Therya

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La portada
Macho de venado cola blanca texano (*Odocoileus virginianus texanus*), ejemplar fotografiado con una cámara DSRL en el norte de Coahuila, México. Fotografía de Jorge Castro Urbiola.

Issue cover
Male Texas whitetail deer (*Odocoileus virginianus texanus*), specimen photographed with a DSRL camera in northern Coahuila, Mexico. Photograph by Jorge Castro Urbiola.

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 y las habilidades. Al signo decimoprimero en la cosmogonía mexica. "Ozomatli" es una representación pictórica del mono araña (*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.

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Consejo Editorial
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Susana González. Departamento Biodiversidad y Genética, Instituto de Investigaciones Biológicas Clemente Estable-MEC, Montevideo, Uruguay.
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Víctor Sánchez Cordero. Universidad Nacional Autónoma de México, Instituto de Biología. Coyoacán, Ciudad de México, México.

THERYA
Lilia Ruiz Ruiz. Editora de formato. Centro de Investigaciones Tropicales, Universidad Veracruzana. E-mail: correo.therya@gmail.com
Malinalli Cortés Marcial. Tesorera de la Revista THERYA. Universidad Autónoma Metropolitana Unidad Xochimilco. E-mail: therya.tesoreria@gmail.com
Alina Gabriela Monroy Gamboa. Difusión. Centro de Investigaciones Biológicas del Noroeste. Av. Instituto Politécnico Nacional 195. La Paz 23096, Baja California Sur. México. E-mail: beu_ribetzin@hotmail.com
María Elena Sánchez Salazar. Traducción.

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Editores Generales

Sonia Gallina Tessaro. Instituto de Ecología, A.C. Carretera antigua a Coatepec 351, Col. El Haya, Xalapa, Veracruz, México. CP 91073. E-mail: sonia.gallina@inecol.mx
Jorge Ortega Reyes. Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Ciudad de México, México. CP 11340. E-mail: artibeus2@aol.com
María Cristina Mac Swiney González. Centro de Investigaciones Tropicales, Universidad Veracruzana, Xalapa, Veracruz, México. CP 91000. Email: cmacswiney@uv.mx

Editora Asistente

Mercedes Morelos Martínez. Centro de Investigaciones Tropicales, Universidad Veracruzana, Xalapa, Veracruz, México. CP 91000. Email: mercedesmorelosm@gmail.com

Editores Asociados
Luis F. Aguirre. Centro de Biodiversidad y Genética. Universidad Mayor de San Simón, Cochabamba, Bolivia. E-mail: laguirre@fcyt.umss.edu.bo
Gabriel P. Andrade Ponce. Stephen F. Austin State University. 1936 North St, Nacogdoches, TX 75965, Estados Unidos. E-mail: gabriel.andrade@sfasu.edu
Nataly Castelblanco Martínez. El Colegio de la Frontera Sur, Chetumal, Avenida del Centenario km 5.5, 77014 Chetumal, Quintana Roo, México. E-mail: nataly.castelblanco@ecosur.mx
Mónica Díaz. CONICET, PIDBA (Programa de Investigaciones de Biodiversidad Argentina), PCMA (Programa de Conservación de los Murciélagos de la Argentina. Facultad de Ciencias Naturales e Instituto Miguel Lillo - Universidad Nacional de Tucumán. Fundación Miguel Lillo, Miguel Lillo 251, (4000) San Miguel de Tucumán, Argentina. E-mail: mmonicadiaz@yahoo.com.ar
Juan Pablo Gallo Reynoso. Centro de Investigación en Alimentos y Desarrollo. Laboratorio de Ecofisiología. Carretera a Varadero Nacional km 6.6. Col. Las Playitas 85480. Guaymas, Sonora. México. E-mail: jpgallo@ciad.mx
Luis M. García Feria. Instituto de Ecología, A.C. Carretera antigua a Coatepec 351, Col. El Haya, Xalapa, Veracruz. CP 91073. E-mail: luis.garcia@inecol.mx
José F. González-Maya. Departamento de Ciencias Ambientales, Universidad Autónoma Metropolitana, Unidad Lerma. Av. de las Garzas #10, El panteón, 52005 Lerma de Villada, México. E-mail: jf.gonzalez@correo.ler.uam.mx
Mircea Gabriel Hidalgo Mihart. División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco. Carretera Villahermosa-Cárdenas Km. 0.5 S/N, Entronque a Bosques de Saloya. CP. 86150, Villahermosa. Tabasco, México. E-mail: mhidalgo@yahoo.com
Miguel Ángel León Tapia. Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, 04510, Ciudad de México. E-mail: mal@st.ib.unam.mx
Luz Irene Loría. Facultad de Ciencias Agropecuarias, Av. José de Fábrega, Panamá, Provincia de Panamá, Panamá. E-mail: lilaloria@gmail.com
Eduardo Mendoza Ramírez. Instituto de Investigaciones sobre los Recursos Naturales (INIRENA) Universidad Michoacana de San Nicolás de Hidalgo. Av. San Juanito Itzicuaro s/n. Col. Nueva Esperanza C.P. 58337. Morelia, Michoacán, México. E-mail: mendoza.mere@gmail.com
Alina Gabriela Monroy Gamboa. Centro de Investigaciones Biológicas del Noroeste. Av. Instituto Politécnico Nacional 195. La Paz 23096, Baja California Sur. México. E-mail: beu_ribetzin@hotmail.com
Olga L. Montenegro. Conservación y Manejo de Vida Silvestre, Instituto de Ciencias Naturales, Universidad Nacional de Colombia. Carrera 45 N° 26-85, Edificio Uriel Gutiérrez, Bogotá, Colombia. E-mail: olmontenegrod@unal.edu.co

Jesús Alonso Panti May. Centro de Investigaciones Regionales "Dr. Hideyo Noguchi", Universidad Autónoma de Yucatán, Mérida, Yucatán, México. E-mail: pantialonso@gmail.com
Rafael Reyna Hurtado. El Colegio de la Frontera Sur, Unidad Campeche. Avenida Rancho s/n, Lerma Campeche, 24500. México. E-mail: rafaelcalakmul@gmail.com
Bernal Rodríguez Herrera. Universidad de Costa Rica, San José, Costa Rica. E-mail: bernal.rodriguez@ucr.ac.cr
César Ricardo Rodríguez Luna. Departamento de Ecología Humana. Cinvestav, Unidad Mérida, Km 6 antigua, Carretera Mérida-Progreso, Loma Bonita, 97310 Mérida, Yucatán, México. E-mail: crodriguezluna@gmail.com
Cintya Segura Trujillo. Universidad de Guadalajara, Jalisco, México. E-mail: c.a.biolsegura@gmail.com
Sergio Solari. Editor asociado. Instituto de Biología. Universidad de Antioquia. Calle 67 No53-108 / AA 1226. Medellín, Colombia. E-mail: solari.udea@gmail.com
Ella Vázquez Domínguez. Laboratorio de Genética y Ecología, Instituto de Ecología, Universidad Nacional Autónoma de México. C.U., Coyoacán, 04510, Ciudad de México, México. E-mail: evazquez@ecologia.unam.mx

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Editorial

Políticas de conservación de los ciervos latinoamericanos basadas en actualizaciones taxonómicas

Los ciervos han sido durante mucho tiempo algunos de los ungulados más importantes de América Latina, manteniendo vínculos profundos y perdurables con las comunidades humanas. La evidencia arqueológica indica que los ciervos constituyeron una importante fuente de proteína animal para las sociedades prehistóricas, mientras que sus pieles eran utilizadas para la elaboración de vestimenta y otros materiales, y sus huesos y astas eran incorporados en herramientas y otros artefactos culturales. A pesar de esta larga historia de aprovechamiento humano, los ciervos permanecieron abundantes en gran parte de su distribución histórica, lo que sugiere que las formas tradicionales de uso fueron, en muchos contextos, compatibles con la persistencia de sus poblaciones a largo plazo.

Los ancestros de los ciervos sudamericanos colonizaron el continente durante el Gran Intercambio Biótico Americano, tras el establecimiento de la conexión terrestre entre América del Norte y América del Sur a través del istmo de Panamá. La evidencia genética molecular indica que los ancestros de varios linajes de venados neotropicales llegaron a América del Sur durante el Plioceno, hace aproximadamente 5 millones de años, seguidos por posteriores procesos de dispersión y diversificación (Duarte *et al.* 2008). Una fase posterior de diversificación durante el Pleistoceno contribuyó aún más a la notable diversidad evolutiva observada entre los ciervos sudamericanos (Figura 1). Comprender esta historia evolutiva es fundamental, ya que los límites actuales entre las especies no siempre reflejan plenamente los procesos que generaron la diversidad que observamos en la actualidad.

Sin embargo, la situación actual es marcadamente diferente. Muchas poblaciones de ciervos latinoamericanos están disminuyendo como consecuencia de la pérdida y fragmentación del hábitat, la expansión agrícola, la cacería, el incremento de las interacciones con el ganado y otras actividades humanas; estas presiones se ven además agravadas por los efectos cada vez más acelerados del cambio climático. Bajo estas condiciones de cambio rápido, las estrategias de conservación deben ser cada vez más precisas, adaptativas y basadas en evidencia. Los recientes cambios taxonómicos entre los ciervos de América Latina constituyen un ejemplo contundente de por qué la taxonomía debe integrarse estrechamente en la planificación y las políticas de conservación.

Entre los cérvidos neotropicales, pocos casos ilustran este punto con mayor claridad que el de los venados temazates de los géneros *Mazama* y *Subulo*, particularmente el venado de cola gris. Durante décadas, esta especie fue ampliamente reconocida como *Mazama gouazoubira*, uno de los ciervos pequeños con mayor distribución geográfica en América del Sur. Sin embargo, estudios moleculares, citogenéticos, morfológicos y filogenéticos han demostrado que el concepto tradicional de *Mazama* no representa un único linaje evolutivo. Se demostró que el género es polifilético y, posteriormente, el venado de cola gris fue incluido en el género *Subulo*, restablecido recientemente, pasando a denominarse *Subulo gouazoubira* (Bernegossi *et al.* 2023).

A primera vista, cambiar *Mazama gouazoubira* por *Subulo gouazoubira* podría parecer una cuestión puramente nomenclatural. No lo es. Este cambio refleja una comprensión fundamentalmente distinta de la historia evolutiva de los ciervos neotropicales y plantea una pregunta importante: **¿cuáles son las consecuencias de los cambios taxonómicos para las políticas de conservación?**

La historia de *Subulo* es particularmente informativa porque demuestra cómo la morfología puede subestimar la diversidad evolutiva. Los venados de los géneros *Mazama* y *Subulo* son animales relativamente pequeños y morfológicamente conservadores, y varios linajes comparten tamaños corporales, morfología de las astas y características ecológicas similares. Estas semejanzas contribuyeron históricamente a su clasificación dentro de *Mazama*. Sin embargo, la evidencia genética, citogenética y filogenética reveló que la similitud morfológica no necesariamente refleja relaciones evolutivas cercanas.

Trabajos recientes han esclarecido aún más este panorama. El concepto previo del venado de cola gris incluía linajes evolutivos que no están estrechamente emparentados. *Subulo gouazoubira*, distribuido predominantemente al

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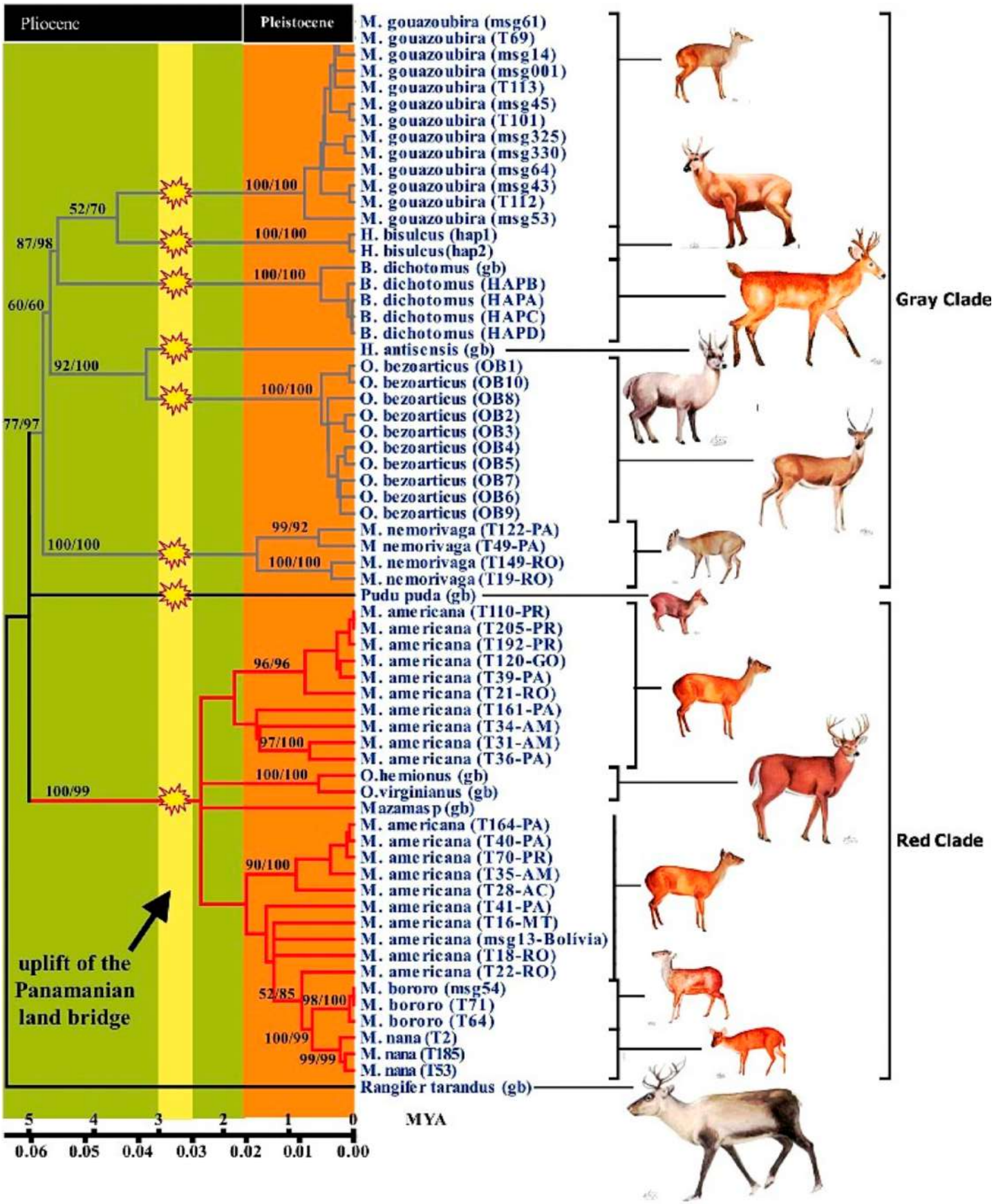

Figura 1. Árbol filogenético que muestra las relaciones entre 59 haplotipos de ciervos, derivados de un fragmento de 934 pares de bases del gen mitocondrial citocromo *b*, elaborado mediante el programa informático MEGA 4 (Tamura *et al.* 2007), después de realizar una prueba de longitud de ramas (Takezaki *et al.* 1995) para evaluar las diferencias en las tasas de sustitución de bases. Los valores de *bootstrap* (1000 réplicas) y las probabilidades posteriores bayesianas (>50 %) se indican sobre los nodos. Árbol modificado de Duarte *et al.* (2008), tomado de Duarte y González (2010).

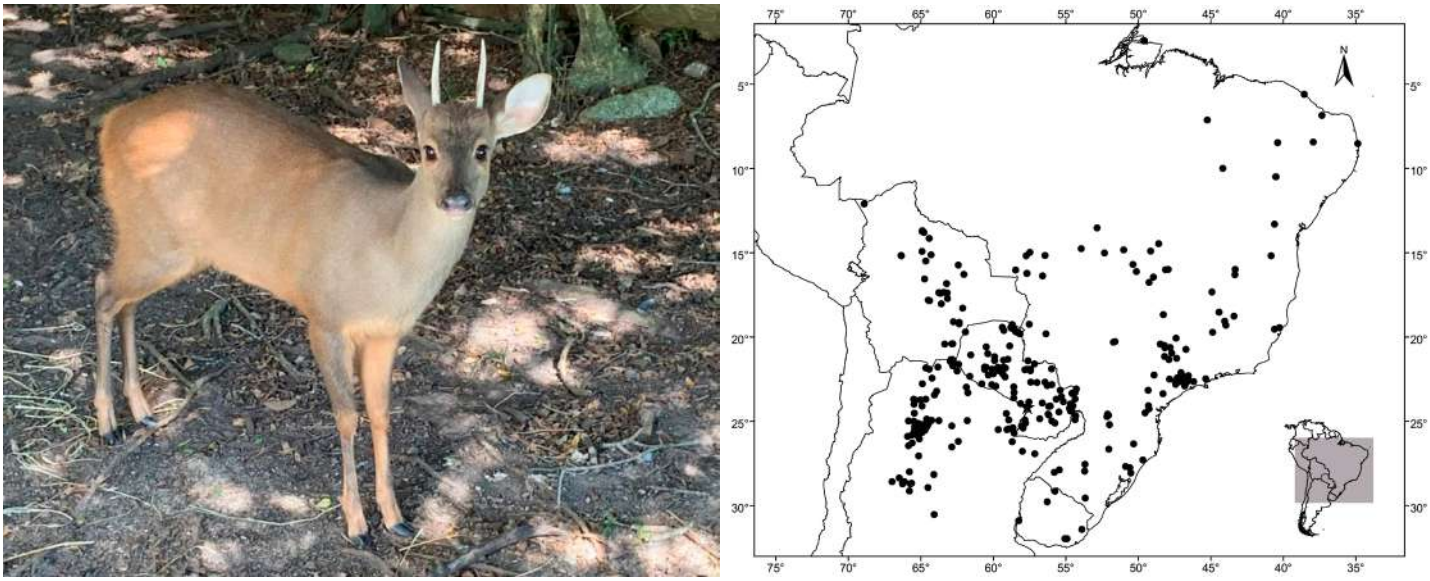

Figura 2. Individuo de *Subulo gouazoubira* y su distribución geográfica, con base en Duarte y González (2010). Fotografía: Susana González.

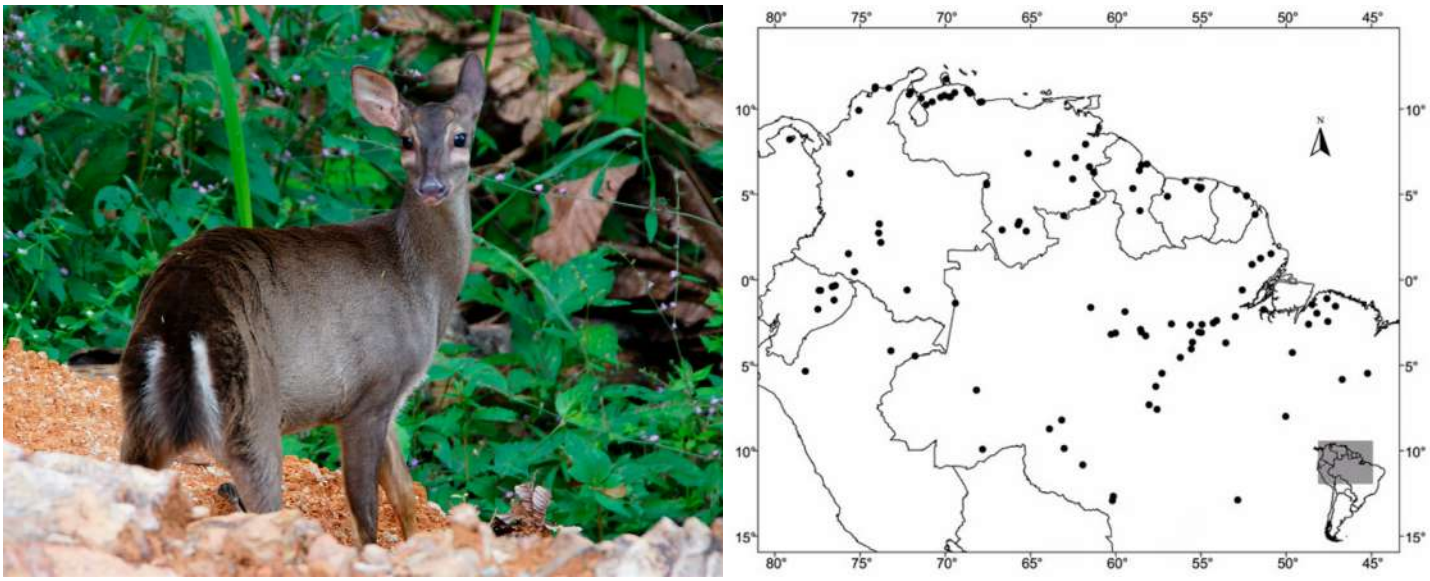

Figura 3. Individuo de *Passalites nemorivagus* y su distribución geográfica, con base en Duarte y González (2010). Fotografía: Christopher Borges.

sur del Amazonas, y *Passalites nemorivagus*, presente en las regiones amazónica y guayanesa, representan linajes evolutivos distintos (Figura 2 y 3).

La reestructuración taxonómica tiene una implicación inmediata para la conservación: **la distribución, abundancia y estado de conservación percibidos de un taxón dependen, en parte, de cómo se defina dicho taxón.**

Cuando *Mazama gouazoubira* era considerada una única especie ampliamente distribuida, su extensa área geográfica contribuía a la percepción de un taxón relativamente seguro. Sin embargo, una vez que los linajes evolutivos previamente no reconocidos son formalmente diferenciados, la distribución, el tamaño poblacional, el grado de fragmentación, las tendencias demográficas y las amenazas potenciales de cada linaje pueden requerir una reevaluación independiente. Es importante señalar que reconocer a *Subulo gouazoubira* como un linaje evolutivo diferenciado no significa, por sí mismo, que la especie esté más amenazada. Por el contrario, proporciona un marco más preciso para evaluar su estado de conservación.

Esta distinción es particularmente importante para los ciervos neotropicales, cuya incertidumbre taxonómica ha complicado históricamente las evaluaciones de las tendencias poblacionales, las distribuciones geográficas y las prioridades de conservación. Una revisión taxonómica puede revelar que lo que anteriormente se consideraba una sola especie ampliamente distribuida es, en realidad, un complejo de linajes evolutivos con diferentes distribuciones geográficas, historias demográficas, características ecológicas y necesidades de conservación. En consecuencia, los cambios taxonómicos pueden requerir la revisión de las evaluaciones de conservación, los planes de manejo, los programas de monitoreo y, cuando corresponda, las medidas de protección legal.

Las implicaciones van más allá de los nombres de las especies. La planificación para la conservación

requiere cada vez más la identificación de la diversidad evolutivamente significativa dentro y entre las especies, incluidas las poblaciones genéticamente diferenciadas y las unidades de manejo. Por lo tanto, el conocimiento taxonómico puede proporcionar una base importante para determinar qué poblaciones deben manejarse de manera independiente, cuáles deben permanecer conectadas y en qué casos la diversidad genética puede requerir una protección particular.

Para los ciervos de América Latina, esto es especialmente relevante porque las políticas de conservación se han desarrollado con frecuencia a partir de evaluaciones a nivel de especie que podrían no reflejar toda la magnitud de la diversidad evolutiva. Un taxón ampliamente distribuido puede parecer relativamente seguro cuando se evalúa como una sola entidad, mientras que los linajes con distribuciones geográficas restringidas dentro de ese taxón pueden enfrentar riesgos considerablemente mayores. Por lo tanto, las revisiones taxonómicas pueden modificar no solo nuestra comprensión científica, sino también la escala a la que deben definirse las prioridades de conservación.

Este aspecto es particularmente relevante en una región donde los recursos destinados a la conservación son limitados y las decisiones de manejo deben establecerse estratégicamente. Si los límites taxonómicos no reflejan con precisión la diversidad evolutiva subyacente, los programas de monitoreo pueden agrupar entidades evolutivas distintas, las tendencias poblacionales pueden quedar ocultas y las inversiones en conservación pueden dirigirse hacia unidades que no representan adecuadamente la diversidad biológica subyacente. Por el contrario, reconocer linajes evolutivos distintos permite orientar las acciones de conservación con mayor precisión y puede ayudar a identificar poblaciones cuya pérdida representaría una erosión desproporcionada de la historia evolutiva.

En consecuencia, la próxima generación de estrategias de conservación para los ciervos de América Latina debería ir más allá del simple conteo de especies. Necesitamos identificar y preservar la diversidad evolutiva, mantener la conectividad genética cuando sea apropiado, proteger poblaciones únicas cuando su diferenciación justifique un manejo independiente y garantizar que las acciones de conservación se basen en evidencia evolutiva y ecológica sólida. Cuando los cambios taxonómicos revelen linajes previamente no reconocidos, las políticas de conservación deberían ser lo suficientemente flexibles como para incorporar nueva evidencia científica en las evaluaciones de las especies, los esquemas de monitoreo, los planes de manejo y, cuando esté justificado, las medidas de protección legal.

En este contexto, el restablecimiento de *Subulo* es más que un cambio de nomenclatura. Es un recordatorio de que **no podemos conservar eficazmente aquello que no hemos reconocido correctamente**.

La taxonomía es importante para la conservación porque cada nombre de especie conlleva una hipótesis implícita sobre su identidad evolutiva. A medida que esa hipótesis cambia con la incorporación de nueva evidencia, las políticas de conservación también deben cambiar. Para los ciervos latinoamericanos, integrar la taxonomía, la genómica, la ecología y la planificación de la conservación no es simplemente deseable: **es esencial para garantizar que la diversidad evolutiva de estos notables mamíferos sea reconocida, evaluada y protegida eficazmente**.

Editorial

Latin American deer conservation policies based on taxonomic updates

Deer have long been among the most important ungulates in Latin America, maintaining deep and enduring connections with human communities. Archaeological evidence indicates that deer were an important source of animal protein for prehistoric societies, while their hides were used for clothing and other materials, and their bones and antlers were incorporated into tools and other cultural artifacts. Despite this long history of human use, deer remained abundant throughout much of their historical range, suggesting that traditional forms of use were, in many contexts, compatible with the long-term persistence of their populations.

The ancestors of South American deer colonized the continent during the Great American Biotic Interchange, following the establishment of the Panamanian land connection between North and South America. Molecular genetic evidence indicates that the ancestors of several Neotropical deer lineages arrived during the Pliocene, approximately 5 million years ago, followed by subsequent dispersal and diversification (Duarte *et al.* 2008). A later phase of diversification during the Pleistocene further contributed to the remarkable evolutionary diversity observed among South American deer (Figure 1). Understanding this evolutionary history is essential because present-day species boundaries do not always fully reflect the processes that generated the diversity we observe today.

Today, however, the situation is markedly different. Many Latin American deer populations are declining as a result of habitat loss and fragmentation, agricultural expansion, hunting, increasing interactions with livestock, and other human activities, with these pressures further compounded by the accelerating effects of climate change. Under these rapidly changing conditions, conservation strategies must become increasingly precise, adaptive, and evidence-based. Recent taxonomic changes among Latin American deer provide a compelling example of why taxonomy must be closely integrated with conservation planning and policy.

Among Neotropical Cervidae, few cases illustrate this point more clearly than the brocket deer, particularly the gray brocket deer. For decades, this species was widely recognized as *Mazama gouazoubira*, one of the most geographically widespread small deer in South America. However, molecular, cytogenetic, morphological, and phylogenetic studies have demonstrated that the traditional concept of *Mazama* does not represent a single evolutionary lineage. The genus was shown to be polyphyletic, and the gray brocket deer was subsequently placed in the resurrected genus *Subulo*, becoming *Subulo gouazoubira* (Bernegossi *et al.* 2023).

At first glance, changing *Mazama gouazoubira* to *Subulo gouazoubira* may appear to be a purely nomenclatural issue. It is not. The change reflects a fundamentally different understanding of the evolutionary history of Neotropical deer and raises an important question: **What are the consequences of taxonomic change for conservation policy?**

The history of *Subulo* is particularly informative because it demonstrates how morphology can underestimate evolutionary diversity. Brocket deer are relatively small and morphologically conservative animals, and several lineages share similar body sizes, antler morphology, and ecological characteristics. These similarities historically contributed to their classification within *Mazama*. However, genetic, cytogenetic, and phylogenetic evidence revealed that morphological similarity does not necessarily reflect close evolutionary relationships.

Recent work has further clarified this picture. The former concept of the gray brocket deer encompassed evolutionary lineages that are not closely related. *Subulo gouazoubira*, occurring predominantly south of the Amazon, and *Passalites nemorivagus*, occurring in Amazonian and Guianan regions, represent distinct evolutionary lineages (Figure 2 and 3).

Taxonomic restructuring has an immediate conservation implication: **the perceived distribution, abundance, and conservation status of a taxon depend, in part, on how that taxon is defined.**

When *Mazama gouazoubira* was treated as a single, widespread species, its extensive geographic distribution contributed to the perception of a relatively secure taxon. Once previously unrecognized evolutionary lineages are formally distinguished, however, the distribution, population size, degree of fragmentation, demographic trends, and potential threats of each lineage may need to be reassessed independently. Importantly, recognizing *Subulo gouazoubira* as a distinct evolutionary lineage does

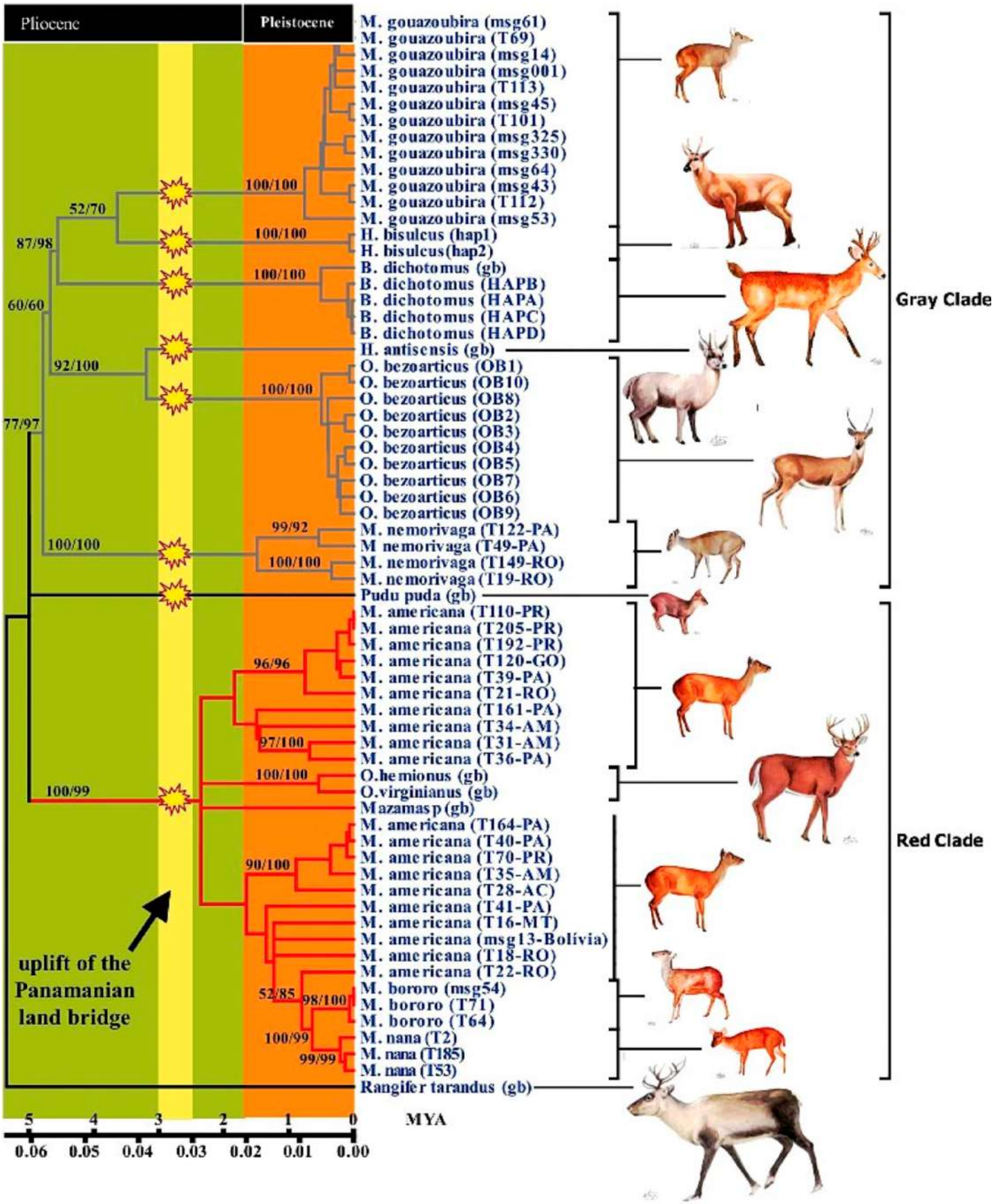

Figure 1. Phylogenetic tree showing the relationships among 59 deer haplotypes derived from a 934 base pair fragment of the mitochondrial cytochrome b compiled with the computer program MEGA 4 (Tamura *et al.* 2007) after performing a branch length test (Takezaki *et al.* 1995) to test for differences in base substitution rates. Bootstrap values (1000 replicates) and Bayesian posterior probabilities (>50%) are denoted above nodes. Tree modified from Duarte et al. (2008) taken from Duarte and González (2010).

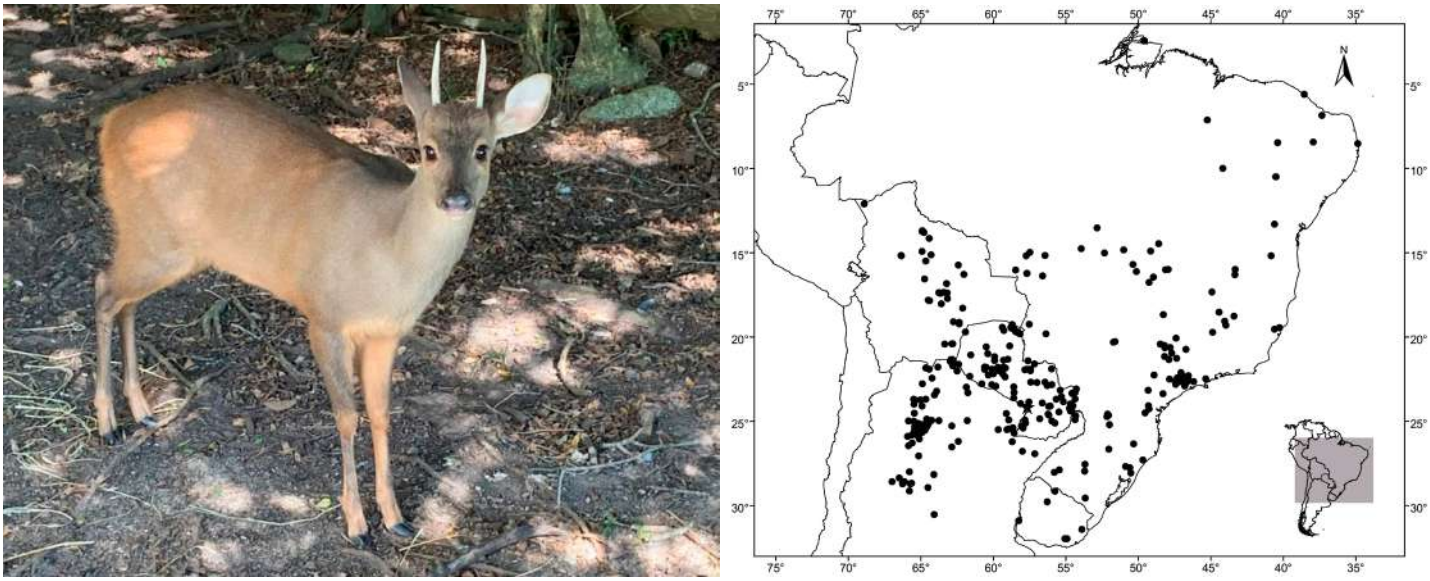

Figure 2. Individual of *Subulo gouazoubira* and its geographic range, based on Duarte and González (2010). Photo: Susana González.

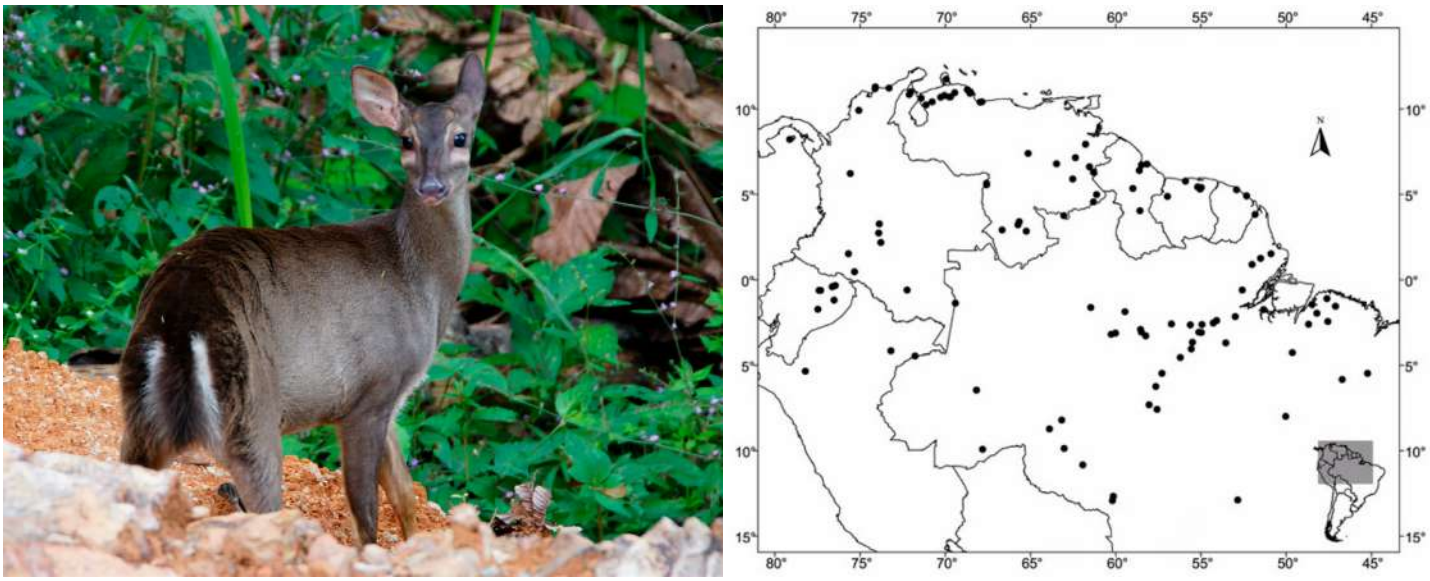

Figure 3. Individual of *Passalites nemorivagus* and its geographic range, based on Duarte and González (2010). Photo: Christopher Borges.

not, by itself, mean that the species is more threatened. Rather, it provides a more accurate framework within which its conservation status can be evaluated.

This distinction is particularly important for Neotropical deer, for which taxonomic uncertainty has historically complicated assessments of population trends, geographic distributions, and conservation priorities. A taxonomic revision can reveal that what was previously considered a single widespread species is, in fact, a complex of evolutionary lineages with different geographic distributions, demographic histories, ecological characteristics, and conservation needs. Consequently, taxonomic changes may require conservation assessments, management plans, monitoring programs, and, where appropriate, legal protection measures to be revisited.

The implications extend beyond species names. Conservation planning increasingly requires the identification of evolutionarily significant diversity within and among species, including genetically differentiated populations and management units. Taxonomic knowledge can therefore provide an important foundation for determining which populations should be managed independently, which should remain connected, and where genetic diversity may warrant particular protection.

For Latin American deer, this is especially relevant because conservation policies have often been developed around species-level assessments that may not capture the full extent of evolutionary diversity. A widespread taxon may appear relatively secure when evaluated as a single entity, while geographically restricted lineages within that taxon may face substantially greater risks. Taxonomic revisions can, therefore, change not only scientific understanding but also the scale at which conservation priorities should be defined.

This issue is particularly important in a region where conservation resources are limited and management deci-

sions must be strategically prioritized. If taxonomic boundaries do not accurately reflect underlying evolutionary diversity, monitoring programs may combine distinct evolutionary entities, population trends may be obscured, and conservation investments may be directed toward units that do not adequately represent biological diversity. Conversely, recognizing distinct evolutionary lineages can allow conservation actions to be targeted more precisely and can help identify populations whose loss would represent a disproportionate erosion of evolutionary history.

The next generation of conservation strategies for Latin American deer should consequently move beyond simply counting species. We need to identify and preserve evolutionary diversity, maintain genetic connectivity where appropriate, protect unique populations where their differentiation warrants independent management, and ensure that conservation actions are based on robust evolutionary and ecological evidence. Where taxonomic changes reveal previously unrecognized lineages, conservation policies should be sufficiently flexible to incorporate new scientific evidence into species assessments, monitoring frameworks, management plans, and, where warranted, legal protection.

In this context, the resurrection of *Subulo* is more than a change in nomenclature. It is a reminder that **we cannot effectively conserve what we have not correctly recognized**.

Taxonomy matters for conservation because every species name carries an implicit hypothesis about evolutionary identity. As that hypothesis changes with new evidence, conservation policy must change with it. For Latin American deer, integrating taxonomy, genomics, ecology, and conservation planning is therefore not simply desirable—**it is essential to ensure that the evolutionary diversity of these remarkable mammals is recognized, evaluated, and effectively protected.**

Susana González[1]

[1]Departamento Biodiversidad y Genética, Instituto de Investigaciones Biológicas Clemente Estable, Uruguay Co-Chair Emérita DSG-SSC-IUCN. E-mail: iconservacionneotropical@gmail.com

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Mammals from Los Mármoles National Park, one of the first protected areas in Mexico

Melany Aguilar-López[1], Jazmín L. Monter-Vargas[2], Josefina Ramos-Frías[1], Jorge I. Ángeles Escudero[3], José Luis Aguilar-López[4], Lázaro Guevara[5], and Pedro Adrián Aguilar-Rodríguez[1*]

[1]Ecoydes, A. C. Avenida Del Bosque 40, 42182, Pachuca, Hidalgo, Mexico. E-mail: mel1983aguilar@gmail.com (MAL); tia_chepis@hotmail.com (JR-F)
[2]Área de Protección de Recursos Naturales Lago Tláhuac-Xico, Progreso Street 3, 04110, Mexico City, Mexico. E-mail: jazminmonter04@gmail.com (JLM-V)
[3]Parque Nacional La Montaña Malinche o Matlalcueyatl, Antiguo camino Real a Ixtulco s/n, Jardín Botánico Tizatlán, 90100, Tlaxcala, Tlaxcala, Mexico. E-mail: jiangeles@conanp.gob.mx (JIAE)
[4]Departamento de Conservación de la Biodiversidad. El Colegio de la Frontera Sur. Carretera Panamericana y Periférico Sur S/N, 29290, San Cristóbal de las Casas, Chiapas, Mexico. E-mail: jose.aguilarlopez@ecosur.mx (JLA-L)
[5]Instituto de Biología, Universidad Nacional Autónoma de México. Circuito exterior 70-153, 04510, Ciudad Universitaria, Mexico City, Mexico. Email: llg@ib.unam.mx (LG)
[*]Corresponding author: pedroaguilarr@gmail.com

Los Mármoles National Park (state of Hidalgo) is one of the oldest protected natural areas in Mexico. Due to its geographical location, it contains both Nearctic and Neotropical species, although the mammal species inhabiting the area have been poorly studied. This information is required to establish conservation actions in the area, which is heavily affected by mining and illegal logging. We sampled mammals across nine non-consecutive years (2013-2018, 2021-2022, and 2025) and searched records in literature to produce the first updated checklist for Los Mármoles. We conducted 62 field trips of varying lengths (1 to 12 days). We used pitfall and Sherman traps, mist nets, camera traps, and scent stations to trap mammals. In addition, we conducted interviews with local people and obtained incidental records (*e.g.*, observations, dead animals, tracks, excrement). We recorded 85 native mammal species, including 10 protected species and 15 endemic species to Mexico. Chiroptera, Carnivora, and Rodentia were the most well-represented groups with the highest number of species in this study, highlighting the presence of large carnivores, such as *Ursus americanus* and *Panthera onca*. We documented domestic and feral animals within the protected area. Although Los Mármoles is home to more than 50% of the state's mammal species, it faces serious threats, such as mining, feral dogs, and livestock.

Keywords. Carnivora, Chiroptera, feral animals, protected areas, Rodentia, temperate forest, trap-cameras.

El Parque Nacional Los Mármoles (estado de Hidalgo) es una de las áreas naturales protegidas más antiguas en México. Debido a su ubicación geográfica, contiene especies tanto Neárticas como Neotropicales, aunque las especies de mamíferos que habitan el área han sido poco estudiadas. Esta información es necesaria para establecer acciones de conservación en el área, la cual es fuertemente impactada por la minería y la tala ilegal. Se conjuntó la información del muestreo de mamíferos durante nueve años no consecutivos (2013-2018, 2021-2022 y 2025) y de la literatura para generar el primer listado actualizado para el parque. Realizamos 62 salidas de campo con duración variable (1 a 12 días). Los mamíferos se capturaron con trampas de caída y Sherman, redes de niebla, cámaras trampa y estaciones olfativas. Además, se realizaron entrevistas entre la gente local y se usaron registros incidentales (*p.ej.*, observaciones, animales muertos, huellas, excretas). Se registraron 85 especies de mamíferos nativos, incluyendo 10 especies protegidas y 15 especies endémicas de México. Chiroptera, Carnivora y Rodentia fueron los grupos con mayor número de especies en este estudio, donde destacan la presencia de grandes carnívoros, como *Ursus americanus* y *Panthera onca*, así como la presencia de mamíferos domésticos y ferales dentro del bosque del área protegida. A pesar de que Los Mármoles alberga más del 50% de las especies de mamíferos del estado, enfrentan graves amenazas como la minería, los perros ferales y el ganado.

Palabras clave: Animales ferales, áreas protegidas, bosque templado, cámaras trampa, Carnivora, Chiroptera, Rodentia.

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Protected Areas (PAs) are an "area-based conservation tool" implemented globally, to counteract the loss of biodiversity by various anthropogenic factors, such as overexploitation of natural resources, population growth, deforestation, and illegal traffic (Gurney *et al.* 2023), with protected areas covering about 15% of land surface and 7.4% of ocean surface (UNEP-WCMC and IUCN 2021). Mexico possesses 232 PAs, extending 98,000,719 ha (*ca.* 35.54% of the territory; CONANP 2025). Of them, 79 (22.12%) are National Parks (NPs; CONANP 2025), defined as "large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities" (*sensu* Dudley 2008, see also LGEEPA 2024), and are primarily characterized by the beauty of their

landscapes (Villalobos 2000). Many of these areas are insufficient to protect some highly diverse groups of flora and fauna (Falcón-Brindis *et al.* 2021; Chávez-Lugo *et al.* 2024), making the continuous actualization of species lists within protected areas fundamental for making appropriate management and conservation decisions.

Hidalgo is a state in central Mexico, known for its mountainous terrain, which lies in a transitional zone between Neartic and Neotropical biogeographic regions (Escalante *et al.* 2004), and located in the Sierra Madre Oriental and the Veracruzan biogeographic province (Morrone *et al.* 2017; Morrone 2019). In Hidalgo, five PAs are federally constituted, covering about 6% of the territory and 131,742 hectares (CONANP 2025). "Los Mármoles National Park" (hereafter, Los Mármoles) was decreed on September 8th, 1936, with a total area of 23,150 ha, being the second federally protected area in the state. Los Mármoles derives its name from the marble deposits found throughout the region (CONANP 2024). Despite being almost 90 years old, it was formally administered by the federal government just in 2010 (M. A. Soto-Martínez personal communication, former director of Los Mármoles), which led to different environmental and political problems, with mining (marble exploitation) and illegal logging being the human activities with the most significant impact (Arroyo-Ruiz and Cuevas-Cardona 2017), which contradicts the current legislations that states "Only activities related to the protection of natural resources, the enhancement of flora and fauna…the preservation of ecosystems and their elements, as well as ecological research, recreation, tourism, and education, may be permitted in national parks" (article 50°, LGEEPA 2024). However, due to its rugged topography, there are areas of difficult access that have allowed the maintenance of well-conserved areas and the conservation of part of its native biodiversity.

Over the last two decades, inventories and systematic revisions have been carried out to finally have a baseline on the biodiversity that Los Mármoles harbors, covering various groups of flora (Ramírez-Cruz *et al.* 2009; Álvarez-Zúñiga *et al.* 2010; Sánchez-González *et al.* 2010; Delgadillo-Moya *et al.* 2011; García-Sánchez *et al.* 2014), invertebrates (Asiain *et al.* 2011), and vertebrates (Aguilar-López *et al.* 2015a, 2015b; Larios-Lozano *et al.* 2017; Aguilar-López *et al.* 2019; Flores-Hernández 2019; CONANP 2020). Mammals play several ecosystem roles, such as pollinators and seed dispersers, predators of various arthropods, and prey of other animals, including humans (Zalapa *et al.* 2005; Bagchi *et al.* 2006; Kunz *et al.* 2011), thus directly influencing human well-being. Despite their ecological importance, mammalian biodiversity in Los Mármoles is poorly known (Mendoza-Vega 2012; CONANP 2024). This information gap influences the proposal and implementation of conservation strategies at the park, in addition to the fact that, in recent years, there has been an insistence on the re-categorization of the area to allow extractive activities (Arroyo-Ruiz and Cuevas-Cardona 2017), which makes it essential to have all the information on the biological diversity of the area for decision-making and appropriate management.

Therefore, our objective was to compile the information generated over nine years of research on mammals conducted with the participation of community brigades in the park, complemented it with data from scientific literature and interviews with local community members, to provide an updated list of the resident mammal species of Los Mármoles, as a basis for revising the management plan.

Materials and methods

Los Mármoles covers an area of 23,150 ha (1.1% of the state area), located northeast of the state of Hidalgo, Mexico (20º45′33″ and 20º58′47″ N; 99º08′55″ and 99º18′37″ W), covering the municipalities of Zimapán, Nicolás Flores, Jacala de Ledezma, and Pacula (CONANP 2024). Los Mármoles is part of the Sierra Gorda (located mainly in Guanajuato, but some parts are included in the states of San Luis Potosí, Guanajuato, and Hidalgo), within the Sierra Madre Oriental (Randell-Badillo 2008). Elevation ranges from 1,000 m to 3,000 m, and the vegetation is predominantly temperate affinity composed mainly of *Quercus*, *Pinus*, *Juniperus,* and *Cupressus* forests, covering most of the area in Los Mármoles, while other vegetation types are less dominant, such as spiny shrubland and deciduous lowland forest (CONANP 2007; Ramírez-Cruz *et al.* 2009). The climate is temperate sub-humid with summer rains (covering 20,008 ha) and semi-warm sub-humid with summer rains (3,142 ha; 450 to 1,500 mm; SARH 1994; CONANP 2007).

For the recording of mammals, we conducted 62 field trips (22 for bat sampling exclusively and two trips for other small mammals), ranging from one to 12 days. We visited 48 localities in four municipalities within and adjacent to Los Mármoles from 2013-2018, 2021-2022, and 2025 (carried out by the community brigade "El Cobre"), covering most of the area and all the vegetation types and heights in the park (Figure 1). Accordingly, field trips were conducted by different people over the years and framed in independent projects with various objectives, therefore, sampling varied among years.

Small mammals (bats, shrews, and mice). For recording bats, we conducted interviews to locate potential roosting sites in 43 localities, within and outside the area of Los Mármoles. These interviews were conducted in 2015 and 2017. At each site, we first contacted a representative from a given community and local officials to reach people who, due to their work, knew the area and may recognize local fauna, such as livestock farmers, agricultural workers, and community brigade members (enrolled in firefighting activities or those responsible for communal lands or resources). Subsequently, we employed the "snowball" sampling technique, in which each interviewee provides contact information about other people who could

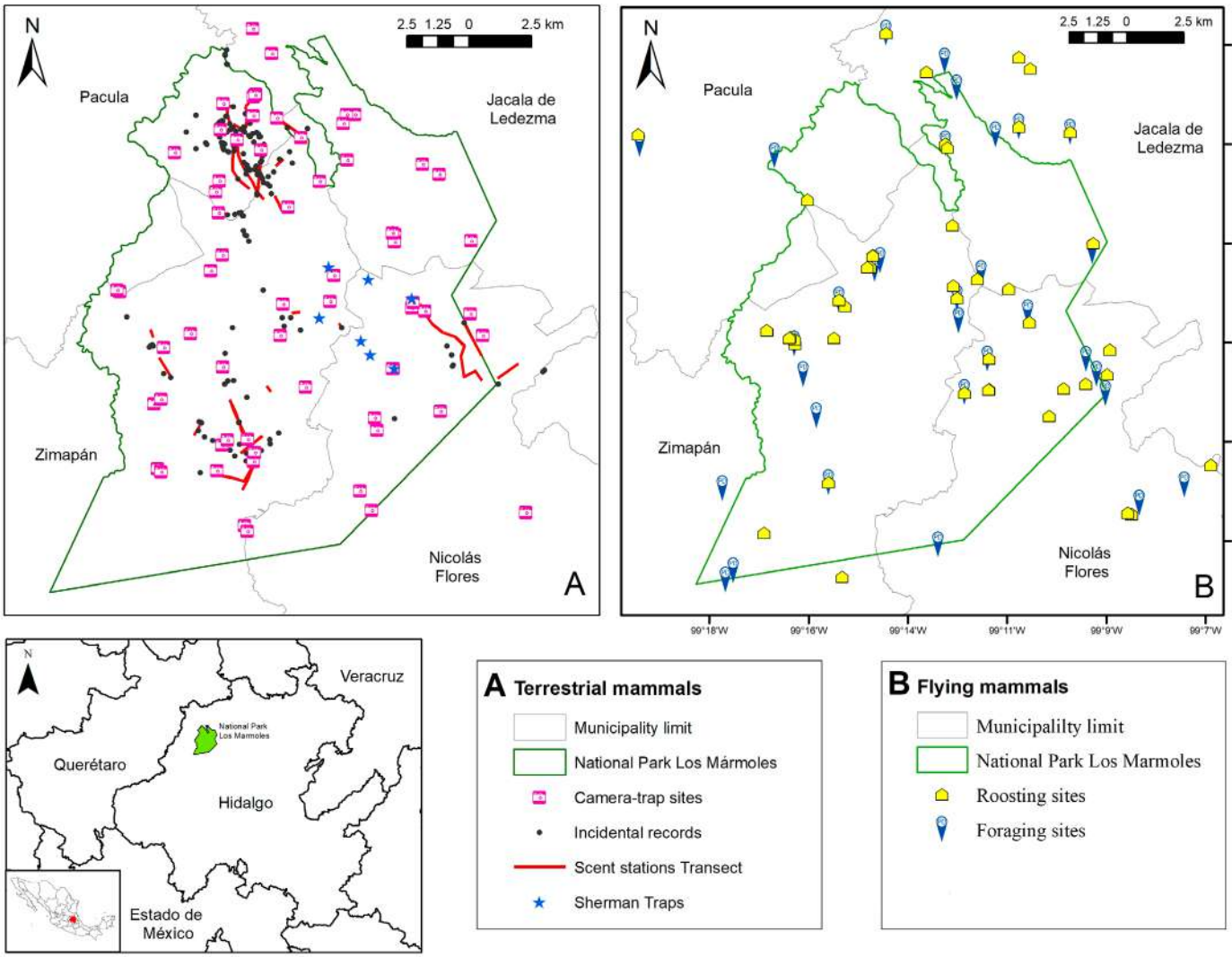

Figure 1. Location of Los Mármoles National Park and sampling sites for this study. A. Location of camera traps and scent stations, and incidental records of terrestrial mammals. B. Mist-netting sites at roosts and in fly corridors in probable roosting foraging areas of bats.

be interviewed (Castillo-Álvarez and Peña-Mondragón 2015). Specifically for bats, we applied semi-structured interviews, each consisting of a total of 14 questions (Supplementary Data 1).

We sampled bats using up to six (minimum of one) mist-nets per night (3, 6, 10, and 12 m long) per site/night (one to three nights per site) in potential flight paths for bats (vegetation boundaries, rural paths, natural ponds, ravines, and similar locations; (Kunz *et al.* 2009; Bracamonte 2018), as well as at the entrance of roosting sites (caves, mines, hollow trees, rooftops). Nets were functional from before astronomical twilight (around 17:00-18:00 hrs. depending on the season) until midnight (seven hours per night). Potential roosting sites were visited during the day to determine if it was a diurnal or a nocturnal (*i.e.*, only used during the night) roost. For species identification, we used morphological criteria (*i.e.,* relative size, forearm, foot, and ear lengths, fur and coloration patterns) and field guides (Hall 1981; Aranda 2000, 2012; Medellín *et al.* 2008; Álvarez-Castañeda *et al.* 2015). For each captured individual, we recorded the following data: date of record, locality, type of vegetation, sex (male or female), age category (juvenile, subadult, adult by the ossification of finer epiphyseal joints, tooth wear, fur coloration), weight (g), reproductive condition (through the visual inspection of the testes and epidydimal position in males, and the distension of lower abdomen, palpation of the abdomen and inspection of the nipples in females), and other somatic measurements (Hall 1981; Brunet-Rossinni and Wilkinson 2009). Captured individuals were handled and released following the suggestions of Kunz *et al.* (2009). Most of the individuals were released at the capture site, with one voucher specimen per species (except species protected by law).

For rodents and shrews, we used 50 pitfall and 160 Sherman traps, which were placed around the bases of trees and along fallen trunks (Lorenzo *et al.* 2019). Sherman traps were baited with a mixture of oatmeal, peanut butter, and vanilla. No bait was used for pitfall traps. We conducted trapping at two locations in the spring of 2019 and the summer of 2022. Due to the region's limited knowledge of small mammals and difficulty identifying some taxa, we

Table 1. Mammalian species registered in this study (by method) and reported in databases/grey literature for the National Park Los Mármoles. The black point (•) indicates species of which a voucher specimen was collected, and the asterisk (*) indicates protected species. Biogeographic realm and endemicity follow the Mammal Diversity Database (2026) (NA= Neartic, NT= Neotropic).

	Order	Family	Species	Biogeographic realm/Endemism	Registered in this study[a]	Databases/ Literature[b]
1	Artiodactyla	Cervidae	*Odocoileus virginianus* (E. A. W. von Zimmermann, 1780)	NA/NT	IR, SS, CT	TH, CTCB[e]
2	Artiodactyla	Cervidae	*Mazama temama* (Kerr 1792)	NA/NT	CTCB	
3	Artiodactyla	Tayassuidae	*Dicotyles tajacu* (Linnaeus, 1758)	NT	IR, SS, CT	TH, CTCB[e]
4	Carnivora	Ursidae	*Ursus americanus** Pallas, 1780	NA	IN, CT	PA[d]
5	Carnivora	Felidae	*Herpailurus yagouaroundi** (É. Geoffroy Saint-Hilaire, 1803)	NA/NT	IN	CTCB[e]
6	Carnivora	Felidae	*Leopardus pardalis** (Linnaeus, 1758)	NT	IN, CT	DB, TH
7	Carnivora	Felidae	*Leopardus wiedii** (H. R. Schinz, 1821)	NT	IR, SS, IN, CT	DB, TH
8	Carnivora	Felidae	*Lynx rufus* (von Schreber, 1777)	NA	IR, SS, IN, CT	TH
9	Carnivora	Felidae	*Panthera onca** (Linnaeus, 1758)	NA/NT	IR, IN, CT	CTCB[e]
10	Carnivora	Felidae	*Puma concolor* (Linnaeus, 1771)	NA/NT	IR, SS, IN, CT	DB, TH
11	Carnivora	Canidae	*Canis latrans* Say in James, 1823	NA/NT	IR, SS, IN, CT	TH, CTCB[e]
12	Carnivora	Canidae	*Urocyon cinereoargenteus* (von Schreber, 1775)	NA/NT	IR, SS, IN, CT	TH, CTCB[e]
13	Carnivora	Mephitidae	*Conepatus leuconotus* (H. Lichtenstein, 1832)	NA/NT	IR, IN, CT	TH, CTCB[e]
14	Carnivora	Mephitidae	*Mephitis macroura* H. Lichtenstein, 1832	NA/NT	IR, IN, CT	DB, TH
15	Carnivora	Mephitidae	*Spilogale angustifrons* A. H. Howell, 1902	NA/NT	IN, CT	
16	Carnivora	Mustelidae	*Eira barbara** (Linnaeus, 1758)	NA/NT	IN, CT	
17	Carnivora	Mustelidae	*Neogale frenata* (H. Lichtenstein, 1831)	NA/NT	IR, IN, TC	TH
18	Carnivora	Procyonidae	*Bassariscus astutus* (H. Lichtenstein, 1830)	NA	IR, SS, IN, CT	DB, TH
19	Carnivora	Procyonidae	*Nasua narica* (Linnaeus, 1766)	NA/NT	SS, IN, CT	TH
20	Carnivora	Procyonidae	*Procyon lotor* (Linnaeus, 1758)	NA/NT	IR, SS, IN, CT	TH
21	Chiroptera	Mormoopidae	*Pteronotus mesoamericanus* J. D. Smith, 1972	NA/NT	MN	TH
22	Chiroptera	Mormoopidae	*Mormoops megalophylla*• W. C. H. Peters, 1865	NA/NT	MN	
23	Chiroptera	Molossidae	*Tadarida brasiliensis* (I. Geoffroy Saint-Hilaire, 1824)	NA/NT	MN	
24	Chiroptera	Natalidae	*Natalus mexicanus*• G. S. Miller, 1902	NA/NT	IR	
25	Chiroptera	Phyllostomidae	*Desmodus rotundus*• (É. Geoffroy Saint-Hilaire, 1810)	NA/NT	MN	TH
26	Chiroptera	Phyllostomidae	*Diphylla ecaudata*• von Spix, 1823	NA/NT	MN	
27	Chiroptera	Phyllostomidae	*Choeronycteris mexicana** von Tschudi, 1844	NA/NT	MN	TH
28	Chiroptera	Phyllostomidae	*Glossophaga mutica*• A. H. Merriam, 1898	NA/NT	MN	TH
29	Chiroptera	Phyllostomidae	*Micronycteris microtis*• G. S. Miller, 1898	NA/NT	MN	DB, TH
30	Chiroptera	Phyllostomidae	*Leptonycteris nivalis** (de Saussure, 1860)	NA	MN	TH
31	Chiroptera	Phyllostomidae	*Leptonycteris yerbabuenae* L. Martínez & Villa-Ramírez, 1940	NA/NT	MN	TH
32	Chiroptera	Phyllostomidae	*Anoura peruana* (von Tschudi, 1844)	NA/NT	MN	
33	Chiroptera	Phyllostomidae	*Artibeus intermedius* J. A. Allen, 1897	NA/NT	MN	
34	Chiroptera	Phyllostomidae	*Artibeus jamaicensis* Leach, 1821	NA/NT	MN	DB, TH
35	Chiroptera	Phyllostomidae	*Artibeus lituratus* (I. von Olfers, 1818)	NA/NT	MN	TH
36	Chiroptera	Phyllostomidae	*Dermanura azteca*• (Andersen, 1906)	NA/NT	MN	DB, TH
37	Chiroptera	Phyllostomidae	*Dermanura tolteca*• (de Saussure, 1860)	NA/NT	MN	TH
38	Chiroptera	Phyllostomidae	*Sturnira hondurensis*• G. G. Goodwin, 1940	NA/NT	MN	TH
39	Chiroptera	Phyllostomidae	*Sturnira parvidens*• E. A. Goldman, 1917	NA/NT	MN	TH
40	Chiroptera	Vespertilionidae	*Antrozous pallidus* (Le Conte, 1856)	NA/NT	MN	
41	Chiroptera	Vespertilionidae	*Corynorhinus mexicanus*• G. M. Allen, 1916	NA/Endemic	MN	DB, TH
42	Chiroptera	Vespertilionidae	*Corynorhinus townsendii*• (G. M. Allen, 1916)	NA	MN	
43	Chiroptera	Vespertilionidae	*Idionycteris phyllotis*• (G. M. Allen, 1916)	NA	MN	
44	Chiroptera	Vespertilionidae	*Eptesicus fuscus*• (Palisot de Beauvois, 1796)	NA/NT	MN	DB, TH
45	Chiroptera	Vespertilionidae	*Lasiurus frantzii*• (W. C. H. Peters, 1871)	NA/NT	MN	DB, TH
46	Chiroptera	Vespertilionidae	*Lasiurus cinereus* (Palisot de Beauvois, 1796)	NA/NT	MN	DB, TH

47	Chiroptera	Vespertilionidae	*Lasiurus intermedius*• H. Allen, 1862	NA/NT	MN	
48	Chiroptera	Vespertilionidae	*Myotis thysanodes* G. S. Miller, 1897	NA	MN	
49	Chiroptera	Vespertilionidae	*Myotis auriculus*• R. H. Baker & Stains, 1955	NA	MN	TH
50	Chiroptera	Vespertilionidae	*Myotis californicus*• (Audubon & Bachman, 1842)	NA	MN	TH
51	Chiroptera	Vespertilionidae	*Myotis ciliolabrum*• H. Merriam, 1886)	NA	MN	
52	Chiroptera	Vespertilionidae	*Myotis volans*• (H. Allen, 1866)	NA	MN	
53	Chiroptera	Vespertilionidae	*Myotis velifer*• (J. A. Allen, 1890)	NA/NT	MN	
54	Chiroptera	Vespertilionidae	*Myotis yumanensis*• (H. Allen, 1864)	NA	MN	
55	Chiroptera	Vespertilionidae	*Parastrellus hesperus*• (H. Allen, 1864)	NA	MN	TH
56	Chiroptera	Vespertilionidae	*Perimyotis subflavus*• (F. Cuvier, 1832)	NA/NT	MN	
57	Chiroptera	Vespertilionidae	*Rhogeessa tumida*• H. Allen, 1866	NA/NT	MN	
58	Cingulata	Dasypodidae	*Dasypus mexicanus* W. C. H. Peters, 1865	NA/NT	IR, SS, IN, CT	TH
59	Didelphimorphia	Didelphidae	*Didelphis virginiana* Kerr, 1792	NA/NT	IR, SS, IN, CT	DB, TH, CTCB[e]
60	Eulipotyphla	Soricidae	*Cryptotis mexicanus*• (Coues, 1877)	NA/Endemic	PF	DB, TH
61	Eulipotyphla	Soricidae	*Sorex altoensis*• Carraway, 2007	NT/Endemic	PF	DB
62	Lagomorpha	Leporidae	*Sylvilagus cunicularius* (G. R. Waterhouse, 1848)	NA/Endemic	CTCB	
63	Lagomorpha	Leporidae	*Sylvilagus floridanus* (J. A. Allen, 1890)	NA/NT	IR, SS, IN, CT	DB, TH
64	Rodentia	Sciuridae	*Glaucomys volans** (Linnaeus, 1758)	NA/NT	IN	
65	Rodentia	Sciuridae	*Otospermophilus variegatus* (Erxleben, 1777)	NA	IR, SS, IN, CT	DB, TH
66	Rodentia	Sciuridae	*Sciurus aureogaster* F. Cuvier in É Geoffroy Saint-Hilaire & F. Cuvier, 1829	NA/NT	IR, SS, IN, CT	DB, TH, CTCB[e]
67	Rodentia	Sciuridae	*Sciurus deppei* W. C. H. Peters, 1864	NA/NT	IR, IN, CT	DB
68	Rodentia	Sciuridae	*Sciurus oculatus** W. C. H. Peters, 1864	NA/Endemic	IR, IN, CT	DB, TH
69	Rodentia	Heteromyidae	*Heteromys irroratus* J. E. Gray, 1868	NA		DB, TH
70	Rodentia	Cricetidae	*Casiomys chapmani*• (O. Thomas, 1898)	NT/Endemic	ST	
71	Rodentia	Cricetidae	*Casiomys alfaroi* (J. A. Allen, 1891)	NT		TH
72	Rodentia	Cricetidae	*Neotoma mexicana* S. F. Baird, 1855	NA/NT		DB, TH
73	Rodentia	Cricetidae	*Peromyscus amplus*• Osgood 1904	NA/Endemic	ST	DB, TH
74	Rodentia	Cricetidae	*Peromyscus aztecus* (de Saussure, 1860)	NA/NT/Endemic		TH
75	Rodentia	Cricetidae	*Peromyscus boylii* (S. F. Baird, 1855)	NA		DB, TH
76	Rodentia	Cricetidae	*Peromyscus collinus*• Hooper, 1952	NA/Endemic	ST	
77	Rodentia	Cricetidae	*Peromyscus gratus*• C. H. Merriam, 1898	NA	ST	DB, TH
78	Rodentia	Cricetidae	*Peromyscus hylocetes* C. H. Merriam, 1898	NA/Endemic		PA[c]
79	Rodentia	Cricetidae	*Peromyscus leucopus* (Rafinesque, 1818)	NA		DB, TH
80	Rodentia	Cricetidae	*Peromyscus levipes*• C. H. Marriam, 1898	NA/Endemic	ST	DB, TH
81	Rodentia	Cricetidae	*Peromyscus zamorae*• Osgood, 1904	NA/Endemic	ST	DB
82	Rodentia	Cricetidae	*Peromyscus mexicanus* (de Saussure, 1860)	NA/NT/Endemic		TH
83	Rodentia	Cricetidae	*Reithrodontomys sumichrasti*• (de Saussure, 1861)	NA/NT/Endemic	ST	
84	Rodentia	Cricetidae	*Reithrodontomys fulvescens* J. A. Allen, 1894	NA/NT		TH
85	Rodentia	Cricetidae	*Sigmodon leucotis*• V. O. Bailey, 1902	NA	ST	DB, TH

a Methods: CT: Camera traps; IN: Interviews; IR: Indirect record; MN: Mist netting; SS: Scent-Station; PF: Pitfall trap; ST: Sherman trap.
b CTCB: Camera Trap and photos from Brigada de vigilancia y monitoreo comunitario del Parque Nacional Los Mármoles; DB; Database; PA: Published article; TH: Thesis.
c Aguilar-López *et al.* 2015a.
d Aguilar-López *et al.* 2019.
e Available at: https://visor.conanp.gob.mx/visor_anp.php.

secured voucher specimens. For scientific collecting, we followed standard recommendations on specimen capture, sacrifice, and preparation (Sikes *et al.* 2016).

Collected small mammals were deposited in the Mammal Collection at the Universidad Autónoma del Estado de Hidalgo (UAEH) and the National Mammal Collection, Universidad Nacional Autónoma de México UNAM (Collection permits SGPA/DGVS/10391, 008327, and 05505/19, granted by the Secretaría de Medio Ambiente y Recursos Naturales).

Medium and large terrestrial mammals. We set up one to 32 camera trap stations per night (Wilview, Stealth Cam, Primos, Reconyx, Cuddeback Attack, Cuddeback LR) with perfume as an attractant, for a total effort of 10,100 tramp/night. Complementary, we set up 486 scent stations, 399 of which were operative during the study, distributed along 28 km of transects. We used fresh fruit, egg, and perfume (unbranded European perfume) as bait to lure

the animals to the stations. We included observations of mammals, dead run-over specimens, carcasses, furs, tracks and feces as indirect records. In addition, we conducted open interviews (Supplementary Data 2) in 2014 and 2015 with local people at 44 localities within Los Mármoles, by selecting the interviewees in the same way as used in the interviews about bats (see above). These interviews aimed to identify which mammal species were known to community members, as well as potential sites to deploy the camera traps, following the observations sites suggested by the interviewees. We used illustrations as a reference for the interviewee (Supplementary Data 2); these were shown at the end of the interview to avoid influencing the participants (García-Alaniz *et al.* 2010).

