

Therya

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La portada

The wolf (*Canis lupus*) is one of the main predators of the boreal parts of the continents. In many places in the world it has been extirpated and its current populations are restricted to different isolated areas in North America, Europe, and Asia. Currently there are several repopulation programs in different countries around the world (Photograph Sergio Ticul Álvarez Castañeda).

Nuestro logo “Ozomatli”

El nombre de “Ozomatli” proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimer en la cosmogonía mexica. “Ozomatli” es una representación pictórica de los 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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**Reglamento interno del Sistema Integral De Difusión y Divulgación Therya de la
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fascículo 45 <http://www.revistas-conacyt.unam.mx/therya/index.php/THERYA/issue/view/44>

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Editorial**Advances and limitations in the trophic ecology of bats in Mexico**

Diet studies are essential for understanding ecology, evolutionary biology, and informing ecosystem management and restoration ([Nielsen et al. 2018](#)). The study of feeding and competitive interactions in bats is considered crucial for understanding their ecology in a rapidly changing environment ([Salinas-Ramos et al. 2020](#)). Nonetheless, studying the bat guild with the greatest species richness, which preys on the largest number of species on the planet in one of the megadiverse countries is a challenge that few researchers have considered, but it must be addressed.

In recent years, there has been a recurring theme in the study of trophic ecology, focusing on the characteristics of bats and their food sources. This approach aims to understand better trophic specialization, particularly in the context of predator-prey interactions between bats and arthropods. These type of studies approach has been made possible mainly by the high level of resolution offered by diet analyses based on high-throughput mtDNA sequencing. Some previous studies had considered this analysis perspective based on diet visually identifying.

However, they were limited in identifying the prey at higher taxonomic levels (e. g., subclass, order, suborder, etc.). Studies in which the presses were classified based on traits such as their hearing ability, hardness, or flight capacity, but with limited precision due to the resolution in taxonomic identification (e. g. [Bogdanowicz et al. 1999](#); [Segura-Trujillo et al. 2016](#)). Limited identification resolution regarding the diet composition of arthropodophagous bats has been achieved since pioneering work of Clare (2009). Since then, the studies addressing the trophic theme in different species of bats that prey on arthropods have increased worldwide. However, challenges in studying the trophic ecology of bats persist. Although studies on the molecular identification of arthropod-predating bats' diets have increased globally in the last decade, however, few studies have been conducted in México. The first DNA barcode-

based study conducted in México described the diet and trophic overlap of three species of Mormoopidos (*P. davyi*, *P. personatus*, and *P. parnellii*) in Chamela, Jalisco ([Salinas-Ramos et al. 2015](#); Figure 1).

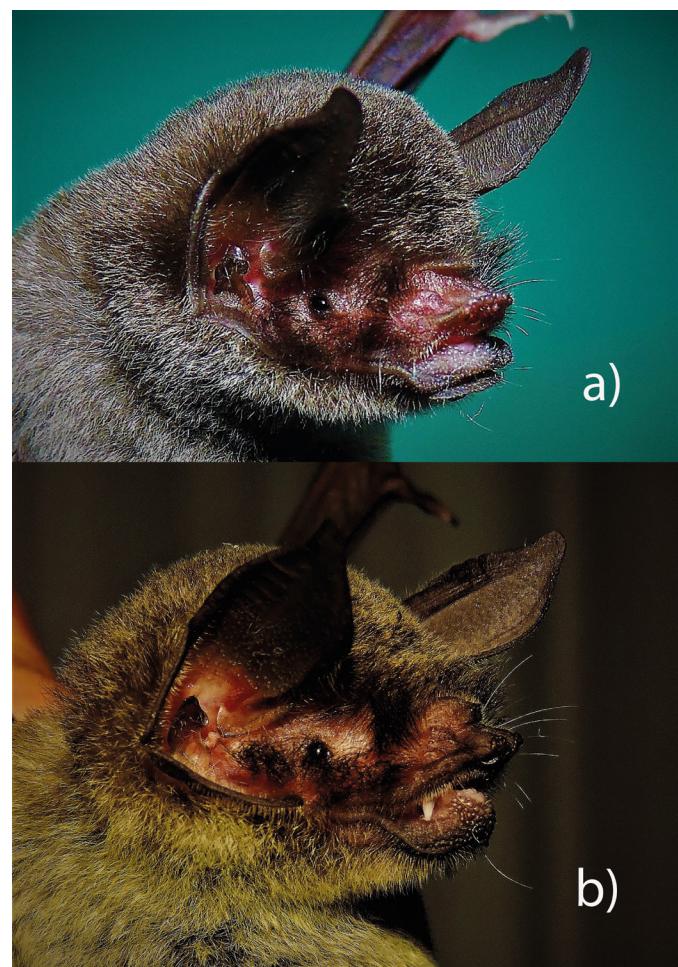


Figure 1. Photographs of two species of Mustached bats, a) *Pteronotus personatus* and b) *Pteronotus parnellii*, currently considered two different species distributed in México, *Pteronotus mexicanus* and *Pteronotus mesoamericanus*. (Photographs by Cintya A. Segura-Trujillo).

Later, 20 species of Mexican bats were researched (*Peropteryx macrotis*, *Balantiopteryx plicata*, *Rhynchonycteris naso*, *Saccopteryx bilineata*, *Pteronotus mexicanus*, *Pteronotus mesoamericanus*, *Pteronotus fulvus*, *Mormoops megalophylla*, *Molossus rufus*, *Nyctinomops laticaudatus*, *Natalus mexicanus*, *Macrotus californicus*, *M. waterhousii*, *Myotis velifer*, *M. melanorhinus*, *M. pilosatibialis*, *Rhogeessa parvula*, *R. aeneus*, *R. tumida*, and *Neoeptesicus furinalis*; Figure 2 and 3), focused in detailing their taxonomic composition and prey traits to describe their trophic segregation and predator-prey interaction based on functional characteristics ([Segura-Trujillo et al. 2022, 2024](#)). Research on the trophic ecology of arthropod-eating bats in México is currently limited, both by direct identification methods and by molecular analysis of their excreta. It can be difficult to accurately describe the diet of bats in this trophic group because their primary food source, arthropods, is so diverse. To identify the specific types of arthropods they consume, we need information from scientific collections and digital databases such as GenBank, which allow us to identify a larger proportion of their prey at more detailed taxonomic levels.

However, taxonomic identification is only the basis, as it is essential to classify prey based on their functional traits. These traits are helpful for defining interactions with bats or identifying whether bats are preying on species relevant to agriculture or human health. One example, in the case of moths, which are the preferred food of bats, it is difficult to detect them visually in bat droppings due to the low keratin content of their bodies. As a result, their remains are largely broken-down during digestion, making their identification at suborder levels difficult. In research using high-throughput sequencing, most moths can be identified at the family level. However, it is difficult to identify them at the genus or species level because there are not enough sequences of moths from México in GenBank to accurately identify their exact species. In some cases, moths can be identified at the species level when they are of agricultural interest. For example, moths such as *Helicoverpa* sp., *Spodoptera* sp., and *Plutella xylostella*, whose larvae are significant pests in agriculture, have been found in the diet of bats. This is possible because reference sequences for comparison and identification are available, thanks to their importance in the agricultural economy.



Figure 2. Some species' diets have been described through molecular studies in México. a) Black mastiff bat *Molossus rufus*, b) Proboscis bat *Rhynchonycteris naso*, c) Hairy-legged myotis *Myotis pilosatibialis*, and d) Lesser dog-like bat *Peropteryx macrotis* (Photographs by Cintya A. Segura-Trujillo).

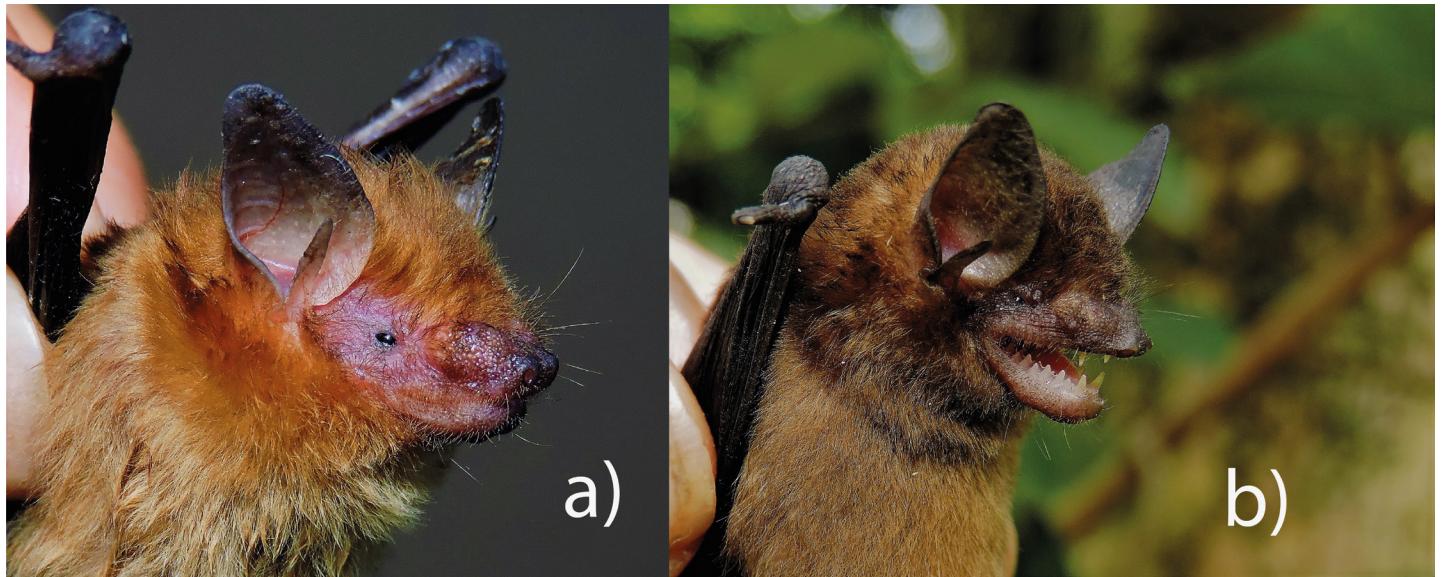


Figure 3. Species' diets have been described through molecular studies in México. a) Little yellow bat *Rhogeessa parvula*, b) Black-winged little yellow bat *R. tumida*, (Photographs by Cintya A. Segura-Trujillo).

In this scenario, we have encountered several significant limitations when conducting research in this field. These include limited funding, lack of infrastructure, and the requirement for collaboration with specialist entomologists. Specifically, when it comes to determining diet through molecular studies, there is a need to expand genetic reference databases to Mexican arthropods. In recent years, bats have become one of the most widespread mammals to study. They have gone from being one of the most mythologized animals to one of mammalogists' favorites. Despite this, we still largely ignore their trophic interactions, their importance as pest biocontrol agents, and their vulnerability to the eradication of their prey. Therefore, an invitation to reflect is made to develop strategies for increasing studies on bats' trophic ecology in México.

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Baird's Tapir (*Tapirus bairdii*) avoid human settlements and roads while searching for water in community-owned forests from the Calakmul region

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Baird's tapir (*Tapirus bairdii*) populations are declining because of deforestation, fragmentation, poaching, and vehicle collisions. Tapirs play an ecological role as seed dispersers and seed predators; therefore, their loss will impact plant communities. This species prefers large areas with continuous native forest where human pressure is low and with permanent water bodies. In the Calakmul region of Southern Mexico, there are no permanent water bodies, only seasonal ponds called locally "aguadas". These ponds have been crucial for tapir survival. Communal lands of the Calakmul region are important for tapirs, offering more surface water than the Calakmul Biosphere Reserve. Therefore, the objective of the present work was to determine the habitat features and anthropic factors influencing Baird's tapir use of ponds on communal lands. Our hypothesis was that Baird's tapirs would use seasonal ponds that are farther from roads and human settlements with higher frequency than ponds near roads and human settlements. We set camera-trap stations for 50 days at 36 ponds on three communal lands from September to November 2022. We measured 3 habitat covariates: presence/absence of water, normalized differential vegetation index, and vegetation type. The disturbance covariates were Euclidean distance to roads and human settlements, and the sampling effort as the number of days stations were active. We evaluated the effect of these covariates in a single occupancy model, where we built detection histories in R v. 4. 2. 2 software. We obtained 60 independent records of Baird's tapir at 27 out of the 36 ponds with a sampling effort of 1,599 camera trap nights. For tapir detection, the effort had a positive effect ($\beta = 0.34 \pm 0.19$, $W_i = 0.66$, $p = 0.08$). Distance to roads had the strongest effect (positive) on Baird's tapir occupancy ($\beta = 1.2 \pm 1.27$, $W_i = 0.39$, $p = 0.34$), while Distance to human settlements also had a positive effect ($\beta = 0.49 \pm 0.65$, $W_i = 0.17$, $p = 0.45$). On communal lands from the Calakmul region, tapirs are searching for water sources on ponds far from roads and settlements to avoid potential conflicts with humans. Although tapirs are not hunted, other factors associated with villages and roads might encourage tapirs to avoid these areas. Communal lands have greater water availability in ponds than in the protected area, so therefore we recommend the creation of communal protected areas to preserve the remaining forests outside the reserve. With the arrival of mega-projects like the Maya train, the economic development of the study region will likely increase. For this reason, it's of great importance that wildlife passages remain available and that mega-projects assure the free movement of tapirs to ponds in the Calakmul region.

Las poblaciones de tapir centroamericano (*Tapirus bairdii*) están disminuyendo globalmente por la deforestación, fragmentación, cacería y atropellos. Los taurinos son dispersores y depredadores de varias semillas; por lo tanto, su extinción afectará a las comunidades vegetales. Esta especie prefiere extensiones grandes de bosque nativo, con presión humana baja y cuerpos de agua perennes. En la región de Calakmul en el sur de México no existen cuerpos de agua perennes, y el agua se almacena en depósitos temporales llamados localmente aguadas, estas aguadas son vitales para la supervivencia del tapir. En la región de Calakmul, los ejidos son importantes para los taurinos, pues hay mayor disponibilidad de agua en comparación con la Reserva de la Biosfera de Calakmul. Por lo tanto, el objetivo de este trabajo fue determinar las características del hábitat y los factores antrópicos que influyen en la ocupación del tapir centroamericano en aguadas de ejidos. La hipótesis fue que el tapir centroamericano utiliza aguadas alejadas de caminos y poblados con mayor frecuencia que las aguadas cercanas a caminos y poblados. Colocamos 36 estaciones de fototrampeo por 50 días, una por aguada en tres ejidos en el periodo de septiembre-noviembre de 2022. Medimos 3 covariables del hábitat: presencia/ausencia de agua, índice de vegetación diferencial normalizado y tipo de vegetación y 2 covariables de perturbación: la distancia Euclídea a carreteras y poblados, y el esfuerzo de muestreo como número de días activos de las estaciones. Evaluamos el efecto de estas covariables con modelos de ocupación simples, donde construimos historias de detección en R v. 4. 2. 2. Registramos 60 eventos independientes del tapir en 27 de las 36 aguadas con un esfuerzo de muestreo de 1,599 noches-trampa. El esfuerzo de muestreo tuvo un efecto positivo ($\beta = 0.34 \pm 0.19$, $W_i = 0.66$, $p = 0.08$) en la detección del tapir. La distancia a caminos fue la covariable con mejor ajuste, con un efecto positivo en la ocupación del tapir ($\beta = 1.2 \pm 1.27$, $W_i = 0.39$, $p = 0.34$), seguida por la distancia a los poblados ($\beta = 0.49 \pm 0.65$, $W_i = 0.17$, $p = 0.45$). En los ejidos de la región de Calakmul los taurinos van a aguadas lejos de caminos y poblados con mayor frecuencia que a aguadas cerca de caminos y poblados, sugiriendo que los taurinos pueden estar evitando conflictos potenciales con los humanos. Aunque no son cazados frecuentemente, puede haber otros factores asociados a los pueblos y caminos que hacen que los taurinos eviten ciertas aguadas. Como los ejidos tienen mayor disponibilidad de agua es necesario estimular la creación de reservas comunitarias, para conservar los bosques remanentes. Con los megaproyectos como el tren Maya, el desarrollo económico de la región de Calakmul aumentará. Por ello, es esencial que la fauna silvestre tenga acceso a las aguadas y que no se interrumpa su movimiento en la región de Calakmul.

Keywords: Communal lands; detection; occupancy; ponds; protected areas.

Introduction

In México, tropical rainforests are among the major reservoirs of biodiversity. They once covered 9 % of the country, but over two-thirds have been cleared ([Calderón-Aguilera et al. 2012](#)). In addition, the loss of wildlife species that have an impact on the structure and composition of vegetation is affecting negatively the dynamics of the remaining ecosystem ([Calderón-Aguilera et al. 2012; Trepel et al. 2024](#)).

One of the species whose populations are declining in the tropics ([García et al. 2016](#)) is Baird's tapir (*Tapirus bairdii*), a megaherbivore that feeds on shoots, leaves, and fruits from a wide variety of plants ([Naranjo 2019](#)). Tapirs play an ecological role as seed dispersers and seed predators of many plant species. They are capable of dispersing large seeds over long distances ([O'Farrill et al. 2012; O'Farrill et al. 2013](#)), contributing to the heterogeneity of the ecosystems ([Trepel et al. 2024](#)). Baird's tapirs prefer areas with continuous native forest with different succession stages where the understory is dense and diverse, with low human pressure, and with permanent water bodies ([Naranjo 2019; Schank et al. 2020; Falconi-Briones et al. 2022; Carrillo et al. 2015](#)).

The Calakmul region, an area with significant amount of habitat for tapirs ([Reyna-Hurtado and Tanner 2005](#)), is part of the Maya Forest, the largest expanse of tropical forest in Mesoamerica, with nearly 30,000 km² under protection in southeast México, northern Guatemala, and northern Belize ([Reyna-Hurtado et al. 2022](#)). The Calakmul region has most of its extension covered in karstic soil that absorbs the precipitation underground. The only water available on the surface are ponds called "aguadas"; these are used by many wildlife species, including tapirs and people from local communities, especially during the dry season ([Reyna-Hurtado et al. 2022; Sandoval-Serés et al. 2016](#)). These ponds have been crucial for the survival of Baird's tapirs in this region where water is a limiting factor since they use water bodies to thermoregulate, flee from potential danger, relieve wounds ([Naranjo 2019](#)), and interact with their conspecifics ([Reyna-Hurtado and Arias-Domínguez 2024](#)).

For these reasons, the importance of ponds has been studied in this region, mainly in the Calakmul Biosphere Reserve (CBR), where several studies demonstrate that water availability in ponds influences the abundance and visitation of Baird's tapir ([Carrillo-Reyna et al. 2015; Reyna-Hurtado et al. 2019; Pérez-Cortez et al. 2012](#)); and confirm tapir site fidelity to the ponds ([Reyna-Hurtado and Arias-Domínguez 2024](#)). Outside the CBR, only one study evaluated the importance of ponds for tapirs ([Sandoval-Serés et al. 2016](#)). [Martinez et al. \(2020\)](#) evaluated Baird's tapir use of ponds in the Runaway Creek Nature Reserve in Belize, in response to human disturbance.

These studies highlight the importance that ponds have on Baird's tapir population patterns and behavior. In this context, occupancy modelling is a valuable tool to assess species distribution while accounting for detection probabilities separately from occurrence probabilities, which can

be modelled by covariates ([Doser et al. 2022; MacKenzie et al. 2002](#)).

These models have been used to evaluate the occurrence of Baird's tapirs as a function of environmental and disturbance factors in several regions. Areas like the protected area of La Frailesca in Chiapas ([de la Torre et al. 2018; Rivero et al. 2022](#)), in communal lands from Los Chimalapas, Oaxaca ([Pérez-Irineo and Santos-Moreno 2016](#)), in San Juan-La Selva Biological Corridor, Costa Rica ([Cove et al. 2014](#)) and in the Mesoamerican Biological Corridor in Panama ([Meyer et al. 2020](#)). Occupancy models have also been used to study habitat preferences in mountain tapir (*Tapirus pinchaque*) in the Tabaconas Namballe National Sanctuary in Perú ([Mena et al. 2020](#)), and in lowland tapirs (*Tapirus terrestris*) at Vale Natural Reserve, Brazil ([Ferrengueti et al. 2017](#)).

Despite the existing literature about the abundance and distribution of Baird's tapir in different habitat types, little is known about the habitat features and anthropic factors that might be influencing the use of ponds outside protected areas. This is crucial for tapir conservation due to the habitat and water availability present in communal lands ([Reyna-Hurtado et al. 2019; Carrillo et al. 2019; O'Farrill et al. 2014](#)). Threats like vehicle collisions, retaliatory hunting, and deforestation ([Serrano-Mac-Gregor et al. 2021; Naranjo 2018; Contreras-Moreno et al. 2013](#)) for a specie with a low reproductive rate like Baird's tapir ([Pukazhenthil et al. 2013](#)) are the reasons why its classified as endangered by the International Union for Conservation of Nature (IUCN; [García et al. 2016; Schank et al. 2017; Reyna-Hurtado et al. 2019](#)).

The objective of the present work was to determine the habitat features and anthropic factors influencing Baird's tapir's use of ponds on communal lands. Our hypothesis was that Baird's tapirs would use seasonal ponds that are farther from roads and human settlements with higher frequency than ponds near roads and human settlements.

Materials and methods

Study site. Our survey was carried out in the communal lands of Alvaro Obregón, Conhuas, and Nuevo Becal adjacent to the CBR, a protected area that preserves the largest tropical forest in México ([Reyna-Hurtado and Tanner 2007](#)). These communal lands were created in the 1970's, when a colonization process encouraged by the government brought people from all over the country ([Reyna-Hurtado and Tanner 2007](#)). Today, 114 rural communities contain approximately 25,000 inhabitants ([INE 2000](#)) whose main activities are agriculture, livestock, logging, apiculture, sport hunting services and subsistence hunting ([INE 2000; Reyna-Hurtado and Tanner 2007](#)). The three community areas we studied are some of the largest communities of the region with 58,000 ha (Conhuas), 52,000 ha (Nuevo Becal) and 24,000 ha (Álvaro Obregón) respectively, of relatively well-conserved sub-perennial tropical forest ([Pennington and Sarukhan 2005](#)).

The climate is sub-humid tropical (Aw), mean annual precipitation is around 1100 mm, with 7 months of dry season, from November to May ([Estrada-Medina et al. 2016](#); [INE 2000](#)). The main forest types are medium sub-perennial forest, low sub-perennial flooded forest, low semi-deciduous forest, and secondary forest ([Reyna-Hurtado and Tanner 2005](#); Figure 1).

Camera trap survey. We deployed 36 stations with a single camera trap (Browning Strikeforce BTC-5HDX®) at 36 different ponds for 50 days from September to November 2022 after the main rainy season, when water is available in most of the ponds and other water bodies, so water is not a limiting factor. We placed 10 cameras in Conhuas, 12 in Zoh Laguna (Alvaro Obregón), and 14 in Nuevo Becal. To have spatial independence between records and considering the radius of the home range (4.1 km^2) of a tapir from CBR ([Reyna-Hurtado et al. 2016](#)), camera stations were at least 1 km apart from each other. We set the cameras on trees at 40 or 50 cm above the ground facing north or south to avoid false triggers from sunlight. We programmed the cameras to take 3 consecutive pictures with 1-second delay between shots and to be active 24 hours. At the end of the survey, all photos were collected, classified, and organized to create detection histories, where the independent records were

the detections of a tapir in each camera station during the 10-day interval of each occasion. These detections are represented with 1 and the non-detections with 0 for the creation of detection histories, using the package CamtrapR in R v. 4. 2. 2 software ([Reyna-Hurtado et al. 2019](#)).

Habitat and disturbance covariates. We analyzed the effect of three habitat and two disturbance covariates on Baird's tapir occupancy. The first habitat covariate was the presence of water in the ponds because water is an essential feature for tapirs ([Pérez-Irineo and Santos-Moreno 2016](#); [Falconi-Briones et al. 2022](#)). For the second habitat covariate, we identified the vegetation type present at each camera station, obtained from the land use vegetation map series VII 1:250,000 ([INEGI 2022](#)), given that tapirs show a preference for different vegetation types ([Reyna-Hurtado and Tanner 2005](#); [Falconi-Briones et al. 2022](#)). The third habitat covariate was the normalized differential vegetation index (NDVI) using SENTINEL 2 satellite imagery with 10 m resolution, using the formula $\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})$ in the raster calculator from Qgis v. 3. 3. 1 software ([QGis 2023](#)). We considered the NDVI as a proxy of primary productivity, which is associated with food availability and quality for herbivores ([Mena et al. 2020](#); [Pettorelli et al. 2011](#)).

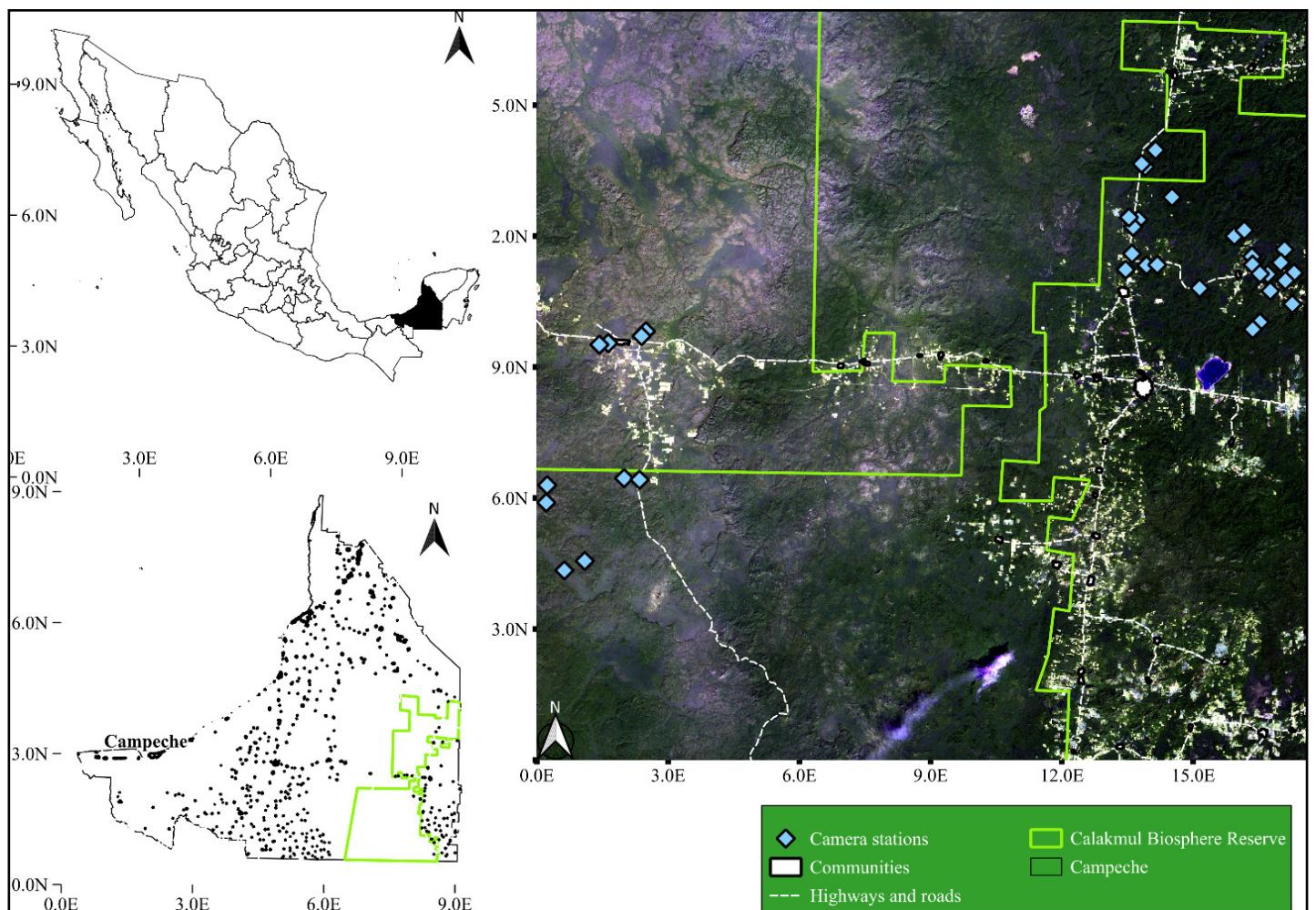


Figure 1. Camera trap survey design in ponds from the communities of Zoh Laguna, Conhuas, and Nuevo Becal, Campeche, México.

The disturbance covariates were the distance to paved highways / paved state roads / unpaved local roads, and distance to the polygon of human settlements (houses, schools, other constructions), both obtained from the shape file "Marco geoestadístico" ([INEGI 2022](#)). Both covariates have had important effects on Baird's tapir and other tapir species at other sites ([Martinez et al. 2020](#); [Mena et al. 2020](#); [Ferreguetti et al. 2017](#); [Cove et al. 2014](#)). We estimated the Euclidean distance from the camera trap station to the nearest road and nearest human settlement using the vector analysis tool "shortest line between objects" in Qgis software ([QGis 2023](#)). Finally, we calculated the sampling effort as the number of days camera traps were active with the package CamtrapR in R software ([Niedballa et al. 2022](#)). Prior previous research in the region suggested that camera traps should be active for at least 45 to 60 days in tropical forests to obtain records for occupancy modelling of ungulate species, so we wanted to evaluate if the effort influenced tapir's detectability ([de la Torre et al. 2018](#); [Martínez Martínez 2023](#)).

Occupancy modelling. To determine the occupancy and detection probabilities of Baird's tapir we constructed detection histories, separating the 50 days of sampling into 5 periods of 10 days each, considering that tapirs take 10 to 12 days to traverse their home range ([Jordan 2015](#); [de la Torre et al. 2018](#)). Then we standardized the numeric covariates to a z-distribution ([MacKenzie et al. 2006](#)) and tested for autocorrelation using the variance inflation factor (VIF), where we excluded variables with a VIF ≥ 3 , a threshold used to minimize collinearity ([Mena et al. 2020](#); [Zuur et al. 2010](#)).

Afterwards, we used a single season occupancy model, where we first built a null model, maintaining occupancy and detection constant, then a global model, which included all covariates to test the goodness of fit, and evaluated whether our data had a good fit to the less-complex models ([MacKenzie and Bailey 2004](#)). We calculated the value of the overdispersion factor (), which determined whether data had under-dispersion (< 1), good fit ($= 1$), or over-dispersion (> 1), with 10,000 bootstrap replications. If models presented over-dispersion, we used the Quasi-Akaike Criterion information (QAIC); otherwise, we used the conventional AIC ([MacKenzie and Bailey 2004](#)).

Subsequently, we evaluated effort as a covariate of detection probability, maintaining occupancy constant, and then we ranked it with the null model to test whether the sampling effort had a significant effect on detection probability. We ranked our models based on ΔAIC , where models with a $\Delta\text{AIC} < 2$ were considered the best ([Burnham and Anderson 2002](#)). To determine whether the covariates from the best models had a significant effect on detection and occupancy, we considered the summed Akaike weights ($W_{\text{all}} > 50\%$) of the models and the p-value ($p \leq 0.05$) ([Mena et al. 2020](#); [de la Torre et al. 2018](#); [Martinez et al. 2020](#)). After determining whether the effort was an important covariate in the detection probability of Baird's tapir, we built five occupancy models using a single covariate in each model,

and then we ranked them and tested their importance for occupancy following the steps described previously. All the occupancy models used the unmarked function in R software v. 4.2.2 ([Fiske and Chandler 2011](#)).

Results

We registered 60 independent records of Baird's tapir at 27 out of 36 ponds with a sampling effort of 1,599 camera trap nights. For occupancy modelling, the global model showed a good fit to the data ($\lambda = 0.88$, $X^2 = 25.3$, $p = 0.64$).

For Baird's tapir detection, the effort had a positive effect ($\beta = 0.34 \pm 0.19$, $W_i = 0.66$, $p = 0.08$; Figure 2) with a mean detection probability of 0.42 ± 0.05 , so we included this covariate for the next analyses (Table 1). We fitted six candidate occupancy models for Baird's tapir records, including the null model (Table 1), where three models tested, including the null model, had a $\Delta\text{AIC} \leq 2$, meaning they were moderately supported ($W_{\text{all}} = 0.72$). Distance to roads was the best-supported covariate, which had a positive effect on Baird's tapir occupancy ($\beta = 1.2 \pm 1.27$, $W_i = 0.39$, $p = 0.34$; Figure 3). The mean distance of ponds to the different roads was 2.2 km, with a minimum distance to roads of 41 m and a maximum distance of 9.7 km. Distance to human settlements was the second-best ranked model with a positive effect ($\beta = 0.49 \pm 0.65$, $W_i = 0.17$, $p = 0.45$; Figure 4) on tapir occupancy. The mean distance of ponds to human settlements was 6.9 km, while the minimum distance was 653 m, and the maximum distance to human settlements was 24.6 km. Considering both covariates, the mean occupancy probability for Baird's tapir was 0.85 ± 0.11 .

Discussion

Our findings supported our hypothesis that in communal lands from the Calakmul region, Baird's tapirs are using ponds far from roads and human settlements with higher frequency than ponds close to roads and human settlements. This contrasts with what was reported in Belize, where tapirs used ponds near roads ([Martinez et al. 2020](#)). However, those roads in Belize were unpaved and with only light vehicle traffic. Paved roads unlike paved with heavy vehicle traffic that are dangerous for tapirs ([Poot and Clevenger 2018](#); [Contreras Moreno et al. 2013](#)). Additionally, roads facilitate access to humans for hunting, logging, or other activities that may pose a threat to tapirs and other animals ([Clements et al. 2014](#)).

In a protected area in Peru, mountain tapirs use habitat away from roads to avoid potential threats like hunting ([Mena et al. 2020](#)). In a protected area in Brazil, lowland tapirs avoided areas with high poaching pressure and near roads ([Ferreguetti et al. 2017](#)). In southeast Asia, the Malayan tapir (*Tapirus indicus*) is affected by roads that cut their preferred habitat and where poaching is a potential threat ([Clements et al. 2014](#)).

As documented in several studies, all tapir species might be affected by roads due to their conditions and traffic, or when they are combined with other potential threats. In

Table 1. Occupancy models selected according to AIC for Baird's tapir.

Common name	Species	Detection Model	k	AIC	ΔAIC	W_i	W_{all}
		p(Effort) $\Psi(.)$	3	225.26	0	0.66	0.66
		p(.) $\Psi(.)$	2	226.61	1.35	0.34	1
		Occupancy Model	k	AIC	ΔAIC	W_i	W_{all}
Baird's tapir	<i>Tapirus bairdii</i>	p(Effort) Ψ (DR)	4	224.83	0	0.39	0.39
		p(Effort) Ψ (DL)	4	226.50	1.67	0.17	0.56
		p(.) $\Psi(.)$	2	226.61	1.79	0.16	0.72
		p(Effort) Ψ (Water)	4	226.86	2.03	0.14	0.86
		p(Effort) Ψ (NDVI)	4	227.18	2.36	0.12	0.98
		p(Effort) Ψ (Veg)	7	230.69	5.86	0.02	1

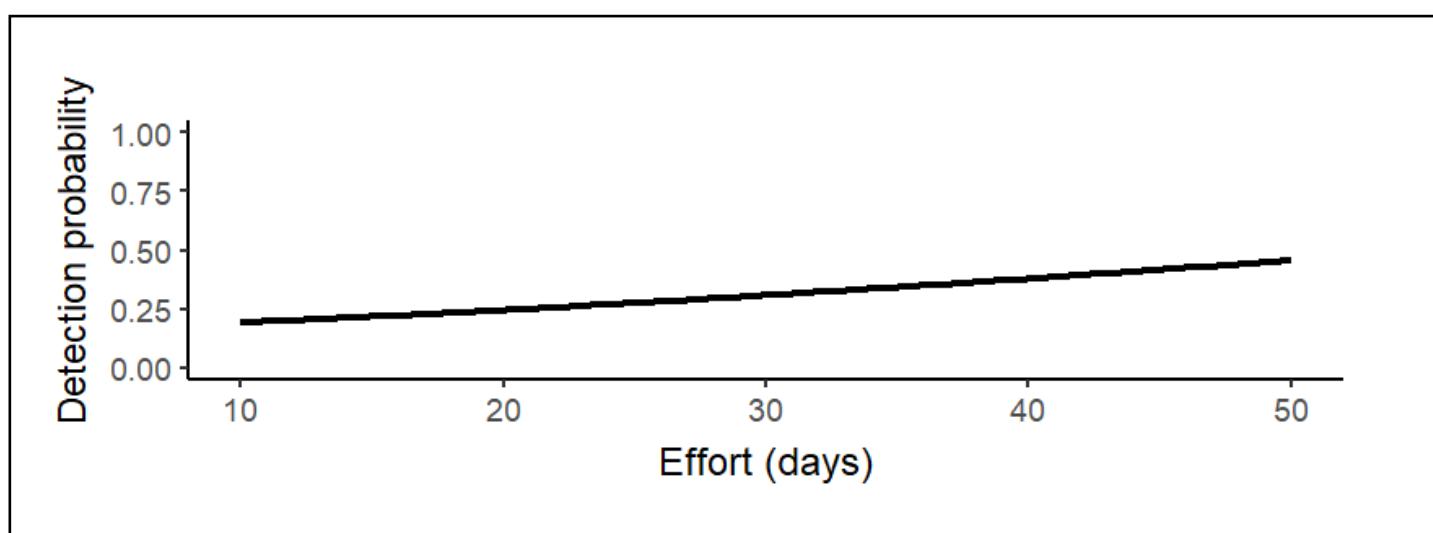
Note: Effort =Number of days cameras were active; DR = Distance to roads; DL = Distance to human settlements; Water =Presence of water in ponds; NDVI =Normalized difference vegetation index; Veg =Vegetation type; k = Number of parameters; AIC = Akaike Criterion Information; ΔAIC = Delta Akaike Criterion Information; W_i = Weighted Akaike Criterion Information; W_{all} = Accumulated weighted Akaike Criterion Information.

the Calakmul region, Baird's tapirs are seldom hunted ([Reyna-Hurtado and Tanner 2005](#)) but there is a growing conflict because of damage to crops and the use of water from apiaries when seeking water by tapirs which may lead people to retaliate against them ([Reyna-Hurtado and Tanner 2005; Pérez-Flores et al. 2021](#)).

In our study site, some ponds were near highway México 186—a paved road with 1,823 vehicles moving daily in the Conhuas portion and 2,710 vehicles daily near Xpujil, according to the Ministry of Communications and Transport ([SCT 2022](#)); other ponds were near the state road CAM 269 where there are no records of the number of vehicles transiting, but the communities use this road to reach Xpujil, the main town in this area. The other paved road is the one to the archaeological site of Calakmul, with less traffic, used mainly by local people and tourists. The rest of the ponds were near local unpaved roads inside the communi-

ties, used only by local people. These roads have different conditions (paved and unpaved) and transit levels, but we did not have sufficient data to evaluate the impact of the different road types.

The distance to human settlements was the other covariate that best explained tapir occupancy. [Martinez et al. \(2020\)](#) also found in Belize that tapirs avoided ponds near villages. This avoidance of human settlements was also reported in Costa Rica in the Cordillera de Talamanca ([Tobler 2002](#)) and in San Juan - La Selva Biological Corridor ([Cove et al. 2014](#)). Although tapirs are not hunted in these sites either, other factors associated with villages-like dogs, deforestation, and hunting in the past--make the tapirs avoid these areas ([Tobler 2002; Zapata-Ríos and Branch 2016](#)). But, in specific conditions, tapirs may tolerate human presence to a certain degree. We observed a group of 3 tapirs in a pond (km 17) adjacent to the road

**Figure 2.** Effect of sampling effort (number of days camera traps were active) on Baird's tapir detection probability in ponds on communal lands.

