Therya

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AMMAC

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La Portada

Logotipo de la Asociación Mexicana de Mastozoología A. C.

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 decimoprimero en la cosmogonía mexica. “Ozomatli” es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. “ Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo.”

Contenido

Therya

Volumen 10, número 3 septiembre 2019

EDITORIAL

ARTICLES

Corrigendum

fascículo 30   http://www.mastozoologiamexicana.org/doi/10.12933/therya-10_3

DERECHOS DE AUTOR Y DERECHOS CONEXOS, año 10, No. 3, septiembre-diciembre del 2019, es una publicación cuatrimestral editada por la Asociación Mexicana de Mastozoología A. C. Hacienda Vista Hermosa 107, Colonia Villa Quietud, Coyoacan 04960. Distrito Federal, México. Telefono (612) 123-8486, www.mastozoologiamexicana.org, therya@cibnor.mx. Editor responsable: Dr. Sergio Ticul Álvarez Castañeda. Reservas de Derechos al Uso Exclusivo No. 04-2009-112812171700-102, ISSN: 2007-3364 ambos otorgados por el Instituto Nacional de Derechos de Autor. Responsable de la última actualización de este número, Unidad de informática de la Asociación Mexicana de Mastozoología A. C. Dr. Sergio Ticul Álvarez Castañeda. Instituto Politécnico Nacional 195. La Paz, Baja California Sur, C. P. 23096. Tel, (612) 123-8486, fecha de la última modificación 30 septiembre 2019.

Therya

El objetivo y la intención de *THERYA* es ser una revista científica para la publicación de artículos sobre los mamíferos. Estudios de investigación original, editoriales, artículos de revisión y notas científicas son bienvenidas.

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Editorial

La revista Therya consuma con este fascículo la impresión de 10 volúmenes, por lo que cumple su primera década de vida. Therya surge como una necesidad de la comunidad mastozoológica de tener vías de difusión del conocimiento académico que se genera tanto en el núcleo de la Asociación Mexicana de Mastozoología (AMMAC) como en otras asociaciones hermanas.

Therya nace cuando la Dra. Sonia Gallina funge como presidente de la Asociación Mexicana de Mastozoología (2008-2010), momento en que ya estaba constituida como una organización madura al ser productora constante de un acervo científico que debe de ser difundido. En esta época se identificó la necesidad de crear un espacio propicio para difundir los resultados que se generan en el campo de la mastozoología. Therya surge con la filosofía de apoyar la publicación de contribuciones académicas de calidad científica, pero con la visión de apoyar a estudiantes en su formación como mastozoólogos. Por ello Therya a apoyados extracurricularmente mediante el proceso de revisión por pares y con la experiencia catedrática de los integrantes su comité editorial . Una de las principales metas de esta revista es apoyar a los jóvenes investigadores y estudiantes a embeber, conocer y aprender el arte de la escritura académica, al mismo tiempo que ha fomentado la difunción los resultados de sus investigaciones.

El apoyo de la AMMAC ha sido continúo a través de las administraciones de los Dres. Luis Ignacio Iñiguez Dávalos, Miguel Ángel Briones Salas, Jorge Ignacio Servín Martínez, Javier Enrique Sosa Escalante y su actual presidente Enrique Martínez Meyer. Es en la administración de Javier Enrique Sosa Escalante y Enrique Martínez Meyer, donde la revista tiene sus primeros financiamientos externos, que le permite poder tener difusión en plataformas más profesionalizadas y la posibilidad de poder ofrecer becas de traducción a inglés a los artículos que se publican. En 2017, Therya consigue un gran logro, al recibir su primer factor de impacto por SCOPUS que se ha mantenido por arriba de 0.5 puntos, lo que la posiciona en el grupo de revistas mexicanas con mayor impacto. Las contribuciones enviadas a Therya se han incrementado desde el primer año en que se publicó, que fue en el 2010, durante el cual se recibieron 24 contribuciones. Este número contrasta con la recibidas hasta el 25 de septiembre del 2019 que han sido106, más las que se acumulen en los próximos cuatro meses, por lo que se espera que para el 2019 se reciban más de 125 manuscritos. Con relación al material publicado, este se ha estabilizado en un promedio anual de 45 artículos y notas académicas, sumando hasta el presente fascículo 386 contribuciones, además de 49 editoriales, de comunicaciones de la propia AMMAC y Corrigendum. Therya se ha nutrido principalmente de contribuciones de autores de México y países latinoamericanos, aunque en los últimos años se han recibido contribuciones de investigadores de Norteamérica, Europa y Asia, lo que le ha permitido posicionarse en el ámbito de la comunidad mastozoológica a internacional.

En la parte académica en estos diez años se ha recibido apoyo de infinidad de revisores, que han dedicado parte de su tiempo a revisar y apoyar a los autores para que la calidad de sus contribuciones sean mejores. Estos revisores han sido coordinados por un grupo de editores asociados a diferentes instituciones, de varias nacionalidades y países, los que son: Sergio Ticul Álvarez-Castañeda, Rafael Ávila Flores, Miguel Briones, Patricia Cortés, Guillermo D'Elía, Mónica Díaz, Jesús Fernández, Mariana Freitas Nery, Sonia Gallina, Juan Pablo Gallo, Lázaro Guevara, William L. Lidicker, Consuelo Lorenzo, Cristina MacSwiney González, Jesús Maldonado, Lía Méndez, Eduardo Mendoza, Robert Owen, Rafael Reyna, Jan Schipper, Jorge Servín, Sergio Solari y Pablo Teta.

Therya también se ha apoyado en quienes han ayudado a llevar acabo la realización difusión y manejo de la revista y que son parte crucial para su elaboración y publicación: Malinalli Cortés Marcial, Gerardo García, Gabriela Monroy Gamboa, Luis Carlos Moreno, Concepción Ramírez Aburto, Evelyn Ríos y Cintya Segura Trujillo.

Con este fascículo de aniversario de 10 años de Therya el que suscribe, sus editores e integrantes del equipo de la revista queremos agradecer a todos aquellos quienes gestaron, permitieron, contribuyeron y fomentaron la consolidación de Therya como una revista de relevancia para la comunidad mastozoológica. Gracias por permitirnos contribuir en la difusión los avances en la mastozoología y en la formación de profesionales amantes de nuestro objeto de estudio los mamíferos.

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Insights into the evolutionary and demographic history of the extant endemic rodents of the Galápagos Islands

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Evolutionary radiations stemming from colonization of archipelagos provide valuable insights into mechanisms and modes of speciation. For this reason, the fauna inhabiting the Galápagos Islands has been the focus of numerous emblematic ecological and evolutionary studies. However, studies focused on rodents have been scarce. Rice rats radiated *in situ* into at least six endemic species: *Aegialomys galapagoensis*, *Nesoryzomys narboroughi*, *N. swarthi*, *N. fernandinae*, *N. indefessus*, and *N. darwini*. Only the first four species remain extant on the archipelago. These species are considered vulnerable, mainly due to human activities and invasive species. Despite their interesting evolutionary history, questions surrounding phylogenetic relationships, colonization events, genetic diversity and demography of populations remain unresolved. We used the D-loop region of mtDNA to infer phylogenetic relationships, colonization events, date divergences, and conduct population genetic analyses of the four extant endemic species inhabiting the Galápagos Islands. We found that all species were monophyletic. *A. galapagoensis* is sister to *A. xanthaeolus* from the continent, and both of them are the sister clade of the genus *Nesoryzomys*. Our results also showed that there were two colonization events to the islands. The first event was the arrival of the ancestor of *Nesoryzomys* during the Pliocene, when divergences between genera occurred. The second was *Aegialomys* during middle Pleistocene, when species diversification began. Populations on each island show high genetic diversity and most show signals of recent expansion. However, future studies are needed to accurately assess the conservation status of these populations. We suggest ongoing monitoring of these vulnerable endemic species, including ecological and population genetic studies. In addition, future studies using genome-wide molecular markers and additional species from the continent, as well as sampling extinct species from the islands, will improve our knowledge about the origin and relationships of the endemic rodents of the Galápagos Islands.

Las radiaciones evolutivas que ocurren en los archipiélagos, posterior a su colonización, proporcionan información relevante sobre las formas y mecanismos de especiación. Por tal motivo, la fauna que habita en las Islas Galápagos ha sido objeto de numerosos y emblemáticos estudios. A pesar de lo anterior, los estudios enfocados a roedores han sido escasos. Las ratas arroceras han radiado *in situ* en al menos seis especies endémicas: *Aegialomys galapagoensis*, *Nesoryzomys narboroughi*, *N. swarthi*, *N. fernandinae*, *N. indefessus* y *N. darwini*. A la fecha, solo las primeras cuatro especies aún se distribuyen en el archipiélago. Dichas especies se encuentran clasificadas como vulnerables, debido principalmente a las actividades humanas y las especies invasoras. A pesar de la interesante historia evolutiva que presentan estas especies, las interrogantes sobre sus relaciones filogenéticas, los eventos de colonización de las islas y la diversidad genética e historia demográfica de sus poblaciones, siguen sin resolverse. Dado lo anterior, usamos la región D-loop del DNA mitocondrial para inferir las relaciones filogenéticas, los eventos de colonización, los tiempos de divergencia y analizar el estado genético poblacional de las cuatro especies endémicas existentes en las Islas Galápagos. Encontramos que todas las especies representan grupos monofiléticos, que *A. galapagoensis* es la especie hermana de *A. xanthaeolus* del continente, y que estas dos especies son el grupo hermano del género *Nesoryzomys*. Nuestros resultados indican dos eventos de colonización en las islas. El primer evento muestra la llegada del ancestro de *Nesoryzomys* durante el Plioceno, siendo contemporáneo a la divergencia entre los dos géneros. El segundo evento de colonización ocurrió a mediados del Pleistoceno, cuando *Aegialomys* invadió el archipiélago y los eventos de diversificación de las especies comenzaron. En general, las poblaciones en las islas muestran una diversidad genética alta y una señal de expansión reciente. A pesar de ello, se requiere de más estudios para evaluar con precisión el estado de conservación de las poblaciones. Sugerimos que las poblaciones de estos roedores endémicos y vulnerables sean monitoreadas, realizando estudios ecológicos y genéticos. Adicionalmente, estudios futuros que utilicen marcadores moleculares distribuidos a través del genoma completo y que incluyan a las especies extintas en las islas y a más especies del continente, mejorarían el conocimiento sobre el origen y las relaciones de los roedores endémicos de las Islas Galápagos.

Key words: *Aegialomys*; colonization; diversification; *Nesoryzomys*; populations; speciation.

Introduction

Remote oceanic islands and archipelagos are biologically simpler than continental regions and therefore provide ideal geographical and historical settings for the study of colonization, adaptation, speciation, and diversification of species. Islands have long been recognized as natural models for the study of evolutionary processes (Parent *et al.* 2008; Losos 2010; Rodrigues and Diniz-Filho 2016; Román-Palacios and Wiens 2018). Compared to continental regions, islands are more ideal places to observe and interpret patterns of evolution due to their geographic isolation, small size, fewer numbers of species, and a high degree of endemism. The development of ecological and evolutionary systems can be directly observed on volcanic islands as we are now better able to date the timing of their emergence above the ocean surface as blank slates for colonization and the timing of subsequent evolutionary diversification (Losos and Ricklefs 2009; Hendriks *et al.* 2019).

The Galápagos Islands are a young oceanic and volcanic archipelago resulting from the eastward passage of the Nazca plate over a hotspot, at a rate of 59 km/My, located in the Pacific Ocean at approximately 960 km west of the coast of South America. It is composed of 13 major islands larger than 10 km^2, six smaller islands, over 40 islets with official names and many smaller unnamed islets and rocks, for a total of approximately 8,000 km^2 of land spread over 45,000 km^2 of water (Snell *et al.* 1996; Parent *et al.* 2008, Geist *et al.* 2014, Harpp *et al.* 2014). The age of the islands increases moving eastward with the oldest islands located towards the southeast of the archipelago. The present islands date from up to 3.5 to 4 million years ago (Ma) for the eastern islands of Española and San Cristóbal, respectively, to 60,000 years ago for Fernandina Island (Geist *et al.* 2014).

Despite their tropical climate, the Galápagos Islands have been the stage of surprisingly few animal diversifications compared with other Pacific tropical island groups. Among vertebrates, the absence of amphibians and the virtual absence of mammals are particularly striking and nearly unique among terrestrial island ecosystems (Parent *et al.* 2008). However, Román-Palacios and Wiens (2018) showed that the Galápagos archipelago drove faster rates of speciation and diversification in tanagers and tortoises, at least three times higher than in other related lineages of birds and tortoises inhabiting different islands.

The rodents of the Galápagos Islands are the only terrestrial mammals that have naturally colonized the islands and diversified within the archipelago. They belong to the Neotropical rice rat family Cricetidae, subfamily Sigmodontinae, tribe Oryzomyini. Two genera of rodents are currently known to be present on the islands: *Aegialomys* (Weksler *et al.* 2006) and *Nesoryzomys* (Heller 1904). There are two commonly recognized and described species in the genus *Aegialomys*: *A. xanthaeolus* the type species from the mainland and *A. galapagoensis*, formerly known from San Cristobal Island but has not been collected since their initial capture by Darwin in 1835 and is presumed extinct there (Patton and Hafner 1983; Dowler *et al.* 2000). In addition, the subspecies *A. galapagoensis bauri*, extant in Santa Fé Island, was previously considered a separate species but has been most often considered synonymous with *A. galapagoensis* (Cabrera 1961; Musser and Carleton 1993, 2005; Weksler *et al.* 2006; Weksler and Percequillo 2011; do Prado and Percequillo 2018). The genus *Nesoryzomys* comprises two extinct and three extant species. The two extinct species are *N. indefessus* from Santa Cruz and Baltra Islands and *N. darwini* from Santa Cruz Island. The extant species include *N. swarthi* from Santiago Island, and *N. narboroughi* and *N. fernandinae* from Fernandina Island (Dowler and Carroll 1996; Dowler *et al.* 2000). *N. narboroughi* has sometimes been synonymized with *N. indefessus* (Heller 1904; Musser and Carleton 1993, 2005), but in this manuscript we retain both *N. indefessus* and *N. narboroughi* as different species as recommended by Dowler (2015). The giant rice rat, *Megaoryzomys curioi*, is known only from subfossil remains from Santa Cruz Island and is not known to have a mainland representative (Patton and Hafner 1983). It is possible that its extinction occurred prior to human settlement of the archipelago.

To date, the only systematic study to include nearly all of the species in the Galápagos, both extinct and extant, is Patton and Hafner (1983). They did not analyze *N. fernandinae* (Hutterer and Hirsch 1980), which was described as a new species after their research was in press (Dowler *et al.* 2000). Based on a variety of data sets, including morphology, anatomy, protein electrophoresis and chromosome number and morphology, they suggested that: a) *Nesoryzomys* should be recognized at the generic level, nevertheless its origin is ambiguous, b) there were at least two independent colonizations of the islands, with *Nesoryzomys* representing an early arrival at 3 to 3.5 Ma, followed considerably later by *Aegialomys* as late as a few hundred to a thousand years ago, c) both *Aegialomys* taxa from the islands derived from *A. xanthaeolus* of the coastal Peruvian river valleys, d) *N. narboroughi, N. swarthi* and *N. indefessus* should be considered as races of a single species; and e) *A. galapagoensis* and *A. bauri* should be considered conspecific.

Dowler *et al.* (2000) performed one of the most recent field surveys during which they discovered a population of *N. fernandinae*; this allowed the first opportunity to describe the appearance of this species, which was previously known only from skeletal remains (Hutterer and Hirsch 1980) from Fernandina Island. They also found a viable population of *N. swarthi* on Santiago Island, which had previously been presumed extinct. These specimens represent the first endemic rodents taken on Santiago Island since the type series was collected in 1906 (Orr 1938), and a single partial skull was found in 1965 (Peterson 1966). However, recent molecular phylogenetic studies included only *A. xanthaeolus*, *N. narboroughi* and *N. swarthi*. Weksler (2003, 2006) and Weksler *et al.* (2006), using a nuclear exon and morphology, found that *N. narboroughi* and *N. swarthi* are monophyletic, and they are closely related to *A. xanthaeolus*. Pine *et al.* (2012), Leite *et al.* (2014), and Machado *et al.* (2014), using morphology and mitochondrial and nuclear genes, supported the results of Weksler (2003, 2006) and the results of Weksler *et al.* (2006).

Outside of what was learned from these studies, little is known about the endemic rodents of the Galápagos Islands; however, it is clear that they are critically threatened by invasive species and human activities. The goal of the present study was to undertake the first study including comprehensive sampling of all four extant endemic rodent species (*A. galapagoensis, N. narboroughi, N. swarthi* and *N. fernandinae*) inhabiting the archipelago, to provide a dated phylogeny, and to elucidate the population genetics status of each species. This information will help to elucidate the evolutionary history of these island taxa and synthesize information about evolution and biogeography at scales that span remote islands, archipelagoes and continents.

Methods

Sample collection. We obtained tissue samples (liver, kidney) from museum specimens deposited at Angelo State Natural History Collections (ASNHC) at Angelo State University and the Museum of Vertebrate Zoology at the University of California, Berkeley (MVZ). Additional samples were from ear biopsies from animals released at the collection site. We sampled 159 individuals of the *Aegialomys* and *Nesoryzomys* genera inhabiting the Galápagos Islands, *A. galapagoensis* (*n* = 43), *N. narboroughi* (*n* = 49), *N. swarthi* (*n* = 43), and *N. fernandinae* (*n* = 24; Figure 1, Appendix 1), and two samples of *A. xanthaeolus* from Ecuador to elucidate its relationship with *A. galapagoensis*. We used *Pseudoryzomys simplex* and *Oligoryzomys microtis* as outgroups for the phylogenetic analyses (sequences downloaded from GenBank, accession numbers AY863422.1 and AY863420.1, respectively).

DNA isolation and mitochondrial gene amplification. We extracted DNA from tissues using the DNeasy® Blood and Tissue Kit (QIAGEN, Inc., Valencia, CA) by cutting approximately 20 µg of tissue into several small pieces and following the manufacturer's protocol. We amplified the mitochondrial control region (D-loop) by polymerase chain reaction (PCR) using the primers designed for *Oligoryzomys* spp. (González-Ittig *et al.* 2002). In rodents, the D-loop has been useful in phylogenetic analyses due to its elevated mutation rate, lack of recombination and maternal inheritance (Robins *et al.* 2014). Also, due to its high mutation rate, this marker has been used to detect signatures of population structure at a scale of just a few kilometers (Hirota *et al.* 2004; Urgoiti *et al.* 2018). The PCR reactions contained 14.85 µL DEPC H2O, 3.0 µL 10X Reaction buffer, 3.0 µL deoxynucleotide triphosphates (dNTPs, 2 mM of each), 1.5 µL each forward and reverse primer (10 µM), 3.0 µL of 0.1 % bovine serum albumin (BSA), 0.15 µL AmpliTaq DNA polymerase (Applied Biosystems, Foster City, CA), and 3 µL of DNA for a final reaction volume of 30 µL. We used 1 % agarose gels stained with ethidium bromide to visualize DNA extractions and to amplify products. Amplification parameters were as follows: initial step of 95 ºC (4 min), followed by 34 cycles of denaturation at 95 ºC (40 sec), annealing at 50 ºC (30 sec), extension at 72 ºC (90 sec), and a final extension at 72 ºC (10 min). Reaction products were purified using AMPure Magnetic Beads (Agencourt Bioscience, Beverly, MA). The *Oligoryzomys* D-loop primers were used in an initial sequencing run. More specific internal forward and reverse primers were designed using the sequence fragments obtained from this initial run. The internal primers GIF (5' - CCACTACCAGCACCCAAAGCTG - 3') and GIREV (5'- GGTTGTGTTGATTAATGATCC - 3') were used in all sequencing reactions. Five microliters of cleaned PCR product were added to 4µL of ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, CA) and 1.0 µL of 1.6 µM internal primer in each sequencing reaction (GIF and GIFREV). Sequencing reaction conditions were: 96 ºC (1 min), 45 cycles of 96 ºC (30 sec), 58 ºC for GIF or 52 ºC for GIREV (15 sec), 60 ºC (4 min), followed by a final holding step of 4 ºC. All sequencing reactions were performed using GeneAmp® PCR System 9700 (Applied Biosystems, Foster City, CA). Final sequencing products were purified using Sephadex G-50 powder then dried in a vacuum centrifuge and stored at - 20 ºC. Sequences were re-hydrated with the addition of 5 µL of HiDi Formamide with 0.1 mM EDTA, denatured at 95 ºC (3 min) and sequenced with capillary action electrophoresis using SCE 9610 Genetic Analysis System (SpectruMedix, State College, PA).

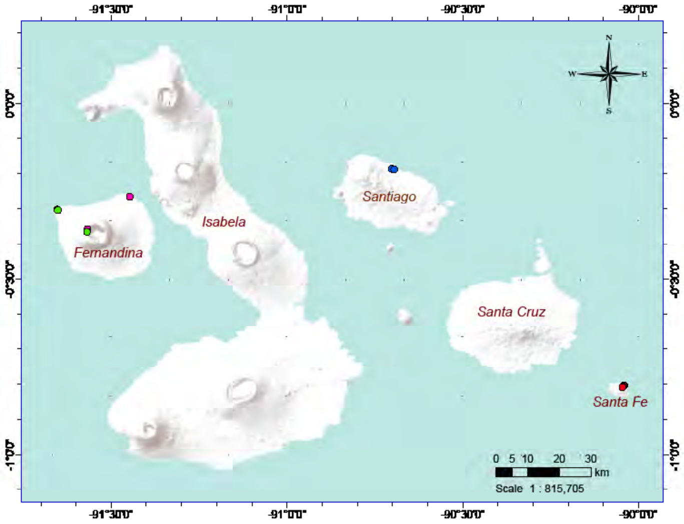

Figure 1. Sampling localities of *A. galapagoensis* (red dots; *n* = 43), *N. narboroughi* (pink dots; *n* = 49), *N. swarthi* (blue dots; *n* = 43) and *N. fernandinae* (green dots; *n* = 24) in the Galápagos Islands.

Phylogenetic analyses and divergence times estimation. We cleaned and edited sequences using Geneious® 11.1.4 (https://www.geneious.com), and performed multiple sequence alignment using ClustalW v.2.1 (Larkin *et al.* 2007) implemented in Geneious. The best evolutionary model of nucleotide substitution was estimated in jModelTest 2.1.1 (Guindon and Gascuel 2003; Darriba *et al.* 2012) using the Akaike information criterion. A Bayesian Inference (BI) analysis was performed in MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), run for 20 million generations sampling every 1,000 generations. Output parameters were visualized using Tracer v1.7.1 (Rambaut *et al.* 2018) to check for convergence between runs, and the first 25 % of the trees were discarded as burn-in.

We used BEAST v2.5.2 (Bouckaert *et al.* 2014) to estimate molecular dates of divergences under an uncorrelated lognormal relaxed molecular clock model. The time to the most recent common ancestor for the main lineages was obtained using Bayesian Markov chain Monte Carlo

(MCMC) searches. We sampled trees and divergence dates for all nodes every 10,000 iterations for 50,000,000 generations. These analyses implemented the Yule speciation processes model and the randomly generated starting tree as priors. We used three calibration points. The first calibration was based on a biogeographical event: the origin of the Galápagos archipelago at 5 Ma (Geist *et al.* 2014). Machado *et al.* (2014) found that the lineage leading to the endemic genus *Nesoryzomys* derived from an ancestor shared with the clade composed of *Melanomys*, *Sigmodontomys* and *Aegialomys* and split around 1.49 (95 % HPD : 0.26 to 3.23) Ma. We used the split between *Nesoryzomys* and *Aegialomys* as a second calibration point. The third calibration point was based on the split of the lineage leading to *Pseudoryzomys* around 2.58 (95 % HPD : 0.43 to 5.38) Ma (Machado *et al.* 2014). We checked convergence statistics for effective sample sizes using Tracer v1.7.1 (Rambaut *et al.* 2018). We used TreeAnnotator v2.5.2 (available in the BEAST package) to get a consensus tree with node height distribution after elimination of 25 % of trees as burn-in. We visualized MrBayes and Beast results using FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

We performed BI and Beast analyses including all samples per species (trees not shown). We chose to perform the phylogenetic and dating analyses using representative samples of each species to reduce the saturation effects. Populations-level analyses included all the samples.

Population analyses. We conducted population genetic analyses separately for each clade determined with the BI analysis, with the exception of *A. xanthaeolus* because of the small sample size. The number of haplotypes (*H*), nucleotide diversity (π) (Nei 1987), haplotypic diversity (*h*), number of polymorphic segregating sites (*S*), singletons (S_1), parsimony informative sites (PIS), and the average number of nucleotide differences (*K*) were estimated using DNAsp v6.12 (Rozas *et al.* 2017). We performed Fu's *Fs* (Fu 1997) and Tajima's *D* (Tajima 1989a) neutrality tests to evaluate whether data departed from a neutral model of evolution due to factors such as population bottleneck or sudden expansion. Statistical significance was determined using the coalescent simulator in DNAsp v6.12 (Rozas *et al.* 2017) with 1000 simulations.

We used the distribution of the number of pairwise mutational differences among individuals, or mismatch distribution, to explore demographic patterns of populations using DNAsp v6.12 (Rozas *et al.* 2017); graphical representation was made by means of the growth-decline model. Raggedness (*r*) index (Harpending 1994) and R_2 statistics of Ramos-Onsins and Rozas (2002) were calculated to analyze goodness of fit of a population expansion model using 1000 simulations in the same program. Populations at demographic equilibrium or in decline should provide a multimodal distribution of pairwise differences, whereas populations that have experienced a sudden demographic expansion should display a star-shaped phylogeny and a unimodal distribution (Tajima 1989b; Slatkin and Hudson 1991; Rogers and Harpending 1992; Harpending and Rogers 2000). However, recent changes in population size may not be detectable in mismatch distribution analyses due to threshold effects, time lags, or earlier demographic events that may mask the effects of recent events (Rogers and Harpending 1992; Harpending and Rogers 2000).

We analyzed the magnitude of historical demographic events by constructing Bayesian Skyline Plots (BSP) using BEAST v2.5.2 (Bouckaert *et al.* 2014). This analysis infers population fluctuations over time by estimating the posterior distribution of the effective population size at specific intervals along a phylogeny (Drummond and Rambaut 2007). Genealogies and model parameters were sampled every 10,000 iterations along 50,000,000 generations under a relaxed molecular clock, with 25 % of burn-in. Convergence statistics for effective sample sizes and demographic plots were visualized using Tracer v1.7.1 (Rambaut *et al.* 2018). In comparison with simple parametric and older coalescent demographic methods, the smoother estimates and sensitivity of this method, together with credibility intervals, provide a realistic population size function and enable retrieval of more details than just summary statistics (Deli *et al.* 2016).

To further investigate the genetic relationships of the haplotypes at the intraspecific level we constructed haplotype networks using the Median-Joining algorithm (Bandelt *et al.* 1999) implemented in PopART v1.7 (Leigh and Bryant 2015).

Results

Phylogenetic lineages and divergence time. We amplified an average of 643 bp of the D-loop gene from 159 individuals of the *Aegialomys* and *Nesoryzomys* genera inhabiting the Galápagos Islands (*A. galapagoensis* $n = 43$, *N. narboroughi* $n = 49$, *N. swarthi* $n = 43$, and *N. fernandinae* $n = 24$, Figure 1, Appendix 1) and two samples of *A. xathaeolus* from the mainland.

The TVM with gamma distribution (+ G) model was recognized as the best fitting model with the following parameters: base frequencies A = 0.3612, C = 0.2445, G = 0.1109, T = 0.2834; nst = 6; and rates = gamma with shape parameter (α) = 0.6020. The BI and Beast analyses including all the samples per species (trees not shown) confirmed the monophyly of each of the species. However, the relationship with the outgroups was not well resolved and the posterior probabilities were lower. This could be due to the high mutation rates that are inherent to the D - loop region which can result in genetic saturation. Distantly related taxa are often affected by saturation effects. When sequences in a multiple alignment have undergone multiple substitutions, the apparent distances largely underestimate the real genetic distances and the alignment is said to be saturated (Philippe *et al.* 2011). In phylogenetics, saturation effects result in long branch attraction, decrease of phylogenetic information, and underestimation of observed divergence times (Wilke *et al.* 2009, Philippe *et al.* 2011). We thus focused our subsequent results and conclusions on the analyses that included only representative samples of each species. The BI analyses showed a topology in which four main clades for the Galápagos species were recognized with high levels of support and one clade including the continental species (Figure 2). All of the Galápagos rodent species analyzed were monophyletic. Clade 1 corresponds to all individuals recognized as *A. xanthaeolus*, which is a sister group of Clade 2, which includes all representatives of *A. galapagoensis*. Clade 3 corresponds to all samples identified as *N. narboroughi*, which is the sister to Clade 4 and Clade 5, corresponding to *N. swarthi*, and *N. fernandinae*, respectively.

The analysis estimating the time to the most recent common ancestor (TMRCA) showed that the oldest divergence event corresponds at the split between the *Nesoryzomys and Aegialomys* genera, dated around 3.84 (95 % HPD : 2.91 – 4.88) Ma (Figure 3). The first split between a continental versus an island species, *A. xanthaeolus* and *A. galapagoensis*, occurred around 1.11 (95 % HPD : 0.37 to 2.11) Ma. Speciation within the genus *Nesoryzomys* started around 2.23 (95 % HPD : 1.32 to 3.12) Ma with the split between *N. fernandinae* and *N. swarthi* versus *N. narboroughi*, followed by the split between the two lineages composed of *N. fernandinae* and *N. swarthi* which occurred around 1.58 (95 % HPD : 0.91 to 2.42) Ma. The estimated dates of divergence for the main nodes and their highest posterior density values are shown in Table 1. According to these results, the main speciation events occurred since the early-middle Pliocene up to the Pleistocene. However, the diversification within each species started at the end of the Pleistocene around 525,500 years ago.

Demographic reconstruction. Genetic diversity and neutrality test per species are shown in Table 2. All of the endemic species of the Galápagos Islands showed high genetic diversity (*Hd* > 0.965). *N. fernandinae* has the highest number of unique haplotypes in proportion with the number of samples, and *N. swarthi* the lowest.

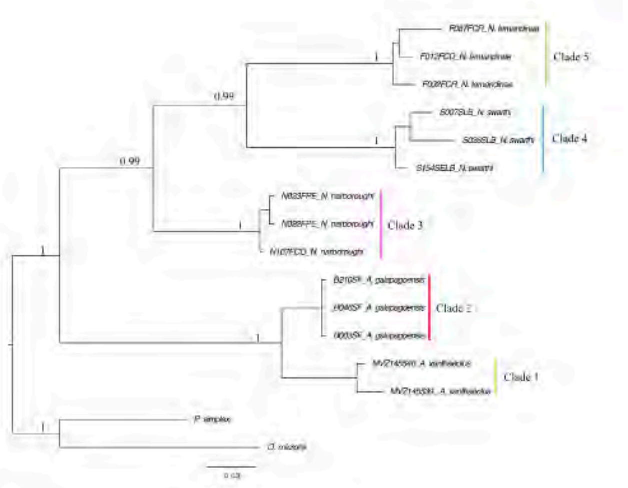

Figure 2. Phylogenetic tree of the four extant endemic rodents of the Galápagos Islands based on Bayesian Inference analysis of mtDNA D-loop sequence data. Numbers at nodes indicate support values of posterior probabilities.

Table 1. Estimated dates of divergence (time to the most recent common ancestor – TMRCA – and 95 % High Posterior Density confidence intervals – HPD – in Ma) for the extant species within the *Nesoryzomys* and *Aegialomys* genera. Clades depicted by letters correspond to those indicated in Figure 2.

Clade	TMRCA	95 % HPD
A	4.26	3.01 – 5.63
B	3.84	2.91 – 4.88
C	2.44	0.72 – 4.01
D	2.23	1.32 – 3.12
E	1.58	0.91 – 2.42
F	1.11	0.37 – 2.11
G	0.52	0.21 – 0.95
H	0.45	0.14 – 0.84
I	0.26	0.03 – 0.58
J	0.16	0.02 – 0.41
K	0.11	0.01 – 0.27

The applied neutrality test revealed significant deviations from mutation-drift equilibrium for all the species inhabiting Galápagos according to Fu´s F_s values, and only for *A. galapagoensis* using Tajima´s *D*. The negative values suggest recent population expansion events in these species (Table 2).

The statistical analyses of mismatch distribution showed unimodal distributions for *A. galapagoensis*, *N. narboroughi* and *N. fernandinae*, which also suggests a recent demographic expansion (Slatkin and Hudson 1991, Rogers and Harpending 1992) or spatial expansion (Ray *et al.* 2003, Excoffier 2004). Statistical analysis of the mismatch distribution *r* index and R_2 were significant (Figure 4).

The Bayesian skyline demographic reconstructions showed a pattern of constant size of populations through time, followed by a recent and small increase (Figure 5). *A. galapagoensis* and *N. fernandinae* show a small growth period, which started around 10,000 and 13,000 years ago, respectively. *N. narboroughi* and *N. swarthi* show a more constant trend of population increase, starting around 50,000 and 90,000 years ago, with a rapid increase starting around

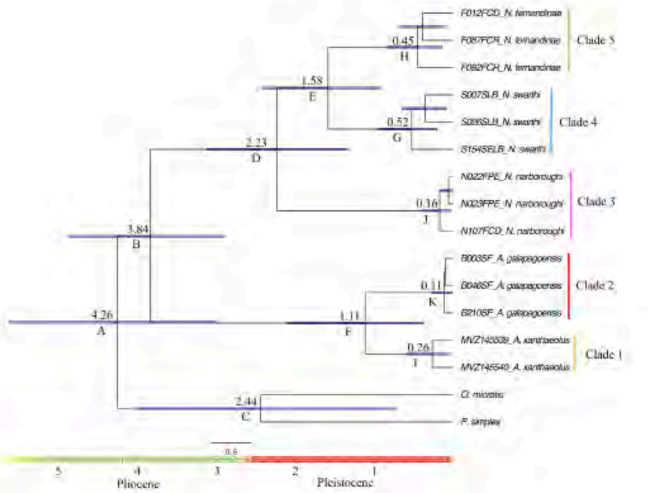

Figure 3. Dated phylogeny of the extant endemic rodents of the Galápagos Islands reconstructed from mtDNA D-loop haplotypes inferred from BEAST. The horizontal bars show the 95 % confidence intervals. Time-scale in millions of years ago. Dates and letters at nodes depict values calculated in Table 1.

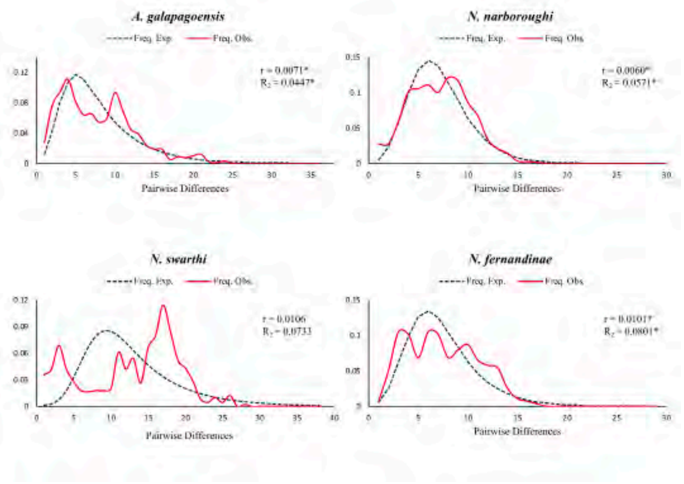

Figure 4. Mismatch distribution of pairwise differences of haplotypes for each of the extant species inhabiting the Galápagos Islands. Shown are observed (red lines) and expected (dark blue square dot lines) frequencies obtained under a model allowing for population size change. Raggedness (*r*) index and R_2 statistics values are shown. Significance is indicated with a star (*).

6,000 and 25,000 years ago, respectively. Skyline reconstruction showed that *A. galapagoensis*, *N. narboroughi*, *N. swar*thi and *N. fernandinae* have similar populations sizes.

Overall, the network analyses including all haplotypes for each species show a few abundant haplotypes, with frequencies between two and six, and numerous unique ones for all the species (Figure 6). *N. fernandinae* showed more unique haplotypes, with two being the highest frequency observed for a haplotype. The four species show long branches with haplotypes that are highly differentiated from the other haplotypes. *N. narboroughi* and *N. fernandinae*, for which samples were collected from three and two localities in Fernandina Island, respectively, do not show that the distribution of the haplotypes follows any structure or differentiation. Only *N. narboroughi* has two shared haplotypes among localities. Though *A. galapagoensis* and *N. narboroughi* do not show networks with a star-like shape, both networks show haplotypes with many connections, suggesting recent populations or with recent demographic expansion. In contrast, the networks of *N. swarthi* and *N. fernandinae* may suggest older or more stable populations.

Discussion

This is the first genetic study to include all extant endemic rodent species of the Galápagos Islands. We implemented different genetic analyses in order to elucidate the phylogenetic relationships among these rodents inhabiting the archipelago, as well as demographic history and relationships of their populations. This information is extremely important for conservation of these endemic species, given that there is very little known about their biology and ecology, and that they are considered vulnerable, mainly due to human activities and the introduction of invasive species. Furthermore, we contributed phylogenetic and demographic information as well as divergence estimates in order to form hypotheses regarding colonization of the islands and compare them with previous hypotheses.

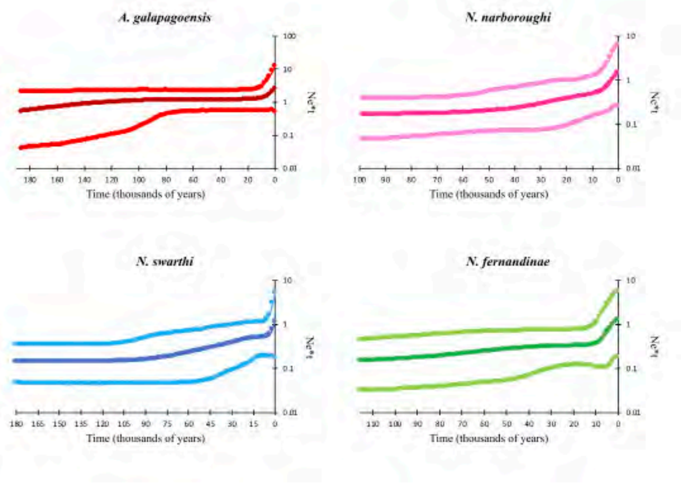

Figure 5. Skyline plots for each extant species of rodents inhabiting the Galápagos Islands. Plots show posterior median (darker lines) and 95 % Bayesian credible intervals (lighter lines on the outside) of the effective population size. The Y axis is in logarithm scale.

Our phylogenetic study corroborated the monophyly of the genera *Aegialomys* and *Nesoryzomys* as Patton and Hafner (1983) and Weksler (2003, 2006), proposed. However, those authors did not include all the extant species. We also corroborated the monophyly of the continental species *A. xanthaeolus* and the island species *A. galapagoensis*, *N. naboroughi*, *N. swarthi* and *N. fernandinae*. Our calibration results suggest that the main speciation events started during the Pliocene with the split between the genus *Aegialomys* and *Nesoryzomys* (3.84 Ma, 95 % HPD:2.9 to 4.88), which agrees with the time proposed by Patton and Hafner (1983), using Nei's methods, dated around 3 to 3.5 Ma; it differs from that proposed by Machado *et al.* (2014), dated around 1.49 Ma (95 % HDP:0.26 to 3.23), and Parada *et al.* (2013) around 2.4 Ma (95 % HDP not available) during the Pleistocene. The difference between Machado *et al.*'s estimate and ours could be due to the genes used; they used IRBP and Cyt b, while we used D - loop. Also, despite the fact that our study and Machado *et al.*'s both used the

Table 2. Variability of the mtDNA D-loop sequences of *Aegialomys* and *Nesoryzomys* from Galápagos Islands. Number of polymorphic segregating sites (*S*), singletons (S_1), parsimony informative sites (PIS), haplotype diversity (*Hd*), nucleotide diversity (π), and average number of nucleotide differences (*K*). Significance is indicated with a star (*).

Species	Total basepairs	Number of samples	Number of haplotypes	*S*	S_1	PIS	*Hd*	π	*K*	Fu's F_s	Tajimas'*D*
Aegialomys galapagoensis	652	43	29	70	46	24	0.972 ∓ 0.012	0.01298∓0.0017	6.970	-14.570*	-2.18653*
Nesoryzomys narboroughi	711	49	32	48	27	21	0.973∓0.011	0.01003∓0.0006	6.179	-19.085*	-1.50303
Nesoryzomys swarthi	629	43	30	71	42	29	0.965∓ 0.016	0.02130∓ 0.0012	11.817	-8.969*	1.20756
Nesoryzomys fernandinae	578	24	22	33	15	18	0.993∓ 0.014	0.01204∓0.0015	6.467	-15.631*	-1.39461

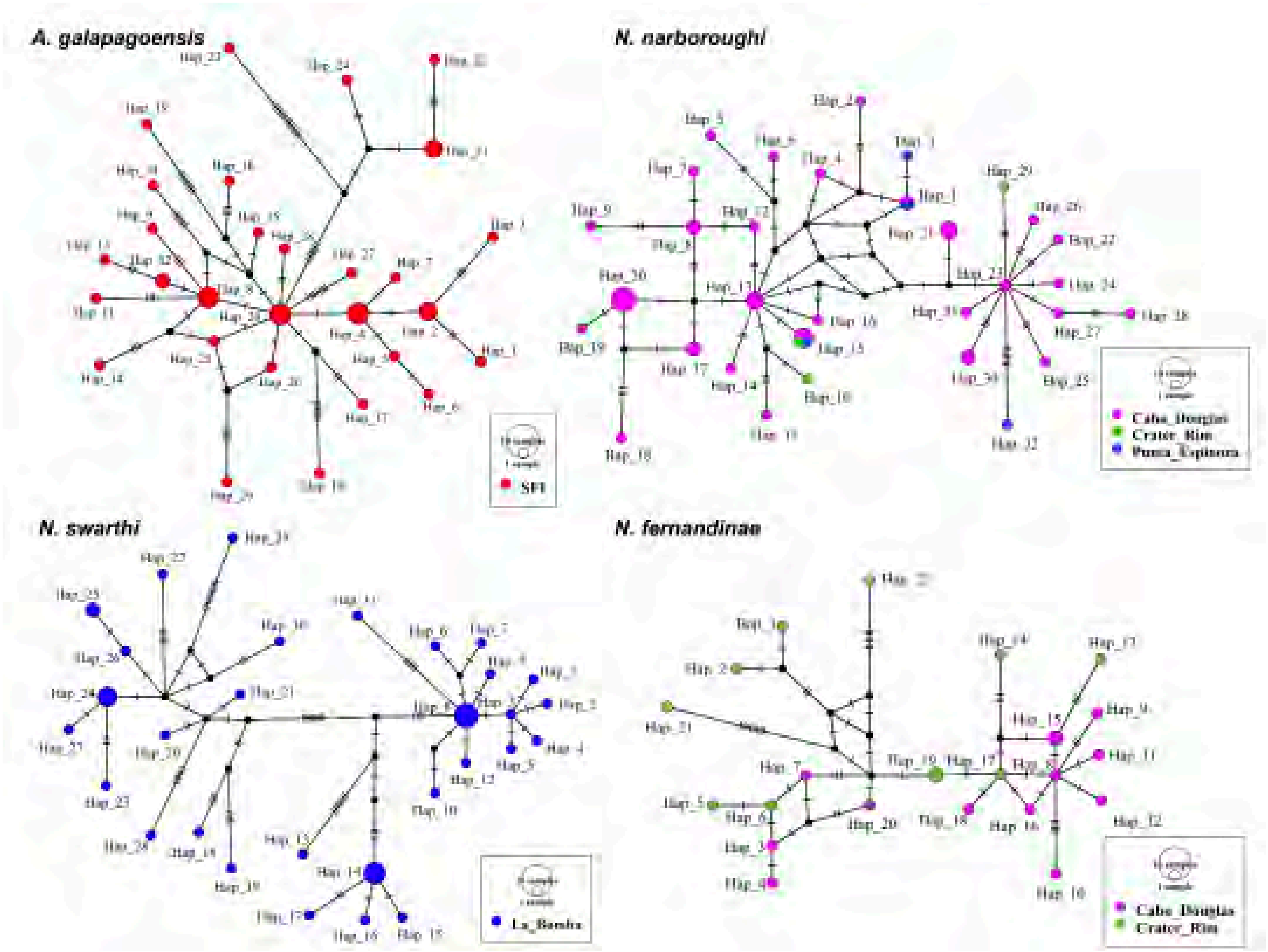

Figure 6. Median-Joining network for each species of the extant rodent of the Galápagos Islands, using mtDNA D-loop haplotypes. Circles sizes are proportional to the haplotype's frequencies in the population. The lines along the branches connecting the haplotypes show the number of substitutions.

origin of the Galápagos as a calibration point, we used the new date proposed by Geist *et al.* (2014) of 5 Ma, while Machado *et al.* used 4 Ma (Geist 1984). We also included *A. galapagoensis* from the islands, while they only used *A. xanthaeolus*. Including the two species of the genus *Aegialomys,* and specifying an older date for the origin of the archipelago, resulted in an older date for the split between these genera, which is well supported with the paleogeographic and biogeographical information. Despite this discrepancy, there is substantial overlap in the credibility intervals of these two assessments.

The second major speciation event occurred within the genus *Nesoryzomys* with the split between *N. narboroughi* versus *N. swarthi* and *N. fernandinae* dated at 2.23 Ma (95 % HDP:1.32 to 3.12) during the Pleistocene. Leite *et al.* (2014) dated the split between *N. narboroughi* and *N. swarthi* around 2 Ma (95 % HDP not available) during the Pleistocene, supporting our results. The third major event occurred at 1.58 Ma (95 % HDP:0.91 to 2.42) during the Pleistocene with the split between *N. swarthi* and *N. fernandinae*. Finally, the speciation between *A. xanthaeolus* and *A. galapagoensis* occurred at 1.11 Ma (95 % HDP: 0.37 to 2.10), also during the Pleistocene.

Rice rats are the only terrestrial mammals that naturally colonized the Galápagos and diversified within the archipelago (Clark 1984, Parent *et al.* 2008). There are some prior hypotheses about how these two genera colonized islands. Patton and Hafner (1983) suggested that *Nesoryzomys* is an old immigrant to the islands while the *Aegialomys* species is quite recent. They based their results on the high degree of morphological and biochemical (allozyme) distinctiveness of *Nesoryzomys* relative to other oryzomyines, including *Aegialomys*. This supported a more ancient origin and a single immigration to the islands, whether of pre-*Nesoryzomys* or *Nesoryzomys* form with subsequent radiation within the islands. In contrast *A. galapagoensis* is nearly morphological identical to the mainland *A. xanthaeolus*, which suggests an introduction to the islands within the last few hundred to thousand years, perhaps via pre-Columbian humans coursing the west coast of Perú (Patton 1984; Pine *et al.* 2012). Parent *et al.* (2008) suggested that colonization events on the Galápagos occurred over the last 3 to 4 Ma during the existence of the present islands, and might have happened earlier when now sunken islands were above sea level. The presence of several drowned seamounts on the Carnegie Ridge east of the Galápagos (Christie *et al.* 1992) suggests that earlier volcanic islands may have served as stepping stones for colonization by some of the terrestrial fauna. Parent *et al.* (2008) also mentioned that rice rat diversity is the result of one colonization event from the South American continent, where their close relatives inhabit, as it has been shown in other species of tortoises and lizards (*i. e.,* Caccone *et al.* 1999; Kizirian *et al.* 2004; Benavides *et al.* 2007).

Our results suggest two colonization events to the Galápagos by the extant species. The first arrival by the ancestor of *Nesoryzomys* was probably a species of *Sigmodontomys* or *Melanomys* that originated from lower montane and lowland forest habitats in South America (Harris and Macdonald 2007). This event should be dated from the early-late Pliocene boundary onwards, as proposed by Leite *et al.* (2014). This was followed by a second arrival of *Aegialomys* from coastal Perú by rafting over recent historical times to the middle Pleistocene, giving rise to the *Aegialomys* of the Galápagos (Patton 1975; Steadman 1985; Hutterer and Oromí 1993; Weksler 2003). It is well known that these species, and the most closely related ones, are excellent dispersers across salt water (Pine *et al.* 2012), making colonization easier for them.

The fauna and flora of the Galápagos Islands is principally derived from western South America, Central America, and the Caribbean (Merlen 2014). So, we assume that colonization from there to the archipelago during the Pliocene was possible because there is strong evidence (Christie *et al.* 1992; Werner *et al.* 1999) that islands have been forming over the hotspot for at least twice as long as the age of the oldest islands, and perhaps as long as 20 Ma. These ancient islands are now seamounts east of the present-day Galápagos along the Carnegie Ridge on the Nazca Plate (Christie *et al.* 1992) and northeast of the archipelago on the Cocos Plate on the Cocos Ridge (Werner *et al.* 1999). There has been a "conveyor belt" of islands produced over millions of years, providing the potential for organic colonization during that time (Merlen 2014).

Once the ancestors of *Nesoryzomys* and *Aegialomys* arrived to the Galápagos Islands, dispersal, colonization, speciation, and diversification were possible during the Pleistocene, in part, because the integrated area of the Galápagos Islands was much greater than today, land bridges existed between a few of the major islands, and many more minor islands and islets were exposed. In fact, there is a hypothesis that between 1 and 5 Ma, at least nineteen major Galápagos Islands existed but are currently submerged; these are in addition to the thirteen that exist today (Geist *et al.* 2014). Later island fragmentation has led to diversification by vicariance as well as dispersal. Dispersal was also possible because the main part of the Galápagos lies in shallow water created by the broad Galápagos platform, which formed by the accumulation of lavas (Geist *et al.* 2008).

Aegialomys galapagoensis, the Galápagos rice rat, is only found in one population on Santa Fé Island and is the latest species to have colonized the archipelago. Our results show high genetic diversity for the species and a signal of recent expansion. This finding is consistent with the fact that *A. galapagoensis* and *N. narboroughi* have been considered common by virtually all researchers visiting the islands (Clark 1980; Patton and Hafner 1983; Clark 1984; Key and Muñoz-Heredia 1994). In fact, Dowler *et al.* (2000) reported that the species was abundant and rice rats could be seen running among the lava rocks before dark. Another reason is that both Santa Fé Island and Fernandina Island are the only two islands that do not have introduced species of rats and mice (Dowler *et al.* 2000), allowing the persistence of the native species. This species is considered vulnerable by the Red List of the International Union for Conservation of Nature (IUCN 2019). We dated the events of speciation and diversification to around 1.11 Ma and 111,200 years ago, respectively; both of them occurred after the emergence of Santa Fé Island, dated at 2.9 Ma (Geist *et al.* 2014). Clark (1980) conducted an ecological study and found that *A. galapagoensis* has high survival and low reproduction relative to congeners of other geographic areas. He did not know if this strategy was specific to *A. galapagoensis* or a common feature of the Galápagos rodent life history (Harris and Macdonald 2007).

Nesoryzomys narboroughi, the large Fernandina rice rat, is only found on Fernandina Island. It is the oldest species within the extant rodents of Galápagos, with a speciation event dated at 2.23 Ma; however, its diversification is the most recent among the extant *Nesoryzomys*, starting around 169,400 years ago. This species is considered vulnerable according to the Red List (IUCN 2019); however, Dowler *et al.* (2000) verified the presence of sustainable populations, which are found from the coastline to the volcano rim. We found that the genetic diversity of this species is high, and their populations are under recent expansion. This could be due to the fact that Fernandina Island does not have introduced species of rats and mice, allowing the persistence of *N. narboroughi*.

Nesoryzomys fernandinae, the small Fernandina rice rat, is also found on Fernandina Island in sympatry with *N. narboroughi* (Hutterer and Hirsch 1980; Dowler *et al.* 2000). Its populations range from the coast up to the volcano rim. Dowler *et al.* (2000) found that this species is more abundant at high elevations along the volcano rim, where vegetation, primarily *Scalasia spp*., is most dense. Meanwhile, *N. narboroughi* is more abundant near the coast, suggesting that the species distributions are influenced by habitat (Dowler and Carroll 1996). *N. fernandinae* was considered extinct (IUCN 1996; Nowak 1999), but now its status is vulnerable according to the Red List (IUCN 2019). This species has the highest genetic diversity within the genus, and it shows a more stable population in comparison with *N. narboroughi*, which showed recent expansion. We dated the events of speciation and diversification to 1.58 Ma and 452,900 years ago, respectively. The presence of *N. narboroughi* and *N. fernandinae* on Fernandina Island suggest that volcanic activity has not occurred on an island-wide scale sufficient to destroy their populations as Merlen (2014) suggested. He also proposed that Fernandina Island is a refuge for biodiversity in Galápagos based on the formation of endemic species, the establishment of terrestrial ecosystems at several altitudes, and climate conditions.

Fernandina Island has the most active volcano and is the youngest major island in the archipelago. Its emergence is suggested to have occurred approximately 32,000 years ago with a maximum emergence around 60,000 years ago (Geist *et al.* 2014). The dates that we obtained for the speciation and diversification of *N. narboroughi* and *N. fernandinae* are older than the dates proposed for the origin of the island.

Nesoryzomys swarthi, the Santiago Galápagos mouse, is endemic to Santiago Island where it exists as a single population in the arid zone of the north-central coast (Dowler *et al.* 2000; Harris *et al.* 2006). This species coexists with *Rattus rattus* and *Mus musculus* on the island. However, the three species are only sympatric near the beach, where the densities of the invasive species are lower (Dowler *et al.* 2000; Harris *et al.* 2006). Brosset (1963) considered that *N. swarthi* was extinct based on the introduction of diseases or parasites by invasive species, and/or competition with them. At present, it is considered vulnerable according to the Red List (IUCN 2019). Our results showed that the species has relatively high genetic diversity, despite being the lowest genetic diversity among the other native rodents. Two of our analyses show a signal of recent expansion, but one of them rejected this hypothesis. We consider that more genetic analyses, including more loci, are necessary to resolve this discrepancy. It is possible that the species underwent a recent bottleneck; however, the genetic signal is not strong. A bottleneck event in the species would be consistent with the fact that it was considered extinct for decades while it went undetected until Dowler *et al.* 2000 rediscovered it. However, we do not have enough data to thoroughly test this hypothesis. The emergence of Santiago Island has been dated to a minimum of 800,000 years ago and a maximum of 1.4 Ma, which agrees with the time of speciation and diversification that we found for *N. swarthi* around 1.58 Ma and 525,500 years ago, respectively. Harris and Macdonald (2007) performed an ecological study and found that the unpredictable environment of the Galápagos arid zone has selected for a strategy of high survivorship and low reproduction in *N. swarthi* that is more typically found among desert Heteromyidae than other members of the Oryzomyini. Clark (1980) found the same result in *A. galapagoensis*. It seems that this strategy is a common feature of native rodents of the Galápagos Islands.

According to our results, we have two main conclusions. The first is that populations of the extant rodents on the Galápagos show high genetic diversity and most show a signal of recent expansion. Despite the challenges that are faced by these species by the extreme arid conditions on the islands, the impact of human activities, and the presence of invasive species, our results suggest that these species do not have genetic signatures implying that they have experienced dramatic population declines and, rather, that populations are demographically stable. However, based on previous studies this conclusion should be considered carefully. For example, the desert-adapted life histories of these species are impressive because their ancestors were not well adapted to dry environments and oryzomyine rodents of semiarid habitats often lack the physiological adaptations to xeric conditions (Best 1988; Meserve 1978; Ribeiro *et al.* 2004; Harris and Macdonald 2007). Moreover, the fact that the abundance of these endemic rodents is positively related to vegetation density suggests that the presence of these species is resource-limited (Clark 1980; Dowler and Carroll 1996; Harris and Macdonald 2007). This could explain why some native species can coexist with invasive species or coexist in sympatry with other native species if there are enough resources to minimize competition. In this sense, there is now evidence that introduced rodents may not be the sole cause of decline in native rodents in Galápagos; feral cats may be a second important factor in rodent decline and extinction (Dowler *et al.* 2000; Dexter *et al.* 2004), as well as loss of habitat and resources or the introduction of pathogens. In light of these previous findings and our results, we should continue to monitor these vulnerable species, performing more fine-scale ecological and population studies in the future.

Our second major conclusion is that the major speciation events of the four extant rice rats occurred within the archipelago during the Pleistocene. In the case of *A. galapagoensis* and *N. swarthi*, their diversification occurred on Santa Fé and Santiago Islands, respectively, and their speciation likely occurred within their current range. However, for the species inhabiting Fernandina Island, *N. narboroughi* and *N. fernandinae*, speciation and diversification likely occurred on a different island, because Fernandina Island is younger than these events. We hypothesize that after speciation on a different island, they dispersed to Fernandina Island. Isabela Island is the largest within the archipelago, and it is close to Fernandina. Its emergence is dated to around 500,000 to 800,000 years ago, and it is therefore possible that diversification of both species occurred there. However, we dated speciation events older than this emergence. Speciation of *Nesoryzomys* likely occurred on islands that emerged at least between 1.5 to 2.3 Ma. It is difficult to know where it occurred because it is recognized that volcanic islands leave little evidence of their ancient biological past, because the lava flows consume organic matter (Steadman 1986). Thus, species may have gone through events of colonization and speciation and subsequently been driven to extinction, leaving no sign (Merlen 2014). Geist *et al.* (2014) suggested that because the Galápagos archipelago is dynamic over evolutionary timescales, for any model of dispersal, colonization, speciation, and radiation involving island geography more than 20,000 years ago, the current map of the Galápagos Islands is close to irrelevant. Despite these problems, we suggest that future studies using genome-wide molecular markers and sampling of extinct species and fossils from the islands, as well as additional continental species, will add further insights into the origin and relationships of the endemic rodents of the Galápagos Islands, which remain ambiguous.

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Literature cited

Bandelt H., P. Forster, and A. Röhl. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37-48.

Benavides, E., R. Baum, D. McClellan, and J. W. Sites Jr. 2007. Molecular phylogenetics of the lizard genus *Microlophus* (Squamata: Tropiduridae): aligning and retrieving indel signal from nuclear introns. Systematics Biology 56:776-797.

Best, T. L. 1988. *Dipodomys spectabilis*. Mammalian Species 311:1-10.

Bouckaert, R., J. Heled, D. Kühnert, T. Vaughan, C-H. Wu, D. Xie, M. A. Suchard, A. Rambaut, and A. J. Drummond. 2014. BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. PLoS Computational Biology 10:e1003537.

Brosset, A. 1963. Statut actuel des mammiferes des iles Galápagos. Mammalia 27:323- 338.

Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'. Ciencias Zoologicas 4:309-732.

Caccone, A., J. P. Gibbs, V. Ketmaier, E. Suatoni, and J. R. Powell. 1999. Origin and evolutionary relationships of giant Galápagos tortoises. Proceedings of the National Academy of Science of the United States of America 96:223-228.

Christie, D. M., R. A. Duncan, A. R. McBirney, M. A. Richards, W. M. White, K. S. Harpp, and G. G. Fox. 1992. Drowned islands downstream from the Galápagos hotspot imply extended speciation times. Nature 355:246–248.

Clark, D. A. 1984. Native land mammals. Pp. 225-231 *in* Key environments: Galápagos (Perry, R. ed.). Pergamon Press. Oxford, U.K.

Clark, D. B. 1980. Population ecology of an endemic Neotropical island rodent: *Oryzomys bauri* of Santa Fe Island, Galapagos, Ecuador. Journal of Animal Ecology 49:185-198.

Darriba D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9:772.

Deli, T., S. Fratini, L. Ragionieri, K. Said, N. Chatti, and C. D. Schubart. 2016. Phylogeography of the marbled crab *Pachygrapsus marmoratus* (Decapoda, Grapsidae) along part of the African Mediterranean coast reveals genetic homogeneity across the Siculo-Tunisian Strait versus heterogeneity across the Gibraltar Strait. Marine Biology Research 12:471-487.

Dexter, N., R. C. Dowler, J. P. Flanagan, S. Hart, M. A. Revelez, and T. E. Lee. 2004. The influence of Feral Cats *Felis catus* on the distribution and abundance of introduced and endemic Galapagos rodents. Pacific Conservation Biology 10:210-215.

do Prado, J. R., and A. R. Percequillo. 2018. Systematics studies of the genus *Aegialomys* Weksler et al., 2006. (Rodentia: Cricetidae: Sigmodontinae): Geography variation, species delimitation, and biogeography. Journal of Mammalian Evolution 25:71-118.

Dowler, R. C. 2015. Genus *Nesoryzomys*. Pp. 390-393 *in* Mammals of South America. Volume 2. (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press. Chicago, U.S.A.

Dowler, R. C., and D. S. Carroll. 1996. The endemic rodents of Isla Fernandina: population status and conservation issues. Noticias de Galápagos 57:8-13.

Dowler, R. C., D. S. Carroll, and C. W. Edwards. 2000. Rediscovery of rodents (Genus *Nesoryzomys*) considered extinct in the Galápagos Islands. Oryx 34:109-117.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214.

Excoffier, L. 2004. Patterns of DNA sequence diversity and genetic structure after a range expansion: lessons from the infinite-island model. Molecular Ecology 13:853-864.

Fu, Y.X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915-925.

Geist, D. 1984. On the emergence and submergence of the Galápagos islands. Noticias de Galápagos 56:5-9.

Geist, D., B. A. Diefenbach, D. J. Fornari, M. D. Kurz, K. Harpp, and J. Blusztajn. 2008. Construction of the Galápagos platform by large submarine volcanic terraces. Geochemestry Geophysics Geosystems 9: doi:10.1029/2007GC001795.

Geist, D. J., H. Snell, H. Snell, C. Goddard, and M. D. Kurz. 2014. A paleogeographic model of the Galápagos Islands and biogeographical and evolutionary implications. Pp. 145-167 *in* The Galápagos A natural laboratory for earth sciences. (Harpp, K. S., E. Mittelstaedt, N. d'Ozouville, and D. W. Graham, eds.). John Wiley and Sons, Inc. Hoboken, U.S.A.

González-Ittig, R. E., G. R. Theiler, and C. N. Gardenal. 2002. A contribution to the subgeneric systematics of *Oligoryzomys* (Rodentia, Muridae) from Argentina by means of PCR-RFLP patterns of mitochondrial DNA. Biochemical Systematics and Ecology 30:23-33.

Guindon S., and O. Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52:696-704.

Harpending, H. C. 1994. Signature of ancient population-growth in a low-resolution mitochondrial DNA mismatch distribution. Human Biology 66:591-600.

Harpending, H., and A. Rogers. 2000. Genetic perspectives on human origins and differentiation. Annual Review of

Genomics and Human Genetics 1:361-385.

Harpp, K.S., E. Mittelstaedt, N. d'Ozouville, and D. W. Graham (eds.). 2014. The Galápagos A natural laboratory for earth sciences. John Wiley and Sons, Inc. Hoboken, U.S.A.

Harris, D. B., S. D. Gregory, and D. W. Macdonald. 2006. Space invaders? A search for patterns underlying the coexistence of alien black rats and Galápagos rice rats. Oecologia 149:276-288.

Harris, D. B., and D. W. Macdonald. 2007. Population ecology of the endemic rodent *Nesoryzomys swarthi* in the tropical desert of the Galápagos Islands. Journal of Mammalogy 88:208-219.

Heller, E. 1904. Mammals of the Galápagos archipelago, exclusive of the Cetacea. Proceedings of the California Academy of Sciences 3:233-251.

Hendriks, K. P., G. Alciatore, M. Schilthuizen, and R. S. Etienne. 2019. Phylogeography of Bornean land snails suggests long-distance dispersal as a cause of endemism. Journal of Biogeography 46:1-13.

Hirota, T., Hirohata, T., Mashima H., Satoh, T., and Y. Obara. 2004. Population structure af large Japanese field mouse, *Apodemus speciosus* (Rodentia: Muridae), in suburban landscape, based on mitochondrial D-loop sequences. Molecular Ecology 13:3275-3282.

Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754-755.

Hutterer, R., and U. Hirsch. 1980. Ein neuer *Nesoryzomys* von der Insel Fernandina, Galápagos. Bonner Zoologische Beitrage 30:276-283.

Hutterer, R., and P. Oromí. 1993. La rata gigante de la Isla Santa Cruz, Galápagos: algunos datos y problemas. Resultados científicos del proyecto Galápagos: patrimonio de la humanidad. Museo de Ciencias Naturales, Tenerife (TFMC) 4:63-76.

IUCN (International Union for Conservation of Nature). 1996. IUCN Red List of Threatened Animals. IUCN, Gland, Switzerland.

IUCN (International Union for Conservation of Nature). 2019. The IUCN Red List of Threatened Species. International Union for Conservancy of Nature and Natural Resources. Version 2019-1. Available on http://www.iucnredlist.org. Downloaded on 05 June 2019.

Key, G., and E. Muñoz-Heredia. 1994. Distribution and current status of rodents in the Galápagos. Noticias de Galápagos 53:21-25.

Kizirian, D., A. Trager, M. A. Donnelly, and J. W. Wright. 2004. Evolution of Galápagos Island lava lizards (Iguania: Tropiduridae: *Microlophus*). Molecular Phylogenetics and Evolution 32:761-769.

Larkin, M. A., G. Blackshields, N. P. Brown, R. Chenna, P. A. McGettigan, H. McWilliam, F. Valentin, I. M. Wallace, A.Wilm, R. Lopez, J. D. Thompson, T. J. Gibson, and D. G. Higgins. 2007. Clustal W and Clustal X version 2.0. Bioinformatics 23:2947-2948.

Leigh, J. W., and D. Bryant. 2015. PopART: Full-feature software for haplotype network construction. Methods in Ecology and Evolution 6:1110-1116.

Leite, R. N., S. O. Kolokotronis, F. C. Almeida, F. P. Werneck, D. S. Rogers, and M. Weksler. 2014. In the wake of invasion: tracing the historical biogeography of the South American Cricetid radiation (Rodentia, Sigmodontinae). PlosOne 9:1-12.

Losos, J. B., and R. E. Ricklefs. 2009. Adaptation and diversification on islands. Nature 457:830-836.

Losos, J. B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. The American Naturalist 175:623-639.

Machado, L. F., Y. L. R. Leite, A. U. Christoff, and L. G. Giugliano. 2014. Phlogeny and biogeography of tetraphodont rodents of the tribe Oryzomyini (Cricetidae: Sigmodontinae). Zoologica Scripta 43:119-130.

Merlen, G. 2014. Plate tectonics, evolution, and the survival of species: A modern day hotspot. Pp. 128-153 *in* The Galápagos A natural laboratory for earth sciences (Harpp, K. S., E. Mittelstaedt, N. d'Ozouville, and D. W. Graham, eds.). John Wiley and Sons, Inc. Hoboken, U.S.A.

Meserve, P. L. 1978. Water dependence in some Chilean arid zone rodents. Journal of Mammalogy 59:217-219.

Musser, G. G., and M. D. Carleton. 1993. Family Muridae. Pp. 501-755 *in* Mammal species of the world: a taxonomic and geographic reference (Wilson, D. E., and D. M. Reeder, eds.). 2nd ed. Smithsonian Institution Press. Washington, U.S.A.

Musser, G. G., and M. D. Carleton. 2005. Superfamily Muroidea. Pp. 894-1531 *in* Mammal species of the world: a taxonomic and geographic reference (Wilson, D. E., and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press. Baltimore, U.S.A.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia University Press, New York, USA.

Nowak, R.M. 1999. Walker's Mammals of the World, 6th edn. The Johns Hopkins University Press. London, U.K.

Orr, R. T. 1938. A new rodent of the genus *Nesoryzomys* from the Galápagos Islands. Proceedings of the California Academy of Sciences Series 4 23:303-306.

Parada, A., U. F. J. Pardiñas, J. Salazar-Bravo, G. D'Elía, and R. E. Palma. 2013. Dating an impressive Neotropical radiation: Molecular time estimates for the Sigmodontinae (Rodentia) provide insights into its historical biogeography. Molecular Phylogenetics and Evolution 66:960-968.

Parent, C. E., A. Caccone, and K. Petren. 2008. Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis. Philosophical Transactions of the Royal Society B 363:3347-3361.

Patton, J. L. 1975. Biosystematics of the rodent fauna of the Galápagos Archipelago. American Philosophical Society Year Book 1975:352-353.

Patton, J. L. 1984. Genetical processes in the Galápagos. Biological Journal of the Linnean Society 21:97-111.

Patton, J. L., and M. S. Hafner. 1983. Biosystematics of the native rodents of the Galápagos Archipelago, Ecuador. Pp. 539-568 *in* Patterns of evolution in Galapagos organisms (Bowman, R. I., M. Berson, and A. E. Leviton, eds.). AAAS Pacific Division. San Francisco, U.S.A.

Peterson, R. L. 1966. Recent mammal records from the Galapagos Islands. Mammalia 30:441-445.

Philippe, H., H. Brinkmann, D. V. Lavrov, D. T. J. Littlewood, M. Manuel, G. Wörheide, and D. Baurain. 2011. Resolving difficult phylogenetic questions: Why more sequences are not enough. Plos Biology 9:1-10.

Pine, R. H., R. M. Timm, and M. Weksler. 2012. A new recognized clade of trans-Andean Oryzomyini (Rodentia:Cricetidae), with description of a new genus. Journal of Mammalogy

93:851-870.

Rambaut A., A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67:901-904.

Ramos-Onsins S. E., and J. Rozas. 2002. Statistical properties of new neutrality tests against population growth. Molecular Biology and Evolution 19:2092-2100.

Ray, N., M. Currat, and L. Excoffier. 2003. Intra-Deme molecular diversity in spatially expanding populations. Molecular Biology and Evolution 20:76-86.

Ribeiro, M. D. S., P. L. B. Da Rocha, L. A. F. Mendes, S. F. Perry, and E. S. De Oliveira. 2004. Physiological effects of short-term water deprivation in the South American sigmodontine rice rat *Oligoryzomys nigripes* and water rat *Nectomys squamipes* within a phylogenetic context. Canadian Journal of Zoology 82:1326-1335.

Robins, J. H., V. Tintinger, K. P. Aplin, M. Hingston, E. Matisoo-Smith, D. Penny, and S. D. Lavery. 2014. Rapid radiation and morphological similarity of New Guinean species. PlosOne 9:e107667.

Rodrigues, J. F. M., and J. A. F. Diniz-Filho. 2016. Ecological opportunities, habitat, and past climatic fluctuations influenced the diversification of modern turtles. Molecular Phylogenetics and Evolution 101:352-358.

Rogers, A. R., and H. C. Harpending. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Molecular Biology and Evolution 9:552-569.

Román-Palacios, C., and J. J. Wiens. 2018. The tortoise and the finch: Testing for island effects on diversification using two iconic Galápagos radiations. Journal of Biogeography 45:1701-1712.

Ronquist, F., and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572-1574.

Rozas J., A. Ferrer-Mata, J. C. Sánchez-Del Barrio, S. Guirao-Rico, P. Librado, S. E. Ramos-Onsins, A. Sánchez-Gracia. 2017. DnaSP 6: DNA Sequence Polymorphism Analysis of Large Data Sets. Molecular Biology and Evolution 34:3299-3302.

Slatkin M., and R. R. Hudson. 1991. Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics 129:555-562.

Snell, H. M., P. A. Stone, and H. L. Snell. 1996. A summary of geographical characteristics of the Galápagos Islands. Journal Biogeography 23:619-624.

Steadman, D. W. 1985. Vertebrate paleontology of the Galápagos Islands. National Geographic Society Research Reports 20:717-724.

Steadman, D. W. 1986. Holocene Vertebrate Fossils from Isla Floreana, Galápagos. Smithsonian contributions to zoology, Number 413, Smithsonian Institution Press. Washington, U.S.A.

Tajima, F. 1989a. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585-595.

Tajima, F. 1989b. The effect of change in population size on DNA polymorphism. Genetics 123:597-601.

Urgoiti, J., Muñoz, A., Espelta, J. M., and R. Bonal. 2018. Distribution and space use of seed-dispersing rodents in central Pyrenees: implications for genetic diversity, conservation and plan recruitment. Integrative Zoology 13:307-3138.

Weksler, M. 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae: Sigmodontinae) based on the nuclear IRBP exon. Molecular Phylogenetics and Evolution 29:331-349.

Weksler, M. 2006. Phylogenetic relationships of oryzomyine rodents (Muroidea: Sigmodontinae): separate and combined analysis of morphological and molecular data. Bulletin of the American Museum of Natural History 296:1-149.

Weksler, M., A. R. Percequillo, and R. S. Voss. 2006. Ten new genera of oryzomyine rodents (Muridae: Sigmodontinae). American Museum Novitates 3537:1-29.

Weksler, M., and A. R. Percequillo. 2011. Key to the genera of the tribe Oryzomyini (Rodentia: Cricetidae: Sigmodontinae). Mastozoología Neotropical 18:281-292.

Werner, R., K. Hoernle, P. van den Bogaard, C. Ranero, and R. von Huene. 1999. Drowned 14-m.y.-old Galápagos Archipelago off the coast of Costa Rica: implications for tectonic and evolutionary models. Geology 27:499–502.

Wilke, T., R. Schultheiss, and C. Albrecht. 2009. A time goes by: A simple fool´s guide to molecular clock approaches in vertebrates. American Malacological Bulletin 27:25-45.

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Appendix 1

List of individuals used in this study, indicating ID (identity) manuscript, ID collection, genus, species, name of the island, locality (if it was available), sex, kind of tissue (L – Liver, K – Kidney, H – Heart, E – Ear, S – Swab, and F – Feces), and GenBank accession number data.

ID manuscript	Collection Number (ASNHC)	Genus	Species	Island	Locality	Sex	Tissue	GenBank accession numbers
B003SF_*A. galapagoensis*	ASK 4110	*Aegialomys*	*galapagoensis*	Santa Fé		M	-	MN398993
B005SF_*A. galapagoensis*	ASK 5643	*Aegialomys*	*galapagoensis*	Santa Fé		F	L	MN398994
B006SF_*A. galapagoensis*	ASK 5644	*Aegialomys*	*galapagoensis*	Santa Fé		F	L	MN398995
B036SF_*A. galapagoensis*	ASK 4106	*Aegialomys*	*galapagoensis*	Santa Fé		M	KL	MN398996
B038SF_*A. galapagoensis*	ASK 4111	*Aegialomys*	*galapagoensis*	Santa Fé		F	-	MN398997
B039SF_*A. galapagoensis*	ASK 5601	*Aegialomys*	*galapagoensis*	Santa Fé		M	L	MN398998
B041SF_*A. galapagoensis*	ASK 5603	*Aegialomys*	*galapagoensis*	Santa Fé		M	L	MN398999
B042SF_*A. galapagoensis*	ASK 5604	*Aegialomys*	*galapagoensis*	Santa Fé		F	L	MN399000
B043SF_*A. galapagoensis*	ASK 5594	*Aegialomys*	*galapagoensis*	Santa Fé		-	L	MN399001
B044SF_*A. galapagoensis*	ASK 5595	*Aegialomys*	*galapagoensis*	Santa Fé		F	L	MN399002
B046SF_*A. galapagoensis*	ASK 5597	*Aegialomys*	*galapagoensis*	Santa Fé		F	L	MN399003
B047SF_*A. galapagoensis*	ASK 5598	*Aegialomys*	*galapagoensis*	Santa Fé		-	L	MN399004
B048SF_*A. galapagoensis*	ASK 5599	*Aegialomys*	*galapagoensis*	Santa Fé		M	L	MN399005
B049SF_*A. galapagoensis*	ASK 5600	*Aegialomys*	*galapagoensis*	Santa Fé		F	L	MN399006
B050SF_*A. galapagoensis*	ASK 5593	*Aegialomys*	*galapagoensis*	Santa Fé		M	L	MN399007
B199SF_*A. galapagoensis*	SF-01	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399008
B200SF_*A. galapagoensis*	SF-02	*Aegialomys*	*galapagoensis*	Santa Fé		F	EF	MN399009
B201SF_*A. galapagoensis*	SF-03	*Aegialomys*	*galapagoensis*	Santa Fé		F	EF	MN399010
B202SF_*A. galapagoensis*	SF-04	*Aegialomys*	*galapagoensis*	Santa Fé		M	EF	MN399011
B203SF_*A. galapagoensis*	SF-05	*Aegialomys*	*galapagoensis*	Santa Fé		F	EF	MN399012
B206SF_*A. galapagoensis*	SF-08	*Aegialomys*	*galapagoensis*	Santa Fé		F	EF	MN399013
B207SF_*A. galapagoensis*	SF-09	*Aegialomys*	*galapagoensis*	Santa Fé		F	EF	MN399014
B208SF_*A. galapagoensis*	SF-10	*Aegialomys*	*galapagoensis*	Santa Fé		M	EF	MN399015
B209SF_*A. galapagoensis*	SF-11	*Aegialomys*	*galapagoensis*	Santa Fé		M	EF	MN399016
B210SF_*A. galapagoensis*	SF-12	*Aegialomys*	*galapagoensis*	Santa Fé		F	EF	MN399017
B211SF_*A. galapagoensis*	SF-13	*Aegialomys*	*galapagoensis*	Santa Fé		-	F	MN399018
B215SF_*A. galapagoensis*	SF-17	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399019
B217SF_*A. galapagoensis*	SF-19	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399020
B218SF_*A. galapagoensis*	SF-20	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399021
B219SF_*A. galapagoensis*	SF-21	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399022
B220SF_*A. galapagoensis*	SF-22	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399023
B221SF_*A. galapagoensis*	SF-23	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399024
B222SF_*A. galapagoensis*	SF-24	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399025
B223SF_*A. galapagoensis*	SF-25	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399026
B224SF_*A. galapagoensis*	SF-26	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399027
B225SF_*A. galapagoensis*	SF-27	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399028
B226SF_*A. galapagoensis*	SF-28	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399029
B227SF_*A. galapagoensis*	SF-29	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399030
B231SF_*A. galapagoensis*	SF-33	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399031
B232SF_*A. galapagoensis*	SF-34	*Aegialomys*	*galapagoensis*	Santa Fé		F	ES	MN399032
B234SF_*A. galapagoensis*	SF-36	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399033
B235SF_*A. galapagoensis*	SF-37	*Aegialomys*	*galapagoensis*	Santa Fé		M	ES	MN399034
B236SF_*A. galapagoensis*	SF-38	*Aegialomys*	*galapagoensis*	Santa Fé		F	E	MN399035
MVZ145539_*A. xanthaeolus*	MVZ145539	*Aegialomys*	*xanthaeolus*	Ecuador		-	L	MN399060
MVZ145540_A. xanthaeolus	MVZ145540	*Aegialomys*	*xanthaeolus*	Ecuador		-	L	MN399061
N018FCD_*N. narboroughi*	ASK 5520	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	HKL	MN399062

N019FCD_*N. narboroughi*	ASK 5521	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	HKL	MN399063
N020FCD_*N. narboroughi*	ASK 5523	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	HKL	MN399064
N021FPE_*N. narboroughi*	ASK 5513	*Nesoryzomys*	*narboroughi*	Fernandina	Punta spinoza	M	HKL	MN399065
N022FPE_*N. narboroughi*	ASK 5514	*Nesoryzomys*	*narboroughi*	Fernandina	Punta spinoza	M	HKL	MN399066
N023FPE_*N. narboroughi*	ASK 5515	*Nesoryzomys*	*narboroughi*	Fernandina	Punta spinoza	F	HKL	MN399067
N024FPE_*N. narboroughi*	ASK 5517	*Nesoryzomys*	*narboroughi*	Fernandina	Punta spinoza	F	HKL	MN399068
N065F_*N. narboroughi*	ASK 7276	*Nesoryzomys*	*narboroughi*	Fernandina	Crater Rim	M	KL	MN399069
N066F_*N. narboroughi*	ASK 7282	*Nesoryzomys*	*narboroughi*	Fernandina	Crater Rim	M	KL	MN399070
N102FCR_*N. narboroughi*	FE-V08	*Nesoryzomys*	*narboroughi*	Fernandina	Crater Rim	F	EF	MN399071
N104FCD_*N. narboroughi*	FE-C02	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	ES	MN399072
N105FCD_*N. narboroughi*	FE-C03	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	ES	MN399073
N106FCD_*N. narboroughi*	FE-C04	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	ES	MN399074
N107FCD_*N. narboroughi*	FE-C05	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	ES	MN399075
N108FCD_*N. narboroughi*	FE-C06	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	ES	MN399076
N109FCD_*N. narboroughi*	FE-C07	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	ES	MN399077
N110FCD_*N. narboroughi*	FE-C08	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	ES	MN399078
N112FCD_*N. narboroughi*	FE-C11	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399079
N113FCD_*N. narboroughi*	FE-C12	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	ESF	MN399080
N114FCD_*N. narboroughi*	FE-C13	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399081
N115FCD_*N. narboroughi*	FE-C14	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399082
N116FCD_*N. narboroughi*	FE-C15	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399083
N118FCD_*N. narboroughi*	FE-C17	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	ESF	MN399084
N119FCD_*N. narboroughi*	FE-C18	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	ESF	MN399085
N120FCD_*N. narboroughi*	FE-C19	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399086
N122FCD_*N. narboroughi*	FE-C21	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399087
N124FCD_*N. narboroughi*	FE-C23	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	ESF	MN399088
N126FCD_*N. narboroughi*	FE-C26	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	ES	MN399089
N127FCD_*N. narboroughi*	FE-C27	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	ES	MN399090
N129FCD_*N. narboroughi*	FE-C30	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399091
N130FCD_*N. narboroughi*	FE-C31	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399092
N131FCD_*N. narboroughi*	FE-C33	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399093
N132FCD_*N. narboroughi*	FE-C34	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399094
N133FCD_*N. narboroughi*	FE-C35	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399095
N134FCD_*N. narboroughi*	FE-C36	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399096
N135FCD_*N. narboroughi*	FE-C37	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399097
N136FCD_*N. narboroughi*	FE-C38	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399098
N137FCD_*N. narboroughi*	FE-C39	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399099
N140FCD_*N. narboroughi*	FE-C42	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399100
N141FCD_*N. narboroughi*	FE-C43	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399101
N143FCD_*N. narboroughi*	FE-C45	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399102
N144FCD_*N. narboroughi*	FE-C46	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399103
N145FCD_*N. narboroughi*	FE-C48	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399104
N146FCD_*N. narboroughi*	FE-C49	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399105
N147FCD_*N. narboroughi*	FE-C50	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399106
N148FCD_*N. narboroughi*	FE-C51	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399107
N149FCD_*N. narboroughi*	FE-C53	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399108
N150FCD_*N. narboroughi*	FE-C54	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	M	EF	MN399109
N151FCD_*N. narboroughi*	FE-C55	*Nesoryzomys*	*narboroughi*	Fernandina	Cabo Douglas	F	EF	MN399110
S002SLB_*N. swarthi*	ASK 5509	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	HKL	MN399111
S007SLB_*N. swarthi*	ASK 4093	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	KL	MN399112
S009SLB_*N. swarthi*	ASK 4094	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	KL	MN399113
S025SLB_*N. swarthi*	ASK 5501	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	HKL	MN399114
S026SLB_*N. swarthi*	ASK 5502	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	HKL	MN399115

S028SLB_*N. swarthi*	ASK 5505	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	HKL	MN399116
S029SLB_*N. swarthi*	ASK 5506	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	HKL	MN399117
S030SLB_*N. swarthi*	ASK 5511	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	HKL	MN399118
S051SLB_*N. swarthi*	ASK 5508	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	HKL	MN399119
S060SLB_*N. swarthi*	ASK 5500	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	HKL	MN399120
S152SELB_*N. swarthi*	SN-B01	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399121
S154SELB_*N. swarthi*	SN-B03	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399122
S155SELB_*N. swarthi*	SN-B04	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399123
S156SELB_*N. swarthi*	SN-B05	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399124
S157SELB_*N. swarthi*	SN-B06	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399125
S158SELB_*N. swarthi*	SN-B07	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399126
S159SELB_*N. swarthi*	SN-B08	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399127
S160SELB_*N. swarthi*	SN-B09	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399128
S161SELB_*N. swarthi*	SN-B10	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399129
S162SELB_*N. swarthi*	SN-B11	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399130
S163SELB_*N. swarthi*	SN-B12	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399131
S164SELB_*N. swarthi*	SN-B13	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399132
S165SELB_*N. swarthi*	SN-B14	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399133
S166SELB_*N. swarthi*	SN-B15	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399134
S167SELB_*N. swarthi*	SN-B16	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399135
S168SELB_*N. swarthi*	SN-B17	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	M	ES	MN399136
S169SELB_*N. swarthi*	SN-B18	*Nesoryzomys*	*swarthi*	Santiago	Beach east of La Bomba	F	ES	MN399137
S170SLB_*N. swarthi*	SN-LB01	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	ES	MN399138
S173SLB_*N. swarthi*	SN-LB04	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	ES	MN399139
S174SLB_*N. swarthi*	SN-LB05	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	ES	MN399140
S175SLB_*N. swarthi*	SN-LB06	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	ES	MN399141
S176SLB_*N. swarthi*	SN-LB07	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	ES	MN399142
S177SLB_*N. swarthi*	SN-LB08	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	ES	MN399143
S179SLB_*N. swarthi*	SN-LB10	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	EF	MN399144
S181SLB_*N. swarthi*	SN-LB12	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	EF	MN399145
S183SLB_*N. swarthi*	SN-LB14	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	EF	MN399146
S184SLB_*N. swarthi*	SN-LB15	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	E	MN399147
S185SLB_*N. swarthi*	SN-LB16	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	EF	MN399148
S186SLB_*N. swarthi*	SN-LB17	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	EF	MN399149
S187SLB_*N. swarthi*	SN-LB18	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	F	EF	MN399150
S188SLB_*N. swarthi*	SN-LB19	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	EF	MN399151
S189SLB_*N. swarthi*	SN-LB20	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	EF	MN399152
S191SLB_*N. swarthi*	SN-LB22	*Nesoryzomys*	*swarthi*	Santiago	La Bomba	M	EF	MN399153
F010FCD_*N. fernandinae*	ASK 5567	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	F	L	MN399036
F011FCD_*N. fernandinae*	ASK 5568	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	L	MN399037
F012FCD_*N. fernandinae*	ASK 5569	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	L	MN399038
F013FCD_*N. fernandinae*	ASK 5571	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	F	L	MN399039
F014FCD_*N. fernandinae*	ASK 5572	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	L	MN399040
F015FCD_*N. fernandinae*	ASK 5562	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	F	L	MN399041
F016FCD_*N. fernandinae*	ASK 5563	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	F	L	MN399042
F017FCD_*N. fernandinae*	ASK 5566	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	F	L	MN399043
F083FCR_*N. fernandinae*	FE-V05	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	M	ESF	MN399044
F084FCR_*N. fernandinae*	FE-V06	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	M	ESF	MN399045
F085FCR_*N. fernandinae*	FE-V07	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	F	ESF	MN399046
F086FCR_*N. fernandinae*	FE-V09	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	M	ESF	MN399047
F087FCR_*N. fernandinae*	FE-V10	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	F	ESF	MN399048
F088FCR_*N. fernandinae*	FE-V11	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	M	ESF	MN399049
F089FCR_*N. fernandinae*	FE-V12	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	M	ESF	MN399050

F090FCR_*N. fernandinae*	FE-V13	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	M	ESF	MN399051
F092FCR_*N. fernandinae*	FE-V15	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	M	ESF	MN399052
F093FCR_*N. fernandinae*	FE-V16	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	F	ESF	MN399053
F095FCR_*N. fernandinae*	FE-V18	*Nesoryzomys*	*fernandinae*	Fernandina	Crater Rim	F	EF	MN399054
F096FCD_*N. fernandinae*	FE-C09	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	EF	MN399055
F097FCD_*N. fernandinae*	FE-C24	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	EF	MN399056
F098FCD_*N. fernandinae*	FE-C29	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	EF	MN399057
F099FCD_*N. fernandinae*	FE-C32	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	EF	MN399058
F101FCD_*N. fernandinae*	FE-C52	*Nesoryzomys*	*fernandinae*	Fernandina	Cabo Douglas	M	EF	MN399059

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Use of linear features by the common vampire bat (*Desmodus rotundus*) in a tropical cattle-ranching landscape

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Linear landscape features are used by many species of insectivorous bats as flight routes and foraging zones, as well as for providing protection against environmental factors and predation. However, very little is known about the role that these landscape features play for non-insectivorous species. In this study, we evaluated the use of linear features by the common vampire bat (*Desmodus rotundus*) in a cattle-ranching landscape in the state of Tabasco, Mexico. We selected 24 sampling sites in 2014 and 24 independent sites in 2016 to 2017, all adjacent to three types of linear landscape features: forest edges, live fences and streams . We monitored each site for two non-consecutive nights between February and April 2014, and every two months from February 2016 to June 2017. We placed 24 m (2014) or 12 m (2016 to 2017) of mist nets perpendicular to the linear feature from its edge. We recorded the height and distance from the edge for each individual captured. In total we captured 50 *D. rotundus* individuals in 2014 and 58 in 2016 to 2017. The average flight height was 77 cm for the 2014 data and 69 cm for 2016 to 2017. According to our results, the most used linear features were forest edges, followed by live fences and streams. Overall, 52 % of the 2014 captures and 62 % of the 2016 to 2017 ones occurred in the first 2 m from the edge, with the number of captures gradually decreasing with increasing distance. This study provides information on the commuting patterns of *D. rotundus* in predominantly open cattle-ranching landscapes.

Los elementos lineales del paisaje son utilizados por muchas especies de murciélagos insectívoros como rutas de vuelo y zonas de forrajeo, además de brindarles protección contra factores ambientales y depredadores. Sin embargo, se conoce muy poco sobre el papel que estos elementos del paisaje juegan para especies no insectívoras. En este estudio, evaluamos el uso de los elementos lineales por el murciélago vampiro común (*Desmodus rotundus*) en un paisaje ganadero del estado de Tabasco, México. Seleccionamos 24 sitios de muestreo en 2014 y 24 sitios independientes en 2016-2017, todos adyacentes a tres tipos de elementos lineales del paisaje: bordes de bosque, cercos vivos y arroyos. Monitoreamos cada sitio durante dos noches no consecutivas entre febrero y abril de 2014 y cada dos meses de febrero de 2016 a junio de 2017. Colocamos 24 m (2014) o 12 m (2016 a 2017) de redes de niebla de manera perpendicular al elemento lineal a partir de su borde. Registramos la altura y distancia desde el borde para cada individuo capturado. En total capturamos 50 individuos de *D. rotundus* en 2014 y 58 individuos en 2016 a 2017. La altura promedio de vuelo fue de 77 cm para los datos de 2014 y de 69 cm para 2016 a 2017. De acuerdo con nuestros resultados, los elementos lineales más utilizados fueron los bordes de bosque, seguidos de los cercos vivos y arroyos. En conjunto, el 52 % de las capturas de 2014 y el 62 % de las capturas de 2016 a 2017 se presentaron en los primeros 2 m a partir del borde, decreciendo gradualmente el número de capturas con el incremento en distancia. Este estudio permite conocer los patrones de movimiento de *D. rotundus* en paisajes ganaderos predominantemente abiertos.

Keywords: forest edges; hematophagous bat; live fences; movement patterns; streams.

Introduction

Throughout the world, large tracts of original natural habitat have been replaced by mosaics of diverse habitats with different levels of human intervention, including forest fragments, areas with secondary vegetation, croplands and induced grasslands for cattle (Mena 2010). In many of these landscapes, there are continuous, structurally contrasting features with respect to adjacent habitats, which connect with each other and with different vegetation remnants (Gurrutxaga and Lozano 2008; García and Abad 2014). These types of linear features, present in heterogeneous landscapes, can be natural, such as rivers, canyons, riparian zones and vegetation strips (Limpens and Kapteyn 1991; Van Geert *et al.* 2010), or artificial, such as roads, railways and live fences (Van der Zanden *et al.* 2013).

For many non-flying land mammals, linear components function as corridors that facilitate movement between patches (Bennet 1998; Gurrutxaga and Lozano 2008; Huber *et al.* 2012). Similarly, some bats use linear landscape features as flight paths and foraging areas (Brandt *et al.* 2007; Loram *et al.* 2011). The linear features most used by bats are hedgerows, rivers and live fences, as well as other landscape components that have continuity such as forest edges and stone walls (Downs and Racey 2006; García and Santos 2014). In the case of insectivorous species, it has been suggested that linear features could be widely used because they offer greater food availability, protection against wind and predators, as well as spatial references that facilitate navigation (Limpens and Kapteyn 1991; Toffoli 2016). In some cases, the use of these spatial components may decrease the energetic cost of searching for foraging sites (Kusch *et al.* 2004; Barragán *et al.* 2010).

The structural characteristics of linear features could be related to the frequency with which they are used by different bat species. For example, it has been observed that the most commonly used live fences are those with the highest heterogeneity levels, height and shrub cover (Fuentes-Montemayor *et al.* 2013). On the other hand, the intensity of use of these landscape components appears to be related to the flight patterns and echolocation of the different bat species. In particular, it has been observed that insectivorous species that emit intense, low frequency echolocation pulses (dominated by constant frequency components) tend to commute in open areas, while insectivorous species that produce weak, high frequency pulses (dominated by modulated frequency components) are those that use the landscape's linear features with greater intensity (Limpens and Kapteyn 1991; Bouhey *et al.* 2011).

The common vampire bat, *Desmodus rotundus* (Chiroptera, Phyllostomidae), is relatively abundant in cattle-ranching landscapes in Latin America (Escobar *et al.* 2015). This species, which feeds mainly on the blood of large herbivorous mammals, leaves its roost every night to search for prey during the periods of greatest darkness (Wimsatt 1969). Unlike insectivorous species, *D. rotundus* may depend on its vision to orient itself in space (Greenhall *et al.* 1983; Eklof 2003). Because its visual field is limited by its tendency to fly very close to the ground, *D. rotundus* is likely to rely heavily on spatial references to orient itself in the landscape. In addition, its limited ability to detect small or distant objects through echolocation (Joermann 1984; Rodriguez and Allendes 2016) would force it to fly close to objects that serve as a reference. According to this hypothesis, *D. rotundus* could be expected to fly very close to linear features in cattle-ranching landscapes dominated by open areas. To test this prediction, we evaluated the use of the different linear features of the landscape by *D. rotundus* in an agroecosystem of the municipality of Tacotalpa, in the state of Tabasco, Mexico. The objectives of the present study were: 1) to estimate the flight height and flight distance relative to linear landscape features by *D. rotundus*; and 2) to compare the use that *D. rotundus* makes of live fences, forest edges and small streams as flight routes. The results of this work allow us to assess the importance of linear landscape features for the spatial navigation of *D. rotundus*, as well as to identify sites where cattle could be more vulnerable to attacks by this predator.

Materials and methods

Study area. This study was conducted in the vicinity of the Xicoténcatl rural settlement, in the municipality of Tacotalpa, Tabasco. The region's characteristic climate is warm and humid, with year-round rainfall, average monthly temperatures ranging from 22 to 28 °C, and average annual rainfall of between 2,000 and 4,000 mm (INEGI 1998). In the low mountainous elevations, vegetation consists of fragments of medium-height semi-evergreen tropical forest and tall evergreen tropical forest with different levels of disturbance, while in the low, slightly undulating plains, induced grasslands predominate (Martínez *et al.* 2013). Large tracts of grassland are crossed by numerous live fences and some rivers, shallow valleys and streams. As in the entire municipality of Tacotalpa, the main economic activity is extensive cattle ranching (Secretaría de la Reforma Agraria 2012).

The main linear features present in the study area are live fences, streams, and forest edges. In this work, we consider forest edges as linear features, based on the classification of landscape components proposed by Downs and Racey (2006). In the study area, live fences represent the boundaries of the pastures, and are made up of small trees, known locally as cocoíte (*Gliricidia sepium*), linked with barbed wire. Initially, the coco*í*tes are planted as small trunks, but later branch again to form live trees arranged in a line. The region's streams are made up of shallow, conspicuous depressions that form in unstable terrain. Although the presence of flowing water is seasonal, they generally maintain small accumulations of water or mud in which hydrophilic grasses and forbs can grow. Some of these streams form small, relatively deep valleys bordered by steep slopes. Forest fragments are generally restricted to the steepest hills, so their edge is often delineated by the base of slopes and some stone walls. Due to deforestation, some forest edges have scattered trees, so the boundaries may be blurred.

Sampling design. In total, we selected 24 sampling sites, spaced at least 150 m, at forest edges (*n* = 9), live fences (*n* = 10) and streams (*n* = 5). The sites were selected in such a way that they were not in the immediate vicinity (at least 60 m around) of other linear features that might interfere with the evaluated site. The first sampling stage was carried out between February 28 and April 29, 2014. A second set of data was collected between February 2016 and June 2017, at 24 sites different from those of the first sampling period. In this second stage, 12 sites were located in the El Paraíso ranch and 12 in the neighboring Poaná ejido; of the total number of sites, 19 corresponded to live fences, 4 to forest edges and 1 to a stream. The data from the second stage are derived from a parallel study carried out by our research group, whose objective depended on the collection of *D. rotundus* data throughout an annual cycle.

Data collection. Considering that *D. rotundus* reduces its activity during periods of greatest moonlight intensity (Flores-Crespo *et al.* 1972), we avoided sampling in the 10 days of most intense moonlight. We monitored each site for two non-consecutive nights per visit (one visit in 2014; six visits in 2016 to 2017). At each site, we placed a mist net perpendicular to the axis of the linear feature, positioning the first supporting pole as close as possible (< 30 cm) to it. During the 2014 sampling, we placed 24 continuous m of net (combinations of 6 and 12 m nets aligned and adjacent, leaving no gaps between them), so the total sampling area covered from the vicinity of the linear feature to the interior of the open areas. We did not attempt to extend the nets beyond 24 m for two reasons: to avoid approaching adjacent linear features, especially in small pastures, and to reduce damage to nets caused by cattle. In addition, available information suggests that *D. rotundus* is rarely captured in open pastures (*e. g.*, Medina *et al.* 2007). Because the sampling effort increased significantly (spatially and temporally) during the second stage, only 12 m of nets were placed at each site in 2016 to 2017. In both stages, nets were placed at dusk and left open for seven hours (stage 2014) or five hours (stage 2016 to 2017). During the first stage, we made a total sampling effort of 8,064 m-net per hour, of which 3,024 m-net per hour was carried out at forest edges, 3,360 m-net per hour at live fences and 1,680 m-net per hour at streams. During the second stage, a total sampling effort of 25,920 m-net per hour was made.

We used a flexometer to measure the height from the ground and distance from the linear feature of each individual found in the net. We identified the captured animals according to the criteria suggested by Medellín *et al.* (2008). To avoid counting newly released specimens twice, we fitted each individual with a plastic necklace containing small beads representing a color code. After obtaining routine morphometric data, the individuals were released at the same capture point.

Data analysis. Chi-square goodness of fit tests were used to assess whether *D. rotundus* tends to fly more frequently at a particular distance from linear landscape features, separately for each type (live fences, forest edges and streams) and together. For this, the number of captures was grouped according to the distance to the linear feature in 2 m intervals and compared with the number of captures that would be expected if the individuals were flying homogeneously in the landscape (equal capture frequency in each distance interval). This analysis was performed separately for the 2014 and 2016 to 2017 samples. To determine whether *D. rotundus* uses all three types of linear features with the same frequency, a non-parametric analysis of variance (Kruskal-Wallis) was performed using the number of captures per site as the unit of analysis (Durán *et al.* 2005). Since only during the first sampling could we include an adequate number of sites corresponding to each type of linear feature, this last analysis was restricted to the 2014 sample.

Results

During the samplings carried out in 2014, we obtained a total of 50 captures corresponding to the species *D. rotundus*. Of the total number of individuals, 24 were caught at live fences, 20 at forest edges and six at streams. Only one individual was recaptured once. From the samplings conducted in 2016 and 2017, we obtained a total of 58 data on flight height and distance from the linear features. Results from both periods show that *D. rotundus* tends to fly very close to the ground (average height: 77 cm in 2014 and 69 cm in 2016 to 2017). Also, 88 % of the 2014 captures and 82 % of the 2016 to 2017 ones were obtained at heights equal to or less than 100 cm. However, no individual was captured more than 160 cm above ground level.

We observed that *D. rotundus* shows a tendency to fly very close to the linear features of the landscape and to avoid open areas; 52 % of the 2014 catches and 62 % of the 2016 to 2017 ones were obtained in the first two meters, with the number of captures gradually decreasing as the distance from the linear feature increased (Figure 1). According to the Chi-square test, the use of the airspace covered by the nets adjacent to the linear features was not homogeneous (2014: $X^2 = 132.59$, $P < 0.001$; 2016 to 2017: $X^2 = 92.57$, $P < 0.001$).

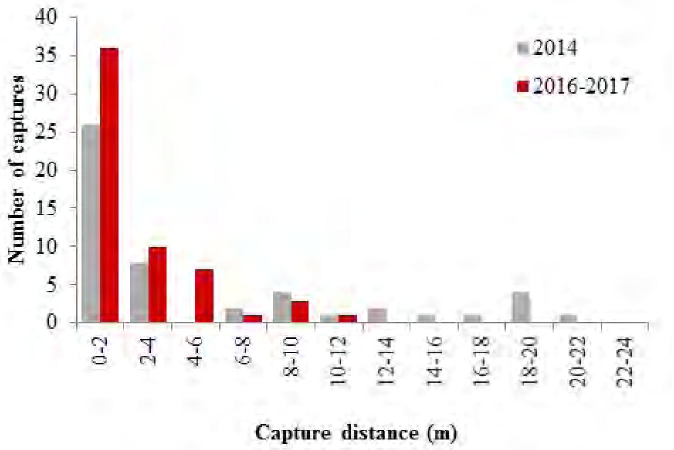

Figure 1. Number of *D. rotundus* individuals captured as a function of distance from linear landscape features (forest edges, live fences and streams) in cattle-ranching landscapes of Tacotalpa, Tabasco, for sampling periods 2014 and 2016-2017.

According to the Kruskal-Wallis test performed with the 2014 data, *D. rotundus* does not preferentially use one particular type of linear feature ($H = 2.15$, $P = 0.342$), regardless of the capture distance. The average number of captures per site was 2.2 individuals for forest edges, 2.4 for live fences and 1.2 for streams. However, the flight pattern was different for each type of linear feature (Figure 2). At the forest edges, ($X^2 = 51.90$, $P < 0.001$), 80 % of the captures were made in the first four meters, with the number of captures notably decreasing in the other distances. A similar pattern was observed in the streams and live fences (streams: $X^2 = 8.62$, $P = 0.03$; live fences: $X^2 = 28.40$, $P < 0.001$), although the percentage of captures in the first 4 m was lower than that of forest edges (Figure 2). Comparing the flight pattern in the three types of linear features, it can be observed that the tendency to fly near the linear features was more pronounced at the forest edges.

Discussion

Despite the extensive knowledge accumulated over several decades about the ecology of *D. rotundus*, this is the first study that describes its commuting patterns in agricultural landscapes. The flight height recorded in this study for *D. rotundus* is similar to that reported in a previous study on the attack behavior of this species, in which it was observed that individuals approached their prey at a height of between 50 and 150 cm (Greenhall *et al.* 1971). In the present study, the average flight height was around 70 cm, indicating that vampires tend to fly at low altitudes while searching for prey or while commuting to and from their roosts.

It was observed that *D. rotundus* flies preferentially near linear landscape features and avoids open areas (grass-

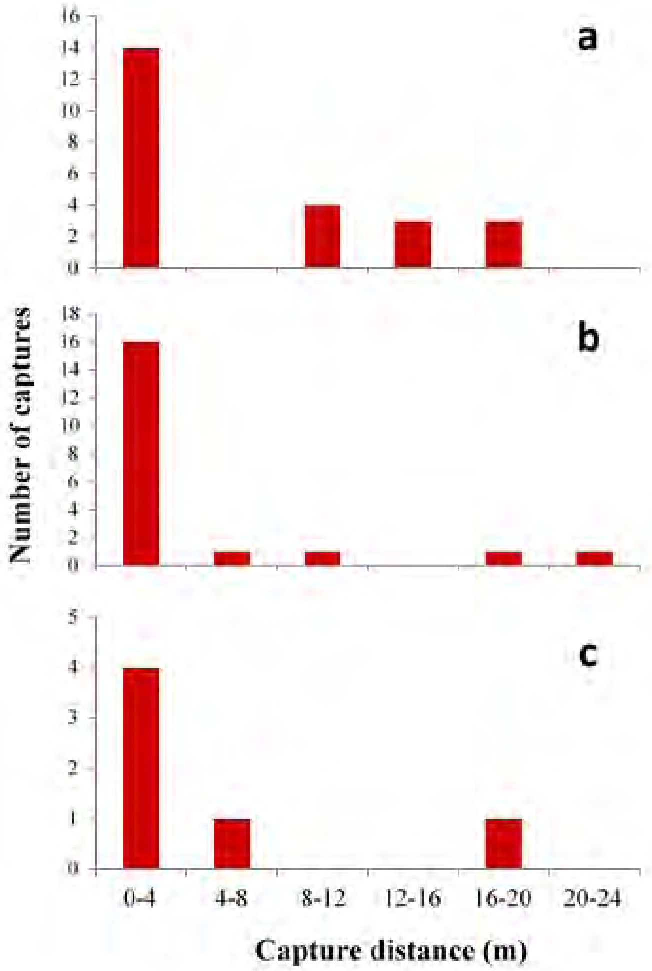

Figure 2. Number of *D. rotundus* individuals captured as a function of distance from three types of linear landscape features: a) live fences, b) forest edges, and c) streams, in cattle-ranching landscapes of Tacotalpa, Tabasco. Data correspond to the period 2014.

lands with scattered trees), as has been reported for several species of insectivorous bats (Lumsden and Bennett 2005; Downs and Racey 2006; Hein *et al.* 2009). Although there was no statistically significant preference for any type of linear feature, the greatest number of captures occurred at live fences and forest edges. The low level of stream use is similar to that observed in insectivorous species (Brandt *et al.* 2007), which could be because these sites increase the risk of predation due to the lack of tree cover (Russ and Montgomery 2002). However, this hypothesis has little support considering that *D. rotundus* avoids commuting during nights or hours with high levels of moonlight as a strategy to decrease the risk of predation (Flores-Crespo *et al.* 1972). Alternatively, lack of tree cover is likely to reduce the effectiveness of streams as spatial reference features in predominantly open landscapes.

Heavy rains and strong winds have been reported to decrease the foraging activity of *D. rotundus* (Wimsatt, 1969). Therefore, flying close to linear features may offer the common vampire bat protection against extreme environmental conditions, as has been suggested for some insectivorous species (Limpens and Kapteyn 1991; Brandt *et al.* 2007). This may explain, in part, why this species was observed more frequently using those linear features that had some degree of tree cover (live fences and forest edges).

Although *D. rotundus* has a moderately developed visual capacity (Greenhall *et al.* 1983; Eklof 2003), its low flight height may limit its field of vision. In addition, the short detection range by echolocation would prevent it from detecting objects at great distances, which in turn would make commuting and orientation difficult in open areas (Joermann 1984). For this reason, we suggest that *D. rotundus* shows a greater tendency to fly near linear landscape features because they act as reference points for spatial orientation (for a discussion on the role of linear features in insectivorous species, see Limpens and Kapteyn 1991).

One factor that may influence the usefulness of linear landscape components as reference points for the spatial orientation of *D. rotundus* is the level of contrast between the linear feature and the open areas. If these features are well defined in space, they could facilitate the commuting of individuals along the landscape (Fuentes-Montemayor *et al.* 2013). This would explain the low level of use observed in streams, which had a more diffuse structure relative to the surrounding pastures, while forest edges and living fences were generally well defined linearly.

It has been suggested that food abundance is a factor promoting the use of linear features by insectivorous bats (Verboom and Huitema 1997; Lumsden and Bennett 2005; Fuentes-Montemayor *et al.* 2013; Kalda 2015). This theory, however, has not been explored in non-insectivorous species, including *D. rotundus*. In a study conducted in a cattle-ranching area of Colombia, it was found that, during the hottest time of the year, cattle explore areas with tree cover in search of a better food supply during the night and part of the early morning (Polania 2012). Therefore, there is a possibility that, at least in some regions and at some times of the year, *D. rotundus* would prefer to commute in the immediate vicinity of wooded areas because they have greater prey availability.

The flight patterns observed in this study suggest that the most vulnerable prey to hematophagous bat attacks would be those resting at night near linear landscape features. This would explain why domestic animals maintained near wooded areas and *D. rotundus* roosting sites are most often bitten by vampire bats (Novaes *et al.* 2010; Costa and Esbérard 2011; Hernández-Pérez *et al.* 2019). In addition, this hypothesis is supported by the results of various experimental studies which documented that *D. rotundus* has a short detection range of objects (including experimental "prey") through the senses of echolocation (Joermann 1984), smell (Bahlman *et al.* 2007), thermoperception (Kürten *et al.* 1982), and passive hearing of sounds emitted by prey (Schmidt *et al.* 1991; Heffner *et al.* 2013). The role of sight is more uncertain (Greenhall *et al.* 1983; Eklof 2003), although the visual detection of prey by *D. rotundus* can be expected to decrease with increasing distance from its flight paths. An additional reason that might explain the preference of *D. rotundus* for linear landscape features (especially wooded ones) is the search for levels of darkness that maximize its ability to visually detect prey, while reducing the likelihood of being detected by them. The three hypotheses (need for spatial references, maximization of visual function in conditions of maximum darkness and minimization of the risk of being detected by prey) are not mutually exclusive and could occur simultaneously.

The flight patterns reported in this study for the common vampire bat are consistent in space and time. Considering that the number of recorded individuals decreases gradually as the distance from the linear features of the landscape increases, we can suggest (with a high level of confidence) that *D. rotundus* prefers to fly close to the linear features in predominantly open landscapes. The results reported herein have strong implications for livestock management in tropical regions, considering that the production animals most vulnerable to attacks by *D. rotundus* (and therefore most at risk of being infected with rabies) are those that rest near linear landscape features.

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Literature cited

Bahlman, J. Wm., and D. A. Kelt. 2007. Use of olfaction during prey location by the common vampire bat (*Desmodus rotundus*). Biotropica 39:147-149.

Barragán, F., C. Lorenzo, A. Morón, M. A. Briones-Salas, and S. López. 2010. Bat and rodent diversity in a fragmented landscape on the Isthmus of Tehuantepec, Oaxaca, México. Tropical Conservation Science 3:1-16.

Bennet, A. F. 1998. Linkages in the landscape: the role of corridors and connectivity in wildlife conservation. IUCN, Gland, Suiza y Cambridge, U.K.

Bernard, E., and M. B. Fenton. 2007. Bats in a fragmented landscape: species composition, diversity and habitat interactions in savannas of Santarém, Central Amazonia, Brazil. Biological Conservation 134:332-343.

Brandt, G., L. Blows, D. Linton, N. Paling, and C. Prescott. 2007. Habitat associations of British bat species on lowland farmland within the Upper Thames catchment area. Centre for Wildlife Assessment & Conservation E-Journal 1:10-19.

Bouhey, K. L., I. R. Lake, K. A. Haysom, and P. M. Dolman. 2011. Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. Biological Conservation 144:1790- 1798.

Costa, L. M., and C. E. L. Esbérard. 2011. *Desmodus rotundus* (Mammalia: Chiroptera) on the southern coast of Rio de Janeiro state, Brazil. Brazilian Journal of Biology 71:739-746.

Downs, C. N., and P. A. Racey. 2006. The use by bats of habitat features in mixed farmland in Scotland. Acta Chiropterologica 8:169-185.

Eklöf, J. 2003. Vision in echolocating bats. Göteborg University, Department of Zoology. Thesis Zoology Department, Göteborg University, Germany.

Escobar, L. E., A. T. Peterson, M. Favi, V. Yung, and G. Medina-Vogel. 2015. Bat-borne rabies in Latin America. Revista do Instituto de Medicina Tropical de São Paulo 57:63-72.

Flores-Crespo, R., S. B. Linhart, R. J. Burns, and G. Clay Mitchell. 1972. Foraging behavior of the common vampire bat related to moonlight. Journal of Mammalogy 53:366-368.

Fuentes-Montemayor, E., D. Goulson, L. Cavin, M. J. Wallace, and J. K. Park. 2013. Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. Agriculture, Ecosystems and Environment 172:6-15.

García, F., and J. Abad. 2014. Los corredores ecológicos y su importancia ambiental: Propuestas de actuación para fomentar la permeabilidad y conectividad aplicadas al entorno del río Cardeña (Ávila y Segovia). Observatorio medioambiental 17:253-298.

García, J., and A. Santos. 2014. Efectos de la estructura del paisaje y de la vegetación en la diversidad de murciélagos filostómidos (Chiroptera: Phyllostomidae) de Oaxaca, México. Revista de Biología Tropical 62:217-240.

Greenhall, A. M., G. Joermann, and U. Schmidt. 1983. *Desmodus rotundus*. Mammalian Species 202:1-6.

Greenhall, A. M., U. Schmidt, and W. Lopez-Forment. 1971. Attacking behavior of the vampire bat, *Desmodus rotundus*, under field conditions in Mexico. Biotropica 3:136-141.

Gurrutxaga, S. M., and P. J. Lozano. 2008. Ecología del paisaje: un marco para el estudio integrado de la dinámica territorial y su incidencia en la vida silvestre. Estudios geográficos 265:519-543.

Heffner, S. R., G. Koay, and E. H. Heffner. 2013. Hearing in American leaf-nosed bats. IV: The Common vampire bat, *Desmodus rotundus*. Hearing Research 296:42-50.

Hein, D. C., B. S. Castleberry, and V. K. Miller. 2009. Site-occupancy of bats in relation to forested corridors. Forest Ecology and Management 257:1200-1207.

Hernández-Pérez, E. L., G. Castillo-Vela, G. García-Marmolejo, M. Sanvicente-López, and R. Reyna-Hurtado. 2019. Wild pig (*Sus scrofa*) as prey of the common vampire bat (*Desmodus rotundus*). Therya 10:195-199.

Huber, P., F. Shilling, J. Thorne, and S. Greco. 2012. Municipal and regional habitat connectivity planning. Landscape and Urban Planning 105:15-26.

Instituto Nacional de Estadística y Geografía. 1998. Cuaderno Estadístico Municipal de Tacotalpa. Estado de Tabasco. Edición 1998. Instituto Nacional de Estadística Geografía e Informática. Gobierno del H. Ayuntamiento Constitucional de Tacotalpa. Tacotalpa, México.

Joermann, G. 1984. Recognition of spatial parameters by echolocation in the vampire bat, *Desmodus rotundus*. Journal of Comparative Physiology 155:67-74.

Kalda, O., R. Kalda, and J. Liira. 2015. Multi-scale ecology of insectivorous bats in agricultural landscapes. Agriculture, Ecosystems and Environment 199:105-113.

