudios Profesionales Superiores Iztacala, Estación de Biología Tropical Los Tuxtlas, and the institutes of Biology and Ecology of Universidad Nacional Autónoma de México (UNAM), have played a key role in this growing trend.



**Figure 1.** Articles published about ethological fields between 1951 and 2018 in 5-year periods (Lustrums). The bars and numbers on bars indicate the number of publications each five years, and the line indicates the cumulative increase in publications.

A large proportion of papers (82.5 %) were published in international, non-Mexican journals, most of which (84 %) are indexed in the Journal Citation Reports - ISI. Not surprisingly, journals specialized in primatology (e. g., *American Journal of Primatology*, *International Journal of Primatology*, *Primates*, *Folia Primatologica*, and others) stand out, as over half of all articles have focused on the order Primates.

Primatology studies of native Mexican species began with several ecological and behavioral studies carried out at Los Tuxtlas Biological Station, in the State of Veracruz (e. g., [Estrada 1984](#)). Eighty-four percent of the original vegetation of the Los Tuxtlas region has been either lost or fragmented ([Dirzo and García 1992](#); [Dirzo et al. 2009](#)); consequently, local populations of primate species have also been significantly reduced ([Escobedo-Morales and Mandujano 2007](#)). The proper design of conservation strategies requires up-to-date information on aspects such as the geographic distribution ([Estrada 1982](#); [Estrada and Coates-Estrada 1988](#)) and ethology ([Estrada et al. 1999](#); [Juan et al. 2000](#)) of the species. As a result, Veracruz is the Mexican state where the highest number of ethological studies ( $n = 31$ ) have been conducted.

Most records of ethological studies are concentrated in the southeast part of the country, roughly matching the geographic distribution of Mexican primates (Figure 2). *Ateles geoffroyi*, *Alouatta palliata*, and *A. pigra* were the most common species studied, with more than 40 % of the publications. In addition, the study of primates such as *Ateles* and *Alouatta* is key for understanding the development

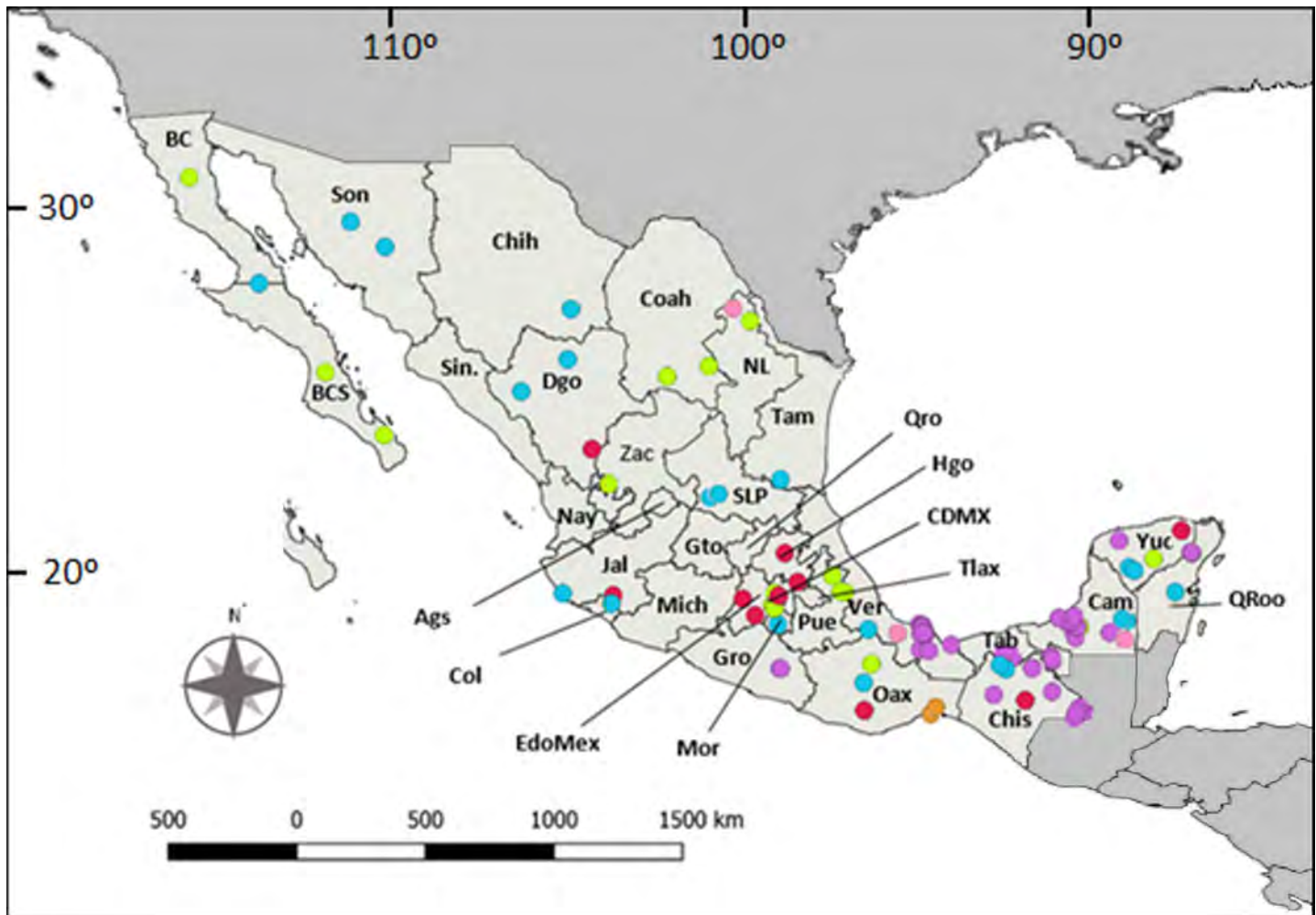
and evolution of the human species (e. g., [Emery Thompson 2019](#)) and is a cornerstone for conserving the tropical ecosystems they inhabit, given their role as umbrella species ([Rodríguez-Luna et al. 2013](#)). Finally, primates are charismatic species whose knowledge can contribute to attract support for conservation projects ([Hill 2002](#)).

Although with a much modest contribution in publications, the orders Rodentia, Carnivora and Chiroptera follow the order Primates ethological studies. The volcano mouse (*Neotomodon alstoni*), an endemic species from central México, is the most studied rodent because its social nature and omnivorous diet facilitates its study in captivity (e. g., [Luis et al. 2000, 2012, 2017](#)). The puma (*Puma concolor*), the jaguar (*Panthera onca*) and the Mexican wolf (*Canis lupus baileyi*) were the most heavily studied carnivores because they are emblematic, charismatic species and because are in some risk category (the last two; e. g., [Servín 1991, 1997](#); [Servín and Huxley 1991](#); [Hernández-SaintMartín et al. 2015](#); [De la Torre et al. 2017](#)). The Jamaican fruit-eating bat (*Artibeus jamaicensis*) has attracted attention due to its dynamics of harem groups presented ([Ortega and Arita 1999](#); [Ortega and Maldonado 2006](#)), and the vampire bat (*Desmodus rotundus*) for attacking cattle ([Wimsatt 1969](#); [Greenhall et al. 1971](#)). Half of México's land mammal orders (Didelphimorphia, Cingulata, Perissodactyla, Pilosa, Soricomorpha) are not the subject of ethology studies.

Ethology became established as a scientific discipline on its own right worldwide in 1973 ([Moreno and Muñoz-Delgado 2007](#)). Prior to that year, only six articles had been

**Table 2.** List of journals according to number of published articles on ethological fields, country of origin and their presence in Journal Citation Reports (JCR) 2018. Number of articles (No.). Country of origin (C.O.). JCR (presence: OK; absence: -).

Journals	No.	C.O.	(ISI)
American Journal of Primatology	16	U.S.A.	OK
Journal of Mammalogy	15	U.S.A.	OK
International Journal of Primatology	14	U.S.A.	OK
Acta Zoológica Mexicana (nueva serie)	9	México	-
Primates	9	Japan	OK
Therya	9	México	-
The Southwestern Naturalist	6	U.S.A.	OK
Folia Primatologica	5	Switzerland	OK
Behavioral Ecology and Sociobiology	4	Germany	OK
Ethology	4	Germany	OK
Mammalian Biology (Zeitschrift für Säugetierkunde)	4	Germany	OK
PLOS ONE	4	U.S.A.	OK
American Journal of Physical Anthropology	3	U.S.A.	OK
Biotropica	3	U.S.A.	OK
Journal of Zoology	3	England	OK
Revista de Biología Tropical	3	Costa Rica	OK
Revista Mexicana de Biodiversidad	3	México	OK
Revista Mexicana de Mastozoología (nueva época)	3	México	-
Western North American Naturalist	3	U.S.A.	OK
Anales del Instituto de Biología, UNAM. Serie Zoología	2	México	-
Acta Chiropterológica	2	Poland	OK
Animal Behaviour	2	England	OK
Biological Rhythm Research	2	England	OK
General and Comparative Endocrinology	2	U.S.A.	OK
Hormones and Behavior	2	U.S.A.	OK
Physiology and Behavior	2	U.S.A.	OK
Zoo Biology	2	U.S.A.	OK
American Midland Naturalist	1	U.S.A.	-
Animal Biology	1	Netherlands	OK
Animal Cognition	1	Germany	OK
Animal Conservation	1	England	OK
Behavioral Ecology	1	England	OK
Biology Letters	1	England	OK
Chiroptera Neotropical	1	Brazil	-
Chronobiology International	1	U.S.A.	OK
Cortex	1	Italy	OK
Current Zoology	1	China	OK
Ethology Ecology and Evolution	1	Italy	OK
Interciencia	1	Venezuela	-
Journal of Arid Environments	1	U.S.A.	OK
Journal of Comparative Psychology	1	Germany	OK
Journal of Zoo and Wildlife Medicine	1	U.S.A.	OK
Mammalia	1	Germany	OK
Mastozoología Netropical	1	Argentina	-
Natural Areas Journal	1	U.S.A.	-
Neotropical Primates	1	Brazil	-
Peer J.	1	England	OK
Salud Mental	1	México	OK
Scientific Reports	1	England	OK
Studies on Neotropical Fauna and Environment	1	England	-
Universidad y Ciencia	1	México	-