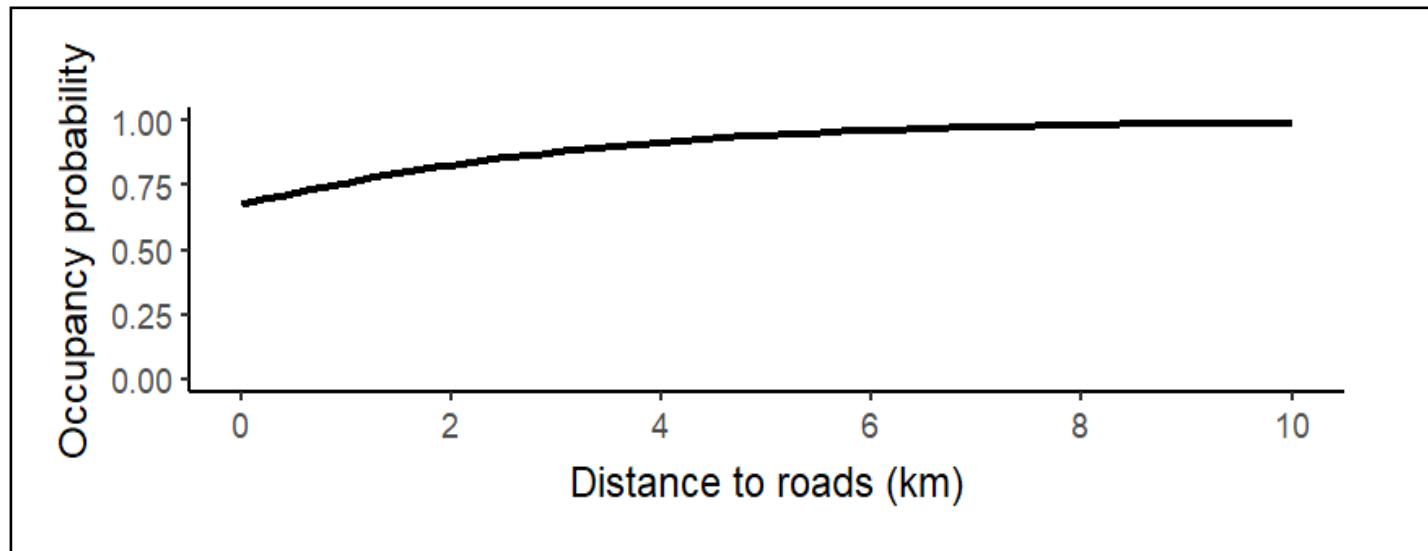


Figure 3. Effect of distance to roads (km) on occupancy probability of Baird's tapir in ponds on communal lands.

to the archaeological site in Calakmul in the months of drought, when water is scarce in the reserve. But when the rainy season comes and water is available in the landscape, they move away from that pond, to avoid being near roads, as our study suggests (authors pers. obs).

In areas where Baird's tapirs have suitable habitat, they will prefer to avoid contact with humans even if they are not hunted (Tobler 2002; Martinez et al. 2020; de la Torre et al. 2018; Cove et al. 2014); but in sub-optimal habitat conditions, they may tolerate a certain degree of disturbance (Reyna-Hurtado and Tanner 2005; 2007; Carrillo et al. 2019). In some places, tapirs would use towns to obtain water when drought is intense (Pérez-Flores et al. 2021) or to avoid potential predators (Pérez-Flores et al. 2022), although this might be an ecological trap if people from the communities retaliate against tapir because of any damage on crops (Medici et al. 2022).

In the Calakmul region, we find forested patches with suitable habitat for Baird's tapirs in the three communities (Carrillo et al. 2019), especially because they have more ponds than in the CBR (Sánchez-Pinzón et al. 2020), but we also find potential threats like roads and human settlements that may reduce pond use (de la Torre et al. 2018; Cove et al. 2014; Carrillo-Reyna et al. 2015). Nonetheless, communal lands may be valuable for tapir conservation if they can be designated as community-protected areas. For example, in Nuevo Becal, a government program called Areas Voluntarily Designated for Conservation (ADVC for its Spanish initials) allows local farmers to extract timber and use different natural resources (Peña-Azcona et al. 2022). They also have legal hunting permits, which are carried out in Wildlife Conservation Management Units (UMA, by its acronym in Spanish). The UMAs are created and approved by the Ministry of Environment and Natural Resources (SEMARNAT, by its acronym in Spanish) so that specific wildlife populations are hunted with regulations (Gallina-Tessaro et al. 2009). These

government programs improve the preservation of the remaining forests and wildlife populations, while helping residents from the communities to obtain economic benefits from those activities (Peña-Azcona et al. 2022). ADVC and UMAs might be useful tools for wildlife conservation outside federal or state reserves. Also, environmental education from academic institutions about the importance of ponds for tapirs and other wildlife (Martinez et al. 2020) can also encourage the people from the communities to protect the ponds by keeping them clean, avoiding deforesting near the ponds and loud noises so as not to scare away wildlife species.

Six months after our study ended, one of the biggest projects in southeast México began its construction, the Maya train, a project that has increased the intensity of use of both the highway and the state road evaluated near CBR. These changes could affect tapirs and other wildlife species. Since the economic development of the Calakmul region will likely increase in the next few years, the roads will probably get busier and the villages larger, which might represent a major threat to the connectivity of an already fragmented landscape (Carrillo et al. 2019). For this reason, it is of great importance that the wildlife passages that are being built allow the free movement of tapirs and other species in their habitat, so they can cross the railways and roads safely. It is also necessary to have strict surveillance of vehicle speed on the highways with speed cameras and patrols (Poot and Clevenger 2018).

Finally, even with our sample size, we obtained a relatively high detection probability for the time surveyed in comparison to other studies (Martinez et al. 2020; de la Torre et al. 2018). This is probably associated with the study design, since we evaluated ponds that may act as lures for tapirs (Martinez et al. 2020). However, we did not evaluate other habitat resources like refuge, understory cover, and food availability for tapirs in these communal lands, which

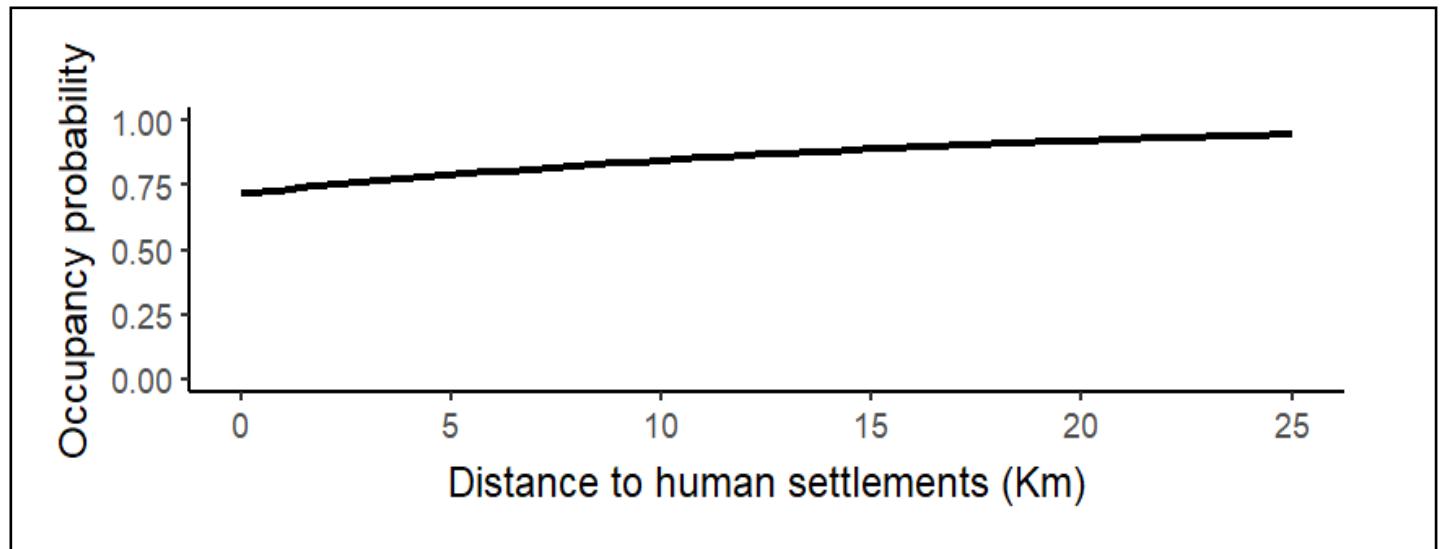


Figure 4. Effect of distance to human settlements (km) on occupancy probability of Baird's tapir in ponds on communal lands.

might affect tapirs' pond use. Therefore, we recommend evaluating other habitat features as well as the impacts of different types of roads, noise, the presence of feral dogs and cattle, and the distance to crops and railways outside the protected area. We also recommend increasing the sample size and effort to monitor ponds and other habitat features in all seasons of the year to reduce the potential bias the design might have on the results.

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Diversity of medium and large mammals in a submontane scrubland

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Studies on mammals are essential due to the rapid changes in land use, habitat fragmentation, and poaching that threaten their survival. Significant changes in the composition of mammal communities due to the elimination or displacement of species have been documented. In the face of accelerated environmental degradation, mammal inventories are vital for understanding the structure and composition of communities and facilitating conservation strategies. In Tamaulipas, mammal studies have focused on protected areas, overlooking ecosystems such as submontane scrublands, which, despite being impacted by human activities, can serve as refuges and biological corridors. Studying these ecosystems is crucial for describing ecological aspects and developing effective conservation and management strategies. Therefore, the objective of this study was to investigate the diversity and richness of medium and large mammals in a submontane scrubland. The study area is located southwest of Casas, Tamaulipas. Ten single camera trap stations were set and remained active from July 2020 to June 2021. Species richness was estimated with Chao 1 and Jackknife 1. Diversity values of orders one and two were estimated, and the species composition and abundance were compared between dry and rainy seasons using PERMANOVA and SIMPER analyses. A total of 457 records of 12 species were obtained, the most abundant being *Odocoileus virginianus*, *Dicotyles tajacu*, and *Leopardus pardalis*. Significant differences in species composition between seasons were detected, with *Dicotyles tajacu*, *Odocoileus virginianus*, *Nasua narica*, and *Leopardus pardalis* accounting for 85.32 % of the differences in species composition between seasons. Although the area is impacted by the introduction of free-grazing cattle, *Leopardus pardalis* is the third-most recorded species and is protected by NOM-059-SEMARNAT-2010. In addition, during the sampling, five of the six Mexican felids were reported and the family Felidae is listed in Appendix II of CITES, so the area should be considered for permanent monitoring to establish conservation strategies.

Los estudios sobre mamíferos son esenciales debido al rápido cambio en el uso del suelo, la fragmentación del hábitat y la caza furtiva que amenazan su supervivencia. Se han documentado cambios significativos en la composición de comunidades de mamíferos debido a la eliminación o desplazamiento de especies. Ante el deterioro ambiental acelerado, los inventarios de mamíferos son vitales para entender la estructura y composición de las comunidades y facilitar estrategias de conservación. En Tamaulipas, los estudios de mamíferos se han centrado en áreas protegidas, dejando de lado ecosistemas como el matorral submontano, que, aunque impactado por actividades humanas, puede servir como refugio y corredor biológico. Estudiar estos ecosistemas es crucial para describir aspectos ecológicos y desarrollar estrategias efectivas de conservación y manejo. Por ello, el objetivo de este estudio fue conocer la diversidad y riqueza de mamíferos medianos y grandes en un matorral submontano. El área de estudio se ubicó al suroeste de Casas, Tamaulipas. Se colocaron 10 estaciones sencillas de cámaras trampa, que permanecieron activas de julio de 2020 a junio de 2021. La riqueza se estimó con Chao 1 y Jackknife 1. Se determinaron los valores de diversidad de orden uno y dos, así mismo, se comparó la composición y abundancias de las especies entre las temporadas de secas y lluvia empleando los análisis de PERMANOVA y SIMPER. Se obtuvieron 457 registros independientes de 12 especies, siendo las más abundantes *Odocoileus virginianus*, *Dicotyles tajacu* y *Leopardus pardalis*. Se detectaron diferencias significativas en la composición de especies entre temporadas abundancias siendo *Dicotyles tajacu*, *Odocoileus virginianus*, *Nasua narica* y *Leopardus pardalis* aportan el 85.32 % de las diferencias en la composición entre temporadas. Aunque el área presenta impacto por la introducción de ganado bovino de libre pastoreo se obtuvo a *Leopardus pardalis* como la tercera especie con más registros y es protegida por la NOM-059-SEMARNAT-2010, además durante el muestreo se reportaron cinco de los seis felinos mexicanos y la familia Felidae se encuentra en el apéndice II del CITES, por lo que el área debería ser tomada en cuenta para monitoreo constante, y establecer estrategias de conservación.

Keywords: Abundance; diversity; dry season; mammals; rainy season; species richness.

Introduction

Biodiversity is an essential component for the balance and health of ecosystems. Mammals play central roles, acting as predators, herbivores, and seed dispersers, to mention a few. In Mexico — one of the most diverse countries worldwide ([Ceballos and Oliva 2005](#)) —, the study of mammals is essential given the rapid change in land use and habitat fragmentation that, together with poaching, threaten their survival ([Aguilar et al. 2000](#)). Significant changes in the composition of mammal communities have been documented around the world, due to the elimination or displacement of species ([Laurance and Yensen 1991](#); [Kirkpatrick and Jarne 2000](#); [Janecka et al. 2014](#)).

Consequently, inventories of mammals should be elaborated because they are essential to acquire comprehensive knowledge, essential for carrying out ecological, conservation, and management studies ([Pacheco et al. 2004](#)). Its importance has grown considerably in the face of the increasing environmental deterioration driven by human population growth and the associated urban, industrial, agricultural, and livestock-raising activities, all of which generate adverse impacts on natural environments ([Chávez and Ceballos 1998](#)). In this context, strategies for the management and conservation of natural resources, particularly flora and fauna, largely depend on the availability of information on biological diversity ([Chávez and Ceballos 1998](#); [Romero and Ceballos 2006](#)). Inventories provide a crucial starting point for understanding changes in the structure and composition of mammal communities in different areas, conserved and disturbed, as well as at different times, facilitating the implementation of conservation and management strategies ([López-Ramírez et al. 2020](#); [Mezhua-Velázquez et al. 2022](#)).

In Tamaulipas, studies on mammals are scarce, and most focus on protected natural areas ([Vargas-Contreras and Hernández-Huerta 2001](#); [Carvajal-Villareal et al. 2012](#); [Carrrera-Treviño et al. 2018](#); [Branney et al. 2023](#); [Ochoa-Espinoza et al. 2023](#)), leaving aside other forest areas that, despite being affected by anthropogenic activities, function as refuges and biological corridors for biodiversity ([López-Ramírez et al. 2020](#)). Such is the case of the submontane scrubland, characteristic of northeastern Mexico, including Tamaulipas. This vegetation type is characterized by a mixture of thorny shrubs, small trees, and perennial herbs ([Rzedowski 2005](#)). It covers 8.3 % of the surface area of Tamaulipas ([INEGI 2017](#)) and undergoes constant changes due to the human activities already mentioned ([Estrada-Castillón et al. 2012](#)), which affect wild mammal populations.

Therefore, studying this ecosystem is essential to describe its ecological aspects, determine the factors that influence their populations, and generate better conservation, management, and use strategies ([Buenrostro-Silva et al. 2017](#); [Salazar-Ortiz et al. 2020](#)). The objective of this study was to evaluate the diversity, structure, and composition of medium and large mammals in a submontane scrubland.

Materials and methods

Study Area. The study area is located southwest of the municipality of Casas, Tamaulipas, Mexico, between coordinates 23° 24' and 23° 21' N, -98° 44' and -98° 38' O, at an altitude of 240 to 420 meters above sea level. ([INEGI 2010](#)). The area is located outside the limits of the western slope of the Sierra de Tamaulipas Biosphere Reserve (Figure 1). The regional climate is semi-warm and semi-dry, with minimum temperatures of 16 °C to 19 °C and maximum temperatures of 34 °C to 36 °C ([INEGI 2021](#)), and a mean annual precipitation of 600 mm to 800 mm. The dominant vegetation type is submontane scrubland ([INEGI 2021](#)).

Sampling design. Ten simple stations (camera traps) were placed with a minimum separation of 3 km and a maximum of 3.5 km from each other. The stations were set on nature trails or close to trails and roads with traces of mammals, such as footprints and feces. Camera traps were installed at 30 cm to 50 cm above the ground and set to capture three photographs at five-second intervals, operating 24 hours a day. They were checked each month to change memory cards and batteries ([Chávez et al. 2013](#); [Maffei et al. 2002](#); [Mattey et al. 2022](#)). The sampling campaign covered 12 months, from July 2020 to June 2021; months were grouped according to climatic seasons (dry and rainy). To determine the dry and rainy seasons, the mean historical precipitation was calculated for the period between 1982 and 2013 based on climatological statistical information available from the national meteorological service of the National Water Commission ([CONAGUA 2010](#)). As a result, the dry season included January, February, March, April, November, and December, while the rainy season spanned from May to October.

Analysis of photographic and taxonomic identification and nomenclature. To determine the independence of the records, the following criteria were considered: a) consecutive photographs of the same species should be separated by 24 h and b) in photographs of gregarious species, each was considered as a separate record ([Monroy-Vilchis et al. 2011](#); [Chávez et al. 2013](#); [Ávila-Nájera et al. 2015](#); [Pozo-Montuy et al. 2019](#)). Individuals were identified based on [Ceballos and Oliva \(2005\)](#) using the nomenclature according to [Ramírez-Pulido et al. \(2014\)](#).

Data analysis. The potential number of species was calculated according to [Moreno \(2001\)](#) and [Magurran \(2004\)](#) by using the non-parametric estimators Chao 1, which uses abundance data, and Jackknife 1, based on species incidence. Estimators were calculated using 100 randomizations with no replacement in the program EstimateS 9.1.0 ([Colwell 2013](#)).

Diversity numbers were calculated using the Hill series of first (q_1) and second (q_2) orders. These were obtained from the exponential of the Shannon-Wiener index: $q_1 = e^h$ (where: q_1 = first-order Hill number, and e^h = Shannon index) and Simpson's reciprocal: $q_2 = 1/D$ (where: q_2 = second-order Hill number and D = Simpson's dominance

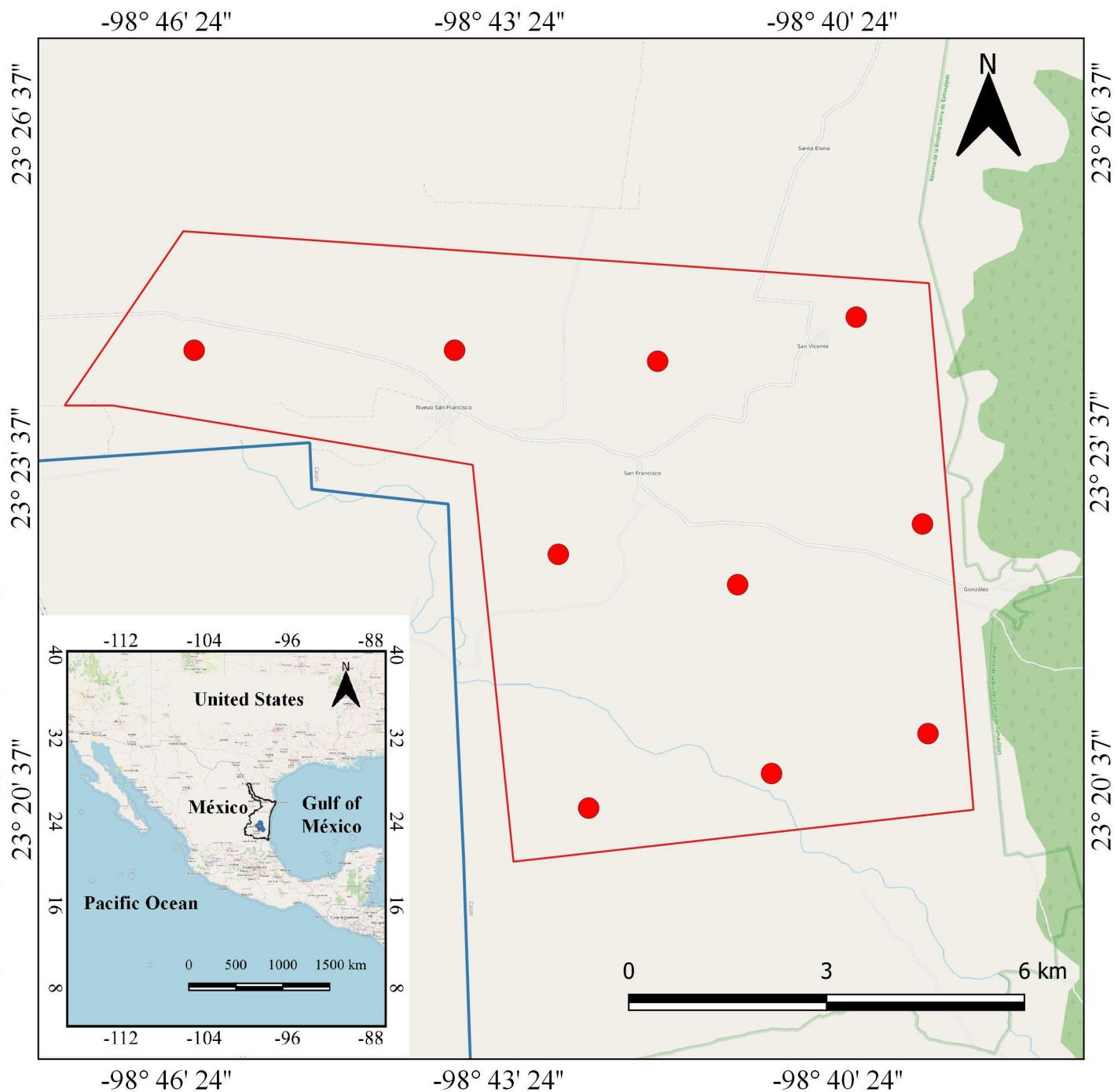


Figure 1. Location of the study area, Casas, Tamaulipas, México.

index); these indicate the number of effective species ([Moreno 2001](#); [Magurran 2004](#); [Magurran 2021](#)).

The species composition of mammal communities and their abundances between seasons were compared with a permutation-based analysis of variance (PERMANOVA); this results in the sum of squares within groups (SS) and the sum of squares within groups (Ss), using the Bray-Curtis index as a measure of distance, with 9999 random permutations ([Anderson 2001](#)). A percentage similarity analysis (SIMPER) was also used to determine which species contributed most to the differences between the seasons ([Clarke 1993](#)).

Results

Species richness. A total of 457 independent records were obtained with a sampling effort of 3,650 trap-days; the mammals recorded belong to three orders, seven families, and 12 species. The order Carnivora presented the highest richness with four families: Canidae, Felidae, Mephitidae, and Procyonidae; of these, Felidae was the best-represented family, with five species (Table 1). The highest species richness was recorded during the rainy season (12 species) vs. the dry season (nine species), while the potential richness for each season was in rainfall from 13.99 (Chao 1) to 16.17

Table 1. Taxonomic list of the records of medium and large mammals in the study area and dry and rainy season, in the municipality of Casas, Tamaulipas.

Order, Family, and Species	Records			NOM-059	
	Dry	Rainy	Area		
DIDELPHIMORPHIA					
DIDELPHIDAE					
<i>Didelphis marsupialis</i>	5	1	6	-	
CARNIVORA					
FELIDAE					
<i>Herpailurus yagouaroundi</i>	-	1	1	A	
<i>Leopardus pardalis</i>	40	18	58	P	
<i>Lynx rufus</i>	6	4	10	-	
<i>Puma concolor</i>	1	2	3	-	
<i>Panthera onca</i>	-	1	1	P	
CANIDAE					
<i>Canis latrans</i>	17	10	27	-	
MEPHITIDAE					
<i>Conepatus leuconotus</i>	2	3	5	-	
PROCYONIDAE					
<i>Nasua narica</i>	25	12	37	-	
<i>Procyon lotor</i>	-	1	1	-	
ARTIODACTYLA					
TAYASSUIDAE					
<i>Dicotyles tajacu</i>	17	86	103	-	
CERVIDAE					
<i>Odocoileus virginianus</i>	118	87	205	-	

(Jackknife 1) and for the dry season from 10.06 to 11.50. Thus, the observed richness relative to the potential richness ranged from 74.21 % to 97.95 % in the rainy season and from 78.26 % to 89.46 % in the dry season (Figure 2).

Records and diversity. The mammal species with the highest number of records were *Odocoileus virginianus*

(white-tailed deer) with 205 records (44.86 %), followed by *Dicotyles tajacu* (collared peccary) with 103 (22.5 %) and *Leopardus pardalis* (ocelot) with 58 (12.7 %) (Figure 3). On the other hand, the species with a single record were *Herpailurus yagouaroundi*, *Panthera onca*, and *Procyon lotor* (Table 1).

For the study area, we estimated $q_1 = 4.908$ abundant species and $q_2 = 3.584$ dominant species that contribute to diversity. The highest number of effective species was observed in the dry season, with 4.468 (Table 2).

The PERMANOVA determined significant differences between the seasons [$SS = 1.331$; $Ss = 0.9798$; $F = 3.586$; $p < 0.019$] (Table 3). The SIMPER analysis indicated that the species that determine the main differences between seasons are *D. tajacu* (34.87 %), *O. virginianus* (28.36 %), *N. narica* (11.26 %), and *L. pardalis* (10.84 %), accounting for 85.32 % of the differences between the seasons. Specifically, *O. virginianus* and *D. tajacu* showed the highest mean abundance per season, with 14.5 and 14.3 in the rainy seasons, while *O. virginianus* (19.7), *L. pardalis* (6.67), and *N. narica* (4.17) showed the highest mean abundance in the dry season; Table 4).

Discussion

The present study reports approximately 8 % of the wild mammal species known for the state of Tamaulipas (152 species) and 24.5 % of the medium and large species (49 species; [Ceballos and Oliva 2005](#); [Moreno 2024](#)). Compared with the study by [Branney et al. \(2023\)](#), which recorded 15 species of the Order Carnivora in the Sierra de Tamaulipas Biosphere Reserve (RBST), an adjacent area, the present study reports nine species of this order despite the impact of livestock ranching. This variation can be attributed to the number of sampling stations, as more camera traps were used in the RBST and a larger area was covered. The pres-

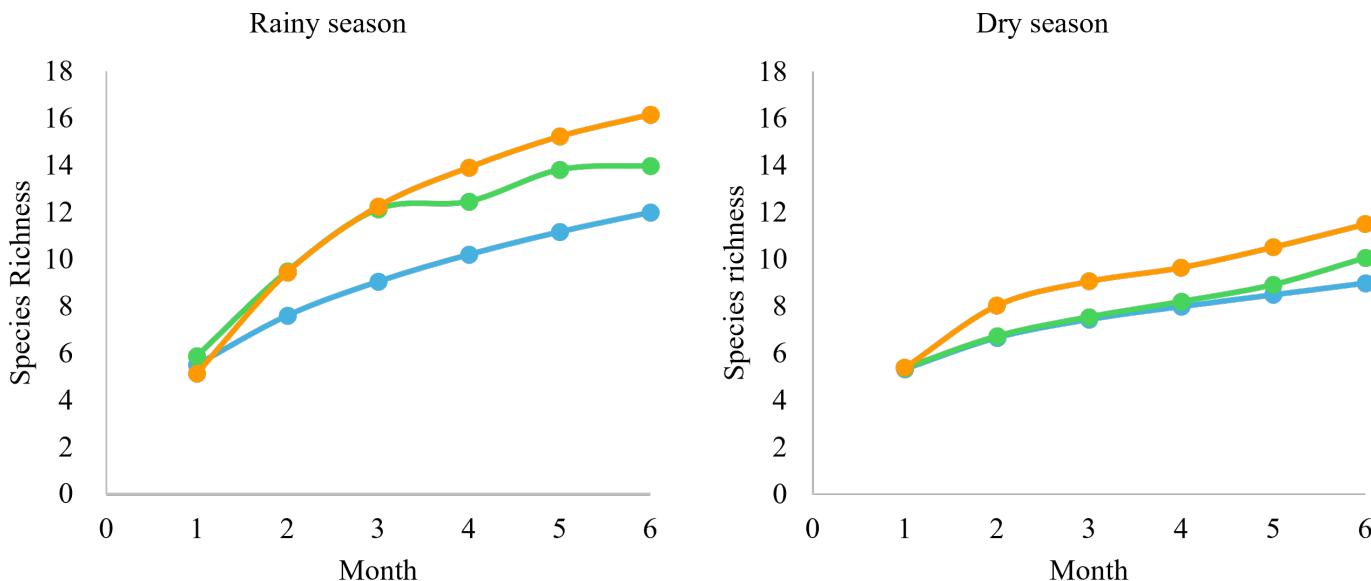


Figure 2. Species accumulation curves during seasons. Light blue = observed species; Green = Chao 1; Orange = Jack 1.

Table 2. Diversity indices by dry and rainy season, in the municipality. Houses, Tamaulipas.

Diversity	Dry	Rainy	Study Area
Richness	9	12	12
Abundance	231	226	457
Effective species			
$e^H(q_1)$	4.544	4.468	4.908
$1/D(q_2)$	3.177	3.280	3.584

Hill Series q_1 = abundant species; q_2 dominant species.

ence of *Sylvilagus* sp. Is worth noting, detected by direct observation, although it was not included in the study because it was not recorded in the sampling stations. The high species richness in the study area may be associated with the vegetation type and food availability ([SEMARNAT 2018](#); [Pozo-Montuy et al. 2019](#)). Diverse habitats, such as submontane scrubland, provide a wide range of resources and microhabitats that offer shelter and suitable feeding areas ([Alanís-Rodríguez et al. 2015](#)).

This study reports five of the six Mexican felines. This finding could indicate that the ecosystem has fragments of vegetation with a good degree of conservation ([Aranda et al. 2012](#); [Hernández-Pérez et al. 2024](#)). According to [Ceballos and Olivia \(2005\)](#), [Aranda et al. \(2012\)](#), [Velazco and Macías and Peña-Mondragón \(2015\)](#), the feline species identified in the area thrive preferentially in arid, xeric (submontane), and subtropical scrublands. These areas, covered by dense vegetation, provide an ideal habitat for these taxa ([Buenrostro-Silva et al. 2015](#)), as they provide them with shelter and camouflage, contributing to their successful hunting.

The submontane scrubland is of great importance because it is home to medium and large mammal species with a high cultural and ecosystem value ([Cortes-Marcial and Briones-Salas 2014](#)). Among these species, there are six with declining populations (*H. yagouaroundi*, *L. pardalis*, *P. concolor*, *P. onca*, *C. leuconotus*, *N. narica*), four with stable populations (*D. marsupialis*, *L. rufus*, *D. tajacu*, and *O. virginianus*), and two with growing populations (*C. latrans* and *P. lotor*; [IUCN 2023](#)). In addition, 11 of these species are classified as Least Concern (LC) and only *P. onca* is listed as Near Threatened (NT) by the [IUCN \(2023\)](#); three of these species are protected by NOM-059-SEMARNAT-2010 ([SEMARNAT 2010](#)). Likewise, *H. yagouaroundi*, *L. pardalis*, and *P. onca* are included in Appendix I of CITES, while *L. rufus* and *P. concolor* are in Appendix II ([CITES 2023](#)).

In both seasons, a similar diversity (orders 1 and 2) was recorded in the mammal communities, with uniform values in terms of the abundant and dominant species in the site. This is consistent with the study conducted by [Ríos-Solís et al. \(2021\)](#) in El Gavilán, Oaxaca, an area covered by tropical dry forest with dense vegetation in some period of the year, similar to some elements of the submontane scrubland. These ecosystems are suitable for the diversity of medium and large mammals.

On the other hand, the mountain cloud forest (BMM, in Spanish) of Tamaulipas shows a higher diversity during the dry season, similar to the submontane scrubland. In the submontane scrubland, diversity values also show a greater presence of abundant and dominant species during the dry season, with a minimal variation between seasons.

It is important to note that the BMM is located in the El Cielo Biosphere Reserve, which could be stabilizing the diversity levels, i.e., it fosters a stable structure and composition of mammals over time, since, being a protected natural area, activities such as hunting are prohibited. In contrast, the submontane scrubland, which lacks this type of protection, shows a constant diversity between the rainy and dry seasons. This suggests an ecosystem that maintains a greater resilience in the face of temporal variations ([De Mazancourt et al. 2013](#); [Loreau and De Mazancourt 2013](#)).

The distribution of mammal abundance varies between seasons. During the dry season, the species with the highest number of records were *O. virginianus*, *L. pardalis*, and *N. narica*; during the rainy season, the abundant species were *O. virginianus*, *D. tajacu*, and *L. pardalis*. To note, *O. virginianus*, *D. tajacu*, and *L. pardalis* maintain reproductive populations, since they were recorded with offspring.

Of the recorded species, *O. virginianus* was very abundant obtained in both seasons, likely due to its high plasticity to different environments. These generalist herbivores thrive in various types of vegetation and, according to several authors ([Ceballos and Oliva 2005](#); [Weber 2014](#); [Gallina and López 2016](#); [Jiménez-Sánchez et al. 2024](#)), are common in arid and scrub areas. In addition, their diet usually includes plants from the families Fabaceae and Asteraceae ([Navarro-Cardona et al. 2018](#)), which are abundant in submontane scrubland areas ([Rzedowski 2005](#)). However, a trend of declining abundance of *O. virginianus* was observed during the rainy season, while the abundance of *D. tajacu* increased. This suggests a more intense competition for food in the rainy season, forcing *O. virginianus* to travel greater distances in search of food ([Sánchez-Pinzón and Arias 2022](#)).

Like *O. virginianus*, *D. tajacu* is adapted to a wide variety of ecosystems ([Zaldivar et al. 2022](#)). In the present study, its abundance was higher during the rainy season. This finding is consistent with the observations reported by [Reyna-Hurtado et al. \(2014\)](#) and [Sánchez-Pinzón et al. \(2020\)](#), who highlighted that water availability is essential for the presence of this species and also influences the rolling behavior for grooming, to regulate temperature, or to eliminate ecto-

Table 3. PERMANOVA, comparisons of the structure of medium and large mammal communities between seasons in the municipality of Casas, Tamaulipas.

Season	Rainy	Dry
Rainy	-	0.0116*
Dry	3.586	-

Upper diagonal = p -values, lower diagonal = F -values. * = significant values.

*Odocoileus virginianus**Dicotyles tajacu**Leopardus pardalis**Lynx rufus**Panthera onca**Nasua narica***Figure 3.** Mammals recorded in the southwest of the municipality of Casas, Tamaulipas, México.

parasites ([García-Marmolejo et al. 2015](#); [Sánchez-Pinzón et al. 2020](#)).

The fact that *L. pardalis* was the feline with the highest number of records may indicate that it is the top predator in the study area, and its presence may lead to the "pardalis effect". In other words, the presence of the ocelot influences the dynamics of the populations of its prey and other predators, affecting the structure and composition of the ecological community ([Silva-Magaña and Santos-Moreno 2020](#)). This may explain the low number of records of *P. onca*, *P. concolor*, *Lynx rufus*, and *H. yagouaroundi*, so they may be occasional visitors. Likewise, *H. yagouaroundi* is a cryptic and rare species, so it is difficult to detect it ([Gordano 2015](#)), and its presence is influenced by the pardalis

effect ([De Olivera et al. 2010](#); [Caso et al. 2015](#)).

Compared to other studies, ocelot records were more frequent in the present study. For example, in the El Cielo Biosphere Reserve in Tamaulipas, 40 records were documented over a 24-month period ([Ochoa-Espinoza et al. 2023](#)); in the northeastern Sierra de Puebla, 33 records were captured over 21 months ([Ordoñez-Pardo et al. 2023](#)); in Tequila, Veracruz, a single record was recorded in eight months ([Salazar-Ortiz et al. 2020](#)); and in the Lagunas de Chacahua National Park, Oaxaca, four records were captured during 12 months ([Buenrostro-Silva et al. 2015](#)). These differences can be attributed to variables such as the vegetation type, degree of human activities, or presence of big cats, in contrast with the area studied in the present

Table 4. Analysis SIMPER: determines the percentage of contribution of mammal species between seasons (rainy and dry) in the municipality of Casas, Tamaulipas.

Species	% Contrib.	% Accum.	Prom. A. Rainy	Prom. A. Dry
<i>Dicotyles tajacu</i>	34.870	34.87	14.300	2.830
<i>Odocoileus virginianus</i>	28.360	63.23	14.500	19.700
<i>Nasua narica</i>	11.260	74.49	2	4.170
<i>Leopardus pardalis</i>	10.840	85.32	3	6.670
<i>Canis latrans</i>	5.770	91.09	1.670	2.830
<i>Didelphis marsupialis</i>	2.575	93.67	0.167	0.833
<i>Lynx rufus</i>	2.177	95.85	0.667	1
<i>Conepatus leuconotus</i>	1.779	97.62	0.5	0.333
<i>Puma concolor</i>	1.03	98.65	0.333	0.167
<i>Procyon lotor</i>	0.566	99.22	0.167	0
<i>Herpailurus yagouaroundi</i>	0.408	99.63	0.167	0
<i>Panthera onca</i>	0.370	100	0.167	0

It indicates % Contrib. = percentage of total contribution per species; % Acum. = cumulative percentage of species; Prom. A. rainfall and dry = Average abundance of species in the seasons.

work, which is covered by a dense submontane scrubland vegetation ([Rzedowski 2005](#)), which favors the presence of *L. pardalis* ([Ceballos and Oliva 2005](#); [Aranda et al. 2012](#); [Galindo-Aguilar et al. 2019](#)). In addition, the study was carried out during the COVID-19 pandemic during which human activities were limited, a circumstance that may have also favored the presence of this feline.

[Ramírez-Bravo et al. \(2010\)](#) and [Galindo-Aguilar et al. \(2019\)](#) point out that the ocelot tolerates fragmented environments that are usually close to mountainous areas within protected areas. Such is the case of this study, which was carried out in an area adjacent to the Sierra de Tamaulipas Biosphere Reserve. In addition, habitat modification and fragmentation are detrimental to feline populations, with ocelots being most affected by the decline in vegetation cover ([Hernández-Pérez et al. 2024](#)).

It should be mentioned that the study area is being affected by the introduction of free-range cattle. The abundance of *Leopardus pardalis* in this area indicates that there are still vegetation remnants or fragments that are suitable for the subsistence of species with a high ecosystem value. Therefore, the area should be considered for monitoring, and federal and state authorities should establish conservation strategies.

The record of a raccoon was interesting because this species thrives in a wide variety of environments associated with permanent water bodies ([Guerrero et al. 2000](#); [Timm et al. 2016](#)). One of the reasons of this distribution is that, as raccoons lack salivary glands, they need to moisten the food to ingest it ([Ceballos and Oliva 2005](#)). In the study area, water bodies are temporary from April to September, so this habitat is not suitable for the species.

Additional research and inventories on mammals should be conducted, especially in unprotected areas, to gain a more complete understanding of mammal diversity and their conservation status. This may contribute to iden-

tify priority areas and develop effective strategies for species conservation.

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Mapping core habitats, landscape permeability, and movement corridors for conservation of desert bighorn sheep in Sonora, México

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The desert bighorn (*Ovis canadensis mexicana*) is under Special Protection in México, but populations in Sonora have declined compared to historical levels and are increasingly isolated despite the high economic and ecological value of species. Consequently, we assessed landscape permeability for desert bighorn in Sonora, using data from 39 GPS/satellite-collared individuals. We modeled connectivity and least-cost corridors among 95 % aKDE core areas using Circuitscape and Linkage Mapper software from habitat association maps developed using maximum entropy modelling. We identified a network of 83 potential corridors connecting 43 core areas; corridors ranged from <1 to 165 km in length. We found two distinct areas in desert bighorn range in Sonora: a southern area characterized by high connectivity with shorter corridors of lesser resistance to movements, and a northern area characterized by much lower connectivity with longer corridors of greater resistance; connectivity between these two areas was limited. These results illustrate the isolated distribution of many populations of desert bighorn and the limited connectivity between populations in northern and southern Sonora. Our connectivity maps provide a background for targeting management actions aimed at facilitating the movement and expansion of desert bighorn populations in Sonora. Consequently, they can guide conservation efforts that identify and promote preservation of key patches or corridors; facilitate habitat restorations within and around corridors; and enhance connectivity and thus viability of populations throughout Sonora.

El borrego cimarrón del desierto (*Ovis canadensis mexicana*) se encuentra bajo Protección Especial en México, pero las poblaciones en Sonora han disminuido en comparación con los niveles históricos y están cada vez más aisladas a pesar del alto valor económico y ecológico de las especies. En consecuencia, evaluamos la permeabilidad del paisaje para el borrego cimarrón del desierto en Sonora, utilizando datos de 39 individuos con collares GPS/satélite. Modelamos la conectividad y los corredores de menor costo entre las áreas núcleo con 95 % de aKDE utilizando el software Circuitscape y Linkage Mapper a partir de mapas de asociación de hábitat desarrollados utilizando modelos de máxima entropía. Identificamos una red de 83 corredores potenciales que conectan 43 áreas núcleo; los corredores variaron de <1 a 165 km de longitud. Encontramos dos áreas distintas en el rango del borrego cimarrón del desierto en Sonora: un área sur caracterizada por una alta conectividad con corredores más cortos de menor resistencia a los movimientos, y un área norte caracterizada por una conectividad mucho menor con corredores más largos de mayor resistencia; la conectividad entre estas dos áreas fue limitada. Estos resultados ilustran la distribución aislada de muchas poblaciones de borrego cimarrón del desierto y la conectividad limitada entre las poblaciones del norte y sur de Sonora. Nuestros mapas de conectividad proporcionan una base para orientar las acciones de gestión destinadas a facilitar el movimiento y la expansión de las poblaciones de borrego cimarrón del desierto en Sonora. En consecuencia, pueden orientar los esfuerzos de conservación que identifican y promueven la preservación de parches o corredores clave; facilitan la restauración del hábitat dentro y alrededor de los corredores; y mejoran la conectividad y, por lo tanto, la viabilidad de las poblaciones en todo Sonora.

Keywords: Biological corridors; connectivity; circuit theory; desert bighorn; least-cost path; Sonora.