Literature and databases revision. We checked published literature, gray literature (undergraduate and graduate thesis), and online databases about mammals (using the terms "Parque Nacional Los Mármoles", "mammals", "Hidalgo", and the names of four municipalities where the park is located: "Zimapán" "Jacala" "Pacula" and "Nicolás Flores" and the names of the different mammalian families known to occur in the state): Sistema Nacional de Información sobre Biodiversidad de México (SNIB), iNaturalistMX, and Global Biodiversity Information Facility (GBIF). Searches were performed between July 4–11 2024. Raw data were cleaned by removing duplicate, incomplete, or suspicious records (with missing or dubious information: dates, invalid or missing coordinates), from unsuitable sources or without updated taxonomical information. Specifically, in case of iNaturalistMX dataset, only information tagged as "Research grade" was taken into account. We considered reports found in at least two databases, including any mammal collection, national or international.

Taxonomical list and conservation status. We follow the accepted nomenclature of the American Society of Mammalogists (Burgin *et al.* 2025; MDD 2026), which includes recent taxonomic updates (Calahorra-Oliart *et al.* 2021; Molinari *et al.* 2023; Pérez-Montes *et al.* 2023; Barthe *et al.* 2024; Voss 2024). For their conservation status, we follow national (SEMARNAT 2019) and international norms (IUCN 2025).

Data analysis. We performed rarefaction and extrapolation sampling curves based on Hill numbers to estimate the sample coverage value, and the species richness estimated by extrapolation to twice the sampling effort (Chao *et al.* 2014), for each sampling method. The calculation was performed using species presence-absence data per year in the online version of iNEXT (Chao *et al.* 2016). The curves were generated based on sampling units in order to present the results for all sampling methods in a consistent manner. Accumulation curves based on individuals are recommended for standardized surveys (Gotelli and Colwell 2001), but our results come from different projects with varying sampling efforts across years; therefore, we used the years as the sampling unit (Jiménez-Valverde and Hortal 2003).

Results

We registered 85 mammal species, 76 during fieldwork conducted in collaboration of community brigades, 50 species are corroborated by this study, with only nine species from literature references (eight orders, 20 families, and 56 genera; Table 1) reported for the park. Fifteen species are endemic to Mexico. Species accumulation curves estimated sample coverage values of 0.89 (89%) for the mist nets sampling method, 0.581 (58%) for Sherman traps, and 0.968 (96%) for camera traps. The estimated total species richness, extrapolated to double the sampling effort, was 40, 14, and 28 species, respectively (Figure 2).

Small mammals (bats, shrews, and mice). We captured 1,222 individuals from 37 bat species (Table 1), of which 73 were collected as museum specimens, and the rest were released. Total sampling effort was 389,350 m/net/night (1198 m/net multiplied by 325 hours of netting). We interviewed 148 people, which allowed us to visit 27 diurnal roosts, identified by local people. The most abundant family was Phyllostomidae (n = 983 individuals, 15 species), whereas Vespertilionidae was the most species-rich (n = 18, Table 1 and Figure 3). Most individuals were captured at roosting sites, mainly caves and tunnels. We collected 99 non-volant small mammals belonging to eight species of rodents and two shrews. Sampling effort for small non-volant mammals was 3,200 trap-nights. The most abundant species were the Saxicoline Deermouse, *Peromyscus gratus* C. H. Merriam, 1898 (family Cricetidae), and the Mexican small-eared shrew, *Cryptotis mexicanus* (Coues, 1877) (family Soricidae), respectively (Table 1; Figure 4).

Medium and large mammals. We registered 13 species at scent stations, and we obtained 9,919 pictures and 1,385 videos of 31 species of wild mammals using camera traps (Figure 2), 21,284 pictures, and 3,663 videos of domesticated mammals (*i.e.*, cows: 23,181 photos and videos, dogs: 582, and pigs: 510; Table 2 and Figure 5). Based on the interviews (n = 333), we recorded 25 terrestrial mammal species, including 21 species recorded from 212 incidental records of dead animals, observations, and photographs (Table 1; Figures 3 and 4). Almost all the mammal species suggested by the interviewees were validated using another method (Table 1), except for *Glaucomys volans* (Linnaeus, 1758), which was observed by several members of the community brigade during tree-pruning activities in the forest.

Chiroptera was the best-represented order in the number of species (n = 37; Figure 3), followed by Rodentia (n = 23) and Carnivora (n = 17; Figs. 3 and 4). Ten species are protected by Mexican laws, including *Sciurus oculatus* W. C. H. Peters, 1864 (Subject to Special Protection, Pr), *Glaucomys volans* (Threatened, A), *Herpailurus yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803) (Threatened, A), *Choeronycteris mexicana* von Tschudi, 1844 (Threatened, A), *Leptonycteris nivalis* (de Saussure, 1860) (Threatened, A), *Ursus americanus* Pallas, 1780 (Endangered, P), *Leopardus pardalis* (Linnaeus, 1758) (Endangered, P),

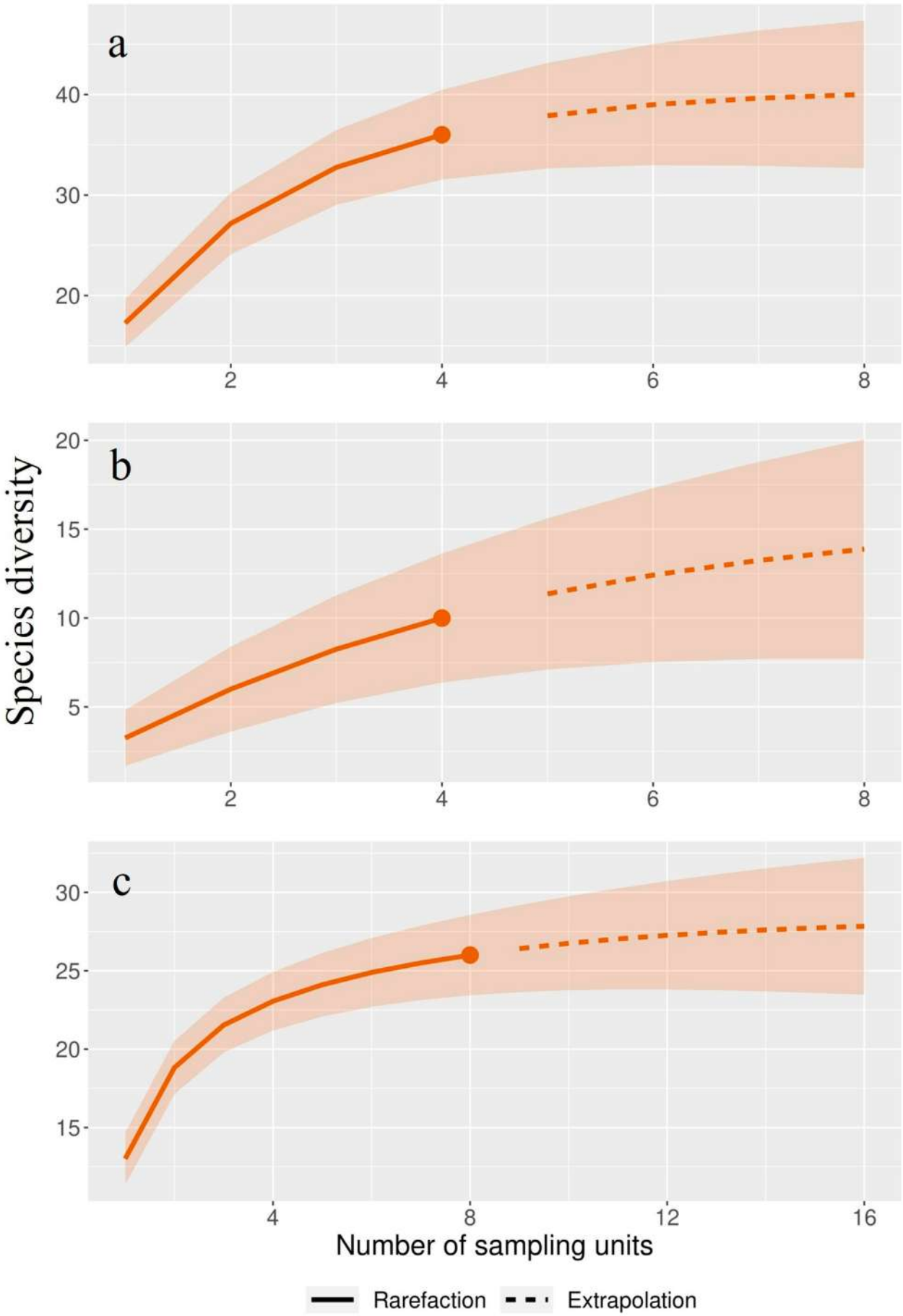

Figure 2. Species accumulation curves of mammals recorded by the sampling methods of a) mist nets, b) Sherman traps, and c) camera traps, for the Los Mármoles National Park.

Figure 3. Some mammals registered within the Los Mármoles National Park. Camera traps: A. *Panthera onca* Linnaeus; B. *Ursus americanus*; C. *Leopardus pardalis*; D. *Eira barbara*. Bats captured by mist-netting: E. *Myotis auriculus*; F. *Myotis yumanensis*; G. *Perimyotis subflavus*; H. *Parastrellus hesperus*. Photos by: M. Aguilar-López and J. Trejo Franco (A, B, D); J. I. Ángeles-Escudero and M. Ramírez (C); M. Aguilar-López (E, F, G, H).

Leopardus wiedii (H. R. Schinz, 1821) (Endangered, P), *Panthera onca* (Linnaeus, 1758) (Endangered, P) and *Eira barbara* (Linnaeus, 1758) (Endangered, P). According to the IUCN Red List, *L. nivalis* is considered endangered (EN), while *L. wiedii, P. onca, C. mexicana, L. yerbabuenae*, and *C. mexicanus* are near threatened (NT). Most species were recorded in areas with dense vegetation cover, including pine-oak forests, oak-pine forests, mixed forests, as well as steep ravines, mainly in the norther portion of Los Mármoles (Figure 1).

Discussion

We presented the first formal mammalian checklist for this protected area that incorporates active sampling, grey

Figure 4. Additional mammals that were reported in this study. A. *Neogale frenata* H. Lichtenstein; B. *Bassariscus astutus*; C. *Mephitis macroura*; D. *Sylvilagus floridanus*; E. *Dicotyles tajacu*; F. *Conepatus leuconotus;* G. *Mazama temama*; H. *Sigmodon leucotis*; I. *Peromyscus amplus*. Photos by: F. Castañón (A); J. Monter-Vargas (B); I. Elizalde Serrano (C); M. Aguilar-López (D, E, F, H, I); Brigada de vigilancia y monitoreo comunitario del Parque Nacional Los Mármoles (G).

literature, databases, and the collaboration of members of the local communities, 90 years after its declaration. Our results show that Los Mármoles harbors >50% of the mammalian fauna reported for the state of Hidalgo (147 spp., Rojas-Martínez *et al.* 2017), which accounts for the importance of this protected area for mammal conservation. The mammal diversity recorded in the park is higher than that reported for other natural protected areas in the central region of Mexico with similar vegetation but a larger surface. For example, the Sierra Gorda Biosphere Reserve (Querétaro, San Luis Potosí, and Guanajuato states), with an area of over 383.5 ha, has 120 reported mammal species (CONANP 1999). Although Los Mármoles represents approximately 6% of it, it harbors almost 67% of

Table 2. Domestic mammal species registered by year in camera traps during this study, in descending order by number of independent records (*i.e.,* pictures and videos), and number of independent records (in parentheses).

	Number of pictures per year						
Species (Family) Common name (in Spanish)	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**Total**
Bos taurus Linnaeus, 1758 (Bovidae) Vaca, toro	2512 (226)	3124 (580)	4736 (926)	1679 (196)	6646 (590)	4484 (972)	**23181**
Canis familiaris Linnaeus, 1758 (Canidae) Perro	142 (8)	85 (59)	99 (61)	18 (94)	158 (94)	80 (29)	**582**
Sus domesticus Erxleben, 1777 (Suidae) Cerdo, cochino, puerco	31 (6)	82 (31)	0	0	147 (12)	250 (22)	**510**
Equus asinus Linnaeus, 1758 (Equidae) Burro, asno	0	200 (50)	88 (19)	0	116 (33)	8 (3)	**327**
Equus caballus (Equidae) Caballo	6 (4)	38 (22)	11 (8)	0	8 (4)	128 (12)	**191**
Capra hircus Linnaeus, 1758 (Bovidae) Cabra, chivo	0	5 (11)	0	0	16 (11)	8 (5)	**29**
Ovis aries Linnaeus, 1758 (Bovidae) Oveja	0	0	3 (3)	0	25 (31)	2 (2)	**27**
Felis catus Linnaeus, 1758 (Felidae) Gato	6 (1)	0	0	0	3 (1)	0	**9**

its mammalian diversity. Other examples are the protected area Desierto de Los Leones (Mexico City; about 1,500 ha and with 14 mammal species; CONANP 2006), and the Zona Protectora Forestal Vedada Cuenca Hidrográfica del Río Necaxa (Puebla and Hidalgo states; 42,100 ha in extension and with 54 mammal species; CONANP 2013; Atonal-Sandoval 2015). Another important and geographically nearby protected area in the state of Hidalgo, El Chico National Park (hereafter El Chico), has 30 reported mammal species within only 2,734 ha (Hernández-Flores and Rojas-Martínez 2010).

Bats were the most species-rich group registered in this study, including arthropodivorous (23 spp.), nectar-feeding (5), fruit-eating (7), and hematophagous (2) species. The Yuma Myotis [*Myotis yumanensis* (H. Allen, 1864)] specimens captured in Los Mármoles, represent the first record of the species in the state in more than 40 years, since Hall (1981) reported the species in the Tasquillo River, a locality about 30 km from Los Mármoles. We also recorded migratory species, such as *C. mexicana*, *Lasiurus cinereus* (Palisot de Beauvois, 1796)*; Lasiurus frantzii* (1871)*; L. yerbabuenae; L. nivalis;* and *Tadarida brasiliensis* (I. Geoffroy Saint-Hilaire, 1824) (Shump Jr and Shump 1982; Arroyo-Cabrales *et al.* 1987; Pfrimmer-Hensley and Wilkins 1988; Wilkins 1989; Cryan 2003; Cole and Wilson 2006). This indicates that Los Mármoles harbors a rich bat-fauna that varies seasonally, including both migratory and endangered species. Based on our estimates, at least four additional species could be recorded (Figure 2). The use of complementary methods, such as active and passive acoustic monitoring of bat-echolocation calls (MacSwiney *et al.* 2008; 2020), we suggest that the bat-fauna inventory for Los Mármoles might increase rapidly, since such methods improve species records, especially among species that fly higher above ground or in open areas, such as members of the Molossidae or Emballonuridae families (Vaughan 1966; Fenton and Griffin 1997; McCracken *et al.* 2021).

Most of the bats reported here came from individuals captured in caves, which almost half of the Mexican bat species use as refugees (Arita 1993). In addition, species such as *Corynorhinus mexicanus* G. M. Allen, 1916; *Corynorhinus townsendii* (W. Cooper, 1837)*; Eptesicus fuscus* (Palisot de Beauvois, 1796)*; Myotis thysanodes* 1897; *Myotis ciliolabrum* (1886)*; Myotis velifer* (1890); *Myotis volans* (H. Allen, 1866); and *Perimyotis subflavus* (F. Cuvier, 1832) are known to use caves in Mexico for hibernation (Ramos-H. *et al.* 2024). Although no hibernation sites have been identified in Los Mármoles, we cannot rule out that some caves or tunnels might be used as hibernacula for some species since cold caves are abundant and within the elevation range of hibernating bat species in Mexico (Ramos-H. *et al.* 2024).

Small non-flying mammals are likely underrepresented in this study primarily due to the limited duration of the sampling effort, which was solely concentrated in Spring and Summer across different years. Rodents (order Rodentia) were mainly represented by the common and widely distributed genus *Peromyscus* (n = 10 spp.), with *P. gratus*, 1898 as the species with the most captures, unlike what was reported by Hernández-Flores and Rojas-Martínez (2010) in other areas in Hidalgo, where *Peromyscus levipes* 1898 and *Peromyscus amplus* Osgood, 1904 were the most common mice. Rodents are highly abundant and play key ecological roles as seed dispersers/predators and prey for many other mammals (Andersson and Erlinge 1977; Fedriani and Manzaneda 2005; Loayza *et al.* 2014; Godó *et al.* 2022), so their presence may indicate the good condition of the forest in the Los Mármoles. The southern flying squirrel, *G. volans*, is a threatened species only reported by the sighting of local people members of the community brigades that regularly patrol the national park, an example of how important it is to capacitate local people to recognize rare species through environmental and scientific communication programs, such as the ones established in the national park for several years (M. Aguilar-López unpublished data). Until now, no camera traps have been deployed in the canopy, and most of the sampling is focused on medium and large land mammals, underrepresenting arboreal species such as *G. volans*.

Figure 5. Domestic and feral animals registered in this study. A. A cow (*Bos taurus*) and a Coyote (*Canis latrans*); B. A herd of cattle grazing in Los Mármoles, far from human settlements; C. Pig (*Sus domesticus*); D. A pair of Donkeys (*Eqqus asinus*) E. Cow´s leg with bite marks, putatively made by feral dogs (arrows); F. A feral dog (*Canis familiaris*) carrying an armadillo (*Dasypus mexicanus*). Photos by: M. Aguilar-López, G. Flores-Sierra and J. Monter-Vargas.

The number of Soricidae species reported here (*n* = 2) is probably an underestimation of the actual number, primarily due to the difficulty of sampling this taxon and its low capture ratio (Carraway 2007), but the environmental conditions in the pine-oak forests, especially in sites far from cultivated areas or sites of disturbance, can benefit the presence of this group (*i.e.*, Flores-Martínez *et al.* 2024). Considering its geographic location and ecosystems, other shrews that could be in the Los Mármoles include *Notiosorex crawfordi* (Coues, 1877) and *Cryptotis pueblensis* H. H. T. Jackson, 1933 (Guevara *et al.* 2015). It is worth noting that, according to our understanding, these shrew specimens are the first to be collected since their first records in Los Mármoles, almost 130 years ago (Guevara 2021). In addition,

they represent the first specimens deposited in Mexican scientific collections.

We highlight records of jaguar (*Panthera onca*), cougar (*Puma concolor* [Linnaeus, 1771]), black bear (*Ursus americanus*), and other carnivores at the park. Their presence is likely associated with the availability of large prey, such as the collared peccary, *Dicotyles tajacu* (Linnaeus, 1758), and the white-tailed deer, *Odocoileus virginianus* (E. A. W. von Zimmermann, 1780), which are known components of their diet (Gutiérrez-González and López-González 2017; Flores-Turdera *et al.* 2021), as well as the availability of forested habitats and rugged terrain. More than 80% of the carnivore species reported for the state (17 of 21) occur in Los Mármoles, including all the Felidae species present in Mexico. Prey diversity and suitable home ranges may allow large felids such as jaguars and cougars to coexist in Los Mármoles (*i.e*, Ávila-Nájera *et al.* 2016). Still, neither species is available for the area. It is noteworthy to mention that an adult jaguar was recently shot, probably by illegal hunters, and died in captivity in August 2024 (Mota-López 2024).

Felidae is a bioindicator group, suggesting healthy ecosystems in the park, since felids have requirements and characteristics that demand greater food availability and larger foraging areas (Aranda 2000). Ravines and canyons and steep slopes (up to 80% for black bears; Monroy-Vilchis *et al.* 2016) may offer refuge for these mammals. As such, these habitats should be considered mainly for conserving the temperate forests of Los Mármoles, where we find other species threatened by human activity, such as the *Leopardus pardalis*, *L. wiedii, Lynx rufus* [von Schreber, (von Schreber, 1777), and *Eira barbara*.

This study confirms the presence of black bears in the area and provides the first photo-evidence of the species in the state of Hidalgo (Aguilar-López *et al.* 2019). Suitable habitat for *U. americanus* includes coniferous forest between 1500 and 3500 m (Monroy-Vilchis *et al.* 2016), which is present in Los Mármoles, but is decreasing due to illegal logging (Arroyo-Ruiz and Cuevas-Cardona 2017).

Feral dogs likely compete with wild carnivores in the area (Table 2), as we noted many instances of dogs chasing small- and medium-sized mammals, in addition to livestock (Figure 5). Feral dogs have a significant impact on fauna through competition, predation, hybridization with wild canids, disease transmission, and changing the behavior of potential prey -by temporarily avoiding dog areas (Jackman and Rowan 2007; Young *et al.* 2011; Waldstein-Parsons *et al.* 2016) and dogs may represent a potential prey for big cats (Carral-García *et al.* 2021), although no interaction of this type was observed or reported during the interviews. Livestock can cause different effects on biodiversity (through grazing and competition with herbivores; Barroso and Gortázar 2024), and cattle are frequently preyed on by big cats (Burgas *et al.* 2014; Khorozyan *et al.* 2015). Hence, a possible conflict may arise from cattle predation. During our study, we encountered some instances of attacks by dogs to cows and wild mammals (Figure 5).

Species richness in Los Mármoles is influenced by its topographic complexity, including rocky areas and ravines that provide refuge for wildlife, as well as by its vegetation, which represents a transition between lowland and highland habitats (Rzedowski, 1978; Flores-Villela and Gerez, 1994). Chávez and Ceballos (1998) noted that localities in the elevational range between 1,500 and 1,700 m above sea level harbor a mixture of temperate and tropical species, consistent with our findings. The sampling effort is another factor contributing to the marked difference in the richness of the temperate forest areas studied so far. This can indirectly influence the composition of the reported mammal species. For example, our sampling was higher and involved more methods than the study at El Chico (Hernández-Flores and Rojas-Martínez 2010), and a bigger area can harbor large mammal species that need bigger foraging areas, like big cats (Hernández-Flores and Rojas-Martínez 2010; de la Torre *et al.* 2017; Núñez-Pérez and Miller 2019). We emphasize that community brigades have been important in registering a large proportion of the mammals reported in the area. This reinforces the need to involve and train local people in biological monitoring programs within protected areas.

Our research fills the information gap on the biodiversity of Los Mármoles, a long-standing protected area in Mexico that still lacks a management plan. Only 12% (10 spp.) of the mammal fauna in Los Mármoles is considered endangered. Our findings highlight the importance of Los Mármoles for the conservation of keystone and threatened mammal species, particularly Carnivora and Chiroptera, which may be vulnerable to extractive activities such as mining. This sector has historically lobbied for the recategorization of the area Los Mármoles to allow mineral extraction (CONANP 2007). In addition, other anthropogenic activities, such as land-use changes for agriculture and housing, may imperil the survival of some species in the coming years. The presence of livestock and feral fauna, such as dogs, might affect the activity patterns and abundance of some mammal species (by predation, competition, etc.; Zapata-Ríos and Branch 2016; Carrasco-Román *et al.* 2021). Therefore, we consider it necessary to implement improved livestock practices and feral dogs' population control strategies.

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Declaration of Artificial Intelligence use

The authors declare that AI Grammarly software was used to assist with style suggestions, textual clarity, and revision of grammar and syntax in English.

Author contributions

Melany Aguilar-López (MA-L), Pedro Adrián Aguilar-Rodríguez (PAA-R), and Lázaro Guevara (LG) developed the idea and structure. MA-L, PAA-R, LG, and José Luis Aguilar-López (JLA-L) wrote the original draft, reviewed and edited all versions of it. MA-L, LG, Jazmín L. Monter-Vargas (JLM-V), Josefina Ramos-Frías (JR-F), and Jorge I. Ángeles Escudero collected data in the field. MA-L, PAA-R, LG, JLA-L, and JR-F provided data curation and formal analysis of the data. MA-L and LG provided funding.

Supplementary data

SD1. Example of the semi-structured interviews presented to local members of the communities to identify the presence of bat roosts in Los Mármoles National Park.

SD2. Example of the semi-structured interviews presented to local members of the communities to identify the presence of medium- and large mammal species in Los Mármoles National Park.

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Camera traps reveal four feline species coexisting, facilitated by temporal segregation in Parque Nacional Tingo María, Perú

Deyvis Cano[1*], Frank Cámara[1], Niler Chahua-García[1], Jhendy Inga[1] and, Homer Sandoval[2]

[1]Programa Académico de Ingeniería Ambiental, Universidad de Huánuco, Huánuco, Perú. E-mail: frank.camara@udh.edu.pe (FC), niler.chahua@udh.edu.pe (NC-G), jhendy.inga@udh.edu.pe (JI)
[2]Parque Nacional Tingo María – Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP), Tingo María, Perú. E-mail: hsandoval@sernanp.gob.pe (HS)
[*]Corresponding author: deyvis.cano@udh.edu.pe

The transformation of natural ecosystems by human activities has significantly reduced the availability of functional habitats for wild felids. In this context, Parque Nacional Tingo María (PNTM), a conservation area of limited extent within a heavily transformed landscape, has confirmed the coexistence of *Herpailurus yagouaroundi*, *Leopardus tigrinus*, *Panthera onca*, and *Puma concolor*. This study determines the locations and frequencies of these species' records and analyzes their hourly activity patterns. For this purpose, 19 camera traps were installed at PNTM from January to December 2024, yielding 52 independent records (with a total of 5,861 camera-days of sampling effort) for felids. *H. yagouaroundi* was the most frequently recorded species (17 records), followed by *L. tigrinus* (12), *P. onca* (12), and *P. concolor* (11). In addition, clear temporal segregation is evident: *H. yagouaroundi* was predominantly diurnal, *L. tigrinus* mainly nocturnal, and *P. onca* and *P. concolor* showed cathemeral activity throughout day and night. These results suggest that the coexistence of the four species in a limited space is facilitated by differences in their activity patterns and support the role of PNTM as a key refuge for territorial felids in an environment undergoing urbanization and landscape fragmentation.

Keywords: Biodiversity, conservation, Felidae, habitats, monitoring, protected natural areas, wildlife.

La transformación de los ecosistemas naturales por las actividades humanas ha reducido significativamente la disponibilidad de hábitats funcionales para los felinos silvestres. En este contexto, el Parque Nacional Tingo María (PNTM), un área de conservación de extensión limitada dentro de un paisaje fuertemente transformado, ha confirmado la coexistencia de *Herpailurus yagouaroundi, Leopardus tigrinus, Panthera onca* y *Puma concolor*. Este estudio determina las ubicaciones y las frecuencias de los registros de estas especies y analiza sus patrones de actividad horaria. Para ello, se instalaron 19 cámaras trampa en el PNTM entre enero y diciembre de 2024, obteniéndose 52 registros independientes de felinos (con 5,861 días-cámara de esfuerzo total de muestreo). *H. yagouaroundi* fue la especie registrada con mayor frecuencia (17 registros), seguida de *L. tigrinus* (12), *P. onca* (12) y *P. concolor* (11). Además, se evidencia una clara segregación temporal: *H. yagouaroundi* fue predominantemente diurno, mientras que *L. tigrinus* fue principalmente nocturno, mientras que *P. onca* y *P. concolor* mostraron actividad catemeral a lo largo del día y de la noche. Estos resultados sugieren que la coexistencia de las cuatro especies en un espacio reducido se ve facilitada por la diferenciación de sus patrones de actividad y respaldan el papel del PNTM como refugio clave para felinos territoriales en un entorno sometido a procesos de urbanización y de fragmentación del paisaje.

Palabras clave: Áreas naturales protegidas, biodiversidad, conservación, Felidae, fauna silvestre, hábitats, monitoreo.

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The transformation of natural ecosystems caused by human activities has considerably reduced the extent of functional habitats for large carnivores worldwide. Deforestation in tropical regions fragments the landscape and forces felids to adapt to smaller territories, thereby altering their spatial use patterns (Anderson *et al.* 2024). From an ecological perspective, wild felids, as they occupy upper trophic levels, require extensive, continuous areas to maintain their regulatory role in the ecosystem, making them sensitive indicators of habitat degradation (Sunquist *et al.* 2014). Moreover, although some species may exhibit similar body sizes, they do not necessarily share the same trophic niche. Coexistence in the same space and time is only possible when resources are diverse and abundant, or when niche partitioning occurs, whether in terms of diet, space, or time, which reduces competition (Ruiz-Gutiérrez *et al.* 2023). Even in protected areas, human presence continues to exert pressure on the spatial occupation of these predators, affecting their distribution and behavior (Poulain *et al.* 2023).

In this context, camera traps emerge as a fundamental tool for studying and monitoring cryptic predators, such as wild felids. These cameras are particularly valuable alternatives in contexts where direct observation is difficult, either because animals are elusive or because understory vegetation is dense (Burton *et al.* 2015). They also make it possible to record, without direct interference, presence, behavior, individual traits, and

demographic variation, including patterns of hourly activity, key aspects for understanding the response and adaptation of mammals to anthropogenic change (Jiménez *et al.* 2010; Allen and Allan 2024).

In the Cordillera Escalera Regional Conservation Area San Martín, Perú, for example, nocturnal records have been obtained of *Panthera onca* (Linnaeus 1758), the largest felid in the Americas and the main apex predator of the Neotropics (Saucedo-Bazalar *et al.* 2023). Similarly, Castagnino Vera (2017) used camera traps in the Peruvian Amazon to study the ecology of the *Leopardus tigrinus* (Schreber 1775), demonstrating their effectiveness for identifying individuals, estimating population density, and analyzing habitat use in tropical environments. Likewise, Mena *et al.* (2020) used spatial capture–recapture models with camera traps to estimate densities of *P. onca* and other vertebrates in fragmented Amazonian landscapes, confirming the value of this methodology for generating robust data to support conservation strategies.

In Perú, Parque Nacional Tingo María (PNTM) stands out as an area of high biological value in the Huánuco region, recognized for its remarkable biodiversity and for the increasing fragmentation of its natural habitats in the surrounding matrix (Puerta and Iannacone 2023; Zuloaga-Obregón and Gabriel-Campos 2023). This area harbors a diverse community of mammals, both prey and predators, that persists in a relatively pristine core despite the anthropogenic pressures recorded in its immediate surroundings (Cossios and Zevallos 2019; Briceño *et al.* 2025). According to Clavijo and Ramírez (2009), the ecological complexity of PNTM and its environmental variability favor the presence of different species along altitudinal gradients. However, systematic studies on felids in this area have been scarce and punctual. Although the presence of several felid species has been confirmed across different sectors of the park, there is still no integrated evidence to explain their ecological interactions, distribution patterns, or spatial use. In this context, Ruiz-Gutiérrez *et al.* (2023) highlight the need to strengthen the scientific basis for decision-making in the conservation and sustainable management of wildlife, especially for felids, which, as apex predators, serve as key indicators of ecosystem health.

Therefore, the present study aims to report the coexistence of four wild felid species, *Herpailurus yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803), *L. tigrinus*, *P. onca*, and *Puma concolor* (Linnaeus 1771), in a habitat of reduced extent, such as PNTM, using camera-trap records. Specifically, it proposes to (i) determine the location and frequency of felid records in the park and (ii) analyze the hourly activity patterns of the recorded species. The results provide ecological information that enables the interpretation of coexistence mechanisms, particularly temporal segregation and spatial use. Likewise, this study seeks to contribute to the design of management and conservation strategies grounded in scientific evidence, strengthening the protection of felids and their habitats, and providing technical inputs for the sustainable management of PNTM and the conservation of biodiversity in Andean–Amazonian ecosystems.

Materials and Methods

Study area. The study was carried out in PNTM, located approximately between 9°19'48" S and 9°09'36" S latitude, and 76°03'36" W and 75°58'12" W longitude (equivalent to the UTM coordinates 382000–392000 m E and 8952000–8970000 m N, zone 18S), the administration of the Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP 2022), in the province of Leoncio Prado, Huánuco region, Perú (Figure 1). The park covers approximately 4,777 hectares and is part of the Premontane Humid Forest of the Peruvian Yungas. It is not formally declared as part of a biological corridor, but it is not completely isolated either, which constitutes partial functional connectivity for large species from an ecological perspective. The area lies between 750 and 1,748 m a.s.l. and has a warm and humid climate, with average temperatures between 22 °C and 29 °C and annual precipitation greater than 3,000 mm, conditions typical of the humid montane forests of the central sector of the Peruvian Amazon, where the dense vegetation cover favors the presence of carnivorous mammals with cryptic habits such as felids.

Felid data source within PNTM. Wildlife monitoring was conducted using 19 Browning camera traps (Recon Force Edge model, BTC-7E) strategically installed across the PNTM from January to December 2024. With the support of park ranger staff, accessible sectors showing evidence of wildlife movement were identified, and monitoring points were selected in accordance with the recommendations of the Peruvian Ministry of the Environment (MINAM 2015). The cameras were distributed along transects, separated by a minimum distance of 250 m to ensure spatial independence among sampling stations and reduce the probability of recording the same individuals at nearby cameras. Their placement prioritized trails, water sources, and areas frequently used by wildlife. During installation, the geographic coordinates of each station were recorded using high-precision GPS receivers. The devices, equipped with passive infrared (PIR) motion sensors, an integrated digital thermometer, a color screen for field configuration, and an invisible infrared flash system, can capture images of up to 20 megapixels and record high-definition videos (1080p) with sound, while also storing metadata such as date, time, and approximate temperature at the moment of capture (Browning 2018).

Each camera was installed at an average height of 60 cm above ground and oriented toward trails or common crossing areas used by felids, a configuration considered one of the most effective methods for estimating species presence. Each unit was programmed to capture a burst of three photographs followed by a 20-second video, with a 30-minute interval before reactivation to avoid the overrepresentation of the same individuals. The system operated continuously throughout the study period, and

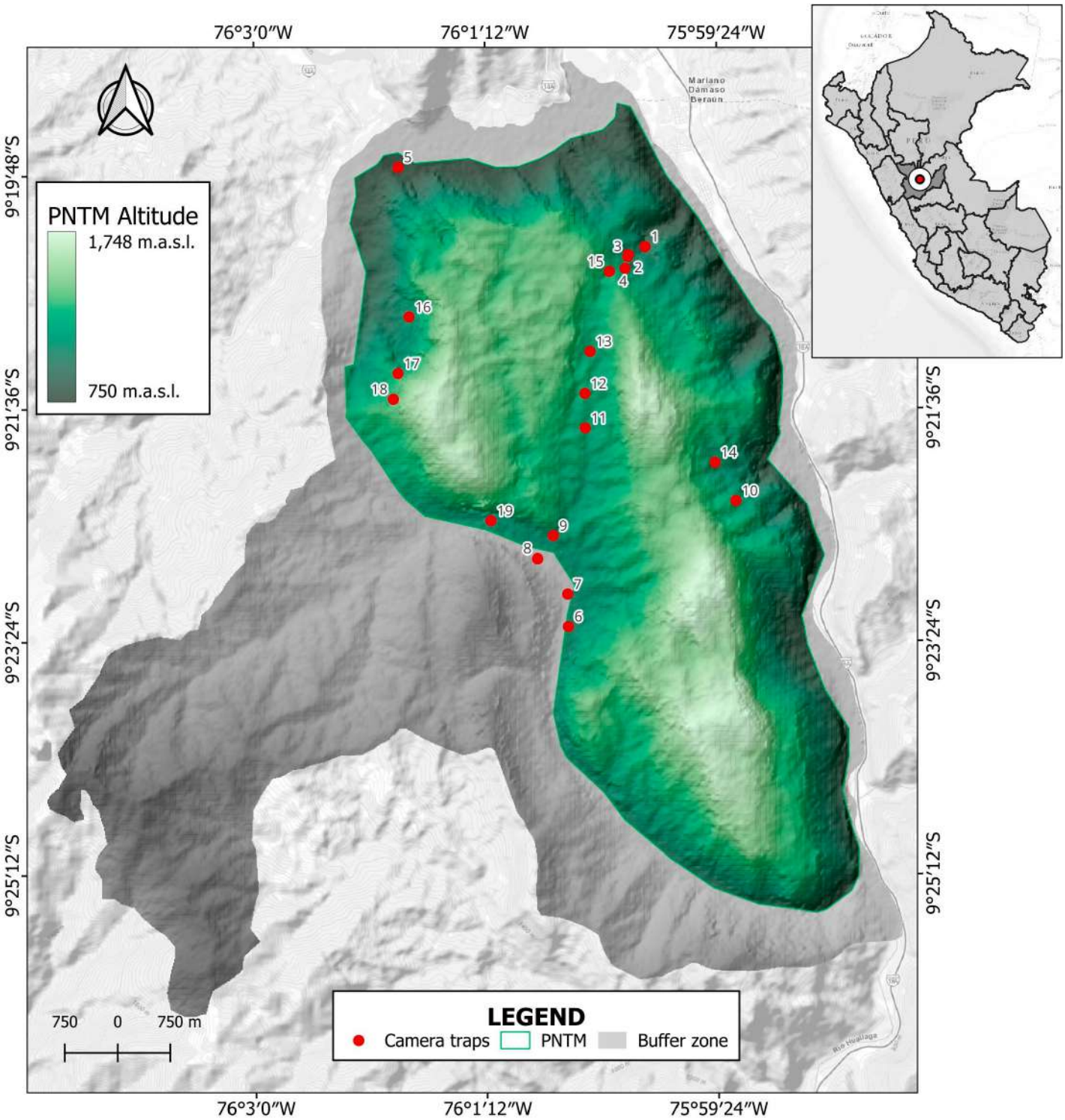

Figure 1. Location map of Parque Nacional Tingo María (PNTM) in Perú. The entire study area is shown in green. In the upper right corner, the legend shows the altitudinal distribution of the PNTM (m a.s.l.), with a gradient from dark green to light green. The red points indicate the locations of the 19 camera traps. The gray outline indicates the boundary of the PNTM buffer zone.

periodic inspections (approximately every two months) were conducted to check battery status and memory cards, ensuring uninterrupted operation of the equipment.

Data processing. The information obtained from photographs and videos recorded by the camera traps was carefully reviewed, organized, and filtered to ensure its quality and consistency before analysis. All records not directly attributable to the presence of felids were excluded. Likewise, indirect evidence, such as the presence of prey or other indicators of their occurrence, was not considered; only images and videos in which individuals of the target felid species were clearly observed were included. Before conducting any analysis, it was ensured that the field-collected information was reliable and accurate for the evaluated area. Photographic and video records were interpreted, recorded, and classified in Microsoft Excel (version 2602, Microsoft 365) by species. Each record was associated with the date, time, and geographic location

Figure 2. Photographic records of felid species obtained using camera traps in the study area: (A) *Herpailurus yagouaroundi* recorded by camera 3 (X = 390020, Y = 8967352); (B) *Leopardus tigrinus* captured by camera 6 (X = 389172, Y = 8962080); (C) *Panthera onca* recorded by camera 1 (X = 388732, Y = 8963046); and (D) *Puma concolor* recorded by camera 13 (X = 389482, Y = 8965996). Coordinates are expressed in UTM, Zone 18S.

recorded by each camera. Events were considered independent when a different individual appeared in front of the camera or when they were separated by intervals of more than 30 minutes, as determined by the camera's technical configuration, for both photographs and videos. (Karanth and Nichols 1998; Zhao *et al.* 2020). For spatial representation, QGIS v.3.34.9 was used; for the generated information, the geographic coordinate system with the WGS 84 datum in UTM zone 18 was used.

Data analysis. Since the study is exploratory and descriptive, simple analyses were employed. Once the database was consolidated, field sightings were quantified by species to determine frequency of occurrence and abundance in the study area. The time intervals analyzed record frequencies in months and by schedule, allowing classification of species according to their activity habits (diurnal, nocturnal, or hourly and monthly). The organization of the data also enabled observation of the frequency of sightings at the spatial level (map) based on recorded coordinates.

To evaluate whether the sampling effort was sufficient to characterize felid richness, a rarefaction analysis of species richness was conducted using camera-trap records. An abundance matrix was constructed with the total number of independent records per felid species, considering camera-days as the unit of effort. Using this matrix, the sample-size–based rarefaction curve was estimated with iNEXT Online version 3.0.2, which implements diversity and sample-coverage estimators for abundance data (Chao *et al.* 2014; 2016). The curve was generated for the diversity order q = 0 (species richness). It included 95% confidence intervals, and the sampling effort was considered to reach the asymptote when the expected richness approached a constant value and the confidence intervals no longer overlapped with lower richness values, that is, when the addition of new camera-days did not produce appreciable increases in the expected number of felid species in the study area. In addition, a sample coverage index greater than 0.95 was considered sufficient to justify and complement the sampling effort.

Results

The 19 cameras installed in the PNTM recorded 2,681 images and videos of various mammals, totaling 5,861 camera-days total sampling effort, for a capture rate of 45.7 records per 100 camera-days. Of these, 14 out of the 19 cameras detected four felid species, with 17 records of *H. yagouaroundi*, 12 of *L. tigrinus*, 12 of *P. onca*, and 11 of *P. concolor*, for a total of 52 independent records; examples of some captures of the four felid species are shown in Figure 2. For more details, see Table 1, which presents all records of felid consolidations, detailing for each event the corresponding camera, date, number of individuals observed, and the UTM coordinates of the detection point, information that serves as the basis for the ecological and comparative analyses developed in this study.

A rapid increase in the number of felid species detected is observed as the number of camera-days increases (Figure

Table 1. Geographic records of the four felid species in PNTM, Perú.

Scientific name	UTM coordinates – Zone 18S		No. / Camera	Date	Recording time (24h format)
	X	Y			
Herpailurus yagouaroundi	386677	8965312	Camera 18	15/5/2024	13:30
	386677	8965312	Camera 18	22/5/2024	12:50
	386745	8968617	Camera 5	24/10/2024	16:30
	386745	8968617	Camera 5	8/11/2024	07:32
	386902	8966488	Camera 16	11/8/2024	14:47
	386902	8966488	Camera 16	1/9/2024	16:30
	386902	8966488	Camera 16	23/10/2024	11:07
	386902	8966488	Camera 16	19/12/2024	07:40
	388732	8963046	Camera 8	20/5/2024	11:30
	388732	8963046	Camera 8	11/7/2024	15:48
	388956	8963374	Camera 9	28/3/2024	16:39
	389408	8965396	Camera 12	25/2/2024	18:35
	389482	8965996	Camera 13	8/11/2024	10:02
	389482	8965996	Camera 13	12/11/2024	16:26
	389507	8966190	Camera 14	2/2/2024	16:05
	389507	8966190	Camera 14	9/2/2024	15:34
	390020	8967352	Camera 3	22/4/2024	16:18
Leopardus tigrinus	386745	8968617	Camera 5	23/8/2024	22:23
	386902	8966488	Camera 16	10/6/2024	18:02
	386902	8966488	Camera 16	27/9/2024	23:39
	388073	8963584	Camera 19	21/3/2024	22:40
	388732	8963046	Camera 1	10/1/2024	02:01
	388732	8963046	Camera 1	19/2/2024	03:31
	388732	8963046	Camera 8	31/5/2024	20:04
	389172	8962080	Camera 6	24/2/2024	00:33
	389172	8962080	Camera 6	25/2/2024	00:21
	389172	8962080	Camera 6	16/4/2024	00:54
	389172	8962080	Camera 6	23/4/2024	22:13
	390020	8967352	Camera 3	14/4/2024	23:25
Panthera onca	386745	8968617	Camera 5	23/8/2024	22:23
	386745	8968617	Camera 5	4/10/2024	04:07
	386745	8968617	Camera 5	12/10/2024	06:16
	386745	8968617	Camera 5	6/11/2024	07:26
	386745	8968617	Camera 5	24/11/2024	12:24
	388732	8963046	Camera 1	29/8/2024	12:32
	388732	8963046	Camera 8	7/5/2024	18:20
	388956	8963374	Camera 9	1/9/2024	00:32
	388956	8963374	Camera 9	1/9/2024	05:25
	388956	8963374	Camera 9	1/9/2024	07:07
	388956	8963374	Camera 9	2/9/2024	15:25
	389162	8962544	Camera 7	30/1/2024	09:05
Puma concolor	386902	8966488	Camera 16	22/12/202	22:02
	388956	8963374	Camera 9	22/8/2024	19:49
	388956	8963374	Camera 9	22/11/2024	12:12
	389162	8962544	Camera 7	29/1/2024	06:45
	389162	8962544	Camera 7	29/1/2024	18:45
	389408	8965396	Camera 12	17/1/2024	07:21
	389482	8965996	Camera 13	17/1/2024	06:53
	389482	8965996	Camera 13	30/3/2024	04:00
	389482	8965996	Camera 13	22/9/2024	01:28
	390020	8967352	Camera 3	29/5/2024	03:16
	390027	8967372	Camera 2	6/6/2024	19:50

3), with a pronounced rise from 1 to approximately 4 species in the first 12 camera-days (sample coverage index = 0.97). From that threshold onward, the curve approaches an asymptote near 4 species. It remains practically stable up to the maximum sampling effort (52 camera-days), while the 95% confidence band (gray-shaded area) narrows progressively, indicating a decrease in uncertainty in the richness estimate. This stabilization of the curve suggests that the sampling effort employed was sufficient to record most, or possibly all, of the felid species present in the study area and that a further increase in effort would have a very low probability of adding new felid species to the inventory.

Figure 4 shows the spatial distribution of records of *H. yagouaroundi*, *L. tigrinus*, *P. onca,* and *P. concolor* in PNTM, where the size of the circles indicates the number of sightings per sampling station. In *H. yagouaroundi* and *L. tigrinus,* a higher concentration of records is observed in the northern and central sectors of the park, with several points showing multiple sightings, suggesting areas of preferential use and a broader spatial distribution. Despite this broad distribution, both species overlap at a few stations (at four common points), suggesting a degree of fine-scale spatial segregation.

By contrast, the records of *P. onca* and *P. concolor* are fewer and appear more dispersed, a pattern that may be related to more solitary habits, lower population densities, or a wider use of space within the study area. Nevertheless, both species show a core of records in the central part of the park and, in the case of *P. onca*, an additional sighting was documented in the northern sector, near the Cueva de las Lechuzas, where visitor presence and human activity are significant.

Activity pattern. In *H. yagouaroundi* (Figure 5A–B), the records were concentrated mainly in February, May, and November, with peaks of up to three events in cameras 14, 12, 18, 8, 13, and 5. Activity was markedly diurnal, with the highest number of sightings between 10:00 and 16:00 h, where two to six events were recorded, indicating a clear preference for daylight hours. In *L. tigrinus* (Figure 5C–D), maximum records were observed in February and April, with up to three events in cameras 1, 6, and 3. Its activity was predominantly nocturnal, with a higher frequency of sightings between 22:00 and 02:00 h, indicating a strong preference for hours of darkness. For *P. onca* (Figure 5E–F), records were concentrated in September (four events) and in August, October, and November (two records in each month), mainly in cameras 1, 9, and 5. Activity was distributed both at night and during the day, with peaks

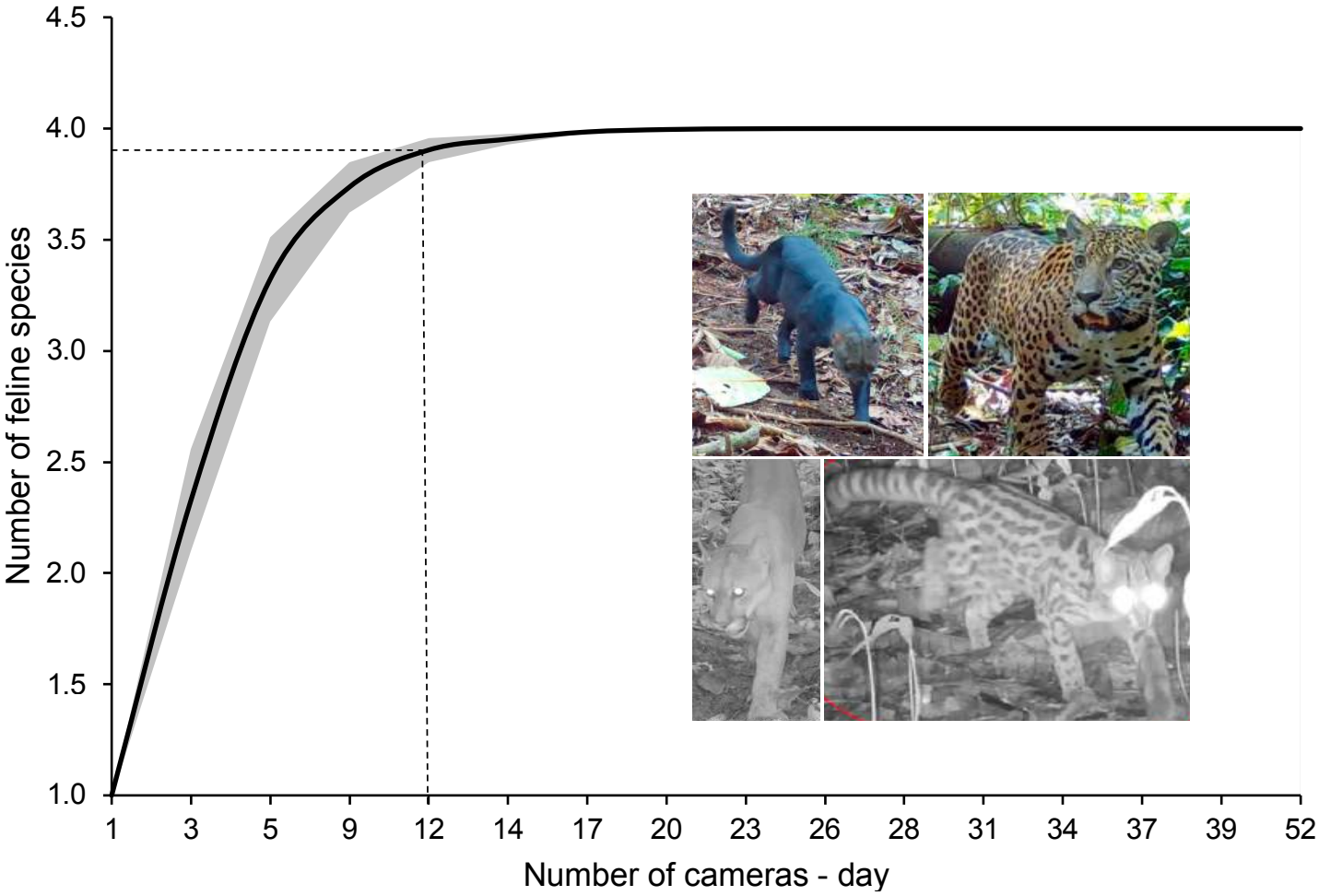

Figure 3. Rarefaction curve analysis showing the number of wild felid species detected as a function of cumulative camera-days. The gray shaded area represents the 95% bootstrap confidence interval for species richness. Dashed black lines indicate the inflection point and horizontal asymptote (sample coverage = 0.97), confirming sampling sufficiency for felid inventory in PNTM.

between 04:00 and 09:00 h (one to two records) and between 18:00 and 00:00 h (one record), without showing a clearly defined hourly pattern in the context of this study. In *P. concolor* (Figure 5G–H), the highest number of records occurred in January, with four events in cameras 7, 13, and 12. Its activity was spread throughout the day and night, with one peak between 01:00 and 06:00 h (two records) and another between 18:00 and 19:00 h (one and two records, respectively), reflecting a mixed activity pattern that could be related to variation in environmental conditions and prey availability.

Discussion

Our results partially agree with those reported by Cossios and Zeballos (2019) for the same park, who, with a sampling effort of 2,940 camera-days over four years of monitoring, recorded 26 events of *P. concolor*, 7 of *H. yagouaroundi*, and 1 of *L. tigrinus*. Taken together, both studies indicate low detectability of felids, consistent with their cryptic behavior and low population densities. Nevertheless, our study, which focused on documenting the coexistence of these species, provides important contributions. We recorded the presence of *P. onca*, a species previously unreported, expanding current knowledge of the felid community in PNTM. In addition, our work involved a more intensive sampling effort over a shorter period: we conducted simultaneous monitoring for one year by deploying 19 active camera traps, accumulating a large number of camera-days compared with the previous study, which was conducted over four years. Similarly, Cossios *et al.* (2022) reported only four *Leopardus pardalis* events in the Allpahuayo Mishana National Reserve, reaffirming the low detectability of felids and their generally low population densities in Amazonian ecosystems. This low recording rate has also been documented by Ruiz-Gutiérrez *et al.* (2023) in the Sierra Madre del Sur, Mexico, where 362 detections of three felids are interpreted as evidence of coexistence mediated by spatial and temporal overlap rather than high abundance. Likewise, Behnke (2015) showed in the lowland Peruvian Amazon that an effort of 2,614 camera-days generated 108,558 photographs of mammals but with very few captures of large felids, suggesting that prolonged efforts are required to detect apex predators and that the low numbers of records reflect reduced densities and extensive home ranges rather than actual absence.

Our results concerning monthly and hourly activity patterns agree with Cossios and Zevallos (2019) in PNTM, where *H. yagouaroundi* was exclusively diurnal, and *L.*

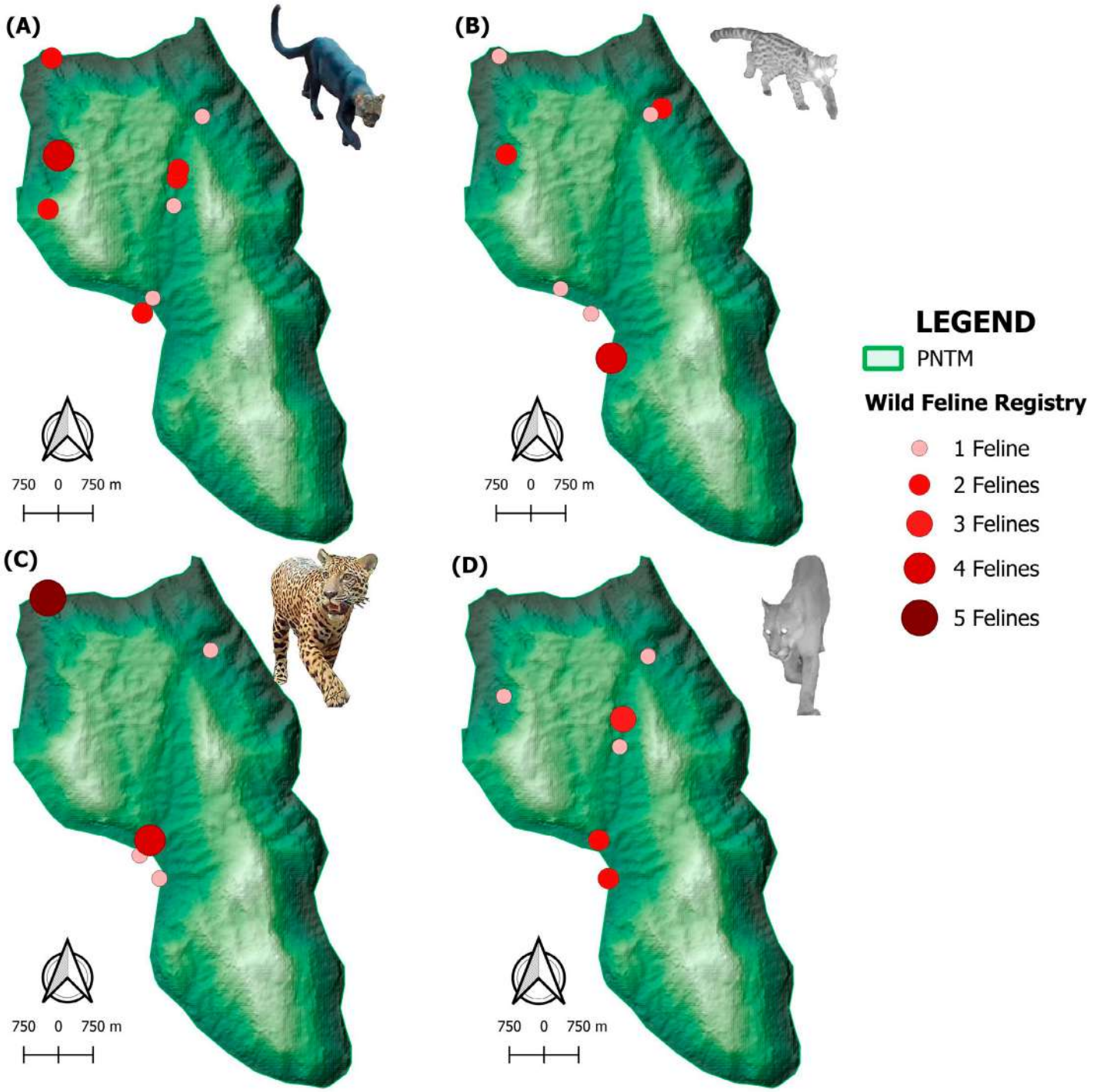

Figure 4. Spatial distribution of records of (A) *Herpailurus yagouaroundi*, (B) *Leopardus tigrinus*, (C) *Panthera onca*, and (D) *Puma concolor* in PNTM, Perú, according to the number of sightings per monitoring station with camera traps.

tigrinus was completely nocturnal, which supports the predominant diurnality and nocturnality observed in this study, as well as *P. concolor,* which showed 30.77% of diurnal records and 53.85% nocturnal. Contrary to what Mosquera-Guerra *et al.* (2018) reported, *L. tigrinus* in the forests of the Bita River (Colombia) exhibits a cathemeral pattern, suggesting some flexibility in its activity. In general, variations among diurnal, nocturnal, and cathemeral habits are usually associated with temperature, humidity, prey availability, and the need to avoid predators or competitors. In the Allpahuayo Mishana Reserve, Cossios *et al.* (2022) pointed out that hunting and tourism can reduce diurnal activity and shift it toward nighttime hours with lower human presence, so the nocturnality of *L. tigrinus* and the mixed patterns of *P. concolor* and *P. onca* in PNTM could be interpreted as behavioral adjustments to coincide with their prey and minimize contact with people.

The spatial distribution of records of *H. yagouaroundi* and *L. tigrinus* is concentrated mainly in the northern and central sectors of PNTM, although with relatively

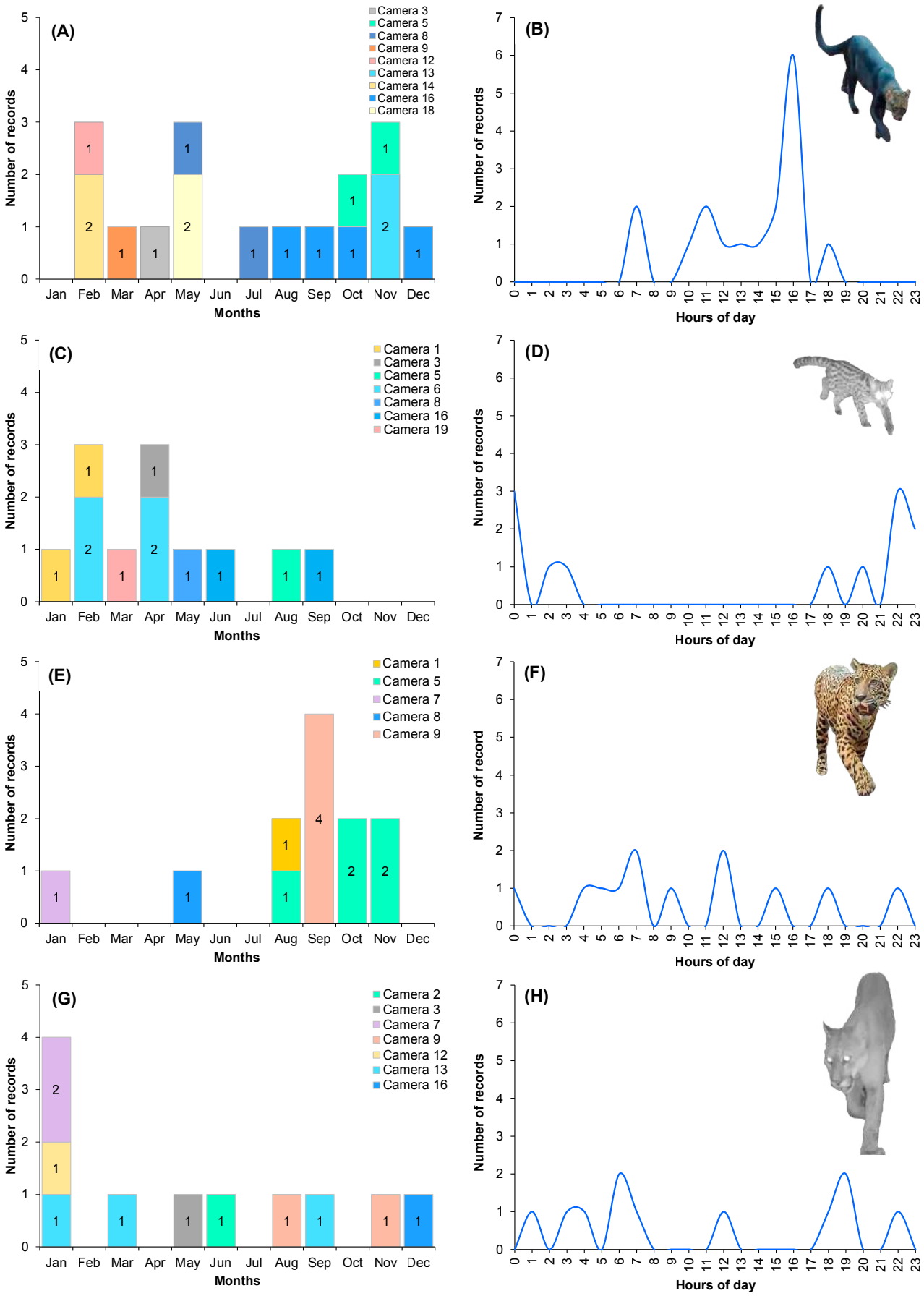

Figure 5. Monthly records and hourly activity of the felids: (A–B) *Herpailurus yagouaroundi*, (C–D) *Leopardus tigrinus*, (E–F) *Panthera onca*, and (G–H) *Puma concolor* in PNTM, Perú. In the first column, the different colors of the bars represent the months in which presence records were captured. In the second column, the blue lines indicate the 24-hour daily activity patterns of the felid species recorded by the camera traps.

wide dispersion among sampling stations. In contrast, records of *P. onca* and *P. concolor* are less frequent and occur in more restricted areas, suggesting lower-density populations or a more limited use of space. This distribution may be related to food availability. In the northern and western sectors of the park, the presence of this felid species appears to be associated with greater prey availability, both domestic (such as chickens) and wild, which constitute its food base. This situation is particularly relevant in areas occupied by users within the Buffer Zone and the Special Use Zone of the protected area (Anderson *et al.* 2024; Briceño *et al.* 2025).

The simultaneous presence of these four species in a relatively small, protected area can be explained by the fact that PNTM acts as one of the few remaining minimally disturbed habitats within a matrix heavily transformed by agriculture, deforestation, urbanization, and hunting, processes documented for the area (Guillén and Reátegui 2014; Puerta and Iannacone 2023). These anthropogenic pressures reduce and fragment the available range, "cornering" felid populations and limiting the availability of safe sites to obtain food, water, and shelter. This scenario has direct implications for both the conservation of apex predators and for wildlife that finds the park one of the few remaining refuges in the landscape (Massara *et al.* 2015).

In addition, the presence of *P. concolor* in the PNTM, a species widely distributed from the Andes to the Amazon, suggests functional ecological connectivity between surrounding montane forests and adjacent forested landscapes. A similar interpretation may apply to *P. onca*, whose occasional records suggest that the park may be part of a broader movement network rather than a fully isolated habitat. Given the extensive spatial requirements of both large felids, it is likely that individuals move through the park while maintaining connections with surrounding forest remnants and buffer zones (Arias-Alzate *et al.* 2022). However, the present study was not designed to estimate population densities or to identify specific corridors, so the degree of connectivity and the size of the populations using the area remain subjects for future research.

The results of this study are relevant to the conservation and management of felids in PNTM because they provide important information on species presence and the sites with the highest activity levels. These data can be incorporated directly into the design of monitoring programs, allowing prioritization of camera placement at stations with concentrated records and focusing effort on areas with a higher probability of detection. In this regard, what was stated by Mosquera-Guerra *et al.* (2018) is relevant, as the information generated through camera traps on activity patterns and spatial distribution of medium- and large-sized mammals constitutes a fundamental input for management planning.

The 52 independent records obtained from 14 monitoring stations confirm the active use of the area by the four species evaluated. A limitation of the study is that no specific individual-identification design was implemented, nor were photographic capture–recapture models applied, which prevents robust estimation of population size or the minimum number of individuals. However, the confirmed evidence of presence, together with information on spatial distribution and observed temporal segregation, provides a strategic baseline to guide zoning processes, threat control, and long-term monitoring programs in the PNTM and in other protected natural areas with similar characteristics.

Nevertheless, the work has limitations that must be considered when interpreting the results: the number of records is relatively low (52 events across 14 cameras), which limits more detailed analyses of diversity, such as overlap in activity or differential habitat use among species. In addition, prey availability and the intensity of human activities at each station were not specifically quantified, so their influence on distribution and activity schedules can only be inferred in general terms. Finally, as in any study based on camera traps, the records reflect the use of the sampled points and not the entire movement range of the felids; therefore, the described patterns should be interpreted with caution and considered an initial approximation of the coexistence of these species in the PNTM. In this regard, future studies could strengthen these results by designing surveys specifically to estimate occupancy, incorporating standardized temporal replicates, increasing station density, and using hierarchical models that allow estimation of detection probability and actual site use. This approach would enable more robust inferences about spatial dynamics and population persistence within the protected area.

Conclusions

This study documents the coexistence of four felid species (*H. yagouaroundi, L. tigrinus, P. onca,* and *P. concolor*) within the relatively small area of PNTM, supported by 52 independent camera-trap records obtained over 5,861 camera-days. The stabilization of the rarefaction curve and the high sample coverage index (0.97) further indicate that the sampling was sufficient to characterize the local felid community. Clear temporal segregation was observed among species: *H. yagouaroundi* was predominantly diurnal, *L. tigrinus* mainly nocturnal, and *P. onca* and *P. concolor* exhibited cathemeral activity. This pattern suggests that temporal niche partitioning is a key mechanism facilitating their coexistence. Considering the wide movement ranges of large felids, particularly *P. onca* and *P. concolor*, PNTM likely functions not only as a local refuge but also as part of a network of connected habitats that supports movement between buffer zones and surrounding fragmented landscapes. In this context, the park may serve as a resident habitat for smaller felids while acting as a functional corridor or use area for larger carnivores within Andean–Amazonian landscapes.

From a management perspective, the results provide strategic information on the sectors of the PNTM where

greater felid activity was recorded and on the periods of the day in which each species shows a higher probability of detection. It is recommended to prioritize installing camera traps in microhabitats, along movement routes, and in sectors of the park where the probability of recording is higher, and to adjust inspection, maintenance, and repositioning of the equipment to the periods of greater species activity. Likewise, it is recommended to expand the sampling effort by increasing the number of stations and extending the temporal series, and to incorporate complementary variables such as prey abundance, human pressure, and microclimate. The integration of these factors, along with the use of occupancy and density models, would allow more precise estimates of space use and a better understanding of how these populations respond to processes such as agricultural expansion, hunting, and other threats in the surrounding landscape.

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Declaration of artificial intelligence use

During the preparation of this manuscript, the authors used Perplexity AI (Grok 4.1) and GPT-5.3 solely to improve the grammar, style, the logical cohesion and translation of the text. These tools were not employed for data generation, statistical analysis, the creation of figures or tables, or the scientific interpretation of the results. The authors critically reviewed and edited the AI-assisted content and hold full responsibility for the integrity, originality, and conclusions presented in this work.

Author contributions

Deyvis Cano: Conceptualization, methodology, research supervision, data analysis and interpretation, visualization, and writing - original draft, review and editing. Frank Cámara: Data collection (fieldwork), data analysis and interpretation, and writing - review and editing. Niler Chahua-García: Data analysis and interpretation, visualization, and writing-review and editing. Jhendy Inga: Visualization and writing -review and editing. Homer Sandoval: Methodology, data collection (fieldwork), visualization, and writing - review and editing.

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Population density of White-tailed deer in a protected area of the Ecuadorian Andes

Michelle Alexandra Rodríguez-Noroña[1,2,3,4*], David Andrés Herrera-Orellana[5], Paúl Monar-Barragán[2], Juan Sebastián Restrepo-Cardona[2,6], Evelyn Edith Araujo[2], and Iván Vinicio Jácome-Negrete[1]

[1]Universidad Central del Ecuador. Facultad de Ciencias Biológicas. Numa Pompilio Llona y Yaguachi.170303, Quito-Ecuador. E-mail: ivjacome@uce.edu.ec (IVJ-N); marodriguezn04@gmail.com (MAR-N).
[2]Fundación Cóndor Andino Ecuador. José Tamayo y Lizardo García. 170523, Quito-Ecuador. E-mail: hpmonarb@gmail.com (PM-B); eearaujoll@gmail.com (EEA); jsrestrepoc@gmail.com (JSR-C); marodriguezn04@gmail.com (MAR-N).
[3]Instituto Nacional de Biodiversidad (INABIO). Calle Rumipamba 341 y Av. de los Shyris, PB 17-07-8976. Quito. Ecuador. E-mail: marodriguezn04@gmail.com (MAR-N).
[4]Fundación de Conservación Jocotoco. Av. Amazonas N40-80 y UNP, Piso 7. E-mail: marodriguezn04@gmail.com (MAR-N).
[5]Universidad Técnica Particular de Loja. San Cayetano Alto, C. París, Loja-Ecuador. E-mail: daho698@gmail.com (DAH-O).
[6]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, USA. E-mail: jsrestrepoc@gmail.com (JSR-C).
[*]Corresponding author: marodriguezn04@gmail.com

The white-tailed deer (*Odocoileus virginianus ustus*) is an ecologically important species as it is part of the diet of carnivores and scavengers. However, there is little research on its population density in the Ecuadorian Andes. We evaluated white-tailed deer population density during two consecutive years (i.e., 2023 and 2024) in three different cover types (i.e., shrubland, grassland, and sandy areas) in the Área de Conservación Hídrica (ACH) Antisana. Data were collected by direct observational counts of individuals in line transects of at least 1 km, between 8:00 and 17:00 h. The average population density was 12.61 ind km^{-2} in 2023 and 14.25 ind km^{-2} in 2024, although these differences were not significant. We also found no differences in deer densities across cover types, although this does not imply a homogeneous distribution of the species in the protected area. There is a clear need for long-term monitoring programs to understand the population dynamics of white-tailed deer and establish management strategies tailored to the unique conditions of each territory. We recommend implementing systematic protocols for estimating white-tailed deer population densities based on direct observation methods, as these provide reliable information on the number of individuals.

Keywords: Antisana, Cervidae, Paramo, Line transects, *Odocoileus virginianus ustus,* Population

El venado cola blanca (*Odocoileus virginianus ustus*) es una especie importante en los ecosistemas naturales, la cual hace parte de la dieta de carnívoros y carroñeros. Sin embargo, existen pocos estudios sobre su densidad poblacional en los Andes. Evaluamos la densidad poblacional del venado de cola blanca durante dos años consecutivos (i.e., 2023 y 2024) en 3 tipos de cobertura distintos (i.e., arbustal, herbazal y arenal) en el Área de Conservación Hídrica (ACH) Antisana. Los datos fueron obtenidos mediante conteo directo por observación de individuos en transectos lineales de al menos 1 km, entre las 08:00 y 17:00 h. La densidad poblacional promedio de venados fue 12.61 ind km^{-2} en 2023 y 14.25 ind km^{-2} en 2024, aunque dichas diferencias no fueron significativas. Tampoco encontramos diferencias en las densidades de venados en los distintos tipos de cobertura, aunque esto no implica una distribución homogénea de la especie en el área protegida. Es necesario realizar programas de seguimiento a largo plazo para conocer la dinámica poblacional del venado de cola blanca y establecer estrategias de manejo que se ajusten a las condiciones propias de cada territorio. Recomendamos implementar protocolos sistemáticos para la estimación de las densidades poblacionales del venado de cola blanca basados en métodos de observación directa, dado que estos proporcionan información confiable sobre el número de individuos.

Palabras clave: Antisana, Cervidae, *Odocoileus virginianus ustus,* Páramo, Población, Transectos lineales

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The tropical Andes are a global biodiversity hotspot due to their high levels of endemism and ongoing habitat loss (Myers *et al.* 2000; Báez *et al.* 2016). High Andean ecosystems, particularly páramos, harbor remarkable plant diversity and play a key role in species evolution due to their unique biogeographical conditions (Arroyo and Cavieres 2013). In addition, these ecosystems provide essential services, including carbon storage, water regulation, and climate refugia for vulnerable species (Cincotta *et al.* 2000; Arroyo and Cavieres 2013). In Ecuador, páramo ecosystems are also fundamental for water supply, agriculture, and hydroelectric power generation, despite covering a small proportion of the national territory. However, they are increasingly threatened by anthropogenic pressures such as agricultural expansion, overexploitation, and population growth (Crespo *et al.* 2010; Etter *et al.* 2017; Sierra *et al.* 2021).