**Figure 2.** Map showing records of ethological studies carried out on native land mammals in México, categorized at order level. The colored circles represent orders and locations worked ( $n$  = number of locations): Primates (purple,  $n$  = 74); Rodentia (green,  $n$  = 33); Carnivora (blue,  $n$  = 25); Chiroptera (red,  $n$  = 22); Cetartiodactyla (pink,  $n$  = 3), and Lagomorpha (orange,  $n$  = 3). Acronyms (BC = Baja California; BCS = Baja California Sur; Son = Sonora; Sin = Sinaloa; Chih = Chihuahua; Dgo = Durango; Coah = Coahuila; Nay = Nayarit; Zac = Zacatecas; NL = Nuevo León; SLP = San Luis Potosí; Gto = Guanajuato; Ags = Aguascalientes; Jal = Jalisco; Col = Colima; Tam = Tamaulipas; Qro = Querétaro; Hgo = Hidalgo; CDMX = Ciudad de México; EdoMex = Estado de México; Tlax = Tlaxcala; Pue = Puebla; Ver = Veracruz; Mich = Michoacán; Gro = Guerrero; Mor = Morelos; Oax = Oaxaca; Tab = Tabasco; Chis = Chiapas; Cam = Campeche; Yuc = Yucatán; QRoo = Quintana Roo).

published in México, most of them authored by foreign researchers. Those studies examined various ethological aspects of mammals. [Russell and Findley \(1954\)](#) documented the first observation of swimming of a myomorph rodent of the genus *Onychomys* from the State of Nuevo León. [Packard \(1958\)](#) described the carnivorous behavior of the Mexican ground squirrel (*Ictidomys mexicanus*) preying on a rabbit (*Sylvilagus* sp.) in the State of Coahuila. Other studies described various aspects of the common vampire bat, *Desmodus rotundus*: foraging behavior and refuge selection in the State of Tabasco ([Wimsatt 1969](#)), mode of attack on cattle in the State of Oaxaca ([Greenhall et al. 1971](#)), biting and feeding habits in captivity at the Instituto Nacional de Investigaciones Pecuarías in México City ([Greenhall 1972](#)), and the relationship between the feeding periods and absence in relation to moonlight in Oaxaca and San Luis Potosí ([Crespo et al. 1972](#)).

Thirteen scientific papers were published between 1973 and 1995. For example, [Gould \(1975\)](#) recorded, described, and compared vocalization patterns related to precocial

and altricial conditions of pups of eight bat species, including two from México (the lesser long-nosed bat, *Leptonycteris yerbabuena*, from Sonora, and the black mastiff bat, *Molossus rufus*, collected by R. Horst and recorded at his laboratory). The mating behavior of four deer-mouse species of the genus *Peromyscus* from Oaxaca and Campeche was described by [Dewsbury \(1979\)](#). The diurnal roosting and resting behavior (in tree holes) of the Mexican fruit bat (*Artibeus jamaicensis*) at Chamela Biological Station, Jalisco, was described by [Morrison \(1979\)](#). [Estrada \(1984\)](#) and [Estrada and Coates-Estrada \(1985\)](#) studied the frugivory habits and range of habitats used by the mantled howler (*Alouatta palliata*) in Los Tuxtlas, Veracruz. [Servín \(1991\)](#) described 37 social behavioral patterns (classified into friendly, submissive, playful, sexual, and aggressive-defensive behaviors) displayed by five Mexican wolves (*Canis lupus baileyi*) over 15 months in captivity in the State of Durango. [Servín and Huxley \(1991\)](#) determined the seasonal and annual foods habits of coyote *Canis latrans* by analyzing 330 scats collected on the buffer zone at the Michilia Biosphere Reserve,



**Table 3.** List of species found in ethological studies according to order, family, and national and international risk categories. A: Number of published articles; B: Endemic (presence: OK; absence: -); C: In NOM 059 Semarnat 2010 categories (E: Probably extinct in the wild; P: endangered; A: threatened; absence: -). D: In IUCN categories (EN: endangered; LC: least concern; VU: vulnerable; NT: near threatened; absence: -). E: In CITES Appendices (I: Highly endangered; II: may become endangered; absence: -).

Order	Family	Species	A	B	C	D	E
Primates							
	Atelidae	<i>Ateles geoffroyi</i>	37	-	P	EN	I, II
		<i>Alouatta pigra</i>	25	-	P	LC	I
		<i>Alouatta palliata</i>	23	-	P	EN	I
Rodentia							
	Cricetidae	<i>Neotomodon alstoni</i>	12	OK	-	LC	-
		<i>Neotoma mexicana</i>	1	-	-	LC	-
		<i>Microtus mexicanus</i>	2	-	-	LC	-
		<i>Onychomys leucogaster</i>	1	-	-	LC	-
		<i>Peromyscus aztecus</i>	1	-	-	LC	-
		<i>Peromyscus melanocarpus</i>	1	OK	-	EN	-
		<i>Peromyscus melanophrys</i>	2	OK	-	LC	-
		<i>Peromyscus mexicanus</i>	1	-	-	LC	-
		<i>Peromyscus melanotis</i>	1	OK	-	LC	-
		<i>Peromyscus yucatanicus</i>	2	-	-	LC	-
		<i>Reithrodontomys megalotis</i>	2	-	-	LC	-
		<i>Sigmodon leucotis</i>	1	-	-	LC	-
	Heteromyidae	<i>Chaetodipus siccus</i>	3	OK	A	LC	-
		<i>Dipodomys merriami</i>	1	-	A	LC	-
		<i>Heteromys gaumeri</i>	2	-	-	LC	-
		<i>Heteromys irroratus</i>	1	-	-	LC	-
	Sciuridae	<i>Cynomys mexicanus</i>	1	OK	P	EN	I
		<i>Ictidomys mexicanus</i>	2	OK	-	LC	-
		<i>Ictidomys spilosoma</i>	1	-	-	LC	-
		<i>Tamiasciurus mearnsi</i>	1	OK	A	EN	-
		<i>Xerospermophilus perotensis</i>	2	OK	A	EN	-
Chiroptera							
	Phyllostomidae	<i>Artibeus jamaicensis</i>	6	-	-	LC	-
		<i>Anoura geoffroyi</i>	2	-	-	LC	-
		<i>Artibeus lituratus</i>	1	-	-	LC	-
		<i>Carollia sowelli</i>	1	-	-	LC	-
		<i>Desmodus rotundus</i>	6	-	-	LC	-
		<i>Diphylla ecaudata</i>	1	-	-	LC	-
		<i>Glossophaga commissarisi</i>	1	-	-	LC	-
		<i>Leptonycteris yerbabuena</i>	3	-	-	NT	-
	Emballonuridae	<i>Balantiopteryx plicata</i>	1	-	-	LC	-
	Molossidae	<i>Molossus rufus</i>	1	-	-	LC	-
		<i>Nyctinomops laticaudatus</i>	1	-	-	LC	-
	Mormoopidae	<i>Pteronotus gymnotus</i>	1	-	A	LC	-
		<i>Pteronotus mesoamericanus</i>	1	-	-	LC	-
	Vespertilionidae	<i>Aeorestes cinereus</i>	1	-	-	LC	-
		<i>Antrozous pallidus</i>	1	-	-	LC	-
		<i>Lasiurus blossevillii</i>	1	-	-	LC	-
		<i>Lasiurus borealis</i>	1	-	-	LC	-
Carnivora							
	Canidae	<i>Canis lupus baileyi</i>	6	-	E	LC	I, II
		<i>Canis latrans</i>	5	-	-	LC	-
		<i>Urocyon cinereoargenteus</i>	1	-	-	LC	-
	Felidae	<i>Lynx rufus</i>	3	-	-	LC	II
		<i>Puma concolor</i>	7	-	-	LC	-
		<i>Panthera onca</i>	6	-	P	NT	I
	Mephitidae	<i>Conepatus leuconotus</i>	1	-	-	LC	-
	Procyonidae	<i>Bassariscus astutus</i>	1	-	A	LC	-
Lagomorpha							
	Leporidae	<i>Lepus flavigularis</i>	4	OK	P	EN	-
Artiodactyla							
	Cervidae	<i>Odocoileus virginianus</i>	3	-	-	-	-
	Tayassuidae	<i>Tayassu pecari</i>	1	-	P	VU	II

finding that mammals (e. g., rodents and ungulates) and fruits (e. g., *Juniperus deppeana* and *Arctostaphylos pungens.*) were the most consumed food categories. In the same Biosphere Reserve, [Servín and Huxley \(1995\)](#) determined the home range of coyotes (*Canis latrans*), registering an average annual of 9.1 km<sup>2</sup>.

The most productive period by far was between 1996 and 2018, with 90 % of the articles retrieved were published over these years. The fields most frequently addressed were foraging with 33 articles (19.5 %), movement with 28 articles (16.6 %) and nesting, rearing, and territoriality, and social behavior, cooperation, and kinship with 20 and 21 articles (12.4 % and 11.8 %), respectively.