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Introduction

Bighorn sheep (*Ovis canadensis mexicana*) historically occupied three main areas of México: 1) Vizcaíno Desert and Mechudo mountains on the Baja California peninsula 2) from northern Sonora to northern Baja California, and 3) from northern Chihuahua to northern Coahuila ([Ceballos and Oliva 2005](#); [Medellín et al. 2005](#); [Romero-Figueroa et al. 2024](#)). However, anthropogenic impacts such as unregulated hunting, habitat loss and modification, overgrazing by livestock, diseases from domestic animals, and loss of water sources have resulted in the extirpation of some local populations, while the remaining populations are highly fragmented and have low population sizes ([Sandoval 1985](#); [Smith and Krausman 1988](#); [Ceballos and Oliva 2005](#); [Romero-Figueroa et al. 2024](#)). Currently, the populations in Sonora and the Baja California peninsula are considered stable ([Lee 2003](#); [Romero-Figueroa et al. 2024](#)), while other populations are maintained under semi-captivity in the states of Chihuahua and Coahuila ([Sánchez 2005](#); [Uranga and Valdez 2011](#)). However, due to the increased extinction risks from population fragmentation caused by human activities, which impacts demographic stability through deterministic and stochastic effects, bighorn sheep are under Special Protection in México (NOM-059-SEMAR-NAT-2010; [DOF 2010](#)).

Like other large herbivores, bighorn sheep are more vulnerable to population collapse and face a higher risk of extinction than smaller-bodied species ([Bowyer et al. 2019](#)). Local populations of bighorn face many potential threats to their persistence associated with habitat modifications (*i.e.*, urbanization, highway development, and agricultural development) ([Monson and Sumner 1980](#); [Smith and Krausman 1988](#)). In particular, land use changes can fragment previously contiguous habitats, resulting in smaller suitable patches scattered throughout the landscape ([Lindermayer 2019](#)). Fragmentation into smaller habitat patches occupied by small remnant populations increases extirpation risks because of demographic issues and vulnerability to stochastic environmental effects, both of which increase likelihood of local extinction and inbreeding ([Bleich et al. 1996](#); [McCullough 1996](#)).

Increasing human impacts and resultant habitat fragmentation makes conservation and recovery of desert bighorn (*Ovis canadensis mexicana*) in Sonora challenging. Maintaining habitat connectivity is an important strategy for mitigating the detrimental effects of fragmentation on populations ([Anděl et al. 2010](#)); hence, there is growing recognition of the need to prioritize management of habitat patches and corridors at the landscape level in México, driven particularly by concern for endangered species (*e.g.*, [Ceballos et al. 2021](#); [González-Saucedo et al. 2021](#); [Balbuena-Serrano et al. 2022](#); [Torres-Romero et al. 2023](#)). Such concerns similarly apply to large herbivores that occur in small isolated populations or metapopulations ([McCullough 1996](#)). Identifying potential movement corridors for bighorn may be particularly important in arid

environments such as Sonora, where populations lack large contiguous habitats as in more northern temperate environments. Instead, desert bighorn are naturally isolated in smaller habitat patches associated with isolated mountain ranges or other rocky habitats ([Bleich et al. 1990](#); [Bleich et al. 1996](#)).

Connectivity among habitat patches is dependent on landscape attributes that facilitate or impede movement between patches ([Taylor et al. 1993](#)). Higher-quality habitats with suitable landscape connectivity can increase the likelihood of species persistence and population viability in response to landscape alterations ([Vasudev et al. 2015](#)). Individuals move more readily through suitable habitats during dispersal or exploratory movements; in contrast, a landscape with less suitable habitat decreases the connectivity among patches ([Keeley et al. 2017](#)). Identifying core habitats with high permeability of movements between these areas (*i.e.*, existence of suitable connectivity corridors) would therefore enhance conservation of bighorn in México, including identifying areas suitable for population expansion and restorations, which is a current focus of desert bighorn management in Sonora and throughout México.

Because desert bighorn are highly valued for their ecological ([Monson and Sumner 1980](#)) and economic contributions ([Lee 2011](#)), comprehensive and adaptive conservation strategies driven by reliable information that address the needs and interests of managers and other stakeholders are needed in Mexico ([Ortega-Arqueta et al. 2016](#)). To address this need for the fragmented populations of desert bighorn in Sonora, our goal was to define locally, individually-based habitat associations of desert bighorn, and use these to model connectivity of the Sonoran landscape for desert bighorn. Our specific objectives included: 1) identify core habitats of extant desert bighorn populations, 2) Construct a habitat likelihood map for desert bighorn to evaluate landscape permeability, and 3) Model functional connectivity and corridors that could facilitate movements of desert bighorn among populations in Sonora.

Materials and methods

Study area. The region is characterized by the Sonora Mountains, which comprise four distinct physiographic provinces: Sierra Madre Occidental, Sierras and Paralelos Valleys at its center, desert, and coastal areas along the Gulf of California (Figure 1). The climate is dry and temperate; precipitation averages 450 mm annually, with most occurring in July (≥ 86 mm) and the least in May (≤ 3.2 mm; [INEGI 2010](#)). Elevations range from 0 to 2,625 m. General vegetation includes primarily grassland and rosetophyllous scrub ([INEGI 2017](#)).

Desert bighorn are primarily found in northwest Sonora, adjacent to the Gulf of California, including six municipalities: Hermosillo, Pitiquito, Caborca, Puerto Peñasco, Plutarco Elías Calles, and San Luis Río Colorado. Desert bighorn occur in mountainous areas characterized by deep valleys

and narrow passageways, including the Sierra of Posada, Noche Buena, and the Sierra del Viejo ([Valverde 1976](#); [Segundo-Galan 2010](#)).

Habitat association and radio-collared desert bighorn data. We used a database of satellite telemetry locations from 30 adult female and nine adult male desert bighorn obtained from the Program for the conservation, repopulation, and sustainable use of bighorn sheep in the state of Sonora (hereafter, the Sonora Bighorn Program), collected April 2019 to October 2022 following capture in March 2019. Desert bighorn were captured throughout extant desert bighorn habitat in Sonora (Figure 1) by aerial net-gunning from a Robinson R-44 helicopter (Robinson Helicopter Company, Torrance, CA) and fitted with a global positioning system (GPS)/satellite radio-collar (TELENAX, El Marques, Querétaro, México) programmed to record one location per day. Following processing, each desert bighorn was released at the capture location. Radio-collared desert bighorn were distributed throughout current desert bighorn distribution in Sonora.

Telemetry data included 24,164 locations from April 2019 through October 2022. We plotted locations in Arc-

Map 10.5 (Environmental Systems Research Institute, Inc, Redlands, CA), using only 3D fixes because these had an accuracy of ≤ 10 m (TELENAX, El Marques, Querétaro, México). Because our short term (*i.e.*, daily) locations were not spatially independent (*i.e.*, they were autocorrelated), we calculated 95 % autocorrelated kernel utilization distributions (aKDEs) from locations to define annual home ranges using continuous-time movement modeling ([Fleming et al. 2014, 2016](#)) in ctmmweb (<https://ctmm.shinyapps.io/ctmmweb/>; [Calabrese et al. 2016, 2021](#)). We then used resultant 95 % aKDEs as core areas or nodes to map connectivity among these patches in Sonora ([Rayfield et al. 2011](#)).

We calculated a composite 100 % minimum convex polygon (MCP) from all locations pooled in ArcMap and added a five km buffer (which corresponded to the mean distance we observed desert bighorn moving between separate rocky ranges in Sonora) to define the overall bighorn use area (*i.e.*, habitat availability). We used the combined 100 % buffered MCP to characterize the study area in terms of habitat attributes available to bighorn. We used 10 habitat variables for assessing habitat associations of desert bighorn, derived from 90 m resolution rasters (Table 1). We

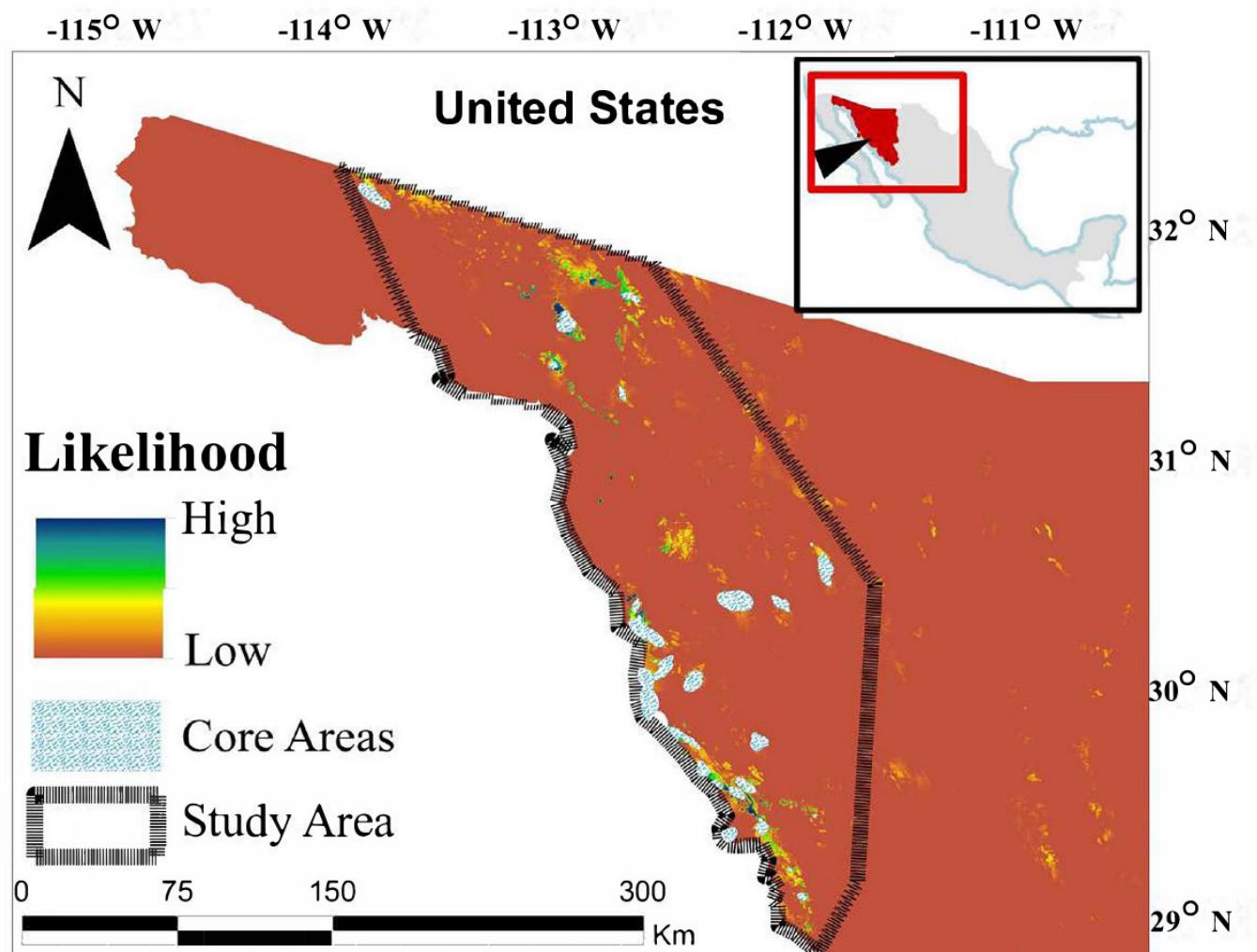


Figure 1. Mean likelihood of presence for desert bighorn (*Ovis canadensis mexicana*) in northwest Sonora, México.

selected habitat variables that have previously been related to distribution and habitat use of bighorn and other large herbivores in arid environments in México and the southwestern USA (e. g., [Monson and Sumner 1980](#); [Andrew et al. 1999](#); [Krausman and Shackleton 2000](#); [Álvarez-Cárdenas et al. 2001](#); [Guerrero-Cárdenas et al. 2003](#); [Bangs et al. 2005](#); [Medellín et al. 2005](#); [Ruiz-Mondragón et al. 2018](#); [Bender et al. 2022](#); [Bender et al. 2023](#); [Whiting et al. 2023](#)). We delineated habitat types from land cover mapping by the National Institute of Statistic and Geographic (<https://www.inegi.org.mx>; series VI, 1:250,000, [INEGI 2017](#)). We used three habitat types for analyses based on proportions within bighorn ranges; sarcocaula shrubland (matorral sarcocaula; 79 % of home ranges), microphyll scrub (matorral desertico microfilo; 19 % of home ranges), and all others (≤ 2 % of home ranges) pooled. We determined distance to rivers/lakes, water bodies, roads, and human settlements using the Euclidean distance metric in ArcGIS (Tédonzong *et al.* 2020). We determined slope and aspect from 90 m resolution digital elevation models (DEMs; [INEGI 2020](#)) in ArcGIS and terrain ruggedness ([Riley et al. 1999](#)) in QGIS (Table 1; [QGIS 2015](#)).

We used maximum entropy modeling (MaxEnt 3.4.1; [Phillips et al. 2006](#)) to model likelihood of desert bighorn presence in Sonora. Maximum entropy is a machine learning response that starts with known locations and compares habitat correlates at those sites to these same correlates at 10,000 random points throughout the study site. The maximum entropy algorithm is deterministic and will converge to the maximum entropy probability distribution ([Phillips et al. 2006](#)). The model results in a non-negative value assigned to each pixel, with values ranging from 0.0 to 1.0 to indicate the likelihood of a site being used by desert bighorn. Importantly, maximum entropy modeling relates presence locations to random locations and not to inferred absences; because this approach utilizes only known locations, it eliminates the need for absence data which are invariably unknown.

We assessed models using receiver operating characteristic (ROC) plots ([Phillips et al. 2006](#)). The ROC is a plot of sensitivity and $1 - \text{specificity}$, with sensitivity representing how well the data correctly predicts presence while specificity provides a measure of correctly predicted absences (Fielding and Bell 1997). We then used the area under the ROC curve (AUC) to assess performance of models ([Fielding and Bell 1997](#); [Phillips et al. 2006](#)). This approach provides an index of model accuracy; values range from 0.5 to 1.0, with values of 0.5 indicating no fit greater than that expected by chance. Standard errors were calculated for AUC values using 30 % of locations as test data ([Phillips et al. 2006](#)).

We constructed separate models for each individual desert bighorn for which annual data were available ($n = 43$) using the habitat variables above. We used the individual as the replicate to incorporate individual variation into the final model of desert bighorn habitat likelihood ([Baldwin](#)

Table 1. Classes, variables, and sources used to model habitats for bighorn sheep in the northeast of Sonora.

Class	Variables	Source
Topographic	Elevation (DEMs)	INEGI 2020
	Slope	INEGI 2020
	Aspect	INEGI 2020
	Terrain Ruggedness Index (TRI)	Riley <i>et al.</i> 1999
Human impact	Distance to settlements	INEGI 2017
	Distance to roads	INEGI 2017
Land cover	Tree cover	Hansen <i>et al.</i> 2013
	Vegetation types	INEGI 2017
Water resources	Distance to rivers	INEGI 2017
	Distance to water bodies	INEGI 2017

[2009](#)). For model development, we used the complementary log-log (clog-log) transformation and automatic features selection with cross-validation to reduce overfitting ([Elith *et al.* 2011](#); [Phillips and Dudík 2008](#)). We used 70 % of locations for model training data and the remaining 30 % for model testing ([Zurell *et al.* 2020](#); [Phillips *et al.* 2006](#)). We first modeled all variables individually to ensure that each provided useful information on distribution of desert bighorn (*i.e.*, variables AUC had a lower 95% CI of >0.50 ; [Swets 1988](#)). We then constructed fully parameterized models for each desert bighorn because we wanted to produce the most generalized model of desert bighorn likelihood possible (rather than identifying individual variables most associated with desert bighorn presence), analogous to minimizing bias in an information-theoretic approach (*i.e.*, drawing the most life-like elephant; [Wel 1975](#); [Burnham and Anderson 1998](#)). Last, we averaged the resultant maps of likelihood of landscape presence from each individual desert bighorn to create a mean likelihood coverage in ArcGIS. We used this mean likelihood map as the habitat association model (HAM) for modeling corridors ([Cushman *et al.* 2006](#)).

Resistance surface layer and connectivity analysis. We calculated a resistance surface layer (R) with values ranging from 1 (least resistance to movements) to 100 (greatest resistance to movements) based on the inverse of the HAM, where $R = 100 - (100 \times \text{HAM})$. The resistance layer illustrates the difficulty of, or resistance to, desert bighorn movement within any given location in the landscape ([Mateo-Sánchez *et al.* 2014](#); [Khosravi *et al.* 2022](#)). We then used Circuitscape V 4.0 ([McRae *et al.* 2013](#)), which uses circuit theory to model population connectivity as analogous to an electrical current ([McRae *et al.* 2008](#)), to generate a connectivity model among core areas (*i.e.*, 95 % akDE ranges). This process uses a graph-theoretical approach to predict movement patterns and quantify the effects of landscape features that impede species movement ([Cushman *et al.* 2013](#)).

We further identified optimal connectivity corridors using the least-cost paths approach ([Adriaensen *et al.* 2003](#); [Balbi *et al.* 2019](#)). Least-cost paths are the routes between two nodes (*i.e.*, core areas) that minimize accumulated resistance across all pixels intersecting the routes. To deter-

mine least-cost paths, we utilized the Linkage Mapper 3.0.0 extension for ArcMap ([McRae and Kavanagh 2011](#)), which calculates all possible routes in the landscape and their costs, with the lowest cost routes identified using the Cost Distance algorithm. This algorithm calculates the minimum accumulated cost distance between two nodes; the result is a vector layer of lines (routes) that establish the optimal routes for the establishment of corridors ([Adriaensen et al. 2003](#)). We then determined cost-weighted distances (CWD) between core areas (*i.e.*, individual desert bighorn 95 % aKDEs) and classed CWD into five categories (low, medium, high, very high, and highest) for presentation and analysis of least-cost paths. Last, we used ANOVA ([Zar 1999](#)) to test for differences in likelihood of desert bighorn presence and length of corridors among classes of corridors.

Results

The OUF-anisotropic continuous time movement model (ctmm) either provided the best fit (85 % of models) or was within $AUC_c < 2$ of the best fit model (15 % of models; size of home ranges did not differ from the lowest AUC_c model in these cases) for all desert bighorn. Consequently, we used OUF-anisotropic models for all 95 % aKDE home

ranges. The OUF-anisotropic movement model is the most general of ctmm, and includes a home range, correlated locations, correlated velocities, and movements varying by direction ([Fleming et al. 2014, 2016; Calabrese et al. 2021](#)). Annual home range sizes averaged 19.8 (SE = 4.0) km^2 for females and 30.7 (SE = 5.1) km^2 for males. From individual movement data, we observed a minimum of 6 dispersal or seasonal movements of desert bighorn among disjunct ranges or rocky islands that were separated by a range of 2 to 8 km (mean = 5.0; SE = 1.0).

Individual desert bighorn maximum entropy models showed extremely high fit (mean = 0.991; SE = 0.001; range = 0.977 to 0.998 [SE range 0.010 to 0.050]). The mean habitat association likelihood map revealed a landscape of scattered small high-quality patches in the human-dominated matrix of Sonora (Figure 1). Resistance to movements characterized two distinct areas of flow within our study area: an extensive patch dominating the southern area with relatively high permeability and a smaller patch with lower permeability in the northern area (Figure 2). Between these two areas was a large region of low permeability to movements (Figure 2). Similarly, within the northern area was a large region of very low permeability between the north-

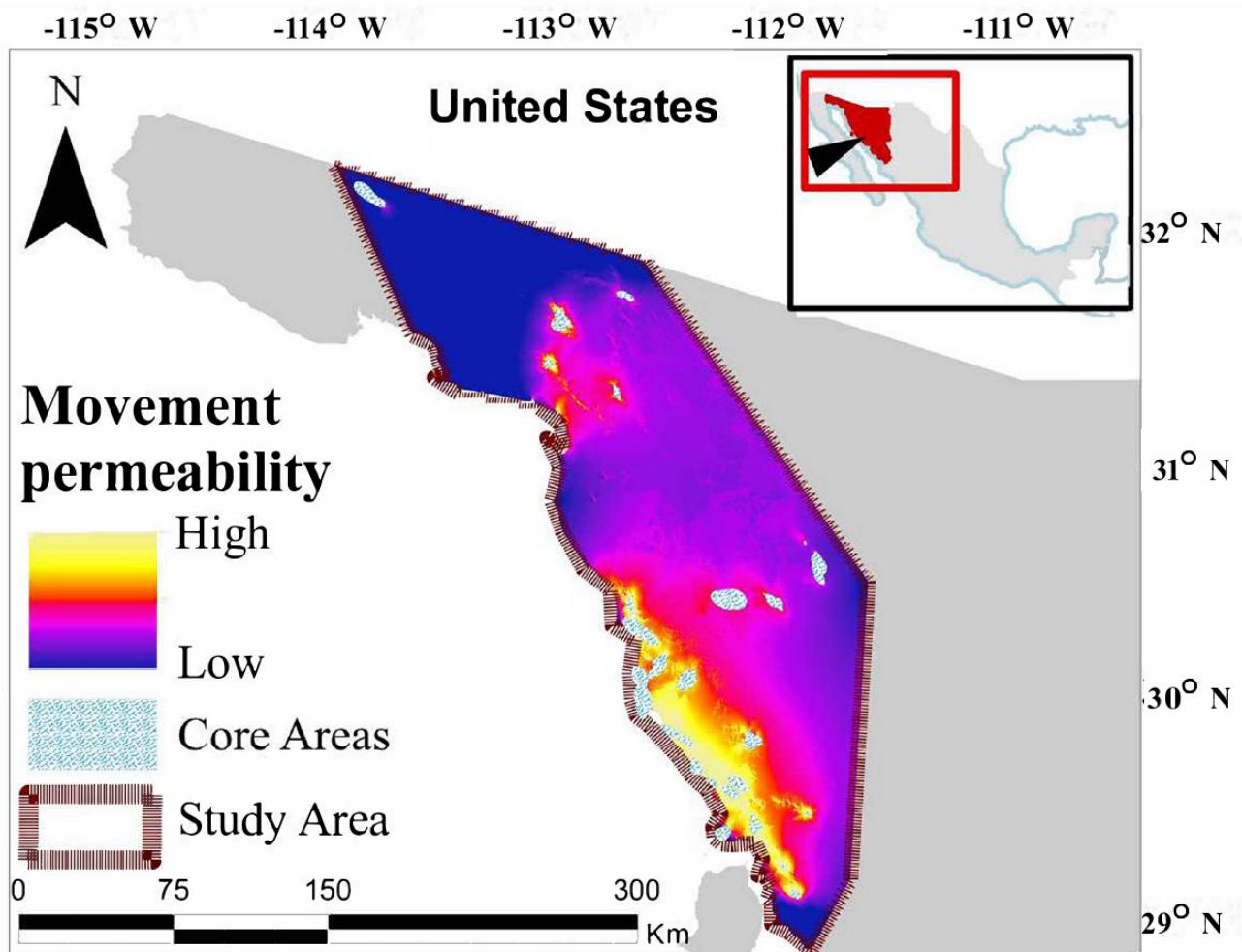


Figure 2. Estimated permeability of the northwest Sonora landscape to movements by desert bighorn (*Ovis canadensis mexicana*).

ernmost and southernmost core areas.

We identified a network of 83 potential corridors spanning 4,276 km that interconnected 43 desert bighorn core areas throughout northeast Sonora (Table 2; Figure 3). The northern portion of our area was the most isolated, with only 19 potential links (including four that connected the northern and southern areas), while the southern area contained 64. Among these, 14 corridors measured < 1 km and were predominantly located in the southern region. A total of 20 corridors spanned a distance of < 10 km, and 42 corridors were < 20 km. A total of eight corridors were > 100 km, and occurred solely in the northern area or between the northern and southern areas (Figure 3).

Mean likelihood of desert bighorn presence declined ($F_{2,80} = 60.6; P < 0.001$) as resistance to movements increased from low resistance (likelihood = 0.44) to moderate (likelihood = 0.25) to high (likelihood = 0.09). Similarly, classes of potential corridors with lower resistance to movement were shorter ($F_{2,80} = 33.7; P < 0.001$) than higher resistance classes (Table 2).

Discussion

Our evaluation of landscape resistance to desert bighorn movements and potential movement corridors identified two distinct areas within current desert bighorn range in Sonora: a northern and a southern area, with low and high connectivity, respectively, and with limited potential connectivity between these areas (Figures 2 and 3). Both of these areas are considered important regions for desert bighorn conservation in Sonora, and thus require attention regarding facilitating the movement of desert bighorn within and between areas, as well as between the northern area and bighorn populations in adjacent northern Baja California (e.g., [Ruiz-Mondragon et al. 2018](#)). Consequently, our connectivity results can guide conservation efforts that identify and promote preservation of key patches or corridors; facilitate habitat restorations within and around corridors; and thus enhance connectivity and viability of populations in both areas of Sonora ([Shepherd and Whittington 2006](#); [Castilho et al. 2015](#); [Dutta et al. 2016](#);

Table 2. Classes of modeled corridors based on resistance to desert bighorn movements, Sonora, Mexico. Characteristics of each class presented include likelihood of desert bighorn presence (Likelihood), total length of corridors, and mean length of corridors. Also presented is the High Class subdivided into 3 subclasses (High, Very High, and Highest).

Resistance		Likelihood		Length			
Class	Subclass	Mean	SE	Total	Mean	SE	N
Low		0.44 A	0.03	66.2	2.5 A	0.6	26
Moderate		0.25 B	0.04	351.3	17.6 B	0.9	20
High		0.09 C	0.02	1924.4	52.1 C	6.1	37
	High	0.09	0.02	527.6	29.3	0.9	18
	Very High	0.06	0.02	548.4	45.7	2.5	12
	Highest	0.09	0.03	853.4	121.9	7.8	7

ABC = Means with different letter differ by Class ($P \leq 0.003$).

[Allen et al. 2016](#).

We found the southern area to be characterized by high connectivity among core areas and relatively short potential movement corridors, e.g., 35 % of potential corridors were <10 km in length, which is considered short and indicates easy movement between areas. Additionally, 67 % of the corridors were < 25 km (mean = 19 km), which, while longer, is still within documented movement distances of bighorn in arid environments ([Schwartz et al. 1986](#)). Short corridors (under 10 km) are typically easier for individuals to traverse, while longer corridors (over 25 km) may represent more significant barriers or challenges, even to species like desert bighorn which readily move among disjunct habitat patches ([Schwartz et al. 1986](#); [Bleich et al. 1990](#); [Bleich et al. 1996](#)).

In the arid Southwestern USA and México, bighorn sheep regularly move between isolated desert mountain ranges or clusters of rocky habitats (as also observed in this study; [Schwartz et al. 1986](#); [Bleich et al. 1990](#); [Bleich et al. 1996](#)). However, the extent of these movements is contingent upon factors such as the distance between sites, sex, and the nature of intervening habitats ([Ough and deVos 1984](#); [Bleich et al. 1996](#); [Allen et al. 2016](#)). Individual bighorn in arid environments often move >20 km between ranges ([Schwartz et al. 1986](#)). While males are more likely to show exploratory or longer distance dispersal movements than females ([Ough and deVos 1984](#); [Bleich et al. 1996](#)), females will also emigrate to neighboring ranges ([McQuivey 1978](#); [Bleich et al. 1996](#)). Consequently, the high level of connectivity and numerous core areas in the southern area suggests that this area does not require immediate active management actions to enhance connectivity. Rather, emphasis in southern areas should be on actions that maintain existing conditions, such as careful environmental review of proposed developments, etc., to minimize or mitigate any potential impacts on movements of desert bighorn. The higher habitat quality associated with the shorter low-resistance corridors facilitates movements in the southern area ([Ough and deVos 1984](#)).

In contrast, the northern Sonora area is characterized by much lower connectivity, with longer distances among core areas; e.g., only 20 % of potential corridors were < 10 km, 30 % were < 25 km, and potential corridors averaged 41 km in length. Even more challenging for desert bighorn in Sonora is the large separation characterized by significant resistance to movements between northern and southern populations (Figure 2 and 3), where the shortest potential corridor is 107 km and the four potential corridors connecting northern and southern areas averaged 131 km. While female bighorn have occasionally been documented to move >50 km ([McQuivey 1978](#)), this level of separation can provide a significant challenge to desert bighorn exchange between northern and southern populations ([Ough and deVos 1984](#); [Bleich et al. 1996](#)), as well as within the northern area (although the latter may possibly be somewhat mitigated by movements to or from Baja California populations).

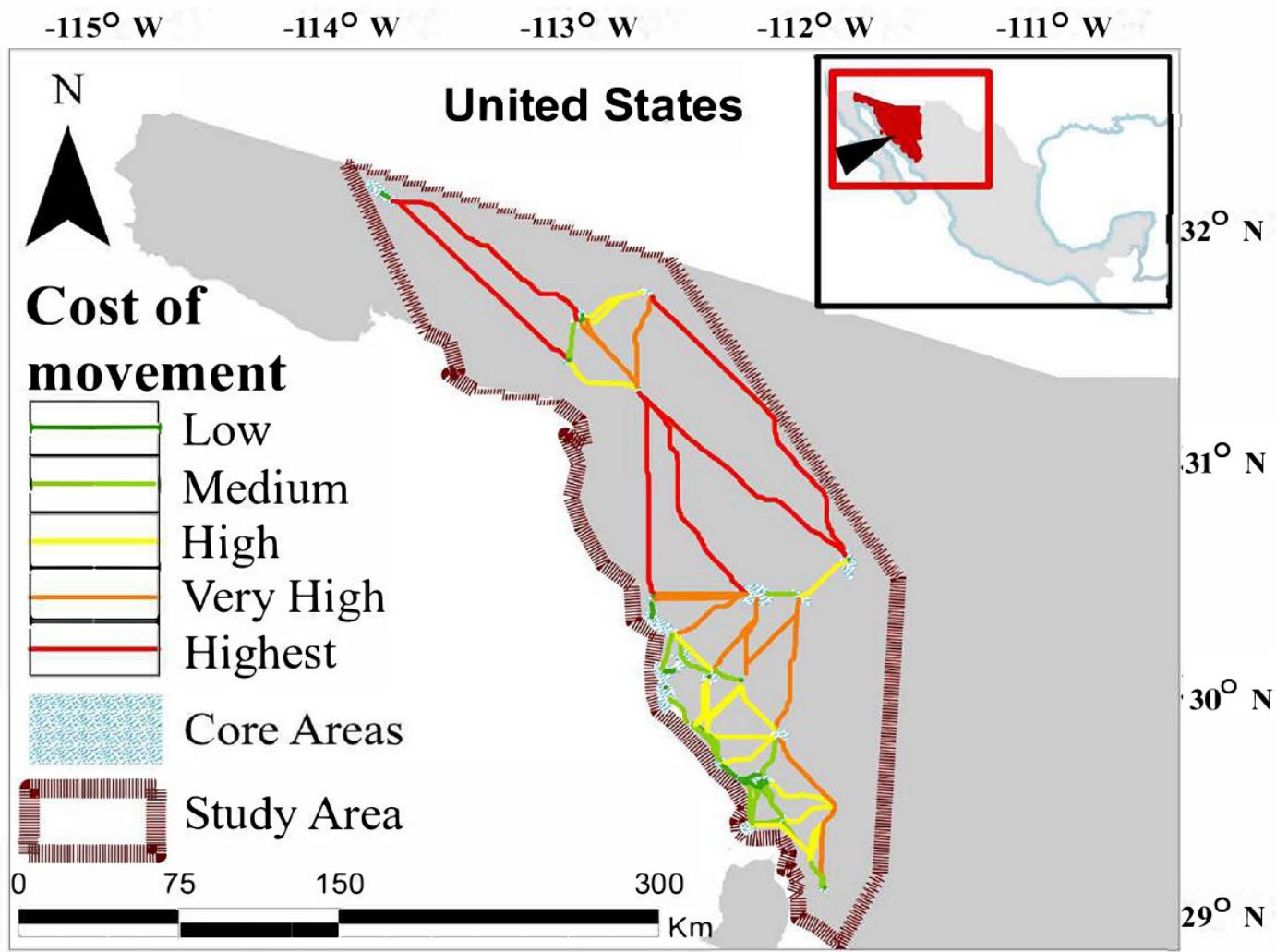


Figure 3. Location and quality of potential linkages between desert bighorn (*Ovis canadensis mexicana*) core areas in northwest Sonora, México. Linkage quality is determined from the ratio of cost-weighted distance to least-cost paths. Higher values indicate higher cost of movement along the path of least resistance and lower values indicate lower costs of movements along the least-cost path.

Consequently, the immediate conservation priority for Sonora should be to enhance connectivity within northern Sonora and between the northern and southern Sonora areas. Connections between the northern and southern areas are compromised by factors such as greater separation between mountainous terrain, agricultural development, human settlements, primary roads, etc. Hence, the potential corridors we identified between northern and southern areas (and within the northern area) highlight ecologically important areas that should be prioritized for actions to facilitate desert bighorn movements or habitat quality between existing core areas. These actions may include minimizing fences, roads, irrigation canals, and other movement impediments between desert bighorn core areas (NDOW 2001). Management actions in the northern area should ideally be in consort with similar actions in northern Baja California, given the proximity between bighorn sites in these States.

Roads, depending on their type, size, traffic, and other features, are a major cause of mortality and impediments to movement for both small and large mammals in México

(González-Gallina and Hidalgo-Mihart 2018; Rubio-Rocha et al. 2022). Hence, new construction or improvements of existing roads should consider including wildlife crossings (i.e., under or over passes) and avoiding continuous guard rails or fences along right-of-ways within potential corridors (NDOW 2001; Manteca-Rodríguez et al. 2021). Because much of desert bighorn range in Sonora is used for livestock grazing, new pasture or right-of-way fencing should follow standard wildlife-friendly recommendations, such as using 99 cm high, three-strand fences with a smooth bottom wire ≥ 51 cm from the ground (NDOW 2001). Such actions can lessen the risk to connectivity between core areas associated with the most common obstructions to desert bighorn movements in Sonora.

Last, we used individual-animal-based habitat data from local desert bighorns to develop inputs to model connectivity among core areas in Sonora. In contrast, most connectivity modelling analyses use expert opinion to identify suitable habitats and barriers to movement, which is vulnerable to several potential biases including lack of local knowledge regarding species habitat use patterns (Due-

ñas-López *et al.* 2015). Resource selection or habitat use by wildlife is an adaptive response of individuals to meet their life requirements given existing environmental circumstances (Manly *et al.* 1993; Bender 2020; Bender *et al.* 2022). Hence, our methodology of using local desert bighorn to identify habitat attributes associated with their presence offers a more targeted and likely accurate approach for identifying potential movement corridors; local desert bighorn are certainly more aware of what constitutes suitable conditions for themselves than are human experts. While individuals may disperse or move through lower-quality habitats, movements are much more likely through suitable areas (Ough and DeVos 1984; Allen *et al.* 2016) and individuals are much more likely to be successful in movements (*i. e.*, stay alive).

Information on core areas and landscape connectivity can provide very targeted information for conserving bighorn sheep in Mexico, where their distribution is primarily limited to two states (Sonora and the Baja California peninsula) and where the overall population status is considered stable, but the current status of many small isolated populations is unknown (Lee 2003; Romero-Figueroa *et al.* 2024). Connectivity mapping can be used to strategically place conservation actions such as habitat restorations within or around corridors (Shepherd and Whittington 2006), as well to identify suitable sites for habitat restorations (Bleich *et al.* 1996). For example, managers should prioritize reestablishing extirpated populations along higher-quality corridors and in proximity to occupied core areas, enhancing the probability of dispersing desert bighorn encountering other populations (Bleich *et al.* 1996). Minimizing isolation, facilitating movements, and restoring extirpated populations is important to ensure the long-term viability of desert bighorn in Mexico. Because of the ecological and economic importance of desert bighorn, actions that enhance the probability of establishment and connectivity of populations can significantly contribute to the overall welfare of northern México.

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Potential distribution of the Curaçaoan Long-nosed Bat, *Leptonycteris curasoae*: implications for monitoring and conservation

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Understanding the spatial distribution of animal species, which involves integrating species occurrence with environmental data, provides crucial information for conservation planning, especially for threatened species. In this study, we used niche-based species distribution models to create a potential distribution map of *Leptonycteris curasoae*, a vulnerable fruit- and nectar-feeding bat. This model incorporated occurrence data from field sampling, mammal collections, scientific literature, and environmental variables. Additionally, we mapped the threats faced by *L. curasoae* and overlaid this data with protected area boundaries to identify priority conservation regions. Our results indicate that the current and potential distribution of this species is considerably smaller (~9 %) than the area previously considered according to the IUCN Red List. The potential distribution of *L. curasoae* is environmentally restricted to arid and semiarid areas and dry forests in Aruba, Bonaire, Curaçao, Northern Colombia, and Venezuela, characterized by high temperatures, low precipitation, and seasonality in temperature and precipitation. Approximately 22 % of the suitable areas for this species are within protected areas, and we observe differences in the magnitude of the area under protection and the impact of identified threats among countries. Roost vandalism is the most critical threat in Curaçao and Venezuela, while mining, tourism, and wind farms are more frequent in Colombia. Expanding or creating protected areas and roosts, jointly with establishing conservation corridors and connected private reserves across political boundaries, are high-priority conservation actions needed to guarantee safe mating and maternity roosts, long-distance movements, and connectivity of *L. curasoae* populations along its entire geographic distribution.

Comprender la distribución espacial de las especies animales que involucran conjuntamente la presencia de especies y los datos ambientales ofrece información crítica para la planificación de la conservación, particularmente para las especies amenazadas. Aquí, utilizamos modelos de nicho para estimar la distribución potencial de *Leptonycteris curasoae*, un murciélagos frugívoro-nectarívoro considerado como Vulnerable. Este modelo incluyó datos de presencia provenientes de muestreos en campo, colecciones de mamíferos, literatura científica, así como variables ambientales. Adicionalmente, mapeamos las amenazas actuales para superponerlas con datos de áreas protegidas y así poder identificar áreas prioritarias para conservación de *L. curasoae*. Nuestros resultados indican que la distribución actual y potencial de esta especie es menor (9 %) que la considerada anteriormente en la Lista Roja de Especies Amenazadas de la UICN. La distribución potencial de *L. curasoae* está ambientalmente restringida a áreas áridas, semiaridas y bosques secos en Aruba, Bonaire, Curazao, el norte de Colombia y Venezuela, caracterizados por altas temperaturas, bajas precipitaciones y estacionalidad en temperatura y precipitación. Aproximadamente el 22 % de las áreas adecuadas para esta especie está dentro de áreas protegidas, y observamos diferencias en la magnitud de área protegida y el impacto de las amenazas identificadas entre países. El vandalismo es la amenaza más crítica en Curazao y Venezuela, mientras que la minería, el turismo y los parques eólicos son más frecuentes en Colombia. Ampliar o crear áreas y refugios protegidos, junto con el establecimiento de corredores de conservación y reservas privadas conectadas más allá de las fronteras políticas, son acciones de conservación de alta prioridad para garantizar la permanencia de refugios de apareamiento y maternidad, los movimientos de larga distancia y la conectividad de las poblaciones de *L. curasoae* a lo largo de su distribución.

Keywords: Chiroptera; Curaçaoan Long-nosed Bats; species distribution models; tropical dry forest; vulnerable bat species.

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Introduction

Global trends indicate that human activities have significantly impacted biodiversity, particularly in the past five decades ([Díaz et al. 2019](#)). Currently, mammals are the second most endangered vertebrate group, comprising 22 % of threatened species ([IUCN 2020](#)). Among mammals, 15 % of bat species are threatened ([Frick et al. 2020](#)). Although bats have a global distribution and high diversity in tropical regions ([Altringham 2011](#); [Burgin et al. 2018](#)), many species are sensitive to habitat disturbances ([Voigt and Kingston 2016](#)).

The Curaçaoan Long-nosed bat, *Leptonycteris curasoae* Miller, 1900, is one of the 19 threatened bat species in South America and the Caribbean islands. This species strongly depends on dry forests and arid ecosystems in Colombia, Venezuela, and the Caribbean islands ([IUCN 2023](#)). This fruit- and nectar-feeding bat species is the primary pollinator of several plant species, mainly of Cactaceae (e. g., *Stenocereus* spp., *Cereus* spp., *Pilosocereus* spp.) and Asparagaceae (*Agave* spp.) families ([Griffiths and Gardner 2007](#)). *L. curasoae* is a migratory bat, undertaking long-distance flights (28 to 89 km) between Caribbean islands, including Aruba, Bonaire, and Curaçao, and between those islands and the mainland of northern Venezuela ([Simal et al. 2015](#)).

The main threats for *L. curasoae* are habitat alteration due to urban expansion, mining, quarrying, wind farms development, and vandalism of roosts, mostly caves ([Nassar 2015](#); [Simal et al. 2021](#)). Furthermore, dry forests, arid and semiarid zones are the most threatened and transformed ecosystems in the Neotropics ([Escribano-Avila et al. 2017](#)), with 66% of the dry forests having already disappeared ([Portillo-Quintero and Sánchez-Azofeifa 2010](#)). In Colombia, Venezuela, and the Caribbean islands, these ecosystems are in critical condition because they are underrepresented in protected areas. In Colombia and Venezuela, only 5 % of their coverage is under protection ([Fajardo et al. 2005](#); [Rodríguez et al. 2010](#); [Pizano and García 2014](#)), and in Caribbean islands, approximately 10 % of these ecosystems are within protected areas ([Portillo-Quintero and Sánchez-Azofeifa 2010](#)).