The ecological importance of white-tailed deer (*Odocoileus virginianus ustus*) is due at least in part to their role as a food source for other wild animals. Changes in deer abundance can cause variation in the diet of the cougar (*Puma concolor*), which can trigger predation of

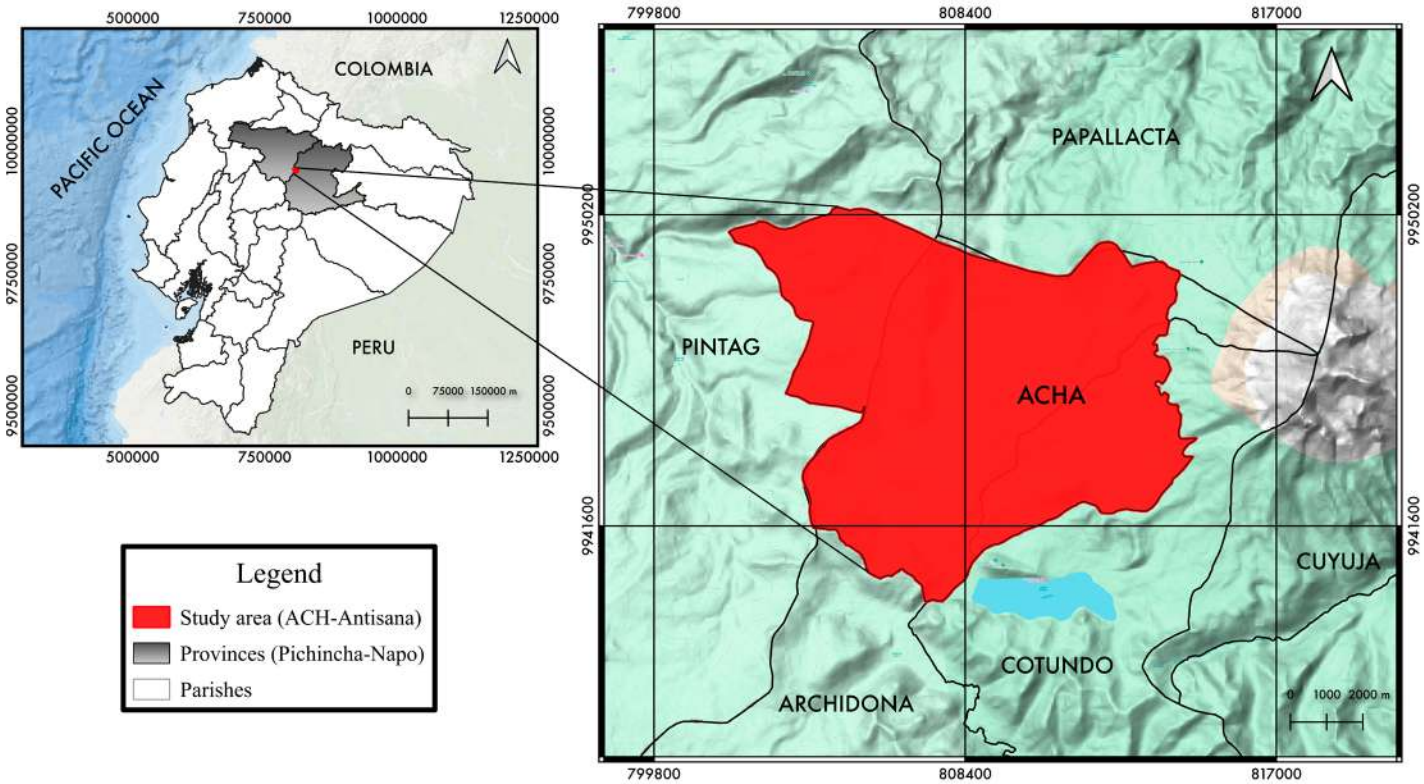

Figure 1. Geographic location of the ACH Antisana, Ecuador, where white-tailed deer data were collected during 2023 and 2024.

domestic animals, thus causing human-wildlife conflicts (Fulbright and Ortega 2007; Piña and Trejo 2014; Tellkamp *et al.* 2019). Likewise, artiodactyls are an important food source for obligate and facultative scavengers (Lambertucci *et al.* 2009; Perrig *et al.* 2017). However, its population status remains unknown, limiting the understanding of its potential effects on threatened species such as the condor, whose populations are declining due to human pressures (Restrepo-Cardona *et al.* 2022).

The methods used to estimate white-tailed deer population density include aerial surveys, mark-recapture techniques, the use of camera traps and remote thermal imaging, and fecal counts. Remote surveys are notable for their cost-effectiveness and efficiency (LaRue *et al.* 2007; Urbanek and Nielsen 2012). Counting individuals through direct observation is especially useful in areas with relatively high abundances and flat, open terrain that offers good visibility (Beltrán and Díaz 2010; Mandujano 2014). However, estimates of the species' abundance and population size are often made using indirect methods such as counting feces in fixed transects (Ortiz-Martinez *et al.* 2005; Piña and Trejo 2014; Mandujano 2016). Nevertheless, this method provides a relative density index due to variation in defecation and feces decomposition rates caused by intrinsic and extrinsic factors (Galindo-Leal 1992; Pérez-Mejía *et al.* 2004; Navarro 2005; Mandujano 2014). Lower defecation rates can cause individuals to be overestimated (Mandujano 2014). In addition, if the substrate and environmental conditions are not suitable, feces may not be preserved long enough to be recorded (Navarro 2005). Thus, estimates of deer density may vary depending on the sampling methods used (Hewitt 2011). Nevertheless, there is little knowledge about the ecology and threats facing the white-tailed deer in the Ecuadorian páramos. Domestic dogs represent a significant threat to the species (Zapata-Ríos and Branch 2018; Restrepo-Cardona *et al.* 2025). Similarly, hunting and wildlife trafficking are latent threats to the species (Sánchez 2009). Although the population density of a species is crucial for determining its conservation status and establishing effective management and conservation strategies (Mandujano *et al.* 2010), the information available on the population status of the white-tailed deer is scarce in Ecuador. Albuja (2007) studied the population density of this species in the Oyacachi-Papallacta and Antisana páramos, reporting a density of 1.6 ind km^{-2}. On the other hand, Tellkamp *et al.* (2019) evaluated the population density in the Área de Conservación Hídrica (ACH) Antisana and reported population densities of deer that ranged between 7.91 ind km^{-2} and 11.31 ind km^{-2} (Tellkamp *et al.* 2019).

Therefore, it is crucial to determine the population status of white-tailed deer in the Ecuadorian Andean páramos, given that changes in population density can affect the populations of native species that feed on these animals (e.g., puma, Andean condor) and thus also the ecosystem services that this biodiversity provides to people (Rojas 2010; Arenas 2011; Hansen *et al.* 2017; Chávez *et al.* 2022). Hence, the objective of this study was to evaluate the population density of white-tailed deer for two consecutive years (i.e., 2023 and 2024) and in three different cover types (i.e., shrubland, grassland, and sandy area) in the ACH Antisana.

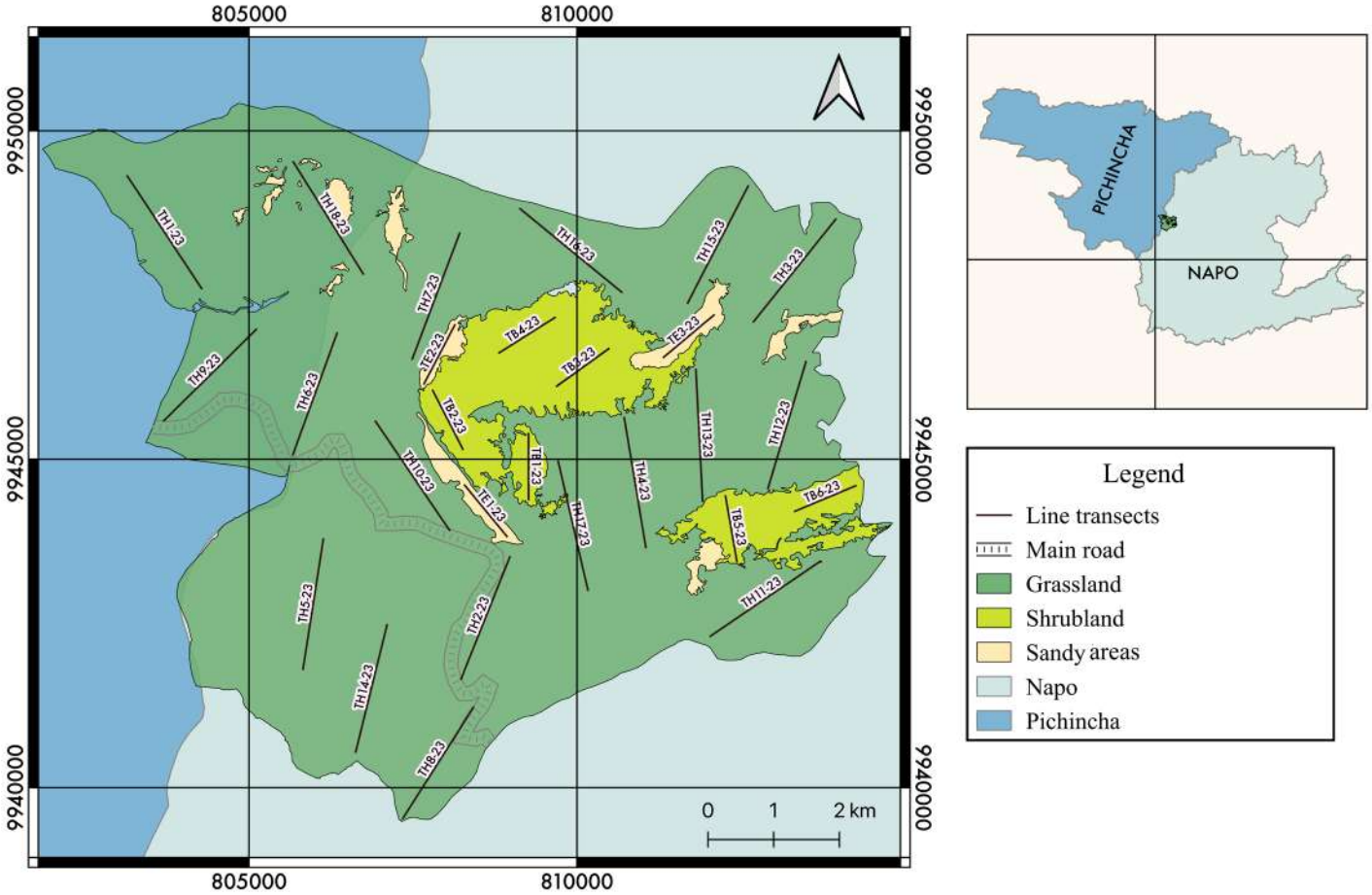

Figure 2. Cover types (grassland, shrubland, and sandy area) and location of 27 transects in grassland (18 transects), shrubland (6 transects), and sandy areas (3 transects) for the study of white-tailed deer in the ACH Antisana during 2023 and 2024.

Materials and methods

Study area. The study was conducted in the ACH Antisana located in the provinces of Napo and Pichincha (Figure 1), which covers an area of 8487 ha. The ACH Antisana is bordered to the north by the Chakana Reserve, to the west by private land, and to the south and east by Antisana National Park (FONAG 2019). Its altitude ranges from 3720 to 4640 meters above sea level, and it has an average annual rainfall of 1098 mm (Sklenář *et al.* 2015; Bécquer 2022). In the páramos of Ecuador, annual precipitation has a bimodal pattern with wet seasons from February to May and from October to December (Hofstede and Mujica 2002). In the study area, rainfall is concentrated between December and June, with a drier period from July to November (Pérez and Zapata 2025). The area provides water for consumption to 2,6 million inhabitants of the Metropolitan District of Quito (Crespo *et al.* 2010). Historically, land use in the site was dedicated to intensive livestock farming, with cattle, sheep, and horses. By 2012, there were an estimated 1500 sheep and 6000 cattle head in the area (FONAG 2024). However, in an effort to conserve its water sources and biodiversity, the area was declared an ACH in 2012, and management actions have subsequently focused on reducing livestock impacts and promoting ecological restoration (Crespo *et al.* 2010; Grubb *et al.* 2020).

The most representative ecosystems of the ACH Antisana are (1) the paramo grassland, characterized by its herbaceous appearance and evergreen phenology, and dominated by *Agrostis* sp., *Calamagrostis* sp., and *Cortaderia* sp. (MAE 2013; Bécquer 2022). And (2) the floodable paramo grassland is distinguished by its flooding regime, with the presence of *Lophozia laxifolia* and *Cortaderia sericantha* plants that form cushions and floating vegetation on compact, thick soil that retains moisture and produces conditions of impermeability and inefficient drainage, which favors the formation of peat bogs and swamps (MAE 2013).

Field data collection. To estimate the population density of white-tailed deer, the direct counting method was used by observing individuals in linear transects. Sampling was carried out between October and November 2023 and between October and December 2024, in accordance with the schedule and logistical framework of the monitoring project under which this study was conducted. The sampling was carried out in three types of cover types: grassland, shrubland, and sandy areas, which cover an area within the ACH Antisana of 72.92 km^2, 8.89 km^2, and 2.43 km^2, respectively (Figure 2). The three cover types are spatially distinguishable within the study area but are not completely isolated, allowing movement of white-tailed deer among them. Therefore, cover types were considered as sampling categories to evaluate relative differences in

Figure 3. Selected cover types in the Área de Conservación Hídrica Antisana in 2023 and 2024: A) grassland, B) grassland transect, C) sandy areas, D) sandy areas transect, E) shrubland, F) shrubland transect.

density rather than independent population units. A total of 27 linear transects were established based on spatial coverage, representation of the different cover types and field accessibility within the study area, ensuring an adequate sampling effort while maintaining logistical feasibility and consistency between surveys. The transects had variable widths and lengths of 2 km for grassland cover types and 1 km for shrubland and sandy area. To avoid sampling bias, a stratified random sampling design was used, where transects were randomly located within each cover type using previously defined polygons (Terán-Valdez *et al.* 2018). Random points were generated in QGIS and used as starting locations, with the number of transects proportional to cover type area. Transect orientation was randomly assigned among cardinal directions (Mandujano 2014). A minimum distance of 1 km between transects was maintained to avoid overlap, and any transect not meeting spatial criteria was re-randomized. The width of the transects was determined by the position of the deer observed. In addition, to reduce possible overlaps in observations, a minimum distance of 1 km between transects in the same cover type was considered to reduce

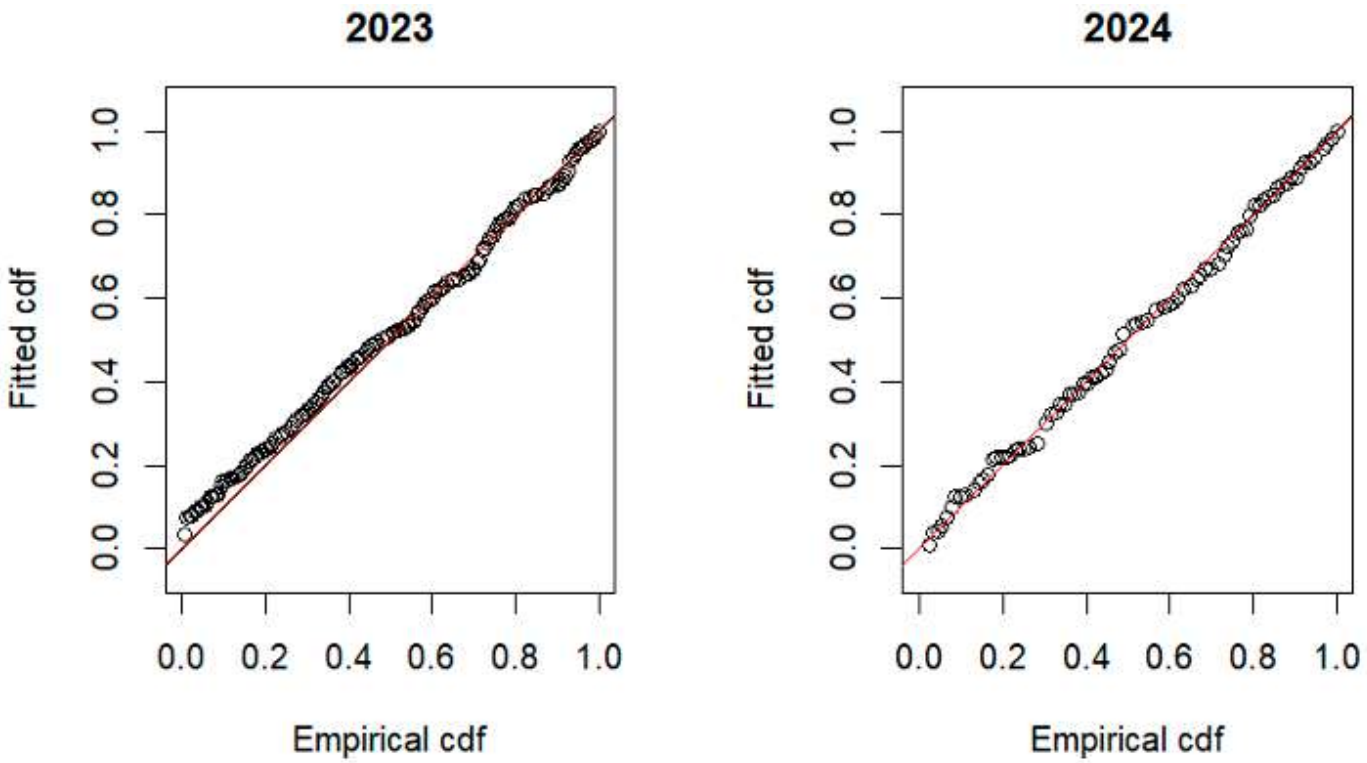

Figure 4. Quantile-quantile plots (Q-Q plots) indicating the fit of the detection function to the data for the years 2023 and 2024.

the likelihood of repeated detections. While specific home range estimates for this species in páramo ecosystems are unavailable, studies in tropical environments have reported home ranges ranging from 0.12 to 0.9 km^2 (Contreras-Moreno *et al.* 2021).

Each transect was surveyed once a year, between 8:00 a.m. and 5:00 p.m., as outside this time frame deer tend to gather to feed and rest. Each transect was surveyed on foot by two researchers, ensuring that a set direction was followed at a constant speed of 2 km/h and without backtracking (Figure 3). All deer on both sides of the transect were recorded (Mandujano 2014; Narváez and Zapata-Ríos 2020). When an individual was detected, the perpendicular distance of the animal from the transect was recorded using a LEUPOLD-RX-1000i/TBR rangefinder, and in the case of grouped deer, the perpendicular distance from the transect to the center of the group was measured (Gallina *et al.* 2014; Adams *et al.* 2020). No sampling was carried out on days with high rainfall because rain reduces the ability to detect animals, while on days with light or passing rain, the surveys were carried out as normal (Adams *et al.* 2020; Narváez and Zapata-Ríos 2020).

Statistical analysis. Deer density was estimated using alternative models, which were chosen based on a detection function adjusted to the data from perpendicular distance measurements to individuals or groups of individuals in each transect (Thomas *et al.* 2010). The R package "Distance" (Buckland *et al.* 2015) was used, which provides four models [unif (unif), half-normal (hn), hazard-rate (hr), and negative exponential] for the detection function, and also allows the addition of series adjustment terms [(cosine (cos), hermite polynomial (herm), simple polynomial (poly), and null adjustments] to the model when the simple model ("key function") alone does not provide an adequate fit. The key function 'unif' was used. It can be used to perform strip transect analysis, but it is also useful for analyzing linear transect data if series adjustment terms are added (Buckland *et al.* 2015). Likewise, the ‹hazard rate› function was used because it has a 'shoulder' (Buckland *et al.* 2015). However, the key function 'negative exponential' was not used because it does not have a 'shoulder' (Buckland *et al.* 2015). Next, a comparative analysis was performed between different selected models with their respective series adjustments: unif (cos, poly), half-normal (cos, herm, poly), and hazard-rate (cos, herm, poly), to find the appropriate detection function.

A plausible and parsimonious model was selected based on the Akaike›s information criterion (AIC), goodness of fit (Cramér-von Mises test and the Quantile-Quantile plot) and the shape criterion of the detection function (presents a 'shoulder'). The model was chosen according to the criterion of parsimony, i.e., the one with the lowest AIC (Martínez *et al.* 2009). The Cramér-von Mises test was used to evaluate the difference between the empirical and theoretical distributions, rejecting the null hypothesis (< 0.05) (Buckland *et al.* 2015). The Q-Q plot compared the empirical distribution function (EDF) with the theoretical cumulative distribution function (CDF), considering the model to be inadequate if the points deviated from the reference line (Miller *et al.* 2019). Finally, the density per m^2 was calculated and transformed to ind km^{-2} for the three cover types in 2023 and 2024.

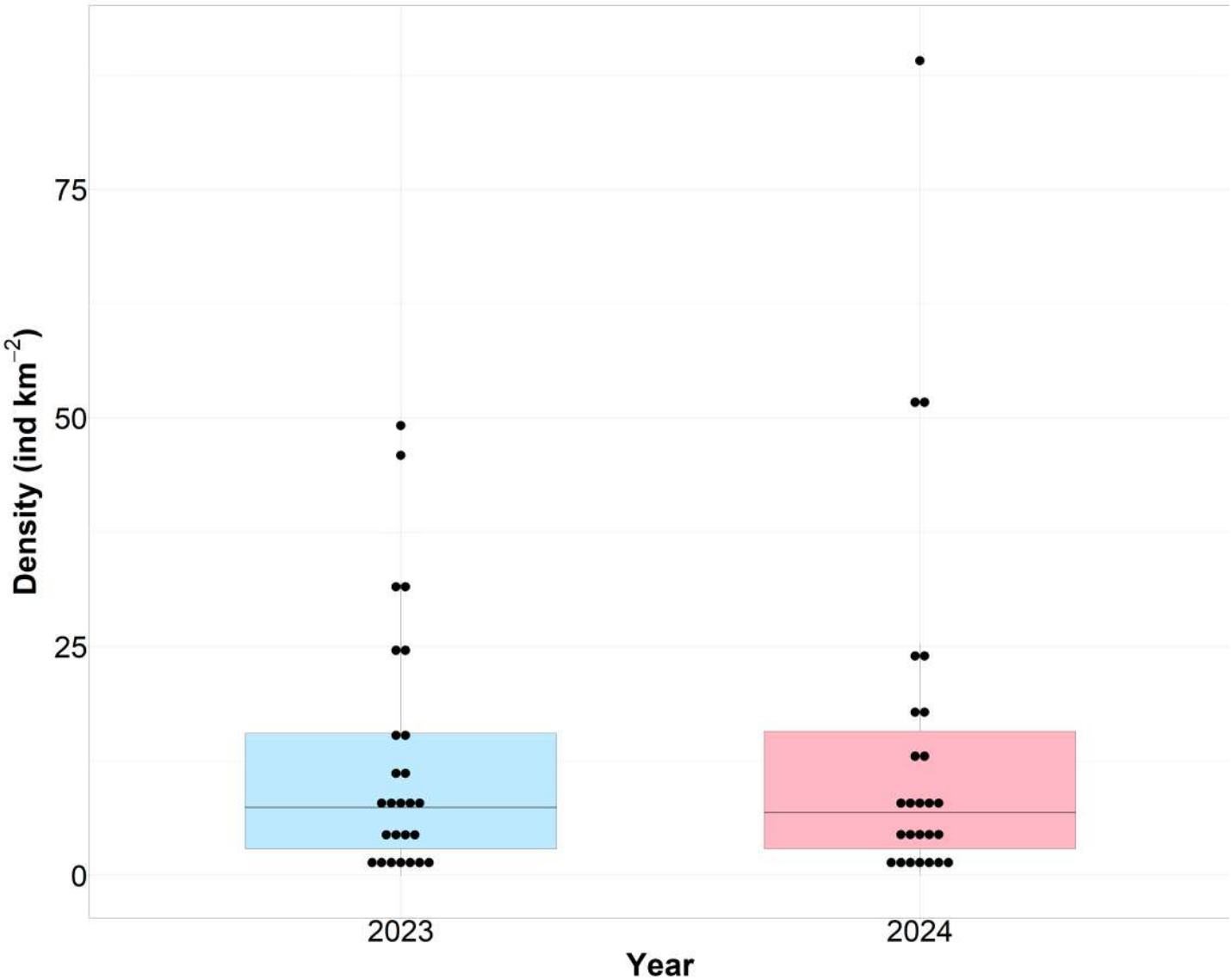

Figure 5. Box plot of white-tailed deer population density in the ACH Antisana transects for the years 2023 and 2024. Wilcoxon test for paired data, $p > 0.05$.

Prior to comparing the annual population density and density per cover type, the Shapiro-Wilk normality test was applied, which indicated that the data did not follow a normal distribution. The Wilcoxon test was used for both cases. To compare the population density between cover types in 2023 and 2024, the Kruskal-Wallis test was used separately for each year. All analyses were performed using statistical software R version 4.3.0 (R CoreTeam 2021).

Additionally, a heat map was generated in QGIS 3.10 (QGIS Development Team 2019). For this, the vector layers of transects by cover type were processed, incorporating density data and transect codes. These layers were then combined into a single file (.shp) and midpoints were generated along each transect. Next, the kernel density estimation algorithm was applied, using the midpoint layer as input, a kernel bandwidth of 2.4 km, and a pixel size of 30 m, and the entities were weighted according to density. Finally, a grayscale raster was obtained, the map was cropped to the study area, and the thermal intensity values were reclassified (QGIS Project 2020).

Results

A total of 45 km was covered in 27 transects in 2023 and 43 km in 26 transects in 2024. One transect could not be covered in 2024 due to logistical difficulties. During the surveys, 617 deer were recorded in 2023 and 470 deer in 2024. Group density decreased between 2023 and 2024, while individual density and expected group size increased. Similarly, estimated abundance was higher in 2024. Overall, the coefficients of variation were not high in both years, although slightly higher in 2024 (see Table 1). Model 4 (Hazard-rate + cos, see Supplementary 2) was selected as the most robust for both years, according to the AIC, Goodness of Fit, and Q-Q plot (Figure 4). Based on this model, average annual population densities were estimated, yielding values of 12.61 ind km^{-2} for 2023 and 14.25 ind km^{-2} for 2024, representing a population increase of 13.01% between the two years.

Population densities were calculated by cover type for each year (see Table 2). In both years, grassland concentrated the highest abundance and density of individuals, whereas

Table 1. White-Tailed Deer Population Density for 2023 and 2024 in the ACH Antisana

Parameters	Year 2023	Year 2024
Sampling Effort (km)	45	43
Number of Deer Groups Observed	161	92
Groups Density (groups km^{-2})	3.19 ± 0.26 (CV= 8.01%)	2.98 ± 0.35 (CV= 11.83 %)
Individuals Density (ind km^{-2})	12.61 ± 0.8 (CV= 6.03%)	14.25 ± 1.5 (CV= 10.41%)
Expected Group Size (ind group^{-1})	3.95 ± 0.27 (CV= 6.82%)	4.79 ± 0.33 (CV= 6.94%)
Estimated Abundance/Population (N)	1061.92 ± 64.08 (CV= 6.03 %)	1200.66 ± 125.05 (CV= 10.41%)

N: Estimated deer population over 84.24 km2 (individual density times total area)
CV: Coefficient of variation

shrubland and sandy areasshowed lower values. From 2023 to 2024, density increased in grassland and shrubland but decreased in sandy area. Coefficients of variation were higher in shrubland and sandy area, reflecting greater variability in these environments. In 2023, the shrubland recorded the highest density of deer (14.07 ind km^{-2}), while the sandy areas had the lowest density. In 2024, the highest density was recorded in grassland cover type and the lowest density in sandy areas. At the transect level, in 2023, transect TB1-23 had the highest density with 49.15 ind km^{-2}, whereas no individuals were recorded in transects TB5-23 and TE3-23. In 2024, transect TH14-24 showed the highest density with 89.05 ind km^{-2}, and no deer were recorded in transects TB3-24, TH1-24, and TH9-24.

The deer population density data for 2023 and 2024 did not follow a normal distribution ($p < 0.05$). The results of the Wilcoxon test (V = 170, $p = 0.901$) indicated that there were no significant differences between the deer densities recorded in 2023 and 2024 (Figure 5). No significant differences were detected in the densities recorded in both years in grassland (V = 76, $p = 1$), sandy (V = 4, $p = 0.75$), and shrubland (V = 6, $p = 0.438$) cover types (Figure 6). Kruskal Wallis tests ($\chi^2 = 0.684$, d.f. = 2, $p = 0.710$) indicated that there were no significant differences between the densities recorded in the three cover types in 2023 (Figure 7) or in 2024 ($\chi^2 = 0.166$, d.f. = 2, $p = 0.920$) (Figure 8).

Table 2. White-Tailed Deer Population Density by cover types for 2023 and 2024 in the ACH Antisana

Cover types	2023			2024		
	Observed Abundance	Estimated Abundance (N)	Density (ind km^{-2})	Observed Abundance	Estimated Abundance (N)	Density (ind km^{-2})
shrubland	91	125.09 ± 71.2 (CV= 56.92%)	8.04 ± 4.35 (CV= 54.1 %)	58	120.90 ± 71.03 (CV= 58.75%)	13.59± 7.99 (CV= 58.75%)
sandy areas	26	19.54 ± 10.57 (CV= 54.10%)	8.04 ± 4.35 (CV= 54.10 %)	13	14.82 ± 4.37 (CV= 29.49%)	6.09 ± 1.80 (CV= 29.49%)
grassland	500	939.2 ± 219.16 (CV= 23.33%)	12.88 ± 3.01 (CV= 23.33%)	399	1203.33 ± 435.57 (CV= 36.20%)	16.50 ± 5.97 (CV= 16.20%)

N: Number of deer in each cover type per year, calculated from the density and the corresponding area (grassland: 72.92 km^2, shrubland: 8.89 km^2, sandy areas: 2.43 km^2).
CV: Coefficient of variation

The shrubland had deer densities ranging from 0 to 49 ind km^{-2} in 2023 and from 0 to 50 ind km^{-2} in 2024. The sandy areas recorded values between 0 and 14 ind km^{-2} in 2023 and between 2 and 8 ind km^{-2} in 2024. The grassland recorded values between 0 and 45 ind km^{-2} in 2023 and between 0 and 89 ind km^{-2} in 2024. In 2023, the highest densities (up to 49 ind km^{-2}) were concentrated in the central region of the study area, decreasing progressively towards the west and north, where no individuals were recorded (Figure 9). The southwest zone had areas with densities of up to 45 ind km^{-2}, while in the southeast, a small area with densities of up to 24 ind km^{-2} was identified. In 2024, the general pattern remained the same, with the highest densities (up to 89 ind km^{-2}) located in the southwest region of the study area, followed by the central region. In the southeast, an area with densities of up to 52 ind km^{-2} was recorded, while the north and northwest continued to show low or zero densities.

Discussion

Our findings differ slightly from those reported for 2018 and 2019 in the ACH Antisana, where using direct methodologies (counts at observation points) and indirect methodologies (fecal accumulation rate, standing fecal culture, and remote fecal sampling), deer population densities ranging from 7.91 ind km^{-2} to 11.31 ind km^{-2} were reported (Tellkamp *et al.* 2019). The differences in results could be due to the sampling times used. White-tailed deer are considered a facultatively or semi-gregarious species, forming small and variable groups depending on season, sex, and behavioral context (Saalfeld *et al.* 2008). Because variation in group size can influence the precision of density estimates obtained through distance sampling, surveys conducted when deer are less aggregated may facilitate the detection of a greater number of groups and reduce variability in group size (Galindo-Leal and Weber 1998; Thomas *et al.* 2010; Buckland *et al.* 2015). The sampling

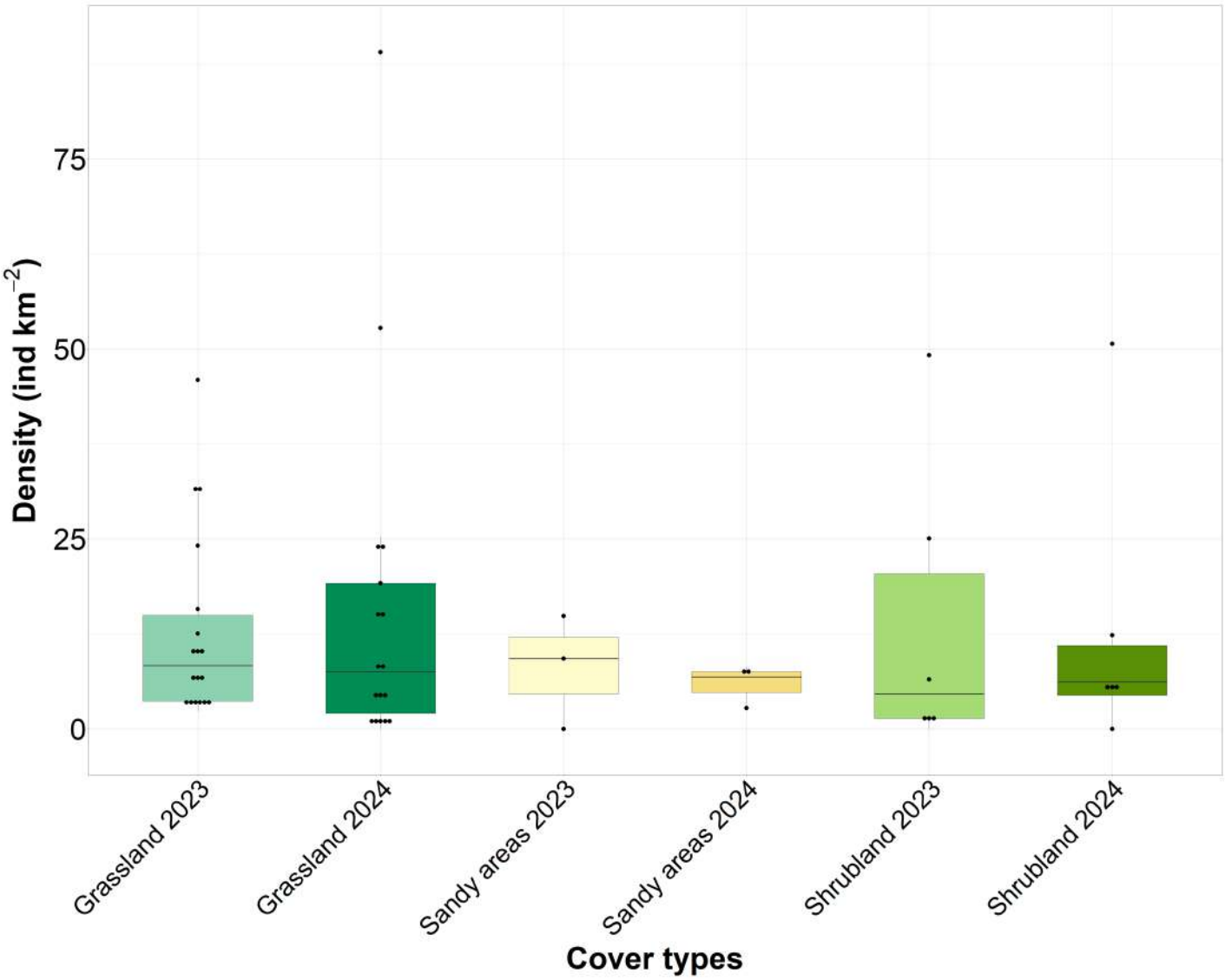

Figure 6. Population density of white-tailed deer in grassland, shrubland, and sandy areas in 2023 and 2024 in the ACH Antisana. Wilcoxon paired test $p > 0.05$ for shrubland, sandy areas, and grassland cover types.

carried out by Tellkamp *et al.* (2019) took place between 06:00 and 09:00 hrs and between 15:00 and 18:00 hrs. In contrast, our observations were made between 08:00 and 17:00 hrs, thus avoiding the species' peak grouping times, as population density estimates can be affected by variability in the size of the groups observed. This strategy may have facilitated the detection of more groups of smaller sizes, potentially improving to more accurate estimates.

Nevertheless, the density values obtained differ significantly from the findings of Albuja (2007) between 1996 and 1997, who, through counts of individuals in transects and observation points, reported a population density of 1.6 ind km^{-2} in the Oyacachi-Papallacta and Antisana moorlands, a figure well below that reported in this study. These differences in deer density after almost two decades could be attributed to various factors. During the 1990s, deer poaching was a relatively common practice in Antisana National Park and its buffer zone, as was intensive livestock management (Albuja 2007). However, control and patrolling by park rangers have been progressively strengthened over the years (Terán-Valdez *et al.* 2018; Grubb *et al.* 2020).

The ACH Antisana has shown a favorable recovery process, which would explain the high number of deer in the area. During the last decade, the reduction of grazing pressure through livestock removal (Crespo *et al.* 2010; Grubb *et al.* 2020) and, in 2017, ecological restoration of sandy areas in this protected area began with the planting of native plants, including the species chocho silvestre (*Lupinus pubescens*), chilca (*Baccharis caespitosa*), achupalla (*Puya clava-herculis*), and chuquiragua (*Chuquiraga jussieui)* which are part of the deer's diet (FONAG 2017). Also, since 2019, hunting control and the removal of introduced species, particularly livestock, camelids and horses have led to an increase in white-tailed deer populations (Crespo *et al.* 2010; Grubb *et al.* 2020). Also, the hunting control and the removal of introduced species, particularly livestock, camelids and horses have led to an increase in white-tailed deer populations (Grubb *et al.* 2020; Crespo *et al.* 2010). Additionally, 2021 human access to the protected area

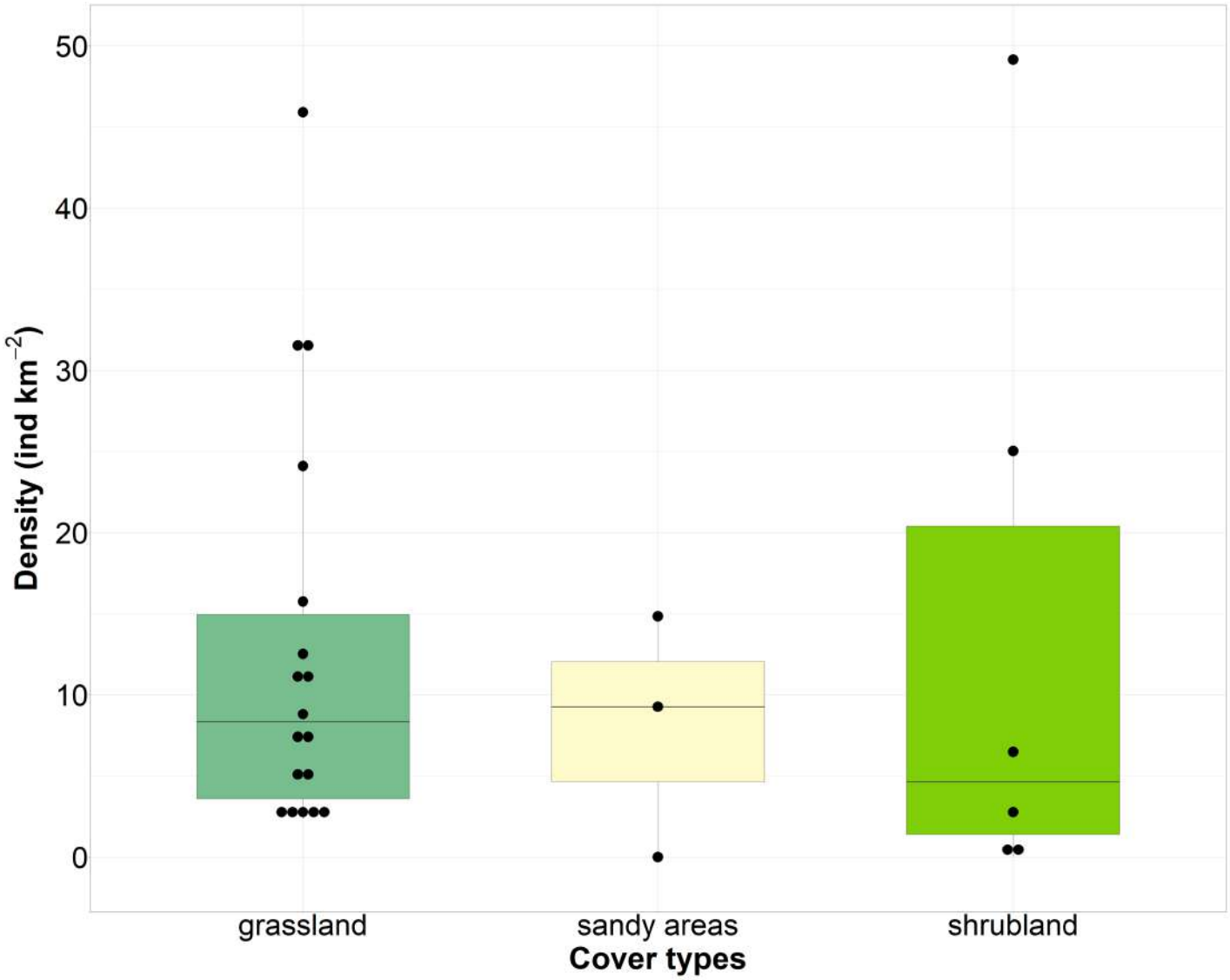

Figure 7. Population density of white-tailed deer in grassland, shrubland, and sandy areas of the ACH Antisana in 2023. Kruskal Wallis test $p > 0.05$.

was restricted, which favored the recovery of vegetation cover (FONAG 2021). This entire process could explain the increase in the deer population and the ability of a recovered ecosystem to sustain these populations. This suggests that the recovery of ecosystem structure and function likely plays a key role in maintaining current deer population levels.

Our density findings are consistent with those reported for other northern Andean páramo ecosystems. In Chingaza National Natural Park, Colombia, and Sierra Nevada de Mérida National Park, Venezuela, white-tailed deer densities ranging from 11.55 to 43 ind km^{-2} and groups of up to 50 individuals have previously been reported (Correa-Viana 1994; Mateus-Gutiérrez 2014). Similarly, in the ACH Antisana, groups of up to 49 white-tailed deer were recorded. However, more recent studies conducted in Chingaza National Natural Park revealed substantially lower densities, ranging from 0.16 to 2.09 ind km^{-2} depending on the study sector and estimation method (Carrillo-Villamizar and López-Arévalo 2024). These authors also reported that deer abundance has declined compared to previous estimates from the same park, where the highest abundances were recorded in 2004, suggesting important temporal and spatial variation in population density within páramo ecosystems. Despite these lower current densities, previous studies in Chingaza documented the formation of large groups of white-tailed deer, which is consistent with the large aggregations observed in the ACH Antisana (Mateus-Gutiérrez 2014; Carrillo-Villamizar and López-Arévalo 2024).

At the local scale, however, no significant differences in deer densities were detected between different cover types (grassland, shrubland, and sandy area) within each year, nor when comparing the same cover type between 2023 and 2024 suggesting that cover type alone does not strongly influence their distribution and abundance in the study area (Pérez-Moreno *et al.* 2020). Nevertheless, this does not imply a homogeneous spatial distribution. White-tailed deer are often associated with heterogeneous environments, where different vegetation types may provide complementary resources, including forage and

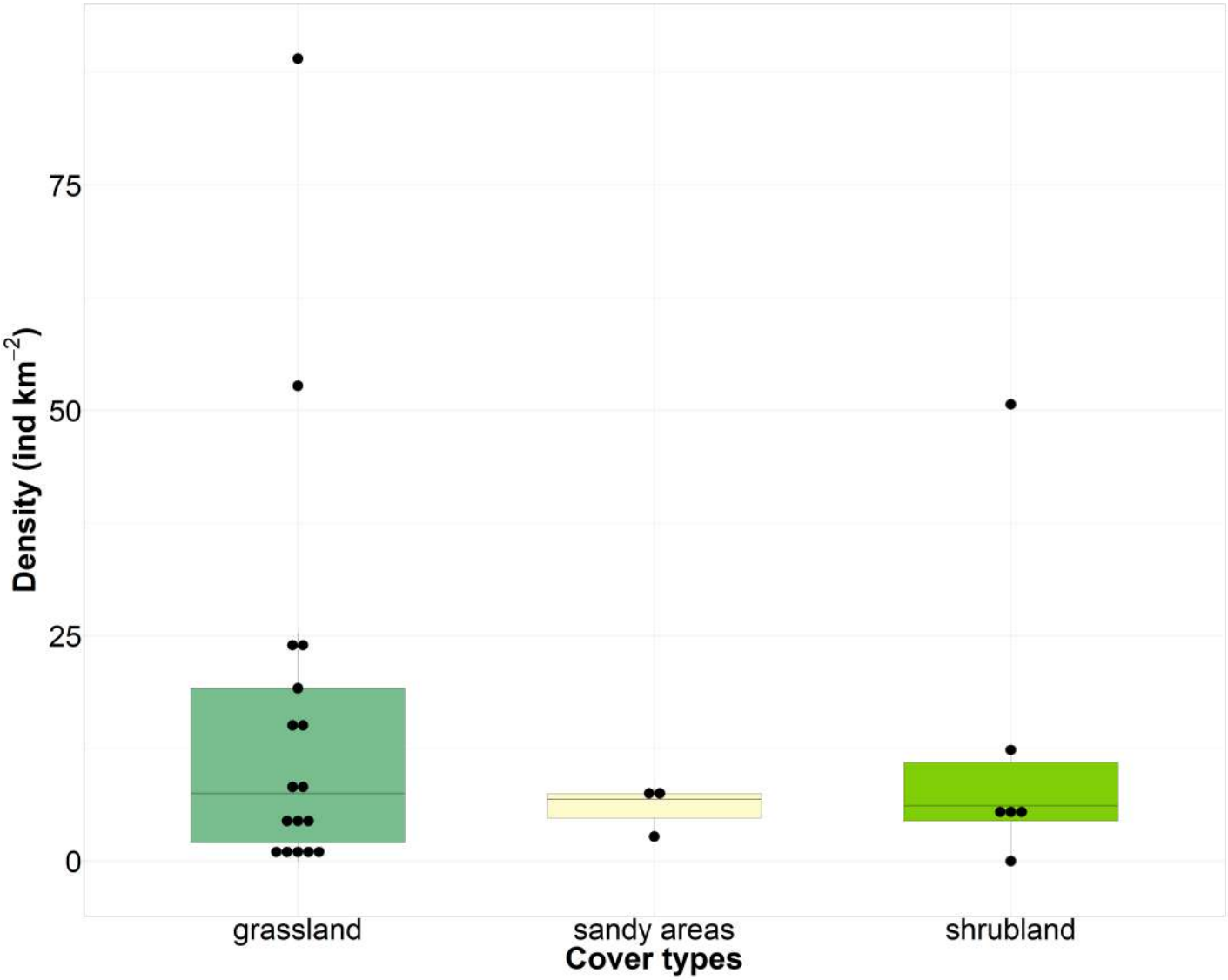

Figure 8. Population density of white-tailed deer in grassland, shrubland, and sandy areas in the Antisana Water Conservation Area in 2024. Kruskal-Wallis test $p > 0.05$.

cover (Fulbright and Ortega 2007; Gastelum-Mendoza *et al.* 2023). In this context, suggesting that patterns of deer density are driven more by the integration of resources of the landscape than by individual cover types. In Mexico, López-Téllez *et al.* (2007) reported variations in deer density in four locations: Mitepec and El Salado exhibited high densities (3.2–3.4 ind km^{-2}), while Huachinantla and Jolalpan exhibited low densities (0.1–0.5 ind km^{-2}). This may be due to spatial and temporal components (availability of vegetation cover, food, and water), which affect the deer distribution patterns (Garavito 2004; Chávez *et al.* 2022).

In this context, variations in cover types of use may also be influenced by population density and perceived predation risk. Under high-density conditions, females with young and other individuals may prefer areas with dense vegetation that provide greater protection (Garavito 2004). Although differences were not statistically significant, higher density values were observed in shrubland and grassland cover types.

Shrublands likely provide both shelter and high-quality forage resources, as white-tailed deer are selective feeders that preferentially consume young leaves and stems of shrubs, which are rich in protein and low in fiber and lignin (Fulbright and Ortega 2006; Pérez-Moreno *et al.* 2020). In addition, woody vegetation often constitutes a major component of their diet, and increases in shrub availability have been linked to population growth in some regions (Taylor and Hahn 1947; Ramírez *et al.* 1996; Arceo *et al.* 2005). Also, their dense structure may reduce detectability and increase protection from predators (Christopher *et al.* 2002; Vargas and Pedraza 2004; Ortiz-Martínez *et al.* 2005).

Grasslands are dominated by grasses and herbaceous plants that serve as key complementary food resources, particularly under conditions of increased competition or seasonal variation in forage availability (Brokx and Andressen 1970; Gallina 1990; Gallina and Bello 2010; Plata *et al.* 2009, 2011). Previous studies have also reported that white-tailed deer use shrublands primarily for cover and

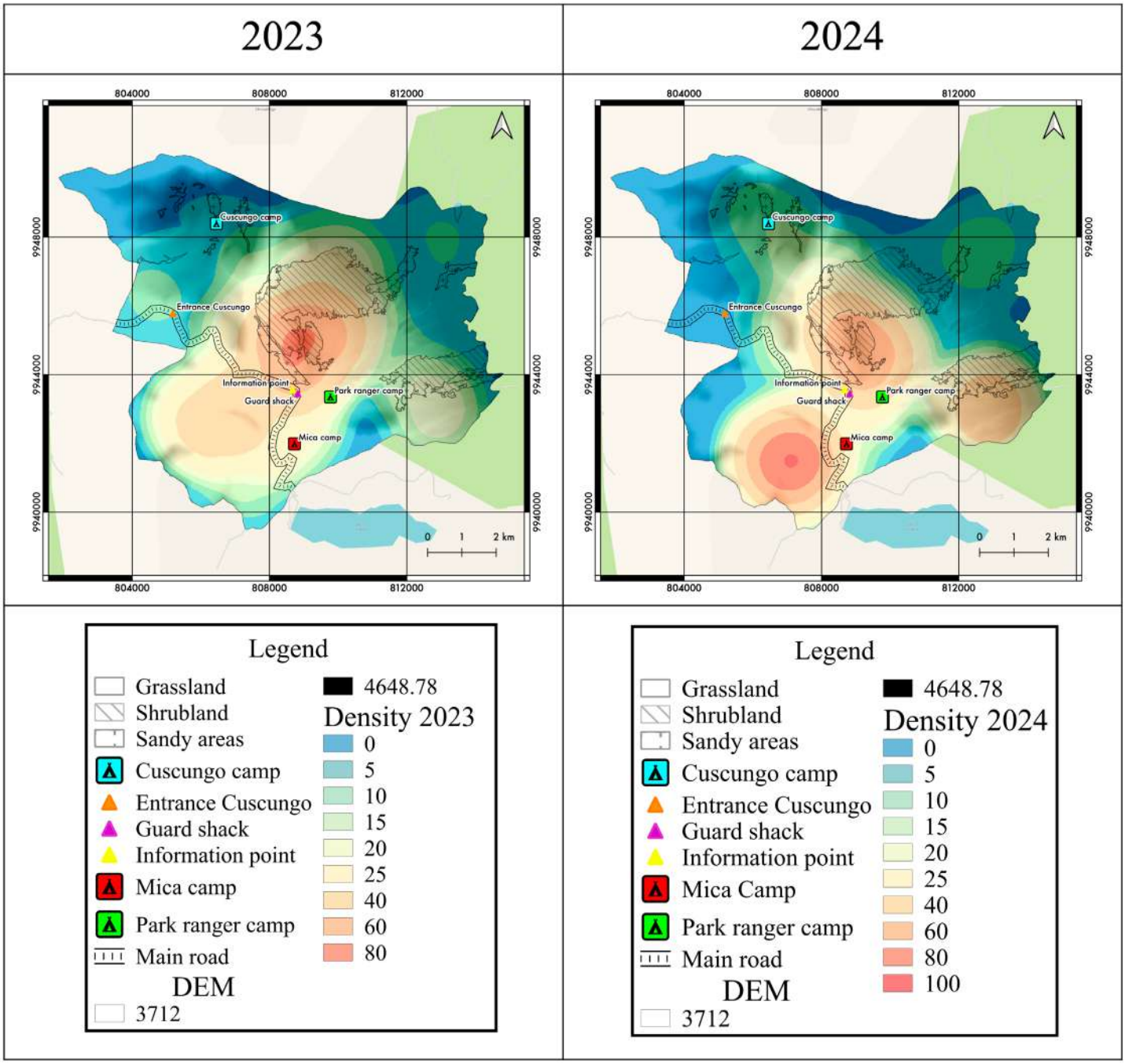

Figure 9. Heat maps of white-tailed deer population density in the grassland, shrubland, and sandy areas of the Antisana Water Conservation Area in 2023 and 2024. Warm colors indicate areas of higher population density, while cool colors represent areas of lower density. Density measured in ind km^{-2}

grasslands for feeding and resting (Correa-Viana 1994). Together, these findings suggest that observed density patterns are better explained by the combined availability of resources across vegetation types than by any single cover type component.

Additionally, other cover types may fulfill complementary functions. Harley (2019) mentions that deer species such as red deer (*Cervus elaphus*) take dust baths using their antlers to dig into the ground. Although this behavior has not yet been documented in white-tailed deer, sandy areas may provide opportunities for similar behavioral activities, as patches of sand with multiple tracks were observed during fieldwork, as if the deer had rolled around there. These observations highlight the need for further studies to confirm the potential role of sandy areas in the species' ecology.

The spatial distribution pattern observed in the ACH Antisana indicates a non-random aggregation of white-tailed deer within specific zones of the landscape. Higher densities concentrated in central and southwestern areas suggest the presence of core use areas within the protected landscape, while lower densities in peripheral zones may reflect reduced cover type suitability or higher levels of disturbance. Ungulate populations in heterogeneous and protected landscapes commonly exhibit core–periphery spatial structures, where individuals concentrate their activity in core areas that maximize access to resources

while minimizing exposure to disturbance and perceived risk (Boyce *et al.* 2016). This pattern coincides with the spatial distribution of anthropogenic pressures in many protected area systems, which are often not uniformly distributed but tend to be concentrated near the edges, while central areas can function as relative refuges with lower levels of disturbance (Dillon *et al.* 2025). In this context, the spatial aggregation of deer over the two years may reveal a non-uniform distribution in the study area, with higher values concentrated in central zones and lower densities toward the periphery. This indicates that broader spatial processes, such as landscape structure and the distribution of resources or disturbances, may play a more important role than cover type per se in shaping deer distribution patterns.

One limitation of this study is that sampling was conducted only during the last half of 2023 and 2024, which restricts a more complete understanding of the species' population dynamics throughout the year. According to López-Téllez *et al.* (2007), deer density estimates can vary between locations and transects depending on the sampling time. In this regard, it is worth noting that sampling took place during the transition between the dry and rainy seasons (October–December), a period in which changes in resource availability and individual activity may occur. Despite this temporal restriction, the study involved an extensive field phase, with a greater sampling effort than that carried out by Albuja (2007) and Tellkamp *et al.* (2019). To the best of our knowledge, there are no specific studies on the reproductive seasonality of the white-tailed deer in the ACH Antisana. Furthermore, the species' reproduction in temperate and cold zones begins in late November, peaking in December (Albuja 2007; Ugarte 2011; Chávez *et al.* 2022). During this period, males and females increase their activity in searching for mates, which can increase their detectability (Hölzenbein and Marchinton 1992; Galindo-Leal and Weber 1998). In 2024, sampling was extended until December 11, partially coinciding with the reproductive season and the beginning of the rainy season, which could partially explain the increase in deer density recorded that year, although the differences were not statistically significant. In contrast, most of the 2023 sampling was conducted in October, during the dry season and outside the breeding season.

Although despite the annual estimates showed good accuracy, evidenced by their low coefficients of variation, which reflect less variability in the data and therefore greater sampling reliability (Shechtman 2013), the smaller number of observations in some cover types may have influenced the ability to detect differences. In distance sampling, small sample sizes can affect the accuracy of the detection function and increase the variability of density estimates (Buckland *et al.* 2015). Therefore, although no significant differences were identified, the presence of subtle variations between cover types cannot be ruled out.

Long-term monitoring programs are essential to better understand the population dynamics of white-tailed deer and establish management strategies tailored to the conditions of each territory (Sánchez-Rojas 2009; Abrante-Hernández *et al.* 2013). These studies should include not only information on the population density of the species but also on its age structure, growth rate, and sex ratio, as this information is key to understanding the dynamics of any animal population (Ezcurra and Gallina 1981; Mandujano and Aranda 1993; Ojasti and Dallmeier 2000). We recommend implementing systematic protocols for estimating white-tailed deer population densities based on direct observation methods, as these provide reliable information on the number of individuals and are a useful tool for establishing long-term monitoring programs.

Conclusions

This study provides updated evidence of relatively high densities of white-tailed deer in the ACH Antisana compared to historical records of the zone, suggesting a positive population trend that is likely associated with ongoing ecological recovery processes, including vegetation restoration, reduction of anthropogenic pressure, and improved cover type conditions.

No significant differences in deer densities were detected among cover types or between sampling years, indicating that cover type alone does not strongly determine deer density. Instead, the species appears to respond to a heterogeneous landscape where cover type elements provide complementary resources that jointly support population maintenance.

Overall, these results highlight that white-tailed deer density is closely linked to ecosystem recovery processes and site heterogeneity. Our findings highlight the importance of continuing restoration and management actions within the ACH Antisana, especially in areas that have been historically degraded by anthropogenic activities. The conservation of this high Andean ecosystem not only guarantees the survival of the white-tailed deer but also contributes to the preservation of other species that depend directly or indirectly on it and to maintaining ecosystem services. Thus, promoting comprehensive conservation strategies in the paramo are essential to ensure the long-term dynamics of the ecosystem.

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Declaration of Artificial Intelligence Use

We declared that we used DeepL Translate for a preliminary translation. Also, we used ChatGPT for brainstorming and outlining purposes.

Author contributions

Michelle Alexandra Rodríguez-Noroña: Conceptualization, fieldwork, data curation, formal analysis, fund acquisition, research, methodology, project administration, resources, software, visualization, original draft writing, writing-reviewing and editing; David Andrés Herrera-Orellana: Fieldwork, data curation, writing-reviewing and editing; Paúl Monar-Barragán: Conceptualization, writing-reviewing and editing, fund acquisition, research, project management, resources, validation, writing-reviewing and editing; Juan Sebastián Restrepo-Cardona: Validation, writing, revision, and editing; Evelyn Edith Araujo: Conceptualization, acquisition of funds, research; Iván Vinicio Jácome-Negrete: Conceptualization, fieldwork, supervision, research, resources, validation, writing-reviewing and editing.

Supplementary data

SD1. Direct observation of white-tailed deer in cover types transects in the Antisana Water Conservation Area in 2023 and 2024: A) Observation with rangefinder, B) male white-tailed deer, C) Observation with rangefinder, D) Group of white-tailed deer, E) Data entry on field form, F) female white-tailed deer

SD2. Summary of detection function models fitted to Deer data. "CvM" stands for Cramér-von Mises, $\hat{P}_a$ is average detectability, se($\hat{P}_a$) is standard error. Models are sorted in ascending order according to their AIC.

SD3. Adjustments to the detection function (Hazard-rate + cos) to the perpendicular distance distribution data for the years 2023 and 2024.

SD4. Database collected in 2023 used to estimate the density of white-tailed deer (*O. virginianus ustus*) using the R-Distance package.

SD5. Database collected in 2023 used to estimate the density of white-tailed deer (*O. virginianus ustus)* in cover types (TH: grassland, TB: shrubland, TE: sandy areas) using the R-Distance package.

SD6. Database collected in 2024 used to estimate the density of white-tailed deer (*O. virginianus ustus*) using the R-Distance package.

SD7. Database collected in 2024 used to estimate the density of white-tailed deer (*O. virginianus ustus*) in cover types (TH: grassland, TB: shrubland, TE: sandy areas) using the R-Distance package.

SD8. R scripts used for density estimates and construction of white-tailed deer figures.

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Molecular identification of mesocarnivores through feces in the Sierra del Abra Tanchipa Biosphere Reserve, San Luis Potosi, Mexico

Octavio César Rosas-Rosas[1], Canuto Muñoz-García[2], Miguel Paul Conde-Hinojosa[3], Luis Antonio Tarango-Arámbula[1], Reyna Isabel Rojas-Martínez[4], Héctor Eduardo Benítez-Alemán[5], and Cesar Cortez-Romero[1,5*]

[1]Posgrado en Innovación en Manejo de Recursos Naturales, Colegio de Postgraduados, Campus San Luis Potosí, Iturbide No. 73, Centro, Salinas de Hidalgo, San Luis Potosí, México. C.P. 78620. E-mail: octaviocrr@colpos.mx (OCR-R); ltarango@colpos.mx (LAT-A); ccortez@colpos.mx (CC-R)
[2]Facultad de Medicina Veterinaria y Zootecnia. Universidad Autónoma de Guerrero. Pungarabato, Guerrero, México C.P. 40610. E-mail: cmunoz@uagro.mx (CM-G)
[3]Instituto de Ciencias Agropecuarias. Universidad Autónoma del Estado de Hidalgo. Avenida Universidad Km. 1 s/n Exhacienda Aquetzalpa, Tulancingo, Hidalgo, México. C.P. 43600. E-mail: miguel_conde@uaeh.edu.mx (MPC-H)
[4]Programa de Fitopatología, Colegio de Postgraduados, Campus Montecillo, km. 36.5 Carretera México-Texcoco, Montecillo, Texcoco, Estado de México, México. C.P. 56264. E-mail: rojas@colpos.mx (RIR-M)
[5]Posgrado en Recursos Genéticos y Productividad, Programa de Ganadería, Colegio de Postgraduados, Campus Montecillo, km. 36.5 Carretera México-Texcoco, Montecillo, Texcoco, México. C.P. 56264. E-mail: benitez.hector@colpos.mx (HEB-A)
[*]Corresponding author: ccortez@colpos.mx

Molecular identification of sympatric carnivore species through feces is not a simple task, especially for those of similar body size and similar droppings. This fact can be a disadvantage for several types of field research, including distribution, demography, and feeding habits. The objective of this study was to identify mesocarnivore species from feces collected in the Sierra del Abra Tanchipa Biosphere Reserve, San Luis Potosí, northeastern Mexico, using the PCR-RFLP technique. We collected 125 fecal samples from roads and latrines during February-May 2018, November 2018, and February 2019. DNA was extracted and a fragment of the cytochrome *b* gene was amplified with two pairs of primers: one specific for five Neotropical feline species and the other for the universal carnivore. To include control samples, DNA was extracted and amplified from hair follicles of the following species: captive ocelot (*Leopardus pardalis*), bobcat (*Lynx rufus*), jaguarundi (*Puma yagouaroundi*), margay (*Leopardus wiedii*), gray fox (*Urocyon cinereoargenteus*), domestic species, dogs (*Canis lupus familiaris*) and cats (*Felis catus*), and one sample from tissue of puma (*Puma concolor*). The PCR products from the control samples were sequenced to identify the restriction enzymes *Hpa II*, *MluC I*, *Hae II*, and *Mbo I,* which were used for the PCR-RFLP. Identification of restriction fragments was performed by banding patterns for each species on 2 % agarose gels. A total of 108 samples were identified (86.4 % of the total collected): 82 (75.3 %) *L. pardalis*, 11 (10 %) *U. cinereoargenteus*, 6 (5.5 %) *Puma concolor*, 6 (5.5 %) *P. yagouaroundi*, and 3 (2.7 %) *L. wiedii*.

Keywords: Feces, felids, molecular tools, restriction enzymes

La identificación molecular de carnívoros simpátricos a partir de heces no es una tarea sencilla, especialmente para aquellas con tamaño corporal y excrementos similares. Esto puede ser una desventaja para investigaciones de campo, distribución, demografía y de hábitos alimentarios. El objetivo de este estudio fue identificar especies de mesocarnívoros a partir de heces recolectadas en la Reserva de la Biosfera Sierra del Abra Tanchipa, San Luis Potosí, noreste de México, mediante la técnica de PCR-RFLP. Se recolectaron 125 muestras fecales de caminos y letrinas, durante febrero-mayo de 2018, noviembre de 2018 y febrero de 2019. Se extrajo ADN y se amplificó parte del gen citocromo b del ADN mitochondrial con dos pares de primers: uno específico para cinco especies de felinos neotropicales y el otro universal para carnívoros. De las muestras testigo se extrajo y se amplificó ADN de folículos pilosos de ocelote (*Leopardus pardalis*), gato montés (*Lynx rufus*), jaguarundi (*Puma yagouaroundi*), tigrillo (*Leopardus wiedii*) y zorro gris (*Urocyon cinereoargenteus*) en cautiverio; de especies domésticas como perros (*Canis lupus familiaris*) y gatos (*Felis catus*), así como de una muestra de tejido de puma (*Puma concolor*). Los productos de PCR de las muestras testigo se secuenciaron para identificar las enzimas de restricción *Hpa II*, *MluC I*, *Hae II* y *Mbo I*, las cuales fueron utilizadas en la técnica PCR-RFLP. La identificación de fragmentos de restricción se realizó mediante patrones de bandas en geles de agarosa al 2 % para cada especie. Se identificó un total de 108 muestras (86.4 % del total recolectadas): 82 (75.3 %) *L. pardalis*, 11 (10.0 %) *U. cinereoargenteus*, 6 (5.5 %) *P. concolor*, 6 (5.5 %) *P. yagouaroundi* y 3 (2.7 %) *L. wiedii*.

Palabras clave: Enzimas de restricción, félidos, heces, herramientas moleculares

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Predators are highly specialized animals that have developed traits to capture and subdue their prey. Mammals of the Order Carnivora are characterized by having teeth capable of cutting and slicing, as they have sharp carnassial teeth and highly developed canines (Kitchener 1991; Ceballos and Oliva 2005). This order encompasses 245 recent terrestrial species, grouped into 107 genera and 13 families (Wilson *et al.* 1995; Bellani 2020). We found in Mexico six of the 37 world species (Ceballos and Oliva 2005), of which the Felidae family is the most morphologically specialized (Bellani 2020). In general, felids are top predators within ecosystems, since

they keep the ecosystem in balance by controlling the population size of primary prey, influencing the diversity and dynamics of the plant community and, consequently, its diversity (Wang 2002; López-Pérez *et al.* 2021).

Medium-sized carnivores (<20 kg), known as "mesocarnivores," are more numerous than large carnivores, both in species richness and abundance, and in their behavior and ecology, given their small size and ability to thrive in diverse habitats. However, these species are assumed to have a lower ecological impact and, consequently, mesocarnivores have received little or no attention (Emmons 1988; Roemer *et al.* 2009). Among the mesocarnivores of felids are: ocelot (*Leopardus pardalis* Linné 1758), margay (*Leopardus wiedii* Schinz 1821), and jaguarundi (*Puma yagouaroundi* Geoffroy Saint-Hilaire 1803). These medium-sized felids have a neotropical distribution and inhabit a wide variety of habitats (de Oliveira 1998; Bianchi *et al.* 2011; Peña-Mondragón and del Val 2022). On the other hand, some canids have a wide distribution across the American continent, including coyote (*Canis latrans* Say 1823) and gray fox (*Urocyon cinereoargenteus* Schreber 1775), which are considered sympatric species that occupy diverse habitats within the same region. Coexistence of these species makes it difficult to identify their feces in the field by shape and color (Alberts *et al.* 2017) and, consequently, makes it difficult to describe their diets and to determine whether they may share certain prey preferences.

The study of wildlife, particularly of elusive species such as carnivores, represents a significant methodological challenge. Conventional methods of direct capture and handling can be costly, logistically complex, and potentially harmful to the individuals studied (Paez *et al.* 2021). In response to these limitations, non-invasive techniques have become increasingly relevant in wildlife research and population monitoring. Among the most widely used tools are camera traps, track transects, hair snares, and fecal collection (Torres-Romero *et al.* 2018). Comparative studies have shown that camera traps are significantly more efficient than live-capture traps and comparable in effectiveness to other non-invasive methods, but only provide information on the ecological aspects of felines; collected data do not distinguish between species or sex (Wearn and Glover-Kapfer 2019), being particularly valuable for detecting nocturnal species and populations at low density. Hair snares, for example, have demonstrated their potential in tropical ecosystems of Mexico for sampling felid populations, including records of rarely detected species such as the jaguarundi and the margay (Garcia-Alaniz *et al.* 2009). Taken together, these minimally invasive approaches (including camera trapping and genetic identification) detect a similar number of individuals compared to conventional trapping, with additional advantages in animal welfare and cost reduction (Paez *et al.* 2021).

Identification of signs, including tracks, burrows, hair, and feces, is an indirect, non-invasive technique that allows researchers to study the biological and ecological aspects of a species in a given ecosystem (Torres-Romero *et al.* 2018). Differentiating feces of Neotropical felids is complicated by their great morphological similarity (Alberts *et al.* 2010; Aranda-Sánchez 2012). Morphological characteristics such as diameter, length, and disjoint segments of feces may guide field identification; however, in many cases morphometric patterns cannot be a reliable technique to distinguish among different sympatric species (Akrim *et al.* 2018). Furthermore, in habitats with similarly sized sympatric carnivores, misidentification of fecal samples in the field is frequent and can lead to significant bias in research results (Laguardia *et al.* 2015), with direct implications for management and conservation decisions.

To address this problem, molecular scatology techniques have been developed to identify species from DNA present in intestinal epithelial cells adhered to the outer surface of feces (Reed *et al.* 1997). These techniques can be used to establish species distributions, model habitat requirements, analyze diet, estimate abundance and population density, and are important for population and conservation analyses (Rodgers and Janečka 2013). Molecular scatology consists of a genetic analysis of fecal samples to extract genetic material (DNA) from an individual without physical contact, thus determining the species, sex, and population size, among other parameters (Nagata *et al.* 2005; Alberts *et al.* 2010; Bach *et al.* 2022). Since DNA obtained from fecal samples is often degraded by environmental conditions, the use of multiple molecular markers is critical for obtaining more reliable identifications (Rodríguez-Castro *et al.* 2020). Among the most frequently used mitochondrial markers for the identification of Neotropical species are regions of the cytochrome *b* gene and, more recently, primers for a region of the ATP6 gene under a DNA mini-barcoding approach (Alberts *et al.* 2017).

Molecular studies offer a more accurate method, such as PCR-RFLP, because they use specific primers (Mukherjee *et al.* 2010). In this way, PCR-RFLP (where a PCR with common primers is followed by restriction digestions targeting species-specific motifs). PCR-RFLP is a technique that differentiates organisms by analyzing patterns derived from the cleavage of a previously amplified DNA strand with restriction enzymes or endonucleases. If two organisms differ in the distance between sites cut by a particular restriction enzyme, the lengths of the fragments will differ when the DNA is digested with the endonuclease (Bidlack *et al.* 2007). The similarities or differences in the patterns generated in an agarose gel can be used to differentiate sequences obtained from sympatric species. Several studies have evaluated and applied this approach in carnivore communities worldwide. In Europe, reliable non-invasive methods based on nested PCR of a mitochondrial D-loop region, followed by restriction enzyme digestion, were developed to differentiate morphologically similar sympatric mustelid species (Gómez-Moliner *et al.* 2004). Researchers in India developed primers for felids and canids targeting the 16S rRNA region of the mitochondrial

genome. They also selected restriction enzymes that differentially cut this region for various species, generating diagnostic banding patterns on agarose gel (Mukherjee *et al.* 2010). For Andean felids, Cossíos and Angers (2006) demonstrated the utility of PCR-RFLP for discriminating feces of sympatric species, while for Neotropical felids with broader distributions, Roques *et al.* (2011) developed the RCP-PCR protocol — a single-tube multiplex PCR system that generates species-specific banding patterns on agarose gel — achieving high identification success rates for puma, jaguar, jaguarundi, and ocelot/margay feces. These precedents confirm the viability and versatility of PCR-RFLP as a non-invasive monitoring tool for carnivores across different biogeographic contexts.