Thirty-three studies focused on foraging, examining for example food preferences and selection strategies of spider monkeys and howler monkeys at Los Tuxtlas, Veracruz ([Dunn et al. 2009, 2010, 2012](#)), Palenque, Chiapas ([Amato et al. 2014](#)), Catemaco, Veracruz ([Reynoso-Cruz et al. 2016](#)), and the Yucatán Peninsula ([Pinacho-Guendulain and Ramos-](#)

[Fernández 2017](#)), as well as the use of non-conventional sources of water (e. g., streams) in Veracruz ([Serio-Silva and Rico-Gray 2000](#)) and Campeche ([Duarte-Dias et al. 2014](#)). The response of monkeys to variations in food availability was studied in a controlled environment at the Hilda Ávila de O'Farrill Management Unit, Veracruz ([Rangel-Negrín et al. 2015](#)) and in fragmented habitats at Los Tuxtlas, Veracruz ([Estrada et al. 1999; Juan et al. 2000; Asensio et al. 2007](#)), Balacán, Tabasco ([Pozo-Montuy and Serio-Silva 2006](#)), and the Lacandona tropical rainforest, Chiapas ([Chaves et al. 2012; Benitez-Malvido et al. 2016](#)). [Horner et al. \(1998\)](#) described that southern long-nosed bats, *Leptonyctis curasoae*, from the State of Sonora visited between 80 to 100 cactus flowers daily to feed on nectar and acquired 40 kilojoules of energy. [Frick et al. \(2009\)](#) documented, based on 143 working nights at 14 sites in Baja California, the first known example of an insectivorous bat, the pallid bat *Antrozous pallidus*, displaying facultative nectarivorous habits. [Hernández-Hernández et al. \(2018\)](#) found that the endemic Perote ground squir-

rel, *Xerospermophilus perotensis*, feeds opportunistically but, under certain conditions, selects plant species that provide a better-quality diet; [Luna-Casanova et al. \(2016\)](#), for his part, determined the preference of Tehuantepec jackrabbit (*Lepus flavigularis*) in Oaxaca to establish feeding and resting sites in the pasture with the presence of cattle. The food habits, based on scats, of different carnivores were also determined, for example; the coyote (*Canis latrans*; [Grajales-Tam et al. 2003](#)), the puma (*Puma concolor*), and jaguar (*Panthera onca*; [Aranda and Sánchez-Cordero 1996](#)), and cacomixtle, (*Bassaris astutus*; [Nava et al. 1999](#)), in different states such as Baja California Sur, Campeche, Hidalgo and San Luis Potosí.

Studies on movement ( $n = 28$ ) focused on the use of space and movement patterns of animals, mostly in the Central American spider monkey (*Ateles geoffroyi*). [Valero and Byrne \(2007\)](#) worked in the Otchma'ax Yetel Koooh reserve (Yucatán) and found that these monkeys are guided by spatial memory and are capable of planning routes. [Smith-Aguilar et al. \(2016\)](#) found a more concentrated use of space and higher rates of association (individuals brought together by resources of common interest) during periods of high fruit abundance. [Campbell et al. \(2005\)](#) investigated the terrestrial behavior of spider monkeys at five study sites in Perú, Ecuador, Panama, Costa Rica, and México (Punta Laguna, Yucatán) and concluded that this behavior occurred rarely, being more restricted in South America, where it occurred only in the context of eating soil or rotten wood and visiting salt licks. This contrasted with the behavior observed in

Central and North America, where terrestrialism occurred more frequently while drinking water from streams during the dry season, when adult females escaped attacks by adult males, or as part of a chase game. [Van-Belle et al. \(2013\)](#) recorded, over 15 months, 691 movements of independent groups of another primate species, *Alouatta pigra*, at Palenque National Park, Chiapas, confirming that adult females showed leadership more frequently than males. Such female actions are beneficial for life as a group because they provide social cohesion by coordinating the timing and direction of travel, a behavior that has been observed in other mammals ([Smith et al. 2015](#); [Tokuyama and Furuichi 2017](#)).

The home range has been determined in other terrestrial mammals for example the coyote (*Canis latrans*), in Durango ([Servín and Huxley 1995](#)) and Oaxaca ([Marín-Sánchez et al. 2015](#)), the gray fox (*Urocyon cinereoargenteus*), in Durango ([Servín et al. 2014](#)), the jaguar (*Panthera onca*) in Quintana Roo ([González-Gallina et al. 2018](#)), the Gaumer's spiny pocket mouse (*Heteromys gaumeri*), in Yucatán ([Cimé-Pool et al. 2002](#); [Hernández-Betancourt et al. 2003](#)), the Mexican spiny pocket mouse (*Heteromys irroratus*) in Oaxaca ([Santos-Moreno and Santiago-Marcial 2012](#)), the bobcat (*Lynx rufus*) in Durango and Chihuahua ([Elizalde-Arellano et al. 2012](#)) and Colima ([Burton et al. 2003](#)), the Tehuantepec Jackrabbit (*Lepus flavigularis*) in Oaxaca ([Carrillo-Reyes et al. 2010](#)), the white-lipped peccaries (*Tayassu pecari*) in Campeche ([Reyna-Hurtado et al. 2009](#)), and the white-tailed deer (*Odocoileus virginianus*) in Nuevo León ([Bello et al. 2004](#)).

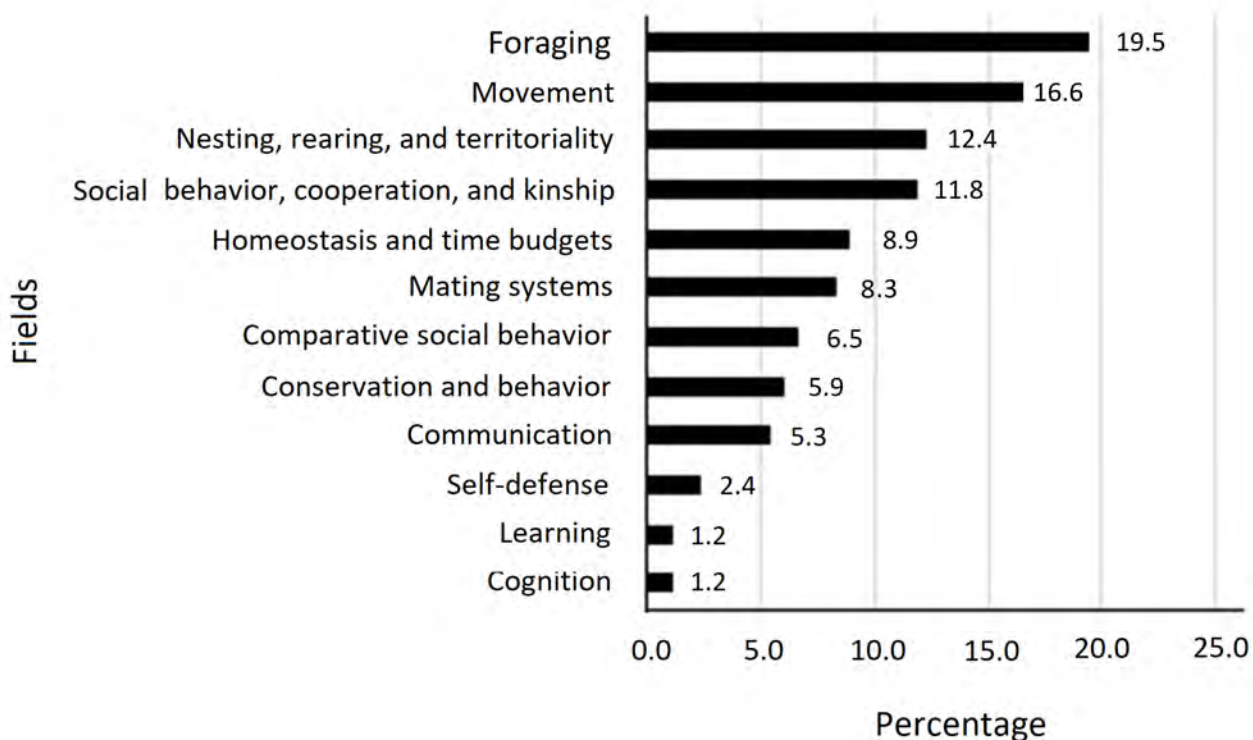


Figure 3. Percentage of published ethological articles organized by field based on Breed and Moore (2012).

A genetic structure study by [Aguilera-Miller \(2016\)](#) on the Cerralvo pocket mouse, *Chaetodipus siccus*, a species endemic to the Baja California Peninsula, revealed that the ethological interactions between individuals (e. g., dominant females more aggressive than subordinates) were responsible for females not dispersing and remaining in small geographic areas, pointing to the presence of female philopatry. In addition, [Aguilera-Miller et al. \(2018\)](#), based on the same molecular markers, found that the haplotypes considered to be ancestral were located at the periphery of the distribution area, while the derived haplotypes were located in the center of the distribution range, supporting again the hypothesis of strong philopatric behavior among females.

The 21 studies on nesting, rearing, and territoriality addressed primarily parental care and aggressive behavior. For example, observations on the endemic Mexican volcano mouse (*Neotomodon alstoni*), in captivity in México City confirmed that this species exhibits monogamous and biparental care behaviors ([Luis et al. 2000](#)). Males looked after the offspring when their testosterone levels were high ([Luis et al. 2009, 2012, 2017](#)), and the presence of males adversely affected maternal care but improved offspring survival ([Luis et al. 2004](#)).

The reproductive behavior of the Tehuantepec jackrabbit (*Lepus flavigularis*), an endemic species listed as endangered in the official Mexican laws ([SEMARNAT 2010](#)), was studied by [Rioja-Paradela et al. \(2011\)](#) in the State of Oaxaca. These authors found that the breeding season lasted 250 days per year; each female gave birth to two leverets that were weaned after 12 days and showed a higher survival rate relative to other leporids; predation by feral dogs (*Canis familiaris*) appeared to be the primary cause of mortality. On the other hand, [Servín \(1997\)](#) determined that, in a captive population of Mexican wolves (*Canis lupus baileyi*) from the La Michilía Biosphere Reserve, Durango, the mating occurred from January to April, the births occurred between April and May and the average number of offspring born per litter was four.

Studies on primates showed that the Guatemalan black howler, *Alouatta pigra*, in the State of Campeche lengthens its foraging periods during lactation ([Duarte-Dias et al. 2011](#)); maternal care by the mantled howler monkey, *A. palliata*, in the State of Veracruz, was directly related to lactation stage and food availability ([Duarte-Dias et al. 2018](#)). [Duarte-Dias \(2005\)](#) provided a detailed description of labor and birth in *A. palliata* under semi-captivity conditions at Agaltepec island in Catemaco, Veracruz. He described the labor and birth stages, behavioral events, and their timing and duration; the patterns described are representative of the birth process in this species.