Kürten, L., and U. Schmidt. 1982. Thermoperception in the common vampire bat (*Desmodus rotundus*). Journal of Comparative Physiology 146:223-228.

Kusch, J., C. Weber, S. Idelberger, and T. Koob. 2004. Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. Folia Zoologica 53:113-128.

Limpens, H. J. G. A., and K. Kapteyn. 1991. Bats, their behavior and linear landscape elements. Myotis 29:39-48.

Loram, A., P. Warren, K. Thompson, and K. Gaston. 2011. Urban domestic gardens: the effects of human interventions on garden composition. Environmental Management 48:808-824.

Lumsden, F. L., and F. A. Bennett. 2005. Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia. Biological Conservation 122:205-222.

Martínez-Encino, C., G. Villanueva-López, and F. Casanova-Lugo. 2013. Densidad y composición de árboles dispersos en potreros en la sierra de Tabasco, México. Agrociencia 47:483-496.

Medellin, R. A., T. H. Arita, and H. O. Sánchez. 2008. Identificación de los murciélagos de México. Clave de campo. Segunda edición. Instituto de ecología UNAM. Ciudad de México, México.

Medina, A., C. A. Harvey, D. S. Merlo, S. Vilchez, and B. Hernández. 2007. Bat diversity and movement in an agricultural landscape in Matiguás, Nicaragua. Biotropica 39:120-128.

Mena, J. L. 2010. Respuestas de los murciélagos a la fragmentación del bosque en Pozuzo, Perú. Revista Peruana de Biología 17:277-284.

Novaes, G. M., M. A. M. Vieira, N. Lewis, C. A. Goncalves, and F. V. Nogueira. 2010. Landscape risk factors for attacks of vampire bats on cattle in Sao Paulo, Brazil. Preventive Veterinary Medicine 93:139-146.

Polania Ortiz, Y. E. 2012. Movimiento de vacunos en un paisaje arbolado y su relación con el gasto de energía. Universidad de Tolima, Facultad De Medicina Veterinaria y Zootecnia.

Rodríguez, S. A., and J. L. Allendes. 2016. Echolocation calls of free-flying common vampire bats *Desmodus rotundus* (Chiroptera: Phyllostomidae) in Chile. Bioacustics 26:153-160.

Russ, J. M., and W. I. Montgomery. 2002. Habitat associations of bats in Northern Ireland: implications for conservation. Biological Conservation 108:49-58.

Secretaria de la Reforma Agraria. 2012. Cuaderno de alternativas de desarrollo y retos del núcleo agrario: ejido Xicotencatl. Tacotalpa, México.

Schmidt, U., P. Schlegel, H. Schweizer, and G. Neuweiler. 1991. Audition in vampire bats, *Desmodus rotundu*s. Journal of Comparative Physiology 168:45-51.

Toffoli, R. 2016. The importance of linear landscape elements for bats in a farmland area: The influence of height on activity. Journal of Ecology 9:1.

Van der Zandena, H. E., H. P. Verburga, and A. C. Mucher. 2013. Modelling the spatial distribution of linear landscape elements in Europe. Ecological Indicators 27:125-136.

Van geert, A., F. Van Rossum y L. Triest. 2010. Do linear landscape elements in farmland act as biological corridors for pollen dispersal? Journal of Ecology 98:178-187.

Verboom, B., and H. Huitema. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. Landscape Ecology 12:117-125.

Wimsatt, W. A. 1969. Transient behavior, nocturnal activity patterns, and feeding efficiency of vampire bats (*Desmodus rotundus*) under natural conditions. Journal of Mammalogy 50:233-244.

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Differences in metal content in liver of Heteromyids from deposits with and without previous mining operations

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Some rodents of the family Heteromyidae can survive without drinking water, as they obtain it from food. All these species have in common that they eat seeds and fruits. The content of trace metals in food varies depending on the local geology and anthropogenic activities. Baja California Sur has mineral deposits that have been exploited; thus, the metals released may be incorporated into seeds and fruits that are consumed by Heteromyidae. Therefore, metal content in the liver is expected to reflect the presence of mining in soil where these rodents thrive. Individuals from different species of Heteromyidae were collected at sites with mineral deposits; these were divided into two groups: rodents captured in sites with a history of mining operations (Santa Rosalia, San Juan de la Costa, and El Triunfo), and rodents captured in areas with no mining activities (El Vizcaíno, Punta Abreojos, Magdalena Island, and Santiago). The liver of these rodents was excised and its manganese, copper, cadmium, lead, zinc, nickel, and iron contents were determined using atomic absorption spectrophotometry. Manganese was the element that showed the highest significant differences between species, followed by zinc and copper. Iron and cadmium showed the lowest differences. Nickel and lead showed no differences. *Chaetodipus arenarius* showed significant differences between sites in copper and lead content; *C. spinatus* did not show significant differences for manganese, copper, nickel, and iron, but it did for cadmium and lead content. Differential accumulation of metals occurs across species. These results indicate that the same species could be used for comparative purposes in pollution monitoring. The comparison of different heteromid species, despite their sharing similar feeding habits and belonging to the same family, can lead to misinterpretation due to the variability of the results. This is probably due to the requirements and tolerances regarding essential elements, such as manganese and zinc, to or tolerance to non-essential elements such as cadmium and lead, which may vary across species.

Algunas especies de roedores de la familia Heteromyidae pueden sobrevivir sin tomar agua debido a que la obtienen del alimento que consumen. Todas las especies de esta familia, tienen en común que se alimentan de semillas y frutos. El contenido de metales en el alimento puede variar dependiendo de la geología y las actividades antropogénicas que se desarrollen en el yacimiento donde habiten. En Baja California Sur se encuentran yacimientos de minerales que han sido explotados a través de la minería. Los metales liberados se pueden incorporar en las semillas y frutos de los que se alimentan los Heteromyidae. Por lo tanto, es de esperar que el contenido de metales en el hígado de los roedores refleje la presencia de minería en el habitat en que viven. Ejemplares de diferentes especies de Heteromyidae fueron colectados en sitios con yacimientos de minerales los cuales se dividieron en dos grupos. Con antecedentes de actividad minera (Santa Rosalía, San Juan de la Costa y El Triunfo) y sin actividad minera (El Vizcaíno, Punta Abreojos, Isla Magdalena y Santiago). Los hígados de los roedores fueron extraídos y analizados en su contenido de manganeso, cobre, cadmio, plomo, zinc, níquel y hierro por espectrofotometría de absorción atómica. El manganeso fue el elemento que presentó mayor cantidad de diferencias significativas entre especies, seguido por el zinc y el cobre y en menor medida de el hierro y el cadmio. El níquel y el plomo no presentaron diferencias. *Chaetodipus arenarius* presentó diferencias significativas entre yacimientos en su contenido de cobre y plomo, mientras que *C. spinatus* no presentó diferencias significativas de manganeso, cobre, níquel y hierro, pero si en cadmio y plomo. Se observa acumulación diferencial de metales entre especies. Los resultados indican que una misma especie debe ser utilizada para fines comparativos en monitoreos de contaminación. Comparar distintas especies, aunque todos sean heterómidos y tengan alimentaciones similares, puede causar interpretaciones erróneas. Esto se debe a que los requerimientos y tolerancias de elementos esenciales para la vida, como son manganeso y zinc, o la tolerancia hacia elementos no esenciales como cadmio y plomo, pueden variar entre especies.

Keywords: bioaccumulation; bioindicators; chemical pollution; rodents; arid soils.

Introduction

The Baja California peninsula, Mexico, includes regions with mineral deposits; El Vizcaíno has copper and nickel streaks; Santa Rosalia has copper, iron, zinc, and manganese deposits; El Triunfo-San Antonio, lead, zinc, and copper; and Sierra de San Francisco, copper (Servicio Geológico Mexicano 2017). In the municipalities of Loreto (San Hilario-Santa Rita), La Paz (Tembabiche, San Juan de la Costa), and Comondú (San Domingo and La Bocana), there are phosphorite deposits, composed of 70 % to 80 % spheroidal phosphate grains, used mainly as agricultural fertilizer (Consejo de Recursos Mineros 1999; Servicio Geológico Mexicano 2017). These deposits also contain trace elements (these elements are named as trace because they are commonly found in environmental concentrations below 0.1 % (Pais and Jones 1997) and lower than 0.01 % of body weight in animal and plant tissues (Adriano 2001), including cadmium, manganese, zinc, and lead (Alshahri and Alqahtani 2015).

These deposits that have been exploited through mining are located in three mining districts. The most important is Santa Rosalia, mainly dedicated to copper extraction; San Juan de la Costa, to phosphorite; and, to a lesser extent, El Triunfo-San Antonio, to gold and silver (Consejo de Recursos Mineros 1999; Servicio Geológico Mexicano 2017).

Santa Rosalia is located in northern Baja California Sur, where mining operations related to copper extractions were conducted from the mid-19th to the late 20th centuries and resumed in the early 21st century (Consejo de Recursos Mineros 1999). Beach sand in this area contains copper (up to 30,380 $\mu g \cdot g^{-1}$), zinc (up to 26,970 $\mu g \cdot g^{-1}$), and lead (up to 2,100 $\mu g \cdot g^{-1}$) in levels above those recorded in sediments polluted from industrial operations in Russia (Shumilin *et al.* 2000). Phosphorite was extracted at San Juan de la Costa from 1975 to 2003, when the mine closed because its facilities were damaged by a hurricane, and resumed operations from 2007 to date (Panorama Minero de Baja California Sur 2008). Mining activities, primarily gold extraction, were also conducted in San Antonio and El Triunfo, in the south of the Baja California peninsula, since the mid-18th century until the early twentieth century; no extraction activities are currently performed (Consejo de Recursos Mineros 1999; Servicio Geológico Mexicano 2017). During more than 150 years of gold mining in the San Antonio-El Triunfo area, several deposits of mineral waste were produced with high contents of trace metals such as cadmium (203 $\mu g \cdot g^{-1}$), copper (882 $\mu g \cdot g^{-1}$), and lead (29,364 $\mu g \cdot g^{-1}$; Méndez-Rodríguez and Álvarez-Castañeda 2016), relative to the values considered as typical of the earth's crust (cadmium: 0.2 $\mu g \cdot g^{-1}$; copper: 55 $\mu g \cdot g^{-1}$, and lead: 12.5 $\mu g \cdot g^{-1}$, Taylor 1964).

Baja California Sur has mineral deposits not yet exploited, as those in Santiago (copper deposits), Magdalena Island, Abreojos (offshore phosphorite deposits) and the Vizcaíno Desert, (scattered copper and nickel streaks; Servicio Geológico Mexicano 2017). Areas with mineral deposits can contain amounts of various metals above the average concentrations in the earth's crust, either in soil or in air (Taylor 1964; Hunter *et al.* 1987). The presence of a trace element such as lead or cadmium in a mineral deposit does not necessarily mean that it is readily available for accumulation by organisms living in the area, that is to say, that it is bioavailable. The bioavailable fraction of a chemical is largely determined by its solubility, which in turn depends on its chemical properties (Allen 2002). The chemical properties of an element may be affected by environmental factors such as water pH and salinity (Kim *et al.* 2015).

Except for a study conducted in the southern Baja California peninsula (Méndez-Rodríguez and Álvarez-Castañeda 2016), the content and variability of trace elements in mammals living in mining areas is still unknown. Heteromid species have been found in all areas with mineral deposits; these have been used as bioindicators of pollution by trace elements (cadmium, lead, manganese, zinc, and nickel; Méndez-Rodríguez and Álvarez-Castañeda 2016).

Heteromids bioaccumulate trace elements taken up from food (Méndez-Rodríguez and Álvarez-Castañeda 2016). Bioaccumulation refers to the elements that are accumulated in organisms from solid intake (food, air inspired, sediments, and grooming); it differs from bioconcentration, which deals with elements taken up by drinking water (Kim *et al.* 2015). Bioaccumulation is not influenced by fluctuations in the composition of trough water, which in turn may depend on several factors such as the time of the year (rainy or dry season) and the occurrence of natural or anthropogenic pollution events.

The objective of this study was to determine potential differences in trace elements content across the species of heteromid rodents living in a site with mineral deposits. It also seeks to establish whether the trace elements content within the same heteromid species may vary significantly between sites with mineral deposits, with and without records of mining operations.

Materials and Methods

The specimens studied were collected in May 1998 from areas with mineral deposits with and without mining operations. To this end, Sherman traps were placed along transects, with a total of 600 nights/traps per locality. The deposits sampled were divided into two groups: A) with mining activity: Santa Rosalia, San Juan de la Costa and El Triunfo, and B) with no mining operations: Vizcaíno, Abreojos, Magdalena Island and Santiago (Consejo de Recursos Mineros 1999; Servicio Geológico Mexicano 2017; Figure 1). The four species collected are associated with different types of substrate: *Chaetodipus arenarius*, areas with sandy substrate; *C. spinatus,* rocky outcrops; *C. rudinoris*, loamy or clayey soils; and *Dipodomys simulans,* clayey or sandy soils of more than 15 centimeters deep (Patton and Álvarez-Castañeda 1999; Gutierrez-Ramos and Álvarez-Castañeda 1999). Since each deposit has limited types of substrates, our expectation was to find not the four species in each locality, but an average of two species per locality. For statistical analysis, we only considered the species for which eight individuals were captured. All specimens analyzed were adults (age 4, *sensu* Hoffmeister 1951).

Analysis of trace elements. The analyses of trace elements were carried out in the liver of specimens collected. This tissue has been useful to reflect environmental differences in trace elements content between substrates associated with small mammals (Talmage and Walton 1991). The specimens were transported to the laboratory in coolers. The liver of the specimens of the four species of was excised and dry-stored individually under freezing until analysis (Méndez-Rodríguez and Álvarez-Castañeda 2016). In the laboratory, each liver was dried in an oven at 70 °C and subsequently weighed. The concentration of trace elements was recorded in milligrams (dry weight). Each sample was digested separately using a solution of 70 % nitric acid (HNO_3) and 30 % hydrogen peroxide (H_2O_2; Analytical grade; Mallinckrodt J. T. Baker, USA) in a microwave oven (Mars 5X, CEM; Mathews, USA; Méndez-Rodríguez and Álvarez-Castañeda 2016). After digestion, 1 ml of hydrochloric acid (HCl) was added to each sample and then brought to 50 mL with distilled water. Manganese (Mn), copper (Cu), cadmium (Cd), lead (Pb), zinc (Zn), nickel (Ni), and iron (Fe) concentrations were determined using an atomic absorption spectrophotometer (Xploraa, GBC Scientific Equipment) with air-acetylene flame (Van Loon 1985). Values were calibrated and validated using the certified reference standard TORT-2 (National Research Council Canada, Ottawa). The analytical values were within the range of the certified values. Metals recovery was higher than 95%. The concentrations of trace elements reported in other studies based on fresh weight were converted to dry weight by multiplying by 3.5 (Talmage and Walton 1991). The limits of detection of the instrument were as follows: Mn, 0.020 μg·g^{-1}; Cu, 0.017 μg·g^{-1}; Cd, 0.017 μg·g^{-1}; Pb, 0.074 μg·g^{-1}; Zn, 0.070 μg·g^{-1}; Ni, 0.030 μg·g^{-1}; Fe, 0.65 μg·g^{-1}.

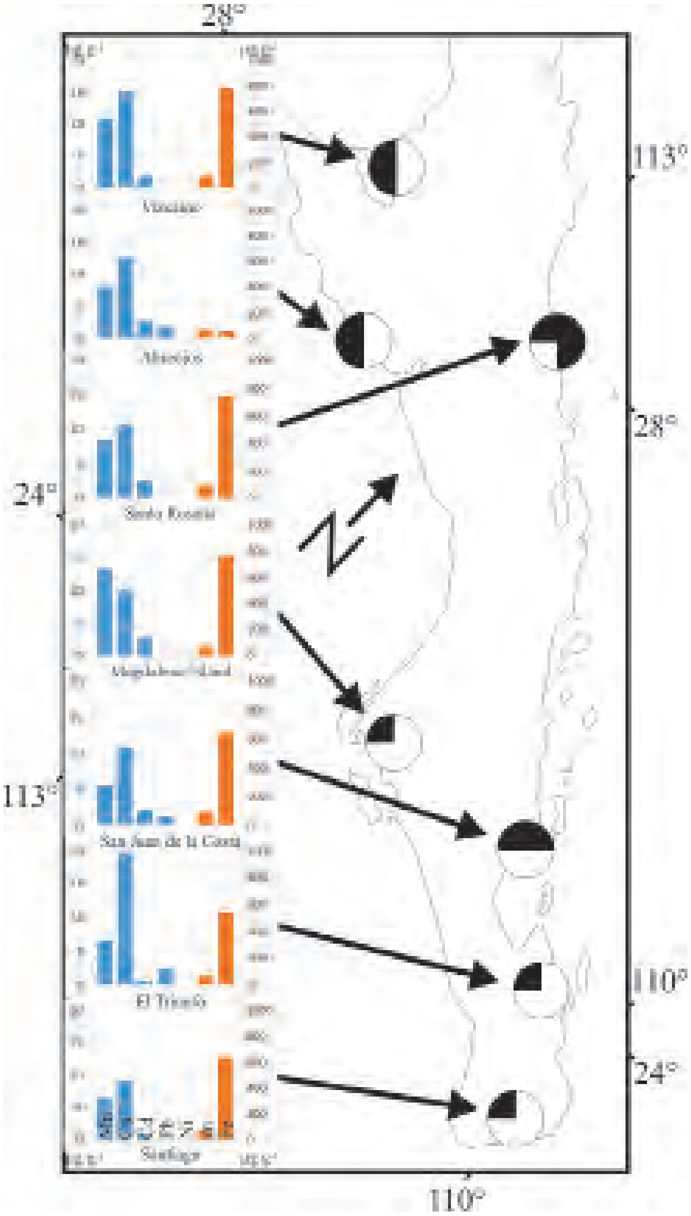

Figure 1. Sites where specimens of *Chaetodipus arenarius, C. spinatus, C. rudinoris,* and *Dipodomys simulans* were collected in Baja California Sur, Mexico. Columns in blue are related to the Y1 axis; columns in orange, with Y2. The presence of the different species in each site is marked. The top left quarter represents the presence of *C. spinatus*, top right = *C. rudinoris;* bottom left = *C. arenarius;* and lower right = *D. simulans.*

Statistical analysis. The normality and homoscedasticity of the concentration data of each trace element were analyzed using the Kolmogorov-Smirnov and Levene tests, respectively. The concentration data of the seven elements were log-transformed and compared by a one-way ANOVA, to test for significant differences in trace element concentrations between different species in a locality or between individuals of the same species from different localities. A Tukey's post-hoc analysis was conducted (Zar 2010). The analyses were carried out using the software STATISTICA (StatSoft, Inc 10). The data are reported as the mean ± standard error. The results with a significance level of $P < 0.05$ were considered statistically significant. The presence of synergies (an element favors the presence of another element in a tissue) or antagonisms (higher concentrations of an element associated with lower levels of another) between elements was explored using Pearson's correlations (Schoendorfer and Davies 2012; Mikolic *et al.* 2016).

Results

Different heteromid species coexisting in a given deposit. A total of four heteromid species were found across the whole study area. In a single deposit, up to two species were found with more than eight individuals, depending on the type of substrate (Table 1). This prevented the comparison of the four species in a single deposit, but pairwise comparisons were performed in different deposits. In sites where individuals belonging to more than one species were found, manganese was the element that showed the greatest number of significant differences between species (Table 1). In El Vizcaino, *C. spinatus* showed significantly higher manganese ($P = 0.005$) and zinc ($P = 0.002$) concentrations, and lower copper levels ($P = 0.0001$), versus *C. arenarius*. There were no significant differences in cadmium, lead, nickel, or iron. In Santa Rosalia, *C. spinatus* showed significantly higher manganese ($P = 0.0002$) and zinc ($P = 0.0058$) concentrations, but a lower cadmium level ($P = 0.0273$), relative to *Dipodomys simulans;* no significant differences were observed for copper, lead, nickel, and iron. In San Juan de la Costa, *C. spinatus* showed significantly higher manganese ($P = 0.0004$) and copper ($P = 0.0114$) concentrations, but lower cadmium ($P = 0.0114$) and iron ($P = 0.0024$) levels, versus *C. rudinoris*, with significant differences in lead, zinc, and nickel. In most deposits, *C. spinatus* showed significantly higher manganese and lower cadmium levels, relative to the other heteromid species coexisting with it.

Same species living in different deposits. The species that prevailed in the deposits studied was *C. spinatus* (Table 1). The metals content in specimens of this species in the seven sites showed no significant differences in manganese, copper, nickel, and iron levels. Cadmium levels in specimens from Magdalena Island were significantly higher versus those in specimens from Santiago ($P = 0.0104$), San Juan de la Costa ($P = 0.0356$) and El Triunfo ($P = 0.0229$). San Juan de la Costa showed significantly higher lead concentrations than Magdalena Island ($P = 0.0126$), Santa Rosalia ($P =$

Table 1. Concentration of trace elements in liver tissue in the heteromids *Chaetodipus arenarius, C. spinatus, C. rudinoris*, and *Dipodomys simulans* collected in sites with mineral deposits in Baja California Sur, Mexico.

	Especie	*n*	Manganese	Copper	Cadmium	Lead	Zinc	Níckel	Iron
				Without mining activity					
El Vizcaino	*C. arenarius*	10	8.37±0.38	18.18±0.98	1.88±0.17	0.41±0.37	86.37±5.18	<0.02	821±43
	C. spinatus	9	13.86±1.78	12.32±0.81	1.94±0.26	<0.17	120.99±8.22	0.16±0.16	758±76
Abreojos	*C. arenarius*	15	7.93±0.43	12.62±0.85	2.85±0.61	1.73±0.50	77.89±4.18	<0.02	852±76
	C. spinatus	1	12.38	15.51	1.29	3.92	89.45	<0.02	796
Isla Magdalena	*C. spinatus*	10	13.50±5.01	10.19±3.35	3.00±0.61	<0.17	79.01±18.05	<0.02	774±147
				With mining activity					
Santa Rosalia	*C. rudinoris*	1	11.31	7.39	5.15	<0.17	97.27	<0.02	549
	C. spinatus	13	10.84±0.87	11.79±1.95	2.15±0.34	0.09±0.08	118.55±8.87	0.12±0.11	807±62
	D. simulans	10	5.66±0.32	9.75±0.61	3.61±0.40	<0.17	78.62±4.99	<0.02	699±40
S. J. Costa	*C. rudinoris*	10	3.60±0.73	9.96±0.62	3.30±0.57	0.58±0.26	103.01±8.54	<0.02	749±64
	C. spinatus	8	8.25±0.64	12.95±0.76	1.35±0.25	2.24±1.05	107.44±4.20	0.50±0.48	449±46
El Triunfo	*C. spinatus*	11	7.77±0.56	13.37±1.23	1.11±0.11	1.92±0.69	75.32±6.61	<0.02	773±88
Santiago	*C. spinatus*	10	6.54±1.26	9.22±1.84	1.13±0.33	0.43±0.30	72.75±13.26	0.22±0.22	642±127

0.0113), and El Vizcaíno ($P = 0.0000$), but these were not significantly different versus Santiago. At El Vizcaíno, *C. arenarius* showed the highest copper levels ($P = 0.0004$) and the lowest lead levels ($P = 0.0450$) relative to Abreojos (Table 1).

Correlations between metals by species and site. In San Juan de la Costa, *C. rudinoris* yielded a direct correlation between manganese and copper contents (r = 0.89), and an inverse correlation between manganese and cadmium (r = -0.84). In *C. spinatus,* nickel was directly correlated to lead (r = 0.82), and inversely correlated to cadmium (r = -0.77). In *C. spinatus* and *C. rudinoris* manganese (r = 0.76) and copper (r = 0.62) show a direct correlation; the opposite, i.e., an inverse correlation between these two species was observed for iron (r = -0.67) and cadmium (r = -0.58). These findings suggest that both species living in the same deposit behave differently in terms of bioaccumulation. Although an increase in manganese and copper levels co-occurs in both species in San Juan de la Costa, iron and cadmium increases in *C. rudinoris* while both elements decreases in *C. spinatus* or vicebersa. Zinc and nickel show non-significant differences between these two species coexisting in the same locality.

In Santa Rosalia, no significant correlation was found between metals in *D. simulans* or *C. spinatus*. However, a direct correlation in manganese (r = 0.52) and zinc (0.53) was evident between these two species, but an inverse correlation in cadmium (r = -0.59) was observed. In other words, in both species, manganese and zinc contents either increased or decreased in parallel in both species; however, when cadmium increases in *D. simulans*, it decreases in *C. spinatus*.

In El Vizcaino, *C. arenarius* showed a direct correlation between manganese and copper (r = 0.69) and between manganese and zinc (r = 0.68); in contrast, *C. spinatus* showed no significant correlations between the content of these metals. Both species showed a direct correlation in manganese (r = 0.61) and zinc (r = 0.66) content, but and inverse correlation in copper (r = -0.74) content. In Abreojos, *C. arenarius* showed a direct correlation between copper and cadmium (r = 0.52), copper and zinc (r = 0.84), and cadmium and zinc (r = 0.63).

In El Triunfo, Santiago and Isla Magdalena, only *C. spinatus* individuals were found. El Triunfo specimens showed no significant correlation between metals content. In Santiago, manganese was significantly correlated ($P < 0.05$) to copper (r = 0.84), zinc (r = 0.79) and iron (r = 0.81). In addition, a direct correlation was observed between copper and zinc (r = 0.93), and between copper and iron (r = 0.97). Lead was directly correlated with nickel (r = 0.84), and iron with zinc (r = 0.94). The specimens collected in Magdalena Island showed a significant direct correlation between copper and zinc (r = 0.80).

Discussion

Mineral deposits have high metal concentrations relative to those considered typical of the earth's crust (Taylor 1964); this does not imply, however, that these metals are bioavailable. The concentrations found in the liver of rodents collected in the different deposits show mean manganese, copper, zinc, and nickel levels that are below the values considered characteristic of non-contaminated sites: manganese (up to 1320 $\mu g \cdot g^{-1}$); copper (up to 23 $\mu g \cdot g^{-1}$); zinc (up to 120 $\mu g \cdot g^{-1}$); nickel (up to 4.80 $\mu g \cdot g^{-1}$; Talmage and Walton 1991; Lewis *et al.* 2001; Torres and Johnson 2001; Milton *et al.* 2003). These four elements are essential for life; hence, their levels in the body are regulated by physiological mechanisms that produce a balance between assimilation, metabolism, and excretion (Fritsch *et al.* 2010).

Cadmium concentrations in the liver of specimens collected in the seven sites studied, regardless of the presence of mining operations, are within the range considered normal for this element (Marques *et al.* 2007; Petkovšek *et al.* 2014), suggesting that the rodents studied are not bioaccumulating this metal. In deposits with presence of foundry facilities, the cadmium levels recorded are almost one order of magnitude higher than those found in the present study (≈ 50µg·g^{-1}; Dimitrov *et al.* 2016). In Slovenia, in deposits affected by lead foundries, which are also sources of cadmium pollution to the environment, the granivorous rodent *Apodemus flavicollis* shows concentrations higher than those recorded in the present study, ranging from about 19.0 ± 20.0 µg·g^{-1} up to 15.5 ± 19.4 µg·g^{-1} (Petkovšek *et al.* 2014; Dimitrov *et al.* 2016), which are twice those recorded in the present study (Table 1).

It is considered that the levels of trace elements in soil will be reflected in the liver of rodents thriving in these sites, since metals in the substrate are likely taken up by local plants (Méndez-Rodríguez and Álvarez-Castañeda 2016) and, in this way, can be incorporated into the food chain. In plants, however, trace elements may be present as a non-bioavailable moiety, for example, if they occur as phytates (Schoendorfer and Davis 2012). Therefore, cadmium levels in sediments or the diet may not be directly related to its concentrations in body tissues. Another factor to consider is that a set of antagonistic or synergistic chemicals are also taken up with food. For example, seeds consumed by rodents in El Triunfo contain cadmium (Méndez-Rodríguez and Álvarez-Castañeda 2016), and its assimilation and retention in the body is affected by the presence of zinc and iron (Schoendorfer and Davis 2012; Méndez-Rodríguez and Álvarez-Castañeda 2016).

The results regarding the accumulation of the various metals showed differences between sites as well as between rodent species. For instance, in San Juan de la Costa, cadmium content in *C. rudinoris* is inversely related to manganese content, while in *C. spinatus* cadmium varies inversely with nickel, and the amount of cadmium between these two species is inversely related. This indicates that, although both species may be sharing one or several types of seeds as food sources (review of cheek pouches, Gutierrez pers. obs.), the amount and composition of each seed type can influence the levels of each trace element that will eventually be bioaccumulated by each species. This is based on the fact that iron can either promote or prevent zinc uptake, depending on the proportion of these two elements (Lonnerdal 2000). In the rodents studied, a similar phenomenon may occur between copper and zinc, since in deposits with mining activity the relationship between these two elements is disrupted.

Mining operations may involve processes that change the chemical nature of elements, thus increasing or reducing their bioavailability (Ramírez *et al.* 2005). For instance, when the bioavailable fraction of copper increases, this element as well as cadmium displace zinc from metallothioneins; in turn, the zinc released induces the synthesis of methallothioneins (Bebianno and Langston 1991). A synergistic relationship between copper and zinc has been observed in tissues, that is, one element promotes the assimilation of the other; however, when the zinc:copper ratio is altered because one of these two elements accumulates at levels far above those of the other, then the relationship becomes antagonistic (Jonker et al. 2005; Nis et al. 2017).

In Santa Rosalia, copper extraction operations led us to expect that rodents accumulate copper in higher amounts relative to specimens of the same species in other locations with no copper mining. This was not observed (Table 1). In soil polluted by metals, the following situations may occur in plants: 1) the element is not bioavailable for uptake by the plant; 2) the plant fails to grow because of excess levels of the bioavailable trace element in soil; 3) the element is taken up from soil to the roots, but is not transported to other parts of the plant; or 4) the element is transported from the root to the seed or fruit (Allen 2002). According to the above, although in Santa Rosalia copper concentrations have been measured at levels up to 5,785 mg kg^{-1} in stream sediments and up to 33,192 mg kg^{-1} in mining waste, it is likely not bioavailable and, therefore, not recorded in rodents.

The bioavailability of a given element in soil is a critical factor for its uptake by an organism; this element may be affected by fluvial discharges or activities such as the application of materials that affect the pH or composition of soil, as is the case when mining takes place according to Ramírez *et al.* 2005. In San Juan de la Costa, Santa Rosalia, and El Triunfo, which are sites with deposits where mining operations have been conducted throughout history, rodents showed no significant increases in the trace elements analyzed in the liver, relative to specimens collected in areas with no mining activities (Table 1).

As regards species collected in the same locality, we expected to find no differences in metal concentrations between them. That is to say, we expected that all species of heteromids from a same deposit would reflect similar concentrations of metals in liver. However, it was found that *C. spinatus* accumulates significantly higher manganese and zinc levels than *C. arenarius* and *D. simulans,* which are the species coexisting with *C. spinatus* in some localities (Table 1). Since these species compete for the same food (Hunter *et al.* 1987; Gutierrez-Ramos and Álvarez-Castañeda 1999), any differences may be associated with the metabolism of each species, rather than with the degree of environmental pollution. It should be considered that manganese and zinc function as enzymatic cofactors (Aschner and Aschner 2005) and some species may require higher levels of these cofactors than others. For instance, it has been observed that more active or faster rodent species show a higher energy demand (Bozinovic and Gallardo 2005). The enzymes involved in energy production include pyruvate carboxylase, which uses manganese as a cofactor (Aschner and Aschner 2005). This element is also a cofactor of arginase, an enzyme associated with the concentration of urine (formed mainly by urea) that is part of a strategy for the optimization of metabolic water (MacMillen and Lee 1967; Brock *et al.* 1994). Urine concentration uses a large amount of energy (Frank 1988; Bozinovic and Gallardo

2005). The various species likely have a differential capacity to concentrate urine and recover water from it, and this physiological process would be reflected in the concentration of chemical elements.

Lead concentrations recorded in the four species and in all deposits are below those considered as toxic for mammals (4.2 µg·g^{-1} dry weight; Ma 1996). The highest lead levels were found in heteromids living in San Juan de la Costa, where phosphorite is extracted; in Abreojos, where there is a non-exploited phosphorite deposit; and in El Triunfo, where gold and silver mining operations have been conducted but with no phosphorite deposits. This implies that the source of bioavailable lead may not be associated with phosphorite or its exploitation, but with another mineral or situation. Traditionally, the presence of lead is associated with the use of gasoline, which contained this metal until the 1990s (Soto-Jimenez and Flegal 2009). Lead is a conservative pollutant that persists in the environment; in addition, its presence in a mineral deposit is also attributed to its capacity to be transported by wind (Soto-Jimenez and Flegal 2009).

The results reported here showed the lack of consistency in the presence of trace elements in species living in a same deposit, as well as between sites. Our findings that the species living in a same deposit exhibit different trace metals levels support the conclusion that the concentration of trace elements in different species is influenced by different physical, chemical, and biological factors that differentially affect the ability to each species to take up the various trace metals. It is therefore relevant to further explore the synergistic and antagonistic processes related to zinc and copper, which together with metallothioneins and other detoxification mechanisms present in living organisms, may directly participate in the bioaccumulation of trace metals.

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Cited literature

Adriano, D. C. 2001. Trace elements in terrestrial environments: biogeochemistry, bioavailability, and risks of metals. Springer. New York, U.S.A.

Allen, H. E. 2002. Bioavailability of metals in terrestrial ecosystems: Importance of partitioning for bioavailability to invertebrates, microbes and plants. Society of Environmental Toxicology and Chemistry.

Alshahri, F., and M. Alqahtani. 2015. Chemical fertilizers as a source of 238 U, 40 K, 226 Ra, 222 Rn, and trace metal pollutant of the environment in Saudi Arabia. Environmental Science and Pollution Research 22:8339-8348.

Aschner, J. L., and M. Aschner. 2005. Nutritional aspects of manganese homeostasis. Molecular aspects of medicine 26:353-362.

Bebianno, M. J., and W. J. Langston. 1991. Metallothionein induction in *Mytilus edulis* exposed to cadmium. Marine Biology 108:91-96.

Bozinovic, F., and P. Gallardo. 2006. The water economy of South American desert rodents: from integrative to molecular physiological ecology. Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology 142:163-172.

Brock, A. A., S. A., Chapman, E. A. Ulman, and G. Wu. 1994. Dietary manganese deficiency decreases rat hepatic arginase activity. The Journal of nutrition 124:340-344.

Brown, J. H., and G. A. Liberman. 1973. Resource utilization and coexistence of seed-eating rodents in sand dune habits. Ecology 54:788-797.

Brown, J. H., O. J. Reichman, and D. W. Davison. 1979. Granivory in desert ecosystems. Annual Review of Ecology and Systematics 10:788-797.

Dimitrov, H. A., V. I. Mitkovska, V. D. Tzekov, and T. G. Chassovnikarova. 2016. Bioaccumulation of Cadmium and Lead in Rodent Species from the Region of Lead-Zinc Smelting Factory–Plovdiv (South Bulgaria). Ecologia Balkanica 8:9-18.

Consejo de Recursos Minerales. 1999. Monografía geológico-minera del estado de Baja California Sur. Secretaría de Comercio y Fomento Industrial. Coordinación General de Minería. Pachuca, México.

Florianczyk, B. 2007. Metallothioneins and its role in metal regulation, binding of reactive oxygen species, apoptosis and cell differentiation. Journal of Pre-clinical and Clinical Research 1:16-18

Frank, C. L. 1988. The relationship of water content, seed selection, and the water requirements of a heteromyid rodent. Physiological Zoology 61:527-534.

Fritsch, C., R. P. Cosson, M. Cœurdassier, F. Raoul, P. Giraudoux, N. Crini, and R. Scheifler. 2010. Responses of wild small mammals to a pollution gradient: host factors influence metal and metallothionein levels. Environmental Pollution 158:827-840.

Gutiérrez-Ramos, A., and S. T. Álvarez-Castañeda. 1999. Seed removal by heteromyid rodents in three habitats of tropical Mexico. Pp 211-222 *in* Ecology and management of forest, woodlands, and scrublands in the dryland region of the United States and Mexico: Perspectives for the 21st Century (Ffolliott, P. F., and A Ortega-Rubio, eds.). University of Arizona, Centro de Investigaciones Biológicas del Noroeste. La Paz, México.

Hoffmeister, D. F. 1951. A taxonomic and evolutionary study of the piñon mouse, *Peromyscus truei*. Illinois Biological Monographs 21:1–104.

Hunter, B. A., M. S. Johnson, and D. J. Thompson. 1987. Ecotoxicology of copper and cadmium in a contaminated grassland ecosystem. III. Small Mammals. Journal of Applied Ecology 24:601-614.

Iwai, T., M. Takahashi, K. Oda, Y. Terada, and K. T. Yoshida. 2012. Dynamic changes in the distribution of minerals in relation to phytic acid accumulation during rice seed development. Plant Physiology 160:2007-2014.

Janzen, D. H. 1970. Herbivores and the number of three species in tropical forest. American Naturalist 104:501-528.

Jonker, M. J., C. Svendsen, J. J. Bedaux, M. Bongers, and J. E. Kammenga. 2005. Significance testing of synergistic/antagonistic, dose level-dependent, or dose ratio-dependent effects in mixture dose-response analysis. Environmental Toxicology and Chemistry: An International Journal 24:2701-2713.

Kim, R. Y., J. K. Yoon, T. S. Kim, J. E. Yang, G. Owens, and K. R. Kim. 2015. Bioavailability of heavy metals in soils: definitions and practical implementation—a critical review. Environmental Geochemistry and Health 37:1041-1061.

Lewis L. A., R. J. Poppenga, W. R. Davidson, J. R. Fischer, and K. A. Morgan. 2001. Lead toxicosis and trace element levels in wild birds and mammals at a firearms training facility. Archives of Environmental Contamination and Toxicology 41:208-214.

Linzey A. V., R. Timm, S. T. Álvarez-Castañeda, I. Castro-Arellano, and T. Lacher. 2008. *Chaetodipus spinatus*. *In*, IUCN 2013. IUCN. Red List of Threatened Species. Version 2015.1. http://www.iucnredlist.org/details/4338/0.

Lonnerdal, B. 2000. Dietary factors influencing zinc absorption. The Journal of Nutrition 130:1378S-1383S.

Ma, W. 1996. Lead in mammals. Pp. 281–296 *in* Environmental contaminants in wildlife: interpreting tissue concentrations (Beyer, W. N., G. H. Heinz, and A. W. Redmond-Norwood, eds). Second edition. Lewis. Boca Raton, U.S.A.

MacMillen, R. E., and A. K. Lee. 1967. Australian desert mice: independence of exogenous water. Science 158:383-385.

Macmillern, E., and D. S. Hinds. 1983. Water regulatory efficiency in heteromyid rodents: a model and its application. Ecology 64:152-164.

Mares, M. A. 1993. Heteromyids and their ecological counterparts: A pandesertic view of rodent ecology and evolution. Pp. 652-701 *in* Biology of the Heteromyidae (Genoways, H. H., and J. H Brown, eds.). The American Society of Mammalogists, Special Publication. Lawrence, U.S.A.

Marques, C. C., A. Sánchez-Chardi, S. I. Gabriel, J. Nadal, A. M. Viegas-Crespo, and M. Da Luz Mathias. 2007. How does the greater white-toothed shrew, *Crocidura russula*, responds to long-term heavy metal contamination?— A case study. Science of the Total Environment 376:128-133.

Milton, A., J. A., Cooke, and M. S. Johnson. 2003. Accumulation of lead, zinc, and cadmium in a wild population of Clethrionomys glareolus from an abandoned lead mine. Archives of Environmental Contamination and Toxicology 44:405-411.

Mikolić, A., Schönwald, N., and M. Piasek. 2016. Cadmium, iron and zinc interaction and hematological parameters in rat dams and their offspring. Journal of Trace Elements in Medicine and Biology 38:108-116.

Méndez-Rodríguez, L. C., and S. T. Álvarez-Castañeda. 2016. Assessment of trace metals in soil, vegetation and rodents in relation to metal mining activities in an arid environment. Bulletin of Environmental Contamination and Toxicology 97:44-49.

Milton, A., Cooke, J. A., and M. S, Johnson. 2003. Accumulation of lead, zinc, and cadmium in a wild population of *Clethrionomys glareolus* from an abandoned lead mine. Archives of Environmental Contamination and Toxicology 44:405-411.

Patton, J. L., and S. T. Álvarez Castañeda. 1999. Family Heteromyidae. Pp. 351-443 *in* Mamíferos del Noroeste Mexicano (Álvarez Castañeda, S. T., y J. L. Patton, eds.). Centro de Investigaciones Biológicas del Noroeste, S. C. La Paz, México.

Nys, C., T. Van Regenmortel, C. R. Janssen, R. Blust, E. Smolders, and K. A. Schamphelaere. 2017. Comparison of chronic mixture toxicity of nickel-zinc-copper and nickel-zinc-copper-cadmium mixtures between Ceriodaphnia dubia and Pseudokirchneriella subcapitata. Environmental Toxicology and Chemistry 36:1056-1066.

Petkovšek, S. A. S., Kopušar, N., and B. Kryštufek. 2014. Small mammals as biomonitors of metal pollution: a case study in Slovenia. Environmental Monitoring and Assessment 186:4261-4274.

Pais, I., and J. B. Jones, Jr. 1997. The handbook of trace elements. CRC Press. Boca Raton, U.S.A.

Ramirez, M., S. Massolo, R. Frache, and J. A. Correa. 2005. Metal speciation and environmental impact on sandy beaches due to El Salvador copper mine, Chile. Marine Pollution Bulletin, 50: 62-72.

Servicio Geológico Mexicano. 2017. Panorama minero del Estado de Baja California Sur. México. Secretaria de Economía, Servicio Geológico Mexicano, Coordinación General de Minería and Secretaría de Gobernación. Ciudad de México, México.

Schmidt-Nielsen, K. 1964. Desert animals. Physiological problems of heat and water. Desert animals. Physiological problems of heat and water. Oxford University Press. London, U.K.

Schmidt-Nielsen, K. 1972. How animals work. Cambridge University Press, London, U.K.

Schoendorfer, N., and P. S. Davies. 2012. Micronutrient interrelationships: Synergism and antagonism, Pp 159-177 *in* Micronutrients (Betancourt, A. I., and H. F. Gaitan, eds). First edition. Nova Science Publishers, Inc. New York, U.S.A.

Shumilin, E. N., Rodríguez-Figueroa, G., Bermea, O. M., Baturina, E. L., Hernández, E., and G. D. R. Meza. 2000. Anomalous trace element composition of coastal sediments near the copper mining district of Santa Rosalía, Peninsula of Baja California, Mexico. Bulletin of Environmental Contamination and Toxicology 65:261-268.

Soto-Jiménez, M. F., and A. R. Flegal. 2009. Origin of lead in the Gulf of California Ecoregion using stable isotope analysis. Journal of Geochemical Exploration, 101:209-217.

Talmage S. S., and B. T. Walton. 1991. Small mammals as monitors of environmental contaminants. Pp. 47-145 *in* Reviews of Environmental Contamination and Toxicology. Springer. New York, U. S. A.

Taylor, S. R. 1964. Abundance of chemical elements in the continental crust: a new table. Geochimica et Cosmochimica Acta 28:1273-1285.

Torres K. C., and M. L. Johnson. 2001. Bioaccumulation of metals in plants, arthropods, and mice at a seasonal wetland. Environmental Toxicology and Chemistry 20:2617-2626.

Van Loon, J. C. 1985. Selected methods of trace metal analysis: biological and environmental samples. John Wiley and Sons. U.S.A.

Vašák, M., and G. Meloni. 2011. Chemistry and biology of mammalian metallothioneins. JBIC Journal of Biological Inorganic Chemistry 16:1067-1078.

Zar, J. H. 2010. Biotatistical analysis. 5th editon. Prentice Hall. Upper Saddle River, U.S.A.

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Identity and distribution of the Nearctic otter (*Lontra canadensis*) at the Río Conchos Basin, Chihuahua, Mexico.

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We have identified a scarcely known river otter population from the Upper Río Conchos basin, northern Mexico, finding a well-established population of the Nearctic otter *Lontra canadensis*. A pioneer study of these otters at Río San Pedro, a tributary of the Río Conchos, described them as Neotropical otters, *Lontra longicaudis*; at that time, no specimens or photographs of these otters were available from the locality. Therefore, its taxonomic status remained unclear for various decades. Río Conchos is one of the major tributaries of Río Grande (Río Bravo in Mexico) and its headwaters are located high in the Sierra Madre Occidental. A juvenile otter fur obtained from Río San Pedro was compared to two furs of Neotropical otters from Oaxaca and Sonora, with the aim to compare the structure of primary hairs (PH) and secondary hairs (SH) in order to know their specific status. Camera traps were set-up at Río San Pedro in Chihuahua and in Arroyo Bamochi (occupied by *L. longicaudis*) in Sonora in 2015 to compare individuals, population structure and occupation in both places. Two other places were surveyed to confirm the presence of river otters: Río Conchos and Río Santa Isabel. Based on hair characteristics (primary and secondary hairs from the juvenile) and photographic evidence from camera-traps, we confirm that otters from Río San Pedro, belong to the Nearctic otter, *Lontra canadensis*. And presumably in other localities visited in the Concho's river basin that also has presence of otters, such as Río Santa Isabel and Río Conchos. The population structure from Arroyo Bamochi and Río San Pedro were similar in both areas, but the density of otters is higher at Arroyo Bamochi than at Río San Pedro, even though there is no significant difference between the two sites. Specimens of river otters from Río Grande basin have been identified as *L. canadensis lataxina*, Cuvier, 1823. The former distribution area of this species ranges from inland US across the Río Grande basin in the Rocky Mountains, the Río Pecos, further East, flowing south and southeast into the Gulf of Mexico. The finding reported here represents a major area occupied by this species, and a significant conservation issue for their protection in Mexico, as well as an indicator of the healthy conservation status of the upper Río Conchos.

Se identificó una población de nutria de río escasamente conocida de la cuenca alta del Río Conchos en el norte de México. Encontramos que la población está bien establecida y corresponde a la nutria Neártica, *Lontra canadensis*. Un estudio pionero de estas nutrias en el Río San Pedro, tributario del Río Conchos, las describió como nutria Neotropical, *Lontra longicaudis*; en ese tiempo no se conocía ningún espécimen o fotografías de nutrias de la localidad. Por lo que su estado taxonómico era poco claro, lo que duró varias décadas. El Río Conchos es uno de los mayores tributarios del Río Bravo (Río Grande en los Estados Unidos) y sus cabeceras se encuentran localizadas en la parte alta de la Sierra Madre Occidental. Se obtuvo la piel de una nutria juvenil del Río San Pedro, la cual fue comparada con dos pieles de nutria Neotropical, una de Oaxaca y otra de Sonora, para cotejar la estructura de los pelos primarios (PH) y de los pelos secundarios (SH) y determinar a qué especie pertenecía el individuo. Se colocaron cámaras trampa en el Río San Pedro en Chihuahua y en el Arroyo Bamochi (ocupado por *L. longicaudis*) en Sonora en el 2015, para comparar la estructura poblacional y la ocupación en ambos lugares. Otros dos lugares fueron visitados para confirmar la presencia de las nutrias, el: Río Conchos y el Río Santa Isabel. Con base en las características del pelo (pelos primarios y secundarios de la piel del juvenil) y evidencia fotográfica de las cámaras-trampa, confirmamos que las nutrias del Río San Pedro, Río Santa Isabel y del Río Conchos pertenecen a la especie Neártica: *Lontra canadensis*. La estructura de la población en el Arroyo Bamochi y en el Río San Pedro fueron similares en ambos sitios, pero la densidad de nutrias es más alta en el Arroyo Bamochi que en el Río San Pedro, aun así, no existe diferencia significativa entre los dos sitios. Los especímenes de nutrias de la Cuenca del Río Grande han sido identificados en el pasado como *L. canadensis lataxina*, Cuvier, 1823. La distribución original de esta especie va desde el interior de los Estados Unidos, a través de la Cuenca del Río Grande y del Río Pecos, de las montañas Rocallosas hacia el sur y sureste hacia el Golfo de México. El hallazgo reportado aquí representa un reto significativo para la conservación de esta especie en México, así como es un indicador del excelente estado de conservación del río.

Key Words: Chihuahua, *Lontra canadensis,* Mexico, Otter identity, Status.

Introduction

Geographical barriers such as high mountain ranges have played a key role for the adaptation and evolution of numerous species whose populations were separated by catastrophic events, including volcanism, glaciations, and subsequent shifts in the flow direction of the major rivers. The rise of large mountain ranges resulting from plate tectonics at a continental scale has conformed impassable barriers for many species. On ecological time scales (thousands of years), these produced changes in local habitats, disruption of habitat connectivity and, over long periods of time, led to genetic differentiation, speciation and endemism. In addition, the distribution and occupancy of species are subject to selection pressures resulting from climatic gradients that affect habitat connectivity.

The high-elevation continental divide at Sierra Madre Occidental causes streams to flow in various directions to several large basins; these steep elevations are formidable geographical barriers that may be difficult for Neotropical otters to cross. This ancient steep-sloped and high-altitude mountain range rose around the Late Cretaceous (~100 mya). Some deposits point to older ages, such as tuffs (volcanic igneous rocks composed mostly of compacted volcanic ash) near Cascada de Basaseachi (Basaseachi fall), which contain lithic fragments of granitic gneiss that are 1.6 billions of years old (Housh *et al.* 2003). Glaciations also formed large barriers that restrained the connection between eastern and western basins. Eight series of glaciations from 600-12 kya (Walker *et al.* 2008), likely shaped the current distribution of the genus *Lontra* in the Americas.

Climatic factors such as precipitation and temperature regimes (significantly colder winters), coupled with the occurrence of drier conditions in the eastern basin, may also have become a major barrier preventing connectivity between suitable habitats for Neotropical otters. This is due to the high mountain ridges with steep slopes and scarcity of running fresh water in the eastern slopes, along with different vegetation assemblages (pine-oak and tropical deciduous forest on the western slope vs. pine-oak and high-altitude grasslands and arid scrubland on the eastern side).

Therefore, geographical barriers imposed by the high mountain ranges or "Sierras" of México have confined the Neotropical otter (*Lontra longicaudis*) to the large river basins in the western slopes and coastal plains, rarely reaching the rivers running across the central plateau (Guerrero *et al.* 2015; see Figure 1). Therefore, it is unlikely the presence of Neotropical otters in both slopes of the continental divide in the Sierra Madre Occidental (*i. e.*, the western slope down to the Gulf of California and the eastern slope down to the Central Plateau and Río Grande basin in northern Mexico) as suggested by Carrillo-Rubio and Lafón (2004). These authors have regarded otters found at Río San Pedro (Chihuahua) as Neotropical otters, although Polechla and Carrillo-Rubio (2009) later questioned their identity.

Nearctic otters, *Lontra canadensis lataxina* Cuvier, 1823, inhabit the basin of Río Grande that ranges from Colorado and New Mexico down to the Gulf of México (Hall 1981), these otters were declared, "apparently extirpated" (Findley *et al.* 1975; Jones and Schmitt 1997; Polechla *et al.* 2004; Polechla and Carrillo-Rubio 2009) due to hunting and habitat degradation. To counter this extirpation, 23 Nearctic otters were reintroduced to the Río Grande watershed in New Mexico in 2008 (Long 2010).

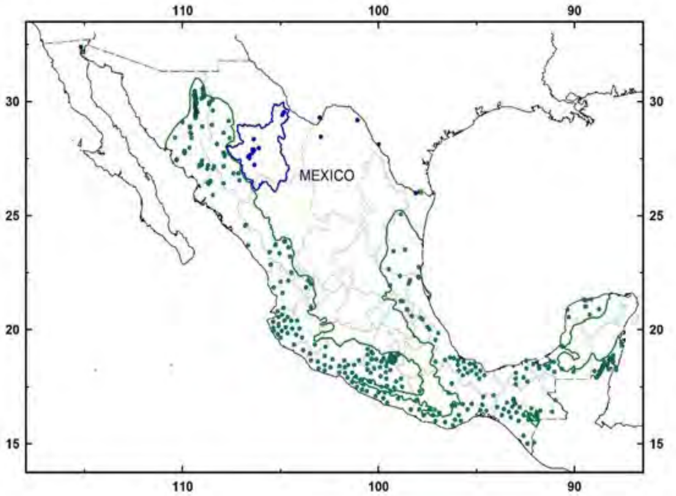

Figure 1. Current distribution of the Neotropical otter (*Lontra longicaudis*) (green dots and lines); and our records of a relict population of Nearctic otter (*Lontra canadensis*) in the Conchos basin, north-western Mexico (blue dots and blue line). Other records of *L. canadensis* in México, also in blue dots. Historic records of *L. canadensis* in green squares.

The Upper Río Conchos basin includes the Río San Pedro, Río San Lorenzo, Río Santa Isabel, Río Satevó, Río Chuviscar, Río Balleza and Río Florido, as well as other minor tributaries (such as Río Parral). This basin is located on the eastern slope of the Sierra Madre Occidental and drains into the high-altitude Central Plateau of Northern México, crossing the Chihuahuan desert towards its confluence with Río Grande to drain into the Gulf of México. There are four records of museum specimens and two recent records of this species from the 1980s in different sites along Río Grande which conforms the border between the United States and México and from affluents from México (Hall 1981; Gallo-Reynoso 1997; López-Wilchis 1998).

Based on the above logic, it is unlikely that the otter population reported here belongs to the Neotropical species. Its nearest populations are found further northwest at the Papigochi-Tutuaca basin (2,073 m, 115 km to the NW straight distance), both tributaries of Río Bavispe-Yaqui, which flows to the west/southwest through the State of Sonora and reaches the Gulf of California. West of the Río Conchos basin and across the Sierra Madre ridges is the Río Mayo basin, whose main tributaries are the Río Candameña, Río Basaseachi and Río El Durazno, which merge to form the Río Mayo, that flows to the Gulf of California. A similar situation is that of the Río Fuerte basin, which includes many tributaries such as Río Batopilas, Río Verde and Río Urique, which flow through Barrancas del Cobre (Cooper Canyon), then merge to form Río Fuerte and drain into the Gulf of California. Although, the recently released otters mentioned above (Long 2010) are not likely to have given rise to the otter population that we are reporting here, because of the long distance that separates the site of reintroduction from the area where the population we are describing inhabits and that Carrillo-Rubio and Lafón (2004) were studying before 2004. Further south of the Río Conchos basin is the Río Nazas basin (in the State of Durango), an endorheic basin that is heavily used for irrigation. It is known that its headwaters were once inhabited by otters regarded as Neotropical otters by Pohle (1920) and Gallo-Reynoso (1997), but their settings is similar to those of the Río Conchos and therefore should be occupied by *L. canadensis*.

The undetermined taxonomic identity of otters of the Río San Pedro, in the Conchos basin by Carrillo-Rubio and Lafón (2004) and the recent depiction as belonging to the Nearctic otter by Ceballos and Carrillo-Rubio (2017), based solely on camera – trap photographs of the rhinarium shape of the species, not in hard evidence, as it is to review a specimen. This situation raises questions on their conservation status along the basin, which in their middle portion has been subject to strong anthropogenic pressure over its probable historical range, particularly in aquatic habitats. Adding to this, an unconfirmed sighting of a river otter reported by Carrillo-Rubio (2002) in the lower Conchos. Later, supported with photographs of an area used by otters in 2009 and with an otter trail in 2010 (Jaen, pers. comm. to J. P. Gallo-Reynoso) in the Pegüis Canyon, near the confluence of Río Conchos with Río Grande, within an area proposed for conservation. The taxonomic status of these specimens remains unknown, although they might be Nearctic otters.

Nearctic otters currently lack protection from the Mexican authorities, since the two subspecies previously reported in Mexico, *i. e.*, *Lontra canadensis sonora* from the Colorado River and *Lontra canadensis lataxina* from the Río Grande, are regarded as extinct in México (Gallo-Reynoso and Casariego 2005). They are not listed under any protection category by wildlife authorities of México (NOM-059-ECOL-2010).

Neotropical otters are regard as 'threatened', their main threat is habitat fragmentation and pollution (Gallo-Reynoso 1989, 1997), which restricts gene flow among populations, thus increasing their risk of extinction (Hedrick 1985; Frankham *et al.* 2002). Habitat fragmentation is most likely the cause for the distribution of Nearctic otters, restricted to the tributaries of the upper Río Conchos in a relict environment. Downstream, river otters are expose to seasonal dry conditions throughout the Chihuahuan desert when runoff is minimum in spring (Hudson *et al.* 2005). Anthropogenic activities play a role as well, including water diversion with reservoirs and channels for large agricultural areas, urbanization, and removal of riparian vegetation by cattle, and water pollution by large cities and industry (Ramos-Rosas *et al.* 2012). In Mexico, all these activities are common for agricultural purposes, while water demand to fulfil the growing population needs has led to extensive construction of dams throughout the country (Sánchez and Gallo-Reynoso 2007). Moreover, the upper Río Conchos probably represents the southernmost limit of the distribution range of the Nearctic otter, which could further compromise the genetic connectivity between otter populations, given that the habitat in this area tends to be more fragmented and of marginal quality (Gaston 2009; Sexton *et al.* 2009).

Further studies will contribute to identify habitat features associated with species occupation, as well as geographic or climatic barriers that restrain gene flow across basins. These will provide valuable information to assess habitat connectivity, a central issue when establishing corridors to ensure the long-term conservation of the species (Pearse and Crandall 2004; Cushman *et al.* 2006; Latch *et al.* 2008). Research on the association between river otters and the habitats in which they live is key, since otters are closely associated with their habitat, and therefore are considered bio-indicators of ecosystem health (Kruuk 2006; Waldemarin and Alvares 2008; Guerrero *et al.* 2015; Rheingantz and Trinca 2015).

In the present study, we used habitat and population approaches aimed at 1) identifying the species that inhabits the Río Conchos basin; 2) assessing the status and population structure of the species inhabiting the San Pedro, Conchos and Santa Isabel rivers; 3) proposing conservation measures for this species and its habitat based on our findings.

Methods

Study Area and Sampling. The Río San Pedro (1,467 m) was survey in November 2015, by walking along riverbanks to record the presence of otters (tracks, spraints, dens, food remains) in the middle and lower portions of the basin. We observed an adult individual at a small creek that flows into Río San Pedro. We collected 14 spraints and set-up four camera traps (Bushnell HD 12 megapixels, with an SD card of 32 gigabytes) facing their latrines. In December 2015 we retrieved the cameras from Río San Pedro and explored Río Conchos near Nonoava, 40 km to the southwest, above the Francisco I. Madero reservoir and the confluence of the San Pedro and Conchos rivers. There we obtained spraints and observed several otter tracks along 5 km of the stream. In addition, the tanned fur of a juvenile otter was given to us and is now in the reference collection of vertebrates at Laboratorio de Ecofisiología, CIAD-Guaymas. In June 2017, we surveyed the middle portion of Río Santa Isabel and found tracks, spraints, food remains and latrines of river otters. No live wild animals were handled in the present study.

The total area monitored spanned along 20 km of river, divided into three portions: two areas in Río San Pedro, each measuring 5 km in length, and separated by a section of 10 km. In both areas of Río San Pedro, we recorded habitat features that are key for otters, such as vegetation cover, presence of pools, fish availability, and rocky areas used for latrines where otter spraints are dump. The third area was located at Río Conchos, and the fourth area was located at Río Santa Isabel, in these two rivers, 5 km of riverbanks were surveyed.

As control, we survey Arroyo Bamochi (1,187 m) in the Bavispe-Yaqui basin, State of Sonora, an area known to be occupied by Neotropical otters (Gallo-Reynoso *et al.* 2016); the same methodology was used to obtain otter records.

Hair examination. Primary (PH) and secondary (SH) hairs from the fur of the juvenile specimen were compared following the methodology of Kuhn and Meyer (2010), with similar hairs from two furs of adult *Lontra longicaudis* (from Río Bavispe in Sonora, and from San Miguel Pochutla, Oaxaca; both furs are deposited in the reference collection of vertebrates at Laboratorio de Ecofisiología, CIAD-Guaymas). PH were obtained from a 1-cm^2 fur section, cut from the right flank; hair length was measured to differentiate PH and SH from the three individuals. All hair samples were observed under an Olympus BX41 XploRA Raman technology microscope at 10X and 40X to differentiate hair medulla and scales of the three specimens.

Habitat. To evaluate the interaction between individuals, and habitat characteristics in the study area, we used a Garmin GPS (GPSmap 78s) to generate the track of the areas surveyed; tracks were upload as a Kml files in Google Earth to produce maps of the distance of the otter habitat surveys, as well as the river elevation profile (slope). The aim was to map the distribution of otters in the upper Río Conchos-San Pedro basin, and Río Bavispe-Yaqui basin, based on geographical features such as elevation and tributary network, since such habitat characteristics are known to affect abundance, dispersal and/or occupancy by otters. Data on river basins were obtained from Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Mexico's National Commission for the Knowledge and Use of Biodiversity, CONABIO).

Camera trap survey and otter behavior. Camera traps (four Bushnell Trophy Cam XLT© IR and Trophy Cam HD© IR, all of 5-8 megapixels with a SD card of 32 gigabytes) were set up to record photographs and videos. Video length was 20 s in all cases, with a separation of 1 min between capture events. In cameras taking still photographs, three photos were taken per event, separated by 1 min between events. Total effort accounted for 100 trap-days. These photographs and videos were used to estimate the otter population structure. By identification of different otter age/sex categories using the latrines (observing their marking behavior and genitalia, we were able to identify males, subadult male, adult female, juvenile, lone individuals of either sex, mother-offspring groups and unidentified individuals), and frequency (number of days) and time (hours) of latrine use in the area. Cameras also collected data on ambient temperature, moon phase and other habitat characteristics, such as changes in flow, all of which might influence the presence of otters at latrines/camera –trap sites (Table 1). Cameras also recorded environmental sounds and vocalizations, such as barks, whistles, grunts, etc., from otters and other species in the area, including birds. Camera traps were tied to tree trunks, positioned near or over otter latrines at 2.5 to 4 m high to avoid flash floods.

We deployed four similar camera traps at Arroyo Bamochi in the Río Bavispe-Yaqui basin (Sonora), with the same methodology to record photographs and videos of Neotropical otters, to ascertain the identity and differences of the two otter populations. In both rivers, cameras positioned at 1.25 km from each other, covering an area of 5 km. Left for a month to record photographs and videos.

Table 1. Location of camera-traps used to record the presence of Nearctic (Río San Pedro, November - December 2015) and Neotropical (Arroyo Bamochi September – October 2015) otters. All cameras were placed on tree trunks at 2.5 to 4 m height.

	Río San Pedro		Arroyo Bamochi	
Camera	Latitude	Longitude	Latitude	Longitude
1	27.86036	-106.34138	30.14022	-109.03294
2	27.86139	-106.34341	30.14211	-109.03019
3	27.86269	-106.34850	30.14386	-109.03038
4	27.86292	-106.34841	30.14536	-109.03202

Relative abundance was estimated by dividing the number of otters recorded by the area covered by all cameras (5 km), to assess the total number of individuals/km.

Relationship between ambient and water temperature was obtained with the frequency of otter records at different times of the day, and the ambient temperature recorded by the camera. Water temperature were obtained by measuring it on the spot at different hours during day light and with records from the nearest agricultural measuring station.

Prey availability. Fish were filmed underwater in large and deep pools in both locations with a GoPro Hero2© camera to estimate prey availability. The camera tied to a 1.5 m pole and moved slowly sideways in a vertical position while filming. Several fish species were filmed and posteriorly identified, at least four large key species in each river, all being present in otter spraints collected in both localities. A Río San Pedro's large pool was measured, length, wide and depth (10 m wide by 30 m long, by 2.5 m deep), containing approximately 96,250 m^3. The pool at Arroyo Bamochi (7 m wide by 25 m long, by 1.70 m deep), equivalent to 65,391 m^3. Fish length and weight were also measured from fishes captured in the localities and compared to the mean sizes of the species reported in the literature, or in FishBase (www.fishbase.org); from these, an estimated mass (kg) of prey available for otters were obtained for each pool. Identification of fish prey were done following Page and Burr (1991), Lima *et al.* (2003), Trewavas (1982) and De La Maza-Benignos (2009).

Results

Otter specimen collected. In 2013, we were informed of a juvenile otter from Río San Pedro that was injured by peasants near its den, taken alive and kept in captivity at the municipality of Belisario Dominguez (Chihuahua), this otter later died in captivity. The local authorities contacted us (Nuñez, V., and J. P. Gallo-Reynoso) and sent photographs of the otter for identification; the specimen possessed characteristics that were clearly different from *Lontra longicaudis*. Based on cephalic traits (lateral view), the specimen otter profile corresponds to the Nearctic otter: the head and nose are straighter than in the Neotropical otter, in which both structures are more concave (Figure 2). The upper lips were more inbound to the mouth than in Neotropical otters, a characteristic of Nearctic otters. The coloration of the individual was paler than in *L. longicaudis*. In Decem-

Figure 2. Comparative morphology and specific rhinarium form of Nearctic otters from Río San Pedro, Chihuahua, México, with a captive Nearctic otter at The Arizona Sonora Desert Museum (Tucson AZ). 1) Lateral view and coloration of the juvenile from Río San Pedro (V. Nuñez 2013). 2) Lateral view and coloration of an adult Nearctic otter (scratching its head sideways) at the Arizona Sonora Desert Museum (I. Barba-Acuña 2016). 3) Rhinarium of the Río San Pedro otter (J. P. Gallo-Reynoso, Bushnell Trophy Cam December. 2015). 4) Rhinarium of a Nearctic otter at the Arizona Sonora Desert Museum (I. Barba-Acuña. 2016).

ber 2015, the fur of that juvenile was donated to us; at a first glance, the rhinarium resembled that of a Neotropical otter, but at close examination, and removing the stiffness of the nose (due to the drying and subsequent tanning process), corresponded to *Lontra canadensis*. To the touch, the fur was fluffier than in Neotropical otters. The soles of the individual had hairs between the pads, which is present in Nearctic otters, and a feature absent in Neotropical otters, whose sole is completely bare of hair.

Hair differences. Guard hairs or PH on the flank and dorsum of the juvenile otter were 20 to 24 mm long, and the underfur or SH were 12 to 18 mm long. According to Kuhn and Meyer (2010), in *L. canadensis* mean PH length is 24 ± 0.9 mm (individual variation from 17 to 29 mm), and mean SH length is 15 ± 1.3 (individual variation from 12 to 20 mm).

While the two *L. longicaudis* furs examined had a PH length of 15 and 16 mm, which SH measured 5 and 7 mm showing some variation between localities being shorter in the more tropical settings (fur from Oaxaca) than in the northern one (fur from Sonora). According to Kuhn and Meyer (2010), in *L. longicaudis* mean PH length is 16 ± 1.5 mm (individual variation from 12 to 22 mm) and mean SH length is 8 ± 0.6 (individual variation from 5 to 10 mm); therefore, based in the above fur differences, the juvenile otter fur from Río San Pedro corresponds to *L. canadensis*.

Primary hairs from the juvenile, observed under microscope at 40X are similar to Nearctic otter PHs as described at *pars intermedia*, hair cuticle scales are "narrow diamond petal", differing from Neotropical otter *pars intermedia* hair cuticle scales that are "diamond petal" (Figure 3).

We observed an adult individual downstream of the Arbolito creek dam, which is a tributary to San Pedro. Its body movement was consistent with a Nearctic otter, later observed in videos of several individuals. Images obtained from the videos show different individuals with the typical rhinarium of Nearctic otters; however, the quality of videos is not sufficiently clear to make an in-depth differentiation; in addition, individuals do not always face the camera. The body shape of adult males filmed is sturdier (rounded and shorter) relative to Neotropical otters, which are longer and slender. Adult individuals from Río San Pedro were compared to an adult individual of *L. canadensis* filmed by us at the Arizona Sonora Desert Museum, Tucson, Arizona (April 2016); their movements, overall body shape, fur color, tail length and broad base of tail are all similar (Figures 2 and 6).

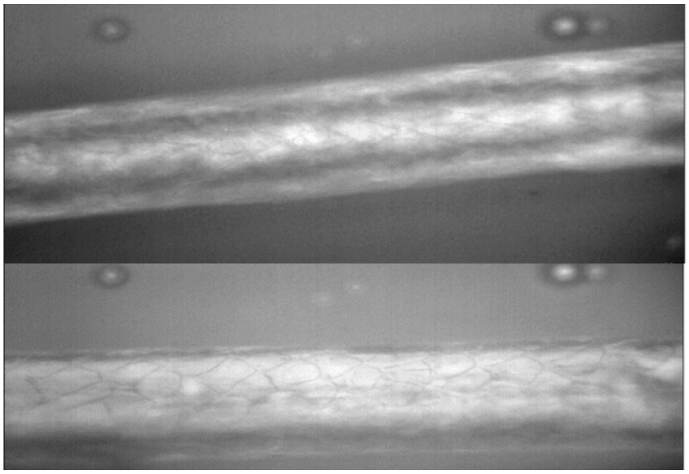

Figure 3. *Pars intermedia* primary hair scales of Nearctic and Neotropical otters as shown under 40X Raman Microscope. Shape of cuticle scales of *L. canadensis* described as "narrow diamond petal" (upper photograph), compared to the shape of cuticle scales of *L. longicaudis* as "diamond petal" (lower photograph) *sensu* Kuhn and Meyer (2010). Hairs of the Nearctic otter are thicker than hairs of the Neotropical otter.

Tracks of the individuals studied at Río San Pedro are similar to tracks of the Nearctic otter and are different from those of *L. longicaudis*. The posterior paws of the Nearctic otter typically steps on the print of the forepaw, producing distinctive tracks that made possible to differentiate between both species. In Neotropical otters, the posterior paw rarely steps on the print of the forepaw when this happens, the posterior feet step sideways of the forepaw print, sometimes stepping over a little, usually by the external side.

Habitat. The sites surveyed at Río San Pedro, Río Santa Isabel and a portion of the Río Conchos comprised a total linear distance of 20 km of continuous otter habitat, including deep pools, rapids, meanders, shallow areas, boulders, and rocky cliffs. Riverbank areas showed a low diversity of trees (*Salix* sp., *Prosopis* sp., *Populus* sp., *Quercus* spp., *Juniperus* sp., *Fraxinus* sp.), while the herb stratum was dominated by batemote or seep willow (*Baccharis salicifolia*) and grass (*Bouteloua* sp.). Otters preferred areas protected by willows than other trees at Río San Pedro, Conchos and Santa Isabel.

The site monitored at Arroyo Bamochi also comprised a linear distance of 20 km of continuous otter habitat, including deep pools, shallow areas, two freshwater springs, boulders and rocky cliffs. Riverbanks were covered with a large diversity of trees (*Acer grandidentatum*, *Alnus oblongifolia*, *Fraxinus velutina*, *Junglans mayor*, *Salix goddingii*, *Prosopis* sp., *Populus fremonti, Populus brandegeei, Platanus wrightii,* *Juniperus deppeana* and *Quercus* spp.), and the herb stratum was composed by batemote or seep willow (*B. salicifolia*), jecota (*Hymenocclea monogyra*), cardo (*Argemone mexicana*), sedge (*Carex* sp.), and others. Due to extended protection by trees, otters did not show preference of areas covered by a particular species of tree.

Camera traps. The total effort was 100 trap-days (no photographs, 2,150 videos) at Río San Pedro, and 136 trap-days (983 photographs, 82 videos) at Arroyo Bamochi, Sonora. We obtained a total of 86 high-quality otter individual identifications at Río San Pedro and 30 at Arroyo Bamochi, 116 positive individual identifications (0.49 identifications/day). The total number of otters with positive individual identifications in the area covered by cameras were nine at Río San Pedro (two large males, two adult females, one juvenile female, one juvenile male, one undetermined-sex juvenile, a large cub and an unidentified individual). There were 11 individuals identified at Arroyo Bamochi (two large males, a female with a large cub, a female with two smaller cubs, a solitaire female, two juvenile males and an unidentified individual). There is no signficative difference (t-test, t = 1.309307, *d. f.* = 9, *P* = 0.265384, *n* = 10) in the number of otters in the two similar area sites. The relative abundance of otters was 1.8 otters/km at San Pedro and 2.2 otters/km at Bamochi. The difference in relative abundance between the two streams is not significant, despite the differences observed in the local habitat, evidenced by the abundance and diversity of riparian vegetation as described above. An important difference between these two watercourses is the amount of pools in the habitat and the available running water, being larger at Río San Pedro than at Arroyo Bamochi.

Associations between trees, secondary vegetation, rocky cliffs and access to large pools where the most common sites where the two otter populations have their dens and/or latrines. *Otter Behavior.* Camera-trap videos were useful to compare the behaviour regarding visits to latrines, vocalizations and general movements of otters while sniffing spraints, dropping and urine marking of latrines. Data on moon phase, ambient temperature and hour of the day serve to evaluate the response of otters to these environmental features. Nearctic otters were more visible during daylight hours than Neotropical otters, which preferred crepuscular and night hours. *Relationship with water temperature.* Río San Pedro is at 1,467 m, while Arroyo Bamochi at 1,187 m, a differential altitude of 280 m. Despite of this, it is notorious that ambient and water temperature behaves very different in each river. The ambient temperature is 8 °C higher at Arroyo Bamochi (range: 16.8 to 24.7), than at Río San Pedro (range: 3 to 19 °C), water temperature behaves similar, with 8 °C higher at Arroyo Bamochi (range: 9.1 to 20.3 °C) than at Río San Pedro (range: 8.8 to 13.3 °C). These differences in temperature might explain why the frequency of visitation of camera – traps – latrine combination is different in both species. Otters at Río San Pedro are visible in the river at almost any hour of the day, avoiding only the warmest hours, while Neotropical otters, preferred to be crepuscular and in the night than in the middle of the day, which is probably very hot for them. This correlates with the type of PH and SH hair, and its size, being longer where the water is significantly colder, and smaller where water is warm. Therefore, temperatures (of water and ambient) might also be an important barrier for the distribution of both species (Figures 4A and 4B).

Prey Availability. Fish species observed in the pool at Río San Pedro, near camera traps were: Largemouth bass (*Micropterus salmoides*), 25 ind. (~30 cm mean length and ~2 kg mean weight = 50 kg). Río Conchos matalote (*Catostomus bernardini*), 52 ind. (~40 cm mean length and ~2 kg mean weight = 104 kg). Sardinita (*Astyanax mexicanus*), 25 ind. (~10 cm mean length and ~75 g mean weight = 1.9 kg). Introduced tilapia (*Oreochromis mossambicus*), 36 ind. (~18 mean length cm and ~1 kg mean weight = 36 kg), as well as smaller unidentified fish. Fish availability in this pool as otter prey was estimated at 192 kg.

Fish species observed at the pool of Arroyo Bamochi, near camera traps were: Largemouth bass (*M. salmoides*); 13 ind. (~30 cm mean length and ~2 kg mean weight = 26 kg). Río Yaqui matalote (*Catostomus yaqui*), 30 ind. (~40 cm mean length and ~2 kg mean weight = 60 kg). Introduced tilapia (*O. mossambicus*), 26 ind. (~18 cm mean length and ~1kg mean weight = 26 kg), and smaller unidentified fish. Total fish estimated availability in the pool was 112 kg.

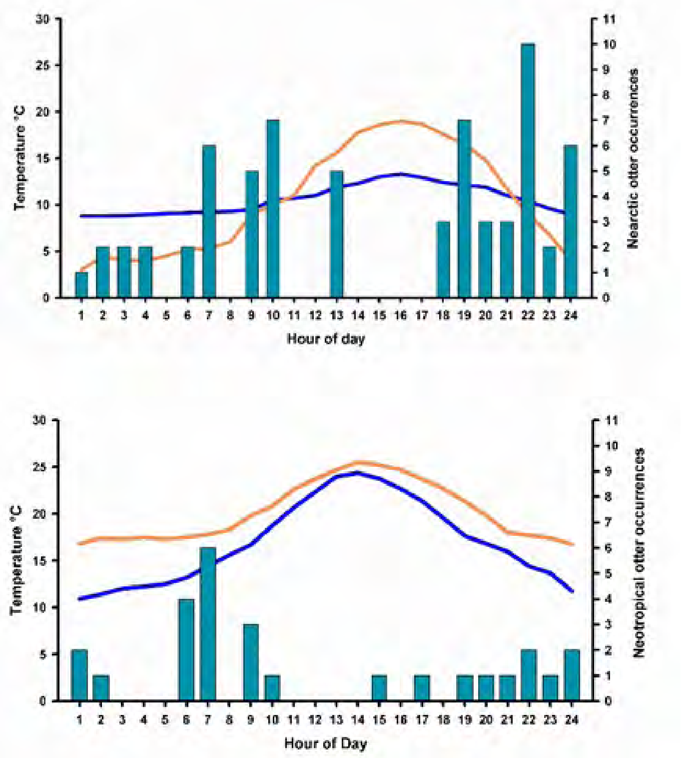

Figure 4. A and 4 B. Differences in observation of Nearctic and Neotropical otters related to ambient and water temperature. Blue line represents water temperature. Orange line represents ambient temperature. Bars are the number of occurrences of otters in one latrine over a 30-day period.

Discussion

Otter species Determination. The different sources of evidence, such as habitat connectivity, photographic confirmation of external morphology and rhinarium shape, as well as hair and fur characteristics of the specimens examined, led us to conclude, that the otter species inhabiting the Río San Pedro, Río Conchos and Río Santa Isabel basins in Central Chihuahua, is *Lontra canadensis*, the Nearctic otter, representing a relict population that has survived the isolation from otters inhabiting Río Grande (Figures 3 and 4). It is notable that the hair coloration and thickness are also different in the specimens analysed, being tan-coloured in the juvenile *L. canadensis* and copper-coloured in the two adult *L. longicaudis,* thicker in *L. canadensis* and slender in *L. longicaudis.* Based on these traits, the fur of the juvenile otter from Río San Pedro correspond to the Nearctic otter.

Additional morphological features when comparing the juvenile specimen vs. individuals of *L. longicaudis* of similar size (Gallo-Reynoso *et al.* 2013) are the following. The tail of the juvenile specimen measures 37 cm, which is shorter than in similar sized specimen of *L. longicaudis*, which measures 42.7 cm. However, the base of the tail is broader in the juvenile specimen than in *L. longicaudis*. In general, the fur is paler in the dorsum (brown-ash), which contrasts with the dark brown color of the two *L. longicaudis* specimens examined.

If the species inhabiting the San Pedro, Santa Isabel and Conchos rivers belonged to the Neotropical otter, there should exist an extensive habitat connectivity along a conspicuous corridor, where the gene flow of the Neotropical otter would have been able to cross the eastern slopes of the Sierra Madre towards the Central Plateau, and across the Chihuahuan Desert.

If such connection ever existed after the past glaciation period, the most likely corridor was the Río Papigochi-Tutuaca to the northwest where we have records of the Neotropical otter (2,079 m), which is the closer one to the Río San Pedro basin at higher elevations. The Río Papigochi-Tutuaca basin serves as a corridor that connects habitats from Chihuahua down to the west reaching as far as Sonora; it is a high-altitude oak-pine grassland habitat, which turns into a desert scrub habitat in Sonora (Gallo-Reynoso *et al.* 2016). The Río San Pedro (1,467 m) is located to the southeast, 116 km away (straight line) from Río Papigochi-Tutuaca. Río Santa Isabel (1,548 m) to the east at 109 km away (straight line) from Río Papigochi-Tutuaca. A large mountain range of 2,350 m separates these basins and the elevation differential is of 569 m; therefore, we can conclude that there is no habitat connectivity. To the south, Río San Pedro and Río Conchos headwaters are located at around 2,100 m, 400 m lower than the more than 2,700 m peaks of the Sierra Madre ridges that divide the Río Conchos basin from the Río Mayo and Río Fuerte basins to the west, inhabited by Neotropical otters. There is a null habitat connectivity of the Conchos basin with Río Bavispe (Papigochi-Tutuaca), Río Mayo and Río Fuerte basins.

In terms of the effect of habitat connectivity on the distribution of otters, elevation and slope are the most important geographic characteristics that separates the two species, implying a reduction in gene flow as elevation and slope increases (Guerrero *et al.* 2015). These results agree with previous findings by Guerrero *et al.* (2015) who used a landscape-genetic approach to examine how the ridges that delineate basins affect the gene flow, and therefore the distribution, of Neotropical otters in Mexico. These authors found a positive correlation between the genetic distance of individuals in different basins and the mean slope separating the basins, showing that steep elevations and dry land restrain otter dispersal. In other studies of habitat suitability, slope and elevation were found to affect otter dispersal (Loy *et al.* 2009; Carranza *et al.* 2011).

In otter species, habitat connectivity is usually assessed by differentiating between longitudinal and lateral connectivity. Longitudinal connectivity refers to the ability of otters to move within a river basin; lateral connectivity, to dispersal movements across basins, resulting in gene flow among populations inhabiting adjacent basins (Gallo-Reynoso 1989; Carranza *et al.* 2011; Van Looy *et al.* 2014; Guerrero *et al.* 2015). Natural boundaries among watersheds, such as ridges, could restrain lateral connectivity; this seems to be the case for this otter population, as high elevations and steep slopes were found to restrict the distribution of Neotropical otters as shown by Guerrero *et al.* (2015).

Conservation Implications. It is general knowledge that well-connected waterways and low levels of human disturbance are key for the occurrence and survival of Neotropical and Eurasian otters (Gallo-Reynoso 1997; Kruuk 2006; Santiago-Plata 2013); accordingly, we assumed that urban and agricultural land would have a detrimental effect on habitat connectivity for Nearctic otters. However, Eurasian and Neotropical otters tolerate heavy human disturbance, as long as there is sufficient prey availability (Gallo-Reynoso 1997; Lariviere 1999; Kruuk 2006; Sales-Luís *et al.* 2009; Reid *et al.* 2013). In this study, we incorporated prey availability as a predictor of habitat stability and use. In studies addressing habitat suitability for both Eurasian and Neotropical otters, riparian vegetation density and riverbank slope have shown to be key drivers for otter habitat connectivity (Jeffress *et al.* 2011; Pardini and Trajano 1999; Loy *et al.* 2009; Santiago-Plata 2013).

Our results show areas with favourable habitat characteristics and large prey availability at lower Río San Pedro, middle Río Santa Isabel and upper Río Conchos, and point to the existence of three potential areas that are suitable for the distribution of the Nearctic otters. However, sampling efforts should increase to unveil additional areas where favourable conditions in terms of habitat connectivity and prey availability are found. Although topographic features (*i. e.,* steep slopes and high elevations) may serve as natural limits between watersheds in the Río Conchos basin, in this study these were not found to restrain otter distribution within the basin. In this regard, a good starting point for identifying management units would be to select basins as sampling units and use non-invasive methods, such as latrine sites coupled with camera traps, to continue the long-term monitoring and characterization of otter populations.

In addition, anthropogenic disturbances affecting river-bed configuration could further hinder connectivity. In this regard, it has been proposed that damming could disrupt the connectivity of otter populations by imposing barriers to dispersal (Mason 1995; Gallo-Reynoso 1997; Pedroso and Santos-Reis 2009). Consequently, we propose that conservation corridors for the Nearctic otter be establish in the Upper Río Conchos basin, where adjacent tributaries are delimited by low elevations and slopes, therefore, conservation corridors interconnecting these three tributaries (San Pedro, Santa Isabel and Conchos) upstream of the dams should be established to guarantee habitat connectivity and longitudinal gene flow. There should not be built new infrastructure such as dams and open mines within their riparian zone that might have significant impacts on otter populations. The latter could prove especially challenging, as three high-capacity dams (*i. e.,* higher than 50 m) were built some time ago along the Conchos' basin. Río Satevó and Río Santa Isabel converge before joining the Río San Pedro, their waters are trapped by the Francisco I. Madero dam. South from this, the Boquillas Dam encloses the Río Conchos waters, downriver the Conchos flow joins the Río Florido and they now flow to the confluence with the Río San Pedro (downriver of the Francisco I. Madero Dam), after this confluence, the Río Conchos is confined again by El Granero Dam. In all this area of the middle Conchos Basin, water is divert to irrigate important agricultural areas. There are no confirmed records (historical or recent) of otters in this area, and therefore there is no corridor across the middle to the lower Conchos Basin through which this otter population could maintain genetic connectivity with this major area of Río Grande basin in northern México and southern U.S. From the continental divide in the Sierra Madre Occidental eastern slope, down to the Gulf of Mexico.

The designation of conservation corridors for these otters will be a key factor (Frankham *et al.* 2002) to prevent the loss of genetic diversity, maintain the evolutionary potential, and protect their population. We consider that the upper Río Conchos basin could be a suitable conservation corridor, not only because it may facilitate gene flow across the different interconnecting tributaries (San Pedro and Santa Isabel tributaries), but also because of its potential role to connect the otter populations inhabiting Río Grande and the Gulf of México. Also, because these Nearctic otters have probably been distributed throughout the Sierra Madre eastern slope in the Río Conchos basin at least since the last glaciation (20 to 12 kya).

A major potential corridor can be delimited (Figure 5) along the Río Grande basin at the Mexico-U.S. border and the state limits between New Mexico and Texas. However, the terrain is largely mountainous due to the Sierra Madre Occidental that becomes the Rocky Mountains to the north; this corridor is restricted to a narrow strip of river running from southwestern Chihuahua to the Río Grande. Nevertheless, it is likely key for maintaining the connectivity between the Rocky Mountains and the Sierra Madre Occidental, and, is the only connection with otter populations that inhabit the Río Conchos basin. Although there are no studies on potential corridors for the Neotropical otter in Mexico, a contemporary study addressed the distribution of the jaguar (*Panthera onca*) in Mexico, and showed that the southern Pacific coastal plains function as a key corridor for this species (Rabinowitz and Zeller 2010). These authors stressed that the limited range of the jaguar is a major concern, and that the jaguar population in the area is affected by human activities. In the case of both species of river otters in Mexico, no study has identified corridors that should be preserved for their survival; the only reference are the proposals of Guerrero-Flores *et al.* (2015) and the one presented here.

The climate in northern México is drier, with extreme temperatures than in western, eastern and southern Mexico, which is mostly humid, subtropical and tropical. The otter populations studied here have prevailed in potentially most extreme and fragmented environments across the species range, which could further restrain the genetic connectivity with northern Nearctic otter populations; the last record of Nearctic otter in the Río Grande is that of Polechla *et al.* (2004). Even though, 23 Nearctic otters were reintroduced to the Río Grande basin in New Mexico (Long 2010), with an unknown outcome in terms of the future genetic composition. Nonetheless, within this area there is a potential corridor connecting the San Pedro, Santa Isabel and Conchos populations with populations living further to the east. The corridor follows the main course of

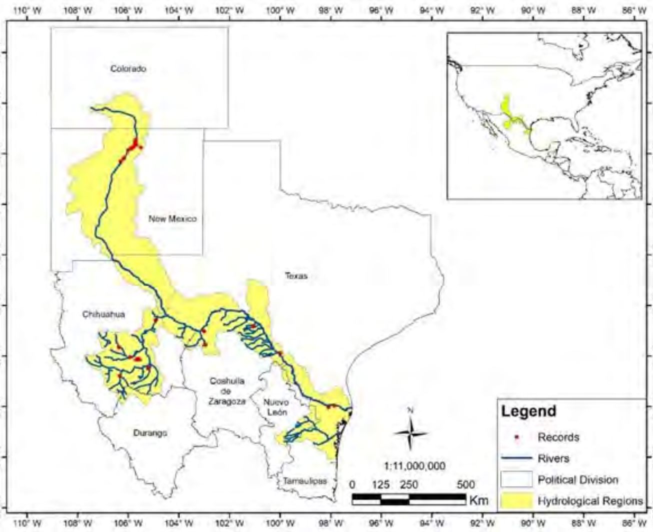

Figure 5. Distribution of the Nearctic otter at the Río Grande and Río Conchos basins in northwestern United States and northern Mexico. Red dots are our records of the species at Río San Pedro, Río Conchos and other records from Río Grande (Gallo-Reynoso 1997; López-Vilchis 1998). Red dots in the upper basin of the Río Grande are recent sightings of reintroduced Nearctic otters (Long, 2010). The area in yellow is a corridor proposed for the conservation of Nearctic otters between Mexico and the U.S.

the Río Grande, highlighting this as a key route to maintain the connectivity with Nearctic otters of New Mexico to the northwest, and of Texas to the east. However, the limited amount of surface water in the San Pedro, Santa Isabel and Conchos rivers, and the fact that natural watercourses are constantly altered to irrigate agricultural lands, used for cattle growing and with the presence of extensive mining operations in this region, are resulting in a long-lasting disruption to river ecosystems (Gallo-Reynoso 1997; Gómez-Álvarez *et al.* 2011). There are other potential conservation corridors within the Nearctic otter range; the challenge will be to control the ever-growing anthropogenic impact within the Conchos basin.

Future directions in conservation. The International Union for Conservation of Nature (IUCN) classifies the Nearctic otter as 'least concern', with a stable population (Serfass *et al.* 2015). Nevertheless, as the relict population studied here is isolated, it must be considered as "Threatened" in México by the IUCN. It is imperative to conduct research on landscape genetics (Guerrero *et al.* 2015) to investigate the distribution range of the species, biogeographic barriers, habitat connectivity, otter populations, habitat relationship and impact by anthropogenic uses and barriers (such as dams) on gene flow. Therefore, allowing the identification of key areas for conservation in the upper Río Conchos basin, including the Río San Pedro and Río Santa Isabel where local populations, well preserved habitats with good relative abundance and large prey availability are now known (Carrillo-Rubio and Lafón 2004; Gallo-Reynoso *et al.* 2016; Ceballos and Carrillo-Rubio 2017). Based on our findings, we hereby propose to classify the population of Nearctic otters of the Río Conchos as an extant and relict population by the Mexican Wildlife and Conservation authorities due to its reduced and the strong human pressure throughout its downstream habitat.

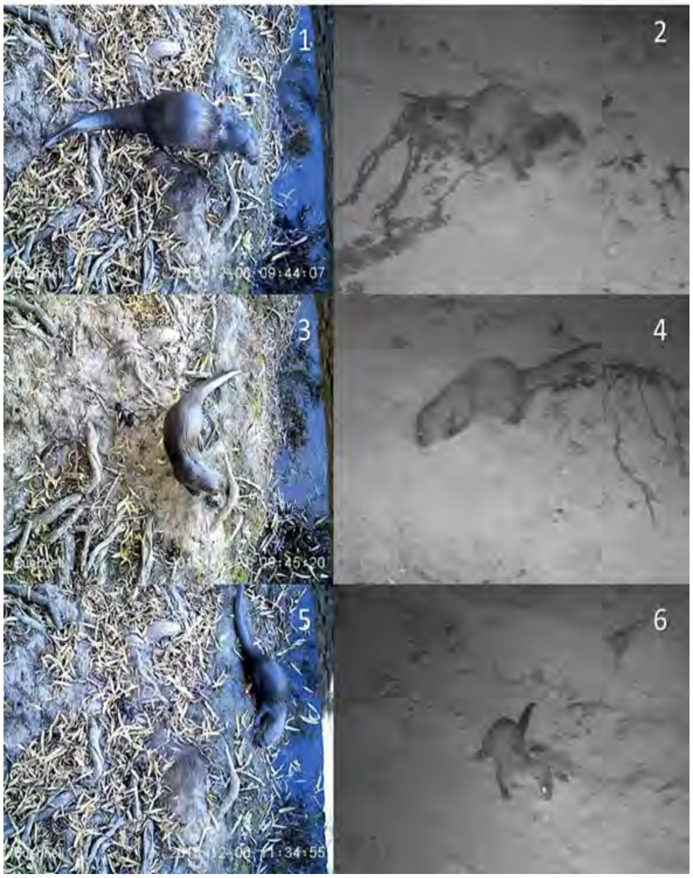

Figure 6. Comparative morphology between sexes of the same species and between both species of the Nearctic from Río San Pedro (Chihuahua, Conchos Basin), and Neotropical otters from Arroyo Bamochi (Sonora, Bavispe Basin). Nearctic otters are more active during daylight hours than Neotropical otters, which are active mainly at crepuscular and night hours. 1) Male of Nearctic otter. Río San Pedro, Chihuahua. 2) Male of Neotropical otter marking with urine. Arroyo Bamochi, Sonora. 3) Female of a Nearctic otter at Río San Pedro. 4) Female of Neotropical otter at Arroyo Bamochi, Sonora. 5) Juvenile of a Nearctic otter at Río San Pedro. 6) Juvenile of Neotropical otter at Arroyo Bamochi, Sonora. All photographs taken with Bushnell Trophy Cam.

Genetic analyses of the spraints collected are underway to confirm these findings. Immediate conservation measures are needed, and have been forwarded to the wildlife authorities in Mexico, Dirección General de Vida Silvestre (General Direction for Wildlife) and Comisión Nacional de Áreas Naturales Protegidas (National Commission of Protected Natural Areas), as the population described here is, to date, the only well-preserved population of this species reported in Mexico.

In terms of further avenues for research, there is a great need for obtaining updated information on the population size of this otter species in Mexico. There is virtually no information on this subject, as a single countrywide survey for the three otter species in México was conducted more than 20 years ago (Gallo-Reynoso 1997). Future studies could take advantage of capture–recapture analyses based on non-invasive genetic data, in order to gain an insight into population sizes (Marucco *et al.* 2010; Trinca *et al.* 2013). These efforts could be replicated spatially and temporally for the long-term monitoring of Nearctic otter populations in Mexico. Finally, there is a need to evaluate the role of this otter as an umbrella species for the lotic ecosystems and/or as an indicator species of watershed conservation status.

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Literature cited

Carranza, M. L., E. D'Alessandro, S. Saura, and A. Loy. 2011. Connectivity providers for semi-aquatic vertebrates: the case of the endangered otter in Italy. Landscape Ecology 27:281–

290.

Carrillo-Rubio, E. 2002. Uso y modelación del hábitat de la nutria de río (*Lontra longicaudis annectens*) en el bajo Río San Pedro, Chihuahua. M. Sc. Thesis. Universidad Autónoma de Chihuahua. Chihuahua, México.

Carrillo-Rubio, E. and A. Lafón. 2004. Neotropical river otter micro-habitat preference in west-central Chihuahua, Mexico. IUCN Otter Specialists Group 21:10-15.

Ceballos, G. and E. Carrillo-Rubio. 2017. Redescubrimiento y estado de conservación de la nutria de río del norte (*Lontra canadensis*) en México. Revista Mexicana de Mastozoología Nueva época 7:1-12.

CONABIO (http://www.conabio.gob.mx/informacion/metadata/gis/).

Cushman, S. A., K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. American Naturalist 168:486-499.

De la Maza Benignos, M. 2009. Los Peces del Río Conchos. Alianza WWF - FGRA y Gobierno del Estado de Chihuahua. Chihuahua, México.

Findley, J. S., A. H. Harris, D. E. Wilson, and C. Jones. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque, U.S.A.

Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. Introduction to conservation genetics Cambridge University Press. Cambridge, U.K.

Gallo-Reynoso, J. P. 1989. Distribución y estado actual de la nutria o perro de agua (*Lutra longicaudis annectens* Major, 1897) en la Sierra Madre del Sur, México. M. Sc. Thesis, Universidad Nacional Autónoma de México. Ciudad de México, México.

Gallo-Reynoso, J. P. 1997. Situación y Distribución de las nutrias en México, con énfasis en *Lontra longicaudis annectens* Major, 1897. Revista Mexicana de Mastozoología 2:10–32.

Gallo-Reynoso, J. P. and M. A. Casariego. 2005. Nutria de río, perro de agua. Pp. 374-376 *in* Los Mamíferos Silvestres de México (Ceballos G., and G. Oliva, eds.). Comisión Nacional para el Conocimiento y uso de la Biodiversidad, Fondo de Cultura Económica, Ciudad de México, México.

Gallo-Reynoso, J. P., S. Macías-Sánchez, E. Arellano-Nicolás, and A. González-Romero. 2013. Length, body mass, and growth of the Neotropical otter (*Lontra longicaudis annectens*) in Mexico. Therya 4:219-230.

Gallo-Reynoso, J. P., S. Macías-Sánchez, L. Armenta- Méndez, I. D. Barba-Acuña, V. A. Nuñez-Ramos, A. Loya Jaquez, G. Ponce-García, and A. Gardea-Béjar. 2016. Letrinas de nutrias y cámaras trampa ¿qué nos dicen? Otter latrines and camera traps, what do they tell us? In: Memorias XIII Congreso Nacional de Mastozoología. Asociación Mexicana de Mastozoología. Tuxtla Gutiérrez, Chiapas. Available at jpgallo@ciad.mx

Gaston, K. J. 2009. Geographic range limits: achieving synthesis. Proceedings. Biological Sciences / The Royal Society 276:1395–406.

Gómez-Álvarez, A., J. L. Valenzuela-García, D., Meza-Figueroa, M., de la O-Villanueva, J. Ramírez-Hernández, J. Armendáriz-Tapia, and E. Pérez-Segura. 2011. Impact of mining activities on sediments in a semi-arid environment: San Pedro River, Sonora, Mexico. Applied Geochemistry 26:2101–2112.

Guerrero, J., J. P. Gallo-Reynoso, and R. Biek. 2015. Mitochondrial DNA diversity, genetic structure, and demographic history of the Neotropical Otter (*Lontra longicaudis*) in Mexico. *Journal of Mammalogy* 96:1162-1173.

Hall, E. R. 1981. The mammals of North America. Wiley Interscience Publication. New York, U.S.A.

Hedrick, P. 1985. Genetics of Populations. Jones & Bartlett Publishers. Portola Valley, U.S.A.

Housh, T. B., F. W. McDowell, and J. N. Connelly. 2003. Early and mid-Proterozoic crust of the Coahuila terrane preserved in xenoliths at Cascada de Basaseachic, southwestern Chihuahua. Geological Society of America. Abstracts with Programs 36:78.

Hudson, P. F., D. A. Hendrickson, A. C. Benke, A. Varela-Romero, R., Rodiles-Hernández, and W. Minckley. 2005. Rivers of Mexico. Pp. 1030-1084 *in Rivers of North America* (Benke A. and C. Cushing, eds). Elsevier. Amsterdam, Netherlands.

Jeffress, M. R., C. P. Paukert, J. B. Whittier, B. K. Sandercock, and P. S. Gipson. 2011. Scale-dependent factors affecting North American river otter distribution in the Midwest. The American Midland Naturalist 166:177-193.

Jones, C. and C. G. Schmitt. 1997. Mammal species of concern in New Mexico. Special publication: Life among the muses; papers in honor of James S. Findley. Museum of Southwestern Biology 3:179-205.

Kruuk, H. 2006. Otters: Ecology, Behaviour and Conservation. Oxford University Press, Oxford, U.K.

Kuhn, R. A. and W. Meyer. 2010. Comparative hair structure in the Lutrinae (Carnivora: Mustelidae). Mammalia 74:291-303.

Lariviere, S. 1999. *Lontra longicaudis*. Mammalian Species 609:1-5

Latch, E. K., D. G. Scognamillo, J. A. Fike, M. J. Chamberlain, and O. E. Rhodes. 2008. Deciphering ecological barriers to North American river otter (*Lontra canadensis*) gene flow in the Louisiana landscape. The Journal of Heredity 99:265–274.

Lima, F. C. T., L. R. Malabarba, P. A. Buckup, J. F. Pezzi, R. P. da Silva, A. Vari, R. Harold, O. T. Benine, C. S. Oyakawa, N. A. Pavanelli, C. A. S. Menezes, M. C. S. L. Lucena, Z. M.S. Malabarba, R. E. Lucena, F. Reis, C. Langeani, C., Moreira, et al. 2003. Genera Incertae Sedis in Characidae. Pp. 106-168 *in* Checklist of the Freshwater Fishes of South and Central America (Reis, R. E., S. O. Kullander and C. J. Ferraris Jr., eds.). EDIPUCRS. Porto Alegre, Brasil.

Long, B. 2010. River otter monitoring in the Upper Rio Grande watershed in northern New Mexico, October 14, 2008 through January 21, 2010. New Mexico Department of Game and Fish.

López-Wilchis, R. 1998. Base de datos de mamíferos de México depositados en colecciones de Estados Unidos y Canadá. Universidad Autónoma Metropolitana. Unidad Iztapalapa. Bases de datos SNIB-CONABIO. Proyecto No. P130. Ciudad de México, México .

Loy, A., M. L. Carranza, C. Cianfrani, E. D. Alessandro, P. Marzio, M. Di Minotti, and G. Reggiani. 2009. Otter *Lutra lutra* population expansion: assessing habitat suitability and connectivity in southern Italy. Folia Zoologica 58:309–326.

Marucco, F., D. Boitani, H. Pletscher, and M. K. Schwartz. 2010. Bridging the gaps between non-invasive genetic sampling and population parameter estimation. European Journal of Wildlife Research 57:1–13.

Mason, C. F. 1995. Habitat quality, water quality and otter distribution. Hystrix (New Series) 7:195–208.

NOM-059-SEMARNAT-2010. 2010. Norma Oficial Mexicana. Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. Diario Oficial, Jueves 30 de diciembre de 2010.

Page, L. M. and B. M. Burr. 1991. A field guide to freshwater fishes of North America north of Mexico. Houghton Mifflin Company, Boston, U.S.A.

Pardini, R. and E. Trajano. 1999. Use of shelters by the neotropical river otter (*Lontra longicaudis*) in an Atlantic forest stream, southeastern Brazil. Journal of Mammalogy 80:600-610.

Pearse, D. E. and K. A. Crandall. 2004. Beyond Fst : Analysis of population genetic data for conservation. Conservation Genetics 5:585-602.

Pedroso, N. M. and M. Santos-Reis. 2009. Assessing otter presence in dams: A Methodological proposal. *IUCN Otter Spec. Group Bull* 26:97–109.

Pohle, H. 1920. Die unterfamilie der Lutrinae. Archiv fur Naturgeschchte 85A:1-247.

Polechla, P. J., A. G. Burns, S. Rist, K. A. Moore, and J. W. Dragoo. 2004. First physical evidence of the Nearctic river otter (*Lontra canadensis*) collected in New Mexico, USA, since 1953. *IUCN Otter Specialist Group Bulletin* 21:70–75.

Polechla, P. J. and E. Carrillo-Rubio. 2009. Historic and current distributions of river otters (*Lontra canadensis*) and (*Lontra longicaudis*) in the Rio Grande or Rio Bravo del Norte drainage of the Colorado and New Mexico, USA, and Chihuahua, Mexico and adjacent areas. IUCN Otter Specialists Group Bulletin 26:81-95.

Rabinowitz, A. and K. A. Zeller. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biological Conservation 143:939–945.

Ramos-Rosas, N. N., C. Valdespino, J. García-Hernández, J. P. Gallo-Reynoso, and E. J. Olguín. 2012. Heavy metals in the habitat and throughout the food chain of the neotropical otter, *Lontra longicaudis*, in protected Mexican wetlands. Environmental Monitoring Assessment 185:1163-73.

Reid, N., D. Thompson, B. Hayden, F. Marnell, and W. I. Montgomery. 2013. Review and quantitative meta-analysis of diet suggests the Eurasian otter (*Lutra lutra*) is likely to be a poor bioindicator. Ecological Indicators 26:5–13

Rheingantz, M. L. and C. S. Trinca. 2015. *Lontra longicaudis*. The IUCN Red List of Threatened Species 2015: e.T12304A21937379. http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T12304A21937379.en. Downloaded on 12 September 2016.

Sales-Luís, T., D. Freitas, and D. Santos-Reis. 2009. Key landscape factors for Eurasian otter *Lutra lutra* visiting rates and fish loss in estuarine fish farms. European Journal of Wildlife Research 55:345–355.

Sánchez, O. and J. P. Gallo-Reynoso. 2007. Evaluación del riesgo de extinción de *Lontra longicaudis* de acuerdo al numeral 5.7 de la NOM-059-SEMARNAT-2001. Pp. 61–89 *in* Método de evaluación del riesgo de extinción de la especies silvestres en México (MER) (Sánchez, O., R. Medellín, A. Aldama, B. Goettsch, J. Soberón and M. Tambutti, eds.). SEMARNAT-INE-IECUNAM-CONABIO. Ciudad de México, México.

Santiago-Plata, V. M. 2013. Ocupación y distribución potencial de la nutria neotropical (*Lontra longicaudis*) asociada a variables ambientales en la cuenca del río San Juan, Costa Rica. Centro Agronómico Tropical de Investigación y Enseñanza 144.

Serfass, T., S. S. Evans, and P. Polechla. 2015. *Lontra canadensis. The IUCN Red List of Threatened Species 2015*: e.T12302A21936349 http://dx.doi.org/10.2305/IUCN.UK.20152.RLTS.T12302A21936349.en

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and Ecology of Species Range Limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Trewavas, E. 1982. Tilapias: taxonomy and speciation. Pp. 3-13 *in* The biology and culture of tilapias (Pullin, R. S. V., and R. H. Lowe-McConnell, eds.). ICLARM Conf. Proc. 7. (Ref. 1).

Trinca, C. S., C. F. Jaeger, and E. Eizirik. 2013. Molecular ecology of the Neotropical otter (*Lontra longicaudis*): non-invasive sampling yields insights into local population dynamics. Biological Journal of the Linnean Society 109:932–948.

Van Looy, K., J. Piffady, C. Cavillon, T. Tormos, P. Landry, and Y. Souchon. 2014. Integrated modelling of functional and structural connectivity of river corridors for European otter recovery. Ecological Modelling 273:228–235.

Waldemarin, H. F. and R. Alvares. 2008. *Lontra longicaudis*. *In* IUCN 2010. IUCN Red List of Threatened Species.

Walker, M., S. Johnsen, S. O. Rasmussen, J. P. Steffensen, T. Popp, P. Gibbard, W. Hoek, J. Lowe, S. Björk, L. Cwynar, K. Hughen, P. Kershaw, B. Kromer, T. Litt, D. J. Lowe, T. Nakagawa, R. Newnham, and J. Schwander. 2008. The Global Stratotype Section and Point (GSSP) for the base of the Holocene Series/Epoch (Quaternary System/Period) in the NGRIP ice core. Episodes 31:264–267.

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Sigmodontine community and species responses to El Niño and precipitation in different levels of forest degradation

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Few studies have focused on rodent communities at the margins of an ecoregion or the limits of species' distributions, where the community may be more sensitive to extrinsic variables, both biotic and abiotic. This study evaluates sigmodontine rodent species diversity and overall abundance, and variation associated with climatic variables, in three locations with differing levels of habitat degradation. The study was conducted in northeastern Paraguay, near the western limit of the Upper Paraná Atlantic Forest and near the distributional limits of the three most abundant species in the study sites. Three mark-recapture grids were established and classified as least, moderately and most-degraded based on an analysis of several vegetation parameters. The grids were sampled for five consecutive nights, six times during two years. Shannon diversity and overall abundance were calculated for each sample. Monthly Multivariate ENSO Index and rainfall values were obtained from publicly available resources. Product-moment correlations were calculated between community and climatic parameters, including cumulative values for the climatic variables. The same correlations were calculated for the three common sigmodontine species. 1,632 captures were recorded, representing 13 sigmodontine species. Species richness in the samples (one session on one grid) varied from four to seven. *Akodon montensis*, *Hylaeamys megacephalus* and *Oligoryzomys nigripes* were the three most abundant species. In general, species diversity was negatively correlated with ENSO index, precipitation and precipitation anomaly, including cumulative one- to six-month cumulative values of each. Total sigmodontine abundance was positively correlated with the climatic variables. However, these correlations were not uniform among the three levels of habitat degradation, nor did the three abundant species show similar correlation patterns. The three most abundant species are each near their distributional limits, whereas several less abundant species have distributions that extend well beyond the study area. This somewhat counterintuitive result bears further investigation in other sites at ecoregional margins, to determine whether it is a commonly observed pattern, or an exception. Overall sigmodontine abundances were generally reflective of *Akodon montensis* abundance, which generally correlated with precipitation (including cumulative amounts). Our analyses of these longitudinal data showed two major effects on sigmodontine species diversity and population. First, they are impacted by habitat and secondly, they are affected by climate (ENSO, precipitation). However, individual species are not impacted similarly. *Akodon montensis* abundances primarily were correlated with abiotic (climatic) variables, and the correlations were consistent across habitats (biotic factors). In contrast, *Hylaeamys megacephalus* abundance was correlated with climatic variables in two habitats, but not the moderately-degraded habitat, and *Oligoryzomys nigripes* abundance was not correlated with climate in the most-degraded habitat.

Pocos estudios se han centrado en las comunidades de roedores en los márgenes de una ecorregión o en los límites de las distribuciones de las especies, donde la comunidad puede ser más sensible a las variables extrínsecas, tanto bióticas como abióticas. Este estudio evalúa la diversidad de especies y la abundancia general de roedores sigmodontinos, y la variación asociada con las variables climáticas, en tres lugares con diferentes niveles de degradación del hábitat. Se establecieron tres parcelas de captura-marca-recaptura y se clasificaron como la menos, moderada y más degradadas basadas en un análisis de vegetación de varios parámetros. Las parcelas fueron muestreadas durante cinco noches consecutivas, seis veces durante dos años. La diversidad de Shannon y la abundancia general se calcularon para cada muestra. El índice mensual de ENOS multivariable y los valores de precipitación se obtuvieron de sitios accesibles en Internet. Las correlaciones producto-momento se calcularon entre los parámetros climáticos y de la comunidad, incluidos los valores acumulados para las variables climáticas. Se calcularon las mismas correlaciones para las tres especies comunes de sigmodontinos. Se registraron 1,632 capturas, representando 13 especies sigmodontinos. La riqueza de especies en las muestras (una sesión en una parcela) varió de cuatro a siete. *Akodon montensis, Hylaeamys megacephalus* y *Oligoryzomys nigripes* fueron las tres especies más abundantes. En general, la diversidad de especies se correlacionó negativamente con el índice ENOS, la precipitación y la anomalía de la precipitación, incluidos los valores acumulativos de uno a seis meses de cada uno. La abundancia total de sigmodontinos se correlacionó positivamente con las variables climáticas. Sin embargo, estas correlaciones no fueron uniformes entre los tres niveles de degradación del hábitat, ni tampoco entre las tres especies abundantes. Las tres especies más abundantes están cada una cerca de sus límites de distribución, mientras que varias especies menos abundantes tienen distribuciones que se extienden mucho más allá de este sitio. Este resultado algo contraintuitivo conlleva una mayor investigación en otros sitios en los márgenes ecorregionales, para determinar si es un patrón observado comúnmente, o una excepción. Las abundancias de sigmodontinos generalmente reflejaron la abundancia de *Akodon montensis*, que generalmente se correlacionó con la precipitación (incluidas las cantidades acumuladas). Las conclusiones destacadas de este estudio fueron: (1) diferentes niveles de degradación del hábitat se correlacionan con la variación en la diversidad de especies y la abundancia general de los sigmodontinos, y las especies individuales no muestran los mismos niveles de correlación entre los diferentes hábitats; y (2) la variabilidad climática (ENOS y precipitación) también afecta la diversidad de especies sigmodontinos y la abundancia de la población, y las especies comunes no muestran correlaciones similares entre sí. Las abundancias de *Akodon montensis* se correlacionaron principalmente con variables abióticas (climáticas), y las correlaciones fueron consistentes en todos los hábitats (factores bióticos). En contraste, la abundancia de *Hylaeamys megacephalus* se correlacionó con las variables climáticas en dos hábitats, pero no en el hábitat moderadamente degradado, y *Oligoryzomys nigripes* no se correlacionó con el clima en el hábitat más degradado.

Key words: Climatic variables; habitat quality; mark-recapture sampling; Paraguay; population abundance; species diversity; upper Paraná Atlantic Forest.

Introduction

The composition and dynamics of terrestrial small-mammal communities in the Neotropics are to date poorly documented (Mares 1982; Lacher and Mares 1986; Mares and Ernest 1995; Willig *et al.* 2000; Owen 2013). Accordingly, studies of terrestrial small-mammal communities are increasingly the focus of intensive studies. However, the majority of these studies are either broad-scale comparisons of faunal communities (Ojeda *et al.* 2000; Willig *et al.* 2000), or are evaluations of a community situated well within the geographic and ecologic boundaries of the ecoregion being evaluated (*e. g.*, Ribeiro and Marinho-Filho 2005; Bernardes 2006; Becker *et al.* 2007; Magnusson *et al.* 2010). With the increasing fragmentation of ecoregions, it will be increasingly important to assess community composition and dynamics in marginal patches of a particular ecoregion (Santos 2008; Owen 2013). Faunal members of such communities are presumed to be living near the limits of their capabilities in terms of their abiotic (*e. g.,* soils, weather, climate) and biotic environment (vegetation composition and structure, predators, competitors). Moreover, such communities are likely to be sensitive to extrinsic variables such as climate change and anthropogenic changes in land use (Willig *et al.* 2000; Carnaval and Moritz 2008; Meserve *et al.* 2011; Owen 2013; de la Sancha *et al.* 2014). Importantly, a detailed understanding of the responses of rodent communities and their more common species to both biotic and abiotic variations in their environment is necessary for developing predictive models for the emergence of rodent-borne zoonotic pathogens (Glass *et al.* 2002; Goodin *et al.* 2006; Keesing *et al.* 2010; Han *et al.* 2015; Eastwood *et al.* 2018; Morand *et al.* 2019).

Most of eastern Paraguay is within the historical distribution of the Upper Paraná Atlantic Forest (UPAF), which is a Biodiversity Hotspot and Conservation Priority Area (Myers *et al.* 2000; Willig *et al.* 2000). This ecoregion has experienced extensive land-use conversion for ranching and agriculture resulting in less than 7 % of the original footprint remaining (Klink and Moreira 2002; Klink and Machado 2005; Silva *et al.* 2006; Huang *et al.* 2007, 2009). This study evaluates the temporal dynamics and particularly the effects of the El Niño / Southern Oscillation (ENSO) and precipitation on the sigmodontine rodent communities occupying three types of habitat degradation, near the western limit of the UPAF in eastern Paraguay. We hypothesized that substantial fluctuations in rodent species diversity and sigmodontine population abundance would result from fluctuations in the abiotic variables mentioned above, and that these effects would be dissimilar in the three communities sampled, due to differing levels of habitat degradation. Moreover, we expected that some species would be more responsive to climatic (abiotic) fluctuations, whereas others might be more sensitive to habitat degradation.

Materials and Methods

Study Site. The study was conducted in the Reserva Natural del Bosque Mbaracayú (RNBM), a natural reserve of ca. 65,000 ha in Canindeyú Department, northeastern Paraguay (*Figure* 1). This site is located within climate type Cfa (temperate, without dry season, hot summer—Peel *et al.* 2007). The RNBM is located near the western margin of the Upper Paraná Atlantic Forest (UPAF—depicted as Moist Broadleaf Forest in the biome map of Olson *et al.* 2001), and receives an annual average precipitation of approximately 1550 mm (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/ge/, accessed 17 March 2019).