Therefore, due to the great diversity of carnivores distributed in the Sierra del Abra Tanchipa Biosphere Reserve, San Luis Potosí, Mexico, a specific protocol is required to accurately identify its feces. The objective of this research was to identify mesocarnivore species from fecal samples collected using the PCR-RFLP technique.

Materials and methods

Study Area. The Biosphere Reserve Sierra del Abra Tanchipa (RBSAT) is a natural protected area (NPA) located in the municipalities of Ciudad Valles and Tamuín, San Luis Potosí, and Antiguo Morelos, El Mante, Tamaulipas, which encompasses about 21,464.44 hectares (22° 24′-22° 03′ N, 90° 59′-98° 53′ W). The vegetation types include tropical deciduous forest, medium subdeciduous forest, low subevergreen forest, tropical oak forest, palm forest, and grassland (de Nova-Vázquez *et al.* 2018).

Collection and preservation of samples. Feces and Hair follicles. We collected fecal samples every two weeks from February to May 2018, November 2018, and February 2019. We conducted field surveys along transects on the main roads in the western section of the RBSAT. We placed feces collected in acid-free paper bags and labeled them, including location, date, collecting time, and habitat type; samples were stored at room temperature.

To validate the extracted DNA from fecal samples, we used a set of genetic material known as "witness samples." For this purpose, we used hair follicles from captive ocelot, bobcat, jaguarundi, margay, gray fox, and puma fur. Chapultepec Zoo, Ciudad de México, donated follicle samples. We also used follicles from local dogs and house cats. We stored the samples in 70% ethyl alcohol.

DNA extraction. Feces. We extracted DNA from 125 field-collected fecal samples using the QIAamp DNA Stool Mini Kit from QIAGEN (QIAGEN®, Mexico) using a protocol modified by Chaves *et al.* (2010) and divided them into two days. On the first day, we cut fine fragments of the cortex of each sample (an average of 200 mg), using a new scalpel, forceps, and a disposable Petri dish. We placed the samples in a 2 mL Eppendorf tube, added 1.5 mL of ASL buffer and mixing gently. Some samples had a large amount of hair and insoluble material, which had to be dissolved in 4 mL of ASL buffer. A 1.5 mL aliquot was taken after the sample was dissolved in a 2.0 mL Eppendorf tube, and then the sample was incubated at 65 °C for 12 h. On the second day, the sample was centrifuged at 6000 x *g* for three min. Subsequently, 1.5 mL of the supernatant was transferred to a new 2.0 mL Eppendorf tube, and an Inhibitex (buffer) tablet was added until it was completely dissolved. After a 1-minute incubation at room temperature, the mixture was centrifuged at 6000 x *g* for 12 min. Subsequently, 25 µL of proteinase K and 600 µL of the supernatant from the pellet precipitation performed earlier were added to the Eppendorf tubes containing the sample, and the mixture was carefully mixed to obtain a homogeneous solution. Next, we added 600 µL of buffer AL to the same tube and incubated at 70 °C for 15 min. After the incubation time, we added 600 µL of 100 % ethanol and stirred for 15 s to form a homogeneous mixture. We transferred 600 µL of the above mixture to a QIAamp spin column with a 2 mL collection tube and centrifuged at 6000 x *g* for one minute. We repeated these steps until the entire sample was filtered. Subsequently, we transferred the column to a clean collection tube, then added 500 µL of buffer AW1 and centrifuged at 6000 x *g* for one minute; the filtrate was discarded. Again, we added 500 µL of buffer AW2, centrifuged at 6000 x g for two min, and discarded the filtrate. Then, we transferred the filtrate column to a 1.5 mL Eppendorf tube and performed two washes within the column with 60 µL of buffer AE directly on the membrane. It was left to incubate for one hour at room temperature for each wash, where we obtained a final volume of 120 µL with DNA in the Eppendorf tube, identified and stored at -20 °C.

For this research, we used two pairs of oligonucleotides; the first pair was an oligonucleotide specific for five species of Neotropical felids (MxCtF 5´-CCATCCAACATCTCAGCATGATG-3´ and MxCtR 5´-GAGGCTCCGTTGGCATGTAT-3´), which was developed by Garcia-Alaniz (2009), where fragments of the cytochrome *b* gene with 165 bp, considering fragments between 148 bp and 486 bp from mitochondrial DNA. These fragments are reported in GenBank with accession numbers FJ490206 (165 bp) puma (*Puma concolor*), FJ490207 (165 bp) ocelot (*Leopardus pardalis*), FJ490208 (165 bp) jaguarundi (*Puma yagouaroundi*) and FJ490209 (165 bp) margay (*Leopardus wiedii*).

The second pair of oligonucleotides, from universal carnivores, amplified a fragment of the mitochondrial DNA cytochrome *b* gene (HCarn200; 5´-ATTCAGCCRTARTTAAC-GTC–3´) (Bidlack *et al.* 2007), used in conjunction with another (CanidL1; 5´-AATGACCAACATTCGAAA-3´) (Paxinos *et al.* 1997). These two oligonucleotides amplified fragments of 234 bp, corresponding to the 148 bp and 486 bp fragments from mitochondrial DNA. These oligonucleotides amplified fragments of the aforementioned species, and we also amplified for coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*) and bobcat (*Lynx rufus*), as well as for domestic dog (*Canis lupus familiaris*) and domestic cat (*Felis catus*).

Hair follicles. We extracted DNA from all control samples

and directly amplified using the Phire Animal Tissue Direct PCR Kit (Termo Fisher Scientific™, Mexico). Samples were dried at room temperature and cut with a clean scalpel to no more than 5 mm in length from the start of the follicle. We placed ten follicles in 1.5 mL Eppendorf tubes, where 25 µL of 2x Phire Animal Tissue PCR Buffer (Termo Fisher Scientific™, Mexico), 25 µM of each oligo, and finally, we added 1 µL of Phire Hot Start DNA Polymerase (Termo Fisher Scientific™, Mexico).

DNA Amplification. Feces samples were amplified by PCR, in a 25 µL final volume reaction containing 100 ng μL^{-1} of DNA, 1X TAE reaction buffer (Tris Acetate-EDTA, Sigma Aldrich®, Mexico), 2.5 mM $MgCl_2$, 0.2 mM (200µM) of dNTP (Promega®, USA), 20 µM of each primer, and 1.5 units per reaction of Taq polymerase (Sigma Aldrich®, Mexico). We used an initial incubation in a thermocycler (Tc-512 brand; Techne®) at 94 °C for three minutes, followed by 40 cycles at 94 °C for one min, 54 °C for one min and 72 °C for two minutes, and a final extension at 72 °C for five minutes. In each test, we added a positive and a negative control. For follicles, we placed the DNA samples in a thermal cycler (Tc-512 brand; Techne®), with an initial denaturation temperature at 98 °C for five minutes, followed by 40 cycles at 98 °C for five seconds, 54 °C for five seconds, and 72 °C for 20 s and a final extension at 72 °C for 1 min.

Although the DNA extracted from the fecal samples had low DNA integrity, the concentration in many samples was greater than 100 ng μL^{-1}; those with concentrations below 50 ng µL-1 were discarded from the study. In some samples with a sweep, PCR amplification could be performed with the specific primer (fragment size of 165 bp) for felids developed by Garcia-Alaniz (2009), from which 91 % of the samples were amplified (Supplementary data SD1). The samples that did not amplify with the previous primer were subjected to amplification with the universal carnivore primer (fragment size of 234 bp) reported by Bidlack *et al.* (2007) which allowed the amplification of the remaining 9.0 % (Supplementary data SD2).

PCR-RFLP technique. We sequenced amplicons from control samples and imported into NebCutter software v. 2.0 (https://academic.oup.com/nar/article/31/13/3688/2904148) to determine the type of restriction enzymes used to obtain restriction fragments, generate positive controls, and identify fecal samples. The enzymatic reactions had a final volume of 15 µL, containing 1.5 µL of 10x buffer, 1 µL of enzyme (5U), 2 µL (20 ng of DNA) of PCR product, and Milli-Q water (Merck®, Mexico) for the remainder of the reaction volume. We added positive and negative controls to each reaction.

Agarose gels. We run by electrophoresis DNA samples, PCR products, and PCR-RFLP in a vertical chamber (Model MVG-216-33; C.B.S Scientific CO®, USA) in agarose gels 1 % in TAE running buffer (Sigma Aldrich®, Mexico) at 247 volts for 90 min, with a molecular weight marker (GeneRuler 1 kb DNA Ladder; Thermo Scientific®, USA). We stained the gel with ethidium bromide, then added it to the agarose gel. Three µL of the amplicon and 3 µL of Green GoTaq® Flexi buffer (Promega©, Wisconsin, USA) were deposited in each well. We viewed the gel on a photodocumenter (Quantum®) with Vision Capt® software.

Results

DNA extraction and amplification from feces. The PCR enabled amplification of DNA from 108 of 125 samples collected (60 from roadsides and 65 from a latrine).-

DNA extraction and amplification from hair follicles. We performed DNA amplification from follicles as control samples using the Phire Animal Tissue Direct PCR Kit with both pairs of primers, and we observed amplification for all samples. With the universal carnivore primer used by Bidlack *et al.* (2007), we also observed that the feline follicle samples amplified (234 bp), but the band in the agarose gel was fainter, unlike the bands from the canid follicles sampled (Figure 1).

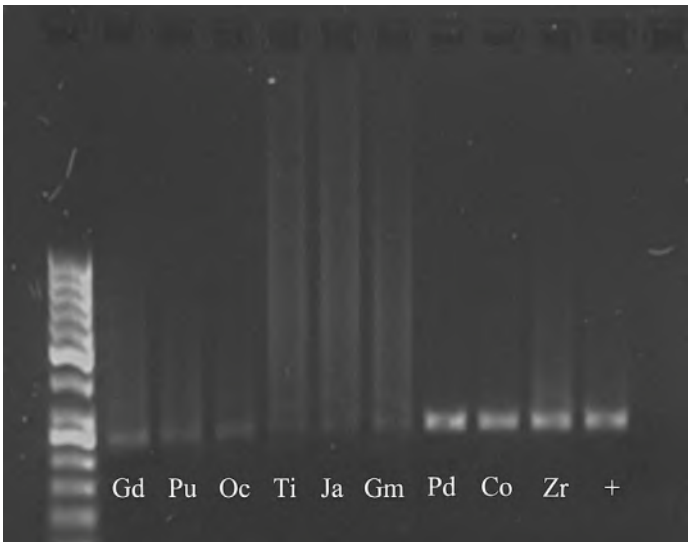

Figure 1. Amplification of samples from follicles using the universal carnivore primer. 50 bp molecular marker (Mm). Gd: Domestic cat, Pu: Puma, Oc: Ocelot. Ti: Margay, Ja: Jaguarundi, Gm: Bobcat. Pd: Domestic dog, Co: Coyote, Zr: Gray fox, + Positive control (Pd), - Negative control.

In the case of the specific primer developed by Garcia-Alaniz (2009), a faint band was observed for the domestic cat and the bobcat. In wild canids, we did not observe amplification. For the ocelot, margay, puma, and jaguarundi control samples, the bands were completely labeled (165 bp, Figure 2). Amplifications of control samples from nine carnivore species for the mitochondrial DNA cytochrome *b* gene are shown in Table 1.

Identification of restriction enzymes. We sequenced PCR-amplified control samples to identify the restriction enzymes used in the PCR-RFLP. The sequences obtained were subjected to BLAST (Basic Local Alignment Search Tool) analysis to verify similarities with other reported cytochrome *b* gene sequences in GENBANK. Similarities ranged from 88% to 98%.

After verification of the sequences of the cytochrome *b* gene fragments for different mesocarnivore species,

Table 1. Fragment of the cytochrome *b* gene sequences obtained from DNA amplification of follicles from nine carnivore species.

Species	Sequence	bp	GenBank accession number
Puma concolor (Puma)	GAGGGGATGATCTCCTCCCAACATTTCAGCATGATGAAACTTTGGCTCCCTACTAGGGGTCTGCCTAATCCTA-CAAATCCTAACCGGCCTCTTCCTGGCCATACACTATACATCAGACACAATGACTGCCTTTTCATCAGTCACTCA-CATCCTGTCGGACGTCAAACTACG	165	FJ490206
Leopardus pardalis (Ocelot)	TGGGTCCTTATTAGCAGTTTGCCTACTTTTACAGATTCTCACAGGCCTCTTTCTAGCCATACACTATACATCAGA-TACAGCAACCGCCTTTTCCATCATTTACCCAGATCTGCCGCGACGTCAACTATGGCTAAATCATCCGATACAT-ACATGCCAACGGAGCCTCA	165	FJ490207
Puma yagouaroundi (Jaguarundi)	GGTTCCTTAATAGGAGTCTGCCTAATCCTACAGATTCTGACCGGCCTATTCCTAGCCATACACTACACATCAGA-CACAACAACCGCCTTCTCATCAGTCACCCACATCTGCCGCGACGTTAACTAGGGCTGAATCATCAGATATATA-CATGCCAACGGGGCTTCCA	165	FJ490208
Leopardus wiedii (Margay)	GGCTCCTTATTAGGAGTTTGCCTAATCCTACAAATTCTCACTGGCCTTTTCCTAGCTATACACTACACATCAGA-CACCACAACCGCTTTCTCATCAGTTACCCACATCTGCCGCGACGTCAACTATGGCTGAATTATCCGATACCTA-CATGCCAACGGAGCCTCC	165	FJ490209
Felis catus (Domestic cat)	AATCACACCCCGTTATCAACATTATTACTCACTCATCCATCGATCTACCTAGCCCATCTTACATCTCAGCATGAT-GAAACTTCGGCTCCCTTCTAGGAGTCTGCCTAACCTTACAAATCCTCACCGGCCTCTTTTTGGCCATACACTA-CACATCAGACACAATAACCGCCTTTTCATCAGTTACCCACATCTGTCGCGACGTTAACTACGGCTGAATAATC-CGATATTTACAC	402	AJ300702
Lynx rufus (Bobcat)	AAAGTCACACCGTATTACTAAAGTATACAACCGATAATTCATCGATTCACCCGCCCCATCAACATCTCAGCAT-GATGAAACTTCGGCTCCCTGCTAGGAGTCTGCCTAATCCTACAGATCCTCACCGGCCTCTTCCTAGCCATACAC-TACACATCAGACACGCTAACCGCCTTTTCATCAGTCACCCATATCTGCCGCGACGTTAACTATGGCTGAATAATC-CGATAC	226	DQ471842
Canis familiaris (Domestic dog)	AAAACCCACCCACTAGCCACAATTGTTAATAACTCATTCATTGACCTCCCAGCGCCGTCTAACATCTCTGCTT-GATGGAACTTCGGATCCTTACTAGGAGTATGCTTGATTCTACAGATTCTAACAGGTTTATTCTTAGCTATGCAC-TATACATCGGACACAGCCACAGCTTTTTCATCAGTCACCCACATCTGCCGAGACGTTAACTACGACTGAATTATC-CGCA	277	DQ236096
Canis latrans (Coyote)	CACCCACTATGCAAAGTTGTCAATAACTCATTCATTGACCTCCCAGCGCCATCTAACATCTCTGCTTGATG-GAATTTCGGATCCTTACTAGGAGTATGCCTGATTCTACAGATTCTAACAGGTTTATTTTTAGCTATACACTATA-CATCGGACACAGCCACAGCTTTTTCATCAGTCACCCACATCTGTCGAGACGTTAACTACGGCTGAATTATCCGC-TACATACA	253	KT946976
Urocyon cinereoargenteus (Gray fox)	AAAACCCACCCGCTCGGTAAAATCGTCAACAGCTCGTTCATCGACCTACCTGCACCATCTAACATTTCTGCAT-GATGGAACTTCGGGTCCCTGTTAGGAATCTGCCTTATTCTACAGATTATAACAGGCTTATTCTTGGCCATACAC-TATACATCAGATACCGCTACAGCCTTTTCATCCGTTACCCATATCTGTCGAGACGTTAACTACGGCTGAATAATC-CGCTATAT	226	DQ471838

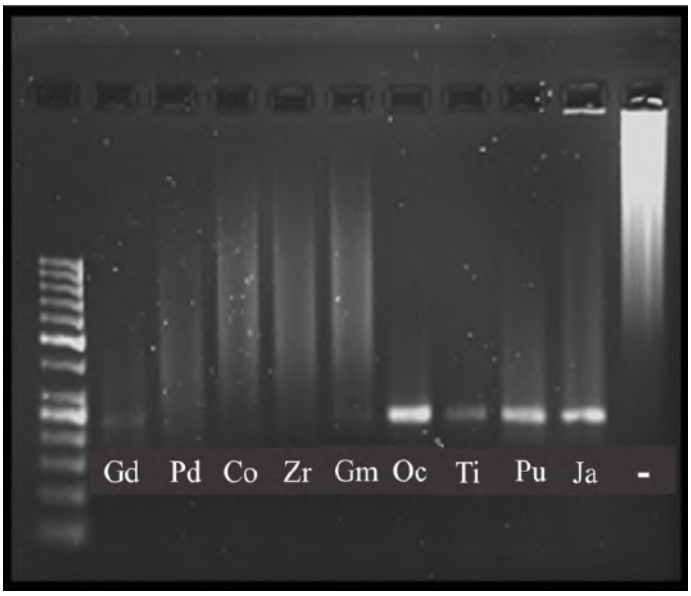

Figure 2. Amplification of follicle samples using the feline-specific primer. 50 bp marker, Gd: Domestic cat, Pu: Puma, Oc: Ocelot. Ti: Margay, Ja: Jaguarundi, Gm: Bobcat. Pd: Domestic dog, Co: Coyote, Zr: Gray fox, (-) Negative control.

we performed PCR-RFLP method. Then we searched for restriction enzymes (endonucleases) using the online NebCutter v. 2.0 program (New England, Biolabs), which cut at different points. We used these sequences to generate banding patterns to differentiate each species. In the first case, we obtained the sequences for ocelot, margay, jaguarundi, and puma. We identified the *Hpa II* enzyme, which had no effect on the ocelot sequences. We cut the puma sequence at base 85, which generated two fragments of similar size, in the same way, *Hpa II* cut the sequence obtained from jaguarundi at base 42, which generated two restriction fragments: the first with a length of 42 bp and the second with a length of 125 bp (Figure 3a). For the sequences obtained from ocelot and jaguarundi, we identified *Hae III* enzyme to be used in conjunction with the *Mbo I* enzyme, which cut the ocelot sequence at base 44, generating two restriction fragments. The first one with a length of 44 bp and the second one of 121 bp. This allowed to differentiate the three fragments generated by this same pair of enzymes for the ocelot sequence, two of 61 bp and one of 46 bp (Figure 3b).

Validation of restriction enzymes. This procedure was first verified using PCR products obtained from follicular samples, then tested with PCR products from fecal samples, and amplified with the species-specific primer for Neotropical felids for identification. We observed a band in the agarose gel, since both fragments in the use of the *Hpa II* enzyme for puma are similar in size (85 bp and 87 bp) (Figure 4a). For the same enzyme in the jaguarundi, we also observed two bands, each of a different size: the lower band is 42 bp and appears faint, while the upper band is 125 bp (Figure 4a). When restriction enzymes *Hae III* and *Mbo I* were used together to select the sequences of the ocelot and

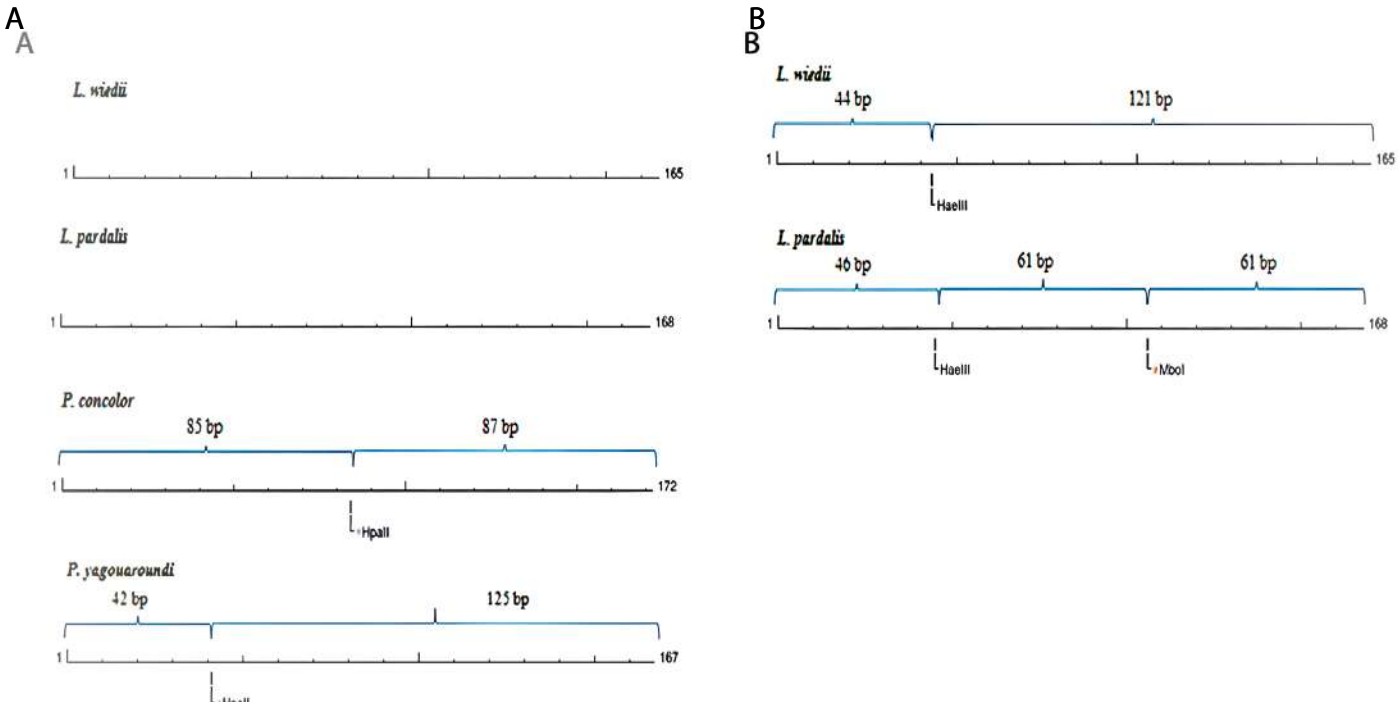

Figure 3. Cutting patterns created by the restriction enzymes *Hpa II*, *Hae II*/*Mbo I* for four feline species: (3a) fragments for margay, ocelot, puma, and jaguarondi, and (3b) fragments for margay and ocelot.

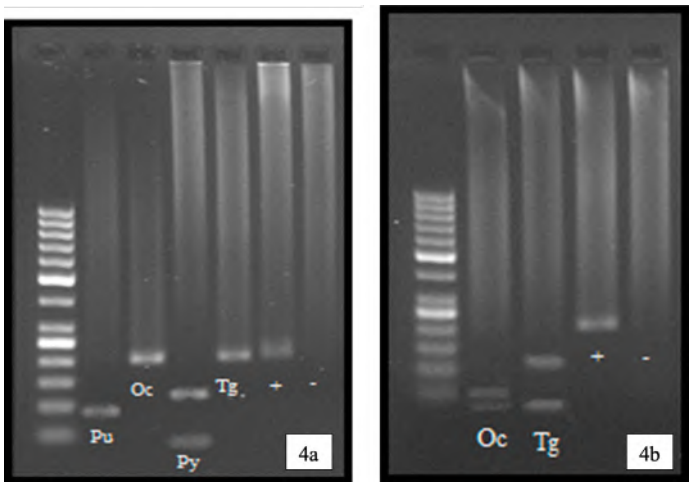

Figure 4. Amplification of feline fecal samples. 50 bp marker. (a) Pu: Puma, Oc: Ocelot, Py: Jaguarundi, Tg: Margay. (b) Oc: Ocelot, Tg: Margay. Positive control (+), Negative control (-).

the margay, two bands were observed in the agarose gel for the ocelot, generated by three fragments: two of 61 bp, which means that only one band is observed, and another smaller fragment of 46 bp. We used this same pair for the margay sequence, where only the *Hae III* enzyme acted, and generated two easily visible bands in the agarose gel: one of 44 bp and a larger one of 121 bp (Figure 4b).

In the case of the samples amplified with the non-specific primer, we identified the enzyme *MluC I*. Additionally, we observed two restriction sites at bases 20 and 215 for the domestic dog, which generated three restriction fragments; the first was 20 bp in size, the second 195 bp, and the third 11 bp. We similarly observed in the coyote sequence two restriction sites at bases 72 and 209, which generated three fragments of 72 bp, 137 bp, and 18 bp, respectively (Figure 5a). The sequences of the gray fox, bobcat, and domestic cat were not cut by this enzyme, but they were cut by the enzymes *Hae III* and *Mbo I* when used together, which identified restriction zones at base 139 in the gray fox sequence, which generated two fragments: the first of 139 bp and another of 91 bp by the simple action of the *Hae III* enzyme. In the bobcat sequence, we found two restriction sites at the height of bases 116 and 128, which generated three fragments of 116 bp, 12 bp and 100 bp. The domestic cat sequence had three restriction sites at the height of bases 41, 127 and 138; therefore, we obtained four restriction fragments of 41 bp, 86 bp, 11 bp, and 95 bp (Figure 5b).

The follicle PCR products as control samples, and the PCR products of the DNA extracted from the fecal samples for identification, both amplified with the nonspecific primer, were subjected to the action of the aforementioned restriction enzymes, their products were placed on an agarose gel and separated by electrophoresis. The *MluC I* enzyme generated two visible bands in the domestic dog sample; one of approximately 195 bp and the second of 20 bp. For the coyote sample, three bands were easily observable: the first of 137 bp, followed by one of 72 bp, and the last, barely visible, of 18 bp. No action of this enzyme was observed in the gray fox, bobcat, and domestic cat samples (Figure 6a), which were subjected to the action of *Hae III* and *Mbo I* together to differentiate these three species. We observed in the gray fox the presence of two bands, one of 139 bp and the other of 91 bp. To differentiate the wildcat sample, is the only band that could be observed, generated by two restriction fragments, which have a size of 116 and

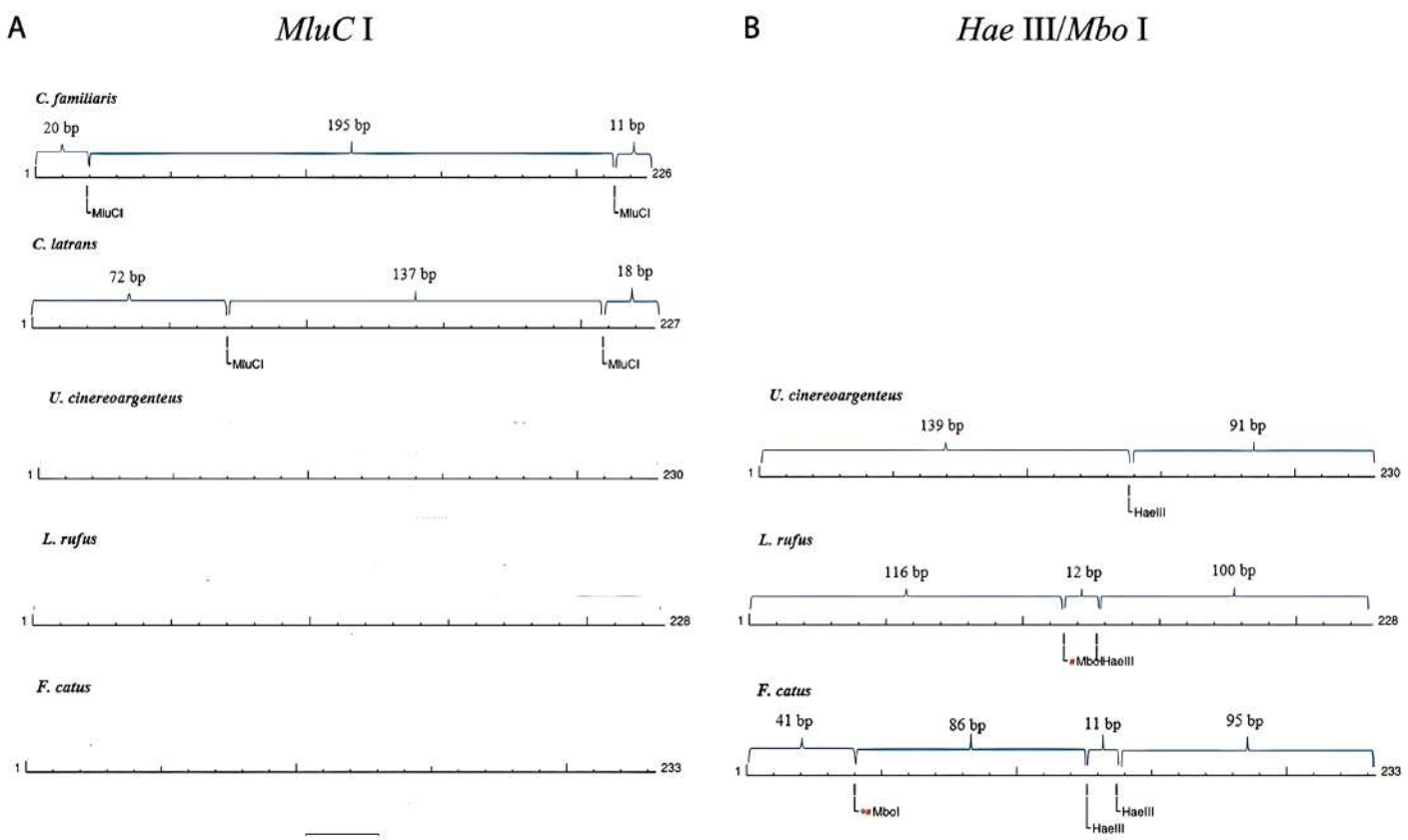

Figure 5. Cutting patterns created by the restriction enzymes *MluC* I and *Hae II/Mbo I* for sequences generated by the nonspecific primer; (5a) fragments for domestic dog, coyote, gray fox, bobcat, and domestic cat, and (5b) gray fox, bobcat, and domestic cat.

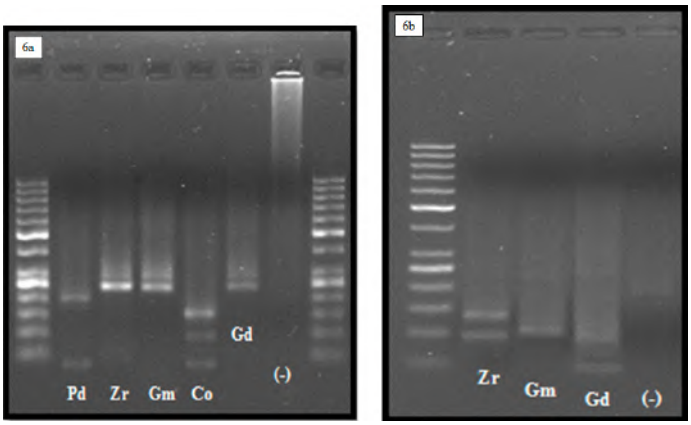

Figure 6. Amplification of feline follicle samples. 50 bp marker. (a) Pd: Domestic dog, Zr: Gray fox, Gm: Bobcat, Co: Coyote, and Gd: Domestic cat. (b) Zr: Gray fox, Gm: Bobcat, Gd: Domestic cat, (-) Negative control.

100 bp, because they are so similar in size, only one band is visible. In the domestic cat sample, we observed two bands: the first, formed by two restriction fragments of 95 and 86 bp, and the second band, barely visible, by a 41 bp fragment (Figure 6b).

Identification of mesocarnivores from fecal samples. Finally, we identified 108 samples (86.4 %) from a total of 125 feces collected in the field (60 on roads and 65 in a latrine), 82 (76.3 %) correspond to *L. pardalis*, 11 (10 %) to *U. cinereoargenteus*, 6 (5.5 %) to *P. concolor*, 6 (5.5 %) *P. yagouaroundi,* and 3 (2.7 %) to *Leopardus wiedii* (Figure 7).

Out of the 60 feces collected on roads, only 51 (85 %) were identified, corresponding to 35 (68 %) of ocelot, 3 (6%) of margay, 5 (10 %) of jaguarundi and 8 (16 %) of gray fox and, of 65 collected in a latrine, 57 (87 %) were identified, belonging to ocelot 47 (82.5 %), 6 (10.5 %) of puma, one (1.7 %) of jaguarundi, 3 (5.3 %) of gray fox (Figure 8).

Discussion

This study demonstrates the efficacy of PCR-RFLP for identifying mesocarnivores from fecal samples in the Sierra del Abra Tanchipa Biosphere Reserve (RBSAT), achieving successful identification in 108 of 125 collected samples (86.4%). The predominant species was the ocelot (*Leopardus pardalis*), representing 82 samples (75.3 %), followed by gray fox (*Urocyon cinereoargenteus*) with 11 samples (10 %), and puma (*Puma concolor*), jaguarundi (*Puma yagouaroundi*), and margay (*Leopardus wiedii*) each with 6, 6, and 3 samples (5.5 %, 5.5 %, and 2.7 %, respectively). Ocelot scats were most abundant on roads (68 % of 51 identified) and especially in latrines (82.5 % of 57 identified), reflecting their behavioral preference for trails in foraging and latrine use for territorial marking and intraspecific communication in Neotropical habitats, as documented by Emmons (1988), Kitchener (1991) and King *et al.* (2017).

These results confirm the sympatric presence of these mesocarnivores in RBSAT tropical deciduous and subdeciduous forests, aligning with prior distribution records for ocelots in the region amid ongoing habitat fragmentation from agriculture and human activities. The high ocelot prevalence suggests sustained

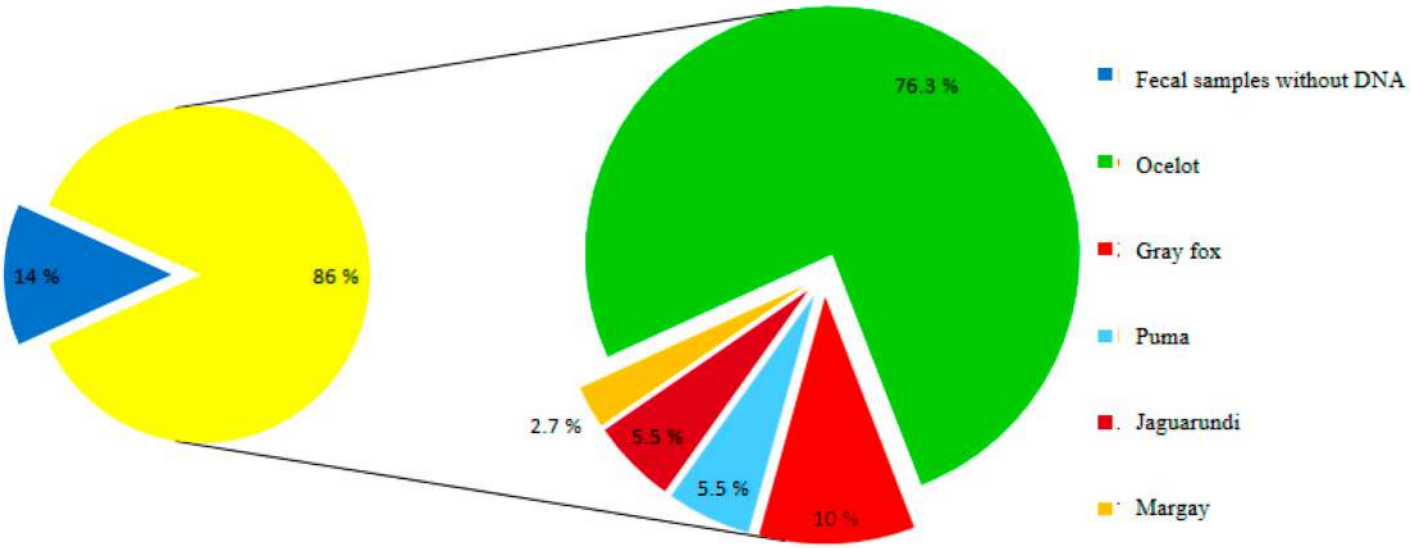

Figure 7. Percentage of samples of mesocarnivore species identified by PCR-RFL.

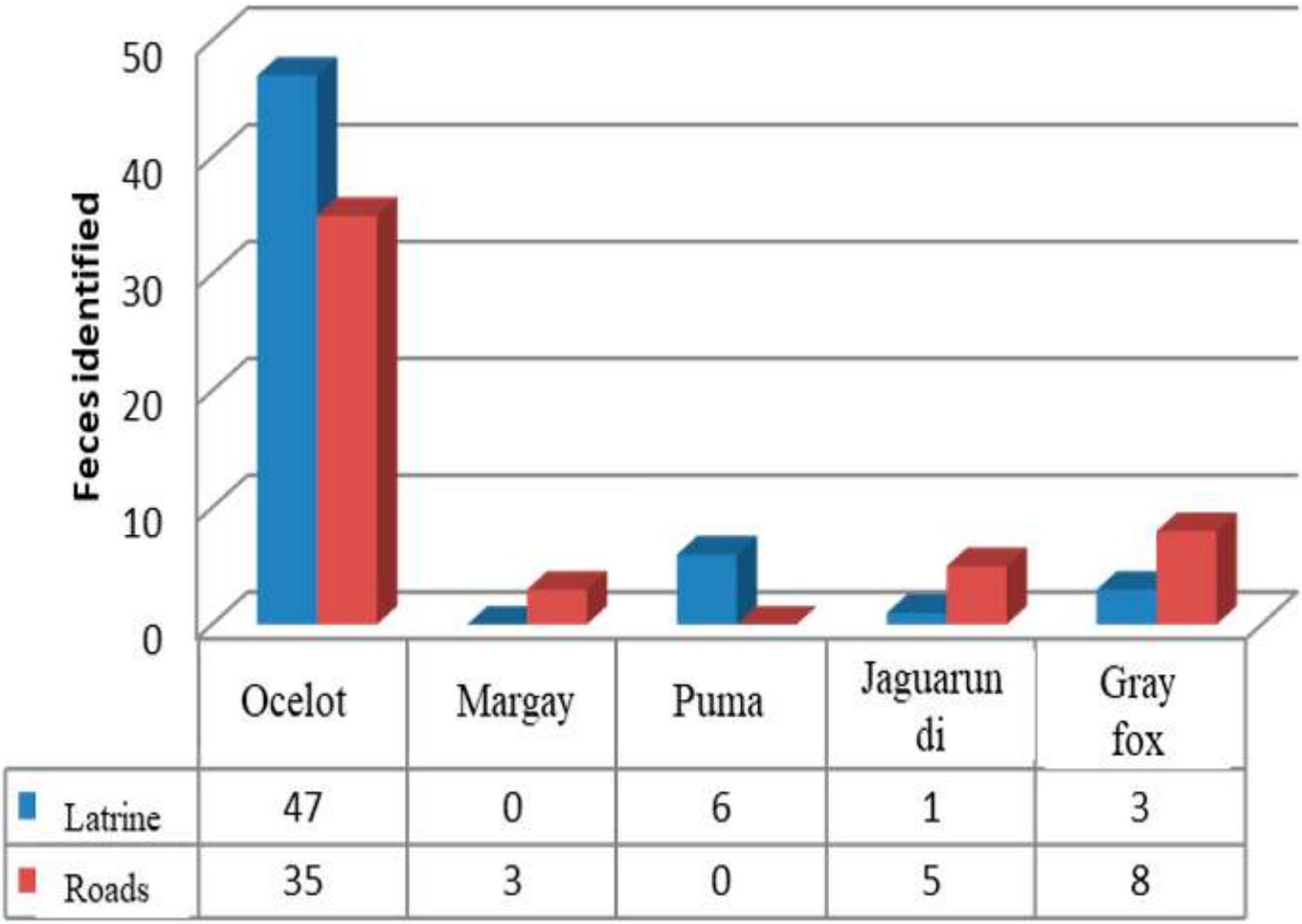

Figure 8. Comparison of feces identified in latrines and roads.

populations capable of regulating prey dynamics, though mesocarnivores generally receive less conservation attention than larger carnivores due to their adaptability and perceived lesser ecological impact (Roemer *et al.* 2009). Detection of puma and jaguarundi primarily in latrines highlights potential spatial overlap in scent-marking sites, offering opportunities for noninvasive monitoring of multi-species interactions, diet, and abundance in this protected area (Moreno and Giacalone 2006; Cacelin-Castillo *et al.* 2020).

DNA extraction from feces yielded fragmented but sufficient material (>100 ng μL^{-1} in most cases), enabled by a modified QIAamp protocol that enhanced lysis despite environmental degradation (Morin *et al.* 2001; Chaves *et al.* 2010). Amplification succeeded in 91 samples (73 %) with felid-specific primers (165 bp; Garcia-Alaniz 2009) and nine more with universal primers (234 bp; Bidlack *et al.* 2007), minimizing bias and capturing canids. Follicle controls validated enzyme specificity: *Hpa II* differentiated puma and jaguarundi; *Hae III*/*Mbo I* distinguished ocelot and margay; *MluC I* separated canids, with *Hae III*/*Mbo I* resolving gray fox, bobcat, and domestic cat patterns (Wilson *et al.* 1995).

PCR-RFLP provided high-resolution identification (86.4 % success) for morphologically cryptic scats, surpassing traditional methods prone to errors among similar-sized sympatric species (e.g., ocelot vs. margay; gray fox vs. domestic dog) (Rosas-Rosas *et al.* 2003; Haag *et al.* 2009; Aranda-Sánchez 2012). This technique's dual-primer strategy—specific for felids, universal for others—followed by targeted restriction digests (*Hpa II*, *MluC I*) generated diagnostic banding patterns without sequencing, proving cost-effective and field-applicable (Zuercher *et al.* 2003; Mukherjee *et al.* 2010). Comparable approaches achieved 86 % accuracy across seven carnivores (Zuercher *et al.* 2003) or Andean felids via 16S rRNA (Cossíos and Angers 2006), while hair-morphology keys reached only 52-70 % reliability (Ruell and Crooks 2007).

In contrast, metabarcoding offers broader taxonomic coverage but requires advanced sequencing infrastructure and risks contamination, whereas PCR-RFLP agarose gel visualization is suitable for resource-limited settings such as RBSAT studies on distribution, demographics, and feeding ecology (Mills *et al.* 2000; Cossíos and Angers 2006). Despite challenges such as low fecal DNA quality, strategic collection (roads/latrines), and controls mitigated failures, supporting scalable noninvasive scatology for mesocarnivore research in biodiverse, fragmented ecosystems (Davison *et al.* 2002). Future enhancements could integrate detection by trained dogs to boost sample recovery 5-15-fold (Long *et al.* 2007).

Conclusions and recommendations

Through identification and analysis of feces, we determined that methods based on molecular scatology, for identifying the origin of fecal samples, are successful methods since up to 90 % of the total samples can be identified when they are in good condition and properly preserved for analysis, in addition to reducing the risk of errors due to identifications based on associated track and sign. Indeed, it is the most accurate technique for the identification of feces collected in the field, therefore for describing food habits of sympatric carnivores. Currently, molecular techniques have decreased in cost, making them more accessible. The availability of kits and technologies reduces the time required to obtain and analyze results. The PCR-RFLP technique for identifying carnivore feces had an 86 % success rate. This could be because samples were selected based on lower levels of disintegration caused by environmental factors such as rain, high temperatures, and sunlight. In addition, the sampling was conducted during seasons with little rainfall. It is recommended that the PCR-RFLP technique for identifying fecal samples be performed on samples from the same sampling site, as discrepancies in banding patterns may occur among species from different populations, caused by variations in polymorphisms in the target sequences. BLAST testing of the obtained sequences is also recommended to avoid errors in fragment amplification. Increasing the number of samples by searching with the help of trained dogs could help achieve greater representativeness of some other species that are more difficult to identify and sample at a simple view. Our results support the identification of individuals through fecal samples in the field, where various species of mesocarnivores are present.

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Declaration of Artificial Intelligence use

The authors declare that they did not use any artificial intelligence tools in writing this article.

Autor contributions

Octavio C. Rosas-Rosas: conceptualization, study design and fieldwork planning, data collection, analysis and interpretation of the results, and preparation of the first draft of the manuscript. Canuto Muñoz-García: conceptualization, study design, and fieldwork planning; reviewed and provided critical revisions to the manuscript. Miguel Paul Conde-Hinojosa: conceptualization, reviewed, and provided critical revisions to the manuscript. Luis Antonio Tarango-Arámbula: conceptualization, study design and fieldwork planning, funding acquisition, reviewed and provided critical revisions to the manuscript. Reyna Isabel Rojas-Martínez: sample processing in the molecular biology laboratory and provided critical revisions to the manuscript. Héctor E. Benítez-Alemán: conceptualization, study design and fieldwork planning, sample processing in the molecular biology laboratory. Cesar Cortez-Romero: conceptualization, study design and fieldwork planning, funding acquisition, reviewed and provided critical revisions to the manuscript.

Supplementary data

SD1. Amplification of DNA extracted from fecal samples using the feline-specific primer (fragment size of 165 bp).

SD2. Amplification of DNA extracted from stool samples using the nonspecific primer (fragment size of 234 bp).

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Medium- to large-bodied mammals in the upper basin of the Barranca del Amatzinac, Hueyapan, Morelos, Mexico

Miguel A. Márquez-Rivera[1,2], Elizabeth Arellano[1], David Valenzuela-Galván[1], and Daryl D. Cruz[1*]

[1]Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos. E-mail: abrahamriveramamr@gmail.com (MAM-R); elisabet@uaem.mx (EA); dvalen@uaem.mx (DV-G).
[2]Facultad de Ciencias Biológicas, Universidad Autónoma del Estado de Morelos.
[*]Corresponding author: daryldavidcf@gmail.com

The Barranca del Amatzinac is the principal hydrological system in northeastern Morelos, crossing several municipalities, including the recently established Indigenous municipality of Hueyapan. Despite its ecological importance, reliable information on the diversity of medium- to large-bodied mammals—and other taxonomic groups—is lacking. Here, we present the first report on the diversity of medium- to large-bodied mammals and describe the activity patterns of species recorded in the upper basin of the Barranca del Amatzinac. We deployed 15 camera traps strategically across the upper basin and conducted 12 monthly sampling sessions from May 2023 to April 2024, each lasting one week. In parallel, we performed transect-based sign surveys (track and sign identification) with two walks per month over the same period. Species richness was estimated using Hill numbers. We also calculated proportional capture rates for each species recorded by camera trapping and encounter rates for each species recorded from signs and inferred activity patterns using the Diel.Niche package in R. In total, we documented 15 species of medium- to large-bodied mammals. With 1,183 trap-days, camera traps recorded 12 species, and nearly 264 km of transect walks yielded 11 species. Alpha diversity (α, using Hill numbers) was 6.57 for camera-trap records and 6.52 for sign surveys. The most common species were *Dasypus mexicanus*, *Didelphis virginiana*, and *Bassariscus astutus*. Consistent activity patterns were obtained for most of the photographed species, as well as seasonal changes in some taxa (*Canis latrans* and *Nasua narica*), suggesting temporal partitioning and responses to seasonal environmental variation. This study provides the first formal data on medium- to large-bodied mammals for the Indigenous municipality of Hueyapan and northeastern Morelos, establishing a baseline for future biological research in the area.

Keywords: activity pattern, Barranca del Amatzinac, camera trapping, capture rate, diversity, signs.

La Barranca del Amatzinac es el principal sistema hídrico en el noreste del estado de Morelos, atraviesa varios municipios, incluido el recientemente creado municipio indígena de Hueyapan. A pesar de su importancia ecológica, carece de información verídica sobre la diversidad biológica de mamíferos medianos y grandes, así como de otros grupos taxonómicos. Por ello, el objetivo de esta investigación fue presentar el primer reporte sobre la diversidad de mamíferos medianos y grandes, y describir los patrones de actividad de las especies registradas en la parte alta de la Barranca del Amatzinac. Se emplearon 15 cámaras trampa, distribuidas estratégicamente en la parte alta de la barranca. Se realizaron 12 muestreos, uno por mes, cada uno de una semana, desde mayo de 2023 hasta abril de 2024. Asimismo, se efectuó un muestreo de búsqueda por transectos (identificación de rastros), con dos recorridos mensuales durante el mismo periodo. La riqueza específica se calculó con base en los números de Hill. También se calcularon tasas proporcionales de captura para cada especie registrada mediante fototrampeo y tasas de detección para cada especie registrada a partir de rastros, y se inferieron los patrones de actividad utilizando el paquete Diel.Niche en R. En total se registraron 15 especies de mamíferos medianos y grandes. Con un esfuerzo de 1,183 trampa-días se identificaron 12 especies mediante fototrampeo, y 11 especies tras un esfuerzo de casi 264 km de recorridos por transecto. La diversidad alfa (α, usando números de Hill) fue de 6.57 para registros fotográficos y 6.52 para rastros. Las especies más comunes fueron *Dasypus mexicanus*, *Didelphis virginiana* y *Bassariscus astutus*. Se obtuvieron patrones de actividad consistentes para la mayoría de las especies fotografiadas, así como cambios estacionales en algunos taxones (*Canis latrans* y *Nasua narica*), lo que sugiere una partición temporal y respuestas a la variación ambiental estacional. Este trabajo aporta la primera información formal sobre la diversidad de mastofauna de talla media-grande para el municipio indígena de Hueyapan y el noreste de Morelos, y sienta las bases para futuras investigaciones biológicas en el área de estudio.

Palabras clave: Barranca del Amatzinac, diversidad, fototrampeo, patrón de actividad, rastros, tasa de captura.

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Although the state of Morelos is the second smallest of Mexico's federal entities, it harbors approximately 113 mammal species distributed across the region (CONABIO 2020; Guerrero *et al.* 2020, 2025), representing roughly 20% of the country's mammalian diversity. The region with the most biodiversity information is the Sierra de Huautla Biosphere Reserve—the most diverse area in the state—where ~66 mammal species have been recorded (CONANP and SEMARNAT 2005; Mason-Romo *et al.* 2008; Orozco-Lugo *et al.* 2013, 2014; Valenzuela-Galván *et al.* 2013, 2015, 2020; Guerrero *et al.* 2025), located in the southern portion of Morelos. In contrast, the forests of northeastern Morelos—dominated by temperate vegetation rather than by tropical dry forest, as in the south—are among the least studied in mammalogy, leaving a significant information gap regarding mammal diversity (Guerrero *et al.* 2020).

Accelerated urban expansion has prompted local communities to implement strategies to conserve their natural areas (Aguilar *et al.* 2000; Kays *et al.* 2022a). However, designing effective management and conservation mechanisms requires first identifying which species are present (Antos and Yuen 2014). In this regard, biological inventories of different taxonomic groups are essential to understand the structure and dynamics of local communities (Heywood and Watson 1995). The information they generate forms the basis for establishing conservation programs and actions, as well as for the sustainable use of biodiversity (Heywood and Watson 1995; Murillo *et al.* 2014).

The ecological importance of mammals is unquestionable: they participate in key processes such as pollination, seed dispersal, and trophic regulation, both as predators and prey (Rumiz 2010; Sánchez-Cordero *et al.* 2014; Escribano-Ávila *et al.* 2015; Cheyne *et al.* 2016). Moreover, many species are considered bioindicators of ecosystem quality (Gittleman *et al.* 2001; Cheyne *et al.* 2016). Although multiple methods exist to obtain records (e.g., specimen collection and track/sign identification; Walker *et al.* 2000; González 2005), the surge in the use of camera traps has proven particularly effective for inventorying species that are cryptic or occur at low densities (González 2005; Kays *et al.* 2022b). Camera trapping provides reliable estimates of species richness (Shek *et al.* 2007; Lyra-Jorge *et al.* 2008), especially for medium- to large-bodied mammals, and yields information on population dynamics (Varma *et al.* 2006), habitat use (Tobler *et al.* 2009), density (Trolle and Kery 2005), abundance (Marnewick *et al.* 2008), and activity patterns (Maffei *et al.* 2007; Arispe *et al.* 2008).

In addition, camera trapping can be complemented with other sampling methods. The use of indirect evidence such as signs (footprints, scats, carcasses, trails, burrows, and territorial marks) increases detection probability, particularly for species with low photographic capture rates or movement patterns that do not coincide with camera placement (Lyra-Jorge *et al.* 2008; Seidlitz *et al.* 2021). Furthermore, indirect signs can provide complementary information on habitat use and diet; genetic information can even be obtained through fecal analyses (Grajales-Tam and González-Romero 2014; Seidlitz *et al.* 2021; Ramírez-García *et al.* 2025). The combination of both methods reduces biases associated with interspecific differences in detectability and provides a more comprehensive assessment of mammal assemblages, strengthening richness estimates and the ecological interpretation of community structure (Lyra-Jorge *et al.* 2008; Burton *et al.* 2015; Cruz-Bazán *et al.* 2025).

Medium- to large-bodied mammal fauna includes non-volant terrestrial and arboreal species that are usually identifiable without capture and generally weigh >250 g (medium-sized) and >20 kg (large-sized) (Rumiz *et al.* 1998; Morrison *et al.* 2007; Benchimol 2016). This group exerts direct and indirect effects on vegetation and other species through herbivory, predation, and seed dispersal (Dirzo and Miranda 1990; Ripple *et al.* 2014). In Morelos, medium- to large-bodied mammals comprise approximately 29 species, of which 18 have potential presence in northeastern Morelos (Mason-Romo *et al.* 2008; Altamirano-Álvarez *et al.* 2009; Valenzuela-Galván *et al.* 2020).

The Barranca del Amatzinac is a key hydrological feature in northeastern Morelos (CONAGUA 2009; Velázquez-Gutiérrez *et al.* 2015). It crosses several municipalities, including the recently established Indigenous municipality of Hueyapan (CONAGUA 2009; Consejo Municipal de Hueyapan 2022). The system originates at ~3,900 masl on the slopes of the Popocatépetl volcano; its upper basin lies within the municipalities of Hueyapan and Tetela del Volcán (CONAGUA 2009; Velázquez-Gutiérrez *et al.* 2015). It is characterized by rugged relief and an assemblage of oyamel fir, pine, and pine–oak forests, vegetation typical of the state's high-elevation temperate zones (CONABIO and UAEM 2004; Rzedowski 2006). These communities are part of the Trans-Mexican Volcanic Belt, one of Mexico's most important biogeographic regions. Despite this, studies on medium- to large-bodied mammals in northeastern Morelos remain scarce (CONAGUA 2009; Guerrero *et al.* 2020), likely underestimating the group's true diversity. From a biocultural perspective, generating this information is key for municipalities and communities to recognize, value, and protect their natural heritage.

Accordingly, we focused on the medium- to large-bodied mammals of the Barranca del Amatzinac. Our objectives were to (i) inventory species and estimate species richness, diversity, and capture rates using camera trapping, and assess encounter rates using sign surveys, and (ii) characterize diel and seasonal activity patterns of the species recorded by camera trapping at the study site.

Materials and methods

Study area. The Amatzinac basin originates on the slopes of the Popocatépetl volcano at approximately 3,900 masl. It traverses several municipalities and communities in the northeastern and eastern regions of the state of Morelos. The basin covers an area of 241.55 km^2, extends 62.57 km in length, and is divided into three sections: upper, middle, and lower (CONAGUA 2009; Velázquez-Gutiérrez *et al.* 2015) (Figure 1).

This study was conducted in the upper part of the Amatzinac basin, within the Indigenous Communal Land of Hueyapan. Characteristic of temperate forests, this area harbors fir, pine, and pine–oak forest assemblages (INEGI 2021; Consejo Municipal Hueyapan 2022), interspersed with agricultural patches. Mean annual temperature ranges from 12 to 18 °C (INEGI 2021), and mean annual precipitation is between 1,500 and 2,000 mm. Precipitation is markedly seasonal, with most rainfall occurring during the rainy season (May–October), while the dry season extends from November to April and is characterized by substantially lower monthly precipitation (CONAGUA 2022). Temperature variation throughout the year is

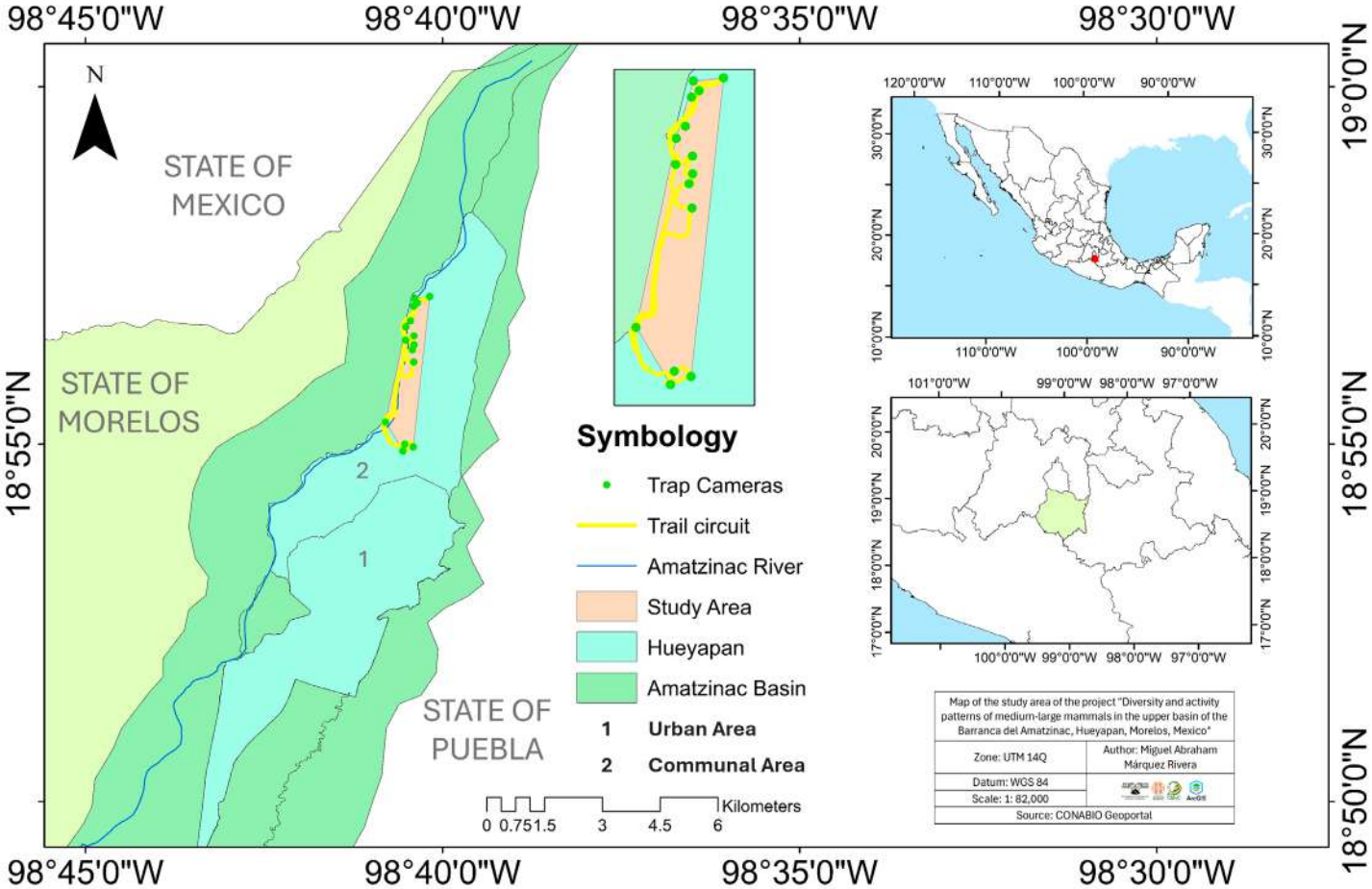

Figure 1. Geographic location of the study site and the Barranca del Amatzinac, Hueyapan, Morelos, Mexico.

moderate, with cooler conditions from December to February and warmer temperatures preceding the onset of the rainy season (INEGI 2021). The sampling area covered by trap cameras comprised 222 ha within the upper basin of the Barranca del Amatzinac and was estimated using a minimum convex polygon based on camera trap locations in ArcGIS. Additionally, 24 surveys of 11 km each were conducted, totaling a cumulative distance of 264 km to identify signs within the study area.

Sampling Design. A total of 12 sampling periods were conducted, one per month, each lasting one week, from May 2023 to April 2024. Fifteen camera traps from Cuddeback® (Non Typical, Inc., Park Falls, Wisconsin) were deployed, specifically the Long-Range IR-E2, Attack Black Flash, and Attack IR models.

Sampling stations were systematically placed in locations with evidence of wildlife presence (e.g., latrines, burrows, tracks, and water bodies), following the relief of the upper basin. Each station consisted of one camera trap mounted on a tree or wooden stake at ~50 cm above ground level, with inter-station distances ranging from 200 to 250 m. The exact spacing was influenced by terrain conditions; similarly, comparable distances (200–500 m) have been reported and used to increase the probability of species detection (Chávez *et al.* 2013; Silva-Rodríguez *et al.* 2024; Yamashita *et al.* 2025). Cameras operated continuously (24 h/day), programmed to capture three photographs per detection event (1-min reactivation interval) and a 20-s video when available.

All stations were georeferenced using a Garmin® GPS device. During each sampling period, memory cards were downloaded and batteries replaced as needed. To enhance detection, attractants were systematically deployed at all stations. During the dry season, canned sardines, chicken pieces, and water containers were placed at each station, whereas during the rainy season only canned sardines and chicken pieces were used.

Complementary Field Surveys. In parallel with camera trapping, 24 field surveys (two per month) were conducted in the study area between May 2023 and April 2024, by walking a trail circuit of ~11 km within the study area. Surveys were conducted during the day between 09:00 and 13:00 h. On each survey, all observed mammalian evidence (signs) was recorded through photographs of footprints, scats, carcasses, and direct sightings. Of these, only well-preserved carcasses and some scats were collected for subsequent identification. Samples were collected under collecting permit FAUT-0136 issued to EA. Collected carcasses were prepared through taxidermy and deposited in the mammal collection of the Centro de Investigación en Biodiversidad y Conservación (CIByC) of the Universidad Autónoma del Estado de Morelos (UAEM). Collected scats

were preserved dry and later analyzed morphologically at the Centro de Investigación en Biodiversidad y Conservación. Identification of these signs was carried out using field guides and relevant literature. For *Sylvilagus* species in particular, taxonomic identification was performed by comparing macroscopic morphological characteristics of field-collected fecal samples (Velázquez *et al.* 1996; Aranda 2000, 2012). An operational criterion of 100 m between records of the same species was established to consider them independent events, in order to avoid counting the same individual multiple times along the transect.

Data Processing. Species identity was assigned based on photographic records and species identification guides (Aranda 2000, 2012). A database was compiled, including coordinates, date and time, species taxonomy, and relevant observations for each record.

To avoid overestimation in subsequent analyses, only independent records per species were considered. Following established criteria, an independent record was defined as a single photograph from the same camera, separated by an exclusion interval of 24 h for all the species (Hernández-Pérez *et al.* 2015). If multiple individuals appeared in the same photograph, or if consecutive photographs depicted different individuals, each was treated as an independent record.

Richness and Diversity. Species richness was assessed using Hill numbers of order 0 (q = 0) (Hill 1973; Moreno *et al.* 2011; Ochoa-Espinoza *et al.* 2023), which are insensitive to species abundances/frequencies and correspond to raw species richness. Sample completeness ($\hat{C}n$) was also estimated, representing the proportion of the community sampled (Chao and Jost 2015; Serna-Lagunes *et al.* 2019). Analyses were conducted with the iNEXT package in R v.4.1.3 (Hsieh *et al.* 2016; R Core Team, 2023), and results were represented with rarefaction and extrapolation curves. Calculations were performed separately for camera trapping and sign surveys.

Alpha diversity (α) was estimated using Hill numbers of order 1 (q = 1), the exponential of Shannon's index (Hill 1973; Moreno *et al.* 2011; Bautista-Plazas 2020), which weights species by their relative incidence (independent events were used as incidence-frequency data in both methods). Analyses and graphical outputs were obtained with iNEXT in R. This approach provides both abundance-insensitive (q = 0) and abundance-weighted (q = 1) perspectives of the recorded species.

Sampling Effort and Capture Rate. For camera trapping, sampling effort (SE) was calculated by summing the number of days each camera trap was operational (cameras damaged or lost in the field were excluded from the calculation of sampling effort) (Medellín *et al.* 2006; Lira-Torres and Briones-Salas 2012). The capture rate (CR) per species was estimated as: $CR=(C/SE)\times1000$ trap-days where C = captures or independent events, SE = sampling effort, and 1000 trap-days = standard unit (Lira-Torres and Briones-Salas 2012; Hernández-Pérez *et al.* 2015; Mandujano 2024).

For sign surveys, sampling effort (SE) was calculated as the product of the distance traveled and the number of surveys. The Sign Encounter Rate (SER) was then estimated by dividing the total number of independent signs recorded per species (including footprints, scats, carcasses, and direct sightings) by the total distance traveled (Carrillo *et al.* 2000; Lira-Torres and Briones-Salas 2012).

Activity Patterns. Activity patterns were obtained using the Diel.Niche package in R (R Core Team 2023; Gerber *et al.* 2024), based on photographic records obtained for each species with at least 1 h of interval on a given camera. Those records were categorized as diurnal, nocturnal, or crepuscular based on the printed hour of each record, corrected with reference to the solar time according to its specific geographic position and date. This classification was performed using the suncalc package in R (R Core Team 2023; Thieurmel and Elmarhraoui 2023). The Diel.Niche package evaluates seven alternative activity hypotheses: traditional diurnal, traditional crepuscular, traditional nocturnal, general cathemeral (irregular periods of activity throughout the 24-hour day), crepuscular–nocturnal, diurnal–nocturnal (a bimodal activity pattern with distinct activity during daytime and nighttime), and diurnal–crepuscular; The method relies on a Bayesian multinomial regression framework, which probabilistically assigns each species to an activity hypothesis and compares alternative models using Bayes factors, balancing fit and complexity (Berger 2013; Gerber *et al.* 2024). Following Gerber *et al.* (2024), a threshold probability of 0.80 was adopted to reduce uncertainty in hypothesis assignment, although the model with the highest probability was ultimately recommended.

To capture the subtleties of temporal activity beyond simple categorical labels, we used the best-supported model for each species (selected from the general hypothesis set of the Diel.Niche package) to estimate activity probabilities for each diel period (diurnal, nocturnal, and crepuscular). These model-based probabilities provide a quantitative and comparable framework, allowing us to describe species-specific patterns and their seasonal variation in greater detail. This analysis was performed using the Diel. Niche package (Gerber *et al.* 2024).

Only species with ≥15 independent photographic records (at least 1 h of interval between them for this calculation) were included, a conservative criterion commonly used to ensure sufficient statistical power and reliability in estimating activity patterns. Additionally, circular histograms (rose plots) divided into 24 classes, each representing one hour of the day, were generated for each species to visualize activity patterns. These were created in R using the tidyverse, lubridate, and ggplot2 packages (R Core Team 2023).

Results

Richness and Diversity. A total of 15 medium- to large-sized mammal species were recorded, belonging to six orders, 11 families, and 14 genera. Of these, 12 species were detected using camera trapping (Table 1; Supplementary Data SD1)

and 11 species using sign surveys (Table 2; Supplementary Data SD2). Eight species were recorded by both sampling methods; only *Lynx rufus, Urocyon cinereoargenteus, Neogale frenata* and *Bassariscus astutus* were recorded by camera trapping. In contrast, *Otospermophilus variegatus, Conepatus leuconotus, Sylvilagus cunicularius* and *Sylvilagus floridanus* were identified from signs (It was not possible to distinguish between the two species of the genus *Sylvilagus* in the photographic records).

Sample coverage (Ĉn) values were 100% for camera trapping and 93% for sign surveys, indicating high sampling completeness. Alpha diversity (α) was estimated at 6.57 (95% CI: 6.06–7.08) for camera trapping (12 species recorded) and 6.52 (95% CI: 4.35–8.58) for sign surveys (11 species recorded). According to season, alpha diversity (α) metrics for the camera trapping method were 6.83 (95% CI: 6.20–7.46) in the dry season and 5.72 (95% CI: 5.08–6.36) in the rainy season. In the case of sign surveys, a value of 5.24 (95% CI: 2.46–8.03) was obtained in the dry season and 6.03 (95% CI: 3.98–8.08) in the rainy season (Figure 2).

Sampling Effort and Capture Rate. Based on photographic records, a total sampling effort of 1,183 trap-days was achieved, yielding 513 independent records corresponding to 12 medium- to large-sized mammal species. The most common species were *D. mexicanus* (N = 162, CR = 136.94), *D. virginiana* (N = 112, CR = 94.67), and *B. astutus* (N = 80, CR = 67.62). Conversely, the least frequent species were *U. cinereoargenteus* (N = 7, CR = 5.92), *L. rufus* and *N. frenata* (N = 2, CR = 1.69) (Figure 3; Tables 1 and 3).

During the dry season, with a sampling effort of 567 trap-days, a total of 300 independent records were obtained, corresponding to 12 mammal species. The most

Table 1. Medium-large-sized mammals recorded in the upper basin of the Barranca del Amatzinac, Hueyapan, Morelos, Mexico. Total independent photographs (TIP), and Capture Rate (CR) total and by season (Dry-Rainy). IUCN status (LC = Least Concern).

Species	Photo-trapping						IUCN
	TIP	CR(T)	TIP(D)	CR(D)	TIP(R)	CR(R)	
Didelphimorphia							
Didelphidae							
Didelphis virginiana Kerr, 1792	112	**94.67**	79	**139.33**	33	**53.57**	LC
Cingulata							
Dasypodidae							
Dasypus mexicanus W. C. H. Peters, 1865	162	**136.94**	77	**135.8**	85	**137.99**	LC
Lagomorpha							
Leporidae							
Sylvilagus sp.	10	**8.45**	6	**10.58**	4	**6.49**	LC
Rodentia							
Sciuridae							
Sciurus aureogaster F. Cuvier, 1829	15	**12.68**	8	**14.11**	7	**11.36**	LC
Carnivora							
Felidae							
Lynx rufus (Schreber, 1777)	2	**1.69**	1	**1.76**	1	**1.62**	LC
Canidae							
Canis latrans Say, 1823	30	**25.36**	18	**31.75**	12	**19.48**	LC
Urocyon cinereoargenteus (Schreber, 1775)	7	**5.92**	6	**10.58**	1	**1.62**	LC
Mustelidae							
Neogale frenata (H. Lichtenstein, 1831)	2	**1.69**	2	**3.53**	-	-	LC
Procyonidae							
Bassariscus astutus (H. Lichtenstein, 1830)	80	**67.62**	57	**100.53**	23	**37.34**	LC
Nasua narica (Linnaeus, 1776)	68	**57.48**	28	**49.38**	40	**64.94**	LC
Procyon lotor (Linnaeus, 1758)	12	**10.14**	8	**14.11**	4	**6.49**	LC
Artiodactyla							
Cervidae							
Odocoileus virginianus (Zimmermann, 1780)	13	**10.99**	10	**17.64**	3	**4.87**	LC

Note: *Mustela frenata* (Sheffield and Thomas 1997) is currently recognized as *Neogale frenata* (Patterson *et al.* 2021), and *Dasypus novemcinctus* (McBee and Baker 1982) is currently recognized as *Dasypus mexicanus* (Barthe *et al.* 2025).