Other studies addressed aggressive patterns in spider monkeys (*Ateles geoffroyi*) from protected areas in Yucatán. [Valero et al. \(2006\)](#) recorded collective aggressions by sexually mature males towards a single younger individual, with a fatal outcome. [Aureli et al. \(2006\)](#) reported, for the first

time, instances of assault groups advancing on the ground in unusual silence, similar to the behavior of chimpanzees ([Kelly 2000; Watts et al. 2006](#)). Although no fatal outcomes were observed, these behaviors may be related to factors such as reduction in mating opportunities, number of males relative to the neighboring community, or strengthening of intra-group ties. These findings suggest that this behavior might have evolved primarily through mutualism where participants gain direct benefits from their physical fitness. Intergroup aggression in defense of the cooperative group was observed in the Guatemalan black howler (*A. pigra*), at Palenque, Chiapas ([Van-Belle et al. 2014](#)); intra-group aggression, even including infanticide, was observed at Balancán, Tabasco ([García-Feria et al. 2016](#)).

The 20 studies on social behavior, cooperation, and kinship focused mostly on primates. [Pastor-Nieto \(2001\)](#) studied spider monkeys, *Ateles geoffroyi*, at the Zoológico Centenario zoo in Yucatán, finding that social relationships such as food sharing were influenced by affiliative behavior (e. g., mutual grooming) rather than by kinship. Social relationships were observed to improve the physical fitness of wild spider monkeys in the Yucatán Peninsula. For example, there was a closer proximity between family dyads, as well as between male-male relationships ([Rebecchini et al. 2011](#)); affiliative behaviors between males were found to be more common when they were young ([Schaffner et al. 2012](#)) and when new members entered the group and acted as bond initiators ([Aureli and Schaffner 2007](#)). [Slater et al. \(2009\)](#) found that competition for resources and the need for cooperation affected social interaction patterns, particularly the social relationships between females as they spent much time on feeding and showed greater aggressiveness. However, the presence of small infants influenced the social behavior of females as, according to [Slater et al. \(2007\)](#), mothers with infants received significantly more approaches and hugs from other females.

The fifteen behavioral studies on homeostasis and time budgets included a radiotelemetry study of activity patterns of the white-tailed deer (*Odocoileus virginianus*), in a xerophilous scrub in the State of Coahuila ([Gallina and Bello Gutiérrez 2014](#)). A study of locomotor activity of the Mexican wolf (*Canis lupus baileyi*), in relation to lunar phases, which recorded the most intense activity during the waxing moon, decreasing activity during the full and last quarter moons, and the lowest locomotive activity during new moon ([Sánchez-Ferrer et al. 2016](#)). Other studies found interspecific differences in the way primates allocate time to different activities: the mantled howler monkey, *A. palliata*, spent a considerable amount of time resting, feeding, and moving around ([Muñoz et al. 2001](#)); Guatemalan black howlers (*A. pigra*), rested more frequently in high-quality habitats ([Rangel-Negrín et al. 2018](#)); separately, the periods of rest and activity of spider monkeys (*A. geoffroyi*), were mainly driven by light-darkness periods and environmental factors such as temperature, precipitation, and humidity ([Muñoz-Delgado et al. 2004](#)). In this last species,

in Catemaco, Veracruz, [Muñoz-Delgado et al. \(2014\)](#) studied the impact of housing conditions and season on the daily timing and pattern, and [Muñoz-Delgado et al. \(2018\)](#), recorded that these primates respond to visitor (tourist) activity since it modified their normally pronounced bimodal diel activity pattern and developed a superimposed infradian activity rhythm peaking on Saturday and Sunday.

The 14 studies on mating systems included a study of the breeding season and reproductive behavior of the Mexican prairie dog (*Cynomys mexicanus*), in Coahuila ([Rioja-Paradela et al. 2008a](#)); an early effort to determine the mating behavior of the Tehuantepec jackrabbit (*Lepus flavigularis*), in the State of Oaxaca ([Rioja-Paradela et al. 2008b](#)); and the first report on the sexual behavior of the Mexican wolf (*Canis lupus baileyi*) at the San Juan de Aragón zoo (México City) in summer ([Soto et al. 2013](#)). All these species are listed as endangered ([SEMARNAT 2010](#); [Álvarez-Castañeda et al. 2019](#); [Lorenzo and Smith 2019](#)).

The structure and social interactions of bats and primates were also studied. [Ortega and Arita \(1999\)](#) found that Mexican fruit bats (*Artibeus jamaicensis*), from the Yucatán Peninsula formed harems consisting of 4 to 18 females and one or two males, where males could play different roles: dominant (one in each harem), subordinate (present only in large harems), or satellite (not associated with a harem). Dominant males actively defended females, particularly during the breeding season when they displayed more agonistic responses towards male visitors ([Ortega and Arita 2000](#)). However, some subordinate males may have associated with harems as satellites, provided that they contributed some benefit to the dominant male ([Ortega and Arita 2002](#)). In addition, [Ortega and Martínez-Rodríguez \(2011\)](#) registered that broad tailed bat (*Nyctinomops laticaudatus*) in the archaeological zone of Uxmal, Yucatán, shows a promiscuous mating system, and the males display agonistic-type behavioral activities.

A study at the Palenque National Park (Tabasco, México) showed that the black howlers (*Alouatta pigra*) with high androgens levels and fecal glucocorticoids, had almost exclusive access to fertile females ([Van-Belle et al. 2009a](#)), in addition males rarely solicited sexual interactions, but instead monitored the females reproductive status by sniffing their genitals, and maintained significantly closer proximity to females during their periovulatory periods ([Van-Belle et al. 2009b](#)). In contrast, studies of spider monkeys (*Ateles geoffroyi*) from Yucatán found that males with fewer reproductive opportunities resorted to infanticide ([Gibson et al. 2008](#)) or attacked females ([Slater et al. 2008](#)), likely as a means of sexual coercion to increase their mating chances.

Studies on comparative social behavior ( $n = 11$ ) addressed, for example, the role of agonistic behavior in explaining the relative abundance of the Mexican volcano mouse (*Neotomodon alstoni*), in a small mammal community at the Sierra del Ajusco mountain range in central México. Habitat partitioning by occupying different micro-

habitats or maintaining discrete central areas were mechanisms likely allowing the coexistence of *N. alstoni* and other species such as the black-eared mouse (*Peromyscus melanotis*), and the Mexican vole (*Microtus mexicanus*), which usually defended their territory in preferred microhabitats against *N. alstoni* ([Fa et al. 1996](#)). The first known cases of infanticide and forced copulation in spider monkeys (*A. geoffroyi*) from two communities in México and four in Perú ([Gibson et al. 2008](#)) were also described. [Gibson et al. 2008](#) and [Hernández-Saintmartín et al. \(2013\)](#) studied activity patterns of jaguars, pumas, and their potential prey species in San Luis Potosí, where the activity peaks of both felids suggest that temporal segregation is a strategy which minimizes interspecific encounters allowing the coexistence of several individuals.

The ten studies that focused on conservation and behavior looked only at primates, addressing the close relationship between anthropogenic disturbance factors and behavioral changes or increased stress levels in animals. [Rangel-Negrín et al. \(2016\)](#) found that Guatemalan black howlers (*A. pigra*) from the State of Campeche exhibited a narrower behavioral repertoire and higher psychosocial stress levels when living in altered or disturbed habitats. The latter was also observed in Guatemalan black howlers from the Yucatán Peninsula ([Rangel-Negrín et al. 2014](#)), Balancán, Tabasco ([Martínez-Mota et al. 2007](#)), and El Zapotal Ecological and Recreational Center, State of Veracruz ([Aguilar-Melo et al. 2013](#)), as a response to tourism in the latter. However, stress has also been recorded in *A. palliata* by translocations in southern Veracruz ([Aguilar-Cucurachi et al. 2010](#)).

However, these behaviors are not unique to howler monkeys. Spider monkeys (*A. geoffroyi*) from an island in Catemaco lake, Veracruz, showed increased agonistic behaviors and fewer vocalizations in the presence of tourists ([Pérez-Galicia et al. 2017](#)). An alternative to address stressful behaviors in captivity was suggested by [Márquez-Arias et al. \(2014\)](#). They showed that, at the Instituto Nacional de Psiquiatría Ramón de la Fuente Muñiz in México City, environmental enrichment ameliorated behavioral issues caused by confinement.

The nine articles that addressed communication behavior looked mostly at vocalization aspects. [Servín \(2000\)](#) found that Mexican wolves (*Canis lupus baileyi*) in captivity at La Michilía, State of Durango, howled more frequently and for longer periods during mating, and were heard more often at dawn and dusk. A comparison of two groups of spider monkeys (*Ateles geoffroyi*) from México and Costa Rica revealed that contact calls in each group showed differential variations between individuals ([Santorelli et al. 2013](#)). On the other hand, the studies by [Briseño-Jaramillo et al. \(2015, 2017, 2018\)](#) on Guatemalan black howlers (*A. pigra*) from Yucatán, provided the first description of a unique behavior associated with the call (placing a hand in front of the mouth while vocalizing), a study that opened up a new line of research on how non-human primates

developed strategies to overcome limitations in acoustic plasticity. These authors identified a repertoire of vocal calls that included twelve distinct calls (three of which are emitted exclusively by females and two only by males) and confirmed the presence of non-random patterns through which individual calls can be differentiated, even those from members of other groups, which might represent potential “conversation rules” (Briseño-Jaramillo et al. 2018).

Self-defense ( $n = 4$ ), learning ( $n = 2$ ), and cognition ( $n = 2$ ) were studied least frequently; altogether, they accounted for less than 5 % of the articles published during this period. Studies on self-defense described aspects such as the evasive behavior of *A. palliata* towards a group of the potential predator tayra, *Eira barbara*, in Playa Escondida, Veracruz (Asensio and Gómez-Marín 2002) and climbing more than 5 m as an escape mechanism of the American hog-nosed skunk (*Conepatus leuconotus*), when chased by humans in Colima (México) and Texas (USA; Brashear et al. 2010).