Most studies assessing habitat and feeding ecology, geographic range, roost location, and populational trends of *L. curasoae* have been carried out in the islands of Aruba, Bonaire, and Curaçao ([Petit 1995, 1997](#); [Simal et al. 2015, 2021](#)) and Venezuela ([Martino et al. 1998, 2002](#); [Nassar et al. 2003](#); [Newton et al. 2003](#)). Much less information is available for Colombia ([Cadena et al. 1998](#); [Sánchez and Cadena 1999](#)). The above topics are vital for updating the risk of extinction assessment provided by the IUCN Red List nearly a decade ago for *L. curasoae* ([Nassar 2015](#)). Information regarding long-distance routes, stopover foraging grounds, and diurnal and mating/maternity roosts along its potential seasonal migration paths remains scarce across *L. curasoae*'s entire geographical distribution, limiting our understanding of the annual migration dynamics attributed to this species.

Niche-based species distribution modeling (SDM) has proved to be valuable in conservation strategies ([Rodríguez et al. 2007](#); [Villero et al. 2017](#)). Such modeling is particularly useful for locating suitable areas for field exploration and identifying key variables limiting the distribution of rare bat species of conservation concern ([Razgour et al. 2011](#)). In this study, we aimed 1) to generate a potential distribution map of *L. curasoae*, 2) to identify threats and underprotected areas within this bat's potential distribution, and 3) to fill in information gaps concerning the current distribution and roosts occurrence for the species, emphasizing understudied countries such as Colombia.

Materials and methods

Study area. We compiled data from all countries where *L. curasoae* is distributed: Colombia, Venezuela, Aruba, Bonaire, and Curaçao islands (ABC islands). Due to the limited information available on the current distribution of *L. curasoae* in Colombia, we conducted field expeditions in 2020, 2022, and 2023 according to the reproductive cycle and the possible annual migration of the species ([Martino et al. 1998](#); [Simal et al. 2021](#)). Field expeditions were conducted in 27 locations across three geographic areas: 1) The Chicamocha River basin (ten sites) in January 2020. 2) the Caribbean coast (nine sites) in February 2020. 3) Tierra Bomba island in February 2020, April and December 2022 and June 2023. 4) La Guajira Peninsula (seven sites, Supplementary material Figure S1) in April 2022.

The Chicamocha River Basin is in the Colombian Eastern Mountain range, at 500 to 1,500 masl ([Albesiano et al. 2003](#)). This area features semi-arid, thorn scrub, and dry forest vegetation ([Latorre et al. 2014](#)). The mean annual temperature in this region ranges from 16 °C to 36 °C, and annual rainfall reaches 731 mm ([Albesiano et al. 2003](#)). Sampled localities in the Caribbean coast and La Guajira Peninsula belong to the Peri-Caribbean Arid Belt. The Caribbean coast is characterized by seasonally tropical dry forests, with an average annual temperature of 27 °C (16 to 36 °C, [IDEAM 2010](#)), while La Guajira Peninsula primarily comprises xerophytic and thorn scrub vegetation, with an average annual temperature of 29 °C (19 to 36 °C, [IDEAM 2010](#)). The Peri-Caribbean Arid Belt province generally has lower average yearly rainfall, strong winds, and higher evaporation rates than the Chicamocha River Basin ([Hernández et al. 1992](#)).

Current geographic distribution of *Leptonycteris curasoae*. We mapped the current geographical distribution of *L. curasoae* revisiting information on specimens deposited in mammal collections, including the Instituto de Ciencias Naturales of Universidad Nacional de Colombia (ICN), Instituto Alexander von Humboldt (IAvH), Universidad Industrial de Santander (UIS-MHN), and Vertebrate collection at Universidad de Los Andes, Venezuela (CVULA). Additional records were obtained from other institutions by revising databases such as GBIF ([GBIF 2022](#)) and VertNet ([VertNet 2022](#)). Furthermore, we examined information about geographical distribution in the scientific literature in Google

Scholar ([Google Scholar 2022](#)) and Web of Science ([Web of Science 2022](#)) using the keywords “Leptonycteris* AND L. curasoae* AND Curaçaoan Long-nosed Bat*” without date restrictions. Also, we checked data compiled in the thesis and technical reports of studies carried out in zones where this bat species was historically found. This resulted in a total of 13 documents conducted in the five countries where *L. curasoae* is distributed. We assessed the Extent of Occurrence (EOO) and the Area of Occupancy (AOO) for the revisited current distribution that we obtained and for the previous distribution published in the last IUCN Red List assessment ([Nassar 2015](#)), using the sRedList platform ([Cazalis et al. 2024](#)).

As described earlier, we complemented the current distribution for Colombia conducting field expeditions across 27 locations. At each location, bat sampling was carried out using six ground-level mist nets (two 6 m, one 9 m, and three 12 m length, 20 mm mesh, ECOTONE, Poland). Mist nets were active from 18:00 to 00:00 and were checked every 25 minutes on average. Our total sampling effort was 16,609 m² x mist net x hours (mnhs). Also, we searched for caves and artificial roosts where bats were captured using mist nets at the entrances of the roosts or an entomological hand net inside the roosts. Capture and handling methods followed the guidelines of the American Society of Mammalogists ([Sikes et al. 2011](#)) and were authorized by licenses from the Environmental Licenses National Agency ([ANLA 2014](#)).

Ecological modeling and climate variables. We used 19 current bioclimatic variables sourced from the Chelsa database ([Karger et al. 2021](#)), which offers data at approximately 1 km² spatial resolution (0.0083 arc seconds). These variables depict annual and seasonal climate patterns over the baseline period from 1970 to 2000. To address collinearity issues among the 19 bioclimatic variables, we employed the *corrSelect* function from the *fuzzySim* package ([Barbosa 2015](#)), available in R ([R Core Team 2022](#)). By using the Pearson method with a threshold value set at 0.8 and a variance inflation factor, this function effectively identifies and excludes highly correlated variables ([Barbosa 2015](#)). To establish a calibration area (M), we intersected a buffer around species occurrences (2.5 °) with ecoregions defined by [Olson et al. \(2001\)](#). This approach considers both dispersal and ecological limitations, enhancing the robustness of our modeling process.

Occurrence records. We generated a database comprising 400 georeferenced records for *L. curasoae* and after a thorough examination, we excluded 63 % of the records due to inconsistent or duplicated coordinates. Furthermore, we implemented a distance-based filter of 5 km to mitigate sample bias, using the *spThin* function ([Aiello-Lammens et al. 2015](#)) of the *Wallace* package ([Kass et al. 2018, 2023](#)). As a result of these procedures, we obtained 148 valid records.

Niche-based species distribution model. We employed the ensemble modeling approach implemented in the *bio-*

mod2 package ([Thuiller et al. 2009](#)) within the R software ([R Core Team 2022](#)) to develop the niche-based distribution model for *L. curasoae*. Ensemble modeling combines multiple individual models to produce a more robust prediction by leveraging the strengths of each constituent model while mitigating the effects of their inherent uncertainties and errors ([Araujo and New 2007](#)).

Out of the ten algorithms available in *biomod2*, we selected seven for our analysis: MaxEnt (MAXENT.Phillips), Generalized Additive Models (GAM), Generalized Boosted Regression Model (GBM), Artificial Neural Networks (ANN), Surface Range Envelope (SRE), and Random Forest (RF). Because our occurrence datasets only included presence-derived information, we randomly generated 10,000 pseudo-absences within the calibration area to balance the dataset. Prevalence was set to 0.5 to assign equal importance to presences and pseudo-absences during the calibration process. Each model was executed ten times, with each run using a different selection of calibration and evaluation datasets, with 70 % of the data allocated for calibration and the remaining 30 % for evaluation in each run.

To evaluate model performance, we used the area under the curve of the receiver operating characteristic (AUC). Models were assembled using a total consensus rule, where algorithms and the ten replicates were assembled based on the weighted sum of evaluations greater than AUC > 0.8 ([Araujo and New 2007](#)). Subsequently, an ensemble model comprising seven algorithms × 10 repetitions was used to project the potential distribution of *L. curasoae* under current climatic conditions. Given the thorough revision of all occurrence records ([Peterson et al. 2011](#)), we are confident that each point contributes to representing the distribution of *L. curasoae*. Therefore, we obtained a binary map by employing the minimum training presence threshold (value of 240).

Pressures and threats. We conducted an overlay analysis, superimposing the current and potential spatial distribution of *L. curasoae* with layers depicting land use transformation and protected areas, and mapped current threats such as mining, wind farms, tourism, and vandalism of roosts across the geographic range of this species. The land-use transformation data were obtained from a global map of land use/land cover (LULC) from 2023 derived from ESA Sentinel-2 imagery at 10 m resolution ([Karra et al. 2021](#)). This map layer was created based on a large dataset of over 5 billion human-labeled Sentinel-2 pixels by developing and deploying a deep-learning segmentation model on Sentinel-2 data. The algorithm generates LULC predictions for nine classes: water, trees, flooded vegetation, crops, built area, bare ground, snow/ice, clouds, and rangeland.

The polygons representing protected areas were sourced from Protected Planet ([Protected Planet 2023](#)), a comprehensive data repository on protected areas and other effective area-based conservation measures (OECMs).

This database is updated monthly and maintained by the United Nations Environment Programme World Conservation Monitoring Centre ([UNEP-WCMC 2024](#)). Only protected areas categorized by the IUCN were considered. Protected areas designated as 'Protective Zones' and 'Critical Areas with Treatment Priority' were excluded from the analysis because they only exist in Venezuela, and the anthropogenic activities allowed include exploitation of natural resources incompatible with the aims of protected areas ([García and Silva 2013](#)). We compiled 340 georeferenced locations of mining, wind farms, and tourism threats obtained from Colombian governmental platforms such as the [Mining and Energy Planning Unit \(2023\)](#) and the [Ministry of Commerce, Industry, and Tourism \(2022\)](#), respectively. For Aruba, Bonaire, Curaçao, and Venezuela, threat information came from published data ([Petit et al. 2006](#); [Molinari et al. 2012](#); [Nassar and Simal 2019](#); [Simal et al. 2021](#)) and data observed directly in the field between 1997 and 2015 (J. Nassar pers. obs.). Similarly, roost vandalism records for Colombia were obtained from our field observations from 2020 to 2023.

By integrating spatial data on land cover change, we identified regions where habitat degradation and fragmentation might pose significant threats to *L. curasoae* populations. Additionally, overlaying data of protected areas allowed us to assess the extent to which current conservation measures cover the bat's distribution range and identify potential gaps in its protection. Mapping current threats enabled us to pinpoint specific areas where human activities pose immediate risks to the survival and habitat integrity of *L. curasoae*.

Results

Current geographic distribution of *L. curasoae*. Most of the occurrence records of *L. curasoae* came from Venezuela (41.2 %) and Colombia (39.9 %), and the remaining occurrence data (18.9 %) correspond to the ABC islands (Supplementary material, Table S1). In Colombia, we captured 200 individuals from six localities in the three geographic areas sampled: the Chicamocha River Basin (5 individuals), the Caribbean Coast (124), and La Guajira Peninsula (71; Table S2). Five localities represent new records of *L. curasoae* in the country (Table S1).

Throughout the geographic range of *L. curasoae*, only 23 locations (15.5 %) correspond to roosts. Ten roosts are in Venezuela, and ten are in the ABC islands. During the field expeditions in Colombia, we explored 23 roosts, including caves, natural shelters, and human-made buildings (Supplementary material, Table S3). We discovered three roosts of *L. curasoae* in Colombia. One roost is in a cave on La Guajira Peninsula, which hosts a large maternity colony (Table S3). The other two roosts are in historical fortresses on Tierra Bomba Island where a smaller colony resides. This colony was observed only in February 2020 and December 2022, using the fortresses as mating roosts (Table S3). Eighteen shelters are maternity roosts: Venezuela (7 shelters), Bonaire (4), Aruba (3), Curaçao (3), and Colombia (1). Mating roosts were found in Venezuela (5), Bonaire (2), and Colombia (2; Supplementary material, Table S1). Our data indicated that the Extent of Occurrence (453,300 km²) was reduced by almost half and the Area of Occupancy (167,500 km²) by nearly a third in the revisited current distribution compared to the previous distribution published in the last IUCN Red List assessment (EOO = 1,028,661 km² and AOO = 614,428 km²; Figure 1).

Niche-based species distribution model. Out of the 60 models created (six algorithms and ten replicates), 45 models exhibited AUC values greater than 0.8. The average sensitivity across these models was 96.5 %, indicating a high proportion of correctly predicted presences, while the average specificity was 89.4 %, reflecting a high proportion of correctly predicted absences (Supplementary material, Table S4).

The potential distribution of *L. curasoae* estimated through the weighted ensemble of these models encompassed most of its currently known distribution in Colombia, Venezuela, and the ABC Islands. Predicted suitable areas were predominantly identified in Aruba, Bonaire, Curaçao, La Guajira Peninsula in Colombia, the Paraguaná Peninsula, and areas south of Falcón and north of Lara states in Venezuela, as well as several intra-Andean arid patches in Venezuela and Colombia. All these areas correspond with most of the currently known locations for this species, however, some exceptions were observed. Suitable areas for *L. curasoae* were identified in the northeast portion of the Sierra de Perijá, north of Monagas state, and

Table 1. Mean, median, maximum, and minimum of bioclimatic variables considered in the potential distribution model of *L. curasoae*.

	Annual mean temperature (°C)	Annual mean diurnal range (°C)	Temperature seasonality (CV, %)	Annual precipitation (mm)	Precipitation of driest month (mm)	Precipitation seasonality (CV, %)	Precipitation of coldest quarter (mm)
	Bio 1	Bio 2	Bio 4	Bio 12	Bio 14	Bio 15	Bio 19
Minimum	8.35	0.9	15.5	276	1.1	25.4	6.2
Median	26.35	7.2	72.8	919.7	12.2	60.9	84.3
Mean	25.91	6.69	71.13	902.5	20.18	58.39	122
Maximum	29.05	11.3	113.6	2356	124.1	110.6	574.1

southeast of the Paraguaná Peninsula in Venezuela, as well as in the south of Sierra del Perijá and south of the Chicamocha River Basin in Colombia. All of them are locations where *L. curasoae* has never been recorded in the past. Additionally, a deviation of the model was detected with no suitable area predicted for an existent record of the species in the south of the Cesar state, in Colombia (Figure 2).

The final set of non-correlated variables was seven (Table 1). Based on the model's predictions, *L. curasoae* can occur in areas with relatively high annual mean temperature, low temperature seasonality, and low variation in annual mean diurnal range temperature. Also, suitable areas are characterized by low to intermediate annual precipitation, intermediate precipitation seasonality, and low precipitation in the driest month and the coldest quarter (Table 1). The potential distribution model indicated that suitable areas for this bat species represent only 9.4 % of the total area reported in the IUCN Red List (Figure 2).

Pressures and threats. According to the LULC map, the most dominant land-use classes were rangeland (47.6 %) and trees (40.2 %). In comparison, the anthropized area covered 8.4 % of the potential distribution area of *L. curasoae* (Supple-

mentary material, Table S5). In general, 133 protected areas overlapped with the potential distribution of *L. curasoae* (Figure 2, Supplementary material, Table S6). Only 40 (30.1 %) protected areas have the highest level of protection, being considered as IUCN categories Ia (1 area) and II (39), which cover only 18.41 % of the potential distribution of *L. curasoae*. Most of the protected areas are in Venezuela (58.6 %). In Colombia, 33.1 % of the protected areas overlapped, while in the ABC islands the overlap was 8.3 %. About 22.2 % of the suitable areas predicted are inside protected areas, most of which are in Venezuela (20.2 %), followed by Colombia (1.9 %) and the ABC islands (0.1 %; Table 2).

We identified 86 threats that overlapped with the potential distribution of *L. curasoae* (Figure 2). Roost vandalism is the most critical threat in Curaçao and Venezuela, while mining, tourism, and wind farms are the most frequent menaces identified in Colombia. Mining and tourism were mainly concentrated in *L. curasoae* suitable areas in the intra-Andean, Caribbean, and La Guajira regions of Colombia. Wind farms are mainly restricted to the ABC islands (1 wind farm in each) and northern Colombia (17; Figure 2, Supplementary material, Table S7).

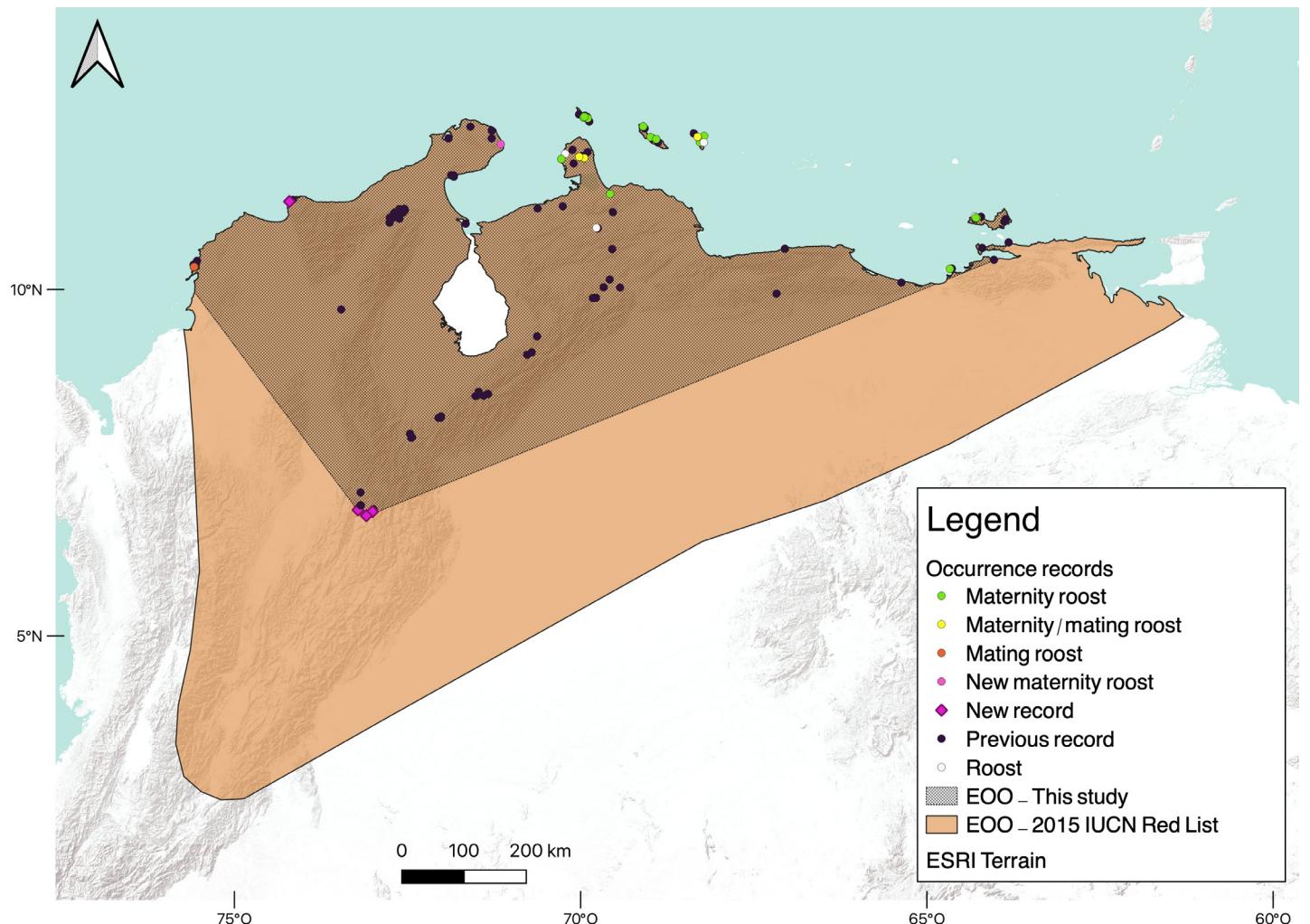


Figure 1. Records of *L. curasoae* used for the Species Distribution Model (SDM). New localities and types of roosts are shown. The Extent of Occurrence (EOO) assessed in this study and from the IUCN Red List (Nassar 2015) for *L. curasoae* are shown.

Table 2. Potential distribution area of *L. curasoae* (extension and percentage), protected areas overlapped (number and percentage) with the potential distribution of *L. curasoae*, and percentage of potential distribution area under protection by country.

Country	Potential distribution area (km ²)	% of potential distribution area	Number and (%) of protected areas	% of potential distribution area inside protected areas
Aruba	172.21	0.22	1 (0.75)	0.04
Bonaire	273.44	0.35	3 (2.26)	0.06
Curaçao	419.53	0.53	7 (5.26)	0.03
Colombia	18,454.38	23.28	44 (33.08)	1.94
Venezuela	59,936.35	75.62	78 (58.65)	20.17
Total potential distribution inside protected areas				22.23
Total potential distribution without protection				77.77
Total potential distribution	79,255.91			

Discussion

The distribution of a species is expected to occur in areas with suitable abiotic conditions and biotic interactions that have been accessible to the species via dispersal over relevant time periods ([Feng et al. 2024](#)). In this study, we found that the current Extent of Occupancy and potential distribution of *L. curasoae* are smaller than previously considered, with environmentally suitable areas found in the ABC islands, northern Colombia and Venezuela. Around 22.3 % of the suitable areas for the species are inside protected areas, and many threats identified occur in countries where the environmentally suitable areas are less represented in national parks or reserves, such as Colombia.

Current geographic distribution of L. curasoae. In Colombia, *L. curasoae* is more abundant in the coastal region (Caribbean and La Guajira Peninsula) than in the Chicamocha River Basin. Similarly, more occurrences of this species were reported by [Cañón and Trujillo \(2014\)](#) in La Guajira. Previous studies have documented a lower capture rate of *L. curasoae* in intra-Andean arid patches of Colombia and Venezuela compared to northern Venezuela ([Sosa and Soriano 1993; Cadena et al. 1998; Martino et al. 1998; Sánchez and Cadena 1999; Soriano et al. 2000](#)). Part of the sampling in the Caribbean coast and La Guajira was conducted at the recently discovered roosts, where the largest colony mainly consisted of pregnant females. On Tierra Bomba Island, the colony uses the fortresses only during the mating season (October–February) and leaves afterward (A. Otálora-Ardila, unpublished data). These reproductive behaviors may explain the large aggregations and high abundance observed of *L. curasoae* in northern Colombia. In contrast, no roosts were found for *L. curasoae* in the Chicamocha River Basin.

The high abundance of *L. curasoae* in the northern part of its range might also be linked with food availability. *Stenocereus griseus* and *Cereus repandus*, two columnar cacti species that are primary food resources for *L. curasoae*, have longer flowering and fruiting periods on the coast of Venezuela compared to the continental and intra-Andean arid areas of Venezuela and Colombia ([Sosa and Soriano](#)

[1996; Ruiz et al. 2000; Nassar and Emaldi 2008](#)). These differences in cacti reproductive patterns are probably mediated by variations in rainfall regimes between the coast and continental arid zones ([Nassar and Emaldi 2008](#)). Although specific data on reproductive phenology of cacti in the north of Colombia is lacking, similar differences in resource availability might exist between the northern regions and intra-Andean arid zones.

Most of the known roosts of *L. curasoae* are in northern Venezuela and the ABC islands, regions characterized by abundant karst formations ([Hoekstra et al. 2010](#)). Consequently, have more potential for cave development than continental regions in northern South America. Only in the ABC islands, the karst extension is nearly 13,000 km² ([Day 2010](#)). This high concentration of caves likely explains the large populations of *L. curasoae* in this part of its range. High capture rates have been recorded in caves of ABC islands and the Paraguaná Peninsula in Venezuela, with population estimates of 14,350 bats in Bonaire and 26,517 in Aruba ([Simal et al. 2015, 2021](#)). Our data suggest a similar pattern in Colombia, where a cave in La Guajira Peninsula hosts a maternity colony of around 10,000 bats. Although the two roosts we found in Tierra Bomba are human buildings ([Otálora-Ardila et al. 2022a, b](#)), they host approximately 700 individuals. These three shelters are the only roosts known for *L. curasoae* in Colombia. Despite exploring roosts in the Chicamocha River Basin, including La Macaregua cave, which was previously reported as *L. curasoae* roost ([Marinkelle and Cadena 1972](#)), we did not find this species in any cave or artificial roost in this region.

Our data indicated that the current EOO is smaller than previously known ([Nassar 2015](#)). Upon revisiting specimens at mammal collections, we identified some specimens with incorrect localization data, confirming that the southern location of *L. curasoae* corresponds to the Chicamocha River Basin. Although our results indicate a reduction in EOO and AOO, the current EOO and AOO are still above the thresholds of 100 km² or 10 km², respectively, which would be necessary to classify *L. curasoae* as an Endangered species. Based solely on the current EOO and AOO values, this

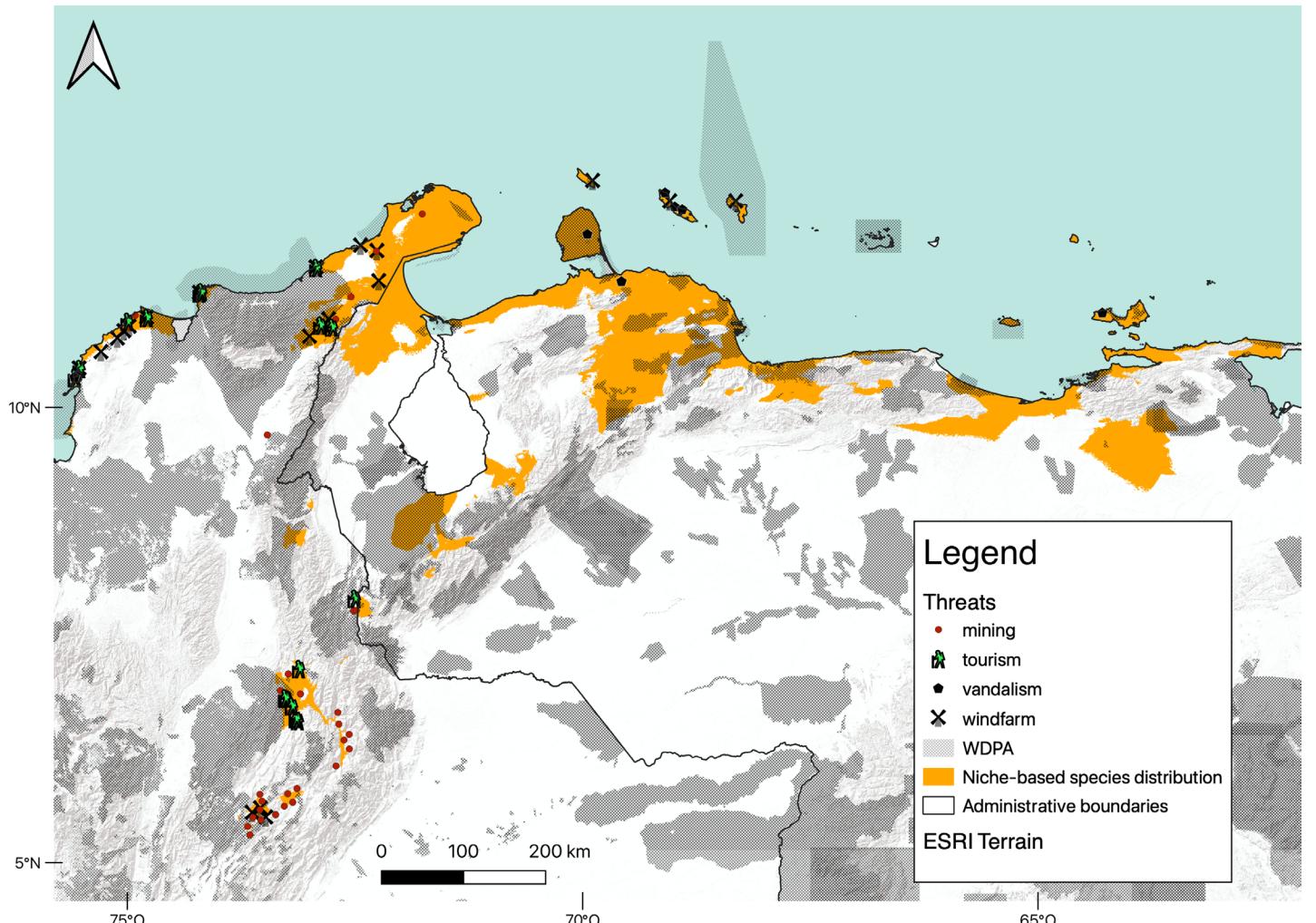


Figure 2. Potential distribution, presence of protected areas (WDPA), and threats (mining, tourism, vandalism, wind farms) for *L. curasoae*.

species would be classified as Near Threatened or Least Concern. However, the A2 criteria applied to *L. curasoae* in the past (inferred population reduction where the causes of reduction may not have ceased, be understood, or be reversible) remain relevant. Additionally, the threats faced by *L. curasoae* and knowledge about its biology and population parameters vary across the countries where it is distributed. The situation is more critical in Colombia because there is limited knowledge of roosts and populational parameters. Moreover, the identified threats are present throughout its known distribution in Colombia and are expected to increase in the near future. Consequently, considering all these factors and adopting a conservative approach, we recommend that *L. curasoae* be maintained as Vulnerable (VU A2c).

Our data showed that the environmentally suitable areas of the potential distribution of *L. curasoae* correspond to only 9.4 % of the area presented in the IUCN Red List ([Nassar 2015](#)). This discrepancy arises because the Extent of Occurrence assessed by the IUCN overestimates the actual distribution because it includes an erroneous record located 170 km to the southwest, corresponding to an indi-

vidual captured in the Chicamocha River Basin. Also, the Extent of Occurrence represents the area encompassing all the known occurrences of a taxon, which includes unsuitable or unoccupied habitats ([IUCN 2012](#)). In contrast, the potential distribution refines the area occupied by a species by delimiting it to suitable areas.

Niche-based species distribution model and threats for *L. curasoae*. Bioclimatic variables such as temperature and precipitation are recognized as environmental factors influencing the potential distribution areas of tropical bats ([da Silva et al. 2018; Debata et al. 2019; Garbino et al. 2023](#)). Specifically, temperature seasonality (Bio 4) and precipitation seasonality (Bio 15) significantly contribute to the potential distribution of other tropical nectarivorous bats associated with arid environments ([Burke et al. 2019](#)). These climatic variables are positively correlated with primary productivity, water availability, and phenology in tropical dry forests ([Stan and Sanchez-Azofeifa 2019](#)). For instance, temperature promotes flowering production in seasonally dry forests ([Pau et al. 2013](#)), while precipitation regimes influence the flowering and fruiting patterns of columnar cacti, which are primary dietary sources for *L. curasoae* ([Nassar et al.](#)

2003; [Nassar and Emaldi 2008](#)). Furthermore, temperature and precipitation contribute to modulate the species and functional composition of chiropterophilous cacti used by *L. curasoae* in the inhabited dry ecosystems ([Ruiz et al. 2002](#); [Nassar et al. 2013](#)). Consequently, these two bioclimatic factors are key drivers of the seasonal availability of food resources for this species.

Additionally, suitable areas for *L. curasoae* were associated with low mean diurnal range, suggesting that temperature is an extrinsic factor that might exert physiological constraints on this species. As noted by [Ortega-García et al. \(2017\)](#), *L. curasoae* has the narrowest thermal niche among Neotropical nectar-feeding bats, ranging from 16.6 to 32.6 °C. Thus, areas with temperature stability and values within these limits provide optimal thermal conditions for this species.

The spatial distribution of threats affecting *L. curasoae* suggests that, despite the relatively small anthropized area (8.4 %), there are marked differences in protected area coverage and the impacts of other threats among countries. Our data indicate that wind farms, mining, and tourism pose important threats in Colombia. For instance, mining has had more impact, with approximately 90 % of Colombia's coal production occurring at La Guajira, and 90 % of gypsum and 30 % of limestone mining operations located in the Chicamocha River Basin ([UPME 2022, 2023a](#)). Wind farms represent another potentially critical threat, particularly in the ABC islands and northern Colombia, where 67 wind farm projects are planned along the Caribbean coast and from the La Guajira Peninsula to northern Cesar state ([UPME 2023b](#)). Although the long-distance flying routes of *L. curasoae* in Colombia are not well known, it is likely that some of the planned wind farms could overlap with the presumed migratory corridor that this species might use from La Guajira Peninsula to the east towards the Caribbean coast and south towards the intra-Andean dry areas ([UPME 2023b](#)).

Our data indicated that only 22.2 % of the suitable areas of *L. curasoae* are within protected areas. Extending or creating new protected areas is a high-priority conservation action for dry forests ([Sánchez-Azofeifa et al. 2014](#); [da Silva et al. 2018](#); [Prieto-Torres et al. 2018](#)). We suggest the creation of new protected areas in La Guajira Peninsula, the Caribbean coast near Cartagena and Tierra Bomba Island, the intra-Andean arid zones of Colombia and Venezuela, and Lara and Falcón states in Venezuela. These efforts are crucial for preserving local bat populations and protecting critical mating and maternity roosts, stopover foraging grounds, and migratory routes.

Although SDM models are valuable tools in conservation planning, they have limitations. For instance, the SDM assumes that species are at equilibrium with the environment, and biotic interactions are usually not considered due to the Eltonian Noise Hypothesis ([Peterson et al. 2011](#)). Our study did not include cave occurrences in the SDM due

to the limited number of known *L. curasoae* roosts and the scarcity of cave inventories. Future research should extend the use of SDM to examine how food resource availability, migratory patterns, and climate change could impact *L. curasoae* populations.

Implications for conservation. Nectar-feeding bats like *L. curasoae* play a crucial role in plant pollination and seed dispersal, essential for maintaining dry forests and arid habitats ([Arita and Wilson 1987](#)). Therefore, preserving *L. curasoae* will contribute to maintaining biotic interactions, plant diversity, and the ecosystem services this species provides in the dry and xerophytic ecosystems of the ABC islands, northern Colombia, and Venezuela. Although representation of dry forests within Colombia's protected areas increased by 68.4 % from 2010 to 2020, these ecosystems remain the least represented in the Colombian protected areas' system ([Corzo et al. 2023](#)). Connectivity between protected areas is also lower in the Caribbean ecoregion due to human transformation and because it has the smallest remnants of natural dry forests ([Castillo et al. 2020](#)).

Given the possible migratory behavior of *L. curasoae*, we recommend not only expanding existing natural areas or creating new ones but also establishing conservation corridors ([Belote et al. 2016](#)) and a network of connected private reserves across political boundaries ([Kark et al. 2009](#)). Conservation corridors should be prioritized along protected areas on the Caribbean coast of Colombia and Venezuela and in Falcón and Lara states in Venezuela. This approach is crucial to guarantee the seasonal movements and connectivity of *L. curasoae* populations throughout its distribution.

Conserving mating and maternity roosts is crucial since *L. curasoae* is strongly cave-dependent ([Cole and Wilson 2006](#)). Currently, seven important areas for bat conservation (AICOMs by its acronym in Spanish) and four important sites for bat conservation (SICOMs by its acronym in Spanish) have been recognized by the Latin American and Caribbean Network for Bat Conservation (RELCOM, <https://www.relcomlatinoamerica.net/>) as of high value to protect areas and caves or human buildings that serve as maternity and mating roosts of *L. curasoae* ([Bárquez et al. 2022](#)). Despite these efforts, our study indicates that roost vandalism remains a significant threat, menacing the species in several locations. For instance, as we completed the preparation of this article, we received a report from the coordinators of the Venezuelan Program for Bat Conservation (PCMV, the Venezuelan node of RELCOM) of a presumed case of massive poisoning of the bat colonies roosting in the Butare Tunnel at Falcón State (Venezuela), one of the identified roosts used by thousands of *L. curasoae* bats (ID L385, Table ST1; A. García-Rawlins, Asociación Civil Topotepuy, *pers. comm.*). More than 200 adults and pups of *L. curasoae* and *Mormoops megalophylla* were found dead on the floor of the tunnel and hanging on the walls (date of sighting May 31st, 2024); however, it is unknown what substance was used. Roosts discovered in Colombia

are particularly sensitive because one of them is the only known maternity roost for *L. curasoae*, and the other two are used by a colony only during mating season. Since its rediscovery in 2020, this colony has returned in 2022 and 2023 (A. Otálora-Ardila, unpublished data). Consequently, these two roosts are vital to maintaining the presumed long-distance movements of this species between the western part of its distribution and the north. Therefore, it is critical to establish effective management actions to protect bat colonies in those sites (see examples in [Simal et al. 2021](#)).

Our findings suggest that *L. curasoae* populations along the Caribbean coast of Colombia and Venezuela and in intra-Andean dry areas face more threats than those in the ABC islands. In the latter, ongoing bat protection initiatives have been implemented or are in the process of being established, having as targets the main bat roosts identified in the three islands ([Simal et al. 2021](#)). Identifying roosts in intra-Andean areas, determining their lapse of use, and assessing routes of migratory movements between coastal and intra-Andean zones is crucial. This is particularly important as planned wind farm developments in Colombia ([UPME 2023b](#)) could disrupt bat navigation ([Jonasson et al. 2024](#)), and interfere with these not yet identified flight routes. We also recommend creating intergovernmental action plans to protect this bat species at a regional level, addressing gaps in knowledge and guiding conservation efforts in a coordinated way to protect *L. curasoae*, with special focus on protection of maternal and mating roosts. Despite being included in general national-level strategies focused on migratory species ([MAVDT et al. 2009](#)), *L. curasoae* lacks specific conservation measures ([Rojas-Díaz and Saavedra-Rodríguez 2014](#)) and is often omitted from strategies aimed at protecting pollinator species ([MADS et al. 2021](#)).

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Distribution and karyotypic variation of Brazilian molossid bats (Chiroptera, Mammalia)

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Recent biogeographic studies have shown that geographically distant populations of different animal groups, including bats, can present genetic differentiation. Given this, the objective here was to study the composition of Molossidae species that occur in Brazil and investigate whether these species present karyotypic differences between populations from different biomes. A bibliographical survey was carried out, and the karyotypes found for each species were analyzed and compared in relation to the diploid number of chromosomes, the fundamental number of arms of the autosomal chromosomes, the centromeric position, and the presence of other structural chromosomal variations. The results showed that of the 32 species of Molossidae recorded for Brazil, 14 have their karyotypes described. Of these, only nine refer to specimens collected in Brazil. For *Molossus molossus*, karyotypic variations were observed between the Amazon and the Atlantic Forest, and within the Amazon, in regions separated by the Amazon River. *Molossops temminckii* showed variations among populations in the state of Minas Gerais. *Eumops perotis* and *Cynomops planirostris* also showed differentiation between populations from the Amazon and the Atlantic Forest. *Molossus rufus* showed variation between populations from the Atlantic Forest and Caatinga. The variations observed were structural in autosomal and sexual chromosomes between different populations. The species *Cynomops brasiliensis*, *Eumops glaucinus*, and *Nyctinomops laticaudatus* have studies only for the Atlantic Forest region, while *Eumops hansae* has karyotypic studies only for the Amazon region. This study showed the existence of karyotypic variation between different populations of five species of molossids. Furthermore, it highlighted the need for investment in knowledge of family karyology, which is scarce, with the aim of better understanding aspects of karyotypic evolution in this group.

Estudios biogeográficos recientes han demostrado que poblaciones geográficamente distantes de diferentes grupos de animales, incluidos los murciélagos, pueden presentar diferenciación genética. Ante esto, el objetivo fue estudiar la composición de las especies de Molossidae presentes en Brasil e investigar si estas especies presentan diferencias cariotípicas entre poblaciones de diferentes biomas. Se realizó un levantamiento bibliográfico y los cariotipos encontrados para cada especie fueron analizados y comparados en relación con el número diploide de cromosomas, el número fundamental de brazos de los cromosomas autosómicos, la posición centromérica y la presencia de otras variaciones cromosómicas estructurales. Los resultados mostraron que de las 32 especies de Molossidae registradas para Brasil, 14 tienen el cariotipo descrito. De ellos, sólo nueve se refieren a ejemplares recolectados en Brasil. Para *Molossus molossus*, se observaron variaciones cariotípicas entre la Amazonía y la Mata Atlántica, y dentro de la Amazonía, en regiones separadas por el río Amazonas. *Molossops temminckii* mostró variaciones entre poblaciones en el estado de Minas Gerais. *Eumops perotis* y *Cynomops planirostris* también mostraron diferenciación entre poblaciones de la Amazonía y la Mata Atlántica. *Molossus rufus* mostró variación entre poblaciones de la Mata Atlántica y Caatinga. Las variaciones observadas fueron estructurales en los cromosomas autosómicos y sexuales entre diferentes poblaciones. Las especies *Cynomops brasiliensis*, *Eumops glaucinus* y *Nyctinomops laticaudatus* tienen estudios sólo para la región de la Mata Atlántica, mientras que *Eumops hansae* tiene estudios cariotípicos sólo para la región amazónica. Este estudio mostró la existencia de variación cariotípica entre diferentes poblaciones de cinco especies de molósidos. Además, destacó la necesidad de invertir en el conocimiento de la cariología familiar, que es escaso, con el objetivo de comprender mejores aspectos de la evolución cariotípica en este grupo.