The three sampling grids were evaluated based on an extensive series of vegetation structural characteristics, measured at each of the trap stations in each grid. Means of these vegetation measures were used as general measures for each grid. These were standardized to a mean of zero and standard deviation of one, to mitigate against effects of character size. Eigenvectors were extracted from the correlation matrix of standardized characters and evaluated using Principal Component Analysis (PCA; Sneath and Sokal 1973). Following preliminary analyses, six characters were included in the final PCA, as being important descriptors of both forest quality and rodent habitat: dead wood on ground, maximum canopy height, distance to nearest trees, percentage coverage by forbs, logs (fallen trees) in vicinity, and presence of orange trees. Degradation levels were judged to be positively associated with the first two principal components, which together represented 95% of the variance (Table 1). Thus, more degraded (poorer) forest habitat is associated with forbs, logs (fallen trees), and orange trees (*Citrus aurantium*, an introduced species which has acclimatized in disturbed forest). Less degraded forest habitat is associated with more dead wood (fallen branches, not fallen trees), higher canopy and lower distance to the nearest tree. Based on these criteria, Grid B (centered at -24.141° S, -55.366° W) was designated as "least degraded", Grid A (-24.123° S, -55.505° W) was "moderately degraded", and Grid G (-24.131° S, -55.537° W) was "most degraded". Grid names and designations are consistent with other publications based on data developed in this project.

Sampling methods and protocol. Each 12 by 12 sampling grid consisted of 144 trap stations, with the traps placed 10 m apart. Sampling was conducted six times (July and November 2015, February, July and November 2016, and February 2017). July is winter, and typically dry, whereas November is the beginning of the summer and the peak of the rainy season, and February is the end of summer, with intermediate rainfall levels. In each sampling session, traps were opened for five nights on each grid. In the first sampling session two traps were placed at each station (one trap on the ground, one on a plywood platform 2 to 3 meters above the ground, in vines or branches). Thereafter (for the remaining five sampling sessions) three traps were placed at each station (two on the ground, one on a platform above ground). Thus, 432 traps were open each night for the remaining five sampling sessions resulting in 2,160 trap-nights per sampling session with the total effort for the six sampling sessions of the study being 36,720 trap-nights.

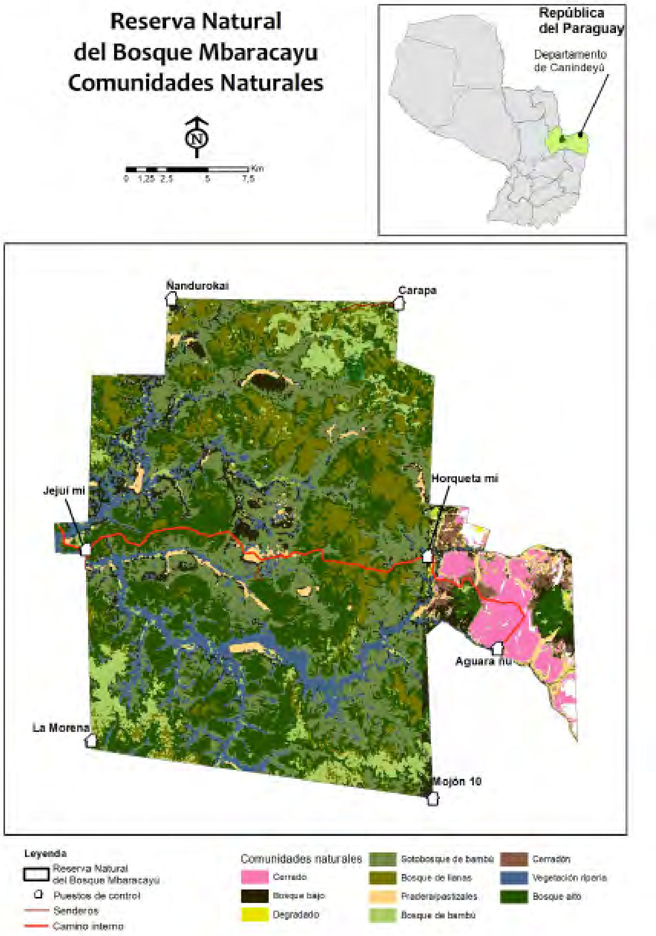

Figure 1. Map of the Reserva Natural del Bosque Mbaracayú and its location within Paraguay, and land cover based on supervised classification of satellite imagery combined with extensive ground-truthing using habitat categorization by local Ache (Indigenous) people. See text for location and description of sampling grids. Map based on Naidoo and Hill (2006) and Peña-Chocarro *et al.* (2010).

Environmental data. Monthly multivariate ENSO index (MEI) values (Wolter and Timlin 1993, 1998) were downloaded from the Physical Sciences Division of the Earth Sciences Laboratory, U.S. National Oceanic and Atmospheric Administration (https://www.esrl.noaa.gov/psd/enso/mei/data/meiv2.data) for the time period beginning one year before rodent sampling began, until the final sampling period. Precipitation data (Precip) were obtained for the same time period from the Climatic Research Unit of the University of East Anglia accessed via a Google Earth application ((https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/ge/). Precipitation data are presented as 0.5-degree grid averages. Because the RNBM lies approximately equally on two of the grid squares, the precipitation values for those two squares were averaged to calculate monthly precipitation values for the study site. Monthly precipitation values were also downloaded for the 30 years prior to the study (1984 to 2013) to calculate historical monthly precipitation means and standard deviations. Monthly precipitation anomaly values (Anom) were calculated by subtracting the monthly means from the recorded precipitation amounts during the study. To evaluate the effect of ENSO on precipitation at the study site, Pearson product-moment correlations were calculated between MEI and Precip (current month and monthly lagged values for from 1-6 months), and between MEI and Anom (current and lagged for from 1 to 6 months).

Table 1. Loadings of six vegetation measures on principal components 1 and 2, and percent of variance explained by these two components.

Vegetation	PC-1	PC-2
Percent coverage by forbs	0.972	0.185
Percent coverage by deadwood	-0.788	0.602
Maximum canopy height	-0.816	-0.533
Minimum distance to trees	0.245	-0.942
Presence of fallen trees	0.947	-0.140
Presence of orange trees	0.960	0.233
% of variance	62.2	32.8

Correlations between rodent community measures and abiotic measures. For comparison with rodent community and population measures, MEI, precipitation and precipitation anomaly values were listed for each of the six sampling months, as well as cumulative MEI, precipitation and anomaly for the two, three, four, six, and twelve-month periods ending with each sampling month (MEI1 – MEI12, Precip1 – Precip12, Anom1 – Anom12). Total sigmodontine abundance (all species included) and species diversity (Shannon index) were calculated for each of the three grids and each of the six sampling sessions. Because abundance values may be expected to conform to a Poisson distribution, a Shapiro-Wilk test was conducted, which failed to reject the null hypothesis of normality ($W = 0.96$, $P = 0.602$). Thus, we did not transform the abundance values. Product-moment correlations were then calculated between each of these two rodent community measures and each of the climatic variables. We arbitrarily considered correlations with an absolute value > 0.70 to indicate potential climatic predictors (MEI, precipitation and precipitation anomaly) of fluctuations in population measures (species diversity, total abundance and species abundances,), which corresponds to a 93 % confidence interval around $r = 0$. All calculations were made in Microsoft Excel™, with the exception of calculations pertaining to the principal components analyses, which were conducted using NTSYSpc ver. 2.2 (Rohlf 2005).

Results

Based on monthly precipitation data from the 30 years prior to this study (1984 to 2013), October – December (spring and early summer) is normally the peak rainy season at the study site, with another shorter period in April – May (autumn). The second period is much less consistent, having a higher standard deviation of precipitation amount than any other month of the year.

Among the abiotic variables, the multivariate ENSO index (MEI) correlated weakly with the current month for both precipitation and precipitation anomaly, with the correlation coefficients for both decreasing non-monotonically for increasing lag times, with very little association after three months. For current and all lagged periods, MEI correlated with the precipitation anomaly than with precipitation, indicating that greater than normal rainfall is received during periods of higher MEI values (El Niño events). However, no value of r was greater than 0.29, and MEI, anomaly and precipitation were treated as independent abiotic variables, for the comparisons with species diversity and sigmodontine and species abundances.

A total of 1,632 captures (4.4 % overall trap success) was recorded in the sampling, involving 1,021 individual animals (611 recaptures). Overall, 13 species were encountered, two of which remain unidentified. Sigmodontine species richness varied from 4 to 6 on Grid B (least degraded), 4 to 7 on Grid A (moderately degraded), and 4 to 7 on Grid G (most degraded). *Akodon montensis* was by far the commonest species, with 64.6 % of the individuals, followed by *Hylaeamys megacephalus* (17.3 %) and *Oligoryzomys nigripes* (9.0 %, Table 2). Shannon species diversity varied from 0.70 to 1.11 on Grid B, 0.73 to 1.32 (Grid A), and 1.00 to 1.41 (Grid G). Total sigmodontine abundance (species combined) ranged from 17 to 88 (B), 27 to 111 (A), and 23 to 53 (G; Table 3).

Correlations between climatic and population measures were quite variable. In general, species diversity was negatively correlated with the three sets of climatic variables (MEI, precipitation, precipitation anomaly, and their cumulative values; Figure 2). In contrast, total sigmodontine abundance was positively correlated with the three climatic variables.

Predictors of species diversity. Notwithstanding a generally negative correlation with the climatic variables, species diversity appeared to be only loosely associated with those variables which we evaluated (Table 4), with only Grids B and G (least and most degraded) showing an "important" (absolute value > 0.70) correlation with current month precipitation, and no other climatic variable. On both grids, species diversity correlated most strongly with current-month values of MEI and precipitation, generally deceasing with increasing cumulative values. In contrast, species diversity on these same two grids correlated best with the six-month cumulative value for precipitation anomaly (Figure 2). On the moderately degraded grid (A), species diversity was negatively correlated with nearly all climatic variables, although strongly with none (Table 4), and the strongest correlations were with the two-month cumulative values of precipitation and precipitation anomaly (Figure 2).

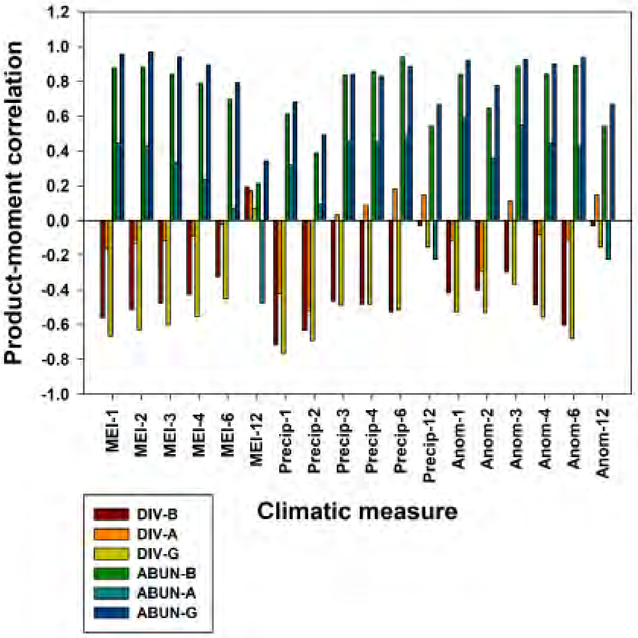

Figure 2. Correlograms showing product-moment correlations between sigmodontine species diversity and total abundance with MEI, precipitation and precipitation anomaly, shown for 1, 2, 3, 4, 6 and 12-month cumulative values. Grid B, least degraded; Grid A, moderately degraded; Grid G, most degraded.

Predictors of sigmodontine abundance. Sigmodontine abundance was strongly positively correlated with 11 of the 18 climatic variables on Grid B (least degraded), showing an immediate increase with higher MEI and anomaly values, as

Table 2. Summary of species encountered on each grid, for all six sampling sessions combined. Least, moderate and most refer to level of habitat degradation, as evaluated using a principal components analysis of six environmental variables, measured at each of 144 trap stations on each grid, and averaged for the grid.

	Grid B (least)		Grid A (moderate)		Grid G (most)		Overall	
Species	**# indiv.**	**Percent.**	**# indiv.**	**Percent.**	**# indiv.**	**Percent.**	**# indiv.**	**Percent.**
Akodon montensis	254	71.9%	279	64.7%	127	53.6%	660	64.6%
Calomys callosus	1	0.3%	2	0.5%	8	3.4%	11	1.1%
Euroryzomys russatus	2	0.6%	0	0.0%	0	0.0%	2	0.2%
Hylaeamys megacephalus	45	12.7%	75	17.4%	57	24.0%	177	17.3%
Juliomys pictipes	2	0.6%	0	0.0%	0	0.0%	2	0.2%
Necromys lasiurus	0	0.0%	3	0.7%	0	0.0%	3	0.3%
Oecomys mamorae	0	0.0%	1	0.2%	0	0.0%	1	0.1%
Oligoryzomys mattogrossae	9	2.5%	17	3.9%	10	4.2%	36	3.5%
Oligoryzomys nigripes	31	8.8%	40	9.3%	21	8.9%	92	9.0%
Oligoryzomys sp.	5	1.4%	12	2.8%	6	2.5%	23	2.3%
Rhipidomys macrurus	1	0.3%	0	0.0%	2	0.8%	3	0.3%
Sooretamys angouya	2	0.6%	2	0.5%	5	2.1%	9	0.9%
Oryzomyine sp.	1	0.3%	0	0.0%	1	0.4%	2	0.2%
Totals	353	100.0%	431	100.0%	237	100.0%	1021	100.0%

Table 3. Species richness and Shannon diversity and total abundance for sigmodontine rodents on three sampling grids during six sampling sessions in the Reserva Natural del Bosque Mbaracayú. Grid B had the least degraded habitat, Grid A was moderately degraded, and Grid G the most degraded. See text for further description of grid habitats.

Year	Month	Session	RICH-B	RICH-A	RICH-G	DIV-B	DIV-A	DIV-G	ABUN-B	ABUN-A	ABUN-G
2015	Jul	2	4	7	6	0.94	1.01	1.22	82	111	53
2015	Nov	3	5	6	4	0.70	0.73	1.00	71	79	47
2016	Feb	4	5	6	7	0.97	1.32	1.30	88	63	52
2016	Jul	5	6	5	6	1.11	1.18	1.41	40	50	32
2016	Nov	6	5	4	5	1.00	0.87	1.31	17	27	23
2017	Feb	7	6	6	5	0.89	1.20	1.28	55	101	30

well as with three, four and six-month cumulative precipitation. No strong correlations were found between abundance and twelve-month cumulative values (Table 4). Similarly, abundance on Grid G (most degraded) showed strong correlations with 13 of the 18 climatic variables, and no strong correlations with twelve-month cumulative values. In contrast, Grid A (moderately degraded) exhibited no strong correlation of sigmodontine abundance with any climatic variable.

Abundant species, species diversity and total abundance. The three most abundant species in this study were *Akodon montensis*, *Hylaeamys megacephalus* and *Oligoryzomys nigripes*, with 64.6 %, 17.3 % and 9.0 % of all individuals, respectively (Table 2). Because *A. montensis* represents nearly two-thirds of the overall population, abundance levels of this species generally correlate strongly and positively with total sigmodontine abundance (Figure 3). Moreover, an increased proportion of *A. montensis* corresponds on each grid with a decrease in species diversity, as measured by the Shannon Index (Figure 4).

The three most abundant species exhibited differing correlation patterns with total sigmodontine abundance, in the different levels of habitat degradation. *Akodon montensis* was consistently strongly correlated with total abundance, across the three grids. In contrast, *H. megacephalus* was strongly correlated with total abundance on Grids B and G (least and most degraded), and essentially uncorrelated on Grid A (moderately degraded), and *O. nigripes* most strongly correlated on Grids B and A, and uncorrelated on Grid G (most degraded; Figure 5).

As mentioned, on Grid A (moderately degraded), *H. megacephalus* showed only a low correlation with total abundance, although it showed a strong positive correlation with species diversity. On grids A and G, *A. montensis* and *H. megacephalus* showed strongly contrasting responses in the sampling session of February 2016 (the end of the strong El Niño event of late 2015), with *Akodon* decreasing and *Hylaeamys* increasing, after which percentages returned to earlier levels. In contrast, neither of these two species were affected by the El Niño event on Grid B (least degraded; Figure 6).

Discussion

The Sigmodontine community composition and relative abundances of the three most abundant species in this study were similar to those from other studies in the Atlantic Forest habitat of the RNBM (Owen *et al.* 2010; Eastwood *et al.* 2018). However, there are considerable differences between this community and others in Atlantic Forest (*e. g*., Cademartori *et al.* 2004; Carmignotto and Aires 2011; Melo *et al.* 2011; Galiano *et al.* 2013; Maestri and Marinho 2014; Barros *et al.* 2015; Machado *et al.* 2019). One noteworthy difference was that while *Hylaeamys megacephalus* was abundant on all sites in our study, it is absent in more southerly latitudes, reflecting its tropical distribution from the north coast of Venezuela southward across Amazonia and terminating in east-central Paraguay. *Akodon montensis* reaches the western limit of its more subtropical distribution in eastern Paraguay and northern Argentina, as does *Oligoryzomys nigripes*, which is distributed from northeastern Brazil southward to Uruguay (D'Elía and Pardiñas 2015). Thus, although each is widely distributed, the three most abundant species in this study are all near the limits of their distributions.

Higher overall sigmodontine abundance was generally associated with lower species diversity in this study, indicat-

Table 4. Climatic variables arranged in order from highest to lowest correlation coefficient with each community measure (sigmodontine species diversity (Shannon Index) and total sigmodontine abundance), for each grid (B, least degraded; A, moderately degraded; G, most degraded). Climatic measures with negative correlation coefficients are shown in parentheses. Measures with absolute value of correlation coefficient > 0.70 are shown in bold face.

Species diversity			Total abundance		
Grid B	**Grid A**	**Grid G**	**Grid B**	**Grid A**	**Grid G**
MEI-12	Precip-6	MEI-12	**Precip-6**	Anom-1	**MEI-2**
(Anom-12)	MEI-12	(Anom-12)	**Anom-6**	Anom-3	**MEI-1**
(Precip-12)	Anom-12	(Precip-12)	**Anom-3**	Precip-6	**MEI-3**
(Anom-3)	Precip-12	(Anom-3)	**MEI-2**	Precip-3	**Anom-6**
(MEI-6)	Anom-3	(MEI-6)	**MEI-1**	Precip-4	**Anom-3**
(Anom-2)	Precip-4	(Precip-4)	**Precip-4**	MEI-1	**Anom-1**
(Anom-1)	Precip-3	(Precip-3)	**Anom-4**	Anom-4	**Anom-4**
(MEI-4)	(MEI-6)	(Precip-6)	**MEI-3**	MEI-2	**MEI-4**
(Precip-3)	(Anom-4)	(Anom-1)	**Anom-1**	Anom-6	**Precip-6**
(MEI-3)	(MEI-4)	(Anom-2)	**Precip-3**	Anom-2	**Precip-3**
(Precip-4)	(Anom-6)	(MEI-4)	**MEI-4**	MEI-3	**Precip-4**
(Anom-4)	(Anom-1)	(Anom-4)	MEI-6	Precip-1	**MEI-6**
(MEI-2)	(MEI-3)	(MEI-3)	Anom-2	MEI-4	**Anom-2**
(Precip-6)	(MEI-2)	(MEI-2)	Precip-1	Precip-2	Precip-1
(MEI-1)	(MEI-1)	(MEI-1)	Precip-12	MEI-6	Precip-12
(Anom-6)	(Anom-2)	(Anom-6)	Anom-12	(Precip-12)	Anom-12
(Precip-2)	(Precip-1)	(Precip-2)	Precip-2	(Anom-12)	Precip-2
(Precip-1)	(Precip-2)	**(Precip-1)**	MEI-12	(MEI-12)	MEI-12

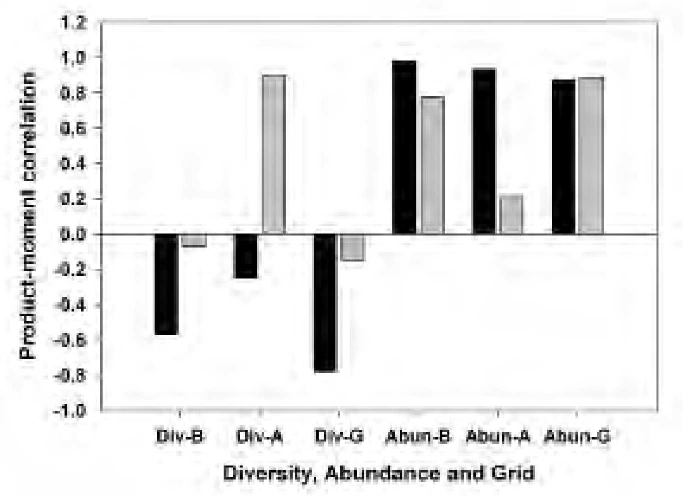

Figure 3. Correlogram showing product-moment correlations between *Akodon montensis* and *Hylaeamys megacephalus* population abundances, with species diversity and total sigmodontine abundance on three sampling grids. Grid B, least degraded; Grid A, moderately degraded; Grid G, most degraded. Black bars, *Akodon montensis*; gray bars, *Hylaeamys megacephalus*.

ing that the diversity index was driven primarily by evenness, rather than species richness. In fact, species richness varied little throughout the study, whereas abundances varied substantially. This finding contrasts with those reported in other studies in which species diversity and abundance were both highest in the same habitat or in the same season (*e. g.*, Gastal 1997; Alho 2005; Asfora *et al.* 2009).

Hannibal and Neves-Godoi (2015) found *Hylaeamys megacephalus* to be more abundant and more broadly distributed among habitats than *Akodon montensis* in a study in Mato Grosso do Sul, Brazil. Similarly, Santos (2008) found *H. megacephalus* to be more abundant than an unidentified *Akodon* species in an Amazon-Cerrado interface area. In our study, increased overall abundance was due primarily to increased abundance of *Akodon montensis*. However, on Grids A and G (moderately and most degraded) in one sampling session (February 2016) an increase in overall abundance resulted from an increase in *Hylaeamys megacephalus*, while the proportion of *A. montensis* in the population decreased. This sampling session coincided with the end of an "exceptionally intense" El Niño event (Dirección Nacional de Aeronautica Civil 2016). This inverse relationship between the two most abundant species, apparently in response to the El Niño event, was negligible on Grid B (least degraded). To our knowledge, this complex interaction of population response by these two abundant species has not been reported elsewhere, and certainly bears further study and confirmation.

Effects of habitat degradation. Several important studies have documented differences in sigmodontine species diversity and abundance in response to different habitat quality or degradation (*e. g.*, Gastal 1997; Cerqueira *et al.* 2003; Alho 2005; Melo *et al.* 2011; Sponchiado *et al.* 2012; Galiano *et al.* 2013; de la Sancha *et al.* 2014). Results of the present study also document such differences associated with differing levels of habitat degradation.

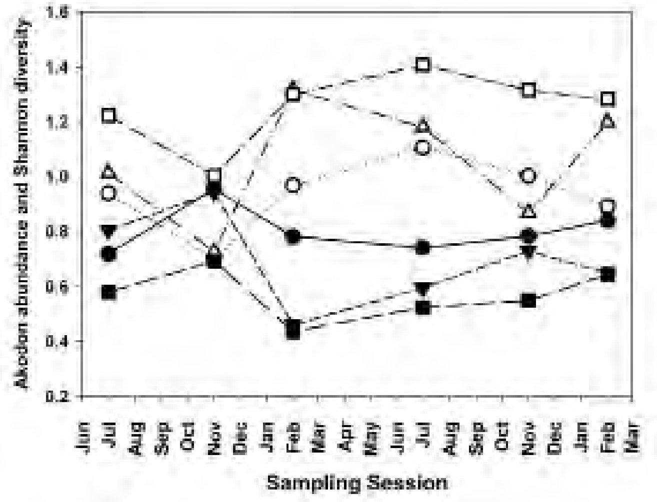

Figure 4. *Akodon montensis* population abundances (expressed as percentage of total sigmodontine abundance) and Shannon species diversity. Closed figures, *A. montensis* abundances; open figures, Shannon diversity. Circles, Grid B; triangles, Grid A; squares, Grid G.

Habitat degradation affects species diversity. Species diversity increased with increased habitat degradation. Diversity was highest in the most degraded habitat (Grid G; Shannon Index $H = 1.25 \pm 0.135$ across six sampling sessions), lowest in the least degraded habitat (Grid B, $H = 0.94 \pm 0.135$), and intermediate in the moderately degraded habitat (Grid A, $H = 1.05 \pm 0.223$). However, the effect of habitat degradation was less consistent in the moderately degraded habitat, as indicated by the higher standard deviation of species diversity levels across sampling sessions.

Habitat degradation affects overall sigmodontine abundance. The moderately degraded habitat had the highest sigmodontine abundance. Abundance was not associated monotonically with degradation extent. Grid A (moderately degraded) had the highest average abundance (72 ± 31.6), as well as being the least consistent (highest standard deviation). The most degraded habitat (Grid G) consistently had the lowest abundance (40 ± 12.8), and the least degraded habitat (Grid B) was intermediate in both mean and standard deviation (59 ± 27.0).

Habitat degradation affects different species differently. Of the three most abundant species, *Akodon montensis* abundance generally correlated highly with overall sigmodontine abundance on all three grids. Nevertheless, it showed a strong reduction in relative abundance (percentage of overall population) on Grids B and G in the February 2016 sample, at the end of a strong El Niño event. *Hylaeamys megacephalus* generally correlated strongly with overall abundance on Grids B and G (least and most degraded), but not on Grid A (moderately degraded). However, on both Grids G and A, *H. megacephalus* strongly increased in relative abundance in the February 2016 sample, benefitting apparently from either the reduction in *A. montensis*, or the heavy rains of the preceding several months, or both. *Oligoryzomys nigripes* abundance correlated with overall abundance on B and A (least and moderately degraded), but did

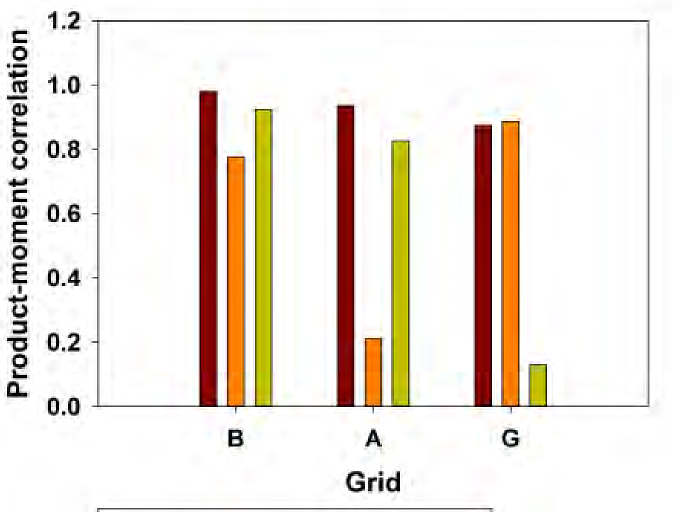

Figure 5. Correlations of population abundances of *Akodon montensis* (brown bar*), Hylaeamys megacephalus* (orange bar), *Oligoryzomys nigripes* (lemon bar), with abundances of all sigmodontine species combined.

not coincide with the overall abundance variations on Grid G (most degraded), apparently not benefiting from conditions that produced increases in the other two species.

Effects of climatic fluctuations. Numerous studies have also demonstrated effects of climatic variability (particularly precipitation) on sigmodontine community diversity, abundance and composition (*e. g*., D'Andrea *et al.* 1999; Melo *et al.* 2011; Lacher 2012; Sponchiado *et al.* 2012; Galiano *et al.* 2013). The present study supports the importance of climatic variability for sigmodontine community parameters, as well as for abundances of common species.

Climate variability affects species diversity. The Multivariate ENSO Index (MEI) of the current month was moderately negatively correlated with species diversity on Grids B and G (least and most degraded) with decreasing strength of correlation with increasing cumulative lengths of MEI scores. On Grid A (moderately degraded), MEI showed only very weak correlations with diversity. Current-month precipitation was also negatively correlated with species diversity on Grids B and G, with two-month cumulative precipitation slightly less strongly correlated. On Grid A, the two-month cumulative precipitation showed the strongest correlation with diversity, and present-month precipitation at a slightly lower correlation strength. In contrast to MEI and precipitation, species diversity was most strong correlated (negatively) with four- and six-month cumulative anomaly values on Grids B and G. Again, Grid A did not follow the response pattern of the other grids, showing only low correlation values with precipitation anomaly.

Climate variability affects overall sigmodontine abundance. MEI was strongly positively correlated with overall sigmodontine abundance for Grids B and G, for current month and cumulative MEI values of up to six months, decreasing to low correlation values at 12 months. Overall abundance on Grid A was much less strongly correlated (also positively) with MEI current and cumulative values.

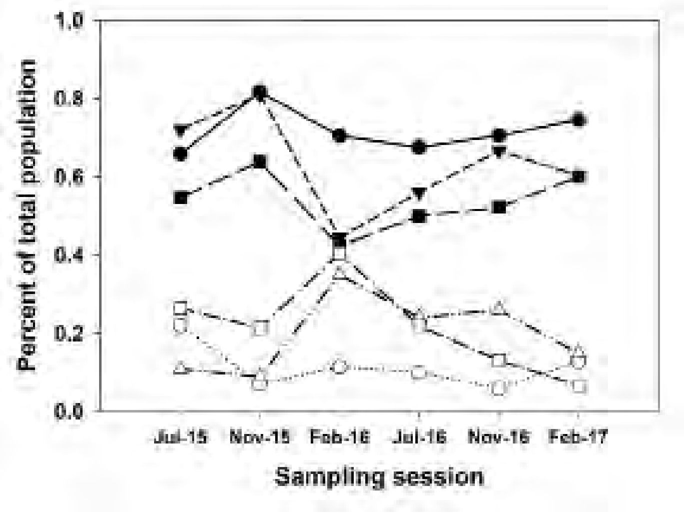

Figure 6. Chart showing relationships of population abundances of *Akodon montensis* and *Hylaeamys megacephalus*, shown as percentages of total sigmodontine abundance for each sampling session on each grid. Solid symbols, *Akodon montensis*; open symbols, *Hylaeamys megacephalus*. Circles, Grid B (least degraded); triangles, Grid A (moderately degraded); squares, Grid G (most degraded). Note the strongly contrasting changes in *A. montensis* and *H. megacephalus* in February 2016, at the end of the strong El Niño event, on Grids A and G. However, the populations on Grid B (least degraded) were not affected by the El Niño event.

Precipitation correlated most strongly with sigmodontine abundance on Grids B and G in the three-, four- and six-month accumulations, again with Grid A less strongly correlated. Precipitation anomaly reflected this same pattern, as well as strong correlations with current-month anomaly for Grids B and G, with Grid A again less strongly correlated.

Climate variability affects common species differently. On Grid B (least degraded), *Akodon montensis* and *Hylaeamys megacephalus* population percentages varied very little across the six sampling sessions. Although the overall populations varied considerably, the percentages of these two species remained relatively constant. On Grids A and G, pronounced variation was seen, with *Akodon* increasing and *Hylaeamys* decreasing in the first part of the El Niño event of late 2015 (Dirección Nacional de Aeronautica Civil 2016), and then reversing those trends toward the end of that event, with *Akodon* and *Hylaeamys* of nearly equal proportions in February 2016, after which both populations returned to pre-El Niño percentages, and *Hylaeamys* decreasing nearly to zero on Grid G (most degraded) by February 2017.

In this two-year study, substantial fluctuations in rodent species diversity and sigmodontine population abundance were noted, and these were often correlated with fluctuations in the abiotic variables examined. We also found that these effects were dissimilar in the three habitats sampled, representing differing levels of habitat degradation. However, this dissimilarity was expressed as an unexpected pattern. In fact, a particularly interesting result of this investigation was that species diversity and overall sigmodontine abundance were both only poorly correlated with abiotic variables on the moderately degraded habitat (Grid A), and also were more highly variable on that grid, than in the least and most-degraded habitats. As a result, populations on the least- and most-degraded grids could be substantially predicted by the abiotic variables, whereas populations on the moderately degraded grid were highly variable, and apparently responding to biotic or abiotic factors which were not included in our study.

Another noteworthy result was that, although several community and species population measures which were correlated with climatic variables, none showed important correlations with 12-month cumulative values of these variables. In other words, the community and its populations were not responsive to cumulative precipitation of the entire preceding year, but were responsive to the preceding half-year's events. We did not test for cumulative values between 6 and 12 months, and further investigation is needed to determine the duration of cumulative climatic events which are important to the sigmodontine populations. Additionally, the deviation of the community and population responses in the moderately habitat (Grid A) require better understanding, and may be particularly important in the context of complex interactions of populations of common species such as *Akodon montensis* and *Oligoryzomys nigripes*, which hosts to Jabora and Juquitiba hantaviruses, respectively (Eastwood *et al.* 2018).

Finally, we found that some species were more responsive to climatic (abiotic) fluctuations, whereas others were more sensitive to habitat degradation. *Akodon montensis* closely followed overall abundance (which correlated positively with climatic variation) on all three grids, whereas *Hylaeamys megacephalus* did so only in the least- and most-degraded habitats, and *Oligoryzomys nigripes* only in the least- and moderately-degraded habitats.

Akodon montensis is primarily terrestrial, although it may also ascend lianas or low branches of bushes (Machado *et al.* 2019). It is primarily an Atlantic Forest species, also occurring in gallery forest of the Cerrado, whose distribution extends from Minas Gerais state to southern Brazil, and westward in Paraguay only to about where the RNBM (our study site) is located (Cáceres *et al.* 2008; Carmignotto and Aires 2011; D'Elía and Pardiñas 2015). Although our study site is near the distributional limit of this species, it was by far the most abundant encountered in the study. It was well represented in most sessions on all grids, the exceptions being Grids B and G (most- and least-degraded habitats) in February 2016, suggesting that although it is unaffected by habitat degradation *per se*, it can be affected by an interaction between biotic and abiotic factors, and in the presence of adverse climatic conditions can best maintain its high abundance levels in moderately degraded habitat (Grid A). This is an important finding, in the context of this species as the primary reservoir for Jabora Virus, a pathogenic hantavirus species.

In contrast to *A. montensis*, *Hylaeamys megacephalus* did not generally follow overall sigmodontine population trends on Grid A, but did so (responding to climatic variables) on Grids B and G. This species is a widespread, terrestrial, primarily tropical mouse of moderate size, reaching its southern limit in the region of the RNBM (D'Elía and Pardiñas 2015). On both Grids A and G (moderately and most-degraded habitats), this species increased its representation in February 2016 (when *A. montensis* declined on those two grids), but did not do so in the least-degraded habitat (Grid B). Thus it appears to be affected by variation in the abiotic factors in habitats that are moderately or more degraded, but not in the least-degraded habitat.

Finally, *Oligoryzomys nigripes* is a scansorial forest species (encountered both on the ground and in bushes or vines above the ground), with primarily an Atlantic Forest distribution, also extending into Cerrado gallery forests (Carmignotto and Aires 2011; D'Elía and Pardiñas 2015). In our study it generally followed overall population trends (*i. e.*, responded to the climatic variables) in the least- and moderately-degraded habitats, but not in the most-degraded habitat, where it was consistently in low numbers, and did not respond to these abiotic variables affecting the other two species in those habitats.

Conclusions

Herein, we evaluated the potential value of three climatic variables for prediction of two sigmodontine community parameters—species diversity and overall abundance—in different levels of habitat degradation. In addition, we examined correlations of these abiotic variables with abundances of the three most common species. To our knowledge, this is the first study to evaluate the influences of both biotic and abiotic factors on a sigmodontine community, and to document temporal variation in abundances of common species in response to both abiotic and biotic variables. The importance of establishing predictive capability for these parameters in these communities under different levels of habitat degradation lies, among other reasons, in the potential for recognizing and predicting conditions portending outbreaks of zoonotic diseases such as hantavirus cardiopulmonary syndrome (Vadell *et al.* 2016).

This report provides an ecological baseline which will be used as context in which to evaluate the effects of resource augmentation and predator exclusion, two characteristics of peridomestic habitats, where increased transmission risk of these and other viral pathogens to humans might be expected. Additional results from this research will report on the effects of these experimental manipulations on the sigmodontine communities and species, as well as various aspects of the zoonotic viral populations associated with these rodents.

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Literature cited

Alho, C. J. R. 2005. Intergradation of habitats of non-volant small mammals in the patchy Cerrado landscape. Arquivos do Museu Nacional, Rio de Janeiro 63:41-48.

Asfora, P. H., and A. R. M. Pontes. 2009. The small mammals of the highly impacted North-eastern Atlantic Forest of Brazil, Pernambuco Endemism Center. Biota Neotropical 9:31-35.

Barros, C. S., T. Püttker, B. T. Pinotti, and R. Pardini. 2015. Determinants of capture-recapture success: an evaluation of trapping methods to estimate population and community parameters for Atlantic forest small mammals. Zoologia 32:334-344.

Becker, R. G., G. Paise, L. C. Baumgarten, and E.M. Viera. 2007. Estrutura de comunidades de pequenos mamíferos e densidade de *Necromys lasiurus* (Rodentia, Sigmodontinae) em áreas abertas de cerrado no Brasil central. Mastozoología Neotropical 14:157-168.

Bernardes, M. L. 2006. Estudo de uma comunidade de pequenos mamíferos, com enfoque na variação da população de *Bolomys lasiurus* (Lund, 1841), em uma área de cerrado no estado de Minas Gerais. Unpubl. M.S. thesis, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brasil.

Cáceres, N. C., M. R. Bornschein, W. H. Lopes, and A. R. Percequillo. 2007. Mammals of the Bodoquena Mountains, southwestern Brazil: an ecological and conservation analysis. Revista Brasileira de Zoologia 24:426-435.

Cáceres, N. C., A. P. Carmignotto, E. Fischer, and C. F. Santos. 2008. Mammals from Mato Grosso do Sul, Brazil. Check List 4:321-335.

Cademartori, C. V., M. E. Fabián, and J. O. Menegheti. 2004. Variações na abundância de roedores (Rodentia, Sigmodontinae) em duas áreas de floresta ombrófila mista, Rio Grande do Sul, Brasil. Revista brasileira do Zoociências Juiz de Fora 6:147-167.

Carmignotto, A. P., and C. C. Aires. 2011. Mamíferos não voadores (Mammalia) da Estação Ecológica Serra Geral do Tocantins. Biota Neotropica 11:313-328.

Carnaval, A. C., and C. Moritz. 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. Journal of Biogeography 35:1187-1201.

Cerqueiera, R., R. T. Santori, R. Gentile, and S. M. S. Guapyassu. 2003. Micrographical ecological differences between two populations of *Akodon cursor* (Rodentia, Sigmodontinae) in a Brazilian restinga. Journal of Advanced Zoology 24:46-52.

D'Andrea, P. S., R. Gentile, R. Cerqueira, C. E. V. Grelle, C. Horta, and L. Rey. 1999. Ecology of small mammals in a Brazilian rural area. Revista Brasileira de Zoologia 16:611-620.

D'Elía, G., and U. F. J. Pardiñas. 2015. Subfamily Sigmodontinae Wagner, 1843. Pp. 63-685 *in* Mammals of South America, Volume 2. Rodents (Patton, J. L., G. D'Elía and U. F. J. Pardiñas, eds.). The University of Chicago Press. Chicago, U.S.A.

de la Sancha, N. U., C. L. Higgins, S. J. Presley, and R. E. Strauss. 2014. Metacommunity structure in a highly fragmented forest: has deforestation in the Atlantic Forest altered historic biogeographic patterns? Biodiversity Research 20:1058-1070.

Dirección Nacional De Aeronáutica Civil (DINAC). 2016. El Episodio de El Niño 2015/16 excepcionalmente intenso. Efectos en Paraguay. Dirección de Meteorología e Hidrología, Asunción, Paraguay.

Eastwood, G., J. V. Camp, Y. K. Chu, A. M. Sawyer, R. D. Owen, X. Cao, M. K. Taylor, L. Valdivieso-Torres,R. D. Sage, A. Yu,D. G. Goodin,V. J. Martinez Bruyn, R. C. McAllister, L. Rodriguez, E. P. William, and C. B. Jonsson. 2018. Habitat, species richness and hantaviruses of sigmodontine rodents within the Interior Atlantic Forest, Paraguay. PLoS ONE 13(8):e0201307.

Galiano, D., B. B. Kubiak, J. R. Marinho, and T. R. Ochotorena de Freitas. 2013. Population dynamics of *Akodon montensis* and *Oligoryzomys nigripes* in an Araucaria forest of Southern Brazil. Mammalia 77:173-179.

Gastal, M. L. de A. 1997. Ecología de comunidades de pequenos mamíferos em matas de galería de Brasília, DF. Tese do Doutor em Ecología, Universidad de Brasília, Brasília, Brazil.

Glass, G. E., T. L. Yates, J. B. Fine, T. M. Shields, J. B. Kendall, A. G. Hope, C. A. Parmenter, C. J. Peters, T. G. Ksiazek, C. Li, J. A. Patz, and J. N. Mills. 2002. Satellite imagery characterizes local animal reservoir populations of Sin Nombre virus in the southwestern United States. Proceedings of the National Academy of Science 99:16817-16822.

Han, B. A., J. P. Schmidt, S. E. Bowden, and J. M. Drake. 2015. Rodent reservoirs of future zoonotic diseases. Proceedings of the National Academy of Science 112:7039-7044.

Hannibal, W., and M. Neves-Godoi. 2015. Non-volant mammals of the Maracaju Mountains, southwestern Brazil: composition, richness and conservation. Revista Mexicana de Biodiversidad 86:217-225.

Harris, I., P. D. Jones, T. J. Osborn, and D. H. Lister. 2014. Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. International Journal of Climatology 34:623-642.

Huang, C., S. Kim, K. Song, J. R. G. Townshend, P. Davis, A. Alstatt, J. R. G. Townshend, P. Davis, K. Song, C. J. Tucker, O. Rodas, A. Yanosky, R. Clay, and J. Musinsky. 2007. Rapid loss of Paraguay's Atlantic forest and the status of protected areas – a Landsat assessment. Remote Sensing of Environment 106:460-466.

Huang, C., S. Kim, K. Song, J. R. G. Townshend, P. Davis, A. Alstatt, J. R. G. Townshend, P. Davis, K. Song, C. J. Tucker, O. Rodas, A. Yanosky, R. Clay, and J. Musinsky. 2009. Assessment of Paraguay's forest cover change using Landsat observations. Global and Planetary Change 67:1-12.

Keesing, F., L. K. Belden, P. Daszak, A. Dobson, C. D. Harvel, H. E. Holt, P. Hudson, A. Jolles, K. E. Jones, C. E. Mitchell, S. S. Myers, T. Bogich, and R. S. Ostfeld. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468:647-652.

Klink, C. A., and A. G. Moreira. 2002. Past and current human occupation, and land use. Pp. 69-88 *in* The Cerrados of Brazil (Oliveira, P. S., and R. J. Marquis, eds.). Columbia University Press. New York, U.S.A.

Klink, C. A., and R. B. Machado. 2005. Conservation of the Brazilian Cerrado. Conservation Biology 19:707-713.

Lacher, T. E., Jr., and M. A. Mares. 1986. The structure of Neotropical mammal communities: an appraisal of current knowledge. Revista Chilena de Historia Natural 59:121-134.

Machado, A. F., C. F. Marks, B. Peres, G. L. Melo, and N. C. Cáceres. 2019. Movement and use of environmental structures, climbing supports and shelters by *Akodon montensis* (Sigmodontinae, Rodentia) in the Atlantic Forest of southern Brazil. Mammalia https://doi.org/10.1515/mammalia-2018-0096.

Maestri, R., and J. R. Marinho. 2014. Singing in the rain. Rainfall and moonlight affect daily activity patterns of rodents in a Neotropical forest. Acta Theriologica DOI 10.1007/s13364-014-0177-x.

Magnusson, W. E., V. M. G. Layme, and A. P. Lima. 2010. Complex effects of climate change: population fluctuations in a tropical rodent are associated with the southern oscillation index and regional fire extent, but not directly with local rainfall. Global Change Biology 16:2401-2406.

Mares, M. A. 1982. The scope of South American mammalian biology: perspectives on a decade of research. Pp. 1-26 *in* Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology Special Publications No. 6. Linesville, U.S.A.

Mares, M. A., and K. A. Ernest. 1995. Population and community ecology of small mammals in a gallery forest of central Brazil. Journal of Mammalogy 76:750-768.

Melo, G. L., J. Sponchiado, A. F. Machado, and N. C. Cáceres. 2011. Small-mammal community structure in a South American deciduous Atlantic Forest. Community Ecology 12:58-66.

Meserve, P. L., D. A. Kelt, M. A. Previtali, W. B. Milstead, and J. R. Gutiérrez. 2011. Global climate change and small mammal populations in north-central Chile. Journal of Mammalogy 92:1223-1235.

Morand, S., K. Blasdell, F. Bordes, P. Buchy, B. Carcy, K. Chaisiri, Y. Chaval, J. .e Jean-François, C. M. Desquesnes, S. Jittapalapong, T. Jiyipong, A. Karnchanabanthoen, P. , J.-M. Rolain, and A. Tran. 2019. Changing landscapes of Southeast Asia and rodent-borne diseases: decreased diversity but increased transmission risks. Ecological Applications e01886.

Muñoz-Pedreros, A., S. Fletcher, J. Yañez, and P. Sánchez. 2010. Diversidad de micromamíferos en tres ambientes de la Reserva Nacional Lago Peñuelas, Región de Valparaiso, Chile. Gayana 74:1-11.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. G. de Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Ojeda, R. A., P. G. Blendinger, and R. Brandl. 2000. Mammals in South American drylands: Faunal similarity and trophic structure. Global Ecology and Biogeography 9:115-123.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'amico, Illanga Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51:933–938.

Owen, R. D. 2013. Ecology of small terrestrial mammals in an isolated Cerrado patch, eastern Paraguay: communities, species, and effects of ENSO, precipitation, and fire. Mastozoología Neotropical 20:97-112.

Owen, R. D., D. G. Goodin, D. E. Koch, Y-K. Chu, and C. B. Jonsson. 2010. Spatiotemporal variation in *Akodon montensis* (Cricetidae: Sigmodontinae) and hantaviral seroprevalence in a subtropical forest ecosystem. Journal of Mammalogy 91:467-481.

Peel, M. C., B. L. Finlayson, and T. A. McMahon. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11:1633-1644.

Ribeiro, R., and J. Marinho-Filho. 2005. Estrutura da comundade de pequenos mamíferos (Mammalia, Rodentia) da Estação Ecológica de Águas Emendadas, Planaltina, Distrito Federal, Brasil. Revista Brasileira de Zoologia 22:898-907.

Rohlf, F. J. 2005. NTSYSpc. Numerical taxonomy and multivariate analysis system, version 2.2. Exeter Software. Setauket, U.S.A.

Santos, P. H. P. dos. 2008. Estudo da comunidade de pequenos mamíferos não-voadores, sob efeito do fogo e da borda, em área de floresta de transição Amazônia-Cerrado, Querência, MT. Dissertação de Mestrado, Universidade Federal do Pará, Belém, Brazil.

Silva, J. F., M. R. Fariñas, J. M. Felfili, and C. A. Klink. 2006. Spatial heterogeneity, land use and conservation in the Cerrado region of Brazil. Journal of Biogeography 33:536-548.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical Taxonomy. The Principles and Practice of Numerical Classification. W.H. Freeman and Company. San Francisco, U.S.A.

Sponchiado, J., G. L. Melo, and N. C. Cáceres. 2012. Habitat selection by small mammals in Brazilian Pampas biome. Journal of Natural History 46:1321-1335.

Vadell, M. V., F. G. Erize, and I. E. G. Villafañe. 2017. Evaluation of habitat requirements of small rodents and effectiveness of an ecologically-based management in a hantavirus-endemic natural protected area in Argentina. Integrative Zoology 12:77-94.

Willig, M. R., S. J. Presley, R. D. Owen, and C. López-González. 2000. Composition and structure of bat assemblages in Paraguay: a subtropical-temperate interface. Journal of Mammalogy 81:386-401.

Wolter, K., and M. S. Timlin. 1993. Monitoring ENSO in COADS with a seasonally adjusted principal component index. Proc. of the 17th Climate Diagnostics Workshop, Norman, OK, NOAA/NMC/CAC, NSSL, Oklahoma Climate Survey, CIMMS and the School of Meteorology, University of Oklahoma. Norman, U.S.A.

Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO events - how does 1997/98 rank? *Weather* 53:315-324.

Wolter, K., and M. S. Timlin. 2011. El Niño/Southern Oscillation behavior since 1871 as diagnosed in an extended multivariate ENSO index (MEI.ext). International Journal of Climatology 31:1074-1087.

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Presence of *Arenavirus* in *Mus musculus*, Chiapas, Mexico

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An outbreak of a highly lethal hemorrhagic fever, caused by an *Arenavirus* whose reservoir was *Peromyscus mexicanus*, occurred in the state of Chiapas, Mexico, in June 1967. In order to determine whether any *Arenavirus* is nowadays present in the same region of the state of Chiapas (municipalities of Ocozocoautla de Espinosa and Berriozábal), we surveyed rodents as potential *Arenavirus* reservoirs. Three species of rodents, *Mus musculus*, *Peromyscus mexicanus,* and *Rattus rattus*, previously identified as *Arenavirus* reservoirs, were registered in the study area. We detected the presence of *Arenavirus* RNA in one *Mus musculus* individual captured in an urban area. It is necessary to continue monitoring wildlife and carry out serological and molecular analyzes to investigate the incidence and future prevalence of *Arenavirus* in the area and propose specific actions for its control.

En junio de 1967, en el estado de Chiapas, ocurrió un brote de fiebre hemorrágica altamente letal, el cual se le atribuyó a un *Arenavirus* cuyo reservorio fue *Peromyscus mexicanus*. Para determinar hoy en día la posible existencia de *Arenavirus* en la misma región del estado de Chiapas (municipios de Ocozocoautla de Espinosa y Berriozábal), se evaluó a los roedores presentes en el área como posibles reservorios de *Arenavirus*. Tres especies de roedores que han sido identificados como reservorios de *Arenavirus*, *Mus musculus*, *Peromyscus mexicanus* y *Rattus rattus* se registraron en el área de estudio. Se detectó la presencia de *Arenavirus* RNA en un individuo de *M. musculus* capturado en un área urbana. Es necesario continuar monitoreando la fauna silvestre y realizar análisis serológicos y moleculares para investigar la incidencia y la prevalencia futura de *Arenavirus* en el área, así como proponer acciones específicas para su control.

Key words: Chiapas; *Mus musculus*; *Rattus rattus*; rodent; virus.

Introduction

An outbreak of a highly lethal hemorrhagic fever occurred in the state of Chiapas in June 1967, in San Leandro ranch at 35 miles (56.3 km) southwest of Palenque (Goldsmith and Shields 1971), in the municipality of Chilón, and 96 km SW (in straight line) of the capital city, Tuxtla Gutiérrez. This hemorrhagic fever in Chiapas clinically resembled hemorrhagic fevers caused by arenaviruses from South America, and the outbreak was preceded by a large-scale deforestation and an increase in the abundance of rodents in and around houses in the epidemic area in the 3-year period before 1967 (Goldsmith and Shields 1971). Hypothetically, Ocozocoautla de Espinosa Virus (OCEV) or an *Arenavirus* phylogenetically closely related to OCEV was the etiologic agent in the hemorrhagic fever epidemic in Chiapas in 1967. At present, OCEV is the cause of a human disease that is clinically indistinct from dengue hemorrhagic fever and other severe febrile illnesses that are endemic to Chiapas (Cajimat *et al.* 2012). Milazzo *et al.* (2010) reported antibody against a Tacaribe serocomplex virus (*Arenavirus*) in 3 (25 %) of 12 Mexican deer mice (*Peromyscus mexicanus*) captured in the municipality of Ocozocoautla de Espinosa, and Cajimat *et al.* (2012) isolated *Arenavirus* RNA from Mexican deer mice (*P. mexicanus*) captured in the same locality. Analyses of nucleotide and amino acid sequence data indicated that the deer mice were infected with a novel Tacaribe serocomplex virus, which was named for the first time Ocozocoautla de Espinosa Virus.

In order to confirm if the *Arenavirus* RNA is current present in Ocozocoautla de Espinosa and Berriozábal, we surveyed rodents as potential reservoirs of this RNA virus.

Materials and Methods

Study area. The study was carried out in the municipalities of Ocozocoautla de Espinosa and Berriozábal, Chiapas. Rodents were surveyed at different sampling sites (one night per locality) in Ocozocoautla de Espinosa (25-26 September 2017 and 1-2 February 2018) and Berriozábal (8-9 February, 27-28 September 2017, and 24-27 September 2018). To capture the rodents, we used 200 Sherman traps in each sampling sites, which were placed in different types of vegetation and in urban areas. Species were identified using specialized mammal guides (Álvarez-Castañeda *et al.* 2017). The animals were collected under the scientific collection permit number FAUT-0143 of CL (official letter No. SGPA/DGVS/002779/18), following the protocols established for capturing and handling mammals by the American Society of Mammalogists (Sikes *et al.* 2016).

Strict biosecurity measures were used while sampling species, including use of disposable laboratory coats, goggles, latex gloves, and masks with filters to avoid inhalation of possible pathogens and other contaminating particles. For each specimen, body measurements, weight, sex, and reproductive condition were recorded, as well as type of habitat and geographic location (Martin *et al.* 2011). Tissue samples (liver) were taken from two specimens of each species and placed in sterile 2 ml tubes with RNAlater™ (Sigma) and preserved at -20 °C. All specimens and tissues were deposited and cataloged in the Mammal Collection of El Colegio de la Frontera Sur (ECO-SC-M), San Cristóbal de Las Casas, Chiapas. The rest of specimens were released in the site in which were captured.

Detection of Arenavirus *RNA.* This analysis was made in the Laboratorio de Ecología Evolutiva, in the Universidad de Ciencias y Artes de Chiapas. RNA was extracted from liver samples RNAlater™ (Sigma) and preserved at -20 °C to determine the presence of *Arenavirus*. RNA extraction was carried out with the QIAamp Viral RNA Mini extraction kit (Qiagen, USA), according to manufacturer instructions.

The molecular detection of *Arenavirus* genes was carried out using the reverse transcription polymerase chain reaction (RT-PCR). The retrotranscription was performed according to manufacturer instructions by the Thermo Scientific RevertAid First Strand cDNA Synthesis Kit for obtaining complementary DNA (cDNA). The reaction mixture was prepared with 5 µl of sample of RNA from liver tissue of 21 samples of rodents: 1 µl of Oligo $(dT)_{18}$ primer and 6 µl of nuclease-free water; it was mixed, briefly centrifuged and incubated at 65 °C for 5 minutes. The following components were added: 4 µl reaction buffer (5x), 1 µl ribonuclease inhibitor (RiboLock Rnase Inhibitor), 12 µl of 10mM deoxynucleotide triphosphate (dNTP's mix) and 1 µl of reverse transcriptase (RevertAid M RT). All was mixed, centrifuged briefly and incubated at 42 °C for 60 minutes and the reaction was terminated by heating at 70 °C for 5 minutes.

The detection of *Arenavirus* positive controls was carried out through the nested RT-PCR reaction with a first round of amplification where the Aren 1+ (5'-CWA TRT ANG GCC AIC CIT CIC C-3') and Aren 1- (5'-TNR WYA AYC ART TYG GIW CIR TKC C-3') primers were used, amplifying approximately 450 base pairs (bp; Castellar *et al.* 2017). The reaction had an initial denaturation time at 94 °C for 2 minutes, followed by 30 cycles of denaturation at 94 °C for 1 minute, an alignment at 60 °C for 1 minute, an extension of 72 °C for 30 seconds; decreasing 0.5 ºC per cycle, then 15 cycles of denaturation at 94 ºC for 1 minute, 45 ºC of alignment for 1 minute and an extension at 72 ºC for 30 seconds and a final extension at 72 ºC for 5 minutes.

In the second round, 1 µl of the amplified product was used, under the following conditions: a denaturation at 94 °C for 2 minutes, 40 cycles of denaturation at 94 °C for 30 seconds, alignment at 45 °C for 1 minute, an extension at 72 °C for 30 seconds and a final extension phase at 72 °C for 5 minutes, using the primers Aren 2+ (5'- CAN ANY TTR TAN ARN AIR TTY TCR TAI GG-3') and Aren 2- (5'- AGY YTN KNN GCN GCI CTI AAR GC-3'), which amplify in an internal fragment of 200 bp. The mixtures for both rounds of amplification were prepared under the following conditions: 5 µl of Green GoTaq Flexi Buffer 1X, 1.5 µl of $MgCl_2$ (25 mM), 0.5 µl of dNTPs (10 mM), 1 µl of each primer (10 pmol), 14.9 µl of nuclease-free water and 0.15 µl of GoTaq DNA polymerase (5µ/µl) Promega ® for a final volume of 24 µl.

The amplified products were visualized on a 2 % agarose gel using 3 µl of sample. In each gel was included a 1 µl line of 100 bp molecular weight marker whose total length is 1,500 bp per line; for 90 minutes at 100 V. The gel was stained with ethidium bromide (3,8-diamino-6-ethyl-5-phenylphenanthridium bromide; 10 mg/ml), taking an image with the Vision Works Software and the GelMaxImager UVP ® equipment.

Results

Rodents as reservoirs of Arenavirus. A total of 26 rodent specimens were collected in Ocozocoautla de Espinosa (3 *Handleyomys rostratus*, 1 *Heteromys desmarestianus*, 2 *Mus musculus*, 5 *Peromyscus aztecus*, 15 *Peromyscus mexicanus*), and 84 in Berriozábal (7 *H. desmarestianus*, 1 *M. musculus*, 1 *Oryzomys couesi*, 21 *P. aztecus*, 1 *P. leucopus*, 44 *P. mexicanus*, 1 *Rattus rattus*, 4 *Scotinomys teguina*, 4 *Sigmodon toltecus*), from which *M. musculus* (Sudia *et al.* 1975; Bowen *et al.* 1997), *P. mexicanus* (Salazar-Bravo *et al.* 2004; Milazzo *et al.* 2010; Cajimat *et al.* 2012), and *R. rattus* (Li *et al.* 2015) have been considered natural reservoirs of *Arenavirus*.

Detection of Arenavirus *RNA.* Of the 20 samples analyzed (5 *P. aztecus*, 9 *P. mexicanus*, 3 *H. rostratus*, 1 *H. desmarestianus*, 2 *M. musculus*), one was positive to the presence of *Arenavirus* RNA. The positive case corresponded to a specimen of *M. musculus* (ECO-SC-M 8945) collected in February 1st, 2018 in Ocuilapa, municipality Ocozocoautla de Espinosa, Chiapas (16.8542° N, -93.4107° W), inside the kitchen of one house located in the center of the city.

Discussion

The finding of *Arenavirus* in a synanthropic rodent species (*M. musculus*), in the same region where an outbreak of a highly lethal hemorrhagic fever occurred 50 years ago, should be a warning sign. In 1967, the outbreak was preceded by a large-scale deforestation in the area and an increase in the abundance of rodents around and inside people's homes (Goldsmith and Shields 1971). In this report, the positive rodent was captured in the kitchen of a rural village, in close proximity with people. In addition, *P. mexicanus, M. musculus* and *R. rattus*, which were captured in our survey, have a long history as reservoirs and transmitters of diseases to humans (Kosoy *et al.* 2015; Williams *et al.* 2018), and have been reported as carriers of antibodies to *Arenavirus* in the area or other places of the world (Sudia *et* al. 1975; Bowen et al. 1997; Salazar-Bravo et al. 2004; Milazzo et al. 2010; Cajimat et al. 2012; Li et al. 2015).

It is important to continue carrying out molecular analyzes to detect *Arenavirus* in mammals (increasing the sample number) that have previously been found to serve as reservoirs of zoonotic virus hemorrhagic fever (VHF) in order to determine recidivism and prevalence of viruses that cause hemorrhagic fevers, and thereby be able to respond to outbreaks of VHF in Mexico.

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Literature cited

Álvarez-Castañeda, S. T., T. Álvarez, and N. González-Ruiz. 2017. Keys for Identifying Mexican Mammals. Johns Hopkins University Press. Baltimore, U.S.A.

Bowen, M. D., C. J. Peters, and S. T. Nichol. 1997. Phylogenetic analysis of the *Arenaviridae*: patterns of virus evolution and evidence for cospeciation between arenaviruses and their rodent hosts. Molecular Phylogenetics and Evolution 8:301–16.

Cajimat, M. N. B., M. L. Milazzo, R. D. Bradley, and Ch. F. Fulhorst. 2012. Ocozocoautla de Espinosa virus and hemorrhagic fever, Mexico. Emerging Infectious Diseases 18:401–405.

Castellar, A., M. Guevara, J. D. Rodas, A. F. Londoño, E. Arroyave, F. J. Díaz, S. Levis, and P. J. Blanco. 2017. Primera evidencia de infección por el virus de la coriomeningitis linfocítica (*Arenavirus*) en roedores *Mus musculus* capturados en la zona urbana del municipio de Sincelejo, Sucre, Colombia. Biomédica 37:75-85.

Goldsmith, R. S., and K. P. Shields. 1971. Epidemic in southern Mexico of disease resembling virus hemorrhagic fevers. Lancet 2:151-154.

Kosoy, M., L. Khlyap, J. F. Cosson, and S. Morand. 2015. Aboriginal and invasive rats of genus *Rattus* as hosts of infectious agents. Vector Borne and Zoonotic Diseases 15:3–12.

Li, K., X. D. Lin, W. Wang, M. Shi, W. P. Guo, X. H. Zhang, J. G. Xing, J. R. He, K. Wang, M. H. Li, J. H. Cao, M. L. Jiang, E. C. Holmes, and Y. Z. Zhang. 2015. Isolation and characterization of a novel arenavirus harbored by Rodents and Shrews in Zhejiang province, China. Virology 476:37–42.

Martin, R. R., R. H. Pine, and A. F. DeBlase. 2011. A Manual of Mammalogy; with Keys to Families of the World. Third Edition. Waveland Press. Long Grove, U.S.A.

Milazzo, M. L., A. Barragán-Gómez, J. D. Hanson, J. G. Estrada-Franco, E. Arellano, F. X. González-Cózatl, I. Fernández-Salas, F. Ramírez-Aguilar, D. S. Rogers, R. D. Bradley, and C. F. Fulhorst. 2010. Antibodies to Tacaribe serocomplex viruses (family Arenaviridae, genus *Arenavirus*) in cricetid rodents from New Mexico, Texas, and Mexico. Vector Borne and Zoonotic Diseases 10:629–637.

Salazar-Bravo, J., B. Armién, G. Suzán, A. Armién, L. A. Ruedas, M. Avila, Y. Zaldívar, J. M. Pascale, F. Gracia, and T. L. Yates. 2004. Serosurvey of wild rodents for hantaviruses in Panama, 2000-2002. Journal of Wildlife Diseases 40:103–109.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688.

Sudia, W. D., V. F. Newhouse, L. D. Beadle, D. L. Miller, J. G. Jr. Johnston, and R. Young. 1975. Epidemic Venezuelan equine encephalitis in North America in 1971: Vector studies. American Journal of Epidemiology 101:17–35.

Williams, S. H., X. Che, A. Paulick, C. Guo, B. Lee, D. Muller, A. C. Uhlemann, F. D. Lowy, R. M. Corrigan, and W. I. Lipkin. 2018. New York City house mice (*Mus musculus*) as potential reservoirs for pathogenic bacteria and antimicrobial resistance determinants. mBio 9:e00624-18.

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The least known with the smallest ranges: analyzing the patterns of occurrence and conservation of South American rodents known only from their type localities

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The identification of taxa with small range sizes is important both from an ecological and conservational perspective. As other small mammals, several species of rodents have restricted geographical distributions, a situation that could increase their immediate risk of extinction. Species having restricted ranges and/or low population sizes have usually lower genetic variation than wide-ranging relatives, being highly susceptive to disruptive treats, such as new or introduced competitors, pathogens, and predators, severe climatic events, cataclysms, and/or population-level phenomena. We reviewed the most recent compilations on South American rodents to identify those only known from their type locality (*i. e.*, an area with a maximum latitudinal and longitudinal range of < 10 km). This restriction is in accordance with an extent of occurrence < 100 km^2, which fits partially with the criterion B1 of the IUCN for an extent of occurrence of a critically endangered species. For each species, we recorded the year of description, country of origin, main habitat use, use of substrate, and conservation status. We identified 58 species of South American rodents that are known only from their type localities or their vicinities. These species belong to two suborders, seven families, and 29 genera. The family with more species in this list is Cricetidae, which accounted for a half of the included species. Most species in our list were described during the decades of 1890-1930 and 1990 to recent. The habitat type with more species in the list was tropical forest. Almost a third of the species are considered under the highest categories of threat, such as CR, EN o VU. Two species within the list are considered to become extinct in historical times, including the akodont *Juscelinomys candango* and the vizcacha *Lagostomus crassus*. Almost half of the species in our list are referred as DD. Fifty eigth rodent species from South American are only known from their type localities and their surroundings; *i. e.*, *ca.* 9 % of the currently approximately 650 recorded species of the subcontinent. The species list provided here need to be depurated trough additional field and collection based work. Even when some species could be removed from this list (due taxonomical changes or additional records from other localities), it is also possible than others could be included. Most species in our list are found at or close to highland areas, such as the Andes or the Serra do Mar, suggesting that at least partially the rarity of some of them could be related to the relative inaccessibility of these places. As in previous contributions focused on geographically restricted taxa, most species in our list are considered as DD in the IUCN Red List. This is unfortunate, since species listed as DD usually do not gain much attention (*i. e.*, conservation programs, founds) as those considered as CR, EN or VU. Previous authors discussed this point, suggesting the need to designate as CR all species geographically restricted to their type localities, at least when no recent records (*i. e.*, in the last 25 years) exists.

La identificación de especies con áreas de distribución pequeña es importante tanto desde una perspectiva ecológica como de conservación. Como es frecuente en mamíferos pequeños, varias especies de roedores tienen distribuciones geográficas restringidas. Las especies que ocupan áreas restringidas y/o tienen tamaños poblacionales pequeños suelen tener una variación genética menor que aquellas de distribución más amplia y son más susceptibles a situaciones disruptivas, como la introducción de competidores, patógenos y depredadores, eventos climáticos severos, cataclismos y/o fenómenos a nivel poblacional. Revisamos las compilaciones más recientes sobre roedores de América del Sur para identificar aquellas especies que únicamente se conocen de su localidad tipo (es decir, un área con un intervalo máximo, latitudinal y longitudinal, de < 10 km). Esta restricción está de acuerdo con una extensión de la ocurrencia < 100 km^2, que se ajusta parcialmente al criterio B1 de la UICN para una extensión de ocurrencia de una especie en peligro crítico. Para cada especie, registramos el año de descripción, país de origen, uso principal del hábitat, uso del sustrato y estado de conservación. Identificamos 58 especies de roedores sudamericanos que se conocen sólo de sus localidades tipo y/o cercanías. Estas especies pertenecen a dos subórdenes, siete familias y 29 géneros. La familia con más especies en esta lista es Cricetidae, que representó la mitad de las especies incluidas. La mayoría de las especies en nuestra lista fueron descritas durante las décadas de 1890-1930 y 1990-2019. El tipo de hábitat con más especies en la lista fue el bosque tropical. Casi un tercio de las especies se consideran en las categorías más altas de amenaza, como CR, EN o VU. Dos especies dentro de la lista están consideradas como extintas en tiempos históricos, incluyendo el ratón *Juscelinomys candango* y la vizcacha *Lagostomus crassus*. Casi la mitad de las especies en nuestra lista son referidas como DD. Hay 59 especies de roedores sudamericanos que se conocen sólo de su localidad tipo; es decir, *ca.* del 9 % de las aproximadamente 650 especies registradas actualmente en el subcontinente. La lista de especies que proporcionamos debe depurarse a través de trabajo adicional, tanto en el campo como en colecciones biológicas. Incluso cuando algunas especies podrían eliminarse de esta lista (debido a cambios taxonómicos o registros adicionales de otras localidades), también es posible que otras puedan incluirse. La mayoría de las especies en nuestra lista se encuentran en o cerca de áreas de tierras altas, como los Andes o la Serra do Mar, lo que sugiere que al menos parcialmente la rareza de algunas de ellas podría ser un artefacto relacionado a la relativa inaccesibilidad a estos lugares. Como en contribuciones anteriores centradas en taxones restringidos geográficamente, la mayoría de las especies en nuestra lista se consideran DD en la Lista Roja de la UICN. Esto es desafortunado, ya que las especies listadas como DD generalmente no reciben tanta atención (es decir, fondos para establecer programas de investigación o conservación) como aquellas consideradas como CR, EN o VU. Autores anteriores discutieron este punto, sugiriendo la necesidad de designar como CR a todas las especies restringidas geográficamente a sus localidades tipo, al menos cuando éstas no tengan registros recientes (es decir, en los últimos 25 años).

Key words: distribution; endemism; extinction; rare species; Rodentia; small mammals.

Introduction

With *ca.* 2600 species, rodents compose the most diverse order within Mammalia, including about 42 % of the living mammal species (D'Elía *et al.* 2019a). Native rodents inhabit almost every habitat on Earth, except Antarctica, New Zealand, and some oceanic islands. They occupy a large variety of terrestrial and freshwater niches, including even gliding species (D'Elía *et al.* 2019a). As other small mammals, rodents play a fundamental role in trophic chains, acting as preys of other vertebrates, and contributing to energy and nutrient flow, providing key functions to the ecosystems, such as seed dispersal or soil removal (Lacher *et al.* 2017). Despite these characteristics, rodents are among the least known mammals, both in terms of their taxonomy and natural history, with many species that are known only from the holotype or type series and frequently from collections made more than a century ago (Amori *et al.* 2016).

From a conservational perspective, even when laudable efforts exists (notable the IUCN Small Mammal Specialist Group, which also covers tree shrews and eulipotyphlans), rodents are not charismatic species as other medium and large mammals (*e. g.*, canids, cetaceans, felids or ungulates), attracting little attention from media and financial founds (Fleming and Bateman 2016). This is an unfortunate situation, since the historical record indicates that rodents are among the most vulnerable mammals to extinction owing to direct or indirect human activities, accounting *ca.* 53 % of the total number of mammal losses during the last 500 years (Turvey 2009).

As other small mammals, several species of rodents have restricted geographical ranges, a fact that could increase their immediate risk of extinction (*e. g.*, Gaston 1994). It is widely accepted that species having restricted distributions and/or low population sizes have usually lower genetic variation than wide-ranging relatives (*e. g.*, Caughley 1994; MacArthur and Wilson 1967), being highly susceptive to disruptive treats, such as new or introduced competitors, pathogens, and predators, severe climatic events (*e. g.*, droughts), cataclysms (*e. g.*, volcanic eruptions), and/or population-level phenomena (*e. g.*, inbreeding depression). An eloquent example of the vulnerability of rodents with restricted distributional ranges is the biological extinctions of *ca.* 21 endemic species from the Caribbean islands since 1500 AD after the European colonization (Turvey 2009).

At the time of description, new species are known at least from one locality (*i. e.*, the type locality) and a single individual (*i. e.*, the holotype), on which the species description is based. The known distribution of most species is normally enlarged as new specimens are recorded in other localities. However, some species remaining being known from only the vicinities of their type localities; sometimes, this fact reflects the existence of microendemisms (*e. g.*, *Phyllotis bonariensis*, which is apparently restricted to the hilly system of Ventania in central-eastern Argentina; see Steppan and Ramírez 2015), but in most cases is only because of the limited field work or to already collected specimens have not been identified as representative of those species.

In this contribution, we reviewed the distribution patterns, main habitats, use of substrate, and conservation implications of South American rodents that are only known from their type locality or its immediate surroundings. We also discussed if these species are geographically distributed in poorly surveyed areas or if they share some life traits that may make them easy to overlook (*e. g.*, fossoriality).

Materials and methods

To identify those species only known from their type localities and/or its immediate surroundings, we reviewed the most recent compilations on Neotropical rodents, using Patton *et al.* (2015) as starting point. For those species described since 2015, we consulted the review of D'Elía *et al.* (2019a) plus the literature published after December 2017, which is the date that ends the period included in this review. We also reviewed the primary literature. In each case, we individually reviewed the distributional range of each taxon, searching in published (*e. g.*, Patton *et al.* 2015) and online data sources (*e. g.*, GBIF, www.gbif.org). Taxonomy follows Patton *et al.* (2015), with minor modifications according to the posterior literature.

We use the definition of type locality given by Meiri *et al.* (2017), which considered a maximum latitudinal and longitudinal range of < 10 km (= 0.1º). This restriction is in accordance with an extent of occurrence < 100 km^2, which fits partially with the criterion B1 of the IUCN for an extent of occurrence of a critically endangered species (IUCN, 2017).

For each species, we distinguished between those known only from old records and those recently described or known by repeated records in the type locality. The cut-off between old and recent records was arbitrarily placed at 50 years ago (1969; see Meiri *et al.* 2017 for a similar procedure).

Use of substrate for each species was taken from the literature (e.g., Patton *et al.* 2015). Six main habitat categories were considered in the analysis, following the proposal of Amori *et al.* (2016): *i*) deserts, *ii*) grasslands, *iii*) scrublands, *iv*) temperate forests, *v*) tropical forest, *vi*) unknown.

Results

We identified 58 species of South American rodents that are known only from their type localities or their vicinities (Figure 1, Table 1). These species belong to seven families, of which six belong to Hystricomopha (Table 1). However, the family with more species ($n = 28$; 48.3 % of the total) in this list is Cricetidae, all belonging to the subfamily Sigmodontinae. The 58 identified species are part of 29 genera; the genus with most species in the list is the ctenomyid *Ctenomys* with 11, followed by the cricetid *Thomasomys* with five. Remarkably, some of the South American rodent species known only from the surroundings of their type localities are relatively large animals as the mountain vizcacha *Lagidium ahuacaense* (2,000 g), recorded at a single rocky outcrop point in the coastal Desert of Ecuador and the chinchilla rat *Cuscomys ashaninka* (910 g) only know from its holotype collected at a Peruvian humid cloud forest (Emmons 1999; Spotorno and Patton 2015).

Most species included in our list were described during the decades of 1890 to 1930 (*n* = 18; 31 %) and 1990 to recent (*n* = 33; 56.9%), with a peak between 1990-2000 (*n* = 14; 24.1 %); Table 1; Figure 2). More than the half of the surveyed species (*n* = 36; 61.1 %) were described since 1969. At least four species of those described prior to 1969 (*i. e.*, *Ctenomys bicolor*, *Phyllomys thomasi*, *Phyllotis bonariensis*, and *Santamartamys rufodorsalis*) were recorded again from their type localities during the last 50 years (cf. Patton *et al.* 2015).

The majority of the selected species were collected at open to brushy and arid-semiarid to temperate habitats, including deserts (*n* = 6; 10.3 %), grasslands (*n* = 14; 24.1 %), and scrublands (*n* = 14; 24.1 %). However, the habitat type with more species in the list was tropical forest (*n* = 21; 36.2 %; Table 1; Figure 3). Looking at the country of origin, we observed that a high number of the species in our list occurs in Argentina (*n* = 21; 36.2 %), Brazil (*n* = 12; 20.7 %), and Peru (*n* = 9; 15.5 %). Other seven countries are represented by 1 (Colombia, Paraguay, Uruguay, Venezuela) to 3 (Bolivia) or 6 (Ecuador) species (Table 1). No species comes from Guyana, Suriname or French Guiana.

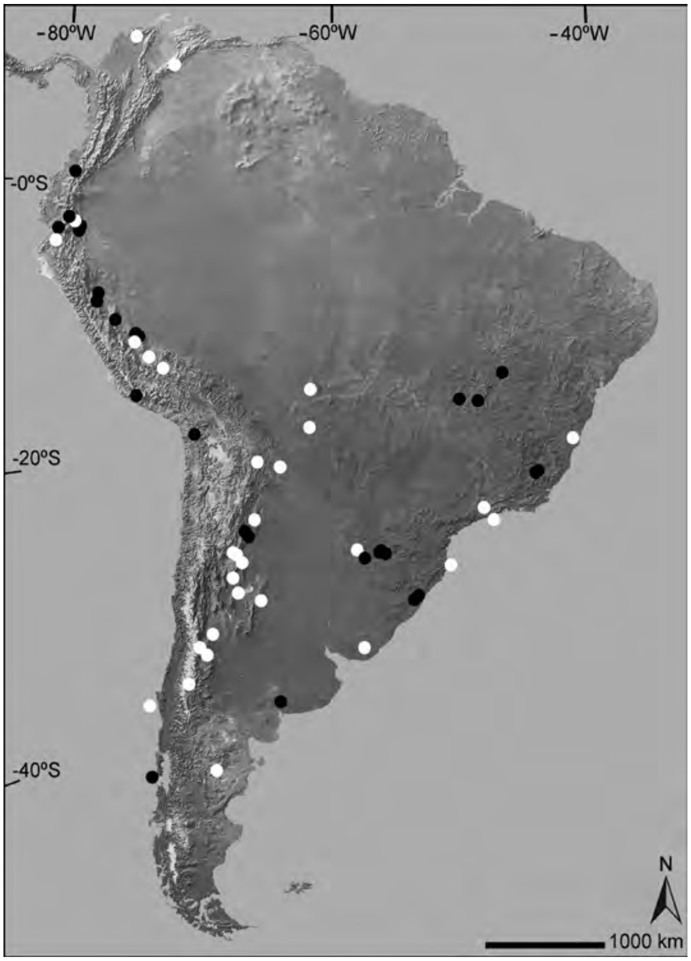

Figure 1. Map of South America depicting the geographical distribution of those rodent species only known from their type localities (black circles = sigmodontine; white circles = caviomorph).

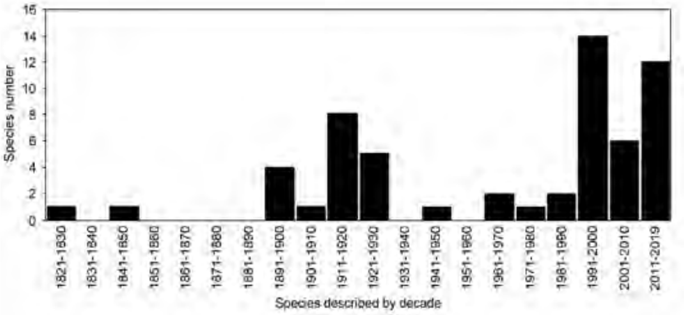

Figure 2. Number of South American rodent species described by decade between 1820 and the present that are only known from their type localities.

Regarding the use of substrate, four major groups can be recognized: cursorial (*n* = 32; 55.2 %), fossorial (*n* = 16; 27.6 %), climber (*n* = 9; 15.5 %), and semiaquatic (*n* = 2; 3.4 %; Table 1).

In terms of conservation status as considered by the IUCN Red List , two species (3.4 %) are considered as extinct (EX), including the akodont *Juscelinomys candango* and the vizcacha *Lagostomus crassus* (Table 1; Figure 4). Almost a third of the remaining species are considered under the highest categories of threat, such as critically endangered (CR; *n* = 8; 13.8 %), endangered (EN; *n* = 3; 5.2 %), vulnerable (VU; *n* = 3; 5.2 %) or near threatened (NT; *n* = 1; 1.7 %). Only one species is considered as of least concern (LC; *n* = 1; 1.7 %); while almost half of the species in our list are referred as data deficient (DD; *n* = 26; 44.8 %). Finally, the IUCN has not yet evaluated most of the species described or removed from the synonymy of other taxa since 2014; consequently these species are listed as not evaluated (NE; *n* = 14; 24.1 %; Table 1; Figure 3).

Discussion

Our study document that 58 rodent species from South American are only known from their type localities and their surroundings; *i. e.*, ~9 % of the currently ~650 recorded species of the subcontinent (Patton *et al.* 2015). The number

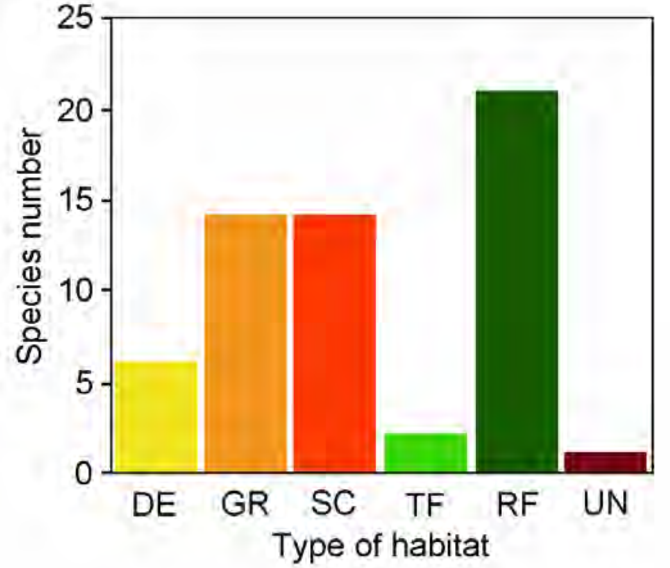

Figure 3. Number of South American rodent species by habitat type that are only known from their type localities. Abbreviations are as follow: deserts (DE); grasslands (GR); scrublands (SC); temperate forests (TF); tropical forest (RF); unknown (UN).

Table 1. List of species of South American rodent that are only known from their type localities.

	Suborder	Family	Year of description	Habitat	Country	Habits	UICN
Akodon kotosh	Supramyomorpha	Cricetidae	2016	tropical forest	Peru	cursorial	NE
Akodon mystax	Supramyomorpha	Cricetidae	1998	grassland	Brazil	cursorial	DD
Akodon philipmyersi	Supramyomorpha	Cricetidae	2005	grassland	Argentina	cursorial	DD
Brucepattersonius guarani	Supramyomorpha	Cricetidae	2000	tropical forest	Argentina	cursorial	DD
Brucepattersonius misionalis	Supramyomorpha	Cricetidae	2000	tropical forest	Argentina	cursorial	DD
Brucepattersonius paradisus	Supramyomorpha	Cricetidae	2000	tropical forest	Argentina	cursorial	DD
Calomys chinchilico	Supramyomorpha	Cricetidae	2007	desert	Peru	cursorial	NE
Cerradomys akroai	Supramyomorpha	Cricetidae	2014	scrubland	Brazil	cursorial	NE
Deltamys araucaria	Supramyomorpha	Cricetidae	2017	tropical forest	Brazil	cursorial	NE
Euneomys fossor	Supramyomorpha	Cricetidae	1899	uncknown	Argentina	uncknown	DD
Geoxus lafkenche	Supramyomorpha	Cricetidae	2016	temperate forest	Chile	fossorial	NE
Hylaeamys tatei	Supramyomorpha	Cricetidae	1998	tropical forest	Ecuador	cursorial	DD
Juliomys ximenezi	Supramyomorpha	Cricetidae	2016	tropical forest	Brazil	climber	NE
Juscelinomys candango	Supramyomorpha	Cricetidae	1965	scrubland	Brazil	cursorial	EX
Microakodontomys transitorius	Supramyomorpha	Cricetidae	1993	scrubland	Brazil	cursorial	EN
Neacomys macedoruizi	Supramyomorpha	Cricetidae	2018	tropical forest	Peru	cursorial	NE
Necromys lilloi	Supramyomorpha	Cricetidae	2016	grassland	Argentina	cursorial	NE
Nectomys saturatus	Supramyomorpha	Cricetidae	1897	tropical forest	Ecuador	semiaquatic	NE
Oxymycterus caparaoe	Supramyomorpha	Cricetidae	1998	grassland	Brazil	cursorial	LC
Phyllotis anitae	Supramyomorpha	Cricetidae	2007	grassland	Argentina	cursorial	DD
Phyllotis bonariensis	Supramyomorpha	Cricetidae	1964	grassland	Argentina	cursorial	NT
Phyllotis osgoodi	Supramyomorpha	Cricetidae	1950	desert	Chile	cursorial	DD
Rhipidomys albujai	Supramyomorpha	Cricetidae	2017	tropical forest	Ecuador	climber	DD
Thomasomys apeco	Supramyomorpha	Cricetidae	1993	tropical forest	Peru	cursorial	VU
Thomasomys fumeus	Supramyomorpha	Cricetidae	1924	tropical forest	Ecuador	cursorial	DD
Thomasomys hudsoni	Supramyomorpha	Cricetidae	1923	scrubland	Ecuador	cursorial	VU
Thomasomys onkiro	Supramyomorpha	Cricetidae	2002	tropical forest	Peru	cursorial	VU
Thomasomys rosalinda	Supramyomorpha	Cricetidae	1926	tropical forest	Peru	cursorial	EN
Abrocoma budini	Hystricomorpha	Abrocomidae	1920	scrubland	Argentina	cursorial	DD
Abrocoma famatina	Hystricomorpha	Abrocomidae	1920	scrubland	Argentina	cursorial	DD
Abrocoma vaccarum	Hystricomorpha	Abrocomidae	1921	scrubland	Argentina	cursorial	DD
Cuscomys ashaninka	Hystricomorpha	Abrocomidae	1999	tropical forest	Peru	cursorial	DD
Cuscomys oblativus	Hystricomorpha	Abrocomidae	1916	tropical forest	Peru	cursorial	DD
Cavia intermedia	Hystricomorpha	Caviidae	1998	grassland	Brazil	climber	CR
Cavia patzeli	Hystricomorpha	Caviidae	1981	grassland	Ecuador	climber	DD
Lagidium ahuacaense	Hystricomorpha	Chinchillidae	2009	desert	Ecuador	cursorial	DD
Lagostomus crassus	Hystricomorpha	Chinchillidae	1910	grassland	Peru	cursorial	EX
Ctenomys andersoni	Hystricomorpha	Ctenomyidae	2014	scrubland	Bolivia	fossorial	NE
Ctenomys bicolor	Hystricomorpha	Ctenomyidae	1914	scrubland	Bolivia	fossorial	NE
Ctenomys brasiliensis	Hystricomorpha	Ctenomyidae	1826	grassland	Uruguay	fossorial	DD
Ctenomys fochi	Hystricomorpha	Ctenomyidae	1919	grassland	Argentina	fossorial	DD
Ctenomys johanis	Hystricomorpha	Ctenomyidae	1921	scrubland	Argentina	fossorial	DD
Ctenomys juris	Hystricomorpha	Ctenomyidae	1920	scrubland	Argentina	fossorial	DD
Ctenomys lessai	Hystricomorpha	Ctenomyidae	2014	grassland	Bolivia	fossorial	NE
Ctenomys osvaldoreigi	Hystricomorpha	Ctenomyidae	1995	grassland	Argentina	fossorial	CR
Ctenomys paraguayensis	Hystricomorpha	Ctenomyidae	2000	grassland	Paraguay	fossorial	NE
Ctenomys pontifex	Hystricomorpha	Ctenomyidae	1918	scrubland	Argentina	fossorial	DD
Ctenomys validus	Hystricomorpha	Ctenomyidae	1977	scrubland	Argentina	fossorial	DD
Ctenomys yatesi	Hystricomorpha	Ctenomyidae	2014	scrubland	Bolivia	fossorial	NE
Ollalamys edax	Hystricomorpha	Echimyidae	1916	tropical forest	Venezuela	climber	DD

Phyllomys mantiqueirensis	Hystricomorpha	Echimyidae	2003	tropical forest	Brazil	climber	CR
Phyllomys thomasi	Hystricomorpha	Echimyidae	1897	tropical forest	Brazil	climber	EN
Phyllomys unicolor	Hystricomorpha	Echimyidae	1842	tropical forest	Brazil	climber	CR
Octodon pacificus	Hystricomorpha	Octodontidae	1994	temperate forest	Chile	cursorial	CR
Tympanoctomys aureus	Hystricomorpha	Octodontidae	2000	desert	Argentina	fossorial	CR
Tympanoctomys kirchnerorum	Hystricomorpha	Octodontidae	2014	desert	Argentina	fossorial	DD
Tympanoctomys loschalchalerosorum	Hystricomorpha	Octodontidae	2000	desert	Argentina	fossorial	CR
Santamartamys rufodorsalis	Hystricomorpha	Octodontidae	1899	tropical forest	Colombia	climber	CR

and identity of species listed may change owing to distinct reasons, in particular as result of both field and taxonomic work. As such, the list provided here is provisory and prone to change in the near future. Having said that, we expect that the general trends discussed here would remain for several years.

The species of our list are not evenly distributed among rodent families. Most belong to the family Cricetidae, a fact that it is not surprising since, in South America, this is the richest species rodent family (Patton *et al.* 2015) and by far the family were more new species are discovered (D'Elía *et al.* 2019a). Moreover, of the three cricetid subfamilies found in South America, none of the listed species belong to Neotominae nor Tylomyinae, but all to Sigmodontinae. The second family with more representatives is Ctenomyidae. No species from our list belongs to the hystricomorph families Erethizontidae, Dinomyidae, Dasyproctidae and Cuniculidae, nor the sciuriomorph Sciuridae and the supramyomorph Heteromyidae.

Amori *et al.* (2016) listed 30 South American rodent species only known from their type localities. Our list includes several restricted species described after Amori *et al.* (2016) closed their data compilation (*i. e.*, 2005), but also several geographically restricted species, such as *Akodon mystax* and *Oxymycterus caparoae*, omitted by Amori *et al.* (2016). In addition, some species listed by Amori (2016) were not included in our list. This fact is consequence of changes prompted by recent taxonomic work (*e. g.*, *Akodon aliquantulus* is now considered a synonymy of *A. caenosus*; *Juscelinomys guaporensis* is now considered a synonym for *J. huancachae*) and because known distributions have been redefined (*e. g.*, *Oecomys cleberi* is now recognized as a widely distribute species in the southern portion of the Brazilian Cerrado; Patton *et al.* 2015).

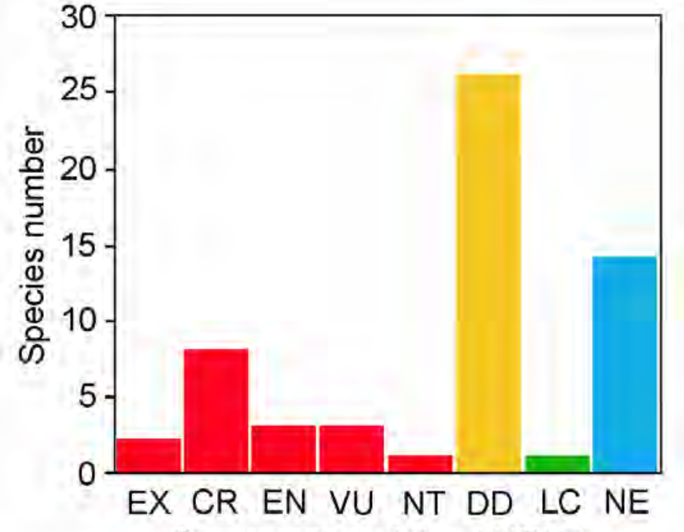

Figure 4. Number of South American rodent species according to their category in the IUCN's Red List that are only known from their type localities. Abbreviations are as follow: EX, extinct; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near treathened; LC, least concern; DD, data deficient, NE, not evaluated

Even when our criterion for inclusion species in the list is clear, some uncertainties persist regarding some species. One of these is *Ctenomys brasiliensis*, the type species of the genus *Ctenomys*. We include it in our list indicating it comes from the Uruguayan grasslands; however, the specific collection locality of the single specimen is unknown (Bidau 2015). Traditionally, *C. brasiliensis* whose collection locality data is consigned as "des parties intérieures du Brésil, de la Province de Las Minas" has been considered as collected in Minas Gerais, Brazil. However, not specimen of *Ctenomys* is known from that Brazilian state, while the holotype of *C. brasiliensis* falls in the morphospace of *C. pearsoni*, an Uruguayan species that inhabits a general area close to the Uruguayan city of Minas (Fernandes *et al.* 2012). In addition, at the time of collection, what is now Uruguay was part of the Brazilian Empire. As such, tentatively *C. brasiliensis* is considered as an Uruguayan form whose distinction of *C. pearsoni* should be further evaluated (Bidau 2015).

The taxonomic distinction of some of the species included in the list is doubtful and, as such, their presence in our list depends on the results of future taxonomic assessments. One of such case is the leaf eared mouse *Phyllotis bonariensis*, a form geographically restricted to the hilly system of Ventania in central-eastern Argentina (Steppan and Ramírez 2015). While some authors maintained this nominal form as a distinct species (being the reason why it is included in our list), others had suggested its conspecificity with *P. xanthopygus*, a species widely distributed in western South America, from Peru to Argentina and Chile (*e. g.*, Teta *et al.* 2018). Another example is that of the vizcacha *Lagostomus crassus*, that may represent an extinct Peruvian population of *L. maximus* (Spotorno and Patton 2015). As an extreme case, it is possibly that the three supposedly endemic species of *Brucepattersonius* from Argentina (*B. guarani*, *B. misionensis*, and *B. paradisus*) could be considered as synonym of *B. iheringi*, a taxon currently distributed in forested areas of southern Brazil (Lanzone *et al.* 2018).

Several reasons could interplay to cause the rarity and/or the absence of recent records for some rodent species;

some of them would be ultimately because of the lack of enough work and others are derived from biological attributes of the species (Amori *et al.* 2016; Meiri *et al.* 2017). For those recently described taxa, rarity could be an artifact of the lack of knowledge, as perhaps not enough time has elapsed for researchers to study them, including their distributional ranges (Meiri *et al.* 2017). If additional fieldwork is conducted, is likely that the known distribution of some species would be enlarged. For example, the fish-eating rat *Neusticomys mussoi* was only known from its type locality in western Venezuela since its description in 1991, being subsequently found at two additional localities in Venezuela and Colombia in 2008 and 2014, respectively (Rodríguez-Posadas 2014). A more eloquent example is that of the Kerr's Atlantic forest rat, *Phyllomys kerri*, that being described in 1950, it was not rediscovered until 68 years later (Abreu-Junior *et al.* 2018). This could be certainly the case of other species in our list, since most of them were described in the last 50 years.

As mentioned above, even when field work is conducted, some biological attributes of the species may hamper the registry of new recording localities, including the fact that some species *i*) could be difficult to observe and collect due to their size, habits (*e. g.*, climber, fossorial), or for being microhabitat specialists; *ii*) could be difficult to distinguish from other species and even when specimens are collected they are misidentified; *iii*) could have low populational densities; or *iv*) could be extinct (Amori *et al.* 2016; Meiri *et al.* 2017). Most species in our list are fossorial (*e. g.*, *Ctenomys*) and some of them are climber (*e. g.*, *Phyllomys*), which make them more difficult to catch trough traditional trapping procedures (Patterson 2002). Two species within our list, *Juscelinomys candango* and *Lagostomus crassus*, are considered extinct by the IUCN Red List; unfortunately, this number could increase in the next years. This could be the case of the water rat *Nectomys saturatus*, which is not observed since 1897 and that has lost most of its habitat owing to growing urbanization and desiccation of the meadows at its type locality (Chiquito and Percequillo 2019).

Most species in our list are found at or close to the Andes, including both forested and desert regions. Thus at least partially, the rarity of some of them could be related to the relative inaccessibility of medium to high altitude Andean areas. This could be the case of the mice of the genus *Thomasomys*, which in addition includes several species that easily confound among them (Pacheco 2015). Montane areas are usually complex geographical systems, in which speciation and microendemism are promoted by physical barriers and vertical succession of habitats (Maestri and Patterson 2016). This could be also the case of the Serra do Mar, in southeastern Brazil, which is included, together with the western Andean ranges, within the high richness areas for rodents in South America (Maestri and Patterson 2016).

At least four species in our list are island endemics; these are *Cavia intermedia* from Moleques do Sul Islands (Santa Catarina, Brazil; Cherem *et al.* 1999), *Geoxus lafkenche* from Guafo Island (Los Lagos, Chile; Teta and D'Elía 2017), *Octodon pacificus* from Mocha Island (Bio Bio, Chile; Hutterer 1994), and *Phyllomys thomasi* from Ilha de São Sebastião (Sao Paulo, Brazil; Emmons *et al.* 2002). Frequently, island endemics are more threatened than their continental counterparts owing to their usually smaller distributions, as well as facing habitat loss and introduction of alien species (Amori and Clout 2003). The four island endemics identified here fall in this trend; the tree of them that have been categorized by the IUCN are listed as CR (*Cavia intermedia* and *Octodon pacificus*) and EN (*Phyllomys thomasi*). We note that none of the endemic oryzomyine species from Galapagos Islands have distributional ranges restricted to their type localities, at least as is here defined; however, all of them occupies small geographical ranges, and are considered as VU (*Aegialomys galapagoensis*, *Nesoryzomys fernandinae*, *N. narboroughi*, *N. swarthi*) or even EX (*N. darwini*, *N. indefessus*).

As in previous contributions focused on geographically restricted taxa, most species in our list are considered as DD in the IUCN Red List (Figure 4), even when the use of this category is explicitly discouraged by the IUCN (IUCN 2017). Amori *et al.* (2016) suggested that this situation reflects a bias produced by the heterogeneity of assessors of the IUCN and the generalized assumption among researchers that extremely rare species are the consequence of suboptimal research efforts rather other causes. This situation is not exempt of consequences; species listed as DD usually do not gain much attention (*i. e.*, conservation programs, founds) as those considered as CR, EN or VU (Amori *et al.* 2016). Almost one fourth of the species in our survey are included under one of the highest three categories of threat defined by the Red List (*e. g.*, CR, EN, VU). Remarkably, there are more caviomorph than sigmodontine rodents on that list, perhaps because vizachas, chinchilla rats, and their relatives are more charismatic than mice and rats. Amori *et al.* (2016) draw attention to the points discussed here, suggesting the need to designate as CR all species geographically restricted to their type localities, at least when there are no recent records (*i. e.*, in the last 25 years).

The identification of those species with the smallest ranges is important both from an ecological and conservational perspective (Meiri *et al.* 2017). On the one hand, most of the geographically restricted species may be functionally analogous to "singletons" in ecological communities, being mostly unknown in their basic aspects of their natural history (*e. g.*, diet, movements, reproduction). True narrow endemic species are also pivotal to understood biogeographical processes (Meiri *et al.* 2017). On the other hand, considering these species is crucial to develop adequate conservation strategies and to decide how to allocate finite resources (Amori *et al.* 2016). As such, the species list provided here needs to be depurated trough additional field and collection based work. Even when some species could be removed from this list, it is also possible that others could be included. We close this contribution by stating that we expect that our list and the considerations expressed will help draw attention to those poorly known South American rodent species, triggering the desire to conduct research on them. Also, we expect that authorities and agencies granting funds and authorizations to conduct field work understand the importance of this activity towards a better knowledge on these species and ultimately towards their conservation (see Thomson *et al.* 2018 and D'Elía *et al.* 2019b).

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Literature Cited

Abreu-Júnior, E. F., A. R. Percequilloa, L. Geise, Y. L. R. Leite, and A. C. Loss. 2018. Unveiling the identity of Kerr's Atlantic tree rat, *Phyllomys kerri* (Rodentia, Echimyidae). Mammalian Biology 91:57–70.

Amori, G., and M.N. Clout. 2003. Rodents on islands: a conservation challenge. Pp. 63-68 *in* Rats, Mice and People: Rodent Biology and Management (Singleton, G. R., C. A. Hinds, C. J. Krebs, and D. M. Spratt, eds.). ACIAR Monographs 96. Sidney, Australia.

Amori, G., G. A. Esposito, and L. Luiselli. 2016. Known from a handful of specimens: analyzing the worldwide patterns of occurrence and conservation of rodents and shrews recorded only from the type locality. Journal of Threatened Taxa 8:8556–8563.

Bidau, C. J. 2015. Familia Ctenomyidae. Pp. 818-877 *in* Mammals of South America (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press. Chicago & London.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244. https://doi.org/10.2307/5542

Cherem, J. J., J. Olimpio, and A. Ximenez. 1999. Descrição de uma nova espécie do gênero *Cavia* Pallas, 1766 (Mammalia-Caviidae) das Ilhas dos Moleques do Sul, Santa Catarina, Sul do Brasil. Biotemas 12:95–117.

Chiquito, E. A., and A. R. Percequillo. 2019. The taxonomic status of *Nectomys saturatus* Thomas, 1897 (Cricetidae: Sigmodontinae). Zootaxa 4550:321–339.

D'Elía, G., P-H. Fabre, and E. P. Lessa. 2019a. Rodent systematics in an age of discovery: recent advances and prospects. Journal of Mammalogy 100:852–871. https://doi.org/10.1093/jmammal/gyy179

D'Elía, G., F. Jaksic, L. D. Bacigalupe, F. Bozinovic, J. L. Canto, C. Correa, F. E. Fontúrbel, F. Lisón, M. A. Méndez, R. Nespolo, J. C. Opazo, E. Palma, J. R. Rau, S. M. Rodríguez, E. Rodríguez-Serrano, P. Sabat, R. A. Vásquez, and P. Victoriano. 2019b. Sugerencias para mejorar la regulación chilena de manipulación de vertebrados terrestres en poblaciones naturales en el contexto de investigaciones científicas. Gayana 83.

Emmons, L. H. 1999. A new genus and species of Abrocomid rodent from Peru (Rodentia: Abrocomidae). American Museum Novitates 3279: 1–14.

Emmons, L. H., Y. L. R. Leite, D. Kock, and L. P. Costa. 2002. A review of the named forms of *Phyllomys* (Rodentia: Echimyidae) with the description of a new species from coastal Brazil. American Museum Novitates 3380:1–40.

Fernandes, F. A., R. Fornel, and T. R. O. Freitas. 2012. *Ctenomys brasiliensis* Blainville (Rodentia: Ctenomyidae): clarifying the geographic placement of the type species of the genus Ctenomys. Zootaxa 3272:57–6 8.

Fleming, P. A., and P. W. Bateman. 2016. The good, the bad, and the ugly: which Australian terrestrial mammal species attract most research? Mammal Review 46:241–254.

Gaston, K. J. 1994. Rarity. Population and community biology series, vol. 13. Springer, Dordrecht.

Hutterer, R. 1994. Island rodents: a new species of Octodon from Isla Mocha, Chile (Mammalia: Octodontidae). Zeitschrift für Säugetierkunde 59:27–41.

IUCN, 2017. The IUCN Red List of Threatened Species. Version 2017-1. Retrieved from http://www.iucnredlist.org

Lacher, T. E., W. J. Murphy, J. Rogan, A. T. Smith, and N. S. Upham. 2017. Evolution, phylogeny, ecology, and conservation of the Clade Glires: Lagomorpha and Rodentia. Pp. 15–26 *in* Handbook of mammals of the world, Volume 6: lagomorphs and rodents (Wilson, D. E., J. T. E. Lacher, and R. A. Mittermeier, eds.). Lynx Ediciones. Barcelona, Spain.

Lanzone, C., C. A. Labaroni, A. Formoso, L. M. Buschiazzo, F. Da Rosa, and P. Teta. 2018. Diversidad, sistemática y conservación de roedores en el extremo sudoccidental del Bosque Atlántico Interior. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 20:151–164.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press. Princeton, U.S.A.

Maestri, R., and B.D. Patterson. 2016. Patterns of species richness and turnover for the South American rodent fauna. PLoS ONE 11(3):e0151895. https://doi.org/10.1371/journal.pone.0151895

Meiri, S., A. M. Bauer, A. Allison, F. Castro-Herrera, L. Chirio, G. Colli, I. Das, T. M. Doan, F. Glaw, L. L. Grismer, M. Hoogmoed, F. Kraus, M. LeBreton, D. Meirte, Z. T. Nagy, C. de C. Nogueira, P. Oliver, O. S. G. Pauwels, D. Pincheira-Donoso, G. Shea, R. Sindaco, O. J. S. Tallowin, O. Torres-Carvajal, J-F. Trape, P. Uetz, P. Wagner, Y. Wang, T. Ziegler, and U. Roll. 2017. Extinct, obscure or imaginary: The lizard species with the smallest ranges. Diversity and Distributions. DOI: 10.1111/ddi.12678.

Pacheco, V. 2015. Genus *Thomasomys* Coues, 1884. Pp. 617–682 *in* Mammals of South America (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press. Chicago, U.S.A.

Patterson, B. D. 2002. On the continuing need for scientific collecting of mammals. Mastozoología Neotropical 9:253–262.

Patton, J. L., U. F. J. Pardiñas, and G. D'Elía (eds.). 2015. Mammals of South America, Volume 2: Rodents. The University of Chicago Press. Chicago, U.S.A.

Rodríguez-Posadas, M.E. 2014. Primer registro del ratón de agua del táchira, *Neusticomys mussoi* (Rodentia, Cricetidae) en Colombia. Mastozoología Neotropical 21: 367–372.

Spotorno, A. E., and J. L. Patton. 2015. Superfamily Chinchilloidea Bennett, 1833. Pp. 762-783 *in* Mammals of South America (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press. Chicago, U.S.A.

Steppan, S. J. and O. Ramírez. 2015. Genus *Phyllotis* Water house, 1837. Pp. 481-507 *in* Mammals of South America (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press. Chicago, U.S.A.

Teta, P., and G. D'Elía. 2017. Taxonomic notes on the long-clawed mole mice of the genus *Geoxus* (Cricetidae), with the description of a new species from an oceanic island of southern Chile. Hystrix, The Italian Journal of Mammalogy, 26. DOI: https://doi.org/10.4404/hystrix-27.2-11996.

Teta, P., J. P. Jayat, C. Lanzone, A. Ojeda, A. Novillo, and R. A. Ojeda. 2018. Geographic variation in quantitative skull traits and systematic of southern populations of the leaf-eared mice of the *Phyllotis xanthopygus* complex (Cricetidae, Phyllotini) in southern South America. Zootaxa 4446:68–80.

Thomson, S. A., R. L. Pyle, S. Ahyong et al. 2018. Taxonomy based on science is necessary for global conservation. PLoS Biology 16(3):e2005075.

Turvey, S. T. 2009. Holocene extinctions. Oxford University Press. Oxford, UK.

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Siphonaptera associated with small mammals (Didelphimorphia, Chiroptera, and Rodentia) from northwestern Argentina

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Northwestern Argentina (NOA) is one of the least studied areas in Argentina with respect to ectoparasites of the order Siphonaptera; previous investigations, until this study, were scarce and specific. The objective of this study was to contribute to the knowledge of the diversity of siphonaptera that parasitize small mammals from the NOA, emphasizing in their systematics and distribution. Specimens of fleas collected in several localities of NOA, and stored in the "Annexes" of the Colección Mamíferos Lillo, Universidad Nacional de Tucuman, Argentina, were studied. Fleas were manually removed from the host pelage, fixed in alcohol 70 % and prepared following conventional techniques for later observation under microscope. For specimen identification, the original descriptions of species and subspecies were reviewed and compared with specimens stored in systematic collections. Nine families, 22 genera, 53 species, and eight subspecies were recorded. A new family, a new genus, and three new species are recorded for the first time in Argentina; five species are new for NOA and nine are new to science. The distribution of 11 species and two subspecies are extended in the NOA, new records are added to different provinces and new flea-hosts associations are reported. The greatest diversity of fleas in the Yungas is the reflection of one of the areas with the highest biodiversity in the Neotropical region, such as the Yungas forests, which also includes mammals, as sigmodontine rodents and bats among them. The similarity analysis among eco-regions showed a major faunistic congruence between the Yungas and the Dry Chaco. The greatest differentiation was given by the High Andes and Puna compared with the other eco-regions, probably because these areas are the least surveyed and with the lowest richness and abundance of small mammal species. From the total of 82 new flea-host associations, 81 belong to sigmodontine rodent hosts and one to a marsupial.

El Noroeste Argentino (NOA) representa una de las áreas de Argentina menos estudiada en lo que respecta a ectoparásitos del orden Siphonaptera; las investigaciones, hasta este estudio, eran escasas y puntuales. El objetivo del presente trabajo fue contribuir al conocimiento de la diversidad de sifonápteros que parasitan micromamíferos del NOA, con énfasis en la sistemática y distribución. Se estudiaron ejemplares de sifonápteros procedentes de varias localidades del NOA depositados en los "anexos" de la Colección Mamíferos Lillo, Universidad Nacional de Tucuman, Argentina. Las pulgas fueron recolectadas manualmente del pelaje de los hospedadores, fijadas en alcohol 70 % y preparadas siguiendo las técnicas convencionales para su posterior observación al microscopio óptico. Para la identificación de los ejemplares se revisaron las descripciones originales de especies y subespecies y se compararon los ejemplares con aquellos depositados en colecciones de referencia. Se registraron nueve familias, 22 géneros, 53 especies y ocho subespecies. Una nueva familia, un nuevo género y tres nuevas especies se citan por primera vez para Argentina, cinco especies son nuevas para el noroeste y nueve son nuevas especies para la ciencia. Se extiende la distribución de 11 especies y dos subespecies en el NOA, se suman nuevos registros para las diferentes provincias y se reportan nuevas asociaciones sifonáptero-hospedador. La mayor diversidad de pulgas en la eco-región de Yungas es un reflejo de una de las áreas de más alta biodiversidad en la región Neotropical como son las selvas de Yungas, incluyendo a los mamíferos y, entre ellos, a los roedores sigmodontinos y los murciélagos. El análisis del grado de afinidad entre eco-regiones mostró una mayor congruencia faunística entre las Yungas y el Chaco Seco. La mayor diferenciación estuvo dada por los Altos Andes y la Puna con respecto al resto, probablemente porque son dos de las áreas menos muestreadas y con menor riqueza y abundancia de especies de micromamíferos. Del total de 82 nuevas asociaciones sifonáptero-hospedador, 81 poseen como hospedadores a los roedores sigmodontinos, y una asociación está constituida por un marsupial.

Key words: Argentina; eco-regions; fleas; host; new records; taxonomic.

Introduction

Fleas are ectoparasites of higher vertebrates, mainly abundant and diverse in mammals, hosting 94 % of the known flea species. In Argentina, the fleas reported mostly represents new distributional records, some increasing the number of species for the studied areas or regions, also extending their geographical range as well as reporting new flea-host associations (Lareschi *et al.* 2003, 2010; Autino *et al.* 2005; Sanchez *et al.* 2009; Claps and Autino 2012; López-Berrizbeitia 2013a, b; Sanchez and Lareschi 2013). Some studies describe new species for science, mainly from central and southern Argentina (see Manhert 1976; Beaucournu and Torres-Mura 1987; Beaucournu and Gallardo 1988, 2005; Beaucournu and Alcover 1990; Hastriter 2001; Beaucournu *et al.* 2004; Hastriter and Sage 2009, 2011; Sanchez and Lareschi 2014b; Ezquiaga *et al.* 2015; Sanchez *et al.* 2015), and more recently from the northwest (Beaucournu and Castro 2002, 2003; López-Berrizbeitia *et al.* 2015a, b, 2016; López-Berrizbeitia *et al.* 2018, 2019).

Until this study, Northwestern Argentina (NOA) represented one of the areas in the country where the studies of ectoparasites of the order Siphonaptera were very scarce and punctual. Even though, in the last years, the small mammals surveys have increased in the region (Díaz *et al.* 1999, 2000; Díaz and Barquez 1999, 2007; Flores *et al.* 2000; Barquez *et al.* 2009; Ferro and Barquez 2009; Jayat and Ortiz 2010; Sandoval *et al.* 2010; Barquez *et al.* 2011; Jayat *et al.* 2011; Gamboa Alurralde *et al.* 2016), in Catamarca, La Rioja, and Santiago del Estero provinces, the small mammals have been scarcely surveyed. The data presented here are the results of extensive field surveys, laboratory work, and collection revision coming from a doctoral thesis (López-Berrizbeitia *et al.* 2018).

In the natural communities, small mammals are the most numerous animals (Ferro 2012), and in the NOA, they are represented by marsupials, bats, and rodents. Rodents are the most diverse taxon and are represented by several families, being the family Cricetidae, subfamily Sigmodontinae, the most numerous, besides being distributed throughout South America (Barquez *et al.* 2006; Patton *et al.* 2015). The sigmodontine rodents are found in every habitat in the NOA, from tropical forests to Andean High deserts (Ferro 2012). Marsupials belong to the order Didelphimorphia, family Didelphidae, this taxon is represented by four genera and 10 species (Barquez *et al.* 2006; Voss and Jansa 2009). Finally, the order Chiroptera is represented by four families and 44 species, being Vespertilionidae the most specious family with 17 species, followed by Molossidae (13), Phyllostomidae (12), and Noctilionidae with two species (Barquez and Díaz 2009; Díaz *et al.* 2016; Urquizo *et al.* 2017; Barquez *et al.* 2017).

In Argentina, most records of fleas come from rodents, perhaps due to the great diversity and abundance of the group, and to a lesser extent come from marsupials and bats (Lareschi *et al.* 2016). On the other hand, studies are mainly restricted to the central and southern parts of Argentina, where a replacement of the hosts species and a decrease of diversity can be observed (Barquez *et al.* 2006; Barquez and Díaz 2009; Udrizar Sauthier and Pardiñas 2014); also in the northwest, marsupial and bat richness is notably greater than in southern Argentina (Barquez *et al.* 2006; Gardner 2008).

For a long time, the identification of host species was considered as not relevant for parasitological studies; in fact, in the literature there are mentioned several flea records collected from unknown hosts, or with their identifications not reaching species or even genus level (Hopkins and Rothschild 1953, 1956, 1966; Smit 1987; Del Ponte 1977; Autino and Lareschi 1998). Sometimes taxonomic identification in poorly known groups can be troublesome, but it is of essential importance since it allows analyses of several aspects of host parasite relationships such as co-evolutionary processes, and even to identify species that can act as disease reservoirs. Based on this, it is important to highlight the importance of developing interdisciplinary studies between parasitologists and mammalogists tending to ensure correct taxonomic identification of both, parasites and hosts, mitigate the gaps in the knowledge of both groups (Fernandez 2019) and to avoid erroneous conclusions in research. In this context, the principal objective of this research was to study the faunistic composition of fleas (Siphonaptera) parasitizing small mammals (Didelphimorphia, Chiroptera, and Rodentia) in Northwestern Argentina.

Materials and methods

Study area. Northwestern Argentina is integrated by the provinces of Catamarca, Jujuy, La Rioja, Salta, Santiago del Estero, and Tucuman (Carlevari 1994; Bolsi *et al.* 1997a, b; Figure 1). The region is complex because it harbors a great variety of landscapes (Santillán de Andrés and Ricci 1998), which is reflected in its diversity of flora and fauna (Burkart *et al.* 1999). Biogeographically, NOA is part of the Neotropical Region, one of the greatest phytogeographical regions on earth, and occupies most part of the Argentine territory, sharing the Amazonian, Chacoan, and Andean-Patagonian Dominions (Cabrera 1976). According to Burkart *et al.* (1999), the eco-regions recorded in the NOA are: Yungas (Amazonian Dominion), High Andes and Puna (Andean-Patagonian Dominion), Dry Chaco, Monte Desert of Mountains and Isolated Valleys, and a small portion of Humid Chaco (Chaco Dominion; Figure 1).