Finally, the articles on learning addressed the cultural transmission of behavior in primates. For example, Santorelli et al. (2011) compared variants of universal behaviors (defined as those used across all communities) of spider monkeys at three communities, two in Punta Laguna, Yucatán, México and one in Santa Rosa, Costa Rica. Six behaviors were identified that were likely maintained through social learning: 1) fruit extraction using the hand instead of the mouth; 2) drinking by licking instead of dribbling; 3) drinking using the left hand instead of the right hand; 4) contact greeting instead of non-contact greeting; 5) resting sitting upright; and 6) resting by leaning laterally. These results may have several implications for the study of spider monkey behavior: on the one hand, they suggest the possibility of a behavioral repertoire larger than the one reported by previous studies (e. g., McGrew 1998; Watson and Caldwell 2009); on the other, that the relative use of universal behavioral variants can reinforce community membership.

Briseño-Jaramillo et al. (2015) provided the first description of a unique behavior (placing a hand in front of the mouth while vocalizing) associated with the call of Guatemalan black howlers at Palenque National Park, Chiapas. They concluded that this behavior is transmitted culturally and plays a role in intergroup competition and intragroup cohesion.

In conclusion, ethological research on mammals in México — as represented by published articles in which this was the main study subject — reveals three distinct periods: the first (1900 to 1953) with no published papers, the second (1954 to 1995) was characterized by a low production of publications, while the third (1996 to 2018) shows a linear increase in the number of articles published, usually in foreign journals, with Mexican authors having an increasing participation. More than 90 % of all the studies focused on primates, rodents, bats, and carnivores and most studies were developed in the State of Veracruz and southeast México. Ethological studies have not explored other mammalian orders nor have focused on the north-

ern part of the country. A diverse set of studies have been addressed, particularly over the last two decades; those such as foraging, movement, nesting, breeding, and territoriality, followed by social behavior, cooperation and kinship stand out in terms of the number of articles published. Despite its relatively recent development compared to disciplines such as paleontology, evolution, biogeography, and others, mammalian ethology in México has already made significant contributions given the growing number of mammalogists interested in this field and the increase in national and international collaborations, which therefore indicates that mammal ethology will surely continue its development and consolidation.

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# Use of mineral licks by mammals in areas of the Amazonia with no hunting pressure

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Mineral licks are areas where several species of animals, including mammals, converge to consume water and soil as a mineral supplement. Certain mammal species are an important source of protein in the diet of indigenous communities. Many of these species are under hunting pressure and their populations have been seriously affected. The purpose of this study was to determine the species of large and medium-sized mammals that use three open mineral licks in the area of the Kichwa Añangu community, within the Yasuní National Park, where hunting used to take place. We calculate the capture frequency for the visiting species and the richness, composition, and similarity of the assemblages recorded in the mineral licks during two climatic seasons of the year (higher rainfall vs. lower rainfall). We installed a single camera trap station (CTS) at each mineral lick during three sampling periods in 2018. In each period, all cameras operated 24 hours a day for 30 to 40 days and were set to capture three photographs upon sensor activation, with 60-second intervals between consecutive activations. With a total sampling effort of 249 days/trap, we obtained 645 photographs and 398 grouped records of 16 species. We recorded 95.2 % of the expected richness according to the Chao1 estimator ( $S = 16.8$ ). The species with the highest capture frequency were: *Mazama zamora* (FC = 62.2), *Tayassu pecari* (FC = 35.7), *Tapirus terrestris* (FC = 28.9), and *Pecari tajacu* (FC = 8.0). ECT-1 and ECT-2 captured 11 species each, and ECT-3 captured nine species. There were no significant differences in the species composition between the three mineral licks or between climatic seasons. Our results show that the focal mineral licks studied attract a rich mammalian fauna, which likely points to the success of the government regulation of wildlife trafficking and the application of sustainable tourism practices in the Añangu community.

Los saladeros son áreas donde convergen varias especies de animales, entre ellos mamíferos, para el consumo de agua y suelo como suplemento mineral. Entre los mamíferos que los visitan se incluyen especies que constituyen una fuente importante de proteína para la dieta de las comunidades indígenas. Las poblaciones de varias de estas especies han sido seriamente afectadas por la cacería. El propósito de este estudio fue conocer las especies de mamíferos grandes y medianos que usan tres saladeros abiertos que se encuentran en el área de la comunidad Kichwa Añangu dentro del Parque Nacional Yasuní, donde antes se realizaba cacería. Se determinaron sus frecuencias de captura, riqueza de especies, así como la composición y similitud de los ensamblajes registrados en los distintos saladeros y temporadas, una con mayor y otra con menor pluviosidad. Realizamos tres periodos de muestreo durante el año 2018 usando una estación de cámara trampa (ECT) simple en cada saladero. En cada periodo las cámaras permanecieron activas las 24 horas, durante 30 a 40 días, y fueron programadas para capturar tres fotografías al activarse el sensor, con intervalos de 60 segundos entre activaciones consecutivas. Con un esfuerzo total de muestreo de 249 días/trampa obtuvimos 645 fotografías, con 398 registros agrupados de 16 especies. Se logró registrar un 95.2 % de la riqueza esperada según el estimador Chao1 ( $S = 16.8$ ). Las especies con mayor frecuencia de captura fueron: *Mazama zamora* (FC=62.2), *Tayassu pecari* (FC = 35.7), *Tapirus terrestris* (FC = 28.9) y *Pecari tajacu* (FC = 8.0). Las ECT-1 y ECT-2 presentaron 11 especies cada una, la ECT-3 presentó 9 especies. No existieron diferencias significativas en la composición de especies entre los tres saladeros o entre temporadas. Nuestros resultados ponen en evidencia la riqueza de mamíferos que usan los saladeros como una fuente de minerales. Esto muy probablemente refleja el éxito de la regulación por parte del gobierno para el control de tráfico de vida silvestre y de la aplicación de las prácticas de turismo sostenibles en la comunidad Añangu.

**Keywords:** Añangu; camera trap; capture frequencies; conservation; Ecuador; richness; sustainable tourism; Yasuní.

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## Introduction

It is very common to observe mammals and birds consuming fragments of soil from certain forest sites where they live, a phenomenon known as geophagy ([Diamond et al. 2008](#); [Gilardi et al. 1999](#); [Setzl et al. 1999](#)). Such sites are known as mineral licks or in the Neotropics as *saladeros* ([Voigt et al. 2007](#)), salt licks (Tracy and Mc Naughton 1995), or natural mineral licks ([Emmons and Stark 1979](#)), as they contain mineral salts of sodium, calcium, potassium, or iron ([Emmons and Stark 1979](#); [Klaus and Schmid 1998](#); [Lizcano and Cavalier 2004](#); [Montenegro 2004](#); [Mah-](#)

[aney et al. 2005](#); [Link et al. 2012](#)). Mineral licks can be classified as “open”, “wall” or “caves”, according to their characteristics ([Montenegro 2004](#)).

The mammals recorded visiting these mineral licks include chiropters, rodents, primates, and ungulates. In the case of birds, species of the orders Galliform (chickenlike birds locally known as *pavas*), Columbiform (pigeons), and in large numbers Psittaciform (parrots) have been recorded ([Izawa 1993](#); [Krishnamani and Mahaney 2000](#); [Brightsmith 2004](#); [Montenegro 2004](#); [Voigt et al. 2007](#); [Bravo et al. 2008](#); [Tobler et al. 2009](#); [Blake et al. 2010](#); [Link et al. 2011](#); [Link et al. 2012](#)).

It has been proposed that geophagy represents a supplementary source of minerals (Davies and Baillie 1988; Klaus and Schmid 1998) that help reduce the absorption of toxins from food (Kreulen 1985; Diamond et al. 2008; Gilardi et al. 1999). It is also thought that geophagy allows ingesting antacid agents to regulate gastric pH (Davies and Baillie 1988). Soil consumption varies according to the species, geography, and climate (Davies and Baillie 1988; Setz 1999; Blake et al. 2010; Blake et al. 2011).

The Yasuní National Park, located in the Orellana and Pastaza provinces in the Ecuadorian Amazon region, is home to the Kichwa and Waorani indigenous peoples (Licona et al. 2011). For these communities, subsistence hunting is a primary activity to obtain protein from the consumption of prey such as monkeys and peccaries (Blake et al. 2013). However, overhunting, in addition to the illegal trade in wildlife facilitated by roads built by oil companies (Bass et al. 2010), has led to the decline of animal populations in the forest and, thus, in mineral licks near these communities (Suárez et al. 2009; Espinosa and Salvador 2017; Blake et al. 2013).

Hunting has a greater impact on mammals than birds, likely because the selective hunting of larger species (Benitez-López et al. 2017). Decades ago, in the Kichwa Añangu community located on the Napo River banks within the Yasuní National Park, wildlife was being overhunted. However, when its decline was noted, a tourism project was launched in 1998 as an alternative for socio-economic development. The book of the History of the Añangu Community states that the commitment to tourism is also a response to the exploitation of the Amazon for oil extraction (Renkert 2019). Another initiative implemented afterward as a community policy was the discontinuation of illegal wildlife hunting and trafficking to allow the recovery of wildlife populations. As a result, after 20 years, there is an evident recovery of landmark wildlife species, such as giant otters, jaguars, and large primates (Suárez and Zapata 2019).

The present work documented the species of large and medium-sized mammal species using three mineral licks in the Kichwa Añangu community area, using camera traps. In addition, capture frequencies and species composition in different climatic seasons were determined.