Keywords: Brazil; karyological variation; Free-tailed bats; Molossidae; Phytophysiology.

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Introduction

Molossids are known as free-tailed bats, morphologically characterized by a tail that extends about one-third beyond the outer edge of the uropatagium and the presence of a "hairbrush" on the outer toes ([Gregorin and Cirranello 2016](#)). This family has fast and long-lasting flight, adapted to open areas, which is reflected in their aerodynamic design of head, ears, and wings, and the quadrupedal habit, rare in Chiroptera ([Vaughan 1966](#)). The Molossidae family

currently includes 23 genera and 132 described species, with a circumtropical distribution ([Gregorin and Cirranello 2016](#); [Simmons and Cirranello 2023](#); see [Wilson and Mittermeier 2019](#)). In Brazil, eight genera and 32 species are registered, widely distributed throughout the national territory ([Garbino et al. 2022](#)).

Currently, many studies have been carried out on the processes that resulted in the current patterns of distribution and differentiation of organisms. These works have

shown that climate fluctuations promoted cycles of expansion and contraction of different vegetation formations in Brazil ([Costa 2003](#); [Werneck et al. 2012](#); [Batalha-Filho et al. 2013](#)). These events would have influenced the dispersal, genetic differentiation of populations, and speciation of different organisms, such as birds ([Beven et al. 1984](#); [Batalha-Filho et al. 2013](#)), reptiles ([Werneck et al. 2012](#)), rodents ([Costa 2003](#)), and bats ([Martins et al. 2009](#); [Pavan et al. 2011](#); [Silva et al. 2023](#)).

Dealing with Chiroptera in more detail, a study carried out by [Martins et al. \(2009\)](#) on *Desmodus rotundus* (Phyllostomidae) indicated through molecular analyses that there is a genetic structuring of species populations coinciding with the division of biomes in South America. [Pavan et al. \(2011\)](#) showed that *Carollia perspicillata* and *C. brevicauda* also exhibited genetic structuring of their populations throughout their distribution, coinciding with phytogeographic variation. A study carried out by [Loureiro et al. \(2020a\)](#) showed that some species of the genus *Molossus* presented structuring between populations distributed both on the continent and on islands suggesting a certain degree of genetic differentiation between populations of different species of the genus north and south of the Amazon River. Therefore, it is possible that other species in the family have been influenced by geoclimatic processes, such as the separation between humid forests, affecting gene flow and leading to the accumulation of distinct characteristics between populations.

Among the several ways of accessing the evolutionary differences between different taxa is cytogenetics, a field of study in biology that, based on the use of different techniques, allows the observation of numerical and structural characteristics of the chromosomes of distinct organisms ([Varella-Garcia and Taddei 1989](#)). Cytogenetics is, therefore, a method of studying karyotypic diversity and the variations that exist between different individuals, populations, species, and biological groups.

This field of research has been aiding in the process of identifying species, especially in groups where there may be taxonomic controversies, such as Rodentia ([Bonvicino and Weksler 1998](#); [Christoff et al. 2000](#)) and Chiroptera ([Eick et al. 2007](#); [Ao et al. 2006](#); [Moratelli et al. 2007](#); [de Lemos Pinto et al. 2012](#)). Furthermore, this tool can be very important for understanding the biogeography of some groups, such as the African murids studied by [Granjon and Dobigny \(2003\)](#), the Neotropical cichlids studied by [Thompson \(1979\)](#), and the species *Rhinophylla fischerae* from Phyllostomidae, which may represent more than one species, according to geographic variation in the karyotype ([Gomes et al. 2010](#)). For molossids, however, studies have generally focused on describing the karyotypes of the species without aiming to cytogenetically compare species collected in different regions or biomes of Brazil. The studies by [Morielle-Versute et al. \(1996\)](#) and [Corrêa \(2016\)](#), for example, described the karyotype of the species *Cynomops planirostris* and *Molossus molossus* for

the Atlantic Forest region and the Amazon, respectively. However, no studies regarding possible karyotypic variations between populations of these species have been conducted. Seeking this information is of great value from a conservation perspective, which aims to protect the diversity and uniqueness of species and their populations ([Palacios-Mosquera et al. 2020](#)), as well as from an evolutionary perspective, which aims to understand the biological processes that led to current diversity ([Santos et al. 2019](#)).

Given this, the central objective of the present study was to conduct a survey of Molossidae species that occur in Brazil and investigate whether they exhibit structural and/or numerical karyotypic differences between their populations. In more detail, the objectives were: (i) to map the distribution of molossid species in Brazil, identifying their distribution across different biomes; (ii) to carry out a karyotypic survey of these species; and (iii) to comparatively analyze the karyotypes obtained from each species, aiming to identify karyotypic variations between populations from different biomes.

Materials and methods

The survey of the karyotypic descriptions of the species and their occurrence records was carried out by consulting the online databases Google Scholar, SCIELO (The Scientific Electronic Library Online), BHL (Biodiversity Heritage Library), GBIF (Global Biodiversity Information Facility), and ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade). The nomenclature of bat species follows [Garbino et al. \(2022\)](#).

A compilation of occurrence records obtained from bibliographic research was carried out to understand the distribution of species across different biomes. The locations of occurrence records for each species were plotted on distribution maps, created using QGIS software. Additionally, the locations of the karyotypes described in the literature were also indicated on maps.

The karyotypes obtained through bibliographic research were reorganized according to the morphology and position of the centromeres, following [Levan et al. \(1964\)](#). The karyological data for each species were analyzed in relation to the diploid number of chromosomes (2n), the fundamental number of autosomal chromosome arms (FN), the centromeric position, and the presence of other structural chromosomal variations. Subsequently, comparisons were made between the different karyotypes described in the literature for each species.

Results

Distribution of species by Biome. Currently, there are records in Brazil for eight genera and 32 species of molossids ([Garbino et al. 20234](#)), which are widely distributed across Brazilian biomes. The species distribution data in the surveyed biomes are organized and summarized in Table 1.

Table 1. Species of Molossidae recorded in Brazil and the respective biomes in which they occur. Amazon (Am); Atlantic Forest (AF); Cerrado (Ce); Caatinga (Ca); Pantanal (Pt); Pampa (Pp).

Species	Biomes	References
<i>Cynomops abrasus</i>	Am, AF, Ce, Ca, Pt	Paglia et al. 2012
<i>Cynomops greenhalli</i>	Am, Ca	Paglia et al. 2012
<i>Cynomops milleri</i>	Am	Moras et al. 2018
<i>Cynomops mastivus</i>	Am	Moras et al. 2016
<i>Cynomops planirostris</i>	Am, AF, Ce, Ca, Pt	Santos et al. 2015; Mendes et al. 2020
<i>Eumops auripendulus</i>	Am, AF, Ce, Ca, Pt	Eger 1977, 2008
<i>Eumops bonariensis</i>	AF, Ce, Pp	Eger 2008; Bordignon, 2006; Bernardi et al. 2009
<i>Eumops chimaera</i>	AF	Gregorin et al. 2016
<i>Eumops dabbenei</i>	Pt	Fischer et al. 2015
<i>Eumops delticus</i>	Am, AF, Ce	Eger 2008; Silva et al. 2013
<i>Eumops glaucinus</i>	Am, AF, Ce, Ca, Pt	Paglia et al. 2012
<i>Eumops hansae</i>	Am, AF, Ce	Paglia et al. 2012
<i>Eumops maurus</i>	Am, AF, Ce	Eger 2008; Sodré et al. 2008; Diaz, 2011
<i>Eumops patagonicus</i>	AF, Pp, Pt	Bernardi et al. 2009; Bordignon et al. 2011; Carvalho et al. 2017
<i>Eumops perotis</i>	Am, AF, Ce, Ca, Pt	Torres et al. 2020
<i>Eumops trumballi</i>	Am	Paglia et al. 2012
<i>Molossops neglectus</i>	Am, AF	Althoff et al. 2018
<i>Molossops temminckii</i>	Am, AF, Ce, Ca, Pt	Nunes et al. 2013
<i>Molossus aztecus</i>	Am, AF, Ce, Ca, Pt	Loureiro et al. 2018
<i>Molossus coibensis</i>	Am, AF, Ce, Ca	Loureiro et al. 2018
<i>Molossus currentium</i>	Am, Pt	Paglia et al. 2012; Loureiro et al. 2018
<i>Molossus fluminensis</i>	AF, Ce, Pt	Loureiro et al. 2020a
<i>Molossus molossus</i>	Am, AF, Ce, Ca, Pt, Pp	Rocha et al. 2010; Barros et al. 2014; Loureiro et al. 2018
<i>Molossus pretiosus</i>	Ce, Pt	Loureiro et al. 2018
<i>Molossus rufus</i>	Am, AF, Ce, Ca, Pt	Souza et al. 2016; Loureiro et al. 2018
<i>Neoplatytmops mattogrossensis</i>	Am, AF, Ce, Ca	Novaes et al. 2013
<i>Nyctinomops aurispinosus</i>	AF, Ce, Ca	Oliveria et al. 2019
<i>Nyctinomops laticaudatus</i>	Am, AF, Ce, Ca, Pt, Pp	Paglia et al. 2012
<i>Nyctinomops macrotis</i>	Am, AF, Ce, Ca, Pt	Rocha et al. 2015
<i>Promops centralis</i>	Am, AF, Ce, Ca, Pt	Hintze, et al. 2020
<i>Promops nasutus</i>	Am, AF, Ce, Ca, Pt, Pp	Paglia et al. 2012
<i>Tadarida brasiliensis</i>	Am, AF, Ce, Ca, Pt, Pp	Tavares et al. 2008

Based on the bibliographic survey of distribution data carried out in this study, it was observed that three of the molossid species recorded in Brazil (*Cynomops mastivus*, *Cynomops milleri* and *Eumops trumballi*) occur only in the Amazon region. Two species (*Eumops chimaera* and *Molossus fluminensis*) have records for the Atlantic Forest in Brazil, both with a probable distribution in the Cerrado and Pantanal, since they are also recorded in Bolivia (Taylor et al. 2019). *Molossops neglectus* occurs only in the Amazon and the Atlantic Forest. *Cynomops greenhalli* is found in the Amazon and Caatinga, while *Molossus currentium* has

records in the Amazon and Pantanal. *Eumops bonariensis* is concentrated in the Atlantic Forest, Cerrado, and Pampas; *Eumops patagonicus* is found in the Atlantic Forest, Pantanal, and Pampas; and *Nyctinomops aurispinosus* occurs in the Atlantic Forest, Caatinga, and Cerrado. *Molossus pretiosus* is recorded only in the Cerrado, Pantanal, and NW Amazon. The remaining 20 species have broader occurrences in Brazilian biomes (Taylor et al. 2019).

Karyotypic variation in Brazilian species. Of the 32 species of Molossidae recorded for Brazil, 14 have published karyotypic descriptions, with only nine referring to specimens collected in Brazil (Table 2). *Cynomops planirostris*, *Eumops perotis*, and *Molossus molossus* have karyotypic studies for both the Amazon and Atlantic Forest regions. *Molossus rufus* has karyotype studies in the Atlantic Forest, Cerrado, and Caatinga regions. *Cynomops abrasus*, *Eumops glauvinus*, *Molossops temminckii*, and *Nyctinomops laticaudatus* have studies only for the Atlantic Forest region, while *Eumops hansae* has a karyotypic study only for the Amazon region (Table 2).

The next section details the distribution of species with available karyotypic studies available in the literature and describes the karyotypic studies identified in the bibliographic survey.

Distribution and description of the karyotypic variation of the species

Molossus E. Geoffroy, 1805

Molossus molossus (Pallas, 1766)

Type locality: Martinique, Lesser Antilles.

Distribution: The distribution of *Molossus molossus* is extensive, covering southern North America, Central America, and South America. Records indicate its occurrence in all Brazilian biomes (Peracchi et al. 2011; Barros et al. 2014; Loureiro et al. 2018; Figure 1).

Karyology: The karyotypes described for *Molossus molossus* by Lopes (1978) for eastern Pernambuco and by Cristoff and Freitas (1987) for Rio Grande do Sul, according to Varella-Garcia et al. (1989), presented $2n = 48$ and FN = 56. However, other karyotypes described for regions in the Amazon (Corrêa and Bonvicino 2016) and Atlantic Forest (Morielle-Versute et al. 1996) have $2n = 48$ and FN = 64. Karyotypic studies for *Molossus molossus* in Brazil generally describe the species' autosomal chromosomes as consisting of one pair of very large submetacentrics, three pairs of medium submetacentrics, five pairs of medium to small subtelocentrics and 14 pairs of medium to small acrocentrics (Morielle-Versute et al. 1996; Faria 2003; Brandão 2015). Leite-Silva et al. (2003) describe a large submetacentric pair, eight pairs of medium-sized two-armed chromosomes, and 14 medium-to-small-sized acrocentric pairs. Corrêa (2016) describes a pair of large metacentric chromosomes, eight pairs of metacentric or submetacentric chromosomes, ranging from large to medium, and 14 pairs of acrocentric chromosomes, ranging from large to small.

Regarding sex chromosomes, [Morielle-Versute et al. \(1996\)](#) and [Leite-Silva et al. \(2003\)](#) describe the X chromosome as a medium-sized submetacentric and the Y chromosome as a small subtelocentric. [Faria \(2003\)](#) described the X chromosome as a medium-sized submetacentric and the Y chromosome as a small acrocentric. [Corrêa and Bonvicino \(2016\)](#) described the X chromosome as a large metacentric and the Y chromosome as a small acrocentric.

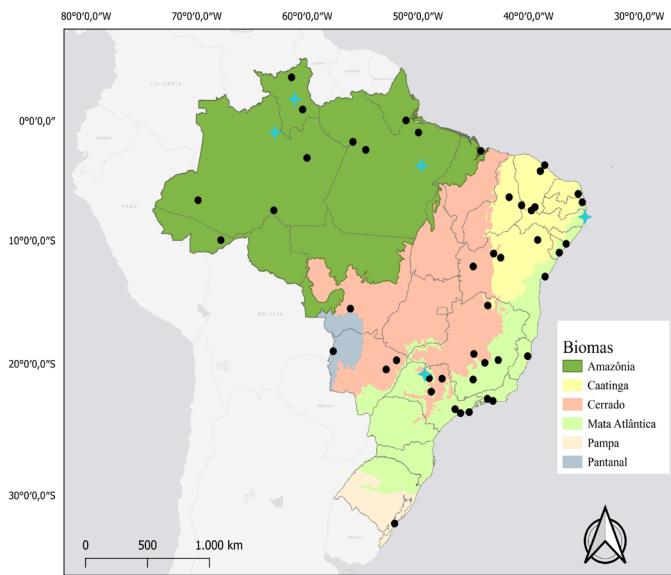


Figure 1. Map of the distribution and location of karyotypic studies of *Molossus molossus*. Black dots: occurrence records. Blue Crosses: records that have karyotypic data described.

Molossus rufus E. Geoffroy, 1805

Type locality: Caiene, French Guiana.

Distribution: *Molossus rufus* is widely distributed in South America. However, [Loureiro et al. \(2020b\)](#) recently revalidated *Molossus fluminensis* as a distinct species, with type locality at Rio de Janeiro, and previously considered a junior synonym of *Molossus rufus*. [Loureiro et al. \(2020b\)](#) describe the distribution of *M. fluminensis* as being in southeastern Brazil, Bolivia, Paraguay, and Argentina, and the distribution of *M. rufus* as being in central and northern Brazil, Bolivia, Ecuador, French Guiana, Guyana, Peru, Suriname, Trinidad and Tobago, and Venezuela. In Brazil, *M. rufus* is recorded in the Amazon, Caatinga, Cerrado, Atlantic Forest. *M. fluminensis* is recorded in Atlantic Forest, Cerrado, Pantanal, and Pampa ([Souza et al. 2016](#); [Loureiro et al. 2018](#); [Loureiro et al. 2020b](#); Figure 2).

Karyology: In studies carried out by [Morielle-Versute et al. \(1996\)](#), [Faria \(2003\)](#), and [Leite-Silva et al. \(2003\)](#) with specimens collected in the Atlantic Forest, the species *Molossus rufus* presented $2n = 48$ and $FN = 64$. In the study by [Leal \(2012\)](#) for the Caatinga, $2n = 48$ and $FN = 62$ was found. [Leal \(2012\)](#) also mentions that Dantas (2004) and Sousa (2007) also found $2n = 48$ and $FN = 62$ in their studies with specimens collected in Pará and Piauí, respectively.

The karyotypic studies of *Molossus rufus* conducted by [Morielle-Versute et al. \(1996\)](#) and [Faria \(2003\)](#) describe the

species' autosomal chromosomes as consisting of one pair of large submetacentrics, three pairs of medium submetacentrics, five pairs of medium to small subtelocentrics, and 14 pairs of medium to small acrocentrics. The study by [Leite-Silva et al. \(2003\)](#) describes the karyotype as having a large submetacentric pair, eight pairs of medium-sized two-armed chromosomes, and 14 medium- to small-sized acrocentric pairs. The study by [Leal \(2012\)](#) reports eight pairs of metacentric and submetacentric chromosomes, one of which is large and the others medium in size, along with 15 acrocentric pairs that range from medium to small. Sex chromosomes were characterized by [Morielle-Versute et al. \(1996\)](#) and [Leite-Silva et al. \(2003\)](#) as having an X chromosome that is medium-sized and submetacentric, and a Y chromosome that is small and subtelocentric. According to [Faria \(2003\)](#) and [Leal \(2012\)](#), the X chromosome is medium-sized and submetacentric, while the Y chromosome is small and acrocentric.

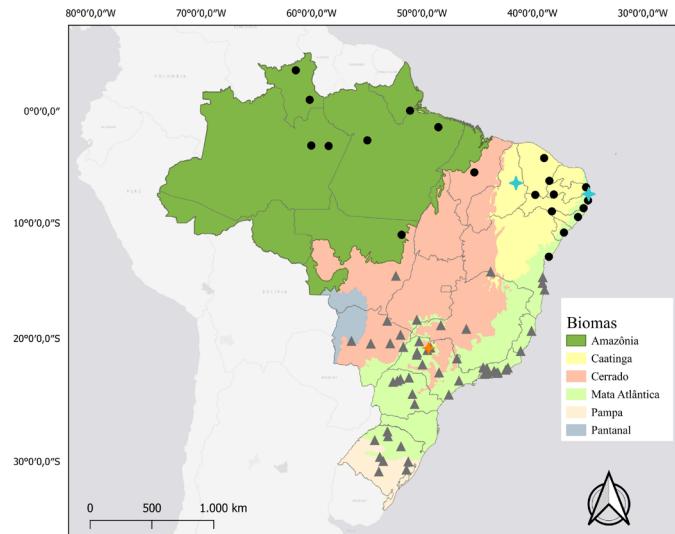


Figure 2. Map of the distribution and location of karyotypic studies of *Molossus rufus* and *M. fluminensis*. Black dots: occurrence records of *M. rufus*. Blue Crosses: records that have karyotypic data described for *M. rufus*. Gray triangle: potential occurrence records of *M. fluminensis*. Orange Crosses: records that have karyotypic data described, potentially, for *M. fluminensis*.

Molossops Peters, 1866

Molossops temminckii (Burmeister, 1854)

Type locality: Lagoa Santa, Minas Gerais, Brazil.

Distribution: *Molossops temminckii* occurs in South America, with records in Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, Paraguay, Peru, Uruguay, and Venezuela ([Eger 2008](#)). In Brazil, it has been recorded in the Amazon, Caatinga, Cerrado, Atlantic Forest, and Pantanal ([Nunes et al. 2013](#); Figure 3).

Karyology: The karyotypic studies of *Molossops temminckii* conducted by [Morielle-Versute et al. \(1996\)](#) and by [Santos \(2013\)](#) observed $2n = 48$ and $FN = 68$. The karyotypic morphology of autosomal chromosomes was described by

[Morielle-Versute et al. \(1996\)](#) as one large submetacentric pair, two medium-sized submetacentric pairs, eight subtelocentric pairs, and 12 medium-to-small acrocentric pairs. [Santos \(2013\)](#) described three metacentric, four submetacentric, five subtelocentric, and 10 acrocentric pairs. It is noted that there may be an error in chromosome counting in [Santos \(2013\)](#), with possibly 11 pairs of acrocentric chromosomes instead of 10. [Morielle-Versute et al. \(1996\)](#) described the sex chromosomes with the X as a medium-sized subtelocentric and the Y as a small subtelocentric. [Santos \(2013\)](#) only analyzed the karyotype of a female, thus describing the X chromosome as subtelocentric.

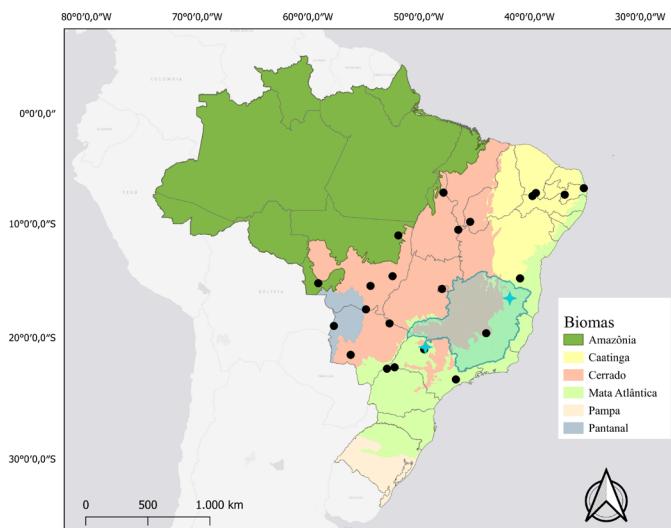


Figure 3. Map of the distribution and location of karyotypic studies of *Molossops temminckii*. Black dots: occurrence records. Blue Crosses: records that have karyotypic data described.

Eumops Miller, 1906

Eumops perotis (Schinz, 1821)

Type locality: Campos dos Goytacazes, Rio de Janeiro, Brazil.

Distribution: According to [Eger \(1977\)](#), *Eumops perotis* has two disjoint populations: one in North America, identified as *Eumops perotis californicus*, and another in South America, recognized as *Eumops perotis perotis*. In Brazil, it has been recorded in the Amazon, Caatinga, Cerrado, Atlantic Forest, and Pantanal ([Torres et al. 2020](#); Figure 4).

Karyology: According to [Varella-Garcia \(1989\)](#), Toledo (1973) describes $2n = 48$ and $FN = 54$. Studies by [Corrêa \(2016\)](#) for the Amazon and by [Morielle-Versute et al. \(1996\)](#) and [Okumura Finato et al. \(2000\)](#) for the Atlantic Forest presented $2n = 48$ and $FN = 58$. [Morielle-Versute et al. \(1996\)](#) described autosomal chromosomes as one pair of large submetacentric chromosomes, three pairs of medium submetacentric chromosomes, two pairs of subtelocentric chromosomes, and 17 pairs of acrocentric chromosomes, ranging from medium to small. [Corrêa \(2016\)](#) describes a pair of large metacentric chromosomes, five pairs of

medium metacentric or submetacentric chromosomes, and 17 pairs of acrocentric chromosomes, ranging from medium to small. In the study by [Morielle-Versute et al. \(1996\)](#), the X chromosome is described as medium submetacentric and the Y chromosome as small acrocentric. In [Corrêa \(2016\)](#), the X chromosome may have been mistakenly described as a medium metacentric, as only females were analyzed, so it is not possible to rule out that it is the same.

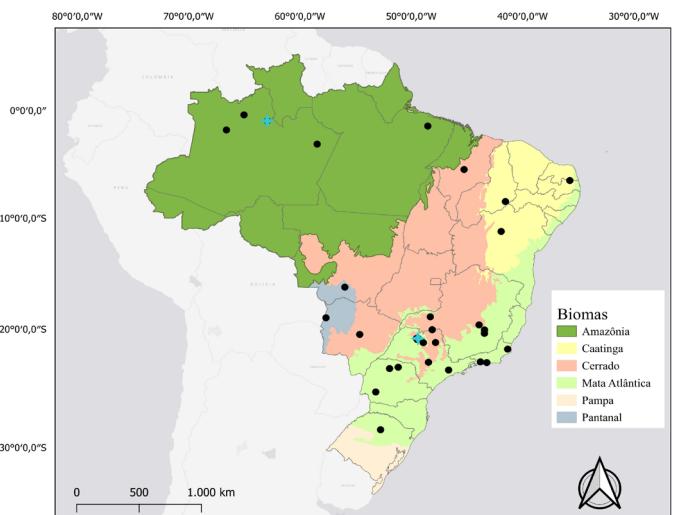


Figure 4. Map of the distribution and location of karyotypic studies of *Eumops perotis*. Black dots: occurrence records. Blue Crosses: records that have karyotypic data described.

Cynomops Thomas, 1920

Cynomops planirostris (Peters, 1866)

Type locality: Caiene, French Guiana.

Distribution: *Cynomops planirostris* is known from Venezuela, Guianas, Suriname, eastern Colombia, Peru, Bolivia, Paraguay, Argentina, and Brazil ([Eger 2008](#)). In Brazil, it has been recorded in all biomes except the Pampa ([Santos et al. 2015; Mendes et al. 2020](#); Figure 5).

Karyology: The karyotype study by [Santos \(2013\)](#), carried out with specimens collected in Itinga (MG) in the central region of the Atlantic Forest, showed $2n = 34$ and $FN = 64$. The autosomal chromosomes were described as 13 meta- or submetacentric pairs, two subtelocentric pairs, and one acrocentric pair. The studies by [Leite-Silva et al. \(2003\)](#), for the northern region of the Atlantic Forest and [Corrêa \(2016\)](#) for the Amazon presented $2n = 34$ and $FN = 60$, with autosomal chromosomes described as 14 pairs of metacentric or submetacentric chromosomes, ranging from large to small, and two pairs of acrocentric chromosomes. The X chromosome in was described as a large metacentric, in [Leite-Silva et al. \(2003\)](#) as a medium submetacentric, and in [Corrêa \(2016\)](#) as a medium metacentric. The Y chromosome in was described as a small metacentric, while in [Leite-Silva et al. \(2003\)](#) and [Corrêa \(2016\)](#) it was described as a small acrocentric.

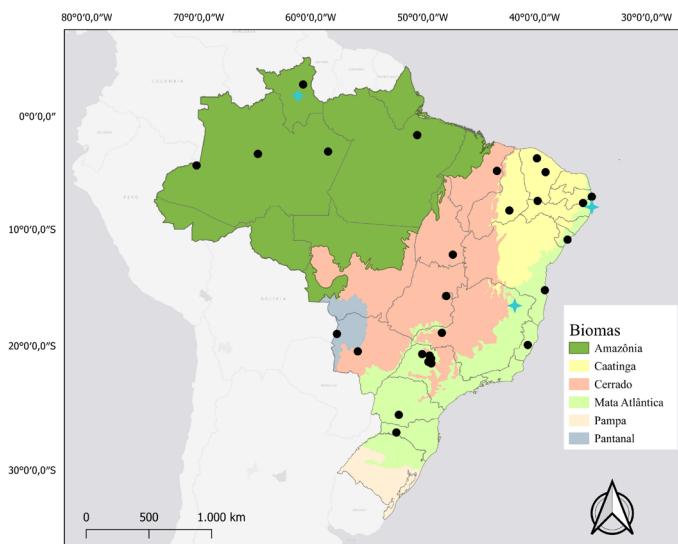


Figure 5. Map of the distribution and location of karyotypic studies of *Cynomops planirostris*. Black dots: occurrence records. Blue Crosses: records that have karyotypic data described.

Discussion

Status of cytogenetic knowledge of molossids in Brazil. Our results showed that although the Molossidae family has 32 species in Brazil, there is limited knowledge about their karyology. Through our bibliographical research, we identified a total of 25 karyotypic studies that included molossid species occurring in Brazil. Of these, 11 studies were carried out with specimens collected within the country (Table 2). It is worth noting that, in general, the studies found were focused on describing the karyotypes of the species but did not aim to investigate karyotypic variations between populations from different phytogeographic regions in Brazil, as is the focus of the present study.

As highlighted in our results, only 14 molossid species have a karyotypic description. When we restrict this number to karyotypes from specimens collected in Brazil, only nine species have been studied (Table 2). Furthermore, even the species that have been studied do not have karyotype descriptions for all the different regions in which they occur in the country. For example, *Cynomops abrasus*, *Eumops glaucinus*, *Molossops temminckii*, and *Nyctinomops laticaudatus* have a wide distribution but only have karyotypic studies within the Atlantic Forest (tables 1 and 2).

The work carried out by [Morielle-Versute et al. \(1996\)](#) was one of the first studies on Brazilian molossids, presenting the karyotypes of seven species. This study was of great importance for understanding the karyotypic variation within the family in Brazil. Since then, other studies have been conducted; however, the karyology of populations of 23 species remains unknown and needs to be investigated.

According to [Sotero-Caio et al. \(2017\)](#), approximately 50 % of molossid bat species have been studied using conventional staining (Giemsa) worldwide, 11 species have been analyzed with G-banding, and four species have been analyzed with the Zoo-FISH technique. Of the species stud-

ied, 41 had $2n = 48$, with the FN varying between 54 and 66. In nine species, the diploid number varied widely, ranging from 34 to 52 (Tables 2). The authors highlight the challenges in determining the number of chromosomal arms in Molossidae, as many species have numerous subtelocentric chromosomes. These difficulties are also related to the level of chromosome condensation and the quality of chromosome preparation. Nevertheless, accurate identification of chromosomal arms is considered crucial for understanding the karyotypic evolution of the family.

Due to the limited variation in diploid and fundamental numbers found in the literature, the most accepted hypothesis is that karyotypic conservatism characterizes the evolution of Molossidae. This conservatism is primarily attributed to pericentric inversions, Robertsonian rearrangements, and translocations ([Morielle-Versute et al. 1996](#); [Sotero-Caio et al. 2017](#)). According to [Sotero-Caio et al. \(2017\)](#), although chromosomal evolution in Molossidae is generally conservative, intrageneric variations were identified within *Cynomops* and between the genera *Cynomops* and *Molossops*, as reported by [Leite-Silva et al. \(2003\)](#). Intraspecific variations were also observed in *Eumops glaucinus*, as documented by [Warner et al. \(1974\)](#), with differences found between specimens from Colombia ($2n = 40$, NF = 64) and those from Mexico and Costa Rica ($2n = 38$, NF = 64). These variations may have been influenced by geographic factors.

Chromosomal variations in Brazilian molossids. In this section, we will individually discuss the variations found between the karyotypic studies carried out for each species.

***Molossus molossus*.** According to [Morielle-Versute et al. \(1996\)](#), the differences in FN observed between the studies by Lopes (1978) and Cristoff and Freitas (1987) compared to others are attributed to the observation of less condensed metaphases obtained from fibroblast cultures. Although the most recent studies do not show numerical chromosomal variations, they do reveal structural differences in autosomal and sexual chromosomes.

In general, the karyotypic descriptions by [Morielle-Versute et al. \(1996\)](#), [Faria \(2003\)](#), and [Brandão \(2015\)](#) are more like each other compared to the description by [Corrêa \(2016\)](#). The latter study not only showed greater differences in autosomal chromosomes but also in the X chromosome. This differentiation aligns with findings by [Loureiro et al. \(2020a\)](#), which indicated genetic differentiation between molossid populations separated by the Amazon River. Corrêa's study was carried out with specimens collected in Barcelos (AM) and Caracaraí (RR), north of the Amazon River, while the other studies focused on populations south of the river. However, further cytogenetic and molecular studies are needed to explore this hypothesis, including research across other South American biomes.

Regarding the description of the Y chromosome, no direct relationship can be identified concerning population differentiation between the Amazon and Atlantic For-

Table 2. Karyotypic data of fourteen species of molossids that occur in Brazil. Diploid number (2n); Fundamental Number (Fn); synthetic nucleotide 5-bromo-2-deoxyuridine (BrdU); Band C (C); G Band (G); conventional staining (Giemsa-); Nucleolus organizing regions (NOR); Fluorescence in situ hybridization (FISH). Biomes: Amazon (Am); Atlantic Forest (AF); Cerrado (Ce); Caatinga (Ca); Pantanal (Pt); Pampa (Pp).

Species	2n	Fn	Method	Biome	References
<i>Cynomops abrasus</i>	34	60	Giemsma	-	27
	34	64	C and G	FA	20
<i>Cynomops greenhalli</i>	34	60	Giemsma	-	2, 9, 16, 27
<i>Cynomops planirostris</i>	34	64	Giemsma	FA	22
	34	60	G, C, NOR and FISH	FA	14, 15
	34	60	C	Am	5
<i>Eumops auripendulus</i>	42	60	Giemsma	-	27
	42	62	Giemsma	-	25
<i>Eumops glaucinus</i>	40	64	G, C and NOR	FA	12, 18, 20,
	40	64	Giemsma	-	27
	38	64	Giemsma	-	27
<i>Eumops hansae</i>	48	58	Giemsma and FISH	Am	5
<i>Eumops perotis</i>	48	54	Giemsma	-	24
	48	56	Giemsma	-	1, 26
	48	58	C and G	FA	12, 20
	48	58	C	Am	5
<i>Molossops temminckii</i>	42	56	Giemsma	-	9
	42	56	Giemsma	FA	22
	48	68	C and G	FA	10
<i>Molossus molossus</i>	48	56	C, G and NOR	Pa, FA	3, 7, 17
	48	58	Giemsma	-	27
	48	64	G, C, RON, BrdU and FISH	FA	10, 15, 20, 21, 18
	48	64	C, G and RON	Am	4, 5, 6
<i>Molossus rufus</i>	48	58	Giemsma	-	27
	48	60	Giemsma	FA	17, 25
	48	62	Giemsma	Ce, Ca	8, 13, 23
	48	64	G, C, NOR, BrdU and FISH	FA	10, 11, 15, 20, 21
<i>Nyctinomops laticaudatus</i>	48	64	C and G	FA	20
<i>Promops centralis</i>	48	58	Giemsma	-	27
<i>Promops nasutus</i>	40	54	Giemsma	-	26
<i>Tadarida brasiliensis</i>	48	56	G	-	2, 27
	48	58	Giemsma	-	27

References: 1. [Baker \(1970\)](#); 2. [Baker et al. \(1982a\)](#); 3. [Baker and Lopez \(1970\)](#); 4. [Brandão \(2015\)](#); 5. [Corrêa \(2016\)](#); 6. [Corrêa and Bovicino \(2016\)](#); 7. [Cristoff and Freitas \(1987a\)](#); 8. [Dantas \(2004\)](#); 9. [Gardner \(1977b\)](#); 10. [Faria \(2003\)](#); 11. [Faria and Morielle-Versute \(2006\)](#); 12. [Finato \(2000\)](#); 13. [Leal \(2012\)](#); 14. [Leite-Silva et al. \(2000\) b](#); 15. [Leite-Silva et al. \(2003\)](#); 16. [Linares and Kiblisky \(1969b\)](#); 17. [Lopes \(1978a\)](#); 18. [Moratelli et al. \(2000\) b](#); 19. [Morielle et al. \(1988a\)](#); 20. [Morielle-Versute et al. \(1996\)](#); 21. [Morielle-Versute and Varella-Garcia \(1994\)](#); 22. [Santos \(2013\)](#); 23. [Sousa \(2007c\)](#); 24. [Painter \(1925b\)](#); 25. [Toledo \(1973a\)](#); 26. [Wainberg \(1966b\)](#); 27. [Warner et al. \(1974\)](#). The citation's final letters indicate the cited author and data source: a - [Varella-Garcia and Taddei \(1989\)](#); b - [Moratelli et al. \(2007\)](#); c - [Leal \(2012\)](#).

est biomes or within the Atlantic Forest biome itself. Both the study by [Morielle-Versute et al. \(1996\)](#), which described the Y chromosome as subtelocentric, and the study by [Faria \(2003\)](#), which described it as acrocentric, were conducted with specimens collected in the Atlantic Forest region of São Paulo. Additionally, the study by [Leite-Silva et al. \(2003\)](#),

which also identified the Y chromosome as subtelocentric, was based on specimens from Pernambuco. Therefore, variations in the Y chromosome of *Molossus molossus* require further investigation.

Molossus rufus. *Molossus rufus* exhibited both numerical and structural chromosomal variations between studies conducted in the Atlantic Forest and those from the Amazon, Caatinga, and Cerrado. Studies from the southern Atlantic Forest provided consistent descriptions for autosomal chromosomes. However, the northern Atlantic Forest study could not adequately identify the centromeric positions of these chromosomes. Research in the Caatinga and Cerrado showed identical 2n and FN values but differed from other biomes in the centromeric positions of chromosomes. Regarding sex chromosomes, no variation was observed for the X chromosome. The Y chromosome did show variation among studies, but this variation does not appear to be related to the different biomes.

The karyotypic variation found among specimens collected in the Atlantic Forest and other biomes may be interspecific. Considering the distribution proposed by [Loureiro et al. \(2020b\)](#), in which *M. fluminensis* occurs in southeastern Brazil, Bolivia, Paraguay, and Argentina, and *M. rufus* in the central and northern regions of Brazil, Bolivia, Ecuador, French Guiana, Guyana, Peru, Suriname, Trinidad and Tobago, and Venezuela, it is possible that the karyotyped specimens from the Atlantic Forest actually correspond to *M. fluminensis*. However, there are questions regarding the actual identification of the specimens in relation to the karyotypic samples from the Cerrado, Caatinga, and Atlantic Forest in the northeast region, since the samples used by [Loureiro et al. \(2020b\)](#) that separate the two species molecularly are from the Guianas and southeastern Brazil. According to the distribution proposed by the author, the FN of *M. rufus* would vary from 58 in Trinidad and Venezuela (Warner et al. 1974) to 64 in Pernambuco, with 62 in Piauí. In this case, new karyotypic studies are necessary to confirm this variation and to determine whether the karyotype from Pernambuco is in fact from *M. rufus* or *M. fluminensis*, and thus to clarify the karyotypic variation of these two species.

Molossops temminckii. The karyotypic study carried out by [Santos \(2013\)](#), based on specimens collected in Itinga (MG), described three pairs of metacentric chromosomes. In contrast, the study by [Morielle-Versute et al. \(1996\)](#) for Minas Gerais found no metacentric chromosomes. This discrepancy resulted in differences in the number of submetacentric, subtelocentric, and acrocentric chromosomes between the karyotypes. No variations were observed in the description of the X chromosome. Since [Santos \(2013\)](#) only analyzed a single female, it was not possible to assess the Y chromosome.

Thus, the karyotypes of *Molossops temminckii* exhibit variations in the morphology of autosomal chromosomes within the state of Minas Gerais. Since the karyotype described by [Morielle-Versute et al. \(1996\)](#) lacks a precise description of the collection location, it is not possible to

determine whether the variation observed relative to [Santos \(2013\)](#) is truly between the Cerrado and Atlantic Forest biomes, or merely within different areas of the Atlantic Forest in Minas Gerais.

Eumops perotis. Considering the studies by [Corrêa \(2016\)](#) and [Morielle-Versute et al. \(1996\)](#), *Eumops perotis* exhibited subtle karyotypic variation between the Amazon and Atlantic Forest regions, particularly in the position of the centromere in five pairs of autosomal chromosomes. Since [Corrêa \(2016\)](#) karyotyped only females, it was not possible to draw conclusions about the X chromosome. Considering the lack of records for *Eumops perotis* in much of central Brazil, the populations in the Amazon and Atlantic Forest biomes may be undergoing isolation. This potential isolation is supported by genetic studies on birds and bats across their distribution in Brazil, which have indicated similar patterns of differentiation and isolation ([Martins et al. 2009; Pavan et al. 2011; Batalha-Filho et al. 2013](#)).

Cynomops planirostris. We observed numerical and structural karyotypic variations, both in autosomal and sexual chromosomes, among three different populations of *Cynomops planirostris* occurring in the Amazon and the Atlantic Forest. The karyotypes for the northern Atlantic Forest ([Leite-Silva et al. 2003](#)) and the Amazon ([Corrêa 2016](#)) differed from the karyotype for the central Atlantic Forest ([Santos 2013](#)) in relation to FN. This variation is largely attributed to differences in the morphology of two pairs of autosomal chromosomes across the studies of these three populations.

The Y chromosome also showed a closer relationship between the populations of the Amazon and the northern Atlantic Forest, differing morphologically from the Y chromosome described for the central region of the Atlantic Forest by [Santos \(2013\)](#). Notably, the Y chromosome described by [Corrêa \(2016\)](#) for the Amazon has a completely heterochromatic short arm, whereas the Y chromosome described by [Leite-Silva et al. \(2003\)](#) for the northern Atlantic Forest lacks constitutive heterochromatin. This variation may indicate a degree of isolation between these populations.

The chromosomal variations observed among the karyotypic descriptions of molossids collected in Brazil may result from several chromosomal rearrangement processes, such as insertions/deletions or pericentric inversions. For instance, in *Eumops perotis*, the main differences between studies were related to the position of the centromeres and/or the size of the chromosome arms. Additionally, these variations may be due to Robertsonian translocations, as suggested by the differences found in *Molossops temminckii* and *Cynomops planirostris*.