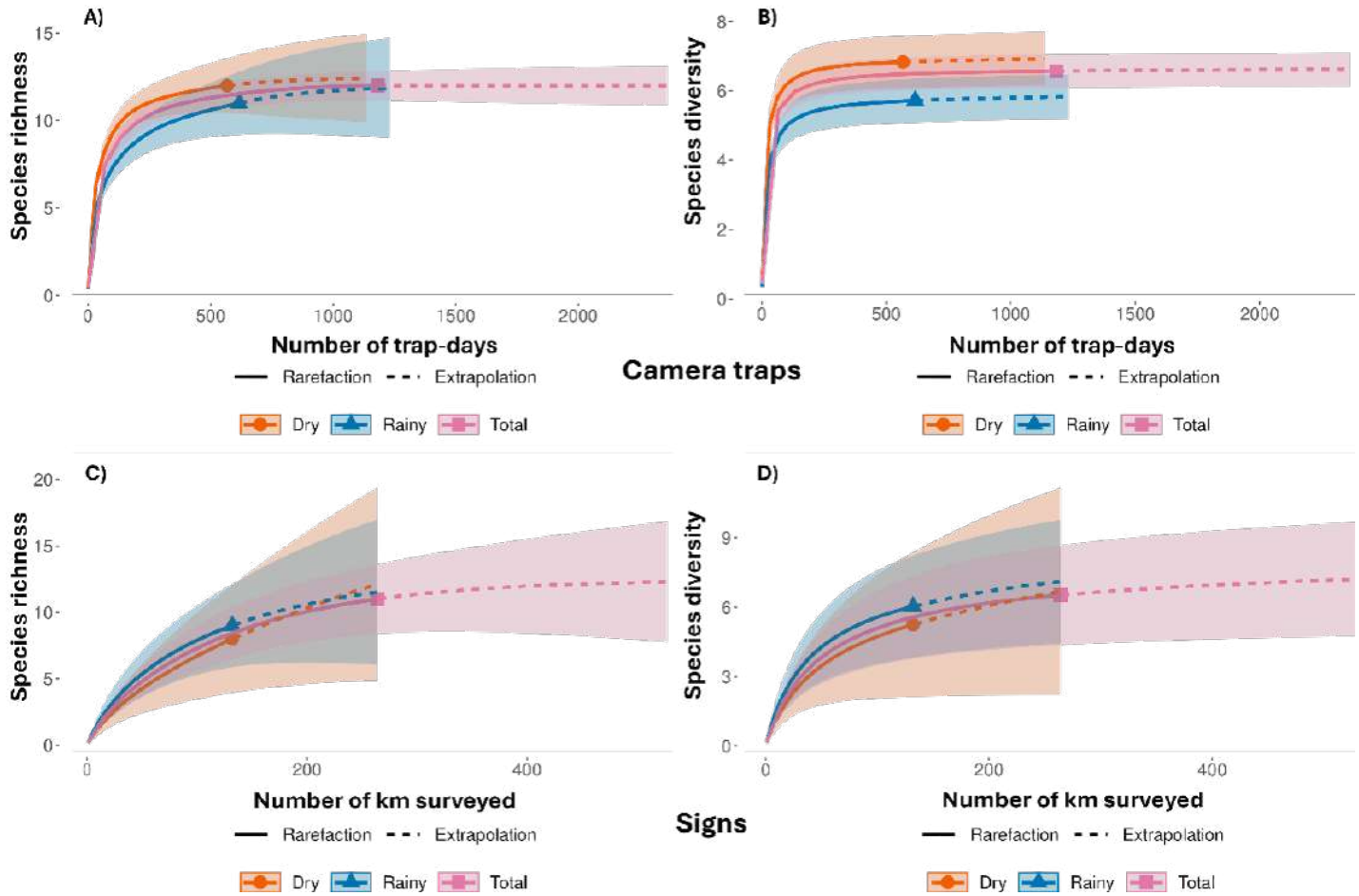

Figure 2. Species richness (A, C) and alpha diversity (B, D) of medium- to large-sized mammals recorded in the upper basin of the Barranca del Amatzinac, Hueyapan, Morelos, Mexico, using camera trapping (A, B) and sign surveys (C, D). Sampling curves are based on rarefaction and extrapolation using sample size. Shaded areas represent 95% confidence intervals derived from 100 bootstrap replicates.

frequent species were *D. virginiana* (N = 79, CR = 139.33), *D. mexicanus* (N = 77, CR= 135.80) and *B. astutus* (N = 57, CR = 100.53). The least common species were *U. cinereoargenteus* (N = 6, CR = 10.58), *N. frenata* (N = 2, CR = 3.53), and *L. rufus* (N = 1, CR = 1.76) (Figure 3; Tables 1 and 3).

For the rainy season, a sampling effort of 616 trap-days produced 213 independent records, corresponding to 11 mammal species. The most frequent species during this period were *D. mexicanus* (N = 85, CR = 137.99), *D. virginiana* (N = 33, CR = 53.57), and *Nasua narica* (N = 40, CR = 64.94). In contrast, the least frequent species were *Sylvilagus sp*. (N = 4, CR = 6.49) and *Odocoileus virginianus* (N = 3, CR= 4.87), as well as *L. rufus* and *U. cinereoargenteus* (N = 1, CR = 1.62) (Figure 3; Tables 1 and 3).

Sign Encounter Rate. Using the sign survey method, a total sampling effort of 264 km was covered, yielding 45 independent records corresponding to 11 medium-to large-sized mammal species. The highest encounter rate from signs (SER) was recorded for *Sciurus aureogaster* (N = 20, SER = 0.076), followed by *O. variegatus* (N = 6, SER= 0.023) and *O. virginianus* (N = 4, SER = 0.015). In contrast, the least frequent species were *D. virginiana*, *Conepatus leuconotus*, and *Procyon lotor* (N = 1, SER = 0.004) (Tables 2 and 3).

During the dry season, a sampling effort of 132 km yielded 19 records, corresponding to eight mammal species. The most frequent species were *S. aureogaster* (N = 9, SER = 0.068) and *O. virginianus* (N = 3, SER = 0.023). The least frequent species were *D. virginiana*, *Sylvilagus cunicularius*, *S. floridanus*, *Canis latrans*, and *P. lotor* (N = 1, SER = 0.008).

In the rainy season, with the same sampling effort of 132 km, 26 independent records were obtained, corresponding to nine mammal species. The highest SER values in this period were observed for *S. aureogaster* (N = 11, SER = 0.083) and *O. variegatus* (N = 4, SER = 0.030). Conversely, the least frequent species were *S. floridanus*, *C. latrans*, *C. leuconotus*, and *O. virginianus* (N = 1, SER = 0.008).

Activity Patterns. Activity patterns were estimated for seven of the 12 species recorded through camera trapping. Based on model fit, *B. astutus*, *D. mexicanus*, *D. virginiana*, and *P. lotor* were classified as nocturnal (model probabilities: 0.95, 1.00, 1.00, and 0.98, respectively). *S. aureogaster* was classified as diurnal (0.97). *C. latrans* was classified as diurnal–nocturnal with a lower model probability (0.66); likewise, *N. narica* was classified as diurnal–nocturnal (0.82) (Table 4; Supplementary Data SD3).

Activity patterns were obtained for five species in both

Table 2. Medium-large size mammals recorded in the upper basin of the Barranca del Amatzinac, Hueyapan, Morelos, Mexico. Total mammalian signs records (TS), and Sign Encounter Rate (SER) total and by season (Dry-Rainy). Type of sign (C= Carcass, SI= Sighting, F= Footprint, S= Scat, B= Burrow). IUCN status (LC= Least Concern).

Species	Signs						Type of Sign	IUCN
	TS	SER(T)	TS(D)	SER(D)	TS(R)	SER(R)		
Didelphimorphia								
Didelphidae								
Didelphis virginiana Kerr, 1792	1	**0.004**	1	**0.008**	-	**-**	C, F	LC
Cingulata								
Dasypodidae								
Dasypus mexicanus W. C. H. Peters, 1865	3	**0.011**	-	**-**	3	**0.023**	C, SI, F	LC
Lagomorpha								
Leporidae								
Sylvilagus cunicularius (Waterhouse, 1848)	3	**0.011**	1	**0.008**	2	**0.015**	S	LC
Sylvilagus floridanus (J. A. Allen, 1890)	2	**0.008**	1	**0.008**	1	**0.008**	S	LC
Rodentia								
Sciuridae								
Sciurus aureogaster F. Cuvier, 1829	20	**0.076**	9	**0.068**	11	**0.083**	SI	LC
Otospermophilus variegatus (Erxleben, 1777)	6	**0.023**	2	**0.015**	4	**0.03**	C, SI	LC
Geomyidae							B	
Carnivora								
Canidae								
Canis latrans Say, 1823	2	**0.008**	1	**0.008**	1	**0.008**	SI, F	LC
Mephitidae								
Conepatus leuconotus (H. Lichtenstein, 1832)	1	**0.004**	-	**-**	1	**0.008**	C	LC
Procyonidae								
Nasua narica (Linnaeus, 1776)	2	**0.008**	-	**-**	2	**0.015**	C, F	LC
Procyon lotor (Linnaeus, 1758)	1	**0.004**	1	**0.008**	-	**-**	F	LC
Artiodactyla								
Cervidae								
Odocoileus virginianus (Zimmermann, 1780)	4	**0.015**	3	**0.023**	1	**0.008**	SI, F, S	LC

seasons. *D. mexicanus*, *B. astutus* and *D. virginiana* were classified as nocturnal in both seasons, as in their general pattern, these species presented model supports above 0.9 in both seasons, except for *B. astutus*, which showed a lower support (0.77) during the rainy season. *C. latrans* presented a different classification between seasons; it was classified as nocturnal during the dry season, although with a much lower model probability (0.47), while in the rainy season it showed a diurnal–nocturnal activity with lower support (0.76), similar to that reported in its general activity. *N. narica* exhibited an activity pattern during the dry season similar to the general activity, being classified as diurnal–nocturnal with lower support (0.78); in contrast, during the rainy season it was classified as diurnal (0.82), differing from its general pattern.

Based on the best-supported model for each evaluated species, the estimated probabilities of diel activity were obtained for the three activity periods (diurnal, nocturnal, and crepuscular). *D. mexicanus*, *B. astutus*, *D. virginiana* and *P. lotor* showed predominantly nocturnal activity with probabilities higher than 0.8. *N. narica* was mainly diurnal (0.66), although it also showed a considerable nocturnal probability (0.26), while *S. aureogaster* exhibited a strong diurnal activity probability (0.92). In contrast to *N. narica*, *C. latrans* showed a higher nocturnal probability (0.65) than diurnal activity (0.25). Total and seasonal activity probabilities are presented in Table 4.

Table 3. Sampling effort (in trap-days for photo-trapping and in kilometers of sampling for sign surveys), independent records and species recorded in each sampling method used in the record of medium-large mammals for the upper basin of the Barranca del Amatzinac, Hueyapan, Morelos, Mexico.

	Photo-trapping			Signs		
	Total	Dry	Rainy	Total	Dry	Rainy
Sampling effort	1183	567	616	264	132	132
Independent records	513	300	213	45	19	26
Registered species	12	12	11	11	8	9
Exclusive species	4	4	3	4	3	4

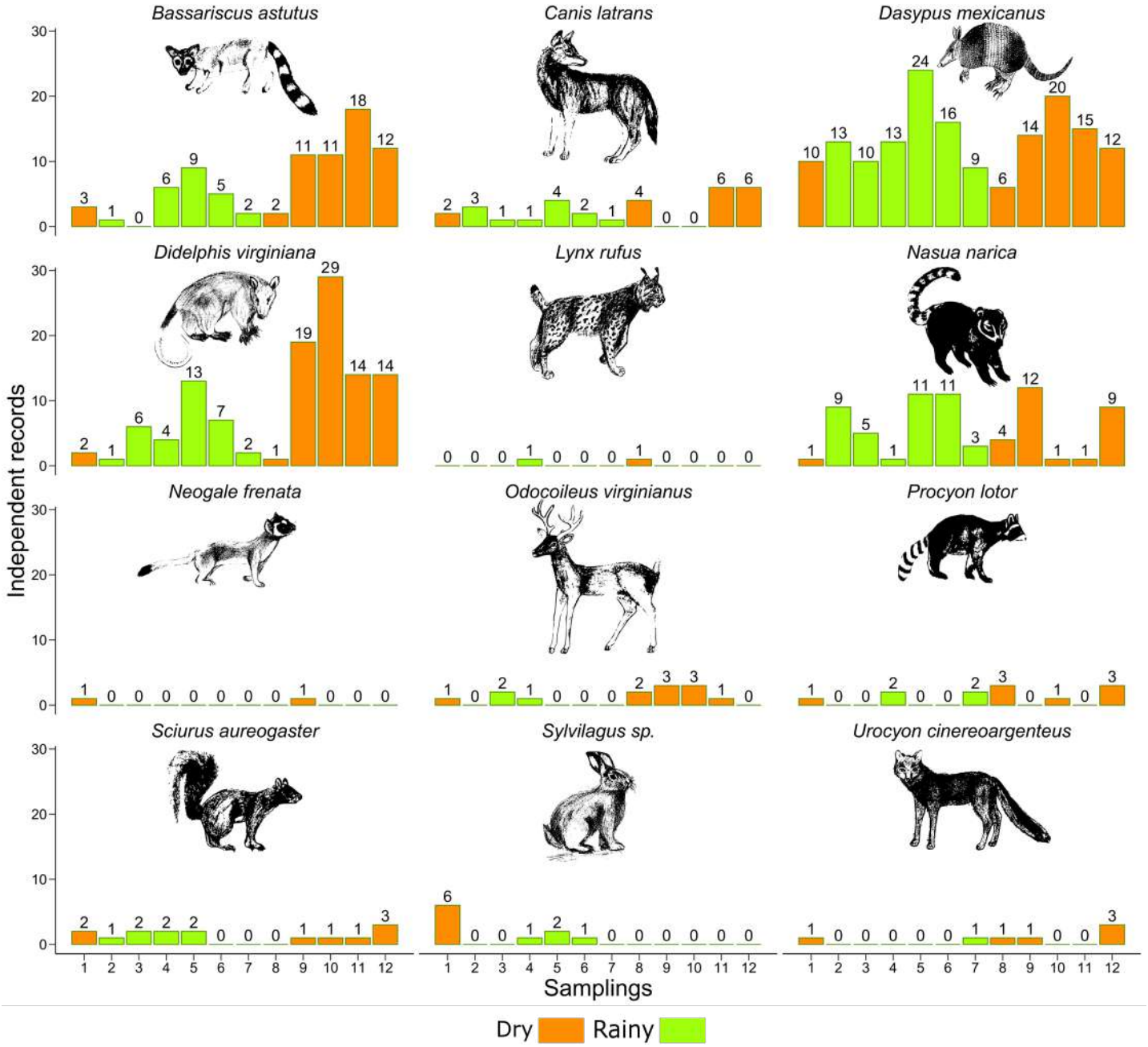

Figure 3. Total frequency of medium and large mammal species recorded in the upper basin of the Barranca del Amatzinac by photo-trapping. X axis= Sampling carried out (one per month from May 2023 to April 2024), Y axis= Number of independent records for each species. Orange indicates the dry season; green indicates the rainy season.

Discussion

This study documents for the first time the presence of 15 medium- to large-sized mammal species in the upper Barranca del Amatzinac basin, representing six orders and 11 families. This richness corresponds to approximately 51.7% of the species reported for the state of Morelos (Álvarez-Castañeda 1996; Altamirano-Álvarez *et al.* 2009; Guerrero *et al.* 2020; Valenzuela-Galván *et al.* 2020). The diversity detected likely reflects the basin's location within the Trans-Mexican Volcanic Belt, one of the most biodiverse biogeographic regions in Mexico (Suárez-Mota and Téllez-Valdés 2014). Comparable richness has been reported in subhumid temperate forests, such as the 20 species recorded in the Sierra Madre de Oaxaca (Cruz-Espinoza *et al.* 2012), 11 species in the Sierra de Juárez Oaxaca (Hernández-Rodríguez *et al.* 2019), and 10 species in Pico de Orizaba National Park (Serna-Lagunes *et al.* 2019).

Sample coverage (Ĉn) analyses indicated high sampling completeness for both sampling methods. Camera trapping detected 12 taxa (11 identified to species level and one to genus level), whereas sign surveys recorded 11 species (Chao and Jost 2012; Serna-Lagunes *et al.* 2019). Although only 15 of the 18 potential species expected for the region were documented, coverage estimates suggest that most detectable species were likely captured. Richness extrapolations (q = 0) also indicated that only a few additional species would be expected with further sampling. Alpha diversity (α) values were similar for the

Table 4. Activity patterns of medium-large mammals in the upper basin of the Barranca del Amatzinac, Hueyapan, Morelos, Mexico. TIP (total independent photographs for the entire sampling and by seasons) (D= diurnal, N= nocturnal and D-N= diurnal-nocturnal).

	Species	Photographic events				Model support	Activity pattern (best-supported model)	Activity probability (based on the best-supported model)		
		TIP	Day	Night	Twilight			Diurnal	Nocturnal	Crepuscular
Total	*Dasypus mexicanus*	212	11	196	5	1	**N**	0.05	0.92	0.03
	Canis latrans	35	8	24	3	0.66	**D-N**	0.25	0.68	0.07
	Bassariscus astutus	129	5	109	15	0.95	**N**	0.04	0.84	0.11
	Didelphis virginiana	205	8	179	18	1	**N**	0.04	0.87	0.09
	Nasua narica	98	64	25	9	0.82	**D-N**	0.66	0.26	0.08
	Procyon lotor	18	0	18	0	0.98	**N**	0.03	0.92	0.03
	Sciurus aureogaster	16	16	0	0	0.97	**D**	0.92	0.03	0.03
Dry	*Dasypus mexicanus*	90	4	84	2	1	**N**	0.05	0.92	0.03
	Canis latrans	20	3	15	2	0.47	**N**	0.09	0.83	0.07
	Bassariscus astutus	95	3	81	11	0.94	**N**	0.04	0.85	0.11
	Didelphis virginiana	144	8	120	16	0.93	**N**	0.06	0.83	0.11
	Nasua narica	42	18	20	4	0.78	**D-N**	0.44	0.49	0.07
Rainy	*Dasypus mexicanus*	122	7	112	3	1	**N**	0.06	0.91	0.03
	Canis latrans	15	5	9	1	0.76	**D-N**	0.35	0.59	0.06
	Bassariscus astutus	34	2	28	4	0.77	**N**	0.06	0.84	0.09
	Didelphis virginiana	61	0	59	2	1	**N**	0.01	0.94	0.04
	Nasua narica	56	46	5	5	0.82	**D**	0.83	0.08	0.08

Activity pattern assigned according to the best-supported model; activity probability for the three diel periods was calculated using the best-supported model from the hypothesis set of the Diel.Niche package.

overall results of both methods. The overlap of confidence intervals suggests that no clear differences in diversity between seasons were detected for each method employed (Chao and Jost 2012; Cultid-Medina and Escobar 2019).

Camera trapping proved effective for detecting a wide range of mammals, including widely distributed species such as *O. virginianus*, *C. latrans*, and *D. mexicanus* (Cruz-Espinoza *et al.* 2012; Cortés-Marcial and Briones-Salas 2014; Grajales-Tam and González-Romero 2014; Hernández-Pérez *et al.* 2015; Ochoa-Espinoza *et al.* 2023), as well as elusive species, such as *N. frenata* (Sheffield and Thomas 1997; Contreras-Moreno *et al.* 2015) and *L. rufus*, a bioindicator species of ecosystem quality (Pacheco 2003; Ríos-Carrillo 2014; Díaz-Bernal 2017). However, no photographic records were obtained for *Mephitis macroura*, *Spilogale angustifrons*, or *Herpailurus yagouaroundi*, species previously reported for Morelos (Altamirano-Álvarez *et al.* 2009). Greater sampling effort and complementary methods may therefore increase detection probability.

Species-level identification of the genus *Sylvilagus* was not possible from photographic records, as *S. cunicularius* and *S. floridanus* share similar morphological traits (Aranda 2012; Kays *et al.* 2022b). Species determination was achieved through fecal samples, which exhibit diagnostic characteristics (Velázquez *et al.* 1996; Aranda 2012) (Supplementary Data SD2). Sign surveys also documented the presence of Geomyidae, identified by characteristic soil mounds produced by their fossorial habits (Aranda 2012).

Capture Rates (CR) indicated that *D. mexicanus*, *D. virginiana* and *B. astutus* were the most common species. Although camera trapping has been suggested to be suboptimal for recording *D. mexicanus* (Monroy-Vilchis *et al.* 2011; Cortés-Marcial and Briones-Salas 2014), other studies have reported it as frequent using the same method (Lira-Torres and Briones-Salas 2012; Ochoa-Espinoza *et al.* 2023), consistent with our findings. Its high frequency may relate to its insectivorous and generalist diet (McBee and Baker 1982), along with its preference for humid habitats with dense vegetation cover (Weckel *et al.* 2006; Harmsen *et al.* 2010), conditions present at the study site. Similar for *D. virginiana* and *B. astutus*, both described as ecologically plastic and tolerant of human-modified environments (McManus 1974; Castellanos-Morales *et al.* 2009; Cisneros-Moreno and Martínez-Coronel 2019), their high CR may reflect adaptability and resource availability.

Carnivora was the most diverse order in this study, with eight species recorded. *C. latrans* was the fifth most frequent species (N = 30, CR = 25.36), likely due to the availability of prey such as *D. mexicanus*, *S. cunicularius*, and *S. floridanus* (Monroy *et al.* 2003; Watine and Giuliano 2017; Serna-Lagunes *et al.* 2019). Its populations may also inhibit those of *U. cinereoargenteus* due to competition and resource overlap, potentially explaining the latter's low CR (Grajales-Tam and González-Romero 2014; Egan *et al.* 2021). Temporal segregation may further reduce direct interactions and facilitate coexistence (Rodríguez-Luna *et al.* 2024). Similarly,

L. rufus showed a low CR, likely constrained by its specialist carnivorous niche, particularly its reliance on lagomorphs (Delibes *et al.* 1997; CONANP 2010; Ríos-Carrillo 2014). For *N. frenata*, the low number of records may reflect its elusive behavior and low detectability in conventional surveys (Sheffield and Thomas 1997; Estrada *et al.* 2002; Jesús-Espinosa *et al.* 2023). Among procyonids, *N. narica* showed relatively high CR (N = 68, CR = 57.48), likely related to its matriarchal social structure, which produces multiple independent events in a single record (Valenzuela-Galván 2002). *B. astutus* also showed multiple events, as young remain with the mother for several months (Pacheco 2003). In contrast, *P. lotor* (N = 12, CR= 10.14) had lower capture rate than other procyonids, possibly reflecting competition with other carnivores or preference for less-represented habitats. Overall, most species exhibited higher CR during the dry season; only *D. mexicanus* and *N. narica* showed greater frequency during the rainy season. Notably, *N. frenata* was not recorded during the rainy season in camera traps.

Sign surveys showed *S. aureogaster*, *O. variegatus*, and *O. virginianus* as the most frequent species. The high frequency of *S. aureogaster* may relate to its diurnal activity pattern and the fact that surveys were conducted during daytime (Mora-Ascencio *et al.* 2010; Ramos-Lara and Cervantes 2011). *O. variegatus* was regularly detected in sign surveys but not by camera traps, likely because cameras were placed inside forest stands, whereas this species was mainly observed along open trails and edge habitats. Future sampling designs should therefore consider different forest strata to increase detection probability. Sign-based encounter rates differed between seasons for most species, partly because many were recorded only once. Consequently, SER values were lower than CR, reflecting fewer overall records. Although sign surveys are valuable for mammal inventories (Lyra-Jorge *et al.* 2008; Cortés-Marcial and Briones-Salas 2014; Swan *et al.* 2014), the low number of records suggests refining the local design (e.g., longer transects, standardized substrates, optimized timing) and combining complementary methods.

Evidence of local reproductive activity was obtained for *D. mexicanus* and *N. narica*. A juvenile *D. mexicanus* was observed in August 2023, and for *N. narica*, one juvenile was photographed in June 2023 and the carcass of another juvenile was found in August 2023. These events occurred during the rainy season, when resource availability is higher, suggesting stable local populations.

Regarding activity patterns, *B. astutus*, *D. mexicanus*, *D. virginiana*, and *P. lotor* were classified as nocturnal (model probability > 0.9). These species have been described as primarily nocturnal in other regions of Mexico (Lira-Torres and Briones-Salas 2012; Hernández-Pérez *et al.* 2015; Hernández-Hernández *et al.* 2018). These results support the idea that species weighing <10 kg tend to be nocturnal–crepuscular (Monroy-Vilchis *et al.* 2011). *Canis latrans* was classified as diurnal–nocturnal, although this pattern can also be considered a specific form of cathemerality (González-Pérez *et al.* 1992; Cortés-Marcial and Briones-Salas 2014; Gerber *et al.* 2024). *N. narica* was classified as diurnal–nocturnal (model probability = 0.82), although it is commonly described as diurnal (Valenzuela-Galván 2002; Reid 2009; Lira-Torres and Briones-Salas 2012), which may reflect sexual and contextual differences in activity (e.g., greater nocturnal activity in adult males) and behavioral adjustments to local conditions (Hernández-Pérez *et al.* 2015). Across seasons, *B. astutus*, *D. mexicanus*, and *D. virginiana* maintained consistent activity patterns, whereas *N. narica* and *C. latrans* exhibited seasonal variation. These shifts may reflect changes in resource availability, temperature, humidity, geographic conditions, population traits (sex, age, reproductive status, mate availability), and human disturbance (Valenzuela 2005; Ridout and Linkie 2009; Monroy-Vilchis *et al.* 2011; Rowcliffe *et al.* 2014).

We observed that activity patterns probabilities (based on the model with the highest support) varied considerably among species: *B. astutus, D. mexicanus, D. virginiana,* and *P. lotor* were predominantly nocturnal (probabilities > 0.8) in both seasons and in the overall dataset. However, *P. lotor* was classified only in the total dataset. For *C. latrans*, nocturnal (~0.7) and diurnal (~0.3) activity probabilities were not similar and consistent between seasons. For *N. narica*, overall probabilities were similar among the three periods, but seasonal variation was observed: in the dry season values were equivalent, whereas in the rainy season diurnal probability was higher (0.83) than nocturnal (0.08) and crepuscular (0.08), explaining its classification as diurnal in that period.

Conclusions

This study provides baseline information on the richness, diversity, capture rates, and activity patterns of medium- to large-sized mammals in the upper Amatzinac basin, Hueyapan, Morelos. Fifteen species were documented in a relatively small area outside a protected natural area, underscoring the biological relevance of the site. Given that this region contributes to aquifer recharge ("water forests") in northeastern Morelos, ecological assessments of different taxonomic groups will support local communities in designing programs and strategies for the sustainable management of natural resources in the upper Barranca del Amatzinac.

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Declaration of Artificial Intelligence use

Grammarly Pro was used solely to check English spelling and grammar.

Author contributions

Miguel A. Márquez-Rivera: Conceptualization, Formal analysis, Investigation, Methodology and Writing – Original Draft Preparation. Elizabeth Arellano: Conceptualization, Project administration, Resources, Reviewing and Editing. David Valenzuela-Galván: Methodology, Resources, Reviewing and Editing. Daryl D. Cruz: Conceptualization, Methodology, Project administration, Supervision, Writing-Reviewing and Editing.

Supplementary data

SD1. Medium- to large-sized mammals recorded by camera traps in the study area: (A) *Didelphis virginiana,* (B) *Dasypus mexicanus,* (C) *Sylvilagus sp.,* (D) *Sciurus aureogaster,* (E) *Lynx rufus*, (F) *Canis latrans,* (G) *Urocyon cinereoargenteus,* (H) *Neogale frenata,* (I) *Bassariscus astutus,* (J) *Nasua narica, (k) Procyon lotor,* (L) *Odocoileus virginianus.*

SD2. Medium- to large-sized mammal species recorded from traces in the study area: (A) *Dasypus mexicanus,* (B) *Didelphis virginiana*, (C) *Conepatus leuconotus*, (D) *Nasua narica*, (E) *Odocoileus virginianus*, (F) *Sciurus aureogaster*, (G) *Otospermophilus variegatus*, (H) *Procyon lotor*, (I) *Canis latrans*, (J) *Sylvilagus floridanus* vs *Sylvilagus cunicularius* and (K) Geomyidae.

SD3. Activity patterns of medium-large mammals recorded by photo-trapping, in the Barranca del Amatzinac, Hueyapan, Morelos, Mexico. (Nocturnal: *D. mexicanus, B. astutus, D. virginiana* and *P. lotor*; Diurnal-Nocturnal: *C. latrans* and *N. narica*; Diurnal: *S. aureogaster*).

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Casuistry of primates in a veterinary center in Paraguay: retrospective report 2004-2025

Joerg Richard Vetter[1,2*], and Mauricio E. Martínez[3].

[1]Departamento de Recursos Faunísticos y Medio Natural, Facultad de Ciencias Veterinarias, Universidad Nacional de Asunción, San Lorenzo – Paraguay.
[2]Refugio Silvestre Urutau, Filadelfia – Paraguay.
[3]Grupo de Iniciación Científica, Facultad de Ciencias Veterinarias, Universidad Nacional de Asunción, San Lorenzo – Paraguay. E-mail: mauricioddo70@gmail.com (MEM)
[*]Corresponding author: jvetter@vet.una.py

Non-human primates play a fundamental role in tropical ecosystems, contributing to key ecological processes such as seed dispersal and the maintenance of community structure, while also holding significant evolutionary, cultural, and social value. Despite their importance, illegal trafficking of primates is rife. In Paraguay, five native primate species are recognized, several of which are affected by illegal trade and inadequate captive management. This study reports the species and main clinical findings of non-human primates transferred to the Departamento de Recursos Faunísticos y Medio Natural of the Facultad de Ciencias Veterinarias, Universidad Nacional de Asunción, between 2004 and 2025. Data were obtained from individual medical records, considering only primary diagnoses, and included information on taxonomy, origin, diet, and clinical condition of individuals. A total of 292 primates of seven genera were registered, with *Sapajus cay* being the most frequent species (50%), followed by *Alouatta caraya* (31.8%) and *Aotus azarae* (10.6%). Across all species, the most common reasons for consultation were routine check-ups, trauma, digestive disorders, infectious diseases, and respiratory conditions. Trauma and tetanus were recurrent findings, highlighting the impact of poor management and exposure to anthropogenic risks. In more than 88% of cases, diets were classified as incomplete or inappropriate, typically characterized by excessive sweet fruits, processed foods, and a lack of fiber, contrasting sharply with species-specific nutritional requirements. Information on animal origin was frequently missing, although available data indicated widespread national and transboundary illegal trafficking. The results emphasize the consequences of illegal possession and inadequate captive conditions on primate health and welfare, as well as the associated risks to conservation and public health due to zoonotic and anthropozoonotic diseases. Strengthening wildlife law enforcement, improving public awareness, and developing standardized protocols for rescue and rehabilitation are urgently needed in Paraguay.

Keywords: Anthropozoonosis, illegal wildlife traffic, Paraguay, primates, zoonosis.

Los primates no humanos desempeñan un papel fundamental en los ecosistemas tropicales, ya que contribuyen a procesos ecológicos clave, como la dispersión de semillas y el mantenimiento de la estructura de las comunidades, al tiempo que tienen un importante valor evolutivo, cultural y social. A pesar de su importancia, el tráfico ilegal de primates es muy frecuente. En Paraguay se reconocen cinco especies de primates nativos, varias de las cuales se ven afectadas por el comercio ilegal y la gestión inadecuada en cautividad. Este estudio informa sobre la composición de las especies y los principales hallazgos clínicos de los primates no humanos trasladados al Departamento de Recursos Faunísticos y Medio Natural de la Facultad de Ciencias Veterinarias de la Universidad Nacional de Asunción entre 2004 y 2025. Los datos se obtuvieron de los expedientes médicos individuales, teniendo en cuenta únicamente los diagnósticos primarios, e incluyeron información sobre taxonomía, origen, dieta y estado clínico. Se registraron un total de 292 primates, siendo *Sapajus cay* la especie más frecuente (50 %), seguida de *Alouatta caraya* (31,8 %) y *Aotus azarae* (10,6 %). En todas las especies, los motivos más comunes de consulta fueron revisiones rutinarias, traumatismos, trastornos digestivos, enfermedades infecciosas y afecciones respiratorias. Los traumatismos y el tétanos fueron hallazgos recurrentes, lo que pone de relieve el impacto de la mala gestión y la exposición a riesgos antropogénicos. En más del 88 % de los casos, las dietas se clasificaron como incompletas o inadecuadas, caracterizadas típicamente por un exceso de frutas dulces, alimentos procesados y una falta de fibra, lo que contrasta fuertemente con los requisitos nutricionales específicos de cada especie. A menudo faltaba información sobre el origen de los animales, aunque los datos disponibles indicaban un tráfico ilegal generalizado a nivel nacional y transfronterizo. Los resultados ponen de relieve las consecuencias de la posesión ilegal y las condiciones inadecuadas de cautiverio para la salud y el bienestar de los primates, así como los riesgos asociados para la conservación y la salud pública debido a las enfermedades zoonóticas y antropozoonóticas. En Paraguay es urgente reforzar la aplicación de la legislación sobre fauna silvestre, mejorar la sensibilización del público y elaborar protocolos normalizados para el rescate y la rehabilitación.

Palabras clave: antropozoonosis, Paraguay, primates, tráfico ilegal de fauna, zoonosis.

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Non-human primates (hereafter primates) are vitally important to tropical biodiversity and to many ecosystem functions, processes, and services, such as seed dispersal and the maintenance of community structures (Estrada *et al.* 2017; Fergnani *et al.* 2020). They are our closest living biological relatives, provide us with fundamental information about human evolution, and play an important role in the livelihoods, cultures, and religions of many societies. Paradoxically, unsustainable human activities are now the main force threatening primate populations (Estrada *et al.* 2017).

Primates face an imminent extinction crisis, with around 93% of species characterized by declining

populations and 65% of species classified as Vulnerable, Endangered, or Critically Endangered (Estrada and Garber 2022). Population declines in approximately 75% of species are associated with deforestation and habitat loss resulting from agricultural expansion, livestock farming, and natural resource extraction. Other pressures that negatively affect primate populations include unsustainable hunting of wild animals, the illegal pet trade, expansion of road networks, transmission of zoonotic diseases, and climate change (Estrada *et al.* 2020).

There are five species of primates recorded in Paraguay: *Alouatta caraya* (Atelidae), *Aotus azarae* (Aotidae), *Mico melanurus* (Callithrichidae), *Sapajus cay* (Cebidae), and *Plecturocebus pallescens* (Pitheciidae). Two species (*A. azarae* and *P. pallescens*) have been classified as Least Concern (LC), while *A. caraya* and *M. melanurus* are classified as Near Threatened (NT), and *S. cay* is classified as Vulnerable (Vu) (Bicca-Marques *et al.* 2021; Milagres *et al.* 2021; Rímoli *et al.* 2021; Rumiz *et al.* 2021; Rímoli *et al.* 2022). On a national level, *S. cay*, *A. caraya* and *A. azarae* are classified as LC, although it has been suggested that *S. cay* be upgraded to Vulnerable (Cartes *et al.* 2017; Smith and Lusseau 2024). On the other hand, *M. melanurus* was categorized as Vulnerable due to habitat loss from land conversion and fragmentation of remaining forests, and probable hunting for the pet trade is mentioned (Cartes *et al.* 2017). In contrast, *P. pallescens* is categorized as Near Threatened (NT) due to the severe deforestation process affecting the Paraguayan Chaco (Cartes *et al.* 2017).

In South America, illegal primate trafficking is a major factor in the decline of native primate populations, but the absence of clear legal frameworks, insufficient financial and human resources allocated to controlling and combating trafficking, and the lack of established protocols for the rescue, rehabilitation, and reintroduction of animals hinder any effort to eliminate established trafficking schemes (Estrada-Cely and González 2008; Tirira 2013; Shanee *et al.* 2017; Shanee *et al.* 2023). Paraguay has been a member of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) since 1976, and the Law 96/92 "On Wildlife" prohibits the trade of wild animals that do not come from legally authorized breeding facilities. As such, there is currently no legal way to obtain a primate for domestic ownership in the country.

The objective of this study is to report on the main clinical findings of the primate species transferred to the Departamento de Recursos Faunísticos y Medio Natural of the Facultad de Ciencias Veterinarias, Universidad Nacional de Asunción, in the city of San Lorenzo, over a twenty-year period (2004-2025).

Materials and methods

The data were obtained from the individual medical records of primates stored in the Departamento de Recursos Faunísticos y Medio Natural of the Facultad de Ciencias Veterinarias (FCV), Universidad Nacional de Asunción (UNA) from 2004 to 2025. All medical records are annual, and in most years the department was closed during the month of January. For all medical records, only the primary diagnosis was considered.

From each medical record we obtained the date of consultation, annual individual medical record number, taxon, weight in grams (if recorded), sex (if recorded), age as recorded (if recorded), origin (if recorded), time with current owner, description of the diet offered by current owner, diagnosis, and subclassification of the diagnosis (e.g., trauma, caused by a vehicle or by another animal). All the data were obtained as registered in the medical records. The diagnosis of the primate upon arrival was established based on the available information and classified into the following categories: routine check-up, dermatological, digestive, unspecified (when a definitive diagnosis could not be reached), poisoning, management (e.g., problems caused by inappropriate housing or husbandry), neoplasia, nutritional (e.g., metabolic bone disease or diabetes), reproductive, respiratory, trauma, infectious, or undefined (when left blank).

As for the food provided, given that the food offered to different animals varied greatly, diets were classified as "incomplete or inadequate" or "adequate," based on the species' known feeding ecology.

To analyze the data, measures of central tendency and dispersion were calculated for quantitative data, and absolute frequency and relative frequency (as percentages) were analyzed for qualitative data.

Results

Between 2004 and 2025, 292 primates were registered in the Departamento de Recursos Faunísticos y Medio Natural, FCV-UNA. The number of individuals per taxon is shown in Table 1.

The most common species was Azara's capuchin monkey (*Sapajus cay*), recorded in 146 clinical records (50% of the total). Of these, 78 were male, 41 were female, and 28 records did not specify sex. Weight was recorded in 107 records, with an average weight of 1350.8 ± 906.6 grams. Age was not recorded uniformly: in 114 records, age was reported numerically, with an average age of 44.3 months;

Table 1. The number of individuals per primate species registered in clinical files.

Taxon	Number
Sapajus cay	146
Alouatta caraya	93
Aotus azarae	31
Callithrix jacchus	8
Callithrix spp.	4
Plecturocebus pallescens	4
Saimiri spp.	3
Saguinus fuscicollis	1
No Data	2
Total	**292**

Figure 1. Individuals of *Sapajus cay* affected by electrocution (A), tetanus (B), and dermatologic affection (C).

Table 2. Most frequent causes of consultation for the main species transferred to the FCV-UNA from 2004 – 2025.

	***S. cay* (n=146)**	***A. caraya* (n=93)**	***A. azarae* (n=31)**
Routine check-up	37 (25.3%)	21 (22%)	6 (19.4%)
Dermatological	16 (11%)	6 (6.5%)	0
Digestive	13 (8.9%)	28 (30.1%)	1 (3.2%)
Respiratory	13 (8.9%)	5 (5.4%)	9 (29%)
Trauma	25 (17.1%)	17 (18.3%)	7 (22.6%)
Infectious	19 (13%)	3 (3.2%)	4 (12.9%)
Undefined	18 (12.3%)	6 (6.5%)	2 (6.5%)

some records reported age by standard classifications, where 12 were recorded as "juvenile" and 10 as "adult"; and in 10 records, age was not recorded. The main reason for consultation was routine check-up (25.3%, n=37), followed by trauma (17.1%, n=25) (Table 2). Trauma was sub-classified according to cause, with four cases due to electricity (Figure 1A), four due to dog attacks, three due to human attacks, two due to burns, and 12 cases with no established cause. Infectious processes accounted for 13% (n=19) of the records, with 16 cases of tetanus (Figure 1B), one case of *Mycobacterium tuberculosis* infection, and two unspecified infections. Finally, 16 cases (11%) of various dermatological conditions (ectoparasites, abscesses, and mycosis) (Figure 1C), 13 cases (8.9%) of digestive disorders (mainly undefined gastroenteritis), and 13 (8.9%) cases of undefined respiratory disorders were reported.

The diet offered to capuchin individuals varied greatly between patients. In 89.7% (n=131) of cases, the capuchin monkeys were provided with an incomplete or inappropriate diet, consisting of an excess of sweet fruits, sweets, cold cuts and sausages, soft drinks, coffee and caffeinated beverages, dairy products, and/or fried foods. Only in four cases was a diet reported that could be considered appropriate for the species. In three files, only "varied diet" is reported, and in eight files, the diet was not described.

Eighty-six (58.9%) records did not include information on the origin of the individuals. However, six records mentioned "Chaco", nine cases reported municipal markets (mainly Mercado N°4 in Asunción), and 45 records reported 35 different cities in the Oriental Region of Paraguay as the origin.

The second most common species recorded was the black-and-gold howler monkey (*Alouatta caraya*), recorded for 93 clinical records (31.8% of total records). Of these, 39 were male, 39 female, and 15 records did not specify sex. Weight was recorded in 78 records, with a mean weight of 2,182.9 ± 210.8 grams. Age was recorded numerically in 77 records, with a mean of 18.8 ± 31.2 months. Other records reported the age by standard classifications, where five were recorded as "juvenile," six as "adult," and in five records, the age was not recorded. The main reason for consultation was digestive disorders, reported for 28 records (30.1%), with six cases of parasitic gastroenteritis, three cases of bacterial gastroenteritis, nine cases of undefined gastroenteritis, one case of stomatitis, one case of hemorrhoids, and eight undefined cases. Routine check-ups were recorded in 21 files (22%). This was followed by trauma in 17 files (18.3%), mainly due to undefined causes (10/17) and electricity (3/17), dermatological conditions in six files, respiratory conditions in five files, three cases of tetanus, and six files without diagnosis (Table 2).

Eighty-two records (88.2%) described a diet that was incomplete or inadequate for the species, mainly due to an excess of sweet fruits, lean meat, pasta, white rice, dairy products, and a general lack of fiber. Only four files reported a diet that could be considered appropriate, and 7 files did not describe the food.

Fifty files (53.8%) did not record the origin of the indi-

Figure 2. Individual of *Aotus azarae* positive to HSV-1 presenting a characteristic palpebral ulcer.

viduals. However, eleven forms mentioned "Chaco", seven report municipal markets (mainly Mercado N° 4 in Asunción), three mention the city of Acahay, and 22 report 17 different cities in the Oriental Region of Paraguay as the origin.

The Azara's owl monkey (*Aotus azarae*, called Ka'i Pyharé in the Guaraní language), was recorded in 31 clinical records (10.6% of total records). Of these, 18 were female, 7 male, and 6 records did not specify the sex. Weight was recorded in 27 records, with a mean of 570.85 ±256.5 grams. Age was recorded numerically in 22 records, with a mean of 8.7 months (±5.4); and some records reported age by standard classifications, where four were recorded as "juvenile", one as "adult", and in four records age was not recorded. The main reason for consultation was undefined respiratory condition (n=9), followed by trauma (n=7), and infectious disease (n=4), including three cases of encephalitis caused by Herpes Simplex Virus (Figure 2) and one case of tetanus. Six records were registered as routine check-ups (19.4%), and two records did not report a diagnosis (Table 2).

Twenty-eight records (90.3%), described an incomplete or inadequate diet for the species, mainly consisting of homemade food, sweets, dairy products, lean meat, bread, and excessive amounts of sweet fruits. Only one clinical record described a diet that could be considered appropriate, and two records did not describe the diet at all.

Sixteen records (51.6%) did not include information on the origin of the individuals. Five records mentioned "Chaco"; six records mentioned four cities in the Oriental Region of Paraguay (Asunción, San Lorenzo, Emboscada, and Loma Grande); two records mentioned municipal markets (Asunción and the other unidentified); and two medical records report two different cities in the Occidental Region of Paraguay (Puerto José Falcón and Pozo Colorado) as the origin.

The medical records of individuals of the genus *Callithrix* did not contain sufficient data. The white-coated titi, *Plecturocebus pallescens* (Ka'i ygau in Guaraní language), was recorded in four medical records. Of these, three were female and one was male, with a mean weight of 338.75 grams (195 - 600) and an average age of 8.8 months (5 - 12). Two records did not indicate the origin of the animals; one mentioned the city of Villarrica, and another mentioned the city of Pozo Colorado. Three patients of the genus *Saimiri* (species not identified) were recorded (two females and one male), with a mean weight of 331.6 grams (305-360), all reported as originating in Bolivia.

It is worth mentioning that one adult female was recorded under the species *Saguinus fuscicollis*. The animal's weight was not recorded, but it was reported as originating from Brazil and was diagnosed with a nonspecific respiratory infection.

Discussion

The Azara's capuchin monkey (*S. cay)* is a species distributed throughout eastern Paraguay, including Asunción (MADES *et al.* 2021), as well as part of the humid Chaco, matching the reported origin of the animals in this manuscript. The species' feeding habits are plastic and opportunistic. Its diet in the wild is complex, consisting of a wide variety of food items, and is closely related to the availability of food in the ecosystem (Smith *et al.* 2022), unlike the limited and nutritionally inadequate range of food items reported in clinical records, including dairy products, excess sweet fruits, lean meat, processed foods, fried foods, sweets, and soft drinks, among others. The mean weight reported in the findings is within the expected mean weight for the species (1200 g in females, 4500 g in males), although closer to the minimum range (Verona and Pissinatti 2014), which could be related to the inadequate diet or to the fact that the published mean weight refers to adult weight.

The black howler monkey (*A. caraya*) is distributed in humid ecosystems associated with riparian forests, mainly present in the Pantanal and Lower Chaco ecoregions, although it has a wide distribution in eastern Paraguay (Cartes *et al.* 2018), matching the origin of the animals recorded. The mean weight reported in the findings is below the expected minimum weight for the species (5800 g), which may be related to the fact that the mean age of the animals was still far from sexual maturity, when they should reach adult weight (Verona and Pissinatti 2014), or inadequate management, due to the complexities of managing the species in captivity and the negative impact on the animals' health (Cubas 1996; Pastor-Nieto 2014).

Regarding these two species, our findings match reports from other countries in that the families Cebidae and Atelidae present the highest number of cases under human care, with trauma also being one of the main reasons for veterinary consultation, albeit also putting particular emphasis on the impact of infectious diseases on the animals' quality of life (Cubas 1996; Varela *et al.* 2010; Nolasco 2017; Yllescas Barrientos 2019).

Azara's owl monkey (*A. azarae*) is an arboreal species that inhabits tropical and xerophytic forests, with its Paraguayan distribution limited to the humid Chaco and the semi-arid forests of the dry Chaco (Cartes *et al.* 2018; Weiler *et al.* 2019). The reported origins of the species indicate widespread trafficking at the national level. The species' diet is flexible and includes flowers, fruits, leaves, and invertebrates (Weiler *et al.* 2019; van der Heide *et al.* 2023), which is very different from the visibly inappropriate diet reported in this study. The mean weight reported is similar to the known lower range expected for the species (600 to 1000 grams), although this range involved a predominance of young individuals, still far from sexual maturity (Calle and Joslin 2014; Verona and Pissinatti 2014), which can differ from the expected adult weight.

The genus *Callithrix* currently comprises six species, all endemic to southern and eastern Brazil, associated with the Atlantic Forest, the Cerrado, and the Caatinga (Malukiewicz *et al.* 2020). *C. jacchus* is one of the smallest species in the genus and is native to the Atlantic Forest and Caatinga (in the states of Maranhao, Piauí, Ceará, Rio

Grande do Norte, Paraíba, Pernambuco, Alagoas, Bahia, and Tocantins; Rylands *et al.* 2009), so the presence of the species in Paraguay is indicative of illegal transnational trafficking. These species feed on fruits, gum, and invertebrates (Castro and Araújo 2007; Abreu *et al.* 2016), representing great complexities for captive management due to the particularities of their digestive system (Caton *et al.* 1996). As for animals classified only as genus *Callithrix* spp., the following alternatives can be assumed: (1) individuals of the species *C. jacchus*, or some other species of the current genus, or (2) individuals classified according to the old nomenclature of *Mico melanurus* (formerly *Callithrix argentata*) (Rylands *et al.* 2009).

White-coated titi, *P. pallescens*, is an arboreal and gregarious species associated with the northern Paraguayan Chaco. It inhabits xerophytic forests as well as transitional Chaco-Chiquitano forests, and feeds mainly on fruits, although it also eats leaves and insects (Cartes *et al.* 2018; Weiler *et al.* 2019; Tomas *et al.* 2022). The mean weight of the species ranges between 510 and 730 grams, notably higher than the values reported in the present study, although this could be associated with the young mean age reported (Calle and Joslin 2014; Tomas *et al.* 2022). The genus *Saimiri* is widely distributed in South America, strongly associated with the Amazon basin, even reaching Central America (Thorington 1985). They weigh between 750 and 1100 grams, depending on the species, and feed on insects, fruits, flowers, and leaves (May 2013; Calle and Joslin 2014). Regardless of the species in question, the animals reported originate from illegal cross-border trafficking, matching with what is reported in the clinical records.

With regard to the report of *Saguinus fuscicollis*, the species' range is far from Paraguayan territory (Buckner *et al.* 2015), and to the authors' knowledge, no other individuals of this species have been reported in the country. There are no morphometric data to corroborate the coincidence with the aforementioned species, and it has not been possible to contact the person responsible for the animal, probably because it is an old clinical record. Considering these limitations, we believe that this report most likely represents a misidentification of a specimen belonging to another species.

Regarding the various digestive disorders reported in different species, in most cases a definitive diagnosis could not be made. Among the etiologies that cause digestive disorders in non-human primates, various forms of viral hepatitis are described; bacterial disorders caused by *Shigella* spp., *Salmonella* spp., *Yersinia* spp., *Campylobacter* spp., *Mycobacterium* spp., various parasitic infections, including those caused by Acanthocephala and Entamoebidae, and even dental caries (Verona and Pissinatti 2014; Dib *et al.* 2023). In captivity, the predisposition to digestive system conditions can increase mainly due to stress, confinement, and inadequate diets offered to animals (Suleman *et al.* 1995; Tarara *et al.* 1995; Suleman *et al.* 2000). In *A. caraya*, for example, the diet in the wild is based mainly on leaves from various plant families, followed by fruits and flowers (Ludwig *et al.* 2008), requiring high amounts of fiber, in stark contrast to what is offered to animals in captivity. Diets high in fiber are essential for maintaining the intestinal microbiota in folivorous species, promoting the development of more diverse microbial populations, which increases nutrient utilization and improves food passage through the digestive tract. This, together with greater foraging opportunities, ultimately results in greater animal welfare (Edwards and Ullrey 1999; Nijboer 2006; Kišidayová *et al.* 2009; Lawless *et al.* 2025).

With regard to respiratory conditions, although in most cases no causative agent is identified, the diagnosis of *Mycobacterium tuberculosis* in one animal was noted. Disease by *Mycobacterium* spp. has already been reported in primates of the genus *Sapajus* in Argentina and Brazil, highlighting the potential impact on public health associated with the fact that these species are often kept as pets (Ehlers *et al.* 2020; Lamattina *et al.* 2025; Vetter and Insfrán 2025). Other microorganisms associated with respiratory conditions in non-human primates are *Klebsiella pneumoniae*, *Staphylococcus* spp., *Streptococcus* spp., *Pasteurella multocida*, and *Bordetella bronchiseptica* (Verona and Pissinatti 2014), with the possible presence of *K. pneumoniae* in non-human primates being of particular importance, as it is a zoonotic agent capable of causing severe respiratory symptoms, leading to multisystemic disease and sepsis (Soto *et al.* 2012; Anzai *et al.* 2017; Saputro *et al.* 2023; Strich *et al.* 2025).

Among the dermatological conditions reported in non-human primates are dermatophytosis (caused by *Trichophyton* spp., *Microsporum* spp., or *Epidermophyton* spp.), dermatophilosis, nocardiosis (Migaki 1986), scabies (caused by *Demodex* spp., *Sarcoptes scabiei*, or *Psorergates* spp.; Bernstein and Didiert 2009), and leishmaniasis (Garcez *et al.* 2002; Voltarelli *et al.* 2009; Santos and de Oliveira 2020), all of which have zoonotic potential. Bacterial infections usually occur as secondary infections following injuries or fights, although under certain conditions, infections can occur from the skin's natural microbiota, such as *Staphylococcus* spp. and *Streptococcus* spp., as well as *Pseudomonas* spp. (Bernstein and Didiert 2009; Oliveira and Santos 2023). Apparently, some species are natural carriers of *Malassezia* spp. (Neves *et al.* 2017; Coutinho *et al.* 2020). Nutritional deficiencies, allergies, and some neoplasms can also have cutaneous manifestations in primates, although there is not much information on this subject (Beniashvili 1989; Juan-Sallés *et al.* 2001; Bernstein and Didiert 2009; Miller 2012; Díaz-Delgado *et al.* 2018; Ehlers *et al.* 2022).

A study from Brazil cites trauma as the leading cause of death in primates, with trauma from vehicle collisions, interspecific aggression, and electrocution being the most common causes in free-living animals (Ehlers *et al.* 2022), matching the present report. In other studies, the casuistry varies, but trauma remains among the three main conditions affecting primates, along with infectious diseases and

nutritional disorders (Varela *et al.* 2010; Yllescas Barrientos 2019). Gram-positive anaerobic bacillus *Clostridium tetani*, present in the soil, can enter the body through skin lesions caused by trauma and produce toxins that cause a condition known as tetanus, causing trismus, opisthotonos, and epileptiform seizures (Luisto 1993; Kessler *et al.* 2006; Springer *et al.* 2009; Oliveira and Santos 2023).

Although not many diagnoses accompanied by the etiological agent are mentioned, it should be noted that non-human primates can be carriers and transmitters of important zoonoses such as the rabies virus (particularly in *Callithrix* spp.), Alphavirus, *Trypanosoma* spp., *Leishmania* spp., *Toxoplasma gondii*, *Plasmodium* spp., as well as suffer from anthropozoonoses such as SARS-CoV-2, Herpes Simplex Virus-1, and *Mycobacterium tuberculosis* (Diaz *et al.* 2007; Estrada-Cely *et al.* 2011; Kotait *et al.* 2019; Ehlers *et al.* 2020; Dubey *et al.* 2021; Rondón *et al.* 2021; Diaz *et al.* 2024; Mendoza *et al.* 2024; Vetter *et al.* 2025). The potential impact of zoonoses and anthropozoonoses on conservation efforts, as well as on public health, must be considered.

In addition to this, debate should be generated regarding the ethical and legal questions surrounding the captive possession of non-human primates outside accredited zoological institutions. In Paraguay, the legal framework prohibits the sale and purchase of wild animals, including primates. Despite this prohibition, there is a provision that allows for the legal registration of wild animals kept in human care without the need to prove their origin beyond a sworn statement. This, combined with the ease of sale and limited oversight, has led to the normalization of domestic ownership of many species, including their display on social media. This fosters a culture of impulsive acquisition of juvenile primates, which are abandoned once they reach puberty. To date, there have been no final convictions for primate trafficking in Paraguay. The constant exposure of primates of unknown origin, with an unknown microbial load and subjected to extremely stressful conditions, combined with a lack of understanding regarding their environmental and nutritional needs, as well as their behavioral requirements, creates conditions conducive to the transmission of pathogens between humans and animals. These pathogens can cause serious illness in both humans and primates and can easily become sources of infection (Mendoza *et al.* 2024). As a countermeasure, various law enforcement agencies must be integrated, and they can utilize new animal welfare laws to discourage the keeping of these animals in homes. The enforcement of exemplary sentences, such as those handed down for animal abuse, combined with educational campaigns featuring real-life cases of zoonoses and anthropozoonoses, can be the first step toward reducing the impact of primate trafficking in the country.

Conclusions

The objective of this study was to report the main clinical findings regarding primates transferred to the Departamento de Recursos Faunísticos y Medio Natural at the Universidad Nacional de Asunción. The data indicate that four of the five species recorded in Paraguay are affected by illegal trafficking and unregulated private ownership, although *Sapajus cay* and *Alouatta caraya* are the most affected. Routine checkups are frequent, but various cases of health issues are also recorded, primarily trauma, digestive and respiratory conditions, and infectious diseases. It is worth noting that many medical records contain incomplete data and/or remain undiagnosed. This is the first case report on primates in Paraguay and may help identify key species for controlling illegal trafficking.

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Declaration of Artificial Intelligence use

No artificial intelligence tools were used in the preparation of this manuscript.

Author contributions

Joerg Richard Vetter contributed to the manuscript's conception, design, data analysis, and writing. Mauricio E. Martínez contributed to the data collection, data analysis, and writing.

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Under blue wings: mammals of the Spix's Macaw Protected Areas, Northeastern Brazil

Thais Pereira dos Santos[1,2], Camile Lugarini[3], Eduardo Martins Venticinque[4], and Paulo Henrique Dantas Marinho[4,5,6,7,8*]

[1]Universidade Federal do Vale do São Francisco (UNIVASF). Petrolina, Pernambuco, Brazil. E-mail: thais.santos.bolsista@icmbio.gov.br (TPS).
[2]Núcleo de Gestão Integrada (NGI) Juazeiro - Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). Juazeiro, Bahia, Brazil.
[3]Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). Antonina, PR, Brazil. E-mail: camile.lugarini@icmbio.gov.br (CL).
[4]Programa de Pós-graduação em Ecologia, Universidade Federal do Rio Grande do Norte (UFRN). Natal, Rio Grande do Norte, Brazil. E-mail: eduardo.venticinque@ufrn.br (EMV).
[5]Programa de Pós-Graduação em Desenvolvimento e Meio Ambiente (PRODEMA), Universidade Federal Rural do Semi-Árido (UFERSA). Mossoró, RN, Brazil.
[6]Escola Estadual de Educação Profissional Professora Elsa Maria Porto Costa Lima, Secretaria de Educação do Estado do Ceará (SEDUC). Aracati, Ceará, Brazil.
[7]Tiger Cat Conservation Initiative (TCCI). São Luís, Maranhão, Brazil.
[8]Instituto Seridó Vivo (ISV). Currais Novos, Rio Grande do Norte, Brazil.
[*]Corresponding author: paulohdmbio@gmail.com

Mammals can be used as indicators of relative biological integrity and environmental quality. Therefore, inventories of this taxon are fundamental for planning and evaluating conservation and management strategies such as the creation of protected areas. This study compared the medium- and large-sized mammalian species' diversity and composition before and after the establishment of the Spix's Macaw protected areas to assess its potential beneficial effects and to provide subsidies for the management and monitoring of the protected ecosystem. Mammal data were collected in two camera trapping surveys carried out in 2017 and between 2020 and 2021, totaling a sampling effort of 3,803 camera-trap days. We obtained a total of 1,141 records of 17 species of wild mammals, including 13 medium- and large-sized species and four small mammal species. We recorded four threatened species. Although species richness and composition were very similar between the periods before and after the establishment of the protected area, diversity was higher which is associated with having greater species evenness. *Cerdocyon thous*, *Euphractus sexcinctus*, and *Dasypus novemcinctus* were the most common wild mammals, while the rarest species were *Puma concolor*, *Procyon cancrivorus*, *Dicotyles tajacu,* and *Dasyprocta prymnolopha*. Seven domestic species were recorded, including the super-abundant *Capra hircus*. Therefore, conservation and habitat restoration strategies, such as the expansion of protected areas and the sustainable management of domestic species, must be reinforced and expanded to ensure the persistence of an important diversity of wild mammals, whose population trends should be monitored.

Keywords: Caatinga, camera trap, medium and large-sized mammals, threatened species, tropical dry forest.

Los mamíferos pueden utilizarse como indicadores de la integridad biológica relativa y la calidad ambiental. Por lo tanto, los inventarios de este taxón son fundamentales para la planificación y evaluación de estrategias de conservación y manejo como la creación de áreas protegidas. Este estudio comparó la diversidad y la composición de las especies de mamíferos de tamaño mediano y grande antes y después del establecimiento de las áreas protegidas del guacamayo de Spix para evaluar sus posibles efectos beneficiosos y proporcionar información para la gestión y el monitoreo del ecosistema protegido. Los datos de mamíferos se recolectaron en dos campañas de fototrampeo realizadas en 2017 y entre 2020 y 2021, totalizando 3,803 días-trampa. cámara Obtuvimos un total de 1,141 registros de 17 especies de mamíferos silvestres, incluyendo 13 especies de tamaño mediano y grande y cuatro especies de mamíferos pequeños. Registramos cuatro especies amenazadas. Aunque la riqueza y la composición de especies fueron muy similares entre los períodos anteriores y posteriores a la protección del hábitat, la diversidad fue mayor tras el establecimiento de áreas protegidas, cuando las poblaciones mostraron una mayor uniformidad. *Cerdocyon thous*, *Euphractus sexcinctus* y *Dasypus novemcinctus* fueron los mamíferos silvestres más comunes; mientras que las especies más raras fueron *Puma concolor*, *Procyon cancrivorus*, *Dicotyles tajacu* y *Dasyprocta prymnolopha*. Se registraron siete especies domésticas, incluyendo la superabundante *Capra hircus*. Por lo tanto, es necesario reforzar y ampliar las estrategias de conservación y restauración del hábitat, como la expansión de las áreas protegidas y el manejo sostenible de las especies domésticas, para asegurar la persistencia de una importante diversidad de mamíferos silvestres, cuyas tendencias poblacionales deben ser monitoreadas.

Palabras clave: Bosque seco tropical, Caatinga, cámara trampa, especies amenazadas, mamíferos medianos y grandes.

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The presence of certain mammal species in an area is an indicator of relative biological integrity and environmental quality (Cheyne *et al.* 2016; Marques *et al.*, 2023). Species inventories, with adequate sampling design, can ensure detailed knowledge of the occurrence, diversity, and distribution of species in this group in a specific region, potentially generating data to be used for assessing the impacts of human actions on the biological community (Tobler *et al.* 2008; Marinho *et al.* 2018a). This type of knowledge is fundamental for planning and evaluating appropriate conservation and management strategies within and outside protected areas (Tobler *et al.* 2008; Falcão *et al.* 2025; Martins *et al.* 2025).

Among mammals, medium and large-sized mammals (*i.e.* > 1 kg) are particularly good indicators of environmental quality, as they generally require large areas, have low population density, and occupy high trophic levels, in the case of top predators (Chiarello 1999; Cardillo *et al.* 2005). Medium- and large-sized mammals are among the vertebrates most affected by hunting (Benítez-López *et al.* 2017) and by habitat loss, fragmentation, and degradation (Crooks *et al.* 2017). They play important ecological roles and provide strategic ecosystem services, such as controlling herbivore populations, modulating the nutrient cycle, and dispersing large seeds, being essential for the structuring and regeneration of tropical forests (Chiarello 1999; Terborgh *et al.* 2001; Cardillo *et al.* 2005; Galetti and Dirzo 2013; Sobral *et al.* 2017; Vale *et al.* 2023). Therefore, their population decline can cause numerous cascading effects on the ecosystem (Vanthomme *et al.* 2010; Gibson *et al.* 2011). Thus, medium- and large-sized mammals are an important target for conservation and systematic monitoring (Balmford *et al.* 2005; Dobson 2005; Silva *et al.* 2018).

On a global scale, the diversity of medium- and large-sized mammals is positively related to the coverage of protected areas (Chen *et al.* 2022). Protected areas represent one of the main strategies for biodiversity conservation (Silva *et al.* 2018; Magioli *et al.* 2021; Sonoda *et al.* 2021), generally harboring greater species richness, including those threatened with extinction (Magioli *et al.* 2021), in addition to protecting species from threats that are present outside their boundaries (Pacifici *et al.* 2020). The positive effect of habitat protection persists at regional scale, especially in tropical ecosystems characterized by high biodiversity and significant anthropogenic pressure (Magioli *et al.* 2021).

Despite constituting the largest and most diverse seasonally dry tropical forest in the Americas, the Caatinga is one of the least protected (Teixeira *et al.* 2021) and most degraded and fragmented ecosystems in Brazil (Antongiovanni *et al.* 2018, 2020). This ecosystem undergoes great pressure from a human population of over 28 million people and nine million goats raised extensively (Tabarelli *et al.* 2018). Moreover, climate change (Moura *et al.* 2023) and the recent advance of large renewable energy projects threaten this ecosystem (MAPBIOMAS 2024). With at least 183 recorded mammal species, 11 of which are endemic, the semiarid Brazilian Caatinga is rich in mammal diversity and endemism (Carmignotto and Astúa 2017). However, knowledge about the distribution and conservation status of mammals in the ecosystem is still scarce, even in protected areas (Marinho *et al.* 2018a; Campos *et al.* 2019).

Created in 2018, the Spix's Macaw protected areas encompass approximately 120,000 hectares of Caatinga ecosystem under different protection levels (Presidência da República do Brasil 2018). Their central objective is to protect natural habitats that are important to the life cycle of the Spix's Macaw (*Cyanopsitta spixii*) (Presidência da República do Brasil 2018), thereby ensuring conditions for the reintroduction of a psittacine species that is extinct in the wild. The region's entire biodiversity may benefit from the conservation and management actions implemented, with a focus on a charismatic bird considered a flagship and umbrella species that requires extensive areas to establish and survive (Simberloff 1998; Lugarini *et al.* 2021). However, studies characterizing the fauna possibly benefited by the protected areas implemented in the region are still incipient, especially for mammals. Therefore, this study aimed to describe the diversity and composition of the medium- and large-sized mammal assemblage (mammals, from now on) before and after the establishment of Blue Spix's Macaw protected areas in northeastern Brazil. We conducted an initial assessment of the effects of habitat protection on mammals to provide subsidies for the management and monitoring of the protected ecosystem.

Materials and methods

Study area. The study area comprises the Spix's Macaw Environmental Protection Area (EPA), with 89,996 hectares, and the Spix's Macaw Wildlife Refuge (WR), which has 29,986 hectares, in addition to a part of the immediate surroundings of these protected areas located in the municipalities of Curaçá and Juazeiro, in northern Bahia, Northeast Brazil (Presidência da República do Brasil 2018; Figure 1). The protected areas are located in the Caatinga morphoclimatic domain, where a hot and semiarid climate predominates (Velloso *et al.* 2002) with an average annual minimum temperature of 25°C and a maximum of 34°C, and an average annual rainfall of 429 mm, with more frequent rains between December and March (Junqueira *et al.* 2020). The phytophysiognomy of the area can be divided into three main formations: open shrubland, including flattened and rocky outcrop environments; dense arboreal vegetation in environments influenced by mountain ranges; and riparian forest, represented by floodplain and lowland environments in banks of temporary rivers and streams (Freitas *et al.* 2005). Human activities have historically degraded the region's vegetation and hampered its natural regeneration, such as excessive grazing pressure by goats, sheep and cattle (Juniper and Yamashita 1991), which reach high densities in the region (Magalhães *et al.* 2024).

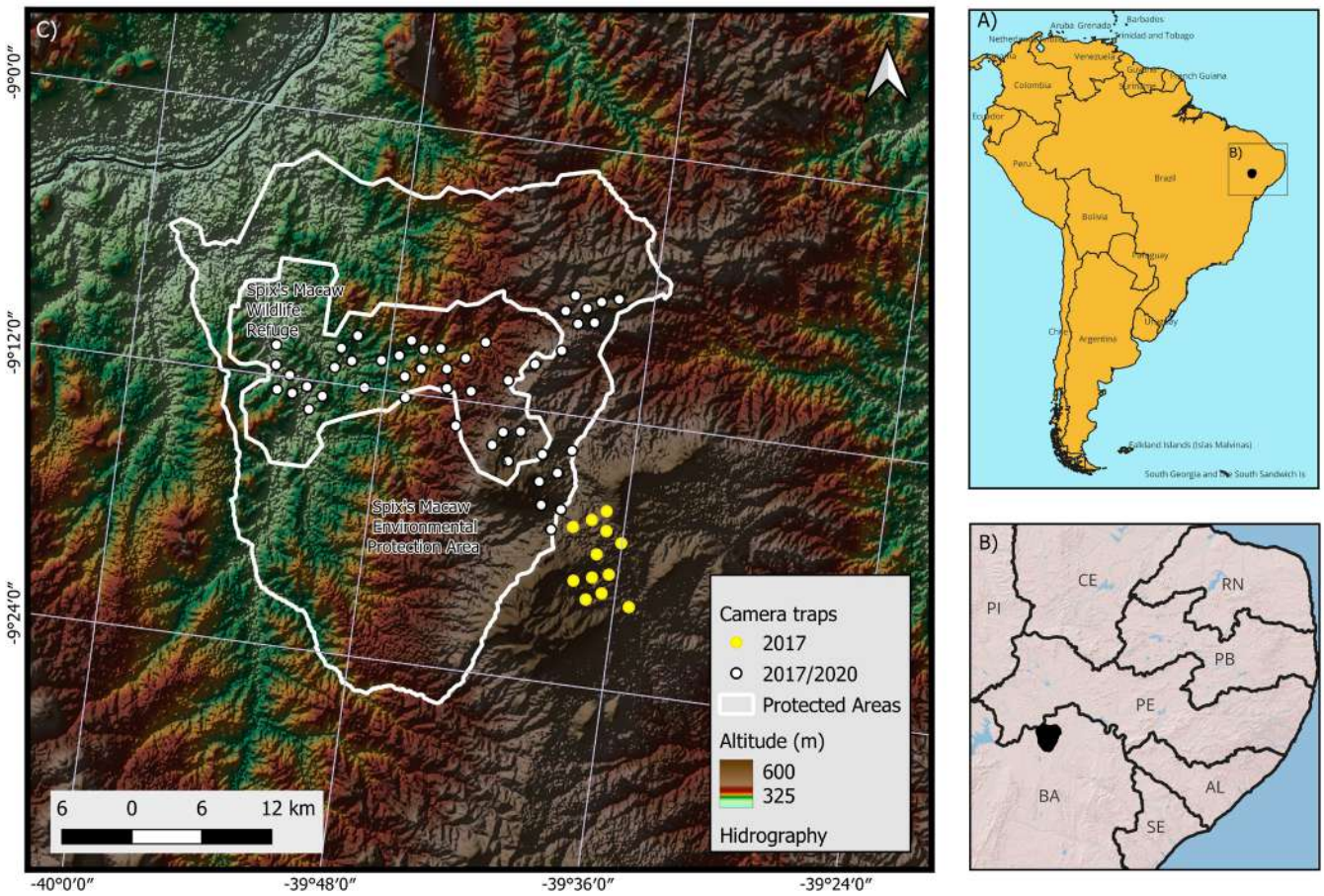

Figure 1. Study area and sampling points in the Spix's Macaw Protected Areas and their surroundings located in Northeastern Brazil (A), northern Bahia (B), between Curaçá and Juazeiro municipalities (C). Brazilian states: Rio Grande do Norte (RN), Ceará (CE), Paraíba (PB), Piauí (PI), Alagoas (AL), Sergipe (SE), and Bahia (BA). The topography presented is based on NASA Shuttle Radar Topography Mission (2013).

Data sampling. Data on mammals were collected in two campaigns conducted between 2017 and 2021, following an adaptation of the Tropical Ecology Assessment and Monitoring protocol (TEAM) (Ahumada *et al.* 2013). Both sampling campaigns followed the same field protocol, varying only in the number of sampling points. From September to November 2017, 60 points were sampled (before the creation of the protected areas) during the dry season. From October 2020 to January 2021, 48 of the 60 points from the first campaign were surveyed again, covering the dry season and the beginning of the rainy season. During this period, the traps were distributed exclusively within the protected areas, excluding the 12 sampled points that were outside the boundaries of the conservation units after their creation. All sampling points were preferably installed on pre-existing trails used by animals and people and established with a minimum distance of approximately 1.5 km between them, considering that the adopted protocol focused primarily on medium to large-sized mammals. We took care to consider the heterogeneity of the environments found in the area, as well as to encompass the altitudinal gradient, including areas from the lowest points to the mountain ranges. No bait was used.

At each sampling point, a Bushnell automatic camera trap (Essential E2 or Trophy Cam HD) activated by movement was installed. The cameras were programmed to take 2 or 3 pictures, with 5-minute resting intervals, and remained active 24 hours a day during the sampling period, for a minimum of 30 consecutive days, except for those that presented any problem. They were installed on pre-existing trails, in dry streambeds, and in riparian forests at 30-40 cm from the ground.

Data analysis. All analyses were conducted for medium- and large-sized mammals (>1 kg; Marinho *et al.* 2018a), while for small mammals only the number of records obtained is presented. We used the grouped records of the same species and site within one-hour periods to calculate the frequency of recording for each species (Marinho *et al.* 2018a). The frequency of recording was calculated as the ratio of the number of grouped records to the sampling effort, multiplied by 100 (O'Brien 2011). We built rank-abundance graphs (Cruz-Bazan *et al.* 2025), based on the recoding frequencies of medium- and large-sized mammal species for the 2017 and 2020 sampling seasons, as well as for the total data obtained from the 60 and 48 sample points, respectively.