## Methods

**Study Area.** Camera trap stations (ECT, for its acronym in Spanish) were installed in three open mineral licks of brown, marshy clay soils with a thin layer of decaying litter. ECT-1 (0° 32' 15.818", -76° 24' 16.083") was installed in a mineral lick of approximately 260 m<sup>2</sup>, ECT2 (-0° 31' 58.068", -76° 22' 11.360") in one of approximately 200 m<sup>2</sup>, and ECT-3 (0° 31' 14.939", 76° 21' 4.527") in one of about 150 m<sup>2</sup>. The three mineral licks were located within the territory of the Kichwa Añangu community in the Yasuní National Park, province of Orellana (Figure 1); this area is part of the Yasuní Biosphere Reserve, considered one of the most biodiverse regions worldwide (Bass et al. 2010). The study area

is mainly covered by periodically flooded forests (*varzea*), non-flooded dryland forests, and marshlands where the buriti palm (*Mauritius flexuosa*) predominates. It is located within the Eastern Tropical zoogeographic region (Albuja et al. 2012), characterized by a humid tropical climate (Unesco 2010). According to the Nuevo Rocafuerte monitoring station of the National Institute of Meteorology and Hydrology (INHIM), in 2018, the total precipitation was approximately 3,300 mm and the average monthly temperature was 26.1 °C. Precipitation is concentrated between February and July and decreases the rest of the year, ranging between 2,881 mm and 3,942 mm (Pitman 2000; Albuja et al. 2012; Blake et al. 2012),

**Sampling Design.** We visited the mineral licks on three occasions to install the ECTs, which remained in operation for three periods of 30 to 40 days. The first period spanned from February to March, the second from June to July, and the third from November to December 2018; we recorded information from nine camera traps in total, three for each period.

The three mineral licks were georeferenced with a Garmin Oregon 650t GPS (Garmin Ltd.); the distance between them ranged from 2.5 to 6.4 km. Each ECT was equipped with one camera trap (Bushnell Trophy Cam HD, Aggressor model, Bushnell Corporation). Cameras were attached to tree trunks at the edge of each mineral lick, at a height of 0.5 to 0.75 m above the ground, and were oriented toward wildlife trails. These were set to capture three photographs each time the motion sensor was activated, with a 60-second interval between activations. The sampling effort varied between 61 and 98 camera trap days between mineral licks. The number of camera trap days was estimated from the time the camera started operating until the last image was captured (based on the date and time stamped on the pictures).

**Data Analysis.** The images captured were entered and processed in the Wild.ID software (<https://www.wildlifeinsights.org/team-network>). Based on the criteria proposed by Tobler et al. (2009), Blake et al. (2011), and Link et al. (2012), "independent" records were those images captured consecutively from clearly distinguishable individuals or individuals of the same species captured by the same camera within a 60-minute interval.

To assess the completeness of the species inventory, the species richness estimators Chao1 and ACE were calculated for each mineral lick and a species accumulation curve was constructed for the data set using the EstimateS 9.1.0 program (Colwell and Coddington 1994; Colwell 2013). To determine whether this variation influenced the estimation of species richness between mineral licks as well as between seasons, an analysis was performed with rarefaction curves interpolated to the smallest sample (Krebs 1989; Colwell et al. 2012) using the program Past 3.03 (Hammer et al. 2001). The Jaccard similarity index was also calculated to evaluate the similarity of species composition between mineral licks as well as between climatic seasons (Moreno 2001).

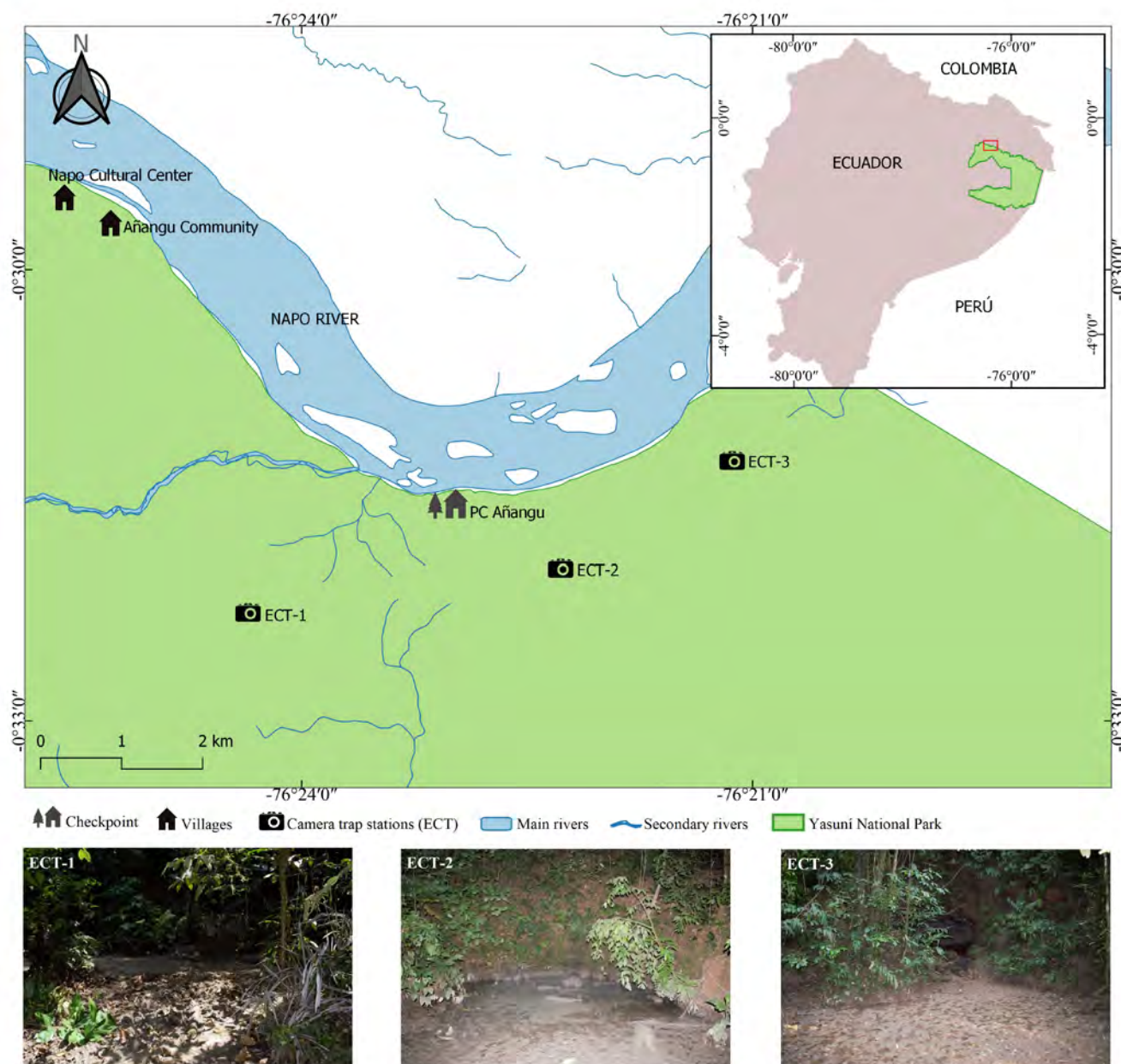
The capture frequency (FC, for its acronym in Spanish) of each species was calculated by dividing the number of capture events by species for the sampling effort (number of camera trap days) in each mineral lick and climatic season and multiplying by 100 to facilitate comparisons with similar studies (Blake *et al.* 2011; Blake *et al.* 2013).

Capture frequency (FC) patterns were compared graphically through rank-abundance curves (Whittaker's plots) based on Magurran (2004). The vertical axis measured capture frequencies and the horizontal axis measured the range of species recorded in each mineral lick (ECT), the total number of species of the whole study, and the number of species by climatic season.

## Results

A total sampling effort of 249 camera trap days yielded 645 images, of which 398 were independent records of 16 species in 11 families and seven taxonomic orders. The number of independent records per mineral lick varied between 112 and 159, with 11 species recorded in the first and second mineral licks and 9 in the third (Table 1). The taxonomic order with the highest number of records was Rodentia, with three families and four species (Table 2).

*Observed Species - Species Richness Estimates.* A total of 16 species ( $S_{obs}$ ) were recorded, accounting for 95.2 % of the figure estimated with Chao1 ( $S = 16.8$ ) and 85.6 % of the figure estimated with ACE ( $S = 18.7$ ). Therefore, a repre-



**Figure 1.** Map of the study area showing the location of the camera trap stations (ECT) in the three mineral licks, Kichwa Añangu community village, and Yasuni National Park checkpoint.

sentative sample was obtained in general terms. However, in ECT-1, the recorded species amounted to 42.5 % of the Chao1 estimate ( $S = 25.9$ ) and 28.6 % of the ACE estimate ( $S = 38.5$ ). In contrast, ECT-2 recorded 100 % of the Chao1 estimate ( $S = 11$ ) and 94.8 % of the ACE estimate ( $S = 11.6$ ). ECT-3 recorded 75.6 % of the species estimated by Chao1 ( $S = 11.9$ ) and 70.9 % of the expected species according to ACE ( $S = 12.7$ ; Table 1).

**Table 1.** Camera-trap data in three mineral licks located in the Yasuní National Park, Kichwa Añangu community. Trap Camera Station (ECT).

	ECT-1	ECT-2	ECT-3	Total
Camera trap days	61	98	90	249
No. of captures	303	137	205	645
Species richness ( $S_{obs}$ )	11	11	9	16
Number of independent records	159	112	127	398
Chao 1	25.9	11.0	11.9	16.8
ACE	38.5	11.6	12.7	18.7