However, the processes and origins of the variations observed require further investigation. Improved banding techniques and the use of chromosomal probes are essential for understanding the evolution of the molossid karyotype throughout their distribution in Brazil. [Sotero-Caio et al. \(2017\)](#) and [Leite-Silva et al. \(2003\)](#) highlighted that in

Molossidae, determining the fundamental number is challenging because the short arms of the chromosomes can be extremely small, complicating the distinction between subtelocentric and acrocentric forms. However, according to these authors, the detection of these differences is important, as they portray the mode of chromosomal evolution of Molossidae, which appears to be based mainly on pericentric inversions.

[Leite-Silva et al. \(2003\)](#) highlight that various studies suggest nucleolus organizing regions (NOR's) are important markers for studies of chromosomal evolution in Chiroptera and emphasize their potential role in the chromosomal evolution of molossids. Analyses carried out on *Cynomops brasiliensis*, *Cynomops planirostris*, and *Molossops temminckii*, revealed that none of these species share the same number of NOR-bearing chromosomes ([Leite-Silva et al. 2003; Morielle-Versute et al. 1996](#)).

Furthermore, *Cynomops brasiliensis* and *C. planirostris* exhibit variation in the number of chromosomes with constitutive heterochromatin. *Cynomops planirostris* shows constitutive heterochromatin on the short arm of the X chromosome and on five autosomal chromosomes, while *C. brasiliensis* and *M. temminckii* have constitutive heterochromatin on all autosomal chromosomes ([Corrêa and Bonvicino 2016; Leite-Silva et al. 2003; Morielle-Versute et al. 1996](#)). Previously, these three species were classified under the genus *Molossops*, given that the hypothesis of intragenetic variation considered by [Leite-Silva et al. \(2003\)](#) and [Morielle-Versute et al. \(1996\)](#) currently also extends to an intergeneric variation.

It is important to highlight that none of the karyotypes found in the literature refer to a type specimen or a specimen collected at the type locality of these species. This highlights the need for investment in karyotypic studies to establish a "type karyotype" for each species and to subsequently describe the diversity and karyotypic evolution among species.

Influences of geoclimatic changes on the karyotypic variation of Brazilian molossid bats. Different studies indicate that Brazilian biomes experienced a highly dynamic history during the Tertiary and Quaternary periods, shaped by various climatic events that led to complex processes of retraction and expansion over time. These events influenced Brazilian biomes and were crucial in shaping the current floristic and faunal composition of Brazil ([Machado et al. 2018; Silveira et al. 2019; Werneck et al. 2012](#)).

Phylogeographic studies based on molecular data with certain groups of rodents and marsupials, as well as suboscine birds occurring in the Amazon and the Atlantic Forest, have identified similar connection routes between these biomes over time. The oldest connections are dated to the middle to late Miocene through central Brazil and Chaco region. Most recent connections likely occurred through the Cerrado and Caatinga in the northeastern Brazil from the Pliocene to the Pleistocene, driven by Quaternary climate

changes that facilitated the expansion of gallery forests through these areas ([Batalha-Filho et al. 2013](#); [Costa 2003](#)).

According to [Werneck et al. \(2012\)](#), during the Last Interglacial, around 120,000 years ago, the climate was hotter and drier, likely promoting an expansion of the Cerrado into areas including the northern Amazon and the eastern coast of South American. Between the Last Interglacial and the Last Glacial Maximum, the Cerrado underwent a process of retraction, reaching its smallest extent during this period. Following this, the Cerrado began to expand again until the Middle Holocene, approximately 6,000 years ago, when it started to stabilize into its current form.

According to a study using molecular data from the vampire bat *Desmodus rotundus*, which is widely distributed across all Brazilian biomes, genetically structured populations were found for the southern Atlantic Forest, northern Atlantic Forest, Amazon, Cerrado, Pantanal, and Central America. This study indicates that Atlantic Forest populations separated from those in the Amazon and Cerrado during the Pleistocene, which is consistent with the emergence of a dry strip separating the Atlantic Forest from the Amazon during that period ([Martins et al. 2009](#)). The authors considered that there are no identifiable physical barriers to dispersal and gene flow within this bat distribution range, suggesting that the population structuring may be influenced by ecological separation barriers.

The same type of study conducted by [Pavan et al. \(2011\)](#) suggested that *Carollia perspicillata* and *C. brevicauda*, from the Phyllostomidae, may have appeared in the Amazon region during the Pleistocene approximately 700,000 years ago. It was also observed that *C. perspicillata* has two main evolutionary lineages that may have diverged during the Pleistocene: one lineage extends from Bahia to Paraná in the southern Brazilian Atlantic Forest, while the other, more geographically widespread, is distributed across the northern part of the Atlantic Forest, Cerrado, and Amazon, as well as in other biomes of South and Central America ([Pavan et al. 2011](#)).

In a comparative phylogeographic analysis of island and continental bat species of the genus *Molossus*, [Loureiro et al. \(2020a\)](#) demonstrated the influence of the Amazon River as a dispersal barrier, as well as the impact of ecological factors and vegetation formations on the genetic structuring of these species in South America.

Thus, recent studies indicate that, although bats are capable of true flight, they are still affected by geographic distance and ecological variants, such as the distinction of vegetation between biomes ([Pavan et al. 2011](#); [Morales et al. 2018](#); [Loureiro et al. 2020a](#)).

The results of this study reveal that, despite the limited number of karyotypic studies on molossids, it was possible to observe variations in the species between karyotypes from different biomes, and even within the same biome. The Molossidae family, which dates back 50 to 31 million years, began its diversification into Neotropical clades approximately 20 million years ([Amador et al. 2016](#)). This

study underscores the critical need for increased investment in karyotypic research on molossid bats to better understand interspecific and intraspecific variations and the evolutionary trajectory of their karyotypes. Above all, this investment is necessary due to the presence of population variations and cryptic species, as seen with *Molossus fluminensis* and *M. rufus*, so that conservation and management plans appropriate to the group can be carried out.

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New findings of mites on small mammals in the Yungas Forest of Argentina

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In Argentina, studies on the systematics of parasitic mites on small mammals have been limited mainly to rodent mites from the Pampas region, followed by some studies in the northeastern region. The mites collected in the province of Jujuy, particularly in the locality of Las Capillas, have not been previously analyzed. The objective of this study was to contribute to the knowledge of the faunal composition of mites parasitizing small mammals in the Yungas eco-region, Jujuy province, Argentina. Specimens of mites deposited in the "Colección de Mamíferos Anexo Lillo, Dra. Analía G. Autino (CMLA)", Universidad Nacional de Tucumán, from bats and rodents were examined. The specimens were fixed in 70 % alcohol and prepared following conventional techniques for taxonomic identification. The specimens were compared to the original descriptions of the species and to specimens in the CMLA. A total of 153 mites of the order Mesostigmata were analyzed, resulting in the identification of 11 species, eight genera, and three families. Three species parasitized the order Chiroptera and eight parasitized the order Rodentia. A total of 152 mites were identified in the adult stage, including 14 males and 138 females, and one protonymphal stage. All species represent new records for the locality Las Capillas, except *Gigantolaelaps gilmorei*. The following species are reported for the first time for the Jujuy Province: *Androlaelaps fahrenholzi*, *Laelaps mazzai*, *Mysolaelaps microspinosis*, *Eulaelaps stabularis*, *Chiroptonyssus robustipes*, *Macronyssus crosbyi* and *Periglischrus iheringi*, as well as the genera *Androlaelaps*, *Mysolaelaps*, *Eulaelaps*, *Chiroptonyssus*, *Macronyssus* and *Periglischrus* and the families *Macronyssidae* and *Spinturnicidae*. Twenty mite-host associations were recognized for Las Capillas. The results increase the inventory of the acarological fauna of small mammals in the northwestern Argentina and particularly in the Yungas of the province of Jujuy, which constitutes an area of influence of bacterial pathogens.

En Argentina, los estudios sobre la sistemática de los ácaros parásitos en pequeños mamíferos han estado restringido principalmente a ácaros de roedores de la región pampeana, seguidos de algunas investigaciones en la región noreste. Los ácaros colectados en la provincia de Jujuy, particularmente en la localidad de Las Capillas, no han sido analizados previamente. El objetivo del presente estudio fue contribuir al conocimiento de la composición faunística de ácaros parásitos de pequeños mamíferos en la ecorregión de las Yungas, provincia de Jujuy, Argentina. Se examinaron ejemplares de ácaros depositados en la "Colección de Mamíferos Anexo Lillo, Dra. Analía G. Autino (CMLA)", Universidad Nacional de Tucumán, provenientes de murciélagos y roedores. Los ejemplares fueron fijados en alcohol 70 % y preparados siguiendo las técnicas convencionales para su identificación. Los especímenes se compararon con descripciones originales de especies y con especímenes depositados en la CMLA. Un total de 153 ácaros pertenecientes al orden Mesostigmata fueron analizados, resultando en la identificación de 11 especies, ocho géneros y tres familias. Tres especies parasitaron el orden Chiroptera y ocho el orden Rodentia. Se identificaron 152 ácaros en estado adulto, incluyendo 14 machos y 138 hembras, y uno en estadio protoninfal. Todas las especies representan nuevos registros para la localidad Las Capillas, excepto *Gigantolaelaps gilmorei*. Se reportan por primera vez para la provincia de Jujuy las siguientes especies: *Androlaelaps fahrenholzi*, *Laelaps mazzai*, *Mysolaelaps microspinosis*, *Eulaelaps stabularis*, *Chiroptonyssus robustipes*, *Macronyssus crosbyi* y *Periglischrus iheringi*, así como los géneros *Androlaelaps*, *Mysolaelaps*, *Eulaelaps*, *Chiroptonyssus*, *Macronyssus* y *Periglischrus* y las familias *Macronyssidae* y *Spinturnicidae*. Asimismo, se reconocieron 20 asociaciones ácaro-hospedador para Las Capillas. Los resultados aumentan el inventario de la fauna acarológica de pequeños mamíferos en el noroeste argentino y particularmente en las Yungas de la provincia de Jujuy que constituye un área de influencia de bacterias patógenas.

Keywords: Bats; Mesostigmata; Northwestern Argentina; rodents.

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Introduction

In Argentina, studies on the systematics of parasitic mites on small mammals have been restricted mainly to mites of rodents from the Pampas region, followed by some investigations in the northeastern region ([Lareschi and Mauri 1998](#); [Lareschi 2023](#)), while records for the northwestern region are extremely scarce ([Lareschi and Mauri 1998](#); [Lareschi et al. 2003](#); [López Berrizbeitia et al. 2013](#)). Las Capillas is located in the province of Jujuy in the northwestern Argentina (NWA). It corresponds to a mountain forest vegetation in very good condition and has remained isolated from human impact for more than 50 years. It has been recognized as an "Area of Importance for the Conservation of Bats" (AICOM; in Spanish, it stands for "Área de Importancia para la Conservación de los Murciélagos") by the Latin American Bat Conservation Network (RELCOM, or "Red Latinoamericana para la Conservación de los Murciélagos"; see www.relcomlatinoamerica.net) on 2013.

[Gamboa Alurralde et al. \(2016\)](#) recorded the three main orders of small mammals in Las Capillas: marsupials (Didelphimorphia), bats (Chiroptera), and rodents (Rodentia). The first is represented by two species from the family Didelphidae, the second by 24 species from four families (Noctilionidae, Phyllostomidae, Molossidae, and Vespertilionidae), and the third by 13 species from two families (Cricetidae and Ctenomyidae).

The mites collected at this locality have not been analyzed previously, thus new findings of geographic and host distribution for parasitic mites of small mammals (Chiroptera and Rodentia) from the Yungas Forest in the Jujuy province, Argentina are added.

Materials and methods

Study area. The fieldwork was conducted within "Finca Las Capillas" (-24° 04' 27.93" S, -65° 08' 42.08" W), an area of 3,500 ha located approximately 2 km north of "Las Escaleras", Manuel Belgrano Department, Jujuy Province, Argentina (Figure 1). The area corresponds to the montane forest district, a part of the Yungas eco-region, which is extended approximately between 700 and 1,500 m ([Burkart et al. 1999](#); [Brown and Pacheco 2006](#)). The observed vegetation is typical of the district, which is dominated by tall trees such as *Cedrela angustifolia*, *Enterolobium contortisiliquum*, *Anadenanthera colubrina*, *Cinnamomum porphyrium*, and *Myrcianthes pungens*. There are also smaller trees, such as *Allophylus edulis* and *Celtis brasiliensis*, among others, that do not exceed 20 m. Bushes such as *Urera baccifera*, *Piper tucumanum*, and *Solanum* spp., as well as herbs ranging from smaller forms to taller than 2 m ([Cabrera 1976](#)), are present. Epiphytes are abundant, and lichens, ferns, bromeliads and mosses are dominant, which are present in more than 70 % of the trees ([Brown et al. 2001](#)). The climate in this altitudinal belt is warm and humid, and the temperature and humidity vary in relation to altitude, latitude, topography, and slope exposure. Annual precipitation varies between 900 and 1,000 mm. Rainfalls are concentrated

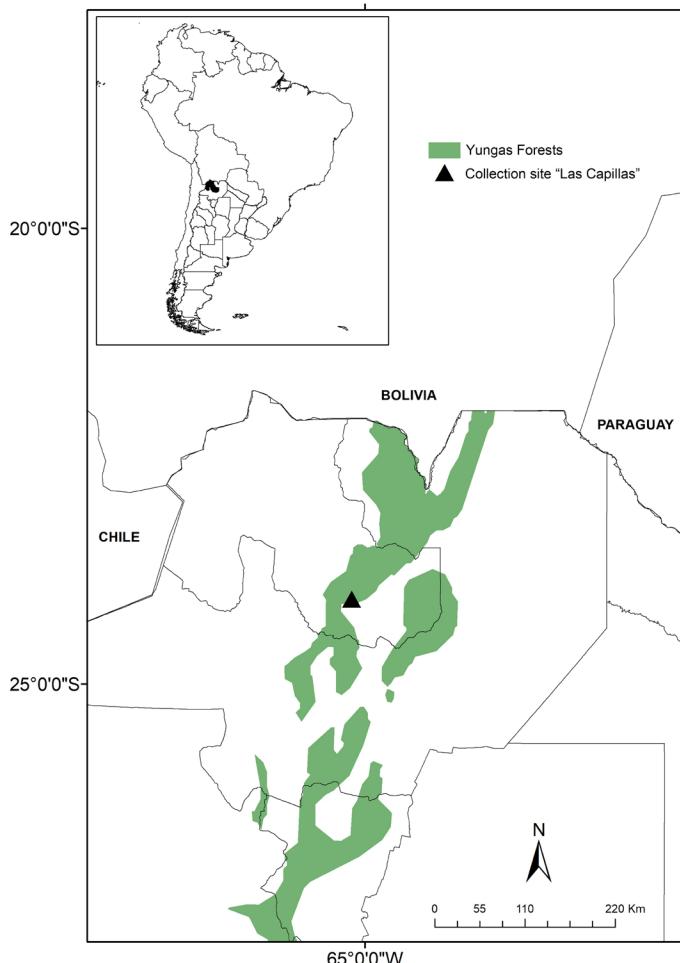


Figure 1. Map illustrating the Jujuy Province and the Yungas Forests eco-region. The black dot (triangle) shows the collection site of mite species, "Las Capillas".

mainly in summer, and last for about 5 to 6 months. During the cooler months, the condensed water mist that characterizes these "cloud forests" is captured and cooperates to partially compensate for the lack of rains in that season ([Burkart et al. 1999](#)). The area includes a hydrographic system that is part of the Basin of the Mojotoro-San Francisco-Lavayen rivers and the sub-basin of the Negro-Upper San Francisco rivers. The main river at the study area is Las Capillas, which changes its name to Negro River before it flows into the San Francisco River ([Paoli et al. 2011](#)).

Collection and preparation of specimens. An important number of mites (Arachnida: Acari) from the study area were deposited in the "annexes" Analía G. Autino (CMLA) of the Colección Mamíferos Lillo, Universidad Nacional de Tucumán (UNT). These specimens are the results of surveys carried out for several years; all specimens were analyzed during this study.

Specimens were removed from hosts with a toothbrush/forceps, preserved in a solution of 70 % ethyl alcohol, and prepared following conventional techniques for taxonomic identification ([Krantz and Walter 2009](#); [Morales-Malacara et al. 2020](#)).

Nomenclature follows [Krantz and Walter \(2009\)](#) and keys and descriptions of [Fonseca \(1939a, b\)](#), [Furman \(1972\)](#), [Herrin and Tipton \(1975\)](#), [Morales-Malacara \(2001\)](#) and [Lareschi \(2010b, 2011\)](#) were used. Specimens were compared with original descriptions of species and with specimens stored in the CMLA.

Voucher specimens of small mammals are deposited at the Colección Mamíferos Lillo (CML), Facultad de Ciencias Naturales e Instituto Miguel Lillo, UNT. A single host has not yet received a collection number; therefore, the collection catalog number is indicated, and its acronym corresponds to PIDBA (specimen catalog of the Argentine Biodiversity Research Institute). To corroborate the taxonomic identification of small mammals, we followed [Patton et al. \(2015\)](#), [Barquez and Díaz \(2020\)](#), and [Teta and Jayat \(2021\)](#). The basic checklist used was based on American Society of Mammalogists (ASM; [Mammal Diversity Database 2024](#)).

Results

A total of 153 mites belonging to 11 species, eight genera, and three families were studied. These mites were recorded on three species of bats, *Artibeus planirostris* (Phyllostomidae), *Myotis albescens* (Vespertilionidae) and *Tadarida brasiliensis* (Molossidae), and eight species of rodents, *Akodon budini*, *Akodon simulator*, *Calomys callosus*, *Calomys musculinus*, *Calomys venustus*, *Euryoryzomys legatus*, *Oligoryzomys brendae*, and *Oligoryzomys flavescens* (Cricetidae). Information of each mite species and respective hosts are given in the following species accounts.

Systematics

Order Mesostigmata

Family Laelapidae

Androlaelaps fahrenholzi (Berlese, 1911)

Distribution in Argentina: Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, La Rioja, Misiones, Neuquén, Rio Negro, Santa Fe, San Juan, San Luis, Tucumán ([Lareschi 2023](#)); herein this species is added to Jujuy Province.

Material examined: 1 ♂ (CMLA 1075), ex *A. budini* (CML 12340), 1 ♂ (CMLA 1076), ex *A. simulator* (CML 12348).

Remarks: *Androlaelaps fahrenholzi* constitutes a species complex ([Lareschi 2011](#)) and although, our specimens present the typical characteristics of the complex such as the inflated *pilus dentalis* and the presence of the serrated Z5 seta ([Savchenko 2022](#)), these will need to be reviewed and studied with other taxonomic techniques, such as morphogeometric and molecular methods.

It has been recorded from a great number of mammal species worldwide, mainly rodents, marsupials, and several birds ([Furman 1972](#)). In Argentina, it was cited on mammals of the orders Rodentia, Didelphimorpha, Microbiotheria, Cingulata, and Chiroptera ([Lareschi and Mauri 1998](#)). The record on *A. budini* represents a new mite-host association.

Gigantolaelaps gilmorei Fonseca, 1939

Distribution in Argentina: Jujuy and Salta ([Lareschi 2023](#)).

Material examined: 5 ♀ (CMLA 1077 to 1081), ex *E. legatus* (CML 4317).

Remarks: It is one of the largest species of the genus *Gigantolaelaps* ([Fonseca 1939a](#)). It can be distinguished from all other species of the genus by the following characters: rectangular sternal plate with the posterior edge wider than the anterior edge, with a slightly pronounced median projection, and without accessory setae ([Furman 1972](#)). This species has a close association with *E. legatus* (originally cited as *Oryzomys russatus*) in southeastern Brazil and Argentina, and in Paraguay with *Euryoryzomys nitidus* (originally cited as *Oryzomys nitidus*). *Gigantolaelaps gilmorei* was recorded on *A. simulator*, but it was considered an accidental association ([Lareschi et al. 2004](#)).

Gigantolaelaps oudemansi Fonseca, 1939

Distribution in Argentina: Chaco, Jujuy, and Tucumán ([Lareschi and Mauri 1998; Lareschi 2023](#)).

Material examined: 18 ♀ (CMLA 1082 to 1099), ex *E. legatus* (CML 12383, 8330).

Remarks: According to [Furman \(1972\)](#), there are three general morphological forms of the species, which were used to separate it into three groups based on the size of the dorsal plate and the size and shape of the proximal and distal setae of the coxa I. The specimen examined in this study corresponds to "group 1", which is characterized by both setae of coxa I being setiform, subequal, or the distal seta being up to 1.2 times longer than the proximal seta.

The species was found parasitizing *Oecomys concolor* in the Chaco province ([Lareschi and Mauri 1998](#)), *O. brendae* (originally cited as *Oligoryzomys destructor*) in the Tucumán province and *E. legatus* (originally cited as *Oryzomys russatus*) in the Jujuy province ([Lareschi et al. 2003](#)).

Gigantolaelaps wolffsohni (Oudemans, 1910)

Distribution in Argentina: Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, Misiones, Salta, San Luis, and Tucumán ([Lareschi 2023](#)).

Material examined: 8 ♀ (CMLA 1100 to 1104, 1111 to 1113), ex *O. brendae* (CML 9523, 12371, 2 released); 6 ♀ (CMLA 1105 to 1110), ex *O. flavescens* (CML 12370, 12380).

Remarks: This species can be distinguished from all other species of the genus by the following characters: the anteroventral seta of the coxa I spiniform and distal setiform, the dorsal plate with setae J5 very long, about 2/3 the length of setae Z5. Furthermore, the posterior margin of the plate is convex ([Furman 1972](#)). Although this species was previously cited on *O. flavescens* and *O. brendae* ([Savchenko et al. 2021](#)), in Jujuy province, only one specimen of the order Rodentia without identification was reported as host ([Lareschi and Mauri 1998; Lareschi 2023](#)),

therefore, the recorded associations in this study are new to the province. *Gigantolaelaps wolffsohni* was also reported on other rodents of the genera *Holochilus*, *Scapteromys*, and *Mus* ([Lareschi 2023](#)).

Laelaps mazzai Fonseca, 1939

Distribution in Argentina: Buenos Aires, Chaco, Chubut, Córdoba, Corrientes, Entre Ríos, Formosa, Salta, and Santa Fe ([Espinoza-Carniglia et al. 2023](#); [Lareschi 2023](#)); herein this species is added to Jujuy Province.

Material examined: 9 ♀ (CMLA 1116, 1117, 1119, 1120 to 1125) and 1 ♂ (CMLA 1118), ex *C. callosus* (CML 12386, 12387), 8 ♀ (CMLA 1126 to 1133), ex *C. musculinus* (CML 12390), 19 ♀ (CMLA 1134 to 1149, 1152, 1153, 1227), ex *C. venustus* (CML 12388, 12393), 2 ♀ (CMLA 1114, 1115), ex *O. flavesiensis* (CML 12370); 2 ♀ (CMLA 1150, 1151), ex *O. brendae* (CML 12369).

Remarks: This species can be distinguished from all other species of the genus by the following characters: hypertrichia, dorsal plate with 60 to 75 pairs of setae, coxa I with proximal seta longer than distal seta, both spiniform ([Furman 1972](#)). This mite is mainly associated with species of the genus *Calomys* from Argentina, Brazil, Paraguay, and Venezuela ([Espinoza-Carniglia et al. 2023](#)). In Argentina, it was also recorded parasitizing other genera of rodents as *Akodon*, *Eligmodontia*, *Necromys*, *Oxymycterus*, *Reithrodontomys*, and *Mus* ([Lareschi et al. 2006](#); [Lareschi 2023](#)). The association with *O. brendae* is recorded for the first time.

Laelaps paulistanensis Fonseca, 1936

Distribution in Argentina: Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, La Rioja, Misiones, Río Negro, and Tucumán ([Lareschi 2023](#)).

Material examined: 2 ♀ (CMLA 1160, 1161), ex *C. musculinus* (CML 12390); 18 ♀ (CMLA 1154, 1155, 1162 to 1177), ex *O. brendae* (CML 9523, 12369, 12371, 1 released); 4 ♀ (CMLA 1156 to 1159), ex *O. flavesiensis* (CML 12370, 12380).

Remarks: This species can be distinguished from all other species of the genus by the following characters: dorsal plate with 36 to 45 pairs of setae, coxa I with spiniform proximal seta and piliform distal seta longer than the proximal seta ([Furman 1972](#)). *Laelaps paulistanensis* was cited on rodents of genera *Akodon*, *Calomys*, *Ctenomys*, *Euryoryzomys*, *Holochilus*, *Mus*, *Oecomys*, *Oligoryzomys*, *Oxymycterus*, *Reithrodontomys* and *Scapteromys* and one record on a marsupial, *Lutreolina* (Didelphimorphia; [Lareschi and Mauri 1998](#); [Savchenko et al. 2021](#)). In Jujuy, it was found on *E. legatus* ([Lareschi et al. 2003](#)), but the associations reported here were expected since these hosts were previously recorded in other provinces as Buenos Aires, Misiones, and Tucumán ([Lareschi et al. 2003, 2019](#); [Navone et al. 2009](#); [Lareschi 2010a, 2023](#); [Colombo et al. 2013](#)).

Mysolaelaps microspinosis Fonseca, 1936

Distribution in Argentina: Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, La Rioja, Misiones, San Luis, Tucumán ([Lareschi 2023](#)); herein this species is added to Jujuy Province.

Material examined: 17 ♀ (CMLA 1178-1187, 1196 to 1202), ex *O. brendae* (CML 9523, 12371); 8 ♀ (CMLA 1188 to 1195), ex *O. flavesiensis* (CML 12370, 12380).

Remarks: This species can be distinguished from all other species of the genus by the following characters: sternal setae, approximately equal in size, first and second pairs of genitoventral setae less than ½ length of third and fourth pairs, metapodial plate smaller than stigma and genitoventral plate slightly concave posteriorly ([Furman 1972](#)). *Mysolaelaps microspinosis* is mainly associated with cricetid rodents of the tribe Oryzomyini, parasitizing the genus *Oligoryzomys* in Argentina, Brazil, Chile, and Uruguay, and the genus *Oryzomys* in Venezuela ([Savchenko et al. 2021](#)). It also was recorded on rodents of the tribes Akodontini and Phyllotini and even other families (Caviidae and Muridae; [Savchenko et al. 2021](#); [Lareschi 2023](#)). [López Berrizbeitia et al. \(2013\)](#) erroneously cited this species for Jujuy.

Subfamily Haemogamasinae

Eulaelaps stabularis (Koch, 1839)

Distribution in Argentina: Buenos Aires, Córdoba, Río Negro, San Luis, and Tucumán ([Lareschi and Mauri 1998](#); [Lareschi 2023](#)); herein this species is added to Jujuy Province.

Material examined: 1 ♀ (CMLA 1203), ex *A. simulator* (CML 12348).

Remarks: This species can be distinguished from all other species of the genus by the following characters: movable digit bidentate, metapodial plate larger than stigma, genitoventral plate straight posteriorly, peritreme extending to posterior third of coxa I, peritrematal plate swollen and truncated subsequently, simple striae; posterior pore small and epistome with approximately six fine, simple processes ([Uchikawa and Rack 1979](#)). In Argentina, was recorded on cricetid rodents (*Akodon*, *Calomys*, *Graomys*, *Necromys*, *Oligoryzomys*, *Reithrodontomys* and *Scapteromys*) and caviids (*Cavia*; [Lareschi 2023](#)). Only one record of *A. simulator* ([Lareschi et al. 2003](#)) was previously known for the NWA, in the Tucumán province.

Family Macronyssidae

Chiroptonyssus robustipes (Ewing, 1925)

Distribution in Argentina: Buenos Aires, Córdoba, La Rioja, San Juan, San Luis, Salta, Río Negro, and Tucumán ([Lareschi and Mauri 1998](#)); herein this species is added to Jujuy Province.

Material examined: 3 ♂ (CMLA 1205-1207), 2 ♀ (CMLA 1204, 1208) and 1 protonymph (CMLA 1209), ex *T. brasiliensis* (2 released).

Remarks: This species can be distinguished from all other species of the genus by the following characters: idiosomal setae serrated and base of tritosternum with a denticulate expansion, gena III with 10 setae. In females, absence of sternal glands. In males, IV femur with prominent internal spine ([Radovsky 2010](#)). This species presents a significant prevalence on *T. brasiliensis* ([Pesenti et al. 2014](#)), although it has also been reported on other genera of bats as *Myotis*, *Neoptesicus*, *Mormoops* and *Nyctinomops* ([Durden et al. 1992](#); [Lareschi 2023](#)).

Macronyssus crosbyi (Ewing and Stover, 1915)

Distribution in Argentina: Formosa, Rio Negro ([Lareschi and Mauri 1998](#)); herein this species is added to Jujuy Province.

Material examined: 3 ♀ (CMLA 1211- 1213) and 1 ♂ (CMLA 1210), ex *M. albescens* (CML 4315, PIDBA 1540).

Remarks: Females of this species can be distinguished by the following characters: the sternal plate with moderately developed anterolateral sculpture, sternal glands with thick striae and epiginal plate with striations; in males, dorsal plate with M11 strongly noticeable and thickened ([Radovsky 2010](#)). This species is associated with the family Vespertilionidae, mainly of the genus *Myotis* and some records on the genus *Eptesicus* (now *Neoptesicus*; [Radovsky 1967](#)). In Argentina, was reported parasitizing to *Myotis chiloensis* and *Myotis nigricans* ([Lareschi 2023](#)), but the association with *M. albescens* had previously only been recorded in Paraguay ([Presley et al. 2015](#)).

Family Spinturnicidae

Periglischrus iheringi Oudemans, 1902

Distribution in Argentina: Salta ([Lareschi and Mauri 1998](#)); herein this species is added to Jujuy Province.

Material examined: 7 ♂ (CMLA 1214, 1215, 1221 to 1225), 6 ♀ (CMLA 1216 to 1220, 1226), ex *A. planirostris* (CML 4158, 2 released).

Remarks: This species can be distinguished from all other species of the genus by the following characters: in females, pyriform sternal plate; in males, the first pair of setae of the genitoventral plate extends to or beyond the insertion of the second pair of setae and intercoxa area IV with eight pairs of setae (7 + 1 adanal; [Herrin and Tipton 1975](#)). The existence of morphologic variations among individuals from different populations suggests that this species may be a species complex ([Morales-Malacara 2001](#); [Gomes-Almeida et al. 2024](#)). *Periglischrus iheringi* is mainly associated with the family Phyllostomidae, preferably with species of the genus *Artibeus*, but it was also recorded on species of the families Emballonuridae, Noctilionidae, Molossidae, and Mormoopidae ([Herrin and Tipton 1975](#); [Lareschi and Mauri 1998](#)). The association with *A. planirostris* is recorded for the first time for Argentina.

Discussion

These results contribute to our knowledge of the mite fauna of NWA and particularly in the Jujuy province. Based on our studies in NWA, one new genus and species are added, increasing the total list of Mesostigmata mites of bats and rodents in the region, to 17 species of 11 genera. In the Jujuy province, seven species are added, increasing the total list of mites to 12 species of nine genera, including the first records of the families Macronyssidae and Spinturnicidae and the genera *Androlaelaps*, *Eulealaps*, *Mysolaelaps*, *Chiroptonyssus*, and *Periglischrus*. One of the families of mites most represented, in terms of the number of individuals and hosts, was Laelapidae. This family comprised eight species (*A. farhenholzi*, *E. stabularis*, *G. gilmorei*, *G. oudemansi*, *G. wolffsohni*, *L. mazzai*, *L. paulistanensis*, and *M. microspinosis*). Two species, *C. robustipes* and *M. crosbyi* (Macronyssidae) were recorded on bats. They included both adult males and females and one nymph (*C. robustipes*). Twenty mite-host associations were recorded, of which two are new to Argentina and two are reported for the first time.

The knowledge for most of the mite species represented in this study, is still scarce. In particular, three species of mites (*G. gilmorei*, *M. crosbyi*, and *P. iheringi*) were recorded in only two provinces in Argentina. This may be due to the sampling effort and the complexity of the study of these arthropods. For some taxa, the differentiation of morphological characters is complex, the intraspecific variation that may exist is still unknown, which makes it difficult in some cases to determine whether it is a simple variation or a different species.

We emphasize the importance of joint research between parasitologists and mammalogists to ensure proper identification of both parasites and their hosts, and to allow a better understanding of these taxa, not only from a systematic point of view, but also from an ecological and epidemiological point of view, since the study area belongs to an area of influence of bacterial pathogens.

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Neotropical Bats play natural predators of medically important Culicidae

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Arthropodophagous bats are crucial to suppressing pest insect species, particularly those of human health interest, such as mosquitoes of the family Culicidae, which are vectors of several diseases. Reports of culicid mosquitoes in the diet of bats are scarce, especially in tropical areas where diseases in which mosquitoes are vectors proliferate. This study aimed to evaluate the presence of culicids in the diet of neotropical arthropodophagous bats using high-throughput sequencing. We specifically aimed to assess bats as biological control agents and determine the presence of culicid mosquitoes in their diet using two sets of COI primers. We assess the presence of culicid mosquitoes in the feces of bats belonging to different families, environments, and foraging strata in several neotropical regions. We compare richness, percentage of reads, and incidence of genera of Culicidae identified with each primers' set. Seventeen of the 19 bat species studied show consumption of culicids. The two primers' sets yielded dissimilar results regarding several reads and culicid species and/or genera taxonomic levels. Our findings indicate that bats from different families and foraging habits are biological control agents consuming different species of mosquitoes associated with diseases affecting the health of humans.

Los murciélagos artrópodofágos son cruciales para suprimir especies de insectos plaga, particularmente aquellas de interés para la salud humana, como son los mosquitos de la familia Culicidae, que son vectores de varias enfermedades. Los registros de mosquitos culícidos en la dieta de murciélagos son escasos, especialmente en áreas neotropicales donde proliferan enfermedades de las que los mosquitos son vectores. Este estudio tuvo como objetivo evaluar la presencia de culícidos en la dieta de murciélagos artrópodófagos neotropicales utilizando secuenciación de alto rendimiento. Nuestro objetivo específico fue evaluar a los murciélagos como agentes de control biológico y determinar la presencia de mosquitos culícidos en su dieta utilizando dos conjuntos de cebadores para el gen COI. Se evaluó la presencia de mosquitos culícidos en las heces de murciélagos pertenecientes a diferentes familias, ambientes y estratos de alimentación de varias regiones neotropicales. Se comparó la riqueza, el porcentaje de lecturas y la incidencia de géneros de Culicidae identificados con cada conjunto de cebadores. Diecisiete de las 19 especies de murciélagos estudiadas presentaron consumo de culícidos. Los dos conjuntos de cebadores arrojaron resultados disímiles en relación con varias lecturas y en niveles taxonómicos de especies y/o géneros de culícidos. Nuestros hallazgos indican que los murciélagos de diferentes familias y hábitos de alimentación son agentes de control biológico que consumen diferentes especies de mosquitos asociados con enfermedades que afectan la salud de los humanos.

Keywords: Bats; biological control agents; mosquitoes; next-generation sequencing; predation.

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Introduction

More than 75 % of bat species feed on arthropods, making them crucial for arthropod pest control ([Wilson 1973](#); [Hutson and Mickleburgh 2001](#); [Kunz et al. 2011](#); [Williams-Guillén 2016](#)). This ecosystem service holds greater significance when it directly impacts the economy by preying on arthropods that are either crop pests or vectors of diseases affecting the health of humans and domestic animals, as is the case of mosquitoes of the family Culicidae ([Dobson 2005](#); [Fenton et al. 2006](#); [Kunz et al. 2011](#)).

The family Culicidae includes hematophagous female mosquitoes, mostly belonging to the genera *Culex*, *Aedes*, and *Anopheles*. Culicidae comprises around 3,583 species

in 110 recognized genera ([Mosquito Taxonomic Inventory 2020](#)); some species of the genus *Culex* are vectors of West Nile Virus, filariasis, equine encephalitis, and avian malaria ([Bolling et al. 2009](#); [Farajollahi et al. 2011](#)); *Aedes* includes vectors of Yellow Fever Virus, Dengue Virus, Zika Virus, and canine dirofilariasis ([Gubler 2002](#)); and *Anopheles*, mainly of malaria ([Manguin et al. 2008](#)).

Arthropodophagous bats have been considered active predators of culicid mosquitoes. This assumption has been explored empirically considering them as biocontrol mosquitoes' species ([Kunz et al. 2011](#); [Williams-Guillén 2016](#)). [Campbell \(1925\)](#) reported mosquito remains in the stomach content of bats, suggesting a potential role of bats in

controlling the spread of malaria. His findings have been questioned on the basis that identification of digested exoskeleton remnants of mosquitoes is impossible at taxonomic levels below the rank of family ([Storer 1926](#); [Whitaker et al. 2009](#)). It has been reported that *Myotis lucifugus* consumes culicid mosquitoes ([Whitaker and Lawehead 1992](#)), with foraging activities in areas where mosquitoes are abundant ([Rydell et al. 2002](#)) and has been estimated that a single bat can consume up to 1,300 mosquitoes in one to two hours ([Wetzel and Boyles 2017](#)). The predation on mosquitoes is critical for vector-borne diseases, mainly in tropical regions ([Githcko et al. 2000](#)). Mosquito species such as *C. quinquefasciatus* and *A. aegypti* are vectors that thrive in warm, humid climates ([Rueda et al. 1990](#); [Couret et al. 2014](#)), where they are more abundant ([Turell 1989](#)). Given this scenario, the confirmation of mosquito predation by bats may play a key role in the promotion of bat species as biological control agents for mosquitoes of public health importance and the importance of the bat's conservation plans. We use the definition of biological control agents as Natural enemies of insects playing an important role in limiting the densities of potential pests ([Flint and Dreistadt 1998](#)).

Accurate reports about the consumption of culicid species that are vectors of diseases are scarce. Under controlled conditions, it has been found that Northern long-eared bats (*Myotis septentrionalis*) prey on mosquitoes of the genus *Culex* ([Reiskind and Wund 2009](#)). To date, however, evidence about the suppression of mosquitoes by bats under natural conditions is scarce and restricted to southern Oceania, northern Europe, and North America (e.g., [Clare et al. 2014](#); [Vesterinen et al. 2013](#); [Vesterinen et al. 2018](#); [Wray et al. 2018](#)). Molecular techniques have been applied successfully to determine that various bat species feed on Culicidae (Table 1).

The mitochondrial gene cytochrome c oxidase subunit I (COI) has been used for improving taxonomic identification

of culicid species ([Laurito et al. 2013](#); [Batovska et al. 2016](#); [Yssouf et al. 2016](#)), being useful for detection of mosquito species in bat feces ([Vesterinen et al. 2013](#); [Clare et al. 2014](#); [Vesterinen et al. 2018](#); [Wray et al. 2018](#)). For the genus *Aedes*, taxonomic studies reported a 100 % species-level identification success, and Culicidae genera are accurately identifiable with COI due to genetic distance between genera greater than 12 % ([Chan et al. 2014](#); [Talaga et al. 2017](#)). For the genera *Culex* and *Anopheles*, COI is not considered successful in species-level identification (69 % success; [Laurito et al. 2013](#); [Batovska et al. 2016](#); [Yssouf et al. 2016](#)). However, greater genetic differentiation is reported with COI than with 16S markers for species of these genera ([Talaga et al. 2017](#); [Vadivalagan et al. 2017](#)). For example, it is possible to identify *C. tarsalis* and *C. pipiens* complex using COI gene ([Pfeiler et al. 2013](#); [Shaikevich et al. 2016](#); [Shahhosseini et al. 2018](#)). More than 36,131 culicid COI sequences are available through GenBank, including those belonging to the genera *Aedes* with 16 species (9,795 sequences), *Anopheles* with 19 species (10,633 sequences), and *Culex* with five species (6,136 sequences; [Sayers et al. 2024](#)).

The purpose of this study is to use genetic data to confirm that, in rural areas, all the arthropodophagous bats show some predation activity on mosquitoes of the family Culicidae, which are vectors of several diseases, and that these arthropodophagous bats are active biological control agents that have positive effects in the human population. This study aims to evaluate the presence of culicids in the diet of neotropical bats of different families, environments, foraging guilds, and foraging strata.

Materials and methods

Three hundred and twenty (320) bat fecal samples were collected throughout the Neotropical region of México (Supplementary Material 1) during the rainy season from June to September 2015. Methodology followed [Segura-Trujillo et al. \(2022\)](#). Samples were collected from 19 dif-

Table 1. Bats species and culicid species were reported in their diet by metabarcoding studies.