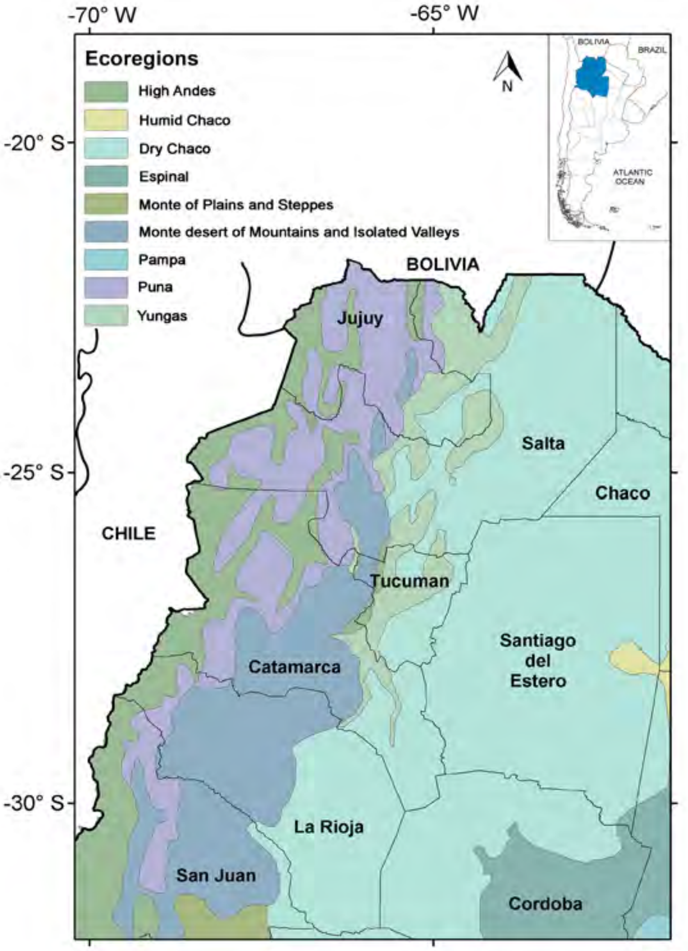

Figure 1. Geographic location of northwestern Argentina, limits, provinces and ecoregions.

Collection and preparation of specimens. In the "annexes" of the Colección Mamíferos Lillo, Universidad Nacional de Tucuman, an important number of flea specimens (Insecta: Siphonaptera) were stored from several localities of NOA. These specimens are the results of surveys carried out over several years; all specimens were reviewed and analyzed during this study. Also, surveys to all provinces of NOA were carried out, prioritizing areas with absence of data (Appendix I).

Collection of small mammals. Small terrestrial mammals were captured with Sherman live traps baited with oats, set on two or three transects of 60 traps each, and placed in different habitats at each sampling locality. For small fossorial mammals we placed traps designed for the live capture of subterranean rodents, modified from the model by Baker and Williams (1972). The traps were placed at fresh mounds, the tunnel hole was opened and the extreme of the pipe was inserted into the burrow with the device activated. Bats were captured using four or six 12 m mist nets set on different habitats. Specimens representing unusual records, or with uncertain identification, or with presence of fleas detected for the first time, were collected as voucher specimens. Permits issued by the provincial authorities for Administration of Natural Resources of each province of the NOA authorized the collection of these specimens. Most of the specimens were deposited at the Colección Mamíferos Lillo (CML), Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucuman, Tucuman, and a small part was deposited at the Sam Noble Oklahoma Museum of Natural History (SNOMNH), University of Oklahoma, Norman, Oklahoma. Some specimens are still being catalogued and acronyms used in the text are: CLH (personal catalogue of Carlos Luis Hoyos), EMG (personal catalogue of Enrique M. Gonzalez), LIF (personal catalogue of Luis Ignacio Ferro), MIC (personal catalogue of María Inés Carma), and MMD (personal catalogue of María Mónica Díaz).

For taxonomic identification of small mammals we followed Díaz *et al.* (1997), Braun and Díaz (1999), and Barquez and Díaz (2009). The basic checklist used was based on Barquez *et al.* (2006), Gardner (2008), and Patton *et al.* (2015).

Processing of Siphonaptera. The specimens were removed manually from the host pelage with toothbrushes and forceps, preserved in a solution of 70 % ethyl alcohol, and prepared following conventional techniques for taxonomic identification (see Hastriter and Whiting 2003).

Systematic analysis of Siphonaptera. Nomenclature follows Whiting *et al.* (2008), and keys and descriptions of Hopkins and Rothschild (1953, 1956, 1962, 1966), Johnson (1957), Smit (1987), Hastriter and Mendez (2000), and Linardi and Guimarães (2000) were used. With the purpose of species identification, specimens were compared with original descriptions of species and subspecies and with specimens stored in the following collections: Annexes of the Colección Mamíferos Lillo (CMLA; Universidad Nacional de Tucuman, Argentina), British Museum (Natural History; BMHN; London, United Kingdom), Muséum d'Histoire Naturelle (MHN; Paris, France), and Monte L. Bean Life Science Museum, Brigham Young University (BYU; Provo, Utah, United States, including the flea collection of Michael W. Hastriter and Vernon J. Tipton).

Localities and maps. A total of 154 localities were recorded. Geographic coordinates for localities sampled by us were obtained with Geographic Positioning System (GPS) and those from the literature were determined using the Google Earth Pro Versión 2016. Some localities were not mapped, because the original localities were imprecise or with absence of data. It is also important to mention that corrected coordinates of some localities, erroneously reported in the literature, were obtained. The map of NOA including provinces and ecoregions (Figures 1) was designed with the ArcGis 10.1 program (ESRI 2011).

All localities were ordered numerically and alphabetically, with the provincial department indicated between parentheses (see Appendix I).

Species accounts. In this section we report all species known from the NOA, including those published on literature with confirmed identity. Accounts include scientific name, author, general distribution, distribution in Argentina, and specimens examined (total numbers between parentheses). In specimens examined we included: specific locality, number of specimens by sex and collection number (when known); host species and collection number (when known). Some included specimens are distributed out the study area (Appendix II), but they were used for description purposes. In additional specimens only the locality and hosts were included. Under "Comments" we summarize available information about natural history and taxonomy of each species.

Similarity analysis. To evaluate the affinity of species among ecoregions in the NOA we carried out a similarity analysis. The similarity was estimated through the simple presence or absence of species in different ecoregions to analyze the degree of interrelationships among them.

We applied Jaccard's Coefficient (*J*), one of the most used qualitative estimators (Jost *et al.* 2011), which allows the use of qualitative data such as presence-absence of the organisms (Moreno 2001); its value varies from 0 (no shared species between two sites) and 1 (the two sites have the same composition of species) and was calculated with the formula:

Where *a* is the number of species present in site A; *b* is the number of species present in site B; and *c* is the number of species present in both sites, A and B.

The index was calculated with the PAST 1.18 program (Hammer *et al.* 2001) using the unweighted pair-group arithmetic averaging cluster algorithm (UPGMA) based on similarity values, and expressed in a dendrogram through an analysis of Clusters using the same program PAST 1.18.

Results

Species Accounts. In the present study, nine families of the order Siphonaptera parasitizing small mammals of the orders Didelphimorphia, Chiroptera, and Rodentia in the NOA were recorded (Table 1). The number of genera, species, and subspecies for each families are detailed as follows: Tungidae, one genus and six species; Pygiopsyllidae, one genus and one species; Stephanocircidae, five genus and seven species; Rhopalopsyllidae, five genus, 27 species, and two subspecies; Ctenophthalmidae, three genus, five species, and three subspecies; Pulicidae, two genus and two species; Leptopsyllidae, one genus and one species; Ischnopsyllidae, three genus, four species, and two subspecies; and Ceratophyllidae, one genus and one species.

Family Tungidae

Subfamily Tunginae

Tribe Hectopsyllini

Genus *Hectopsylla* Frauenfeld 1860

Hectopsylla (*Hectopsylla*) *gracilis* Mahnert 1982

General distribution. Endemic to Argentina (Lareschi *et al.* 2016).

Distribution in Argentina. This species was previously known from the provinces of Chubut, Jujuy, Mendoza, Neuquén, Río Negro (Lareschi *et al.* 2016), Salta (López-Berrizbeitia 2013a) and La Rioja (López-Berrizbeitia *et al.* 2013b, 2017); in this study it is added to Catamarca and Tucuman provinces.

Specimens Examined (24). Catamarca: Las Juntas, 1 female (no number), ex *Akodon spegazzinii* Thomas 1897 (MIC 86). Chubut: Puerto Madryn, 1 paratype female (BMNH no number), ex *Eligmodontia typus* F. Cuvier 1837 (unknown number). Jujuy: Arroyo La Horqueta, a 6 km al SE de las Lagunas de Yala, 1 female (no number), ex *Akodon caenosus* Thomas 1918 (CML 4617); Sobre ruta 40, 29 km al N del empalme con ruta 52, 1 female (no number), ex *Akodon albiventer* Thomas 1897 (CML 4574), 3 females (no numbers), ex *Eligmodontia hirtipes* (Thomas 1902; CML 8315, 9443, 9445), 4 females (no numbers), ex *Eligmodontia puerulus* (Philippi 1896; CML 8316, 9466, 9468). La Rioja: 2 km al S pasando río de La Punta sobre ruta provincial 7, 1 male (CMLA 600), ex *Graomys chacoensis* (J.A. Allen 1901; CML 12948); a 800 m al E de la entrada de Anillaco sobre ruta Nacional 75, 4 females (CMLA 594, 595, 596, 597), ex *Andalgalomys olrogi* Williams and Mares, 1978 (CML 9747), 2 females (CMLA 598, 599), ex *E. typus* (CML 9751), 1 female (CMLA 593), ex *G. chacoensis* (CML 9748); Anillaco, atrás del cementerio, 2 females (CMLA 601, 602), ex *Eligmodontia moreni* (Thomas 1896; CML 12943). Salta: Vega Cortadera, 1 female (no number), ex *E. puerulus* (SNOMNH 34757). Tucuman: La Olorosa, 1 female (no number), ex *Abrothrix andina* (Philippi 1858; released); Peña Colorada, 2 females (no number), *ex A. andina* (released).

Additional Records. Jujuy: Salar Cauchari, 31 km al N de Cauchari, sobre ruta provincial Nº 70, Susques, ex *E. puerulus* (Lareschi *et al.* 2010).

Remarks. This species is endemic to Argentina (Lareschi *et al.* 2016). Recently, three new associations were recorded with the following hosts: *A. olrogi*, *G. chacoensis* (López-Berrizbeitia 2013a) and *E. moreni* (López-Berrizbeitia *et al.* 2017). Others hosts are: *Abrothrix olivacea* (Waterhouse 1837), *Akodon iniscatus* Thomas 1919; *Abrothrix longipilis* (Waterhouse 1837; originally cited as *A. hirta*); *Reithrodon auritus* (G. Fischer 1814); *Eligmodontia morgani* J.A. Allen 1901, and *G. griseoflavus* (Waterhouse 1837; see Sanchez 2012).

Hectopsylla (*Hectopsylla*) *cypha* Jordan 1942

General distribution. Argentina and Chile (Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. La Rioja, Mendoza, Río Negro, and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined (2). Mendoza: San Rafael, 1 holotype male (BMNH 1940-217), 1 allotype female (BMNH 1940-217), ex *Microcavia maenas* (Thomas 1898; unknown number; originally identified as *Microcavia australis* I. Geoffroy and d'Orbigny 1833).

Additional Records. La Rioja: Zapallar, ex *Lagostomus* sp. (Hastriter and Méndez 2000). Tucuman: not specific locality, unknown host (Beaucournu and Castro 2003).

Remarks. Examined specimens correspond to deposited specimens in the Natural History Museum. Originally, the type host species was *M. australis*, but according to geographical distribution in Teta *et al.* (2017) this species is not distributed in Mendoza Province and it corresponds to *M. maenas*. Regarding the recorded host in the La Rioja Province, it could be *Lagostomus maximus* (Desmarest 1817), since it is the only extant species of the genus. This species was recorded parasitizing others rodents in the Mendoza Province: *Graomys griseoflavus*, *Octomys mimax* Thomas 1920, and *Tympanoctomys barrerae* (Lawrence 1941; see Lareschi *et al.* 2016).

Hectopsylla (*Hectopsylla*) *gemina* Jordan 1939

General distribution. Argentina and Chile (Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, La Pampa, Mendoza, Río Negro, San Juan, and Santiago del Estero provinces (Lareschi *et al.* 2016); in this study it is added to Tucuman Province.

Specimens Examined (3). Mendoza: Puesto "La Carpa", 1 male (BMNH 1959-683), ex *M. maenas* (unknown number; originally identified as *M. australis*). Rio negro: Fortín Uno, 1 holotype female (BMNH 1940-217), ex *M. australis* (unknown number). Tucuman: Parque Nacional Campo de Los Alisos, El Kerqueo, 1 female (no number), ex *Phyllotis osilae* J. A. Allen, 1901 (CML 11676).

Additional Records. Santiago del Estero: not specific locality, ex *Microcavia jayat* Teta, Ojeda, Lucero, and D'Elía 2017 (originally cited as *M. australis*; Autino and Lareschi 1998).

Remarks. Others recorded hosts for this species in Argentina are: *Akodon* sp., *G. griseoflavus* (Cricetidae), *Cavia* sp., *Galea leucoblephara* Burmeister 1861 (originally cited as *G.*

musteloides Meyen 1833; Caviidae), *Ctenomys* sp. (Ctenomyidae), and *T. barrerae* (Octodontidae; Hastriter and Méndez 2000; Lareschi *et al.* 2016). *Phyllotis osilae* represents a new host for this species of flea. According to Hastriter and Mendez (2000) this species shows preference for *M. australis*; however, in this study, we recorded the species *P. osilae*, a cricetid rodent of the tribe Phyllotini.

Hectopsylla (*Hectopsylla*) *psittaci* Frauenfeld 1860

General distribution. Argentina, Brazil, Chile, United States, and Great Britain (Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, La Rioja, and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined. None.

Additional records. Tucuman: not specific locality, ex *Eumops perotis* (Schinz 1821; originally cited as *Promops perotis*; Del Ponte and Riesel 1939).

Remarks. This species is primarily a parasite of birds. It is native to the southern cone of South America, but with populations dispersed by migratory birds in Europe and southwestern United States (Hastriter and Méndez 2000). The associtation with *E. perotis* is accidental (Del Ponte and Riesel 1939).

Hectopsylla (*Hectopsylla*) *stomis* Jordan 1925

General distribution. Endemic to Argentina (Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, La Pampa, Mendoza, Salta, and Santiago del Estero provinces (Lareschi *et al.* 2016).

Specimens Examined (1). Buenos Aires: Cañada Mariano, 1 holotype female (BMNH 1923-615), ex bird (unknown number).

Additional Records. Salta: El Quebrachal, ex *L. maximus* (Hopkins and Rothschild 1953). Santiago del Estero: El Ojito, pica de Santiago del Estero, ex *L. maximus* (Hopkins and Rothschild 1953).

Remarks. The only examined specimen corresponds to a female deposited in the Natural History Museum, London, England. Like *H.* (*H.*) *gracilis*, it is an endemic species to Argentina. Other recorded hosts are: *G. griseoflavus* and *M. maenas* in La Pampa and Mendoza provinces, respectively (Lareschi *et al.* 2016); and although, this species was recorded on *L. maximus* in Northwestern Argentina, its presence on small mammals is highly probable.

Hectopsylla (*Rhychopsyllus*) *pulex* (Haller 1880)

General distribution. Argentina, Brazil, United States, and Mexico (Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, Catamarca, La Pampa, Salta, and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined (6). Jujuy: Río Lavayén, aproximadamente 1 km al N de Santa Rita, 2 females (no number), ex *Tadarida brasiliensis* (I. Geoffroy St. Hilaire 1824; CML 7077). Salta: Parque Nacional El Rey, 3 females (no number), ex *T. brasiliensis* (released). Tucuman: Dique Escaba, 1 female (no number), ex *T. brasiliensis* (released).

Additional Records. Catamarca: El Rodeo, ex *T. brasiliensis* (Del Ponte 1977). Jujuy: Parque Provincial Potrero de Yala, ex *T. brasiliensis* (Autino *et al.* 2016). Salta: 8 km al O de Piquirenda Viejo; Río Las Conchas, 2 km al N y 6 km al O de Metán, ex *T. brasiliensis* (Autino *et al.* 2009). Tucuman: San Miguel de Tucuman, ex *E. perotis* (Schreiter and Shannon 1927).

Remarks. Traditionally *H.* (*H.*) *pulex* was included in the genus *Rhinchopsyllus,* but later Hastriter and Mendez (2000) proposed the synonymy with the genus *Hectopsylla*. This species parasitizes mainly bats of the family Molossidae but also the family Vespertilionidae (Hastriter and Méndez 2000). In this study, only one female was examined; the males are rare, in fact, previous studies recorded males specimens only associated with the guano of species of the genus *Molossus* in Colombia and Panama (Tipton and Méndez 1966; Hastriter and Méndez 2000).

Family Pygiopsyllidae

Genus *Ctenidiosomus* Jordan 1931

Ctenidiosomus austrinus López-Berrizbeitia, Hastriter and Díaz 2015

General distribution. Endemic to Argentina (López-Berrizbeitia *et al.* 2015a).

Distribution in Argentina. Only known from the type locality in Salta Province (López-Berrizbeitia *et al.* 2015b).

Specimens Examined (1). Salta: Aproximadamente 15 km O de Escoipe, sobre ruta Provincial Nº 33, 1 holotype male (no number) ex *P. osilae* (CML 8044).

Remarks. The single male holotype was collected from a juvenile male specimen of the sigmodontine rodent, *Phyllotis osilae*, on May during the dry season. The type locality of *Ct. austrinus* corresponds to the ecoregion Monte Desert of Mountains and Isolated Valleys and similar to all other species of *Ctenidiosomus*, the new species was collected at a high elevation (2680 m.). With this report, the geographical distribution of the genus *Ctenidiosomus* is extended ~2600 km further south from its previously known southern limits of El Tambo, Huancayo Province, Junín Department, Peru (Mardon 1981). The presence of this species in Bolivia is highly probable due to its location among Peruvian and Argentine records.

Family Stephanocircidae

Subfamily Craneopsyllinae

Tribe Craneopsyllini

Genus *Cleopsylla* Rothschild 1914

Cleopsylla barquezi López-Berrizbeitia, Hastriter and Díaz 2016

General distribution. It is only found in NOA (Lopez-Berrizbeitia *et al.* 2016).

Distribution in Argentina. Catamarca, Salta, and Tucuman provinces (Lopez-Berrizbeitia *et al.* 2016).

Specimens Examined (20). Catamarca: Cumbre de Humaya, 1 paratype male (CMLA 26), ex *Akodon spegazzinii*

Thomas 1897 (MIC 302), 1 paratype female (CMLA 29) ex *A. spegazzinii* (MIC 312), 2 males (CMLA 27, 30), 2 females (CMLA 28, 31), ex *A. spegazzinii* (MIC 263, 266, 311); Las Juntas, 1 female (CMLA 22), 2 males (CMLA 23, 24), ex *P. osilae* (MIC 79), 1 female (CMLA 25), ex *A. spegazzinii* (MIC 85). Salta: aproximadamente 15 km O Escoipe, sobre ruta Provincial N° 33, 1 paratype male (CMLA 15), 3 paratypes females (CMLA 17, 18, 19), ex *A. spegazzinii* (CML 9236, SNOMNH 33007), 2 males (CMLA 16, 20), 1 female (CMLA 21), ex *A. spegazzinii* (CML 9236). Tucuman: 10 km S Tafí del Valle, Santa Cruz, 1 holotype male (CMLA 13), 1 allotype female (CMLA 14), ex *P. osilae* (SNOMNH 30102); Ciénaga Grande, San José de Chasquivil, 1 female (no number), ex *A. spegazzinii* (CML 7478).

Remarks. The elevation for hosts and specimens of the new species of flea was similar among the localities, fluctuating within a range of 1750–2680 m. The type locality of *C. barquezi* corresponds to highland pastures (2278 m), the last stratum of the eco-region Yungas Forests. Colombetti *et al.* (2008) misidentified the new species of *C. barquezi* referring to it as *C. townsendi*. The hosts reported by Colombetti *et al.* (2008) were not available for our review; therefore, we could not verify their identity.

Genus *Craneopsylla* Rothschild 1911

Craneopsylla minerva (Rothschild 1903)

General distribution. Argentina, Brazil, Chile, Ecuador, Paraguay, Peru, Uruguay, and Venezuela (Johnson 1957; Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, Catamarca, Cordoba, Chubut, Jujuy, La Pampa, Mendoza, Neuquen, Rio Negro, Salta, Santa Fe, Santiago del Estero, Tierra del Fuego, and Tucuman provinces (Lareschi *et al.* 2016), and it has been recently included in La Rioja Province (López-Berrizbeitia *et al.* 2017).

Specimens Examined (203). Argentina. Buenos Aires: Estancia La Daniela, 1 lectotype male (BMNH 1923-615), 1 allotype female (BMNH 1923-615), ex *Lutreolina crassicaudata* (Desmarest 1804; unknown number; originally identified as *Didelphis crassicaudata*). Catamarca: 22 km al SE de Villa de Escaba sobre ruta Prov. Nº 9, 1 female (no number), ex *Akodon glaucinus* Thomas 1919 (CML 12346); 3.4 km al S de la unión entre las rutas 18 y 9 provinciales, sobre ruta provincial N° 18, 5 females (no numbers), ex *Akodon lutescens* J. A. Allen 1901 (SNOMNH 37530); Estancia Narvaez, 5.5 km N La Chacritas en ruta Provincial 1, 3 females (no numbers), ex *A. spegazinii* (CML 7198, 7200); Las Juntas, 1 male (no number), 3 females (no numbers), ex *Akodon simulator* Thomas 1916 (MIC 104, 130) 6 females (no numbers), 1 male (no number), ex *A. spegazzinii* (MIC 128), 1 male (no number), 1 female (no number), ex *P. osilae* (MIC 114). Jujuy: 17 km al O y 3 km al S de la Quiaca, sobre ruta provincial Nº 5, 1 female (no number), ex *Phyllotis xanthopygus* (Waterhouse 1837; CML 8006); 3 km del cruce Río Las Capillas y ruta prov. N˚ 20, 3 females (no numbers), ex *Calomys venustus* (Thomas 1894; CML 12393); 9 km NO Bárcena, 1 male (no number), 4 females (no numbers), ex *Phyllotis caprinus* Pearson 1958 (SNOMNH 30082), 3 males (no numbers), 15 females (no numbers), ex *P. osilae* (CML 6501, 8068), 2 males (no numbers), 4 females (no number), ex *P. xanthopygus* (SNOMNH 34028, 30192); Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional 9, 1 female (no number), ex *Akodon toba* Thomas 1921 (CML 4893); Arroyo Los Matos, 7 km N de Las Capillas, 2 males (no numbers), 5 females (no numbers), ex *Akodon budini* (Thomas 1918; CML 12340, released), 1 male (no number), 5 females (no numbers), ex *A. spegaziinii* (CML 12362), 1 female (no number), ex *Oxymycterus paramensis* Thomas 1902 (CML 12364); Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 1 female (no number), ex *Euryoryzomys legatus* (Thomas 1925; CML 9628); Cuesta del Hurón, 29 km al O de Cieneguillas, sobre ruta provincial 64, 1 male (no number), 7 females (no numbers), ex *P. xanthopygus* (CML 7969, 7970), 1 female (no number), ex *Tapecomys wolffsohni* (Thomas 1902; CML 8070); Río Blanco, 9 km SO, San Antonio, 1 female (no number), ex *Oligoryzomys brendae* Massoia 1998 (SNOMNH 37035); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial 20, 1 male (no number), 1 female (no number), ex *Tapecomys primus* Anderson and Yates 2000 (CML 12398); Ruta 83 camino a Valle Grande, 9 km al N de San Francisco, 2 females (no numbers), ex *T. primus* (CML 7556). La Rioja: 2 km al E de Malanzán, camping El Descanso, 1 female (CMLA 611), ex *G. griseoflavus* (CML 13005); 5 km al S del Cañón del Ocre, 1 female (CMLA 608), ex *P. xanthopygus* (CML 13020); Cuesta La Cébila, 22 km al NO de Chumbicha, sobre ruta 60, 1 female (no number) ex *A. glaucinus* (CML 3752); Puesto Tres Piedras, 2 females (no numbers), ex *Akodon* sp. (CML 12900); RP 11, km 81, El Potrerillo, Río El Potrerillo, 1 male (no number), ex *G. chacoensis* (CML 12960); Ulapes, 1 km al O de la plaza principal de Ulapes, 2 females (CMLA 609, 610), ex *G. chacoensis* (CML 12991). Salta: 12.6 km O de Piquirenda Viejo, 1 female (no number), ex *E. legatus* (CML 9694); A 43.7 km del cruce de las rutas 50 y 18, camino a Isla de Cañas, sobre ruta 18, 1 female (no number), ex *Lutreolina massoia* Martínez-Lanfranco, Flores, Jayat, and D'Elía 2014 (CML 7650; originally identified as *L. crassicaudata*), 1 female (no number), ex *Thylamys sponsorius* (Thomas 1921; CML 7511); ~ 15 km al O de Escoipe, sobre Ruta Provincial N° 33, 9 females (no numbers), ex *A. spegaziinii* (CML 7213); ~ 2 km al N y 6 km al O de Metán, sobre Río Las Conchas, 3 males (no numbers), 4 females (no numbers), ex *A. lutescens* (CML 12363), 1 female (no number), ex *Akodon puer* Thomas 1902 (CML 12345), 1 female (no number), ex *A. simulator* (CML 12349), 1 female (no number), ex *O. brendae* (CML 12374), 1 male (no number), 1 female (no number), ex *Oligoryzomys flavescens* (Waterhouse 1837; CML 12377); ~ 3 km N Cachi Adentro, 2 males (no numbers), 2 females (no numbers), ex *G. griseoflavus* (SNOMNH 33335); ~ 3.5 km al O de Metán, 1 male (no number), 2 females (no numbers), ex *A. simulator* (CML 12352), 3 males (no numbers), 4 females (no numbers), ex *O. brendae* (CML 12374, 12375, 12376), 1 male (no number), 1 female (no number), ex O. *flavescens* (CML 12379); Cuesta Chica, 35 km O del Oculto, 4 km E de San Andrés, 1 female (no number), ex *O. paramensis* (CML 11498); El Oculto, ruta provincial N° 18, km

25 sobre Río Blanco (camino a San Andrés), 1 female (no number), ex *E. legatus* (CML 11600); Hipólito Yrigoyen, 1 male (no number), 3 females (no numbers), ex *Calomys boliviae* (Thomas 1901; CML 49, 52), *Akodon tartareus* Thomas 1919 (CLH 59); Laguna de Pintascayo, 1.5 km N sobre Río Pescado frente a Quebrada del Café, 1 female (no number), ex *A. simulator* (LIF 935); Pintascayo, campamento Lima (Propiedad de GMF S.A), 2 females (no numbers), ex *Akodon* cf. *fumeus* (MMD 5172), 1 male (no number), 2 females (no numbers), ex *T. sponsorius* (CML 10109); Río Los Sauces, 12 km NO del Jardín, ruta 6 km 110, 1 female (no number), ex *C. venustus* (LIF 190). Santiago del Estero: Salinas de Ambargasta, ~ 8 km SE Cerro Rico, 2 females (no numbers), ex *C. venustus* (CML 6763, 6764). Tucuman: 1.9 km NE Hualinchay sobre ruta provincial 311, 1 male (no number), ex *O. brendae* (SNOMNH 34359); Arroyo Aguas Chiquitas, Reserva Provincial Aguas Chiquitas, 1 male (no number), 2 females (no numbers), ex *A. simulator* (CML 3807); Ciénaga Grande, San José de Chasquivil, 1 male (no number), 1 female (no number), ex *A. spegazzinii* (CML 7478), 1 female (no number), ex *P. osilae* (CML 8461); Dique San Ignacio, 1 female (no number), ex *A. simulator* (CML 7170), 1 female (no number), ex *Calomys callosus* (Rengger 1830; CML 7176), 2 males (no numbers), 2 females (no numbers), ex *L. massoia* (CML 2895), 1 male (no number), 1 female (no number), ex *T. sponsorius* (CML 7159, released); El Ceibal Chico, 4 km al E de la rotonda de San Isidro de Lules por ruta provincial 321 y 1.5 km al S, por calle Julio C. Berrizbeitia, 1 female (no number), ex *Akodon tucumanensis* J. A. Allen 1901 (released); Lagunas de Huaca Huasi (Cumbres Calachaquíes), 1 female (no number), ex *A. andina* (CML 11762); Las Tipas, Parque Biológico Sierra de San Javier, 1 male (no number), ex *Graomys domorum* (Thomas 1902; CML 5986); Los Chorrillos 13 km NO, límite norte estancia Los Chorrillos, 1 male (no number), ex *A. spegazzinii* (CML 6466); Pie de la Cuesta a Chasquivil, 5 km de la Hoyada sobre Río Hoyada, 2 females (no numbers), ex *Abrothrix illutea* Thomas 1925 (CML 11791), *O. brendae* (CML 7279); Piedra Blanca, 1 female (no number), ex *Akodon alterus* Thomas 1919 (CML 7275); Reserva La Florida, 7 km O Ibatín , sobre Río Pueblo Viejo, 3 males (no numbers), 2 females (no numbers), ex *A. simulator* (CML 6087), 1 male (no number), ex *E. legatus* (CML 5981), 1 female (no number), ex *O. brendae* (SNOMNH 34347); Reserva Provincial Aguas Chiquitas, sobre Río Aguas Chiquitas, 1 male (no number), 1 female (no number), ex *A. caenosus* (CML 11942), 1 male (no number), 1 female (no number), ex *A. spegazzinii* (CML 11942), 1 male (no number), ex *C. venustus* (CML 11949), 1 male (no number), 2 females (no number), ex *O. flavescens* (CML 11944); Río Grande, 5 km al S de El Siambón, 1 male (no number), ex *O. brendae* (CML 9653), 1 female (no number), ex *Thylamys cinderella* (Thomas 1902; CML 7775); Río Nio, 4 km al O, camino hacia Alto de Medina, 1 female (no number), ex *C. boliviae* (SNOMNH 35288); Santa Cruz, 10 km al S de Tafí del Valle, 8 males (no numbers), 10 females (no numbers), ex *P. osilae* (SNOMNH 30102); Tapia, cruce de ruta 9 y Río Tapia, 1 female (no number), ex *O. brendae* (CML 11558). Brazil: Serra do Cipo, Minas Gerais, 1 male (BMNH 1948-516), ex *Nectomys squamipes* Brants 1827 (unknown number). Paraguay: Sapucay, 1 lectotype female (BMNH 1923-615), ex *Didelphis aurita* Wied-Neuwied 1826 (unknown number; originally identified as *Didelphis azarae* Tschudi 1845).

Additional Records. Catamarca: Otro Cerro, Rancho de los Crisho, ex Rodentia (Hopkins and Rothschild 1956). Jujuy: Laguna La Brea, 25 km antes de Palma Sola, ex *E. legatus* (Lareschi *et al.* 2003); Villa Carolina, Río Lavallén, a unos 20 km al E de San Pedro de Jujuy, ex *Holochilus chacarius* Thomas 1906 (originally cited as *Holochilus balnearum*; Hopkins and Rothschild 1956). Salta: 12.6 km O de Piquirenda Viejo, ex *Chrotopterus auritus* (Autino *et al.* 2009); El Quebrachal, ex *G. griseoflavus*, *M. maenas* (originally cited as *M. australis*) and *Rattus rattus* Linnaeus 1758 (Hopkins and Rothschild 1956); J. V. González, ex *Galea leucoblephara* Burmeister 1861 (originally cited as *G. musteloides*; Hopkins and Rothschild 1956). Santiago del Estero: El Quemado, ex *A. tucumanensis*; Las Carpas, ex *G. griseoflavus*, *C. venustus* (originally cited as *Hesperomys venustus*) and *M. jayat* (originally cited as *M. australis*); not specific locality, *ex G. griseoflavus* (Hopkins and Rothschild 1956). Tucuman: Cerro San Javier, a unos 20 km al O San Miguel de Tucuman, ex *L. massoia* (originally cited as *L. crassicaudata*) and *O. brendae* (originally cited as *O. destructor*); not specific locality, ex *Rattus* sp. (Del Ponte 1977).

Remarks. Traditionally two subspecies, *Craneopsylla minerva minerva* (Rothschild, 1903) and *Craneopsylla minerva wolffhuegeli* (Rothschild, 1909) are recognized, differentiated by the number of spines present in genal ctenidium (Hopkins and Rothschild 1956). Del Ponte (1977) treated both as valid species, *C. minerva* and *C. wolffhuegeli*. Despite this, other authors have continued to treat them as subspecies (Beaucournu *et al.* 2014; Lareschi *et al.* 2016). Here, we consider *C. m. minerva* and *C. m. wolffhuegeli* as synonyms, based on the study of the morphology of our collected specimens and their comparison with specimens from other collections, which include an allotype and lectotypes. We have determined that the character traditionally used to differentiate them as subspecies is highly variable and presents intermediate states. We have registered individuals with four, five, six or seven genital spines, and even in some specimens the number of spines can vary on each side. In addition, no differences were found in the genitalia of the males of both subspecies.

Twenty one new flea-host associations were recorded with following hosts: *L. massoia* (Didelphimorphia, Didelphidae), *A. spegazzinii* (López-Berrizbeitia *et al.* 2013b), *A. andina*, *A. illutea*, *A. budini*, *A. lutescens*, *A. simulator*, *A. tucumanensis*, *C. boliviae*, *C. callosus*, *C. venustus*, *E. legatus*, *G. chacoensis*, *G. domorum*, *O. brendae*, *O. flavescens*, *O. paramensis*, *P. caprinus*, *P. osilae*, *T. primus*, and *T. wolffsohni* (Rodentia, Cricetidae).

In the review of fleas of Argentina, Lareschi *et al.* (2016) mistakenly mentioned as host of *Craneopsylla minerva* to

Holochilus vulpinus (Brants 1827) for the locality of "Villa Carolina" (Jujuy Province), but this species of rodent is not in NOA, therefore it corresponds to *H. chacarius*. Regarding the host mentioned by Hopkins and Rothschild (1956) as *H. venustus* for the locality "Las Carpas" (Santiago del Estero Province), it was cited by Lareschi *et al.* (2016) as *Calomys musculinus* (Thomas, 1913), but it corresponds to *C. venustus.*

Genus *Nonnapsylla* Wagner 1938

Nonnapsylla rothschildi Wagner 1938

General distribution. Argentina, Bolivia, Chile, and Perú (Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. It is only found in the Jujuy Province (Lareschi *et al.* 2016).

Specimens Examined (9). Argentina. Jujuy: Cuesta del Hurón, 29 km al O de Cieneguillas, sobre ruta provincial 64, 1 male (no number), 5 females (no numbers), ex *Octodontomys gliroides* (P. Gervais and d'Orbigny 1844; CML 7143, 7144); Curques, 24 km al N de Susques sobre ruta 74, 1 female (no number), ex *E. puerulus* (CML 7974). Bolivia: Río Yapacani, Santa Cruz, 1 female lectotype (BMNH 1923-615), ex *Opisthocomus hoazin* (Muller 1776; unknown number). Peru: Puno, 4 km NO Pomata, 1 paratype female (BMNH 1957-239), ex *Galea musteloides* Meyen 1833 (unknown number).

Additional Records. Jujuy: Cuesta del Hurón, 29 km al O de Cieneguillas, sobre ruta provincial 64, ex *Galea comes* Thomas 1919 (originally cited as *G. leucoblephara*) and *P. xanthopygus* (Lareschi *et al.* 2011).

Remarks. This species was not recorded in this study, the specimens examined correspond to those deposited in collections. The recorded localities in Argentina belong to the Puna at an elevation close to 4000 m. The recorded hosts are typical inhabitants of this environment as *O. gliroides*, the only octodontids distributed in the Puna, from the Jujuy to La Rioja (Verzi *et al.* 2015), or *E. puerulus* (Cricetidae), found in the Puna and High Andes in Jujuy, Salta, and Catamarca provinces (Lanzone *et al.* 2015). According to this, the presence of this species in other provinces of NOA is highly probable, so to increase the sampling effort in this type of habitat is fundamental.

Genus *Plocopsylla* Jordan 1931

Plocopsylla (*Plocopsylla*) *chicoanaensis* López-Berrizbeitia, Sanchez, Barquez, and Díaz 2018

General distribution. Endemic to Argentina (López-Berrizbetia *et al.* 2018).

Distribution in Argentina. Salta and Catamarca provinces (López-Berrizbetia *et al.* 2018).

Specimens Examined (21). Catamarca: Las Juntas, 1 male (CMLA 697), ex *A. caenosus* (MIC 94), 2 paratypes males (CMLA 689, 690), 1 paratype female (CMLA 691), *ex A. spegazzinii* (MIC 110, 121, 126), 3 males (CMLA 699, 700, 701), 4 females (CMLA 702, 703, 704, 705), ex *A. spegazzinii* (MIC 91, 108, 113, 121), 1 male (CMLA 706), ex *Oligoryzomys* sp. (MIC 204), 1 female (CMLA 698), ex *P. osilae* (MIC 79). Salta: Aproximadamente 15 km O Escoipe, sobre ruta provincial Nº 33, 1 male holotype (CMLA 687), 1 allotype female (CMLA 688), ex *A. spegazzinii* (SNOMNH 33007), 3 paratypes males (CMLA 692, 694, 695), 2 paratypes females (693, 696), ex *A. spegazzinii* (CML 9236, 9240); 26 km noroeste de Santa Rosa de los Pastos Grandes, 1 female (CMLA 707), ex *P. osilae* (CML 7234).

Remarks. *Plocopsylla* (*P.*) *chicoanaensis* belongs to the complex '*angusticeps-lewisi*'. The complex also comprises *Plocopsylla* (*P.*) *angusticeps*, *P.* (*P.*) *lewisi*, *P.* (*P.*) *wilesi*, *P.* (*P.*) *silewi*, and *P.* (*P.*) *linardii,* all recorded in Argentina. *Plocopsylla* (*P.*) *linardii*, recently described from San Juan Province, Argentina (Sanchez *et al.* 2015), is closest geographically to *P.* (*P.*) *chicoanaensis*. The type locality of *P.* (*P.*) *chicoanaensis* corresponds to the Monte Desert of Mountains and Isolated Valleys. The habitat in which the paratypes were collected corresponds to the montane forest stratum of the Yungas Forest ecoregion. The hosts recorded for *P.* (*P.*) *chicoanaensis* belong to different tribes of rodents, including Akodontini (*A. caenosus* and *A. spegazzinii*), Phyllotini (*P. osilae*) and Oryzomyini (*Oligoryzomys* sp.); the record of these associations was probable because the other species of the complex were also found parasitizing species of these tribes (see Sanchez *et al.* 2015).

Plocopsylla (*Plocopsylla*) *hastriteri* López-Berrizbeitia, Sanchez, Barquez and Díaz 2018

General distribution. Endemic to Argentina (López-Berrizbetia *et al.* 2018).

Distribution in Argentina. It has only been recorded in one locality from La Rioja Province (López-Berrizbetia *et al.* 2018).

Specimens Examined (2). La Rioja: 8 km al NE del Cañón del Ocre, 1 male holotype (CMLA 708), 1 male paratype (CMLA 709), ex *P. osilae* (CML 13011).

Remarks. The type locality of *P.* (*P.*) *hastriteri* corresponds to the Puna. This species was recorded on *P. osilae*, a species of the tribe Phyllotini, which coincides with the recorded hosts in other species of the genus, either to the same genus (*Phyllotis*) or, as *P.* (*P.*) *pallas*, collected on the genus *Eligmodontia* (Schramm and Lewis 1988).

Plocopsylla (*Plocopsylla*) *inti* Johnson 1957

General distribution. Perú (Johnson 1957) and Argentina (López-Berrizbetia *et al.* 2018).

Distribution in Argentina. This species is only found in one locality from Catamarca Province (López-Berrizbetia *et al.* 2018).

Specimens Examined (1). Catamarca: Paycuqui, 1 female (CMLA 710), ex *Abrothrix andina* (CML 9218).

Remarks. This species constitutes a new record for Argentina, extending its distribution ~ 970 km southward. Johnson (1957) described *P.* (*P.*) *inti* from Tacna (Peru) in *Phyllotis magister* Thomas 1912 and *P. xanthopygus*; this new record represents the second one of the species after 60 years. The collection locality corresponds to the Puna. *Plocopsylla* (*P.*) *inti* infesting *Abrothrix andina,* a new flea–host association (López-Berrizbeitia *et al*. 2018).

Genus *Tiarapsylla* Wagner 1937

Tiarapsylla argentina Jordan 1942

General distribution. Endemic to Argentina (Lareschi *et al.* 2016).

Distribution in Argentina. Chubut, Jujuy, La Pampa, Mendoza, Santa Fe, and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined. None.

Additional records. Jujuy: Pucará de Tilcara, ex *Graomys* o *Bolomys*. Tucuman: Los Cardones, ex *Ctenomys* sp. (Beaucournu and Castro 2003).

Remarks. *Tiarapsylla argentina* is endemic to Argentina (Lareschi *et al.* 2016). Other recorded hosts for this species in other provinces are: *Ctenomys mendocinus* Philippi 1869 and *M. australis* in Mendoza Province, and *Reithrodon auritus* (G. Fischer 1814) in Chubut Province (see Lareschi *et al.* 2016).

Family Rhopallopsyllidae

Subfamily Parapsyllinae

Genus *Delostichus* Jordan 1942

Delostichus talis (Jordan 1936)

General distribution. Endemic to Argentina (Smit 1987).

Distribution in Argentina. Buenos Aires, Chubut, La Pampa, Mendoza, Rio Negro, San Juan (Lareschi *et al.* 2016), and La Rioja provinces (López-Berrizbeitia *et al.* 2017); in this study it is added to Catamarca Province.

Specimens Examined (21). Catamarca: 21 km SO El Desmonte, 4 males (no numbers), ex *M. maenas* (SNOMNH 30232). La Rioja: Quebrada de Santo Domingo, 30 km SO de Jagüé, 6 males (CMLA 619, 620, 621; 3 specimens no numbers), 9 females (CMLA 613, 614, 615, 616, 617, 618; 3 specimens no numbers), ex *Microcavia* sp. (CML 13052, 13053). Rio Negro: Fortín Uno, 1 lectotype male (BMNH 1923-615), 1 allotype female (BMNH 1923-615), ex *M. australis*.

Remarks. This species is endemic to Argentina (Lareschi *et al.* 2016); being the rodents of the family Caviidae its main hosts (Smit 1987). However, others hosts, in provinces not belonging to NOA, are: *G. griseoflavus* (Cricetidae) from Rio Negro, *T. barrerae* (Octodontidae) from Mendoza, *R. rattus* (Muridae) from La Pampa, and in some carnivores as *Conepatus chinga*, *Lycalopex griseus* y *L. gymnocercus* from Mendoza (Smit 1987; Lareschi *et al.* 2016). Regarding to the species of *Lycalopex*, Teta *et al.* (2018) consider them as synonyms, but in this study both species are accepted as valid (Díaz and Lucherini 2006). The recorded localities in NOA correspond to the Puna with an elevation of 3000 m, and to the Monte Desert of Mountains and Isolated Valleys with an elevation that exceeds 2000 m.

Genus *Ectinorus* Jordan, 1942

Ectinorus (*Ectinorus*) *budini* (Jordan and Rothschild 1923)

General distribution. Argentina (Lareschi *et al.* 2016).

Distribution in Argentina. It is only found in one locality in Catamarca Province (Lareschi *et al.* 2016).

Specimens Examined (2). Catamarca: Otro Cerro, 1 lectotype male (BMNH 1923-614), ex *Andinomys edax* Thomas 1902 (unknown number), 1 paralectotype male (BMNH 1923-615), ex *P. xanthopygus* (unknown number; originally identified as *Phyllotis arenarius* Thomas 1902).

Remarks. During this study, specimens of this species were not collected; the examined specimens correspond to those deposited specimens in the BMNH. Female is unknown. The females recorded of the type series (Jordan and Rothschild 1923) and described within this species were misidentified, they could be related to *Ectinorus* (*Ectinorus*) *simonsi* (Smit 1987).

Ectinorus (*Ectinorus*) *disjugis* Jordan 1942

General distribution. Argentina and Perú (Smit 1987).

Distribution in Argentina. It is only found in one locality in Jujuy Province (Lareschi *et al.* 2016).

Specimens Examined (2). Argentina. Jujuy: El Chaguaral, Villa Carolina, 1 holotype female (BMNH 1923-615), ex *Ctenomys juris* Thomas 1920 (unknown number; originally identified as *Ctenomys mendocinus juris* Cabrera 1961). Peru: Cailloma, Arequipa, 1 female (BMNH 1948-97), ex Rodentia (unknown number).

Remarks. This species was not collected in this study, the examined specimens correspond to those deposited in the BMNH. Male is unknown. The only recorded locality in NOA corresponds to Dry Chaco ecoregion.

Ectinorus (*Ectinorus*) *hapalus* (Jordan 1942)

General distribution. Endemic to Argentina (Smit 1987).

Distribution in Argentina. Buenos Aires, Chubut, Mendoza, Neuquén, San Luis, and Santa Cruz provinces (Lareschi *et al.* 2016); in this study it is added to La Rioja Province.

Specimens Examined (3). La Rioja: 2 km al S pasando Río de La Punta sobre ruta provincial Nº 7, 1 male (no number), ex *G. chacoensis* (CML 12948). Mendoza: Santa Rosa, 1 lectotype male (BMNH 1940-217), 1 paralectotype female (BMNH 1940-217), ex nest of *G. griseoflavus*.

Remarks. This species is endemic from Argentina (Lareschi *et al.* 2016), being this record the first for NOA, extending its geographical distribution ~ 600 km northward; the nearest locality is Santa Rosa (Mendoza Province). The NOA record corresponds to the Monte Desert of Mountains and Isolated Valleys, at an elevation ~ 1000 m. *Graomys chacoensis* represents a new association flea-host. Others rodent hosts are: *Abrothrix longipilis* (Waterhouse 1837) in the Chubut, *Abrothrix olivacea* (Waterhouse 1837) in Neuquén and Santa Cruz, and *Akodon azarae* (J. B. Fischer 1829; originally cited as *A. arenicola* Thomas 1917) in Buenos Aires (Sanchez and Lareschi 2013, 2014a; Lareschi *et al.* 2016).

Ectinorus (*Ectinorus*) *nomisis* Smit 1987

General distribution. Argentina and Chile (Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. It is only found in one locality in Jujuy Province (Lareschi *et al.* 2016).

Specimens Examined (1). Jujuy: 5 km NE de Humahuaca, 1 holotype male (BMNH 1971-662), ex *O. gliroides* (unknown number).

Remarks. During this study, this species was not recorded; the specimen examined corresponds to a male deposited in the BMNH from Argentina. The collecting locality is placed in the Puna at ~ 4000 m.

Ectinorus (*E.*) *nomisis* is closely related to *E.* (*E.*) *simonsi*. Beaucournu *et al.* (2013), based on the finding of three males with intermediate characters between these two species, raised the possibility that *E.* (*E.*) *nomisis* could be a subspecies of *E* (*E.*) *simonsi*. The examined specimen from Jujuy has all characters belonging to this species, therefore there is no doubt about its identity. It is necessary to increase the sample number of this species that may allow the study of morphology in order to study variation among them.

Ectinorus (*Ectinorus*) *pilosus* Beaucournu and Castro 2002

General distribution. Argentina and Chile (Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. It is only found in one locality in Catamarca Province (Lareschi *et al.* 2016).

Specimens Examined. None.

Additional Records. Catamarca: Santa María Department, ex *Ctenomys knighti* Thomas 1919 (originally cited as *Ctenomys* sp.; Beaucournu and Castro 2002; Lareschi *et al.* 2016).

Remarks. During this study, this species neither was recorded nor revised specimens in systematic collection. This species was recorded for the first time in Argentina in the Monte Desert of Mountains and Isolated Valleys at an elevation of ~ 2000 m (Beaucournu and Castro 2002); later Beaucournu *et al.* (2013) published the second record of the species parasitizing *Ctenomys* sp. in Chile. It is probable that *E.* (*E.*) *pilosus* could have a preference for this genus, although records are very scarce (Beaucournu *et al.* (2013)).

Ectinorus (*Panallius*) *galeanus* (Jordan 1939)

General distribution. Endemic to Argentina (Smit 1987).

Distribution in Argentina. Buenos Aires, Mendoza, Neuquen, Rio Negro, San Juan, San Luis, and Santiago del Estero provinces (Lareschi *et al.* 2016).

Specimens Examined (2). San Juan: Las Casuarinas, 1 lectotype male (BMNH 1940-217), 1 allotype female (BMNH 1940-217) ex *G. leucoblephara* (unknown number).

Additional Records. Santiago del Estero: El Ojito, ex *L. maximus*; El Quemado, ex *Akodon [boliviensis] tucumanensis;* Las Carpas, ex *G. chacoensis* (originally cited as *G. griseoflavus*) and *M. jayat* (originally cited as *M. australis*; Smit 1987; Lareschi *et al.* 2016).

Remarks. This species was not recorded in this study, the examined specimens correspond to those deposited in the BMNH. *Ectinorus* (*Panallius*) *galeanus* is endemic to Argentina and was recorded parasitizing *Akodon dolores* Thomas 1916 in Neuquen (Lareschi *et al.* 2016). The hosts of this species are diverse, including rodents of different habits belonging to the families Cricetidae (two tribes) and Caviidae. The host cited from Santiago del Estero (locality "El Quemado") is doubtful because *A. tucumanensis* is not distributed in the province. The species is distributed in arid environments, Dry Chaco and Monte Desert of Mountains and Isolated Valleys.

Genus *Tetrapsyllus* Jordan 1931

Tetrapsyllus (*Phylliver*) *bleptus* (Jordan and Rothschild 1923)

General distribution. Argentina, Peru, and Chile (Smit 1987; Beaucournu *et al.* 2014).

Distribution in Argentina. Catamarca, Jujuy, Mendoza, Neuquen (Lareschi *et al.* 2016), La Rioja, Salta, and Tucuman provinces (López-Berrizbeitia *et al.* 2019).

Specimens Examined (22). Catamarca: Otro Cerro, 1 holotype female (BMNH 1923-615), 1 paratype female (BMNH 1923-615), ex *R. auritus* (unknown number; originally identified as *Reithrodon caurinus* Thomas 1920). Jujuy: Quebrada Seca, Alfarcito, 10 km al O de Tilcara, 1 male (no number), ex *Phyllotis* sp. (CML 12308). LA RIOJA: Puesto Tres Piedras, 2 males (no numbers), ex *Akodon* sp. (CML 12900); Quebrada de Santo Domingo 30 km al SO de Jagué, 1 female (no number), ex *P. xanthopygus* (CML 13046). Mendoza: Puesto "Pugin", Algarrobito, 1 male (BMNH 1959-683), ex Rodentia (unknown number). Salta: Finca Barba Yaco, 8.5 km SE Ojo de Agua, 1 female (no number), ex *A. simulator* (SNOMNH 29996). Tucuman: Ciénaga Escondida, 1 male (no number), ex *A. spegazzinii* (released), 1 male (no number), 1 female (no number), ex *P. xanthopygus* (released); La Olorosa, 1 female (no number), ex *P. osilae* (released); Los Chorrillos 13 km NO, límite norte estancia Los Chorrillos, 1 female (no number), ex *A. simulator* (CML 9053).

Additional Records. Jujuy: El Chaguaral, ex *C. juris* (originally cited as *C. mendocinus juris*); Reserva Provincial Olaroz--Cauchari, ex *A. albiventer* (Smit 1987; Lareschi *et al.* 2010).

Remarks. The new flea–host associations recorded are: *Tetrapsyllus* (*Phylliver*) *bleptus* with *A. simulator*, *A. spegazzinii*, and *P. osilae* (López-Berrizbeitia *et al.* 2019); another recorded host is *G. griseoflavus* from Mendoza (Smit 1987). In the study area, the species was recorded in Monte Desert of Mountains and Isolated Valleys, Dry Chaco, High Andes, Puna, Yungas, and in the ecotone between Yungas and High Andes.

Tetrapsyllus (*Tetrapsyllus*) *spegazzinii* Lopez-Berrizbeita, Hastriter, Barquez and Diaz 2019.

General distribution. Argentina (López-Berrizbeitia *et al.* 2019).

Distribution in Argentina. It is only recorded in Salta Province (López-Berrizbeitia *et al.* 2019).

Specimens Examined (5). Salta: ~ 15 kmW Escoipe, on Provincial road No. 33, 1 holotype male (CMLA 818), ex *A. spegazzinii* (SNOMNH 33007), 1 allotype female (CMLA 819), 1 paratype male (CMLA 820) ex *A. spegazzinii* (CML 9236); Finca Barba Yaco, 8.5 km SE Ojo de Agua, 1 paratype male (CMLA 821), 1 paratype female (CMLA 822) ex *A. simulator* (CML 9050, SNOMNH 33147).

Remarks. The localities of examined specimens belong to the Monte Desert of Mountains and Isolated Valleys and Yungas.

Subfamily Rhopalopsyllinae

Genus *Polygenis* Jordan 1939

Polygenis (*Neopolygenis*) *pradoi* (Wagner 1937)

General distribution. Argentina, Brazil, and Colombia (Smit 1987).

Distribution in Argentina. Buenos Aires (Lareschi *et al.* 2016) and Misiones provinces (Urdapilleta *et al.* 2019); and in this study, it is included in Catamarca and Salta provinces.

Specimens Examined (5). Argentina. Catamarca: Las Juntas, 2 females (no numbers), ex *A. spegazzinii* (MIC 86, 119). Salta: Aproximadamente 15 km O de Escoipe, sobre ruta provincial Nº 33, 1 female (no number), ex *A. spegazzinii* (SNOMNH 33007). Brazil: Brasilien, Nova Teutonia, Catharina, 1 topotype male (BMNH 1956-476), ex Rodentia (unknown number), 1 topotype female (BMNH 1956-476), unknown host.

Remarks. Here, a new flea-host association, *P.* (*N.*) *pradoi*-*A. spegazzinii*, is recorded. Others recorded hosts in Argentina are: *Didelphis albiventris* Lund 1840, *A. azarae*, *Oligoryzomys nigripes* (Olfers 1818), *Oxymycterus rufus* (G. Fischer 1814), and *Scapteromys aquaticus* Thomas 1920 (Lareschi *et al.* 2016). The records of this species extend its geographical distribution ~ 1550 km northwest of Argentina. In order to complete the gap between the records of Buenos Aires Province and NOA, is necessary to increase the sampling efforts of *Polygenis* (*Neopolygenis*) *pradoi*. Also, the presence of this species in Ecuador, Peru, and Bolivia is highly probable due to its location among records from Colombia, Brazil, and Argentina.

Polygenis (*Neopolygenis*) *puelche* Del Ponte 1963

General distribution. Endemic to Argentina (Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, La Pampa, Mendoza, and Tucuman provinces (Lareschi *et al.* 2016), and in this study, it is included in Catamarca and Salta provinces.

Specimens Examined (16). Catamarca: 22 km al SE de Villa de Escaba sobre ruta provincial Nº 9, 1 female (no number), *A. spegazzinii* (CML 12356); 3.4 km al S de la unión entre las rutas provinciales 18 y 9, sobre ruta provincial Nº 18, 2 males (no numbers), 2 females (no numbers), ex *A. simulator* (CML 7219), 3 females (no numbers), 1 male (no number), ex *A. lutescens* (SNOMNH 37302, 37308). Salta: Aguas Blancas, Estación de Aforo a 30 m del puente internacional sobre ruta provincial N° 19, a orillas del Río Bermejo, 1 male (no number), ex *Akodon simulator* (CML 11014); ~ 2 km al N y 6 km al O de Metán, sobre río Las Conchas, 1 female (no number), ex *A. simulator* (CML 12349). Tucuman: 26 km al S de San Pedro de Colalao sobre ruta provincial 364, 1 female (no number), ex *A. simulator* (SNOMNH 33188); Los Chorrillos 13 km NO, límite norte estancia Los Chorrillos, 1 male (no number), 1 female (no number), ex *A. simulator* (CML 9053); Río Nío, 4 km al O, camino hacia Alto de Medina, 2 males (no numbers), ex *O. brendae* (CML 4475, 4480).

Additional Records. Tucuman: Cerro San Javier, unknown host (Smit 1987).

Remarks. This species is endemic to Argentina (Lareschi *et al.* 2016). In this study, three new flea–host associations are recorded: *P.* (*N.*) *puelche* with *A. simulator*, *A. spegazzinii*, and *A. lutescens*. Others recorded hosts are: *L. crassicaudata, A. azarae, Calomys laucha* (G. Fisher 1814), *C. musculinus, Ctenomys talarum* Thomas 1898, *O. rufus*, and *O. nigripes* in Buenos Aires; *G. griseoflavus* in Buenos Aires and La Pampa; and *A. dolores* in Mendoza (Lareschi *et al.* 2016. The distribution of the species extends ~ 300 km to the west and ~ 500 km to the north from of the nearest locality belonging to the Trancas Department, Tucuman Province.

Polygenis (*Polygenis*) *acodontis* (Jordan and Rothschild 1923).

General distribution. Argentina, Brazil, and Venezuela (Smit 1987).

Distribution in Argentina. Buenos Aires, Catamarca, Cordoba, Jujuy, La Pampa, Salta, Tucuman (Lareschi *et al.* 2016), and La Rioja provinces (López-Berrizbeitia *et al.* 2017); in this study the Santiago del Estero Province is added.

Specimens Examined (92). Catamarca: Otro Cerro, 1 lectotype male (BMNH 1923-615), ex *A. simulator* (unknown number), 1 paralectotype female (BMNH 1923-615), *Homo sapiens* Linnaeus 1758; 21 km SO El Desmonte, 1 male (no number), ex *M. maenas* (SNOMNH 30232); 22 km al SE de Villa de Escaba sobre ruta provincial Nº 9, 1 male (no number), ex *A. glaucinus* (CML 12347), 1 male (no number), 2 females (no numbers), ex *A. spegazzinii* (CML 12356, 12360); 3.4 km al S de la unión entre las rutas provinciales 18 y 9, sobre ruta provincial Nº 18, 1 female (no number), ex *A. lutescens* (SNOMNH 37307); Estancia Narváez, 5.5 km N La Chacritas en ruta provincial 1, 3 males (no numbers), 1 female (no number), ex *A. spegazzinii* (CML 7198); Las Juntas, 1 male (no number), 4 females (no numbers), ex *A. simulator* (MIC 66, 104, 130, 182, 207), 3 males (no numbers), 5 females (no numbers) ex *A. spegazzinii* (MIC 86, 113, 119, 121, 173), 1 male (no number), ex *Necromys lactens* (Thomas 1918; MIC 64), 3 females (no numbers), ex *Oligoryzomys* sp. (MIC 117, 170, 201), 1 male (no number), 1 female (no number) ex *P. osilae* (MIC 180, 181). Jujuy: Arroyo Los Matos, 7 km N de Las Capillas, 3 females (no numbers), ex *A. budini* (CML 12340), 2 females (no numbers), ex *C. venustus* (2 released), 1 female (no number), ex *O. brendae* (CML 12372), 1 male (no number), 1 female (no number), ex *O. paramensis* (CML 12364), 1 female (no number), ex *T. sponsorius* (released); Río Blanco, 9 km SO, San Antonio, 1 female (no number), ex *O. brendae* (CML 9550); Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N° 29, 1 male (no number), ex *O. brendae* (CML 9537). La Rioja: Cuesta La Cébila, 22 km al NO de Chumbicha, sobre ruta 60, 1 male (CMLA 674), ex *A. glaucinus* (CML 3751). Salta: 3 km al N de Potrerillos sobre ruta provincial Nº 6, 10 males (no numbers), 11 females (no numbers), ex *A. simulator* (CML 9037, SNOMNH 29992); ~ 2 km al N y 6 km al O de Metán, sobre Río Las Conchas, 1 female (no number), ex *A. caenosus* (CML 12342), 1 female (no number), ex *A. puer* (CML 12345), 2 females (no numbers), *ex A. simulator* (CML 12349); ~ 3.5 km al O de Metán, 2 females (no numbers), ex *A. simulator* (CML 12352); Finca Barba Yaco, 8.5 km SE Ojo de Agua, 2 males (no numbers), 1 female (no number), ex *A. simulator* (SNOMNH 29995, 29996, 33147), 2 females (no numbers), ex *O. brendae* (CML 9572), 1 male (no numbers), 2 females (no numbers), ex *P. xanthopygus* (SNOMNH 30198); Pintascayo, Campamento Lima (Propiedad de GMF S.A), 1 male (no number), ex *A.* cf. *fumeus* (MMD 5172); Río Los Sauces, 12 km NO del Jardín, ruta 6 km 110, 2 males (no numbers), 1 female (no number), ex *C. venustus* (LIF 190). Santiago del Estero: La Puerta, 27 km al SE de Las Termas de Río Hondo, sobre ruta Nacional Nº 9, 2 females (no numbers), ex *A. dolores* (CML 12343). Tucuman: 1.9 km NE Hualinchay sobre ruta provincial 311, 1 male (no number), ex *P. osilae* (CML 8085); Dique San Ignacio, 1 female (no number), ex *T. sponsorius* (CML 7159); Los Chorrillos 13 km NO, límite norte estancia Los Chorrillos, 1 male (no number), ex *A. simulator* (CML 9053), 1 female (no number), ex *Akodon* sp. (CML 6466), 1 male (no number), ex *T. sponsorius* (CML 7814); Reserva Provincial Aguas Chiquitas, sobre Río Aguas Chiquitas, 1 male (no number), 1 female (no number), ex *C. venustus* (CML 11945, 11947).

Additional Records. Catamarca: Otro Cerro, ex *A. alterus*. Jujuy: El Chaguaral, ex *C. juris* (originally cited as *C. m. juris*; Johnson 1957; Smit 1987; Lareschi *et al.* 2016).

Remarks. In this study, *P.* (*P.*) *acodontis* infesting *A. budini*, *A. glaucinus*, *A. lutescens*, *N. lactens*, *O. brendae*, and *P. osilae*, all constitute new flea–host associations, and it was also recorded on *P. xanthopygus* (López-Berrizbeitia *et al.* 2013b). The localities from NOA belong to Dry Chaco, Yungas, and Monte Desert of Mountains and Isolated Valleys.

Polygenis (*Polygenis*) *bohlsi* (Wahlgren 1901)

Polygenis (*Polygenis*) *bohlsi bohlsi* (Wahlgren 1901)

General distribution. Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Paraguay, Peru, and Venezuela (Smit 1987).

Distribution in Argentina. Buenos Aires, Chaco, Cordoba, Corrientes, and Mendoza provinces (Lareschi *et al.* 2016); in this study, La Rioja Province is included.

Specimens Examined (4). Buenos Aires: Chivilcoy, 1 male (BMNH 1962-699), 1 female (BMNH 1962-699), ex *C. laucha* (unknown number). La Rioja: Ulapes, 1 km al O de la plaza principal de Ulapes, 2 females (no numbers), ex *G. chacoensis* (CML 12991).

Remarks. The association *P.* (*P.*) *b. bohlsi-G. chacoensis* is new. Moreover, this species was recorded on others rodents in Argentina such as *A. azarae*, *C. aperea*, *S. aquaticus*, *A. dolores*, *G. griseoflavus*, *Mus musculus* Linnaeus 1758, and *Deltamys kempi* Thomas 1917 (Lareschi *et al.* 2016). The record from La Rioja corresponds to Dry Chaco and extends the geographical distribution of the species ~ 360 km northwest of Argentina.

Polygenis (Polygenis) byturus (Jordan and Rothschild 1908)

General distribution. Argentina and Bolivia (Smit 1987).

Distribution in Argentina. Antarctica and South Atlantic Islands, Buenos Aires, Cordoba, Jujuy, La Pampa, Rio Negro, Salta, Santa Fe, San Luis, Santiago del Estero, Tierra del Fuego, and Tucuman provinces (Lareschi *et al.* 2016); in this study the Catamarca and La Rioja provinces are added.

Specimens Examined (20). Catamarca: Estancia Narváez, 5.5 km N La Chacritas en ruta Provincial 1, 1 female (no number), ex *A. alterus* (SNOMNH 32997). La Rioja: 2 km al E de Malanzán, camping El Descanso, 1 male (no number), 1 female (no number), ex *Akodon* sp. (CML 12897); 26 km SO Quimilo, 1 female (no number), ex *A. dolores* (SNOMNH 36034); Ambil, 23 km al S de Catuna, 2 females (no numbers), ex *G. chacoensis* (CML 12983); Chepes, puesto La Escondida, 42 km al S de Chepes, 1 female (no number), ex *G. chacoensis* (CML 12990); Olta, Dique de Olta, 2 males (no numbers), 2 females (no numbers) ex *G. chacoensis* (CML 12962); Ulapes, 1 km al O de la plaza principal de Ulapes, 1 female (no number), ex *P. xanthopygus* (CML 13037). Salta: Finca Chato Méndez, 1 male (no number), 4 females (no numbers), ex *C. callosus* (CLH 1, 2). Santa Fe: Las Rosas, 1 male lectotype (BMNH 1923-615), 1 female allotype (BMNH 1923-615), ex *L. crassicaudata* (unknown number). Santiago del Estero: La Puerta, 27 km al SE de Las Termas de Río Hondo, sobre ruta Nacional Nº 9, 1 male (no number), ex *G. chacoensis* (CML 12397).

Additional Records. Jujuy: not specific locality, ex *H. chacarius* (originally cited as *Holochilus* [*brasiliensis*] *vulpinus*); El Chaguaral, ex *C. juris* (originally cited as *Ctenomys* [*mendocinus*] *juris*; Smit 1987). Salta: Cerillos, not specific locality, ex *G. leucoblephara* (originally cited as *G. musteloides*); El Quebrachal, ex *G. leucoblephara* (originally cited as *G. musteloides*), *G. griseoflavus, R. rattus*; J. V. González, ex *G. leucoblephara* (originally cited as *G. musteloides*; Smit 1987). Santiago del Estero: not specific locality, ex *G. chacoensis* (originally cited as *G. griseoflavus*); El Ojito, ex *L. maximus*; El Quemado, ex *Akodon* (*boliviensis*) *tucumanensis, C. musculinus* (originally cited as *Hesperomys murillus*); Las Carpas, ex *C. venustus* (originally cited as *Hesperomys venustus*), *G. chacoensis* (originally cited as *G. griseoflavus*), *M. jayat* (originally cited as *M. australis*); Pozo Betbeder, ex *R. rattus* (Smit 1987). Tucuman: Taco Ralo, unknown host (Smit 1987).

Remarks. The longitude degrees of the locality La Rosas (Santa Fe Province) were corrected. The host cited from Santiago del Estero (locality "El Quemado") is doubtful because *A. tucumanensis* is not distributed in the province. In this study, new flea–host associations were recorded: *P.* (*P.*) *byturus* with *A. alterus*, *A. dolores*, *C. callosus* and *P. xanthopygus*. The species is distributed in all provinces of NOA except Tucuman, although the presence of this species is highly probable. The ecoregions of the localities correspond to the Yungas and Dry Chaco.

Polygenis (*Polygenis*) *platensis* (Jordan and Rothschild 1908).

General distribution. Argentina, Bolivia, Brazil, Chile, and Uruguay (Smit 1987).

Distribution in Argentina. Buenos Aires, Cordoba, Chubut, Entre Rios, Jujuy, La Pampa, La Rioja, Mendoza, Rio Negro, Salta, San Juan, San Luis, Santa Cruz, and Santiago del Estero (Lareschi *et al.* 2016) and Misiones provinces (Urdapilleta *et al.* 2016).

Specimens Examined (18). Buenos Aires: Chivilcoy, 1 male (BMNH 1944-88), ex *A. azarae* (originally cited as *A. arenicola*; unknown number); La Plata, 1 holotype female (BMNH 1923-615), ex *Ctenomys* sp. (unknown number); not specific locality, 1 male (BMNH 1923-615), ex *Didelphis* sp. (unknown number). La Rioja: 2 km al S de la entrada al Parque Geológico Sanagasta, sobre RN 75, 1 male (no number), 1 female (no number), ex *G. chacoensis* (CML 13001, 13002), 1 male (no number), ex *P. osilae* (CML 13015), 1 male (no number), ex *P. xanthopygus* (CML 13015); 4 km al O de Anillaco, Reserva Aguada de las Alturas, 1 male (CMLA 605), ex *A. glaucinus* (CML 9767); Ulapes, 1 km al O de la plaza principal de Ulapes, 4 females (3 CMLA 622, 623, 624; 1 no number), ex *G. chacoensis* (CML 12991, 12992), 2 males (CMLA 625, 626), 2 females (CMLA 627, 628), ex *G. griseoflavus* (CML 13007). Mendoza: not specific locality, 1 holotype male (BMNH 1940-217), 1 paratype female (BMNH 1940-217), ex *M. australis* (unknown number).

Additional Records. Jujuy: San Pedro, unknown host. La Rioja: Guayapa, 13 km SO de Patquía cerca de la ruta 150, unknown host. Salta: Rosario de Lerma, *G. leucoblephara* (Smit 1987).

Remarks. Traditionally two subspecies of this species are recognized: *P.* (*P.*) *p. platensis* and *P.* (*P.*) *p. cisandinus*. Lareschi and Linardi (2009), through the review of type specimens and the diagnostic characters, questioned their validity of the subspecies and consider them as synonyms. This study follows Lareschi and Linardi (2009) and considers *Polygenis* (*Polygenis*) *platensis* as valid species.

According to the geographic coordinates in Smit (1987), the locality Guayapa (La Rioja Province) was wrongly placed at approximately 3 km N of El Milagro, but in this study is relocated to ~ 180 m SE of that site, next route 150 and 13 km SW Patquia (corrected coordinates: -29°51’41.18” S, -67°14’22.99” W). López-Berrizbeitia *et al.* (2013b) cited as host to *A. simulator*, but following to Coyner *et al.* (2013) the species belong to *A. glaucinus*. López-Berrizbeitia *et al.* (2017) reported a new flea-host association from Ulapes, *Polygenis* (*P.*) *platensis*-*G. chacoensis*. The examined specimen collected from the genus *Didelphis* from Buenos Aires, would correspond to *Didelphis albiventris*, because it is the only species of the genus present in this province.

Polygenis (*Polygenis*) *rimatus* (Jordan 1932)

General distribution. Argentina, Brazil, Paraguay, and Perú (Smit 1987).

Distribution in Argentina. Buenos Aires, Chubut, Formosa, La Rioja, Misiones, Neuquen, San Juan, Santiago del Estero (Lareschi *et al.* 2016), and Salta provinces (Smit 1987).

Specimens Examined (3). Argentina. Salta: Gran Chaco, 1 paratype female (BMNH 1923-615), ex *D. albiventris* (unknown number; originally identified as *Didelphis azarae* Tschudi 1845). Paraguay: Sapucay, 1 holotype male (BMNH 1923-615), 1 paratype female (BMNH 1923-615), ex *D. albiventris* (unknown number; originally identified as *D. azarae*).

Additional Records. La Rioja: not specific locality, ex *Cavia aperea* (Smit 1987). Santiago del Estero: Not specific locality, ex *M. jayat* (originally cited as *M. australis*; Autino and Lareschi 1998).

Remarks. During this study, this species was not recorded, the examined specimens are those deposited in the BMNH. The host *Cavia aperea* was probably misidentified, because the presence of the genus *Cavia* (family Caviidae) in La Rioja province is unknown (Patton *et al.* 2015).

Polygenis (Polygenis) roberti (Rothschild 1905)

Polygenis (Polygenis) roberti beebei (Fox 1947)

General distribution. Argentina, Bolivia, Brazil; Colombia, Costa Rica, Ecuador, French Guiana, Panama, Peru, Surinam, and Venezuela (Smit 1987; Lareschi *et al.* 2016).

Distribution in Argentina. Jujuy (Lareschi *et al.* 2016), and Misiones provinces (Urdapilleta *et al.* 2019); in this study the Salta Province is added.

Specimens Examined (3). Argentina. Salta: 12.6 km O de Piquirenda Viejo, 1 male (no number), ex *E. legatus* (CML 9694); Río Las Conchas, 2 km al N y 6 km al O de Metán, 1 female (no number), ex *E. legatus* (CML 9710). Bolivia: Buen Retiro, 1 female (BMNH 1955-277), ex *Cuniculus paca* (Linnaeus 1766; unknown number).

Additional Records. Jujuy: Laguna La Brea, 25 km antes de Palma Sola, ex *E. legatus* (Lareschi *et al.* 2016).

Remarks. The records cited in this study constitute the third one for Argentina and the second for NOA, extending the distribution ~ 200 km north (in Jujuy Province) and ~ 170 km to the south (Salta Province). The records correspond to the Yungas Forests. The main hosts are rodents of the family Cricetidae, especially members of the tribe Oryzomyinii (Smit 1987).

Polygenis (Polygenis) tripus (Jordan 1933)

General distribution. Argentina, Bolivia, and Brazil (Smit 1987).

Distribution in Argentina. Buenos Aires, Salta (Lareschi *et al.* 2016), and Misiones provinces (Lareschi *et al.* 2019).

Specimens Examined (5). Salta: Hipólito Yrigoyen, 3 males (no numbers), ex *A. tartareus* (CLH 57); Rosario de Lerma, 1 lectotype male (BMNH 1923-615), 1 allotype female (BMNH 1923-615), ex *G. leucoblephara* (unknown number; originally identified as *G. musteloides*).

Additional Records. Salta: not specific locality, ex *G. leucoblephara* (originally cited as *G. musteloides*; Smit 1987).

Remarks. The association recorded in this study, *P. (P.) tripus-A. tartareus* is a new flea–host association; in Argentina, others recorded hosts are: *A. azarae*, *Oligoryzomys* sp., *Oxymycterys rufus*, *Phyllotis* sp., *S. aquaticus* and *Rattus norvegicus* Berkenhout 1769 (Lareschi *et al.* 2016).

Genus *Tiamastus* Jordan 1939

Tiamastus cavicola (Weyenbergh 1881)

General distribution. Argentina, Bolivia, Chile, Ecuador, and Peru (Smit 1987; Beaucournu *et al.* 2014).

Distribution in Argentina. Buenos Aires, Catamarca, Cordoba, Jujuy, La Pampa, Mendoza, Rio Negro, Salta, and Santiago del Estero provinces (Lareschi *et al.* 2016).

Specimens Examined (19). Buenos Aires: Bonifacio, 1 male (BMNH 1923-615), ex *C. aperea* (unknown number). Jujuy: 3 km al E de Purmamarca por ruta nacional N° 52, 6 males (no numbers), 11 females (no numbers), ex *M. maenas* (CML 12400). Not specific locality: 1 lectotype female (BMNH 1923-615) ex *C. aperea* (unknown number; originally identified as *Cavia leucopyga* Brandt 1835).

Additional Records. Catamarca: La Merced, ex *G. leucoblephara* (originally cited as *G. musteloides*). Jujuy: El Chaguaral, ex *C. juris*. Salta: Rosario de Lerma; Cerillos (=Cerrillos), ex *G. leucoblephara*; Capital, unknown host (Smit 1987).

Remarks. The main hosts of this species are rodents of the family Caviidae (Smit 1987), but in Argentina it was recorded on others families of rodents: *A. azarae* (Cricetidae) and *Ctenomys* spp. (Ctenomyidae; Lareschi *et al.* 2016). The records of NOA correspond to Dry Chaco, Puna, and Yungas Forests.

Tiamastus helicis Beaucournu and Castro 2003

General distribution. Endemic to Argentina (Beaucournu and Castro 2003).

Distribution in Argentina. It is only found in one locality from Tucuman Province (Beaucournu and Castro 2003; Lareschi *et al.* 2016).

Specimens Examined. None.

Additional Records. Tucuman: Tapia, ex *Ctenomys latro* (Beaucournu and Castro 2003).

Remarks. This species is endemic from Argentina (Lareschi *et al.* 2016). During this study the species was not collected. The only known record corresponds to the Yungas Forests.

Tiamastus palpalis (Rothschild 1911)

General distribution. Argentina (Lareschi *et al.* 2016).

Distribution in Argentina. Catamarca, Jujuy, La Pampa, Mendoza, Santa Fe, Santiago del Estero, Tucuman (Lareschi *et al.* 2016), and La Rioja provinces (López-Berrizbeitia *et al.* 2017).

Specimens Examined (27). Catamarca: 9.2 km O Andalgalá, 2 males (no numbers), 3 females (no numbers), ex *Ctenomys* sp. (SNOMNH 30256); Chumbicha, alrededores, 2 females (no numbers), ex *Ctenomys* sp. (CML 12409). La Rioja: 2 km al S pasando Río de La Punta sobre ruta provincial Nº 7, 1 male (no number), ex *E. moreni* (CML 12941); 700 m al E de ruta nacional 40, 1 female (CMLA 631), ex *Ctenomys* sp. (CML 11030); Anillaco, 500 m al O de la plaza de Anillaco, 7 males (1 CMLA 629, 6 no numbers), 11 females (5 CMLA 630, 632, 633, 634, 635, 6 no numbers), ex *Ctenomys* sp. (released).

Additional Records. Jujuy: El Chaguaral, cerca de Villa Carolina, ex *C. juris*. Santiago del Estero: not specific locality, ex *Ctenomys brasiliensis* (Johnson 1957; Smit 1987).

Remarks. This species is endemic from Argentina (Lareschi *et al.* 2016). The main hosts are rodents of the family Caviidae (Smit 1987); however, in this study, the species was collected on rodents of the families Cricetidae and Ctenomyidae. Others recorded hosts belong to mammals of the order Carnivora, in Mendoza (Smit 1987). Regarding to type host *C. brasiliensis*, it was misidentified because this species is not distributed in Argentina (Lareschi *et al.* 2016), probably the host correspond to *Ctenomys argentinus*, the only species of the genus present in Santiago del Estero. In NOA, most records correspond to the Monte Desert of Mountains and Isolated Valleys, and only two to the Dry Chaco.

Tiamastus plesius Jordan 1942

General distribution. Argentina and Chile (Smit 1987; Beaucournu *et al.* 2014).

Distribution in Argentina. Buenos Aires, Jujuy, La Pampa, Mendoza, and Rio Negro provinces (Lareschi *et al.* 2016).

Specimens Examined. None.

Additional Records. Jujuy: Pucará de Tilcara, ex *N. lactens* (Beaucournu and Castro 2003).

Remarks. In this study, this species neither was recorded nor specimens were reviewed. Others recorded hosts are: *M. maenas* (originally cited as *M. australis*) from Mendoza; *Ctenomys fulvus* Philippi 1860 (originally cited as *Ctenomys robustus* Philippi 1896) from Chile (Beaucournu *et al.* 2014; Bidau 2015). In NOA, the record corresponds to the Puna.

Tiamastus subtilis (Jordan and Rothschild 1923)

General distribution. Endemic to Argentina (Lareschi *et al.* 2016; Smit 1987).

Distribution in Argentina. Chubut and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined. None.

Additional Records. Tucuman: Los Cardones, ex *Ctenomys* sp. (Beaucournu and Castro 2003).

Remarks. In this study, this species neither was recorded nor specimens were reviewed. *Tiamastus subtilis* is known from two localities, one in the south and the other in NOA, separated by ~ 2500 km. Other recorded host is *P. xanthopygus* from Chubut (Smit 1987). In the NOA, the record corresponds to the Yungas Forest.

Family Ctenophthalmidae

Subfamily Ctenophthalminae

Tribe Agastopsyllini

Genus *Agastopsylla* Jordan and Rothschild 1923

Agastopsylla hirsutior Traub 1952

General distribution. Peru (Hopkins and Rothschild 1966), and recently it will be added to Argentina (López-Berrizbeitia *et al*. in press).

Distribution in Argentina. It is only known from one locality from Tucuman province (López-Berrizbeitia *et al*. in press).

Specimens Examined (2). Tucuman: Ciénaga Grande, San José de Chasquivil, 1 male (no number), 1 female (no number), ex *A. spegazzinii* (CML 7478).

Remarks. The type material is a female specimen deposited in the Field Museum of Natural History; but a new type was designed because the specimen was lost (López-Berrizbeitia *et al*. in press). The record corresponds to the Monte Desert of Mountains and Isolated Valleys.

Agastopsylla nylota Traub 1952

Agastopsylla nylota nylota Traub 1952

General distribution. Peru (Hopkins and Rothschild 1966), and recently it will be added to Argentina (López-Berrizbeitia *et al*. in press).

Distribution in Argentina. It is only known from one locality from Salta Province (López-Berrizbeitia *et al*. in press).

Specimens Examined (4). Salta: aproximadamente 15 km O Escoipe, sobre ruta provincial Nº 33, 3 males (no numbers), 1 female (no numbers), ex *P. osilae* (CML 8044).

Remarks. The type material, a male specimen, deposited in the Field Museum of Natural History, was lost, then a new type for the species was designed (López-Berrizbeitia *et al*. in press). One of the male specimens examined was misidentified as *A. pearsoni* in López-Berrizbetia *et al.* (2013a).

Tribe Neotyphloceratini

Genus *Neotyphloceras* Rothschild 1914

Neotyphloceras chilensis Jordan 1936

General distribution. Argentina, Chile, and Peru (Hopkins and Rothschild 1966; Lareschi *et al*. 2016).

Distribution in Argentina. Until now, this species was only known from the southern provinces of Argentina, Neuquén and Rio Negro (Lareschi *et al*. 2016); in this study three provinces from northwestern Argentina (Catamarca, Jujuy, and Salta) were added.

Specimens Examined (20). Catamarca: Paycuqui, 1 female (no number), ex *Neotomys ebriosus* Thomas 1894 (SNOMNH 30069), 1 female (no number), ex *A. andina* (CML 9217). Jujuy: 6.8 km al SE de Suripujio, sobre ruta provincial N° 5, 1 female (no number), ex *P. xanthopygus* (SNOMNH 30197); Sierra de Tilcara, El Hueco, 21 km SE de Tilcara, 1 male (no number), ex *N. lactens* (CML 9377). Salta: aproximadamente 15 km O Escoipe, sobre ruta provincial Nº 33, 1 female (no number), ex *A. spegazzinii* (CML 9240); Vega Cortadera, 4 males (no numbers), 4 females (no numbers), ex *A. andina* (CML 6874, SNOMNH 30219), 3 males (no numbers), 1 female (no numbers), ex *E. puerulus* (CML 9478, SNOMNH 34755). Chile: Valparaíso, 1 lectotype male (BMNH 1923-615), 1 paratype female (BMNH 1923-615), ex *Thylamys elegans* (Waterhouse 1839; unknown number; originally identified as *Marmosa elegans*), 1 allotype female (BMNH 1923-615), ex *A. longipilis* (unknown number).

Remarks. Traditionally, this species was considered as subspecies of *N. crassispina*, later Sanchez *et al.* (2012) redescribed it and considered it as valid species. In Argentina, this species was restricted to the south through few records (Beaucournu and Alcover 1990; Lareschi *et al*. 2016); therefore, this records, in three provinces of NOA, are relevant because extend the distribution of *N. chilensis* ~ 2000 kms northward. In this study, five new flea–host associations are recorded: *N. chilensis* with *N. ebriosus*, *P. xanthopygus*, *N. lactens, A. andina*, and *E. puerulus*.

Neotyphloceras crassispina Rothschild 1914

Neotyphloceras crassispina hemisus Jordan 1936

General distribution. Argentina, Bolivia, Chile, and Peru (Lareschi *et al*. 2016).

Distribution in Argentina. Catamarca, Jujuy, Mendoza, Neuquen, Rio Negro, Salta (Lareschi *et al*. 2016), and La Rioja provinces (López-Berrizbeitia *et al*. 2013b); in this study the Tucuman Province is added.

Specimens Examined (131). Catamarca: 17 km N Barranca Larga, 1 female (no number), ex *P. xanthopygus* (CML 8035), 1 female (no number), ex *P. xanthopygus* (SNOMNH 30201); 21 km SO El Desmonte, 1 male (no number), ex *M. maenas* (SNOMNH 30232); 3.4 km al S de la unión entre las rutas provinciales N° 18 y 9, sobre ruta provincial N° 18, 1 female (no number), ex *P. osilae* (CML 7229), 1 female (no number), ex *N. lactens* (SNOMNH 34512); Estancia Narváez, 5.5 km N La Chacritas en ruta provincial 1, 3 males (no numbers), 2 females (no numbers), ex *A. alterus* (SNOMNH 32997), 1 male (no number), ex *C. musculinus* (SNOMNH 35315), 2 females (no numbers), ex *A. spegazzinii* (CML 7198, 7202); Laguna Blanca, 1 male (no number), 1 female (no number), ex *Eligmodontia bolsonensis* Mares, Braun, Coyner and van den Bussche 2008 (CML 9436); Las Juntas, 3 males (no numbers), 2 females (no numbers), ex *A. simulator* (MIC 66, 104, 130), 2 females (no numbers), ex *A. spegazzinii* (MIC 87, 128), 1 male (no number), 2 females (no numbers), *ex P. osilae* (MIC 69); Otro Cerro, Rancho de los Crisho, 1 holotype male (BMNH 1923-615), ex *A. edax* (unknown number), 1 paratype female (BMNH 1923-615), ex *R. auritus* (unknown number; originally identified as *R. caurinus*), 1 topotype male (no number), unknown host; Pasto Ventura, 1 male (no number), ex *E. bolsonensis* (CML 7182); Paycuqui, 5 males (no numbers), 7 females (no numbers), ex *A. andina* (CML 6878, 6879, 9217, 9218; SNOMNH 30214), 3 males (no numbers), 2 females (no numbers), ex *N. ebriosus* (SNOMNH 30069, 33874), 1 female (no number), ex *P. xanthopygus* (SNOMNH 30205). Jujuy: 3

km al E de Purmamarca por ruta nacional N° 52, 4 females (no numbers), ex *M. maenas* (CML 12400); 9 km NO Bárcena, 1 female (no number), ex *P. caprinus* (SNOMNH 30081), 2 males (no numbers), 4 females (no numbers), ex *P. caprinus* (CML 6499), 4 males (no numbers), 8 females (no numbers), ex *P. osilae* (CML 6501, 8068, SNOMNH 30082), 5 males (no numbers), 14 females (no numbers), ex *P. xanthopygus* (SNOMNH 30191, 30193, 30194, 34028); Chilcayoc, 1 male (no number), ex *P. xanthopygus* (SNOMNH 30196); Sierra de Tilcara, Toro Arita, 12 km ESE de Maimará, 14 km ESE de Tilcara, 1 female (no number), ex *A. jelskii* (CML 8479). LA RIOJA: 4 km al O de Anillaco, Reserva Aguada de las Alturas, 2 males (CMLA 603, 604), ex *P. xanthopygus* (CML 9753); 5 km al S del cañón del Ocre, 1 male (no number), 2 females (no numbers), ex *P. xanthopygus* (CML 13020); 8 km al NE del Cañón del Ocre, 2 males (no numbers), 1 female (no number), ex *P. osilae* (CML 13011), 4 females (CMLA 606, 607, no numbers), ex *P. xanthopygus* (CML 13021); Quebrada de Santo Domingo 30 km al SO de Jagué, 1 female (no number), ex *P. xanthopygus* (CML 13047). Salta: Finca Barba Yaco, 8.5 km SE Ojo de Agua, 1 female (no number), ex *P. xanthopygus* (SNOMNH 30198). Tucuman: Lagunas de Huaca Huasi (Cumbres Calchaquíes), 1 male (no number), ex *P. xanthopygus* (CML 11746).

Additional Records. Jujuy: Cuesta de Lipán, 15 km O de Purmamarca, sobre ruta 52, ex *P. xanthopygus*; La Quiaca, 17 km O y 3 km S, sobre ruta provincial Nº 5, ex *P. xanthopygus* (Lareschi *et al.* 2010).

Remarks. López-Berrizbeitia *et al.* (2015b) redescribed the subspecies amending the diagnosis. Hastriter *et al.* (2002) considered that *N. c. hemisus* could be synonymous of the nominal subspecies, but a comprehensive and detailed study is necessary in order to reach a conclusion. Five new flea–host associations were previously recorded with the following hosts: *A. spegazzinii*, *O. brendae*, *A. andina* (López-Berrizbeitia *et al.* 2013b), and *E. bolsonensis*, *N. lactens* (López-Berrizbeitia *et al.* 2015b); and in this study new six flea–host associations are reported with: *M. maenas*, *A. alterus*, *C. musculinus*, *N. ebriosus*, *P. caprinus*, and *A. jelskii*.

Subfamily Doratopsyllinae

Tribe Tritopsyllini

Genus *Adoratopsylla* Ewing 1925

Adoratopsylla (Tritopsylla) intermedia (Wagner 1901)

Adoratopsylla (Tritopsylla) intermedia intermedia (Wagner 1901)

General distribution. Argentina, Bolivia, Brazil, Ecuador, Paraguay, Peru, and Venezuela (Johnson 1957; Hopkins and Rothschild 1966; Lareschi *et al.* 2016).

Distribution in Argentina. Jujuy, Salta, Tucuman (Lareschi *et al.* 2016) and Misiones provinces (Urdapilleta *et al.* 2016).

Specimens Examined (67). Argentina. Jujuy: Casa Colorada, ~ 2 km al N de Alfarcito, 1 male (no number) ex *P. osilae* (CML 8062). Salta: a 43.7 km del cruce de las rutas 50 y 18, camino a Isla de Cañas, sobre ruta 18, 2 males (no numbers), 5 females (no numbers), ex *Marmosa* (*Micoureus*) *constantiae* Thomas 1904 (CML 7765), 6 males (no numbers), 6 females (no numbers), ex *L. massoia* (CML 7650, SNOMNH 32543), 7 females (no numbers), ex *T. sponsorius* (CML 6502, 7821). Tucuman: Dique San Ignacio, 1 male (no number), 2 females (no numbers), ex *L. massoia* (CML 2895), 25 females (no numbers), 4 males (no numbers), ex *T. sponsorius* (CML 7158, 7159, 7160, 1 released); Reserva La Florida, 7 km O Ibatín, sobre Río Pueblo Viejo, 1 male (no number), 2 females (no numbers), ex *T. sponsorius* (SNOMNH 29979); Río Grande, 5 km al S de El Siambón, 1 male (no number), 2 females (no numbers), ex *T. cinderella* (CML 7775). Paraguay: not specific locality, 1 male paralectotype (BMNH 1923-615), unknown host; Villarica, 1 female (BMNH 1964-287), ex *Didelphis marsupialis* Linnaeus 1758 (unknown number).

Additional records. Tucuman: Dique San Ignacio, ex *L. massoia* (Lareschi *et al.* 2016).

Remarks. During this study, this species was not recorded. Most hosts reported are marsupials, except in Jujuy where the species was recorded parasitizing a phyllotine rodent. Although *L. massoia* is not a small marsupial, is important to mention because *A.* (*T.*) *i. intermedia* exhibits a great preference for this host. The records from northwestern Argentina correspond to the Yungas Forests and Puna.

Family Pulicidae

Subfamily Pulicinae

Tribe Pulicini

Genus *Pulex* Linnaeus 1758

Pulex (*Pulex*) *irritans* Linnaeus 1758

General distribution. Cosmopolitan (Hopkins and Rothschild 1953).

Distribution in Argentina. Buenos Aires, Catamarca, Chubut, Cordoba, Formosa, La Rioja, Mendoza, Neuquen, Rio Negro, Salta, San Luis, Santiago del Estero, and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined (5). Argentina. Salta: 7.8 km NNE Pampa Grande, sobre ruta provincial Nº 6, 1 male (no number), 2 females (no numbers), ex *Lycalopex gymnocercus* Fischer 1814 (CML 7125). Hungary: Budapest, 1 neotype male (BMNH 916267), unknown host. France: Marsella, 1 female (BMNH 1923-615), ex Rodentia (unknown number).

Additional Records. La Rioja: not specific locality, ex *Dolichotis patagonum* Zimmermann 1780; entre Olta y Santa Rita de Catuna, ex *Lepus* sp. Salta: El Quebrachal, ex *L. maximus*. Santiago del Estero: not specific locality, unknown host. Tucuman: not specific locality, ex *D. albiventris* (originally identified as *D. azarae*; Hopkins and Rothschild 1953).

Remarks. The host mentioned by Hopkins and Rothschild (1953) as *Lepus* sp. probably corresponds to *Lepus europaeus* Pallas 1778, because it is the only species of the genus of the order Lagomorpha in Argentina. The same authors not recorded the coordinates for the locality between Olta and Santa Rita de Catuna, La Rioja; in the present study, we indicate the coordinates for the two main localities cited by them (Olta: -30°37'53.26" S, -66°15'48.87" W and Santa Rita de Catuna: -30°57'03.87" S, -66°13'02.48" W), but the exact locality of the record is still unknown. Although in NOA the species was only recorded on medium to large mammals, the records are included because its presence on small mammals is highly probable; also in other provinces of Argentina it was recorded on rodents such as *G. griseoflavus*, *M. musculus*, and *Ctenomys* sp. (Lareschi *et al.* 2016).

Subfamily Xenopsyllinae

Tribe Xenopsyllini

Genus *Xenopsylla* Glinkiewiez 1907

Xenopsylla cheopis (Rothschild 1903)

Xenopsylla cheopis cheopis (Rothschild 1903)

General distribution. Cosmopolita (Hopkins and Rothschild 1953).

Distribution in Argentina. Buenos Aires and La Rioja provinces (Lareschi *et al.* 2016).

Specimens Examined (3). Nigeria: Olokemeji, 2 males (BMNH 379), 1 female (BMNH 379), ex *Praomys daltoni* Thomas, 1891 (unknown number; originally identified as *Myomys daltoni*).

Additional Records. La Rioja: not specific locality, ex *R. norvegicus* (originally cited as *Epymis norvegicus*), *Rattus* sp. (originally cited as *Epimys* sp.; Hopkins and Rothschild 1953).

Remarks. *Xenopsylla cheopis cheopis* is one of the most efficient vectors of *Yersinia pestis* (Lehmann and Neumann 1896), responsible for the bubonic plague (Boyer *et al.* 2014). The only known records of this species in the NOA corresponds to old records from La Rioja. The absence of new records of this species probably reflects the deficiency of sampling and studies in exotic rodents (López-Berrizbeitia *et al.* 2017); however, it is necessary to emphasize that the species was also recorded on a marsupial and a rodent of the family Cricetidae in Argentina (Lareschi *et al.* 2016).

Family Leptopsyllidae

Subfamily Leptopsyllinae

Tribe Leptosyllini

Genus *Leptopsylla* Jordan and Rothschild 1911

Leptopsylla (*Leptopsylla*) *segnis* (Schönherr 1811)

General distribution. Cosmopolitan (Hopkins and Rothschild 1971).

Distribution in Argentina. Buenos Aires, Jujuy, and Santa Fe provinces (Lareschi *et al.* 2016).

Specimens Examined. None.

Additional Records. Jujuy: not specific locality, unknown host (Lareschi *et al.* 2016).

Remarks. The species is originated in western Asia, but transported by man and is now found in almost the entire world. The main host is *M. musculus*, but it was also recorded on species of the genus *Rattus* (Hopkins and Rothschild 1971). The only record in NOA is doubtful; it was published in a bulletin of the First Argentine Entomo-epidemiological Conference (Bejarano *et al.* 1959) and except in Lareschi *et al.* (2016), it was not cited in the reviews of fleas from Argentina. The distribution in Argentina is disjunct, with records in Santa Fe and Buenos Aires provinces (central-eastern Argentina) and in Jujuy (NOA), with an absence of information in the intermediate provinces.

Family Ischnopsyllidae

Subfamily Ischnopsyllinae

Tribe Ischnopsyllini

Genus *Myodopsylla* Jordan and Rothschild 1911

Myodopsylla isidori (Weyenbergh 1881)

General distribution. Argentina, Chile, and Uruguay (Autino *et al.* 2004; Beaucournu *et al.* 2014; Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, Catamarca, Cordoba, Corrientes, Entre Rios, Jujuy, La Rioja, Neuquen, Rio Negro, San Luis, Salta, Santiago del Estero, and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined (40). Catamarca: 22 km al SE de Villa de Escaba sobre ruta provincial Nº 9, 1 male (no number), ex *Myotis dinellii* Thomas 1902 [originally identified as *Myotis levis* (Geoffroy, 1824)] (released); Cuesta del Clavillo, 5 km al SO de La Banderita, 5 females (no numbers), ex *M. dinellii* (originally identified as *M. levis*; CML 3164, released). Jujuy: Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial Nº 20, 1 female (no number), ex *M. dinellii* (CML 4317); Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N° 29, 2 males (no numbers), 4 females (no numbers), ex *Myotis keaysi* J. A. Allen, 1914 (CML 6224). La Rioja: Anillaco 1.7 m al E del CRILAR, 1 female (CMLA 612), ex *M. dinellii* (released). Salta: 3 km al N de Potrerillos sobre ruta provincial N° 6, 1 male (no number), 2 females (no numbers), ex *M. dinellii* (CML 8068, SNOMNH 27932); 7.8 km al NNE de Pampa Grande, sobre ruta provincial 6, sobre Río Cachi, 2 males (no numbers), 1 female (no number), ex *M. dinellii* (SNOMNH 27933); Río Los Sauces, 12 km NO del Jardín, ruta 6 km 110, 1 male (no number), 6 females (no numbers), ex *M. dinellii* (CML 11066). Tucuman: Arroyo El Saltón, Reserva Provincial Santa Ana, 1 female (no number), ex *M. dinellii* (originally identified as *M. levis*; CML 5451); Escaba de Abajo, Casa abandonada a 150 m de la Hostería Ekay Apu, 1 female (no number), ex *M. albescens* (Geoffroy, 1806; released); 2 males (no numbers), 6 females (no numbers), ex *M. dinellii* (released); Parque Provincial El Cochuna, camping, 1 female (no number), ex *Myotis nigricans* (Schinz, 1821; CML 4225). Not specific locality: 1 lectotype male (BMNH 1923-615), 1 allotype female (BMNH 1923-615), ex *M. albescens* (originally identified as *Vespertilio isidori*; unknown number).

Additional Records. Catamarca: La Puerta, ex *M. nigricans* (Del Ponte 1977). Jujuy: Cuesta de Jaire, ex *M. keaysi* (Autino *et al.* 2016). La Rioja: not specific locality, ex Chiroptera (Hopkins and Rothschild 1956). Santiago del Estero: Sumampa, ex *M. nigricans* (Del Ponte 1977). Tucuman: Arroyo Aguas Chiquitas, Reserva Provincial Aguas Chiquitas, ex *M. dinellii* (originally cited as *M. levis*); Arroyo El Saltón, Reserva Provincial Santa Ana, ex *M. albescens* (Autino *et al.* 1999); Arroyo Mista, ex *T. brasiliensis* (Autino *et al.* 2009); Dique San Ignacio, ex *M. albescens* (Autino *et al.* 1999); Parque Provincial El Cochuna, camping, ex *M. nigricans* (Autino *et al.* 2000).

Remarks. *Myodopsylla isidori* exhibits a great preference for bats of the genus *Myotis* throughout its distribution (Autino *et al.* 2004; Beaucournu *et al.* 2014; Lareschi *et al.* 2016); although, in Argentina, it was also recorded on the genus *Tadarida* (Autino *et al.* 2009). In NOA, the records correspond to the Dry Chaco, Monte Desert of Mountains and Isolated Valleys, and Yungas Forests.

Myodopsylla wolffsohni (Rothschild 1903)

Myodopsylla wolffsohni wolffsohni (Rothschild 1903)

General distribution. Argentina, Brazil, Paraguay, and Uruguay (Linardi and Guimarães 2000; Claps and Autino 2012). Beaucournu *et al.* (2014) reported that the subspecies was misidentified in Chile and that specimen corresponds to *M. isidori*. However, Lareschi *et al.* (2016) sustained the error and mentioned it wrongly for Chile and Mexico (Salceda-Sánchez and Hastriter 2006; Acosta-Gutiérrez 2014).

Distribution in Argentina. Corrientes, Entre Rios, Salta, and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined (2). Paraguay: Tacuaral, 1 holotype male (BMNH 1923-615), 1 female allotype (BMNH 1923-615), ex *M. albescens* (unknown number). Uruguay: Paso Pache, Río Santa Lucia, Puente Viejo, 1 male (no number) ex *M. albescens* (EMG 1183).

Additional Records. Salta: La Estrella, ex *M. nigricans* (Autino *et al.* 2016); Río El Naranjo, 14 km al O de ruta provincial Nº 5, sobre camino de acceso a Parque Nacional El Rey, ex *M. albescens* (Claps and Autino 2012). Tucuman: not specific locality, ex *E. perotis* (Schinz 1821).

Remarks. During this study, the subspecies was not recorded. The records correspond to the Dry Chaco and Yungas Forests.

Tribe Sternopsyllini

Genus *Hormopsylla* Jordan and Rothschild 1921

Hormopsylla fosteri (Rothschild 1903)

General distribution. Argentina, Brazil, Paraguay, and Venezuela (Hastriter and Guerrero 1998).

Distribution in Argentina. Cordoba and Tucuman provinces (Lareschi *et al.* 2016).

Specimens Examined. None.

Additional Records. Tucuman: Capital, ex *E. perotis* (Hopkins and Rothschild 1956; Del Ponte 1977).

Remarks. In this study, this species neither was recorded nor specimens were reviewed. Although the species was recorded mainly on insectivorous bats of the family Molossidae, there is a record on a hematophagous bat, *Desmodus rotundus* (Familia Phyllostomidae) from Brazil (Linardi and Guimarães 2000).

Genus *Sternopsylla* Jordan and Rothschild 1921

Sternopsylla distincta (Rothschild 1903)

Sternopsylla distincta speciosa (Rothschild 1903)

General distribution. Argentina, Colombia, Panama, Paraguay, Peru, and Venezuela (Del Ponte 1977; Lareschi *et al.* 2016).

Distribution in Argentina. Buenos Aires, Catamarca, Jujuy, Mendoza, Salta, and Tucuman provinces (Lareschi *et al.* 2016). In this study, the subspecies is added in the La Rioja province.

Specimens Examined (6). Argentina. Buenos Aires: Estancia San José, sobre Río Negro (Partido Patagones), 1 female (no number), ex *T. brasiliensis* (released). Jujuy: San Salvador de Jujuy, 1 male (no number), 2 females (no numbers), ex *T. brasiliensis* (unknown number). La Rioja: Ulapes, 1 km al O de la plaza principal de Ulapes, 1 female (no number), ex *T. brasiliensis* (CML 12871). Tucuman. Dique San Ignacio, 1 male (no number), ex *M. albescens* (CML 5614). Panama: Chiriquí, Bambito-Cerro Punta, 1 female (BMNH 10087), ex guano of Chiroptera.

Additional Records. Catamarca: El Rodeo, ex *T. brasiliensis* (Del Ponte 1977). Salta: Rosario de La Frontera, ex *T. brasiliensis* (Autino *et al.* 1999). Tucuman: Dique Escaba; Dique San Ignacio; San Miguel de Tucuman, ex *T. brasiliensis* (Del Ponte 1977).

Remarks. *Sternopsylla distincta* exhibits a great preference for bats of the family Molossidae (Johnson 1957; Tipton and Machado-Allison 1972), although it also was recorded on bats of the genus *Myotis* (family Vespertilionidae), in Argentina and Panama (Del Ponte 1977; Lareschi *et al.* 2016). Del Ponte (1977) and Beaucournu and Castro (2003) questioned the validity of the subspecies and suggested that it could be a synonym of the nominal. The examined specimens show all characters diagnostic for the subspecies; although, it is necessary to carry out morphological studies of the males and females of both subespecies in order to verify the existence of variation between them. In NOA the records correspond to the Dry Chaco and Yungas Forests.

Family Ceratophyllidae

Subfamily Ceratophyllinae

Genus *Nosopsyllus* Jordan 1933

Nosopsyllus (*Nosopsyllus*) *fasciatus* (Bosc 1800)

General distribution. Cosmopolitan (Lewis 1990).

Distribution in Argentina. Buenos Aires, Cordoba, Jujuy, Neuquen, Rio Negro, Santa Fe, Tierra del Fuego, Antarctica and Southern Atlantic Islands, and Islas Malvinas (Lareschi *et al.* 2016).

Specimens Examined (2). Hungary: Budapest, 1 male (BMNH 1923-615), ex *R. norvegicus* (originally identified as *Mus decumanus*; unknown number). France: Bure, 1 female (BMNH 1923-615), nest of Rodentia.

Additional Records. Jujuy: not specific locality, ex *R. norvegicus* and *R. rattus* (Bejarano *et al.* 1959; Lareschi *et al.* 2016).

Remarks. In Argentina, others hosts for this species are: *Abrothrix longipilis*, *Akodon olivaceus*, and *O. longicaudatus* (Lareschi *et al.* 2016). The only record in NOA was published in a bulletin of the First Argentine Entomo-epidemiological Conference (Bejarano *et al.* 1959), except in Lareschi *et al.* 2016 it not was cited in the reviews of fleas from Argentina.

Index of similarity (I_j)

The index of similarity among ecoregions was calculated based on 49 species and five subspecies, including four new species in the process of description [*Ectinorus* (*E.*) sp. n. 1, *Ectinorus* (*E.*) sp. n. 2, *Ectinorus* (*E.*) sp. n. 3 and *Polygenis* (*P.*) sp. n.], and three species and one subspecies were excluded because no specific localities were available.

The coefficient of Jaccard discriminated two main clusters, one constituted by High Andes and Puna and another by Yungas Forests, Dry Chaco, and Monte Desert of Mountains and Isolated Valleys (Figure 2). The highest similarity value was recorded between Yungas Forests and Dry Chaco (I_j = 0.29), and this cluster is grouped with the Monte Desert of Mountains and Isolated Valleys. The greatest differentiation was recorded between High Andes and Puna (Figure 2, Table 2).

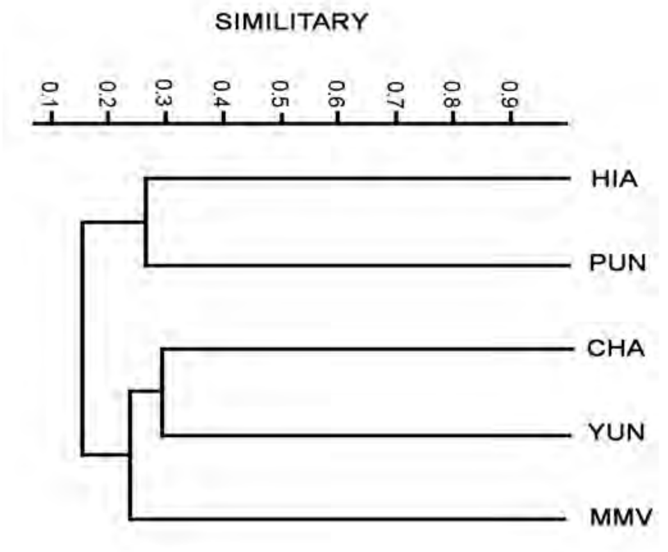

Figure 2. Consensus phenogram of ecoregions in northwestern Argentina at species and subspecies levels. Acronyms: HIA=High Andes, CHA=Dry Chaco, MMV=Monte Desert of Mountains and Isolated Valleys, PUN=Puna, YUN=Yungas.

Discussion

A total of 971 flea specimens were studied, of which 851 correspond to species from NOA and 120 are specimens from other localities used for comparative purposes. The specimens examined included 35 holotypes, 21 allotypes, 43 paratypes, 22 lectotypes, 12 paralectotypes, four neotypes, and six topotypes. Until now eight families, 19 genera, 40 species and seven subspecies of Siphonaptera, parasites of small mammals (Didelphimorphia, Chiroptera, and Rodentia), were known from NOA. The family Pygiopsyllidae, the genus *Agastopsylla* and three species and one subspecies (*Agastopsylla hirsutior*, *Agastopsylla nylota nylota*, and *Plocopsylla* (*P.*) *inti*) are new records for Argentina; five species and one subspecies: *Neotyphloceras chilensis*, *Delostichus talis*, *Ectinorus hapalus*, *Polygenis* (*P.*) *pradoi*, and *Polygenis bohlsi bohlsi* are new for NOA. In this study we have recorded nine species that are new to science, five of which were recently published (*Ctenidiosomus austrinus*, *Cleopsylla barquezi*, *Plocopsylla* (*P.*) *chicoanaensis*, *Plocopsylla* (*P.*) *hastriteri*, and *Tetrapsyllus* (*T.*) *spegazzinii*; Lopez-Berrizbeitia *et al.* 2016, 2018, 2019), and four more which are in process of description, belonging to the genus *Polygenis* and *Ectinorus* (Rhopalopsyllidae).

Six species are considered as probable for the study area, due to records obtained in other regions of the country, but cited on small mammals whose distributions include the NOA [*Hectopsylla* (*Hectopsylla*) *cypha*, *Hectopsylla* (*Hectopsylla*) *stomis*, and *Pulex irritans*], or referenced for the area but without punctual records [*Hectopsylla* (*Hectopsylla*) *psittaci*, *Leptopsylla* (*Leptopsylla*) *segnis*, and *Nosopsyllus fasciatus*]. Additionally species and subspecies are added for almost all provinces of the NOA, four species and one subspecies are added in Tucuman: *H.* (*H.*) *gracilis, H.* (*H.*) *gemina, N. c. hemisus,* and *T.* (*P.*) *bleptus*; five in Catamarca: *H.* (*H.*) *gracilis, D. talis, P.* (*N.*) *pradoi*, *P.* (*N.*) *puelche*, and *P.* (*P.*) *byturus*); eight species and one subspecies in La Rioja: *H.* (*H.*) *gracilis*, *N. c. hemisus*, *D. talis*, *T.* (*P.*) *bleptus, P.* (*P.*) *acodontis*, *P. (P.) byturus*, *T. palpalis*, and *C. minerva*; five species and one subspecies in Salta: *H.* (*H.*) *gracilis*, *T.* (*P.*) *bleptus*, *P.* (*N.*) *pradoi*, *P.* (*N.*) *puelche*, and *P. (P.) r. beebei*); and one species in Santiago del Estero: *P.* (*P.*) *acodontis*. The record of *H.* (*H.*) *gemina* obtained in Tucuman allows us to confirm its presence in the study area through a punctual locality. It is important to mention that some species are still known only by historical records, such as *E.* (*E.*) *budini* only collected in the type locality, Otro Cerro (Catamarca), 70 years ago; for this reason, it is important to increase the sampling efforts in the areas where these species were long ago collected.

On the other hand, most of the ecoregions from NOA suffers an accelerated degradation process such as the Chaco (Torrella *et al.* 2007, 2011) and Yungas Forests (Brown *et al.* 2001). The natural vegetation is changing and their replacement by crop areas affect on the small mammal hosts in this type of habitats (Ewers and Didham 2006; Peters *et al.* 2006), with the consequent reduction of its population, probably a reason why during the fieldwork some species were not collected even with a great trapping effort. As an example, for *E.* (*E.*) *disjugis*, the only known locality (El Chaguaral) for the presence of this species in Argentina, belongs to the Dry Chaco in Jujuy Province, a highly disturbed and fragmented area with almost no traces of well-preserved natural vegetation which implies reduction or lost of the small mammals communities in the area (Torres and Jayat 2010). Other examples are *H. stomis*, *E. galeanus*, and *E. rimatus*, collected in localities in Santiago del Estero, a province where the Dry Chaco is almost restricted to the Copo National Park or some small mountainous areas in the province (Torrella and Adámoli 2005; Díaz and Barquez 2007).

The distribution and amplitude of the geographical range of a flea species result from the interaction between the responses to the geographical range of its hosts and the environmental conditions of its microhabitats (Krasnov 2008). In this study the flea species were recorded in five of the six ecoregions represented in the NOA: Dry Chaco, Monte Desert of Mountains and Isolated Valleys, High Andes, Puna, and Yungas Forests (Table 1). The Yungas Forests have the greatest number of species of fleas, followed by the Monte Desert of Mountains and Isolated Valleys, Dry Chaco, High Andes, and Puna. The higher diversity in the Yungas Forests is a reflection of an area with the greatest diversity in the Neotropical region (Mittermeier *et al.* 1999), including mammals (Barquez *et al*. 2006; Gamboa-Alurralde *et al.* 2015) with the sigomodontine rodents and bats (Díaz and Barquez 2007; Barquez and Díaz 2009; Gamboa Alurralde *et al*. 2016; Gamboa Alurralde 2017). These small mammals were the main hosts for the families Rhopalopsyllidae and Ischnopsyllidae, two of the most diverse in the Yungas Forests. The family Tungidae, only represented by the genus *Hectopsylla*, was mainly distributed in the Yungas and the Dry Chaco, with records agreeing with previous citations that show this family with a distribution mainly neotropical (Sanchez 2012, Lareschi *et al.* 2016). *Ctenidiosomus austrinus*, the only species of the family Pygiopsyllidae, was restricted to the Monte Desert of Mountains and Isolated Valleys, following the distribution of their host, *P. osilae*, found along the Oriental Altiplano and the Andean slopes (Jayat and Pacheco 2006; Steppan and Ramirez 2015). Most species of the family Stephanocircidae were recorded in the Puna, representing mainly an Andean distribution; these species were also found in the Patagonia parasitizing rodents of the same genera as those recorded in our study area, *Abrothrix*, *Akodon* and *Calomys* (Sanchez 2012); this situation would support the idea of a close relationship between Puna and Patagonian Steppes proposed by Cabrera (1976) and Burkart *et al*. (1999). *Craneopsylla minerva* was the only species found in all analyzed ecoregions, which would be related to the large number of hosts parasitized by this species because, in general, the specialist fleas have restricted geographical ranges whereas the generalist fleas have wide ranges allowing them not only to exploit more host species, but also to hosts species which are not necessary phylogenetically related (Krasnov *et al.* 2005).

The analysis of degree of affinity among ecoregions showed a great faunistic congruence between Yungas Forests and Dry Chaco, sharing 11 species of the families Tungidae, Stephanocircidae, Rhopalopsyllidae, and Ischnopsyllidae. This result was expected because studies developed on other group of animals, for example mammals, were similar (Díaz and Barquez 2007). The ecoregions with the highest differentiation were the High Andes and the Puna ecoregions, being the ecoregions that share less species compared with the other ecoregions; these areas were also the least sampled and containing the lowest richness and abundance of small mammal species, specially marsupials and bats (Figure 2, Table 2).