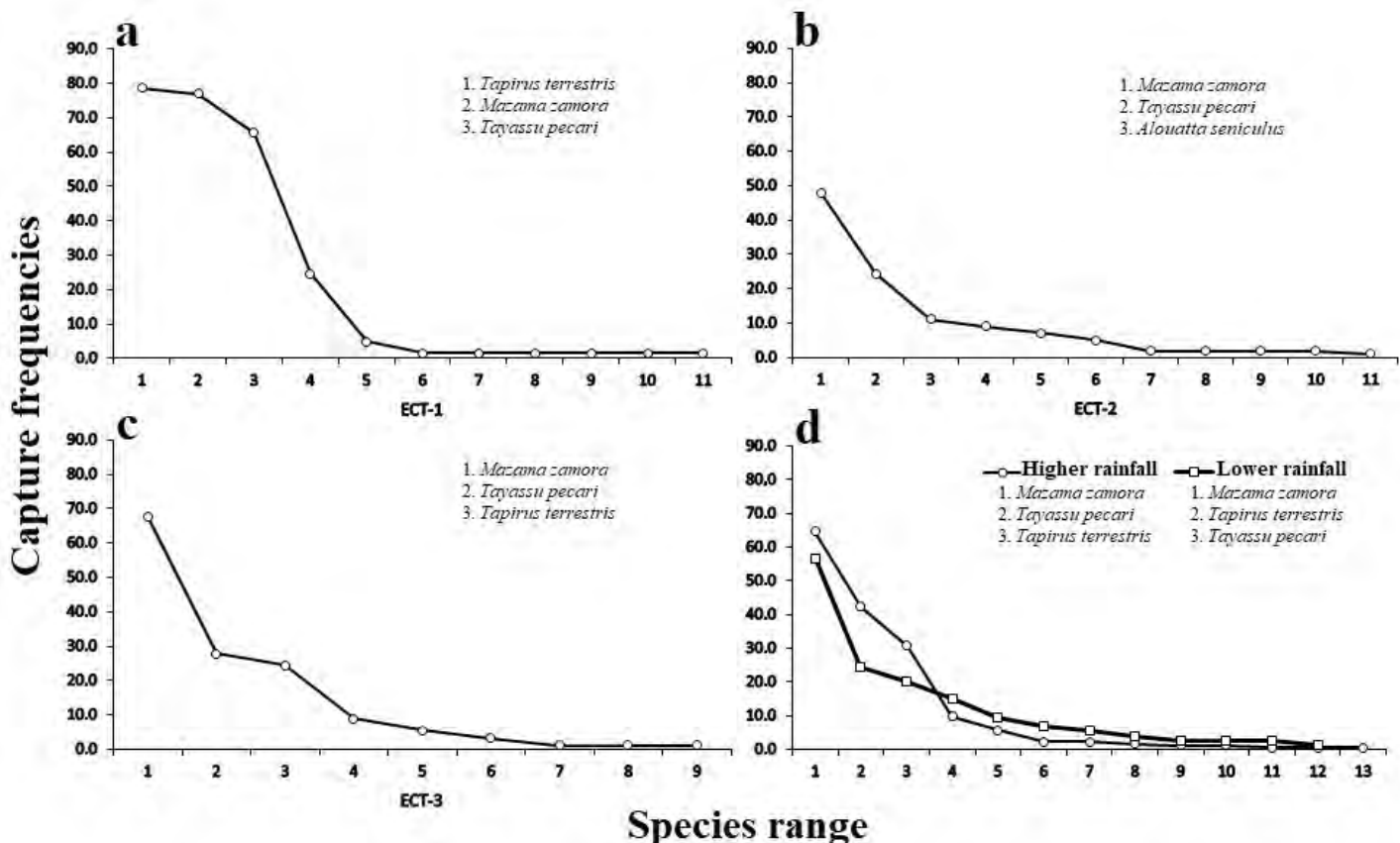
**Capture Frequency of Mammalian Species.** The species recorded most frequently over the three sampling periods were the red brocket (*Mazama zamora*; 155 independent records,  $FC = 62.2$ ), white-lipped peccary (*Tayassu pecari*; 89 independent records,  $FC = 35.7$ ), South American tapir (*Tapirus terrestris*; 72 independent records,  $FC = 28.9$ ), and

collared peccary (*Pecari tajacu*; 20 independent records,  $FC = 8.0$ ). The species with the lowest number of records were the collared anteater (*Tamandua tetradactyla*), white-fronted Capuchin (*Cebus yuracus*), and green acouchi (*Myoprocta pratti*), with one independent record ( $FC = 0.4$ ) in each case (Table 2).

The most frequent species in the three mineral licks were *M. zamora*, *T. terrestris*, *T. pecari*, and *A. seniculus*. These species obtained different capture frequencies in each ECT, thus attaining a different rank. These were the most abundant species and were relatively easy to capture with camera traps; the exception was *A. seniculus*, which appeared among the dominant species only in ECT-2 (Figure 2).

**Rarefaction and Interpolation.** It was found that by interpolating to the smallest number of independent records (112 records), ECT-2 was the mineral lick with the highest number of species ( $S = 11$ ). This indicates that species richness in this site was significantly higher relative to ECT-3 ( $S = 8.6$ ) under the same number of records since the confidence intervals did not overlap. However, the confidence intervals of ECT-1 ( $S = 9.2$ ) overlapped with those of the other sites, so differences were non-significant (Figure 3).

**Climate Temporality: Rarefaction and Interpolation, Capture Frequency and Species Composition.** During the higher rainfall season, the sampling effort was 175 days/trap, resulting in 286 independent records of 13 species, ten families,



**Figure 2.** Range-abundance curves (Whittaker's plots) with capture frequencies for the mineral licks a) ECT-1. b) ECT-2. c) ECT-3. d) Seasons of higher and lower rainfall.

**Table 2.** List of orders, families, and species recorded according to higher or lower rainfall, FC value and the threat category in IUCN, LRE=Libro Rojo de Ecuador (Red Book of Ecuador) and CITES.

List	Higher rainfall				Lower rainfall		Total		IUCN	LRE	CITES
	Feb-Mar		Jun-Jul		Nov-Dec		No. Rec.	FC			
	No. Rec.	FC	No. Rec.	FC	No. Rec.	FC					
ARTIODACTYLA											
Cervidae											
<i>Mazama zamora</i>	55	54.5	58	78.4	42	56.8	155	62.2	DD	NT	*
<i>Mazama murelia</i>	0	0.0	4	5.4	2	2.7	6	2.4	LC	NT	*
Tayassuidae											
<i>Tayassu pecari</i>	47	46.5	27	36.5	15	20.3	89	35.7	VU	CR	II
<i>Pecari tajacu</i>	1	1.0	16	21.6	3	4.1	20	8.0	LC	NT	II
CARNIVORA											
Felidae											
<i>Leopardus pardalis</i>	0	0.0	3	4.1	7	9.5	10	4.0	LC	NT	I
CINGULATA											
Dasypodidae											
<i>Dasypus pastasae</i>	0	0.0	0	0.0	2	2.7	2	0.8	LC	DD	*
<i>Dasypus novemcinctus</i>	8	7.9	2	2.7	1	1.4	11	4.4	LC	LC	*
PERISSODACTYLA											
Tapiridae											
<i>Tapirus terrestris</i>	35	34.7	19	25.7	18	24.3	72	28.9	VU	EN	II
PILOSA											
Myrmecophagidae											
<i>Tamandua tetradactyla</i>	1	1.0	0	0.0	0	0.0	1	0.4	LC	LC	*
PRIMATES											
Atelidae											
<i>Alouatta seniculus</i>	0	0.0	0	0.0	11	14.9	11	4.4	LC	LC	II
<i>Ateles belzebuth</i>	0	0.0	0	0.0	2	2.7	2	0.8	EN	EN	II
Cebidae											
<i>Cebus yuracus</i>	1	1.0	0	0.0	0	0.0	1	0.4	LC	NT	*
RODENTIA											
Dasypodidae											
<i>Myoprocta pratti</i>	0	0.0	1	1.4	0	0.0	1	0.4	LC	LC	*
<i>Dasypodactyla fuliginosa</i>	1	1.0	1	1.4	4	5.4	6	2.4	LC	LC	*
Cuniculidae											
<i>Cuniculus paca</i>	4	4.0	0	0.0	5	6.8	9	3.6	LC	NT	III
Erethizontidae											
<i>Coendou prehensilis</i>	1	1.0	1	1.4	0	0.0	2	0.8	LC	DD	*

and seven orders. In the season of lower rainfall, the sampling effort was 74 camera trap days, yielding 112 independent records of 12 species in eight families and six orders.

Between the two seasons, the rarefaction analysis interpolating to the lowest number of independent records (112) revealed that ten species were recorded during the higher rainfall season and 12 in the lower rainfall season. The 95 % confidence intervals overlapped, so no significant difference in species richness from climatic seasonality was observed (Figure 3).

In the higher rainfall season, the most frequent species were *M. zamora* (113 records, FC = 64.6), *T. pecari* (74 records, FC = 42.39), *T. terrestris* (54 records, FC = 30.9), and *P. tajacu*

(17 records, FC = 9.7). In the lower rainfall season, the most frequent species were *M. zamora* (42 records, FC = 56.8), *T. terrestris* (18 records, FC = 24.3), *T. pecari* (15 records, FC = 20.3), and red howler (*Alouatta seniculus*; 11 records, FC = 14.9).

When the range-abundance (FC) curves are compared between the two seasons, *M. zamora* is the predominant species in both seasons, followed by *T. pecari* and *T. terrestris*. These were the most abundant species that were observed most frequently in mineral licks (Figure 2).