Bat Species	Location	Culicid species reported in diet	Source
<i>Vespadelus pumilus</i> and <i>Vespadelus vulturnus</i>	Australia	<i>Aedes vigilax</i>	Gonsalves et al., 2013
<i>Myotis daubentonii</i>	Finland	<i>Anopheles cinereus</i> , <i>Anopheles messeae</i> , <i>Coquillettidia richiardii</i> , <i>Culex pipiens</i> , and <i>Ochlerotatus communis</i>	Vesterinen et al., 2013; Vesterinen et al., 2018
<i>Eptesicus nilssonii</i>	Finland	<i>Aedes vexans</i> , <i>Anopheles cinereus</i> , <i>Anopheles messeae</i> , and <i>Culex pipiens</i>	Vesterinen et al., 2018
<i>Myotis brandtii</i>	Finland	<i>Anopheles cinereus</i> , <i>Anopheles claviger</i> , <i>Anopheles messeae</i> , and <i>Culex pipiens</i>	Vesterinen et al., 2018
<i>Myotis mystacinus</i>	Finland	<i>Anopheles messeae</i> and <i>Culex pipiens</i>	Vesterinen et al., 2018
<i>Pipistrellus pygmaeus</i>	Iberian Peninsula	<i>Culex pipiens</i> and <i>Culex spp.</i>	Puig-Montserrat et al., 2020
<i>Plecotus auritus</i>	Finland	<i>Aedes vexans</i> and <i>Culex pipiens</i>	Vesterinen et al., 2018
<i>Eptesicus fuscus</i>	Canada/ United States	<i>Aedes vexans</i> , <i>Culex pipiens</i> , and <i>Culex restuans</i>	Clare et al., 2014; Wray et al., 2018
<i>Myotis lucifugus</i>	United States	<i>Aedes vexans</i> , <i>Culex restuans</i> , and <i>Culex territans</i>	Wray et al., 2018
<i>Myotis sodalis</i>	United States	<i>Culex erraticus</i> , and <i>Culex territans</i>	O'Rourke, et al. 2021

ferent bat species with varying foraging habits, strategies, and habitats, as detailed in Table 2. For molecular analysis, 32 samples were pooled (each sample composed of 2 fecal pellets of 10 specimens); each sample pool consisting of 0.08 to 0.2 g of feces from 10 individuals of the same species and location (two fecal pellets from each bat). We followed the guidelines and procedures of the American Society of Mammalogists to capture bats and collect the samples (Sikes et al. 2016). All collected fecal samples were stored in 90 % ethanol, placed in ice coolers while conducting fieldwork, and promptly placed in a -20 freezer upon return to the lab.

DNA was extracted from feces using the QIAamp DNA Stool Kit (Qiagen Inc., Valencia, CA, USA). DNA was PCR amplified using two sets of primers for the DNA barcoding region of the Cytochrome Oxidase Subunit 1. The first set (Zbj) is specific to arthropods, yielding a 150 base-pair fragment (Zbj-ArtF1c-AGATATTGGAACWTTATTTTATTTGG and Zbj-ArtR2c-WACTAATCAATTWCCAAATCCTC; Zeale et al. 2011). The second set (Folmer) included universal primers, yielding a 710 bp product (LCO1490-5'-GGTCAACAAAT-CATAAAGATATTGG-3' and HCO2198:5'- TAAACTTCAGGGT-GACCAAAAAATCA-3'; Folmer et al. 1994). Standard conditions were used for each set of primers according to Zeale et al. (2011) and Herbert et al. (2004), respectively.

Positive amplicons were sent to the Center for Conservation Genomics at the Smithsonian Conservation Biology Institute. Each PCR reaction (50 µl - irrespective of the starting concentration) was prepared as a dual-indexed library using the Agilent SureSelect^{XT} Target Enrichment System for Illumina Paired-End Sequencing following the manufacturer's protocol (Version C1, July 2017). Dual indexing PCR was performed with Nextera-style indices using Kapa HiFi with an initial denaturation of 98 °C for 2 minutes followed by 14 cycles of 98 °C for 30 seconds, 65 °C for 30 seconds, 72 °C for 60 seconds, and a final extension of 72 °C for 10 minutes. The resulting indexed libraries were purified using 1.6x magnetic beads and visualized on a 1.5% agarose gel. The fragment size and quality of the libraries were evaluated using a Bioanalyzer High Sensitivity DNA Kit (Agilent). Library concentration was measured using a Qubit 2.0 fluorometer (Life Technologies) with a dsDNA high-sensitivity kit. Indexed amplicons using the Folmer primers were pooled in an equimolar ratio, and the indexed amplicons prepared with Zbj primers were pooled. The quantity and quality of each end pool were evaluated using a Bioanalyzer 2100 (Agilent Technologies) and Qubit fluorometer (Life Technologies) before sequencing. The Folmer library pool was sequenced on an Illumina MiSeq with a 600-cycle Reagent Kit v3 (2x300 bp), and the Zbj library pool was sequenced independently on an Illumina MiSeq with a 300-cycle Reagent Kit v2 (2x150 bp). We used negative controls to avoid biases during lab work, and we sequenced them to control and characterize contamination. Base calling and demultiplexing were generated per standard protocols on the Illumina MiSeq platform, producing paired FASTQ files for each sample.

After sequencing, we first assessed the quality of the resulting Illumina paired-end reads using FastQC v0.11.5 (Andrews 2010, www.bioinformatics.babraham.ac.uk/projects/fastqc). We used Trimmomatic v0.36 (Bolger et al. 2014) to remove adapter sequences and low-quality reads. The trimmed DNA sequencing reads were then analyzed by PrintSeq-lite v0.20.4 (Schmieder and Edwards 2011) to remove exact duplicates (-derep1,4). We used high-quality forward reads to perform a BLAST analysis on the Smithsonian Institution High Performance Cluster (SI/HPC). We converted FASTQ files to FASTA format using seqtk version 1.2 (Li 2013; <https://github.com/lh3/seqtk>). For a taxonomic assignment, we follow the bioinformatics analyses described by Segura-Trujillo et al. (2024). The bioinformatics files of the sequences obtained from Culicidae in bat feces are available upon request to the corresponding author.

We calculated the incidence rate of the genera of Culicidae identified with each set of primers by type of vegetation and foraging habit, by dividing the number of records by the total number of samples of each type of vegetation and foraging habit (Schnitzler and Kalko 2001). Also, we analyzed taxonomic richness (number of taxa identified to genus and/or species) recorded with each primer set by vegetation foraging habit and taxonomic family.

Results

The 32 sample pools that we analyzed included 19 species of Arthropodophagous bats belonging to families Emballonuridae, Mormoopidae, Molossidae, Phyllostomidae, and Vespertilionidae, from seven different habitats and four foraging guilds (aerial in uncluttered space; aerial background-cluttered space; aerial highly cluttered space; and gleaning highly cluttered space Table 2).

Only 29 of the 32 pooled samples were amplified and sequenced with Zbj primers, yielding an average of 166,738 (3,589 sd) sequence reads for arthropods and an average of 59,952 (6,215 sd) reads for culicid mosquitoes. Culicids were detected in 25 (86.2 %) of the samples analyzed with the Zbj primers. In addition, 28 of the 32 pooled samples were also amplified and sequenced with the Folmer primers, yielding an average of 7,416 (18,492 sd) sequence reads for arthropods and an average of 69 (198 sd) reads for Culicidae. Folmer primers detected culicids in only 18 samples (60.7 % of the samples with positive sequencing). Both sets of primers showed, for the same samples, different amplification in species recorded and their frequency (Table 2, Figure 1). Assays using the Zbj primers detected *Aedes aegypti* in 20 samples, *Aedes* sp. in 9, *Anopheles* sp. in 1, *Culex tarsalis* in 6, *Culex pipiens* complex in 3, and *Culex* sp. in 9 (Table 2; Figure 1). Folmer primers detected *Aedes aegypti* in one sample, *Anopheles* sp. in 5, and *Culex* sp. in 17 (Figure 1). The sequences obtained matched 3,968 GenBank sequences of mosquitoes (*Aedes aegypti* with 2,698, *Aedes* sp. with 43, *Anopheles* sp. with 10; *Culex tarsalis* with 132, *C. pipiens* complex with 10, and *Culex* sp. with 1075).

Table 2. Foraging guild type, species of bats, and vegetation type of each set of samples analyzed with Folmer and Zbj primers. Percentage reads of culicid in proportion of reads of all arthropod's genus identified in each pooled sample. Foraging guilds: Aus = aerial in uncluttered space; Abcs = aerial background-cluttered space; Ahcs = aerial highly cluttered space, and Ghcs = gleaning highly cluttered space. Type of vegetation: Gf = gallery forest; df = deciduous forest; Ddf=dry deciduous forests; Ms-df = medium semi-deciduous forests; Hef = high evergreen forest; Xs = xeric scrublands; and Msf = medium subdeciduous forests.

Foraging guild	Species	Type of vegetation	Folmer				Zbj					
			<i>Aedes aegypti</i>	<i>Anopheles</i> sp.	<i>Culex</i> sp.	% Reads culicid	<i>Aedes aegypti</i>	<i>Aedes</i> sp.	<i>Anopheles</i> sp.	<i>Culex tarsalis</i>	<i>Culex pipiens complex</i>	<i>Culex</i> sp.
Emballonuridae												
ABcs	<i>Peropteryx macrotis</i>	Ms-df	1	1	1	1				1	0.39	
AUs	<i>Balantiopteryx plicata</i>	Xs		1	2.12		1			1	8.46	
AHcs	<i>Rhynchoycteris naso</i>	Gf			-	1			1	9.83		
AHcs	<i>Saccopteryx bilineata</i>	Ms-df			-	1			1	9.22		
Mormoopidae												
AHcs	<i>Pteronotus parnellii</i>	Gf			0	1	1			1.25		
		Df	1	1	1	0.17	1	1		0.31		
		Ms-df			1	5.05	1		1	0.48		
		Hef				0	1		1	2.18		
ABcs	<i>Pteronotus fulvus</i>	Gf			0	1	1			1.23		
		Ms-df			1	1.92	1			0.07		
		Hef			1	8.07				-		
ABcs	<i>Mormoops megalophylla</i>	Ms-df			0					0.02*		
		Hef			0	1			1	0.84		
		Ddf			0	1				0.07		
		Gf			0	1			1	0.30		
Molossidae												
AUs	<i>Molossus rufus</i>	Msf		1	2.4	1		1		3.71		
		Ms-df			-	1	1		1	0.10		
AUs	<i>Nyctinomops laticaudatus</i>	Hef			-	1	1		1	4.31		
Natalidae												
AHcs	<i>Natalus mexicanus</i>	Ddf	1	1	0.08					0		
		Hef		1	0.91					-		
		Msf		1	7.33					-		
		Xs			0					0.08*		
Phyllostomidae												
GHcs	<i>Macrotus californicus</i>	Df			0					0		
GHcs	<i>Macrotus waterhousii</i>	Xs			0					0		
Vespertilionidae												
ABcs	<i>Myotis velifer</i>	Ddf	1	1	4.4	1			1	0.64		
ABcs	<i>Myotis melanorhinus</i>	Xs		1	0.29	1	1	1	1	8.91		
ABcs	<i>Myotis pilosatibialis</i>	Msf	1	1	4.08	1				0.10		
		Ms-df		1	0.22	1	1		1	1.00		
ABcs	<i>Rhogeessa parvula</i>	Xs		1	0.23		1	1	1	1.78		
ABcs	<i>Rhogeessa aeneus</i>	Ms-df		1	11.5		1			0.05		
ABcs	<i>Rhogeessa tumida</i>	Ms-df			0	1		1		14.40		
ABcs	<i>Neoptesicus furinalis</i>	Ms-df			1	0.41				-		

1 = indicates that the taxon was found in the diet of that species; 0 = not sequenced for this primer set, and * sequences identified to the family level but not identified to the genus or species level of culicid mosquitoes.

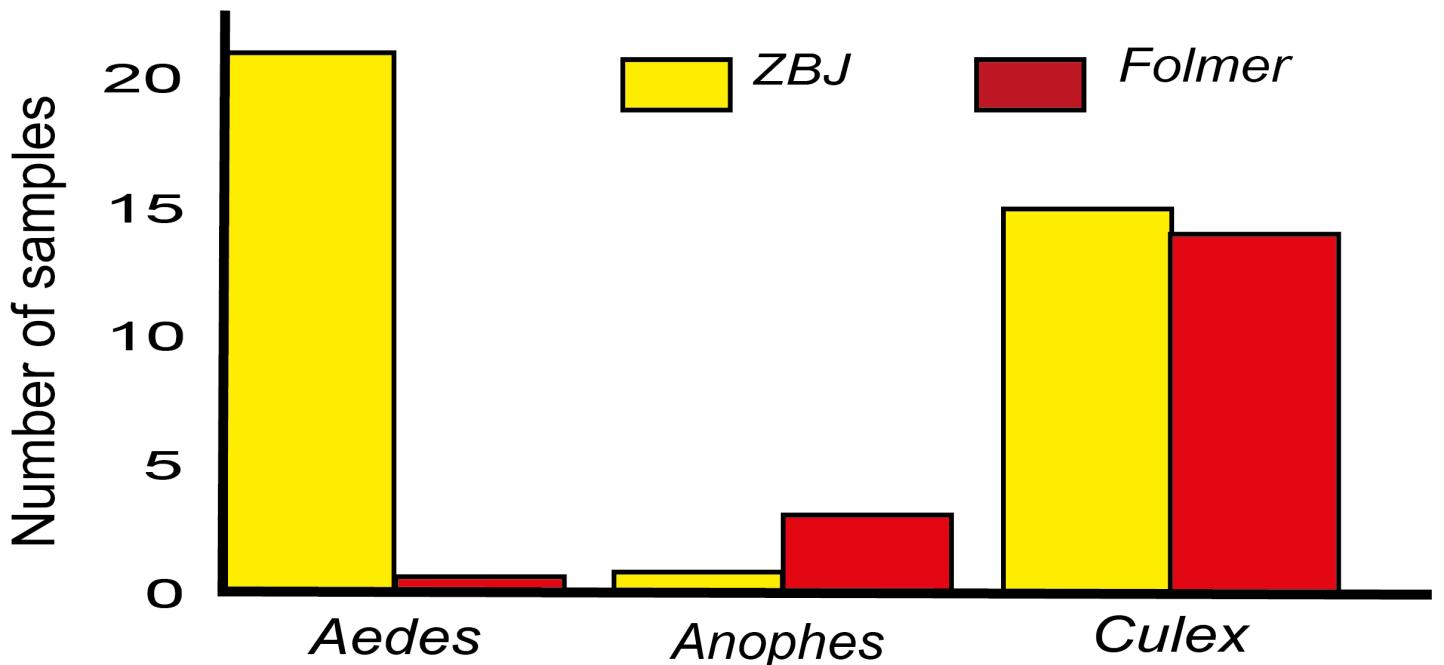


Figure 1. Frequency of each genus of Culicidae identified in the fecal samples of 19 neotropical bat species overall by each set of primers.

In the seven different habitat types we registered at least one species of culicid, with *Anopheles* and *Aedes* as the least and most frequently detected, respectively. In general, the gallery forest and mid-height sub-deciduous forest were the habitats with the lowest incidence of culicids in bat diets, while low- or mid-height deciduous tropical forests showed the highest values (Figure 2). The only foraging guild type for which culicid mosquitoes were not identified with any of the two primer sets (*i. e.*, Folmer and Zbj) was that of gleaners in highly cluttered space (GHcs). Three genera of mosquitoes were found in samples of aerial guild bats that fed in open spaces, at the edge of vegetation, and among vegetation. The incidence differences in *Anopheles* and *Aedes* were observed when using the two sets of primers (Figure 3). Culicid mosquitoes were not detected in either of the two species of the phyllostomid genus *Macrotus* that glean among vegetation and are associated with arid areas.

Culicid richness recorded (number of genera or species) varied across the types of vegetation; the average number of genera and species identified per vegetation type between primers were different. For example, the determined sequences with Folmer primers were around one, while the average number of sequences with Zbj primers ranged between one and two (Figure 4A). On the other hand, regarding the foraging guild, Folmer primers recorded an incidence index lower than one, whereas the value for Zbj primers up to 2.5. The Zbj primers recorded a higher number of taxa (average 2.5) for bats in the aerial-open space foraging guild (AUs; Figure 4B).

Sequence detection was different between bat families, using Zbj primers in Vespertilionidae and Molossidae yielded a higher average richness of Culicidae (2.3 and 2.6,

respectively, Figure 4C), but no Culicidae was recorded for Phyllostomidae. Instead, Folmer primers recorded values less than 1.5, but for each of the three families.

Discussion

The results of the study can be categorized into two main groups: the methodological findings, that indicate that the two sets of primers yield different results and therefore should be used in conjunction, and the biological data, which highlights the importance of arthropod-eating bats from various families and ecological groups in controlling Culicidae mosquitoes. Below, we break down the discussion regarding these two main topics.

Methodological analyses. The results obtained from using both Zbj (general for insects) and Folmer (general, broad-spectrum) primer sets confirmed that 17 out of the 19 arthropodophagous bat species analyzed in this study consume insects belonging to the Culicidae family (Table 2). Mosquitoes from the Culicidae family are blood-feeding insects known to transmit various diseases, posing a significant public health concern.

The low detection of mosquitoes in previous molecular diet analyses of bats has been attributed to the use of standard, low-specificity primers ([Wray et al. 2018](#); [Jusino et al. 2017](#)). In past studies, the selection of COI primers for metabarcoding has been mostly based on their ability to provide high taxonomic diversity coverage and fine taxonomic resolution ([Clarke et al. 2014](#); [Brandon-Mong et al. 2015](#); [Piñol et al. 2015](#)). The Zbj primers have been widely used in metabarcoding bat diet studies, but they have been shown to yield distinct percentages of amplification efficiency for different arthropod orders ([Clarke et al. 2014](#); [Rubbmark et al. 2018](#); [Jusino et al. 2017](#)). Never-

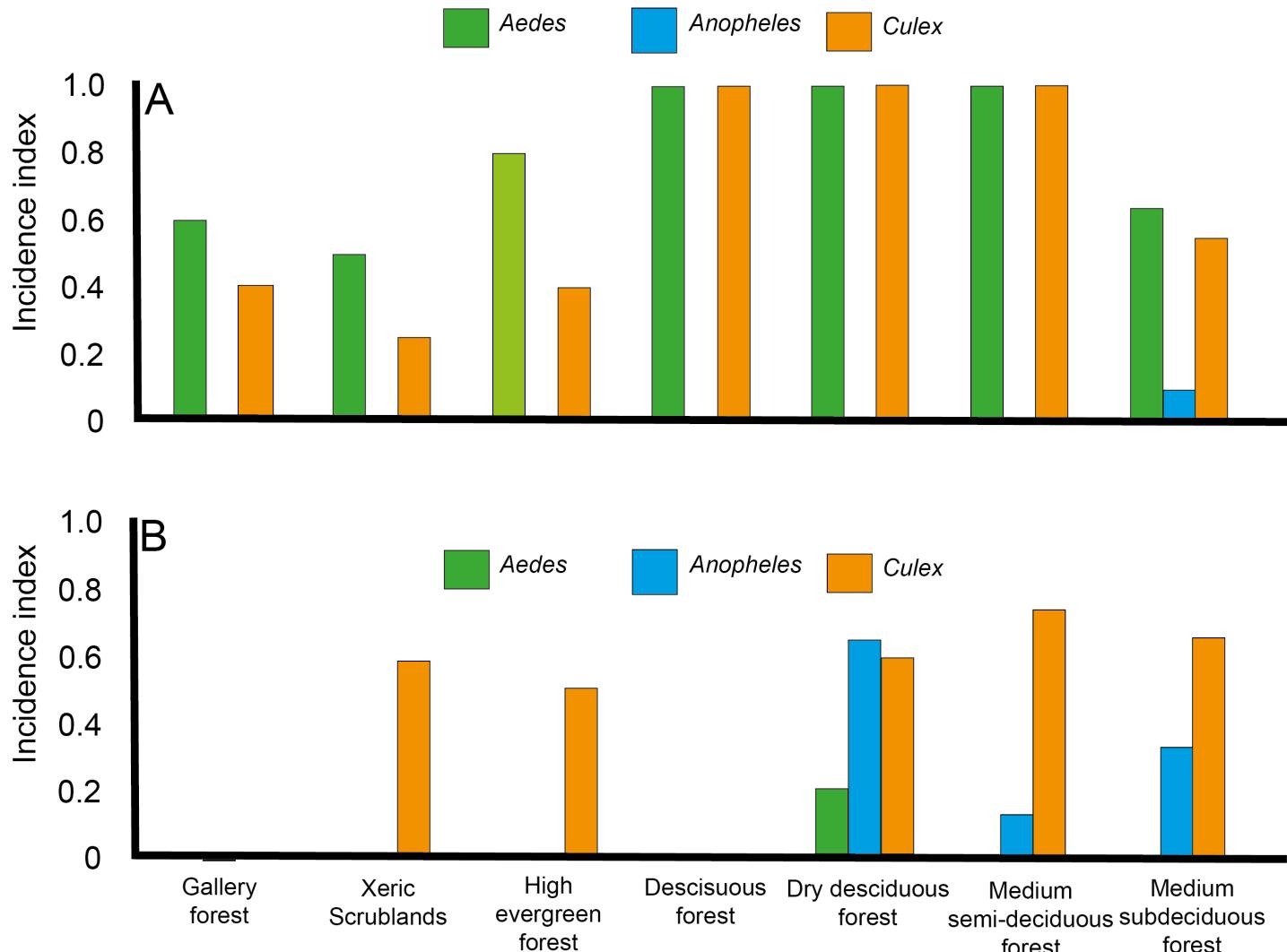


Figure 2. Incidence of Culicidae detected bat diet samples by vegetation type. A) incidence with Zbj primers; B) incidence with Folmer primers.

theless, these primers do show an adequate percentage of taxonomic assignment to species level ([Clarke et al. 2014](#); [Alberdi et al. 2018](#)). Specifically, empirical studies have demonstrated a success rate of around 50 % for the order Diptera ([Clarke et al. 2014](#); [Rubbmark et al. 2018](#); [Jucino et al. 2019](#)). Despite this low efficiency, several bat diet studies have specifically demonstrated the utility of Zbj primers for the detection of culicids ([Vesterinen et al. 2013](#); [Clarke et al. 2014](#); [Vesterinen et al. 2018](#); [Wray et al. 2018](#)). More recently, studies that have used Zbj primers have reported the detection of sequences of many arthropod orders ([Vesterinen et al. 2018](#); [Eitzinger et al. 2019](#); [Koskinen et al. 2019](#)). On the other hand, the use of primers that amplify longer fragments, such as the Folmer primers, is uncommon in metabarcoding studies because they are not easy or cost-efficient to amplify. However, the longer sequence fragments produced by Folmer primers reduce the probability of an erroneous taxonomic assignment ([Alberdi et al. 2018](#)). For example, [Jusino et al. \(2019\)](#) reported Dipteran sequence detection in 50 to 63 % of samples with Zbj primers and 88 % of samples with Folmer primers. Therefore, in

this study, we also used the Folmer primers to complement the Zbj data to have greater power for identification at the lowest possible taxonomic level and both primer sets were found to be valuable for the detection of culicids in our bat fecal samples.

Since data from both primer sets were obtained from the same fecal DNA extracts, the difference in the detection results cannot be attributed to habitat type, latitude, or seasonality that may affect the abundance of culicids. As discussed above, differences in the number of culicid taxa and frequency among samples analyzed with different primers can be the result of differences in the size of fragments and amplification efficiency in the number of different taxa between these primers ([Herbert et al. 2004](#)). The Folmer primers are broad-spectrum primers and of greater length of bases than the Zbj; hence, a large proportion of reads corresponded to species other than culicid mosquitoes, such as those from bats from which the fecal samples were collected. In contrast, Zbj primers amplify a shorter COI length than Folmer primers and yielded mostly sequences corresponding to arthropods. However, [Jusino et al. \(2019\)](#), in

their study of simulated samples (artificial mixture of arthropods) with Folmer primers, were able to detect two species of *Aedes* (*Aedes albopictus* and *A. vexans*) that were not detected with Zbj primers. Nevertheless, in this study, we detected a greater number of taxa with the Zbj primers than with the Folmer primers. For this reason, the use of both primers is recommended herein for the evaluation of the impact of arthropodophagous bats on the control of mosquitoes of medical importance in different regions. In addition, these primer sets have a broad spectrum and can also detect the different types of arthropods that bats feed on.

Biological interaction analyses. The culicid taxa identified in feces from bats in this analysis (*i.e.*, *Aedes* sp., *A. aegypti*, *Anopheles* sp., *Culex tarsalis*, *C. pipiens* complex, and six different *Culex* sp.) transmit diseases including the West Nile virus, filariasis, equine encephalitis, avian malaria, yellow fever, dengue, zika, and canine dirofilariasis ([Gubler 2002](#); [Bolling et al. 2009](#); [Farajollahi et al. 2011](#)). The genera and species identified as bats' prey in this study belong to taxa of medical importance for North America, where samples were collected. This implies that arthropodophagous bats could be contributing to the control of vectors associated

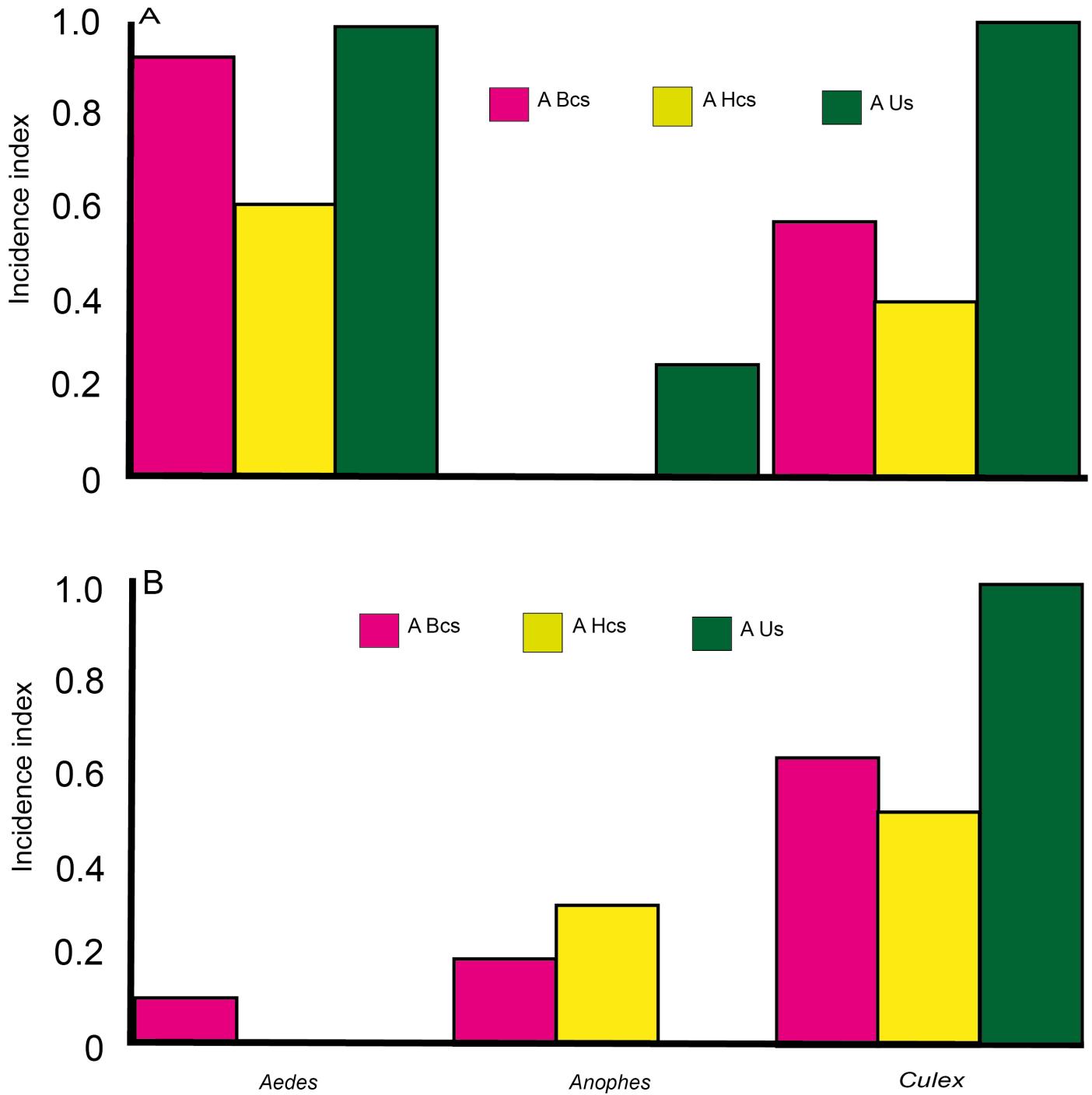


Figure 3. Incidence of Culicidae in the samples by foraging habit of bats. A) incidence registered with Zbj primers. B) incidence with Folmer primers. Categories of aerial foraging bats, bat gleaners were not recorded. Foraging guilds: Us = Aerial uncluttered space; Bcs = Aerial background-cluttered space; Hcs = Aerial highly cluttered space.

with the following diseases of medical importance: yellow fever, dengue, zika, canine dirofilariasis, lymphatic filariasis, and other pathogens (*Aedes*; [Gubler 2002](#); [Kraemer et al. 2015](#); [Sarwar 2015](#); [Bonds et al. 2022](#)); the different types of malaria, transmission of filarial worms, and around 20 different viruses (*Anopheles*; [Manguin et al. 2008](#); [Simonsen and Mwakitalu 2013](#)), and West Nile virus, filariasis, equine encephalitis, and avian malaria (*Culex*; [Bolling et al. 2009](#); [Farajollahi et al. 2011](#)). Therefore, the potential positive impact of bats on public health may be higher than previously thought. The spread of viruses transmitted by culicid mosquitoes depends almost exclusively on controlling these vectors ([Achee et al. 2015](#)), mainly using chemicals agents, while bats serve as biological control agents.

The detection success of Culicidae in our study may be attributed to the fact that the samples analyzed were collected in the Neotropics in México during the summer, a season when moisture and temperature boost the abundance of mosquitoes ([Rueda et al. 1990](#); [Couret et al. 2014](#)). Our results also indicate that the largest number of records of mosquito consumption and the highest number of genera and species are associated with bats foraging on the edge of vegetation and open spaces and, to a lesser extent, with bats that forage among vegetation. Species belonging to various foraging guilds were analyzed in all localities; hence, if culicids were detected in one pooled sample of bat feces, this indicates that culicids were present in that study area. The difference in the incidence rate could be due to three leading causes: 1) bats that forage among the vegetation were the least represented in terms of the number of species analyzed; 2) the small size of mosquitoes makes them hard to capture in closed environments, hence leading to a lower incidence; and, 3) aerial guild bats can forage in urbanized environments, in addition to being attracted to lights where mosquitoes congregate and are easy to capture. The data currently available are insufficient to discern among these hypotheses. Mosquito-borne disease control is a complex task that requires different efforts and strategies for pest management. This includes maintaining natural biocontrol (such as bats as predators of mosquitoes), intra-domiciliary eradication, staying away from water containers where mosquitoes can breed, employment of genetically modified mosquitoes, etc. ([Medlock et al. 2012](#); [Baldachino et al. 2015](#); [Carvalho et al. 2024](#)).

The consumption of culicid mosquitoes determined through molecular techniques had been previously recorded only for bat species of the family Vespertilionidae ([Gonsalves et al. 2013](#); [Clare et al. 2014](#); [Vesterinen et al. 2018](#); [Wray et al. 2018](#)). However, this is the first time that culicid mosquitoes have been found in the feces of bats from the Emballonuridae, Molossidae, and Mormoopidae families in the Neotropics. In addition, more culicid genera and species were documented in the Vespertilionidae and Molossidae families. The family Phyllostomidae was the only group for which we did not detect culicid mosquitoes.

This diversity of predators of mosquitoes may be related to the fact that soft arthropods such as mosquitoes can be predated by different feeding guilds ([Segura-Trujillo et al. 2016, 2022](#)), because of its soft texture that can be eaten by different bat species ([Rabinowitz and Tuttle 1982](#)).

Notably, the samples analyzed from the Phyllostomidae belonged to bat species that gleaned among highly cluttered vegetation (such as *Macrotus californicus* and *M. waterhousii*) that feed on hard apterans such as arachnids ([Segura-Trujillo et al. 2016](#)) but, according to our study, not on culicid mosquitoes. This can be because gleaning bats catch mainly hard and non-flying prey items, preferably those located on a substrate ([Segura-Trujillo et al. 2016](#)). These traits contrast with those of mosquitoes, which are soft-bodied flying prey. This is reflected in the high incidence of culicid mosquitoes across all vegetation types and in the other three bat foraging guilds analyzed. All species of culicid mosquitoes share similar textures and flight speeds, which have been identified as critical factors for prey selection by arthropodophagous bats ([Segura-Trujillo et al. 2016](#)). Unsurprisingly, bats prey on all species of mosquitoes in tropical areas worldwide. The samples analyzed confirm the widespread consumption of Culicidae by bats in neotropical areas during the rainy season, from low tropical deciduous forests to high evergreen forests. Bats' consumption of *A. aegypti* predominates in rainforests, such as the mid-height sub-deciduous forest, gallery forest, and high evergreen forest.

The presence of mosquitoes as preys of bats of different species, foraging guilds, and type of vegetation demonstrate that culicids can be found in practically all microenvironments and are preyed upon by bats. The different species of bats, foraging guilds, vegetation types, and primers functioned as statistical replicates to evaluate mosquito consumption. Which in summary leads to the fact that, except for the species of the guilds gleaned highly cluttered space, which are very specific, bats consume some of the mosquito species. Therefore, we could expect that other arthropodophagous species in these same guilds, which are most of the guilds present, would consume mosquitoes as well.

The result of this study shows that metabarcoding of samples using Zbj and Folmer COI primers, combined with high-throughput DNA sequencing, is a rapid and effective method for detecting Culicidae in bat feces. Although both the Zbj and Folmer primers provide sufficient resolution at the genus level, they are recommended as complementary methods. The large number of sequences obtained for culicid mosquitoes in fecal samples also suggests that the different aerial guilds of arthropodophagous bats, regardless of their taxonomic groups, are effective predators of culicid mosquitoes in various environments and foraging strata. The detection of culicid mosquitoes in different taxa and foraging guilds supports the hypothesis that all species of arthropodophagous bats in aerial guilds likely participate as biological control of mosquitoes,

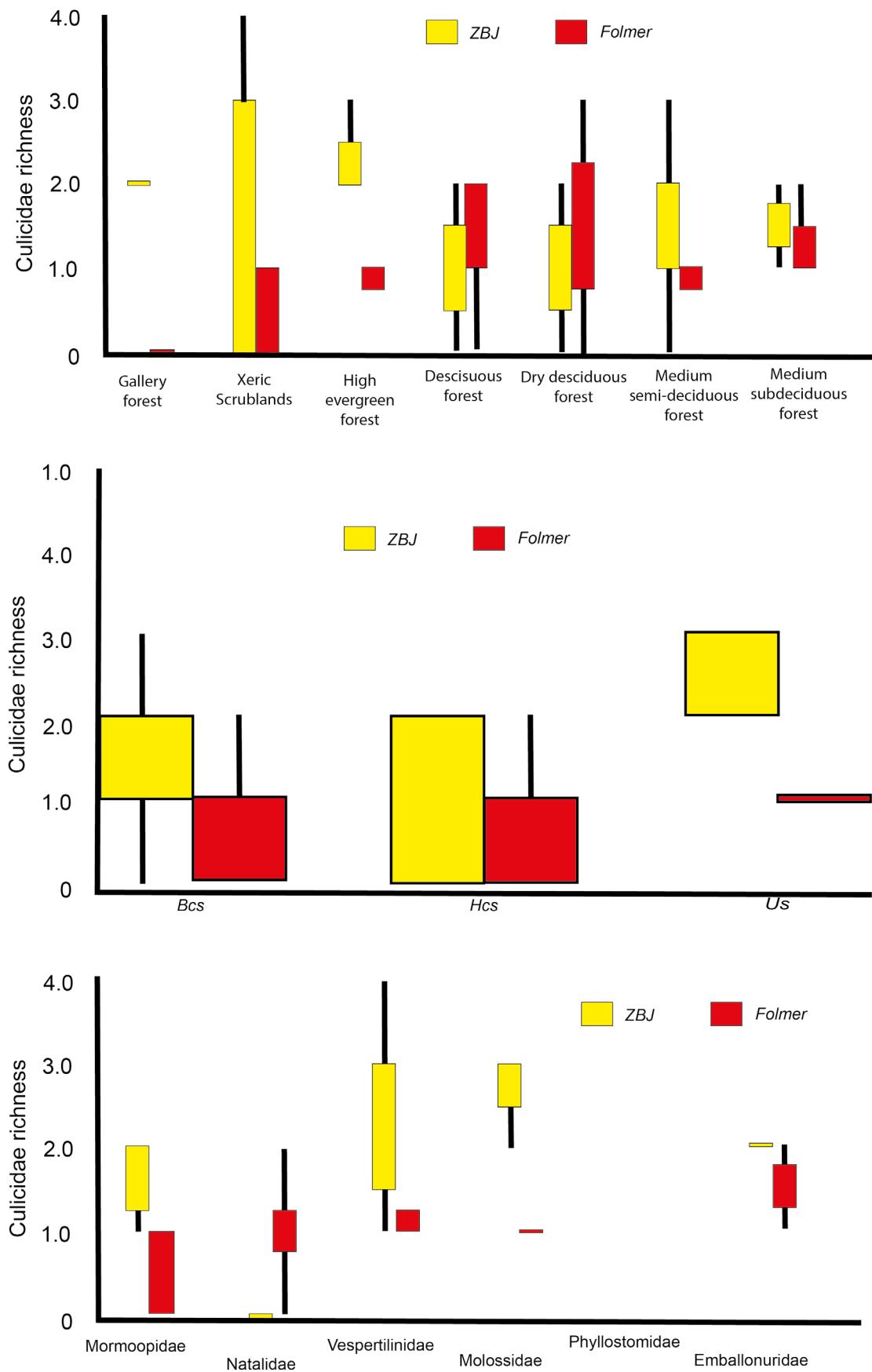


Figure 4. Number of taxa of Culicidae (at the level of genus and species) identified with each set of primers. It represents the minimum and maximum (whiskers), the first quartile, median (horizontal line) and third quartile, X represents the arithmetic mean. A) type of habitat, B) foraging stratum, and C) family of bats. Foraging guilds: A = aerial, G = gleaning, foraging stratum: Us = uncluttered space, BCS = background-cluttered space, Hcs = highly cluttered space. Type of vegetation: Gf = gallery forest; df = deciduous forest; Ddf = dry deciduous forests; Ms-df = medium semi-deciduous forests; Hef = high evergreen forest; Xs = Xeric scrublands; and Msf = medium sub-deciduous forests.

Our study suggests that the role of arthropod-eating bats in controlling mosquito populations needs to be thoroughly evaluated, given the high prevalence of mosquitoes that are vectors for diseases in neotropical regions ([Turell 1989](#); [Rueda et al. 1990](#); [Couret et al. 2014](#)). It also establishes and confirms that different species of bats from various families and different guilds actively consume mosquito species that are considered vectors of diseases that affect human populations. This confirms the importance of bats as biological control agents and their positive effect on human populations.

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Supplementary material

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REGLAMENTO INTERNO DEL SISTEMA INTEGRAL DE DIFUSIÓN Y DIVULGACIÓN THERYA DE LA ASOCIACIÓN MEXICANA DE MASTOZOOLOGÍA A. C.

I. Considerando:

- I.1. Que mediante escritura sesenta y nueve mil ciento treinta y tres, extendida el diecisésis de marzo de mil novecientos ochenta y cuatro, ante el entonces notario cincuenta y ocho del Distrito Federal, Licenciado Mario D. Reynoso Obregón, inscrita en el Registro Público de la Propiedad del Distrito Federal, en el Folio de Personas Morales siete mil ochocientos cincuenta y cinco, y previo permiso de la Secretaría de Relaciones Exteriores, se constituyó la "AMMAC", con domicilio en México Distrito Federal (hoy Ciudad de México – CDMX) y duración de noventa y nueve años.
- I.2. Que por escritura nueve mil trescientos trece, extendida el veinte de junio de mil novecientos noventa y uno, ante el notario ciento veintidós del Distrito Federal, Eugenio Ibarrola Santoyo, inscrita en el Registro Público de la Propiedad de esta ciudad en el folio de personas morales siete mil ochocientos cincuenta y cinco, se reformaron los estatutos de la "AMMAC".
- I.3. Que por escritura ciento sesenta y un mil quinientos cuatro, extendida el treinta y uno de agosto de mil novecientos noventa y nueve, ante el notario treinta y uno del Distrito Federal, Alfonso González Alonso, inscrita en el Registro Público de la Propiedad del Distrito Federal, el doce de octubre de mil novecientos noventa y nueve, en el Folio Real Número siete mil ochocientos cincuenta y cinco de Personas Morales, se reformaron los estatutos sociales de la "AMMAC".
- I.4. Que por escritura ciento cincuenta y siete mil trescientos cinco, extendida a los dos días del mes de junio de dos mil catorce, ante el notario cuarenta y dos del Distrito Federal, Licenciado Salvador Godínez Viera, inscrita en el Registro Público de la Propiedad del Distrito Federal, el diecisésis días del mes de junio de dos mil catorce, en el Folio de Personas Morales trescientos siete mil trescientos ochenta y ocho; se reformaron los artículos segundo, vigésimo noveno y trigésimo segundo de los estatutos sociales de la "AMMAC".
- I.5. Que por escritura ciento cincuenta y ocho mil novecientos setenta y cinco, extendida a los trece días del mes de febrero de dos mil quince, ante el notario cuarenta y dos del Distrito Federal, Licenciado Salvador Godínez Viera, inscrita en el Registro Público de la Propiedad y de Comercio del Distrito Federal, el tres de marzo de dos mil quince, en el Folio de Personas Morales ciento cuarenta y nueve mil dos cientos sesenta y nueve; se ratifican los miembros de la Mesa Directiva de la "AMMAC" durante el bienio dos mil catorce a dos mil diecisésis.
- I.6. Que por escritura ciento sesenta y un mil seiscientos sesenta y seis, extendida a los tres días del mes de marzo de dos mil diecisésis, ante el notario cuarenta y dos del Distrito Federal, Licenciado Salvador Godínez Viera, inscrita en el Registro Público de la Propiedad y de Comercio del Distrito Federal, el catorce de marzo de dos mil diecisésis, en el Folio de Personas Morales ciento cuarenta y seis mil quinientos noventa y uno; se actualizan los estatutos sociales de la "AMMAC".
- I.7. Que el artículo cuarto de los estatutos sociales vigentes de la "AMMAC" establece entre sus medios en su inciso "e" publicar periódicamente por lo menos una revista científica sobre mastozoología y mantener un sitio WEB como medio de divulgación y comunicación con la sociedad.