Mammal diversity was assessed using alpha and beta diversity metrics calculated for the 2017 and 2020 sampling periods, as well as for the pooled dataset. We

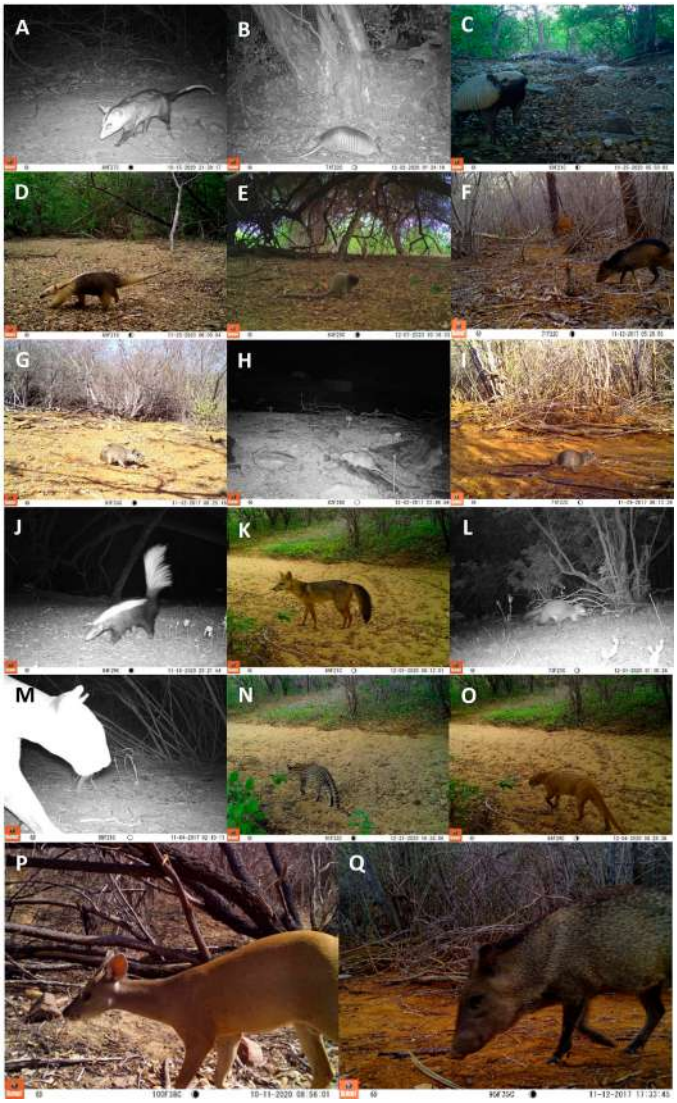

Figure 2. Mammals recorded between 2017 and 2021 in the Spix's Macaw protected areas and their surroundings, Bahia, northeast Brazil. A) *Didelphis albiventris*, B) *Dasypus novemcinctus*, C) *Euphractus sexcinctus*, D) *Tamandua tetradactyla*, E) *Callithrix penicillata*, F) *Dasyprocta prymnolopha*, G) *Kerodon rupestris*, H) *Galea spixii*, I) *Thricomys laurentius*, J) *Conepatus semistriatus*, K) *Cerdocyon thous*, L) *Procyon cancrivorus*, M) *Puma concolor*, N) *Leopardus emiliae*, O) *Herpailurus yagouaroundi*, P) *Subulo gouazoubira*, and Q) *Dicotyles tajacu*.

generated a rarefaction (interpolation) and extrapolation (prediction) curve based on Hill numbers (q = 0 [richness], q = 1 [Shannon], and q = 2 [Simpson]) using abundance data (number of records) from all sampling points across both periods. This method allows for robust comparisons between samples with differing sampling efforts (Cruz-Bazan *et al.* 2025). A curve based on Hill numbers also provides sample coverage through rarefaction and extrapolation curves, which can indicate the degree of completeness of the mammal inventory. On the other hand, we considered only the 48 points sampled during the two sampling periods to estimate the Shannon diversity index (H') and Simpson diversity index (D), as well as Pielou's evenness (J'). Similarly, we estimated Sørensen beta diversity (βsor) between the two sampling periods (2017 and 2020) to assess potential changes in species composition. Diversity indices were obtained using the vegan package (Oksanen *et al.* 2026), and rarefaction and extrapolation curves were constructed using the iNEXT package (Hsieh *et al.* 2016). Statistically significant differences were based on a significance threshold of α = 0.05. All analyses were performed using R software (R Core Team 2026).

Finally, we conducted an assessment of the habitats in which each species was recorded, through assessments of the vegetation at each field point and its comparison with the habitat type classification adapted from Freitas *et al.* (2005), as follows: open shrub vegetation (including flat and rocky outcrop environments; 22 sampling points), riparian forest vegetation (including lowland and floodplain; 22 points), and dense arboreal vegetation (mountain range; 16 points). There was no standardization in the number of points per habitat, so we once again used rarefaction and extrapolation curves in the iNEXT package to compare mammal diversity based on data from the entire sample while accounting for unequal sampling effort.

Species identification was carried out using image guides of potential species and consultation with specialists. The taxonomic classification of the species followed Abreu *et al.* (2025), and the conservation status was based on the red lists of Bahia (Cassano *et al.* 2017; SEMA 2017), Brazil (MMA 2026), and the IUCN (2025). In turn, the classification of species according to trophic guilds followed Paglia *et al.* (2012). Data collection was authorized by the Biodiversity Authorization and Information System of ICMBio (SISBIO Nº75795), and data tabulation and organization were performed using the CamtrapR package (Niedballa *et al.* 2016).

Results

The 2017 and 2020-2021 surveys accumulated a total sampling effort of 3,803 camera-days. There were 2,250 camera-days in 2017, with the cameras remaining active for an average of 37.5 days (SD = ± 2.9), and 1,553 camera-days in 2020-2021, with the cameras remaining in the field for an average of 33 days (SD = ± 5).

We obtained a total of 1,141 grouped records of wild mammals in the two samplings (642 records in 2017 and 499 records in 2020-2021). Based on these records, we obtained a total richness of 17 species of wild mammals (15 species in each sampling season) distributed across seven orders and 13 families, including 13 medium- and large-sized species and four small mammal species, including three rodents and one arboreal primate species (Figure 2; Table 1). Four of the recorded species are considered threatened with extinction at different levels: *Kerodon rupestris* (Bahia), *Herpailurus yagouaroundi* (Bahia and Brazil), *Puma concolor* (Bahia), and *Leopardus emiliae* (Bahia, Brazil and IUCN) (Table 1). In addition to native species, we recorded seven species of domesticated mammals (Table 1).

The richness rarefaction curves (q = 0) for both sampling periods and the pooled data did not tend toward stabilization, indicating that more species would be recorded with increased sampling effort; however, the sample coverage

Table 1. Wild and domesticated mammals recorded in the Spix's Macaw protected areas and their surroundings between 2017 and 2021, using camera trapping, in the municipalities of Curaçá and Juazeiro, Bahia, northeastern Brazil. Recording location: EPA (Environmental Protection Area), WRE (Wildlife Refuge), SUR (surroundings of the two protected areas). Conservation status in Bahia (BA), Brazil (BR) and IUCN (global): VU (Vulnerable), EN (Endangered), NT (Near Threatened). Habitat types: dense arboreal vegetation (DA), open shrubby vegetation (OS) and riparian forest vegetation (RF). Guild: fr (frugivore), om (omnivore), in (insectivore), hb (herbivore), ca (carnivore), according to Paglia *et al.* (2012). Small mammals are marked with one asterisk (*). Exotic/domesticated species are marked with two asterisks (**).

Taxon	Number of records			Status	Local	Habitat	Guild
	2017	2020-21	Total				
Didelphimorphia							
Didelphis albiventris	1	18	19		EPA, WRE	DA, OS, RF	fr/om
Cingulata							
Dasypus novemcinctus	85	82	167		EPA, WRE, SUR	DA, OS, RF	in/om
Euphractus sexcinctus	66	113	179		EPA, WRE, SUR	DA, OS, RF	in/om
Pilosa							
Tamandua tetradactyla	18	12	30		EPA, WRE, SUR	DA, OS, RF	in
Primates							
*Callithrix penicillata**	0	4	4		WRE	RF	on
Rodentia							
*Galea spixii**	33	1	34		EPA, WRE, SUR	DA, OS	hb
*Kerodon rupestris**	25	55	80	VU (BA)	EPA, WRE, SUR	DA, OS, RF	hb
Dasyprocta prymnolopha	2	0	2		SUR	DA	fr
*Thrichomys laurentius**	7	16	23		EPA, WRE, SUR	DA, OS	fr/hb
Cetartiodactyla							
Subulo gouazoubira	17	4	21		EPA, SUR	DA, OS	fr/hb
Dicotyles tajacu	1	1	2	NT (BA)	EPA, SUR	DA	fr/hb
*Bos taurus***	0	35	35		EPA e WRE	DA, OS, RF	
*Capra hircus***	1745	1018	2763			DA, OS, RF	
*Ovis aries***	512	289	801			DA, OS, RF	
Carnivora							
*Canis lupus familiaris***	12	5	17		EPA, WRE, SUR	OS, DA	
Cerdocyon thous	317	127	444		EPA, WRE	DA, OS, RF	in/on
Conepatus semistriatus	11	35	46		EPA, WRE	DA, OS, RF	in/on
Procyon cancrivorus	0	1	1		WRE	RF	fr/on
*Felis catus***	1	9	10		WRE	DA, OS, RF	
Herpailurus yagouaroundi	7	3	10	VU (BA, BR)	WRE, SUR	DA, OS, RF	ca
Leopardus emiliae	40	27	67	VU (BA), EN (BR), VU (IUCN)	EPA, WRE, SUR	DA, OS, RF	ca
Puma concolor	1	0	1	VU (BA), NT (BR)	SUR	DA	ca
Perissodactyla							
*Equus asinus***	59	68	127		EPA, WRE, SUR	DA, OS, RF	
*Equus caballus***	10	6	16		EPA e WRE	DA, OS, RF	

curves suggest a high level of representativeness and that the majority of the species present were recorded (Supplementary Data SD1). The species richness of wild medium- and large-sized mammals in the 2017 and 2020-21 surveys was very similar, with no significant differences between mammal surveys as demonstrated by the overlap of the 95% confidence intervals (Figure 3). Regarding Hill numbers, while richness (q = 0) was virtually identical given the same sampling effort (11 species with nearly 400 individuals recorded in both samples) (Figure 1A), the significantly higher values for q1 (Shannon) and q2 (Simpson) in the second survey suggest greater diversity and evenness in 2020 compared to 2017 (Figures 3B and 3C).

This result is reinforced by the diversity indices calculated from data obtained at the 48 sampling points investigated in 2017 and 2020 (Table 2). Species richness also did not show a statistically significant difference (Supplementary Data SD2), even though 2020 yielded two more species of the medium- and large-sized mammals (11 species) than 2017 (9 species) across the 48 sampling points (Table 2). On the other hand, both diversity indices (Shannon and Simpson) were significantly higher in 2020 (Supplementary Data SD2; Table 2), as was Pielou's evenness index (Table 2). Despite the difference in alpha diversity, the low value of

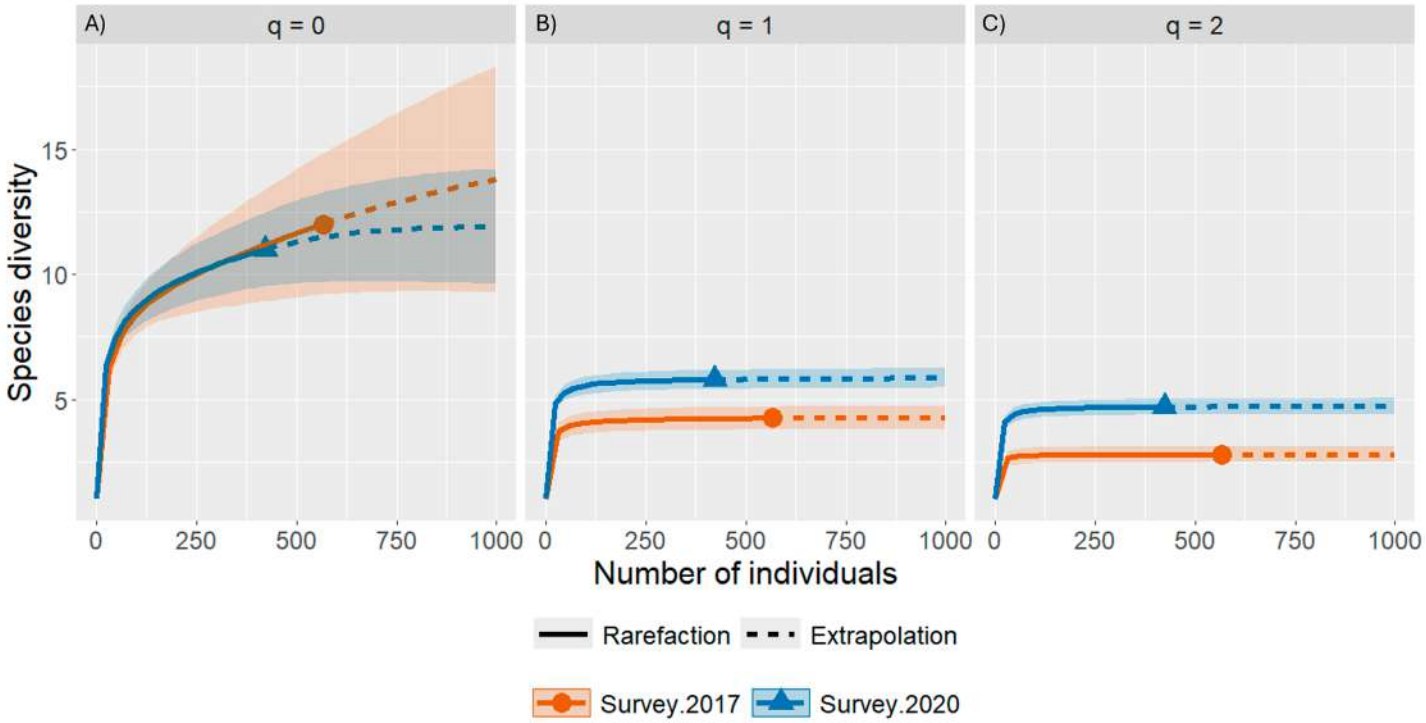

Figure 3. Species diversity curves according to Hill numbers (q = 0, richness [A]; q = 1, Shannon [B]; and q = 2, Simpson [C]) based on number of records (individuals) of wild medium- and large-sized mammals detected in 2017 (orange curve) and 2020-2021 (blue curve) in the Spix's Macaw protected areas and their surroundings, northeastern Brazil.

Table 2. Diversity, evenness, and dissimilarity (beta diversity) indices calculated based on medium- and large-sized mammals recorded at 48 sampling points in 2017 and 2020 in the protected areas of the Spix's Macaw, northeastern Brazil.

Survey	Richness (S)	Shannon (H')	Simpson (D)	Pielou (J')	Sørensen (βsor)
2017	9	1.41	0.66	0.64	
2020	11	1.76	0.79	0.73	
Total/Comparative	12	1.65	0.75	0.66	0.20

the estimated Sørensen beta diversity index (0.20) suggests low species turnover (0.11) and nestedness (0.09) between 2017 and 2020 surveys (Table 2).

In terms of the composition of the mammal assemblage, *P. concolor* and *Dasyprocta prymnolopha* were recorded only in 2017, while *Procyon cancrivorus* was recorded only in 2020 (Table 1). However, considering the data collected only within protected areas, *Didelphis albiventris*, *Dicotyles tajacu*, and *P. cancrivorus* were recorded only in 2020, whereas *P. concolor* was recorded only in 2017, and *D. prymnolopha* was never recorded in the protected areas (Table 1). All other species were recorded in both campaigns.

The species with the highest frequency of records, considered the most common species in both sample periods, was *Cerdocyon thous*, which dominated mainly the first sampling period, followed by *Euphractus sexcinctus* and *Dasypus novemcinctus* (Figure 4). On the other hand, among the species that showed the lowest number of records were *P. concolor*, *P. cancrivorus*, *D. tajacu* and *D. prymnolopha* (Figure 4).

There were many records of domestic animals. The seven species detected by the camera traps are divided into four families and three orders (Table 1). The goat (*Capra hircus*) was the most abundant species with 2,763 records, considering both samplings; followed by sheep (*Ovies aries*) with 801 records, donkey (*Equus asinus*) with 127 records, cow (*Bos taurus*) with 35 records, dog (*Canis lupus familiaris*) with 17 records, horse (*Equus caballus*) with 16 records, and cat (*Felis catus*) with 10 records.

Regarding the habitat types where the species were recorded, *P. cancrivorus* was recorded in a single riparian forest point; while *D. prymnolopha*, *D. tajacu*, and *P. concolor* were recorded only in arboreal vegetation associated with mountain ranges; and *Subulo gouazoubira* were recorded in areas with arboreal and shrubby vegetation, but not in riparian forest (Table 1). The rest of the wild mammals and almost all domesticated exotic species were recorded in all habitats, except for *C. lupus familiaris*, which was not recorded in riparian forest (Table 1). Despite the apparent differences between the habitats, the analysis of rarefaction and extrapolation curves suggests no significant difference in wild mammal richness (q = 0) or diversity (q = 1 or q = 2) between the environments (Supplementary Data SD3).

Discussion

The 17 species of mammals recorded in the Spix's Macaw protected areas and their surroundings, especially the 13 medium- and large-sized species, reinforce the biological importance of the region, which harbors just over 18% of the wild mammal species expected for the entire Caatinga biome (Carmignotto and Astúa 2017). Considering only the medium- and large-sized species, the richness found corresponds to 27% of the 45 mammal species weighing more than 1 kg expected for the Brazilian dry tropical forest (Carmignotto and Astúa 2017). Studies conducted in

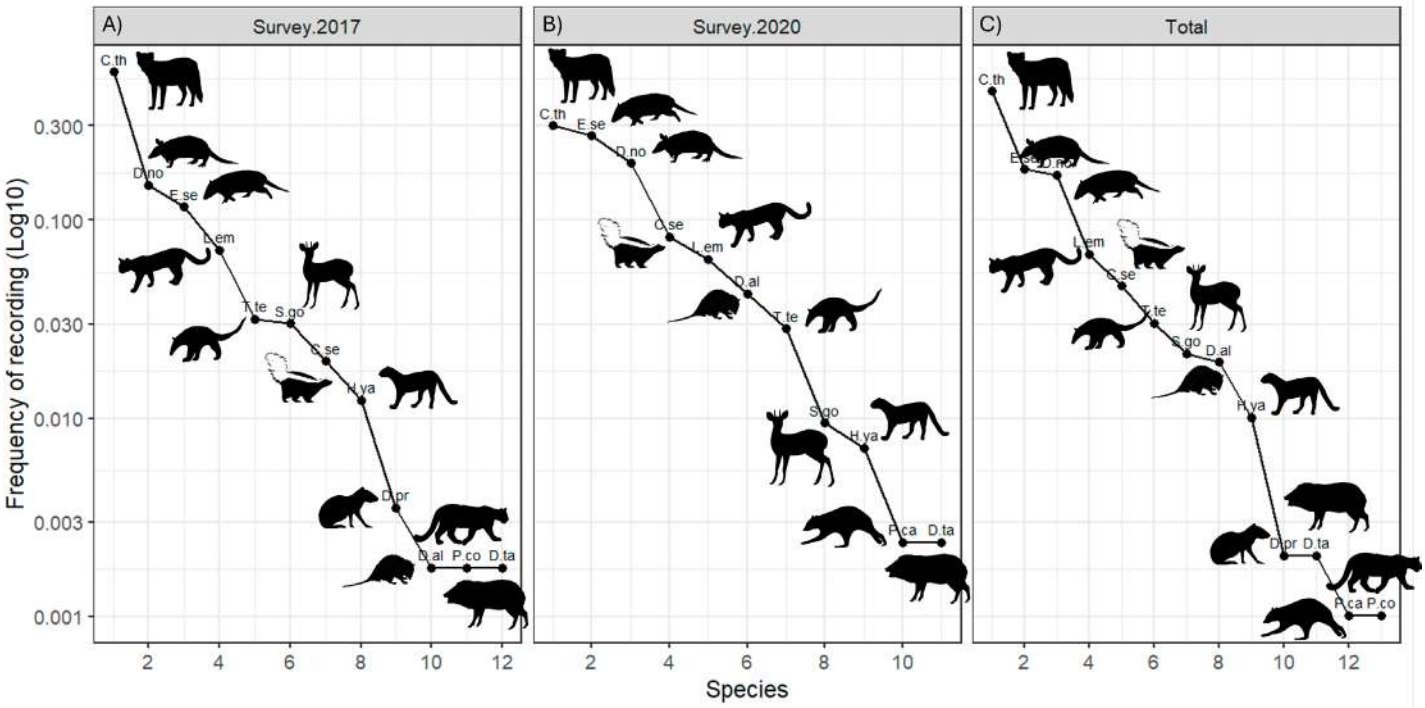

Figure 4. Rank abundance graphs based in frequency of recording of wild medium- and large-sized mammals recorded during 2017 (A), 2020-2021 (B), and considering the total data (C) in the Spix's Macaw protected areas and their surroundings, northeastern Brazil. D.al: *Didelphis albiventris*, D.no: *Dasypus novemcinctus*, E.se: *Euphractus sexcinctus*, T.te: *Tamandua tetradactyla*, D.pr: *Dasyprocta prymnolopha*, C.se: *Conepatus semistriatus*, C.th: *Cerdocyon thous*, P.ca: *Procyon cancrivorus*, P.co: *Puma concolor*, L.em: *Leopardus emiliae*, H.ya: *Herpailurus yagouaroundi*, S.go: *Subulo gouazoubira*, and D.ta: *Dicotyles tajacu*. Source of the mammal illustrations: https://www.phylopic.org/.

other protected areas of the Caatinga have found varying levels of mammal species richness. A survey carried out in the Boqueirão da Onça protected areas, including the National Park and the Environmental Protection Area, also located in northern Bahia, recorded 22 species of wild non-flying mammals using camera traps, including species likely extinct in our study area such as *Panthera onca* and *Myrmecophaga tridactyla* (Campos *et al.* 2019). In contrast, in the Catimbau National Park, in Pernambuco state, only eight species of wild non-flying mammals were found, in addition to seven exotic species that are very abundant in the area (Alves *et al.* 2020). The differences in species richness recorded in these areas and in the present study are related to the conservation status and environmental heterogeneity of the study areas, but also to the sampling effort employed.

The establishment of the Spix's Macaw Environmental Protection Area and Wildlife Refuge in 2018 appears to have benefited the mammals, resulting in a more diverse assemblage characterized by more equitable species abundances. Management actions, habitat restoration, environmental law enforcement and education initiatives, which emerged or were strengthened following the formalization of protected status (Lugarini *et al.* 2021; Vercillo *et al.* 2025), may have facilitated the recovery of mammal species with stricter habitat requirements or those subject to intense hunting pressure, such as *D. tajacu* (Alves *et al.* 2016). However, these results should be interpreted with caution, given the short timeframe since the creation of the EPA and WR. Furthermore, in 2020, the region was recovering from the most severe drought of the last century in the Caatinga that lasted from 2012 to 2017 (Silva *et al.* 2018), which likely also contributed to the recovery of populations most affected by the extended period of resource scarcity. *Procyon cancrivorus*, for example, was not recorded in 2017 and was recorded only once in 2020, possibly affected by scarcity of aquatic environments in the area, especially during the first sampling season, given its strong relationship with this type of habitat (Cheida *et al.* 2013).

The most generalist species in terms of habitat use and diet were the most frequently recorded among wild mammals. The omnivorous *C. thous* was the most common species, especially in the 2017 survey, following the pattern found in other areas of the Caatinga (Dias and Bocchiglieri 2016; Marinho *et al.* 2018a; Dias *et al.* 2019; Santos *et al.* 2024). The two armadillo species detected (*E. sexcinctus* and *D. novemcinctus*) are also considered common in the area. However, they are subjected to hunting in this ecosystem (Alves *et al.* 2016), which can reduce population levels or cause local extinctions in certain areas, especially in the case of *D. novemcinctus* (Bezerra *et al.* 2014; Marinho *et al.* 2018a).

Large mammals such as *D. tajacu* and *P. concolor* are among the species most impacted by habitat degradation and hunting. These species are intensely hunted and persecuted in the Caatinga for their meat or due to conflicts with livestock farmers, respectively (Alves *et al.* 2016), which explains their current absence in much of the biome (Marinho *et al.* 2019). *D. prymnolopha* is another very rare frugivore in the area, recorded infrequently and only in dense arboreal vegetation environments outside protected

areas. This is concerning in terms of maintaining ecosystem services primarily performed by these species, such as the dispersal of large seeds (Vale *et al.* 2023). In turn, *P. concolor* may be affected by the low availability of prey and retaliatory killing (Alves *et al.* 2016; Borges *et al.* 2017; Zanin *et al.* 2020), especially in a region where extensive goat and sheep farming is so economically important. These factors, combined with the extensive home range and low densities of *P. concolor*, may explain why the species was recorded only once during the entire study.

In addition to species with low abundances, some species expected for the region and not detected in this study are also likely to be affected by anthropogenic and climatic impacts. Among them is *Leopardus pardalis*, a mesopredator that naturally exhibits low population densities and that seems to be related to more preserved environments in the Brazilian semiarid region (Penido *et al.* 2016; Dias *et al.* 2017; Campos *et al.* 2019). Among the armadillos with predicted distribution in the region is the threatened *Tolypeutes tricinctus* (Feijó *et al.* 2015). If it still occurs in the region, the population must also be at very low density and restricted to more protected environments. *Galictis cuja* is another carnivore that should also occur in the area but was not detected, a pattern that is repeated in other studies in the biome (Falcão *et al.* 2025; Marinho *et al.* 2018a). Regarding small mammals, *Wiedomys pyrrhorhinos*, *Gracilinanus agilis*, and *Monodelphis domestica* are species known to the area (Freitas *et al.* 2005), thus increasing to 20 the number of confirmed wild mammal species of the protected areas of the Spix's Macaw.

In the Caatinga biome, deforestation and degradation are mainly caused by agriculture and livestock farming, which, along with hunting, represents one of the main threats to wild species (ICMBio 2018). Large herds of goats and sheep, which together exceeded the number of wild mammal records in the present study, compete with wild animals for resources that are commonly scarce in the semiarid Caatinga (Marinho *et al.* 2016). These domestic animals were recorded in all types of habitats. Therefore, it is necessary to reduce their impact by protecting sensitive habitats, limiting access by domestic mammals, restoring degraded areas, and promoting more sustainable herd management strategies (Alves *et al.* 2020).

Indeed, the Caatinga consists of a mosaic of vegetation types shaped by environmental and anthropogenic factors that can determine the availability of resources and refuges for mammals (Freitas *et al.* 2005; Marinho *et al.* 2018b). Although our analysis did not detect significant variations in mammal richness or diversity among the different habitats studied, environments with arboreal vegetation showed a trend toward higher diversity, a pattern recognized in the literature (Marinho 2020). Therefore, future research should further investigate this issue using more appropriate sampling designs to identify priority habitats for enhanced protection or restoration.

The species recorded here reinforce the biological importance of the Spix's macaw protected areas for the conservation of non-flying mammal fauna in the Caatinga. Wild mammals have benefited from conservation and management strategies linked to the reintroduction process of *C. spixii* into the wild (Purchase *et al.* 2024), including the management of protected areas that guarantee the presence of rare and threatened species, as well as large mammals considered keystone species for the health of Brazilian semiarid ecosystems. However, it is important that long-term research investigates the population trends and potential recovery of the mammal assemblage, since the data presented here were collected a few years after the establishment of the protected areas. Actions for managing domestic species and conserving and restoring habitats should be reinforced and expanded to ensure the persistence of threatened and large wild mammals. For instance, records of threatened and rare species in the Caatinga biome obtained only in areas outside or on the periphery of reserves suggest the need to expand protection, as initially planned by the Institute of Environment and Water Resources of the State of Bahia (INEMA 2013), especially considering large-scale projects that may impact the landscape and biodiversity of the region (Bourscheit 2022).

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Declaration of Artificial Intelligence use

We declare that the authors have not used any Artificial Intelligence in the elaboration of this paper.

Author contributions

Thais Pereira dos Santos: Conceptualization, methodology, data curation, formal analysis, writing - original draft & writing - review and editing; Camile Lugarini: conceptualization, methodology, writing - original draft, writing - review and editing & funding; Eduardo Martins Venticinque:

conceptualization, formal analysis, writing - original draft & writing - review and editing; Paulo Henrique Dantas Marinho: conceptualization, methodology, data curation, formal analysis, writing - original draft & writing - review and editing.

Supplementary data

SD1. Diversity rarefaction and extrapolation (R/E) curves (q = 0) (A), sample completeness curves (B), and coverage-based R/E sampling curves (C) for wild medium- and large-sized mammals recorded in Spix's Macaw protected areas during 2017 (survey 2017) and 2020 (survey 2020) samplings and for the whole sample (total), considering 60 points sampled unevenly between 2017 and 2020.

SD2. Species diversity curves according to Hill numbers (q = 0, richness [A]; q = 1, Shannon [B]; and q = 2, Simpson [C]) representing wild medium- and large-sized mammals detected at 48 sampling points in 2017 (orange curve) and 2020-2021 (blue curve) in the Spix's Macaw protected areas, northeastern Brazil.

SD3. Species diversity curves according to Hill numbers (q = 0, richness [A]; q = 1, Shannon [B]; and q = 2, Simpson [C]) representing wild medium- and large-sized mammals detected in different habitat types (dense arboreal vegetation, riparian forest, and open shrub vegetation) of the Spix's Macaw protected areas and their surroundings, Bahia, northeastern Brazil, considering 60 points sampled unevenly between 2017 and 2020.

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Reservas provinciales de Tucumán, Argentina: diversidad y sistemática de murciélagos (Mammalia: Chiroptera)

Melanie Rodríguez De La Fuente[1,2*], Rubén M. Barquez[1], Camila S. González Noschese[1,2] y M. Mónica Díaz[1,2,3]

[1]PCMA (Programa de Conservación de los Murciélagos de Argentina) y PIDBA (Instituto de Investigaciones de Biodiversidad Argentina), Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán. Miguel Lillo 205, CP. 4000, San Miguel de Tucumán, Tucumán, Argentina. E-mail: rubenbarquez@gmail.com (RMB); camilasgn95@gmail.com (CSGN); mmonicadiaz@yahoo.com.ar (MMD)
[2]CCT NOA Sur, CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Crisóstomo Álvarez 722, San Miguel de Tucumán, Tucumán, Argentina.
[3]Fundación Miguel Lillo. Miguel Lillo 205, CP. 4000, Argentina.
[*]Autor de correspondencia: melanierodriguezdlf@gmail.com

The Yungas Forest represent a biodiversity "hotspot" and a conservation challenge for the Tucumán Province due to habitat loss and fragmentation in recent years. Bats from the Yungas represent 66% of the species in Argentina. However, information regarding their diversity in protected natural areas of Tucumán is scarce. The objective of this study was to systematize and analyze the available information on bats occurring in four provincial reserves in Tucumán Province. Subsequently, species diversity, richness, and abundance were evaluated, and bat assemblages were compared among reserves and between the dry and wet seasons. In addition, the systematic identity of specimens deposited in the Colección Mamíferos Lillo (CML) was reviewed, and a bibliographic search was conducted. A total of 950 specimens belonging to 20 species, 12 genera, and 3 families of bats were recorded. Although the recorded diversity was high, it only represented 68% of the total species in Tucumán Province and 50% of the total species present in the Yungas. The Reserva Provincial Santa Ana was identified as the most diverse and even among the reserves studied. The review of the specimens deposited in the CML resulted in the reidentification of one specimen, thereby adding one species to the fauna of Tucumán Province (*Histiotus montanus*). However, due to differences in sampling effort and data sources among reserves, ecological comparisons should be interpreted descriptively. The results did not support the existence of a north–south latitudinal gradient. This study constitutes the first systematic compilation of bat diversity data for these provincial reserves and provides key information for their conservation.

Keywords: assemblages, biological collections, natural protected areas, species richness, Yungas.

Las Yungas representan un "hotspot" de biodiversidad y un reto de conservación para la provincia de Tucumán debido a la pérdida y fragmentación del hábitat en los últimos años. Los murciélagos de las Yungas representan el 66% de las especies de Argentina. Sin embargo, la información sobre su diversidad en áreas naturales protegidas de Tucumán es escasa. El objetivo de este trabajo fue sistematizar y analizar la información disponible sobre murciélagos presentes en cuatro reservas provinciales de la provincia de Tucumán. Posteriormente, se evaluaron la diversidad, riqueza y abundancia de especies, y se compararon los ensamblajes entre las reservas tanto en la estación seca como en la húmeda. Además, se revisó la identidad sistemática de ejemplares depositados en la Colección Mamíferos Lillo (CML) y se realizó una búsqueda bibliográfica. Se registraron 950 individuos de murciélagos, pertenecientes a 20 especies, 12 géneros y 3 familias. Aunque la diversidad registrada fue elevada, solo representó el 68% del total de las especies de la provincia de Tucumán y el 50% del total de las especies presentes en las Yungas. La Reserva Provincial Santa Ana resultó ser la más diversa y equitativa entre las reservas estudiadas. La revisión de los ejemplares depositados en la CML permitió reidentificar a uno de ellos y agregar una especie a la fauna de la provincia de Tucumán (*Histiotus montanus*). Sin embargo, debido a diferencias en el esfuerzo de muestreo y las fuentes de información entre reservas, las comparaciones ecológicas deben interpretarse de forma descriptiva. Los resultados no permitieron corroborar un gradiente latitudinal de norte a sur. Este trabajo constituye la primera sistematización de la diversidad de murciélagos en estas reservas provinciales y aporta información clave para su conservación.

Palabras clave: áreas naturales protegidas, colecciones biológicas, ensamblajes, riqueza de especie, Yungas.

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En Argentina, las selvas de Yungas se distribuyen desde la frontera con Bolivia hasta la provincia de Catamarca, en el noroeste del país (Lomáscolo *et al.* 2014). Las Yungas cuentan con una biodiversidad notable, incluyendo elementos propios, como también el aporte de otros de ecorregiones vecinas como el Chaco Seco (Lomáscolo *et al.* 2014). Se caracterizan por poseer un gradiente latitudinal de norte a sur, donde la riqueza de especies disminuye a medida que aumenta la latitud, encontrándose un número menor de especies de murciélagos en las áreas más australes, sumado a un recambio de especies (Ojeda y Mares 1989; Hillebrand 2004; Ojeda *et al.* 2008; Gamboa Alurralde y Díaz 2021). En su porción más austral, en las provincias de Tucumán y Catamarca, se registran los límites australes de la distribución de muchas especies de mamíferos tropicales (Tabeni *et al.* 2004).

Las Yungas cumplen un importante rol como proveedoras de servicios ecosistémicos (Peri 2021). No

obstante, son consideradas como uno de los sistemas naturales más frágiles, representando un área crítica por el acelerado proceso de degradación y transformación que sufre (Brown *et al.* 2005). Por esta razón, la protección de los parches de selva remanentes es fundamental. En este sentido, la provincia de Tucumán es pionera en destinar parte de sus ecosistemas para la conservación, manteniendo así un 26% de su superficie como Áreas Naturales Protegidas (Lomáscolo *et al.* 2014).

En Argentina, las Yungas albergan una alta diversidad de murciélagos, que representan el 66% de las especies registradas en el país. En esta ecorregión habitan 40 especies pertenecientes a 24 géneros y 5 familias: Emballonuridae, Noctilionidae, Phyllostomidae, Vespertilionidae y Molossidae (Barquez y Díaz 2001, 2020). Sin embargo, se trata de una diversidad menor en comparación con la ecorregión del Chaco Seco, donde se han registrado 46 especies (Barquez y Díaz 2001, 2020; Novaes *et al.* 2025).

Los murciélagos son excelentes bioindicadores del estado de conservación de un ecosistema, debido a su longevidad, amplio rango de distribución, diversidad trófica, tasas reproductivas lentas, los servicios ecosistémicos que brindan y por el hecho de ocupar varios niveles en las cadenas tróficas (Díaz *et al.* 2013; Medellín y Víquez 2014). Estas características hacen que los ensamblajes de murciélagos respondan de manera sensible a cambios en la estructura y calidad del hábitat, variando su diversidad y composición en función del grado de perturbación asociado al cambio de uso del suelo (Fenton *et al.* 1992; Medellín *et al.* 2000). Por su diversidad ecológica y facilidad para muestrear mediante redes de niebla y monitoreos acústicos, además de las características mencionadas anteriormente, los murciélagos conforman un grupo muy interesante de estudio y apropiado para describir la estructura de los ensamblajes en un área o región determinada. A pesar de su relevancia ecológica, existe una notable carencia de estudios sistematizados y publicados focalizados en la diversidad de murciélagos dentro de áreas protegidas provinciales de Tucumán. Esto lleva a que la información no esté al alcance de investigadores locales e internacionales, como tampoco de aquellas personas tomadoras de decisiones y el público en general (Salcedo *et al.* 2015).

El objetivo de este trabajo fue sistematizar y analizar la información disponible sobre las especies de murciélagos presentes en cuatro reservas provinciales de la provincia de Tucumán. Posteriormente, se evaluaron la diversidad, riqueza y abundancia de especies, y se compararon los ensamblajes entre las reservas tanto en la estación seca como en la húmeda.

En una de las hipótesis de trabajo se planteó que la Reserva Provincial Aguas Chiquitas mostraría la mayor diversidad debido a la influencia de la ecorregión del Chaco Seco. Asimismo, se planteó que las reservas del norte de la provincia presentarían mayor diversidad de murciélagos que las del sur, debido a un gradiente latitudinal donde la riqueza de especies disminuye a medida que aumenta la latitud (Ojeda y Mares 1989; Hillebrand 2004; Ojeda *et al.* 2008), pero no se incorporaron otras variables como el área de la reserva.

Materiales y métodos

Área de estudio. La provincia de Tucumán está ubicada en el noroeste de Argentina. Cuenta con una superficie de 22 524 km^2 y un rango de elevación que se extiende desde los 551 hasta los 5 552 msnm. Presenta una estacionalidad muy marcada, predominando una estación húmeda, con lluvias durante los meses de octubre a marzo, y una estación seca, con suaves y prolongadas lloviznas entre los meses de abril a septiembre (Grau y Kortsarz 2012; Lomáscolo *et al.* 2014).

El estudio se centró en cuatro de las reservas con jurisdicción provincial que resguardan las selvas de Yungas (Figura 1):

• Reserva Provincial La Florida (RLF), departamento Monteros (coordenada del punto medio: 27°10'S 65°44'O); posee una superficie aproximada de 15 000 ha, con un gradiente altitudinal de 550 a 900 msnm (Brown *et al.* 2002). Preserva los cuatro pisos altitudinales de la Selva de Yungas: Selva Pedemontana, Montana, Bosques Montano y Pastizal de Neblina (Lomáscolo *et al.* 2014).

• Reserva Provincial Los Sosa (RLS), departamento Monteros (coordenada del punto medio: 27°01'19"S 65°40'16"O); protege una franja de 18 km de largo y 1 km de ancho (1 800 ha), de Selva Montana y parte de Bosque Montano, ascendiendo desde los 650 a los 1750 msnm (Brown *et al.* 2002; Lomáscolo *et al.* 2014).

• Reserva Provincial Santa Ana (RSA), departamento Río Chico (coordenada del punto medio: 27°30'S 65°51'O); es el área protegida con mayor superficie boscosa (casi 20 000 ha), con un gradiente de 600 a 1900 msnm, resguardando la selva Pedemontana (Brown *et al.* 2002; Lomáscolo *et al.* 2014).

• Reserva Provincial Aguas Chiquitas (RACH): está localizada en los departamentos Burruyacú y Tafí Viejo (coordenada del punto medio: 26°35'12"S 65°11'34"O) y cuenta con bosques de transición entre Yungas y Chaco Seco (Lomáscolo *et al.* 2014), ocupando un área de 3 300 ha aproximadamente. En diciembre de 2021, fue reconocida como un AICOM (Área de Importancia para la Conservación de los Murciélagos), por la RELCOM (Red Latinoamericana y del Caribe para la Conservación de los Murciélagos), constituyendo así la segunda AICOM de las tres presentes en la provincia de Tucumán (Sánchez *et al.* 2022).

En la RACH, se realizaron 14 muestreos en la estación húmeda y 9 en la estación seca. La RLF, cuenta con 3 muestreos realizados en la estación húmeda y 4 en la estación seca. En la RLS, se realizaron 5 muestreos durante la estación húmeda y 4 durante la seca. Por último, la RSA cuenta con solo 2 muestreos realizados durante la estación húmeda.

Material de estudio. Se examinaron ejemplares preservados en alcohol, pieles, cráneos y esqueletos, depositados en la Colección Mamíferos Lillo (CML), de la Universidad Nacional de Tucumán (UNT), Argentina. Además, se consideraron registros obtenidos en colectas

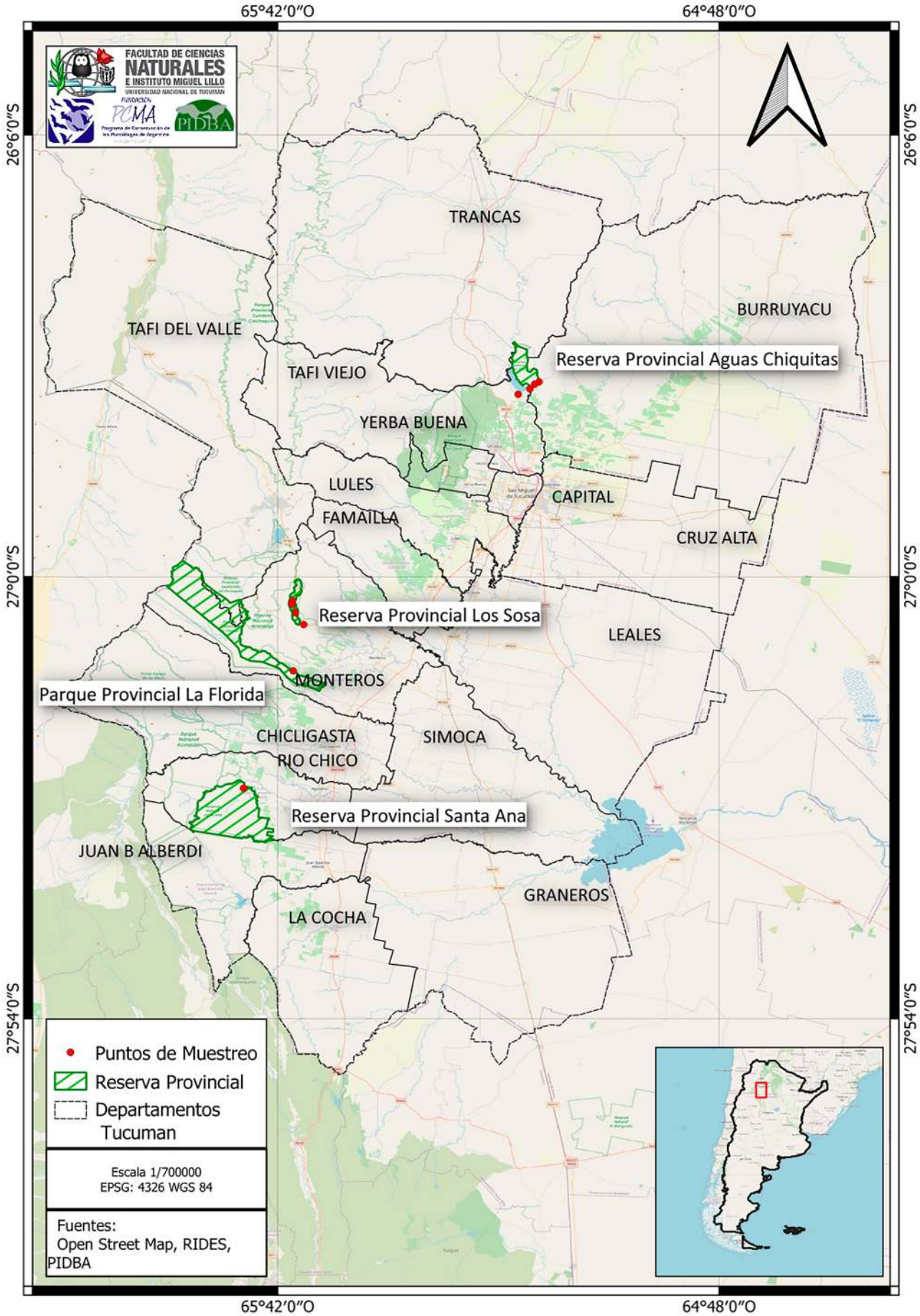

Figura 1. Mapa de la provincia de Tucumán donde se señalan las cuatro reservas provinciales muestreadas (en verde) y los puntos de muestreo (en rojo).

previas, incluyendo los de ejemplares liberados y citas bibliográficas relevantes. También se incluyeron datos de especímenes depositados en el Carnegie Museum of Natural History (CM) en Pittsburgh, Pennsylvania, Estados Unidos y en el Sam Noble Oklahoma Museum of Natural History (OMNH), de la University of Oklahoma en Norman, Oklahoma, Estados Unidos; y de los catálogos personales de Rubén M. Barquez (RMB) y de Santiago Gamboa Alurralde (SGA). Los registros sobre murciélagos liberados se encuentran en los catálogos y planillas del instituto PIDBA. Todos los ejemplares registrados fueron capturados con redes de niebla.

De cada individuo se registraron los datos incluidos en las etiquetas y en los catálogos de la colección y de los coleccionistas. Los datos considerados para las medidas externas siguen a Barquez *et al.* (2021) y las medidas craneales a Barquez *et al.* (1999). La identificación sistemática sigue a Barquez *et al.* (2025). La condición reproductiva se detalla en la Tabla DS1, por reserva, especie, estación, sexo y condición reproductiva. Además, de cada especie se registraron los gremios tróficos siguiendo a Aguirre (2002) y Denzinger y Schnitzler (2013).

Análisis estadísticos. Se evaluó la diversidad alfa y beta, siguiendo metodologías propuestas por Medellín *et al.* (2000), Moreno (2001) y Smith y Smith (2007). Para la diversidad alfa se utilizaron los índices de Shannon, Simpson y equitatividad (J), calculados con EstimateS (Colwell 2011) y PAST versión 4.12b (Hammer *et al.* 2001).

La diversidad beta se evaluó mediante los índices de Jaccard (presencia/ausencia) y Morisita-Horn (abundancia ponderada), los cuales permiten diferenciar las variaciones en la composición de especies de aquellas en la estructura de dominancia (Cuevas y Martori 2007; Mendoza 2013). Asimismo, se representó la estructura de comunidades mediante gráficos de abundancia relativa, siguiendo a Feinsiger (2004).

Debido a las diferencias en el esfuerzo de muestreo entre reservas, la comparación de la riqueza se realizó mediante curvas de rarefacción y extrapolación calculadas con el paquete iNEXT en R (Chao *et al.* 2014; Hsieh *et al.* 2016). Se utilizó el número de Hill de orden q = 0, correspondiente a la riqueza de especies, obteniéndose curvas de interpolación y extrapolación con intervalos de confianza del 95%. Además, se calculó la cobertura muestral (sample coverage, SC), utilizada como medida de completitud del muestreo (Chao *et al.* 2014).

Es importante señalar que en los análisis solo se incluyeron las especies confirmadas para las reservas, excluyendo aquellas consideradas probables, que se describen en una sección final de los resultados.

Resultados

En esta sección se ofrece información sobre las 20 especies registradas (Tabla 1). Se indican la familia (subfamilia para Phyllostomidae), género y especie, autor y año de la cita original, y especímenes examinados. Para los especímenes examinados se indica, entre paréntesis, el número total de ejemplares examinados y para cada localidad se indica el departamento provincial, seguido de la localidad específica; al final se indica la abreviatura de la colección, número de colección de los ejemplares examinados y registros adicionales, incluyendo registros de la literatura y ejemplares liberados por otros colectores. En la sección de comentarios se agregan observaciones sobre su biología, distribución y sistemática.

Orden Chiroptera
Familia Phyllostomidae
Subfamilia Phyllostominae

Chrotopterus auritus (W. C. H. Peters, 1856)

Ejemplares examinados: (1). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 1 (CML 5431).

Comentarios. Es la especie de mayor tamaño que habita en la provincia de Tucumán (Barquez *et al.* 1991). Este ejemplar, que representa el primer registro para la reserva y el segundo para la provincia (Barquez *et al.* 1994), era un macho con testículos abdominales, capturado en junio de 1994.

Subfamilia Stenoderminae

Artibeus planirostris (von Spix, 1823)

Ejemplares examinados: (17). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Aguas Chiquitas, Sierras de Medina, 800 m, 1 (CM 42825); Arroyo Aguas Chiquitas, 605 m, 1 (CML 3144); Reserva Provincial "Aguas Chiquitas", 15 (4 RMB 609-612; 11 liberados).

Registros adicionales: (13). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: 500 m al NO de la casa del guardaparque, 1 (SGA liberado); Arroyo Aguas Chiquitas, 650 m, 11 (SGA liberados); MONTEROS, Reserva Provincial Los Sosa, 1 (Lomáscolo *et al.* 2014).

Comentarios. Esta especie solo fue registrada en dos de las reservas analizadas, siendo común en las Yungas de Argentina (Barquez y Díaz 2001). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Sturnira erythromos (von Tschudi, 1844)

Ejemplares examinados: (280). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 10 (2 CML 5576, 5635; 8 liberados); Bosque Primario-Arroyo Aguas Chiquitas, 6 (liberados); Reserva Aguas Chiquitas, 43 (1 CM 86379; 42 liberados); Reserva Provincial Aguas Chiquitas, zona de crecimiento secundario, 5 (liberados); Río Loro, 18 (liberados). MONTEROS, Parque Provincial de Flora y Fauna La Florida: 7 km al O de Ibatín, sobre Río Pueblo Viejo, 515 m, 63 (26 CML 5424-5429, 5752, 6503- 6507, 6788-6801; 37 liberados); Camping a la par de la represa, 441 m, 5 (CML 10295-10298, 10908); Pueblo Viejo, 3 (CML 3113- 3115); Reserva Provincial La Florida, 57 (liberados); Reserva Provincial La Florida, selva basal, 5 (liberados); Río

Tabla 1. Diversidad de murciélagos en cuatro reservas provinciales de Argentina. Para cada especie se incluye familia, número total de individuos y gremio trófico. RACH= Reserva Provincial Aguas Chiquitas, RLF= Reserva Provincial La Florida, RLS= Reserva Los Sosa, RSA= Reserva Provincial Santa Ana. Gremios tróficos: Car= carnívoro, Fru= frugívoro, San= sanguívoro, Ins VR= insectívoro de vuelo rápido, Ins VL= insectívoro de vuelo lento.

				Reservas provinciales					
Familias	**Subfamilias**	**Especies**	**Acrónimos**	**RACH**	**RLF**	**RLS**	**RSA**	**TOTAL**	**Gremios**
Phyllostomidae	Desmodontinae	*Desmodus rotundus*	D.r	24	0	3	5	32	San
	Stenodermatinae	*Artibeus planirostris*	A.p	29	0	1	0	30	Fru
		Sturnira erythromos	S.e	85	152	32	14	283	Fru
		Sturnira lilium	S.l	256	147	59	24	486	Fru
		Sturnira oporaphilum	S.o	0	0	1	0	1	Fru
	Phyllostominae	*Chrotopterus auritus*	C.a	1	0	0	0	1	Car
Molossidae		*Eumops bonariensis*	E.b	31	0	0	0	31	Ins VR
		Eumops patagonicus	E.p	0	0	0	4	4	Ins VR
		Molossus molossus	M.m	0	0	0	1	1	Ins VR
		Tadarida brasiliensis	T.b	2	2	4	2	10	Ins VR
Vespertilionidae		*Aeorestes villosissimus*	A.v	0	0	1	0	1	Ins VR
		Dasypterus ega	D.e	1	0	0	0	1	Ins VR
		Histiotus macrotus	H.m	0	4	1	0	5	Ins VL
		Lasiurus blossevillii	L.b	6	1	1	1	9	Ins VR
		Myotis albescens	M.a	1	0	0	1	2	Ins VL
		Myotis dinellii	M.d	12	3	0	3	18	Ins VL
		Myotis keaysi	M.k	4	0	1	0	5	Ins VL
		Myotis riparius	M.r	2	1	0	1	4	Ins VL
		Neoeptesicus diminutus	N.d	6	0	0	0	6	Ins VL
		Neoeptesicus furinalis	N.f	19	0	0	1	20	Ins VL
				479	310	104	57	**950**	

Pueblo Viejo, casa de Recursos Naturales, 19 (liberados). MONTEROS, Reserva Provincial Los Sosa: Casa de Piedra, Río Los Sosa, Ruta 307 km 24.9, 850 m, 5 (OMNH 18703- 18707); El Indio, 6 (liberados); El Indio, km 27, bosque secundario, 9 (liberados); Río Los Sosa, Ruta 307 km 19.7, camino a Tafí del Valle, 750 m, 1 (OMNH 18699); Río Los Sosa, Ruta 307 km 23.9, camino a Tafí del Valle, 850 m, 1 (OMNH 18702); Río Los Sosa, Ruta 307 km 24.9, camino a Tafí del Valle, 850 m, 2 (OMNH 18700, 18701); Ruta 307 km 26, 2 (CML 4014, 4015); Ruta 307 km 35, campamento de Vialidad, 5 (liberados); Ruta 307, km 24, sobre río Los Sosa, 1 (CML 3118). RÍO CHICO, Reserva Provincial Santa Ana: Arroyo El Saltón, 14 (1 CML 5432; 13 (liberados).

Registros adicionales: (3). BURRUYACÚ, Reserva Aguas Chiquitas: 500 m al NO de la casa del guardaparque, 661 m, 1 (SGA liberado); Arroyo Aguas Chiquitas, 605 m, 2 (SGA liberados).

Comentarios. Es una de las especies de filostómidos más común en las Yungas de Argentina; según Barquez y Díaz (2001), es menos abundante que *Sturnira lilium*. Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Sturnira lilium (É. Geoffroy Saint-Hilaire, 1810)

Ejemplares examinados: (307). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 23 (4 CML 3117, 4618, 5587, 5629; 19 liberados); Bosque primario, 1 (liberado); Reserva Aguas Chiquitas, 36 (liberados); Río Loro, 2 (liberados); Río, 3 (liberados); Zona alterada, inundable, 7 (liberados); Zona de crecimiento secundario, 5 (liberados). MONTEROS, Reserva Provincial La Florida: 7 km al O de Ibatín sobre río Pueblo Viejo, 515 m, 72 (liberados); Parque Provincial de Flora y Fauna La Florida, camping a la par de la represa, 441m, 15 (CML 10544-10558); Reserva de La Florida, 7 km al O de Ibatín, sobre Río Pueblo Viejo, 25 (11 CML 3116, 5433, 5590-5596, 6377, 6378; 14 liberados); Reserva La Florida, selva basal, 35 (liberados). MONTEROS, Reserva Provincial Los Sosa: El Indio km 27, bosque secundario, 3 (liberados); Río Los Sosa, Ruta 307 km 19.7, camino a Tafí del Valle, 700 m, 1 (OMNH 18932); Río Los Sosa, Ruta 307 km 19.7, camino a Tafí del Valle, 750 m 5 (OMNH 18928, 18929, 18933, 18934, 18936); Río Los Sosa, Ruta 307 km 23.9, camino a Tafí del Valle, 850 m 1 (OMNH 18930); Río Los Sosa, Ruta 307 km 24.9, camino a Tafí del Valle, 850 m, 2 (1 RMB 822; 1 OMNH 18931); Ruta 307, km 19.7, 5 (RMB 1631-1635); Ruta 307, km 19.7, camino a Tafí del Valle, 700 m, 27 (RMB 1801-1816, 1818-1828); Ruta 307, km 23.9, 850 m, 15 (RMB 1630, 1829-1834, 1870-1877). RÍO CHICO: Reserva Provincial Santa Ana: Arroyo El Saltón, Río Chico, 5 (1 CML 3130; 4 liberados); Río El Saltón, 19 (liberados).

Registros adicionales: (179). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 177 (SGA liberados); Reserva Aguas Chiquitas, 500 m al NO de la casa del guardaparque, 661 m, 2 (SGA liberados).

Comentarios. Es una de las especies de murciélagos más comunes en los bosques del noroeste argentino (Barquez y Díaz 2001); prefiere los estratos bajos de la vegetación del bosque (Barquez *et al.* 1991). Hasta recientes investigaciones (ver Velazco y Patterson 2013, 2014), *S. lilium* se consideraba una especie con amplia distribución (desde México hasta Argentina), pero estudios filogenéticos demostraron que se trata de un complejo de 7 especies y que *S. lilium s. s.* se encuentra restringida al escudo brasileño (norte de Argentina, Uruguay, Paraguay, este de Bolivia y sureste de Brasil). Una de las especies del complejo, recientemente descrita, *Sturnira giannae* Velazco y Patterson, 2019 (Velazco y Patterson 2019), fue registrada en Bolivia (Garrido y Siles 2023), en el límite con Argentina, por lo que los ejemplares de *S. lilium* del noroeste necesitan una profunda revisión para determinar si corresponden a dos especies diferentes.

El período reproductivo de esta especie puede, aparentemente, ser amplio en la provincia (Barquez *et al.* 1991). En este estudio se registraron hembras preñadas y lactando en la estación húmeda: en enero y febrero en la Reserva Provincial Aguas Chiquitas, en noviembre y febrero en Reserva Provincial La Florida, marzo y octubre en Reserva Provincial Santa Ana, y octubre en la Reserva Provincial Los Sosa (ver detalles en la Tabla DS1).

Sturnira oporaphilum (von Tschudi, 1844)

Ejemplares examinados: (1). MONTEROS: Reserva Provincial Río Los Sosa: Casa de Piedra, Río Los Sosa, Ruta 307, km 24.9, 850 m, 1 (OMNH 18687).

Comentarios. Es una especie rara, en comparación con las otras dos especies del género que habitan en Argentina, con escasos ejemplares registrados (Barquez y Díaz 2020). El ejemplar de Casa de Piedra, un macho con testículos escrotales, fue capturado en el mes de enero de 1985 (Barquez *et al.* 1991).

Subfamilia Desmodontinae

Desmodus rotundus (É. Geoffroy Saint-Hilaire, 1810)

Ejemplares examinados: (20). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 4 (CML 4287, 4305-4307); Arroyo Aguas Chiquitas, 605 m, 5 (liberados); Reserva Aguas Chiquitas, 3 (liberados). MONTEROS, Reserva Provincial Río Los Sosa: El Indio km 27 bosque secundario, 1 (liberado); Río Los Sosa, Ruta 307 km 23.9, camino a Tafí del Valle, 850 m, 2 (liberados). RÍO CHICO, Reserva Provincial Santa Ana: Arroyo El Saltón 4 (liberados); Río El Saltón, 1 (liberado).

Registros adicionales: (12). BURRUYACÚ, Reserva Aguas Chiquitas: 500 m al NO de la casa del guardaparque, 661 m, 5 (SGA liberados); Arroyo Aguas Chiquitas, 605 m, 7 (SGA liberados).

Comentarios. Esta especie es común en casi todos los ambientes en el norte del país (Barquez *et al.* 1991). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Familia Molossidae

Eumops bonariensis (W. C. H. Peters, 1874)

Ejemplares examinados: (27). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Aguas Chiquitas, 14 (3 CML 2073-2075; 8 CM 42953-42960; 3 liberados); Arroyo Aguas Chiquitas, 605 m, 3 (liberados); Arroyo Aguas Chiquitas, 7 (CML 5284-5288, 5604, 5980); Sobre Arroyo Aguas Chiquitas, 605 m, 3 (CML 11932-11934).

Registros adicionales: (4). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Reserva Aguas Chiquitas, sobre Arroyo Aguas Chiquitas, 605 m, 4 (SGA liberados).

Comentarios. Esta especie habita zonas de vegetación densa del bosque de transición, áreas rurales y terrenos abiertos (Barquez *et al.* 1991). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Eumops patagonicus O. Thomas, 1924

Ejemplares examinados: (4). RÍO CHICO: Reserva Provincial Santa Ana, sobre Río El Saltón, 4 (1 CML 5434; 3 liberados).

Comentarios. La presencia de esta especie en las Yungas está asociada a zonas alteradas, poblaciones y campos de cultivos, y es básicamente una especie chaqueña (Barquez y Díaz 2001), que habita generalmente en áreas abiertas suburbanas (Barquez *et al.* 1991). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Molossus molossus (Pallas, 1766)

Ejemplares examinados: (1). RIO CHICO, Reserva Provincial Santa Ana: Río El Saltón, 1 (CML 5455).

Comentarios. *Molossus molossus* es una especie común en zonas urbanas y suburbanas, encontrándose en grupos numerosos (Barquez y Díaz 2001). Habita en huecos de árboles, techos de viviendas, túneles y alcantarillas (Barquez *et al.* 1991). El único ejemplar registrado es un macho colectado en el mes de marzo.

Tadarida brasiliensis (I. Geoffroy Saint-Hilaire, 1824)

Ejemplares examinados: (8). MONTEROS, Reserva Provincial La Florida: Río Pueblo Viejo, casa de recursos naturales, 2 (liberados). MONTEROS, Ruta 307, km 19.7, camino a Tafí del Valle, 700 m, 4 (3 RMB 816, 817, 826; 1 OMNH 18858). RIO CHICO, Reserva Provincial Santa Ana: Río El Saltón, 2 (liberados).

Registros adicionales: (2). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 2 (SGA liberados).

Comentarios. Es una de las especies de más amplia distribución de Argentina (Barquez *et al.* 1991), en prácticamente todo tipo de hábitats, incluidas casas y edificios en zonas urbanas; viven en grandes colonias y es migratoria (Barquez y Díaz 2001). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Familia Vespertilionidae

Aeorestes villosissimus (É. Geoffroy Saint-Hilaire, 1806)

Ejemplares examinados: (1). MONTEROS, Reserva Provincial Los Sosa: Ruta 307, km 19.7, camino a Tafí del Valle, 700 m, 1 (liberado).

Comentarios. Anteriormente era tratada como subespecie de *Lasiurus cinereus*, pero actualmente se considera especie válida; siguiendo a Baird *et al.* (2015, 2017) la consideramos perteneciente al género *Aeorestes*. El ejemplar liberado fue capturado en el mes de octubre de 1984.

Dasypterus ega (P. Gervais, 1855)

Ejemplares examinados: (1). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 1 (CML 11905).

Comentarios. Si bien algunos autores consideran a *Dasypterus* como subgénero de *Lasiurus*, en este trabajo lo consideramos como género válido siguiendo a Barquez y Díaz (2020). Esta especie tiene una amplia distribución en el país (Barquez y Díaz 2020). Barquez y Díaz (2001) han observado individuos de esta especie en hojas de palmeras exóticas, en jardines de la provincia de Tucumán. También se ha registrado en varias áreas protegidas (Barquez y Díaz 2020). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Histiotus macrotus (Poeppig, 1835)

Ejemplares examinados: (5). MONTEROS, Reserva Provincial La Florida: Pueblo Viejo, 4 (CML 6059-6063). MONTEROS, Reserva Provincial Los Sosa: Río Los Sosa, Ruta 307 km 23.9, camino a Tafí del Valle, 850 m, 1 (liberado).

Comentarios. Esta especie habita en zonas de alturas de la Puna y en pastizales y bosques ribereños de Las Yungas (Barquez y Díaz 2001). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Lasiurus blossevillii (Lesson y Garnot, 1826)

Ejemplares examinados: (7). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 2 (liberados); Arroyo Aguas Chiquitas, 605 m, 1 (CML 5257); Arroyo, 1 (liberado). MONTEROS, Reserva Provincial La Florida: 7 km al O de Ibatín, sobre Río Pueblo Viejo, 1 (CML 5435). MONTEROS, Reserva Provincial Los Sosa: El Indio km 27 Bosque secundario, 1 (liberado). RIO CHICO, Reserva Provincial Santa Ana: Arroyo El Saltón, 1 (CML 5454).

Registros adicionales: (2). BURRUYACÚ: Reserva Aguas Chiquitas, sobre Arroyo Aguas Chiquitas, 605 m 2 (SGA liberados).

Comentarios. Esta especie es común en diversos ambientes, y prefiere áreas abiertas (Barquez *et al.* 1991). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Myotis albescens (É. Geoffroy Saint-Hilaire, 1806)

Ejemplares examinados: (2). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Aguas Chiquitas, Sierras de Medina, 800 m, 1 (CM 42933). RÍO CHICO, Reserva Provincial Santa Ana: Arroyo El Saltón, 1 (CML 3159).

Comentarios. Esta especie habita en la ecorregión de las Yungas, con desplazamientos hacia la región chaqueña (Barquez *et al.* 1991; Barquez y Díaz 2020). El ejemplar CML 3159 corresponde a un macho, colectado en octubre de 1992; mientras que el ejemplar CM 42933 es un macho colectado en enero de 1976. A pesar de los muestreos realizados recientemente en la Reserva Provincial Aguas Chiquitas no se han colectado más ejemplares de esta especie.

Myotis dinellii Thomas, 1902

Ejemplares examinados: (18). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Aguas Chiquitas, Sierras de Medina, 800 m, 12 (5 CM 42938-42942; 7 liberados). MONTEROS, Reserva Provincial La Florida: Pueblo Viejo, 2 (CML 3160, 3161); Reserva La Florida, 1 (liberado). RIO CHICO, Reserva Provincial Santa Ana: Arroyo El Saltón, 3 (CML 5451-5453).

Comentarios. Esta es una especie común en la provincia de Tucumán; se encuentra en áreas naturales y urbanas, y prefiere zonas abiertas, chaqueñas y de alturas hasta 3500 msnm (Barquez *et al.* 1991). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Myotis keaysi J. A. Allen, 1914

Ejemplares examinados: (5). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 4 (3 CML 3152, 3153, 8938; 1 liberado). MONTEROS, Reserva Provincial Los Sosa: El Indio, km 27, Bosque secundario, 1 (liberado).

Comentarios. La distribución de esta especie está asociada a los bosques húmedos de los Andes, en las provincias de Catamarca, Jujuy, Salta y Tucumán (Barquez *et al.* 1991; Barquez y Díaz 2001, 2020). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Myotis riparius Handley, 1960

Ejemplares examinados: (3). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 1 (CML 3156). MONTEROS, Reserva Provincial La Florida: 7 km al O de Ibatín, sobre Río Pueblo Viejo, 1 (CML 5468). RIO CHICO, Reserva Provincial Santa Ana: Arroyo El Saltón, Río Chico, 1 (CML 3158).

Registros adicionales: (1). BURRUYACÚ: Reserva Aguas Chiquitas, 1 (SGA liberado).

Comentarios. Los ejemplares colectados en la Reserva Provincial Aguas Chiquitas y en la Reserva Provincial Santa Ana constituyen los primeros registros de esta especie para la provincia de Tucumán (Barquez *et al.* 1994). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Neoeptesicus diminutus (Osgood, 1915)

Ejemplares examinados: (5). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Aguas Chiquitas, 1 (CM 86380); Aguas Chiquitas, Sierras de Medina, 800 m, 4 (3 CM 42880-42882; 1 liberado).

Registros adicionales: (1). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 1 (SGA liberado).

Comentarios. En este trabajo tratamos a las especies de Argentina dentro del género *Neoeptesicus* (ver Barquez *et al.* 2025). La distribución de esta especie es muy amplia en Argentina, pero con escasos registros conocidos (Barquez *et al.* 1991; Barquez *et al.* 2025). Ver detalles de sexo y condición reproductiva en la Tabla DS1.

Neoeptesicus furinalis (d'Orbigny y P. Gervais, 1847)

Ejemplares examinados: (13). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Aguas Chiquitas, Sierras de Medina, 800 m, 4 (CM 42883-42886; 1 liberado); Arroyo Aguas Chiquitas, 605 m, 2 (liberados); Arroyo Aguas Chiquitas, 605 m, 5 (CML 5225-5227, 11914, 11915). RIO CHICO, Reserva Provincial Santa Ana: Río El Saltón, 1 (CML 5430).

Registros adicionales: (7). BURRUYACÚ, Reserva Provincial Aguas Chiquitas: Arroyo Aguas Chiquitas, 605 m, 7 (SGA liberados).

Comentarios. Los ejemplares CML corresponden a 3 hembras con vagina cerrada colectadas en mayo y agosto y 3 machos colectados en agosto y octubre. Los individuos CM corresponden a 3 hembras y 1 macho colectados en enero y diciembre. El ejemplar CM 42884, tipo de *N. furinalis findleyi* (Williams 1978), corresponde a una hembra colectada en el mes de diciembre. Barquez *et al.* (1999) consideran a esa subespecie como sinónimo de *N. furinalis furinalis*. Ver detalle de la condición reproductiva y sexo en la Tabla DS1.

Especies probables. En esta sección se mencionan algunas especies probables debido a que fueron colectadas y observadas en las cercanías de la Reserva Provincial Aguas Chiquitas, principalmente en la zona de El Cadillal o alrededores. Esos individuos no se incluyeron en los análisis realizados para este trabajo.

Familia Molossidae

Molossops temminckii (Burmeister, 1854)

Ejemplares examinados: (1). TAFI VIEJO: El Cadillal, 1 (CML 724).

Comentarios. El ejemplar examinado corresponde a un macho colectado en el mes de mayo de 1950. Si bien por la ubicación de la localidad su presencia en dicha reserva sería altamente probable, debe tenerse en cuenta que el registro es histórico, ya que fue colectado hace 73 años, y el cambio del paisaje en los alrededores de la zona ha sido significativo en las últimas décadas. Cabe destacar, además, que es una especie que no se colecta fácilmente con redes de niebla, pero sus registros con acústica son más frecuentes.

Promops nasutus (von Spix, 1823)

Ejemplares examinados: (2). TAFI VIEJO: El Cadillal, al lado de la usina, sobre río Loro, 2 (OMNH 36592, 36593).

Comentarios. Barquez *et al.* (1991) mencionaron que dos machos fueron capturados en el mes de junio de 1986, saliendo de sus refugios ubicados en grietas de las laderas del río Loro.

Familia Vespertilionidae

Histiotus montanus (R. A. Philippi y Landbeck, 1861)

Ejemplares examinados: (1). TAFI VIEJO: El Cadillal, 1 (CML 1094).

Comentarios. Esta especie era considerada probable para Tucumán, pero recientemente su presencia fue confirmada en la provincia por González Noschese *et al.* (2024) a partir de un nuevo ejemplar. El ejemplar examinado estaba registrado como *H. laephotis*, pero fue reidentificado durante esta revisión, correspondiendo a un macho colectado en octubre de 1985.

Análisis de datos. Los ejemplares examinados, depositados en la CML fueron 118, 56 en alcohol, 61 en piel y cráneo y 1 con solo cráneo; los ejemplares depositados en otros museos (CM - OMNH) o colectores (RMB, SGA) suman 101 y los liberados fueron 508. Por último, los registros adicionales corresponden a 224 ejemplares. Esto representa un total de 950 individuos de murciélagos registrados en las 4 reservas estudiadas de Tucumán, pertenecientes a 20 especies, 12 géneros y 3 familias. Los ejemplares fueron muestreados entre 1974 y 2022 con un pico de registros en la década de 1990.

La familia mejor representada en el análisis fue Vespertilionidae (10 especies), seguida por Phyllostomidae (6 especies) y Molossidae (4 especies). Las especies más abundantes fueron *Sturnira lilium* (51.1%), seguida por *S. erythromos* (29.8%) y *Desmodus rotundus* (3.4%). *Sturnira oporaphilum, Chrotopterus auritus* (Phyllostomidae), *Dasypterus ega*, *Aeorestes villosissimus* (Vespertilionidae) y *Molossus molossus* (Molossidae) fueron las especies más raras, con solo un individuo cada una (Tabla 1).

Se registraron 5 gremios tróficos: carnívoro (Car), frugívoro (Fru), sanguívoro (San), insectívoro de vuelo rápido (Ins VR), insectívoro de vuelo lento (Ins VL) (Tabla 1). Teniendo en cuenta la riqueza de especies, el gremio de los insectívoros fue el mejor representado, mientras que, considerando la abundancia, el gremio mejor representado fue el de los frugívoros. Para una descripción detallada de la composición sistemática, abundancias y gremios tróficos por reserva, ver Tabla 1.