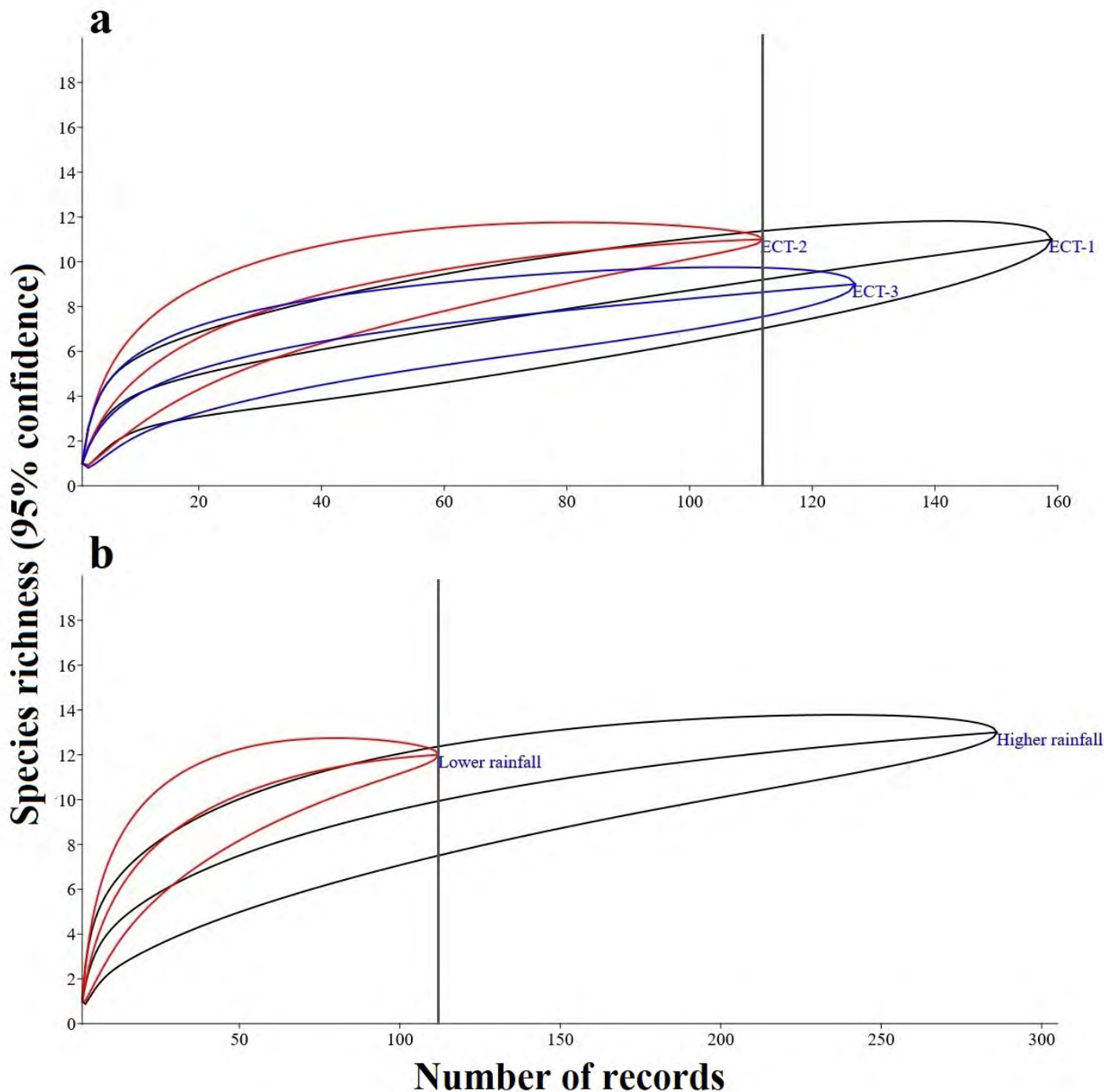
*Similarity.* ECT-1 (*C. albifrons*, *T. tetradactyla*, and *M. pratti*) and ECT-2 (*C. prehensilis*, *A. seniculus*, and *A. belzebuth*) showed three species that were not observed in any other mineral lick; ECT-3 had no unique species. Accord-

ing to the Jaccard similarity index, stations ECT-1 and ECT-2 shared 37.5 % of the recorded species. For their part, ECT-1 and ECT-3 shared 53.8 % of species, the same percentage shared by ECT-2 with ECT-3.

The higher rainfall season recorded four unique species (*C. yaracus*, *C. prehensilis*, *T. tetradactyla*, and *M. pratti*) and the lower rainfall season recorded three unique species (*A. seniculus*, *A. belzebuth*, and *D. pastasae*). Altogether, the two climatic seasons yielded 56.3 % of species similarity, according to the Jaccard index.

### Discussion

*Fauna Recorded in Mineral licks.* According to the richness estimators Chao1 ( $S = 16.8$ ) and ACE ( $S = 18.7$ ), a considerable sample was obtained to determine the richness of species visiting mineral licks. However, species richness would probably increase with a higher sampling effort as the species accumulation curve ( $S_{obs} = 16$ ) shows no asymptotic trend. Whittaker's plots are similar for the three mineral licks, showing equal species capture frequencies and the same dominant species (Figure 2). On the other hand, rarefaction



**Figure 3.** Rarefaction curves based on species richness for a standard sample of 112 independent records in a) ECT-1. ECT-2. ECT-3 mineral licks. b) Seasons of higher and lower rainfall, with a 95 % confidence interval in both cases.



curves evidenced a non-significant difference in the species recorded in the three mineral licks (Figure 3), thus stressing the importance of conserving mineral licks as sources of mineral supplements for the visiting fauna. As in previous studies carried out in the Neotropics (Tobler *et al.* 2009; Blake *et al.* 2011; Blake *et al.* 2013), the red brocket, collared peccary, white-lipped peccary, and South American tapir were the species most frequently recorded in these habitats, also being commonly hunted (Blake *et al.* 2013).

Comparing the capture frequencies of four species with those obtained by Blake *et al.* (2013) in two locations -one disturbed from the proximity of a road and under hunting pressure (YRS) and the other being hard to access and under minimum hunting pressure (TBS)-, the capture frequencies in the present study are in between those observed in TBS and YRS (Table 3); the exception was *T. pecari*, which showed a higher capture frequency. It is worth mentioning that this was one of the most heavily hunted species in the Añangu community area some 20 years ago (Suárez and Zapata 2019). For this reason, we assume that in the mineral licks included in this study, animal populations that were previously overhunted may be undergoing a recovery process; this deserves to be further explored in future research.

Other recorded species, such as the nine-banded armadillo (*Dasytus novemcinctus*) and the ocelot (*Leopardus pardalis*), are rare in mineral licks (Blake *et al.* 2011), but both have been recorded more frequently along trails (Blake *et al.* 2012, 2013; P. Macas-Pogo, personal observation). Ocelots are usually attracted by bats that visit certain mineral licks and are part of their diet (Tinoco and Camacho 2015; Contreras-Moreno *et al.* 2019) and have also been seen hunting amphibians (P. Macas-Pogo, personal observation). The red howler (*A. seniculus*) and the yellow-bellied spider monkey (*A. belzebuth*) are two of the most hunted primate species (Mena *et al.* 2000), so much so that their populations have been decimated in some areas of the Yasuní National Park (Franzen 2006). This study recorded these two species only in ECT-2 and with low capture frequencies (FC = 4.4 and FC = 0.8, respectively), especially the yellow-bellied spider monkey, a frequent visitor to mineral licks (Blake *et al.* 2010; Link *et al.* 2011). The black agouti (*Dasyprocta fuliginosa*) is another species preferred by hunters; this work recorded it at the three study sites. However, compared to data from studies performed by Blake *et al.* (2011) and Blake *et al.* (2013), the number of records is minimal, as is the number of other small species; this could be related to the sampling

effort or even to the position of camera traps at the time of installation.

**Climatic Seasonality.** Several research studies on geophagy indicate that climatic seasonality influences the use of mineral licks (Jones and Hanson 1985; Atwood and Weeks 2003; Link *et al.* 2012) and that animals prefer visiting these sites on sunny days with no mist, wind, or rain (Brightsmith 2004). By contrast, according to Link *et al.* (2011), they display reduced activity in days of heavy rains. However, the rarefaction analysis indicated no significant differences between climatic seasons for the species recorded. The species composition was similar in the two seasons, with a Jaccard index higher than 0.5 (56.3 % similarity); the red brocket, white-lipped peccary, and South American tapir were the dominant species in both seasons. The slopes of Whittaker's plots are steep, suggesting a low evenness of species (Figure 2).

The species recorded only in the lower rainfall season and those captured exclusively in the higher rainfall season with one or two records are insufficient to determine whether the use of mineral licks is related to the season of the year. Factors such as water accumulation in mineral licks are attractive to some individuals (Link *et al.* 2011). The consumption of fruits, seeds, or plants that produce secondary metabolites varies seasonally (Brightsmith 2004; Voigt *et al.* 2007) and induces mammals to search for mineral salts.

For the inhabitants of Añangu, based on a self-managed internal regulation, the discontinuation of wildlife overhunting and, most importantly, wildlife trafficking, has yielded favorable results since today the fauna that can be observed is attractive for tourists visiting the area. A central factor in preventing wildlife trafficking has been that there are neither main roads nor alternate roads near mineral lick sites, and thus the hunting pressure has dropped significantly. This contrasts with areas crossed by the Maxus road where, according to Suárez and Zapata (2018), wildlife has been severely affected and the indirect effects of roads and the oil industry have been underestimated. Besides, excess hunting by the Waorani has led to the local extinction of the hunted species (Mena *et al.* 2000; Franzen 2006; Espinosa *et al.* 2014; Blake *et al.* 2013).

In conclusion, the results presented herein evidence the richness of mammalian species that use these mineral licks as an important source of minerals, which are undoubtedly essential for the normal development of organisms. As mentioned earlier, there is no marked climatic seasonality in this region; therefore, this factor is not a driver for peccaries, brockets, and tapirs when visiting a mineral lick since they were recorded in the three mineral licks over the three sampling periods studied, being the species with the highest capture frequencies. Besides, we recorded species unique to two of the three mineral licks to each climatic season. Therefore, the use of a given mineral lick may also be determined by home range, the particular behavior of each species, hunting pressure, or other factors that deserve further investigation in future research.

**Table 3.** Comparison of capture frequencies (FC) of four species reported by Blake *et al.* (2013) versus the figures obtained in the present study.

Species	Blake <i>et al.</i> 2013		Present study
	TBS (FC)	YRS (FC)	ECT-Total (FC)
<i>Mazama zamora</i>	211.2	57.7	62.2
<i>Tapirus terrestris</i>	37.1	25.5	28.9
<i>Pecari tajacu</i>	48.2	5.5	8
<i>Tayassu pecari</i>	28.1	0	37.5

Mineral licks might be an important resource for local human populations if these are given proper use as subsistence hunting sites or even as sites for wildlife-watching tourism. It is evident that the sustainable practices adopted by the Añangu community support the sustainable management of these sites, making a positive contribution to the conservation of biodiversity in the Yasuní National Park. These mineral licks represent areas that should be valued for their role in the ecosystem, mainly in the diet of the fauna using them. Additional studies are needed to advance our understanding of their characteristics and contributions to forest dynamics. In addition to continuing the application of sustainable tourism practices, the local community should be advised to implement clear guidelines setting restrictions, visiting hours, and behavior of visitors of mammalian mineral licks to ensure their protection.

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# Corrigendum

Change in name of the author

## Morphological differentiation of *Peromyscus leucopus* and *P. maniculatus* in East Texas

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