- I.8. Que el artículo décimo tercero de los estatutos sociales vigentes de la "AMMAC" establece en su numeral cuatro que la Asamblea General puede designar comisiones permanentes o transitorias que auxilien a la Mesa Directiva; y el numeral cinco que es una atribución de la Asamblea General, conocer, discutir y aprobar los reglamentos y procedimientos internos que se requieran, como los de la Revista Científica, Reconocimientos y otros que pudieran ser útiles para la Asociación.
- I.9. Que el artículo décimo quinto de los estatutos sociales vigentes de la "AMMAC" establece como una de las atribuciones de la Mesa Directiva en su numeral cuatro, proponer a la Asamblea General los reglamentos y procedimientos internos que se requieran para el funcionamiento de la AMMAC y que la asamblea decidirá su creación por medio de votación.
- I.10. Que en la Asamblea General realizada el ocho de octubre de dos mil dieciséis durante las Quintas Jornadas Mastozoológicas realizadas en la ciudad de Tuxtla Gutiérrez del estado de Chiapas, se aprobó que la Mesa Directiva formara una comisión para elaborar la propuesta del reglamento interno de la Revista Científica de la AMMAC.
- I.11. Que la comisión constituida para elaborar la Propuesta del Reglamento Interno de la Revista Científica Therya de la AMMAC estuvo formada por el Editor General, el Consejo Editorial, los Editores Asociados y la Mesa Directiva Activa, se tiene a bien expedir la siguiente:

REGLAMENTO INTERNO DEL DEL SISTEMA INTEGRAL DE DIFUSIÓN Y DIVULGACIÓN THERYA DE LA ASOCIACIÓN MEXICANA DE MASTOZOOLOGÍA A. C.

Del Sistema Integral de Difusión y Divulgación THERYA

ARTÍCULO 1. Definición

1.1 Las revistas científicas que conforman El Sistema Integral de Difusión y Divulgación THERYA son los medios de comunicación académica de la Asociación Mexicana de Mastozoología, A. C. (AMMAC). Tienen como propósito difundir información y conocimientos originales e inéditos relacionados con el estudio de los mamíferos en todas las disciplinas de su conocimiento. Es un foro abierto para profesores, investigadores, profesionales y estudiantes de todo el mundo, en el que se publican artículos y comunicaciones científicas cortas en español e inglés.

1.2 Las revistas de divulgación del Sistema Integral de Difusión y Divulgación THERYA son el órgano de difusión y divulgación científica de la Asociación Mexicana de

Mastozoología, A. C. (AMMAC). Tienen como objetivo poner el conocimiento de los mamíferos para el público en general de manera objetiva, amena y asequible. Que este conocimiento esté disponible para todo público, en el que se publican artículos cortos en español.

1.3 El Sistema Integral de Difusión y Divulgación THERYA tendrá una Junta Editorial constituida por los Editores Generales de las revistas y cuyo representante será electo por y entre los mismos Editores Generales.

ARTÍCULO 2. Política.

El Sistema Integral de Difusión y Divulgación THERYA, tiene como base la política de acceso abierto, permitiendo la descarga en forma gratuita del contenido por manuscrito, o del número completo de la revista en formato digital. El Sistema Integral de Difusión y Divulgación THERYA tiene la capacidad de autorizar al (a la) autor (a) a colocar el manuscrito en el formato publicado por la revista en su sitio web personal, o en un repositorio de acceso abierto, distribuir copias del manuscrito publicado en formato electrónico o impreso a quien él o ella considere conveniente, así como reutilizar parte o la totalidad del manuscrito en sus documentos institucionales o libros futuros, siempre y cuando se den los créditos correspondientes y/o añadiendo la cita correspondiente de el o los manuscritos en cuestión.

ARTÍCULO 3. Periodicidad.

En el Sistema Integral de Difusión y Divulgación THERYA se publicará un volumen por año con tres números de manera cuatrimestral.

ARTÍCULO 4. Contenido.

4.1 La revista científica THERYA contará con hasta cinco secciones: Editorial; Contribuciones especiales; Artículos; Revisiones; y Comunicados THERYA-AMMAC. No será necesaria la publicación de las cinco secciones en cada uno de los números.

4.2. La revista científica THERYA Notes contará con hasta cinco secciones: Editorial; Contribuciones especiales; Notas; Revisiones; y Comunicados THERYA-AMMAC. No será necesaria la publicación de las cinco secciones en cada uno de los números.

4.3. La revista de divulgación THERYA Ixmana publicará artículos en temas como: Generalidades de los mamíferos y temas de interés y relevancia actual en el estudio de los mamíferos.

ARTÍCULO 5. Proceso en el Sistema Integral de Difusión y Divulgación THERYA.

El Sistema Integral de Difusión y Divulgación THERYA tiene el proceso de revisión por pares. Los manuscritos recibidos serán sujetos a un proceso editorial que incluyen una evaluación preliminar por parte del (de la) Editor (a) General, y alguno (a) de los (las) miembros del Comité Editorial, quienes determinarán la pertinencia de su publicación.

Los manuscritos que cumplan con los requisitos temáticos y de formato conforme a las normas de publicación serán arbitrados al menos por dos pares académicos, expertos en la disciplina de interés, quienes determinarán si el material reúne las características previamente descritas para su publicación; en caso de discrepancia entre los resultados de los revisores, el escrito puede ser enviado a un (a) tercer revisor (a), en el que se apoyará el (la) Editor (a) Asociado (a) para la recomendación final del manuscrito a (el, la) Editor (a) General. La decisión final la tomará el (la) Editor (a) General.

Los manuscritos se someten a un proceso de evaluación de doble ciego, en el que los (las) autores (as) desconocen a los (las) evaluadores y viceversa. El resultado del proceso de dictamen académico es inapelable. Los manuscritos deberán cumplir con las recomendaciones de el o la Editor (a) General antes de ser considerados para su publicación.

ARTÍCULO 6. Derechos de autor.

Se solicitará a los (las) autores (as), tras la aceptación de un manuscrito, el transferir el derecho de autor (a) del artículo a la Asociación Mexicana de Mastozoología, A. C. (AMMAC).

Es responsabilidad del (de la) autor (a) de correspondencia informar a los (las) co-autores (as) sobre el envío del manuscrito y tener derechos por escrito del uso del material, datos, secuencias o espécimen que no pertenezca directamente a los (las) autores (as) de la contribución.

De la Junta Editorial

ARTÍCULO 7. Representante de la Junta Editorial

- Acorde al Artículo 1 Inciso 1.3 del presente reglamento, la Junta Editorial estará integrada por los (las) Editores (as) Generales de las revistas que conformen el Sistema Integral de Difusión y Divulgación THERYA.
- Los (Las) Editores (as) Generales en su conjunto elegirán a un representante por medio de una votación directa.

ARTÍCULO 8. Atribuciones del representante de la Junta Editorial

- Ser el (la) portavoz del Sistema Integral de Difusión y Divulgación THERYA ante la Mesa Directiva de la AMMAC y entidades externas.
- Asistir como testigo a las reuniones de la Mesa Directiva de la AMMAC, cuando éstas aborden temas relativos al Sistema Integral de Difusión y Divulgación THERYA.
- Asistir a convocatoria extraordinaria por la Mesa Directiva de la AMMAC.

ARTÍCULO 9. Duración de la representación

- El (La) representante de la Junta Editorial durará en el cargo 2 años, con posibilidad de reelección hasta por un periodo consecutivo en caso de ser propuesto, aceptar el cargo y ser electo.
- La reelección se hará efectiva si la persona propuesta acepta el cargo.

Del Comité Editorial

ARTÍCULO 10. El Comité Editorial

El Comité Editorial de cada revista que conforma el Sistema Integral de Difusión y Divulgación THERYA estará constituido por:

- Un (a) Editor (a) General.
- El (La) Editor (a) Asistente.
- Los Miembros del Consejo Editorial.
- Los Editores (as) Asociados (as).

ARTÍCULO 11. Atribuciones del Comité Editorial.

Son atribuciones del Comité Editorial:

- Realizar un análisis e informe en conjunto con el (la) Editor (a) General en los temas en referencia a la calidad académica del Sistema Integral de Difusión y Divulgación THERYA.
- Asesorar al (a la) Editor (a) General en los temas inherentes a la publicación, difusión y distribución del Sistema Integral de Difusión y Divulgación THERYA.
- Emitir opiniones sobre las actividades y acontecimientos que afecten o promuevan la

publicación de las revistas del Sistema Integral de Difusión y Divulgación THERYA de la Asociación Mexicana de Mastozoología, A. C

- d) Aprobar las propuestas del (de la) Editor (a) General, Editor (a) Asistente y Editores (as) Asociados (as) que se requieran para el buen funcionamiento de las revistas del Sistema Integral de Difusión y Divulgación THERYA de la Asociación Mexicana de Mastozoología, A. C.; así como el análisis del desempeño de los vigentes.
- e) Hacer cumplir y fomentar el cumplimiento de los objetivos de la Asociación Mexicana de Mastozoología, A. C., a través del Sistema Integral de Difusión y Divulgación THERYA.
- f) Al ser un trabajo voluntario el que se realiza en el Sistema Integral de Difusión y Divulgación THERYA, los miembros del Comité Editorial de las revistas del Sistema Integral de Difusión y Divulgación THERYA no recibirán ningún estímulo o remuneración económica por sus funciones como Comité Editorial, Editores (as) Generales, Asistentes o Asociados (as).
- g) Los miembros del Comité Editorial de la Revistas Sistema Integral de Difusión y Divulgación THERYA serán considerados como miembros honorarios de la AMMAC. Las cuotas de inscripción a cursos y congresos no estarán exentas de pago. Al ser la AMMAC una asociación que realiza actividades académicas con base en el pago de membresías, los miembros del Comité Editorial que deseen realizar el pago de su membresía de forma voluntaria contarán con un descuento del 50% del costo de la misma.
- h) Ningún miembro del Comité Editorial puede pertenecer a la Mesa Directiva de la AMMAC. En el caso que algún miembro del Comité Editorial aceptara un cargo en la Mesa Directiva de la AMMAC, deberá renunciar a su cargo en el Comité Editorial de las revistas del Sistema Integral de Difusión y Divulgación THERYA mientras esté vigente su participación como miembro de la Mesa Directiva. Al finalizar su periodo en la Mesa Directiva, podrá reingresar al Comité Editorial, si así lo juzga pertinente el propio Comité Editorial.

ARTÍCULO 12. Presidencia del Comité Editorial.

El Comité Editorial de cada revista estará presidido por el (la) Editor (a) General de la misma. En caso de llegar a votaciones para su elección, los miembros del

Consejo Editorial serán los que tengan el voto de calidad (desempate).

ARTÍCULO 13. Funciones del Comité Editorial.

El Comité Editorial es el órgano superior académico de las revistas y debe velar por la constante superación académica, mejorar la difusión, garantizar la continuidad y el crecimiento de las revistas del Sistema Integral de Difusión y Divulgación THERYA.

Del (De La) Editor (a) General

ARTÍCULO 14. Del (De la) Editor (a) General y sus atribuciones.

Son atribuciones del (de la) Editor (a) General.

- a) Hacerse cargo de la parte académica de las revistas científicas o de divulgación del Sistema Integral de Difusión y Divulgación THERYA de la Asociación Mexicana de Mastozoología, A. C.
- b) Organizar y coordinar los aspectos inherentes a la publicación, traducción, difusión y distribución de las revistas científicas o de divulgación del Sistema Integral de Difusión y Divulgación THERYA de la Asociación Mexicana de Mastozoología, A. C.
- c) Mantener informados al Comité Editorial y a los miembros de la Asociación Mexicana de Mastozoología, A. C. a través de un informe anual que se presenta ante la Asamblea, sobre las actividades y acontecimientos que promuevan y afecten la publicación de las revistas científicas o de divulgación de dicha asociación.
- d) Proponer Editores (as) Asociados (as), Editores (as) Especiales, miembros del Consejo Editorial, que se requieran para el buen funcionamiento de las revistas científicas o de divulgación del Sistema Integral de Difusión y Divulgación THERYA de la Asociación Mexicana de Mastozoología, A. C. Todas estas propuestas serán comunicadas a la Mesa Directiva de la Asociación Mexicana de Mastozoología A.C. previamente al inicio de su función.
- e) Proponer Tesorero (a), y servicios externos (como encargados de maquetación, traductores, enlaces con plataformas o sistemas necesarios para el funcionamiento de las revistas y todo lo relacionado con la publicación de las revistas). Todas estas propuestas serán comunicadas y tendrán que ser autorizadas por la Mesa Directiva de la Asociación

- Mexicana de Mastozoología A.C. al inicio del año fiscal y previamente al inicio de su función.
- f) Hacer cumplir y fomentar el cumplimiento de los objetivos de la Asociación Mexicana de Mastozoología, A. C., a través de las revistas científicas o de divulgación del Sistema Integral de Difusión y Divulgación THERYA de la Asociación Mexicana de Mastozoología A. C.
 - g) Solicitar a la Mesa Directiva recursos financieros de manera anual al Sistema Integral de Difusión y Divulgación THERYA para su funcionamiento. El recurso será aportado con base en la disponibilidad del mismo.
 - h) Cualesquiera que por ley le correspondan.
- ARTÍCULO 15. Obligaciones del (de la) Editor (a) General.**
- Son obligaciones del (de la) Editor (a) General:
- a) Revisar la documentación que sea entregada por los (las) autores (as) y turnarla a los (las) diferentes Editores (as) Asociados (as).
 - b) Supervisar el proceso de revisión de los manuscritos a cargo de los (las) Editores (as) Asociados (as).
 - c) Llevar un registro minucioso de la documentación recibida, de la que deberán mandar los (las) autores (as), revisores (as), editor (a) de estilo y editores (as) asociados (as).
 - d) Velar porque los procesos de evaluación sean lo más objetivos y constructivos posibles, con la finalidad de fomentar las publicaciones y formar a los (las) autores (as) participantes.
 - e) Coordinarse con el (la) editor (a) de estilo (externo, en caso de que se tenga) para realizar el formato de los artículos, pruebas de edición, pruebas de autor (a), pruebas de galera e impresión final.
 - f) Coordinarse con el (la) encargado (a) de la página de internet para la publicación en tiempo y forma de cada número de la revista.
 - g) Coordinarse con la persona encargada de difusión para que la publicación alcance a la mayor cantidad de lectores, haciendo uso de las herramientas necesarias para este propósito.
 - h) Estar obligado (a) a que la revista se publique en o antes de la fecha de cierre de cada número cuatrimestral.
 - i) Es el (la) responsable de realizar todos los trámites ante el CONAHCYT y de que la revista se mantenga como revista de excelencia, y de otras instancias académicas nacionales o internacionales.
 - j) Delegar las funciones que considere convenientes para el buen funcionamiento de la revista, pero no, la responsabilidad que ellas impliquen.
 - k) Todo lo que sea tratado dentro del Consejo Editorial y Comité Editorial deberá de mantenerse en confidencialidad y no difundir la información, ni ser usada para beneficio personal.
 - l) La violación de los puntos anteriores será considerada para la destitución del puesto, previo análisis por parte del Consejo Editorial y el consejo de exPresidentes de la Asociación Mexicana de Mastozoología A.C.
 - m) Entregar por escrito y presentar un informe anual a la Mesa Directiva de la Asociación Mexicana de Mastozoología A.C. sobre las actividades académicas, así como los acontecimientos que promuevan y afecten la publicación de las revistas científicas o de divulgación de dicha asociación. Dicho informe será presentado a la Asamblea General de la AMMAC para su aprobación. Dependiendo de las circunstancias, la Mesa Directiva puede solicitar información adicional en cualquier momento del año.
- ARTÍCULO 16. Requisitos del (de la) Editor (a) General**
- Los requisitos para ser propuesto como candidato (a) al puesto de Editor (a) General de alguna de las revistas del Sistema Integral de Difusión y Divulgación THERYA son:
- a) Ser socio (a) de la AMMAC por al menos los 5 años anteriores a su postulación.
 - b) Haber ocupado la posición de Editor (a) Asociado (a) por 3 años de la revista a la que se proponga como Editor (a) General o haber fungido por un periodo como Editor (a) General de una revista del Sistema Integral de Difusión y Divulgación de AMMAC.
 - c) Haber publicado como autor de correspondencia al menos dos artículos en la revista del Sistema Integral de Difusión y Divulgación THERYA de la AMMAC en la que postule como Editor General.
 - d) Comprobar su estancia y permanencia en el SNII, es deseable con por lo menos nivel II o superior (o

equivalente por el panel revisor de la candidatura) para las revistas científicas y nivel I (o equivalente por el panel revisor de la candidatura) para las revistas de divulgación.

- e) Para los extranjeros miembros del Sistema Integral de Difusión y Divulgación THERYA, su equivalente al nivel II en el SNII o más para cualquiera de las revistas.
- f) Aceptar la candidatura.

ARTÍCULO 17. Elección del (de la) Editor (a) General.

- a) La Mesa Directiva de la Asociación Mexicana de Mastozoología A. C, en conjunto con el Consejo Editorial del Sistema Integral de Difusión y Divulgación THERYA, abrirá la convocatoria correspondiente para la recepción de propuestas para Editor (a) General de las revistas científicas del Sistema Integral de Difusión y Divulgación THERYA. La convocatoria deberá emitirse al menos 6 meses antes de la finalización del periodo del (la) Editor (a) General para garantizar un proceso de transición entre el (la) Editor (a) General saliente y el (la) entrante.
- b) El Comité Editorial realizará una votación secreta a partir de los posibles candidatos inscritos al puesto de Editor (a) General, compuesta por candidatos (as) que cumplan con los requisitos del artículo 16 de las atribuciones del (de la) Editor (a) General y tomando en cuenta la trayectoria académica de cada uno de los candidatos, emitiendo cada miembro su voto por escrito al Consejo Editorial. Un miembro del Consejo Editorial y un miembro del Consejo de Expresidentes fungirán como responsables del proceso y llevarán a cabo el proceso de la votación, la cual será por votación de mayoría simple (50 por ciento más uno). Los integrantes de la Mesa Directiva de la Asociación Mexicana de Mastozoología A.C. participarán en calidad de testigo de honor.
- c) En caso de no existir candidaturas o que los perfiles de los candidatos no cumplan con el nivel académico o de experiencia después de la evaluación realizada por el Comité encargado de la selección del Editor General, éste podrá declarar la candidatura desierta. De declararse la candidatura

desierta, se abrirá una convocatoria pública donde los (las) participantes a Editor General podrán no cumplir parcialmente los requisitos mencionados en el artículo 16 del presente reglamento a criterio del consejo editorial.

ARTÍCULO 18. Nombramiento del (de la) Editor (a) General.

El (La) Editor (a) General deberá de ser nombrado (a) por el (la) Presidente de la AMMAC a partir de los resultados de la votación.

ARTÍCULO 19. Duración del cargo de (de la) Editor (a) General.

- a) La duración como Editor (a) General será de un período de 5 años, con la posibilidad de presentar su candidatura por un segundo período, si la revista mantiene o supera los estándares de calidad.
- b) El (La) Editor (a) General podrá presentar su candidatura por un segundo período al término del primer período si:
 - i) El Consejo Editorial de la revista a la que pertenece lo postula y evalúa positivamente.
 - ii) El (La) Editor (a) General acepta el cargo por otro período.
 - iii) La Mesa Directiva de la AMMAC no tiene ninguna objeción respecto a su continuidad y no emite una negativa derivada de mal desempeño comprobado en el cargo o falta ética o académica.
- c) El período como Editor General iniciará en el momento de la publicación del primer número de la revista a su cargo.

ARTÍCULO 20. Causas de cesado del (de la) Editor (a) General.

Causas por la que el (la) Editor (a) General puede ser separado de su nombramiento:

- a) Demostrada falta de ética en la publicación de las revistas del Sistema Integral de Difusión y Divulgación THERYA.
- b) Manipulación con dolo del proceso editorial, revisión, arbitraje y cualquier otro referente a las revistas del Sistema Integral de Difusión y Divulgación THERYA.
- c) La no publicación en tiempo y forma de más de dos números de las revistas del Sistema Integral

- de Difusión y Divulgación THERYA durante el periodo a su cargo.
- d) Malos manejos de los recursos materiales y financieros de las revistas del Sistema Integral de Difusión y Divulgación THERYA.
 - e) Reducción en los estándares de calidad de las revistas del Sistema Integral de Difusión y Divulgación THERYA, con base en los parámetros internacionales y nacionales de evaluación de las revistas científicas o de divulgación.
 - f) A petición del Comité Editorial después de una votación con mayoría simple del mismo Comité Editorial.
 - g) A petición de la Mesa Directiva de la AMMAC, con base en uno o varios argumentos que presente y detalle. El planteamiento será evaluado por el Comité Editorial y votado.
 - h) A petición escrita de un grupo de al menos el 25% del promedio de socios (as) de la AMMAC de un promedio de 4 años. El Comité Editorial y la Mesa Directiva de AMMAC realizarán un análisis de su desempeño para la toma de la decisión definitiva.

ARTÍCULO 21. Designación de un (a) Editor (a) General interino (a).

Designación de un (a) Editor (a) General interino. Este (a) será designado (a) por consenso por el Comité Editorial, de manera temporal mientras se asigna un (a) Editor (a) General siguiendo los artículos correspondientes. El (La) Editor (a) General interino (a) deberá de

cumplir con los requisitos mencionados en el Artículo 16 de este reglamento. El Editor Asistente podrá ser nombrado como Editor General Interino en lo que se realiza el proceso de selección y toma de posesión del nuevo Editor General, teniendo el cargo una duración máxima de tres meses.

Los casos por el cual se designe un (a) Editor (a) General interino (a) serán:

- a) El (La) Editor (a) General no pueda continuar por motivos de salud o fallecimiento en el puesto dentro del periodo para el que fue electo.
- b) En el caso de una eventualidad personal que no permita al (a la) Editor (a) General continuar temporalmente con las responsabilidades y obligaciones del cargo.

- c) Por la aplicación del artículo 16 de este reglamento.

Del Consejo Editorial

ARTÍCULO 22. Del Consejo Editorial

22.1. El Consejo Editorial de las revistas científicas del Sistema Integral de Difusión y Divulgación THERYA estará constituido por:

Por lo menos tres investigadores nacionales e internacionales con el más alto nivel académico. Es deseable que tenga el nivel II en el SNII o superior o su equivalente si es extranjero (a), y con experiencia editorial en una revista indexada de circulación internacional asociada al área de mastozoología o afines.

22.2. El Consejo Editorial de la revista de divulgación estará constituido por:

Por lo menos tres investigadores nacionales o internacionales con alto nivel académico, preferentemente con SNII. El número de integrantes deberá ser impar. Los integrantes deben contar con experiencia editorial en una revista y actividades de divulgación de la ciencia asociadas al área de mastozoología o afines.

ARTÍCULO 23. Funciones del Consejo Editorial.

Las funciones del Consejo Editorial serán:

- a) Acordar con el (la) Editor (a) General en las políticas de publicación que deban de seguir las revistas académicas del Sistema Integral de Difusión y Divulgación THERYA de la AMMAC.
- b) Sugerir cambios y mejoras que deban hacerse a la revista para incrementar su impacto académico.
- c) Intervenir con su consejo cuando exista alguna disputa entre el (la) Editor (a) General, Editor (a) Asistente y Editores (as) Asociados (as) o entre Editores (as) Asociados (as).
- d) Tomar las medidas pertinentes cuando las revistas del Sistema Integral de Difusión y Divulgación THERYA tenga algún problema académico y deba de tomarse una decisión en beneficio de la revista.
- e) Otorgar su consejo ante cualquier situación inesperada y de la que sea necesario tomar alguna acción correctiva, de emergencia o de otra índole.

ARTÍCULO 24. Requisitos para pertenecer al Consejo Editorial.

24.1. Los requisitos para ser nombrado (a) miembro del Consejo Editorial de las revistas científicas del Sistema Integral de Difusión y Divulgación THERYA son:

- a) Ser investigador (a) reconocido internacionalmente por sus investigaciones publicadas sobre mamíferos.
- b) Haber ocupado la posición de Editor (a) General, Editor (a) Asociado (a), Editor (a) de publicaciones especiales o dentro del Consejo Editorial en una revista indexada con alto valor de impacto (más de 1.5), se recomienda, además, que haya publicado en las revistas del Sistema Integral de Difusión y Divulgación THERYA de la AMMAC.
- c) Comprobar su estancia y permanencia en el SNII con por lo menos nivel II o superior, para los extranjeros un nivel equivalente.
- d) Tener demostrada productividad científica con al menos 50 artículos en revistas indexadas o reconocidas por el CONAHCYT.
- e) Aceptar la candidatura.

24.2. Los requisitos para ser nombrado (a) miembro del Consejo Editorial de las revistas de divulgación son:

- a) Ser investigador (a) reconocido (a) internacionalmente por sus investigaciones publicadas sobre mamíferos.
- b) Haber ocupado la posición de Editor (a) General, Editor (a) Asociado (a), Editor (a) de publicaciones especiales o dentro del Consejo Editorial en una revista de divulgación, se recomienda que haya publicado en el Sistema Integral de Difusión y Divulgación THERYA.
- c) Preferentemente comprobar su estancia y permanencia en el SNII.
- d) Tener demostrada productividad de divulgación y difusión de la ciencia.
- e) Aceptar la candidatura.

ARTÍCULO 25. Nombramiento de los (las) miembros del Consejo Editorial.

Los (Las) miembros del Consejo Editorial serán nombrados (as):

- a) Los (Las) consejeros (as) Editoriales deberán de ser propuestos (as) por el (la) Editor (a) General y tener una mayoría simple por parte del Comité Editorial y del (de la) Presidente en funciones de la AMMAC.

- b) La votación de los miembros del Comité Editorial y del (de la) Presidente en funciones de AMMAC será secreta, emitiendo cada miembro su voto por escrito al (la) Editor (a) General. La votación será por mayoría simple.

ARTÍCULO 26. Duración de los (las) miembros del Consejo Editorial.

La duración dentro del Consejo Editorial es de cinco años y pueden ser reelectos después de un análisis de su desempeño por el Comité Editorial, previa aceptación de la continuidad en el puesto.

Del (De La) Editor (a) Asistente.

ARTÍCULO 27. Obligaciones del (de la) Editor (a) Asistente de las revistas científicas y de divulgación.

Son obligaciones del (la) Editor (a) Asistente:

- a) Auxiliar en los procesos editoriales al Editor (a) General.
- b) Ayudar a los (las) Editores (as) Asociados (as) y a los (las) Autores (as) durante el proceso de sometimiento, revisión y edición de los manuscritos propuestos para su publicación.
- c) Brindar soporte técnico a los usuarios de la plataforma de la revista.
- d) Verificar que no haya errores de gramática, puntuación, ortografía o sintaxis en el contenido de los escritos aceptados, así mismo que cumplan las normas editoriales de la revista antes de enviarse a maquetación y elaboración de pruebas de galera.
- e) Coordinar el proceso de corrección de pruebas de galera de los escritos, cerciorándose que se hayan cumplido a cabalidad las correcciones conforme a las normas editoriales de la revista.
- f) Ser vínculo entre el (la) Editor (a) General y los (las) proveedores (as) de servicios de maquetación de los archivos PDF, HTML y XML.
- g) Verificar que los metadatos de la plataforma correspondan exactamente a la información que se presenta en las pruebas de galera corregidas.
- h) Auxiliar al (a la) Editor (a) General para la publicación de los artículos y elaboración de los volúmenes y fascículos de la revista.

- i) Asistir y colaborar con el (la) Editor (a) General en las gestiones editoriales que considere pertinente.

ARTÍCULO 28. Los requisitos del (la) Editor (a) Asistente.

Los requisitos para ser nombrado (a) Editor (a) Asistente de las revistas científicas del Sistema Integral de Difusión y Divulgación THERYA son:

- a) Ser especialista en el campo de los mamíferos.
- b) Haber publicado en las revistas del Sistema Integral de Difusión y Divulgación THERYA de la AMMAC o en una revista internacional de prestigio y alto factor de impacto del campo de los mamíferos.
- c) Es deseable su estancia y permanencia en el SNII.
- d) Tener demostrada productividad científica en revistas indexadas o reconocidas por el CONAHCYT.
- e) En caso de ser extranjero demostrar un nivel equivalente al de SNII nivel I o más y haber realizado investigación sobre mamíferos en México.
- f) Aceptar la candidatura.

ARTÍCULO 29. Elección del (de la) Editor (a) Asistente.

El (La) Editor (a) Asistente deberá de ser nombrados por el (la) Editor (a) General y después de obtener una mayoría simple por parte del Comité Editorial.

ARTÍCULO 30. Duración del (de la) Editor (a) Asistente.

La duración del nombramiento como Editor (a) Asistente tendrá vigencia de cinco años y puede ser reelecto (a) por el mismo periodo después de un análisis de su desempeño por el Consejo Editorial, debiendo aceptar la continuidad en el puesto.

ARTÍCULO 31. Causas de cesado como Editor (a) Asistente.

Causas por la que el (la) Editor (a) Asistente puede ser separado (a) de su cargo:

- a) Demostrada falta de ética en la publicación de las revistas del Sistema Integral de Difusión y Divulgación THERYA.
- b) Manipulación con dolo parte del cualquiera de los procesos editoriales, revisiones, arbitraje y cualquier otro referente a las revistas del Sistema Integral de Difusión y Divulgación THERYA.

- c) Reducción en los estándares de calidad de las revisiones realizadas bajo su cargo.
- d) Retraso continuo en el proceso de revisión, evaluación y dictaminación de manuscritos asignados.
- e) A petición escrita por parte del Comité Editorial y después de una votación con mayoría simple.
- f) A petición de la Mesa Directiva de la AMMAC, con base en un argumento académico que será evaluado por el Comité Editorial.

De los (las) Editores (as) Asociados (as)

ARTÍCULO 32. Obligaciones de los (las) Editores (as) Asociados (as)

Son obligaciones de los (las) Editores (as) Asociados (as):

- a) Revisar la documentación que les sea turnada por el (la) Editor (a) General. En caso de conflicto de interés deberá de notificar al (a la) Editor (a) General para que sea turnada a otro (a) Editor (a).
- b) Realizar el proceso de revisión de los manuscritos lo más rápido posible, con la mejor calidad académica.
- c) Llevar un registro minucioso de la documentación recibida, de la que deberán de mandar copia al (a la) Editor (a) General antes de la publicación de cada número.
- d) Velar por que los procesos de evaluación sean lo más objetivos y constructivos posibles, con la finalidad de alentar a los (las) autores participantes a seguir publicando en la revista.
- e) Todo lo que sea tratado dentro del Comité Editorial deberá de mantenerse en privado y no difundir la información ni ser usada para beneficio personal.
- f) La violación de algunos de estos puntos puede ser considerado para la destitución del nombramiento, previo análisis por parte del Consejo Editorial y el (la) Editor (a) General.
- g) Participar en la votación de los (as) nuevos (as) editores (as) asociados (as).

ARTÍCULO 33. Los requisitos de los (las) Editores (as) Asociados (as)

33.1. Los requisitos para ser nombrado (a) Editor (a) Asociado (a) de las revistas científicas del Sistema Integral de Difusión y Divulgación THERYA son:

- a) Ser especialista en el campo de los mamíferos, de preferencia haber ocupado la posición de Editor (a) General o Editor (a) Asociado (a) de alguna revista o publicación.
- b) Haber publicado en las revistas del Sistema Integral de Difusión y Divulgación THERYA de la AMMAC o en una revista internacional de prestigio y alto factor de impacto del campo de los mamíferos.
- c) Comprobar su estancia y permanencia en el SNII por lo menos en el nivel I, aunque se recomienda más alto.
- d) Tener demostrada productividad científica con al menos 20 artículos en revistas indexadas o reconocidas por el CONAHCYT.
- e) En caso de ser extranjero demostrar un nivel equivalente al de SNII nivel I o más.
- f) Aceptar la candidatura.

33.2. Los requisitos para ser nombrado (a) Editor (a) Asociado (a) de las revistas de divulgación son:

- a) Ser especialista en el campo de los mamíferos.
- b) Haber publicado en el Sistema Integral de Difusión y Divulgación THERYA de la AMMAC o en una revista en revistas indexadas o reconocidas por el CONAHCYT del campo de los mamíferos.
- c) Tener grado de Doctorado y de preferencia estar adscrito (a) a alguna institución de investigación. Preferentemente pertenecer al SNII.
- d) Aceptar la candidatura.

ARTÍCULO 34. Elección del (de la) Editor (a) Asociado (a).

Los (Las) Editores (as) Asociados (as) deberán de ser nombrados (as) por el (la) Editor (a) General y después de obtener una mayoría simple en votación del Comité Editorial.

ARTÍCULO 35. Número de Editores (as) Asociados (as).

El número de Editores (as) Asociados (as) estará definido en función del número promedio de manuscritos recibidos por la revista en los últimos dos años. Considerando una proporción de revisión aproximada de seis artículos por año por cada Editor (a) Asociado (a). La especialidad de

los (las) Editores (as) Asociados (as) estará en función de la temática que se reciba para ser evaluada con objeto de publicación dentro de las revistas del Sistema Integral de Difusión y Divulgación THERYA.

ARTÍCULO 36. Duración del (de la) Editor (a) Asociado (a).

La duración del nombramiento como Editor (a) Asociado (a) tendrá vigencia de cinco años y puede ser reelecto (a) por el mismo periodo después de un análisis de su desempeño por el Consejo Editorial, debiendo aceptar la continuidad en el puesto.

ARTÍCULO 37. Causas de cesado como Editor (a) Asociado (a).

Causas por la que el (la) Editor (a) Asociado (a) puede ser separado (a) de su cargo:

- a) Demostrada falta de ética en la publicación de las revistas del Sistema Integral de Difusión y Divulgación THERYA.
- b) Manipulación con dolo parte del cualquiera de los procesos editoriales, revisiones, arbitraje y cualquier otro referente a las revistas del Sistema Integral de Difusión y Divulgación THERYA.
- c) Reducción en los estándares de calidad de las revisiones realizadas bajo su cargo.
- d) Retraso continuo en el proceso de revisión, evaluación y dictaminación de manuscritos asignados.
- e) A petición escrita por parte del Comité Editorial y después de una votación con mayoría simple.
- f) A petición de la Mesa Directiva de la AMMAC, con base en un argumento académico que será evaluado por el Comité Editorial.

De los (las) editores (as) especiales

ARTÍCULO 38. Editores (as) Especiales.

Los (Las) Editores (as) Especiales son aquellos (as) profesores (as)-investigadores (as) de prestigio, invitados (as) por el (la) Editor (a) General para que colaboren en una sección especial de la revista o en un compendio de manuscrito de una temática de interés. La invitación será específicamente para solamente un número por cada dos volúmenes.

ARTÍCULO 39. Obligaciones de los (las) Editores (as) especiales.

Son obligaciones de los (las) Editores (as) especiales:

- a) Invitar a los especialistas para conformar una sección especial de la revista o en un compendio de manuscritos de una temática de interés, la invitación será para presentar manuscritos dentro de la temática de la sección especial.
- b) Revisar la documentación que les sea turnada por el (la) Editor (a) General. En caso de que por algún motivo no lo pueda realizar deberá de notificar al (a la) Editor (a) General para que sea turnada a otro (a) Editor (a).
- c) Realizar el proceso de revisión de los manuscritos lo más rápido posible, pero con la mejor calidad académica.
- d) Llevar un registro minucioso de la documentación recibida, de la que deberán de mandar copia al (a la) Editor (a) General antes de la publicación de cada número.
- e) Velar por que los procesos de evaluación sean lo más objetivos y constructivos posibles, con la finalidad de fomentar y formar a los (las) autores participantes.
- f) Todo lo que sea tratado dentro del Comité Editorial deberá de mantenerse en confidencialidad y no difundir la información ni ser usada para beneficio personal.
- g) La violación de algunos de estos puntos puede ser considerado para la destitución del nombramiento, previo análisis por parte del Consejo Editorial y el (la) Editor (a) General.

ARTÍCULO 40. Requisitos para ser invitado (a) como Editor (a) Especial.

Los requisitos para ser nombrado (a) Editor (a) Especial:

- a) Ser especialista en el campo de los mamíferos, ser especialista en la temática de la edición especial; de preferencia haber ocupado la posición de Editor (a) General o Editor (a) Asociado (a) de alguna revista o publicación.
- b) Comprobar su estancia y permanencia en el SNII con por lo menos nivel I, aunque se recomienda más alto.

- c) En caso de ser extranjero demostrar un nivel equivalente al de SNII nivel I o más.
- d) Aceptar la candidatura.

Del Consejo de Editores (as) Generales del Sistema Integral de Difusión y Divulgación THERYA

ARTÍCULO 41. Los (Las) Editores (as) Generales de las revistas de Difusión y Divulgación de la Asociación Mexicana de Mastozoología formarán parte del Consejo de Editores (as) del Sistema Integral de Difusión y Divulgación THERYA.

Es actividad del Consejo de editores (as) del Sistema Integral de Difusión y Divulgación THERYA:

- a) Trabajar en conjunto para buscar la superación de las revistas.
- b) Apoyarse en compartir recursos que puedan ser utilizados por más de una de las revistas como son páginas web, personal de apoyo, acciones necesarias conjuntas, contratación de servicios externos relacionados con la publicación de las revistas.
- c) Seleccionar y nombrar una persona encargada de la Tesorería del Sistema Integral de Difusión y Divulgación THERYA.
- d) Escoger a los (las) interlocutores (as) específicos para diferentes actividades o acciones que necesite el Sistema Integral de Difusión y Divulgación THERYA.

De la Tesorería

ARTÍCULO 42. La persona encargada de la Tesorería del Sistema de Difusión y Divulgación THERYA será propuesta por el Consejo de Editores (as) del Sistema Integral de Difusión y Divulgación THERYA. La propuesta será avalada por la Asamblea General de la AMMAC.

ARTÍCULO 43. Obligaciones de la persona encargada de la Tesorería del Sistema Integral de Difusión y Divulgación THERYA.

Es obligación de la persona encargada de la Tesorería:

- a) Administrar correctamente los recursos económicos del sistema.

- b) Efectuar las contrataciones y los pagos correspondientes del sistema en coordinación con el (la) Tesorero (a) de la AMMAC.
- c) Presentar un informe periódico al (a la) Editor (a) General de las revistas del Sistema Integral de Difusión y Divulgación THERYA y un informe anual a la Mesa Directiva y Asamblea General de la Asociación Mexicana de Mastozoología, A. C.
- d) Mantener una comunicación directa con el (la) Tesorero (a) de la AMMAC sobre aspectos financieros de la revista.

ARTÍCULO 44. Requisitos para ser invitado (a) como encargado (a) de la Tesorería del Sistema Integral de Difusión y Divulgación THERYA.

- a) Ser socio (a) de la AMMAC por al menos los 5 años anteriores a su postulación.
- b) De preferencia haber ocupado el puesto de Tesorería en la Mesa Directiva de alguna asociación o demostrar experiencia en el manejo y administración de recursos.
- c) Haber publicado en revistas científicas.
- d) Aceptar la candidatura.

ARTÍCULO 45. Duración de la persona encargada de la Tesorería del Sistema Integral de Difusión y Divulgación THERYA.

- a) Hasta que el Consejo de Editores (as) del Sistema Integral de Difusión y Divulgación THERYA en conjunto con la Mesa Directiva de AMMAC lo propongan.
- b) Hasta que la persona encargada lo decida.

ARTÍCULO 46. Causa de cese de la persona encargada de la Tesorería del Sistema Integral de Difusión y Divulgación THERYA.

- a) Cuando no haya cumplido con alguna de sus obligaciones.
- b) Cuando el Consejo de Editores (as) del Sistema Integral de Difusión y Divulgación THERYA lo proponga con una carta de exposición de motivos.

Transitorios

ARTÍCULO PRIMERO. Este reglamento aplicará a partir de su aprobación por la Mesa Directiva y la Asamblea General de la Asociación Mexicana de Mastozoología A. C.

ARTÍCULO SEGUNDO. Cualquier modificación al presente reglamento, deberá ser aprobada por la Asamblea General de Socios (as).

Información publicada por la Mesa Directiva de la Asociación Mexicana de Mastozoología Asociación Civil. El reglamento fue votado y aprobado en la asamblea de socios del 26 de septiembre del 2024 en la ciudad de Pachuca de Soto, México.'