In the Neotropical region the fleas parasitize mainly on small mammals, as sigmodontine and caviomorph rodents, as well as on marsupials of the orders Didelphimorphia and Paucituberculata (Krasnov 2008). A total of 82 new flea-host associations were recorded; 81 associations have sigomodontine rodents (Family Cricetidae) as hosts, and one association was found with a marsupial (Order Didelphimorphia; Table 1). According to Krasnov (2008), the high diversity of fleas associated to rodents suggests, from an evolutionary perspective, that diversification of the fleas was associated to the great diversification of rodents.

Table 1. Species and subspecies of Siphonaptera and their hosts, provinces and ecoregions of northwestern Argentina. Acronyms: CA = Catamarca, JU = Jujuy, LR = La Rioja, SA = Salta, SE=Santiago del Estero, TU = Tucuman. HIA = High Andes, CHA = Dry Chaco, MMV = Monte Desert of Mountains and Isolated Valleys, PUN = Puna, and YUN = Yungas.

Siphonaptera	Hosts	Provinces	Ecoregions
Hectopsylla (*H.*) *cypha*	*Lagostomus* sp.	LR, TU	MMV
Hectopsylla (*H.*) *gemina*	*P. osilae, M. jayat*	SE, TU	CHA, YUN
Hectopsylla (*H.*) *gracilis*	*A. andina, A. albiventer, A. caenosus, A. spegazzinii, A. olrogi, E. hirtipes, E. puerulus, E. moreni, E. typus, G. chacoensis*	CA, JU, LR, SA, TU	HIA, MMV, PUN, YUN
Hectopsylla (*H.*) *psittaci*	*E. perotis*	TU	-
Hectopsylla (*H.*) *pulex*	*E. perotis, T. brasiliensis*	CA, JU, TU, SA	CHA, YUN
Hectopsylla (*H.*) *stomis*	*L. maximus*	SE, SA	CHA
Ctenidiosomus austrinus	*P. osilae*	SA	MMV
Cleopsylla barquezi	*A. spegazzinii, P. osilae*	CA, SA, TU	MMV, YUN
Craneopsylla minerva	*C. auritus, L. massoia, T. sponsorius, A. andina, A. illutea, A. alterus, A. budini, A. caenosus, A.* cf. *fumeus, A. glaucinus, A. lutescens, A. puer, A. simulator, A. spegazzinii, A. tartareus, A. toba, A. tucumanensis, C. boliviae, C. callosus, C. venustus, E. legatus, G. leucoblephara, G. chacoensis, G. domorum, G. griseoflavus, H. chacarius, M. jayat, M. maenas, O. brendae, O. flavescens, O. paramensis, P. caprinus, P. osilae, P. xanthopygus, R. rattus, Rattus* sp.*, T. wolffsohni, T. primus.*	CA, JU, LR, SA, SE, TU	HIA, CHA, MMV, PUN, YUN
Nonnapsylla rothschildi	*E. puerulus, G. comes, O. gliroides, P. xanthopygus*	JU	PUN

Plocopsylla (*P.*) *chicoanaensis*	*A. caenosus*, *A. spegazzinii*, *P. osilae*, *Oligoryzomys* sp.	CA, SA	MMV, PUN, YUN
Plocopsylla (*P.*) *hastriteri*	*P. osilae*	LR	MMV
Plocopsylla (*P.*) *inti*	*A. andina*	CA	PUN
Tiarapsylla argentina	*Ctenomys* sp.	JU, TU	PUN, YUN
Delostichus talis	*M. maenas*	CA, LR	MMV, PUN
Ectinorus (*E.*) *budini*	*A. edax*	CA	MMV
Ectinorus (*E.*) *disjugis*	*C. juris*	JU	CHA
Ectinorus (*E.*) *hapalus*	*G. chacoensis*	LR	MMV
Ectinorus (*E.*) *nomisis*	*O. gliroides*	JU	PUN
Ectinorus (*E.*) *pilosus*	*C. knighti*	CA	MMV
Ectinorus (*E.*) sp. n. 1	*A. spegazzinii*, *P. osilae*	CA, SA	MMV, YUN
Ectinorus (*E.*) sp. n. 2	*A. spegazzinii*	CA	YUN
Ectinorus (*E.*) sp. n. 3	*A. andina*, *P. xanthopygus*	TU	HIA
Ectinorus (*P.*) *galeanus*	*G. chacoensis*, *M. jayat*, *L. maximus*	SE	CHA
Tetrapsyllus (*P.*) *bleptus*	*A. andina*, *A. albiventer*, *A. simulator*, *A. spegazzinii*	JU, CA, LR, SA, TU	HIA, CHA, MMV, PUN, YUN
Tetrapsyllus (*T.*) *spegazzinii*	*A. spegazzinii*, *A. simulator*	SA	MMV, YUN
Polygenis (*N.*) *pradoi*	*A. spegazzinii*	CA, SA	MMV, YUN
Polygenis (*N.*) *puelche*	*A. lutescens*, *A. simulator*, *A. spegazzinii*, *O. brendae*	CA, SA, TU	YUN
Polygenis acodontis	*T. sponsorius A. alterus*, *A. budini*, *A. caenosus*, *A.* cf. *fumeus*, *A. dolores*, *A. glaucinus*, *A. lutescens*, *A*, *puer*, *A. simulator*, *A. spegazzinii*, *C. boliviae*, *C. venustus*, *C. juris*, *M. australis*, *N. lactens*, *O. brendae*, *Oligoryzomys* sp., *O. paramensis*, *P. osilae*, *P. xanthopygus*	CA, JU, LR, SA, SE, TU	CHA, MMV, YUN
Polygenis (*P.*) *bolhsi bolhsi*	*G. chacoensis*	LR	CHA
Polygenis (*P.*) *byturus*	*A. alterus*, *A. dolores*, *C. callosus*, *C. musculinus*, *C. venustus*, *C. juris*, *G. leucoblephara*, *G. chacoensis*, *G. griseoflavus*, *H. chacarius*, *L. maximus*, *M. australis*, *P. xanthopygus*, *R. rattus*	CA, JU, LR, SA, SE	CHA, YUN
Polygenis (*P.*) *platensis*	*A. glaucinus*, *G. leucoblephara*, *G. chacoensis*, G. *griseoflavus*, *P. osilae*, *P. xanthopygus*	JU, LR, SA	CHA, MMV, YUN
Polygenis (*P.*)*rimatus*	*D. albiventris*, *C. aperea*, *M. australis*	LR, SA	CHA
Polygenis (*P.*) *roberti bebeei*	*E. legatus*	JU, SA	YUN
Polygenis (*P.*) *tripus*	*A. tartareus*, *G. leucoblephara*	SA	YUN
Polygenis (*P.*) sp. n.	*A. spegazzinii*	SA	MMV
Tiamastus cavicola	*C. juris*, *G. leucoblephara*, *M. maenas*	CA, JU, SA	CHA, PUN, YUN
Tiamastus helicis	*C. latro*	TU	YUN
Tiamastus palpalis	*Ctenomys* sp., *C. juris*, *E. moreni*	CA, JU, LR, SE	CHA, MMV
Tiamastus plesius	*N. lactens*	JU	PUN
Tiamastus subtilis	*Ctenomys* sp.	TU	YUN
Agastopsylla hirsutior	A. spegazznii	TU	YUN
Agastopsylla nylota nylota	*P. osilae*	SA	MMV
Neotyphloceras chilensis	*A. andina*, *A. spegazzinii*, *E. puerulus*, *N. lactens*, *N. ebriosus*, *P. xanthopygus*	CA, JU, SA	MMV, PUN
Neotyphloceras crassispina hemisus	*A. andina*, *A. jelskii*, *A. albiventer*, *A. alterus*, *A. simulator*, *A. spegazzinii*, *A. edax*, *C. musculinus*, *C. lepidus*, *E. bolsonensis*, *E. hirtipes*, *E. puerulus*, *G. chacoensis*, *M. australis*, *M. maenas*, *N. lactens*, *N. ebriosus*, *O. brendae*, *P. alisosiensis*, *P. caprinus*, *P. osilae*, *P. xanthopygus*, *Phyllotis* sp., *R. auritus*	CA, JU, LR SA, TU	HIA, MMV, PUN, YUN
Adoratopsylla intermedia intermedia	*L. massoia*, *M. constantiae*, *T. cinderella*, *T. sponsorius*, *P. osilae*.	JU, SA, TU	PUN, YUN
Pulex irritans	*D. albiventris*, *D. patagonum*, *L. maximus*	LR, SA, SE, TU	CHA
Xenopsylla cheopis cheopis	*R. norvegicus*, *Rattus* sp.	LR	-
Leptopsylla (*L.*) *segnis*	Rodentia	JU	-
Hormopsylla fosteri	*E. perotis*	TU	YUN
Myodopsylla isidori	*M. albescens*, *M. dinellii*, *M. keaysi*, *M. nigricans*, *T. brasiliensis*	CA, JA, LR, SA, SE, TU	CHA, MMV, YUN
Myodopsylla wolffsohni wolffsohni	*E. perotis*, *M. albescens*, *M. nigricans*	SA, TU	CHA, YUN
Sternopsylla distincta speciosa	*M. albescens*, *T. brasiliensis*	CA, JU, LR, SA, TU	CHA, YUN
Nosopsyllus fasciatus	-	JU	-

Table 2. Results of the Jaccard index among the ecoregions of northwestern Argentina. Acronyms: HIA = High Andes, CHA = Dry Chaco, MMV = Monte Desert of Mountains and Isolated Valleys, PUN = Puna, and YUN = Yungas.

	PUN	MMV	CHA	YUN	HIA
PUN	1	0.20	0.11	0.24	0.27
MMV	0.20	1	0.18	0.29	0.13
CHA	0.11	0.18	1	0.29	0.10
YUN	0.24	0.29	0.29	1	0.14
HIA	0.27	0.13	0.10	0.14	1

Finally, the results reported here mainly contribute to the knowledge and clarification of the systematics of the species of the order Siphonaptera parasitizing small mammals in NOA, providing new information not only for the region but also for Argentina and for science.

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Literature cited

Acosta-Gutiérrez, R. 2014. Biodiversidad de Siphonaptera en México. Revista Mexicana de Biodiversidad 85:345–352.

Autino, A. G., and M. Lareschi. 1998. Siphonaptera. Pp. 279–290 *in*: Biodiversidad de Artrópodos Argentinos (Morrone J. J. and S. Coscarón, Dir.). Ediciones Sur, La Plata, Argentina.

Autino, A. G., G. L. Claps and F. Ortiz. 2005. Primera cita de *Sternopsylla distincta speciosa* (Siphonaptera: Ischnopsyllidae) para la provincia de Jujuy, Argentina. Revista de la Sociedad Entomológica Argentina 64:34–36.

Autino, A. G., G. L. Claps, and E. M. González. 2004. Nuevos registros de insectos (Diptera y Siphonaptera) ectoparásitos de murciélagos (Vespertilionidae) del norte de Uruguay. Mastozoología Neotropical 11:81–83.

Autino, A. G., G. L. Claps, and R. M. Barquez. 1999. Insectos ectoparásitos de murciélagos de las yungas de la Argentina. Acta Zoológica Mexicana 78:119–169.

Autino, A. G., G. L. Claps, and R. M. Barquez. 2000. Nuevos registros de Diptera y Siphonaptera en la Argentina. Boletín de Entomología Venezolana 15:109–112.

Autino, A. G., F. Ortiz, G. L. Claps, and J. C. Bracamonte. 2016. New host and locality records for chiropteran ectoparasites from Jujuy and Salta provinces, Argentina. Check List 12:1895.

Autino, A. G., G. L. Claps, M. Sánchez, and R. M. Barquez. 2009. New records of bat ectoparasites (Diptera, Hemiptera and Siphonaptera) from northern Argentina. Neotropical Entomology 38:165–177. https://doi.org/10.1590/s1519-566x2009000200002

Baker, R. J., and S. L. Williams. 1972. A live trap for pocket gophers. Journal of Wildlife Management 36:1320–1322.

Barquez, R. M., and M. M. Díaz. 2009. Los Murciélagos de Argentina-Clave de Identificación. Publicación Especial N° 1. PCMA (Programa de Conservación de los Murciélagos de Argentina), Editorial Magna, Tucumán, Argentina.

Barquez, R. M., M. M. Díaz, and R. A. Ojeda. 2006. Mamíferos de Argentina. Sistemática y distribución. Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Mendoza, Argentina.

Barquez, R. M., M. S. Sánchez, and J. C. Bracamonte. 2009. Nueva especie de *Eptesicus* (Chiroptera, Vespertilionidae) para Argentina. Mastozoología Neotropical 16:199–203.

Barquez, R. M., M. S. Sánchez, and M. L. Sandoval. 2011. Nuevos registros de murciélagos (Chiroptera) en el norte de Argentina. Mastozoología Neotropical 18:10–24. http://ref.scielo.org/5mrcwb

Barquez, R. M., D. Miotti, F. Idoeta, and M. M. Díaz. 2017. Two new species of *Myotis* (Chiroptera: Vespertilionidae from Argentina. Papéis Avulsos de Zoologia 57:287-294.

Beaucournu, J. C., and D. Castro. 2002. *Ectinorus pilosus* sp. n. (Siphonaptera: Rhopalopsyllidae), puce nouvelle d'Argentine. Bulletin de la Société entomologique de France 107:367–369.

Beaucournu, J. C., and D. Castro. 2003. Contribution á un Inventaire des Puces d´Argentina. Beiträge zur Entomologie 53:449–479.

Beaucournu, J. C., and J. A. Alcover. 1990. Puces récoltées dans la Province de Neuquén (Argentine); description de 4 nouveau taxa (Insecta, Siphonaptera). Annales de Parasitologie humaine et comparée 64:489–505.

Beaucournu, J. C., and J. C. Torres-Mura. 1987. Un nouveau *Delostichus* (Siphonaptera, Rhopalopsyllidae) d'Argentine. Bulletin de la Société Française de Parasitologie 5:257–260.

Beaucournu, J. C., and M. H. Gallardo. 1988. Puces nouvelles d' Argentine (Insecta, Siphonaptera). *Revue Suisse de Zoologie* 95:99–112.

Beaucournu, J. C., and M. H. Gallardo. 2005. Deux puces nouvelles (Siphonaptera: Rhopalopsyllidae: Parapsyllinae) d' Argentine, parasites d' Abr. uspallata Braun et Mares, 2002 (Rod.: Abrocomidae). Parasite 12:39–43. http://dx.doi.org/10.1051/parasite/2005121039

Beaucournu, J. C., L. Moreno, and D. González-Acuña. 2014. Fleas (Insecta-Siphonaptera) of Chile: a review. Zootaxa 2:151–203.

Beaucournu, J. C., M. H. Gallardo, and K. Ménier. 2004. Deux puces nouvelles du Chili et d' Argentine (Insecta-Siphonaptera: Stephanocircidae et Rhopalopsyllidae) et érection d'un sous-genre chez *Plocopsylla* Jordan, 1931. Parasite 11:249–252. http://dx.doi.org/10.1051/parasite/2004113249

Beaucournu, J. C., S. Belaz, S. Muñoz-Leal, and D. González-Acuña. 2013. A new flea, *Ectinorus* (*Ectinorus*) *insignis* sp. n. (Siphonaptera, Rhopalopsyllidae, Parapsyllinae), with notes on the subgenus *Ectinorus* in Chile and comments on unciform sclerotization in the Superfamily Malacopsylloidea. Parasite, 20:1–12. http://dx.doi.org/10.1051/parasite/2013033

Bejarano, J. F. R., E. del Ponte, and R. N. Orfila. 1959. Primeras Jornadas Entomoepidemiológicas Argentinas, segunda parte. Buenos Aires, Argentina, 581–586.

Bidau, C. J. 2015. Family Ctenomyidae. Pp: 818-876 *in*: Mammals of South America, Volume 2 - Rodents (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, Eds.). The University of Chicago Press. Chicago, U.S.A.

Bolsi, A. S. C, C. Caponio, A. Batista, M. Madariaga, A. Nieva, R. Pucci, and A. Rivas. 1997a. Subproyecto III. Estructuras productivas I. Universidad Nacional de Tucumán. Facultad de Filosofía y Letras. Instituto de Estudios Geográficos. Instituto de Estudios Geográficos. San Miguel de Tucumán, Argentina.

Bolsi, A. S. C, C. Caponio, A. Batista, M. Madariaga, A. Nieva, R. Pucci, and A. Rivas. 1997b. Subproyecto II. Universidad Nacional de Tucumán. Facultad de Filosofía y Letras. Instituto de Estudios Geográficos. Instituto de Estudios Geográficos. San Miguel de Tucumán, Argentina.

Boyer, S., A. Miarinjara, and N. Elissa. 2014. *Xenopsylla cheopis* (Siphonaptera: Pulicidae) susceptibility to deltamethrin in Madagascar. PLoS ONE 9:e111998. https://doi.org/10.1371/journal.pone.0111998

Braun, J. K., and M. M. Díaz. 1999. Key to the native mammals of Catamarca province. Occasional Papers of the Oklahoma Museum of Natural History 4:1–16.

Brown, A. D., H. R. Grau, L. R. Malizia, and A. Grau. 2001. Argentina. Pp. 623–659 in: Bosques nublados del Neotrópico (Kappelle, M. and A. D. Brown, eds.). Editorial Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

Burkart, R., N. O. Bárbaro, R. O. Sánchez, and D. A. Gomez. 1999. Eco-regiones de la Argentina. Administración de Parques Nacionales. Programa Desarrollo Institucional Ambiental. Buenos Aires, Argentina.

Cabrera, A. L. 1976. Regiones fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería 1:1–85.

Carlevari, I. 1994. La Argentina 1994: estructura humana y económica. Editorial Macchi, Buenos Aires, Argentina.

Claps, G. L., and A. G. Autino. 2012. *Myodopsylla wolffsohni wolffsohni* (Rothschild) (Siphonaptera, Ischnopsyllidae) sobre murciélagos de la Argentina y Uruguay. Revista de la Sociedad Entomológica Argentina 71:155–157. http://www.scielo.org.ar/pdf/rsea/v71n1-2/v71n1 2a16.pdf

Colombetti, P. L., A. G. Autino, G. L. Claps, M. I. Carma, and M. Lareschi. 2008. Primer registro de *Cleopsylla townsendi* (Siphonaptera: Stephanocircidae: Craneopsyllinae) en la Argentina. Revista de la Sociedad Entomológica Argentina 67:179–182.

Coyner, B. S., J. K. Braun, M. A. Mares, and V. D. Bussche, R. A. 2013. Taxonomic validity of species groups in the genus *Akodon* (Rodentia, Cricetidae). Zoologica Scripta 42:335–350. https://doi.org/10.1111/zsc.12014

Del Ponte, E. 1977. Notas sobre Suctoria argentinos VIII. Revisión de las familias Hystrichopsyllidae, Stephanocircidae e Ischnopsyllidae (Ceratophylloidea). Revista del Museo argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigaciones de las Ciencias Naturales. Entomología 5:1–141.

Del Ponte, E., and M. A. Riesel. 1939. Notas sobre "Siphonaptera" argentinos. II. Primera lista de especies. Physis, Argentina 17:543–549.

Díaz, M. M, and M. Lucherini. 2006. Familia Canidae. Pp: 89-107 *in*: Mamíferos de Argentina. Sistemática y distribución. (Barquez, R. M., M. M. Díaz, and R. A. Ojeda, eds.) Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Tucumán, Argentina.

Díaz, M. M., and R. M. Barquez. 1999. Contributions to the Knowledge of the mammals of Jujuy Province, Argentina. The Southwestern Naturalist 44:324–333.

Díaz, M. M., and R. M. Barquez. 2007. The Wild Mammals of Jujuy Province, Argentina: Systematics and Distribution. Pp. 417–578 *in*: The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson (Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology. Berkeley, U.S.A.

Díaz, M. M., J. K. Braun, M. A. Mares, and R. M. Barquez. 1997. Key to mammals of Salta Province, Argentina. Occasional Papers, Oklahoma Museum of Natural History 2:1–10.

Díaz, M. M., J. K. Braun, M. A. Mares, and R. M. Barquez. 2000. An update of the taxonomy, systematics, and distribution of the mammals of Salta Province, Argentina. Occasional Papers, Sam Noble Oklahoma Museum of Natural History 10:1–52.

Díaz, M. M., R. M. Barquez, J. K. Braun, and M. A. Mares. 1999. A new species of *Akodon* (Muridae: Sigmodontinae) from Northwestern Argentina. Journal of Mammalogy 80:786–798.

ESRI. 2011. ArcGIS Desktop: Release 10. Redlands, California: Enviromental Systems Research Institute.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81:117–142.

Ezquiaga, M. C., P. M. Linardi, D. M. De Avelar, and M. Lareschi. 2015. A new species of *Tunga* perforating the osteoderms of its armadillo host in Argentina and redescription of the male of *Tunga terasma*. Medical and Veterinary Entomology 29:196–204.

Fernandez, J. E. 2019. The holistic specimen and parasites of mammals. Therya 10:65–67.

Ferro, L. I. 2012. Micromamíferos del noroeste argentino: gradientes altitudinales y la transición bosque puna monte. Doctoral Thesis. San Miguel de Tucumán: Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Tucumán, Argentina

Ferro, L. I., and R. M. Barquez. 2009. Species Richness of Nonvolant Small Mammals Along Elevational Gradients in Northwestern Argentina. Biotropica 41:759–767.

Flores, D. A., M. M. Díaz, and R. M. Barquez. 2000. Mouse opossums (Didelphimorphia, Didelphidae) of northwestern Argentina: Systematic and distribution. Zeitschrift für Säugetierkunde 65:1–19.

Gamboa Alurralde, S. 2017. Ensambles de Murciélagos (Mammalia, Chiroptera) en zonas con distinto grado de perturbación de las Yungas de Argentina. [Doctoral Thesis]. Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán.

Gamboa Alurralde, S., M. F. López-Berrizbeitia, R. M. Barquez, and M. M. Díaz. 2015. Diversity and richness of small mammals at a well-conserved site of The Yungas in Jujuy Province, Argentina. Mammalia 80:253–262.

Gamboa Alurralde, S., R. T. Sánchez, R. M. Barquez, and M. M. Díaz. 2016. New records of bats (Chiroptera, Mammalia) from Argentina. Check List 12:1–11.

Gardner, A. L. 2008. Mammals of South America. Volume 1.

Marsupials, Xenarthrans, Shrews, and Bats. The University of Chicago Press, California, USA. https://doi.org/10.7208/chicago/9780226282428.001.0001

Hammer, O., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological Statistic software package for education and data analysis. Paleontologia Eletronica 4:1–9.

Hastriter, M. W. 2001. Fleas (Siphonaptera: Ctenophthalmidae and Rhopalopsyllidae) from Argentina and Chile with two new species from the rock rat *Aconaemys fuscus* in Chile. Annals of Carnegie Museum 70:169–178.

Hastriter, M. W., and E. Méndez. 2000. A review of the flea genera *Hectopsylla* Frauenfeld and *Rhynchopsyllus* Haller (Siphonaptera: Pulicidae). Proceedings of the Entomological Society of Washington 102:612–624.

Hastriter, M. W., and M. F. Whiting. 2003. Siphonaptera (Fleas). Pp. 1040–1044 in: Encyclopedia of Insects (V. H. Resh and R. Carde Eds.). Academic Press, San Diego, United States.

Hastriter, M. W., and R. D. Sage. 2009. A description of two new species of *Ectinorus* (Siphonaptera: Rhopalopsyllidae) from Laguna Blanca National Park, Neuquén Province, Argentina. Proceedings of the Entomological Society of Washington 11:581–597.

Hastriter, M. W., and R. D. Sage. 2011. Description of a new species of *Ectinorus* (*E. spiculatus*) (Siphonaptera, Rhopalopsyllidae) from Argentina and a review of the subgenus *Ichyonus* Smit, 1987. Zookeys 124:1–18.

Hastriter, M. W., and R. Guerrero. 1998. A review of the bat flea genus *Hormopsylla* (Siphonaptera: Ischnopsyllidae). Proceedings of the Entomological Society of Washington 100:247–251.

Hastriter, M. W., M. D. Zyzak, R. Soto, R. Fernández, N. Solárzano, and M. F. Whiting. 2002. Fleas (Siphonaptera) from Ancash department, Peru with the description of a new species, *Ectinorus alejoi* (Rhopalopsyllidae), and the description of the male of *Plocopsylla pallas* (Rothschild, 1914) (Stephanocircidae). Annals of the Carnegie Museum 71:87–106.

Hopkins, G. H., and M. Rothschild. 1953. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History) with keys and short descriptions for the identification of families, genera, species and subspecies. Volume I, Tungidae and Pulicidae. The Trustees of the British Museum, London, United Kingdom.

Hopkins, G. H., and M. Rothschild. 1956. An illustrated catalogue of Rothschild collection of fleas (Siphonaptera) in the British Museum (N. H.). Volume II. Coptopsyllidae, Vermipsyllidae, Stephanocircidae, Ischnopsyllidae, Hypsophthalmidae, and Xiphiopsyllidae. British Museum (Natural History) London, United Kingdom.

Hopkins, G. H., and M. Rothschild. 1962. An illustrated catalogue of Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. III. Hystrichopsyllidae. British Museum (NH), London, United Kingdom.

Hopkins, G. H., and M. Rothschild. 1966. An illustrated catalogue of the Rothschild Collection of fleas (Siphonaptera) in the British Museum (Natural History). Volume IV. Hystrichopsyllidae. British Museum (NH), London, United Kingdom.

Hopkins, G. H., and M. Rothschild. 1971. An illustrated catalogue of Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. V. Leptopsyllidae and Ancistropsyllidae. British Museum (NH), London, UK.

Jayat, J. P., and P. E. Ortiz. 2010. Mamíferos del pedemonte de Yungas de la alta cuenca del río Bermejo en Argentina: una línea de base de diversidad. Mastozoología Neotropical 17:69–86.

Jayat, J. P., and S. Pacheco. 2006. Distribución de *Necromys lactens* y *Phyllotis osilae* (Rodentia: Cricetidae: Sigmodontinae) en el noroeste argentino: modelos predictivos basados en el concepto de nicho ecológico. Mastozoología Neotropical 3:69–88.

Jayat, J. P., P. E., Ortiz, S. E. Pacheco, and R. González. 2011. Distribution of sigmodontine rodents in Northwestern Argentina: main gaps in information and new records. Mammalia 75: 53–68.

Johnson, P. T. 1957. A classification of the Siphonaptera of South America. Memoirs of the Entomological Society of Washington 3:1–298.

Jost, L., A. Chao, and R. L. Chazdon. 2011. Compositional similarity and β (beta) diversity. Pp. 66–335 *in*: Biological diversity: frontiers in measurement and assessment (Magurran, A. E., and B. J. McGill, eds.). Oxford University Press, Oxford, UK.

Krasnov, B. R. 2008. Funtional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology. Cambridge University Press, Cambridge, UK.

Krasnov, B. R., D. Mouillot, G. I. Shenbrot, I. S. Khokhlova, and R. Poulin. 2005. Spatial variation in species diversity and composition of flea assemblages in small mammal hosts: geographic distance or faunal similarity? Journal of Biogeography 32:633–644.

Lanzone, C., J. K. Braun, J. L. Patton, and U. F. J. Pardiñas. 2015. Genus *Eligmodontia*. Pp. 508–522 *in*: Mammals of South America. Volume 2. Rodents (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press, Chicago, USA.

Lareschi, M., and P. M. Linardi. 2009. Morphological variability in *Polygenis* (*Polygenis*) *platensis* (Jordan and Rothschild) (Siphonaptera: Rhopalopsyllidae: Rhopalopsyllinae) and taxonomic consequences. Zootaxa 2310:35–42.

Lareschi, M., E. Savchenko, and M. Urdapilleta. 2019. Ectoparasites associated with sigmodontine rodents from northeastern Argentina. Therya 10:103–108. DOI: 10.12933/therya-19-758 ISSN 2007-3364

Lareschi, M., J. P. Sanchez, and A. G. Autino. 2016. Review of the fleas (Insecta: Siphonaptera) from Argentina. Zootaxa 3:239–258.

Lareschi, M., R. A. Ojeda, and P. M. Linardi. 2004. Flea parasites of small mammals in the Monte Desert biome in Argentina with new host and locality records. Acta Parasitológica 49:63–66.

Lareschi, M., A. G. Autino, M. M. Díaz, and R. M. Barquez. 2003. New host and locality records for mites and fleas associated with wild rodents from northwestern Argentina. Revista de la Sociedad Entomológica Argentina 62:60–64.

Lareschi, M., A. G. Autino, M. M. Díaz, and R. M. Barquez. 2011. Taxonomy and Distribution of *Nonnapsylla* Wagner, 1938 (Stephanocircidae: Craneopsyllinae). Journal of Parasitology 97:954–955. http://dx.doi.org/10.1645/ge-2738.1

Lareschi, M., J. P. Sanchez, M. C. Ezquiaga, A. Autino, M. M. Díaz, and R. M. Barquez. 2010. Fleas associated with mammals from northwestern Argentina, with new distributional reports. Comparative Parasitology 77:215–221.

Linardi, P. M., and L. R. Guimarães. 2000. Sifonápteros do Brasil. Ed. MZUSP, FAPESP. São Paulo, Brazil.

López-Berrizbeitia, M. F. 2018. Sifonápteros de micromamíferos (Didelphimorphia, Chiroptera y Rodentia) del Noroeste Argentino: sistemática y distribución. Doctoral Thesis. San Miguel de Tucumán: Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán. Tucumán, Argentina

López-Berrizbeitia, M. F., M. W. Hastriter, and M. M. Díaz. 2016. A new flea species of the genus *Cleopsylla* (Siphonaptera: Stephanocircidae) from northwestern Argentina. Journal of Parasitology 102:514–519.

López-Berrizbeitia, M. F., J. P. Sanchez, R. M. Barquez, and M. M. Díaz. 2018. Descriptions of two new species of flea of the genus *Plocopsylla* in northwestern Argentina. Medical and Veterinary Entomology 2:1–12. doi: 10.1111/mve.12303

López-Berrizbeitia, M. F., J. P. Sanchez, R. M. Barquez, and M. M. Díaz. In press. Taxonomic revision of the flea genus *Agastopsylla* Jordan and Rothschild 1923 (Siphonaptera: Ctenophthalmidae). Anais da Academia Brasileira de Ciências.

López-Berrizbeitia, M. F., M. M. Díaz, R. M. Barquez, and M. Lareschi. 2013a. Pulgas (Siphonaptera) parásitas de roedores (Rodentia: Cricetidae) de la provincia de Salta, Argentina: Nuevos registros de distribución. Revista de la Sociedad Entomológica Argentina 72:141–146.

López-Berrizbeitia, M. F., M. W. Hastriter, R. M. Barquez, and M. M. Díaz. 2015a. A new flea of the genus *Ctenidiosomus* (Siphonaptera, Pygiopsyllidae) from Salta Province, Argentina. Zookeys 512:109–120.

López-Berrizbeitia, M. F., M. W. Hastriter, R. M. Barquez, and M. M. Díaz. 2019. Fleas of the genus *Tetrapsyllus* (Siphonaptera: Rhopalopsyllidae) associated with rodents from Northwestern Argentina. International Journal for Parasitology: Parasites and Wildlife 9:80–89.

López-Berrizbeitia, M. F., R. T. Sánchez, M. M. Díaz, and M. Lareschi. 2013b. Los ectoparásitos de La Rioja: resultados preliminares. Revista de la Asociación Parasitológica Argentina 1:40–44.

López-Berrizbeitia, M. F., R. T. Sánchez, R. M. Barquez, and M. M. Díaz. 2017. An update on the distribution and nomenclature of fleas (Order Siphonaptera) of bats (Order Chiroptera) and rodents (Order Rodentia) from La Rioja Province, Argentina. Zookeys 678:139–154. https://doi.org/10.3897/zookeys.678.12006

López-Berrizbeitia, M. F., J. P. Sanchez, M. M. Díaz, R. M. Barquez, and M. Lareschi. 2015b. Redescription of *Neotyphloceras crassispina hemisus* Jordan (Siphonaptera: Ctenophthalmidae: Neotyphloceratini). Journal of Parasitology 10:145–149. https://doi.org/10.1645/14-648.1

Manhert, V. 1976. *Alectopsylla unisetosa* nov. gen., nov. spec. (Siphonaptera, Ischnopsyllidae) from Argentina. Revue Suisse de Zoology 83:769–776.

Mardon, D. K. 1981. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Volume VI. Pygiopsyllidae. Trustees of The British Museum (Natural History), London, England.

Mittermeier, R. A., N. Myers, P. Robles Gil, and C. G. Mittermeier. 1999. Hotspots: earth's biologically richest and most endangered terrestrial ecoregions. Cemex, Ciudad de México, México.

Moreno, C. E. 2001. Métodos para medir la biodiversidad. M y T–Manuales y Tesis SEA, Zaragoza, Spain.

Patton, J. L., U. F. J. Pardiñas, and G. D'Elia. 2015. Mammals of South America. Rodents. Vol. 2. University of Chicago Press, Chicago, Illinois, United States.

Peters, S. L., J. R. Malcolm, and B. L. Zimmerman. 2006. Effects of selective logging on bat communities in the South-eastern Amazon. Conservation Biology 20:1410–1421.

Roccatagliata, J. A. 1998. La Argentina: Geografía general y los marcos regionales. Planeta. Buenos Aires, Argentina.

Rothschild, M., and R. Traub. 1971. A revised glossary of terms used in the taxonomy and morphology of fleas. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. V. British Museum (Natural History), London, England.

Salceda-Sánchez, B., and M. W. Hastriter. 2006. A list of the fleas (Siphonaptera) of Mexico with new host and distribution records. Zootaxa 1296:2–43.

Sanchez, J. P. 2012. Sifonápteros parásitos de los roedores sigmodontinos de la Patagonia norte de la Argentina: estudios sistemáticos y ecológicos. Doctoral Thesis. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina.

Sanchez, J. P., and M. Lareschi. 2013. The fleas (Insecta: Siphonaptera) parasites of sigmodontine rodents (Cricetidae) from Northern Patagonia, Argentina. Comparative Parasitology 80:110–117.

Sanchez, J. P., and M. Lareschi. 2014a. New records of fleas (Siphonaptera: Ctenophthalmidae: Rhopalopsyllidae and Stephanocircidae) from Argentinean Patagonia, with remarks on the morphology of *Agastopsylla boxi* and *Tiarapsylla argentina*. Revista Mexicana de Biodiversidad 85:383–390. DOI:10.7550/rmb.42071

Sanchez, J. P., and M. Lareschi. 2014b. Two new species of *Neotyphloceras* (Siphonaptera: Ctenophthalmidae) from Argentinean Patagonia. Zootaxa 3784:159–170.

Sanchez, J. P., D. E. Udrizar-Sauthier, and M. Lareschi. 2009. Nuevos registros de pulgas (Insecta, Siphonaptera) parásitas de roedores sigmodontinos (Cricetidae) de la Patagonia Austral, Argentina. Mastozoología Neotropical 16:243–246.

Sanchez, J. P., J. C. Beaucournu, and M. Lareschi. 2015. Revision of fleas of the genus *Plocopsylla* belonging to the 'angusticeps–lewisi' complex in the Andean biogeographic region, with the description of a new species. Medical and Veterinary Entomology 29:147–158.

Sanchez, J. P., V. Amor, E. A. Bazan-Leon, R. A. Vasquez, and M. Lareschi. 2012. Redescription of *Neotyphloceras chilensis* Jordan, new status (Siphonaptera: Ctenophthalmidae: Neotyphloceratini). Zootaxa 3259: 51–57.

Sandoval, M. L., M. S. Sánchez, and R. M. Barquez. 2010. Mammalia, Chiroptera Blumenbach, 1779: new locality records, filling gaps, and geographic distribution maps from northern Argentina. Check List 6:64–70.

Santillán de Andrés, S., and R. Ricci. 1998. La región del Noroeste Argentino: paisajes heterogéneos con economía mixta. Pp. 579-612 *in*: La Argentina. Geografía General y los marcos regionales (Roccatagliata, J. A., ed.). Editorial Planeta Buenos Aires, Argentina.

Schramm, B. A., and R. E. Lewis. 1988. A taxonomic revision of the flea genus *Plocopsylla.* Pp. 1-157 *in*: Theses Zoologicae (Fricke, R., ed.). Vol. 9. Koeltz Scientific Books, Koenigstein, Germany.

Schreiter, R., and R. C. Shannon. 1927. Un nuevo e interesante género y especie de una pulga del murciélago. Boletín del Museo de Historia Natural, Universidad Nacional de Tucumán 1:1–15.

Smit, F. G. A. M. 1987. An illustrated catalogue of the Rothschild fleas (Siphonaptera) in the British Museum (Natural History) 7: Malacopsylloidea (Malacopsyllidae and Rhopalopsyllidae). Oxford University Press, Oxford, United Kingdom.

Steppan, S. J. and O. Ramírez. 2015. Genus *Phyllotis.* Pp. 535–555 *in*: Mammals of South America. Volume 2. Rodents (Patton, J. L., U. F. J Pardiñas, and G. D'Elía, eds.) The University of Chicago Press, Chicago, United States.

Teta, P., R. A. Ojeda, S. O. Lucero, and G. D'Elía. 2017. Geographic variation in cranial morphology of the Southern Mountain Cavy, *Microcavia australis* (Rodentia, Caviidae): taxonomic implications, with the description of a new species. Zoological Studies Vol. 56. doi:10.6620/ZS.2017.56-29.

Teta, P., A. M. Abba, G. H. Cassini, D. A. Flores, C. A. Galliari, S. O. Lucero, and M. Ramírez. 2018. Lista revisada de los mamíferos de Argentina. Mastozoología Neotropical 25:163–198.

Tipton, V. J., and C. E. Machado-Allison. 1972. F leas of Venezuela. Brigham Young University Science Bulletin, Biological Series 17:1–115.

Tipton, V. J., and E. Méndez. 1966. The fleas (Siphonaptera) of Panamá. Pp. 289-385 *in*: Ectoparasites of Panama (Wenzel, R. L. and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, USA.

Torrella, S. A., and J. M. Adámoli. 2005. Situación ambiental de la eco-región del Chaco Seco. La situación ambiental Argentina 73–75.

Torrella, S. A., R. G. Ginzburg, and J. M. Adámoli. 2007. Expansión agropecuaria en el Chaco Argentino: Amenazas para la conservación de la biodiversidad. Pp. 53-63 *in*: Panorama de la ecología de paisajes en Argentina y países sudamericanos (Matteucci, S.D., ed.). INTA-UNESCO, Buenos Aires, Argentina.

Torrella, S. A., R. G. Ginzburg, J. M. Adámoli, and L. Galetto. 2011. Estructura, composición y estado de conservación de la comunidad de plantas leñosas del bosque de tres quebrachos en el Chaco Subhúmedo Central. Ecología Austral 21:179–188.

Torres, R., and J. P. Jayat. 2010. Modelos predictivos de distribución para cuatro especies de mamíferos (Cingulata, Artiodactyla y Rodentia) típicas del Chaco en Argentina. Mastozoología Neotropical 17:335–352.

Udrizar Sauthier, D., and U. F. J. Pardiñas. 2014. Estableciendo límites: distribución geográfica de los micromamíferos (Rodentia y Didelphimorphia) de Patagonia centro-oriental. Mastozoología Neotropical, Mendoza 21:79–99.

Urdapilleta, M., P. M. Linardi, and M. Lareschi. 2019. Fleas associated with sigmodontine rodents and marsupials from the paranaense forest in northeastern Argentina. Acta Tropica 193:71–77.

Urquizo, J., M. M. Díaz, and R. M. Barquez. 2017. Una nueva especie de *Myotis* (Chiroptera: Vespertilionidae) para la Argentina. Mastozoología Neotropical 24:257-261.

Verzi, D. H., C. C. Morgan, and A. I. Olivares. 2015. The history of South American octodontoid rodents and its contribution to evolutionary generalisations. Pp. 139–163 *in*: Evolution of the rodents, advances in phylogeny, functional morphology and development (Cox, P., and L. Hautier, eds.). Cambridge University Press, United Kingdom, UK.

Voss, R. S., and S. A. Jansa. 2009. Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. Bulletin of the American Museum of Natural History 322:1–177.

Whiting, M. F., A. S. Whiting, M. W. Hastriter, and K. Dittmar. 2008. A molecular phylogeny of fleas (Insecta: Siphonaptera): origins and host associations. Cladistics 24:677–707.

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APPENDIX I

List of localities

Alphabetical list of localities of each province of northwestern Argentina: Specific locality, Department between parentheses, Geographic coordinates and Elevation are included.

Catamarca

1. 17 km N Barranca Larga (Belén) -26º 51’ 11.6” S, -66º 45’ 18.8” W, 3,219 ± 51 m.
2. 21 km SO El Desmonte (Santa María) -26º 59’ 57.5” S, -66º 14’ 33.7”W, 2,172 ± 150 m.
3. 22 km al SE de Villa de Escaba sobre ruta provincial Nº 9 (Paclín) -27º 47’ 48.48” S, -65º -46’ 56.70”W, 538 m.
4. 3.4 km al S de la unión entre las rutas provinciales 18 y 9, sobre ruta provincial Nº 18 (Paclín) -27º 49’ 48.3” S, -65º 47’ 53.3”W, 1,529±53 m.
5. 5.2 km S El Bolsón (Belén) -27º 02’ 36.6” S, -66º 47’ 14” W, 2,404±55 m.
6. 9.2 km O Andalgalá (Andalgalá) -27º 35’ 33.1” S, -66º 24’ 56.2” W, 1,089±150 m.
7. Chumbicha (Capayán) -28º 54’ S, -66º 15’W, 379 m.
8. Chumbicha, alrededores (Capayán) -28º51’ 43” S, -66º 14’ 41.9”W, 407 m.
9. Cumbre de Humaya (Ambato) -27º 56’ 12.08” S, -65º 56’ 46.30” W, 1900 m.
10. El Rodeo (Ambato) -28º 13’ S, -65º 52’W, 1361 m.
11. Estancia Narváez, 5.5 km N Las Chacritas sobre ruta provincial Nº 1 (Ambato) -27º 39’ 46.3” S, -65º 56’ 34.2” W, 1782±150 m.
12. Inta (Santa María) -26º 41’ 38.20” S, -66º 02’ 49.10”W, 1,889 m.
13. La Merced (Paclín) -28º 10’ S, -65º 38› W, 931 m.
14. La Puerta (Ambato) -28º 13’ S, -65º 24’W, 797 m.
15. Laguna Blanca (Belén) -26º 34’ 53.4” S, -66º 56’ 38.6” W, 3,350±70 m.
16. Las Juntas (Ambato) -28º 06’ S, -65º 55’W, 1,750 m.
17. Otro Cerro (Capayán) -28º 48’ S, -66º 17’W, 2,154 m.
18. Otro Cerro, Rancho de los Crisho (Capayán) -28º 41’ 33.06” S, -66º 15’ 9.00”W, 2,300 m.
19. Pasto Ventura (Antofagasta de la Sierra) -26°41’ 37.4” S, -67°10’ 55.6”W, 3,831±32 m.
20. Paycuqui (Antofagasta de la Sierra) -25º54’ 53” S, -67º 21’ 15” W, 3,664±22 m.

Jujuy

21. 17 km al O y 3 km al S de la Quiaca, sobre ruta provincial Nº 5 (Yavi) -22º 09’ S, -65º 44’W, 3,631 m.
22. 3 km al E de Purmamarca por ruta nacional Nº 52 (Tumbaya) -23º 43’ 47.11” S, -65º 31’ 11.12”W, 2,453 m.
23. 3 km del cruce Río Las Capillas y ruta provincial Nº 20 (Dr. Manuel Belgrano) -24º 5’ 35.77” S, -65º 9’ 7.86”W, 1,141 m.
24. 5 km NE de Humahuaca (Humahuaca) -23º 13’ S, -65º 20’W, 3,103 m.
25. 6.8 km al SE de Suripujio, sobre ruta provincial N° 5 (Yavi) -22º 13’ 27” S, -65º 16’ 12.2”W, 3,991±29 m.
26. 9 km NO Bárcena (Tumbaya) -23º 67’ 5.9” S, -65º 30’ 1.2” W, 2,655±73 m.
27. Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional 9 (El Carmen) -24º 29’ 54.00” S, -65º 18’ 24.00” W, 1,381 m.
28. Arroyo La Horqueta, 6 km al SE de las Lagunas de Yala (Dr. Manuel Belgrano) -24º 07’ S, -65 º 27’W, 1,950 m.
29. Arroyo Los Matos, 7 km N de Las Capillas (Dr. Manuel Belgrano) -24º 04’ 27.93” S, -65º 08’ 42.08”W, 1,193 m.
30. Casa Colorada, ~ 2 km al N de Alfarcito (Tilcara) -23°35’ S, -65°21’W, 3,157 m.
31. Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado (San Antonio) -24º 19’ S, -65º 24’W, 1,643 m.
32. Chilcayoc (Tumbaya) -23º 56’ 30” S, -65º 28’ 33” W, 2,239±50 m.
33. Cuesta de Jaire (Dr. Manuel Belgrano) -24º 01’ 29.14” S, 065º 24’ 50.70”W, 1, 961 m.
34. Cuesta de Lipán, 15 km O de Purmamarca, sobre ruta 52, (Tumbaya) -23º 40’ S, -65º 35’W, 3,092 m.
35. Cuesta del Hurón, 29 km al W de Cieneguillas, sobre ruta provincial 64 (Santa Catalina) -22º 06’ S, -66º 03’W, 3,829 m.
36. Curques, 24 km al N de Susques sobre ruta 74 (Susques) -23º 14’ S, -66º 23’W, 3,917 m.
37. El Chaguaral, cerca de Villa Carolina (San Pedro) -24º 12’ S, -64º 49’W, 514 m.
38. Laguna La Brea, 25 km antes de Palma Sola (Santa Bárbara) -23º 56’ S, -64º 28’W, 882 m.
39. La Quiaca, 17 km O y 3 km S, sobre ruta provincial 5, (Yavi) -22º 09’ S, -65º 44’W, 3,630 m.
40. Parque Provincial Potrero de Yala (Dr. Manuel Belgrano) -24º 06’ 45.81” S, -65º 28’ 41.05”W, 2,031 m.
41. Pucará de Tilcara (Tilcara) -23º 35’ 09.79” S, -65º 24’ 09.53”W, 2,508 m.
42. Quebrada Seca, Alfarcito, 10 km al O de Tilcara (Tilcara) -23º 34’ 40.53” S, -65º 29’ 29.58”W, 3,558 m.
43. Reserva Provincial Olaroz-Cauchari (Susques) -23º 19’ S, -66º 35’W, 3,963 m.
44. Río Blanco, 9 km SO San Antonio (San Antonio) -24º 24’ 52.80” S, -65º 22’ 34.20”W, 1,456 m.
45. Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial 20 (Dr. Manuel Belgrano) -24º 02’ S 65º 07’W, 1,059 m.
46. Río Lavayén, aproximadamente 1 km al N de Santa Rita (San Pedro) -24º 28’ S, -64º 48’W, 553 m.
47. Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N˚ 29 (Dr. Manuel Belgrano) -23º 59’ S, -65º 19’W, 1,669 m.

48. Ruta 83 camino a Valle Grande, 9 km al N de San Francisco (Valle Grande) -23º 35′ S, -64º 58′W, 1,448 m.
49. Salar Cauchari, 31 km al N de Cauchari, sobre ruta provincial Nº 70 (Susques) -23º 50′ S, -66º 47′W, 3,915 m.
50. San Pedro (San Pedro) -24º 12′ S, -64º 55′W, 738 m.
51. San Salvador de Jujuy (Dr. Manuel Belgrano) -24º 12′ S, -65º 19′W, 1,357m.
52. Sierra de Tilcara, El Hueco, 21 km SE de Tilcara (Tilcara) -23º 42′ 26.82″ S, -65º 14′ 42.54″W, 3,044 m.
53. Sierra de Tilcara, Toro Arita, 12 km ESE de Maimará, 14 km ESE de Tilcara (Tilcara) -23º 39′ 55.56″ S, -65º 17′ 55.02″ W, 4,092 m.
54. Sierra de Zenta, ruta provincial 13, entre Chaupe Rodeo e Iruya, 12 km N de Chaupe Rodeo (Humahuaca) -22º 53′ S, -65º 15′W, 3,982 m.
55. Sobre ruta 40, 29 km al N del empalme con ruta 52 (Tumbaya) -23º 24′ S, -65º 46′W, 3,479 m.
56. Villa Carolina, Río Lavallén, a unos 20 km al E de San Pedro de Jujuy (San Pedro) -24º 13′ 09.02″ S, -64º 39′ 58.50″W, 485 m.

La Rioja

57. 1 km al N de Los Tambillos (Coronel Felipe Varela) -29º 22′ S, -67º 47′W, 1,939 m.
58. 2 km al E de Malanzán, camping El Descanso (General Facundo J. Quiroga) -30º 48′ 37.7″ S, -66º 34′ 40.3″W, 957 m.
59. 2 km al S pasando Río de La Punta sobre ruta provincial N˚ 7 (Arauco) -28º 45′ 28.8″ S, -66º 47′ 09.3″W, 996 m.
60. 2 km al S de la entrada al Parque Geológico Sanagasta, sobre ruta nacional 75 (Sanagasta) -29º 16′ 48.73″ S, -67º 2′ 11.92″W, 1,122 m.
61. 26 km SO Quimilo (Chamical) -30º 02′ 43.4″ S, -65º 31′ 13.4″ W, 581 m.
62. 4 km al O de Anillaco, Reserva Aguada de las Alturas (Castro Barros) -28º 47′ 56.52″ S, -66º 59′ 44.94″W, 1,738m.
63. 5 km al S del Cañón del Ocre (Famatina) -28º 51′ 55.9″ S, -67º 41′ 26.3″W, 2,495 m.
64. 700 m al E de RN 40 (San Blas de los Sauces) -28º 24′ 17.4″ S, -67º 04′ 48.4″W, 1,123 m.
65. 8 km al NE del Cañón del Ocre (Famatina) -28º 57′ 37.3″ S, -67º 41′ 26.3″W, 3,127 m.
66. A 800 m al E de la entrada de Anillaco (Castro Barros) -28º 48′ 34.32″ S, -66º 55′ 11.58″W, 1,329 m.
67. Ambil, 23 km al S de Catuna (General Ocampo) -31º 07′ 36.5″ S, -66º 20′ 45.3″W, 597 m.
68. Anillaco, 1.7 m al E del CRILAR (Castro Barros) -28º 48′ 46.00″ S, -66º 55′ 50.44″W, 1,357 m.
69. Anillaco, 500 m al O de la plaza de Anillaco (Castro Barros) -28º 48′ 40.30″ S, -66º 55′ 55.55″W, 500 m.
70. Anillaco, atrás del cementerio (Castro Barros) -28º 48′ 49.04″ S, -66º 56′ 0.75″W, 1,365 m.
71. Chepes, puesto La Escondida, 42 km al S de Chepes (Rosario V. Peñaloza) -31º 39′ 54.2″ S, -66º 41′ 18.1″W, 431 m.
72. Cuesta La Cébila, 22 km al NW de Chumbicha, sobre ruta 60 (Capital) -28º 50′ S, -66º 24′W, 850 m.
73. Guayapa, 13 km SO de Patquía cerca de la ruta 150 (Independencia) -30º 07′ 13.92″ S, -66º 58′ 25.34″W, 502 m.
74. Olta, Dique de Olta (General Belgrano) -30º 38′ 22.55″ S, -66º 17′ 46.6″W, 635 m.
75. Puesto Tres Piedras (Famatina) -28º 50′ 39.8″S , 67º 46′ 58.7″ W, 3,304 m.
76. Quebrada de Santo Domingo 30 km al SO de Jagué (Vinchina) -28º 31′ 34.7″ S, -68º 46′ 13.8″W, 3,131 m.
77. Ruta Provincial 11, km 81, El Potrerillo, río El Potrerillo (Famatina) -28º 23′ 52.6″ S, -67º 40′ 35.6″W, 1,685 m.
78. Ulapes, 1 km al O de la plaza principal de Ulapes (San Martín) -31º 34′ 35″ S, -66º 14′ 55″W, 493 m.
79. Zapallar (Coronel Felipe Varela) -29º 18′ 24.74″ S, -68º 40′ 9.24″W, 1,634 m.

Salta

80. 12.6 km O de Piquirenda Viejo (San Martín) -22º 20′ S, -63º 50′W, 750 m.
81. 26 km NO de Santa Rosa de los Pastos Grandes (Los Andes) -24º 30′ S, -66º 47′ 24″W, 3,949±17 m.
82. 3 km al N de Potrerillos sobre ruta provincial N˚ 6 (Candelaria) -26º 03′ 52.9″ S, -65º 30′ 01.2″W, 1,214±94 m.
83. 7.8 km al NNE de Pampa Grande, sobre ruta provincial N˚ 6, sobre Río Cachi (Guachipas) -25º 47′ 57.8″ S, -65º 27′ 7.3″ W, 1,750±72 m.
84. 8 km O de Piquirenda Viejo (San Martín) -22º 21′ S, -63º 50′ W, 678m.
85. A 43.7 km del cruce de las rutas 50 y 18, camino a Isla de Cañas, sobre ruta 18 (Orán) -23º 00′ S, -64º 33′ 02.40″ W, 679 m.
86. Aguas Blancas, estación de aforo a 30 m del puente internacional sobre ruta provincial N° 19, a orillas del Río Bermejo (Orán) -22º 43′ 29.7″ S, -64º 21′ 49.8″W, 418 m.
87. Aproximadamente 3 km N Cachi adentro (Cachi) -25º 04′ 24.8″ S, -66º 12′ 40.2″W, 2,724±51 m.
88. Aproximadamente 15 km al O de Escoipe, sobre ruta provincial N˚ 33 (Chicoana) -25º 10′ 25.2″ S, -65º 49′ 31.6″ W, 2,680±73 m.
89. Aproximadamente 2 km al N y 6 km al O de Metán, sobre Río Las Conchas (Metán) -25º 28′ 09″ S, -65º 01′ 72″W, 986 m.
90. Cerillos (=Cerrillos) -24º 55′ S, -65º 30′W, 1,250 m.
91. Cuesta Chica, 35 km O del Oculto, 4 km E de San Andrés (Orán) -23º 4′ 20.51″ S, -64º 50′ 12.75″W, 1,539 m.
92. El Quebrachal (Anta) -25º 21′ S, -64º 02′W, 337 m.
93. El Oculto, ruta provincial N° 18, km 25 sobre Río Blanco (camino a San Andrés) (Orán) -23º 6′ 22.21″ S, -64º 32′ 25.40″ W, 528 m.

94. Finca Barba Yaco, 8.5 km SE Ojo de Agua (Rosario de la Frontera) -25º 58’ 36.8” S, -64º 55’ 36.9” W, 1,347±57 m.
95. Finca Chato Méndez (Orán) -23º 13’ 34.67” S, -64º 13’ 1.59” W, 311 m.
96. Gran Chaco (San Martín) -23º 36’ S, -62º 35’ W, 211 m.
97. Hipólito Yrigoyen (Orán) -23º 14’ 34.47” S, -64º 16’ 14.67” W, 328 m.
98. Joaquin V. González (Anta) -25º 06’ S, -64º 07’ W, 379 m.
99. La Estrella (Orán) -23º 48’ 51.06” S, -64º 05’ 50.49” W, 400 m.
100. Laguna de Pintascayo, 1.5 km N sobre Río Pescado, frente a Quebrada del Café (Orán) -22º 51’ 66” S, -64º 29’ 43” W, 465 m.
101. Parque Nacional El Rey (Anta) -24º 58’ S, -64º 38’ W, 915 m.
102. Pintascayo, Campamento Lima (Propiedad de GMF S.A.) (Iruya) -22º 51’ 44.2” S, -64º 37’ 41.1” W, 832 m.
103. Río El Naranjo, 14 km al O de ruta provincial Nº 5, sobre camino de acceso a Parque Nacional El Rey (Anta) -24º 58’ S, -64º 38’ W, 915 m.
104. Río Los Sauces, 12 km NO del Jardín, ruta 6 km 110 (Candelaria) -26º 4’ 33.6” S, -65º 28’ 58.8” W, 993 m.
105. Rosario de la Frontera (Rosario de la Frontera) -25º 48’ S, -64º 58’ W, 792 m.
106. Rosario de Lerma (Rosario de Lerma) -24º 59’ S, -65º 35’ W, 1,330 m.
107. Salta (Capital) -24º 46’ S, -65º 28’ W, 1,258 m.
108. Vega Cortadera (Los Andes) -25º 07’ 13” S, -67 º 02’ 39” W, 3,897±16 m.

Santiago del Estero

109. El Ojito (Pellegrini) -26º 01’ S, -63º 45’ W, 255 m.
110. El Quemado (Figueroa) -27º 06’ S, -63º 33’ W, 174 m.
111. Las Carpas (Alberdi) -26º 30’ S, -63º 10’ W, 204 m.
112. La Puerta, 27 km al SE de Las Termas de Río Hondo, sobre ruta nacional Nº 9 (Río Hondo) -27º 38’ 12” S, -64º 36’ 39” W, 284 m.
113. Pozo Betbeder (Pellegrini) -26º 23’ S, -64º 20’ W, 326 m.
114. Salinas de Ambargasta, ~ 8 km SE Cerro Rico (Choya) -29º 03’ 33.6” S, -64º 38’ 01.5” W, 141±22 m.
115. Sumampa (Quebrachos) -29º 22’ S, -63º 28’ W, 246 m.
116. San Pedro de Guasayán, en el techo de un galpón abandonado (Guasayán) -27º 52’ S, -64º 51’ W, 481 m.

Tucuman

117. 11 km S Tafí del Valle (Tafí del Valle) -26º 53’ 34.90” S, -65º 45’ 52.28” W, 2,278 m.
118. 1.9 km NE Hualinchay sobre ruta provincial N° 311 (Trancas) -26º 18’ 44” S, -65º 35’ 52” W, 1,732±150 m.
119. 26 km al S de San Pedro de Colalao sobre ruta provincial N° 364 (Trancas) -26º 23’ 0.80” S, -65º 33’ 18.80” W, 1,540±64 m.
120. Arroyo El Saltón, Reserva Provincial Santa Ana (Río Chico) -27º 28’ S, -65º 45’ W, 523 m.
121. Arroyo Mista (Leales) -27º 13’ S, -65º 10’ W, 323 m.
122. Cañada del Fuerte Viejo, Cerro Muñoz (Tafí del Valle) -26º 53’ 41” S, 065º 48’ 40.32” W, 3,300 m.
123. Cerro San Javier (Tafí Viejo) -26º 33’ S, -65º 26’ W, 1,780 m.
124. Cerro San Javier, a unos 20 km al O de San Miguel de Tucuman (Tafí Viejo) -26º 48’ 33.55” S, -65º 25’ 7.47” W, 919 m.
125. Ciénaga Escondida (Tafí del Valle) -26º 53’ 33.69” S, -65º 49’ 25.48” W, 3,781 m.
126. Ciénaga Grande, San José de Chasquivil (Tafí Viejo) -26º 41’ 8.74” S, -65º 39’ 30.79” W, 2,830 m.
127. Cuesta del Clavillo, 5 km al SO de La Banderita (Andalgalá) -27º 20’ S, -66º 00’ W, 1,910 m.
128. Dique Escaba (Alberdi) -27º 40’ S, -65º 45’ W, 656 m.
129. Dique San Ignacio (La Cocha) -27º 46’ S, -65º 37’ W, 501 m.
130. El Ceibal Chico, 4 km al E de la rotonda de Lules por ruta provincial 321 y 1.5 km al S, por calle Julio C. Berrizbeitia (Lules) -26º 56’ 57.42” S, -65º 18’ 9.50” W, 393 m.
131. El Papal, Parque Nacional Campo de Los Alisos (Chicligasta) -27º 11’ 29.88” S, -65º 57’ 1.62” W, 2,175 m.
132. Escaba de Abajo, casa abandonada a 150 m de la Hostería Eskay Apu (Alberdi) -27º 40’ 12.03” S, -65º 45’ 52.42” W, 668 m.
133. Los Cardones (Tafí del Valle) -26º 31’ 08.12” S, -65º 59’ 50.81” W, 1,780 m.
134. Lagunas de Huaca Huasi, Cumbres Calchaquíes (Tafí Viejo) -26º 39’ S, -65º 43’ W, 4,169 m.
135. La Olorosa (Tafí del Valle) -26º 53’ 20.06” S, -65º 49’ 48.17” W, 3,940 m.
136. Los Planchones, Cerro Muñoz, aproximadamente 15 km O de Rodeo Grande (Tafí del Valle) -26º 53’ 32.08” S, -65º 50’ 41.72” W, 4,325 m.
137. La Quebradita (Tafí del Valle) -26º 49’ 34.11” S, -65º 42’ 56.69” W, 2,304 m.
138. Las Tipas, Parque Biológico Sierra de San Javier (Tafí Viejo) -26º 39’ 16.20” S, -65º 22’ 57.60” W, 968 m.
139. Los Chorrillos 13 km NO, límite norte estancia Los Chorrillos (Burruyacú) -26º 16’ 10.96” S, -65º 0’ 53.31” W, 1,592 m.
140. Parque Nacional Campo de Los Alisos, El Kerqueo (Chicligasta) -27º 10’ 21.30” S, -65º 58’ 45” W, 3,156 m.
141. Parque Provincial El Cochuna, camping (Chicligasta) -27º 41’ S, -65º 46’ 30” W, 748 m.
142. Peña Colorada (Tafí del Valle) -26º 53’ 12.99” S, -65º 50’ 14.47” W, 4,138 m.
143. Peña Con Gente, Cerro Muñoz (Tafí del Valle) -26º 53’ 30.15” S, -65º 50’ 25.60” W, 4,250 m.
144. Pie de la Cuesta a Chasquivil, 5 km de la Hoyada sobre Río Hoyada (Tafí Viejo) -26º 39’ 37.6” S, -65º 33’ 65” W, 1,700 m.
145. Piedra Blanca (Tafí Viejo) -26º 41’ 8.74” S, -65º 39’ 30.80” W, 2,830 m.
146. Reserva La Florida, 7 km O Ibatín, sobre Río Pueblo Viejo (Monteros) -27º 11’ 30” S, -65º 40’ 6.6” W, 549 m.

147. Reserva Provincial Aguas Chiquitas, sobre Río Aguas Chiquitas (Burruyacú) -26º 36’ 32.40” S, -65º 10’ 36.6” W, 605 m.
148. Río Grande, 5 km al S de El Siambón (Tafí Viejo) -26º 46’ 6” S, -65º 28’ 6” W, 937 m.
149. Río Nío, 4 km al O, camino hacia Alto de Medina (Burruyacú) -26º 26’ 43.20” S, -65º 01’ 36” W, 1,072±26 m.
150. San Miguel de Tucuman (Capital) -26º 51’ S, -65º 25’ W, 1,012 m.
151. Santa Cruz, 10 km al S de Tafí del Valle (Tafí del Valle) -26º 56’18.51” S, -65º 43’22.54” W, 1,989 m.
152. Taco Ralo (Graneros) -27º 50’ S, -65º 12’ W, 343 m.
153. Tapia (Trancas) -26º 36’ 15.83” S, -65º 15’ 36.10” W, 685 m.
154. Tapia, cruce de ruta 9 y Río Tapia (Trancas) -26º 36’ 37.84” S, -65º 15’ 58.03” W, 674 m.

APPENDIX II

List of localities

Alphabetical list of localities that do not belong to northwestern Argentina. It is included by Country, Specific location, Department, Province, State or Party in parentheses, Geographic Coordinates and Elevation.

Argentina

Bonifacio (Guaminí, Buenos Aires) -36º 48’ 56” S, -63º 13’ 22. 5” W, 130 m.

Chivilcoy (Chivilcoy, Buenos Aires) -34º 53’ 50.2” S, -60º 01’ 7.64” W, 55 m.

Estancia La Daniela (Buenos Aires) not located

Estancia San José, sobre Río Negro (Patagones, Buenos Aires) 40º 57’ S, -62º 48’ W, 31 m.

Fortín Uno (Avellaneda, Río Negro) -38º 50’ S, -65º 26’ W, 169 m.

La Plata (La Plata, Buenos Aires) -34º 55’ 16.5” S, -57º 57’ 15.6” W, 3 m.

Las Casuarinas (25 de mayo, San Juan) -31º 49’ S, -68º 19’ W, 562 m.

Las Rosas (Belgrano, Santa Fe) -32º 28’ 30.43” S, -61º 34’ 36” W, 107 m.

Puerto Madryn (Biedma, Chubut) 42º 46’ S, -65º 03’ W, 101 m.

Puesto La Carpa (Lavalle, Mendoza) -32º 46’ S, -68º 15’ W, 597 m.

Puesto Pugin, Algarrobito (Lavalle, Mendoza) -32º 53’ S, -67º 18’ W, 471 m.

San Rafael (San Rafael, Mendoza) -34º 37’ S, -68º 24’ W, 752 m.

Santa Rosa (Santa Rosa, Mendoza) -33º 15’ S, -68º 10’ W, 613 m.

Bolivia

Buen Retiro (Sara, Santa Cruz) 17º 17’ 36.29” S, -63º 42’ 52.52” W, 290 m.

Río Yapacani (Ichilo, Santa Cruz) 16º 00’ S, -64º 25’ W, 174 m.

Brazil

Nova Teutônia (Seara, Santa Catarina) -27º 03’ S, -52º 24’ W, 865 m.

Chile

Valparaíso (Valparaíso, Valparaíso) -33º 02’ 50.06” S, 71º 36’ 45.68” W, 18 m.

Hungary

Budapest (Capital, Hungría Central) 47º 29’ 52.48” N, 19º 02’ 24.85” E, 109 m.

France

Bure (Mosa, Lorena) 48º 30’ 20.36” N, 5º 21’ 30.24” E, 342 m.

Marsella (Bocas del Ródano, Provenza-Alpes-Costa Azul) 43º 17’ 47.34” N, 5º 22’ 11.21” E, 34 m.

Nigeria

Olokemeji (Ekiti) 7º 36’ 52.90” N, 5º 14’ 29.6” E, 420 m.

Panama

Bambito-Cerro Punta (Tierras Altas, Chiriquí) 8º 52’ 22.67” N, 82º 35’ 0.58” W, 1943 m.

Paraguay

Sapucay (Paragaurí) -25º 40’ S, -56º 55’ W, 193 m.

Tacuaral (Central) -25º 07’ 07” S, -56º 13’ 59.8” W, 164 m.

Villarica (Guairá) -25º 46’ 33.82” S, -56º 26’ 58.53” W, 179 m.

Peru

4 km NO Pomata (Puno, Chucuito) -16º 16’ S, -69º 16’ W, 3819 m.

Caylloma (Caylloma, Arequipa) -15º 09’ S, 71º 45’ W, 4493 m.

Uruguay

Paso Pache Antiguo puente, Río Santa Lucia (Canelones, Canelones) -34º 22’ 21.02” S, -56º 16’ 29.96” W, 18 m.

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Genetic relationships of Caribbean lowland spiny pocket mice (*Heteromys desmarestianus*: Rodentia; Heteromyidae): evidence of a distinct mitochondrial lineage

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Genetic studies provide important insights into the evolutionary history and taxonomy of species, allowing us to identify lineages difficult to distinguish morphologically. The relationships among species in the genus *Heteromys* have been in flux as new species have been described, and candidate species have been suggested in the *H. desmarestianus* group. One new potential species may be in Costa Rica's Caribbean lowlands. Herein, we test the phylogenetic relationships of individuals from Costa Rica's Caribbean lowlands to individuals from throughout the species' range using mitochondrial sequences from cytochrome-*b* (*cytb*). We captured 116 individuals from the lowlands, sequenced their *cytb* gene, and incorporated 74 GenBank sequences from throughout the species' range to test if individuals from Costa Rica's Caribbean lowlands potentially constitute an undescribed species. Our results document a distinct mitochondrial lineage in the Caribbean lowlands of Costa Rica. Our results from extensive sampling within the lowlands show a unique mitochondrial DNA lineage, which suggests the presence of an undescribed species. The Caribbean lowlands of Costa Rica may hold other cryptic diversity, and further phylogenetic studies should incorporate samples from this area, as it may have a unique evolutionary history.

Los estudios genéticos proporcionan información importante sobre la historia evolutiva y la taxonomía de las especies, lo que nos permite identificar linajes difíciles de distinguir morfológicamente. Las relaciones filogenéticas entre las especies del género *Heteromys* han estado cambiando a medida que se han descrito nuevas especies y se han sugerido especies candidatas en el grupo *H. desmarestianus*. Una nueva especie potencial podría encontrarse en las tierras bajas del Caribe de Costa Rica. En este trabajo analizamos las relaciones filogenéticas entre individuos de las tierras bajas del Caribe de Costa Rica con individuos de todo el rango de la especie utilizando secuencias mitocondriales del citocromo-b (*cytb*). Capturamos 116 individuos de las tierras bajas, secuenciamos su gen *cytb* e incorporamos 74 secuencias GenBank de todo el área de distribución de la especie para probar si los individuos de las tierras bajas del Caribe de Costa Rica constituyen potencialmente una especie no descrita. Nuestros resultados indican la presencia de un linaje distinto basado en el ADN mitocondrial, que sugiere que los individuos de las tierras bajas del Caribe de Costa Rica probablemente son una especie distinta. Las tierras bajas del Caribe de Costa Rica pueden tener una diversidad críptica significativa. Por ello sugerimos que estudios filogenéticos adicionales deberían incorporar muestras de esta área, ya que puede tener una historia evolutiva única.

Key words: Central America; cryptic species; cytochrome *b*; Heteromyidae; species boundaries.

Introduction

Understanding the relationships among evolutionary lineages is critical to estimating species diversity at varying spatial scales, reconstructing the evolutionary history of taxa, delineating ecological communities, and in making informed conservation decisions (Crozier 1992; Faith 1992; Crandall *et al.* 2000; Sinclair *et al.* 2005; Chave *et al.* 2007). Molecular data are increasingly used for evaluating relationships among species, identifying potential species-level clades, and identifying so-called cryptic species and thus can have significant impact on our understanding of evolutionary relationships (Sinclair *et al.* 2005; Beheregaray and Caccone 2007; Bickford *et al.* 2007; Mort *et al.* 2015).

With the continual improvement of molecular techniques and analyses, and broader sampling of natural populations, our understanding of phylogenetic relationships is often in flux. A group that has proven particularly difficult to delineate with traditional morphological characters are the species of spiny pocket mice of the genus *Heteromys* (Rodentia: Heteromyidae; see Anderson 2015 and references therein). Goldman (1911), in the first revision of the genus, recognized 13 species of *Heteromys* dividing them into two subgenera: *Heteromys* containing 12 species and *Xylomys* with a single species. This author further recognized the subgenus *Heteromys* as comprising two distinct species groups with the *H. desmarestianus* group containing eight species, including the first named *Heteromys* and most widely distributed species, *H. desmarestianus* (Gray, 1868). Recent research based on mitochondrial DNA indicates, however, that the lowland dry forest spiny pocket mice that were long recognized as a separate and sister genus, *Liomys*, are paraphyletic with respect to the species of *Heteromys*, thus should either be recognized as species of *Heteromys* or as another generic level clade (see Anderson *et al.* 2006; Hafner *et al.* 2007; Anderson and Gutiérrez 2009; and references therein). The current trend is to consider all species as belonging in the genus *Heteromys*.

Heteromys desmarestianus has remained a recognized taxon through several revisions (Hall 1981; Rogers and Schmidly 1982; Williams *et al.* 1993; Patton 2005; Rogers and González 2010), although new species have since been recognized (Anderson and Jarrín-V 2002; Anderson 2003; Anderson and Timm 2006; Anderson and Jansa 2007; Anderson and Gutiérrez 2009). Recently, Rogers and González (2010) suggested four additional clades within *H. desmarestianus* should be recognized. This research focuses on one of those four proposed clades that is located within the Caribbean lowlands of Costa Rica.

Heteromys desmarestianus, as currently defined, is common and widespread, ranging from southern Mexico to Colombia (Reid 2009). This species is found in evergreen and semideciduous forests, from sea level to high elevation cloud forests (Timm *et al.* 1989; Reid 2009). In Central America's Caribbean lowlands, the forest spiny pocket mouse is difficult to study because populations are often found at low densities (Fleming 1974; Timm *et al.* 1989), and anthropogenic disturbances often have negative impacts on density and species diversity (Romero, pers. obs.). Based on molecular evidence from mitochondrial and nuclear DNA of three individuals from Caribbean lowlands of Costa Rica, Rogers and González (2010) suggested that these individuals may actually represent a separate species from what is recognized as *H. desmarestianus*. Herein, we test across multiple sites in the lowlands, if individuals from the Caribbean lowlands of Costa Rica are genetically distinct from what is recognized as *H. desmarestianus* and how this population(s) and others of the *H. desmarestianus* species complex are related to each other. In order to build a better understanding of the species diversity in this lineage and to test the hypothesis that there is greater diversity than is currently recognized we, herein, evaluate the relationship within the lineage currently recognized as the species *H. desmarestianus*.

Materials and methods

We trapped mice in several locations throughout the Caribbean lowlands of Costa Rica from 2007–2010 (Figure 1, Table 1). The Caribbean lowlands have similar ambient temperature throughout, but annual precipitation can vary from 2,400 to 4,800 mm per year (McClearn *et al.* 2016). Our localities (Table 1) ranged in elevation and size of forested area; our individuals from the highest elevation were from the Berlin property (Destierro) ranging from 210 to 280 masl. Samples from Berlin also represented our southern-most sample. Our northern-most samples were from the Refugio Nacional de Vida Silvestre Mixto Maquenque, close to the Costa Rica–Nicaragua border on the Río San Juan (Figure 1).

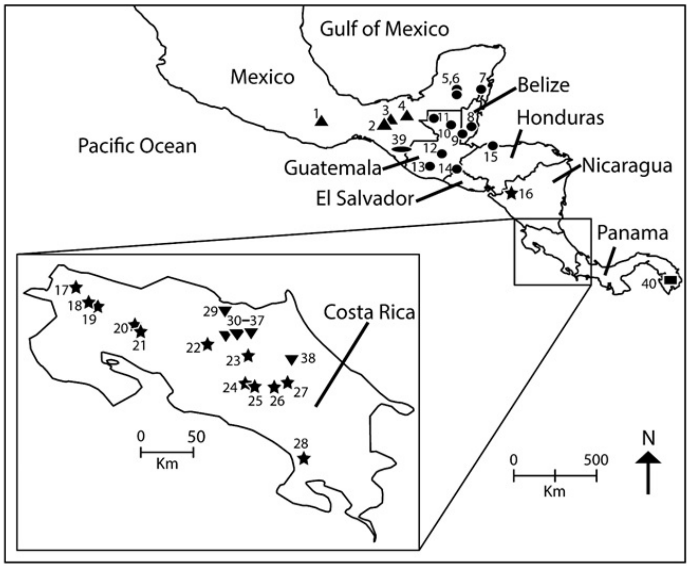

Figure 1. Map of localities for all specimens used in the study. Localities 29–38 represent specimens from Costa Rica's Caribbean lowlands. Symbols correspond to lineages depicted in the maximum likelihood tree (Figure 2). *H. anomalus* from Venezuela not depicted herein. Specific data regarding localities can be obtained from Appendix 1.

We used Sherman live traps (8 cm × 9 cm × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, FL) placed at ground level and baited with cracked corn, oats, and mixed bird seed. Traps were checked daily, and when an individual was caught, a toe was removed with surgical scissors and immediately placed in 95 % ethanol. All vials with tissue and ethanol were stored frozen within hours of collection. Voucher specimens of both complete specimens and toe samples are deposited at the University of Kansas Natural History Museum, Lawrence, Kansas. This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes *et al.* 2016).

Laboratory procedures—116 samples from 10 sites in the Caribbean lowlands were used (Table 1) for genetic comparisons. Tissues were soaked in deionized water for one hr prior to beginning the digestion process. Standard digestion and DNA extraction were conducted following the protocol for mouse tails in Sambrook *et al.* (1989). The mitochondrial

Table 1. Sampling areas in the Caribbean lowlands of Costa Rica. Locality numbers refer to numbers from Figure 1.

Site (locality)	Max elevation (m)	Min elevation (m)	Latitude	Longitude
Maquenque (29)	70.1	47	10° 40′ 48.96″ N	-84° 10′ 39.65″ W
Water Tower (34)	98	42	10° 27′ 52.90″ N	-84° 00′ 29.47″ W
Agrícola Sofía (35)	68.58	51.21	10° 27′ 32.01″ N	-83° 58′ 41.40″ W
Juan Enriques (31)	189.59	45.72	10° 27′ 20.46″ N	-84° 04′ 01.70″ W
Selva Verde (30)	164.59	84.43	10° 26′ 46.36″ N	-84° 04′ 00.62″ W
Starky (36)	69	43	10° 26′ 31.73″ N	-83° 59′ 09.16″ W
Fragment A (37)	162	131	10° 26′ 03.92″ N	-84° 07′ 42.76″ W
La Selva (32)	146	22	10° 25′ 47.90″ N	-84° 00′ 55.15″ W
Tirimbina (33)	224.03	149.35	10° 24′ 45.58″ N	-84° 07′ 02.55″ W
Berlin (38)	280	210	10° 07′ 59.73″ N	-83° 36′ 18.38″ W

cytochrome-*b* (*cytb*) gene was amplified in full using the primers 765 and 766 (Bickham *et al.* 2004). Polymerase chain reaction (PCR) was performed using 50 µl reactions of the following reagents: 5 µl of 10× buffer, 5 µl of 10× $MgCl_2$, 5 µl of 10× solution of dNTP, 0.5 µl of Taq DNA polymerase, 5 µl of a 10× solution of each primer, 25 µl of deionized water, and 1–2 µl of extracted DNA. Thermal cycle conditions consisted of initial heating at 94°C for 3 min, then 36 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 30 s, and extension at 70°C for 2.5 min. PCR products were purified using the QiAquick PCR purification kit (Qiagen, Valencia, CA) and were subsequently used in standard sequencing reactions using Big Dye version 3.0 (Applied Biosystems, Foster City, CA). Sequencing reactions were cleaned using Sephadex spin columns and analyzed with an ABI 3100 automated genetic analyzer (Applied Biosystems, Forster City, CA). Sequence data were manually aligned using Sequencher v. 4.9 (Gene Codes Corporation, Ann Arbor, MI). We used the complete *cytb* gene, and all flanking regions were discarded prior to phylogenetic analysis.

To expand our dataset, we used *cytb* sequences of *H. desmarestianus* available from GenBank (Benson *et al.* 2013). We incorporated 74 individuals representing samples from throughout the range of the species, including specimens from near the type locality of *H. desmarestianus*, Cobán, Guatemala. *Heteromys anomalus*, *H. australis*, and *H. nelsoni* were used as outgroups (Appendix 1). We aligned all sequences with Muscle v.3.8.31 (Edgar 2004) implemented in Jalview 2.8 (Waterhouse *et al.* 2009).

Phylogenetic analysis—Phylogenetic relationships were obtained by performing a maximum likelihood (ML) analysis. We estimated models of molecular evolution using jModelTest v.2.1.1 with the corrected Akaike information criterion test (Guindon and Gascuel 2003; Darriba *et al.* 2012). We used GARLI v. 2.0 (Zwickl 2006) for ML analyses, using two independent search runs, with a maximum of five million generations each. Support values were calculated using bootstrap with 500 replications in GARLI, and results visualized and edited in FigTree v.1.4 (Rambaut 2007).

Results

The aligned data set comprises 1,142 characters of which 738 were constant, 335 characters were parsimony-informative, and 69 variable characters were parsimony-uninformative. The model of DNA substitution inferred from jModeltest 2.1.1 is TIM2+I+G.

The ML tree topology (Figure 2) shows two highly supported lineages for all individuals currently considered *H. desmarestianus*. One clade comprises all samples from the Caribbean lowlands of Costa Rica and had very strong (99 %) bootstrap support. The other lineage comprises all of the *H. desmarestianus* sequences obtained from Belize, Costa Rica (in part), El Salvador, Guatemala, Honduras, México, and Nicaragua and also have strong bootstrap support (83%). Within the clade containing samples from the Caribbean lowlands of Costa Rica (not shown in Figure 2), the individuals from two sites, Berlin and Maquenque, formed clades supported by strong bootstrap support (90 % and 86 %, respectively). Two individuals from the eight sampled at Maquenque were placed elsewhere within the tree, and thus the nonexclusive nature of the branching pattern complicates lower level population patterns from these data. Maquenque is biologically quite interesting being in the floodplain of the Río San Juan and our continued studies there are elucidating other unexpected patterns with other rodent species.

Specimens collected near Baja Verapas, Guatemala (GU646966, GU646967, GU646968; Appendix) ~30 km from the type locality, Cobán, cluster with specimens from Belize, El Salvador, Honduras, and parts of México, but not with specimens from the Caribbean lowlands of Costa Rica (Figure 2). The specimen that clustered closest to Cobán from our Costa Rican lowland dataset was from the Costa Rica–Nicaragua border region ~ 850 km away. Genbank accession numbers of new sequences are reported in the Appendix.

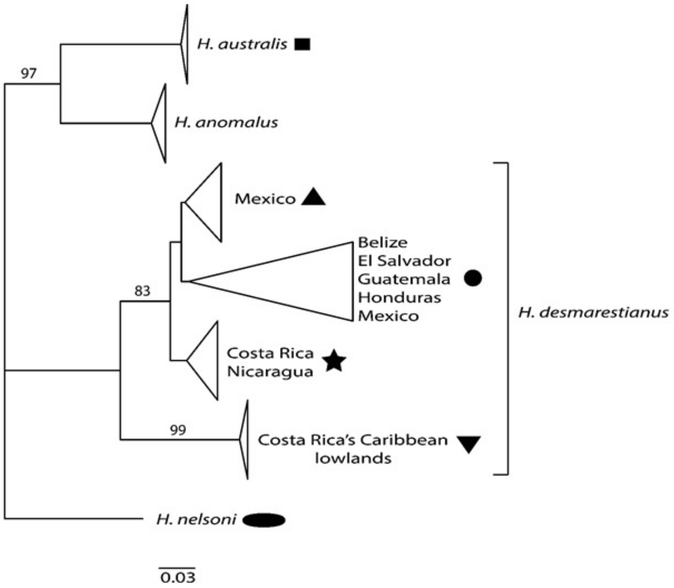

Figure 2. Maximum likelihood tree of our *Heteromys* dataset, based on *cytb* sequences. The maximum likelihood tree is collapsed for visual clarity, and shows the results with bootstrap values. These results indicate that individuals from Costa Rica's Caribbean lowlands harbor unique mitochondrial lineages that could reflect reproductive isolation. Symbols in tree are used in Figure 1 to show the geographic range of lineages. Tree is rooted with *H. golmani*.

Discussion

The results of this study strongly support the hypothesis that what is currently called *Heteromys desmarestianus* in Central America and northern-most South America comprises two very distinct clades, one being found in the Caribbean lowlands of Costa Rica and the other comprising all other populations. Our results show a clear geographic pattern; individuals currently considered *H. desmarestianus* in the Caribbean lowlands of Costa Rica harbor distinct mtDNA haplotypes from individuals considered *H. desmarestianus* found elsewhere in the Neotropics, including other areas in Costa Rica (Figure 2). The specimens from near the type locality of *H. desmarestianus*, Cobán, Guatemala form a well-supported clade with specimens from southern México, Belize, El Salvador, and Honduras. Specimens from western Costa Rica and one specimen from western Nicaragua all form another distinct clade.

Costa Rica is only ~51,000 km^2, yet its variable topography and climate result in diverse habitats with unique flora and fauna (Janzen 1983). Currently, four main mountain ranges divide the country into the Pacific and Caribbean sides. These mountain ranges span southeast to northwest, and are of diverse ages and origins (Anderson and Timm 2006). Extending from western Panama to northern Costa Rica, the Cordillera de Talamanca, Cordillera Central, and Cordillera de Tilarán form an expansive mountain range with peak elevations of over 3,000, 2,500, and 2,000 masl, respectively. The Cordillera de Guanacaste is the northern-most range in Costa Rica, and is comprised of several isolated volcanoes, with passes of ~500 to 700 masl in elevation that connect the Pacific and Caribbean sides (Anderson and Timm 2006). The historical and current topography of these mountain ranges probably shaped the diversification and speciation patterns in the flora and fauna observable today.

The family Heteromyidae originated on the North America continent (Wood 1935; Schmidly *et al.* 1993), and fossil remains for the subfamily Heteromyinae are known from the Pliocene, Pleistocene, and Holocene (Rogers 1990). Rogers (1990) estimated that the major groups within this subfamily diverged ~12 to 13 mya, yet the historical events that produced the *H. desmarestianus* group are largely unknown. The geologic history of the Caribbean, and Central and South America has been a debated topic (Bartoli *et al.* 2005; Montes *et al.* 2012a, 2012b, 2015; Bacon *et al.* 2015; O'Dea *et al.* 2016), but it is thought that islands of volcanic origin between Central and South America may have allowed faunal exchanges prior to the formation of a permanent land bridge (Bartoli *et al.* 2005; Woodburne 2010; O'Dea *et al.* 2016). The time of the emergence of a permanent Panamanian land bridge is disputed, and estimates range from 2 to 7 mya (Montes *et al.* 2012b; but see Bacon *et al.* 2015). Because of the widespread distribution pattern of the *H. desmarestianus* group, a hypothesis similar to the one suggested for other rodent groups has been proposed for this clade (Patterson and Pasqual 1972; Baskin 1978; Simpson 1980; Rogers 1990; Almendra and Rogers 2012; Pine *et al.* 2012); It is thought that considerable radiation occurred in the Miocene and Pliocene throughout Central America, with a subsequent entry to South America via the Panamanian land bridge (Rogers 1990; Schmidly *et al.* 1993).

Our results herein document a broad distribution of this distinct and unrecognized Costa Rican lowland lineage. The northern-most samples within this clade are from the Costa Rica–Nicaraguan border, while the southern-most are ~86 km southeast of there. Unfortunately, little is known about spiny pocket mice in the lowlands of Nicaragua and southern Costa Rica, and we are unable to demarcate northern and southern boundaries of this mtDNA lineage. In terms of elevation, the lowland specimens came from forests that ranged in elevation from ~22 to 280 masl. In our analysis, we included a single GenBank sequence from Cerro Honduras in Parque Nacional Braulio Carrillo. The park, along with privately owned reserves and biological stations, is part of a continuously forested transect that expands from the lowlands at La Selva Biological Station and reaches elevations > 2,700 masl. Although we do not have specific data on the elevation from which this particular specimen came, our results do show that this higher elevation specimen is a member of the clade with *H. desmarestianus* proper from throughout Central America and does not group with our samples from the lowlands, including specimens from the nearby La Selva Biological Station. While our results suggest two distinct clades, we are unable to delineate at this time limits of their specific elevational range, or if there are areas of overlap or hybridization that await discovery.

Our results expand upon, compliment, and confirm Rogers and González (2010), who used both *cytb* and nuclear data, and identified three individuals from the Caribbean lowlands of Costa Rica as a potential candidate species. Although useful to characterize species that are difficult to establish based on morphological data, DNA sequence data do have limitations, particularly when a single marker is used (Farias *et al.* 2001; Rogers and González 2010). Now that we provide more extensive sampling of individuals from the Caribbean lowlands of Costa Rica, we recommend that future studies determine if population structure based on nuclear markers correlates with the distinctive mtDNA lineage of the Costa Rican lowland. Further investigation focused on nuclear DNA is also important because mitochondrial DNA and nuclear DNA can be discordant (Lack *et al.* 2010, Bernardo *et al.* 2019). This can result in distinct mitochondrial DNA lineages within a population or species that are not supported by nuclear DNA.

The diversity of rodent communities in the Caribbean lowlands of Costa Rica have been vastly understudied and we believe underestimated, in part, because of low densities resulting in low trap success (Romero, pers. obs.). Consequently, the lack of data and specimens has hindered our understanding of the basic phylogenetic relationships and biogeographic patterns of species in the area. Other widespread rodent species have been found to hold similar patterns reported herein, where individuals from the Caribbean lowlands of Costa Rica are genetically distinct and potentially new species (Timm, unpublished data). These data suggest that there may be significant cryptic diversity in the lowlands, and that more phylogenetic studies should include samples from this region to identify potential biogeographic patterns for rodents in the Neotropics. This information is necessary not only to understand phylogenetic relationships, but also to have a grasp on the patterns and levels of diversity for the area, and make large-scale conservation decisions based on this information. We believe that our results, in conjunction with future studies that aim to identify and delineate diversity in the *H. desmarestianus* species complex, and the relationships between these species, will allow for a greater understanding of the historical events leading to speciation in this group.

Clearly much remains to be learned about the diversity of these widespread and common rodents that are considered keystone species in the Neotropics.

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Literature Cited

Almendra, A. L., and D. S. Rogers. 2012. Biogeography of Central American mammal: patterns and processes. Pp. 203–229 *in* Bones, clones, and biomes: the history and geography of Recent Neotropical mammals (Patterson, B. D., and L. P. Costa, eds.). University of Chicago Press. Chicago, U.S.A.

Anderson, R. P. 2003. Taxonomy, distribution, and natural history of the genus *Heteromys* (Rodentia: Heteromyidae) in western Venezuela, with the description of a dwarf species from the Península de Paraguaná. American Museum Novitates 3396:1–43.

Anderson, R. P. 2015. Family Heteromyidae. Pp. 51–58 *in* Mammals of South America, Volume 2: Rodents (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). University of Chicago Press. Chicago, U.S.A.

Anderson, R. P., and E. E. Gutiérrez. 2009. Taxonomy, distribution, and natural history of the genus *Heteromys* (Rodentia: Heteromyidae) in central and eastern Venezuela, with the description of a new species from the Cordillera de la Costa. Pp. 33–93 *in* Systematic mammalogy: contributions in honor of Guy G. Musser. (Voss, R. S., and M. D. Carleton, eds.). Bulletin of the American Museum of Natural History 331.

Anderson, R. P., and S. A. Jansa. 2007. Genetic comparisons between *Heteromys desmarestianus* and the recently described *H. nubicolens* (Rodentia: Heteromyidae) in northwestern Costa Rica. Mammalian Biology 72:54–61.

Anderson, R. P., and P. Jarrín-V. 2002. A new species of spiny pocket mouse (Heteromyidae: *Heteromys*) endemic to western Ecuador. American Museum Novitates 3382:1–26.

Anderson, R. P., and R. M. Timm. 2006. A new montane species of spiny pocket mouse (Heteromyidae: *Heteromys*) from northwestern Costa Rica. American Museum Novitates 3509:1–38.

Anderson, R. P., M. Weksler, and D. S. Rogers. 2006. Phylogenetic analyses of spiny pocket mice (Heteromyidae: Heteromyinae) based on allozymic and morphological data. Journal of Mammalogy 87:1218–1233.

Bacon, C. D., D. Silvestro, C. Jaramillo, B. T. Smith, P. Chakrabarty, and A. Antonelli. 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. Proceedings of the National Academy of Sciences 112:6110–6115.

Bartoli, G., M. Sarthein, M. Weinelt, H. Erlenkeuser, D. Garbe-Schönberg, and D. W. Lea. 2005. Final closure of Panama and the onset of northern hemisphere glaciation. Earth and Planetary Science Letters 237:33–44.

Baskin, J. A. 1978. *Bensonomys*, *Calomys*, and the origin of the phyllotine group of Neotropical cricetines (Rodentia: Cricetidae). Journal of Mammalogy 59:125–135.

Beheregaray, L. B., and A. Caccone. 2007. Cryptic biodiversity in a changing world. Journal of Biology 6:9.1–9.5.

Benson, D. A., M. Cavanaugh, K. Clark, I. Karsch-Mizrachi, D. J. Lipman, J. Ostell, and E. W. Sayers. 2013. GenBank. Nucleic Acids Research 41:36–42.

Bernardo, P. H., et al. 2019. Extreme mito-nuclear discordance in a peninsular lizard: the role of drift, selection, and climate. Heredity: 1.

Bickford, D., D. J. Lohman, N. S. Sodhi, P. K. Ng, R. Meier, K. Winker, K. K. Ingram, and I. Das. 2007. Cryptic species as a window on diversity and conservation. Trends in Ecology and Evolution 22:148–155.

Bickham, J. W., J. C. Patton, D. A. Schlitter, I. L. Rautenbach, and R. L. Honeycutt. 2004. Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae). Molecular Phylogenetics and Evolution 33:333–338.

Chave, J., G. Chust, and C. Thébaud. 2007. The importance of phylogenetic structure in biodiversity studies. Pp. 150–167 *in* Scaling biodiversity (Storch, D., P. L. Marquet, and J. H. Brown, eds.). Cambridge University Press. Cambridge, U.K.

Crandall, K. A., O. R. P. Bininda-Emonds, G. M. Mace, and R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. TREE 15:290–295.

Crozier, R. H. 1992. Genetic diversity and the agony of choice. Biological Conservation 61:11–15.

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9:772.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32:1792–1797.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation 61:1–10.

Farias, I. P., G. Ortí, I. Sampaio, H. Schneider, and A. Meyer. 2001. The cytochrome *b* gene as a phylogenetic marker: the limits of resolution for analyzing relationships among cichlid fishes. Journal of Molecular Evolution 53:89–103.

Fleming, T. H. 1974. The population ecology of two species of Costa Rican heteromyid rodents. Ecology 55:493–510.

Goldman, E. A. 1911. Revision of the spiny pocket mice (genera *Heteromys* and *Liomys*). North American Fauna 34:1–70.

Gray, J. E. 1868. Synopsis of the species of Saccomyinae, or pouched mice in the collection of the British Museum. Proceedings of the Zoological Society of London 1868:199–206.

Guindon, S., and O. Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52:696–704.

Hafner, J. C., J. E. Light, D. J. Hafner, M. S. Hafner, E. Reddington, D. S. Rogers, and B. R. Riddle. 2007. Basal clades and molecular systematics of heteromyid rodents. Journal of Mammalogy 88:1129–1145.

Hall, E. R. 1981. The mammals of North America. John Wiley & Sons, Inc. New York, U.S.A.

Janzen, D. H. 1983. Costa Rican natural history. University of Chicago Press. Chicago, U.S.A.

Lack, J. B., J. E. Wilkinson, and R. A. Van Den Bussche. 2010. Range-wide population genetic structure of the pallid bat (*Antrozous pallidus*)—incongruent results from nuclear and mitochondrial DNA. Acta Chiropterologica 12:401–413.

McClearn, D., et al. 2016. The Caribbean lowland evergreen moist and wet forests. Pp. 527–587 *in* Costa Rican ecosystems (M. Kappelle, ed.). University of Chicago Press. Chicago, U.S.A.

Montes, C., et al. 2012a. Arc-continent collision and orocline formation: closing of the Central American seaway. Journal of Geophysical Research: Solid Earth 117(B4):1–25.

Montes, C., et al. 2012b. Evidence for middle Eocene and younger land emergence in central Panama: implications for isthmus closure. Bulletin of the Geological Society of America 124:780–799.

Montes, C., et al. 2015. Middle Miocene closure of the Central American Seaway. Science 348(6231):226–229.

Mort, M. E., et al. 2015. Multiplexed-shotgun-genotyping data resolve phylogeny within a very recently derived insular lineage. American Journal of Botany 102:634–641.

O'Dea, A., et al. 2016. Formation of the Isthmus of Panama. Science Advances 2(e1600883):1–11.

Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. Pp. 247–309 *in* Evolution, mammals, and southern continents (Keast, A., F. C. Erk, and B. Blass, eds.). State University of New York Press. Albany, U.S.A.

Patton, J. L. 2005. Family Heteromyidae. Pp. 844–858 *in* Mammal species of the world: a taxonomic and geographic reference (Wilson, D. E., and D. M. Reeder, eds.). 3rd edition. Johns Hopkins University Press. Baltimore, U.S.A.

Pine, R. H., R. M. Timm, and M. Weksler. 2012. A newly recognized clade of trans-Andean Oryzomyini (Rodentia: Cricetidae), with description of a new genus. Journal of Mammalogy 93:851–870.

Rambaut, A. 2007. FigTree. http://tree.bio.ed.ac.uk/software/figtree. Accessed 13 February 2013.

Reid, F. A. 2009. A field guide to the mammals of Central America & Southeast Mexico. 2nd edition. Oxford University Press. New York, U.S.A.

Rogers, D. S. 1990. Genic evolution, historical biogeography, and systematic relationships among spiny pocket mice (subfamily Heteromyinae). Journal of Mammalogy 71:668–685.

Rogers, D. S., and M. W. González. 2010. Phylogenetic relationships among spiny pocket mice (*Heteromys*) inferred from mitochondrial and nuclear sequence data. Journal of Mammalogy 91:914–930.

Rogers, D. S., and D. J. Schmidly. 1982. Systematics of spiny pocket mice (genus *Heteromys*) of the *desmarestianus* species group from México and northern Central America. Journal of Mammalogy 63:375–386.

Sambrook, J., E. Fritsch, and T. Maniatis. 1989. Molecular cloning: a laboratory manual, 2nd edition. Cold Spring Harbor Laboratory Press. New York, U.S.A.

Schmidly, D. J., K. T. Wilkins, and J. N. Derr. 1993. Biogeography. Pp 319–356 *in* Biology of the Heteromyidae (Genoways, H. H., and J. H. Brown, eds.). Special Publications 10, American Society of Mammalogists. Lawrence, U.S.A.

Sikes, R.S., et al. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Simpson, G. G. 1980. Splendid isolation: the curious history of South American mammals. Yale University Press. New Haven, U.S.A.

Sinclair, E. A., M. Pérez-Losada, and K. A. Crandall. 2005. Molecular phylogenetics for conservation biology. Pp. 19–56 *in* Phylogeny and conservation (Purvis, A., J. L. Glittleman, and T. Brooks, eds.). Cambridge University Press. Cambridge, U.K.

Timm, R. M., D. E. Wilson, B. L. Clauson, R. K. LaVal, and C. S. Vaughan. 1989. Mammals of the La Selva–Braulio Carrillo complex, Costa Rica. North American Fauna 75:1–162.

Waterhouse, A. M., J. B. Procter, D. M. A. Martin, M. Clamp, and G. J. Barton. 2009. Jalview version 2–a multiple sequence alignments editor and analysis workbench. Bioinformatics 25:1189–1191.

Williams, D. F., H. H. Genoways, and J. K. Braun. 1993. Taxonomy. Pp. 38–196 *in* Biology of the Heteromyidae (Genoways, H. H., and J. H. Brown, eds.). Special Publication 10, American Society of Mammalogists. Lawrence, U.S.A.

Wood, A. E. 1935. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. Annals of Carnegie Museum 24:73–262.

Woodburne, M. O. 2010. The great American biotic interchange: dispersals, tectonics, climate, sea level and holding pens. Journal of Mammalian Evolution 17:245–264.

Zwickl, D. J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Dissertation, University of Texas. Austin, U.S.A.

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Appendix 1.

Localities and specimen information for samples utilized in the study. Map numbers correspond to numbers on Figure 1. Data for specimens not from the Caribbean lowlands of Costa Rica were obtained from GenBank and the published papers associated with the GenBank accession numbers.

Map	Species	Specimen information	GenBank	Locality	Country
N/A	*H. anomalus*	CM 78170 = MDE 2087 = AK 3468	GU646919	Miranda, 25 km N Altagracia de Orituco, 500 m	Venezuela
N/A	*H. anomalus*	CM 78168 = MDE 2034 = AK3437	GU646924	Sucre, 40 km NW Caripito, 250 m	Venezuela
40a	*H. australis*	LSUMZ 35452 = MSH 1187 = TK 22565	GU646926	Darién, approximately 6 km NW Cana, E. slope Cerro Pirre, 1,200 m	Panama
40b	*H. australis*	ROM 104356 = F38215	GU646927	Darién, Cerro Pirre, Parque Nacional Darién	Panama
8a	*H. desmarestianus*	CM 91988 = AK7663	GU646929	Stann Creek District, 3.4 km WNW Quam Bank, Cockscomb Basin	Belize
8b	*H. desmarestianus*	CM91980 = AK7688	GU646930	Stann Creek District, 6.8 km WNW Quam Bank, Cockscomb Basin	Belize
8c	*H. desmarestianus*	CM 91951 = AK 7665	GU646932	Stann Creek District, 7.7 km WNW Quam Bank, Cockscomb Basin	Belize
9a	*H. desmarestianus*	CM 91991 = AK 7540	GU646933	Toledo District, 1.0 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9b	*H. desmarestianus*	CM 91989 = AK 7555	GU646934	Toledo District, 2.4 km NNW Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91993 = AK 7588	GU646935	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91994 = AK 7586	GU646936	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91995 = AK 7589	GU646937	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
18	*H. desmarestianus*	KU 158615 = MK 00-112	DQ450094	Guanacaste, Area de Conservación Guanacaste, approximately 20 km NNE Liberia, Pailas, Sendero Pailas, near Rio Colorado, 800 m	Costa Rica
17	*H. desmarestianus*	KU 158508 = MK 99-088	DQ450095	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Orosilito	Costa Rica
17	*H. desmarestianus*	KU 158509 = MK 99-090	DQ450096	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Orosilito	Costa Rica
17	*H. desmarestianus*	KU 158512 = MK 99-093	DQ450097	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla	Costa Rica
17	*H. desmarestianus*	KU 158513 = MK 99-094	DQ450098	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla	Costa Rica
17	*H. desmarestianus*	KU 158514 = MK 99-102	DQ450099	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Carica	Costa Rica
22	*H. desmarestianus*	ROM 113310 = F 48617	GU646938	Alajuela; 10 km E of Sucre, Parque Nacional, Juan Costro Blanco	Costa Rica
22	*H. desmarestianus*	ROM 113311 = F 48618	GU646939	Alajuela; 10 km E of Sucre, Parque Nacional, Juan Costro Blanco	Costa Rica
24	*H. desmarestianus*	ROM 113130 = F 48436	GU646940	Cartago, Iztaru, Cerros de la Carpintera	Costa Rica
24	*H. desmarestianus*	ROM 113131 = F 48437	GU646941	Cartago, Iztaru, Cerros de la Carpintera	Costa Rica
27	*H. desmarestianus*	MVZ 164823 = DSR 2153	GU646942	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164823 = DSR 2154	GU646943	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164825 = DSR 2166	GU646944	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164826 = DSR 2167	GU646945	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164827 = DSR 2246	GU646946	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
26	*H. desmarestianus*	ROM 97324 = FAR 111	GU646947	Cartago, 4 km SE of Turrialba by road, Catie, 600 m	Costa Rica
26	*H. desmarestianus*	ROM 97325 = FAR 112	GU646948	Cartago, 4 km SE of Turrialba by road, Catie, 600 m	Costa Rica
20	*H. desmarestianus*	MVZ 164828 = DSR 2123	GU646949	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164829 = DSR 2124	GU646950	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164831 = DSR 2134	GU646952	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164833 = DSR 2124	GU646953	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164835 = DSR 2143	GU646954	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
21	*H. desmarestianus*	MVZ 164839 = DSR 2121	GU646955	Guanacaste: 5.0 km NE (by road) Tilarán, 675 m	Costa Rica
21	*H. desmarestianus*	MVZ 164840 = DSR 2122	GU646956	Guanacaste: 5.0 km NE (by road) Tilarán, 675 m	Costa Rica
19	*H. desmarestianus*	ROM 113244 = F 48551	GU646957	Guanacaste: Volcán Santa Maria	Costa Rica
19	*H. desmarestianus*	ROM 113245 = F 48552	GU646958	Guanacaste: Volcán Santa Maria	Costa Rica
28	*H. desmarestianus*	LSUMZ 28354 = MSH 1260	GU646959	Puntarenas, 1 km N, 5 km W Palmar Norte, 33 m	Costa Rica
25	*H. desmarestianus*	BYU 15197 = EA 21	GU646960	San José, Bajo de Iglesia, SW Volcán Irazu, Cascajal de Coronado	Costa Rica
25	*H. desmarestianus*	BYU 15198 = EA 22	GU646961	San José, Bajo de Iglesia, SW Volcán Irazu, Cascajal de Coronado	Costa Rica
23	*H. desmarestianus*	BYU 15195 = EA 78	GU646962	San José, Parque Nacional Braulio Carillo, Moravia, Cerro Honduras	Costa Rica
23	*H. desmarestianus*	BYU 15196 = EA 79	GU646963	San José, Parque Nacional Braulio Carillo, Moravia, Cerro Honduras	Costa Rica

29	*H. desmarestianus*	No specimen available	MN335341	Alajuela: Maquenque, 10°40’48.96”N, 84°10’39.65”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335416	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335415	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335420	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335369	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335417	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335429	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335422	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335368	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335428	Heredia: Selva Verde, 10°26’46.36”N, 84°04’00.62”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335344	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335353	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335356	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335351	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335379	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335345	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335412	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335382	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335405	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335363	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335404	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335411	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335403	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335350	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335389	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335362	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335383	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335336	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335381	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335343	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335387	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335354	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335386	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335407	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335359	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335376	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335391	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335357	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335361	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335349	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335399	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335350	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335355	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335390	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335380	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335358	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335384	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335352	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335342	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335347	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335340	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335346	Heredia: La Selva Biological Station, 10°25’47.90”N, 84°00’55.15”W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335392	Heredia: Tirimbina, 10°24’45.58”N, 84°07’02.55”W	Costa Rica

33	*H. desmarestianus*	No specimen available	MN335378	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335395	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335364	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335371	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335365	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335367	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335338	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335337	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335394	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335372	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335385	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
38	*H. desmarestianus*	No specimen available	MN335406	Limon Province: Berlin, 10°07'59.73"N, 83°36'18.38"W	Costa Rica
38	*H. desmarestianus*	No specimen available	MN335397	Limon Province: Berlin, 10°07'59.73"N, 83°36'18.38"W	Costa Rica
38	*H. desmarestianus*	No specimen available	MN335398	Limon Province: Berlin, 10°07'59.73"N, 83°36'18.38"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335409	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335348	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335334	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335410	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335402	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335401	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335333	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335370	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335414	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335332	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335413	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335385	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335393	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335335	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335375	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335332	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335419	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335388	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335360	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335373	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335374	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
37	*H. desmarestianus*	No specimen available	MN335424	Heredia: 10°26'03.92"N, 84°07'42.76"W	Costa Rica
37	*H. desmarestianus*	No specimen available	MN335418	Heredia: 10°26'03.92"N, 84°07'42.76"W	Costa Rica
14	*H. desmarestianus*	ROM 101369 = F 35547	GU646964	Santa Ana, Parque Nacional Montecristi, Bosque Nebuloso, 2,200 m	El Salvador
14	*H. desmarestianus*	ROM 101389 = F 35567	GU646965	Santa Ana, Parque Nacional Montecristi, Bosque Nebuloso, 2,200 m	El Salvador
11	*H. desmarestianus*	LVT 5499	AY926358	Tikal, El Peten	Guatemala
12	*H. desmarestianus*	ROM 98405 = FN 31394	GU646966	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
12	*H. desmarestianus*	ROM 98406 = FN 31395	GU646967	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
12	*H. desmarestianus*	FN 31402	GU646968	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
10a	*H. desmarestianus*	ROM 99603 = FN 32272	GU646969	El Peten: Biotope, Cerro Cahui, El Remate	Guatemala
10a	*H. desmarestianus*	ROM 99604 = FN 32273	GU646970	El Peten: Biotope, Cerro Cahui, El Remate	Guatemala
10b	*H. desmarestianus*	ROM 99469 = FN 32318	GU646971	El Peten: Campo los Guacamayos, Biotopo Laguna del Tigre, 40 km N El Naranjo	Guatemala
11	*H. desmarestianus*	ROM 99292 = FN 31842	GU646973	El Peten, Tikal	Guatemala
11	*H. desmarestianus*	ROM 99293 = FN 31843	GU646974	El Peten, Tikal	Guatemala
13	*H. desmarestianus*	ROM 98266 = FN 31252	GU646975	Sacatepequez, 5 km W San Miguel Duanas, 1,765 m	Guatemala
13	*H. desmarestianus*	ROM 98265 = FN 31254	GU646976	Sacatepequez, 5 km W San Miguel Duanas, 1,765 m	Guatemala
15	*H. desmarestianus*	TCWC 52259 = BEL 865 = AK 9696	DQ168466	Atlántida, Lancetilla	Honduras
1a	*H. desmarestianus*	MVZ 161229 = DSR 1685	DQ168467	Oaxaca; Distrito Ixtlán, Vista Hermosa, 1,000 m	Mexico
5	*H. desmarestianus*	ROM 97050 = FN 30853	GU646977	Campeche, 10 km N El Refugio	Mexico

5	*H. desmarestianus*	ROM 97051 = FN 30854	GU646978	Campeche, 10 km N El Refugio	Mexico
6	*H. desmarestianus*	ROM 96089 = FN 29880	GU646979	Campeche: 25 km N Xpujil	Mexico
2	*H. desmarestianus*	ASNHC 3515 = LAF 1689	GU646980	Chiapas, 12 km N (by road) Berriozábal	Mexico
2	*H. desmarestianus*	ASNHC 1424 = ASK 660	GU646981	Chiapas, 12 km N (by road) Berriozábal	Mexico
2	*H. desmarestianus*	ASNHC 1425 = ASK 689	GU646982	Chiapas, 12 km N (by road) Berriozábal	Mexico
4a	*H. desmarestianus*	ASNHC 1426 = ASK 51	GU646983	Chiapas, 6.6 km S Palenque	Mexico
4b	*H. desmarestianus*	ASNHC 5826 = ASK 49	GU646984	Chiapas, 9.0 km S Palenque	Mexico
4c	*H. desmarestianus*	ROM 96096 = FN 29887	GU646985	Chiapas, 12.5 km S Palenque	Mexico
4c	*H. desmarestianus*	ROM 96105 = FN 29896	GU646986	Chiapas, 12.5 km S Palenque	Mexico
4d	*H. desmarestianus*	ASNHC 1440 = ASK 29	GU646987	Chiapas, 1.2 km E Ruinas de Palenque	Mexico
4d	*H. desmarestianus*	ASNHC 1441 = ASK 31	GU646988	Chiapas, 1.2 km E Ruinas de Palenque	Mexico
3a	*H. desmarestianus*	ROM 97542 = FN 33018	GU646989	Chiapas, 6 km E of Rayon, 1,560 m	Mexico
3b	*H. desmarestianus*	ASNHC 1431 = ASK 589	GU646990	Chiapas, 9 km SE Rayon	Mexico
3b	*H. desmarestianus*	ASNHC 1432 = ASK 591	GU646991	Chiapas, 9 km SE Rayon	Mexico
7	*H. desmarestianus*	ROM 97520 = FN 30995	GU646992	Quintana Roo, 1 km N Noh-Bec	Mexico
7	*H. desmarestianus*	ROM 97521 = FN 30996	GU646993	Quintana Roo, 1 km N Noh-Bec	Mexico
1b	*H. desmarestianus*	CM 79530 = DSR 934 = AK 3108	GU646994	Oaxaca, Vista Hermosa, 1,000 m	Mexico
1b	*H. desmarestianus*	MVZ 161230 = DSR 1686	GU646995	Oaxaca; Distrito Ixtlán, Vista Hermosa, 1,000 m	Mexico
16	*H. desmarestianus*	ROM 112284 = F 48170	GU646996	Esteli, Esteli	Nicaragua
39	*H. nelsoni*	BYU 20644 = DSR 7189	GU647014	Chiapas, Cerro Mozotal, 15º25.866'N, 92º20.274'W, 2,930 m	Panama

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Music and dance in mammals

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A long-standing belief among humans is that the behaviors we call making music and dancing are thought to be strictly human activities. Rapidly accumulating evidence, however, tells a different story. Both music and dance are characterized by sensitivity to and moving in response to rhythms. Among humans, these two behaviors are ubiquitous in all living cultures and can be traced back in our Neanderthal ancestors at least 50,000 years, and probably much longer. It is well established that in humans these two rhythmic behaviors play important social functions, and in recent years have been increasingly noted as well for their health benefits. All of this has called attention to similar behaviors in non-humans. Many examples have been noted among mammals, birds, reptiles, amphibians and even bony fish. Neurologists became interested in understanding the neural mechanisms for these rhythmic behaviors and found that rhythmic behaviors are organized in one of the most ancient parts of the vertebrate brain, namely the subcortical posterior parietal cortex which is located just on top of the uppermost ending of the spinal cord. This anatomy was then found to be the same in almost all vertebrates going back in history for many millions of years to the bony fish. So, now it is understandable why music and dance are so widespread among the vertebrates and why there seems to be the potential for these rhythmic behaviors to appear in most of the vertebrates. This discovery also emphasizes the potential availability of the beneficial effects of these behaviors. Needless to say, there is also the prospect of an emerging opportunity for much exciting and important research on mammals.

Una creencia antigua entre los humanos es que los comportamientos que llamamos hacer música y bailar se consideran actividades estrictamente humanas. Sin embargo, la evidencia que se acumula rápidamente cuenta una historia diferente. La música como la danza se caracterizan por la sensibilidad y el movimiento en respuesta a los ritmos. Entre los humanos, estos dos comportamientos son ubicuos en todas las culturas vivas y se remontan a nuestros antepasados neandertales, al menos 50,000 años, y probablemente mucho más. Está bien establecido que en los humanos estos dos comportamientos rítmicos desempeñan funciones sociales importantes y en los últimos años también se han observado cada vez más por sus beneficios para la salud. Todo esto ha llamado la atención sobre comportamientos similares en los no humanos. Se han observado muchos ejemplos entre mamíferos, aves, reptiles, anfibios e incluso peces óseos. Los neurólogos se interesaron en comprender los mecanismos neurales para estos comportamientos rítmicos y descubrieron que los comportamientos rítmicos están organizados en una de las partes más antiguas del cerebro de los vertebrados, a saber, la corteza parietal posterior subcortical que se encuentra justo en la parte superior del extremo superior de la medulla espinal. Se descubrió que esta anatomía es la misma en casi todos los vertebrados que se remontan a la historia durante millones de años hasta los peces óseos. Por lo tanto, ahora es comprensible por qué la música y la danza están tan extendidas entre los vertebrados y por qué parece existir la posibilidad de que estos comportamientos rítmicos aparezcan en la mayoría de los vertebrados. Este descubrimiento también enfatiza la disponibilidad potencial de los efectos beneficiosos de estos comportamientos. No es necesario decir que también existe la posibilidad de una oportunidad emergente para realizar investigaciones muy interesantes e importantes sobre mamíferos.

Key Words: health benefits; Neanderthals; neural integration; posterior parietal cortex; rhythms; social behavior; vertebrates.

Introduction

Music and dance are still widely considered to be exclusive behaviors of humans (Hanna1983). In this essay I will argue that this is not a realistic conclusion, and in fact these two behaviors greatly pre-date the origins of *Homo sapiens*. Of course there is no argument that humans have developed music and dance to amazing levels of complexity unmatched by any other species on this planet. It is appropriate to begin with some dictionary definitions in order to make sure that there are not misunderstandings or unintended misinterpretations about our subject matter.