De acuerdo con los índices de diversidad, la RSA es la reserva con mayor diversidad (H'= 1.824 y D'= 3.91) y equitatividad (0.76); la segunda más diversa corresponde a la RACH (H'= 1.615 y D'= 3.04) con una equitatividad de 0.59. Para la RLS, los índices de diversidad (H'= 1223 y D'= 2.34) representan una menor diversidad y equitatividad (0.53), y finalmente, la RLF (H'= 0.884 y D'= 2.15) es la reserva con menos diversidad y equitatividad (0.45).

La curva de rango-abundancia de la RSA presenta una dominancia numérica menos marcada, dando lugar a una pendiente más plana y mayor igualdad entre especies

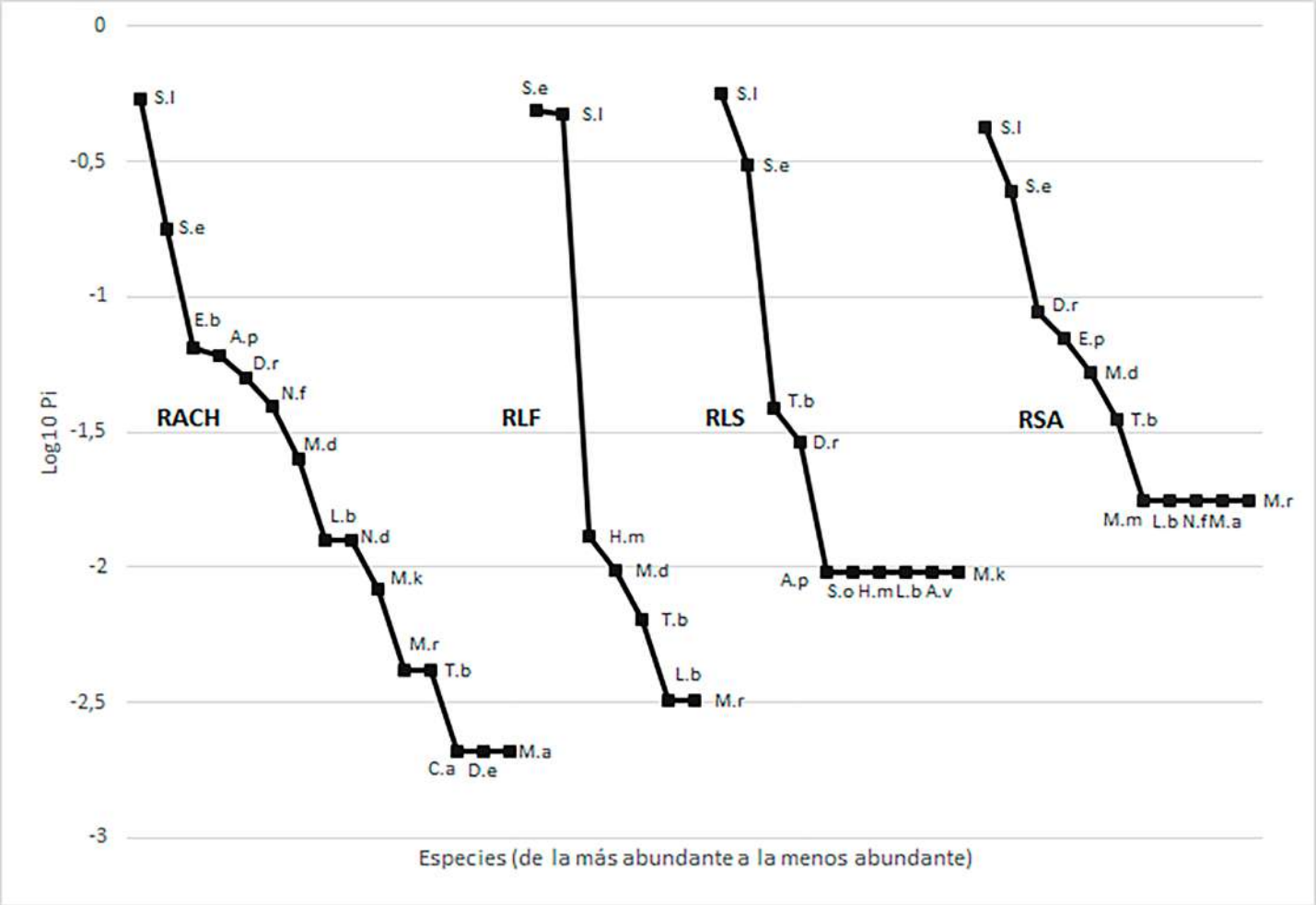

Figura 2. Curvas rango-abundancia de murciélagos registrados en las cuatro reservas provinciales. RACH = Reserva Provincial Aguas Chiquitas, RLF = Reserva Provincial La Florida, RLS = Reserva Provincial Los Sosa, RSA = Reserva Provincial Santa Ana. Para los acrónimos de las especies, ver la Tabla 1.

(Figura 2). Las más comunes son *S. lilium* y *S. erythromos*, seguidas por especies con densidad intermedia. La cola de la gráfica incluye 5 especies con un ejemplar cada una: *M. molossus*, *N. furinalis*, *L. blossevillii*, *M. albescens* y *M. riparius*. La curva de la RACH cuenta con una dominancia numérica muy marcada de *S. lilium* y *S. erythromos*; 3 especies conforman la cola de la gráfica con un ejemplar cada una: *C. auritus*, *D. ega* y *M. albescens*. La curva de la RLS presenta una fuerte dominancia de *S. lilium* y *S. erythromos*. El ancho de la curva está influido por la longitud de la cola de la gráfica, conformada por 6 especies con un ejemplar cada una: *A. planirostris*, *S. oporaphilum*, *A. villosissimus, H. macrotus*, *L. blossevillii*, y *M. keaysi*. Por último, la curva de la RLF cuenta con una dominancia numérica muy pronunciada, donde las dos especies más comunes son *S. erythromos* y *S. lilium*. La cola de la gráfica incluye 2 especies con 1 ejemplar cada una: *L. blossevillii* y *M. riparius* (Figura 2).

Excepto en la RLS, donde Phyllostomidae fue la familia mejor representada, en el resto de las reservas fue Vespertilionidae, pero de cada una de las especies fueron muy pocos los ejemplares registrados, mientras que la mayor abundancia estuvo siempre representada por dos especies del género *Sturnira*, muy comunes en el noroeste de Argentina.

El análisis de similitud entre las reservas provinciales de Tucumán, sobre la base del coeficiente de Jaccard, reflejó una mayor semejanza entre la RSA y la RACH (Ij = 0.52). Mientras que el índice de Morisita-Horn mostró mayor semejanza entre la RLS y la RACH (0.96).

En la RACH se registró una riqueza total de 15 especies: 11 en la estación húmeda y 14 en la seca. Cuatro de ellas fueron exclusivas de la estación seca (*C. auritus*, *D. ega*, *M. riparius* y *T. brasiliensis*), mientras que *M. albescens* se detectó solo en la estación húmeda; las restantes se registraron en ambas estaciones. Las especies más abundantes corresponden al género *Sturnira*, con *S. erythromos* mayormente presente en la estación seca (34% del total de las especies en la estación seca), a diferencia de *S. lilium* que predominó en la estación húmeda (64%).

De las 7 especies registradas en la RLF, 5 estuvieron presentes solo en la estación seca: *H. macrotus, L. blossevillii, M. dinellii, M. riparius* y *T. brasiliensis.* Al igual que la RACH, el género más abundante fue *Sturnira*, presentando el mismo patrón, con un mayor número de ejemplares de *S. erythromos* en la estación seca (68%) y *S. lilium* durante la estación húmeda (74%).

En la RLS de las 10 especies, 9 se colectaron durante la estación húmeda, 3 en ambas estaciones (*D. rotundus S.*

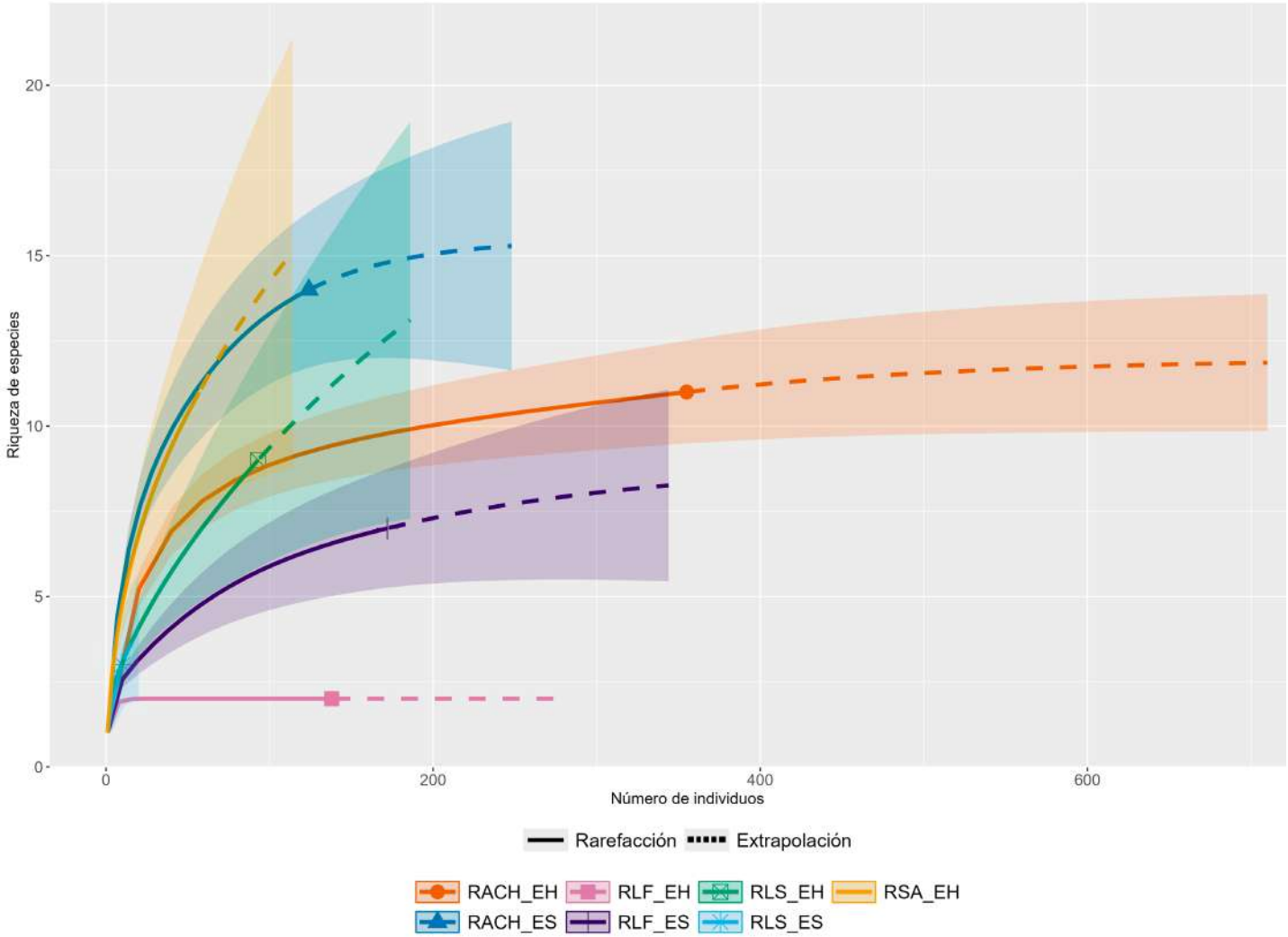

Figura 3. Curvas de rarefacción (líneas continuas) y extrapolación (líneas discontinuas) de la riqueza de especies de murciélagos, estimadas a partir de datos de abundancia para las reservas RACH = Reserva Provincial Aguas Chiquitas, RLF = Reserva Provincial La Florida, RLS = Reserva Provincial Los Sosa, RSA = Reserva Provincial Santa Ana, durante las estaciones húmeda (EH) y seca (ES). Las bandas sombreadas representan intervalos de confianza del 95%. La diversidad se expresa como números de Hill de orden q = 0 (riqueza de especies).

erythromos y *S. lilium*); estas últimas presentan el mismo patrón mencionado anteriormente en las otras reservas analizadas, con *S. erythromos* (80%) en la estación seca y *S. lilium* (62%) durante la estación húmeda. Por último, en la RSA se registraron 11 especies en la estación húmeda, donde S. *lilium* fue la especie más abundante (42%), cumpliéndose el patrón registrado en las otras 3 reservas.

Las curvas de rarefacción y extrapolación permitieron evaluar diferencias en la riqueza de especies entre reservas y estaciones (Figura 3), registrándose en la RACH la mayor riqueza. En ambas estaciones, las curvas mostraron elevados valores de cobertura muestral (SC=0,99 EH; SC=0,97 ES), indicando una alta completitud del muestreo. En la RLF se observó una marcada diferencia estacional; sin embargo, los valores de cobertura (SC=1 EH; SC=0,98 ES), sugieren que el muestreo representó adecuadamente la riqueza en ambos períodos. En contraste, la cobertura en la RLS fue considerablemente menor durante la estación seca (SC=0,94; SC=0,83), y la tendencia ascendente de la curva durante la extrapolación indica que podrían detectarse especies adicionales con un mayor esfuerzo de muestreo. Finalmente, en la RSA se registraron especies solo en estación húmeda, con una cobertura de SC= 0,91, mostrando una buena representatividad, aunque la tendencia ascendente de la curva de extrapolación sugiere que un incremento en el muestreo permitiría detectar nuevas especies.

Discusión y conclusiones

Esta es la primera vez que se sistematizan y publican datos de diversidad de murciélagos para estas reservas provinciales, a pesar de que se realizaron colectas durante muchos años. Este estudio permitió reidentificar un ejemplar en la colección CML como *H. montanus*, especie no reportada previamente para la provincia (ver González Noschese *et al.* 2024). En este sentido, este trabajo responde a la necesidad señalada por Costello *et al.* (2013) de publicar datos de biodiversidad de manera sistemática, con alta calidad y una correcta identificación sistemática, asegurando su permanencia, accesibilidad y mayor impacto científico. La integración de estos registros no solo actualiza el conocimiento sobre los murciélagos de Tucumán, sino que además aporta información base para monitorear cambios

futuros en la composición de los ensamblajes y orientar acciones de manejo y conservación en las áreas protegidas.

La diversidad de murciélagos obtenida fue elevada, representando el 68% del total de especies registradas en la provincia de Tucumán y el 50 % del total de las especies de las Yungas. Sin embargo, las comparaciones ecológicas realizadas deben considerarse de carácter descriptivo.

En este contexto, la RSA presentó los mayores valores observados de diversidad y equitatividad de las cuatro estudiadas, mientras que la RACH registró la mayor riqueza. Es necesario recalcar que la RACH es donde se realizó la mayor cantidad de muestreos, incluyendo relevamientos recientes, mientras que en la RSA los dos únicos muestreos se realizaron hace 30 años. Por ello, llama la atención la diversidad presente en la misma, sumado al hecho de que se ubica al sur de la provincia. De este modo, los resultados no permitieron corroborar la existencia de un gradiente latitudinal de norte a sur (Ojeda *et al.* 2008). Es importante considerar, por un lado, que la RSA es una de las reservas que conserva la Selva Pedemontana (Lomáscolo *et al.* 2014), y por otro, que la matriz en la que se encuentran inmersas las reservas, puede influir en la composición de los ensambles (Gamboa Alurralde y Díaz 2021), aspectos que no fueron abordados en este trabajo. A su vez, la RSA presenta registros de especies no capturadas en las otras áreas estudiadas, como *Eumops patagonicus* y *Molossus molossus*.

En todas las reservas se observó un patrón de presencia-ausencia dado por dos de las especies de *Sturnira* (*S. erythromos* y *S. lilium*), si bien ambas fueron registradas en las dos estaciones, se observó que *S. lilium* predomina en la estación húmeda y *S. erythromos* en la estación seca. Estos resultados coinciden con otros estudios realizados en ambas especies (Autino y Barquez 1994). Estas especies poseen una dieta muy similar (Giannini 1999; Sánchez y Dos Santos 2015) y, de acuerdo con Giannini (1999), hay una tendencia altitudinal en el uso de los recursos y una disminución en la abundancia de los murciélagos de este género durante la estación seca. Por lo tanto, una posible explicación sería la segregación competitiva en tiempo y espacio, debido al uso compartido de los recursos, lo que permite la coexistencia de las mismas especies (Giannini 1999; Gamboa Alurralde y Díaz 2021).

Analizando los gremios tróficos, si bien la mayoría de las especies registradas son insectívoras (14), se observa claramente la dominancia del gremio de los frugívoros, considerando las abundancias. Probablemente estos resultados estén influenciados por las limitaciones del único método de muestreo utilizado, las redes de niebla, que funcionan de una manera más eficaz para la familia Phyllostomidae (Flores-Saldaña 2008; Pech-Canché *et al.* 2010; López Berrizbeitia y Díaz 2013). Debido a sus hábitos de alimentación, los filostómidos utilizan con mayor frecuencia los estratos bajos de la vegetación (Pech-Canché *et al.* 2010); las especies insectívoras, por su parte, usan los estratos superiores (Pech-Canché *et al.* 2010), un comportamiento que dificulta su captura con redes de niebla, lo que explica la razón por la que están subrepresentados en función de su abundancia.

Estos resultados deberían ser interpretados de manera descriptiva y considerando las limitaciones inherentes al conjunto de datos analizados, así como otros factores. Por un lado, el rango latitudinal comprendido por las reservas estudiadas es pequeño, un poco más de un grado. Asimismo, debe tenerse en cuenta que las causas en las variaciones de riqueza, abundancia y diversidad de los murciélagos podrían no estar influenciadas solo por el gradiente latitudinal, sino también por otros factores como la heterogeneidad espacial (Flores-Saldaña 2008), por lo que sería fundamental revisar la matriz del paisaje donde están inmersas las reservas, así como su variación a lo largo del tiempo.

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Declaración del uso de Inteligencia Artificial

Los autores declaran el uso de la herramienta de Inteligencia Artificial ChatGTP como recurso de apoyo exclusivamente para tareas de revisión gramatical, sintáctica y traducción preliminar de algunos artículos científicos.

Contribución de los autores

Melanie Rodríguez De La Fuente: identificación de especies, búsqueda bibliográfica, diseño y preparación de tablas y figuras, y redacción del manuscrito; Rubén M. Barquez: muestreos y redacción del manuscrito; Camila S. González Noschese: muestreos y redacción del manuscrito; M. Mónica Díaz: muestreos, búsqueda bibliográfica, diseño y preparación de figuras y redacción del manuscrito. Todos los autores revisaron y aprobaron este artículo.

Datos suplementarios

DS1. Condición reproductiva de las hembras (♀) y machos (♂) registradas por especie y por reserva.

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50 years of trace element pollution: mammals as biomonitors of environmental degradation in Latin America

Leticia Anaid Mora-Villa[1, 2, 4*], Livia Socorro León-Paniagua[1], Joaquín Arroyo-Cabrales[3], and Joel Cuauhtémoc Rosas-Avila[4]

[1]Museum of Zoology "Alfonso L. Herrera", Department of Evolutionary Biology, Faculty of Sciences, National Autonomous University of Mexico, Circuito Exterior s/n, Ciudad Universitaria, Coyoacán, Mexico City, Mexico, 04510. E-mail: llp@ciencias.unam.mx (LLP)
[2]Postgraduate Program in Biological Sciences, Faculty of Sciences, National Autonomous University of Mexico, Circuito de los Posgrados s/n, Ciudad Universitaria, Coyoacán, Mexico City, Mexico, 04510.
[3]Laboratory of Archaeozoology, Sub-Directorate of Laboratories and Academic Support, National Institute of Anthropology and History, Moneda 16, Colonia Centro, Cuauhtémoc, Mexico City, Mexico, 06060. E-mail: arromatu@yahoo.com.mx (JAC)
[4]Laboratory of Plant Ecology, Department of Botany, National School of Biological Sciences, National Polytechnic Institute, Prolongación Carpio y Plan de Ayala s/n, Miguel Hidalgo, Mexico City, Mexico, 11340. E-mail: jcrosas@hotmail.com (JCRA)
[*]Corresponding author: psdanaid@live.com

Mammals are excellent biomonitors for pollutants such as trace elements; however, there is a lack of studies on this subject in wild mammals across Latin America. This review provides a comprehensive and updated overview of the current state and trends in mammalian toxicology, offering an integrative regional perspective. A systematic literature review was conducted, identifying and synthesizing data on date of publication, country of study, analyzed pollutants, taxonomic group and trophic guild involved, biological matrix used, analytical techniques, and sample origin. Publications show a constant increase in their number and diversity. However, research remains concentrated in high-biodiversity or polluted areas within large countries such as Brazil, Mexico, and Argentina, leading to significant geographical biases. At present, the most frequently analyzed elements have been Hg, Pb, and Cd, reflecting their relevance as environmental pollutants generated from extractive industries and fossil fuel combustion. Aquatic carnivores are highly susceptible to bioaccumulation, making the order Cetacea and the piscivorous trophic guild the most studied groups, underscoring their well-documented issue of mercury contamination in aquatic ecosystems. On the other hand, terrestrial mammals remain comparatively understudied. Due to their central role in metabolic pathways and detoxification of contaminants, liver and kidney have been the most analyzed matrices. Atomic absorption spectrometry has been the most frequent quantification technique, favored for its suitable cost-benefit balance. Future research should incorporate non-invasive techniques and reevaluate the importance of scientific collections, as they offer valuable historical baselines for ecotoxicological studies. We strongly recommend prioritizing further research in mammal species populations living in urban areas and mining regions, to better understand and mitigate the ecological impacts of metal pollution in these threatened ecosystems.

Keywords: biomonitoring, cadmium, lead, mercury, nickel, vanadium

Los mamíferos son excelentes biomonitores de contaminantes, tales como los elementos traza, sin embargo, existe una falta de estudios sobre este tema en mamíferos silvestres de América Latina. Esta revisión proporciona una visión integral del estado y las tendencias actuales en toxicología de mamíferos, ofreciendo una perspectiva regional integradora. Se realizó una revisión sistemática de la literatura, identificando y sintetizando datos sobre: año de publicación, país de estudio, elementos analizados, grupo taxonómico, matriz biológica, gremio trófico, técnica analítica y procedencia de los especímenes. Las publicaciones muestran un aumento constante en número y diversidad. Sin embargo, la investigación se concentra en áreas de alta biodiversidad o bien, contaminadas, dentro de países extensos como Brasil, México y Argentina, generando sesgos geográficos significativos. Los elementos más analizados son Hg, Pb y Cd, reflejando su prevalencia en industrias extractivas y combustión de combustibles fósiles. Los carnívoros acuáticos son altamente susceptibles a la bioacumulación, haciendo del orden Cetacea y del gremio trófico piscívoro los grupos más estudiados. Este enfoque acentúa el problema bien documentado de la contaminación por mercurio en ecosistemas acuáticos, mientras que los mamíferos terrestres permanecen comparativamente poco estudiados. El hígado y el riñón son las matrices más analizadas, lo que concuerda con su papel central en el metabolismo y la desintoxicación de contaminantes. La espectrometría de absorción atómica es la técnica de cuantificación más frecuente, favorecida por su costo-efectividad. Las investigaciones futuras deberían incorporar técnicas no invasivas y reevaluar la importancia de las colecciones científicas, pues ofrecen valiosas líneas base históricas para estudios ecotoxicológicos. Recomendamos incrementar la investigación en áreas urbanas y mineras para comprender y mitigar los impactos ecológicos de la contaminación por metales en estos ecosistemas amenazados.

Palabras clave: biomonitoreo, cadmio, mercurio, níquel, plomo, vanadio.

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Currently, some of the most ubiquitous pollutants derived from human activity are toxic metals and metalloids. These trace elements (Fe, Cu, Mn, Hg, Ni, Zn, Cd, Cr, Al, Pb, Sn, Ag, V, Au, Ga, Sb, As, Ti, Sr and Co) are major byproducts of mining, industrial operations, and fossil fuel combustion (Heim and Schwarzbauer 2013; Kozlowski *et al.* 2014; Buriticá 2019; Jiang *et al.* 2019). Furthermore, they are susceptible to bioaccumulation in living tissues and biomagnification

across trophic chains. This phenomenon poses a substantial threat to wildlife and human populations, as chronic or acute exposure to these substances can lead to poisoning (Nordberg 2001; Gall et al. 2015).

The detrimental health effects of trace elements on humans have been recognized since ancient times and were extensively studied throughout the 20th century (Dooyema *et al.* 2012; Wiłkomirski 2013). In contrast, their consequences for wildlife have been addressed more recently using distinct methodologies, among which biomonitoring is the most frequent (Asif *et al.* 2018).

A biomonitor is an organism that, due to its ecological traits, exhibits high sensitivity to environmental changes and responds to them gradually as to specific stimuli (Capó 2002). The response of a bioindicator reflects the impact of the perturbation on other elements within its community, as it is sensitive enough to display quantifiable effects yet sufficiently tolerant to survive at concentrations that would be lethal to other species (Markert *et al.* 2012).

An effective biomonitor exhibits a correlation between the environmental concentration of a contaminant and its concentration within the organism's tissues (Gorman and Conway 2005). Additionally, basic aspects of its biology are well-documented; it also possess a long life cycle with distinct developmental stages. Species that are readily available, easy to handle, provide ample tissue samples, and have a broad geographical distribution are preferred (Kolf-Clauw *et al.* 2007; Wiłkomirski 2013). Mammals generally fulfill these criteria. Moreover, the evolutionary proximity of some mammal species to humans renders them particularly relevant study subjects, positioning them among the most utilized bioindicators (Tataruch and Kierdorf 2003). An additional advantage of mammals is the presence of hair, which shows a robust correlation with internal matrices such as liver, blood, and kidneys (Brait *et al.* 2009; McLean *et al.* 2009). Hair also accumulates metals throughout its growth and can be sampled in the field or from scientific collections without harming the specimens (Flache *et al.* 2015).

Frequently, the use of mammals as biomonitors has been concentrated in Global North countries, which created a significant knowledge gap compared to the rest of the world (Kalisińska 2019; López-Berenguer *et al.* 2020). Although improvements in instrumental sensitivity and cost have facilitated studies in other regions, such as Latin America, ecotoxicological investigations are still scarce, and a comprehensive compilation of the state of knowledge on mammals in this region is lacking (Di Marzio *et al.* 2019; Canham *et al.* 2020). This study addresses this critical gap by providing an updated, integrative regional synthesis of metal biomonitoring in wild mammals across Latin America, consolidating fragmented information from diverse sources to establish a cohesive baseline for future research. This topic is relevant, as the study area hosts the highest number of megadiverse countries globally, while simultaneously experiencing a severe crisis of species loss and anthropogenic pollution.

Historically, gold and silver mining in Latin America have been primary sources of contamination by toxic elements such as mercury since the 16th century; however, from the second half of the 20th century onward, increased fossil fuel exploitation, industrialization, mining, agrochemical use and urban growth have led to elevated emissions of multiple trace elements. Thus, understanding the distribution and biological effects of these pollutants in mammalian fauna is essential for informing conservation strategies and environmental policy in this region (Driscoll *et al.* 2013).

The objectives of this work are: to synthesize relevant data from the literature, to describe the main groups of mammals employed as biomonitors, the characteristics of the most studied areas, and the regions with information gaps. We also emphasize the use of different biological matrices, analytical techniques employed, and associated potential pollution sources. By systematically identifying taxonomic, geographical, and methodological trends, this review offers a critical evaluation of existing research, while highlighting priority areas for future investigation. Finally, we discuss emerging approaches in the ecotoxicological study of mammals, highlighting historical trends, the need for targeted research in areas affected by specific issues like mining or urbanization, and the future challenges in this field.

Materials and methods

A literature search was conducted to identify digital publications on mammals as biomonitors of metals in Latin America. The study area was defined as the region comprising Mexico, Central America, the Caribbean, and South America, including their respective islands and territorial waters. The search spanned publications from 1960 to 2025, and the study subjects included all groups of wild mammals from the region. Studies involving only laboratory specimens and humans were excluded.

The search included journal articles and theses; review articles were considered in a separate category. The search engines used were Google Scholar, Scopus, PubMed, and the internal search portals of institutions with which one or more authors from previously identified studies were affiliated. The primary search string for all search engines was: ("mammals" OR "wild mammals") AND ("metals" OR "heavy metals" OR "trace elements" OR "toxic metals" OR "biomonitor" OR "sentinel species") AND ("Latin America" OR "Caribbean" OR "Antigua and Barbuda" OR "Argentina" OR "Bahamas" OR "Barbados" OR "Belize" OR "Bolivia" OR "Brazil" OR "Chile" OR "Colombia" OR "Costa Rica" OR "Cuba" OR "Dominica" OR "Dominican Republic" OR "Ecuador" OR "El Salvador" OR "Grenada" OR "Guatemala" OR "Guyana" OR "Haiti" OR "Honduras" OR "Jamaica" OR "Mexico" OR "Nicaragua" OR "Panama" OR "Paraguay" OR "Peru" OR "Saint Kitts and Nevis" OR "Saint Lucia" OR "Saint Vincent and the Grenadines" OR "Suriname" OR "Trinidad and Tobago" OR "Uruguay" OR "Venezuela").

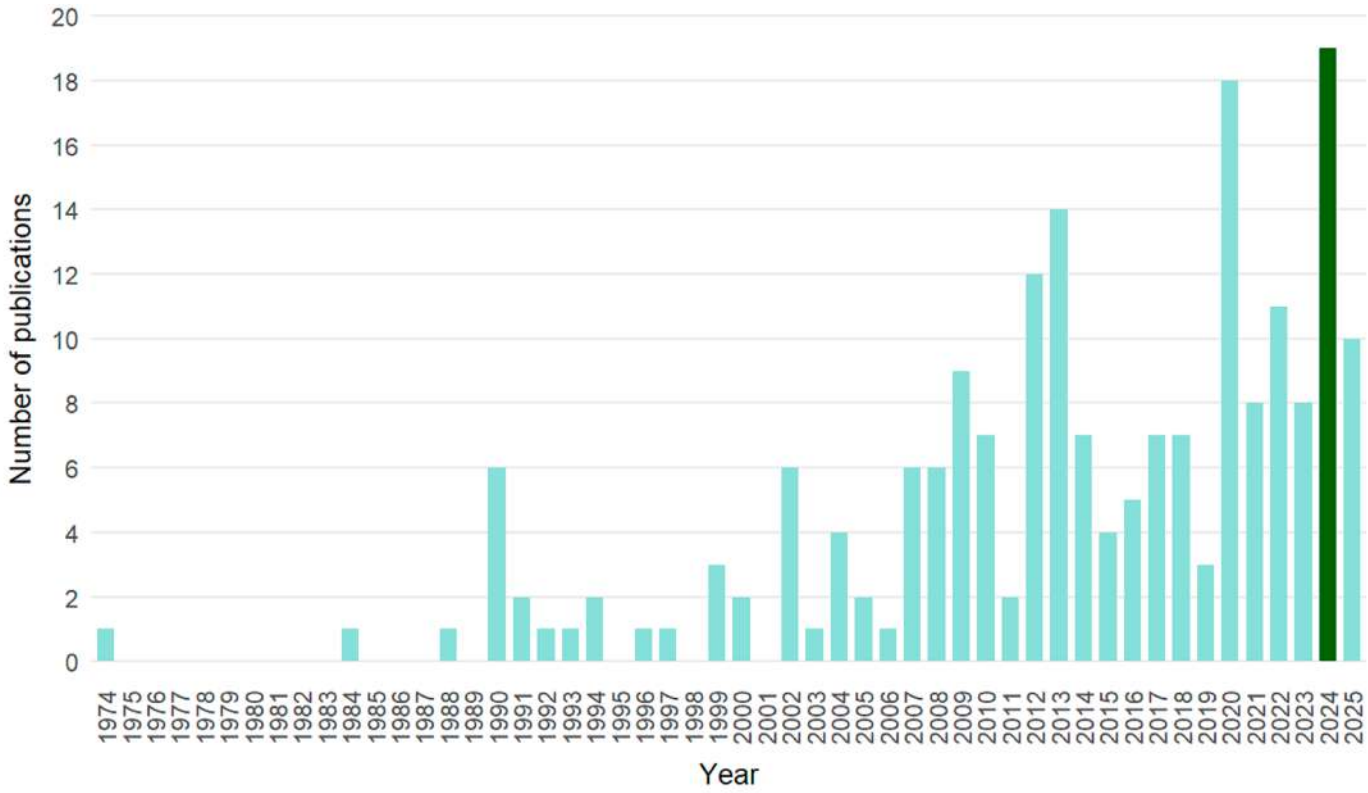

Figure 1. Number of studies on trace element biomonitoring in wild mammals in Latin America from 1974 to 2025.

A complementary search was performed, targeting 22 specific metals with the following search string: ("mammals" OR "wild mammals") AND ("aluminum" OR "antimony" OR "arsenic" OR "cadmium" OR "chromium" OR "cobalt" OR "copper" OR "gallium" OR "gold" OR "iron" OR "lead" OR "manganese" OR "mercury" OR "molybdenum" OR "nickel" OR "selenium" OR "silver" OR "strontium" OR "tin" OR "titanium" OR "vanadium" OR"zinc") AND ("Artiodactyla" OR "Carnivora" OR "Cetacea" OR "Chiroptera" OR "Cingulata" OR "Didelphimorphia" OR "Diprotodontia" OR "Eulipotyphla" OR "Lagomorpha" OR "Microbiotheria" OR "Paucituberculata" OR "Perissodactyla" OR "Pilosa" OR "Primates" OR "Rodentia" OR "Sirenia"). The search was performed in triplicate using keywords in Spanish, Portuguese, and English. The final search date was December 20, 2025.

To eliminate duplicate data and discrepancies, data from each article were reviewed to verify that the information provided by each study was original. Only articles published in peer-reviewed journals and undergraduate or graduate theses that had undergone committee review were included. Undergraduate dissertations not requiring a thesis defense, scientific outreach texts, and works lacking data on the presence or quantification of trace elements were excluded. Additionally, studies conducted on species living exclusively under domesticated or captive zoo conditions were also removed. Chemical speciation of the analyzed elements was not considered, as the majority of original articles did not make this distinction.

The retrieved results were organized according to the following criteria: year of publication; country of origin; chemical element(s) analyzed; taxonomic group(s) included in each publication; biological matrix used; trophic guild(s); quantification or detection technique; and the system of origin (e.g., terrestrial, aquatic). Furthermore, records exceeding reference limits associated with neurotoxicity in mammals (EPA 2022; FAO/WHO 2024) were selected (Tables 1 and 2; Supplementary data). Essential elements such as Fe, Mn, Zn, and Cu are natural constituents of living organisms but were included in this review because they exhibit potential toxicity in mammals when present in excessive amounts, particularly due to anthropogenic sources.

To homogenize the data across different tissue types, all concentrations were expressed in wet weight, following tissue-specific conversion factors established by Lu and Kacew (2009) and Landis *et al.* (2011): Water content correction factors applied were 0.745 for liver, 0.78 for kidney, and 0.10 for hair. Based on these results, the species with the highest pollutant concentrations were identified.

Results

A total of 197 digital records were obtained, of which 160 correspond to journal articles and 17 to theses. Additionally, 20 global or local reviews that include information on Latin America have been published. Because they lack experimental data, reviews were not included in the numerical analysis of the present article. The most frequently used language was English, followed by Spanish and Portuguese. The earliest record for marine mammals corresponds to Gaskin *et al.* (1974), while the oldest for terrestrial mammals is that of Burger *et al.* (1994). Since then, a consistent increase in the

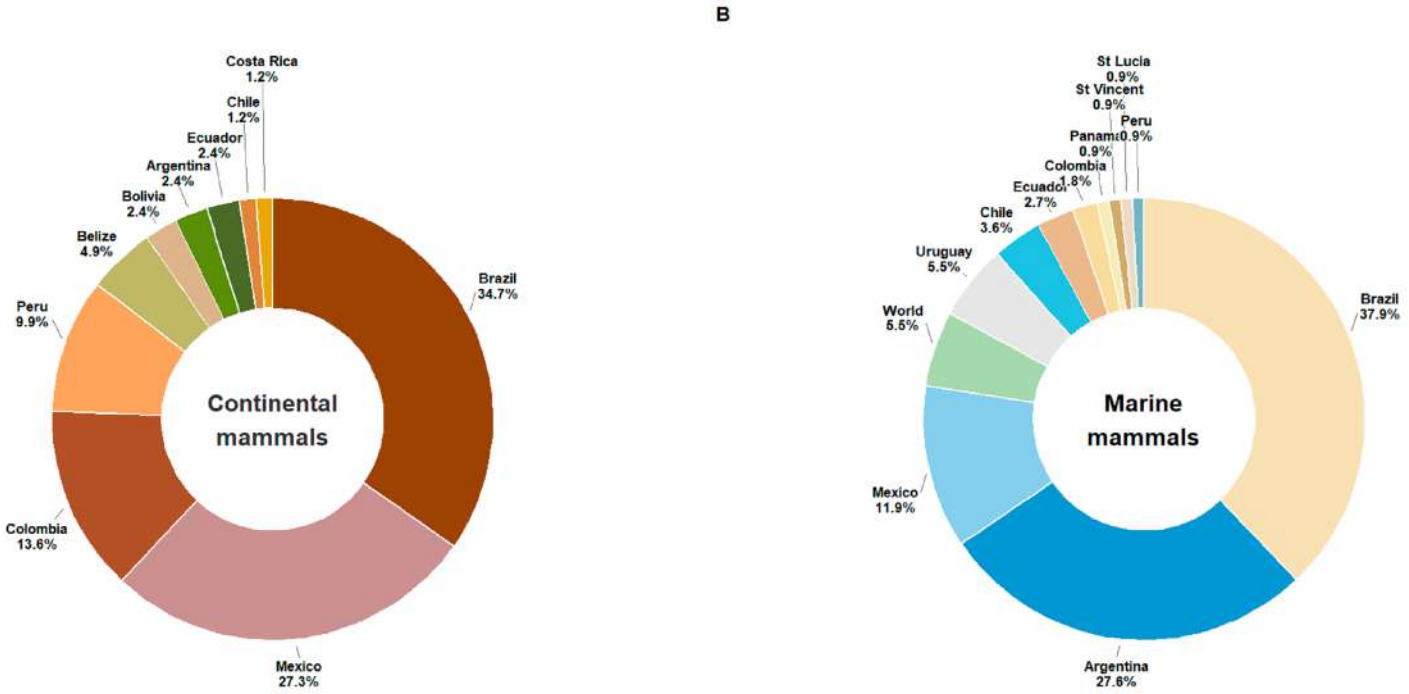

Figure 2. Number of articles and theses per country on mammals as bioindicators of trace elements in Latin America.

number and diversity of published articles on the topic has been observed (Figure 1). The year with the highest activity in this field was 2024, with 19 articles.

Geographically, studies are concentrated in the largest and most populous countries in the region. Consequently, Brazil, Mexico, and Argentina account for over 70% of the total publications (Figure 2). Within these countries, the Amazon River Basin and the Cerrado in Brazil, as well as the mining systems of Morelos in Mexico, are the most studied terrestrial areas. Meanwhile, the coasts of Argentina and Brazil have been the most significant areas for the study of marine mammals.

In total, 22 trace elements have been identified, with mercury being the most frequently studied, followed by cadmium, lead, copper, and zinc (Figure 3). The most frequent objective of the publications was the analytical detection of trace element presence (173), followed by the study of damage biomarkers (22), while the least common objective was the implementation of exposure assays to complement field data (4). Research on this topic has involved seven mammalian orders; the most studied order is Cetacea, and within it, odontocetes have been the subject of the most assessments (Figure 4a). In turn, studies on bat communities have simultaneously involved the largest number of species and trophic guilds from the same locality. Piscivorous species have received particular attention as biomonitors for mercury, whose accumulation pathway often involves aquatic systems (Figure 4b). Quantification in internal organs has been concentrated in the liver and kidney, which are key structures in the transformation and elimination of metallic elements. In turn, hair is the most utilized integumentary annex (Figure 5).

Various techniques have been employed for the detection and quantification of metals. The most used has been Atomic Absorption Spectrometry (AAS), with 112 mentions (Figure 6). The analyzed samples were mostly obtained through direct field collection of specimens. A fraction of the studies utilized material previously housed in scientific collections. The best-studied ecosystems are marine and coastal systems (Figure 7). In contrast, arid and semi-arid zone ecosystems, as well as tropical sub-deciduous forests, have the lowest number of studies.

Discussion

The primary focus of the recorded studies has been to quantify trace elements and infer their impact on wild mammals, with pollution often linked to specific activities like mining and urbanization. Although contamination sources have existed for centuries in Latin America, they intensified markedly during the second half of the 20th century, driven by rapid industrial expansion and resource extraction. Early studies from this review identify these specific sources (Moreno *et al.* 1984; Peña *et al.* 1988).

Geographically, research has concentrated in Brazil, Mexico, and Argentina—countries containing extensive natural areas threatened by human activities alongside some of the region's most densely populated urban zones with high land conversion rates (Di Marzio *et al.* 2019). The Amazon River Basin exemplifies this pattern, being one of the most researched areas from a toxicological perspective due to its vast biodiversity and intense anthropogenic pressure. Notable studies in this region include Contreras Luna and Chavez Estibur (2017) and Moreno-Brush *et al.* (2018), who quantified mercury in bats from the Madre de Dios River Basin in Peru. The work of Dias Fonseca (2004) and Dias Fonseca *et*

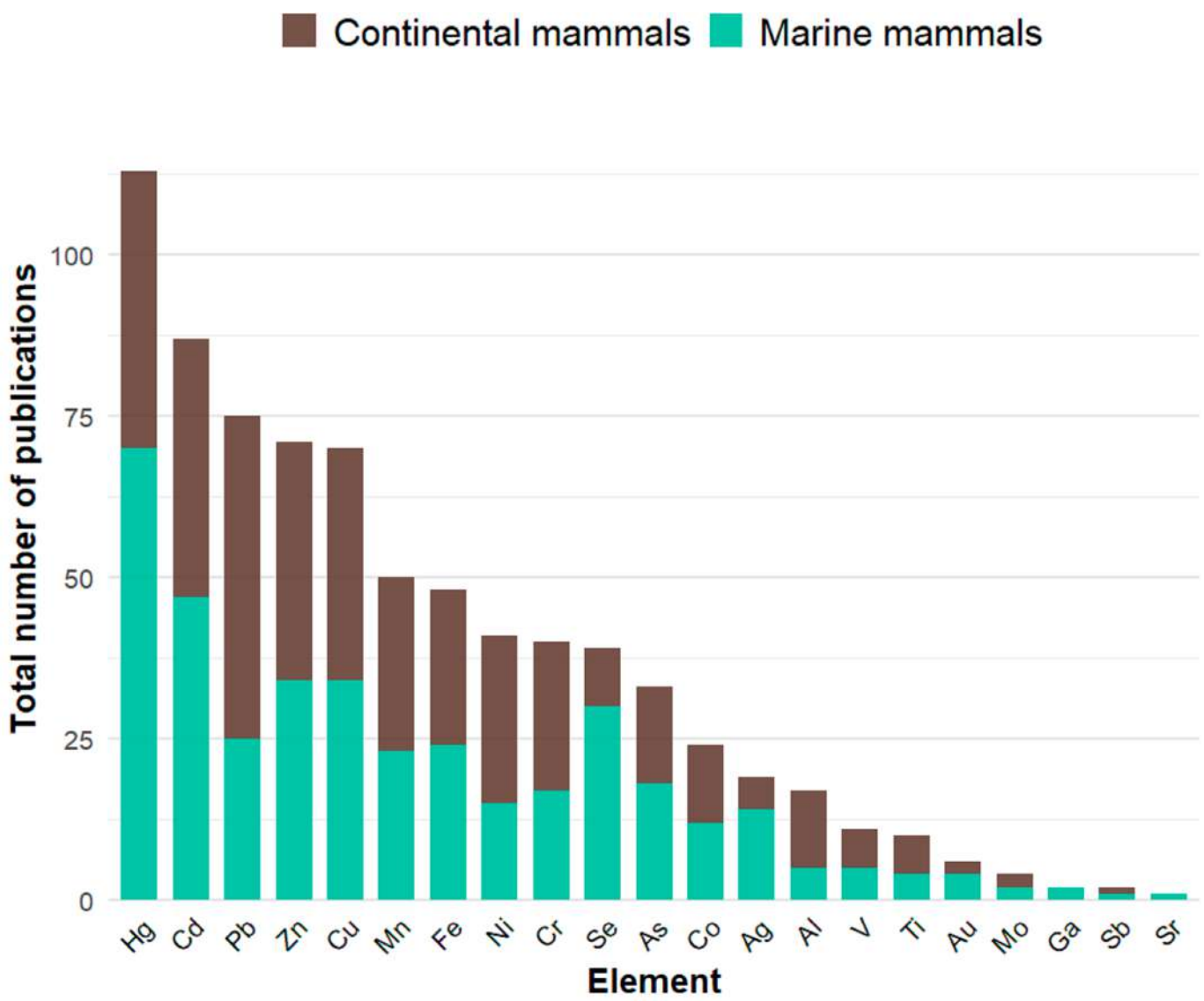

Figure 3. Trace elements quantified in wild mammals in Latin America from 1974 to 2025.

al. (2005) on mercury accumulation in giant otters (*Pteronura brasiliensis*) is also significant. These studies are crucial as both areas experience metal contamination from artisanal mining, a widespread activity estimated to release over 2.5 tons of mercury annually into Amazonian rivers (Lucchini *et al.* 2025). This not only poses a direct threat to aquatic and terrestrial food webs but also establishes a benchmark for studies in tropical zones worldwide. On the other hand, Central America and the Caribbean have fewer publications, and countries with significant mining impacts—such as Bolivia, Chile, and Peru—would benefit from implementing wildlife metal biomonitoring programs.

Globally, mercury, lead, and cadmium are among the most studied contaminants, with established environmental and biological thresholds due to their health effects (Lewis *et al.* 2001; FAO/WHO 2024). Latin America follows this trend, with these elements being the most frequently quantified and their presence is common in most multi-element studies. This focus is justified, as Cd, Pb, As and Hg are associated with mining, an activity with profound historical and economic significance for the region and the continent (Di Marzio *et al.* 2019). Furthermore, Pb, Hg, Cd, Al, As, Mn and Tl are directly associated with neurotoxic effects in mammals. However, this concentration on a few elements may overlook the potential synergistic effects of metal mixtures prevalent in contaminated sites, as well as emerging contaminants such as titanium, vanadium, and gallium, whose effects on wildlife remain poorly described.

In marine environments, most studies have documented bioaccumulation of Hg, Pb, Cd, and As. Beyond dietary influences, identified point sources include mining, agrochemical use, agricultural burning, and even seafloor tectonic activity (Table 2, Supplementary data). Mercury is the most studied element, and its association with marine trophic chains is widely documented. In the study region, the species in which concentrations above neurotoxic thresholds have been most frequently found are Franciscana dolphin (*Pontoporia blainvillei*) (14 studies) and South American fur seal (*Arctocephalus australis*) (9). Both are marine predators found in cold waters (Table 1 and 2,

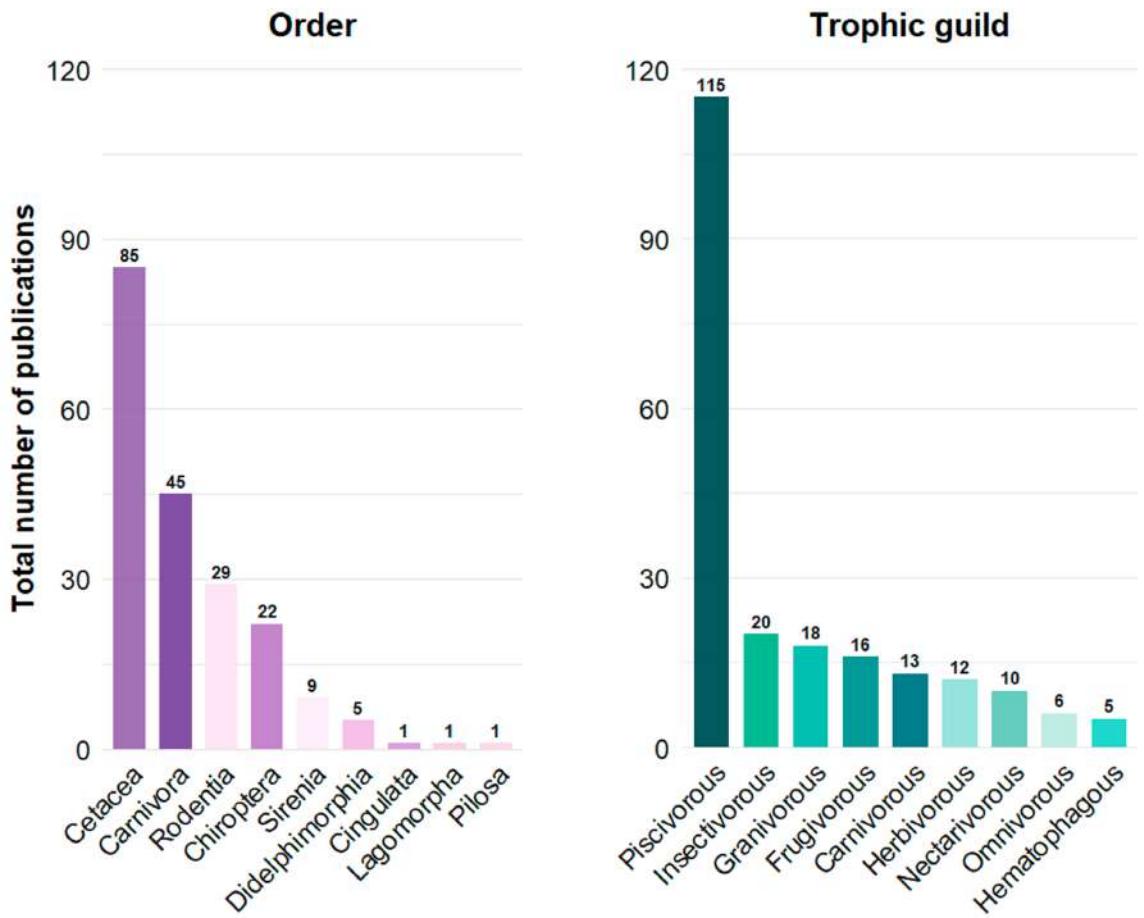

Figure 4. Wild mammal groups in which the presence and effect of trace elements have been evaluated in Latin America from 1974 to 2025. a) Orders; b) Trophic guilds.

Supplementary data). Furthermore, in *P. blainvillei*, mercury has been recorded at concentrations above the toxic limit even in fetuses, highlighting this species' vulnerability and the urgency for better environmental practices and policies (Romero *et al.* 2016).

In terrestrial systems, insectivorous bats such as Brazilian Free-tailed bat (*Tadarida brasiliensis*), Black myotis (*Myotis nigricans*), and Velvety Free-tailed bat (*Molossus molossus*) have proven to be efficient biomonitors for lead, as their concentration in liver and hair is consistently higher in urban centers and agricultural/livestock areas than in other systems (Ramos-H *et al.* 2020; Sánchez-Antonio and Gómez-Martinez 2020; Baquerizo and Salas 2021). In turn, rodents of the genera *Heteromys*, *Peromyscus*, and *Rattus* exhibit lead concentrations exceeding neurotoxic limits, mainly in mining, urban, and industrial influence zones compared to less impacted areas (Mussali-Galante *et al.* 2013; Hernández-Plata *et al.* 2020; Tripodi *et al.* 2020; De la Cruz-Guarneros *et al.* 2021). An additional lead source is hunting ammunition, suggesting that bushmeat consumption may pose health risks to humans who eat it regularly. For cadmium, the kidney serves as the primary target organ, with toxic concentrations detectable earlier than in the liver. The Franciscana dolphin shows the highest recorded cadmium concentrations, with adult females accumulating more than males, suggesting correlations with diet, age, and sexual maturity (Baraj *et al.* 2009; Panebianco *et al.* 2013).

Despite the presence of studies on mercury, lead, cadmium, and arsenic, the effects of other metals like titanium, vanadium, and gallium on wildlife have not yet been fully described. This represents a critical knowledge gap, especially as these metals are increasingly used in modern technologies and may become emerging contaminants. Increasing the number and specificity of studies is essential to understand their mechanisms of action and the true exposure levels for mammals. Such programs could serve as early-warning systems for ecosystem health and human exposure risks.

Taxonomically, research has focused on the orders Cetacea and Carnivora. Their role as predators makes them ideal for toxicological investigation, as they are more susceptible to bioaccumulation of substances like trace elements and pesticides through the abiotic environment and their prey (Kucera 1983). This top-down perspective is vital for understanding contaminant flow through entire ecosystems. In contrast, large continental predators like the jaguar remain understudied. Exceptions include work by May Junior *et al.* (2001) in Brazil and Racero-Casarrubia *et al.* (2012) in Colombia. Their semi-aquatic habits in parts of their range and their status as carnivores make them particularly vulnerable to exposure to metals like mercury (Driscoll *et al.* 2013). The conservation status of jaguar and other continental large predators further underscores the urgency of understanding such anthropogenic threats.

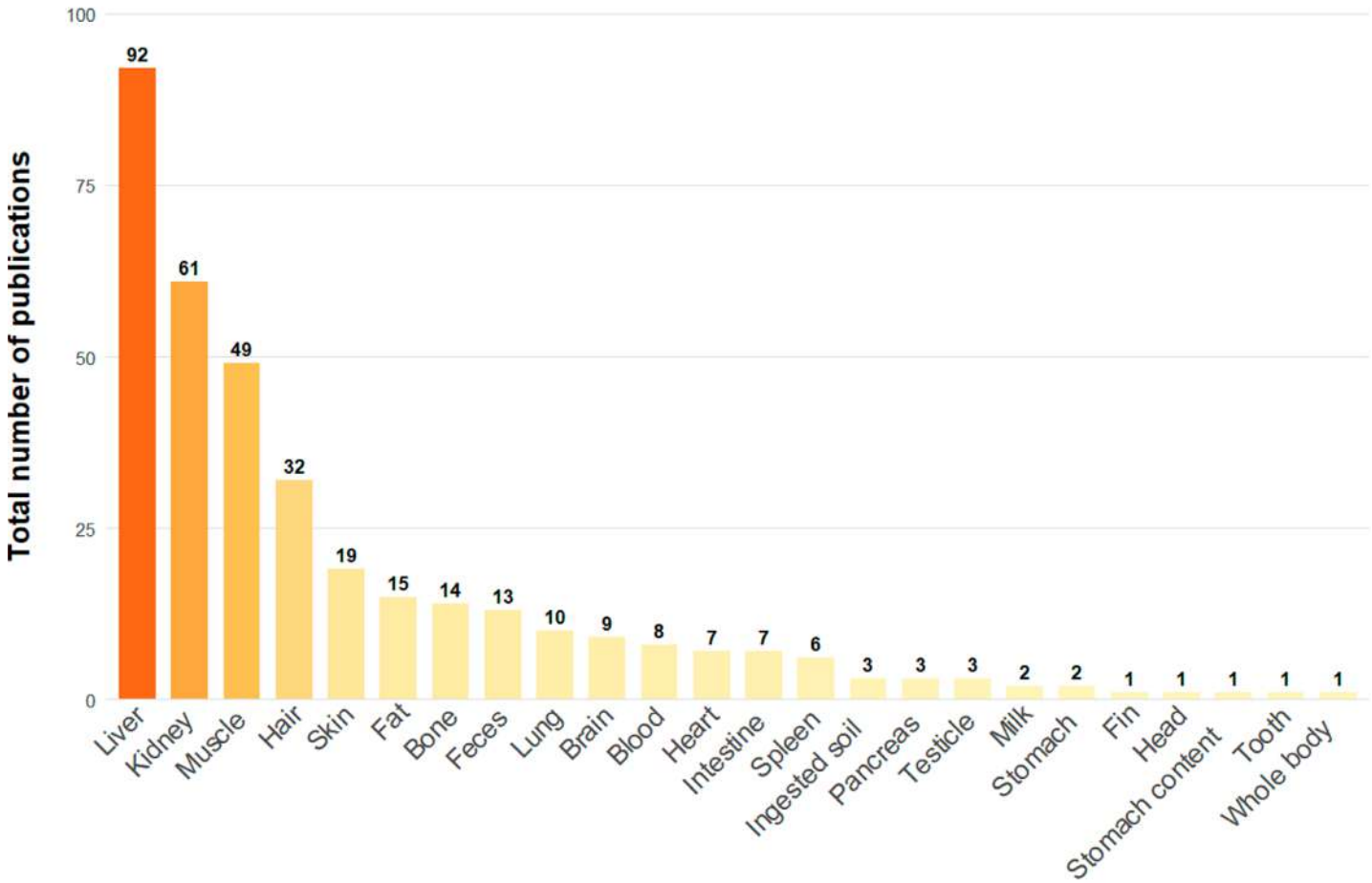

Figure 5. Main matrices used for trace elements quantification in wild mammals in Latin America from 1974 to 2025.

Rodents constitute another group of ecotoxicological importance. Their habits create a link between soil contaminants and higher ecosystem strata (Méndez-Rodríguez and Álvarez-Castañeda 2016; Da Silva *et al.* 2017). As the most abundant mammalian group, with some burrowing species, they are highly susceptible to contamination from extractive industries. Their small home ranges also make them excellent sentinels for local-scale contamination (Smith *et al.* 2002). On the other hand, bats (Chiroptera) offer an additional advantage; by occupying different trophic levels, they provide multiple perspectives on accumulation processes and contaminant pathways within a single study. This makes them powerful, yet underutilized, indicators for assessing landscape-level pollution (Jones *et al.* 2009).

The choice of a biological matrix depends on study objectives and target substances. Trace elements exhibit distinct mechanisms of accumulation, transformation, and elimination, with different tissue residence times, though these processes often involve the liver or kidneys. Therefore, these organs are valuable for assessing recent and chronic exposure and understanding metabolic pathways (Akerstrom *et al.* 2017).

Hair is an excellent indicator of endogenous contamination from ingestion (Hernout *et al.* 2016). Depending on the technique, it can also reveal external accumulation of elements such as lead, cadmium, and copper on its surface (Rendón-Lugo *et al.* 2017). Trace elements accumulate through both pathways during hair growth, providing a broader temporal window than blood or excreta (Varsha 2013). This integrative nature, combined with non-invasive collection, makes hair a highly recommended matrix for future studies, facilitating long-term monitoring and research on rare or endangered species.

Analyzing different trophic guilds provides valuable information on metal transit through ecosystems. For instance, studies on nectarivores, frugivores, and herbivores elucidate contaminant passage from soil to nectar or leaves (Tataruch and Kierdorf 2003; Kalisińska 2019). Thus, expanding research to include all guilds, particularly understudied omnivores, sanguinivores, and nectarivores, is essential for a holistic understanding of contaminant dynamics.

Most reviewed studies employed direct elemental detection techniques, notably spectroscopic analysis, which is rapid but requires meticulous sample preparation (Wiłkomirski 2013). Atomic Absorption Spectrometry (AAS) was the most used analytical method, followed by ICP-MS. The use of the latter has recently increased due to its superior sensitivity and power and multi-element detection capabilities, albeit at higher cost (Gorman and Conway 2005). This trend towards more sensitive

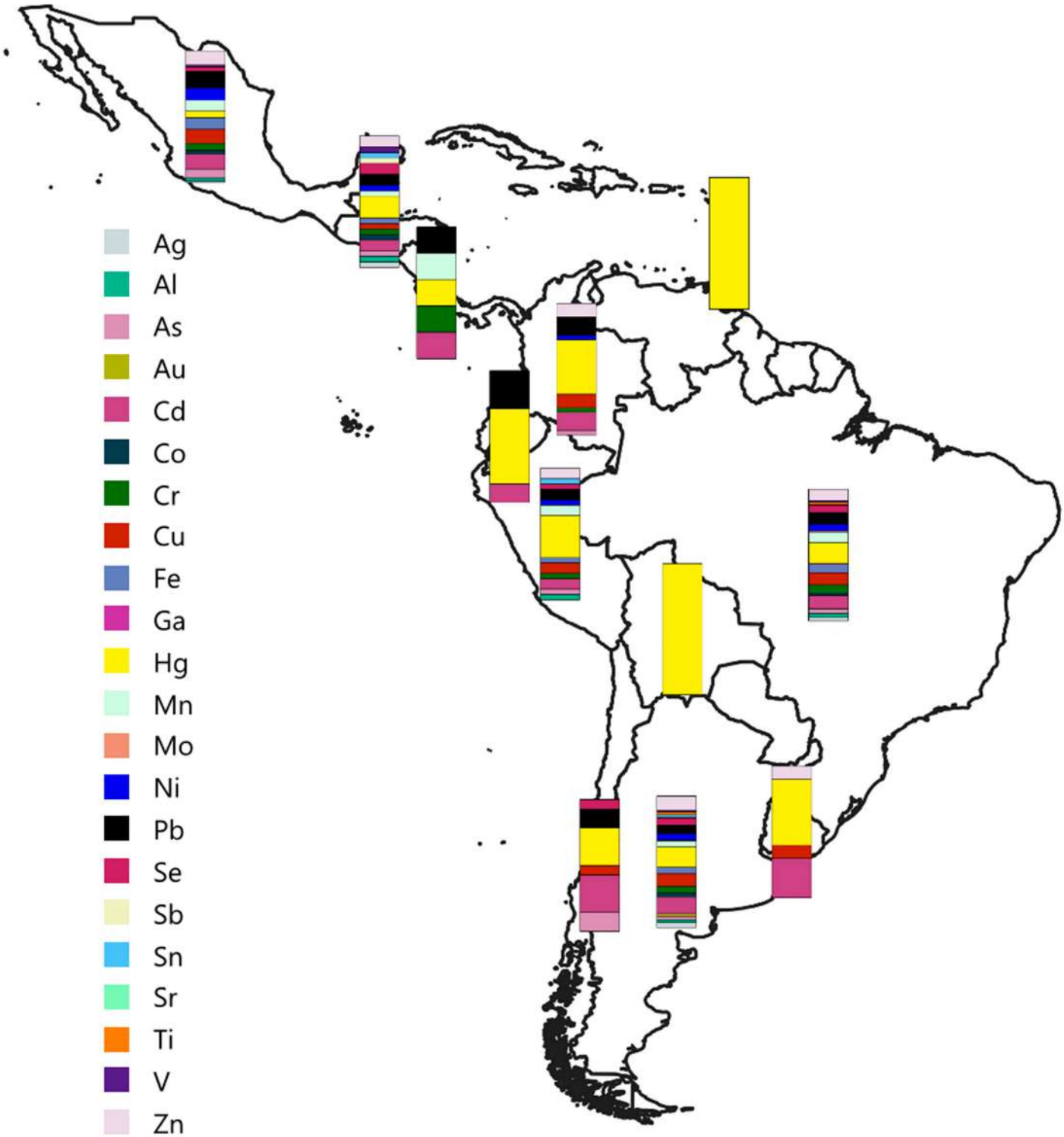

Figure 6. Proportion of trace elements studied in wild mammals in Latin America from 1974 to 2025.

techniques will likely continue, enabling the detection of a wider range of contaminants at lower concentrations and improving risk assessments. Additionally, techniques have diversified to include histochemical damage assessment, behavioral analysis, mathematical modeling, and genotoxicity assays (Banse-Bueno and Aguayo-Lobo 2020; Fernández-Macías *et al.* 2020; Hernández-Plata *et al.* 2020) (Figure 8). This methodological expansion is a positive step, moving beyond mere quantification of metal concentrations to understanding their biological effects at the individual, population, and ecosystem levels. This opens the possibility for multidisciplinary research lines to address this complex issue.

Most samples originated from natural ecosystems via direct collection (Figure 9). However, trace elements can also be detected in non-perishable matrices such as hair, bone, and teeth (Racero-Casarrubia *et al.* 2012; Tovar-Sánchez *et al.* 2012; Rendón-Lugo *et al.* 2017). This presents an

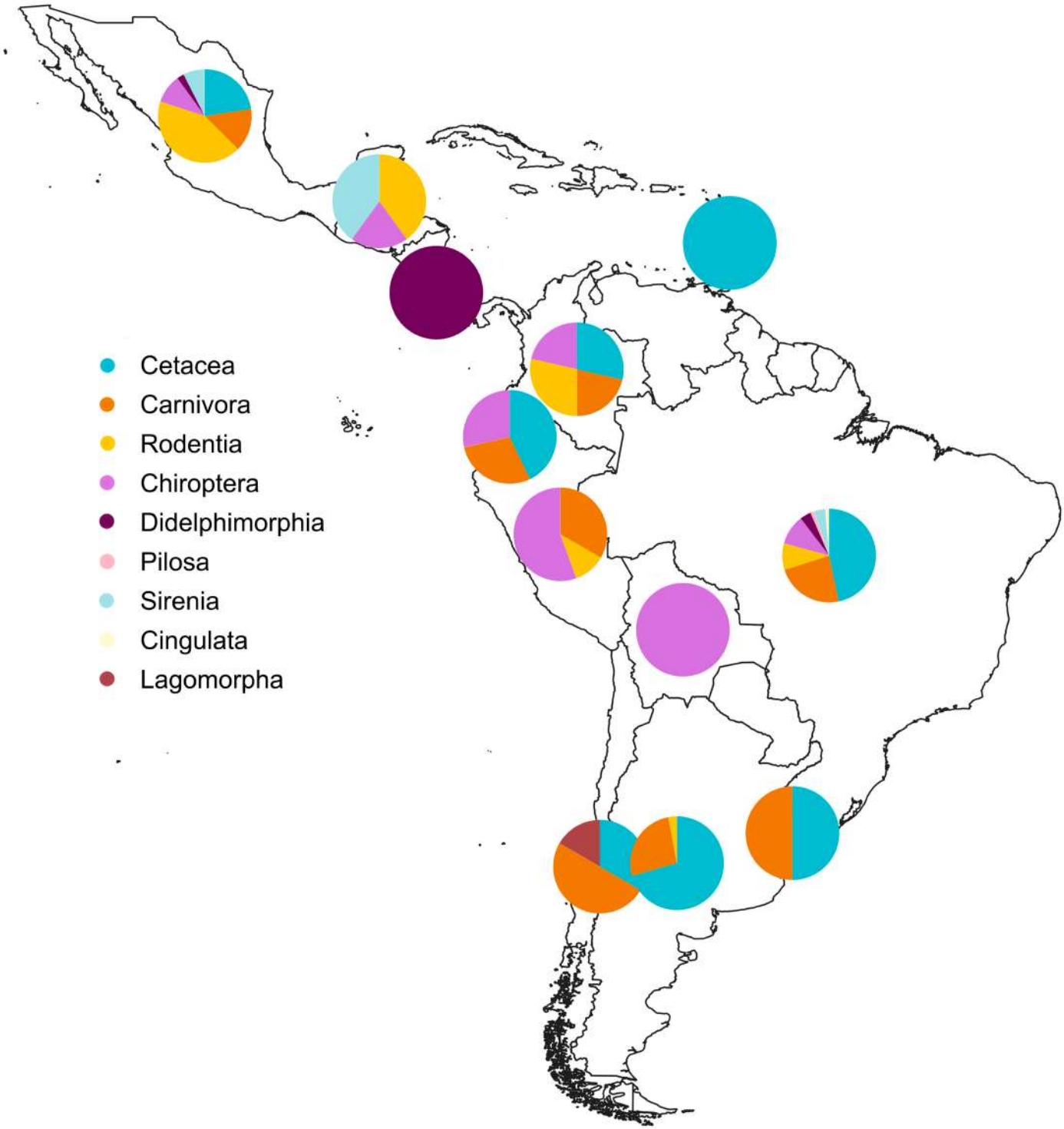

Figure 7. Main mammalian groups used as biomonitors of trace elements in Latin America from 1974 to 2025.

effective opportunity to leverage scientific collections and even paleontological contexts for establishing temporal baselines and historical contamination trends, providing critical context for current levels.

The emergence of studies in urban systems (Pinzón 2010; Ramos-H *et al.* 2020; Tripodi *et al.* 2020) and mining areas (Tovar-Sánchez *et al.* 2012; Mussali-Galante *et al.* 2013; De la Cruz Guarneros 2018; Hernández Plata *et al.* 2020) is noteworthy. These studies are pivotal as they directly assess the impact of pollution from human activity hubs, including emerging contaminants from electronic waste or chemical industry byproducts.

Considering these findings, intensified efforts are recommended in the continent's arid and semi-arid zones. These areas have scant information, have undergone intense land-use change, and in many cases have given way to extractive industries—a primary source of metal pollution—whose impact on wildlife remains largely

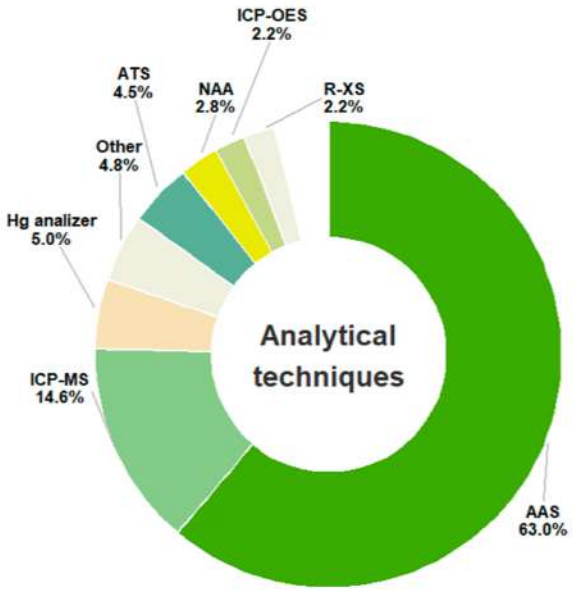

Figure 8. Trace elements assessment techniques in ecotoxicological studies with wild mammals in Latin America between 1974 and 2025.

unknown (Gorman and Conway 2005; De la Cruz-Guarneros *et al.* 2021; Mora-Villa *et al.* 2024). The unique hydrology and ecology of these fragile ecosystems may lead to distinct exposure pathways and heightened vulnerability, warranting immediate investigative attention. Also, the geographical bias toward a few countries implies an overrepresentation of taxonomic groups and ecosystems distributed within those nations, while underestimating contaminant presence in countries with fewer studies. This constitutes a regional concern, as many of the countries with limited published research also face severe socio-environmental problems caused by pollution. Future research can mitigate this imbalance by focusing on underexplored areas and simultaneously, fostering collaborations among countries sharing common pollution issues.