Music – The art and science of combining vocal and/or instrumental sounds or tones in varying melodies, harmonies, rhythms, and timber. In some definitions the following phrase is added: "so as to express emotionally expressive compositions." The art of arranging tones in orderly sequences so as to produce a unified and continuous composition.

Dance – To move the body and feet in rhythm, ordinarily to music. To move rhythmically to music using improvised or prescribed gestures and steps. These are obviously human-oriented definitions, but we can use them cautiously.

Mammals

These two behaviors are strongly associated with social contexts and are powerful signals of emotional states. In the human lineage they can be traced back in time at least to the Neanderthal culture (Mithin 2006). This book is subtitled, "the origin of music, language, mind, and body," and the author brings a formidable interdisciplinary background to bear on developing a plausible history for how and when humans developed verbal language. He makes the argument that non-verbal gestures, rhythmic sensitivity, and musical sounds are necessary precursors to the evolution of verbal language. Moreover, Neanderthal remains have revealed no archaeological evidence of symbolic reasoning and hence they could not have had a verbal language since words are symbolic phenomena (Lidicker 2012). It is now incontrovertible that before vocal language evolved music and dance were, and continue to be powerful means of communication and coordination among humans (Balter 2004). An interesting historical tidbit of these early times was that the earliest known flute was aged at 32,000 years (Balter 2004).

The overall and continuing importance of music and dance in human evolution is indicated by the fact that virtually all existing human cultures include music and dance. In an early paper on this subject, Balter (2004) emphasizes the importance of music in this process, but hardly acknowledges the critical role of dance as well. Since then it has become increasingly apparent that both these activities are adaptive, especially in social contexts. They strengthen social bonding, group recognition, mate finding, and are powerful signals of emotional states. Rapidly increasing evidence also points to significant health benefits from exercise (Hogan 2008; Gitler 2011, Spires-Jones and Ritchie 2018), and this is particularly the case for dance which combines the benefits from exercise with those from music. For example, dancers have been shown to have better immune systems, reduced stress, and improved moods (Sarich 2013), and even premature infants have improved vital signs if provided with music (Loewy 2013). Schellenberg (2004) makes the case that music lessons improve IQ scores. Brown and Parsons (2008) emphasize the vital importance of rhythmic movements (dance) in this pre-vocal language stage of human history. Rapidly accumulating evidence also reveals that dance is a particularly effective choice for health-related exercises, and also has positive effects on the brain (Verghese *et al.* 2003; Powers 2007). It is no accident that orchestral conductors with their intricate knowledge and exposure to music combined with often vigorous accompanying rhythmic movements typically have unusually long life spans. The healthful effects of music and dance were known to the classical Greeks. Given that music and dance are important to humans going back at least to the Neanderthal era, we now need to consider the extent to which these skills go farther back in time and specifically to explore the extent to which they may be found in mammals generally. One theory that has been around for a long time is that since mammals, except for monotremes, are viviparous and so have the ubiquitous experience of developing in association with their mother's heart beat and breathing rhythms. Beyond that, newborns also often experience rhythmic vocalizations as well as rhythmic movements of their mothers, and close body contact through nursing and other parental behaviors. Human infants certainly have good rhythm perception. In general, rhythmic experiences lead to rhythmic sensitivities. Moreover, most mammals make vocalizations, although in many cases these sounds are in high frequencies and not audible to humans. Nevertheless, these sounds have rhythmic musical properties and are subjects of increasing research interest.

Our first step for finding evidence in support of our general conclusion that music and dance are widespread in mammals is to look at our closest non-human relatives, the great apes. Rapidly growing evidence leads to the conclusion that all of these species have recognizable rhythmic activities and sensitivities, including vocalizations *(*Williams 1967; King 2009). A case in point is that chimpanzees (*Pan troglodytes*) are clearly capable of keeping time to music (Gannon 2014; Kotz 2014; Large and Gray 2015), and of listening critically to music (Gannon 2014). In one experiment a chimp expressed a clear preference for music from India and West Africa and disdain for Western music (Mingle 2014). Also, bonobos, a close chimp relative *(Pan paniscus*), can entrain drum beats with head bobbing (Large and Gray 2015).

Other mammals that have been observed to respond to musical rhythms include gorillas, dogs (Bloom 2004; Kaminski *et al.* 2004), sea lions *(Zalophus californicus*; Cook *et al.* 2013), singing mice (*Scotinomys*; Okobi *et al.* 2019), house mice (*Mus musculus*; Spires-Jones and Ritchie 2018), and elephants. Also, almost all bats have complex vocalizations most of which are at too high frequencies for humans to hear. It is therefore reasonable to conclude with confidence that mammals in general seem to be endowed with rhythmic sound capabilities and sensitivities. If they respond with body movements to these rhythms, as many seem to do, we can consider this dance.

Non-mammals

Although our focus here is on mammals, it turns out that our general conclusion is significantly reinforced if we look beyond mammals to other vertebrates. While phylogenetically distant from mammals, birds are an obvious example of widespread music and dance in non-mammal vertebrates (Gess 2007; Pennisi 2012). With the exception of the ratites, birds in general vocalize, mostly with rhythmic components. A particularly spectacular example is the complex duetting exhibited by some tropical species in which the two members of a pair alternate inserting musical components into a single integrated song (Fortune *et al.* 2011). One aspect of this interesting life history feature is that females of a duetting pair have significantly fewer offspring that are fathered by a different male than her mate (extra-pair copulations) than do non-duetting individuals (Douglas *et al.* 2012). Some birds have dance-like behaviors in some cases performed on an arena or lek. These behaviors serve for males to attract females with their dance and vocal skills. In general bird vocalizations involve mate choice, territorial defense, and emotional signaling.

Among reptiles, many lizards display rhythmic head bobbing behaviors. Frog choruses are classic examples of critically important vocal communications. Less well studied are rhythmic sounds made by air bladders in bony fish. The general conclusion is that forms of music and dance are widespread in vertebrates going back in evolution to bony fish (Actinopterygii and Sarcopterygii). It has recently become clear that brains love rhythms. Routine brain activities include integration of information both from an individual's body and sensory inputs from the environment. Often this integrated information then requires rapid behavioral responses. This is a complex challenge. It turns out that all of this coordination is enhanced by rhythmic neuronal communication. Signals from individual neurons are quickly organized into functional groups (Freeman 1951; Canolty 2010). Perhaps this explains why dancing with all of its varied rhythms is much easier and more natural for brains than would be organizing non-rhythmic tasks.

Vertebrates in general

Finally, we come to the most persuasive evidence that supports the widespread importance of various forms of music and dance in mammals. As it turns out, it is not only mammals in which music and dance is widespread, but most of the vertebrates as well. Recent neurophysiological research on the brain (Bass *et al.* 2008; Margoliash and Hale 2008) has discovered that the location in the brain where rhythmic behaviors are organized is not in the cerebral cortex where you might expect to find it, but instead it is in the most primitive subcortical parietal part of the brain located just above the anterior end of the spinal cord (Posterior parietal cortex). This most revealing finding says clearly that rhythmic organization is an ancient component of vertebrate evolution. This new insight means that vertebrate vocalizations (many of which would qualify as music) and rhythmic body movements (many of which would qualify as dance) had a common ancestor more than 400 million years ago. Another corollary of this anatomy is that music and dance are functionally coordinated but are disconnected from verbal language which is organized in more recent or higher parts of the brain. This arrangement explains why persons with brain damage affecting speech will likely not have any diminution of functions involving music and dance. Conversely, damage to the subcortical location of music and dance coordination will not damage verbal language functioning. A related consequence is that music and dance skills can penetrate the "fog" of dementia or even Alzheimer's disease which are centered in more advanced parts of the brain. Lastly, it is increasingly evident that human infants can mimic rhythmic movements, and show enjoyment in doing this (Phillips-Silver and Trainor 2005). All of this means that organized rhythmic behavior is potentially present in vertebrates going back in time to bony fish (Actinopterygii and Sarcopterygii). Mammals certainly have the neuronal architecture for indulging in rhythmic sound production (singing) as well as rhythmic body movements (dance), and many species seem to have taken advantage of this potential capability.

Some of the evidence for music and dance in non-human mammals presented here can be considered as anecdotal. This could tempt skeptical readers to conclude that the evidence for widespread rhythmic sensitivities in mammals is unreliable or unimportant. On the other hand, even anecdotal evidence clearly supports the conclusion that the neural apparatus for rhythmic sensitivities is present in diverse species of mammals, and hence is available for exploitation. Furthermore, most mammals have the capability of making vocal sounds, and hence the potential for rhythmic utterings is real. Given also the evidence that music and dance have important social and health benefits opens the possibility for major research opportunities. Let's take advantage of this relatively little-explored component of mammalogy.

Literature Cited

Balter, M. 2004. Seeking the key to music. Science 306:1120-1122.

Bass, A. H., E. H. Gilland, and R Baker. 2008. Evolutionary origins for social vocalization in a vertebrate hindbrain-spinal compartment. Science 321: 417-421.

Bloom, P. 2004. Can a dog learn a word? Science 304: 1605-1606.

Brown, S., and L. M. Parsons. 2008. Recent brain imaging studies reveal some of the complex neurochoreography behind our ability to dance: the neuroscience of dance. Scientific American (July): 78-83.

Canolty, R. J. 2010. Oscillatory phase coupling coordinates anatomically dispersed functional cells. Proceedings of the National Academy of Sciences B. 107(40):17356-17361.

Cook, P., *et al*. 2013. California sealion (*Zalophus californicus*) can keep the beat: motor entrainment for rhythmic auditory stimuli in a non vocal mimic. Journal of Comparative Psychology 127: 412-427.

Douglas, S. B., D. D. Heath, and D. J. Mennill. 2012. Low levels of extra-paternity in a Neotropical duetting songbird, the Ruffous- and -White wren (*Thryothorus rufalbus*). The Condor 114 :393-400.

Fortune, E. S., C. Rodriguez, D., D. li, G. F. Ball, and M. L. Coleman. 2011. Neural mechanisms for the coordination of duetting in singing in wrens. Science 334: 666-670.

Freeman, W. J. 1995. Societies of brains: A study in the neuroscience of love and hate. Lawrence Erdbaum Associates,Pub., Hillside, N.J., 204 pp.

Gannon, M. 2014. Chimps reveal their taste in music. Journal of Experimental Psychology: Animal learning and cognition. vol. 139?:

Gess, A. 2007. Birds like music, too. Science 317: 1864.

Gitler, A. D. 2011. Another reason to exercise. Science 334:606-607.

Hanna, J. L. 1983. To dance is human, a theory of non-verbal communication. University of Texas Press, 327 pp.

Hogan, P. J. 2008. More evidence on value of dance. Aging and physical activity 16:435-445.

Jensvold, M. L. A., and R. P. Gardner. 2000. Interactive use of sign language by cross-fostered chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology 114:335-346.

Kaminski, J., J. Call, and J. Fischer. 2004. Word learning in a domestic dog: evidence for fast mapping. Science 304:1682-1683.

King, B. J. 2009. The dynamic dance, non-vocal communication in African great apes. Harvard University Press. Cambridge, Massachuset and London, England.

Kotz, I. 2014. Bonobos, like humans, keep time to music. Ageing and Physical Activity 16:435-445.

Large, E., and P. M. Gray. 2015. Spontaneous tempo and rhythmic entrainment in a bonobo (*Pan paniscus*). Journal of Comparative Psychology 29:317-328.

Lawler, A. 2012. Uncovering civilizations roots. Science 335: 790-793.

Lidicker, W. Z., Jr. 2012. Which came first, music or dance? Let's Dance! (Folk Dance Federation of California) 69:13-14.

Loewy, J. 2013. Premature babies and music. Pediatrics162 (supplement 3 May): 902-918.

Margoliash, D., and M. Hale. 2008. Vertebrate vocalizations. Science 321: 347-348.

Mingle, M. E., T. M. Eppley, M. W. Campbell, K. Hall, V. Horner, and F. B. de Waal. 2014. Chimpanzees prefer African and Indian music over silence. Journal of Experimental Psychology: Animal Learning and Cognition 40:502-505.

Mithin, S. 2006. The singing Neanderthals: the origin of music, language, mind, and body. Harvard University Press. Cambridge, U.S.A.

Okobi, D. E., Jr., A. Banerjee, A. M. M. Matheson, S. M. Phelps, and M. A. Long. 2019. Motor cortical control of vocal interaction in Neotropical singing mice. Science 363:983-988.

Pennisi, E. 2012. Preening the troops. Science 136:828.

Phillips-Silver, J., and L. J. Trainor. 2005. Feeling the beat: movement influences infant rhythm perception. Science 308:1430.

Powers, R. 2007. Dancing makes you smarter. Let's Dance! (Folk Dance Federation of California) Feb.: 12-13.

Sarich, C. 2013. Research links music to increased immunity and better mood. Natural society News 14 May: 1-2. http.// www.nationofchange.org/

Schellenberg, E. G. 2004. Music lessons enhance IQ. Psychological Science 15:511-514.

Spires-Jones, T. L., and C. W. Ritchie. 2018. A mouse model of Alzheimer's disease provides clues about why exercise is good for memory. Science 361:975-976.

Verghese, J., *et al*. 2003. Leisure activities and the risk of dementia in the elderly. New England Journal of Medicine 348:2508-2516.

Williams, L. 1967. The dancing chimpanzee: study of primitive music in relation to vocalizing and rhythmic actions of apes. Norton, U.S.A.

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Activity patterns and their relationship to the habitat use of mule deer (*Odocoileus hemionus*) in the Chihuahuan Desert, Mexico

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In desert regions, species have adapted physiologically and behaviorally to the extreme conditions of their environment, such as a lack of water and extreme temperatures. This is the case of the mule deer (*Odocoileus hemionus*) a species which many aspects of its relationship between behavioral ecology and habitat characteristics are unknown. The objectives of this study were: 1) to characterize the daily activity pattern of female mule deer in relationship to three behavioral patterns: resting, feeding and moving, and 2) assess the relationship between these behavioral patterns and the characteristics of the habitat. This study was conducted in the Chihuahuan Desert, where six females of mule deer were monitored using VHF radiotelemetry between 2012 and 2014. We distinguish the behavioral patterns by sensors in the collar and we quantified the number of beeps emitted per minute. Moreover, we described the daily pattern associated with these activities using Kernel density graphs and evaluated the effect of habitat variables on the frequency of resting and feeding behaviors applying a generalized linear model (GLM). We identified the location in which feeding and resting behaviors occurred, and the type of plant associations present and the percentage of area they occupied. We recorded locations over 328 days/deer. Female mule deer spent most of their time resting (63.41 %), followed by moving (21.26 %), and feeding (15.34 %). Deer movement and feeding behaviors were most frequent during the crepuscule. The temperature was the only variable that influenced resting and feeding behaviors (deviance = 4.7; *d. f.* = 1; *P* = 0.02). The estimated area used for resting was 10.35 km^2, while the corresponding area for feeding was 6.45 km^2, in which the plant association with dominance of *Larrea tridentata, Opuntia rastrera* and *Fouquieria splendens* was the most common. Considering the high temperatures prevailing on the region, resting most of the day likely helps deer to have an adequate thermoregulation. The time dedicated to feeding is less than the dedicated to other activities; deer may be spending more time moving than feeding due to the spatial distribution of suitable food patches, or to avoid predators. The mule deer occupy the same areas to feed and rest; however, feeding areas are smaller those used to rest, these areas have been identified in previous studies as those with the greatest use (core areas). In the plant association with greater occupation within the feeding zones, there are species reported as an essential for the deer diet; these areas are located at the foot of the hill, which gives the deer thermal protection.

En regiones desérticas las especies se han adaptado fisiológica y conductualmente a la falta de agua, así como a las temperaturas extremas. Tal es el caso del venado bura (*Odocoileus hemionus*), especie de la cual muchos aspectos de su ecología conductual y su relación con el hábitat aún son desconocidos. Los objetivos de este estudio fueron: 1) caracterizar el patrón diario de actividad de hembras de venado bura con relación a tres pautas de comportamiento: descanso, alimentación y movimiento, y 2) evaluar la relación entre estas pautas y las características del hábitat. Este estudio se realizó en el Desierto Chihuahuense, donde se monitorearon mediante radiotelemetría VHF seis hembras de venado bura entre el 2012 y el 2014. Las pautas se distinguieron mediante un sensor en el collar y la cuantificación del número de pulsaciones que emite por minuto. Se caracterizó el patrón de actividad asociado con las pautas utilizando gráficos de densidad Kernel y se evaluó el efecto de variables del hábitat sobre la frecuencia de las mismas aplicando un modelo lineal generalizado (GLM). Se identificaron las áreas que las venadas usan para alimentarse y descansar, así como las asociaciones vegetales presentes en esas áreas y el porcentaje que ocupaban. Se registraron localizaciones durante un total de 328 días/venado. Las hembras de venado bura dedican la mayor parte del tiempo a descansar (63.41 %), seguido de realizar movimientos (21.26 %) y por último a alimentarse (15.34 %). Tienen horarios crepusculares de movimiento y alimentación. La temperatura fue la única variable que afectó a las pautas de descanso y alimentación (devianza = 4.7; *g. l.* = 1; *P* = 0.02). El área estimada para las zonas que seleccionan para descansar fue de 10.35 km^2 y la de alimentación fue de 6.45 km^2, donde predominó la asociación vegetal con dominancia de *Larrea tridentata, Opuntia rastrera* y *Fouquieria splendens*. Considerando las altas temperaturas que predominan en el sitio, el permanecer echadas la mayor parte del día puede ser necesario para una adecuada termorregulación. El tiempo dedicado a alimentarse es menor al de las otras pautas, esto podría indicar que, las venadas están invirtiendo mayor tiempo en desplazarse que en alimentarse debido a la distribución espacial de parches adecuados para su alimentación, o para evadir depredadores. Las venadas ocupan los mismos sitios para alimentarse y descansar, sin embargo, las áreas para lo primero son menores, dichas áreas han sido identificadas en trabajos previos como las zonas de las áreas núcleo de actividad. En la asociación vegetal con mayor ocupación dentro de las zonas de alimentación se encuentran especies reportadas como parte esencial de la dieta del venado, ubicadas al pie del cerro, lo cual confiere a los venados protección térmica.

Key words: arid ecosystems; behavior patterns; cervid; Mapimí; radiotelemetry.

Introducción

El estudio de la ecología conductual de la fauna busca describir el comportamiento de los animales en función de la adaptación a las condiciones ecológicas, incluyendo tanto el entorno físico como al entorno ecológico (competidores, depredadores, etc.; Davies *et al.* 2012). Las respuestas conductuales de los individuos dependen de las condiciones de su hábitat (Gallina y Bello 2002) y pueden llegar a ser muy complejas y diferentes, tanto entre individuos como dependiendo del sexo y edad (Marchinton y Hirth 1984; Gallina y Bello 2014).

El venado bura (*Odocoileus hemionus*) se distribuye principalmente en zonas templadas y áridas, desde el sur de Alaska hasta el norte de México (Anderson y Wallmo 1984; Geist 1998), donde se extiende por los estados de Baja California, Sonora, Chihuahua, Coahuila y Durango (Heffelfinger *et al.* 2006). En las regiones áridas y semiáridas de su distribución, la especie se ha adaptado morfológica y conductualmente a las condiciones extremas del desierto como la falta de agua y las temperaturas extremas. La actividad del venado bura ha sido asociada con la presencia de pendientes pronunciadas y terrenos accidentados (que además facilitan su escape ante los depredadores) o la existencia de cobertura vegetal de altura media, estos rasgos del paisaje le permiten tener una mejor protección térmica. De igual modo, los venados bura tienden a modificar sus movimientos y ámbitos hogareños a través del día y temporadas del año para hacer más eficiente el uso de los recursos (Sánchez-Rojas y Gallina 2000; Avey *et al.* 2003; Marshal *et al.* 2006; Pérez-Solano *et al.* 2016; 2017). Al interior de los ámbitos hogareños de los venados se presentan zonas con mayor densidad de recursos críticos, que son, por lo tanto, más importantes para su actividad (Burt 1943; Powell 2000). Conocer estas áreas de uso de los venados bura ofrece un importante marco de referencia para definir las características de los sitios seleccionados para su refugio y la obtención de recursos alimenticios seguros, además de contribuir a entender la ecología de su comportamiento (Burt 1943; Kaufman 1962; Samuel y Green 1988).

En México, muchos aspectos biológicos y ecológicos sobre el venado bura, necesarios para su manejo, son desconocidos, o la información es muy escasa, por lo que se utiliza información de estudios realizados en Estados Unidos (Pérez-Solano *et al.* 2016). En comparación con el venado cola blanca (*O. virginianus*), los trabajos de investigación que abordan aspectos conductuales del venado bura son muy pocos, por ejemplo, la conducta en relación a su ecología espacial en el desierto de Sonora (Alcalá-Galván y Krausman 2013) y en el Desierto Chihuahuense (Pérez-Solano *et al.* 2016; 2017). De acuerdo con la última revisión de estudios de cérvidos en México, únicamente un 13 % de estos estudios incluyen a *O. hemionus*, y se enfocan principalmente en sus hábitos alimentarios, dinámica y densidades poblacionales, uso de hábitat y posibles reintroducciones en ciertas áreas (Mandujano 2004). Por lo tanto, resulta altamente relevante el estudio de aspectos conductuales de esta especie para comprender su ecología, mantener sus poblaciones y contar con información que contribuya a definir estrategias de conservación y mejores programas de aprovechamiento de este cérvido. Los objetivos de este estudio fueron: 1) caracterizar el patrón diario de actividad de hembras de venado bura con relación a tres pautas de comportamiento: descanso, alimentación y movimiento; y 2) evaluar la relación entre estas pautas de comportamiento y las características del hábitat.

Material y métodos

Área de estudio. El estudio se realizó en la región central del Desierto Chihuahuense, en la Reserva de la Biosfera de Mapimí (RBM), México, ubicada en la intersección de los estados de Durango, Chihuahua y Coahuila (CONANP 2006). Al centro de la RBM se localiza el cerro San Ignacio (26° 42´, 26° 38´ N, -103° 42´, -103°48´ W; Figura 1), alrededor del cual se realizó este estudio. La vegetación dominante son los matorrales xerófilos, micrófilos y chaparrales de distintas composiciones, con vegetación halófita en las planicies (CONANP 2006; Rzedowski 2006). El clima es seco y extremoso semi-cálido con lluvias en verano, con una precipitación promedio anual de 271 mm. La temporada de lluvias ocurre de julio a octubre y la de secas de noviembre a junio. La temperatura media anual es 20.8 °C, la mínima promedio de invierno 3.9 °C y la máxima promedio en verano 36.1 °C (Montaña y Breimer 1988; CONANP 2006).

Captura y monitoreo de venados bura. Las capturas se realizaron en los años 2011 y 2012 usando redes de caída de 15 x 15 m con una luz de 10 x 10 cm. A las venadas capturadas se les colocaron radiocollares de colores distintos, con transmisores VHF (150 y 152 MHz) y sensor de movimiento (modelo 400, TELONICS, Mesa, Arizona), se monitorearon de enero de 2012 a agosto de 2014. Las localizaciones fueron registradas cada hora en ciclos continuos de 24 horas, se realizaron de dos a tres ciclos continuos por venada, aproximadamente cada dos meses y durante todo el periodo de estudio. Las lecturas se obtuvieron en forma

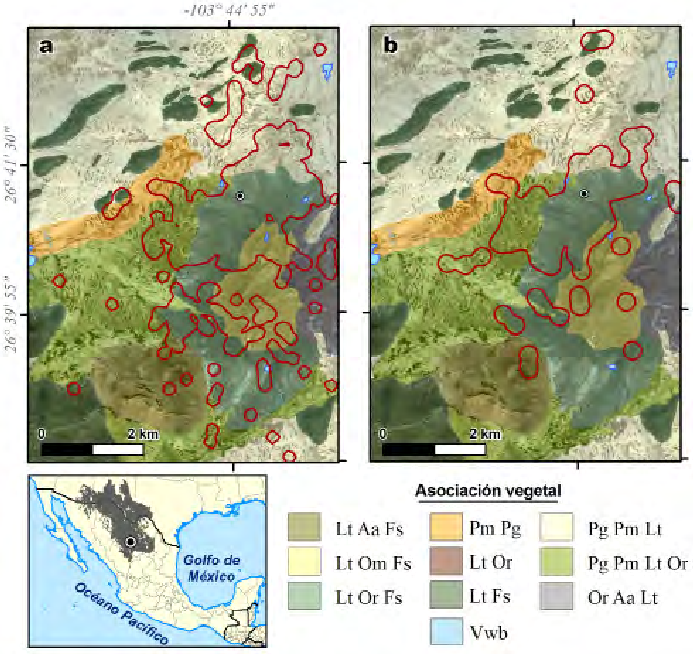

Figura 1. Áreas usadas por las hembras de venado bura para descansar (a) y alimentarse (b), así como las asociaciones vegetales presentes al interior de cada área. El Laboratorio del Desierto de Mapimí (circulo blanco y negro) se ubica al interior del Desierto Chihuahuense (polígono gris). Asociación vegetal: *Pleuraphis mutica* y *Prosopis glandulosa* (Pm Pg); *Larrea tridentata* y *Fouquieria splendens* (Lt Fs); *Larrea tridentata, Agave asperrima* y *Fouquieria splendens* (Lt Aa Fs); *Larrea tridentata, Opuntia microdasys* y *Fouquieria splendens* (Lt Om Fs); *Larrea tridentata, Opuntia rastrera* y *Fouquieria splendens* (Lt Or Fs); *Opuntia rastrera, Agave asperrima* y *Larrea tridentata* (Or Aa Lt); *Prosopis glandulosa, Pleuraphis mutica* y *Larrea tridentata* (Pg Pm Lt); *Prosopis glandulosa, Pleuraphis mutica, Larrea tridentata* y *Opuntia rastrera* (Pg Pm Lt Or) y vegetación asociada a cuerpos de agua (Vwb).

simultánea en dos estaciones fijas, con antenas receptoras tipo "Yagui" (2 de 4 elementos) de pico nulo, ubicadas en sitios elevados. El error de estimación fue calculado usando radiocollares con una ubicación georeferenciada (White y Garrott 1990; Withey *et al.* 2001); el polígono de error de las localizaciones se consideró bajo el cálculo de extensión de 0.09 km^2.

Pautas de comportamiento y patrón de actividad. Las pautas de comportamiento se determinaron a través del uso del sensor de movimiento que posee el radiotransmisor de los collares, el cual emite una señal o pulsación ("beeps") generada por una bola de mercurio ubicada en un tubo dentro del radiotransmisor. Al desplazarse el mercurio se producen cierres en un interruptor, lo que incrementa o disminuye el número de "beeps" emitidos por minuto. El movimiento de los animales al levantar o bajar la cabeza genera cambios en el número de "beeps" que se emiten, los cuales van de 50 a 87 dependiendo la posición de la cabeza, correspondiendo los valores más bajos cuando están echados y los más altos cuando están comiendo (Mandujano *et al.* 1996).

Durante cada localización hecha para cada venada, se contabilizó el número de "beeps" emitidos por minuto, y durante cinco minutos para minimizar el error de asignación de pauta. La asignación de la pauta correspondiente a la localización se hizo considerando la variación observada durante los cinco minutos de conteo (Mandujano *et al.* 1996). Se utilizaron los siguientes valores de beeps por minuto para identificar las tres pautas de comportamiento: descanso de 50 a 55 beeps/minuto, en movimiento (que incluye las posibles pautas de caminando, parado o alimentándose intermitentemente) de 56 a 69 beeps/minuto y alimentándose (casi exclusivamente en el mismo sitio) de 70 a 87 beeps/minuto. Esto se hizo siguiendo los resultados obtenidos con venados en cautiverio por Mandujano *et al.* (1996). Se caracterizó el patrón diario de actividad relacionado con estas tres pautas de comportamiento usando gráficas de densidad Kernel, con el paquete *overlap* (Ridout y Linkie 2009) en el programa R 3.6.0 (R Core Team 2019). Se consideró como actividad crepuscular de las 6:00 a 8:00 horas y de 18:00 a 20:00 horas, actividad diurna de 8:00 a 18:00 horas y actividad nocturna de 20:00 a 6:00 horas (Monroy-Vilchis *et al.* 2011).

Sitios de alimentación y descanso. Ya que los sitios de alimentación y descanso son importantes en la actividad de los individuos, por encontrarse en ellos algunos recursos críticos para sobrevivir, se evaluó cómo las pautas de alimentación y descanso eran afectadas por algunas variables del hábitat aplicando un modelo lineal generalizado (GLM, por sus siglas en inglés) con error tipo binomial en el programa R 3.6.0 (R Core Team 2019). Las localizaciones espaciales identificadas con estas pautas se relacionaron con las variables: pendiente del terreno, asociación vegetal presente, temperatura y humedad relativa. Las primeras dos variables se derivaron usando el sistema de información geográfica QGIS v.2.18 (QGIS Development Team 2017), donde la variable pendiente (grados) se extrajo de un modelo digital de elevación, con una resolución de 15 m por pixel. Las asociaciones vegetales fueron nombradas de acuerdo a las especies más dominantes (Montaña 1988), usando el mapa digital generado por Pérez-Solano *et al.* (2016), que identifica diez tipos de asociaciones vegetales (Figura 1). La temperatura y humedad relativa se obtuvieron cada hora durante los ciclos de muestreo mediante un termohigrómetro colocado en una de las dos estaciones de monitoreo (Extech RH101, Nashua, New Hampshire, USA). Consideramos que, dada la poca variación del terreno y de los sitios que ubicamos donde se movían las venadas, la temperatura y humedad no varía significativamente entre las localizaciones obtenidas por radiotelemetría y las estaciones de monitoreo.

Aunado a esto, se identificaron los sitios donde los individuos se alimentaban y descansaban, así como la extensión (km^2) de dichas áreas. Esto fue hecho estimando "la distribución del uso" ("utilization distribution", UD) con el método Kernel fijo, usado comúnmente para estimar los ámbitos hogareños. El UD proporciona una densidad de probabilidad para reubicar al animal en cualquier lugar de acuerdo con las coordenadas (X, Y) de su localización espacial (Calenge 2006). Se usó el 95 % de las observaciones y un valor de suavizado (h) calculado mediante validación cruzada de mínimos cuadrados (LSCV), en el paquete *AdehabitatHR* (Calenge 2006) dentro del programa R 3.6.0 (R Core Team 2019). Los polígonos obtenidos de este análisis se usaron como referencia para clasificar en QGIS v.2.18 (QGIS Development Team 2017), los tipos de vegetación y el porcentaje que éstas ocupan dentro de las áreas que se identificaron que fueron usadas para alimentarse y como refugio para descanso.

Resultados

Siete hembras fueron capturadas en 95 días de esfuerzo, sin embargo, el sensor de actividad de un collar falló desde el inicio, por lo que el análisis se realizó con seis individuos. Se registraron localizaciones de las seis venadas durante un total de 328 días/venado. Durante los tres años de seguimiento se obtuvo una media ± desviación estándar de 87.50 ± 53.04 registros por individuo para la pauta descanso, 29.33 ± 21.81 para en movimiento y 21.17 ± 19.32 para alimentándose.

Se encontró que las venadas dedican la mayor parte del tiempo a descansar (63.41 %), seguido de pautas como caminar, estar paradas o alimentándose intermitentemente (en movimiento, 21.26 %) y la menor cantidad de tiempo es dedicada a estar detenidas alimentándose (15.34 %). La alimentación y los movimientos de las hembras de venado bura son realizados principalmente en horas crepusculares, y presentan dos picos de actividad (Figura 2). De acuerdo con el GLM, la temperatura (devianza = 4.7; *g. l.* = 1; $P = 0.02$) tuvo una relación positiva con las pautas de descanso y alimentándose. El área estimada para los sitios que los individuos seleccionan para descansar fue de 10.35 km^2, mientras que las áreas donde se alimentan están restringidas a una

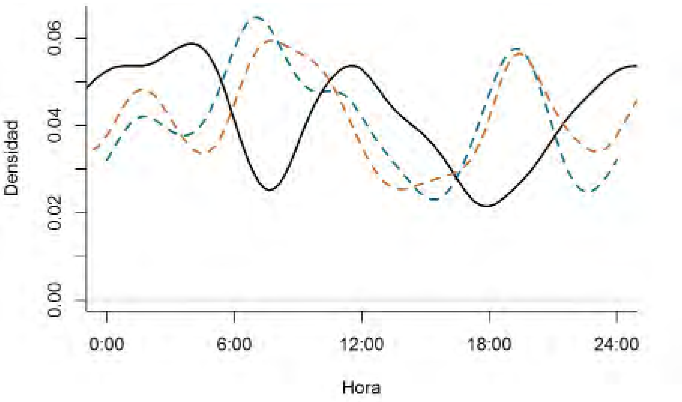

Figura 2. Patrón de actividad diario relacionado con tres pautas de comportamiento de seis hembras de venado bura al interior del Desierto Chihuahuense, México. La pauta descanso está representada por la línea negra, la pauta alimentación por la línea punteada marrón y la pauta movimiento por la línea punteada azul.

extensión de 6.45 km^2 (Figura 1). Al interior de estas dos áreas se identificó la presencia de nueve de los diez tipos de asociaciones vegetales presentes en el área de estudio, la asociación de *Larrea tridentata* y *Opuntia rastrera* (Lt Or) estuvo ausente. La asociación vegetal con dominancia de *Larrea tridentata, Opuntia rastrera* y *Fouquieria splendens* (Lt Or Fs) fue la que tuvo mayor presencia dentro de las áreas de alimentación y descanso (44 y 40 % respectivamente; Figura 1 y 3), seguido de la asociación con *Prosopis glandulosa, Pleuraphis mutica, L. tridentata* y *O. rastrera* (Pg Pm Lt Or) también para ambos casos (22 y 20 % respectivamente; Figura 1 y 3).

Discusión

En este estudio se encontró un patrón diario de actividad crepuscular para la especie, con picos de actividad al amanecer y anochecer, lo cual previamente ha sido reportado en trabajos en Estados Unidos (Relyea y Demarais 1994; Webb *et al.* 2013; Harris *et al.* 2015; Lendrum *et al.* 2017). En regiones desérticas los cérvidos, como el caso del venado bura, evaden las condiciones ambientales extremas a través del comportamiento (Wallmo 1981). De acuerdo con los resultados obtenidos, las venadas bura dedican la mayor proporción de tiempo a descansar (Figura 2). Considerando las altas temperaturas que predominan en el sitio así como la escases de agua en estas zonas áridas, el permanecer echadas la mayor parte del día les permite tener una adecuada termorregulación, al evitar la pérdida de agua por transpiración, y maximizar su energía (Gallina y Bello 2014), esto se refuerza con los resultados obtenidos en el GLM, donde la temperatura ambiental fue la única variable del hábitat que tuvo un efecto estadísticamente significativo sobre las pautas conductuales.

Por otra parte, las actividades de movimiento y alimentación tienen picos de actividad similar, sin embargo, el tiempo dedicado a alimentarse es menor del dedicado al desplazamiento (Figura 2). Al respecto, estudios con venado cola blanca han mostrado que los requerimientos diarios de energía disminuyen en latitudes más sureñas, en comparación con las norteñas, aunado a esto, en zonas áridas la disponibilidad de recursos (agua y alimento) es limitada y los individuos se han adaptado a través de mecanismos tanto conductuales como fisiológicos (Strickland *et al.* 2005; Gallina y Bello 2010), esto ayudaría a explicar por qué las venadas en el área de estudio requieren dedicar menos tiempo a esta actividad. La necesidad de desplazarse está también relacionada con la distribución espacial de los recursos, y las venadas podrían estar invirtiendo más tiempo en esto, pues pueden estar desplazándose entre diversos parches de vegetación adecuada para alimentarse o para evadir a los depredadores (Esparza-Carlos *et al.* 2016).

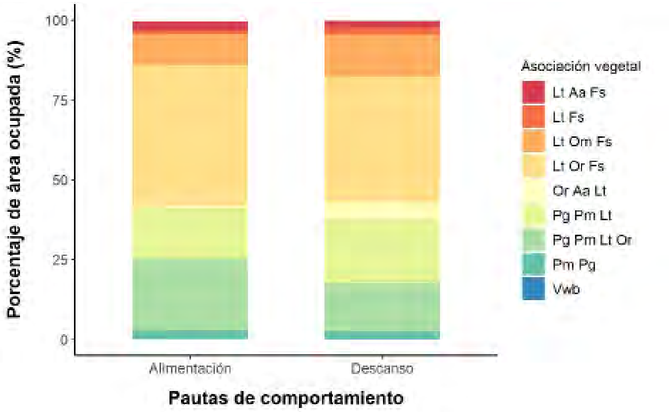

Figura 3. Porcentaje de área ocupada por las asociaciones vegetales presentes en las zonas de alimentación y descanso. Asociación vegetal: *Pleuraphis mutica* y *Prosopis glandulosa* (Pm Pg); *Larrea tridentata* y *Fouquieria splendens* (Lt Fs); *Larrea tridentata, Agave asperrima* y *Fouquieria splendens* (Lt Aa Fs); *Larrea tridentata, Opuntia microdasys* y *Fouquieria splendens* (Lt Om Fs); *Larrea tridentata, Opuntia rastrera* y *Fouquieria splendens* (Lt Or Fs); *Opuntia rastrera, Agave asperrima* y *Larrea tridentata* (Or Aa Lt); *Prosopis glandulosa, Pleuraphis mutica* y *Larrea tridentata* (Pg Pm Lt); *Prosopis glandulosa, Pleuraphis mutica, Larrea tridentata* y *Opuntia rastrera* (Pg Pm Lt Or) y vegetación asociada a cuerpos de agua (Vwb).

La identificación de las áreas que las venadas usan para alimentarse y descansar indicó que están ocupando los mismos sitios (Figura 1), sin embargo, las áreas que usan para alimentarse son más pequeñas (6.45 km^2) y se localizan al pie del Cerro San Ignacio, donde predomina la asociación vegetal dominada por *Larrea tridentata, Opuntia rastrera* y *Fouquieria splendens*, especies que han sido identificadas como parte esencial de la dieta del venado bura en la zona de estudio (Guth 1987; Gallina *et al.* 2017). Estas mismas áreas han sido previamente reportadas como las zonas de mayor uso por los venados por lo que son considerados como áreas núcleo de actividad (Pérez-Solano *et al.* 2017).

Finalmente, este es el primer trabajo que reporta el patrón de actividad para el venado bura en México con base en un método directo como la radiotelemetría, lo cual nos ayuda a entender un poco más sobre su ecología conductual y las estrategias adaptativas en ambientes áridos. Aún es necesario seguir estudiando otros aspectos biológicos y ecológicos de la especie, por ejemplo, la conducta de los machos, pues al ser una especie con una marcada segregación sexual los patrones conductuales, así como sus áreas de alimentación y refugio, probablemente son diferentes a las encontradas con las hembras en este estudio. De igual modo, sería importante considerar las etapas fisiológicas por las que pasan los individuos (por ejemplo, durante la temporada de apareamiento o gestación), para evaluar el efecto que tienen sobre la conducta de estos animales (Hungerford *et al.* 1981; Geist 1998).

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Literatura citada

Alcalá-Galván, C. H., y P. Krausman. 2013. Home range and habitat use by desert mule deer in altered habitats. California Fish and Game 99:65-79.

Anderson, A. E., y O. C. Wallmo. 1984. *Odocoileus hemionus*. Mammalian Species 219:1-9.

Asensio, N., C. D. m Lusseau, M. Schaffner, y F. Aureli. 2012. Spider monkeys use high-quality core areas in a tropical dry forest. Journal of Zoology 287:250-258.

Avey, J. T., W. B. Ballard, M. C. Wallace, M. H. Humphrey, P. R. Krausman, F. Harwell, y E. B. Fish. 2003. Habitat relationships between sympatric mule deer and white-tailed deer in Texas. The Southwestern Naturalist 48:644-653.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519.

CONANP (Comisión Nacional de Áreas Naturales Protegidas). 2006. Programa de conservación y manejo Reserva de la Biosfera de Mapimí, México. Comisión Nacional de Áreas Naturales Protegidas. Distrito Federal, México.

Davies, N. B., J. R. Krebs, y S. A. West. 2012. An introduction to behavioural ecology. John Wiley and Sons. New York, U.S.A.

Esparza-Carlos, J. P., J. W. Laundré, L. Hernández, y L. I. Íñiguez-Dávalos. 2016. Apprehension affecting foraging patterns and landscape use of mule deer in arid environments. Mammalian Biology 81:543-550.

Gallina, S., L. García, y R. González-Trápaga. 2017. Ocotillo flowers as food resource for the mule deer during the dry season. Therya 8:185-188.

Gallina, S., y J. Bello. 2002. Ecología conductual del venado cola blanca texano. Memorias VIII Simposio sobre venados en México "Ing. Jorge Villarreal González", Tlaxcala, México.

Gallina, S., y J. Bello. 2010. El gasto energético del venado cola blanca (*Odocoileus virginianus texanus*) en relación a la precipitación en una zona semiárida de México. Therya 1:9-22.

Gallina, S., y J. Bello. 2014. Patrones de actividad del venado cola blanca en el noreste de México. Therya 5:423-426.

Geist, V. 1998. Deer of the World, their evolution, behavior and ecology. Stackpole books. Pennsylvania, U.S.A.

Guth, M. C. G. A. 1987. Hábitos alimenticios del venado bura (*Odocoileus hemionus, Rafinesque* 1817) en la Reserva de la Biosfera de Mapimí, Durango. Tesis de Licenciatura, ENEP-I UNAM. Distrito Federal, México.

Harris, G., J. G. Sanderson, J. Erz, S. E. Lehnen, y M. J, Butler. 2015. Weather and prey predict mammals' visitation to water. PLoS ONE 10:1-21.

Heffelfinger, J. R., C. Brewer, C. H. Alcalá-Galván, B. Hale, D. L. Weybright, B. F. Wakeling, L. H. Carpenter, y N. L. Dodd. 2006. Habitat Guidelines for Mule Deer: Southwest Deserts Ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies. Arizona, U.S.A.

Hungerford, C. R., M. D. Burke, y P. F. Ftolliot. 1981. Biology and population dynamics of mule deer in Southwestern United States. Pp. 109-131 *in* Deer biology, habitat requirements, and management in Western North America. (Ftolliot, P. F., y S. Gallina, eds.). Instituto de Ecología. Distrito Federal, México.

Kaufman, J. H. 1962. Ecology and social behavior of the coati *Nasua narica* on Barro Colorado Island, Panama. University of California publications in zoology 60:95-222.

Lendrum, P. E., K. R., Crooks, y G. Wittemyer. 2017. Changes in circadian activity patterns of a wildlife community post high-intensity energy development. Journal of Mammalogy 98:1265-1271.

Mandujano, S. 2004. Análisis bibliográfico de los estudios de venados en México. Acta Zoológica Mexicana (n. s.) 20:211-251.

Mandujano, S., S. Pérez, R. Sánchez, y S. Gallina. 1996. Diferenciación de pautas de actividad del venado con ayuda de radiotransmisores con sensor de movimiento. Acta Zoológica Mexicana (n. s.) 67:67-78

Marchinton, R., y D. Hirth. 1984. Behavior. Pp. 129-168 *in* White-tailed deer, ecology and management (Halls, L. K., ed.) A Wildlife Management Institute Book. Stackpole books. Pennsylvania, U.S.A.

Marshal, J. P., V. C. Bleich, P. R. Krausman, M.L. Reed, y N. G. Andrew. 2006. Factors affecting habitat use and distribution of desert mule deer in an arid environment. Wildlife Society Bulletin 34:609-619.

Monroy-Vilchis, O., M. M. Zarco-González, C. Rodríguez-Soto, L. Soria-Díaz, y V. Urios. 2011. Fototrampeo de mamíferos en la Sierra Nanchititla, México: abundancia relativa y patrón de actividad. Revista de Biología Tropical 59:373-383.

Montaña, C. 1988. Las formaciones vegetales. Pp. 167-197 *in* Estudio integrado de los recursos vegetación, suelo y agua en la reserva de la biosfera de Mapimí (Montaña, C. ed.). Instituto de Ecología. Distrito Federal, México.

Montaña, C., y R. F. Breimer. 1988. Major vegetation and environment units. Pp. 99-114 *in* Estudio integrado de los recursos vegetación, suelo y agua en la Reserva de la Biosfera de Mapimí (C. Montaña, ed.). Instituto de Ecología. Distrito Federal, México.

Morrison, M. L., B. Marcot, y W. Mannan. 2006. Wildlife-habitat relationships: concepts and applications. Island Press. Washington, U.S.A.

Pérez-Solano, L. A., S. Gallina-Tessaro, y G. Sánchez-Rojas. 2016. Individual variation in mule deer (*Odocoileus hemionus*) habitat and home range in the Chihuahuan Desert, Mexico.

Journal of Mammalogy 97:1228-1237.

Pérez-Solano L. A., L. M. García-Feria, y S. Gallina-Tessaro. 2017. Factors affecting the selection of and displacement within core areas by female mule deer (*Odocoileus hemionus*) in the Chihuahuan Desert, Mexico. Mammalian Biology 87:152-159.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65-110 *in* Research techniques in animal ecology: controversies and consequences (Boitani, L., y T. K. Fuller, eds.) Columbia University Press. New York, U.S.A.

QGIS Development Team. 2017. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rzedowski, J. 2006. Vegetación de México. Comisión Nacional para el Conocimiento y uso de la Biodiversidad. Distrito Federal, México.

Relyea, R.A., y S. Demarais. 1994. Activity of Desert Mule Deer during the Breeding Season. Journal of Mammalogy 75:940-949.

Ridout, M., y M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322-337.

Samuel, M. D., y R. E. Green. 1988. A revised test procedure for identifying core areas within the home range. Journal of Animal Ecology 57:1067-1068.

Sánchez-Rojas, G., y S. Gallina. 2000. Factors affecting habitat use by mule deer (*Odocoileus hemionus*) in the central part of the Chihuahuan Desert, Mexico: an assessment with univariate and multivariate methods. Ethology Ecology and Evolution 12:405-417.

Strickland, B. K., D. G. Hewitttt, C. A. Deyoung, y R. L. Bingham. 2005. Digestible energy requirements for maintenance of body mass of white-tailed deer in southern Texas. Journal of Mammalogy 86:56-60.

Wallmo, O. 1981. Mule and black-tailed deer of North America. A Wildlife Management Institute Book. University of Nebraska Press. Nebraska, U.S.A.

Webb, S. L., M. R. Dzialak, D. Houchen, K. L. Kosciuch, y J. B. Winstead. 2013. Spatial ecology of female mule deer in an area proposed for wind energy development. Western North American Naturalist 73:347-356.

White, G. C., y R. A: Garrott. 1990. Analysis of radio-tracking data. Academic. San Diego, U.S.A.

Withey, J. C., T. D Bloxton, y J. M. Marzluff. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. Pp. 43-75 *in* Radio tracking and animal populations (Millspaugh, J. J., y J. M. Marzluff, eds.). Academic Press. San Diego, U.S.A.

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A checklist of the parasitic helminths of cricetid and heteromyid rodents in Mexico

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We present an updated checklist of helminth species infecting cricetid and heteromyid rodents (Rodentia: Cricetidae and Heteromyidae) distributed in Mexico. For each helminth record, we include information on helminth taxonomy, location within the host, life stage, host associations, collection localities, citation, and museum collections, when available. We recorded more than 73 helminth species from 47 host species distributed across 21 states in Mexico. The present list represents the most up-to-date knowledge of helminth species infecting cricetid and heteromyid rodents in Mexico.

En el presente trabajo se da a conocer el registro actualizado de los helmintos parásitos que se encuentran en roedores cricétidos y heterómyidos (Rodentia: Cricetidae y Heteromyidae) distribuidos en México. Para cada registro de helminto se incluye la información taxonómica, su localización en el huésped así como su estado de desarrollo y asociación con éste; además de proveer los datos del lugar de colecta, la citas bibliográficas donde han sido registrados y los datos de la colección donde se encuentran depositados, siempre y cuando los datos estén disponibles. Se enlistan más de 73 especies de helmintos que parasitan a 47 especies de huéspedes, distribuidos en 21 estados de la República Mexicana. El presente listado representa el conocimiento más actualizado de las especies de helmintos que infectan roedores cricétidos y heterómidos en México.

Keywords: checklist; Cricetidae; helminth; Heteromyidae; México; parasites.

Introduction

Rodentia is the most diverse order of mammals with 2,552 described species wordwide (Burgin *et al.* 2018). Only In Mexico, there are over 254 rodent species and nearly half of those are endemic (Sánchez-Cordero *et al.* 2014). The families Cricetidae and Heteromyidae are particularly well-represented in Mexico, with approximately 150 and 60 species, respectively (Fernández *et al.* 2014, Burgin *et al.* 2018). Studies of the parasitic helminths (nematodes, cestodes, trematodes, and acanthocephalans) of some of these rodents began in the early to mid 1900s (*e. g.*, Ochoterena and Caballero y Caballero 1932, Chitwood 1938, Zerecero 1943). Since then, multiple studies have surveyed the parasitic fauna of rodents, although these studies are scattered across various journals, books, and museum records. Most recently, García-Prieto *et al.* (2012) compiled a checklist of helminths of mammals in Mexico, including at least 52 helminth species from 30 cricetid and heteromyid host species. However, the checklist by García-Prieto *et al.* (2012) lacks recent host-parasite records. Examination of additonal checklists, publications, and specimens from new field collections is necessary to better understand the helminth fauna of Mexican cricetid and heteromyid species.

Similar to previous checklists, we consolidated records from published checklists and new records to provide an updated and extensive list of helminth species infecting cricetid and heteromyid host species in Mexico. Specifically, we searched for new host-parasite records using Web of Science, using host genus AND "Mexic*", AND "helminth*", "parasit*", "nematod*", "cestod*", or "trematod*" as search terms, and combined these with records from previous checklists (*e. g.*, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Helminth records are grouped by phylum and arranged alphabetically at the order, family, genus, and species levels. For each helminth species, we included data on helminth taxonomy, location within the host, life stage, host associations, collection localities, citation (including both the original citation and subsequent checklists), and museum collections, when available. Specimens listed as collected during the present study were provided by Jesús A. Fernández who collected the hosts in august of 2017 and january of 2018. These registers represent previously unpublished data. Parasite species listed as "sp." from different localities, host species, or publications may represent different species. The host genera *Chaetodipus*, *Dipodomys*, *Heteromys*, and *Perognathus* belong to the family Heteromyidae; all other genera are representatives of Cricetidae. We follow the mammal taxonomy of Burgin *et al.* (2018); for heteromyids, the genus *Liomys* is now recognized as *Heteromys* and all "*Liomys*" host associations are recorded under the genus *Heteromys*.

Abbreviations for the museum records are as follows: CHE-UAEH = Colección de Helmintos, Universidad Autónoma del Estado de Hidalgo in Pachuca, Hidalgo, Mexico; CINZ = Colección de Invertebrados no Artrópodos, Universidad Autónoma de Zacatecas, Zacatecas, Mexico; CNHE = Colección Nacional de Helmintos at the Universidad Nacional Autónoma de México in Mexico City, Mexico; HWML = Harold W. Manter Laboratory of Parasitology, University of Nebraska-Lincoln in Lincoln, Nebraska, United States; MLP-He = Museo de la Plata, Colección Helmintológica, La Plata, Buenos, Aires Argentina; MNHN = Muséum National d'Histoire Naturelle in Paris, France; MZFC-M = Museo de Zoología "Alfonso L. Herrera," Universidad Nacional Autónoma de México in Mexico City, Mexico; UNAM = Universidad Nacional Autónoma de México in Mexico City, Mexico; USNPC = United States National Parasite Collection in Beltsville, Maryland, United States; WHO = World Health Organization Collaborating Centre for Filaroidea Reference Collection, Commonwealth Institute of Parasitology London School of Hygiene and Tropical Medicine, England.

Parasite-Host list

Platyhelminthes Gegenbaur, 1859

Trematoda Rudolphi, 1808

Digenea Carus, 1863

Diplostomida (Poche, 1926) Olson, Cribb, Tkach, Bray, and Littlewood, 2003

Brachylaimidae (Joyeux and Foley, 1930)

Brachylaimidae gen. sp.

Location within Host: Life Stage.

Intestine: Adult.

Estado de México: Cerro Gordo, Otumba: *Peromyscus difficilis* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7563.

Brachylaima bravoae Caballero-Deloya, 1970

Intestine: Adult.

Jalisco: Chamela: *Heteromys pictus* (Caballero-Deloya, 1970, García-Prieto *et al.* 2012). Specimens in collections: CNHE 715, 1495.

Brachylaima chiapensis Ubelaker and Dailey, 1966

Intestine: Adult.

Chiapas: Volcán del Tacaná: *Peromyscus guatemalensis* (Ubelaker and Dailey 1966, García-Prieto *et al.* 2012). Specimens in collections: USNPC 60493.

Brachylaima sp.

Intestine: Adult.

Hidalgo: San Miguel Allende, Tepeapulco: *Peromyscus difficilis* (Pulido-Flores *et al.* 2013, Falcón-Ordaz *et al.* 2015). No specimens in collections.

Diplostomidae Poirier, 1886

Diplostomidae gen. sp.

Intestine: Metacercaria.

Guanajuato: 3 km W of Mineral de Pozos, San Luis de la Paz: *Peromyscus* sp. (Present study). Specimens in collections: CNHE 10887.

Plagiorchiida La Rue, 1957

Dicrocoeliidae Looss, 1899

Caballerolecythus ibunami Lamothe-Argumedo, Falcón-Ordaz, García-Prieto, and Fernández 2005.

Liver: Adult.

Hidalgo: San Miguel Allende, Tepeapulco: *Peromyscus difficilis* (Pulido-Flores *et al.* 2013, Falcón-Ordaz *et al.* 2015). No specimens in collections. Puebla: 1.5 km S of Oriental: *Heteromys irroratus* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7754. Tlaxcala: El Piñonal, El Carmen Tequexquitla: *Heteromys irroratus*, *Peromyscus difficilis* (Lamothe-Argumedo *et al.* 2005, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5211, 5213, USNPC 095892.

Dictyonograptus chamelensis Lamothe-Argumedo, 1980

Bile Ducts: Adult.

Jalisco: Chamela: *Osgoodomys banderanus* (Lamothe-Argumedo 1980, García-Prieto *et al.* 2012). Specimens in collections: CNHE 777.

Cestoda Rudolphi, 1808

Cyclophyllidea van Beneden in Braun, 1900

Cyclophyllidea gen sp.

Stomach: Larva.

Oaxaca: Km. 134 Oaxaca-Tuxtepec Highway: *Peromyscus megalops* (Lynggaard-Islas 2013). Specimens in collections: CNHE 8653.

Anoplocephalidae Cholodkovsky, 1902

Monoecocestus sigmodontis (Chandler and Suttles, 1922)

Intestine: Adult.

Nuevo León: Casas Blancas, Apodaca; El Brasil, Apodaca; Granja La Perla, Apodaca: *Neotoma micropus*, *Peromyscus maniculatus*, *Sigmodon hispidus* (Gutiérrez-González 1980, García-Prieto *et al.* 2012). No specimens in collections.

Paranoplocephala sp.

Intestine: Adult.

Oaxaca: Km. 134 Oaxaca-Tuxtepec Highway: *Microtus oaxacensis*. El Punto, Santa Catarina Ixtepeji: *Peromyscus* sp. (Lynggaard-Islas 2013). Specimens in collections: CNHE 8474, 8475, 8651, 8652.

Catenotaeniidae Spasskii, 1950

Catenotaeniidae gen. sp.

Intestine.

Zacatecas: San Pedro Dam, Ciudad Cuauhtémoc: *Peromyscus* sp. (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ 137, 138.

Catenotaenia peromysci Smith, 1954

Intestine: Adult.

Hidalgo: Paso de León, Metztitlán: *Peromyscus difficilis* (Carmona-Huerta 1994, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015).

Specimens in collections: CNHE 489.

Xihuingo, Tepeapulco: *P. difficilis* (Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 9662.

Catenotaenia sp.

Intestine: Adult.

Guanajuato: 2 km & 7 km W of Mineral de Pozos, San Luis de la Paz: *Peromyscus* sp. (Present study). Specimens in collections: CNHE 10888.

Davaineidae Braun, 1900

Raillietina baeri Meggitt and Subramanian, 1927

Intestine: Adult.

Hidalgo: Huehuetla: *Heteromys irroratus* (Carmona-Huerta 1994, García-Prieto *et al.* 2012). Specimens in collections: CNHE 488.

Note: *Raillietina baeri* is likely misidentified, given that this species is distributed in Africa (Schmidt 1986, García-Prieto *et al.* 2012).

Raillietina celebensis (Janicki, 1902)

Intestine: Adult.

Oaxaca: Cuicatlán: *Oryzomys* sp. (Flores-Barroeta and Hidalgo-Escalante 1960, García-Prieto *et al.* 2012). No specimens in collections.

Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp.

Note: This specimen was originally recorded as *Inermicapsifer* (*Raillietina*) *formosana*, a synonym of *R. celebensis*. *Raillietina celebensis* is distributed in Asia, Australia, and South America, parasitizing *Rattus* and *Bandicota* (Schmidt 1986, García-Prieto *et al.* 2012).

Raillietina sp.

Intestine: Adult.

Durango: La Zarca: *Heteromys pictus* (García-Prieto *et al.* 2012).

Specimens in collections: CNHE 7561.

Puebla: 2 km W of Guadalupe Victoria: *Dipodomys phillipsii* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7756. San Luis Potosí: 32-40 km W of Ciudad Valles: *Oryzomys couesi, Handleyomys melanotis* (recorded as *O. melanotis*) (Underwood *et al.* 1986, García-Prieto *et al.* 2012). No specimens in collections. Note: *H. melanotis* is not distributed in San Luis Potosí according to Téllez and Medellín (2014). Tlaxcala: Barranca Huehuetitla, Panotla: *Heteromys irroratus* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7562. Veracruz: 3 km S of El Frijol Colorado, Perote: *Dipodomys phillipsii* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7755. Yucatán: Xkalakdzonot, Chankom: *Sigmodon toltecus* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7422, CNHE 10714. Zacatecas: Montemariana, Fresnillo: *Chaetodipus* sp. (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ 196, CNHE 8195.

Dilepididae Railliet and Henry, 1909

Dilepididae gen. sp.

Intestine: Adult.

Estado de México: Cerro Gordo, Otumba: *Peromyscus difficilis* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7710.

Choanotaenia sp.

Intestine: Adult.

Colima: La Yerbabuena, Comala: *Peromyscus levipes* (Lynggaard-Islas 2013). Specimens in collections: CNHE 8283. Note: *P. levipes* is not distributed in Colima according to Chávez-Tovar (2014).

Hymenolepididae Ariola, 1899

Hymenolepis diminuta (Rudolphi, 1819) Weiland, 1858

Intestine: Adult.

Colima: Comala: *Hodomys alleni* (Miyazaki *et al.* 1980, García-Prieto *et al.* 2012). No specimens in collections. Hidalgo: Paso de León, Metztitlán: *Peromyscus difficilis* (Carmona-Huerta 1994, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 490.

Hymenolepis horrida (Von Linstow, 1901) Lühe, 1910

Intestine: Adult.

Hidalgo: Paso de León, Metztitlán: *Peromyscus difficilis* (Carmona-Huerta 1994, Falcón-Ordaz *et al.* 2015). No specimens in collections.

Hymenolepis sp.

Intestine: Adult.

Durango: La Zarca, Hidalgo del Parral: *Peromyscus* sp. (Present study). Specimens in collections: CNHE 10889.

Morelos: Tepoztlán: *Baiomys musculus* (Ortiz 1999, García-Prieto *et al.* 2012). No specimens in collections. Puebla: 2 km W of Guadalupe Victoria: *Heteromys irroratus, Reithrodon-*

tomys megalotis (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7757, 7781. Querétaro: Highway junction, el Tejocote, Highway 200 Querétaro-Tequisquiapan: *Heteromys irroratus* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7560. Zacatecas: Rancho La Barranca, Pánuco: *Dipodomys merriami* (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ 130-131.

Rodentolepis nana (vonSiebold, 1952) Blanchard, 1891

Intestine: Adult.

Hidalgo: Paso de León: *Peromyscus difficilis* (Carmona-Huerta 1994, Falcón-Ordaz *et al.* 2015). No specimens in collections. Veracruz: Sierra de Santa Martha: *Peromyscus mexicanus* (Carmona-Huerta 1994, García-Prieto *et al.* 2012). Specimens in collections: CNHE 486. Note: These specimens were collected as *Vampirolepis nana*, which is a synonym of *Rodentolepis nana* (Czaplinski and Vaucher 1994, García-Prieto *et al.* 2012).

Rodentolepis sp.

Intestine: Adult.

Estado de México: Apaxco, Apaxco: *Peromyscus melanotis* (Present study).

Specimens in collections: CNHE 10890.

Hidalgo: Paso de León, Metztitlán: *Peromyscus difficilis* (Carmona-Huerta 1994, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 487. Note: These specimens were collected as *Vampirolepis* sp. and likely represent *Rodentolepis* sp. (García-Prieto *et al.* 2012). Veracruz: Estación de Biología Los Tuxtlas: *Peromyscus* sp. (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7709.

Taeniidae Ludwig, 1886

Hydatigera taeniaeformis (Batsch, 1786) Lamarck, 1816

Liver: Cysticerci.

Nuevo León: Casas Blancas, Apodaca; El Brasil, Apodaca: *Sigmodon hispidus* (Gutiérrez-González 1980, García-Prieto *et al.* 2012). No specimens in collections. Yucatán: Xkalakdzonot, Chankom: *Sigmodon toltecus* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7425, 7361, 7362, CNHE 10701, 10702, 10707. Note: The specimens from Nuevo León were recorded as *Cysticercus fasciolaris* which refers to the larval stage of *Taenia taeniformis* (Martínez *et al.* 2013). Using phylogenies generated by nuclear and mitochondrial genes, Nakao *et al.* (2013) demonstrated that *T. taeniformis, T. krepkogorski* and *T. parva* are only distantly related to the other members of *Taenia*, and proposed the resurrection of genus *Hydatigera* Lamarck, 1816 for these species.

Taenia multiceps Leske, 1780

Dermis: Coenuri.

Hidalgo: Paso de León, Metztitlán: *Peromyscus leucopus* (Carmona-Huerta 1994, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 491. Note: Specimens were originally collected as *Multiceps multiceps*, a synonym of *T. multiceps* (Schmidt 1986, García-Prieto *et al.* 2012).

Taenia pisiformes (Bloch, 1780) Gmelin, 1790

Mesentary: Cysticerci.

Hidalgo: Paso de León, Metztitlán: *Peromyscus difficilis* (Carmona-Huerta 1994, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 485.

Taenia sp.

Liver, Dermis: Cysticerci.

Hidalgo: San Miguel Allende, Tepeapulco: *Peromyscus difficilis*, *Peromyscus* sp. (Pulido-Flores *et al.* 2013, Falcón-Ordaz *et al.* 2015). No specimens in collections. Rancho Santa Elena, Tulancingo: *P. maniculatus* (Pulido-Flores *et al.* 2005, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CHE-UAEH F00012.

Acanthocephala (Rudolphi, 1808)

Archiacanthocephala Meyer, 1931

Moniliformida Schmidt, 1972

Moniliformidae Van Cleave, 1924

Moniliformis sp.

Intestine: Adult.

Jalisco: Puerto el Floripondio, San Gabriel: *Peromyscus* sp., *Peromyscus hylocetes*. (Lynggaard-Islas 2013). Specimens in collections: CNHE 8646-8650, 9472.

Nematoda Rudolphi, 1808

Enoplea

Trichinellida Hall, 1916

Trichuridae (Ransom, 1911) Railliet, 1915

Calodium hepaticum (Bancroft, 1893)

Liver: Adult.

Estado de México: Cerro Gordo, Otumba: *Peromyscus difficilis* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7567.

Capillaria sp.

Intestine: Adult.

Hidalgo: Xihuingo, Tepeapulco: *Peromyscus difficilis* (Falcón-Ordaz *et al.* 2015). No specimens in collections.

Eucoleus gastricus (Baylis, 1926)

Intestine: Adult.

Hidalgo: Rancho Santa Elena: *Peromyscus maniculatus* (Pulido-Flores *et al.* 2005, García-Prieto *et al.* 2012). Specimens in collections: CHE-UAEH F00009. Note: This specimen was collected as *Capillaria gastrica* (García-Prieto *et al.* 2012).

Trichuris dipodomis Read, 1956

Intestine.

Guanajuato: 3 km N of San Luis de La Paz: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE: 9839. Note: *D. merriami* is not distributed in Guanajuato according to Castillo (2014). Veracruz: 3 km S of El Frijol Colorado, Perote: *Dipodomys phillipsii* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7750. Zacatecas: Rancho La Barranca, Pánuco; Rancho El Godillo, Loreto: *Dipodomys merriami*. Tlalticoaloya, Susticacán; Villa de Cos, Villa de Cos: *Chaetodipus* sp. Montemariana, Fresnillo: *D. merriami*, *Peromyscus* sp. (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ: 134, 135, 175, 197, 200-202, CNHE 10003, 10004. Note: *T. dipodomis* is often spelled as *T. dipodomys* in the literature.

Trichuris elatoris Pfaffenberger and Best, 1989

Intestine: Adult.

San Luis Potosí: El Carranco: *Dipodomys ordii*. 15 km NE of Villa de Reyes: *Chaetodipus hispidus, D. merriami* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7706-7708.

Trichuris fossor Hall, 1916

Caecum: Adult.

Hidalgo: Huehuelta: *Peromyscus difficilis* (Falcón-Ordaz 1993, Lamothe-Argumedo *et al.* 1997, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2013, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 2283. Morelos: Reserva Estatal Sierra de Monte Negro: *Heteromys irroratus* (Eslava-Araujo 2005, García-Prieto *et al.* 2012). No specimens in collections.

Trichuris muris (Schrank, 1788)

Intestine, Caecum: Adult.

Morelos: Reserva Estatal Sierra de Monte Negro: *Heteromys irroratus* (Eslava-Araujo 2005, García-Prieto *et al.* 2012). No specimens in collections.

Trichuris silviae Panti-May and Robles, 2016

Caecum: Adult.

Yucatán: Rancho Hobonil, Municipality of Tzucacab: *Heteromys gaumeri* (Panti-May and Robles, 2016). Specimens in collections: MLP-He 7113-7115, CNHE 9987. Xkalakdzonot, Chankom: *H. gaumeri* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7428, CNHE 10704.

Trichuris sp.

Intestine, Caecum: Adult.

Chiapas: Mapastepec: *Heteromys pictus* (Caballero y Caballero 1958, García-Prieto *et al.* 2012). Specimens in collections: CNHE 2366. Chihuahua: Área de Protección de Flora y Fauna Cerro del Mohinora, Guadalupe y Calvo: *Microtus* sp., *Microtus mexicanus, Peromyscus melanotis* (Present study). Specimens in collections: CNHE: 10843, 10848, 10850. Hidalgo: Xihuingo, Tepeapulco: *Peromyscus difficilis* (Falcón-Ordaz *et al.* 2015). No specimens in collections. Morelos: Tepoztlán: *Heteromys pictus* (Ortiz 1999, García-Prieto *et al.* 2012). No specimens in collections. Note: *H. pictus* is not distributed in Morelos according to Ceballos (2014). Yucatán: Paraíso, Maxcanú: *Peromyscus yucatanicus* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7429.

Trichuris sp.

Feces: Eggs.

Chihuahua: Biosphere Reserve, Janos-Casas Grandes: *Dipodomys spectabilis* (Rendón-Franco *et al.* 2014). No specimens in collections.

Chromadorea

Rhabditida Chitwood, 1933

Gongylonematidae (Hall, 1916) Sobolev, 1949

Gongylonema peromysci Kruidenier and Peebles, 1958

Stomach: Adult.

Puebla: 2 km W of Guadalupe Victoria: *Reithrodontomys megalotis* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7753.

Gongylonema sp.

Intestine: Adult.

Zacatecas: Rancho La Barranca, Pánuco: *Dipodomys merriami* (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ 132.

Heteroxynematidae Skrjabin and Shikhobalova, 1948

Aspiculuris americana Erickson, 1938

Caecum: Adult.

Chihuahua: Área de Protección de Flora y Fauna Cerro del Mohinora, Guadalupe y Calvo: *Peromyscus boylii* (Present study). Specimens in collections: CNHE 10845, 10917, 10918.

Aspiculuris sp.

Intestine, Caecum: Adult.

Morelos: Tepoztlán: *Neotoma mexicana* (Ortiz 1999, García-Prieto *et al.* 2012). No specimens in collections. Oaxaca: Km. 134 Oaxaca-Tuxtepec Highway: *Microtus oaxacensis* (Lynggaard-Islas 2013). Specimens in collections: CNHE 8658-8661.

Aspiculuris n. sp.

Rectum: Adult.

Hidalgo: San Miguel Allende, Tepeapulco: *Peromyscus difficilis*, *Peromyscus* sp. (Pulido-Flores *et al.* 2013, Falcón-Ordaz *et al.* 2015). No specimens in collections.

Lamotheoxyuris ackerti (Kruidenier and Mehra, 1959)

Intestine: Adult.

Veracruz: 3 km S of El Frijol Colorado, Perote: *Neotoma nelsoni* (Falcón-Ordaz *et al.* 2010, García-Prieto *et al.* 2012). Specimens in collections: CNHE 6839.

Lamotheoxyuris cf. *ackerti* Falcón-Ordaz, Fernández, and García-Prieto, 2010

Intestine: Adult.

Zacatecas: Rancho La Barranca, Pánuco: *Neotoma mexicana* (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ 136.

Onchocercidae (Leiper, 1911)

Dunnifilaria meningica Gutiérrez-Peña, 1987

Cerebellum: Adult.

Nuevo León: Municipio Dr. Coss: *Neotoma micropus* (Gutiérrez-Peña 1987, García-Prieto *et al.* 2012). Specimens in collections: CNHE 2563, 2564, WHO B-572, USNPC 080270.

Litomosoides carinii (Travassos, 1919)

Body cavity, heart, mesentery: Adult.

Nuevo León: Casas Blancas, Apodaca: *Sigmodon hispidus* (Gutiérrez-González 1980, García-Prieto *et al.* 2012). No specimens in collections.

Litomosoides sigmodontis Chandler, 1931

Body cavity, heart, mesentery: Adult.

Jalisco: *Sigmodon hispidus* (Ochoterena and Caballero y Caballero 1932, García-Prieto *et al.* 2012). No specimens in collections. Note: *S. hispidus* is not distributed in Jalisco according to Ramírez *et al.* (2014). Michoacán: *Sigmodon hispidus* (Ochoterena and Caballero y Caballero 1932, García-Prieto *et al.* 2012). Specimens in collections: CNHE 2573-2579. *Sigmodon fulviventer* (Zerecero 1943, García-Prieto *et al.* 2012). Specimens in collections: CNHE 3015. Note: *S. hispidus* is not distributed in Michoacán according to Ramírez *et al.* (2014). Note: These specimens were originally recorded as *Micropleura sigmodonti* (García-Prieto *et al.* 2012).

Onchocercidae gen. sp. 1

Zacatecas: Estación Camacho, Mazapil: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9840.

Onchocercidae gen. sp. 2

San Luis Potosí: La Tinaja, Soledad de Graciano Sánchez: *Chaetodipus hispidus* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9841.

Oxyuridae Cobbold, 1864

Heteromyoxyuris longejector Quentin, 1973

Intestine.

Durango: Cuencamé. La Zarca, Hidalgo: *Chaetodipus hispidus* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9831, 9834. Guanajuato: Mineral de Pozos, San Luis de La Paz: *Chaetodipus hispidus* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9832, 9833. San Luis Potosí: La Tinaja, Soledad de Graciano Sánchez: *Chaetodipus hispidus* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9836. 15 km NE of Villa de Reyes: *C. hispidus* (García-Prieto *et al.* 2008, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5479, 5729. Sonora: Mazatán: *Perognathus amplus* (García-Prieto *et al.* 2008, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5262. Zacatecas: Rancho La Barranca, Pánuco: *Dipodomys merriami*, *Chaetodipus* sp. Rancho El Godillo, Loreto: *Chaetodipus* sp. Ojocaliente, Ojocaliente: *Peromyscus* sp. Villa de Cos, Villa de Cos: *Dipodomys merriami*, *Chaetodipus* sp. (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ 139, 145-147, 188-190, 192, CNHE 9996-9999. Estación Camacho, Mazapil: *Chaetodipus eremicus, Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9835, 9837.

Heteromyoxyuris otomii García-Prieto, Falcón-Ordaz, Lira-Guerrero, and Mendoza-Garfias, 2008

Caecum: Adult.

Guanajuato: Mineral de Pozos, San Luis de La Paz: *Perognathus flavus* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9838. Hidalgo: Ignacio Zaragoza, Ajacuba: *Perognathus flavus* (García-Prieto *et al.* 2008, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 5480-5482.

Heteromyoxyuris sp.

Guanajuato: 3 km N of San Luis de La Paz: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 5678. Note: *D. merriami* is not distributed in Guanajuato according to Castillo (2014).

Syphacia (*Seuratoxyuris*) *obvelata* (Rudolphi, 1802) Seurat, 1918

Caecum: Adult.

Yucatán: Chichen-Itzá: *Ototylomys phyllotis* (Chitwood 1938, García-Prieto *et al.* 2012). Specimens in collections: CNHE 1950.

Syphacia (*Seuratoxyuris*) *peromysci* Harkema, 1936

Caecum, Large Intestine: Adult and Larva.

Chihuahua: Área de Protección de Flora y Fauna Cerro del Mohinora, Guadalupe y Calvo: *Peromyscus* sp., *Peromyscus boylii*, *P. maniculatus*, *P. melanotis* (Present study). Specimens in collections: CNHE 10847, 10915, 10916, 10980. Hidalgo: Rancho Santa Elena, Tulancingo: *Peromyscus maniculatus* (Pulido-Flores *et al.* 2005, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CHE-UAEH F00011, CNHE 5317. Veracruz: 3 km S of El Frijol Colorado, Municipality of Perote: *Peromyscus difficilis* (Falcón-Ordaz *et al.* 2016). Specimens in collections: CNHE 5671. Yucatán: Paraíso, Maxcanú: *Peromyscus yucatanicus* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7436, CNHE 10709.

Syphacia sp.

Caecum, Intestine: Adult.

Chihuahua: Área de Protección de Flora y Fauna Cerro del Mohinora, Guadalupe y Calvo: *Microtus* sp., *Microtus mexicanus* (Present study). Specimens in collections: CNHE 10844, 10849. Guanajuato: Mineral de Pozos, San Luis de La Paz: *Reithrodontomys* sp. (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9845. Hidalgo: Camino a Zempoala; Xihuingo, Tepeapulco: *Peromyscus difficilis*. Huehuetla: *Peromyscus mexicanus* (Falcón-Ordaz *et al.* 2013, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 6888. Morelos: Reserva Estatal Sierra de Monte Negro: *Heteromys irroratus* (Eslava-Araujo 2005, García-Prieto *et al.* 2012). No specimens in collections. Oaxaca: La Hierba Buena: *Oryzomys* sp., *Peromyscus aztecus* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 6888, 7701. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. San Luis Potosí: 32-40 km W of Ciudad Valles: *Oligoryzomys fulvescens, Handleyomys melanotis* (recorded as *Oryzomys melanotis*) (Underwood *et al.* 1986, García-Prieto *et al.* 2012). No specimens in collections. Note: *H. melanotis* is not distributed in San Luis Potosí according to Téllez and Medellín (2014). Veracruz: 3 km S of El Frijol Colorado, Perote: *Peromyscus difficilis* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7752. Yucatán: Xkalakdzonot, Chankom: *Heteromys gaumeri* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7437, CNHE 10715.

Syphacia sp.

Feces: Eggs.

Chihuahua: Biosphere Reserve, Janos-Casas Grandes: *Perognathus flavus*. (Rendón-Franco *et al.* 2014). No specimens in collections.

Physalopteridae (Railliet, 1893)

Physalopteridae gen. sp.

San Luis Potosí: La Tinaja, Soledad de Graciano Sánchez: *Onychomys arenicola* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9904.

Physaloptera sp.

Stomach, Intestine: Larva, Adult.

Hidalgo: Chacaya, Eloxochitlán: *Peromyscus* sp. (Present study). Specimens in collections: CNHE 10919. Morelos: Tepoztlán: *Sigmodon hispidus* (Ortiz 1999, García-Prieto *et al.* 2012). No specimens in collections. Note: *S. hispidus* is not distributed in Morelos according to Ramírez *et al.* (2014).

Turgida sp.

Stomach: Adult.

Oaxaca: Teotitlán: *Oryzomys* sp. (Donated by H. Wagner, 1941, García-Prieto *et al.* 2012). Specimens in collections: CNHE 2589. Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. Note: These specimens were originally recorded as *Turgida torresi* but due to the poor condition of specimens, specific identification was not possible (Lamothe-Argumedo *et al.* 1997, García-Prieto *et al.* 2012).

Rictulariidae (Hall, 1915) Railliet, 1916

Pterygodermatites baiomydis Lynggaard, García-Prieto, Guzmán-Cornejo, and Osorio-Sarabia, 2014

Intestine: Adult.

Colima: La Yerbabuena: *Baiomys taylori* (Lynggaard *et al.* 2014). *Specimens in collections:* MZFC-M 11988, 12294.

Pterygodermatites dipodomis Tiner, 1948

Intestine: Adult.

Guanajuato: 3 km N of San Luis de La Paz: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9844. Note: *Dipodomys merriami* is not distributed in Guanajuato according to Castillo (2014). San Luis Potosí: 15 km NE of Villa de Reyes: *Dipodomys merriami* (Present study). Specimens in collections: CNHE 10893l. La Tinaja, Soledad de Graciano Sánchez: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017).

Specimens in collections: CNHE 9843. El Carranco: *Dipodomys ordii*. 15 km NE of Villa de Reyes: *Dipodomys merriami* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7702, 7703. Zacatecas: San Pedro Dam, Ciudad Cuauhtémoc: *Peromyscus* sp. Rancho La Barranca, Pánuco; Rancho El Godillo, Loreto: *Dipodomys merriami*. Villa de Cos, Villa de Cos: *Dipodomys merriami*, *Chaetodipus* sp. (Martínez-Salazar *et al.* 2016). Specimens in collections: CNHE 10000, 10001, CINZ 144, 191, 194, 199. Estación Camacho, Mazapil: *Dipodomys merriami*. (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9842.

Pterygodermatites (*Paucipectines*) *parkeri* Lichtenfels, 1970

Intestine: Adult.

Estado de México: Hueypoxtla, Hueypoxtla: *Peromyscus* sp. (Present study). Specimens in collections: CNHE 10912.

Puebla: 2 km W of Guadalupe Victoria: *Dipodomys phillipsii* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7704.

Pterygodermatites (*Paucipectines*) *peromysci* Lichtenfels, 1970

Intestine: Adult.

Chihuahua: Granjas Universitarias, Chihuahua: *Peromyscus melanotis* (Present study). Specimens in collections: CNHE 10846. Hidalgo: Xihuingo, Tepeapulco: *Peromyscus difficilis* (Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 9072. Peñas Cargadas, Epazoyucan: *Peromyscus gratus*. (Present study). Specimens in collections: CNHE 10914. Veracruz: 3 km S of El Frijol Colorado, Perote: *Peromyscus maniculatus* (Falcón-Ordaz *et al.* 2012, García-Prieto *et al.* 2012). Specimens in collections: CNHE 7751.

Pterygodermatites sp.

Intestine: Adult.

Hidalgo: Pachuca de Soto: *Peromyscus leucopus*. Xoxafi, Santiago de Anaya: *Heteromys irroratus* (Present study). *Specimens in collections*: CNHE 10862, 10913.

Spiruridae Oerlèy, 1885

Mastophorus dipodomis Read and Millemann, 1953

Stomach.

Durango: Cuencamé: *Chaetodipus* sp. (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE: 9942. Guanajuato: Mineral de Pozos, San Luis de La Paz: *Chaetodipus* sp. 3 km N of San Luis de La Paz: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE: 9943. Note: *Dipodomys merriami* is not distributed in Guanajuato according to Castillo (2014). Zacatecas: Estación Camacho, Mazapil: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE: 9944. Rancho La Barranca, Pánuco: *Dipodomys merriami*, *Chaetodipus* sp. Rancho El Godillo, Loreto: *Dipodomys merriami*. Villa de Cos: *Chaetodipus* sp. (Martínez-Salazar *et al.* 2016). Specimens in collections: CINZ: 133, 140-143, 193, 198, CNHE 10002. Notes: *Mastophorus dipodomis* (Martínez-Salazar *et al.* 2016) is likely a synonym of *Protospirura dipodomis* (Iturbe-Morgado *et al.* 2017) (see Yamaguti 1961, King and Babero 1974).

Mastophorus muris (Gmelin, 1790)

Intestine: Stomach.

San Luis Potosí: 15 km NE of Villa de Reyes: *Dipodomys merriami* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7705.

Protospirura mexicana Falcón-Ordaz & Sanabria-Espinoza, 1995

Intestine: Adult.

Hidalgo: Huehuetla: *Peromyscus difficilis* (Falcón-Ordaz and Sanabria-Espinosa 1995, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 2291, 2292.

Protospirura sp.

Stomach: Adult and Larva.

Chihuahua: Granjas Universitarias, Chihuahua: *Chaetodipus* sp., *Sigmodon hispidus* (Present study). Specimens in collections: CNHE: 10894, 10923. Note: *S. hispidus* is not distributed in Chihuahua according to Ramírez *et al.* (2014). Durango: La Zarca: *Onychomys torridus* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7566. Note: *O. torridus* is not distributed in Durango according to Ceballos (2014). San Luis Potosí: 15 km NE of Villa de Reyes: *Dipodomys merriami* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7569.

Subuluridae Yorke and Maplestone, 1926

Subulura sp.

San Luis Potosí: La Tinaja, Soledad de Graciano Sánchez: *Onychomys arenicola* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 9903.

Strongylida Diesing, 1851

Heligmonellidae (Skrjabin and Schikhobalova, 1952)

Carolinensis carolinensis (Dickmans, 1935) Travassos, 1937

Intestine: Adult.

Hidalgo: Rancho Santa Elena, Tulancingo: *Peromyscus maniculatus* (Pulido-Flores *et al.* 2005, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 5321, CHE-UAEH P-00010.

Carolinensis huehuetlana Falcón-Ordaz and Sanabria-Espinoza, 1996

Intestine: Adult.

Hidalgo: Huehuetla: *Peromyscus difficilis, Peromyscus mexicanus* (Falcón-Ordaz and Sanabria-Espinoza, 1996, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2013, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 2298, UNAM 199-194. San Miguel Allende; Xihuingo, Tecocomulco: *Peromyscus difficilis* (Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 6887.

Carolinensis perezponcedeleoni Jiménez, 2012

Intestine: Adult.

Veracruz: Adolfo López Mateos: *Nyctomys sumichrasti* (Jiménez, 2012). Specimens in collections: CNHE 7665-7667, HWML 67094-67097.

Carolinensis peromysci (Durette-Desset, 1974)

Intestine: Adult.

Yucatán: Paraíso, Maxcanú: *Peromyscus yucatanicus* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7440.

Carolinensis petteri (Denke, 1977)

Intestine: Adult.

Veracruz: Estación de Biología Los Tuxtlas: *Peromyscus mexicanus* (Denke 1977, García-Prieto *et al.* 2012). Specimens in collections: MNHN 1052. Note: This specimen was originally recorded as *Boreostrongylus*, a synonym of *Carolinensis* (Durette-Desset 1983, García-Prieto *et al.* 2012).

Carolinensis sp.

Intestine: Adult.

Oaxaca: *Peromyscus* sp. (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7695, 7696.

Hassalstrongylus aduncus (Chandler, 1932)

Intestine: Adult.

Hidalgo: Huehuetla: *Sigmodon hispidus* (García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2013, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 6887. Note: *Sigmodon hispidus* is not distributed in Hidalgo according to Ramírez *et al.* (2014). Jalisco: Viborillas, Encarnación de Díaz: *Sigmodon hispidus* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 8064. Note: *S. hispidus* is not distributed in Jalisco according to Ceballos (2014). Yucatán: Xkalakdzonot, Chankom: *Sigmodon toltecus* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7431, 7442, CNHE 10713.

Hassalstrongylus bocqueti Denke 1977

Intestine: Adult.

San Luis Potosí: 32-40 km W of Ciudad Valles: *Oligoryzomys fulvescens*, *Oryzomys couesi*, *Handleyomys melanotis* (recorded as *Oryzomys melanotis*) (Underwood *et al.* 1986, García-Prieto *et al.* 2012). No specimens in collections. Note: *Handleyomys melanotis* is not distributed in San Luis Potosí according to Téllez and Medellín (2014). Veracruz: Estación de Biología Los Tuxtlas: *Handleyomys alfaroi* (recorded as *Oryzomys alfaroi*) (Denke 1977, García-Prieto *et al.* 2012). Specimens in collections: MNHN 1045.

Hassalstrongylus musculi (Dickmans, 1935)

Intestine: Adult.

San Luis Potosí: 32-40 km W of Ciudad Valles: *Oligoryzomys fulvescens*, *Oryzomys couesi*, *Handleyomys melanotis* (recorded as *Oryzomys melanotis*) (Underwood *et al.* 1986, García-Prieto *et al.* 2012). No specimens in collections. Note: *Handleyomys melanotis* is not distributed in San Luis Potosí according to Téllez and Medellín (2014).

Hassalstrongylus sp.

Intestine: Adult.

Oaxaca: La Hierba Buena: *Peromyscus aztecus* (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7697.

Paraheligmonella sp.

Intestine: Adult.

Oaxaca: Km. 134 Oaxaca-Tuxtepec Highway: *Microtus oaxacensis*, *Peromyscus megalops* (Lynggaard-Islas 2013). Specimens in collections: CNHE 8654-8657.

Stilestrongylus hidalguensis Falcón-Ordaz and Sanabria-Espinoza, 1999

Intestine: Adult.

Hidalgo: Atlatilpan Huitzotlalco: *Peromyscus* sp. (Falcón-Ordaz and Sanabria-Espinoza, 1999, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 2293-2295, 2297, 3293.

Stilestrongylus peromysci Falcón-Ordaz and Sanabria-Espinoza, 1999

Intestine: Adult.

Hidalgo: Huehuetla: *Peromyscus difficilis* (Falcón-Ordaz and Sanabria-Espinoza, 1999, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 2296, 3263.

Stilestrongylus sp.

Intestine: Adult.

Oaxaca: La Hierba Buena: *Oryzomys* sp. (García-Prieto *et al.* 2012). Specimens in collections: CNHE 7698.

Note: *Oryzomys* sp. was recorded in the original literature but may represent *Handleyomys* sp. Yucatán: Paraíso, Maxcanú: *Peromyscus yucatanicus* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7439.

Heligmosomidae (Travassos 1914)

Longistriata sp.

Intestine: Adult.

Nuevo León: Casas Blancas, Apodaca; El Brasil, Apodaca; La Perla, Apodaca: *Neotoma micropus, Peromyscus maniculatus, Sigmodon hispidus* (Gutiérrez-González 1980, García-Prieto *et al.* 2012). No specimens in collections.

Ornithostrongylidae (Travassos, 1937)

Vexillata armande Gardner, Fong, Al-Banna, and Raymond, 1994

Intestine: Adult.

Estado de México: Atla, Axapusco: *Perognathus flavus* (Escalante *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5840. Note: These specimens were listed as *Vexillata* cf. *armande* (García-Prieto *et al.* 2012). Guanajuato: Mineral de Pozos, San Luis de La Paz: *Chaetodipus* sp. (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 5677.

Vexillata dessetae Denke 1977

Intestine: Adult.

Veracruz: Adolfo López Mateos: *Heteromys desmarestianus* (Escalante *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5847. Estación de Biología Los Tuxtlas: *H. desmarestianus* (Denke 1977, García-Prieto *et al.* 2012). Specimens in collections: MNHN 1047, CNHE 4817.

Vexillata legallae Denke 1977

Intestine: Adult.

Veracruz: Adolfo López Mateos: *Heteromys desmarestianus* (Escalante *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5846. Estación de Biología Los Tuxtlas: *Heteromys desmarestianus* (Denke 1977, García-Prieto *et al.* 2012). Specimens in collections: MNHN 1054, CNHE 4818.

Vexillata liomyos Falcón-Ordaz, Gardner, and Pérez-Ponce de León, 2001

Intestine: Adult.

Jalisco: Chamela: *Heteromys pictus* (Falcón-Ordaz, Gardner, and Pérez-Ponce de León, 2001, Escalante *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 3911-3914. Morelos: Reserva Estatal Sierra de Monte Negro: *Heteromys irroratus* (Ortíz-Villaseñor *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5294. Nayarit: 1.4 km N of Tacote: *Heteromys pictus* (Escalante *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5616. Tlaxcala: Barranca Huehuetitla, Panotla; 2 km E of San Andrés Cuajimalpa: *Heteromys irroratus* (Escalante *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 5294, 5296, 5845. Zacatecas: Estación Camacho, Mazapil: *Dipodomys merriami* (Iturbe-Morgado *et al.* 2017). Specimens in collections: CNHE 5676.

Vexillata vexillata (Hall, 1916) Durette-Desset, 1971

Intestine: Adult.

Chiapas: Mapastepec: *Heteromys pictus* (Caballero y Caballero 1958, Escalante *et al.* 2011, García-Prieto *et al.* 2012). Specimens in collections: CNHE 2355. Note: These specimens were originally collected as *Longistriata vexillata*. Hidalgo: Atlatilpan; Huehuetla: *Heteromys irroratus*, *Peromyscus difficilis* (Sanabria-Espinosa *et al.* 1996, Falcón-Ordaz and Sanabria-Espinosa 1997, Escalante *et al.* 2011, García-Prieto *et al.* 2012, Falcón-Ordaz *et al.* 2013, Falcón-Ordaz *et al.* 2015). Specimens in collections: CNHE 2282, 2290, 5295. Morelos: Tepoztlán: *Heteromys irroratus* (Ortiz 1999, García-Prieto *et al.* 2012). No specimens in collections. Yucatán: Xkalakdzonot, Chankom: *Heteromys gaumeri* (Panti-May *et al.* 2018). Specimens in collections: MLP-He 7430, CNHE 10705.

Strongylidae Baird, 1853
Unknown genus

Feces: Eggs.

Chihuahua: Biosphere Reserve, Janos-Casas Grandes: *Onychomys leucogaster* (Rendón-Franco *et al.* 2014). No specimens in collections. Note: *Onychomys leucogaster* is not distributed in Chihuahua according to Tobón-García (2014).

Discussion

In our updated checklist, we increase the number of known host-parasite records to at least 73 helminth species from 35 cricetid and 12 heteromyid species collected across 21 states in Mexico. The reported number of helminth species of these rodents is likely underestimating the total helminth diversity of cricetids and heteromyids in Mexico for two reasons. First, this checklist reports some parasite specimens identified only to genus. Specific identification of these specimens and descriptions of new species will likely result in additional species. Second, with only 47 of 190 cricetid and heteromyid rodent species in Mexico sampled, much of the parasite fauna of these host families is unknown. Sampling of additional host species not represented here will likely result in more helminth species.

While we report a checklist of helminths of cricetid and heteromyid rodents in Mexico, Light *et al.* (2019) similarly compiled a checklist of all ectoparasites (fleas, mites, ticks, and lice). Although these checklists represent the most up-to-date knowledge of the macroparasite fauna of cricetid and heteromyid rodents in Mexico, there are still large gaps in our knowledge. We therefore encourage “holistic” collections of rodents, where all available data, including ecto- and endoparasites, are recorded during specimen collections (Cook *et al.* 2016, 2017, Webster 2017, Cook and Light 2019). We also urge researchers to deposit parasites into appropriate natural history collections, as parasites are often underrepresented in these collections (Bell *et al.* 2018), to ensure their availability and continued contribution to future research.

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Literature cited

Bell, K. C., C. J. Carlson, and A. J. Phillips. 2018. Parasite collections: overlooked resource for integrative research and conservation. Trends in Parasitology 34:637–639.

Burgin, C. J., J. P. Colella, P. L. Kahn, and N. S. Upham. 2018. How many species of mammals are there? Journal of Mammalogy 99:1–14.

Caballero y Caballero, C. E. 1958. Estudios helmintológicos de la región oncocercosa de México y de la República de Guatemala. Nematoda 10ª Parte. Anales de la Escuela Nacional de Ciencias Biológicas 9:61–76.

Caballero-Deloya, J. 1970. Descripción de *Brachylaemus* (*Brachylaemus*) *bravoae* sp., nov., (Trematoda: Digenea) de roedores del Estado de Jalisco, México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México 41:39– 44.

Carmona-Huerta, A. 1994. Contribución al conocimiento de céstodos en roedores silvestres (Rodentia) del Estado de Hidalgo y Veracruz. B. S. Thesis, Escuela Nacional de Estudios Profesionales, Iztacala, Universidad Nacional Autónoma de México, Los Reyes, Estado de México, México.

Castillo, R. A. 2014. *Dipodomys merriami* Mearns, 1890; Merriam's kangaroo rat. Pp 201–202 *in* Mammals of Mexico. (Ceballos, G., ed). Johns Hopkins University Press.

Ceballos, G. 2014. *Onychomys torridus* (Coues, 1874); Southern grasshopper mouse. Pp 324–325 *in* Mammals of Mexico. (Ceballos, G., ed). Johns Hopkins University Press.

Ceballos, G. (ed). 2014. Mammals of Mexico. Johns Hopkins University Press. Baltimore, U.S.A.

Ceballos, G., and J. Arroyo-Cabrales. 2012. Lista actualizada de los mamíferos de México. Revista Mexicana de Mastozoología, Nueva Época 2:27–80.

Chávez-Tovar, J. C. 2014. *Peromyscus levipes* Merriam, 1898, Nimble-footed deermouse. Pp 368–369 *in* Mammals of Mexico. (Ceballos, G., ed). Johns Hopkins University Press. Baltimore, U.S.A.

Chitwood, B. G. 1938. Some nematodes from the caves of Yucatan IV. Carnegie Institution of Washington Publication 491:51–66.

Cholodkovsky, N. 1902. Contributions à la connaissance des ténias des des ruminants. Archives de Parasitologie 6:145–148.

Cook, J. A., S. Greiman, S. Agosta, R. P. Anderson, B. S. Arbogast, R. J. Baker, W. Boeger, R. D. Bradley, D. R. Brooks, R. Cole, J. R. Demboski, A. P. Dobson, J. L. Dunnum, R. P. Eckerlin, J. Esselstyn, K. Galbreath, J. Hawdon, H. Hoekstra, S. Kutz, J. E. Light, L. Olson, B. D. Patterson, J. L. Patton, A. J. Phillips, E. Rickart, D. S. Rogers, M. E. Siddall, V. Tkach, and E. P. Hoberg. 2016. Transformational principles for NEON sampling of mammalian parasites and pathogens: a response to Springer and colleagues. BioScience 66:917–919.

Cook, J. A., K. E. Galbreath, K. C. Bell, M. L. Campbell, S. Carrière, J. P. Colella, N. G. Dawson, J. L. Dunnum, R. P. Eckerlin, S. E. Greiman, V. Fedorov, G. M. S. Hass, V. Haukisalmi, H. Henttonen, A. G. Hope, D. Jackson, T. Jung, A. V. Koehler, M. Kinsella, D. Krejsa, S.J. Kutz, S. Liphardt, S. O. MacDonald, J. L. Malaney, A. Makarikov, J. Martin, B. S. McLean, R. Mulders, B. Nyamsuren, S. L. Talbot, V. V. Tkach, A. Tsvetkova, H. M. Toman, E. C. Waltari, J. L. Whitman, and E. P. Hoberg. 2017. The Beringian coevolution project: Holistic collections of mammals and associated parasites reveal novel perspectives on evolutionary and environmental change in the north. Arctic Science 3:585–617.

Cook, J. A. and J. E. Light. 2019. The emerging role of mammal collections in 21st century mammalogy. Journal of Mammalogy 100:733–750.

Czaplinski, B., and C. Vaucher. 1994. Family Hymenolepididae Ariola, 1899. Pp. 595–663 *in*: Keys to the cestode parasite of vertebrates (Khalil, L. F., A. Jones, and R. A. Bray, Eds.). CAB International, Wallingford, UK.

Denke, M. A. 1977. Quatre nouveaux Nématodes Héligmosomes parasites de Rongeurs du Mexique. Bulletin du Musée Nationelle d' Histoire Naturelle 470:777–787.

Domínguez, Y. and G. Ceballos. 2014. *Liomys pictus* (Thomas, 1893), Painted spiny pocket mouse. Pp 215–216 *in* Mammals of Mexico (Ceballos, G., ed). Johns Hopkins University Press.

Escalante, T., E. A. Martínez, J. Falcón-Ordaz, M. Linaje, and R. A. Guerrero. 2011. Análisis panbiogeográfico de *Vexillata* (Nematoda: Ornithostrongylidae) y sus huéspedes. Acta Zoológica Mexicana (nueva serie) 27:25–46.

Eslava-Araujo, A. G. 2005. Helmintos en la mastofauna silvestre de la Sierra de Monte Negro, Morelos, México. B. S. Thesis, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, México.

Falcón-Ordáz, J. 1993. Estudio taxonómico de los nemátodos parásitos de roedores de los géneros *Peromyscus y Liomys*, de Huehuetla y Atlatilpan, Estado de Hidalgo. B. S. Thesis, Escuela Nacional de Estudios Profesionales, Iztacala, Universidad Nacional Autónoma de México, Los Reyes, México.

Falcón-Ordáz, J., and M. A. Sanabria. 1995. Especie nueva del género *Protospirura* (Nemata: Spiriridae) de *Peromyscus difficilis* (Rodentia: Cricetidae) de Hidalgo, México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México 66:17–26.

Falcón-Ordáz, J., and M. A. Sanabria. 1996. Especie nueva del género *Carolinensis* (Nemata: Heligmosomidae) de *Peromyscus difficilis* de Hidalgo, México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México 67:67–75.

Falcón-Ordaz, J., and M. A. Sanabria-Espinoza. 1997. *Vexillata vexillata* (Nematoda: Ornithostrongylidae) parásito de roedores de México. Revista de Biología Tropical 45:1693-1694.

Falcón-Ordáz, J., and M. A. Sanabria. 1999. Dos nuevas especies de *Stilestrongylus* (Nematoda: Heligmonellidae) parásitos de *Peromyscus* (Rodentia: Cricetidae) de México. Revista de Biología Tropical 47:929–937.

Falcón-Ordaz, J., S. L. Gardner, and G. Pérez-Ponce de León. 2001. *Vexillata liomyos* n. sp. (Nemata: Ornithostrongylidae) from *Liomys pictus* (Rodentia: Heteromyidae) from Mexico, with comments on the synlophe of *Vexillata armandae*. Journal of Parasitology 87:656–659.

Falcón-Ordaz, J., J. A. Fernández, and L. García-Prieto. 2010. *Lamotheoxyuris ackerti* n. gen., n. comb. (Nematoda: Heteroxynematidae) parasite of *Neotoma* spp. (Rodentia: Muridae). Revista Chilena de Historia Natural 83:259–266.

Falcón-Ordaz, J., R. Acosta, J. A. Fernández, and G. Lira-Guerrero. 2012. Helmintos y sifonápteros parásitos de cinco especies de roedores en localidades de la Cuenca Oriental, en el centro de México. Acta Zoológica Mexicana (n. s.) 28:287-304.

Falcón-Ordaz, J., S. Monks, and G. Pulido-Flores. 2013. Nemátodos parásitos de roedores de Huehuetla Hidalgo, México. Pp 64-68 *in* Estudios Científicos en el estado de Hidalgo y Zonas Aledañas, Volumen II (Pulido-Flores, G. and S. Monks, eds). Zea Books, University of Nebraska. Lincoln, U.S.A.

Falcón-Ordaz, J., S. Monks, G. Pulido-Flores, L. García-Prieto, and G. Lira-Guerrero. 2015. Riqueza de helmintos parásitos de vertebrados silvestres del estado de Hidalgo, México. Pp 20-37 *in* Estudios en Biodiversidad, Volumen I (Pulido-Flores, G., S. Monks, and M. López-Herrera, eds). Zea Books, University of Nebraska. Lincoln, U.S.A.

Falcón-Ordaz, J., J. A. Fernández, and B. A. Ruíz-Vázquez. 2016. Distribution extension of *Syphacia* (*Seuratoxyuris*) *peromysci* Harkema, 1936 (Nematoda, Syphaciinae) parasitizing the rock mouse, *Peromyscus difficilis* (J. A. Allen 1891) (Rodentia, Neotominae) in central Mexico. Checklist 12:1912.

Fernández, J. A., M. S. Hafner, D. J. Hafner and F. A. Cervantes. 2014. Conservation status of rodents of the families Geomyidae and Heteromyidae of Mexico. Revista Mexicana de Biodiversidad. 85:576–588.

Flores-Barroeta, L., and E. Hidalgo-Escalante. 1960. Céstodos de Vertebrados. VII. Pp. 357–376 *in* Libro Homenaje al Dr. Eduardo Caballero y Caballero (Bravo-Hollis, M., C. Zerecero, L. Flores-Barroeta, E. Hidalgo-Escalante, and H. A. Winter, eds.). Secretaría de Educación Pública e Instituto Politécnico Nacional. Ciudad de México, México.

García-Prieto, L., J. Falcón-Ordaz, G. Lira-Guerrero, and B. Mendoza-Garfias. 2008. A new species of *Heteromyoxyuris* (Nematoda: Oxyuridae), parasite of *Perognathus flavus* (Rodentia: Heteromyidae) from Mexico. Journal of Parasitology 94:860–865.

García-Prieto, L., J. Falcón-Ordaz, and C. Guzmán-Cornejo. 2012. Helminth parasites of wild Mexican mammals: list of species, hosts and geographical distribution. Zootaxa 3290:1–92.

Gutiérrez-González, J. 1980. Algunos helmintos parásitos en ratas silvestres de Apodaca, Nuevo León, México. B. S. Thesis, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Monterrey, Nuevo León, México.

Gutiérrez-Peña, E. J. 1987. *Dunnifilaria meningica* sp. n. (Filarioidea: Onchocercidae) from the central nervous system of the wood rat (*Neotoma micropus*) in Mexico. Tropical Medicine and Parasitology 38:275–350.

Iturbe-Morgado, J. C., J. Falcón-Ordaz, G. Lira-Guerrero, J. A. Fernández, and R. Acosta. 2017. Nematofauna of rodents of the families Heteromyidae and Cricetidae from the Mexican Plateau. Journal of Parasitology 103:127–131.

Jiménez, F. A. 2012. A new species of *Carolinensis* (Nematoda: Heligmonellidae) from Sumichrast's vesper rat *Nyctomys sumichrasti*. Comparative Parasitology 79:208–213.

King, S. R., and B. B. Babero. 1974. Helminths of kangaroo rats (*Dipodomys* spp.) in Nevada with reports of other worm parasites from these hosts. Proceedings of the Helminthological Society of Washington 41:241–248.

Lamothe-Argumedo, R. 1980. Tremátodos de mamíferos II. Una especie nueva del género *Dictyonograptus* Travassos, 1919, (Trematoda:Dicrocoeliidae). Anales del Instituto de Biología, Universidad Nacional Autónoma de México 51:61–68.

Lamothe-Argumedo, R., L. García-Prieto, D. Osorio-Sarabia, and G. Pérez-Ponce de León. 1997. Catálogo de la Colección Nacional de Helmintos. Universidad Nacional Autónoma de México y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Ciudad de México, México..

Lamothe-Argumedo, R., J. Falcón-Ordaz, L. García-Prieto, and J. Fernández-Fernández. 2005. A New dicrocoeliid (Digenea: Dicrocoeliinae) parasite of rodents from Tlaxcala, Mexico. Journal of Parasitology 91:1410–1412.

La Rue, G. R. 1957. The classification of digenetic Trematoda: a review and a new system. Experimental Parasitology 6:3016–344.

Light, J. E., L. A. Durden, B. M. OConnor, W. C. Preisser, R. Acosta, and R. P. Eckerlin. 2019. Checklist of ectoparasites of cricetid and heteromyid rodents in México. Therya 10:

Lynggaard-Islas, C. 2013. Estudio taxonómico de la helmintofauna de algunos cricétidos (Rodentia) de México. B. S. Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City.

Lynggaard, C., L. García-Prieto, C. Guzmán-Cornejo, and D. Osorio-Sarabia. 2014. *Pterygodermatites* (*Paucipectines*) *baiomydis* n. sp. (Nematoda: Rictulariidae), a parasite of *Baiomys taylori* (Cricetidae). Parasite 21:58

Martínez, M. L., M. G. Domínguez, G. E. Morici, R. Cavia, D. P. Montes de Oca, R. Lovera, J. H. Schapiro, and J. L. Caracostantogolo. 2013. Identificación morfológica y molecular de *Cysticercus fasciolaris* aislado de un roedor (*Rattus norvegicus*) de la provincia de Buenos Aires (Argentina). Revista Argentina de Microbiología 45:150–153.

Martínez-Salazar, E. A., V. Flores-Rodríguez, R. Rosas-Valdez, and J. Falcón-Ordaz. 2016. Helminth parasites of some rodents (Cricetidae, Heteromyidae, and Sciuridae) from Zacatecas, Mexico. Revista Mexicana de Biodiversidad 87:1203–1211.

Miyazaki, I., T. Kifune, and R. Lamothe-Argumedo. 1980. Taxonomical and Biological studies on the lung flukes of Central America. Occasional Publications University of Fukuoka 2:1–28.

Nakao, M., A. Lavikainen, T. Iwaki, V. Haukisalmi, S. Konyaev, Y. Oku, M. Okamoto, and A. Ito. 2013. Molecular phylogeny of the genus *Taenia* (Cestoda: Taeniidae): Proposals for the resurrection of *Hydatigera* Lamarck, 1816 and the creation of a new genus *Versteria*. International Journal for Parasitology 43:427–437.

Ochoterena, I., and Caballero y Caballero, E. 1932. Filaria parásita de las ratas de campo *Micropleura sigmodoni* spec., nov. Anales del Instituto de Biología, Universidad Nacional Autónoma de México 3:123–125.

Ortiz, M. U. 1999. Helmintos gastrointestinales en ratas y ratones silvestres del Municipio de Tepoztlán, Morelos, México. B. S. Thesis, Facultad de Biología, Universidad Autónoma del Estado de Morelos. Cuernavaca, México.

Ortiz-Villaseñor, A. L., A. Eslava-Araujo, and M. A. Lozano-García. 2011. *Vexillata liomyos* (Nemata: Ornithostrongylidae) de *Liomys irroratus* (Rodentia: Heteromyidae) de Sierra de Monte Negro, Morelos, México. Acta Zoológica Mexicana (n. s.) 27:207–211.

Panti-May, J. A., and M. D. R. Robles. 2016. A new species of *Trichuris* Roederer, 1761 (Nematoda: Trichuridae) from *Heteromys gaumeri* Allen & Chapman (Rodentia: Heteromyidae) in Yucatan, Mexico. Systematic Parasitology 93:721–730.

Panti-May, J. A., M. C. Digiani, E. E. Palomo-Arjona, Y. M. Gurubel-González, G. T. Navone, C. Machain-Williams, S. F. Hernández-Betancourt, and M. D. R. Robles. 2018. A checklist of the helminth parasites of sympatric rodents from two Mayan villages in Yucatán, México. Zootaxa 4403:495–512.

Poirier, J. 1886. Sur les Diplostomidae. Archives de Zoologie Expérimentale et Générale: Hitorire Naturelle, Morphologie, Histologie, Évolution des Animaux, Série 2 4:327–346

Pulido-Flores, G., S. Moreno-Flores, and S. Monks. 2005. Helminths of rodents (Rodentia: Muridae) from Metztitlán, San Cristóbal, and Rancho Santa Elena, Hidalgo, Mexico. Comparative Parasitology 72:186–192.

Pulido-Flores, G., S. Monks, and J. Falcón-Ordaz. 2013. Helmintos parásitos de algunos roedores (Mammalia: Rodentia) en San Miguel de Allende, Tepeapulco, Hidalgo, México. Pp 35-40 *in* Estudios científicos en el estado de Hidalgo y zonas aledañas, Volumen II (Pulido-Flores, G., and S. Monks, eds.). Zea Books, University of Nebraska. Lincoln, U.S.A.

Ramírez, J. R., C. Chávez-Tovar and G. A. Oliva V. 2014. *Sigmodon hispidus* Say and Ord, 1825; Hispid cotton rat. Pp 426–428 *in* Mammals of Mexico (Ceballos, G., ed). Johns Hopkins University Press. Baltimore, U.S.A.

Rendón-Franco, E., C. I. Muñoz-García, E. Romero-Callejas, K. I. Moreno-Torres, and G. Suzá. 2014. Effect of host species diversity on multiparasite systems in rodent communities. Parasitology Research 113:447–450.

Rudolphi, K. A. 1808 Entozoorum, sive vermium intestinalium historia naturalis 1:1–26.

Sanabria-Espinosa, M. A., J. A. Martínez, and M. P. Villeda. 1996. Redescripción de *Vexillata vexillata* (Nemata: Ornithostrongylidae) en roedores silvestres de las familias Cricetidae y Heteromyidae en dos zonas del estado de Hidalgo, México. Revista de Zoología 8:9–14.

Sánchez-Cordero, V., F. Botello, J. J. Flores-Martínez, R. A. Gómez-Rodríguez, L. Guevara, G. Gitiérrez-Granados and Á. Rodríguez-Moreno. 2014. Biodiversidad de Chordata (Mammalia) en México. Revista Mexicana de Biodiversidad 85 supl.:496–504.

Téllez, G. and R. A. Medellín. 2014. *Oryzomys melanotis* Thomas, 1893, Black-eared oryzomys. Pp 329–331 *in* Mammals of Mexico (Ceballos, G., ed). Johns Hopkins University Press. Baltimore, U.S.A.

Tóbon-García, E. D. 2014. *Onychomys leucogaster*, Northern grasshopper mouse. Pp 323 *in* Mammals of Mexico (Ceballos, G., ed). Johns Hopkins University Press. Baltimore, U.S.A.

Schmidt, G. D. 1986. CRC Handbook of tapeworm identification. CRC Press, Boca Raton, U.S.A.

Ubelaker, J. E., and M. D. Dailey. 1966. Taxonomy of the genus *Brachylaima* Dujardin (Trematoda: Digenea) with description of *B. chiapensis* sp. n. from *Peromyscus guatemalensis* in Mexico. Journal of Parasitology 52:1062–1065.

Underwood, H. T., J. G. Owens, and M. D. Engstrom. 1986. Endohelminths of three species of *Oryzomys* (Rodentia: Cricetidae) from San Luis Potosí, Mexico. The Southwestern Naturalist 31:410–411.

Webster, M. S. 2017. The extended specimen: emerging frontiers in collections-based ornithological research. Studies in Avian Biology (no. 50), Boca Raton, U.S.A.

Yamaguti, S. 1961. The Nematoda of Vertebrates. Systema Helminthum III (Parts I and II). Intersci. Publ. Inc. New York, U.S.A.

Zerecero, M. C. 1943. Algunos helmintos de las ratas domésticas y silvestres de México con descripción de dos nuevas especies. M. Sc. Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México. Coyoacan, México.

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Contributions to the natural history of *Mormopterus kalinowskii* (Chiroptera: Molossidae) in the southwest of Peru

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Mormopterus kalinowskii, is an insectivorous species restricted to the Andean western slopes of Peru and Chile, it is rare and has very scarce available information. We evaluated sex ratio, roost use, and relationship between reproductive patterns and monthly seasonal variation throughout a 13-month period. In addition, we performed the first description and characterization of its echolocation calls. The study area was located in the Ite Valley, Tacna department (southwestern Peru) at the northernmost part of the Atacama Desert, one of the driest deserts in the world. Bats were caught using mist-nets. Sex ratio in the population was calculated from all individuals captured, and its difference with regard to a 1:1 ratio was assessed through a Binomial Coefficient Test. Roost use was assessed through observation and inspection of the study area. Pearson and Spearman correlation coefficients were calculated to establish the relationship between the number of captures and temperature and precipitation data. Echolocation calls were recorded using a Petterson D240x Ultrasound detector plugged to a digital recorder. Spectrogram displays of recorded calls allowed describing structural patterns within echolocation calls and to measure frequency and time parameters. 79 individuals of *M. kalinowskii* were captured; 30 males and 49 females. Sex ratio obtained, 1:1.63, evidenced more females in the study area. *M. kalinowskii* uses crevices as roosts and has a single reproductive cycle per year. Higher capture rates are correlated with temperature ($r = 0.526$), but not precipitation ($r = 0.096$). Calls in search phase exhibited long duration pulses and a descending quasi-constant frequency (QCF) component from 39 to 33 kHz, reducing length and increasing bandwidth when attempting to catch prey. The sex ratio, 1:1.63 (≈ 2), suggests that *M. kalinowskii* is a polygamous species, as occurs in the others molossids, whereas the single annual reproductive cycle shown by *M. kalinowskii* would indicate a seasonal monoestrous reproductive pattern. Echolocation calls share several traits observed in other molossids; however, the frequency values for *M. kalinowskii* search phase pulses could be the highest recorded among the molossid bats of the Pacific coastal desert, allowing them to detect smaller prey as a strategy to mitigate food competition among insectivorous bats in arid environments.

Mormopterus kalinowskii, es una especie insectívora restringida a la vertiente occidental de Perú y Chile, monotípica y rara con muy escasa información disponible. Evaluamos la proporción de sexos, uso de refugios y la relación entre el patrón reproductivo de la especie y las épocas de calor y precipitación durante 13 meses en una población de *M. kalinowskii* en el Valle de Ite, departamento de Tacna (al suroeste del Perú), al comienzo del desierto de Atacama, uno de los más secos del mundo. Además, realizamos la primera descripción y caracterización de las llamadas de ecolocalización de la especie. Los murciélagos fueron capturados usando redes de niebla. La proporción de sexos en la población se calculó a partir de todos los individuos capturados, y su diferencia con respecto a una proporción 1:1 fue evaluada mediante una Prueba de Coeficientes Binomiales. El uso de refugios fue evaluado a través de la observación e inspección del área de estudio. Coeficientes de correlación de Pearson y Spearman fueron calculados para establecer la relación entre el número de capturas y datos de precipitación y temperatura. Las llamadas de ecolocalización fueron grabadas usando un detector de ultrasonido Petterson D240x conectado a una grabadora digital. Los espectrogramas de las llamadas resultantes permitieron describir patrones estructurales dentro de las llamadas y medir parámetros de frecuencia y tiempo. 79 individuos de *M. kalinowskii* fueron capturados; 30 machos y 49 hembras. La proporción sexual obtenida, 1:1.63, evidenció más hembras en el área de estudio. *M. kalinowskii* usa grietas como refugios y tiene un evento reproductivo anual. Mayores capturas están correlacionadas con la temperatura ($r = 0.526$) pero no con la precipitación ($r = 0.096$). Las llamadas en fase de búsqueda exhibieron pulsos de larga duración y un componente de frecuencia cuasi constante descendente (QCF) de 39 a 33 kHz, reduciendo su duración y aumentando su ancho de banda durante intentos de captura. La proporción de sexos, 1:1.63 (≈ 2), sugiere que *M. kalinowskii* es una especie polígama, como ocurre en otros molósidos, mientras que un único evento reproductivo anual mostrado por *M. kalinowskii* indicaría un patrón reproductivo de monoestría estacional. Las llamadas de ecolocalización comparten varias características observadas en otros molósidos, sin embargo, los valores de frecuencia para los pulsos de *M. kalinowskii* en fase de búsqueda podrían ser los más altos de los registrados entre los molósidos del desierto costero del Pacífico, permitiéndoles detectar presas más pequeñas como una estrategia para mitigar la competencia por el alimento entre los murciélagos insectívoros en ambientes áridos.