A consensus exists on the need for more studies using diverse matrices and cost-effective techniques. This review underscores that while there is growing interest in

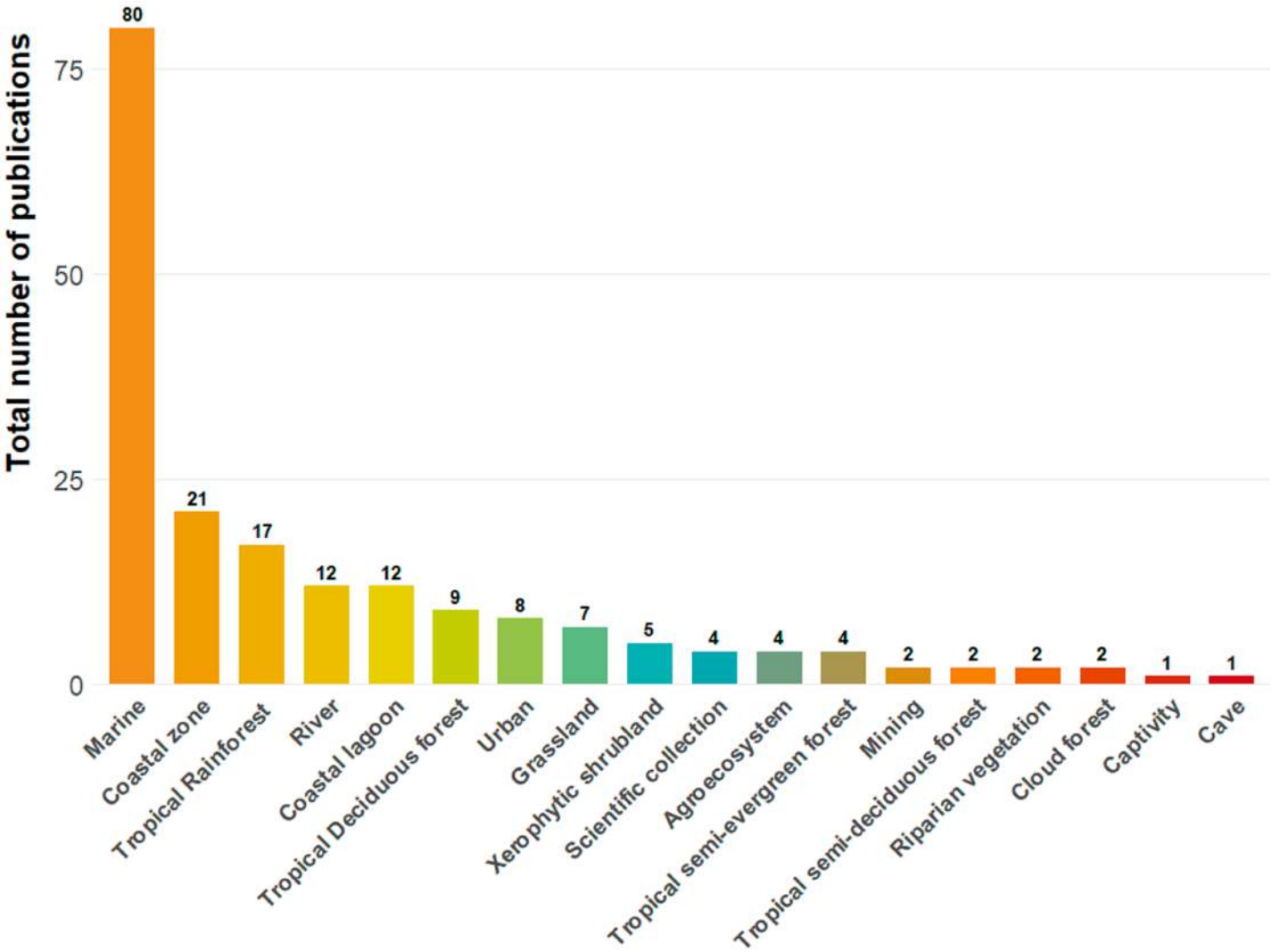

Figure 9. Origin of mammal specimens analyzed in trace elements studies across Latin America between 1974 and 2025.

assessing wildlife health in contaminated ecosystems, the field in this region is still maturing. We also highlight the pressing need to integrate contaminant quantification into environmental management and restoration plans across Latin America, ensuring that conservation strategies are informed by robust ecotoxicological data.

Conclusions

This integrative regional synthesis shows general patterns of metal biomonitoring in wild mammals across Latin America: research efforts are geographically biased, with Brazil, Mexico, and Argentina accounting for over 70% of publications, while Central America, the Caribbean, and arid and semi-arid ecosystems remain largely unknown. Cetaceans and piscivorous species dominate the literature due to phenomena as mercury bioaccumulation, whereas many groups of terrestrial mammals, including large predators, remain mostly understudied. Also, liver and kidney are the most frequently analyzed matrices, but hair offers a non-invasive alternative that can be relevant for endangered species or material from scientific collections.

Given its reliability, AAS is the most widely used analytical technique, though the increasing adoption of ICP-MS reflects a shift toward more sensitive multi-element analyses. On the other hand, the focus on Hg, Pb, and Cd, while justified by their neurotoxicity and links to mining, may overlook synergistic effects of emerging pollutants such as titanium, vanadium, and gallium, requiring broader analytical approaches and multinational collaboration.

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Declaration of artificial intelligence use

The software DeepSeek was used to perform a preliminary translation.

Author contributions

All authors contributed substantially to the design of this study, the analysis and interpretation of the data and the drafting and critical revision of the manuscript. All approved the final version to be published.

Supplementary data

SD1. Studies on toxic metals in mammals from 1974 to 2025 in Latin America.

SD2. Records exceeding international maximum permissible limits (EPA, WHO) for toxic metals in mammals from 1974 to 2025 in Latin America.

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Forty-five years of puma research in Chile: trends, knowledge gaps, and conservation implications

Jorge Leichtle[1,2*], and Cristián Larraguibel-González[2]

[1]Escuela de Medicina Veterinaria, Facultad de Ciencias Médicas, Universidad Bernardo O'Higgins, Santiago 8320165, Chile.
[2]Doctorado en Conservación y Gestión de la Biodiversidad, Facultad de Ciencias, Universidad Santo Tomás, Santiago 8370003, Chile. E-mail: c.larraguibel1@alumnos.santotomas.cl
[*]Corresponding author: jleichtle@docente.ubo.cl

Research on the puma (*Puma concolor*) in Chile has progressively developed over the past 45 years; however, no comprehensive synthesis had previously evaluated its spatial, thematic, and temporal development. We conducted a systematic review of peer-reviewed studies published between 1980 and 2025, identifying 34 articles addressing ecological, behavioral, genetic, sanitary, and socio-environmental aspects of the species. Research effort was spatially uneven across the country. Although central Chile currently accounts for the largest proportion of studies, early research was historically concentrated in the Magallanes Region, while northern ecosystems remain comparatively underrepresented. Trophic ecology dominated the initial decades of research, whereas studies on behavior, distribution and density, health, genetics, and human–puma interactions increased markedly after 2010. Temporal analyses and Correspondence Analysis revealed clear shifts in research priorities, with the most recent period (2016–2025) characterized by greater thematic diversification and the incorporation of molecular and socio-ecological approaches. Despite these advances, important gaps persist, particularly in long-term monitoring, telemetry-based studies, disease ecology, and research in arid or highly fragmented landscapes. Socio-ecological research remains limited relative to the growing challenges of human–puma coexistence in human-dominated environments. By providing the first integrated assessment of four and a half decades of puma research in Chile, this review establishes a baseline to guide future interdisciplinary and geographically representative conservation efforts.

Keywords: apex predator; carnivore conservation; ecological connectivity; human–wildlife conflict; large carnivores.

La investigación sobre el puma (*Puma concolor*) en Chile ha aumentado progresivamente durante los últimos 45 años; sin embargo, no existía previamente una síntesis integral que evaluara su desarrollo espacial, temático y temporal. En este estudio realizamos una revisión sistemática de publicaciones científicas indexadas publicadas entre 1980 y 2025, identificando 34 artículos que abordan aspectos ecológicos, conductuales, genéticos, sanitarios y socioambientales de la especie. El esfuerzo de investigación se distribuye de manera desigual a lo largo del país. Aunque la zona central concentra actualmente la mayor proporción de estudios, las primeras décadas estuvieron históricamente enfocadas en la Región de Magallanes, mientras que los ecosistemas del norte permanecen comparativamente subrepresentados. La ecología trófica dominó las etapas iniciales de investigación, mientras que los estudios sobre comportamiento, distribución y densidad, salud, genética e interacción humano–puma aumentaron de forma marcada después de 2010. Los análisis temporales y el análisis de correspondencias evidenciaron cambios claros en las prioridades de investigación, destacándose que el período más reciente (2016–2025) presentó mayor diversificación temática e incorporación de enfoques moleculares y socio-ecológicos. A pesar de estos avances, persisten vacíos relevantes, particularmente en monitoreo de largo plazo, estudios basados en telemetría, ecología de enfermedades e investigaciones en paisajes áridos o altamente fragmentados. Las investigaciones socio-ecológicas siguen siendo limitadas en relación con los crecientes desafíos de coexistencia humano–puma en entornos dominados por actividades antropogénicas. Al proporcionar la primera evaluación integrada de cuatro décadas y media de investigación sobre el puma en Chile, esta revisión establece una base para orientar futuros esfuerzos de conservación interdisciplinarios y con mayor representatividad geográfica.

Palabras clave: conflicto humano–fauna; conectividad ecológica; conservación de carnívoros; depredador tope; grandes carnívoros.

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The puma, *Puma concolor* (Linnaeus, 1771), is one of the most widely distributed terrestrial predators in the world, occupying a latitudinal range of over 100 degrees from northern Canada to the southern tip of Chile and Argentina (Iriarte and Jaksic 1986; Iriarte *et al.* 1990; Nielsen *et al.* 2025; IUCN 2025). It is a large, solitary felid characterized by a predominantly uniform tawny coat, a long cylindrical tail typically measuring approximately one third of its total body length, rounded ears without prominent tufts, and the absence of rosettes or stripes in adults. These features distinguish it from other felids present in Chile, such as *Leopardus guigna* and *Leopardus colocolo*, as well as from medium-sized canids like *Lycalopex culpaeus*, which differ in cranial morphology, non-retractile claws, and overall body conformation (Iriarte and Jaksic 2012). Across this vast distribution, the species fulfils a key ecological role as an apex predator, influencing herbivore populations and shaping community dynamics through top-down processes (Franklin *et al.* 1999; Bank *et al.* 2002).

Beyond its contemporary ecological relevance, *P. concolor* has been a component of southern South American ecosystems since at least the Late Pleistocene. Fossil

remains attributed to the species have been documented in southern Chile, including deposits from Cueva de los Chingues in Pali Aike National Park, Magallanes (San Román *et al.* 2000). Paleoecological analyses of the Late Pleistocene carnivore guild in southern South America further support the role of large felids, including pumas, as established predators within these ecosystems prior to the Holocene (Prevosti and Vizcaíno 2006). Although paleontological studies fall outside the primary ecological scope of the present review, acknowledging this deep temporal record situates the puma as a longstanding structural component of Chilean ecosystems.

In Chile, *P. concolor* occurs along a remarkable environmental gradient—from the xeric highlands of the northern Andes to Mediterranean shrublands, temperate forests, and the Patagonian steppe (Wilson 1984; Muñoz-Pedreros *et al.* 1995; Guzmán-Marín *et al.* 2023; Ministerio del Medio Ambiente 2024). This ecological plasticity has enabled the species to persist in landscapes under varying degrees of human transformation, including agricultural basins, forestry-dominated areas, and peri-urban environments (Rodríguez *et al.* 2019; Ramírez-Álvarez *et al.* 2021).

Despite its broad presence, scientific knowledge of pumas in Chile has historically been fragmented and geographically uneven. Early research, concentrated primarily in the southern regions, focused on predator–prey dynamics with native ungulates, especially guanacos (*Lama guanicoe*) (Wilson 1984; Iriarte *et al.* 1991; Rau *et al.* 1991; Bank *et al.* 2002). Although foundational, these studies provided limited insights into the ecological variability of pumas across the country. As a result, extensive biogeographic areas—including the central Andes, Mediterranean ecosystems, and the northern highlands—remained largely absent from the scientific record for decades (Zúñiga *et al.* 2009; Guarda *et al.* 2017; Dumont *et al.* 2022).

In the 2000s, methodological innovations began to reshape carnivore ecology globally, including camera trapping, genetic barcoding, stable isotope analysis, and spatially explicit capture–recapture models. These tools gradually permeated Chilean research efforts, enabling new insights into behavior, movement patterns, population density, and genetic structure (Elbroch and Wittmer 2013a; Elbroch *et al.* 2024). More recently, studies have begun to integrate socio-ecological dimensions, reflecting the growing importance of human–puma interactions in landscapes increasingly shaped by agriculture, livestock production, and urban expansion (Rodríguez *et al.* 2019; Ramírez-Álvarez *et al.* 2021; Iranzo *et al.* 2025). These conflicts—including livestock depredation and sightings near rural or peri-urban homes—have broadened conservation concerns beyond ecological patterns alone.

Although individual studies have yielded important contributions, national knowledge remains dispersed across decades, regions, and thematic domains (Hidalgo *et al.* 2013; Landaeta-Aqueveque *et al.* 2015). No comprehensive synthesis has evaluated how research on *P. concolor* in Chile has evolved over time, which themes have dominated or emerged, how regional biases have shaped the available evidence, or what methodological transitions have influenced scientific perspectives. This gap limits the ability to identify knowledge deficits, prioritize conservation needs, and align Chilean research with global directions in carnivore ecology (Pullin and Stewart 2006; Grant and Booth 2009; Haddaway *et al.* 2015; Snyder 2019).

This review addresses this gap by conducting the first systematic synthesis of peer-reviewed studies on *P. concolor* in Chile spanning 45 years (1980–2025). Specifically, we examine (1) the spatial distribution of research effort across administrative regions, (2) thematic patterns and their temporal evolution, (3) changes in publication frequency over time, (4) statistical associations between research topics and historical periods, and (5) major methodological and conceptual transitions. By integrating these dimensions, we provide a comprehensive assessment of the intellectual development of puma research in Chile and propose future directions to strengthen national capacity for conservation and human–puma coexistence.

Material and methods

We conducted a systematic review of peer-reviewed scientific literature on *P. concolor* in Chile published between 1980 and 2025. This period encompasses the earliest contemporary ecological research on the species within the country and captures 45 years of scientific development, including major methodological and conceptual advances in carnivore ecology.

Although several studies and published accounts referring to *P. concolor* in Chile predate 1980, these earlier contributions were predominantly descriptive, embedded within broader natural history syntheses, or lacking a specific ecological focus on the species. Peer-reviewed research explicitly addressing ecological questions—such as diet, spatial ecology, population dynamics, or human–wildlife interactions—began to consolidate more consistently from the early 1980s onward. In addition, pre-1980 publications are often inconsistently indexed in major scientific databases, limiting traceability and reproducibility under standardized search protocols. Establishing 1980 as the starting point therefore acknowledges the existence of earlier contributions while defining a temporal boundary aligned with the emergence of contemporary ecological research and standardized scientific publishing in Chile.

Literature search and eligibility criteria. Searches were performed in Scopus, Web of Science, SciELO, Google Scholar, and institutional repositories using combinations of English and Spanish keywords, including *Puma concolor*, puma, león de montaña, mountain lion, Chile, ecology, diet, behavior, genetics, conflict, coexistence, and conservation. Additional studies were identified through backward and forward citation tracking.

To ensure methodological consistency, we applied strict inclusion criteria. Studies were included if they (1) were published in peer-reviewed journals; (2) focused wholly or partially on pumas within Chile; (3) presented empirical, descriptive, or synthetic contributions related to ecology, behavior, genetics, distribution, health, or human–puma interactions; and (4) provided sufficient information to allow thematic classification. Theses, unpublished reports, government documents, conference abstracts, and other sources of grey literature were excluded because they do not correspond to peer-reviewed scientific literature (Donthu *et al.* 2021; Moher *et al.* 2009).

Data extraction and thematic classification. For each publication, we extracted the year of publication, administrative region(s) of study, main research theme, methodology, sample type, analytical approaches, and principal findings. Publications were classified into the following thematic categories: trophic ecology; distribution and density; behavior; health; genetics; human–puma interaction; and historical conservation. A synthesis of all reviewed studies is presented in Table 1.

Temporal and thematic analyses. To evaluate long-term patterns in scientific output, we analyzed (1) annual publication counts, (2) the frequency of research themes, and (3) the temporal distribution of thematic categories across the study period. To examine changes in research focus, studies were grouped into three publication periods reflecting major methodological transitions: 1980–2000, 2001–2015, and 2016–2025. The second categorical variable corresponded to research theme, classified into seven mutually exclusive categories: trophic ecology; distribution and density; behavior; health; genetics; human–puma interaction; and historical conservation. Although some categories had relatively low frequencies, thematic classifications were retained separately to preserve conceptual resolution and accurately reflect the diversification of research topics over time.

To assess whether thematic composition varied across publication periods, we constructed a 3 × 7 contingency table crossing publication period (three levels) with research theme (seven levels). We then applied a chi-square test of independence to evaluate whether thematic distribution

Table 1. Peer-reviewed studies on *Puma concolor* conducted in Chile between 1984 and 2025. For each study, we summarize the primary research topic, methodological approach, the specific knowledge gap addressed regarding puma ecology, population dynamics, health, genetics, behavior, or human interaction, and the principal findings directly related to the species. The column "Knowledge gap addressed by the study" refers explicitly to the research question or informational deficiency concerning *Puma concolor* that motivated the study at the time of publication, rather than to general limitations in wildlife research or other taxa. "Main findings" summarize the key results as they pertain specifically to puma biology, conservation, or management within the Chilean context. This structure allows direct correspondence between the research gap identified and the contribution made by each study to advancing knowledge of the species.

ID	Year	Authors	Region	Main topic	Methodology	Knowledge gap addressed by the study	Main findings
1	1984	Wilson	Austral	Community ecology	Telemetry	Lack of quantitative data on puma predation patterns and seasonal effects on guanaco populations	Puma predation increased winter mortality of female guanacos
2	1986	Iriarte and Jaksic	National	Historical conservation	Secondary data	Lack of historical assessment of human exploitation affecting puma populations	Fur trade records revealed strong historical hunting pressure on pumas
3	1987	Jaksic and Simonetti	Southern Cone	Community ecology	Literature review	Lack of synthesis of predator–prey interactions involving pumas in southern South America	Puma research primarily focused on mammalian prey; taxonomic bias identified
4	1990	Iriarte *et al.*	Americas	Community ecology	Comparative analysis	Lack of standardized dietary comparisons across regions for pumas	Significant regional variation in puma diet
5	1991	Rau *et al.*	South	Community ecology	Fecal analysis	Limited dietary data for pumas in southern Chile	Diet dominated by guanacos and European hares
6	1991	Iriarte *et al.*	Austral	Community ecology	Fecal analysis	Lack of interannual dietary studies for pumas	Hare (50%) and guanaco (32%) dominated diet
7	1995	Muñoz-Pedreros *et al.*	South	Distribution and density	Camera trapping	Lack of puma occurrence data in temperate forest habitats	Low densities detected in forested areas
8	1999	Franklin *et al.*	Austral	Community ecology	Telemetry	Lack of demographic and density estimates for Neotropical puma populations	Estimated density: 1 puma per 17 km^2
9	2002	Rau and Jiménez	South	Community ecology	Fecal analysis	Lack of temporal dietary comparisons between ranges	Dietary differences observed across study areas
10	2002	Bank *et al.*	Austral	Community ecology	Carcass analysis	Limited understanding of puma predation impact under extreme climatic conditions	74% of guanaco deaths attributed to pumas
11	2005	Borrero *et al.*	Austral	Behavioral ecology	Carcass analysis	Lack of understanding of carcass use and abandonment patterns	Pumas partially abandoned carcasses, influencing scavenger dynamics
12	2009	Zúñiga *et al.*	South	Behavior	Camera trapping	Limited knowledge of puma response to habitat fragmentation	Forest plantations used as habitat
13	2009	Elbroch *et al.*	Austral	Behavior	Telemetry	Lack of dispersal and long-distance movement data	Movements exceeding 100 km documented
14	2012	Skewes *et al.*	South	Community ecology	Fecal analysis	Lack of information on invasive prey incorporation into puma diet	First record of wild boar in diet

15	2013b	Elbroch and Wittmer	Austral	Distribution and density	Telemetry	Lack of density estimates in open Patagonian habitats	Density estimated at 3.4 ind / 100 km^2
16	2013	Hidalgo *et al.*	National	Health	Fecal analysis	Lack of sanitary data for Chilean pumas	First record of *Trichinella* infection
17	2014	Zúñiga and Muñoz-Pedreros	South	Community ecology	Fecal analysis	Limited data on dietary adaptation to altered habitats	Diet included pudú, rabbit, coypu
18	2015	Landaeta-Aqueveque *et al.*	National	Health	Comparative study	Limited understanding of zoonotic parasite transmission involving pumas	Domestic mammals identified as potential transmission vectors
19	2016	Leichtle *et al.*	National	Genetics	Morphogenetic review	Lack of taxonomic clarity within Chilean puma populations	Proposed north–south subspecific differentiation
20	2016	Guarda *et al.*	Central	Distribution and density	Camera trapping	Lack of density data in central Chile	Density estimated at 0.74–0.83 ind / 100 km^2
21	2019	Rodríguez *et al.*	National	Human–puma interaction	Literature review	Lack of spatial evaluation of conflict distribution	91% of conflicts concentrated in 18 municipalities
22	2020	Osorio *et al.*	Central	Community ecology	Comparative study	Limited understanding of interspecific interactions in altered ecosystems	Puma–culpeo coexistence documented
23	2021	Echeverry *et al.*	National	Health	DNA analysis	Lack of updated zoonotic parasite confirmation in pumas	Confirmed *T. spiralis* in poached puma
24	2021	Ramírez-Álvarez *et al.*	Central	Human–puma interaction	Telemetry	Lack of data on puma movement near urban settlements	Low densities recorded near human settlements
25	2022	Dumont *et al.*	Central	Distribution and density	Camera trapping	Lack of coastal occurrence records	First documented record in Putaendo
26	2023	Guzmán-Marín *et al.*	Central	Distribution and density	Camera trapping	Limited understanding of connectivity under fragmentation	Range extension of 170 km documented
27	2023	Rodríguez-Arancibia and Escobar	Central	Distribution and density	Camera trapping	Lack of coastal-edge occurrence data	First record at coastal edge
28	2024	Elbroch *et al.*	Austral	Genetics	DNA analysis	Lack of genetic monitoring in southern populations	Low evidence of inbreeding detected
29	2024	Mac Allister *et al.*	Austral	Genetics	DNA analysis	Limited knowledge of population structure in southern extreme	Unique genetic diversification documented
30	2025a	Leichtle and Bonacic	Northern	Population ecology	Camera trapping; modeling	Lack of ecological data for northern Andean pumas	Lowest densities; nocturnal activity; preference for high-Andean shrublands
31	2025b	Leichtle and Bonacic	Northern	Trophic ecology	Fecal analysis	Lack of trophic studies for northern Andes	Diet dominated by wild artiodactyls; conflict linked to pastoral change
32	2025	Guzmán-Aguayo *et al.*	Austral	Behavior	Camera trapping	Limited data on behavioral responses to tourism	Temporal avoidance of high-use trails
33	2025	Iranzo *et al.*	Austral	Human–puma interaction	Interviews; modeling	Lack of integration between ecological data and human perception	Fear persisted despite stable ecological indicators
34	2025	Calvo and Skewes	South-central	Community ecology	Camera trapping	Scarce data in Araucaria forest ecosystems	Puma detected at low frequency

was statistically associated with historical period. Expected frequencies were calculated under the null hypothesis that research theme and publication period were independent. Prior to interpretation, we verified that the assumptions of the chi-square test were satisfied. Given the relatively small sample size (n = 34), results were interpreted cautiously and complemented with Correspondence Analysis (CA), which provides a multivariate visualization of associations among categorical variables. To characterize longitudinal thematic trajectories, we also generated temporal trend plots showing annual changes in study themes.

Spatial analysis: Spatial patterns of research effort were assessed by linking each publication to the administrative region(s) addressed in the study. Regional boundaries were obtained from the Natural Earth dataset (level-1 subdivisions), and publication counts were mapped to illustrate the geographic distribution of research effort and identify spatial biases in study representation across Chile. No standardization by regional area, habitat extent, or puma distribution range was applied, as the objective was to describe relative research effort rather than infer proportional sampling intensity.

Statistical environment and reproducibility: All analyses were conducted in R 4.3.1 (R Core Team 2024), using the packages ggplot2 (Wickham 2016), igraph (Csardi and Nepusz 2006), and the tidyverse collection (Wickham *et al.* 2019). Scripts for data processing, visualization, and statistical analysis are available upon request to ensure full reproducibility (Aria and Cuccurullo 2017).

Limitations and scope of literature inclusion: Because this review aimed to provide a standardized and reproducible synthesis of scientific knowledge, only peer-reviewed publications were included. Grey literature—such as theses, technical reports, environmental impact assessments, governmental documents, monitoring program reports, and non-indexed institutional publications—was deliberately

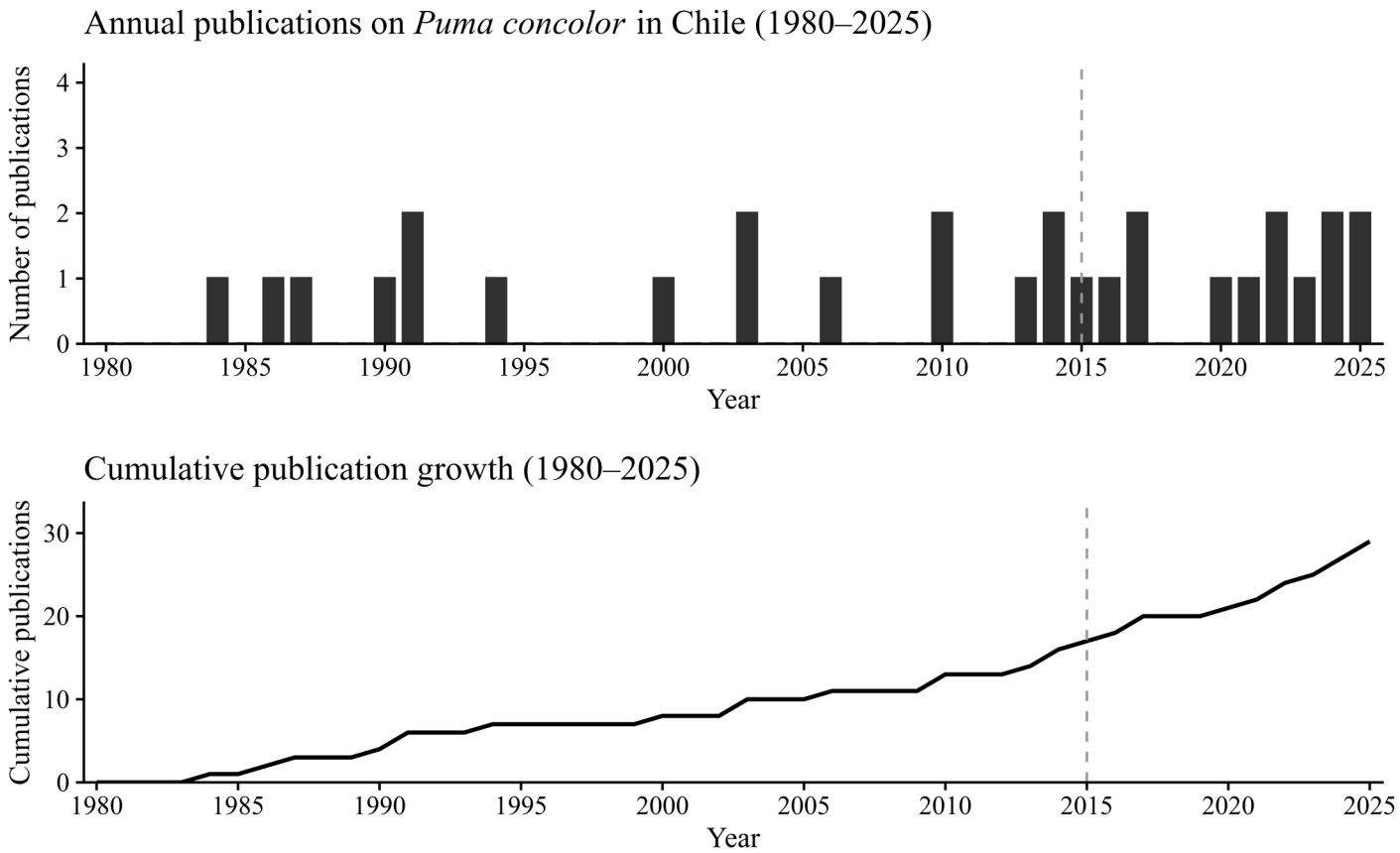

Figure 1. (A) Annual number of peer-reviewed publications on *Puma concolor* in Chile (1980–2025). (B) Cumulative publication growth over the same period. The dashed vertical line marks 2015, corresponding to the beginning of a more consistent publication frequency and a noticeable change in the slope of cumulative growth, indicating progressive consolidation of national research output during the most recent decade.

excluded. Although these sources may contain valuable ecological information, their methodological heterogeneity, variable accessibility, and lack of standardized peer-review processes can limit comparability across studies.

Restricting the analysis to peer-reviewed literature ensured consistency in quality control, traceability of sources, bibliographic verification, and analytical standardization. This decision also enhances reproducibility, allowing future researchers to replicate search strategies, update the dataset, and reassess temporal trends under equivalent criteria. Consequently, the knowledge gaps identified in this review reflect gaps within the indexed scientific literature rather than the totality of information that may exist in technical or unpublished formats.

Results

We identified 34 peer-reviewed publications addressing pumas in Chile between 1980 and 2025. The resulting synthesis reveals substantial spatial concentration, thematic evolution, and temporal shifts in research priorities.

Spatial distribution: Research effort was unevenly distributed across Chile. The highest proportion of studies was conducted in central Chile (38%), particularly during the last decade, followed by the Magallanes Region (32%). Studies conducted at a national scale represented 20%, whereas northern ecosystems accounted for only 10% of publications. Despite this recent increase in central Chile, extensive areas of northern and south-central regions remain poorly documented.

Temporal patterns: Publication output remained relatively low and stable during the first two decades (1980–2000), typically averaging one article per year or less. From the mid-2000s onward, publication frequency became more consistent, generally fluctuating between one and two articles annually. Although no abrupt surge is observed, the cumulative growth curve indicates a gradual acceleration in scientific production after 2010, culminating in the highest annual output recorded in 2025 (Figure 1). This pattern reflects progressive consolidation rather than a sudden expansion of research activity.

Thematic patterns: Trophic ecology dominated the literature (13 publications), reflecting Chilean ecology's early focus on predator–prey interactions. Distribution and density (6), behavior (5), genetics (3), health (3), and human–puma interaction (3) constituted the remaining themes (Figure 2). These patterns show that, while feeding ecology played a foundational role in national puma research, more diverse and multidisciplinary approaches have emerged in the last decade.

Temporal structure of themes: The temporal distribution of thematic categories showed that trophic ecology remains the only theme consistently represented across all decades.

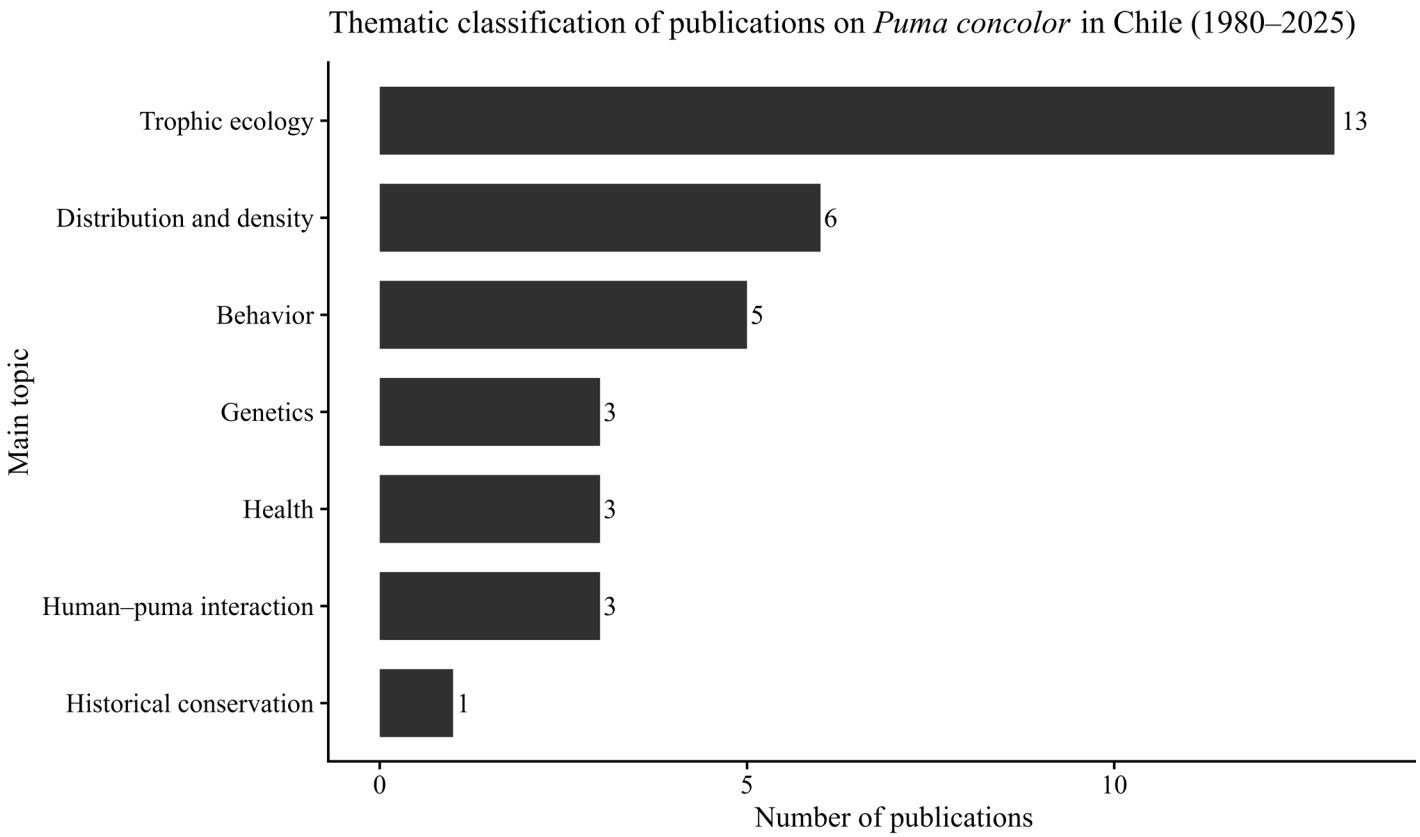

Figure 2. Thematic classification of peer-reviewed publications on *Puma concolor* in Chile (1980–2025) based on the main topic assigned to each study.

Distribution and density studies first appeared in 1995 but remained sporadic during the following decade and became more frequent and methodologically consolidated after 2010. Behavior studies intensified after 2005 and again after 2020, whereas genetics and human–puma interaction emerged almost exclusively in the last decade. Trend analyses further indicated a marked decline in the relative dominance of trophic ecology and a progressive increase in behavioral, spatial, and socio-ecological research (Figure 3).

Period comparison: To evaluate whether the distribution of research themes differed among historical periods, we applied a chi-square test of independence using a 3 × 7 contingency table crossing publication period (1980–2000, 2001–2015, 2016–2025) and research theme (trophic ecology; distribution and density; behavior; health; genetics; human–puma interaction; historical conservation). The test did not detect a statistically significant association between period and research theme ($\chi^2 = 20.43$, df = 12, $p = 0.059$). Although the association did not reach the conventional threshold for statistical significance, descriptive patterns indicated temporal clustering in thematic composition. Early studies (1980–2000) were predominantly focused on trophic ecology; the 2001–2015 period incorporated behavioral and health-related perspectives; and the most recent period (2016–2025) showed greater representation of genetics and socio-ecological research themes.

Correspondence Analysis: The Correspondence Analysis revealed clear temporal structuring in thematic composition. The first dimension explained 84.3% of the total inertia, indicating that most variation in research themes across periods is captured along a single dominant axis. The second dimension accounted for 15.7% of the inertia.

The earliest period (1980–2000) was positioned toward the side of the ordination space associated with trophic ecology and historical conservation. The intermediate period (2001–2015) was located closer to behavioral and health-related research themes, reflecting diversification beyond purely ecological approaches. In contrast, the most recent period (2016–2025) was situated near genetics, human–puma interaction, and distribution and density, indicating a shift toward socio-ecological and population-oriented research perspectives.

Overall, the ordination supports a progressive temporal reorganization of research themes, with early ecological emphasis transitioning toward greater thematic diversity and increasing incorporation of human dimensions in recent years (Figure 4).

Discussion

This review reveals a structured and progressive evolution of puma research in Chile over the past four decades, reflecting broader global patterns in large carnivore science. Worldwide, research on apex predators has transitioned from descriptive ecological studies toward increasingly integrative frameworks incorporating spatial modelling, genetics, disease ecology, and human dimensions (Treves

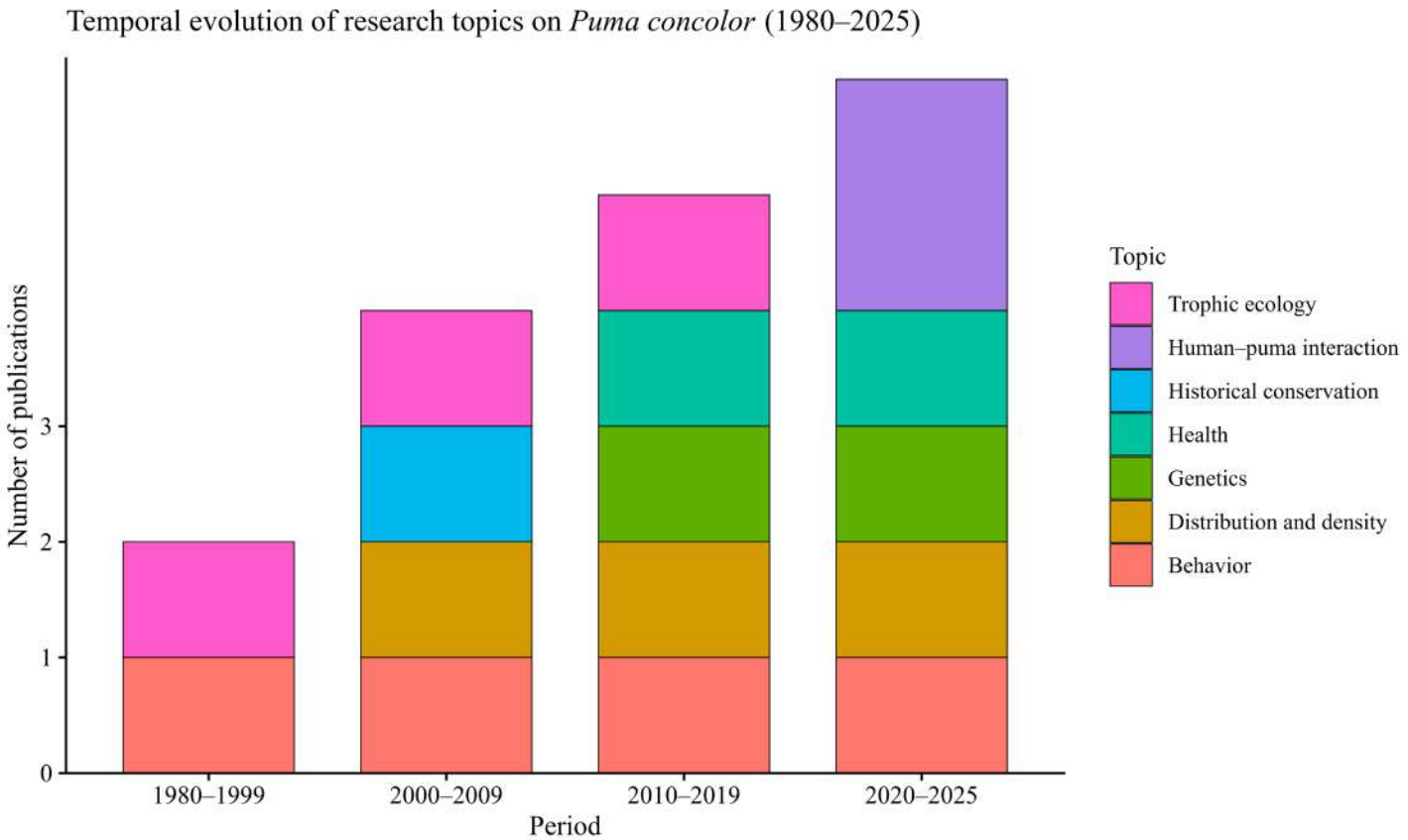

Figure 3. Temporal trends in research topics on *Puma concolor* in Chile (1980–2025). The figure illustrates the emergence, persistence, and occasional disappearance of thematic categories over time. Trophic ecology predominated during the early decades, whereas research on behavior, distribution and density, genetics, health, and human–puma interaction increased notably after 2010, reflecting a progressive diversification of the field.

and Karanth 2003; Ripple *et al.* 2014). A similar trajectory is evident in Chile. Although annual publication rates remained relatively modest throughout much of the study period, the thematic breadth of research expanded markedly after 2010, suggesting qualitative diversification rather than purely quantitative growth. This pattern aligns with global shifts in carnivore research, where methodological innovation and conservation urgency have reshaped research priorities (Crooks 2002; Chapron *et al.* 2014). In addition, increasing human expansion into formerly natural landscapes has intensified interactions between people and large carnivores, generating new research agendas focused on coexistence, conflict mitigation, and human dimensions of conservation (Randa and Yunger 2006; Bombieri *et al.* 2018).

In addition to broader global trends, the historical concentration of Chilean puma studies in southern regions likely reflects structural and institutional drivers. Ecological research effort commonly clusters around areas with long-term field programs, consolidated protected areas, and sustained logistical support, generating spatially uneven knowledge production (Haddaway *et al.* 2015; Gusenbauer and Haddaway 2020). In Chile, Patagonia has historically hosted internationally connected conservation initiatives and well-established research networks focused on large mammals, which may have facilitated repeated sampling and multi-year data continuity (Franklin *et al.* 1999; Bank *et al.* 2002; Elbroch *et al.* 2009). Thus, the regional concentration observed in early decades likely reflects research infrastructure and funding continuity rather than intrinsic ecological priority.

Shifts in thematic and methodological focus: The early predominance of trophic ecology in Chilean puma research reflects a combination of logistical feasibility, methodological accessibility, and regional research infrastructure rather than ecological exclusivity of any particular biome. During the 1980s and 1990s, many studies were conducted in southern Chile, particularly in Patagonian landscapes, where open habitats and abundant ungulate prey facilitated diet assessments through scat analysis and carcass inspection. Similar reliance on dietary studies characterized early phases of large carnivore research globally, as predator–prey interactions were more readily quantified than demographic, genetic, or movement parameters (Treves and Karanth 2003). These foundational studies generated important insights into prey selection, seasonal mortality, and predator–prey dynamics. However, their geographic concentration in southern ecosystems inherently constrained the ability to extrapolate findings across Chile's highly heterogeneous environmental gradient, which includes Mediterranean shrublands, temperate forests, high-Andean plateaus, and arid northern systems.

Importantly, the historical prominence of Patagonian

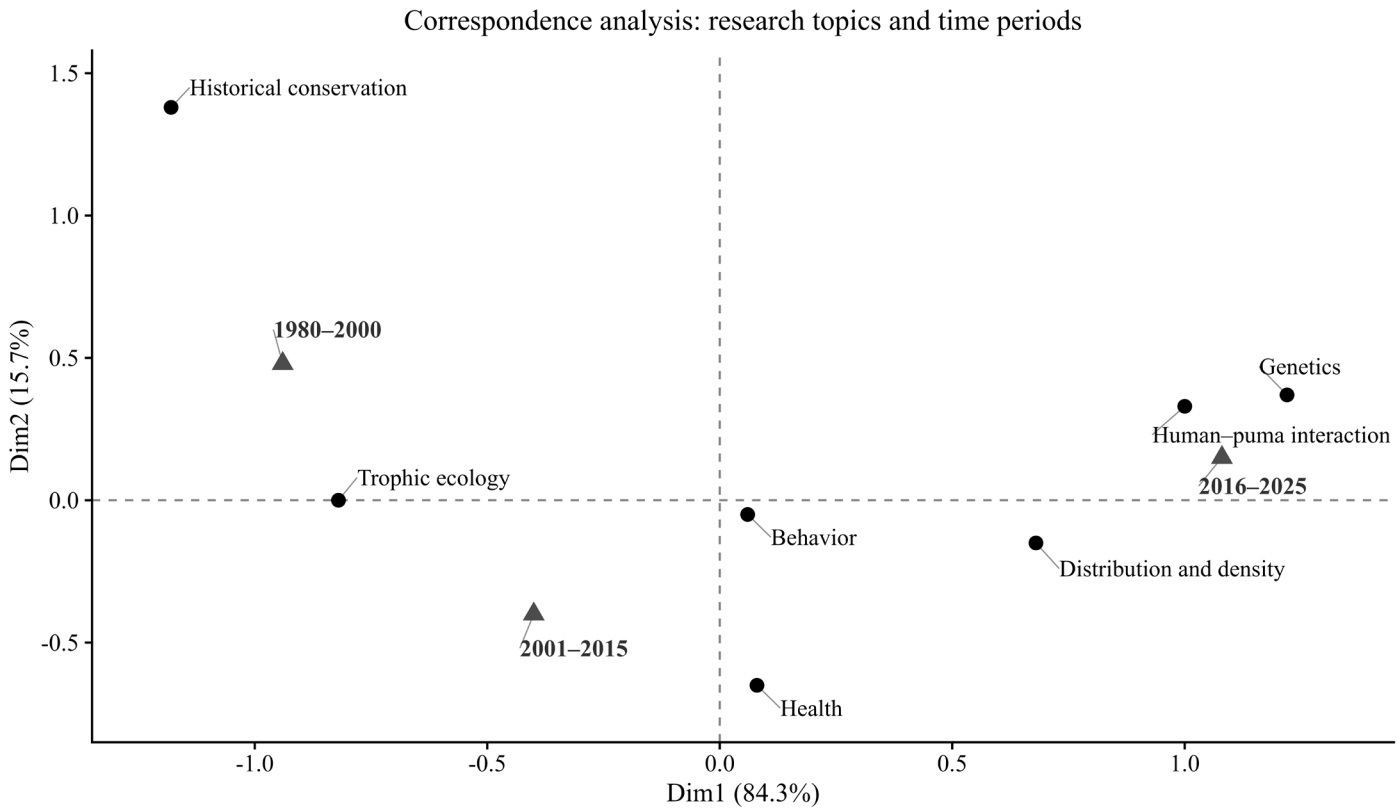

Figure 4. Correspondence Analysis (CA) ordination of research themes and publication periods for *Puma concolor* studies in Chile (1980–2025). Points represent thematic categories (blue) and historical periods (red). The first two dimensions explain 84.3% and 15.7% of the total inertia, respectively. The ordination illustrates temporal structuring in thematic focus, with early studies (1980–2000) associated primarily with trophic ecology and historical conservation, the intermediate period (2001–2015) linked to behavioral and health-related research, and the most recent period (2016–2025) positioned closer to genetics, distribution and density, and human–puma interaction themes.

systems in the literature should not be interpreted as ecological centrality of these landscapes for *P. concolor* in Chile. Most studies relied on indirect methodologies—including camera trapping, scat analysis, carcass inspection, and genetic sampling—rather than direct visual observation. In open southern environments, ecological evidence such as kills, tracks, and scats may have been more detectable, facilitating early research implementation. This pattern reflects detectability and logistical continuity of long-term field programs rather than greater biological importance of southern populations. Given the pronounced biogeographic diversity of Chile, extrapolating ecological patterns derived primarily from Patagonian systems may obscure region-specific dynamics operating in central and northern ecosystems, including variation in prey assemblages, habitat use, population density, movement ecology, and the intensity and form of human–puma interactions.

Beginning in the 2000s, Chilean puma research underwent a methodological transition consistent with broader developments in carnivore ecology. The incorporation of camera trapping, telemetry, and spatially explicit analytical frameworks expanded the scope of inquiry beyond diet-based studies. Advances in spatial capture–recapture models and individual tracking transformed large carnivore monitoring worldwide, enabling robust density estimation and movement analyses (Kelly *et al.* 2012; Royle *et al.* 2014). In Chile, these approaches produced the first standardized density estimates for both central and southern regions and documented dispersal movements and spatial behavior under varying degrees of anthropogenic influence. More recently, genetic analyses have begun to clarify patterns of population structure and connectivity, aligning with global recognition that molecular tools are essential for evaluating fragmentation and long-term demographic viability (Crooks 2002; Frankham 2005).

The emergence of health-related and socio-ecological studies during the last decade further reflects a shift toward interdisciplinary conservation science. As pumas increasingly overlap with livestock systems, forestry landscapes, and peri-urban environments, research attention has expanded to include pathogen transmission, livestock depredation, human perception, and coexistence dynamics (Treves *et al.* 2006; Ripple *et al.* 2014). In Chile, documented cases of zoonotic parasites and spatial concentration of conflicts illustrate this diversification of thematic focus. Nevertheless, despite increasing breadth, several methodological and geographic gaps persist.

Telemetry remains comparatively limited relative to its demonstrated value for understanding movement ecology, habitat selection, survival, and behavioral responses to anthropogenic disturbance (Logan and Sweanor 2001; Elbroch and Wittmer 2013b). The scarcity of long-term monitoring frameworks similarly constrains

robust demographic inference. Globally, sustained multi-year telemetry programs have been central to evaluating carnivore recovery, dispersal dynamics, survival rates, and population viability (Chapron *et al.* 2014). In Chile, however, comparable longitudinal datasets remain rare, limiting the ability to assess population trajectories, climate-related responses, and functional connectivity across heterogeneous landscapes—an approach that has proven critical for understanding large carnivore population dynamics elsewhere (Chapron *et al.* 2014).

Long-term telemetry has been extensively developed in North American puma populations, where multi-decadal collaring programs have generated comprehensive demographic and behavioral datasets (Logan and Sweanor 2001). These programs have provided foundational insights into survival, dispersal, habitat selection, and landscape-scale ecological processes.

The limited implementation of telemetry in Chile should therefore be interpreted within a broader continental context rather than as an isolated national shortcoming. Across much of Latin America, capture-based monitoring of large carnivores remains comparatively limited and often project-dependent. Telemetry requires specialized capture teams, veterinary supervision, long-term permits, and sustained financial support—conditions that are frequently difficult to maintain in South American research systems. As a result, non-invasive approaches such as camera trapping and genetic sampling have become more accessible and scalable alternatives (Kelly *et al.* 2012; Royle *et al.* 2014). Consequently, the relatively low representation of telemetry-based studies in Chile reflects broader structural constraints in regional research capacity. Expanding long-term telemetry programs would nonetheless substantially strengthen national capacity to evaluate demographic trends, ecological connectivity, and adaptive responses to ongoing landscape transformation.

Spatial bias and its implications: Research effort on *P. concolor* in Chile remains unevenly distributed across regions. Although central Chile currently accounts for the largest proportion of peer-reviewed studies, the Austral region—particularly Patagonia—historically concentrated research activity during the early decades. Geographic bias is not unique to Chile; systematic reviews in ecology consistently reveal clustering of research in accessible or institutionally supported regions (Haddaway *et al.* 2015; Gusenbauer and Haddaway 2020). In the Chilean context, long-standing research programs within protected Patagonian landscapes, together with sustained international collaborations, likely facilitated multi-year field continuity and repeated sampling.

Importantly, this historical concentration should not be interpreted as reflecting greater biological centrality or direct visibility of pumas in southern ecosystems. Most Chilean studies have relied on indirect methodologies—including scat analysis for dietary reconstruction, genetic identification from fecal samples (barcoding), carcass inspection, and camera trapping for detection and density estimation—rather than direct visual encounters. In open southern landscapes, early research feasibility was likely enhanced by greater detectability of ecological evidence (e.g., prey remains, tracks, and scats) and improved camera-trap performance in structurally simple habitats. Thus, the spatial pattern observed reflects detectability and institutional continuity rather than intrinsic ecological priority.

Northern Chile, by contrast, remains comparatively underrepresented despite its distinctive high-Andean and arid ecological conditions. Differences in prey assemblages, pastoral systems, climatic variability, and habitat structure suggest that puma ecology in these environments may differ substantially from patterns described in southern systems. However, the limited research effort in northern regions cannot be attributed solely to ecological variation. High-Andean and desert landscapes impose substantial logistical constraints, including seasonal inaccessibility, extreme environmental conditions, elevated field costs, and low infrastructure density, all of which can restrict sustained monitoring. Furthermore, pastoralist land-use systems and dispersed property regimes may complicate research access relative to regions characterized by large, consolidated protected areas.

Such structural conditions likely contributed to the delayed emergence of systematic research in northern ecosystems. Spatially biased research coverage can obscure national-scale patterns of connectivity, demographic resilience, and adaptive responses, particularly for wide-ranging carnivores whose conservation depends on landscape-level processes (Crooks 2002; Ripple *et al.* 2014). Extrapolating ecological patterns derived primarily from southern populations may therefore mask important regional dynamics. Future comparative analyses explicitly evaluating research effort relative to accessibility, institutional presence, or estimated regional densities would help disentangle ecological from structural drivers of spatial research bias and strengthen geographically representative conservation planning.

Knowledge gaps and future directions: The synthesis identifies several priority areas for future research. First, expanded geographic sampling is necessary to address uneven coverage and to evaluate ecological variation across Chile's diverse biomes. Second, greater integration of telemetry and spatial modelling would strengthen understanding of dispersal, habitat connectivity, and behavioral plasticity under fragmentation pressures (Logan and Sweanor 2001; Royle *et al.* 2014). Third, broader genetic monitoring is required to assess population structure and potential isolation, particularly in regions experiencing rapid land-use change (Frankham 2005).

Disease ecology represents another critical frontier. Increasing interaction between domestic animals and wildlife elevates opportunities for cross-species pathogen transmission, a phenomenon widely documented in carnivore systems worldwide (Bevins *et al.* 2012; Foley

et al. 2013; Escobar *et al.* 2022). In Chile, confirmed records of *Trichinella* infection highlight the relevance of integrating epidemiological surveillance into carnivore research. Beyond these cases, evidence from other regions demonstrates exposure of pumas to pathogens commonly associated with domestic carnivores, including feline retroviruses such as Feline Leukemia Virus and Feline Immunodeficiency Virus (Biek *et al.* 2006; Brown *et al.* 2008), as well as associations between domestic animal proximity and pathogen exposure risk (Foley *et al.* 2013). Multi-host parasites such as *Toxoplasma gondii* represent additional ecological and public health concerns in felid systems (Hatam-Nahavandi *et al.* 2021), and emerging panzootics such as sarcoptic mange further illustrate the permeability of wildlife–domestic interfaces (Escobar *et al.* 2022). Although systematic epidemiological monitoring of Chilean puma populations remains limited, increasing overlap among wildlife, livestock, and free-ranging domestic carnivores underscores the need to integrate disease ecology into national research agendas under a One Health framework.

Finally, socio-ecological research must continue to expand. Perception-driven conflict can persist independently of ecological indicators, as demonstrated in multiple carnivore systems (Treves *et al.* 2006). Understanding how fear, economic vulnerability, and cultural narratives shape coexistence outcomes is essential for designing effective management interventions.

Broader conservation implications: Taken together, these findings indicate that Chile's puma populations exhibit ecological adaptability across diverse habitats yet remain insufficiently studied to support a fully integrated and spatially representative national conservation strategy. Apex predators exert disproportionate influences on ecosystem structure and trophic regulation (Ripple *et al.* 2014), and incomplete understanding of their spatial ecology, demographic processes, and landscape connectivity may limit effective long-term management. Although the diversification of research themes since 2010 reflects substantial scientific progress, persistent gaps remain in long-term monitoring, northern geographic representation, telemetry-based studies, and interdisciplinary integration.

At the same time, four decades of research have generated a substantial foundation of knowledge. Chilean studies have elucidated key aspects of trophic ecology, produced regional density estimates, documented movement patterns and dispersal events, identified emerging health risks, and increasingly incorporated socio-ecological dimensions of human–puma interactions. This cumulative body of work demonstrates a clear maturation of puma research in Chile, evolving from predominantly localized ecological descriptions toward more integrative, conservation-oriented and multidisciplinary frameworks.

Strengthening national conservation capacity will require coordinated efforts that link ecological monitoring, genetic surveillance, epidemiology, and social science within a coherent long-term strategy. As Chile continues to experience rapid land-use transformation, infrastructure expansion, and intensifying human–wildlife interfaces, maintaining functional connectivity across heterogeneous landscapes will become progressively more critical (Crooks 2002). By synthesizing four and a half decades of research, this review provides both a retrospective evaluation of scientific development and a forward-looking framework to guide future research and management. Consolidating methodological advances while addressing remaining spatial and thematic gaps will be essential for advancing robust, evidence-based conservation of *P. concolor* in Chile.

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Declaration of artificial intelligence use

This manuscript used artificial intelligence tools (ChatGPT) exclusively to assist with linguistic editing, text refinement, and verification of internal coherence. All ideas, study design, analyses, interpretations, and conclusions are solely the responsibility of the authors. The authors thoroughly reviewed and corrected all content generated or suggested by AI to prevent errors, biases, or inaccuracies. No data, results, or scientific evidence were created using AI, in full compliance with the ethical standards of *Therya*.

Author contributions

Jorge Leichtle conceived the study, designed the review protocol, compiled and classified the literature, conducted the statistical analyses, generated the figures, and led the writing of the manuscript. Cristián Larraguibel-González contributed to study design, validated thematic classifications, supported interpretation of temporal and spatial patterns, and performed critical revisions that substantially improved the structure and clarity of the manuscript. Both authors approved the final submitted version and agree to be accountable for all aspects of the work.

Data availability

All data matrices and R scripts used to perform classification, statistical analyses, and figure generation are available from the corresponding author upon reasonable request. The dataset includes study metadata, thematic categories, regional assignments, temporal classifications, and analysis scripts (R 4.3.1).

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In Memoriam:

M. en. C. Jaime Marcelo Aranda Sánchez (1954-2026)

Tributo a una vida dedicada al aprendizaje y a la enseñanza para comprender y conservar la fauna silvestre de México

Jürgen Hoth von der Meden[1], e Ignacio J. March Mifsut[2]

[1]Fondo de Conservación del Eje Neovolcánico A.C. (FOCEN), México. E-mail: khoth029@uottawa.ca
[2]Consultor independiente, México. E-mail: ijmarchmifsut@gmail.com

Foto: Jürgen Hoth von der Meden

"El rastreo de los mamíferos silvestres es una actividad que permite entrar a un mundo casi mágico, aprendiendo y descubriendo de la naturaleza a través del conocimiento y la imaginación. Es un proceso sin fin de aprendizaje y descubrimiento" (Aranda, M. 10 de abril, 2013, ver Hoth 2013).

Con el reciente fallecimiento el pasado 4 de abril del 2026 de **Jaime Marcelo Aranda Sánchez,** México perdió a un gran miembro de la comunidad académica y a un conservacionista del país. Después de más de cuatro décadas de trabajo ininterrumpido en favor del conocimiento y la protección de la biodiversidad mexicana, en las que se desempeñó como biólogo, mastozoólogo, profesor, investigador y servidor público, Marcelo no escatimó ningún esfuerzo para dejarnos un valioso legado con sus detallados manuales sobre huellas y rastros de mamíferos, edificadores consejos y un gran ejemplo de dedicación y entrega para entender mejor el entramado de la naturaleza. Sus aportaciones han ayudado en gran medida a que la interpretación de las huellas y rastros en México sea reconocida como una técnica formal, útil y accesible en el estudio y gestión de la fauna silvestre; aplicada cotidianamente en la elaboración de inventarios faunísticos y en el manejo de vertebrados silvestres.

Raíces familiares, infancia y primeros pasos de un naturalista

Marcelo nació en la Ciudad de México el 29 de octubre de 1954, el séptimo de diez hijos del matrimonio de Hugo Eduardo Aranda Pamplona (1907–1980) y María del Pilar Sánchez Arizmendi (1923–1989). Su entorno familiar estuvo profundamente vinculado a las letras y al campo. Su padre, de formación contable y amante del campo, publicó varios libros, incluyendo la biografía del distinguido novelista mexicano Luis Inclán, y le inculcó a su hijo, la fascinación por la vida rural y la investigación documental. Su madre, dedicada al hogar y pianista, le brindó un entorno de sensibilidad artística.

Desde los cinco años acompañó a su padre a excursiones en la Sierra del Ajusco. Ya desde sus caminatas tempranas, Marcelo comenzó a interesarse en las huellas de los animales silvestres. A los 13 años, recibió un regalo que le abrió rumbos de vida: el volumen *Los Mamíferos* de la *Colección de la Naturaleza de Time-Life*. En él descubrió dos páginas dedicadas a las huellas de mamíferos norteamericanos; fascinado, copió y dibujó las figuras e hizo su primer cuaderno de campo artesanal enfocado en el rastreo (ver Sicilia 2024, 2026).

Formación académica y años formativos en FAUNAM

En 1975 ingresó a la Facultad de Ciencias de la Universidad Nacional Autónoma de México (UNAM). Durante sus primeros semestres se integró al Laboratorio de Investigación Herpetológica (LIH) de la Facultad. Su mayor interés académico en los mamíferos medianos y grandes lo llevó a incorporarse al Grupo Estudiantil de Trabajo Académico FAUNAM (formado por Víctor Sánchez-Cordero, Ramón Pérez-Gil, Manuel Lemus y Susana López de Lara, entre otros). Su paso por FAUNAM fue clave para establecer una base de investigaciones para estudiantes de Biología de la UNAM en la comunidad El Capulín (Mpio. de Xalatlaco, Estado de México) y consolidó su interés definitivo en el rastreo de mamíferos medianos y grandes.

Entre 1976 y 1980, El Capulín y el Parque Nacional Desierto de los Leones representaron un espacio fundamental para la formación de Marcelo, quien de manera autodidacta ahí forjó sus habilidades para interpretar el paisaje a través del rastreo. Armado con sus propias colecciones de referencia de huellas –integradas por moldes de yeso de rápido fraguado y observaciones de campo– y en libros como la guía de campo de Murie (Murie 1954), comenzó a explorar la posibilidad de aplicar el rastreo a investigaciones biológicas. Así desarrolló sus primeras estimaciones de densidad del venado cola blanca (*Odocoileus virginianus*) en el Desierto de los Leones, realizado mediante el conteo de excretas. De este trabajo pionero también surgió su primera obra publicada en 1980, *Los Mamíferos de la Sierra del Ajusco* (Aranda *et al*. 1980).

En El Capulín, convivió con la jovial y hospitalaria familia de Don Prócoro Palacios y Doña Leonila, quienes, además de alimentar frecuentemente a los voraces miembros de FAUNAM y asociados (en pleno crecimiento… académico), fueron una importante fuente de conocimientos sobre la fauna, la vegetación, así como de usos y costumbres locales.

Después de haber completado varios potenciales trabajos de tesis, incluyendo la historia socioambiental de El Capulín, el 11 de julio de 1980, Marcelo presentó su examen profesional para obtener el título de Biólogo por la Facultad de Ciencias de la UNAM. Su tesis se intituló *Importancia y Utilidad de los Rastros para el Estudio de Mamíferos Silvestres*, y su jurado estuvo integrado por el Dr. Bernardo Villa Ramírez (+), el Dr. Cornelio Sánchez Hernández y la Dra. Luz del Carmen Colmenero.

Trayectoria institucional y contribuciones a la mastozoología

La carrera profesional de Marcelo Aranda se caracterizó por la combinación de investigación de campo, docencia, conservación aplicada, gestión pública y un persistente trabajo artístico a través de la fotografía y el dibujo científico (Figura 1).

Figura 1. Lámina sobre los mamíferos de la selva de Chiapas ilustrada por Marcelo Aranda (2016; Técnica de lápiz sobre papel, 11 x 17 pulgadas/ 29.9 x 43.2 cm, propiedad Ignacio March).

Tuxtla Gutiérrez, Chiapas, 1980–1984. Inicios de la vida profesional y familiar.

En agosto de 1980, recién egresado de la licenciatura, llegó a Tuxtla Gutiérrez para incorporarse al Instituto de Historia Natural de Chiapas (IHN). Allí comenzó una relación profesional que habría de marcar su vida; fue contratado por Don Miguel Álvarez del Toro como encargado de la Sección de Mamíferos. Allí participó en uno de los episodios fundamentales de la historia del IHN: la mudanza de las colecciones y de la fauna del Parque Madero a *El Zapotal*, donde surgiría el Zoológico Miguel Álvarez del Toro (ZOOMAT). El trabajo con los animales del zoológico le permitió desarrollar y ampliar su colección de moldes de huellas y participar en la evaluación y desarrollo de técnicas de contención física y química de fauna silvestre (véase López de Buen y Aranda 1986).

Aquellos años marcaron también el comienzo de una nueva etapa en su vida personal. En 1982 contrajo matrimonio con Lorena López de Buen (MVZ), a quien conoció en el ZOOMAT y juntos tuvieron dos hijos: Lorena Irazú, nacida en 1984, y Andrés Marcelo, nacido en 1986.

San Cristóbal de las Casas, Chiapas, 1984 - 1988. Investigador del INIREB y su trabajo sobre ecología del jaguar

En 1984 se incorpora al Programa Fauna de México del Instituto Nacional de Investigaciones sobre Recursos Bióticos (INIREB) en San Cristóbal de las Casas, trabajando en colaboración con investigadores como Mario Ramos e Ignacio March Mifsut. En este periodo inició sus evaluaciones sobre la situación del jaguar (*Panthera onca*) en Chiapas, en los manglares de la costa del Pacífico (Pijijiapan, Chiapas).

Costa Rica 1988-1990. Nuevamente estudiante de la Maestría en Ciencias

Entre 1988 y 1990 realizó sus estudios de Posgrado en la Universidad Nacional de Costa Rica en el Programa Regional en Manejo de Vida Silvestre para Mesoamérica y el Caribe (PRMVS). Obtuvo su Maestría en Ciencias con la tesis *El Jaguar (Panthera onca) en la Reserva Calakmul, México: Morfometría, Hábitos Alimentarios y Densidad de Población* (Aranda 1990; dirigida por el M. en C. Jorge Fallas). Este trabajo, financiado por la Wildlife Conservation Society (WCS), lo convirtió en el primer biólogo mexicano en realizar investigaciones de campo sistemáticas, así como publicar sobre la ecología del jaguar en el país.

Xalapa, Ver. 1989-2000. Investigador del Instituto de Ecología, A.C. (INECOL)

Tras la desaparición del INIREB, en 1989 Marcelo se incorpora como Investigador Asociado al Instituto de Ecología, A.C. (INECOL) en Xalapa, Veracruz. Durante más de una década en esta institución desarrolló proyectos sobre ecología de carnívoros, patrones alimentarios de félidos, conservación de la biodiversidad y metodologías de monitoreo. Participó activamente en la formación de la Asociación Mexicana de Mastozoología, A.C. (AMMAC), siendo Vicepresidente en el período 2000–2002 y Presidente en el período 2002–2004. Además, organizó el VI Congreso Nacional de Mastozoología en la ciudad de Oaxaca en 2002.

Gestión Pública: 2001-2006, CORENA DF; 2007-2018 CONANP

A partir del 2001, Marcelo complementó su formación académica participando en la administración pública y la gestión ambiental. De 2001 a 2006 trabajó para la Comisión de Recursos Naturales (CORENA, Gobierno del Distrito Federal), con el cargo de Director de Áreas Naturales Protegidas, donde lideró la reorganización técnica y territorial de las Áreas Naturales Protegidas (ANP) de la capital e impulsó la creación del Programa de Educación Ambiental del Parque Nacional Desierto de los Leones. De 2007 al 2018 se sumó a la Comisión Nacional de Áreas Naturales Protegidas, CONANP, en diversas ANP de México.

De 2007 a 2009 dirigió la Reserva de la Biosfera Sierra de Manantlán (Jalisco/Colima), donde impulsó proyectos pioneros de foto-trampeo que registraron la coexistencia de las seis especies de felinos de México. Del 2009 a 2019 asumió la dirección de la Sierra de Morones en Zacatecas (Área de Protección de Recursos Naturales, APRN, Pabellón, 2009–2010), enfocada en la protección del pino azul (*Pinus maximartinezi*). Finalmente, de 2010–2016 se desempeñó como director del Parque Nacional El Tepozteco, Parque Nacional Lagunas de Zempoala y Corredor Biológico Chichinautzin (COBIO).

A partir de 2018 hasta 2026 continuó aportando a la conservación de los ecosistemas como consultor e investigador independiente. Lo hizo de manera notable con iNaturalistMx donde desde 2014 se convirtió en su principal curador de observaciones y –literalmente– hasta el último de sus días todavía estuvo aprobando registros (Galindo 2026).

Obras bibliográficas de referencia y producción científica

La labor académica de Marcelo quedó plasmada en decenas de artículos arbitrados en revistas nacionales e internacionales, capítulos de libros y publicaciones de divulgación.

Algunos temas sobresalientes en los que participó como autor o coautor son los siguientes[1]:

- Estudio sobre la distribución del Conejo de los volcanes (su primer artículo arbitrado).
- Guía de los mamíferos silvestres de Chiapas.
- Hábitos alimentarios del coyote en la Sierra del Ajusco, México.
- Distribución y abundancia del jaguar en el estado de Chiapas.
- Espectro de presas del jaguar y el puma en los bosques tropicales de México.
- Densidad y estructura de una población del jaguar en la Reserva de la Biosfera Calakmul.
- Registro de pequeños mamíferos en la Reserva de la Biosfera Calakmul.
- Análisis de la alimentación de la nutria en un sector del río Los Pescados, Veracruz.
- Registro del águila elegante en la Reserva de la Biosfera Sierra de Manantlán.
- Primer registro de ocelote en el Parque Nacional Lagunas de Zempoala.
- Registro notable de margay en el bosque mesófilo de montaña de Morelos.

Figura 2. Evolución de los manuales de huellas y rastros realizados por Marcelo: a) 1980; b) 1981; c) 2000; y d) 2012. (Diseño J. Hoth.)

[1]Para un listado completo realizado por Marcelo ver Aranda M. (s.f.). *Curriculum vitae.* UNAM -FC (URL) y ResearchGate

Figura 3. Marcelo Aranda, preparando moldes de huellas como parte de sus investigaciones de mamíferos, silvestres de México y cursos de enseñanza asociados. El Cuyo, Yucatán, julio 2000. Autor: M. Cristina MacSwiney G.

No obstante, sus mayores contribuciones fueron sus manuales y guías de campo sobre rastros de mamíferos, las cuales se convirtieron en la referencia técnica indispensable para la formación de biólogos, guardaparques y técnicos en América Latina (Figura 2). Sus libros emblemáticos son:

- *Rastros de los Mamíferos Silvestres de México. Manual de Campo* (INIREB, 1981): La obra primigenia, ilustrada íntegramente por la pluma del propio Marcelo, que sentó la metodología formal para el estudio de huellas en el país.
- *Huellas y otros rastros de los mamíferos grandes y medianos de México* (CONABIO / Instituto de Ecología, A.C., 2000): Edición ampliada que sistematizó la identificación de carnívoros, ungulados y otros grupos mastozoológicos.
- *Manual para el rastreo de mamíferos silvestres de México* (2012): Obra cumbre de consulta obligada en el ámbito científico y de divulgación ambiental.

Su agudo sentido de observación y talento visual se reflejaron también en la fotografía científica, ámbito en el cual fue galardonado con el Segundo Lugar (1985) y el Primer Lugar (1993) en el Concurso Nacional de Fotografía Científica de la UNAM por sus secuencias fotográficas sobre el comportamiento de pumas y jaguares.

Legado

Más allá de sus icónicas publicaciones, Marcelo poseía la capacidad única de los naturalistas clásicos: la lectura del paisaje a través de sus detalles más sutiles, pero también se distinguió por su incesante ánimo de compartir sus conocimientos. Mediante la impartición de más de una docena de cursos especializados de rastreo en México, Costa Rica y Colombia, así como en los diplomados de manejo de fauna de DUMAC, donde se destacó por la formación de generaciones de profesionistas en la observación de la naturaleza (Figura 3). Para Marcelo, una huella en el lodo o en la hojarasca no era una mera marca fortuita, sino el punto de partida para reconstruir la historia del comportamiento animal y fundamentar decisiones reales de conservación.

En el plano personal, tras afrontar procesos complejos de salud y vida familiar, Marcelo volvió a encontrar un nuevo periodo de plenitud con Verónica Aguilar, contrayendo nupcias en febrero de 2020.

Con Marcelo, la mastozoología y la conservación en México ganó a un incansable naturalista e investigador comprometido con el trabajo de campo y a un gran defensor del patrimonio natural. Abrió brecha y nos trilló una amplia vereda tanto con sus manuales mejorados durante cuatro décadas, sus colecciones de huellas donadas al Instituto de Biología de UNAM y a la Facultad de Ciencias UNAM, y seguramente a nivel internacional en otros centros de investigación donde impartió cursos; aunado a la experiencia acumulada y diseminada a través de sus edificantes cursos de campo. Un gran legado que nos toca a todos honrar y seguir cultivando.

Además de salir al campo con su bolsa de yeso para registrar huellas, Marcelo se distinguió por estar siempre acompañado de su cámara. Con ella siguió la huella a eventos clave, incluyendo las vertiginosas transformaciones de sus amados paisajes. Ojalá que ese legado gráfico, junto con las huellas y sus diarios de campo, también pueda ser resguardado y sistematizado como valioso testamento para futuras generaciones. Descansa en paz, Marcelo. Misión cumplida.

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