Key words: arid; desert; echolocation; molossids; monoestry; Tacna; valley.

Introduction

Mormopterus is a widespread bat genus of the Molossidae family, with 13 species spread throughout Africa, Oceania, Central America, and South America. Ten of these species can only be found in Africa and Oceania (*M. setigeren*, *M. petrophilus*, *M. acetabulosus*, *M. francoismoutoui*, *M. jugularis*, *M. doriae*, *M. planiceps*, *M. beccarii*, *M. norfolkensis*, and *M. eleryi*; Hutson *et al.* 2001; Jacobs and Fenton 2002; Goodman *et al.* 2008; McConville 2013), while the other three are only found in America (*M. minutus*, *M. phrudus*, and *M.* kalinowskii; Eger 2007; Mancina 2015).

The Kalinowski's Mastiff Bat, *Mormopterus kalinowskii* (Thomas 1983) occurs in Peru and northern Chile (Figure 1a). It is considered a rare species, due to its low frequency of capture and limited available information, and has a restricted distribution to the arid coasts, dry forests, and the highland steppes of the Andean western slopes of Peru and the arid north coast of Chile. *M. kalinowskii* is associated to diverse habitats from sea level to around 2,598 m elevation, mainly in inter-Andean valleys and creeks with bushy vegetation (Warner *et al.* 1974; Galaz and Yañez 2006; Eger 2007; Iriarte 2008; Pacheco *et al.* 2009; Aragón and Aguirre 2014; Pari *et al.* 2015). Additionally, this species occurs in low abundance in urban areas and flies quite low compared to other members of the Molossidae family (Solari *et al.* 2008). Eger (2007) mentions two notable records for specimens of the Yungas of Cajamarca and Cuzco departments. This author states that the record for Cuzco (AMNH 91553) had been previously identified as *M. phrudus* by Freeman (1981) having the district of Machu Picchu as locality for this record and that the specimen, in fact, corresponds to *M. kalinowskii*; however, information or support for this affirmation was not given. Under this assumption, *M. kalinowskii* would share habitat with *M. phrudus*, which has two unique records (USNM 194449; 194450) with Machu Picchu as type locality. This probable sympatry has not also been discussed by Eger (2007). Unfortunately, information of both species regarding their distribution and habitat use comes from specimens deposited in mammal collections since no study that offers natural history data exists (Eger 2007).

In the present study, we introduce natural history data that include sex ratio, roost use, and the relationship between reproduction cycles and seasonal variation in temperature and precipitation for a population of *M. kalinowskii* within the Tacna department, Peru. Additionally, we present the first description of the echolocation calls for this species as an attempt to increase the available information for bats distributed in the Pacific coastal desert, a remarkable step for the construction of acoustic libraries in the country.

Materials and methods

Study area. The research was carried out in the Ite Valley, Jorge Basadre province in Tacna department, Peru (-17° 52′ 39.327″ S, -70° 58′ 23.8758″ W; 82 m; Figure 1b), which is located in the Pacific desert eco-region (0 to 1,000 m; Brack 1986) towards the extreme Peruvian southwest that coincides with the border between the Coastal Peruvian desert and the Atacama Chilean desert. Here, despite the narrowness of the Ite valley and its desert surroundings, agricultural activities are conducted in the area by local residents (Figure 1c).

Fieldwork. Eight mist-nets of 12 m in length and 2.5 m wide were set up in places, such as abandoned buildings, agricultural areas, water reservoirs, and probable roosts. Mist-nets remained open overnight from 18:00 to 5:00 h of the next day and were checked at one-hour intervals (Pacheco *et al.* 2007; Garcés-Restrepo *et al.* 2016). Sampling took place over two consecutive nights per month, from January 2013 to January 2014 (13 months). The sampling effort was of 2,288 mist-net hours (88 mist-net hours per night).

Taking into consideration the similarities between *Tadarida* and *Mormopterus* genus at external level, we followed taxonomic keys made by Eger (2007) and Díaz *et al.* (2011). This allowed us to identify *M. kalinowskii* individuals based on measurements of the forearm (34.4 to 39 mm) and the external morphological characters, such as pale gray hair, wrinkled lips with deep folds, separated ears with a reduced keel, a well-developed tragus, a wider than high antitragus, and one upper premolar. To avoid bias by recapture, a piece of hair was cut on the right side of the dorsum.

The bats were examined to determine their age, sex, and reproductive stage. The age of each bat was obtained through the observation of the ossification degree of the large bones of the wings allowing us to differentiate among adults, sub adults, and juveniles (Paz and Benzal 1990). The reproductive stage was determined by the observation and palpation of their genitals; males were categorized in accordance to the position of their testicles: non-reproductive males (abdominal position) and reproductive males (scrotal position). While this is not definitive to determine the reproductive condition of male bats (Racey 2009), it is well-known that in most bats spermatogenesis process requires low temperatures, triggering that testes to be found external to the body, inside an external sac, and in inguinal or scrotal position (Garrido-Rodriguez *et al.* 1984; Krutzsch 2000). Males of certain species of bats have permanent abdominal testes, coinciding the spermatogenesis with hibernation that favors spermatozoids generation (Bernard and Tsita 1995). Some species can even have migratory testes, moving them from the abdomen to the scrotum or to the inguinal ring daily or seasonally for reproduction (Baker and Baker 1936; Ratcliffe 1932; Krutzsch and Crichton 1987). Since in the tropical and subtropical regions of the Old and the New World the reproductive pattern of male bats is timed to that of females and is given in response to optimal ecological and nutritional conditions (Krutzsch 2000), in this study, we consider the scrotal position as a sign that evidences the reproductive activity of males of *M. kalinowskii*. In the case of the reproductive stage of females, they were classified as non-reproductive (with closed vagina, normal abdomen, reduced breast, or without pigmentation) and reproductive (with open vagina, and in stage of pregnancy or lactation) (Kunz *et al.* 1996; León 2004; Racey 2009).

In order to determine the sex ratio of the species, we divided the total number of females by the total number of males obtained during the sampling, the result was used to establish a population sex ratio. Then, a Binomial Coefficient Test was performed to assess if the sexual proportion obtained was significantly different from a 1:1 relation (Pérez-Lustre and Santos-Moreno 2010; Santos-Moreno *et al.* 2010). This criterion may be used to infer the existence of monogamy or polygamy among the population (Santos-Moreno *et al.* 2010). Following Graham (1988), we explored about seven kilometers around the study area in order to look for some probable roosts of *M. kalinowskii*, taking into account roosting features of the Molossidae family, presence of guano (feces) and asking local people for information regarding the presence of bats.

Data analysis. We obtained temperature and precipitation data from the SENAMHI (Servicio Nacional de Meteorología e Hidrología del Perú). These data were correlated with the number of captures of *M. kalinowskii*. Previously to the statistical analysis, both number of captures and climatic variables were subjected to a Shapiro-Wilk normality test in order to know whether applying Pearson or Spearman correlations. The statistical analysis was performed through the software STATGRAPHIC Centurion XVI, version 16.1.11 (StartPoint Technologies Inc. 2010).

Ultrasound recording. We used the Pettersson D240x ultrasound detector (Pettersson Elektronik AB, Uppsala, Sweden) in heterodyne mode for real-time pulse detection and the time-expansion mode to convert 3.4 seconds-length segments into recorded audible sequences ten times longer. The detector was plugged to a Tascam DR-100 digital recorder (Teac America Inc., California, USA), with the following settings: sampling rate of 44.1 kHz and 16-bit virtual resolution for stereo PCM wav recordings.

Ultrasonic vocalizations recorded several seconds after hand-released bats took flight allowed us to obtain echolocation calls mostly in search phase. Therefore, reference calls were used to identify the acoustic repertoire of free flying *M. kalinowskii* individuals in the area (Rodríguez-San Pedro *et al.* 2015).

Analysis of recordings. Spectrograms obtained from field recordings were analyzed using the software Avisoft SASLab Pro 5.2 (Avisoft Bioacoustics, Germany). Spectrogram parameters were set at a sampling rate of 44.1 kHz, a 256 point FFT (Fast Fourier Transform) and 75 % Hamming window overlap. Other settings were part of the default software configuration. We chose pulses with a signal to noise ratio over 20 dB (Russo and Jones 2002) and measured six quantitative acoustic parameters: a) initial frequency, b) final frequency, c) maximum amplitude frequency (peak frequency), d) bandwidth (difference between the maximum and minimum frequency values), e) pulse duration,

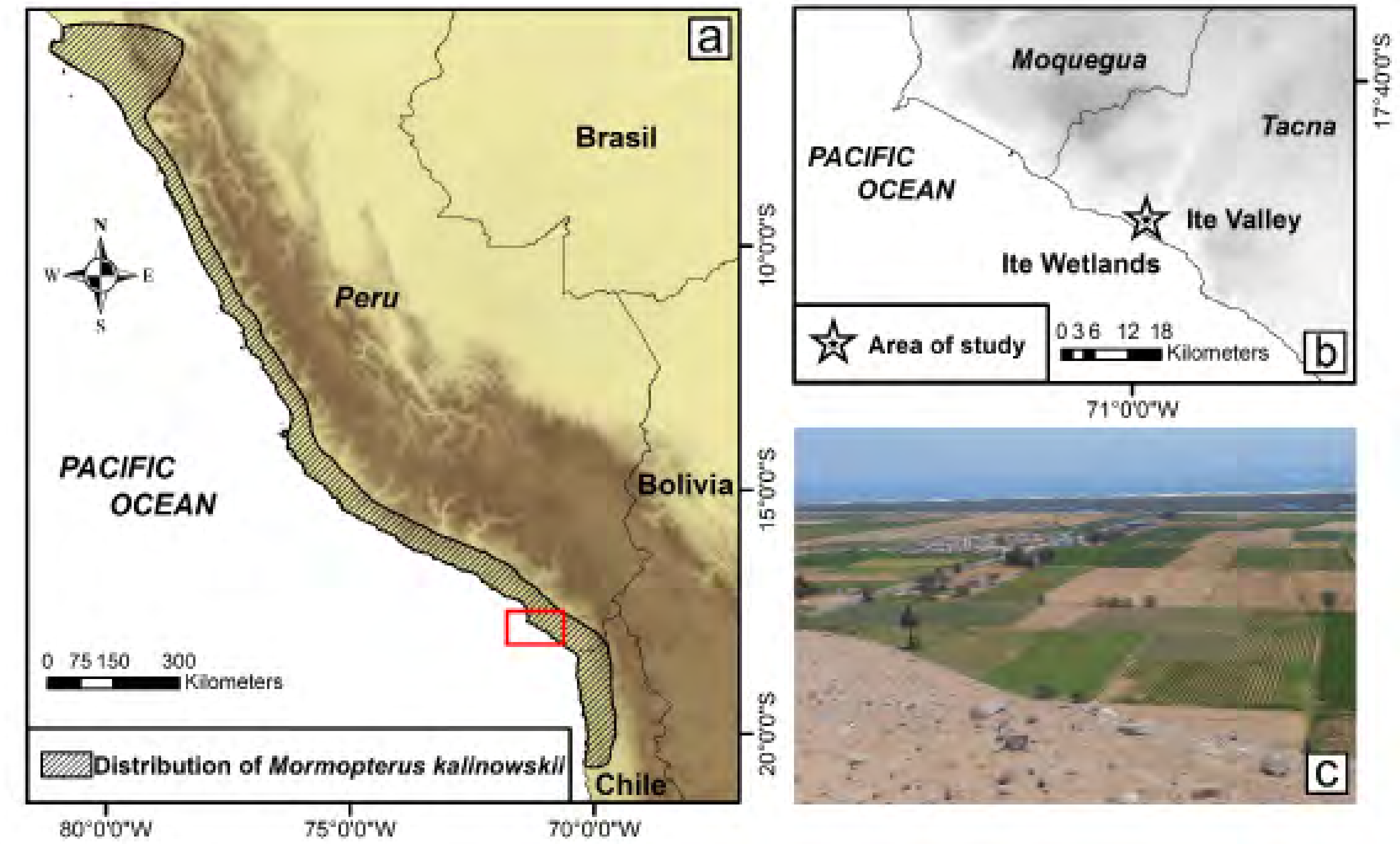

Figure 1. a) Geographic distribution of *M. kalinowskii* in the Peruvian Yungas and the Andean western slopes of Peru and Chile without considering the record given by Freeman (1981) and modified by Eger (2007). b) Geographic localization of Ite Valley, Jorge Basadre province, Tacna department. c) Panoramic view of the Ite Valley surrounded by desert areas and agricultural lands.

and f) interpulse duration (Papadatou *et al.* 2008). To prove if acoustic parameters within the calls from released and free-flying bats belong to the same species, a Wilk's Lambda value was assessed for statistical significance with a multivariate analysis of variance (MANOVA).

In addition, we described structural qualitative traits such as harmonics presence and frequency components sequence (pulse shape in spectrogram according to a modulated or constant frequency). Descriptive statistics (mean ± standard deviation) were calculated for each echolocation phase registered in the acoustic recordings (search, approach, and terminal phase).

Results

A total of 79 individuals of *M. kalinowskii* (Figure 2) were captured: 49 females (43 adults, 2 sub-adults, 4 juvenile) and 30 males (23 adults, 5 sub-adults, 2 juvenile). Of these, 31 females and 17 males were in reproductive stage (3 pregnant females, 28 lactating females, and 17 males with descended testes).

The sex ratio estimated was of 1:1.63. The binomial coefficient test showed that this sexual proportion differed statistically ($Z = 2.025$; *g.* l. = 1; $P = 0.043$) from 1:1, suggesting more than one female per male, so we might infer that there would be almost a relation 1:2 ($1.63 \approx 2$); two females per each male, which is discussed later.

After walking the arid hills that surround the Ite Valley, potential roost sites of *M. kalinowskii* were identified, based on the presence of narrow crevices situated about 3 m above gravel slopes of at least 50 m (remnant sediments of an ancient river). The presence of feces inside the crevices confirmed they had been recently occupied by bats. On one occasion during the survey, 203 individuals were counted leaving a gravel crevice, those are very likely to have been *M. kalinowskii* individuals due to their color and size, and because when we made a closer inspection of the roost, this still had individuals of the species inside about to fly. Thus, we believe this would be a colony of this species.

Figure 2. Adult male specimen of *M. kalinowskii* after being captured using mist nets in the Ite Valley, Jorge Basadre province, Tacna department, Peru.

January (2013, 2014) and February (2013), during the dry season, and December (2013), at the end of the wet season, were the months with the highest number of captures. The extensive dry season was characterized by the lack of precipitation with temperatures between 28.8 °C (February) and 10.2 °C (June). The captures increased towards December during the wet season with temperatures between 10 °C (July) and 26 °C (December). These temperatures were accompanied by small peaks of light precipitation (typical in arid environments) during August (0.3 mm), September (1.1 mm) and December (0.4 mm). After applying Shapiro-Wilk test, precipitation data did not exhibit a normal distribution ($p < 0.05$); hence, Pearson correlation was used to analyze data of bat captures and temperature, while Spearman correlation for assessing data of bat captures and precipitation. Pearson correlation coefficient confirmed a moderate correlation between the number of captures and temperature ($r = 0.526$, $r^2 = 0.277$, $p = 0.065$). In contrast, the Spearman coefficient showed no correlation between the number of captures and precipitation (Spearman correlation coefficient = 0.096, $p = 0.754$).

On the other hand, reproductive individuals were reported mainly during the dry season (January-February) with females being pregnant or in the period of lactation (January-February-December). Reproductive activity peaks of the species, evidenced by a higher number of captures of individuals in reproductive stage, occurred in January (1 male and 12 females), February (2 males and 2 females), and December (3 males and 11 females) in 2013, and January (4 males and 6 females) in 2014. Those were, coincidentally, the months with higher temperatures and very light or null precipitation. We also captured 6 reproductive males from June to September in 2013. However, reproductive females were only captured in the months of reproductive activity peaks, being absent during the rest of the study (Figure 3). Along the assessment, 48 (60.76 %) individuals showed reproductive activity, 3 (6.25 %) females were pregnant and 28 (58.33 %) lactating. With regard to reproductive males, 17 (35.42 %) showed descended testes. On the contrary, 31(39.24 %) individuals were non-reproductive, 18 (58.06 %) females and 13 (41.94 %) males.

Acoustic evaluation. M. kalinowskii recordings sequences were obtained from five captured and 23 free-flying individuals. No statistically significant differences were found in acoustic parameters between released and free-flying bats (MANOVA, Wilk's Lambda = 0.685, $F_{(6, 21)} = 1.613$, $p > 0.05$).

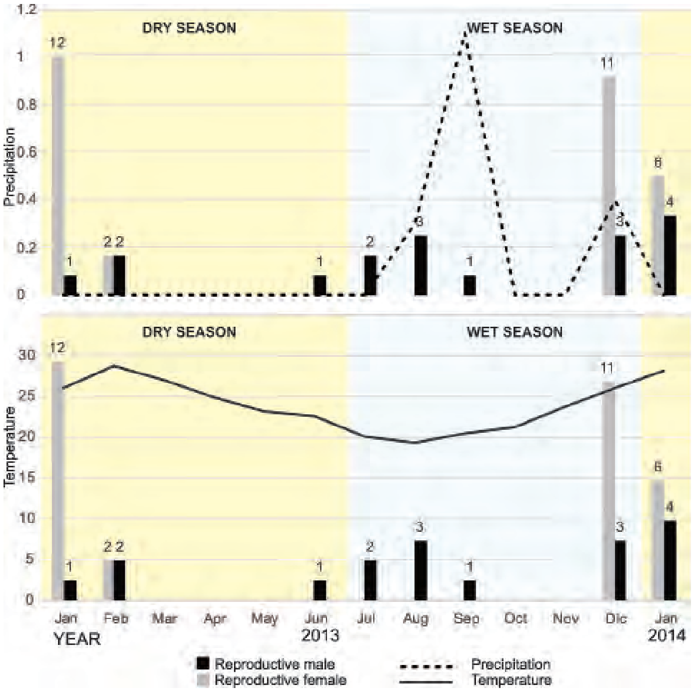

Figure 3. Reproductive females (in black) and reproductive males (in gray) with respect to the environmental temperature and precipitation.

Echolocation calls showed sequences of pulses divided into search, approach, and terminal phases, although few sequences with all three echolocation phases were recorded (Figure 4). In sequences of up to 3.4 seconds, 70 % of the time corresponded to the search phase, 21 % to the approach phase and 9 % to the terminal phase.

Search phase calls consisted of pulses with one harmonic and a flat or slightly concave shape displayed on the spectrogram. These pulses had short bandwidths (< 4 kHz) because of a mild decrease in ultrasonic frequency over time, which was represented by a downward quasi-constant frequency component (dQCF). The search pulse frequency parameters ranged from 39 kHz to 33 kHz and exhibited a longer duration and pulse interval than the subsequent phases (Table 1; Figure 4a).

The approach phase consisted of one-harmonic pulse with pronounced concave shape. Moreover, pulses showed a broad bandwidth which was on average four times greater than the search phase, and an abrupt decline in frequency in the first half of the pulse followed by a slight decrease in the last half, representing a sequence of a downward modulated frequency component (dFM) followed by a dQCF component. During the approach phase, bats emitted pulses ranging between 50 kHz to 37 kHz with shorter duration and pulse intervals than in search phase (Table 1; Figure 4b).

Terminal phase calls consisted of sequences of very short rapid pulses. The average bandwidths for terminal phase pulses were the highest compared to other phases and comprised a frequency range between 45 kHz and 25 kHz. The sharp decline in frequency values over time resulted in a structure defined by a dFM component (Table 1; Figure 4c).

Table 1. Descriptive statistics (mean ± standard deviation) for acoustic parameters in pulses from three echolocation phases of *M. kalinowskii*. IF: Initial Frequency. FF: Final Frequency. PF: Peak Frequency. BW: Pulse Bandwidth. D: Duration. PI: Pulse Interval.

Acoustic Parameter	Search phase (*n* = 37 pulses; 26 calls)	Approach phase (*n* = 11 pulses; 3 calls)	Terminal phase (*n* = 21 pulses; 2 calls)
IF (kHz)	36.8 ± 2.6	51.5 ± 6.4	39.4 ± 4.9
FF (kHz)	33.6 ± 0.8	37.6 ± 1.9	24.1 ± 1.9
PF (kHz)	34.6 ± 1.1	40.3 ± 2.0	30.8 ± 1.4
BW (kHz)	3.2 ± 2.3	13.9 ± 6.8	15.3 ± 3.4
D (ms)	10.7 ± 1.4	7.6 ± 2.5	1.8 ± 0.3
PI (ms)	211.3 ± 76.9	75.2 ± 16.1	9.1 ± 6.3

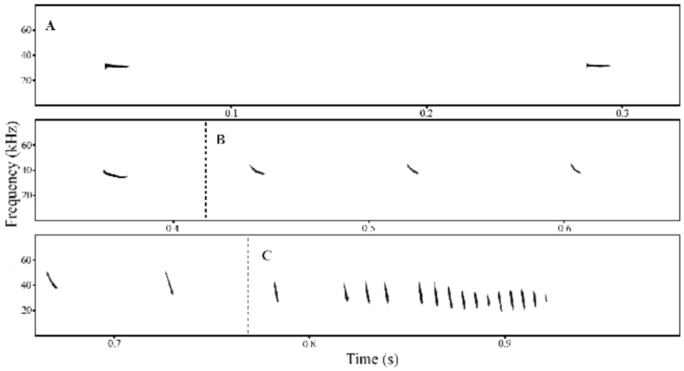

Figure 4. Echolocation call of a free-flying individual of *M. kalinowskii* displayed in a time-frequency spectrogram. a) Search phase. b) Approach phase. c) Terminal phase. View from Avisoft SAS-Lab Pro 5.2, software for bat call analysis. Sampling rate adjusted to 160 kHz.

Discussion

Knowledge about natural history of species in the genus *Mormopterus* in South America is poor (Eger 2007). There are no precedents of previous research related to species of this genus, thus, many aspects of *M. kalinowskii* remain unknown. This survey represents a novel source of information about the genus and the target species.

Sex proportions of different mammals have been evaluated in the Neotropics (Santos-Moreno *et al.* 2007; Pérez-Lustre and Santos-Moreno 2010; Pérez-Irineo and Santos-Moreno 2014), however, this aspect is still unknown for most of species. The measure of sex proportions in bats as an indirect indication to determine the likelihood of monogamy or polygamy was made for some Mexican bat species like *Dermanura tolteca* and *Centurio senex,* applying a test based on binomial coefficients to assess the statistical significance of a sexual ratio different from 1:1 (García-García *et al.* 2010; Santos-Moreno *et al.* 2010). Precisely, the sexual proportion that we obtained for *M. kalinowskii* (1:1.63) was statistically different from a 1:1 ratio when applying this test, suggesting that it is a polygamous species (with polygynous males). This is a common sexual trait, both in molossid species of the New World (*Molossus pretiosus* and *Tadarida brasiliensis*) and in species from the Old World (*Mops condylurus* and *Mormopterus planiceps*; McCracken and Gustin 1991; Bouchard 2001; Krutzsch *et al.* 2002; Keeley and Keeley 2004; Krutzsch and Crichton 2005; Nogueira *et al.* 2008; Ortega and Martínez-Rodríguez 2011).

In this sense, *M. kalinowskii* is likely a promiscuous species, which makes it possible to infer social structure and association conforming mixed groups based on the relation of almost two females for each male (Ortega *et al.* 2010; Keeley and Keeley 2004). Nonetheless, we cannot infer a mating system for the species because the possible existence of "harems" or other mating groups needs to be thoroughly proven (McCracken and Wilkinson 2000).

With regards to reproductive pattern, it is important to point out that a reproductive cycle is usually understood as the period where several reproductive events (mating, pregnancy, births, lactation, and parental care) take place (Martin and Bernard 2000). Our fieldwork data showed that the target species has a single annual reproductive cycle shown by females in reproductive stage and it would last from the end of June to February. Therefore, *M. kalinowskii* is likely to follow a seasonally monoestrous reproductive pattern. Fabian and Marques (1989) and Ortega and Martínez-Rodríguez (2011) concluded that in molossids species of the New World, this kind of reproductive pattern is linked to environmental conditions, which suggests that in *M. kalinowskii* this event would occur in a time where individuals have the best chances for their successful reproduction. Polyestry, and going into estrus soon after giving birth on the other hand, are less common in the family since these traits have only been reported for species in the genera *Molossus* and *Eumops*. Initially, species, such as *Molossus molossus* and *M. ater* were considered as monoestrous (Krutzsch and Crichton 1985; Fabian and Marques 1989), however, it was later reported that *M. molossus* has up to three reproductive cycles with different durations (Fabian and Marques 1989; Alberico *et al.* 2005). At this point, monoestrous cycles in *M. kalinowskii* cannot directly be linked to local food availability because there is not a quantitative analysis of the temporal variability of the alimentary resources (insects) in the Ite Valley. Nevertheless, the relationship between the abundance of food and the reproductive cycles of bats is well-recognized (Fleming *et al.* 1972; Wilson 1979; Mena and Williams 2002; Aguirre 2007). This evidence appears to suggest a strong delimitation in reproductive periods of insectivorous bats based on the availability of insects (Fleming *et al.* 1972) because of the great energetic demand that these events involve (Racey 1982; Zortéa 2003).

The mating season of *M. kalinowskii* was shown to occur between the end of fall and the onset of winter, that is, at the end of June and the beginning of July (transition to the wet season) unlike other species of insectivores (molossids and vespertilionids) of the eastern Andean slopes of Peru (dry season; Graham 1989; Ascorra *et al.* 1996). Consequently, our results suggest that pregnancy of *M. kalinowskii* would occur between the end of winter and the onset of spring, that is to say, late September and early October (wet season) with births at the beginning of the summer (around late December and in transition to the dry season) unlike other monoestrous species of molossids with births associated only to spring in the New World (wet season; Fabian and Marques 1989). For Peruvian bats, Graham (1989) reported 22.2 % of births during both seasons for some insectivorous species, as would occur for *M. kalinowskii*. Additionally, Graham (1989) mentioned that bat species from the Pacific coastal and slope region of Peru showed a high rate of births in the dry season, reinforcing and supporting our results for *M. kalinowskii*. Along the field survey, lactation in our target species was only registered during summer in December, January and February (transition to dry season onwards). This has a strong relation to the pattern recently described by Pari *et al.* (2015), who reported four lactating females for Arequipa department (north of Tacna), two in November and two in March, months adjacent to the limits of our findings for lactation of the species. Based on what has been described, this further supports our data and suggests a relationship between the environmental temperature and the reproduction in accordance with Pearson correlation, where the number of captures of *M. kalinowskii* shows a significant correlation with temperature, which varied between 28.8 °C and 10 °C during 13 months of survey (SENAMHI 2017).

It is necessary to mention that the value of Pearson correlation coefficient does not imply causation but an important degree of association between variables (Cangelosi *et al.* 1983; Rebekić *et al.* 2015). While it is true that the resultant *p*-value (0.06) for Pearson correlation coefficient seems to be statistically non-significant, it is very close to the typical *p*-value of 0.05 used to express statistical significance and would indicate a 93.5 % of probability of our variables being truly related and not merely by chance (Fenton and Neil 2013). In fact, we also used the coefficient of determination (r^2), which has been used in several researches as a stable measure of the relation between two variables (Taylor 1990; Rebekić *et al.* 2015) since *p*-value is highly influenced by the sample size and number of pairs of data (Ziliak and McCloskey 2008). In this case, the value of the coefficient of determination obtained ($r^2 = 0.277$) explains the 27.7 % of the direct and positive relationship between the number of captures and temperature (Kehr 1994).

Thus, *M. kalinowskii* are likely to be mating during the colder months and taking advantage of the warmer months of the year, with more favorable environmental conditions, for pregnancy, births, and lactation (Mena and Williams 2002). Similarly, the reproductive cycle of insectivorous species, such as *Promops davisoni*, *Myotis atacamensis, Histiotus macrotus*, *Histiotus montanus*, and *Tadarida brasiliensis,* with which *M. kalinowskii* shares habitat (Aragón and Aguirre 2014; Flores *et al.* 2015), is also likely to be influenced by temperature. In regard to precipitation, Spearman correlation showed no relationship between the number of captures of *M. kalinowskii* and rain events, possibly as a consequence of low and inconsistent rain in the Ite Valley. Individual rain events in this area reached a maximum of 4 mm at the time of assessment, however, a real relationship between the number of captures and precipitation must not be discarded because so small values of the latter could make it difficult to measure. Consequently, the percentage in response to a single environmental factor about the relationship between the number of captures and temperature, as well as the numerical results obtained from the relationship between the number of captures and precipitation could be increased and made measurable, respectively when more detailed researches involving other environmental factors potentially related to the reproductive pattern of *M. kalinowskii* are completed and give us a better approach of how reproduction of the species behaves in relation with the environment.

All crevices used as roosts by *M. kalinowskii* were found at least 53 meters above the ground; this is consistent with the characteristics described for roosts of molossids species. Since they, in general, have narrow wings, roosts of many species of the Molossidae family must be located in high places, such as buildings, escarpments, and trees in order to reach enough speed to take the necessary impulse to fly over the ground (Vaughan *et al.* 2015). Galaz and Yañez (2006), Iriarte (2008), and Aragón and Aguirre (2014) also report *M. kalinowskii* living in crevices along hills, consistent with other members of the Molossidae family which have been studied in the Pacific coastal desert in southern Peru, such as *Molossus molossus*, *Nyctinomops aurispinosus*, *N. laticaudatus*, *N. macrotis*, *P. davisoni*, *T. brasiliensis*, and *Tomopeas ravus*. These species, besides of living in hillside crevices, are also reported to be found in human constructions, caves, abandoned mines, cliffs, and hollow trees (Pari *et al.* 2015).

We counted approximately 203 individuals leaving their roosts, being the highest quantity of individuals of the target species reported up to now, but an inferior number in comparison to other colonies of molossids like *Molossus molossus* in Colombia, where more than 500 individuals have been registered roosting in human buildings, or *Tadarida brasiliensis* in Mexico and Argentina with records ranging from 700,000 to millions of individuals, respectively (Barquez and Díaz 2001; Alberico *et al*. 2005; Gándara *et al.* 2006). The differences with *M. kalinowskii* represent different social structures and ecology given by important factors, like the environment where these species live, food and roost resource availability, and their own evolutionary history (Kunz 1982; Olival 2012).

The acoustic recording analysis was achieved to describe the echolocation calls of Kalinowski's mastiff bat. Pulses in search, approach, and terminal phases suggest that *M. kalinowskii* is adapted to detect and locate small insects in open spaces as observed around their natural roosts in the Ite valley. We recognized three acoustical traits shared between single search phase pulses emitted by *M. kalinowskii* and other species of the Molossidae family: a) long-duration pulses over 10 ms, b) pulse structure defined by a quasi-constant frequency component, and c) a narrow bandwidth (Jung *et al.* 2014). Moreover, these traits may allow a rapid and efficient discrimination among *M. kalinowskii* and other bats that cohabit in the southern region of the Pacific desert like vespertilionids, such as *H. montanus*, *H. macrotus*, and *M. atacamensis* (Aragón and Aguirre 2014), which produce short-duration search pulses (less than 7 ms) with broad bandwidth and pulse structure corresponding to a modulated frequency followed by a quasiconstant frequency component (Ossa *et al.* 2015; Pacheco *et al.* 2015; Rodríguez-San Pedro *et al.* 2015).

Another species of the genus *Mormopterus* (*M. minutus*) exhibits plasticity in the design of search phase pulses as an adaptation for efficient prey detection in areas of variable vegetation cover with pastures and forests patches of different height (Mora *et al.* 2011). However, no evidence of plasticity was found in *M. kalinowskii* as all echolocation calls were recorded in a habitat constituted by extensive arid zones and low-altitude shrub vegetation. The approach and terminal phase pulses of *M. kalinowskii* are very similar to those described for *M. minutus* and molossids in general (Mora *et al.* 2011), where bandwidth increases up to three times more than in search phase. Duration and pulse interval are gradually reduced, which allows a better determination of the distance, position, size, and shape of the prey (Simmons and Stein 1980).

From our research, *M. kalinowskii* can be considered as one of the species of the Molossidae family with the highest frequency parameters for pulses in search phase, since it is known that the majority of molossids emit pulses between 15 kHz and 40 kHz (Jung *et al.* 2014). In addition, based on the inverse ratio between maximum amplitude frequency and detectable prey size (Jones 1999), this species is able to detect the smallest prey compared to other molossids in the Pacific coastal desert (Aragón and Aguirre 2014; Rodriguez-San Pedro *et al.* 2016), which may provide some clues about possible mitigation of food competition, thus warranting future research on this topic.

The results of this study showed that *M. kalinowskii* in the Ite Valley, Tacna department, has a polygamous mating system (promiscuous), the reproductive pattern is seasonal monoestrus with mating during the colder months (July and August) of the wet season and births during the warmer months (November, December, and January), where the species finds favorable conditions for raising young. It was observed that this species uses hillside crevices as roosts where there could be hundreds of individuals living together.

The acoustic analyses described the echolocation calls of *M. kalinowskii* for the first time, detecting and identifying *M. kalinowskii* employing bioacoustics methods. The Kalinowski's mastiff bat's echolocation calls consist of long and quasiconstant frequency pulses during the search for insects which are shortened and vary their frequency sharply as they approach prey in the air when attempting to capture it. The design of *M. kalinowskii* search phase pulses meets the expected characteristics for the Molossidae family; however, the frequency at which they are emitted could be considered one of the highest reached among the free-tailed bats known to inhabit the Chilean-Peruvian Pacific coastal desert. This allows *M. kalinowskii* to detect smaller prey, leading to a possible mitigation of resource competition between insectivorous bats in desert areas.

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Literature cited

Aguirre, L. 2007. Historia natural, Distribución y Conservación de los Murciélagos de Bolivia. Centro de Ecología y Difusión Simón Patiño. Santa Cruz de la Sierra, Bolivia.

Alberico, M., C. A. Saavedra, and H. García-Paredes. 2005. Murciélagos caseros de Cali (Valle del Cauca-Colombia). Caldasia 27:117-126.

Aragón, G., and M. Aguirre. 2014. Distribución de murciélagos (Chiroptera) en la región de Tacna, Perú. Idesia 32:119-127.

Ascorra, C. F., S. Solari, and D. E. Wilson. 1996. Diversidad y ecología de los quirópteros en Pakitza. Pp. 585-604 in Manu, the Biodiversity of southeastern Peru (Wilson, D. E. and A. Sandoval, eds.). Editorial Horizonte. Lima, Perú.

Baker, J. R., and Z. Baker. 1936. The seasons in a tropical rainforest (New Hebrides). Part 3. Fruit-bats (Pteropodidae). Journal of the Linnean Society (Zoology) 40:123-141.

Barquez, R. M., and M. M. Díaz. 2001. Bats of the Argentine Yungas: a systematic and distributional analysis. Acta Zoológica Mexicana 82:1-81.

Bernard, R. T. F., and J. N. Tsita. 1995. Seasonally monoestrous reproduction in the molossid bat, *Tadarida aegyptica*, from low temperate latitudes (33°S) in South Africa. South African Journal of Zoology 30:18-22.

Bouchard, S. 2001. Sex discrimination and roostmate recognition by olfactory cues in the African bats, *Mops condylurus* and *Chaerephon pumilus* (Chiroptera: Molossidae). Journal of Zoology 254:109-117.

Brack, A. 1986. Las ecorregiones del Perú. Boletín de Lima 44:57-70.

Cangelosi, V. E., P. H. Taylor, and P. F. Rice. 1983. Basic statistics: A real world approach, third edition. West Publishing Co. Minnesota, USA.

Díaz, M. M., L. F. Aguirre, and R. M. Bárquez. 2011. Clave de identificación de los murciélagos del cono sur de Sudamérica. Imprenta ETREUS. Cochabamba, Bolivia.

Eger, J. L. 2007. Family Molossidae P. Gervais, 1986. Pp. 399-436 in Mammals of South America, Volume 1. Marsupials, xenarthrans, shrews, and bats (Gardner, A. L. Ed.). The University of Chicago Press. Chicago, USA.

Fabian, M. E., and R. V. Marques. 1989. Contribuição ao conhecimiento da biologia reprodutiva de *Molossus molossus* Pallas, 1766 (Chiroptera: Molossidae) en Brazil. Revista Brasileira de Zoologia 6:603-610.

Fenton, N., and M. Neil. 2013. Risk assessment and decision analysis with bayesian networks. CRC Press. New York, USA.

Fleming, T. H., E. T. Hooper, and D. E. Wilson. 1972. Three Central American bat communities: structure, reproductive cycles and movement patterns. Ecology 53:653-670.

Flores, M., G. Calizaya, V. Pacheco, and G. Aragón. 2015. Distribution of *Promops davisoni* Thomas, 1921 (Chiroptera: Molossidae) in Peru with a new record and southward range extension. Check List 11:1573.

Freeman, P. W. 1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): Morphology, ecology, evolution. Fieldiana, Zoology 7:1-13.

Galaz, J., and J. Yáñez. 2006. Los Murciélagos de Chile. Guía para su reconocimiento. Ediciones del Centro de Ecología Aplicada. Santiago, Chile.

Gándara, G., A. N. Correa, and C. A. Hernández. 2006. Valoración económica de los servicios ecosistémicos que prestan los murciélagos *Tadarida brasiliensis* como controladores de plagas en el norte de México. Working Papers, Escuela de Graduados en Administración Pública y Políticas Públicas, Campus Monterrey 2006:1-18.

Garcés-Restrepo, M. F., A. Giraldo, C. López, and N. F. Ospina-Reina. 2016. Diversidad de murciélagos del Campus Meléndez de la Universidad del Valle, Santiago de Cali, Colombia. Boletín Científico. Centro de Museos. Museo de Historia Natural 20:116-125.

García-García, J. L, A. Santos-Moreno, and A. Rodríguez-Alamilla. 2010. Population dynamics of the bat *Dermanura tolteca* (Chiroptera: Phyllostomidae) in a tropical forest in Mexico. Revista de Biología Tropical 58:1323-1334.

Garrido-Rodríguez, D., P. Fuentes-Servin, M. Gasca-Boyer, and S. Juárez-Vergara. 1984. Patrón de reproducción del murciélago insectívoro *Pteronotus parnellii mexicanus* Miller, 1902 (Chiroptera: Mormoopidae). Revista de Biología Tropical 32:253-262.

Goodman, S., J. Vuuren, F. Ratrimomanarivo, J. Probst, and R. Bowie. 2008. Specific status of populations in the Mascarene Islands referred to *Mormopterus acetabulosus* (Chiroptera: Molossidae), with description of a new species. Journal of Mammalogy 89:1316-1327.

Graham, G. L. 1988. Interspecific associations among Peruvian bats at diurnal roosts and roost sites. Journal of Mammalogy 69:711-720.

Graham, G. L. 1989. Seasonality of Reproduction in Peruvian Bats. Fieldiana, Zoology 39: 173-186.

Hutson, A. M., S. P. Mickleburgh, and P. A. Racey. 2001. Microchiropteran bats: global status survey and conservation action plan. IUCN/SSC Chiroptera Specialist Group, IUCN. Information Press. Oxford, UK.

Iriarte, A. 2008. Mamíferos de Chile. Lynx Editions. Barcelona, España.

Jacobs, D., and M. Fenton. 2002. *Mormopterus petrophilus*. Mammalian Species 703:1-3.

Jones, G. 1999. Scaling of echolocation parameters in bats. Journal of Experimental Biology 202:3359-3367.

Jung, K., J. Molinari, and E. K. Kalko. 2014. Driving factors for the evolution of species-specific echolocation call design in new world free-tailed bats (Molossidae). PLoS ONE 9:e85279.

Keeley, A. T. H., and B. W. Keeley. 2004. The mating system of *Tadarida brasiliensis* (Chiroptera: Molossidae) in a large highway bridge colony. Journal of Mammalogy 85:113-119.

Kehr, A. 1994. Usos y abusos de las correlaciones en biología. Cuadernos de Herpetología 8:225-228.

Krutzsch, P. H.2000. Anatomy, Physiology and Cyclicity of the Male Reproductive Tract. Pp. 92-137 *in* Reproductive Biology of Bats (Crichton, E. G., and P. H. Krutzsch, eds.). Academic Press. London, UK.

Krutzsch, P. H., and E. G. Crichton. 1985. Observations on the reproductive cycle of female *Molossus fortis* (Chiroptera: Molossidae) in Puerto Rico. Journal of Zoology 207:137-150.

Krutzsch, P. H., and E. G. Crichton. 1987. The reproductive biology of the male little mastiff bat, *Mormopterus planiceps* (Chiroptera: Molossidae) in southeastern Australia. The American Journal of Anatomy 178:369-386.

Krutzsch, P. H., T. H. Fleming, and E. G. Crichton. 2002. Reproductive biology of male Mexican free-tailed bats (*Tadarida brasiliensis mexicana*). Journal of Mammalogy 83:489-500.

Krutzsch, P. H., and E. G. Crichton. 2005. Reproductive biology of the male little mastiff bat, *Mormopterus planiceps* (Chiroptera: Molossidae), in Southeast Australia. American Journal of Anatomy 178:352-368.

Kunz, T. H. 1982. Roosting Ecology. Pp. 1-46 *in* Ecology of bats (Kunz, T. H. Ed.). Plenum Press. New York, USA.

Kunz, T. H., C. Wemmer, and V. Hayssen. 1996. Sex, age, and reproductive condition of mammals. Pp. 279-290 *in* Measuring and monitoring biological diversity, standard methods for mammals (Wilson, R., C. Nichols, and R. Foster, eds.). Smithsonian Institution Press. Washington, U. S. A.

León, P. N. 2004. Estudio preliminar de los patrones reproductivos de *Dermanura phaeotis* y *Artibeus intermedius* (Chiroptera: Phyllostomidae) en petenes del noreste de la península de Yucatan, México. Tesis de Pregrado, UADY, Mérida, Yucatán, México.

Mancina, C. 2015. *Mormopterus minutus*. In: IUCN. 2017. The IUCN Red List of Threatened Species. Version 2017.3. www.iucnredlist.org. Consulted on February 27th 2018.

Martin, L., and R. T. F. Bernard. 2000. Endocrine regulation of reproduction in bats: The role of circulating gonadal hormones. Pp. 27-64 *in* Reproductive Biology of Bats (Crichton, E. G., and P. H. Krutzsch, eds.). Academic Press. London, UK.

McCracken, G. F., and M. K. Gustin. 1991. Nursing behaviour in Mexican free-tailed bat maternity colonies. Ethology 89:305-321.

McCracken, G. F., and G. S. Wilkinson. 2000. Bat mating systems. Pp. 321-357 in Reproductive Biology of Bats (Crichton, E. G., and P. H. Krutzsch, eds.). Academic Press. London, UK.

McConville, A. 2013. The ecology of the east-coast free-tailed bat (*Mormopterus norfolkensis*) in the Hunter region. Thesis for the degree of Doctor of Philosophy. The University of Newcastle, Australia.

Mena, J., and M. Williams. 2002. Diversidad y patrones reproductivos de quirópteros en un área urbana de Lima, Perú. Ecología Aplicada 1:1-8.

Mora, E. C., C. Ibáñez, S. Macías, J. Juste, I. López, and L. Torres. 2011. Plasticity in echolocation inventory of *Mormopterus minutus* (Chiroptera: Molossidae). Acta Chiropterologica 13:179-187.

Nogueira, M. R., A. Pol, L. R. Monteiro, and A. L. Peracchi. 2008. First record of Miller's mastiff bat, *Molossus pretiosus* (Mammalia: Chiroptera), from the Brazilian Caatinga. Chiroptera Neotropical 14:346-353.

Olival, K. J. 2012. Evolutionary and ecological correlates of population genetic structure in bats. Pp. 268-316 *in* Evolutionary History of Bats. Fossils, Molecules and Morphology (Gunnel, G. F., and N. B. Simmons, eds.). Cambridge University Press. New York, USA.

Ortega, J., B. Hernández-Chávez, A. Rizo-Aguilar, and J. A. Guerrero. 2010. Estructura social y composición temporal en una colonia de *Nyctinomops laticaudatus* (Chiroptera: Molossidae). Revista Mexicana de Biodiversidad 81:853-862.

Ortega, J., and J. L. Martínez-Rodríguez. 2011. Conductas de apareamiento y agresión entre machos en una colonia de *Nyctinomops laticaudatus* (Chiroptera: Molossidae) en México. Mastozoología Neotropical 18:95-103.

Ossa, G., L. Forero, F. Novoa, and C. Bonacic. 2015. Caracterización morfológica y bioacústica de los murciélagos (Chiroptera) de la Reserva Nacional Pampa de Tamarugal. Biodiversidata 3:21-29.

Pacheco, V., E. Salas, L. Cairampoma, M. Noblecilla, H. Quintana., F. Ortiz, P. Palermo, and R. Ledesma. 2007. Contribución al conocimiento de la diversidad y conservación de los mamíferos de la cuenca del río Apurímac, Perú. Revista Peruana de Biología 14:169-180.

Pacheco, V., R. Cadenillas, E. Salas, C. Tello, and H. Zeballos. 2009. Diversidad y endemismo de los mamíferos del Perú. Revista Peruana de Biología 16:5-32.

Pacheco, V., A. Zevallos, K. Cervantes, J. Pacheco, and J. Salvador. 2015. Mamíferos del Refugio de Vida Silvestre Los Pantanos de Villa, Lima-Perú. Científica 12:26-41.

Papadatou, E., R. K. Butlin, and J. D. Altringham. 2008. Identification of bat species in Greece from their echolocation calls. Acta Chiropterologica 10:127-143.

Pari, A., K. Pino, C.E. Medina, E. López, and H. Zeballos. 2015. Murciélagos de Arequipa, Historia Natural y Conservación. Impresiones Juve E.I.R.L. Arequipa, Perú.

Paz, O. de, and J. Benzal. 1990. Clave para la identificación de los murciélagos de la Península Ibérica (Mammalia, Chiroptera). Miscelánea Zoológica 13:153-176.

Pérez-Irineo, G., and A. Santos-Moreno. 2014. Density, distribution, and activity of the ocelot *Leopardus pardalis* (Carnivora: Felidae) in Southeast Mexican rainforests. Revista de Biología Tropical 62:1421-1432.

Pérez-Lustre, M., and A. Santos-Moreno. 2010. Movements and capture-recapture data analysis of the Vesper Rat (*Nyctomys sumichrasti*: Rodentia, Muridae) in a tropical forest in northeastern Oaxaca, México. Acta Zoológica Mexicana 26:627-638.

Racey, P. A. 1982. Ecology of bat reproduction. Pp. 57-104 *in* Ecology of bats (Kunz, T. H. Ed.). Plenum Press. New York, USA.

Racey, P. A. 2009. Reproductive assessment of bats. Pp. 249-264 *in* Ecological and behavioral methods for the study of bats (Kunz, T. H., and S. Parsons, eds.). The Johns Hopkins University Press. Maryland, USA.

Ratcliffe, F. 1932. Notes on the fruit bats (*Pteropus* spp.) of Australia. Journal of Animal Ecology 1:32-37.

Rebekić, A., Z. Lončarić, S. Petrović, and S. Marić. 2015. Pearson's or Spearman's correlation coefficient – which one to use? Poljoprivreda 21:47-54

Rodríguez-San Pedro, A., D. A. Peñaranda, J. L. Allendes, and M. L. C. Castillo. 2015. Update on the distribution of *Myotis atacamensis* (Chiroptera: Vespertilionidae): southernmost record and description of its echolocation calls. Chiroptera Neotropical 21:1342-1346.

Rodríguez-San Pedro, A. J. L. Allendes, and G. Ossa. 2016. Lista actualizada de los murciélagos de Chile con comentarios sobre taxonomía, ecología y distribución. Biodiversity and Natural History 2:18-41.

Russo, D., and G. Jones. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. Journal of Zoology 258:91-103.

Santos-Moreno, A., M. Briones-Salas, and R. López-Wilchis. 2007. Diferencias en algunos parámetros demográficos de *Oryzomys chapmani* (Rodentia: Muridae) asociada a tres estados sucesionales de bosque mesófilo de montaña en Oaxaca, México. Acta Zoológica Mexicana 23:123-137.

Santos-Moreno, A., J. L. García-García, and A. Rodríguez-Alamilla. 2010. Ecología y reproducción del murciélago *Centurio senex* (Chiroptera: Phyllostomidae) en Oaxaca, México. Revista Mexicana de Biodiversidad 81:847-952.

SENAMHI. 2017. Servicio Nacional de Meteorología e Hidrología del Perú. Base de datos meteorológicos, datos históricos, Perú. http://www.senamhi.gob.pe/. Consulted on December 1st 2017.

Simmons, J. A., and R. A. Stein. 1980. Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. Journal of Comparative Physiology 135:61-84.

Solari, S., R. Barquez, and M. Díaz. 2008. *Mormopterus kalinowskii*. In: IUCN 2017. The IUCN Red List of Threatened Species. Version 2017.3. www.iucnredlist.org. Consulted on February 27th 2018.

StartPoint Technologies Inc. 2010. Statgraphics Centurion XVI v16.1.11 Program distributed by the author. StartPoint Technologies Inc. Herndon, USA.

Taylor, R. 1990. Interpretation of the correlation coefficient: A basic review. Journal of Diagnostic Medical Sonography 1:35-39.

Vaughan, T. A., J. M. Ryan, and N. J. Czaplewski. 2015. Mammalogy. Sixth edition. Jones and Bartlett Publishers. Massachusetts, USA.

Warner, J. W., J. L. Patton, A. L. Gardner, and R. J. Baker. 1974. Karyotypic analyses of twenty-one species of molossid bats (Molossidae: Chiroptera). Canadian Journal of Genetics and Cytology 16:165-176.

Wilson, D. E. 1979. Reproductive patterns. Special Publications, the Museum, Texas Tech University 16:317-378.

Ziliak, S. T., and D. N. McCloskey. 2008. The cult of statistical significance: how the standard error costs us jobs, justice and lives. The University of Michigan Press. Michigan, USA.

Zortéa, M. 2003. Reproductive patterns and feeding Habits of three nectarivorous bats (Phyllostomidae: Glossophaginae) from the Brazilian Cerrado. Brazilian Journal of Biology 63:159-168.

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Tapir population patterns under the disappearance of free-standing water

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[10] Ejido Nuevo Becal, Calakmul. Campeche, México. (NAD).

Baird's tapir is the largest Neotropical tapir species, and it is considered Endangered by the IUCN. The Calakmul Biosphere Reserve (CBR) is the largest protected tropical forest in Mexico. The CBR is at the heart of the Maya Forest, a tri-national forest located in Mexico, Guatemala, and Belize that is the largest tropical forest outside the Amazon River basin. Free-standing water in the CBR occurs in only a few ephemeral ponds. These ponds are rare in the landscape, with a mean density of one pond in every 10 km^2, and with an average distance among ponds of 3 km. Only some of these ponds have free-standing water in every year. A decreasing trend in water availability from these ponds was detected from 2008 to 2018. Our present objective was to document population of the tapirs during these 11 years, and reveal any relationship to the pattern of water availability. Using the technique of photo-trapping, we monitored from 9 to 15 ponds over a period of 8 years (a total of more than 18,000 camera-days) during the 11-year period. Results showed that although the population remained relatively stable, the index of relative abundance indicated a slight decrease in population abundance and in some sites seemed at least superficially associated with decreasing water availability. Such long-term population studies are becoming more important for estimating the impacts of possible changes and for predicting the future of populations. In turn, they assist the conservation of endangered and sensitive species such as Baird's tapir.

El tapir de Baird es el más grande de las especies de tapires Neotropicales y está considerado como en peligro por la UICN. La Reserva de la Biosfera de Calakmul (CBR por sus siglas en ingles) es el área de bosque tropical protegido mas grande de México y se encuentra en el corazón de la Selva Maya, un bosque tri-nacional localizado entre Belice, Guatemala y México considerado el bosque tropical mas extenso de Mesoamérica. El agua de lluvia en la CBR percola al subsuelo y solamente en pocos sitios (localmente conocidos como aguadas) se almacena agua en el suelo. Estos sitios son raros en el paisaje con una densidad de uno cada 10 km^2 y una distancia promedio de 3 km entre aguadas. Solamente algunos de esos sitios conserva agua durante la época seca de cada año. Se detectó una reducción de la disponibilidad de agua desde el 2008 al 2018. Documentamos la población de tapires durante estos años y examinamos la relación con este patrón de reducción de la disponibilidad de agua. Usando la técnica de foto-trampeo monitoreamos entre 9 a 15 aguadas en 8 años dentro de este periodo de 11 años. Con un total de mas de 18,000 días-cámaras encontramos que aunque la población de tapires de la CBR permanece estable en promedio el índice de abundancia relativa detectó una ligera disminución en la abundancia y en algunas aguadas se asoció con la falta de agua. Estudios de largo plazo de especies en peligro asociadas a cuerpos de agua son importantes porque permiten estimar los efectos de la disponibilidad de agua y predecir futuros escenarios para las poblaciones de fauna silvestre. Esta información es esencial para elaborar planes de conservación de especies en peligro y sensibles tales como el Tapir de Baird.

Keywords: Calakmul Biosphere Reserve; ponds; *Tapirus bairdii*; *Tapirella bairdii*; water availability

Introduction

Wildlife, especially large mammals and birds, are suffering dramatic reductions across the globe, due mainly to hunting and habitat reduction (Ripple *et al.* 2016). Baird's tapir (*Tapirus bairdii,* also known as *Tapirella bairdii,* see: Alvarez-Castañeda *et al.* 2015 for a review of the species and its taxonomy) is the largest of the Neotropical wildlife and is the only Perissodactyl species living in the Mesoamerican forest (García *et al.* 2016). This solitary species lives in well-conserved humid tropical forest from Mexico to Ecuador. Baird's tapir is the largest tapir species in America, and it is considered Endangered by the IUCN (Red List, International Union for the Conservation of Nature; García *et al.* 2016). Baird's tapir is ranked 34th among species that need conservation attention (Issac et al. 2007; Ripple et al. 2016) and is ranked 10th among the rarest Neotropical species (Dobson and Yu 1993).

Tapirs are the only species able to disperse some large seeds in Neotropical forest (O'Farrill *et al.* 2013), and play the role of the largest herbivores, feeding especially on seedlings and herbs (Naranjo 2009; Tobler *et al.* 2006). Baird's tapir populations are decreasing throughout the entire population range due mainly to poaching, habitat loss and fragmentation (García *et al.* 2016). Estimations about how many tapirs are in the wild vary from 3000 (García *et al.* 2016) to more than 5000 (Schank *et al.* 2017).

Calakmul Biosphere Reserve (CBR hereafter) is the largest protected tropical forest in Mexico and is at the heart of the Maya Forest, a tri-national forest located in Mexico, Guatemala and Belize. The CBR is the largest tropical forest outside the forests of the Amazon River basin (Reyna-Hurtado 2007). In CBR, the forest is seasonal and most of the precipitation percolates underground, and only in a few places have free-standing water (Reyna-Hurtado *et al.* 2010). These few ponds (locally known as "*aguadas*") are the only source of water for wildlife and for some human communities in the dry season. These ponds are rare in the landscape, with a mean density of one pond almost every 10 km^2 and with an average distance of 3 km among them (Reyna-Hurtado *et al.* 2009). In addition, these ponds do not contain free-standing water every year (Reyna-Hurtado *et al.* 2012). These ponds are essential for the survival of some species, such as the white-lipped peccary (*Tayassu pecari*) that was documented that some groups of peccaries moved as far as 17 km to reach "aguadas". Also, for tapirs, "aguadas" are essential for survival and tapirs visit them frequently (Sandoval *et al.* 2016, Carrillo *et al.* 2015).

Recently, the technique of photo-trapping, or camera traps, is becoming popular among ecologists for estimating parameters of population and behavior of cryptic or secretive species (O'Connell *et al.* 2011). Additionally, ecologists have developed theoretical models of animal occupancy (detection or non-detection of the species in a specific site) as a surrogate for animal abundance (Royle and Dorazio 2006; MacKenzie and Nichols 2004). Occupancy rate estimation is based on the idea that animal detection is imperfect, and every species has some probability of being detected in any given site (MacKenzie *et al.* 2006). Thus, occupancy rate is estimated based on the detection probability, and is estimated from a series of repetitive samplings, where detection (1) or non-detection (0) of the species is recorded. It assumes that the population is closed and that the occupancy rate of the species remains stable (O'Connell and Bailey 2011)

In 2008, a group of conservationists and researchers from several Mexican institutions initiated a monitoring program of a set of ponds that are located in the center of the southern core of CBR, with the aim of monitoring annual changes in wildlife populations that might be associated with water availability patterns. We present the results of this long-term monitoring for the tapir population of the CBR. This dataset is one of the longest on tapir populations, and water availability was recorded during the same period.

Our research focused on the following questions: What was the trend of the tapir population over 11 years in the CBR, concurrent with pond monitoring? Were the population changes related to water availability changes? Did tapirs favor specific ponds? The general objective was to identify population trends in the CBR over an 11 years period, and any relationship with changes in water availability. Specific objectives were: 1) comparing the population occupancy rate and relative abundance along 11 years in a set of ponds, and 2) examine the relationship of population occupancy and relative abundance of tapir with water availability.

Methods

Study site. The CBR is a seasonal tropical semidry forest located in Southern Mexico in the Yucatan Peninsula. The CBR extends over 7,238 km^2 and was decreed as a protected area in 1989 (Figure 1). The CBR is part of the Great Calakmul Region that includes the Maya Biosphere Reserve in Guatemala and the Rio Bravo-Dos-Milpas conservation area in Belize, which together comprise one of the largest tropical forests in Meso-America with an extent of more than 20,000 km^2. The CBR is bordered on the west, north and east sides by more than 100 human communities (*ejidos*) with a total population around of 30,000 people (INEGI 2015). The southern area of the CBR is contiguous with the Maya Biosphere Reserve in Guatemala without any dispersal barrier between them. The Calakmul climate is warm and sub-humid (Aw), with a mean annual temperature of 24.6° C (Köppen modified by Garcia 1988). There is seasonal rainfall, mainly in summer and early fall, with an annual average of 1076.2 mm. The forest is classified as medium sub-perennial tropical forest (Pennington and Sarukhan 1998). The area's topography is very flat with some gently rolling hills. Mean elevation is 250 m above sea level with a few hills that reach 340 m. Water in the CBR is obtained through precipitation, since there is no permanent river system. Most of the rainfall percolates through the limestone, but some drains above ground into ephemeral ponds. These ponds constitute the only source for water for wildlife through the dry season (Reyna-Hurtado *et al.* 2009; Reyna-Hurtado *et al.* 2010; Reyna-Hurtado *et al.* 2012).

Population Relative Abundance and Occupancy Rates. Since 2008, a set of 9 to 15 ponds was selected so as to occur at least 1.5 km from each other. All these ponds are in the southern area of the CBR, an area that is isolated from any human community by two checkpoints of the CBR authorities, and have one single road that leads to an archeological site but with very few cars every day (less than 10 on average).

These ponds were monitored by setting up a single camera trap (Reconyx PC800 Hyperfire professional Reconyx, Inc. and Cuddeback Inc) at 50 cm high in each of 15 ponds from April to July of 2008, 2009 and 2010 and in 12 ponds

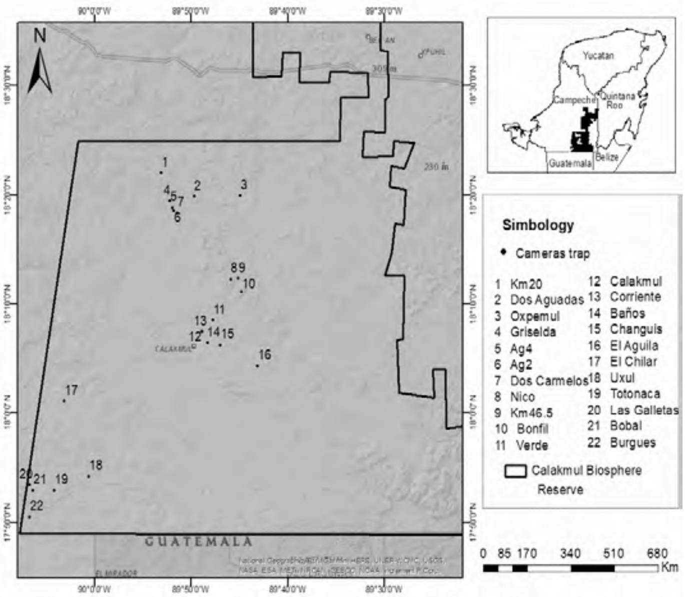

Figure 1. Map of the study area and the ponds monitored in Calakmul Biosphere Reserve.

from February 2014 to December 2018. The cameras were programmed to take five consecutive photos (1 photo per second) each time the sensor detected movement and were checked every 15 days in the period 2008 to 2010 and every 2 months in the period 2014-2018 to change batteries and memory cards.

To consider records independent, we used a 24-hour filter between tapir sequences to avoid having repetitive sequences of the same individual, unless individuals could clearly be distinguished, *e. g*., female vs male; adult vs juveniles, or individual with unique marks or scars (Lira-Torres *et al.* 2014; Figure 2). We determined the Relative Abundance Index (RAI hereafter) using classical method with the following equation: *RAI=N/(SE*1000 camera-trap days*). Where: *N*= Number of independent records and *SE*=Sampling effort measured as the number of days multiplied by the number of cameras active. At the same time than cameras were active, we recorded water availability on each pond that was monitored every month and sometimes twice per month. We only recorded water presence or absence and not the amount, or the percentage of it.

Statistical Analyses. We estimated RAI for each year and for each pond. We estimated average RAI per year and per site, and also per period. We compared RAI between periods by running a T- test and among years and sites by running ANOVA tests. We also estimated occupancy rate (*Psi*) and detection probability (*p*) based on the occupancy theoretical models developed by MacKenzie *et al.* (2006), that are based on species having different probabilities of being detected at any given site. Thus, once the detection probability was estimated, the model estimated the real occupancy rate of any given site. These models work with a series of repetitive samplings, where the species detection (1) or non-detection (0) is recorded (MacKenzie *et al.* 2006). Detection and occupancy probabilities were estimated through 72 (monthly) sampling occasions using a single season model, assuming that tapir occupancy was constant through the sampling period (MacKenzie *et al.* 2006). We estimated the null models without covariates for the occupancy rate (*Psi*) and detection probability (*p*). These models were estimated in the software PRESENCE V. 12.7 developed by J. Hines based on MacKenzie *et al.* (2006).

Figure 2. A tapir and a calf recorded in a pond in Calakmul Biosphere Reserve, Mexico.

We tested differences between occupancy rate of the two periods and among years and sites using non-parametric statistical methods such as U Mann-Whitney and Kruskal Wallis tests. Finally, we tested the relationships between water availability, average rainfall (obtained at a coarse scale for the Campeche State) and the RAI and occupancy rate separately using regression and correlation analysis. We ran these analyses in R Studio software 3.1.3 (R Core Team 2016).

Results

The camera trap effort totaled 18,184 days and covered a time lapse of 11 years divided into two periods, one from 2008 to 2010 and the second from 2014 to 2018; there was no sampling from 2011 to 2013. The sampling effort varied from 9 to 15 ponds per year and resulted in 457 independent records of tapir.

Population trends along years and sites. The average tapir population RAI from all sites and years was 27.6 (records/1000 camera days) and exhibited a decreasing trend from the first period to the second period with an average of 33.1 from 2008 to 2010 versus 22.5 from 2014 to 2018 although not significantly different (t = -1.55, P value = 0.13, *d. f.* = 26). The highest and smallest RAI per year were found in the second period with 50.7 in 2015 and 9.4 in 2017, respectively (Figure 3).

Of all the ponds monitored in the first period the pond “Bonfil” was the one with the largest RAI followed by the ponds “Bobal” and “Totonaca”. There were no significant differences among ponds in the first period (Anova F = 1-34, P value = 0.24, *d. f.* = 44). In the second period, pond “Bonfil” together with pond “Ag1” were the most important for tapirs

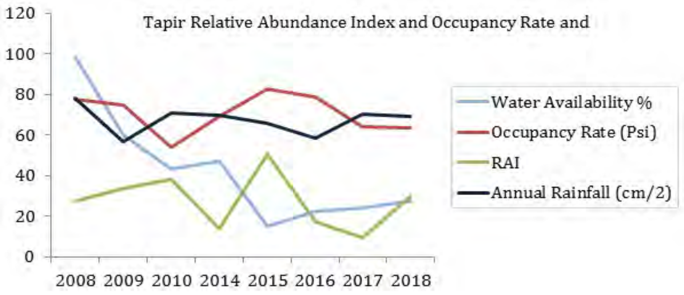

Figure 3. Water availability on ponds (as percentage of ponds with water), Average Annual Rainfall and Tapir Relative Abundance Index (RAI) and Occupancy Rate (Psi) estimated for all ponds. Occupancy rate was multiplied by 100 times to visualize the trend along the water availability trend. Rainfall in cm was divided by 2 to be on the same scale. Calakmul Biosphere Reserve, Mexico.

and "Bonfil" was the one with the highest RAI of all the ponds (Figure 4). There were statistically significant differences among ponds for this period (Anova *F* = 2.65, *P* value = 0.015, *d. f.* = 50) and Tukey post-hoc analyses showed that "Bonfil" differed from "Baños", "Dos Aguadas", "Km46.5" and "Nico" ponds. Some ponds were monitored in both periods. "Bonfil" was as the preferred pond in terms of relative abundance for tapirs, although the RAI variability was very large across years (Fig 4). A decreasing population trend was observed among all the ponds with the exception of Bonfil (Figure 4).

The average occupancy rate (*Psi*) for all years and sites was 0.70 (0.14 SE) with a probability of detection (*p*) of 0.40 (0.09 SE) again, for all sites and years. Occupancy rate (*Psi*) showed a slightly different pattern than RAI and remained relatively stable from the first period (0.69) to the second period (0.72), and a U Mann-Whitney test did not show significant differences among these periods (*p* value = 0.82). The year with the highest occupancy rate was, again, the year of 2015, and the smallest was 2010 (Figure 3). A Kruskal-Wallis test did not reveal statistical differences on occupancy rates (Psi) across years (*p* value = 0.457).

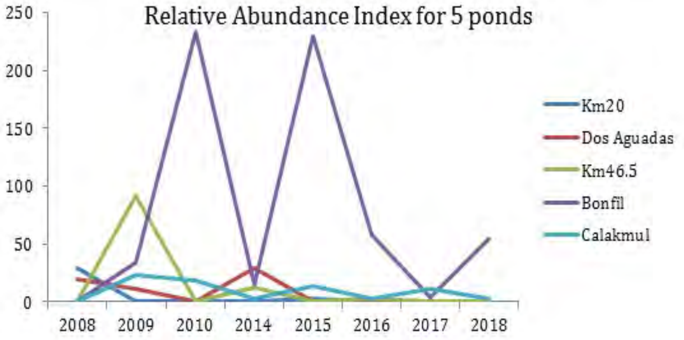

Figure 4. Annual average Relative Abundance Index (RAI) in a set of ponds that were monitored in the two periods. Calakmul Biosphere Reserve, Mexico.

Occupancy rate (*Psi*) of the ponds monitored showed different results than the RAI with "Bobal", "Uxul", "Totonaca", "Dos Carmelos" and "Aguila" as the most important for tapirs in the first period. "Bonfil" was not identified as the best pond according to the occupancy rate in this period, but, in the second period "Bonfil", "Corriente", "Verde", "Ag4" and "Nico" were the ponds with the largest occupancy rates (*Psi*). A Kruskal-Wallis test on the occupancy rate (*Psi*) among ponds revealed that the differences were statistically significant (*p* value=0.023), with the above-mentioned ponds as the most important and "Changuis" and "Km20" as the least important for the first and second period respectively.

Population trends and water availability. Rainfall patterns over the years did not show a decreasing trend state-wide in Campeche (Figure 3) and were not correlated with water availability in the ponds, neither with tapir's RAI, or tapir's occupancy rate (*P* = 0. 294, *P* = 0.878 and *P* = 0.450 respectively according to Pearson correlation test). However, water availability in ponds did show a decreasing trend from 2008 to 2018, with 70 % of ponds being dry from 2008 to 2018. The year with lowest water availability was 2015 where only 15 % of ponds had water (Figure 3). Despite this decreasing trend in water availability of ponds, tapir population on average did not show a decreasing trend and there were not statistically significant relationships between either RAI and water (R^2 = 0.001, *F* = 0.007, *P* value = 0.935) or the occupancy rate and water (R^2 = -0.009, *F* = 0.052, *P* value = 0.827) (Figure 3).

Discussion

We conducted a uniquely long-term study of Baird's tapir population in a Neotropical forest. The main results indicated that Baird's tapir populations in the Calakmul Biosphere Reserve were stable but slightly decreasing. At the same time, there was a dramatic decrease in water availability in the ponds. This was an interesting result because water availability on the ground dropped drastically from the initiation of the study through 2018. During this period, however, tapirs appeared to continue to visit ponds in a similar rate. In fact, in-depth analyses of the visitation rate indicated that in the year with lowest water availability (2015) a peak in the population index occurred, counter to our expectations.

However, this may have been due in great part to visits to a single pond "Bonfil" (64 %), that had free-standing water during that year while other ponds' visitation rate decreased dramatically. This fine detail analyses of each pond visitation rate, provides evidence that tapirs are becoming stressed due to water scarcity and that can have important consequences at the population and behavioral level.

This finding agrees with the events that occurred in the first half of 2019 in the Calakmul municipality when several tapirs, in at least 12 separate incidents, were seen near villages, roads or water containers looking apparently for water. Several of them were in very bad physical conditions and several of them died (RR-H, DSP, and NAD pers. obs.). As far as we are aware, that situation has not occurred in these numbers in the area before (RRH pers. obs.).

Occupancy models did not detect a decreasing trend at the general level but the Relative Abundance Index of some ponds that were monitored the whole time did, with the average RAI of each period shows a decreasing trend for the second period. This finding indicates that in spite of the theoretical expectation that occupancy models are more robust statistically (MacKenzie *et al.* 2006; O'Connell and Bailey 2011), they miss relevant information because they reduce the estimate of the population to only detection or non-detection of the species. We recommend use of a systematically collected index of relative abundance because it can better indicate changes in the population, especially when these changes are not very dramatic, as in the case of tapirs in the CBR.

Monitoring several ponds in the CBR gave us the opportunity to recognize some of them as very important for the tapir population. "Bonfil" is located in the center of the southern area of the CBR and is a very important area for tapirs. Another important pond is "Ag4" which is located at 22 km north of "Bonfil." Identifying important ponds should allow dedicated conservation efforts. For example, since 2015 the authorities of the CBR are setting artificial ponds (2 meters long x 0.5 meters wide) in some specific areas of the CBR. These efforts should be directed to sites important for tapirs. Additionally, some of these ponds can be treated as wildlife sanctuaries by giving them additional protections from tourists.

Climate change is affecting the CBR as well as the Yucatan peninsula (Magrin *et al.* 2007; Mardero *et al.* 2012). It is highly probable that the effects of climate change will intensify in the near future, or will intensify events that appeared periodically such as "El Niño" event that hit the area in 1998, 2003 and apparently between 2015 and 2016 causing less rains in some areas but heavy rains in other areas, or hurricanes that from time to time land in the Mesoamerica region causing damages to the forest and altering tapir behavior as was documented in Nicaragua by Jordan *et al.* (2019). So continued monitoring of tapir populations is needed to record population changes and to apply adaptive measures when possible.

For example, in the near future, if the population trend continues decreasing, the population of tapir in the area may be increasingly encountered in the communal forest of the municipalities that are outside the CBR as was predicted by O'Farrill *et al.* (2014). The communal forests have more water and large water bodies due to a natural precipitation gradient of the area (Reyna-Hurtado *et al.* 2009). If that happens, we will need to work with the communities around CBR to protect tapirs living in their forests.

Long-term wildlife population monitoring is advisable for detecting changes in population trends and relating these changes to environmental or human induced changes. Endangered species such as Baird's tapir need to be monitored closely because their sensitivity to changes in the environment (Naranjo *et al.* 2015; García *et al.* 2016). The CBR is the stronghold for the Baird's tapir population in Mesoamerica (Schank *et al.* 2017), and the dramatic decrease in water availability necessitates detailed monitoring of population and behavioral changes. Additional studies to determine tapir movements are also advisable, as the species can be resilient. For example, tapir movement abilities were demonstrated by a tapir that in the CBR moved as far as 10 km to visit some ponds (Naranjo 2009). In Nicaragua, in the Indio Maiz region, tapir changed movements in response to a hurricane (Jordan *et al.* 2019).

Wildlife is being affected by environmental and human induced changes at alarming rates. Long-term population studies are becoming more important for estimating the impacts of these changes and for predicting the future of the populations. Conservation measures are needed for endangered and sensitive species such as Baird's tapir.

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Literature cited

Alvarez-Castañeda, S., T. Alvarez, and N. Gonzalez-Ruiz. 2015. Keys for identifying Mexican Mammals in the field adn in the Laboratory. CIBNOR, Escuela Nacional de Ciencias Biólogicas, UAM-Metropolitana. Ciudad de México, México.

Carrillo-Reyna, N. L., R. Reyna-Hurtado, and B. Schmook 2015. Abundancia relativa y selección de hábitat de *Tapirus bairdii* en las reservas de Calakmul y Balam Ku, Campeche. Revista Mexicana de biodiversidad 86:202-207.

Dobson, F. S., and J. Yu. 1993. Rarity in Neotropical Forest Mammals Revisited. Conservation Biology 7:586–591.

Garcia, M., C. Jordan, G. O'Farril, C. Poot, N. Meyer, N. Estrada, R. Leonardo, E. Naranjo, A. Simons, A. Herrera, C. Urgilés, C. Schank, L. Boshoff, L. and M. Ruiz-Galeano. 2016. *Tapirus bairdii*. The IUCN Red List of Threatened Species 2016:e. T21471A45173340. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T21471A45173340.en. Downloaded on 05 July 2019.

Garcia, E. 1988. Adaptación del sistema climatológico de Koppen a la República Mexicana. Ciudad de México, México.

Hines, J. E. 2009. PRESENCE 6.9. Software to estimate Patch Occupancy and Related Parameters: USGS-PWRC. Http//www.mbr-pwrc.usgs.gov/software/presence.html (accessed 19 October 2018).

Isaac, N. J. B., S. T. Turvey, B. Collen, C. Waterman and J. E. M. Baillie. 2007. Mammals on the EDGE: Conservation priorities based on threats and phylogeny. PloS ONE 2(3):e296.

Inegi (Instituto Nacional de Estadística Geografia e Informática). 2015. Conteo socio-económico del 2015. Estado de Campeche. INEGI. Campeche, México.

Jordan, C.A., B. Hoover, A. J. Dans, C. Schank and J. A. Miller. 2019.

The Impact of Hurricane Otto on Baird's Tapir Movement in Nicaragua's Indio Maíz Biological Reserve. Pp. 5-19 *in* Movement Ecology of Neotropical Forest Mammals (Reyna-Hurtado, R., and C. Chapman, eds.). Springer International Publishing.

Lira-Torres, I., M. Briones-Salas, and G. Sánchez-Rojas. 2014. Abundancia relativa, estructura poblacional, preferencia de hábitat y patrones de actividad del tapir centroamericano *Tapirus bairdii* (Perissodactyla: Tapiridae), en la Selva de Los Chimalapas, Oaxaca, México. Revista de Biología Tropical 62:1407-1419.

MacKenzie, D.I., J. D. Nichols, J. D. Royle, K. H. Pollock, L. L. Bailey and J. E. Hines. 2006. Occupancy Estimation and modeling. Academic Press. Burlington, U.S.A.

MacKenzie, D. I., and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal biodiversity and conservation 27:461-467.

Magrin, G. C., D. Gay García, J. C. Cruz-Choque, A. R. Gímenez, G. J. Moreno, C. Nagy, and A. Villamizar. 2007. Latin América. Climate change 2007: Impacts, adaptability and vulnerability. Pp. 581-615 *in* Contribution of working group II to the fourth assessment report of the Intergovernmental panel on climate change. Eds., Cambridge University Press. Cambridge, U.K.

Mardero, S., E. Nickl, B. Shmook, L. Schnieder and J. Rogan. 2012. Sequias en el sur de la península de Yucatán: Análisis de la variabilidad anual y estacional de la precipitación. Investigación Geográficas, Boletín del instituto de Geografía, UNAM, Mexico 78:19-33.

Naranjo, E. 2009. Ecology and conservation of Baird's tapir in Mexico. Tropical Conservation Science 4:140–158.

Naranjo, E. J., S. A. Amador-Alcala, F. A. Falconi-Briones, and R. Reyna-Hurtado. 2015. Distribución, abundancia y amenazas a las poblaciones de tapir centroamericano (*Tapirus bairdii*) y pecarí de labios blancos (*Tayassu pecari*) en México. Therya 6:227-249.

O'Connell, A. F. and L. L. Bailey. 2011. Inference for occupancy and occupancy dynamics. Pp. 191-204 *in* Camera traps in animal ecology. Springer, Tokyo, Japan.

O'Connell, A.F., J. D. Nichols, and U. K. Karanth. 2011. Camera Traps in Animal Ecology: Methods and Analyses. Springer. Tokyo, Japan.

O'Farrill, G., M. Galetti, and A. Campos-Arceiz. 2013. Frugivory and seed dispersal by tapirs: an insight on their ecological role. Integrative Zoology 8:4–17.

O'Farrill, G., K. Gauthier-Schampaert, B. Rayfield, O. Bodin and S. Calme. 2014. The Potential Connectivity of Waterhole Network and the Effectiveness of Protected Areas Under Various Drought Scenarios. PLoS ONE 9(5):e95049.

Pennington, T. and J. Sarukhan. 1998. Arboles Tropicales de Mexico. UNAM-Fondo de cultura Economica. Ciudad de México, México.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria.

Reyna-Hurtado, R. 2007. Social ecology of the white-lipped peccary (*Tayassu pecari*) in the Calakmul forest, Mexico. PhD Thesis. Department of Wildlife Ecology and Conservation, University of Florida. Gainesville, U.S.A.

Reyna-Hurtado, R., E. Rojas-Flores, and G. W. Tanner. 2009. Home range and habitat preferences of white-lipped peccary groups (*Tayassu pecari*) in a seasonal tropical forest of the Yucatan Peninsula, Mexico. Journal of Mammalogy 90:1199-1209.

Reyna-Hurtado, R. 2009. Conservation status of the white-lipped peccary (*Tayassu pecari*) outside the Calakmul Biosphere Reserve in Campeche, Mexico: a synthesis. Tropical Conservation Science 2:159-172

Reyna-Hurtado, R. A., G. O'Farril, D. Sima, M. Andrade, A. Padilla, and L. Sosa. 2010. Las aguadas de Calakmul. CONABIO/ Biodiversitas 93:1-5.

Reyna-Hurtado, R., C. A. Chapman, S. Calme, and E. Pedersen. 2012. Searching in heterogeneous environments: foraging strategies in the white-lipped peccary (*Tayassu pecari*). Journal of Mammalogy 93:124-133

Reyna-Hurtado, R., M. Sanvicente, N. Carrillo, J. Pérez-Flores, and S. Calme. 2016. Insights into a multiannual estimates of home range if a Baird's tapir in the Maya forest. Therya 7:271-276

Ripple, W. J., K. Abernethy, M. G. Betts, G. Chapron, R. Dirzo, M. Galetti and T. M. Newsome. 2016. Bushmeat hunting and extinction risk to the world's mammals. Royal Society open science 3:60498.

Royle, J. A. and R. M. Dorazio. 2006. Hierarchical models of animal abundance and occurrence. Journal of Agricultural, Biological, and Environmental Statistics 11:249-263.

Sandoval-Seres, E., R. Reyna-Hurtado, M. Briceño-Mendez, and R. Cerda-Vega. 2016. Pond use and relative abundance of *Tapirus bairdii* in the Calakmul region, Campeche, Mexico. Therya 7:39-50.

Schank, C., M. V. Cove, M. J. Kelly, E. Mendoza, G. O'Farrill, R. Reyna-Hurtado, et al. 2017. Using a novel model approach to assess the distribution and conservation status of the endangered Baird's tapir. Diversity and Distributions 23:1459–1471.

Tobler, M., E. J. Naranjo and I. Lira-Torres. 2006. Habitat Preference,Feeding Habits and Conservation of Baird's Tapir in Neotropical Montane Oak Forests. Pp. 347–359 *in* Ecology and Conservation of Neotropical Montane Oak Forests (Kappelle, M. Ed),. Springer-Verlag, Berlin, Heidelberg.

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Relación de los pequeños mamíferos terrestres (Rodentia y Didelphimorphia) con la estructura de la vegetación en el Bosque Atlántico Interior – un análisis multivariado

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The ecological importance of small mammals includes their role as dispersers of seeds, spores and propagules of plants, fungi and lichens, decomposers of organic matter and controllers of invertebrates as well as prey of a great number of vertebrates. The objective of this research was to determine the relationship between non-volant small mammals (Rodentia and Didelphimorphia) to vegetation structure and the extent of degradation of the forest in an area near the western boundary of the Upper Parana Atlantic Forest, and to evaluate seasonal and interannual variation in species' abundances. The study was conducted in the Mbaracayú Forest Natural Reserve, Paraguay. Mark-capture methodology was employed in three sites with different degrees of degradation, in two seasons of the year (dry and rainy), in 2015 and 2016. A multivariate analysis was performed with ANOVA and MANOVA, evaluating degree of habitat disturbance and annual and seasonal variation as independent variables and species abundances as dependent variables. Sixteen small-mammal species were recorded, with 1,161 captures of 598 individuals and 563 recaptures throughout the sampling. Twelve species were of the Order Rodentia (all of the family Cricetidae, subfamily Sigmodontinae), and four of the Order Didelphimorphia (family Didelphidae). Variables that were significant for the most abundant species (*Akodon montensis*) were interannual variation and habitat degradation. The most common didelphid species in the study was *Gracilinanus agilis*, which appears well-adapted to different degrees of habitat degradation, given its occurrence in all sites. Plant communities, including their composition and degree of habitat disturbance, are important for small-mammal communities which are interacting in the different habitats of the forest. In this study we observed that *Akodon montensis* was most abundant in the habitat of moderate disturbance in the dry season (June). This habitat was characterized by large trees with grasses predominant in the understory. *Hylaeamys megacephalus* was most abundant in the dry season (June) and less so in the rainy season (November). *Oligoryzomys nigripes* is a habitat generalist and is less specialized in food preference. Abundance of the didelphid species *Gracilinanus agilis* was quite variable among sampling periods, but the species was present in all three levels of habitat degradation. The various species (especially the most abundant) exhibited different responses to habitat degradation and to interannual and seasonal variations.

La importancia ecológica de los micromamíferos radica en el rol que desempeñan en los bosques, donde actúan como dispersores de semillas, esporas y propágulos de plantas, hongos y líquenes, descomponedores de materia orgánica, controladores de invertebrados y a la vez, como presas de gran número de vertebrados. El objetivo de esta investigación fue determinar la relación de los micromamíferos no voladores (Rodentia y Didelphimorphia) con la estructura de la vegetación y el nivel de degradación del bosque en una zona del límite occidental del Bosque Atlántico del Alto Paraná y evaluar variación estacional e interanual en las abundancias de estas especies. Se llevó a cabo en la Reserva Natural del Bosque Mbaracayú, Paraguay. La metodología utilizada fue de captura marca recaptura, en tres sitios con diferentes niveles de degradación, en dos épocas del año (seca y lluviosa), en el 2015 y 2016. Se realizó un análisis multivariado con ANOVA y MANOVA considerando el año, época del año y parcela como variables independientes y las abundancias de especies como variables dependientes. El total de especies registradas fue de 16, con 1,161 capturas de 598 individuos, con 563 recapturas. Doce especies fueron del orden Rodentia (todos de la familia Cricetidae, subfamilia Sigmodontinae) y cuatro del orden Didelphimorphia (familia Didelphidae). Las variables que resultaron significativa para la especie más abundante, *Akodon montensis*, fueron el año y el hábitat (nivel de degradación). La especie de didélfido más común en todo el estudio fue *Gracilinanus agilis*, que podría estar adaptado a los diferentes niveles de degradación del hábitat, dada su ocurrencia en todos los sitios. Las comunidades vegetales son principalmente importantes para las comunidades de micromamíferos que se encuentran interaccionando en los diferentes hábitats del bosque. En este estudio se observó que *Akodon montensis* fue más abundante en el hábitat de degradación media en la época seca (junio). En este hábitat estaban presentes comunidades vegetales de árboles de gran porte con predominio de gramíneas en el sotobosque. La población de *Hylaeamys megacephalus* disminuyó en la época lluviosa, observándose una mayor abundancia en la época seca. *Oligoryzomys nigripes* podría ser generalista en lo referente al hábitat por ser una de las especies menos especialistas en cuanto a la alimentación. *Gracilinanus agilis* fluctuó durante todos los periodos de muestreos en las diferentes estaciones del año y estuvo asociado a los tres niveles de degradación. Las asociaciones entre comunidades de micromamíferos y comunidades vegetales indicarían preferencia hacia los diferentes tipos de microhábitats por parte de los micromamíferos. Las distintas especies (sobre todo las más abundantes) responden de diferentes maneras a las modificaciones del hábitat y a lo largo del ciclo anual y en las diferentes épocas debido a sus preferencias u ocurrencia en el hábitat.

Keywords: analysis of variance; canonical coordinates analysis; cluster analysis; Didelphidae habitat association: Reserva Natural del Bosque Mbaracayú; Sigmodontinae.

Introducción

Los micromamíferos pueden llegar a ser indicadores del estado de los bosques, dado que la heterogeneidad del espacio en que se encuentran promueve la diversificación de sus nichos espaciales, además de ser dispersores de semillas, esporas y propágulos de plantas, hongos y líquenes, descomponedores de materia orgánica, controladores de los invertebrados y a su vez, presas de un gran número de vertebrados (Aragón *et al.* 2009).

En el Neotrópico, los roedores sigmodontinos constituyen una parte importante de la riqueza de las comunidades faunísticas (Emmons 1999; Patton *et al.* 2015). Sin embargo, muchas preguntas sobre selección de hábitat dentro de este grupo siguen sin respuesta. Probablemente, las respuestas a estas preguntas permitirían una mejor comprensión de la composición y la dinámica de las comunidades de roedores a una escala local (es decir, la escala a la que un roedor experimenta su entorno).

En las últimas dos décadas, numerosos estudios han investigado las asociaciones de hábitats de roedores Sigmodontinos en todo el Neotrópico. Schnell *et al.* (2010) evaluaron las preferencias de hábitat de *Sigmodon mascotensis* en una zona costera seca del occidente de México, y Poindexter *et al.* (2012) evaluaron cuatro especies comunes de roedores en la misma área. Delciellos *et al.* (2016) informaron que la estructura del hábitat era un determinante importante de ensamblajes de pequeños mamíferos en fragmentos de Mata Atlántica en el estado de Río de Janeiro, Brasil. Además, se han reportado distintas asociaciones de hábitats para una variedad de especies de sigmodontinos en marismas de agua dulce (Bonaventura *et al.* 2003), remanentes de Bosques Atlánticos secundarios (Püttker *et al.* 2008), Bosque Atlántico del sur (Melo *et al.*, 2011, 2013), y la región pampeana en el sur de Brasil (Sponchiado *et al.* 2012). Owen *et al.* (2010) encontraron asociaciones de hábitats distintas para *Akodon montensis* en una región del Bosque Atlántico Occidental. Polop *et al.* (2014) también informaron sobre asociaciones de hábitat para tres especies de Sigmodontinae, *Oligoryzomys longicaudatus, Abrothrix hirta* (reportado como *A. longipilis*) y *A. olivacea,* en una región del sur de los Andes.

Las comunidades de micromamíferos no voladores presentes en áreas boscosas del Bosque Atlántico Interior, al estar relacionadas con las comunidades vegetales, permiten inferir acerca del nivel de degradación del hábitat, ya que responderían de distintas maneras a los cambios que ocurren en el bosque al ser sometidos a una comparación entre sitios, épocas y años. Los niveles de degradación de los bosques afectan la composición de las especies de micromamíferos no voladores tanto a escala temporal como espacial. Se producen comúnmente fluctuaciones irregulares en el número de individuos debido a variaciones climáticas, tales como tiempo particularmente frío, caliente o seco, o también por catástrofes naturales como fuegos o tormentas, y estos factores son independientes de la densidad (Hickman *et al.* 2002). La explosión demográfica en las poblaciones de roedores puede estar ligada a factores ambientales como el fenómeno de El Niño, lo que en países de América del Sur se pudo observar en los últimos años (Jaksic y Lima 2003, Dirección Nacional de Aeronáutica Civil 2016).

En las zonas limítrofes del Bosque Atlántico del Alto Paraná esporádicamente aparecen algunas especies de pequeños mamíferos terrestres encontrados generalmente en bosques o vegetación secundaria y en esas zonas marginales de las ecorregiones la fauna característica de cada ecorregión puede llegar a ser sensible a cambios de su ambiente biótico o abiótico (Owen 2013).

En este trabajo se realizaron evaluaciones de la dinámica de la comunidad de micromamíferos y su asociación con la estructura vegetal en dos épocas del año (seca y lluviosa), a lo largo de un periodo de dos años, utilizando métodos de captura-marca-recaptura en tres parcelas distintas, establecidas de acuerdo a las comunidades vegetales y a los distintos niveles de degradación.

Material y Métodos

Sitio del estudio. El Bosque Atlántico del Alto Paraná (BAAPA) abarca una superficie de 483.800 km^2 y representa uno de los *Biodiversity Hotspots* del planeta, es decir uno de los sitios claves para la conservación por la diversidad que representa (Myers *et al.* 2000). Se caracteriza por estar predominantemente conformado por bosque subtropical semicaducifolio húmedo a subhúmedo (Dinerstein *et al.* 1995; Cartes 2006). Actualmente, los bosques de esta ecorregión existen en fragmentos remanentes que en conjunto totalizan sólo el 7 % de su extensión original (Cartes 2006).

El área de estudio comprende la Reserva Natural del Bosque Mbaracayú (RNBM), que cuenta con 64.405 hectáreas correspondiente al área núcleo de la Reserva de Biosfera del Bosque Mbaracayú (Owen *et al.* 2019; Owen y Smith 2019). Se localiza al noreste de la región Oriental del Paraguay, entre los 24° 00′ y 24° 15′ de latitud Sur, y 55° 00′ y 55° 32 ′ de longitud Oeste, en el Departamento de Canindeyú (Fundación Moisés Bertoni/Banco Mundial 2005). Toda el área en que se encuentra la RNBM está ubicada en la cuenca del Río Jejuí, un tributario importante del Río Paraguay. La RNBM representa uno de los más grandes fragmentos de bosques que se encuentran protegidos en Paraguay lo que significa tener a disposición una de las pocas oportunidades para estudiar comunidades de roedores en sus hábitats (Eastwood *et al.* 2018).

El clima se caracteriza por presentar una temperatura media anual de 22 ºC y precipitaciones medias de 2,000 mm/año, siendo la temporada de lluvia durante los meses de octubre a marzo (primavera-verano). La época seca y fría se da entre los meses de junio y octubre (invierno-primavera). Sin embargo, durante las épocas de El Niño ocurren incrementos de las precipitaciones (Di Bitetti *et al.* 2003).

Estructura de la vegetación y nivel de degradación. Las tres parcelas de muestreo se evaluaron basándose en una serie extensa de características estructurales de la vegetación, medidas en cada una de las estaciones de trampa en cada parcela. Las medias de estas medidas de vegetación se utilizaron como medidas generales para cada parcela. Estos se estandarizaron a una media de cero y una desviación estándar de uno, para mitigar los efectos del tamaño del carácter. Los eigenvectores se extrajeron de la matriz de correlaciones de caracteres estandarizados y se evaluaron mediante el análisis de componentes principales (PCA; Sneath y Sokal 1973). Luego de los análisis preliminares, se incluyeron seis caracteres en el PCA final, como descriptores importantes de la calidad del bosque y el hábitat de roedores: árboles caídos cercanos (AC), distancia al árbol más cercano (DAC), porcentaje de cobertura de hierbas (PCH), restos de madera en el suelo (MM), árbol de naranjo (AN), altura máxima del dosel (AMD). Se consideró que los niveles de degradación estaban asociados positivamente con los dos primeros componentes principales, que en conjunto representaban el 95 % de la varianza. Por lo tanto, un hábitat de bosque más degradado se asocia con las hierbas, los troncos (árboles caídos) y los naranjos (*Citrus aurantium*, una especie introducida que se ha aclimatado en bosques perturbados). El hábitat de bosque menos degradado se asocia con más madera muerta (ramas caídas, no árboles caídos), un dosel más alto y una menor distancia al árbol más cercano. De los datos de vegetación se analizaron los valores promedios para cada parcela y en cada época de muestreo del año 2015 (Tabla 1). En las dos épocas de muestreo (seca y lluviosa) realizadas, se consideraron las mismas características de la vegetación.

Se designaron las tres parcelas de acuerdo a la calidad del hábitat definida en términos de degradación: Parcela B (degradación baja, con su centro a las 24.141° S, 55.366° W), A (degradación media, 24.123° S, 55.505° W) y G (degradación alta, 24.131° S, 55.537° W), distantes mínimos a 3.3 km una de otra. Los nombres y designaciones de las parcelas son consistentes con otras publicaciones en preparación o en revisión basadas en datos desarrollados en este proyecto.

Métodos de muestreo. El tamaño de cada parcela fue de 12 x 12 = 144 estaciones. Las estaciones en cada parcela estuvieron separadas unos 10 metros entre sí. En cada estación se colocaron dos trampas Sherman (7.5 x 9.0 x 23.0 cm; H. B. Sherman Traps, Tallahassee, Florida) en el suelo, y otra a 1-3 m por encima del suelo (lianas o ramas de árboles). En la primera sesión de muestreo (periodo de junio/julio de 2015) se utilizaron una trampa a nivel del suelo y una trampa arriba, aumentando en los siguientes muestreos a una trampa más por estación a fin de aumentar el esfuerzo de muestreo. Las trampas fueron cebadas con una mezcla de avena y mantequilla de maní y revisadas cada mañana.

Se utilizó el método de captura-marca-recaptura. Los muestreos se realizaron en los meses de junio/julio (época seca) y noviembre (época lluviosa) de los años 2015 y 2016. Cada muestreo abarcaba cinco noches en cada parcela. El procedimiento consistió en identificar al animal capturado por medio de una etiqueta PIT (Passive Integrated Transponder, Biomark Inc., Boise, Idaho) de 8.4 mm de largo implantada por vía subcutánea entre los hombros con una jeringa. Luego de la recaptura estos animales podían ser identificados por medio de un lector electrónico de mano.

Se extrajeron muestras de tejido (1 a 2 mm de la punta de la cola) para su identificación posterior por ADN si fuera necesario, además de la preparación de espécimen de cráneo y fluido, de los especímenes encontrados muertos en trampa, para corroborar las identificaciones hechas en campo. Los especímenes colectados y preparados están albergados en la colección de mamíferos del segundo autor. Se utilizó para la nomenclatura taxonómica y claves de identificación de Patton *et al.* (2015) para roedores sigmodontinos, y de Gardner (2008) y Voss y Jansa (2009) para marsupiales.

Se tomaron datos de cada individuo capturado como el código de PIT, fecha, parcela, número de estación de trampeo, lugar de colocación de la trampa (suelo, encima del suelo), identidad específica del individuo, sexo, clase de edad, condición reproductiva, peso y la salud en general. Los procedimientos con animales en este estudio se llevaron a cabo bajo los Permisos de Colecta Científica No. 011/2014, 132/2015 y 269/2016 (Secretaría del Ambiente, actualmente el Ministerio de Ambiente y Desarrollo Sostenible, Paraguay), y se siguieron las pautas del Comité de Cuidado y Uso de Animales del Sociedad Americana de Mastozoólogos para el uso de mamíferos silvestres en investigación y educación (Sikes *et al.* 2011, 2016). Todos los procedimientos con animales fueron aprobados (Aprobación No. 14024-03) por el Comité Institucional de Cuidado y Uso Animal de la Universidad de Texas Tech (IACUC), que sigue la 8ª Edición de la Guía para el Cuidado y Uso de Animales de Laboratorio (Guía), NRC 2011.

Tabla 1. Datos de vegetación para cada parcela tomados en el año 2015. Hábitat con degradación baja, parcela B (baja), hábitat con degradación media, parcela A (media) y hábitat con degradación alta, parcela G (alta).

	Parcela B (baja)		Parcela A (media)		Parcela G (alta)	
Características de la vegetación	Junio	Noviembre	Junio	Noviembre	Junio	Noviembre
Madera muerta en el suelo (%)	11.0 (12.3)	8.0 (15.3)	7.5 (11.0)	5.1 (9.1)	11.1 (13.3)	5.5 (9.8)
Altura máxima del dosel (m)	16.0 (5.1)	14.6 (5.2)	15. 6 (4.8)	14.3 (5.0)	15.6 (3.0)	13.8 (3.3)
Distancia a los árboles más cercanos (m)	4.6 (1.4)	4.6 (1.4)	4.8 (1.6)	4.8 (1.7)	4.2 (1.4)	4.2 (1.4)
Porcentaje de cobertura de hierbas (%)	19.1 (10.0)	22.3 (7.8)	17.5 (10.4)	18.8 (10.0)	4.9 (4.1)	27.4 (13.0)
Árboles caídos (por unidad)	0.6 (0.5)	0.6 (0.5)	0.6 (0.5)	0.6 (0.5)	0.1 (0.3)	0.1 (0.3)
Arboles de naranjo (por unidad)	0.0 (0)	0.0 (0)	0.3 (0.4)	0.3 (0.4)	0.6 (0.5)	0.2 (0.4)

La colección de mamíferos donde los *vouchers* están depositados cuenta con Habilitación Nº. 004/2015 (Secretaria del Ambiente, Paraguay).

Análisis de datos. Se utilizó el Número Mínimo de Conocidos Vivos (Minimum Number Known Alive: MNKA), que es el número total de individuos de una especie encontrado en una parcela durante una sesión de muestreo. Para probar si los datos seguían una distribución normal se realizó la prueba de normalidad de Shapiro-Wilks, para los datos de los dos años. Se rechazó la hipótesis nula que afirma que el conjunto de datos sigue una distribución normal para el 2015 y para el año 2016. Se transformó los datos por medio de Ln (logaritmo natural) para llegar a una distribución normal.

Se utilizó el Análisis de Correspondencia Canónica (CCA) para evaluar la relación especie-ambiente, teniendo en cuenta un conjunto común en donde se asume las respuestas de las especies. Este método se centra principalmente en las relaciones entre especies y mediciones de las variables ambientales, obteniendo una interpretación brindada por los ejes de ordenación. Ha sido desarrollado para estudios de ecología en donde se relaciona la abundancia de especies con las variables ambientales (Ter Braak 1986).

Para evaluar la similitud de las tres parcelas durante los cuatro periodos se empleó el método de Agrupación Pareado no Ponderados con Media Aritmética (Unweighted Pair Group Method using Arithmetic averages - UPGMA, Sokal y Michener 1958). El análisis se tuvo en cuenta para las especies, así como también para las parcelas y las estaciones del año. Este método calcula el promedio de grupos de pares sin ponderar, los clústeres se unen de acuerdo a la distancia media que existe entre todos los miembros de los dos grupos (Hammer 2016).

Para el análisis de las variables independientes (año, época del año, parcela) y dependientes (abundancias de las especies) se realizó un ANOVA y posteriormente un MANOVA, para ver si los cambios en las variables independientes tienen efectos significativos en las dependientes. El ANOVA factorial ayuda a evaluar el efecto de dos o más variables independientes sobre una variable dependiente. El análisis de MANOVA analiza la relación entre dos o más variables independientes (Hernández Sampieri *et al.* 2010) y puede demostrar asociaciones significativas no indicadas por los análisis univariados (Willig *et al.* 1986, Willig y Owen 1987).

Estos análisis multivariados ayudan a comparar y visualizar los efectos que el año, la parcela, o la época del año tienen en las abundancias de las especies de micromamíferos y en cuáles especies. Al visualizar al menos una diferencia entre las medias de los datos, es decir al rechazarse la hipótesis nula, se procedió con pruebas *a posteriori* de Tukey para saber cuáles medias fueron significativamente diferentes.

La prueba de normalidad de los datos, así como las pruebas de Análisis de la Varianza (ANOVA), Análisis Multivariado (MANOVA) y Análisis de Agrupamiento (clúster) se realizaron en el Programa Infostat (Di Rienzo *et al.* 2008). El análisis de Correspondencia Canónica (CCA) se realizó en el Programa Past (Hammer 2016).

Resultados

En total se registraron 16 especies de micromamíferos no voladores encontrados en los sitios de muestreo, con 1.161

Tabla 2. Abundancias (número mínimo conocido en vivo) para cada especie en cada cuadrícula durante cada sesión de muestreo.

	Parcela B (Baja)				Parcela A (Media)				Parcela G (Alta)				
	2015		2016		2015		2016		2015		2016		
Taxón/Especies	Jun	Nov	Jun	Nov	Jun	Nov	Jun	Nov	Jun	Nov	Jun	Nov	**Total**
Didelphidae													
Cryptonanus chacoensis	0	0	0	0	0	1	0	0	0	0	0	0	1
Gracilinanus agilis	5	0	4	0	1	1	2	4	3	2	6	1	29
Marmosa paraguayana	1	0	0	0	0	0	0	0	0	0	0	0	1
Monodelphis dimidiata	0	0	0	1	0	0	0	0	0	0	0	0	1
Cricetidae													
Akodon montensis	53	45	23	12	59	59	28	18	29	28	16	12	382
Calomys callosus	0	1	0	0	1	0	0	0	4	3	0	0	9
Cerradomys maracujensis	0	0	1	0	0	0	0	0	0	0	0	0	1
Hylaeamys megacephalus	15	4	3	1	8	6	12	6	14	7	7	3	86
Juliomys pictipes	0	0	1	0	0	0	0	0	0	0	0	0	1
Necromys lasiurus	0	0	0	0	2	1	0	0	0	0	0	0	3
Oecomys cf. mamorae	0	0	0	0	0	0	0	1	0	0	0	0	1
Oligoryzomys mattogrossae	3	0	3	0	3	1	2	0	1	0	3	0	16
Oligoryzomys nigripes	7	5	4	0	7	5	6	1	4	4	3	4	50
Oligoryzomys sp.	0	0	0	0	4	0	2	0	1	0	2	0	9
Rhipidomys macrurus	0	0	1	0	0	0	0	0	0	0	0	0	1
Sooretamys angouya	0	0	0	2	0	1	0	0	0	0	1	3	7
Total	84	55	40	16	85	75	52	30	56	44	38	23	598

capturas de 598 individuos y 563 recapturas (Tabla 2). Del total, doce especies fueron del orden Rodentia (todos de la familia Cricetidae, subfamilia Sigmodontinae), y cuatro del orden Didelphimorphia (familia Didelphidae). Barreto Cáceres (2017) proporcionó los datos, y detalló los niveles de la riqueza y diversidad de especies, así como la acumulación de especies a través de tiempo.

Análisis de Correspondencias Canónicas. Para el análisis de correspondencias canónicas (CCA) con las características de la vegetación en cada sitio asociado a los distintos niveles de degradación, las variables medidas distancia al árbol más cercano (DAC) y árbol caído (AC), están relacionados positivamente a degradación media y tiene relación negativa con el hábitat de degradación alta. Las variables altura máxima del dosel (AMD) y madera muerta (MM) son asociadas con degradación baja. Árbol de naranjo (AN) y el porcentaje de cobertura de hierba (PCH) se observó mayormente asociado a hábitats con alto nivel de degradación (vectores de hábitats no mostrados).

Las especies *Akodon montensis* (Am) y *Oecomys cf. mamorae* (Oem) se asociaron a las variables de distancia al árbol más cercano (DAC) y árbol caído (AC), relacionados con el hábitat de degradación media. Las especies *Cerradomys maracajuensis* (Cm), *Rhipidomys macrurus* (Rm) y *Juliomys pictipes* (Jp) se encontraron influenciadas por la presencia de madera muerta (MM) en el hábitat con degradación baja. Mientras que la distribución de las especies *Hylaeamys megacephalus* (Hm), *Necromys lasiurus* (Nl), *Oligoryzomys mattogrossae* (Om), *Oligoryzomys* sp. (Osp), *Calomys callosus* (Cc) junto con *Gracilinanus agilis* (Ga) *Cryptonanus chacoensis* (Cch) y *Marmosa paraguayana* (Mp) estuvo asociada al hábitat con degradación alta e influenciada por la presencia de árbol de naranjo (AN). Las especies S*ooretamys angouya* (Sa) *Monodelphis dimidiata* (Md) aparentemente no presentaron alguna relación estrecha con las variables mencionadas (Figura 1). En el análisis de los eigenvectores del análisis de correspondencia canónica, se observa que la mayor parte del análisis es explicada por el primer eje que aporta el 46.67 % de la varianza y el segundo eje que aporta el 33.88 % (Tabla 3).

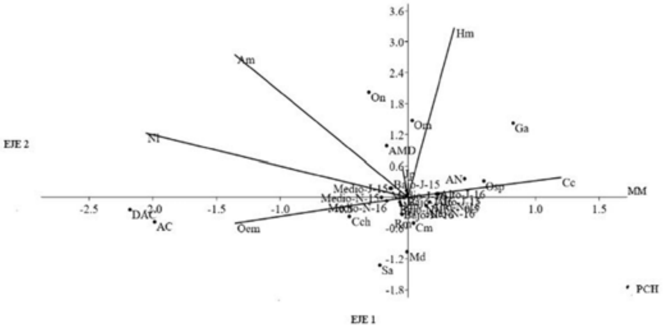

Figura 1. Análisis de Correspondencias Canónica (CCA) para las especies de micromamíferos y los sitios de estudio y las variables de vegetación. Referencias. Especies: *Akodon montensis* (Am), *Calomys callosus* (Cc), *Cerradomys maracujensis* (Cm), *Cryptonanus chacoensis* (Cch), *Gracilinanus agilis* (Ga), *Hylaeamys megacephalus* (Hm), *Juliomys pictipes* (Jp), *Marmosa paraguayana* (Mp), *Monodelphis dimidiata* (Md), *Necromys lasiurus* (Nl), *Oecomys cf. mamorae* (Oem), *Oligoryzomys mattogrossae* (Om), *Oligoryzomys nigripes* (On), *Oligoryzomys* sp (Osp), *Rhipidomys macrurus* (Rm), *Sooretamys angouya* (Sa). Variables: Árbol caído (AC), Distancia al árbol más cercano (DAC), Porcentaje de cobertura de hierbas (PCH), Madera muerta (MM), Árbol de Naranjo (AN), Altura máxima del dosel (AMD).

Agrupamiento de especies. La Figura 2 muestra para la composición de especies para todos los sitios y épocas de muestreos. El grupo de las especies *Akodon montensis* (Am) y *Hylaeamys megacephalus* (Hm) con *Oligoryzomys nigripes* (On) y *Gracilinanus agilis* (Ga) forman un nudo con la especie *Oligoryzomys mattogrossae* (Om) que se separa de los demás grupos. Las especies *Juliomys pictipes* (Jp), *Rhipidomys macrurus* (Rm) y *Cerradomys maracujensis* (Cm), conforman otro grupo junto con las especies *Oecomys* cf. *mamorae* (Oem), *Marmosa paraguayana* (Mp) y *Monodelphis dimidiata* (Md), y juntos se encuentran conformando un punto de unión con las especies *Necromys lasiurus* (Nl) y *Cryptonanus chacoensis* (Cch). La especie *Sooretamys angouya* (Sa) se une a los grupos anteriores. Las especies *Calomys callosus* (Cc) y *Oligoryzomys* sp. (Osp) se encuentran conformando otro grupo.

Agrupamiento de sitios, épocas y años. En la asociación con los tipos de hábitats y época del año, se relacionaron el grupo de los sitios de degradación alta y baja de la época lluviosa del 2016. Estos grupos se separan de los otros conformado por el hábitat con degradación alta y media de la época seca y lluviosa respectivamente del año 2016, conectados a su vez con el hábitat de degradación baja de la época seca del mismo año. Los otros tipos de hábitats que son degradación media y degradación baja de la época seca del año 2016 y 2015, respectivamente, se encuentran asociados al hábitat de degradación media de la época seca del 2015, y este a la vez con los hábitats de degradación alta de la época seca y lluviosa del 2015, relacionados con el hábitat de degradación media de la época lluviosa del 2015. Todos estos grupos se encuentran asociados formando un grupo con el hábitat de degradación baja de la época lluviosa del año 2015 (Figura 3).

Análisis de la varianza (ANOVA). En el ANOVA las variables analizadas fueron época del año, parcela y año. El análisis muestra que cinco especies presentaron diferencias significativas: Akodon montensis (año, parcela), Calomys callosus y Oligoryzomys nigripes (año), y Oligoryzomys mattogrossae y Hylaeamys megacephalus (época del año). Al realizar la prueba a posteriori de Tukey, para Akodon montensis las variables que demostraron ser significativas fueron año y parcela. La diferencia entre las parcelas se debe a que en el sitio con degradación alta (G) se registró un número menor de individuos y en el sitio con degradación media (A) se observó un número mucho mayor de individuos (Tabla

Tabla 3. Componentes y valores de los porcentajes de varianza del análisis de CCA.

Axis	Eigenvalue	%
1	0.15995	46.67
2	0.11613	33.88
3	0.04223	12.32
4	0.01588	4.63
5	0.00856	2.49
6	0.00000	0.00

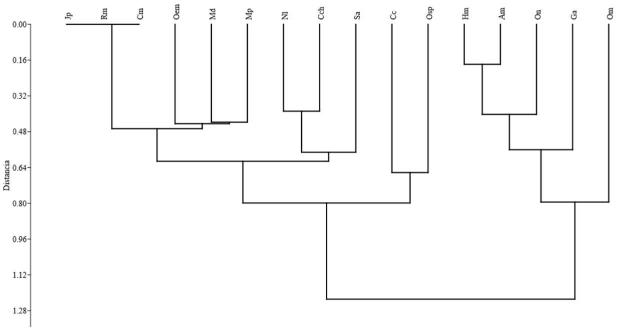

Figura 2. Análisis de agrupamiento para la composición de especies en todos los sitios, época y año que se realizaron los muestreos. *Akodon montensis* (Am), *Calomys callosus* (Cc), *Cerradomys maracujensis* (Cm), *Cryptonanus chacoensis* (Cch), *Gracilinanus agilis* (Ga), *Hylaeamys megacephalus* (Hm), *Juliomys pictipes* (Jp), *Marmosa paraguayana* (Mp), *Monodelphis dimidiata* (Md), *Necromys lasiurus* (Nl), *Oecomys cf. mamorae* (Oem), *Oligoryzomys mattogrossae* (Om), *Oligoryzomys nigripes* (On), *Oligoryzomys* sp. (Osp), *Rhipidomys macrurus* (Rm), *Sooretamys angouya* (Sa).

4). Se rechaza así la hipótesis nula de igualdad de medias de todas las variables; por lo mismo, se acepta la hipótesis alternativa en la cual se indica que al menos una variable produce una influencia sobre la especie.

Para *Hylaeamys megacephalus* la variable que resultó significativa fue la época del año. La diferencia se debió a un número mayor en la época seca (junio) y menor en la época lluviosa (noviembre; Tabla 4). Sin embargo, en el modelo estadístico no resultó significativo ($P = 0{,}096$).

Para *Calomys callosus* lo que resultó significativo fue la variable año. Esto se debe a que no se encontró ningún ejemplar en el 2016, por eso resultó significativo para esa especie en el análisis (Tabla 4). Sin embargo, en el modelo estadístico no resultó significativo ($P = 0{,}095$).

Para *Oligoryzomys nigripes* también resultó significativa la variable año. Esto se debe a que se presentó un menor número en el 2016 (Tabla 4). Sin embargo, en el modelo estadístico no resultó significativo ($P = 0{,}112$).

Para *Oligoryzomys mattogrossae* lo que resultó significativo fue la variable época del año. Esto se debe a que solamente un individuo se encontró en la época lluviosa (Tabla 4). Sin embargo, en el modelo estadístico no resultó significativo ($P = 0{,}009$).

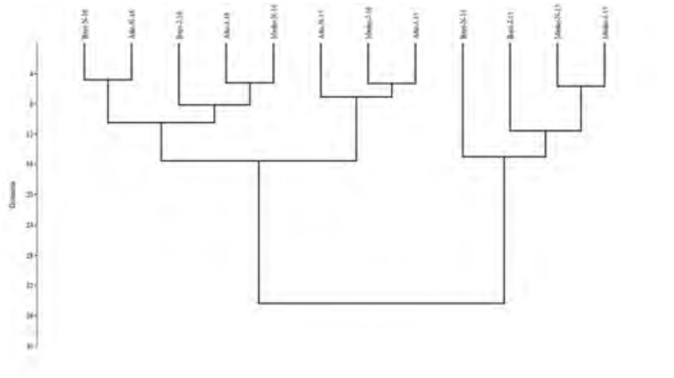

Figura 3. Análisis de agrupamiento para la composición de especies entre todos los sitios, época y año que se realizaron los muestreos. Alto-J-15 (nivel de degradación alto, junio de 2015), Alto-N-15 (nivel de degradación alto, noviembre de 2015), Alto-J-16 (nivel de degradación alto, junio de 2016), Alto-N-16 (nivel de degradación alto, noviembre de 2016), Bajo-J-15 (nivel de degradación bajo, junio de 2015), Bajo-N-15 (nivel de degradación bajo, noviembre de 2015), Bajo-J-16 (nivel de degradación bajo, junio de 2016), Bajo-N-16 (nivel de degradación bajo, noviembre de 2016), Medio-J-15 (nivel de degradación medio, junio de 2015), Medio-N-15 (nivel de degradación medio, noviembre de 2015), Medio-J-16 (nivel de degradación medio, junio de 2016), Medio-N-16 (nivel de degradación medio, noviembre de 2016).

Análisis de la varianza multivariado (MANOVA). El análisis de la varianza multivariado demostró que el año fue el patrón más significativo para la especie *Akodon montensis*. En el estadístico de Wilks se observan valores de la aproximación *F* 2,16; 50,31 y 8,89 para las variables época del año, año y parcela respectivamente (Tabla 5).

Discusión

Especies comunes. En Paraguay oriental, *Akodon montensis* es una especie común encontrada en los bosques, así también lo es por ejemplo en la zona de Misiones, Argentina, donde es más frecuente en diversos ambientes, sin incluir los bordes de arroyos (Cirignoli *et al.* 2011, de la Sancha 2014). En el presente estudio se observó que *A. montensis* estaba asociado a hábitats de degradación media en la época seca. En dicho sitio, estaban presentes comunidades vegetales de árboles de gran porte, hasta 25 m de altura, arbustos hasta 3 m de altura y con predominio de gramíneas en el sotobosque.

Lima *et al.* (2010) registraron una correlación positiva entre el número de capturas de *A. montensis* con la abun-

Tabla 4. Pruebas a posteriori de Tukey para las especies *Akodon montensis, Hylaeamys megacephalus, Calomys callosus, Oligoryzomys nigripes* y *Oligoryzomys mattogrossae* y las variables época del año, año y parcela. Medidas con la misma letra no son significativamente diferentes ($P > 0{,}05$). n: *número de muestreos (4 = muestreos por parcela en los dos años; 6 = muestreos por* época del año y año en los dos años).

	Akodon montensis			*Hylaeamys megacephalus*			*Calomys callosus*			*Oligoryzomys nigripes*			*Oligoryzomys mattogrossae*		
Efecto	Medias	*n*	Grupos	Medias	*n*	Grupos	Medias	*n*	Grupos	Medias	*n*	Grupos	Medias	*n*	Grupos
Época del año															
Nov.	29.00	6	A	4.50	6	A	0.67	6	A	3.17	6	A	0.17	6	A
Jun.	34.67	6	A	9.83	6	B	0.83	6	A	5.17	6	A	2.50	6	B
Año															
2016	18.17	6	A	5.33	6	A	0.00	6	A	3.00	6	A	1.33	6	A
2015	45.50	6	B	9.00	6	A	1.50	6	B	5.33	6	B	1.33	6	A
Parcela															
G	21.25	4	A	7.75	4	A	1.75	4	A	3.75	4	A	1.00	4	A
B	33.25	4	A B	5.75	4	A	0.25	4	A	4.00	4	A	1.50	4	A
A	41.00	4	B	8.00	4	A	0.25	4	A	4.75	4	A	1.50	4	A

dancia de bambú, pudiendo estar asociado a la protección contra los depredadores. En contraste, Goodin *et al.* (2009) indican que *A. montensis* es conocido por ser generalista en cuanto al hábitat, pero muestra preferencia por áreas boscosas semicaducifolias, donde los estratos superiores son menos densos y la cobertura vegetal más densa cerca del suelo. La mayor abundancia de *A. montensis* se registró en los microhábitats que mostraban un grado de actividad antropogénica con mayor penetración de luz, pero donde el bosque nativo estaba aun sustancialmente intacto. Las áreas con vegetación densa y la superficie del suelo desnuda o con poca vegetación tenían menos probabilidades de estar asociadas con la presencia de *A. montensis* (Goodin *et al.* 2009). Melo *et al.* (2013), observaron una relación positiva entre *A. montensis* con los helechos y troncos caídos en el Bosque Atlántico del estado de Rio Grande do Sul, Brasil. Püttker *et al.* (2008) señalan a *A. montensis* como una especie no vulnerable a la fragmentación de los bosques. Las variables significativas en este estudio para *A. montensis* fueron la variable año y la variable parcela o hábitat. Esto se debe a que en el 2016 el número de ejemplares de esta especie fue menor. Además, se podría inferir en una preferencia del hábitat (con nivel de degradación media) para esta especie.

Tabla 5. Análisis de la varianza multivariado, para la especie *Akodon montensis*. Esta especie resultó significativa en el modelo estadístico de ANOVA. Cuadro de Análisis de la Varianza (Wilks). Obsérvese el $p < 0.05$ para la variable año ($p = 0.0002$) y parcela ($p = 0.0120$), ambas variables fueron significativas. Sin embargo, la variable año influenció en mayor medida en la población de la especie. gl: grados de libertad

Efecto	Estadístico	F	gl (num)	gl (den)	*P*
Época del año	0.76	2.16	1	7	0.1849
Año	0.12	50.31	1	7	0.0002
Parcela	0.28	8.89	2	7	0.0120

La especie segunda más común fue *Hylaeamys megacephalus*, que no demostró una preferencia en el hábitat y que podría ser generalista, ya que se encuentra en los bosques primarios, secundarios y degradados (Percequillo *et al.* 2016). Se observó una variabilidad a nivel estacional, que sin embargo en el modelo estadístico no resultó significativa. En la época seca se encontró mayor registro de esta especie, en contraste a la disminución de la población en noviembre durante la época lluviosa. En las zonas boscosas y el cerrado de la parte central de Brasil, *H. megacephalus* se encontró solamente en la época húmeda (Santos-Filho *et al.* 2012). Sin embargo, en este estudio la población de *H. megacephalus* disminuyó en la época lluviosa. Se observó mayor abundancia de esta especie en la época seca (junio) y menor en la época lluviosa (noviembre).

Para la especie *Oligoryzomys nigripes* ninguna de las variables resultó significativa. Sin embargo, estuvo presente en los cuatro periodos de muestreo del estudio excepto en la época lluviosa del 2016. En la época seca de los dos años, mostró asociación con el sitio de degradación media, que podría deberse a características de la vegetación en esa época. Sponchiado *et al.* (2012) encontraron una relación positiva entre *O. nigripes* y las bromelias terrestres, junto con la cercanía a cuerpos de agua. Esta asociación no se observó en este estudio, ya que el predominio de bromelias se encontraba en el sitio de degradación alta. Esta es una de las especies menos especialistas en cuanto a la alimentación, por lo tanto, podría ser generalista en lo referente al hábitat. En la época seca, prefiere sitios más abiertos, también con algunos arbustos y árboles (Bonvicino *et al.* 2016). Se registró la presencia de *O. nigripes* asociado al dosel bajo y a un sotobosque denso en el Bosque Atlántico de Brasil, en zonas con vegetación característica de un bosque perturbado (Püttker *et al.* 2008; Lima *et al.* 2010). Se considera a *O. nigripes* como una especie no vulnerable a la fragmentación de los bosques (Püttker *et al.* 2008). Galiano *et al.* (2013) encontraron que la dominancia poblacional entre *A. montensis* y *O. nigripes* alternó en un Bosque de *Araucaria*, en el sur de Brasil. La abundancia de *A. montensis* no correspondió a ningún factor extrínseco (precipitación, temperatura, etc.), mientras la de *O. nigripes* aumentó en el invierno. Eastwood *et al.* (2018) determinaron que las especies *A. montensis* y *O. nigripes* son simpátricas en la RNBM, en el que fue el primer estudio para determinar los hábitats naturales de dos especies simpátricas de roedores.

En cuanto a los marsupiales, *Gracilinanus agilis* resultó más común dentro del grupo de los didélfidos. Sin embargo, sus poblaciones se mostraron muy variables a través del tiempo y entre sitios. En Mato Grosso do Sul, Brasil se observó que la población de *G. agilis* presentó fluctuación marcadamente estacional, con una alta concentración de la especie en la época lluviosa. Se presume que *G. agilis* tiene tolerancia a algún grado de modificación del hábitat (Carmignotto *et al.* 2015). En esta investigación se observó que *G. agilis* fue fluctuando de igual manera durante todos los periodos de muestreos en las diferentes estaciones del año y asociado a los tres niveles de degradación.

Efectos de caracteres vegetales y degradación. Las asociaciones entre comunidades de micromamíferos y comunidades vegetales, indicarían preferencia hacia los diferentes tipos de microhábitats por parte de los micromamíferos. Estas preferencias podrían ser un factor considerable que influye en los pequeños mamíferos para habitar zonas que pueden estar alteradas (Püttker *et al.* 2008; Lima *et al.* 2010). Sin embargo, el estado de conservación de las especies de micromamíferos de la zona de estudio se encuentra dentro de la categoría de Preocupación Menor (LC) según la lista roja de la UICN (2009). Esto podría deberse a que se reproducen rápidamente y tienen un ciclo de vida relativamente corto. Sin embargo, la alteración de los bosques y hábitats de pequeños mamíferos podría poner en riesgo a las especies más sensibles, sobre todo de marsupiales. Cabe destacar que tres especies (*Marmosa paraguayana, Delomys dorsalis* y *Juliomys pictipes*) que se encuentran en la Reserva Natural del Bosque Mbaracayú son endémicas del BAAPA (Owen y Smith 2019). En este estudio se registraron a *Marmosa paraguayana* y *Juliomys pictipes*.

Las comunidades vegetales son principalmente importantes para las comunidades de micromamíferos que se encuentran interaccionando en los diferentes hábitats del bosque. La alteración o degradación del bosque puede llegar a intervenir con el desequilibrio temporal de las poblaciones y comunidades de pequeños mamíferos (Pardini y Umetsu 2006). Las especies consideradas no vulnerables a la fragmentación se asocian a zonas con características de la vegetación de un bosque más perturbado. En cambio, las especies vulnerables a la fragmentación se encontrarían en áreas con características de los bosques primarios (Püttker *et al.* 2008). Estos patrones se observaron en este estudio ya que se encontraron especies más asociadas a áreas perturbadas y otras especies en zonas de degradación baja. De la Sancha (2014) encontró patrones similares en la Reserva Natural del Bosque Mbaracayú con los bosques megadiversos como el Amazonas. Sin embargo, a pesar de ser uno de los fragmentos de bosques más grandes del BAAPA, Mbaracayú mostró números considerablemente bajos de muestra para pequeños mamíferos comparando con otros fragmentos. Asimismo, en la Amazonía peruana se llegó a reportar números de capturas extremadamente bajas para micromamíferos no voladores, es decir en bosques vírgenes (Hice y Velazco 2012; de la Sancha 2014). En este estudio también se registraron bajos números de muestras, sobre todo en marsupiales y algunos roedores, a pesar de que el esfuerzo de muestreo invertido fue considerable. Sin embargo, podría ser un patrón seguido para los bosques de grandes fragmentos como el Bosque del Mbaracayú.

Efectos de época del año. Para las especies *Hylaeamys megacephalus* y *Oligoryzomys mattogrossae* solo la época del año resultó significativa en el análisis de la varianza. Sin embargo, el modelo estadístico para éste análisis no demostró significancia alguna. Este patrón asociado a una de las especies más abundantes como *H. megacephalus*, sugiere que la época del año (seca y lluviosa) es un factor de importancia a tener en cuenta para las zonas del Bosque Atlántico. Esta variable no resultó significativa para las especies más comunes de roedor (*Akodon montensis*) y de didélfido (*Gracilinanus agilis*). En un estudio realizado en la zona del Cerrado en Brasil, Carmignotto *et al.* (2014) observaron mayor abundancia para la especie *H. megacephalus* en la época lluviosa que en la época seca, presumiendo una mayor actividad en la primera por la disponibilidad de alimentos. En contraste en esta investigación se observaron más individuos en la época seca, pudiendo deberse a que en la zona boscosa se encuentra una disponibilidad de recursos igualmente en la época seca. Para *O. mattogrossae* se podría deber a que se encontró solo un ejemplar en la época lluviosa del 2015, posiblemente debido a el fenómeno de El Niño, que será tratado más adelante. En una zona centro de Brasil la abundancia de micromamíferos resultó alta en la temporada seca y baja en la temporada húmeda (Santos-Filho *et al.* 2012). Así mismo, en este estudio se encontraron más especies de micromamíferos en la época seca que en la época lluviosa. Es importante conocer cómo influye un factor puntual como la época del año, ya que ayudaría a predecir la dinámica de las poblaciones de micromamíferos, sobre todo de las especies que encontramos más abundantes.

En una zona de la Mata Atlántica de Brasil encontraron que el promedio de especies de micromamíferos obtenidas por sitio de muestreo al término de la época lluviosa prácticamente duplicó lo que se obtuvo al final de la época seca (Pardini y Umetsu 2006), en contraste a este estudio donde se observó que en la época lluviosa disminuyen las abundancias.

Efectos del año. La variable año resultó significativa para la especie *Akodon montensis* en el análisis de la varianza multivariado. Los valores bajos de *p* para esta variable sugieren que las abundancias de esta especie cambian de acuerdo a la época del año y más aún entre años. El año 2015 fue un año de altas poblaciones para *A. montensis*. Sin embargo, la abundancia de roedores disminuyó en el año 2016, y algunas especies de marsupiales sólo estuvieron presente en un año de estudio, lo que podría deberse a las constantes precipitaciones que se dieron a finales del 2015, cuando la región experimentó un evento extremo de El Niño (Dirección Nacional de Aeronáutica Civil 2016). Este fenómeno pudo incidir en algunas características o cambios de la vegetación y por ende en la preferencia o presencia o no de las especies a los sitios muestreados (Owen 2013). Para *Calomys callosus* y *Oligoryzomys nigripes* solo el año resultó significativo en el análisis de la varianza. Sin embargo, el modelo estadístico para este análisis no demostró significancia. Esto se debe a que la especie *C. callosus* se encontró solo en el 2015 y no hubo alguna asociación con el siguiente año de estudio. Su ocurrencia en un solo año podría deberse a que es considerada una especie rara en este estudio ya que los patrones de distribución de esta especie no son considerados para esta ecorregión (de la Sancha 2014). En el caso de *O. nigripes* podría deberse a su abundancia mayor en el año 2015, relacionado posiblemente al efecto de El Niño.

Conclusiones

El sitio con mayor riqueza fue el de degradación media, en las estaciones seca y lluviosa del año 2015 y el de degradación baja en la época seca del año 2016. En el 2016 se registró la menor cantidad de especies en la época lluviosa en el hábitat con degradación media y degradación alta, así como también en el hábitat con degradación baja y alta en la época lluviosa del 2015. Los miembros de la familia Cricetidae fueron los más numerosos en todo el muestreo, en donde se encuentran *Akodon montensis* y *Hylaeamys megacephalus*. Para la familia Didelphidae, la especie con más ocurrencia fue *Gracilinanus agilis,* encontrado en todos los hábitats.

Las especies *Akodon montensis* (Am), *Oligoryzomys nigripes* (On) así como *Oecomys cf. mamorae* (Oem) se asociaron más a la distancia al árbol más cercano (DAC) y árbol caído (AC), relacionados con el hábitat de degradación media. Las especies *Cerradomys maracujensis* (Cm), *Rhipidomys macrurus* (Rm) y *Juliomys pictipes* (Jp) se encontraron influenciadas por la presencia de madera muerta (MM) en el hábitat con degradación baja. Mientras que la distribución de las especies *Hylaeamys megacephalus* (Hm), *Necromys lasiurus* (Nl) *Oligoryzomys mattogrossae* (Om), *Oligoryzomys* sp. (Osp), *Calomys callosus* (Cc) junto con *Gracilinanus agilis* (Ga) *Cryptonanus chacoensis* (Cch) y *Marmosa paraguayana* (Mp) estuvo asociada al hábitat con degradación alta e influenciada por la presencia deárbol de naranjo (AN)..

El sitio con degradación media fue el sitio con más riqueza en el 2015. Sin embargo, hubo una variación en el siguiente año siendo uno de los sitios con menos especies. La variable año resultó significativa para *Akodon montensis,* ya que hubo un descenso en la población de estas especies en el 2016. Las distintas especies (sobre todo las más abundantes) responden de diferentes maneras a las modificaciones del hábitat (variable parcela) y a lo largo del ciclo anual y en las diferentes épocas debido a sus preferencias u ocurrencia en el hábitat. La mayoría de las especies que no fueron muy abundantes serían más específicas de cada sitio o estructura de la vegetación. Al igual que la época del año, la diferencia que marcaron los dos años de estudio es un patrón que predice el comportamiento de las poblaciones de micromamíferos en ese periodo de tiempo. Esto ayuda a visualizar por ejemplo cómo cambian las poblaciones de micromamíferos no voladores a lo largo de un año.

Se recomienda estudios longitudinales para observar la dinámica de la población, observar las respuestas de las especies poco comunes y de las especies de roedores y marsupiales en general.

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Literatura citada

Aragón, E. E., A. Garza, y F. A. Cervantes. 2009. Estructura y organización de los ensambles de roedores de un bosque de la Sierra Madre occidental, Durango, México. Revista Chilena de Historia Natural 82:523–542.

Barreto Cáceres, M. B. 2017. Relación de los micromamíferos no voladores (Rodentia y Didelphimorphia) con la estructura de la vegetación y el grado de perturbación del bosque en una zona del límite occidental del Bosque Atlántico del Alto Paraná. M. C. tesis, Universidad Nacional de Asunción, San Lorenzo, Paraguay.

Bonaventura, S. M., V. Pancotto, N. Madanes, y R. Vicari. 2003. Microhabitat use and density of sigmodontine rodents in *Spartina densiflora* fresh water marshes, Argentina. *Mammalia* 67:367-377.

Bonvicino, C., G. D'elia, y P. Teta. 2016. *Oligoryzomys nigripes*. *In* the IUCN Red List of Threatened Species. Version 2016. www.iucnredlist.org. Consultado el 22 de de abril de 2017.

Carmignotto, A. P., A. M. R. Bezerra, y F. H.G. Rodrigues. 2014. Nonvolant small mammals from a southwestern area of Brazilian Cerrado: diversity, habitat use, seasonality, and biogeography. Therya 5:535-558.

Carmignotto, A. P., S. Solari, N. de La Sancha, y L. Costa. 2015. *Gracilinanus agilis*. . *In* the IUCN Red List of Threatened Species. Version 2015. www.iucnredlist.org. Consultado el 22 de de abril de 2017.

Cartes, J. (ed.). 2006. El Bosque Atlántico en Paraguay: Biodiversidad, Amenazas y Perspectivas. Asociación Guyrá Paraguay / Conservation Internacional Center for Applied Biodiversity Science. Asunción, Paraguay.

Cirignoli, S., C. Galliari, U. F. J. Pardiñas, D. H. Podestá, y R. Abramson. 2011. Mamíferos de la reserva Valle del Cuña Pirú, Misiones, Argentina. Mastozoología Neotropical 18:25–43.

de la Sancha, N. U. 2014. Patterns of small mammal diversity in fragments of subtropical Interior Atlantic Forest in eastern Paraguay. Mammalia 78:437–449.

Delciellos, A. C., M. Vieira, C. E. V. Grelle, P. Cobra, y R. Cerqueira. 2016. Habitat quality versus spatial variables as determinants of small mammal assemblages in Atlantic Forest fragments. *Journal of Mammalogy* 97:253–265.

Di Bitetti, M. S., G. Placci, y L. A. Dietz. 2003. A biodiversity vision for the Upper Parana Atlantic Forest ecoregion: designing a biodiversity conservation landscape and setting priorities for conservation action. World Wildlife Fund. Washington, EE.UU.

Dirección Nacional De Aeronáutica Civil (DINAC). Dirección de Meteorología e Hidrología. 2016. El Episodio de El Niño 2015/16 Excepcionalmente intenso. Efectos en Paraguay. Gerencia de Climatología e Hidrología. Asunción, Paraguay.

Dinerstein, E., D. Olson, D. Graham, A. Webster, S. Primm, M. Bookbinder, y G. Ledec. 1995. Una evaluación del estado de conservación de las ecorregiones terrestres de América Latina y el Caribe. WWF, Banco Mundial. Washington, EE.UU.

Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, L. Gonzalez, M. Tablada, y C. W. Robledo. 2008. InfoStat, versión 2008, Grupo InfoStat, FCA, Universidad Nacional de Córdoba. Córdoba, Argentina.

Eastwood, G., J. V. Camp, Y. K. Chu, A. M. Sawyer, R. D. Owen, X. Cao, M. K.Taylor, L. Valdivieso-Torres, R. D. Sage, A. Yu, D. G. Goodin, V. J. Martínez Bruyn, R. C. McAllister, L. Rodriguez, E. P. Williams, y C. B. Jonsson. 2018. Habitat, species richness and hantaviruses of sigmodontine rodents within the Interior Atlantic Forest, Paraguay. PloS ONE 13:1-20.

Emmons, L. H. 1999. Mamíferos de los Bosques Húmedos de América Tropical. Fundación Amigos de la Naturaleza FAN. Santa Cruz de la Sierra, Bolivia.

FMB/BM. (eds). 2005. Reserva Natural del Bosque Mbaracayú. Plan de Manejo 2005-2010. Fundación Moisés Bertoni para la Conservación de Naturaleza (FMB). Banco Mundial (BM). Asunción, Paraguay.

Galiano, D., B. Busnelo Kubiak, J. Reppold Marinho, y T. R. Ochotorena De Freitas. 2013. Population dynamics of *Akodon montensis* and *Oligoryzomys nigripes* in an Araucaria forest of Southern Brazil. Mammalia 77:173-179.

Gardner, A. L. (ed). 2008. Mammals of South America, Marsupials, Xenarthrans, Shrews, and Bats. Volume 1. The University of Chicago Press. Chicago, EE.UU.

Goodin, D. G., R. Paige, R. D. Owen, K. Ghimire, D. E. Koch, Y-K. Chu, y C. B. Jonsson. 2009. Microhabitat characteristics of *Akodon montensis*, a reservoir for hantavirus, and hantaviral seroprevalence in an Atlantic forest site in eastern Paraguay. Journal of Vector Ecology 34:104–113.

Hammer, Ø. 2016. Paleontological Statistics. Version 3.14. Reference manual. Natural History Museum. University of Oslo. Oslo, Noruega.

Hernández Sampieri, R., C. Fernández, y M. Baptista. 2010. Metodología de la Investigación. Quinta edición. Mc Graw Hill. México, México.

Hice, C. L., y P. M. Velazco. 2012. The non-volant mammals of the Reserva Nacional Allpahuayo-Mishana, Loreto, Peru. Special Publications Museum of Texas Tech University. Texas Tech University. Lubbock, Texas:1–135.

Hickman, C., L. Roberts, y A. Larson. 2002. Principios Integrales de Zoología. Undécima Edición. Interamericana McGraw Hill. Madrid, España.

Jaksic, F., y M. Lima. 2003. Myths and facts on ratadas: Bamboo blooms, rainfall peaks and rodent outbreaks in South America. Austral Ecology 28:237–251

Lima, D. O. de, B. O. Azambuja, V. L. Camilotti, y N. C. Cáceres. 2010. Small mammal community structure and microhabitat use in the austral boundary of the Atlantic Forest, Brazil. Zoologia (Curitiba) 27:99-105.

Melo, G. L., J. Sponchiado, A. F. Machado, y N. C. Cáceres. 2011. Small-mammal community structure in a South American deciduous Atlantic Forest. Community Ecology 12:58-66.

Melo, G. L., B. Miotto, B. Peres, y N. C. Cáceres. 2013. Microhabitat of small mammals at ground and understorey levels in a deciduous, southern Atlantic Forest. Anais da Academia Brasileira de Ciências 85:727-736

Myers, N., R. A. Mittermeir, C. G. Mittermeir, G. A. G. de Fonseca y J. Kents. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Naidoo, R., y K. Hill. 2006. Emergence of indigenous vegetation classifications through integration of traditional ecological knowledge and remote sensing analyses. Environmental Management 38: 377–387.

Owen, R. D. 2013. Ecology of small terrestrial mammals in an isolated Cerrado patch, eastern Paraguay: communities, species, and effects of ENSO, precipitation, and fire. Mastozoología Neotropical 20:97-112.

Owen R. D., y P. Smith. 2019. Mamíferos de la Reserva Natural del Bosque Mbaracayú, Departamento Canindeyú Representadas en Colecciones Científicas. Revista de la Sociedad Científica del Paraguay 24:163- 172.

Owen, R. D., D. G. Goodin, D. E. Koch, Y-K. Chu, y C. B. Jonsson. 2010. Spatiotemporal variation in *Akodon montensis* (Cricetidae: Sigmodontinae) and hantaviral seroprevalence in a subtropical forest ecosystem. Journal of Mammalogy 91:467–481.

Owen, R. D., H. Sánchez, L. Rodríguez, y C. B. Jonsson. 2018. Composition and characteristics of a diverse didelphid community (Mammalia: Didelphimorphia) in sub-tropical South America. Occasional Papers, Museum of Texas Tech University 358:1-18.

Owen, R. D., J. V. Camp, y C. B. Jonsson. 2019. Sigmodontine community and species responses to El Niño and precipitation in different levels of forest degradation. Therya 10:255-256.

Pardini, R., y F. Umetsu. 2006. Pequenos mamíferos não-voadores da Reserva Florestal do Morro Grande–distribuição das espécies e da diversidade em uma área de Mata Atlântica. Biota Neotropica 6:1–22.

Patton, J., U. F. J. Pardiñas, y G. D'elía (eds.). 2015. Mammals of South America. Vol 2. Rodents. The University of Chicago Press. Chicago and London.

Peña-Chocarro, M. C., C. Espada-Mateos, M. Vera, G. Céspedes, y S. Knapp. 2010. Updated checklist of vascular plants of the Mbaracayú Forest Nature Reserve (Reserva Natural del Bosque Mbaracayú), Paraguay. Phytotaxa 12:1-224.

Percequillo, A., J. Patton, L. Pires-Costa, G. D'Elía, y B. Patterson. 2016. *Hylaeamys megacephalus*. En: IUCN 2016. The IUCN Red List of Threatened Species. Version 2016. www.iucnredlist.org. Consultado el 22 de de abril de 2017.

Poindexter, C. J., G. D. Schnell, C. Sánchez-Hernández, M. de L. Romero-Almaraz, M. L. Kennedy, T. L. Best, M. C. Wooten, y R. D. Owen. 2012. Co-occurrence of small mammals in a tropical dry deciduous forest: comparisons of communities and individual species in Colima, Mexico. Journal of Tropical Ecology 28:65–72.

Polop, F., L. Sepúlveda, A. Pelliza Sbriller, J. Polop, y M. C. Provensal. 2014. Food habits of *Oligoryzomys longicaudatus* (Rodentia) in a steppe – forest transitional area of Argentinean Patagonia. Ecología Austral 24:304-310.

Püttker, T., R. Pardini, Y. Meyer-Lucht, y S. Sommer. 2008. Responses of five small mammal species to micro-scale variations in vegetation structure in secondary Atlantic Forest remnants, Brazil. BioMed Central Ecology 8:1-10.

Santos-Filho, M., F. Frieiro-Costa, I. Ára, y M. N. F. Silva. 2012. Use of habitats by non-volant small mammals in Cerrado in Central Brazil. Brazilian Journal of Biology 72:893-902.

Schnell, G. D., M. de L. Romero-Almaraz, S. T. Martínez-Chapital, C. Sánchez-Hernández, M. L. Kennedy, T. L. Best, M. C. Wooten, y R. D. Owen. 2010. Habitat use and demographic characteristics of the west Mexican cotton rat (*Sigmodon mascotensis*). Mammalia 74:379–393.

Sikes, R. S., W. L. Gannon, y The Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Sikes, R., y The Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Sneath, P. H., y R. R. Sokal. 1973. Numerical Taxonomy: The Principles and Practice of Numerical Classification. 1st Edition, W. H. Freeman. San Francisco, EE.UU.

Sokal, R. R., y C. D. Michener. 1958. A Statistical Methods for Evaluating Relationships. University of Kansas Science Bulletin 38:1409-1448.

Sponchiado, J., G. L. Melo, y N. C. Cáceres. 2012. Habitat selection by small mammals in Brazilian Pampas biome. Journal of Natural History 46:1321-1335.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

UICN. 2009. The UICN species survival Commission 2009 (en línea). The UICN Red List of Threatened Species. www.iucnredlist.org. Consultado abril 2017.

Voss, R., y S. Jansa. 2009. Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. Bulletin of The American Museum of Natural History 322:142-156.

Willig, M. R., R. D. Owen, y R. L. Colbert. 1986. Assessment of morphometric variation in natural populations: the inadequacy of the univariate approach. Systematic Zoology 35:195-203.

Willig, M. R., y R. D. Owen. 1987. Univariate analyses of morphometric variation do not emulate the results of multivariate analyses. Systematic Zoology 36:398-400.

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Activity patterns of terrestrial frugivorous mammals in a Mexican Neotropical forest

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Fruits reaching the floor of tropical forests constitute an attractive resource for a variety of mammals. Study of the characteristics of the frugivory interaction can help to advance in the understanding of the mechanisms favoring animal's coexistence. However, there are few studies focused on analyzing patterns of activity of mammals feeding on fruits in the forest floor. Camera traps were used to record consumption of *Licania platypus* and *Pouteria sapota* fruits by *Cuniculus paca*, *Dasyprocta punctata*, *Nasua narica, Dycotiles crassus* and *Tapirella bairdii*. Patterns of mammal activity were characterized based on the day, time and tree in which they were recorded. Overlap in daily (delta coefficient) and spatial occurrence (same tree and day, Jaccard, Ochiai indices and V ratio) was assessed. High segregation in the activity of frugivores occurred during the day (mean delta = 0.291 and 0.191 for *L. platypus* and *P. sapota*, respectively) and among trees/days (max. Jaccard = 0.14 and 0.19 for *L. platypus* and *P. sapota*, respectively). Our results suggest that activity overlap among mammalian frugivores feeding in the forest floor is lower than expected. This likely relates to the fact we conducted our analysis at a finer detail than previous studies (for example those focusing exclusively on dietary overlap). Thus, our study increases our understanding of the possible factor that can favor coexistence of tropical frugivorous mammals.

Los frutos depositados en el piso del bosque tropical son un recurso sumamente atractivo para una amplia variedad de mamíferos. El estudio de las características de esta interacción puede permitir avanzar en el entendimiento de los mecanismos que favorecen la coexistencia entre especies de mamíferos. Se usaron cámaras trampa para registrar el consumo de frutos de *Licania platypus* y *Pouteria sapota* por *Cuniculus paca*, *Dasyprocta punctata, Nasua narica, Dycotiles crassus* y *Tapirella bairdii*. Con base en la información del día, la hora y el árbol donde se registró la fauna, se caracterizó el nivel de traslape en actividad a lo largo del día (coeficiente de traslape, delta) y espacialmente (visitas a los mismos árboles en los mismos días, índices de asociación de Jaccard, Ochiai y cociente V). Se encontró una alta segregación en la actividad diaria (delta promedio = 0.291 y 0.191 en *L. platypus* y *P. sapota*, respectivamente) y entre árboles/días (máx. Jaccard = 0.14 y 0.19 en *L. platypus* y *P. sapota*, respectivamente). Nuestros resultados indican que el grado de traslape en la actividad de mamíferos alimentándose de frutos en el piso de la selva es en general bajo. Esto puede deberse al hecho de que nuestro estudio analiza los patrones de actividad de la fauna con un mayor nivel de detalle que estudios previos que, por ejemplo, se han concentrado exclusivamente en la dieta de la fauna. Nuestro estudio permite avanzar en el entendimiento de los mecanismos que permiten la coexistencia entre distintas especies de mamíferos frugívoros.

Key words: Activity patterns; Bayesian statistics; camera-trapping; frugivory; mammal ecology; medium/large tropical mammals; México, temporal partitioning, tropical fruits.

Introduction

It is estimated that between 70 and 90 % of tropical rain forest tree species produce fleshy, nutritious fruits which can be exploited by vertebrates (Jordano 2000). Importance of this resource for animals is evidenced by the fact that when marked drops in fruit availability occur, as those associated with climate fluctuations such as El Niño, mortality among the fauna can drastically increase due to famine (Wright *et al.* 1999). A large proportion of fruits are consumed *in situ* (in the tree canopy) or taken by animals to be consumed elsewhere (Bonaccorso *et al.* 1980; Jayasekara *et al.* 2007; Sampaio *et al.* 2019). As a consequence of this or by mere gravity, a significant amount of fruits falls and accumulate at the base of trees. These fruits attract a wide variety of mammals who are constantly seeking for food in the forest floor (Camargo-Sanabria *et al.* 2015). The study of the activity patterns of this fauna can help to further understand fundamental ecological issues such as the mechanisms of vertebrate coexistence (MacArthur and Levins 1967; Sridhara *et al.* 2016). Thus, information on how ecologically similar or sympatric species coexist is of great importance in understanding community diversity (HilleRisLambers *et al.* 2012). The most commonly used dimensions to explore patterns of animal activity are those corresponding to food types, spatial and temporal activity (Stewart *et al.* 2003).

Most of our current knowledge of frugivory interactions concentrates on primates, bats and birds foraging in the canopy (Sridhara *et al.* 2016). In comparison, much less is known about the patterns of activity of medium and large body-sized mammals consuming fruits on the floor of tropical forest (but see Miura 1997; Camargo-Sanabria and Mendoza 2016; Sampaio *et al.* 2019). Yet, mammals in this group can have a significant impact on seedling recruitment and diversity (Camargo-Sanabria *et al.* 2015) and are amongst the most threatened by human activity (Ripple *et al.* 2015).

At least partially, this lack of information relates to the difficulty of recording the activity of secretive species such as those included in the mammalian frugivore guild. Fortunately, camera trapping has emerged as a very effective tool to tackle this type of issues (Cruz *et al.* 2014; Edwards *et al.* 2015). The characteristics of camera-traps greatly increase the chances of recording interactions between fruits and secretive terrestrial mammals (Camargo-Sanabria and Mendoza 2016).

In this study, we analyze spatial and temporal activity patterns of terrestrial frugivorous mammals consuming the fruits of two tropical trees: *Licania platypus* and *Pouteria sapota*. Fruits of these tree species are highly attractive to terrestrial mammals (Camargo-Sanabria and Mendoza 2016). Yet, these tree species have dissimilar abundances (common vs. rare) and fruit composition (protein-rich vs. sugar-rich), thus providing the opportunity to analyze mammal frugivory activity in two contrasting settings. We calculated two descriptors of mammal activity. First, we characterized patterns of daily activity of mammals consuming fruits deposited at the base of focal trees. Second, we combined information about the day and the focal tree in which mammal species were active to assess their level of co-occurrence. We used these data to estimate the degree of overlap in daily and spatial activity among mammals consuming fruits of focal trees. We expected to find larger overlap in mammal activity in the case of the less abundant and sugar-rich tree species (*P. sapota*) than in the more abundant and protein-rich (*L. platypus*). Moreover, we expected to find greater activity overlap among primarily frugivorous mammalian species (*e. g.*, Baird's tapir, collared peccary, agouti and spotted paca) than among those with more generalist feeding habits (*e. g.*, white-nosed coati).

Materials and methods

Study area. The Montes Azules Biosphere Reserve (MABR) protects the largest and most diverse remnant of tropical rainforest in southern México. The MABR has an extent of 3,312 km^2 and is located between 19° 05' to 20° 07' N and -90° 45' to -91° 30' W (Appendix 1). Average temperature ranges between 24 °C and 26 °C and average annual precipitation is 2,200 mm (Guacamayas Weather Station). Fieldwork for this study was conducted in the southern portion of the MABR, which is part of the Chajul Field Station (CFS). The MABR supports a rich mammalian fauna including large body-sized species such as: puma (*Puma concolor*), jaguar (*Panthera onca*), Baird´s tapir (*Tapirella bairdii*), white tailed-deer (*Odocoileus virginianus*), Central American brocket deer (*Mazama temama*), collared peccary (*Dicotyles crassus*), and white-lipped peccary (*Tayassu pecari*). Moreover, it includes some medium-sized species such as: nine-banded armadillo (*Dasypus novemcinctus*), agouti (*Dasyprocta punctata*), spotted paca (*Cuniculus paca*), tayra (*Eira barbara*), striped hog-nosed skunk (*Conepatus semistriatus*) and white-nosed coati (*Nasua narica*; Medellin 1994).

Focal tree species. Licania platypus (sonzapote; Hemsl.) Fritsch (Chrysobalanaceae) is a canopy tree (10 to 30 m tall) distributed from México to Colombia (Pennington and Sarukhán 2005). Its fruits are drupes (14 cm in length and 12 cm in width) containing a sweet fleshy yellow mesocarp surrounded by a fibrous and stony endocarp that encloses a single seed averaging 10 cm in length and 6 cm in width (Pennington and Sarukhán 2005). In the MABR, fruits fall from May to August (Camargo-Sanabria and Mendoza 2016). Dried *L. platypus* (hereafter *Licania*) fruit pulp has the following macronutrient composition: 25.8 % protein, 0.75% lipids, 56.5 % non-structural carbohydrates, 3.3 % minerals, 13.4 % fiber and moisture content equal to 65 % (Camargo-Sanabria and Mendoza 2016).

Pouteria sapota (mamey; Jacq.) H. E. Moore and Stearn (Sapotaceae) is a tree up to 40 m tall, occurring from México to northern South America (Pennington and Sarukhán 2005). Fruits are 20 cm long and 8 cm wide and present a very fleshy and red mesocarp covering one brown seed up to 10 cm long (Pennington and Sarukhán 2005). In the MABR fruits ripen from December to March and fall from April to August or September (Camargo-Sanabria and Mendoza 2016). Composition of macronutrients in dried *P. sapota* (hereafter *Pouteria*) fruit pulp is as follows: 8.8 % protein, 0.11 % lipids, 89.6 % non-structural carbohydrates, 0.8 % minerals, 0.6 % fiber and moisture percentage is 61 % (Camargo-Sanabria and Mendoza 2016).

Both, *Pouteria* and *Licania* occur primarily on alluvial terraces of our study area (Martínez-Ramos 2006). Surveys of trees with a diameter at breast height (DBH) > 10 cm show that density of *Licania* is much higher than *Pouteria´s* (14.7 individuals/ha *versus* < 1 individual/ha; Martínez-Ramos 2006).

In a previous paper we report the most common terrestrial mammalian fauna consuming fruits of *Licania* and *Pouteria* trees in our study area (Camargo-Sanabria and Mendoza 2016). The mammals with the highest capture frequencies (number of events / sampling effort * 100 camera-days) were: Baird's tapir, collared peccary, agouti, spotted paca and white-nosed coati (Table 1). For this study we focus on these species. The Baird's tapir, collared peccary, agouti and paca are species whose diet relies heavily on fruits, although they also consume other plant parts such as leaves, seeds and even bark (Beck-King *et al.* 1999; Naranjo and Cruz 1998; Dubost and Henry 2006; Pérez-Cortez and Reyna-Hurtado 2008). Fruits are also an important element in the diet of coatis, but this mammal also includes in its diet a wide variety of items ranging from invertebrates to small vertebrates (Valenzuela 1998). All these mammal species spend most of their time in the forest floor, but the coati has a great ability to climb to reach the forest canopy (Emmons and Feer 1997). There is a ten-fold variation in the body weight of this fauna being the extremes the Baird's tapir (*ca.* 293.8 kg) and agouti (*ca.* 2.3 kg; Jones *et al.* 2009).

Table 1. Capture frequency (number of events / sampling effort * 100 camera-days) of five focal mammals species recorded, by camera-traps, eating fallen fruits at focal trees species at the Montes Azules Biosphere Reserve, Chiapas. Modified from Camargo-Sanabria and Mendoza (2016).

Species	*Licania platypus*	*Pouteria sapota*
Cuniculus paca (Paca)	13.5	23.9
Dasyprocta punctata (Agouti)	16.7	35
Nasua narica (White-nosed coati)	22.4	9.2
Dycotiles crassus (Collared peccary)	8.4	22.9
Tapirella bairdii (Baird´s tapir)	16.5	25.5

Recording of mammal visitation to focal fruiting trees. We conducted a several days search of fruiting *Licania* and *Pouteria* trees in alluvial terraces in the vicinity of the CFS. We located a total of 10 trees (six of *Licania* and four of *Pouteria*) with abundant fruits accumulated at their bases. We found other *Licania* and *Pouteria* trees but they had immature or no fruits or were too close to focal trees. Each tree was georeferenced with a handheld GPS unit (Garmin, 62sc, UTM coordinate system, region 15). We did not directly measure fruit production but there were no clear contrasts in fruit abundance among trees. Mean distance between focal trees, measured using ArcMap 10 (ESRI 2011) were 1,472 m and 4,325 m for *Licania* and *Pouteria*, respectively. DBH of focal trees were 102.7 cm ± 28 (mean ± SD) in *Licania* and 78.5 cm ± 23 in *Pouteria*. Tree crown dimensions averaged 21 x 18 m and 20 x 17 m for *Licania* and *Pouteria*, respectively.

We conducted a camera-trapping survey during the fruiting season of May to July 2014. We set up one camera-trap (Ltl Acorn 5210A) to monitor each focal tree. These camera-traps were attached to the trunk of trees in the vicinity of focal trees at a height between 0.6 and 1.5 m, aimed at fallen fruits. Distances from the cameras to the fruits ranged between 4 and 6 m. Each camera was protected against the rain using a small plastic sheet. Cameras were programmed to be active throughout the day and night and to take three pictures each time they were activated. Time between activations was set to its minimum (1 s) and motion sensors were set to normal sensitivity. Monitoring of focal trees ranged from 10 to 30 days and stopped once fruits on the floor were absent.

Data analyses. Mammal pictures were uploaded (with their metadata: date, time, etc.) and tagged with the corresponding species scientific name in a database built using the free software CameraBase v1.5.1 (Tobler 2010).

Description of frugivore daily activity patterns and calculation of activity overlap. We used the R package Overlap (Meredith and Ridout 2014) to construct kernel density plots, based on information of time of recording of each mammal picture. These density plots constituted the basis for describing species daily activity patterns and conducting paired measurements of their overlap. Prior to analysis in Overlap, we converted the timestamp of photos from hours and minutes to radians. We calculated nonparametric estimators of the overlapping coefficients based on the size of the smaller of the two samples; we used delta$_1$ when the smaller sample was less than 50 photos and delta$_4$ when it was greater than 75 (Meredith and Ridout 2014). This coefficient takes values from 0 to 1, where 1 indicates total overlap. To estimate their confidence intervals, we generated 1000 smoothed bootstrap samples for each comparison and selected the option "basic0" in the bootCI output.

Co-occurrence of frugivore in focal trees. To assess the level of co-occurrence of frugivorous species in both tree species, we combined two data sources: *i*) records of presence of each mammalian species in each focal tree and *ii*) dates in which each mammal species was recorded in each of these focal trees. Based on these data we created a binary presence-absence matrix to indicate occurrence of mammal species on a particular date and tree (one matrix per tree species). We used these matrices to calculate Jaccard, Ochiai and V ratio indices (Jackson *et al.* 1989; Zhang 2013). Calculation of these indices for a pair of species (A and B) is based on the frequencies of the following cases: a) both species are present, b) both species are absent, c) species A is present but species B is missing, and d) species A is missing but species B is present (see Appendix 2). These frequencies (fa, fb, fc and fd) define a 2 x 2 contingency table and when divided by the total number of cases (N) are the usual estimates of the true probabilities of the four cases. Each index makes use of the frequencies in such a way that it can be interpreted as an estimate of a function of these four probabilities. Thus, the Jaccard index, defined as fa / (fa + fc + fd), can be interpreted as an estimate of the probability of case (a) given that at least one of the species is present. Similarly, the V ratio index is an estimate of the difference of the probability of cases (a) + (b) minus the probability of cases (c) + (d). Finally, if q_1 is the probability of case (a) given that species A is present, and q_2 is the probability of case (a) given that species B is present, the Ochiai index estimates the geometric mean of q_1 and q_2. The Ochiai and Jaccard indices have their lowest value (0) when both species are absent and their maximum (1) when both species are present (Janson and Vegelius 1981; Ludwig and Reynolds 1988). In comparison, the V ratio index takes a positive value if the number of concordant pairs (both species present or both species absent) is larger than the number of discordant pairs (one species present and the other absent). Otherwise, it takes a negative value.

We applied a Bayesian approach in which we used the observed frequencies, in combination with a non-informative prior distribution, to obtain a posterior distribution for the probabilities of the four cases in the contingency table. On this basis, we obtained a posterior distribution for each of the functions estimated by the indices (see Appendix 2). These posterior distributions are informative about the function each index is estimating. For example, in the case of the Jaccard index (JI), in addition to the estimate JI = fa / (fa + fc + fd), the corresponding posterior distribution allows us to describe what we know with respect to JI* = Pa / (Pa + Pc +Pd) where Pj is the true probability being estimated by fj / N. From the posteriors, we computed a 0.95 posterior probability interval for each function (see Appendix 2).

Our statistical analysis of activity patterns between pairs of mammal species was based on the comparison of estimated overlap coefficients and association indices and their corresponding confidence intervals.

Results

Throughout 194 camera-trap days (130 and 64 for *Licania* and *Pouteria,* respectively) we recorded a total of 1591 pictures of our five focal mammal species (Figure 1, Table 1). In one *Licania* focal tree we did not record any mammal species; therefore, we excluded this tree from the analyses.

Patterns of daily activity and overlap among frugivorous mammals. There was a clear variation in daily activity among frugivorous mammals and between tree species. Most mammal species were more active during the day and close to dawn or dusk, with the only exception of the paca whose activity was completely nocturnal (Figures 2 and 3). Most frugivores showed between one or two main peaks of activity with the exception of the coati which had three peaks of activity, in *Pouteria* focal trees, although one of them was comparatively minor (Figure 3). Activity patterns of tapir and paca were very similar between tree species both in the number and timing of their main peaks (Figures 2 and 3). In comparison, activity patterns of the agouti, collared peccary and coati were more contrasting between tree species (Figures 2 and 3).

As a consequence of the observed contrasts in mammal daily activity patterns there was a wide variation in their degree of overlap. Overlap in *Licania* trees ranged between 0.05 and 0.67 (Figure 2). Lowest levels of overlap occurred in the pairs paca-agouti (delta$_1$ = 0.05) and agouti-tapir (delta$_1$ = 0.09). In contrast, the greatest overlap occurred in the pairs paca-tapir (delta$_1$ = 0.67) and agouti-peccary (delta$_1$ = 0.62). The remaining species pairs had intermediate levels of overlap (Figure 2).

Figure 1. Ensemble of mammalian frugivores recorded eating fruits of *Licania platypus* and *Pouteria sapota* in the tropical rainforest of the Montes Azules Biosphere Reserve. From left to right: spotted paca, agouti (first row); white-nosed coati, collared peccary (second row); Baird's tapir (third row).

There was also wide variation in activity overlap among mammalian species consuming fruits of *Pouteria* (range = 0-0.68; figure 3). In fact, there were two cases in which there was essentially no overlap (peccary vs. tapir and coati vs. tapir; Figure 3). In contrast, greatest overlap occurred between the pairs paca-tapir (delta$_4$ = 0.68) and agouti-peccary (delta$_4$ = 0.4; Figure 3). Overall, overlap was greater in *Licania* than in *Pouteria* (average coefficients: 0.29 vs. 0.19, respectively).

Patterns of frugivorous co-occurrence in focal trees. The paca was recorded at the five focal *Licania* trees, whereas, the collared peccary, coati and tapir were recorded at four and the agouti was recorded at only one. In comparison, the tapir and agouti were recorded at the four focal *Pouteria* trees, the coati and paca at three of them and the collared peccary at only two. The paca showed the greatest variation in the proportion of days it was recorded at focal *Licania* trees (0.03 to 0.33), whereas the collared peccary showed the lowest variation (0.07

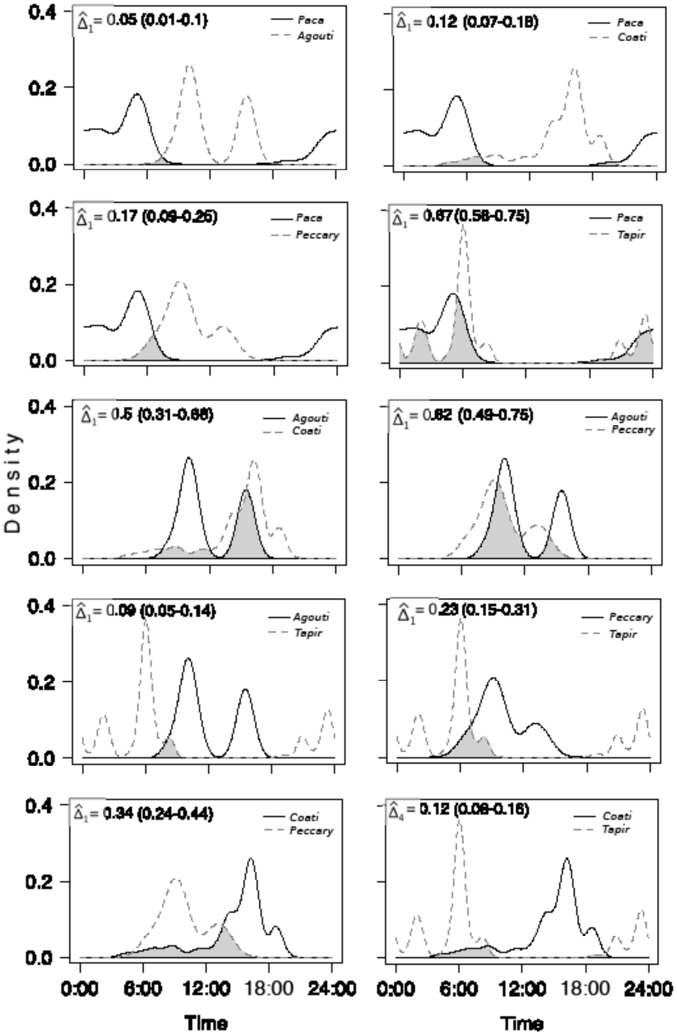

Figure 2. Overlap in the patterns of daily activity of mammalian species interacting with *Licania platypus* fruits.

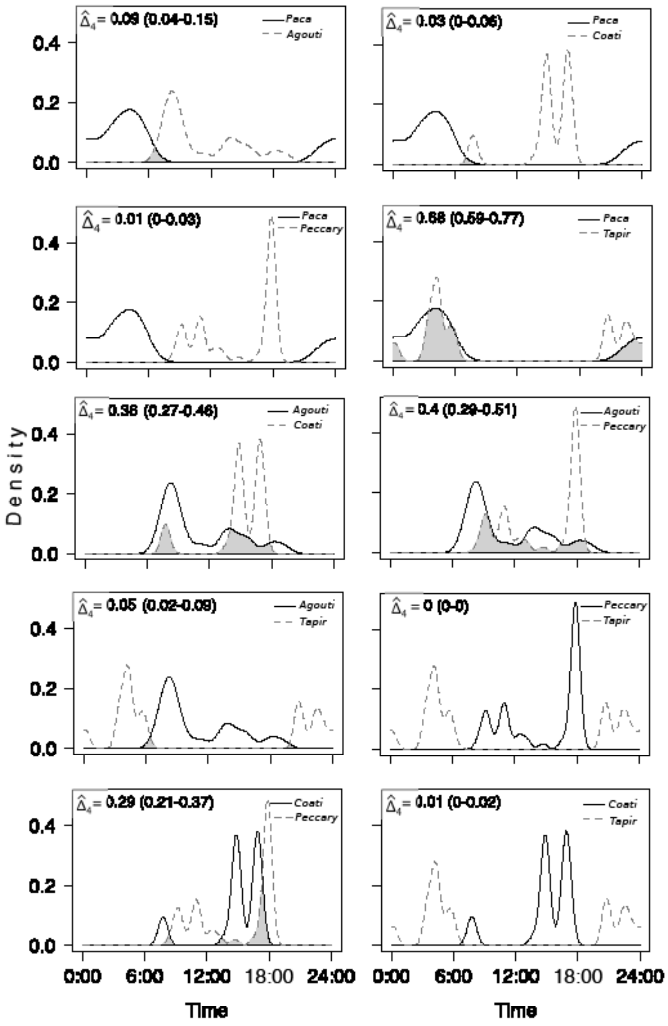

Figure 3. Overlap in the patterns of daily activity of mammalian species interacting with *Pouteria sapota* fruits.

to 0.12). At *Pouteria* the agouti showed the greatest variation in the proportion of days it visited focal trees (0.08 to 0.58), while the coati showed the lowest variation (0.06 to 0.12).

In general, we found low co-occurrence between pairs of mammalian frugivores in both tree species. In *Licania,* the paca-tapir pair had the greatest estimated probability of positive concordances (*i. e*., presence of both species; 0.10). In comparison, in *Pouteria*, the agouti-paca pair had the greatest estimated probability of positive concordances (0.12). Values of the Jaccard index for species using *Licania* fruits were on average lower than those of mammals associated with *Pouteria* (0.06 vs. 0.12; Table 2). Likewise, values of the Ochiai index were on average lower for *Licania* than for *Pouteria* (0.11 vs. 0.21; Appendix 3). Largest values of both the Jaccard and Ochiai indices for *Licania* corresponded to the paca-tapir pair (Table 2 and Appendix 3). In comparison, largest values of the both indices in *Pouteria* corresponded to the collared peccary-paca pair (Table 2 and Appendix 3).

On the other hand, the largest values of the V ratio index in *Licania* corresponded to the pair agouti-peccary (positive association), coati-paca (negative association) and coati-tapir (negative association; Appendix 4). In *Pouteria* the highest values of the V ratio index corresponded to agouti-tapir (negative association), coati-peccary (positive association) and paca-peccary (positive association; Appendix 4).

Table 2. Median values of Jaccard species association index and corresponding 95% probability intervals, within parentheses, for species recorded in *Licania platypus* (above diagonal) and *Pouteria sapota* (below diagonal).

	Paca	Agouti	Coati	Peccary	Tapir
Paca	----	0.02 (0, 0.11)	0.08 (0.01, 0.19)	0.06 (0, 0.19)	0.15 (0.05, 0.30)
Agouti	0.18 (0.07, 0.33)	----	0.07 (0, 0.21)	0.04 (0, 0.19)	0.02 (0, 0.11)
Coati	0.03 (0, 0.13)	0.14 (0.04, 0.29)	----	0.06 (0, 0.18)	0.08 (0.01, 0.19)
Peccary	0.20 (0.06, 0.41)	0.13 (0.03, 0.27)	0.04 (0, 0.18)	----	0.06 (0, 0.19)
Tapir	0.15 (0.04, 0.32)	0.10 (0.03, 0.23)	0.08 (0.01, 0.24)	0.13 (0.02, 0.31)	----

When we plotted both co-occurrence data and overlap in daily activity we found that most of the pairs of mammals were located in the lower left-hand quadrant of the graph with relatively minor exceptions such as those corresponding to the paca-tapir and agouti-peccary pairs (Figure 4).

Discussion and conclusions

We found just partial support for our predictions. Regarding our first expectation of finding a greater level of mammal activity overlap in the case of the less abundant and sugar-rich tree species (*P. sapota*) than in the more abundant and protein-rich tree species (*L. platypus)*. We found that overlap in mammal activity in both tree species was overall low yet, in average, mammal species visited more often the same trees in the same days in the case of *P. sapota* than in the case of *L. platypus*. However, when comparing daily activity, the result was the other way around, with greater average overlap occurring in the case of *L. platypus* than in the case of *P sapota*. In relation with our second prediction, in which we were expecting to find greater activity overlap in species pairs including primarily frugivorous mammalian species than in those including the species with more generalist feeding habits (*i. e*., white-nosed coati), we found that the pair of species having the greatest overlap (delta$_1$ ≥ 0.67) in their daily activity patterns, in both tree species, was indeed constituted by the highly frugivore mammals paca and tapir (Naranjo 2009; Martínez-Ceceñas *et al.* 2018). Moreover, we found that coatis (the species with the more generalist feeding habits) had in most of the cases a low degree of overlap in their daily activity with the other mammal species feeding on the fruits of the focal tree species but, in 3 out 8 paired comparison this overlap was relatively high (delta$_1$ ≥ 0.29).

There are several factors, not mutually exclusive, whose examination might help to gain a better understanding of the underlying causes behind the observed low levels of activity overlap among the focal frugivorous mammals. A first possibility is that these patterns are reflecting the effect of earlier strong competitive interactions established among mammalian frugivorous species ("the ghost of past competition") occurring in our study area (Connell 1980). This possibility would include the effect of species currently present

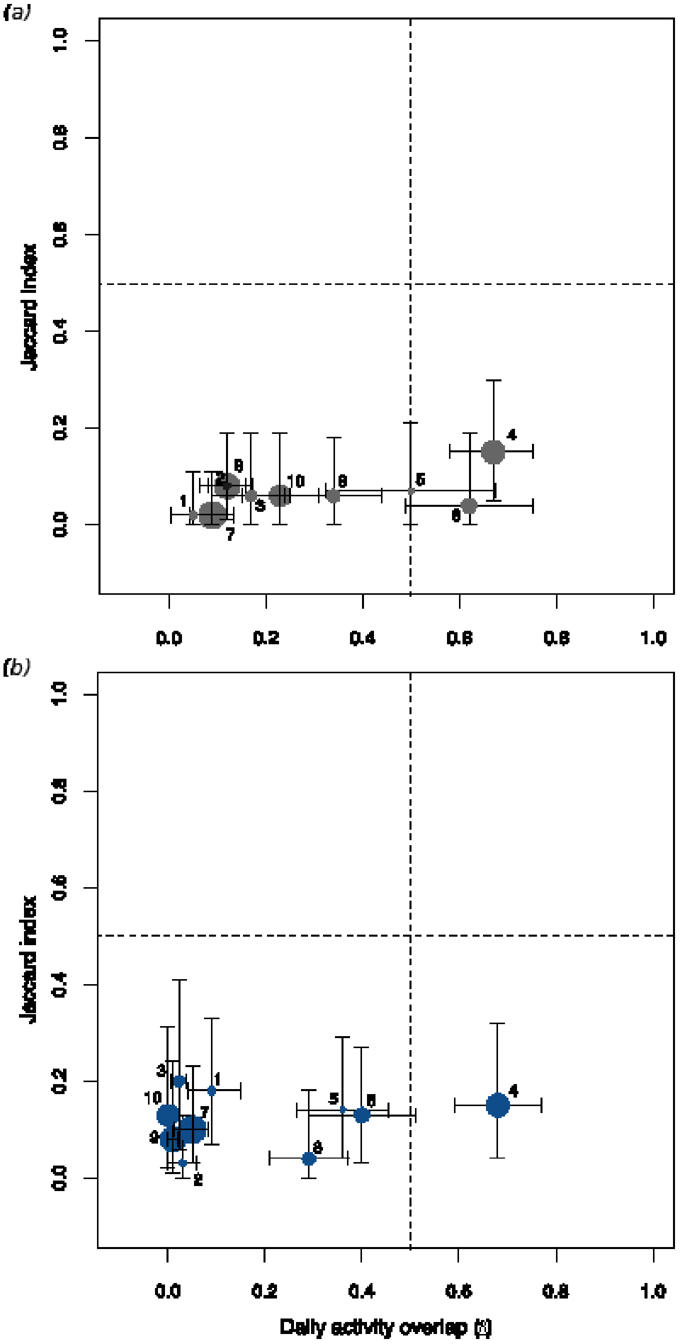

Figure 4. Diagram combining spatial (Jaccard) and daily activity patterns. a) *Licania platypus* and b) *Pouteria sapota*. Key: 1 = paca-agouti, 2 = paca-coati, 3 = paca-peccary, 4 = paca-tapir, 5 = agouti-coati, 6 = agouti-peccary, 7 = agouti-tapir, 8 = coati-peccary, 9 = coati-tapir, 10 = peccary-tapir. Horizontal and vertical lines indicate 95 % confidence intervals and different circle sizes indicate contrasts in body size between pair of species.

but also of those formerly occurring in our study area but currently extinct (Ceballos *et al.* 2010). A potential counterargument of this possibility is that mammalian frugivores usually are able to use a variety of food sources; for example, tapirs in addition to consuming a variety of fruits consume plant leaves, stems, and even tree bark (Naranjo 2009). Thus, one of the main requirements for competition to emerge (*i. e*, exploiting of a shared highly demanded resource which occur in a limited supply) might not apply due to the possibility that mammals rely on different feeding sources. Yet, on the other hand, it is important to take into consideration that fruits and seeds can have an energetic and nutritive content (e.g., carbohydrates, proteins and lipids) hard to find in other plant material (*e. g*., leaves; Smythe 1986). Moreover, despite the fact that in the forest there are a wide variety of fruit species that can be exploited by mammals, plant phenology causes that at a given time, only a few of them are available (Van Schaik *et al.* 1993). It would be interesting to compare mammal activity in forests with different degrees of defaunation to assess if in the absence of some frugivorous mammalian species, others increase their range of activity; certainly this issue warrants further research.

A second possibility to explain low activity overlap is that focal animal species occur at low densities within the local mammal community. However, previous studies conducted in the Montes Azules Biosphere Reserve give little support to this possibility. For example, Azuara (2005) found, in a camera-trap survey of the local mammalian community, that *Cuniculus paca* and *Tapirella bairdii* were two of the most recorded species (no. of records/100 camera-trap days) closely followed by peccaries. Likewise, Towns (2013) found that tapirs and pacas were the first and third most recorded species in a camera-trap study conducted in our same study area. Finally, a more recent camera-trap study conducted in parallel, but independently, to our frugivory study, indicates that pacas, tapirs, peccaries, and in less degree agouties and coatis, are common members of the local mammalian community (A. Dueñas Navarro, com. pers.).

A third possible explanation of the observed patterns of mammal activity is related to our methodological approach. Our results contrast with some previous studies which have suggested the existence of high levels of niche overlap in tropical terrestrial frugivorous mammals. For example, Desbiez *et al.* (2009) measured food and habitat selection in sympatric white-lipped and collared peccaries in the Brazilian Pantanal, finding high levels of overlap in both cases (Pianka's index values were > 0.664 and > 0.864, respectively). Assessment of dietary and habitat use overlap in that study was based on the detection of the focal species along transects and fecal sample analysis. Likewise, Steinmetz *et al.* (2013) analyzed foraging signs and scats as a way to explore if food selection helped to explain extensive geographic coexistence of ecologically similar Asiatic black bear (*Ursus thibetanus*) and sun bears (*Helarctos malayanus*). They found diet overlap was similarly high during periods of diminished and high fruit availability. In contrast to these studies we analyzed activity overlap at a finer scale, by focusing on mammal visitation to the same trees in the same days (co-occurrence). Previous studies have pinpointed the need to take into consideration species microhabitat use differences, to explain coexistence of species that seemingly overlap in diet and activity (Noor *et al.* 2017).

In addition to the above mentioned factors, there are other aspects that likely have some influence over the mammal activity patterns we documented. For example, it is known that the adequate performance of animals in a specific environment (*e. g.*, night habit) requires acquiring particular capabilities (such as night vision) which involve physiological and anatomical adaptations. Thus, there might be evolutionary constraints that can limit the possibility for some animal species to greatly alter their daily activity patterns in response to interspecific interactions (Bennie *et al.* 2014). For example, pacas and agouties share some characteristics such as being large frugivorous rodent species but, on the other hand, they contrast in terms of their daily activity patterns with agouties having most of its activity during the day and paca being active mostly during the night. Clearly, these contrasting activity patterns greatly reduce the likelihood of the species to affect the other behavior. Finally, in some instances presence of frugivore mammals with gregarious and potentially aggressive behavior (such as peccaries) could negatively affect the presence of other frugivores (Smythe 1986).

The combination of an approach like the one we applied in this study, together with the use of other technological tools such as dietary isotope and molecular analyses (Phillips 2012; Pompanon *et al.* 2012) and fine-scale radio tracking of frugivorous (Kays *et al.* 2011), appears as a promissory path to fill the gap regarding our knowledge of terrestrial mammal frugivorous ecology. A better knowledge of frugivorous species' niche differentiation can help managers to understand the capacity of species to coexist under different conservation scenarios (HilleRisLambers *et al.* 2012). Moreover, a clearer understanding of the way mammalian frugivorous interact, among themselves and with plants, will help to appreciate in its full extent the consequences of mammal defaunation (Dirzo *et al.* 2014; Camargo-Sanabria *et al.* 2015).

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Literature cited

Azuara, D. 2005. Estimación de abundancia de mamíferos terrestres en un área de la Selva Lacandona, Chiapas. Tesis de maestría. Universidad Nacional Autónoma de México. México.

Beck–King, H., O. V. Helversen, and R. Beck–King. 1999. Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: a study using alternative methods. Biotropica 31:675-685.

Bennie, J. J., J .P., Duffy, R. Inger, and K. J. Gaston. 2014. Biogeography of time partitioning in mammals. Proceedings of the National Academy of Sciences 111:13727-13732.

Bonaccorso, F. J., W. E. Glanz, and C. M. Sandford. 1980. Feeding assemblages of mammals at fruiting *Dipteryx panamensis* (Papilionaceae) trees in Panama: seed predation, dispersal, and parasitism. Revista de Biologia Tropical 28:61-72.

Camargo-Sanabria, A. A., E. Mendoza, R. Guevara, M. Martínez-Ramos, and R. Dirzo. 2015. Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. Proceedings off the Royal Society of London B: Biological Sciences 282: 20142580.

Camargo-Sanabria, A. A., and E. Mendoza. 2016. Interactions between terrestrial mammals and the fruits of two neotropical rainforest tree species. Acta Oecologica 73: 45–52.

Ceballos, G., J. Y. Arroyo-Cabrales, and E. Ponce. 2010. Effects of Pleistocene environmental changes on the distribution and community structure of the mammalian fauna of Mexico. Quaternary Research 73: 464-473.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Cruz, P., A. Paviolo, R. F. Bó, J. J. Thompson, and M. S. Di Bitetti. 2014. Daily activity patterns and habitat use of the lowland tapir (*Tapirus terrestris*) in the Atlantic forest. Mammalian Biology 79: 376-383.

Desbiez, A. L. J., S. A. Santos, A. Keuroghlian, and R. E. Bodmer. 2009. Niche partitioning among white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*). Journal of Mammalogy 90: 119-128.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345: 401-406.

Dubost, G., and O. Henry. 2006. Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. Journal of Tropical Ecology 22: 641-651.

Edwards, S., A. C. Gange, and I. Wiesel. 2015. Spatiotemporal resource partitioning of water sources by African carnivores on Namibian commercial farmlands. Journal of Zoology 297: 22-31.

Emmons, L. H., and F. Feer. 1997. Neotropical rainforest mammals. A field guide, Second Ed. University of Chicago Press, Chicago.

HilleRisLambers J., P. B. Adler, W. S. Harpole, J. M. Levine, and M.M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. Annual review of ecology, evolution, and systematics 43: 227–248.

Jackson, D. A., K. M., Somers, and H. H. Harvey. 1989. Similarity coefficients: measures of co-occurrence and association or simply measures of occurrence? The American Naturalist 133: 436-453.

Janson, S., and J. Vegelius. 1981. Measures of ecological association. Oecologia 49: 371-376.

Jayasekara, P., U. R. Weerasinghe, S. Wijesundara, and S. Takatsuki. 2007. Identifying diurnal and nocturnal frugivores in the terrestrial and arboreal layers of a tropical rain forest in Sri Lanka. Ecotropica 13: 7-15.

Jones, K.E., J. Bielby, M. Cardillo, S.A. Fritz, J. O'dell, C.D.L. Orme, K. Safi, W. Sechrest, E.H. Boakes, C. Carbone, and C. Connolly. 2009.

Pantheria: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648-2648.

Jordano, P. 2000. Fruits and frugivory. Pp.125-166 in Seeds: the ecology of regeneration in plant communities. (Fenner, M., ed.), 2nd edition. CABI Publ., Wallingford, UK.

Kays, R., S. Tilak, M. Crofoot, T. Fountain, D. Obando, A. Ortega, F. Kuemmeth, J. Mandel, G., G. Swenson, T. Y. Lambert, and B. Hirsch. 2011. Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. The Computer Journal P.Bxr072.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology: a primer in methods and computing, Vol. 1. John Wiley and Sons, New York.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101: 377-385.

Martínez-Receñas, Y., E. J. Naranjo, Y. Hénaut, and A. Carrillo-Reyes. 2018. Ecología alimentaria del tepezcuintle (*Cuniculus paca*) en áreas conservadas y transformadas de la Selva Lacandona, Chiapas, México. Revista mexicana de biodiversidad 89: 507-515.

Martínez-Ramos, M. 2006. Aspectos ecológicos de la selva húmeda en la región Lacandona: perspectivas para su estudio y conservación. Pp. 279-292 in Manejo, conservación y restauración de recursos naturales en México: perspectivas desde la investigación científica. (Oyama, K. and A. Castillo, eds.). Siglo XXI Editores/Unam, México.

Medellin, R. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, México. Conservation Biology 8: 780-799.

Meredith, M., and M. Ridout. 2014. Overlap: estimates of coefficient of overlapping for animal activity patterns R package Version 0.2.3. <http://cran.r-project.org/package=overlap>.

Miura, S., M. Yasuda, and L.C., Ratnam. 1997. Who steals the fruits? Monitoring frugivory of mammals in a tropical rain-forest. Malayan Nature Journal 50: 183-193.

Naranjo, E.J., 2009. Ecology and conservation of Baird's tapir in Mexico. Tropical Conservation Science, 2: 140-158.

Naranjo, E., and E. Cruz-Aldan. 1998. Ecología del tapir (*Tapirus bairdii*) en la Reserva de la Biósfera La Sepultura, Chiapas, México. Acta Zoológica Mexicana n.s. 73: 111-125.

Noor, A., Z. R. Mir, G. G. Veeraswami, and B. Habib. 2017. Activity patterns and spatial co-occurrence of sympatric mammals in the moist temperate forest of the Kashmir Himalaya, India. Folia Zoologica 66: 231-242.

Pennington, T. D., and J. Sarukhán. 2005. Árboles tropicales de México. Manual para la identificación de las principales especies, third ed. Universidad Nacional Autónoma de México-Fondo de Cultura Económica, México.

Perez-Cortez, S., and R. Reyna-Hurtado. 2008. La dieta de los pecaries (*Pecari tajacu* y *Tayassu pecari*) en la región de Calakmul, Campeche, México. Revista Mexicana de Mastozoología (Nueva época) 12: 17-42.

Phillips, D. L. 2012. Converting isotope values to diet composition: the use of mixing models. Journal of Mammalogy 93: 342–352.

Pompanon, F., B. E., Deagle, W. O., Symondson, D. S., Brown, S. N. Jarman, and P. Taberlet. 2012. Who is eating what: diet assessment using next generation sequencing. Molecular Ecology 21:1931-1950.

Ripple, W.J., T.M. Newsome, C. Wolf, R. Dirzo, K.T. Everatt, M. Galetti, M.W. Hayward, G.I. Kerley, T. Levi, P.A. Lindsey, and D. W. Macdonald. 2015. Collapse of the world's largest herbivores. Science advances 1:P.E1400103.

Sampaio, R. A., D. O. Moreira, A. M. de Assis, S. L. Mendes, and A. Gatti. 2019. Interaction between frugivorous vertebrates and two plant species of the genus *Spondias*. Animal Biology 1: 1-16.

Smythe, N. 1986. Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals. Annual Review of Ecology and Systematics 17: 169-188.

Sridhara, S., K. McConkey, S. Prasad, and R.T., Corlett. 2016. Frugivory and seed dispersal by large herbivores of Asia. Pp. 121-150 in The ecology of large herbivores in South and Southeast Asia, Ecological Studies 225. (Ahrestani, F.S. and M. Sankaran, eds.). Springer, Dordrecht.

Steinmetz, R., D. L. Garshelis, W. Y. Chutipong, and N. Seuaturien. 2013. Foraging ecology and coexistence of asiatic black bears and sun bears in a seasonal tropical forest in Southeast Asia. Journal of Mammalogy 94: 1-18.

Stewart, K.M., R.T. Bowyer, J. Kie, B.L. Dick, and M. Ben-David. 2003. N iche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? Ecoscience 10: 297-302.

Tobler, M. W. 2010. Camera Base. 1.5.1. Botanical Research Institute Of Texas.

Towns, V.S., 2013. Monitoreo poblacional de algunas especies de mamíferos de talla mayor en la selva alta perennifolia del estado de Chiapas, México. Tesis de maestría. Universidad Nacional Autónoma de México. México.

Valenzuela, D. 1998. Natural history of the white-nosed coati, *Nasua narica*, in a tropical dry forest of Western Mexico. Revista Mexicana de Mastozoología (Nueva época) 3: 26-44.

Van Schaik, C.P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of ecology and Systematics, 24: 353-377.

Wright, S. J., C. Carrasco, O. Calderon, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. Ecology 80: 1632-1647.

Zhang, J. 2013. Species association analysis: miscellaneous functions for analyzing species association and niche overlap R package version 0.2.1. <https://cran.r- project.org/web/packages/spaa/index.html>.

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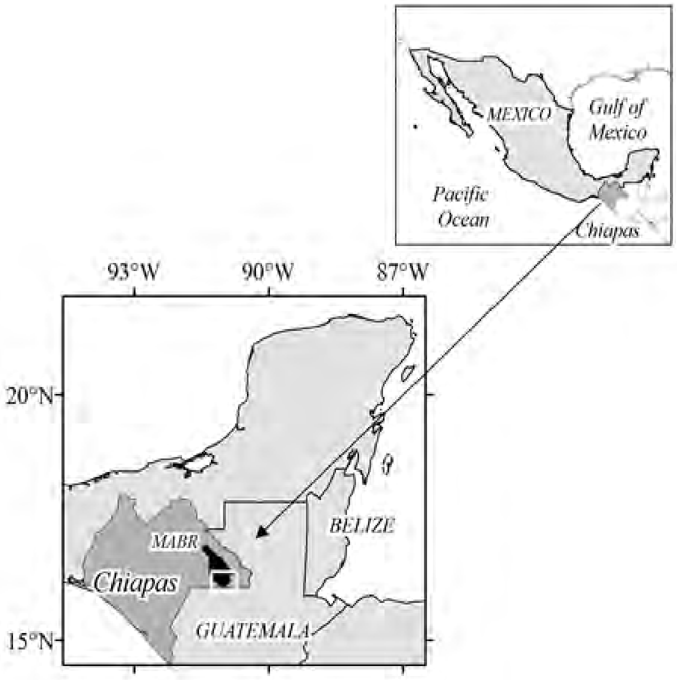
Appendix 1.

Location of the study area (white quadrate in the lower panel) in the Montes Azules Biosphere Reserve (MABR), state of Chiapas, southeast México.



Appendix 2.

Formulas to calculate species association indices.

Frequencies of co-ocurrence for species A and B.

a = both species (species A and species B) are present.

b = both species are absent.

c = only species A is present.

d = only species B is present.

1. Ochiai index:

   Ochiai = a/sqrt((a+c) * (a+d))

2. Jaccard index:

   Jaccard =a / (a + c + d)

3. V ratio:

   V = ((a+b)-(c+d)) / (a + b + c + d)

Example of estimation of species co-occurrence indices and posterior distributions applying Bayesian approach.

Tree species: *Pouteria sapota*

Pair: *Dasyprocta punctata – Nasua narica*

A) Positive concordances

[1] Posterior mean:

0.0838

[2] Posterior median

0.0768

[3] Posterior variance

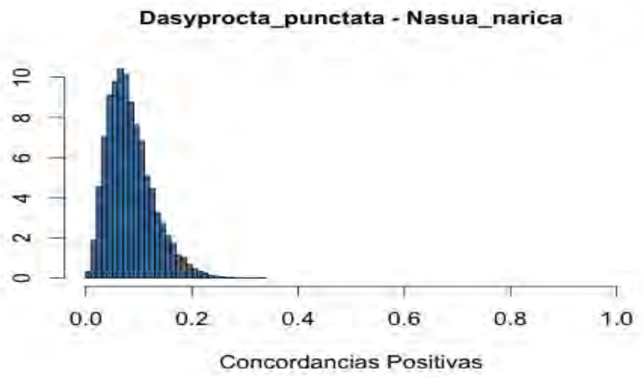
0.0018

[4] 95% posterior probability interval

0.0210, 0.1855

[5] "Classic" value of the index

0.0833



B) V ratio index

[1] Posterior mean

-0.0465

[2] Posterior median

-0.0487

[3] Posterior variance

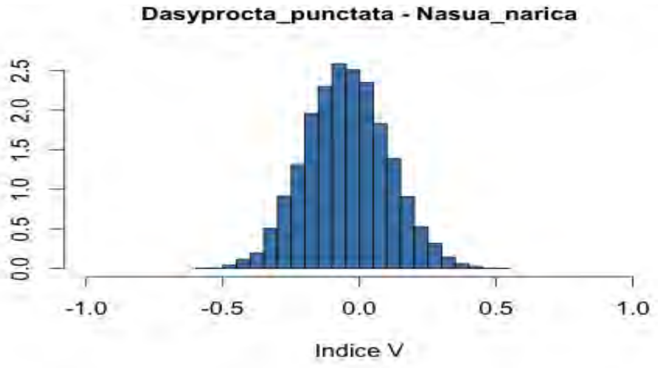
0.0227

[4] 95% posterior probability interval

-0.3358, 0.2556

[5] Value "classic" index

-0.0476



C) Jaccard index

[1] Posterior mean

0.1380

[2] Posterior median

0.1283

[3] Posterior variance

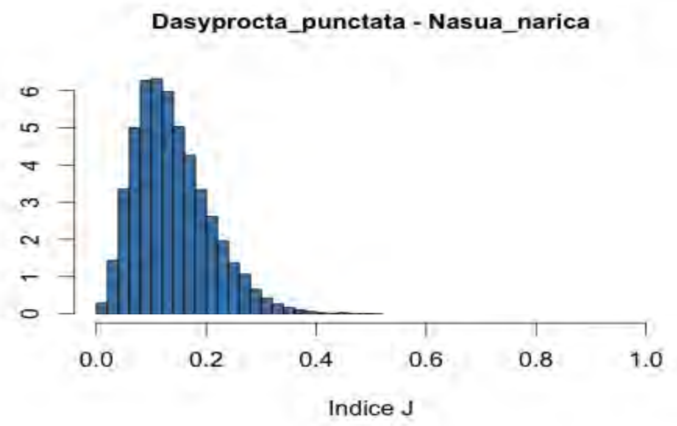
0.0045

[4] 95% posterior probability interval

0.0355, 0.2945

[5] Value "classic" index

0.1372



D) Ochiai index

[1] Posterior mean

0.2929

[2] Posterior median

0.2894

[3] Posterior variance

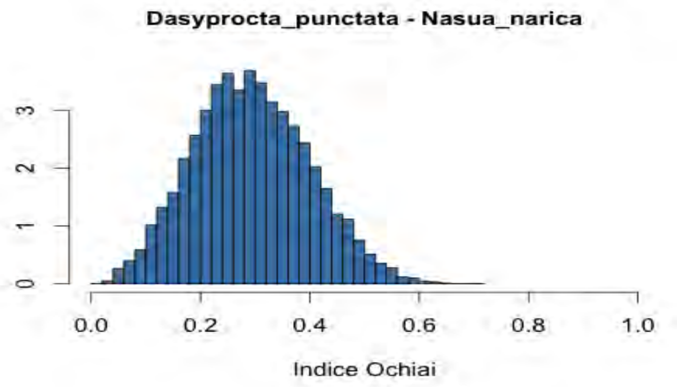
0.0113

[4] 95% posterior probability interval

0.0982, 0.5073

[5] Value "classic" index

0.2979



Appendix 3.

Median values of Ochiai species association index and corresponding 95% probability intervals, within parentheses. *Licania platypus* (above diagonal) and *Pouteria sapota* (below diagonal).

	Paca	Agouti	Coati	Peccary	Tapir
Paca	-	0.03 (0, 0.24)	0.13 (0.03, 0.32)	0.11 (0.01, 0.33)	0.26 (0.10, 0.47)
Agouti	0.31 (0.14, 0.51)	-	0.14 (0.01, 0.40)	0.04 (0, 0.34)	0.03 (0, 0.23)
Coati	0.03 (0, 0.25)	0.29 (0.10, 0.51)	-	0.10 (0.01, 0.32)	0.13 (0.03, 0.32)
Peccary	0.34 (0.11, 0.59)	0.25 (0.08, 0.46)	0.04 (0, 0.32)	-	0.11 (0.01, 0.34)
Tapir	0.25 (0.08, 0.48)	0.18 (0.04, 0.38)	0.14 (0.01, 0.41)	0.22 (0.05, 0.48)	-

Appendix 4.

Median values of V ratio species association index and corresponding 95% probability intervals, within parentheses. *Licania platypus* (above diagonal) and *Pouteria sapota* (below diagonal).

	Paca	Agouti	Coati	Peccary	Tapir
Paca	-	0 (-0.30, 0.29)	-0.44 (-0.68, -0.15)	-0.05 (-0.34, 0.24)	-0.19 (-0.47, 0.12)
Agouti	-0.19 (-0.47, 0.11)	-	0.05 (-0.25, 0.34)	0.44 (0.15, 0.68)	0 (-0.30, 0.30)
Coati	0.14 (-0.16, 0.43)	-0.05 (-0.34, 0.26)	-	-0.10 (-0.38, 0.20)	-0.43 (-0.67, -0.14)
Peccary	0.34 (0.04, 0.60)	-0.14 (-0.43, 0.16)	0.39 (0.09, 0.64)	-	-0.05 (-0.34, 0.26)
Tapir	0.05 (-0.26, 0.34)	-0.43 (-0.68, -0.14)	0.19 (-0.10, 0.47)	0.19 (-0.11, 0.47)	-

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Landscape Genetics of Mammals in American Ecosystems

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Since the term was coined in 2003, landscape genetics (LG) is a field that integrates population genetics, landscape ecology, and spatial analytical techniques to quantify the effects of landscape on microevolutionary processes. Despite the growing interest in LG, there is little knowledge about the trends in LG research for America in general and regarding mammals in particular, as well as about which ecosystems are being most studied. Deserts represent nearly one-third of the Earth's surface and are characterized by high heterogeneity and species richness. However, they are underrepresented in the LG literature. Hence, we performed a thorough review of published scientific articles addressing LG of mammals in America, with emphasis on deserts. The objectives were to 1) determine the mammal groups that have been most studied; 2) establish the representation of desert ecosystems; 3) describe the research questions and analytical methods most frequently used; and 4) summarize the key landscape factors and environmental variables associated with genetic diversity and structure patterns of mammals in America. We conducted a comprehensive literature search of published articles between 2003 and 2019 in the Web of Science (http://apps.webofknowledge.com) based on search words specific to the revision subject. We verified and screened the articles recovered, and gathered basic information (species, authors, publication year), together with the research questions addressed and the genetic and statistical methods used. We recovered 36 publications on LG involving mammals in America; of these, only eight were conducted on desert ecosystems (Table 1). Rodentia was the most represented order in all American ecosystems ($n = 20$), while Artiodactyla ($n = 4$) was specifically represented in deserts. Of all studies, the most common research questions focused on estimating 'connectivity' ($n = 14$) and 'genetic structure' ($n = 12$), and the most frequent analytical methods were Mantel and partial Mantel tests. Dispersal capabilities and vegetation cover were the most important variables regarding the genetic structure of desert populations. Most studies evaluated connectivity with simple and partial Mantel tests, but the use of novel methodologies (*i. e.,* genomics) was also identified. Ecological traits of species, particularly for rodents, and vegetation cover were the main factors related to genetic patterns in deserts. Notably, we identified that North America is the most studied region, while LG studies with mammals are scarce in Mexico and South America (one study encompassed North and Central America), as well as in desert ecosystems, hence the urgency to conduct studies in those regions and in deserts.

La genética del paisaje (GP) integra conceptos y herramientas de la genética de poblaciones, ecología del paisaje y estadística espacial, para cuantificar los efectos de la matriz del paisaje en los procesos microevolutivos. Los ecosistemas de desierto están caracterizados por una alta heterogeneidad y riqueza de especies; sin embargo, están poco representados en la literatura de GP. Los objetivos de la presente revisión fueron: 1) conocer los grupos de mamíferos más estudiados, 2) determinar la representatividad de los ecosistemas desérticos, 3) describir las preguntas más frecuentes y los métodos y análisis utilizados, 4) resumir los principales factores del paisaje y del ambiente asociados con la diversidad y estructura genética de los mamíferos de América. Realizamos una búsqueda exhaustiva de estudios publicados sobre GP con mamíferos en ecosistemas de América (2003-2019, en Web of Science). Recopilamos información de referencia (especies, autores, año de publicación), y preguntas de investigación, aproximaciones metodológicas y análisis estadístico-espaciales. Obtuvimos 36 publicaciones, ocho desarrolladas en ecosistemas desérticos (Tabla 1). El orden más representado en ecosistemas de América fue Rodentia ($n = 20$) y en particular en desiertos fue Artiodactyla ($n = 4$). Del total de trabajos, las preguntas enfocadas a estimar 'conectividad' ($n = 14$) y 'estructura' ($n = 12$) fueron las más estudiadas, y los análisis más utilizados se basaron en pruebas de Mantel (simple y parcial). La capacidad de dispersión y la presencia de vegetación fueron variables clave. Aunque predominó la evaluación de conectividad mediante análisis de correlación entre matrices de distancias y pruebas de Mantel, identificamos el uso de metodologías novedosas, como la construcción de redes genéticas y demográficas a partir de matrices de resistencia. Cabe resaltar que las variables ecológicas de las especies, en particular de roedores, y la cobertura vegetal fueron clave en desiertos. Finalmente, identificamos que Norteamérica es la región más estudiada, mientras que existen pocos trabajos de GP con mamíferos en México y Sudamérica (un trabajo abarcó Norteamérica y Centroamérica) y en ecosistemas desérticos, por lo que es urgente realizar estudios en dichas regiones y en desiertos.

Key words: connectivity; gene flow; genetic structure; Mexico; rodents; spatial analysis.

Introduction

Genetic variation is considered to be the basic level of biological diversity (McNeely *et al.* 1990) and is essential for the adaptation and survival of individuals, the viability of populations, and the ability of species to adapt to environmental changes (Frankham *et al.* 2010). Particularly since 1970, genetic variation started being regarded as a key element of conservation (Frankel 1974). On the other hand, the acknowledgment of the impact of human activities on the environment in the 1980s — mainly fragmentation and habitat loss — gave rise to landscape ecology as the discipline that investigates the interactions between spatial heterogeneity and ecological processes (Turner 2005). In 2003, the conceptual and methodological development of both disciplines laid the foundations for the recognition of Landscape Genetics (LG) as a discipline that evaluates the impact of environmental heterogeneity and the landscape elements on the variation and genetic structure of individuals and populations (Manel *et al.* 2003). LG integrates the concepts and tools of population genetics, landscape ecology, and spatial statistics, to quantify the effects of the landscape matrix (composition, configuration, and quality) on microevolutionary processes such as gene flow, drift and selection, based on neutral or adaptive genetic variation (Manel *et al.* 2003; Holderegger and Wagner 2006; Storfer *et al.* 2007; Balkenhol *et al.* 2015).

The impact of LG in the scientific community has led to a marked increase in the number of publications related to the topic, from 3 to 60 articles per year, over 10 years (Storfer *et al.* 2010). A variety of analytical and methodological approaches have emerged, including the stages that a LG study should follow (Garrido-Garduño and Vázquez-Domínguez 2013; Hall and Beissinger 2014), the consideration of temporal and spatial scales (Anderson *et al.* 2010), the sampling design and selection of molecular markers (Landguth *et al.* 2012), statistical analyses (Balkenhol *et al.* 2009a), and certain limitations and perspectives of LG (Balkenhol *et al.* 2009b; Richardson *et al.* 2016). In this sense, Storfer *et al.* (2010) analyzed empirical studies published up to that date; from their results, five points stand out: 1) there is a taxonomic bias toward vertebrates; 2) most works have been conducted in America; 3) forests are the most studied habitats; 4) the topic most frequently addressed is the identification of barriers affecting gene flow; and 5) deserts are scarcely represented ecosystems, with 3 % of LG studies. Other revisions also point out that vertebrates are the dominant taxonomic group in LG studies at the global level (Garrido-Garduño and Vázquez-Domínguez 2013; Dyer 2015); of these, mammals have prevailed (Montgelard *et al.* 2014). It should be noted that although America is the region most represented in LG studies, there is no information currently available identifying the main topics of research, analytical methods used, and environments studied from an LG perspective.

Deserts are one of the Earth's more widespread environments, occupying approximately one-third of the Earth's surface (Schimel 2010). The environmental characteristics of deserts, such as high temperatures and low rainfall, have favored a variety of microhabitats that, in addition to hosting a large number of taxonomic groups, many of them endemic, also confer temporal and spatial heterogeneity (Whitford 2002; WWF 2019). Temporal heterogeneity emerges from highly variable environmental conditions throughout the day, between seasons of the year, or between years (Polis 1991); for its part, spatial heterogeneity influences species composition, distribution, and abundance (Whitford 2002; Ludwig *et al.* 2005). Thus, heterogeneity renders deserts ideal systems for hypothesis testing within the LG framework (Challenger and Soberón 2008). For instance, in the Chihuahuan desert, vegetation tends to be distributed in small patches (Grünberger 2004), producing a heterogeneous matrix that allows evaluating structural and functional connectivity (Manel and Holderegger 2013).

It is worth stressing that in the current context of global climate change, it is predicted that change rates toward warmer and more arid environments will rise in deserts relative to other regions. This, coupled with the transformation and loss of natural habitats in desert ecosystems (Mittermeier *et al.* 2003; Zeng and Yoon 2009; WWF 2019), have supported that deserts be presently considered as vulnerable regions, particularly the deserts of North America (Bachelet *et al.* 2016; WWF 2019). Therefore, due to the overall scarce representation of deserts in the literature of landscape genetics (Storfer *et al.* 2010), we deem it essential to determine the state of the art of LG research in American deserts. Its relevance lies in the fact that the persistence of species inhabiting desert ecosystems depends on the dispersal ability of individuals and the movement of genes within and between their populations across the landscape (Scribner *et al.* 2005; Reding *et al.* 2013).

Based on the above arguments, in the present work we conducted a review of the scientific literature aiming to 1) determine the most studied groups of mammals; 2) determine the representativeness of desert ecosystems; 3) describe the research questions most frequently addressed and the methods and analysis used; and 4) summarize the main factors of the landscape and the environment associated with genetic diversity and structure of the mammals of America.

Materials and Methods

Literature review. We surveyed articles about landscape genetics (LG) with mammals in ecosystems of America published between 2003 — when the term was first coined — and May 2019. We used the Web of Science website (http://apps.webofknowledge.com) based on different combinations of terms as keywords: 'landscape genetics', 'functional connectivity' and 'mammals'; 'landscape genetics', 'mammals' and 'desert'; 'landscape genetics', 'mammals', 'desert' and 'America'; 'functional connectivity', 'mammals' and 'desert'. This literature search method has proved to be efficient in different review works (*e. g.*, Storfer *et al.* 2010; Dyer 2015; Rico 2019), which also allows a systematic and repeatable analysis, although it certainly may exclude some works.

Literature validation and analysis. We conducted a detailed revision of the works obtained to the last screen (revision of the title, abstract, and methods), aiming to eliminate duplicated works and confirm that studies matched the search criteria (mammals, America, and desert). We considered only works that reported empirical data and that strictly corresponded to genetic landscape analysis, *i. e.*, including at least one landscape variable and evaluating its relationship with genetic patterns. We collected information on species, authors, year of publication, environments (considering the most represented environment in the study area according to each work), research questions (classified by 'type'), and statistical-spatial LG analysis used. The research questions were classified according to six types: 'connectivity', 'structure', 'gene flow', 'comparative analysis', 'association analysis' and 'adaptation'.

Results

Taxonomy, geographic region, and diversity of deserts. The results obtained for each combination of terms and search screened were as follows: 'landscape genetics', 'functional connectivity' and 'mammals' (*n* = 85 works); 'landscape genetics', 'mammals' and 'desert' (*n* = 78); 'landscape genetics', 'mammals', 'desert' and 'America' (*n* = 38); 'functional connectivity', 'mammals' and 'desert' (*n* = 10). After a thorough validation of the literature (elimination of duplicates, inclusion of works with empirical data only involving the analysis of landscape variables), a total of 36 publications were obtained (Table 1). We identified six orders of mammals, of which Rodentia was the most represented taxon (*n* = 20; Table 1). The main geographic region studied was North America (*n* = 25), mostly in the United States of America (*n* = 19). For South America (*n* = 10), we identified works conducted in Brazil (*n* = 3), Argentina (*n* = 6), and Uruguay (*n* = 1). We recorded one study that covered countries of North America (Mexico) and Central America (Belize, Costa Rica, Guatemala, and Honduras), which was counted separately. The environments involved included forests (*n* = 6), urban areas (*n* = 6), cropland (*n* = 4), mountains and rivers (*n* = 5), sand dunes (*n* = 5), and shrub steppe (*n* = 2), while desert ecosystems were addressed in eight studies.

Specifically for deserts, Artiodactyla was the order most represented (*n* = 4), although with a single species (the desert bighorn sheep *Ovis canadensis nelsoni*), followed by the orders Carnivora (*Ursus americanus* and *Bassariscus astutus*) and Rodentia (*Dipodomys spectabilis* and *Dipodomys merriami*), with two works each. The deserts of North America (Mojave, *n* = 3; Chihuahuan, n = 3; Sonoran *n* = 2) were the only arid environments where LG studies have been carried out (Table 1). No studies were found addressing the deserts of South America (Atacama and Patagonia). For Mexico, we found only three LG works, two in the tropical deciduous forest of Oaxaca and San Luis Potosí, and the other one the coast of Jalisco; only a single study was conducted in the desert (Chihuahuan; Table 1).

Research questions and statistical-spatial methods. The classification of the research questions addressed in all the publications reviewed (North America) revealed that those dealing with 'connectivity' and 'structure' were the most common ones (*n* = 14 and 12, respectively), followed by 'gene flow' (*n* = 7). The 'comparative', 'association' and 'adaptation' approaches were represented by one work each. To note, the 'association' and the 'adaptation' approaches were unique to desert environments (Table 1).

All studies analyzed genetic aspects that included assessment of deviations from the Hardy-Weinberg equilibrium and linkage disequilibrium, as well as genetic diversity measures by estimating allelic richness and observed and expected heterozygosity. Four works performed allocation and structure analyses to define genetic groups and to detect migrants (Figure 1).

Regarding spatial data handling and recording (landscape and environmental variables), all studies used a Geographic Information System (GIS) to represent the study area. In addition, five works estimated the Normalized Difference Vegetation Index (NDVI) to obtain vegetation cover data. A study selected sampling sites based on the method of environmental domains (Figure 1). In the remaining works, the landscape was characterized through a classification based on the literature reported for the area, or from repositories of specific environmental information.

In all the studies at least two analytical methods were used for assessing the genetics-landscape relationship. The methods most commonly utilized were the Mantel and partial Mantel tests, followed by linear regression models and their variants (*n* = 14; Figure 1). Some works addressing 'connectivity' and 'gene flow' questions constructed resistance layers to quantify the effects of landscape through the estimation of effective distances based on least-cost path algorithms (*n* = 6), resistance distance (estimated based on circuits theory; *n* = 6), and both (*n* = 4). One work used species distribution models (SDM) for the construction of these resistance layers (Figure 1).

Landscape factors that determine the genetic structure and diversity. The results obtained for America show that the environmental and landscape characteristics, represented as effective distances, are the ones that best explained genetic structure and diversity patterns in most works (Figure 2a), followed by geographic distance (*i. e.*, with a pattern of isolation by distance). The main landscape variables

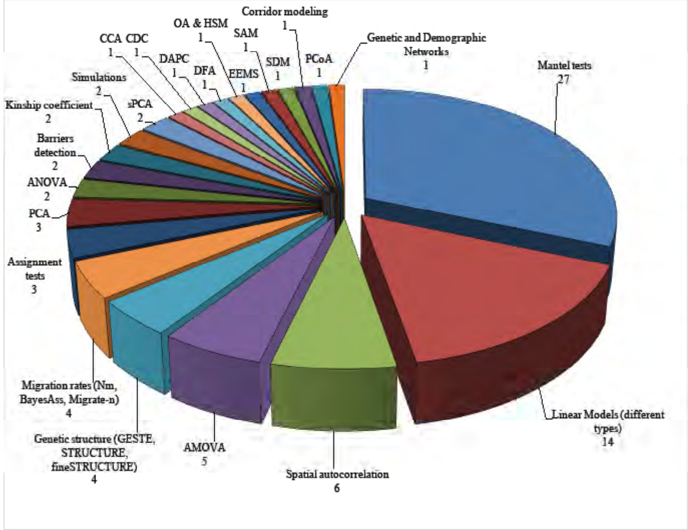

Figure 1. Analytical methods used in landscape genetics studies with mammals in North America. Numbers indicate the number of studies that used each method; all works used more than two methods. Abbreviations: ANOVA = Analysis of variance; AMOVA = Analysis of molecular variance; CEC = Canonical correspondence analysis; CDC = Climatic domain classification; DAPC = Discriminant principal component analysis; DFA = Discriminant functional analysis; EEMS = Estimated effective migration rates; OA and HSM = Occupancy analyses and Habitat suitability model; PCA = Principal component analysis; PCoA = Principal coordinate analysis; sPCA = Spatial principal component analysis; SAM = Spatial autoregressive modeling; SDM = Species distribution models.

included topography, vegetation cover (evaluated as NDVI and extent of available habitat in the landscape), rivers, and water bodies (Figure 2b). Additional relevant factors were anthropogenic constructions (highways and roads) and the ecological characteristics of species, such as dispersal capacity and population density. In particular in deserts, the factors most frequently associated with genetic structure and diversity were vegetation cover, dispersal, and anthropogenic constructions (Figure 2b).

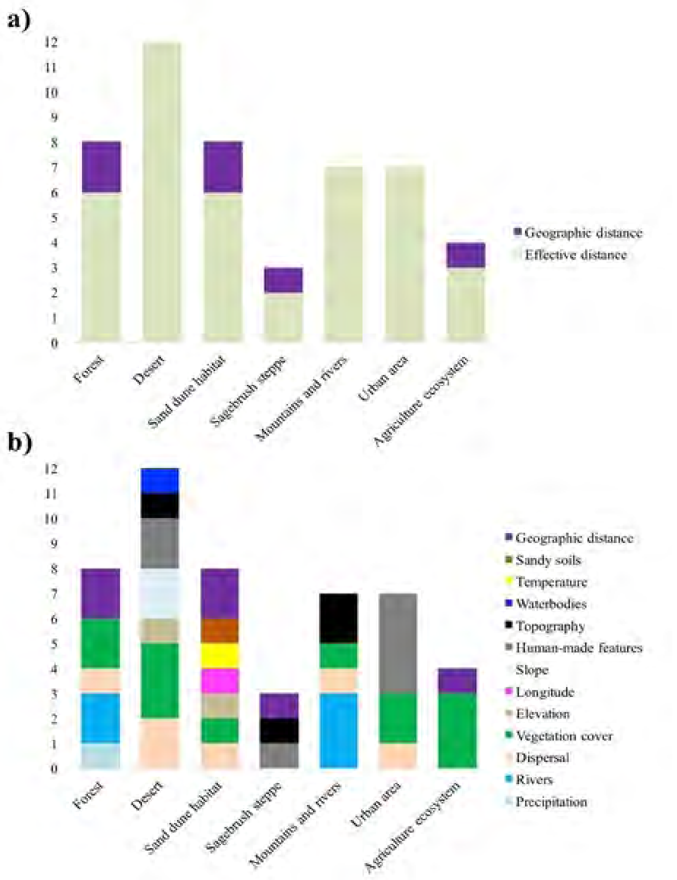

Figure 2. Factors that determine the genetic structure and diversity of mammals, expressed as accumulated frequencies in each of the environments analyzed. "Vegetation cover" includes the different approaches used to assess that characteristic (NDVI, habitat patches), as well as for "anthropogenic constructions" (roads, highways). a) Factors in terms of geographic and effective distance; b) environmental and landscape variables that constitute effective distances in each environment. "Longitude" refers to the geographic position in the coordinate system.

Discussion

Since the term was first coined to the steady construction of the theoretical, methodological, and analytical frameworks (Manel *et al.* 2003; Holderegger and Wagner 2006; Balkenhol *et al.* 2015), landscape genetics (LG) has been broadly accepted in the scientific community to address questions related to the effect of the environmental variables in the genetic structure and variation of natural populations (Storfer *et al.* 2010; Garrido-Garduño and Vázquez-Domínguez 2013; Dyer 2015). Mammals comprise 6,399 species worldwide (of the 6,495 recognized species, 96 have become extinct); of these, 697 are located in the Nearctic region, which covers North America (Burgin *et al.* 2018). Our results show that this region is the best represented in LG studies with mammals, covering a great diversity of ecosystems. A study that encompasses North America and Central America is worth mentioning (Wultsch *et al.* 2016), and could be considered as one of the first addressing LG for this region. In addition, we found scarce research efforts done (and published) on landscape genetics involving the mammals of Mexico and South America, as well as in desert ecosystems.

Rodents and carnivores, models in landscape genetics in North America. Rodentia is considered the largest order, with 2,409 species that account for approximately 44 % of the diversity of mammals worldwide (Wilson *et al.* 2017). The characteristics of rodents, namely high species richness, small size (most species), limited dispersal capabilities, and diverse life stories, make them an ideal taxonomic group to address questions at the landscape scale, together with genetics and ecology. It is striking, however, that it was only recently that the qualities of this group were recognized within the context of landscape studies (Waits *et al.* 2015).

Studies involving rodents in America have been conducted mainly in areas with anthropogenic impact, including urban areas (Gardner-Santana *et al.* 2009; Chambers and Garant 2010; Mapelli *et al.* 2012; Munshi-South 2012; Marrotte *et al.* 2014; Anderson *et al.* 2015; Chiappero *et al.* 2016; Combs *et al.* 2018). On the other hand, we found only two works that were conducted with rodents in desert environments, specifically kangaroo rats in the Chihuahuan desert. In the first study, Cosentino *et al.* (2015) evaluated the population genetics of *D. spectabilis* from a spatial perspective, considering the configuration of the landscape matrix; they found that genetic differentiation patterns of its populations are determined by biological aspects of the species, specifically the dispersal capacity and population densities. In the second work, Flores-Manzanero *et al.* (2019) found higher gene flow in a population of *D. merriami* along areas with shrub vegetation, which in turn is associated with the construction of burrows and as a food source (seeds); accordingly, based on a LG approach these authors found a relationship between genetic patterns and ecological processes.

Carnivores were the second most represented order in landscape genetics studies in America, encompassing both medium-sized species such as the fisher (*Martes pennanti*; Hapeman *et al.* 2011) and the "cacomixtle" (ringtail, *Bassariscus astutus*; Lonsinger *et al.* 2015), as well as large species, including the gray wolf (*Canis lupus*; Cullingham *et al.* 2016), the black bear (*Ursus americanus*; Atwood *et al.* 2011; Draheim *et al.* 2018), and the jaguar (*Panthera onca*; Wultsch *et al.* 2016). Notably, carnivores are recognized as the most vulnerable to extinction group of mammals, due to their biological characteristics and anthropogenic impacts (Cardillo *et al.* 2004). The few studies identified in this review highlight the importance of conducting genetic landscape research to explore, among others, the effect of landscape elements (mountains, rivers) and anthropogenic features (habitat fragmentation) on the diversity and genetic structure of this group.

Evaluation of connectivity. Landscape genetics has focused primarily on terrestrial organisms (Storfer *et al.*

Table 1. Summary of landscape genetics studies with mammals analyzed in this review.

ORDER/ Species	F	Region	Environment/ landscape	Research question	Type of question	Statistical-spatial analysis	Genetic structure and diversity drivers
DIDELPHIMORPHIA							
Marmosops incanus	1	Atlantic Plain, Brazil	Forests with different degrees of fragmentation	Comparative landscape genetics Response of genetic diversity to fragmentation	Comparative analysis	ANOVA, regression models, and Mantel tests	Amount of available habitat across the landscape (% patch cover)
PRIMATES							
Leontopithecus rosalia	2	Uniao Biological Reserve, Brazil	Fragmented Atlantic forest	Evaluate the effect of the landscape in gene flow	Gene flow	Spatial autocorrelation, kinship indices, and generalized linear models	The spatial configuration of vegetation cover affects the dispersal of individuals
LAGOMORPHA							
Brachylagus idahoensis	3	Wyoming, Estados Unidos	Shrub steppe	Evaluate whether the spatial genetic structure pattern is due to isolation by distance or by barriers	Structure	Analysis of isolation by distance at individual and population levels	Geographic distance, with a road as a likely barrier
Ochotona princeps	4	Oregon, Estados Unidos	Mountains and rivers	Identify the factors that limit or facilitate gene flow	Gene flow	Genetic distance, resistance distances, simple and partial Mantel tests, simulations	Topographic complexity is the main driver of gene flow
Sylvilagus transitionalis	5	Eastern United States	Fragmented habitat / Urban zone	Assess connectivity	Connectivity	Resistance matrix, partial Mantel tests, Least-cost path and mixed-effect models	Linear anthropogenic constructions and shrub habitats (effective distance)
RODENTIA							
Calomys venustus	6	Córdoba, Argentina	Farming areas with roads	Assess spatial and temporal genetic structures	Structure	Spatial autocorrelation analysis, Mantel and partial Mantel tests. Correlation between genetic and "geographic" distances	Geographic distance only
Ctenomys "chasiquensis"	7	Las Pampas, Argentina	Sand dunes and cropland	Evaluate the environmental factors that shape population structure and those that promote the connectivity between populations	Structure	AMOVA, simple and partial Mantel tests, spatial principal component analysis (sPCA), generalized linear models	Plant cover (NDVI) and Longitude promote gene flow between populations
Ctenomys lami	8	Coxilha Lombas, Brasil	Matrix of rivers, lagoons and cropland	Assess the spatial genetic structure	Structure	Correlation between genetic and geographic distances, Mantel tests, assignment analysis, AMOVA	Geographic distance, probably due to the species limited dispersal
Ctenomys porteousi	9	Buenos Aires, Argentina	Cultivation and farming areas	Evaluate the effect of landscape configuration on genetic structure and connectivity. Migration rates	Connectivity	Connectivity between habitat patches. Correlation between genetic and geographic distances. Mantel and partial Mantel tests, generalized linear model.	Amount of available habitat across the landscape and distance between good-quality patches.
Ctenomys rionegrensis	10	Río Negro, Uruguay	Dune and river systems	Evaluate the geographic factors that shape population structure	Structure	Mixed generalized models	Elevation
Ctenomys sp.	11	Corrientes, northeast Argentina	Flood-prone area including lagoons, marshes, and cropland	Evaluate the geographic factors that shape population structure	Structure	Analysis of structure (GESTE), species distribution models and linear models	The presence of well-drained sandy soils and temperature are the drivers for the distribution and differentiation of populations
** Dipodomys merriami*	12	Mapimí, Durango, México	Chihuahuan desert	Evaluate the landscape features that limit or facilitate gene flow	Gene flow	Linear mixed-effect models from resistance surfaces and model evaluation using AIC	Effective distance (NDVI) best explains gene flow patterns, which is favored in areas with vegetation cover
** Dipodomys spectabilis*	13	Nuevo México, Estados Unidos	Chihuahuan desert	Evaluate the presence of a founder effect on recolonized sites based on genetic diversity, size, and connectivity between sites	Connectivity	Correlation between genetic and geographic distances. Mantel test, mixed generalized models	Dispersal characteristics associated with population density
Hydrochoerus hydrochaeris	14	Basins of Venezuela, Paraguay, and Argentina	River systems	Assess spatial genetic structure	Structure	AMOVA. Principal Coordinate Analysis and Canonical Correspondence. Resistance distance	Rivers determine the structure pattern
Lagidium viscacia	15	Neuquén, Argentina	Steppe and mountains	Evaluate functional connectivity	Connectivity	Correlation between genetic, geographic and cost distances. Mantel tests	Functional connectivity is influenced by landscape geology

Liomys pictus	16	Western Mexico	Tropical deciduous forest	Evaluate the effect of landscape elements on genetic structure and gene flow.	Gene flow	Environmental domains. Wombsoft, Barrier. Correlation between genetic and geographic distances. Effective distance: Least-cost path and circuit theory. Mantel and partial Mantel tests	Effective distance, precipitation and streams
Microtus californicus	17	Jasper Ridge Reserve, California, United States	Grasslands and oak forest	Evaluate gene flow	Gene flow	Principal component analysis, Mantel tests	Only geographic distance, due to the ecological characteristics.
Ondatra zibethicus	18	Sudbury, Ontario, Canada	Watersheds	Evaluate the effect of landscape characteristics on structure and connectivity.	Connectivity	Spatial autocorrelation by sex. Assignment analysis. Correlation between genetic, linear and resistance distances (least-cost path). PATHMATRIX. Partial Mantel tests	Roads and anthropogenic elements seem to facilitate the movement of organisms
Peromyscus leucopus	19	New York, United States	Urban zone	Evaluate the landscape characteristics that foster connectivity between populations in an urban environment	Connectivity	Migration rates (Nm, BayesAss and Migrate-n). Linear, effective (least-cost) and resistance distances. Mantel and partial Mantel tests	Effective distance (based on vegetation cover)
P. leucopus	20	Montérégie, Quebec, Canada	Farming land with rivers and roads	Evaluate the effect of the landscape characteristics on genetic structure and connectivity.	Connectivity	Correlation between genetic and ecological distances. Mantel tests. Multiple regression analysis between ecological and linear distances. Connectivity between patches with resistance distance	Forest fragments facilitate the movement of individuals
Rattus norvegicus	21	Baltimore, Maryland, United States	Urban zone	Characterize the genetic structure and evaluate gene flow	Gene flow	Genetic distance, kinship relations, and Mantel tests	Habitat fragmentation (urban area); the ecology of organisms contribute to homogenize diversity and genetic structure
R. norvegicus	22	New York, United States	Urban zone	Explore spatial genetic structure patterns	Structure	Spatial autocorrelation, Mantel tests, PCA, sPCA, estimated effective migration surfaces (EEMS), population structure (fineSTRUCTURE)	Closely related individuals and ecological characteristics of the species
Tamias striatus	23	south Quebec and Ontario, Canada	Forested areas, rivers, and urban areas	Explore the geographic factors that shape population structure; sex-biased dispersal	Structure	Correlation between genetic and geographic distances Mantel test. Identification of barriers (Barrier). AMOVA	The river is the main barrier, as well as sex-biased dispersal (males)
T. striatus	24	Indiana, United States	Patches of forest and farmland	Evaluate functional connectivity	Connectivity	Assignment analysis. Correlation between genetic and geographic distances. Mantel test. Coverage distances. Regression models	Vegetation cover promotes gene flow
Zapus trinotatus	25	Olympic Peninsula, Washington, United States	River systems, presence of mountains and forest	Assess connectivity in among rivers using three environmental distances. Migration rate	Connectivity	Spatial autocorrelation analysis. Mantel test. Estimation of migration rates	Effective distance (topographic and riparian landscape features) and limited species dispersal
CARNIVORA							
* *Bassariscus astutus*	26	Southwest United States	Desert and mountains Chihuahuan	Assess connectivity patterns associated with genetic structure: IBD, IBR, IBE	Connectivity	Partial Mantel tests. Discriminant function analysis. ANOVAs	Environmental characteristics: elevation, slope, and vegetation type (IBE-effective distance)
Canis lupus	27	Rocky Mountains, Canada	Mountains	Evaluate gene flow between herds considering the landscape characteristics	Gene flow	Regression between genetic and geographic distances (resistance model and coverage distance). Multiple regressions of distance matrices. Partial Mantel tests	Effective distance (based on vegetation cover)
Martes pennanti	28	Northeast United States	Mountains and rivers	Characterize genetic structure and its association with landscape features and human disturbance	Structure	Correlation between genetic, geographic and barrier distances. Mantel and partial Mantel tests. Recent migration rates	Orographic and hydrological characteristics (i.e. river and great lakes)
Panthera onca	29	In Mexico: Sierra Mixe, Oaxaca, and Sierra de Abra-Tanchipa, San Luis Potosí. In Central America: Belize, Costa Rica, Guatemala, Honduras	Tropical deciduous forest and medium tropical forest	Evaluate genetic structure at different spatial scales	Structure	Analysis of population structure, PCA, AMOVA, spatial autocorrelation, and Mantel tests.	Geographic distance, probably due to habitat fragmentation

* *Ursus americanus*	30	Arizona, United States	Mountains and Sonoran and Chihuahuan deserts	Evaluate connectivity and identify potential corridors	Connectivity	Analysis of occupation based on landscape characteristics (e.g. coverage). Habitat availability model. Resistance layers and corridor modeling	Fragmentation/barrier associated with the construction of the border wall
U. americanus	31	Michigan, United States	Cultivation and farming areas	Evaluate the effect of landscape changes on spatial genetic structure through time.	Structure	Simple and partial Mantel tests, resistance distances, FRAGSTATS, autoregressive spatial model, selection of models based on AIC	Vegetation cover showed a better relationship with genetic distance, while variables associated with environmental heterogeneity better predicted the genetic change over time
ARTIODACTYLA							
Odocoileus hemionus	32	Southern California, United States	Mountains and urban areas	Assess connectivity	Connectivity	Genetic structure (STRUCTURE and DAPC), genetic distances between individuals, habitat accumulated cost distance (HAC), least-cost path, generalized linear mixed-effect models	Highways restrain the connectivity between populations and individuals
* *Ovis canadensis nelsoni*	33	Southeast California, United States	Mojave and Sonoran deserts	Assess connectivity between populations, considering the effect of slope and anthropogenic presence	Connectivity	Migration rates. Correlation between genetic and geographic distances. Least-cost path. Partial Mantel test	Effective distance (based on topography)
* *O. c. nelsoni*	34	Southwest United States	Mojave desert	Combine connectivity by landscape resistance models and network theory to prioritize patches or corridors for conservation purposes	Connectivity	Effective resistance distance (least-cost path). Partial Mantel tests. Genetic and demographic network models. Correlations	Effective distance (based on maximum dispersal)
* *O. c. nelsoni*	35	Southwest United States	Mojave desert	Implementing NDVI as a predictor of food quality and genetic diversity	Association	Linear quadratic regression models to measure the association between NDVI and genetic diversity (response variables). Connectivity metrics as an additional predictor variable	Patches with high NDVI values
* *O. c. nelsoni*	36	Southwest United States	Mojave desert	Explore the effects of landscape on the spacing of adaptive genetic variation	Adaptation	Linear regression models from resistance (least-cost) surfaces and simulations	Effective distance (terrain slope, water bodies,and roads determine gene flow)

Abbreviations: IBD= isolation by distance (Isolation by Distance), IBR= isolation by barrier (Isolation by Barrier), IBE= isolation by ambient (Isolation by Environment); ANOVA = Analysis of variance; AMOVA= analysis of molecular variance; PCA = Principal component analysis.

*= study explicitly conducted in a desert.

F= Source. 1: Balkenhol *et al.* (2013); 2: Moraes *et al.* (2018); 3: Thimmayya and Buskirk (2012); 4: Castillo *et al.* (2014); 5: Amaral *et al.* (2016); 6: Chiappero *et al.* (2016); 7: Mora *et al.* (2017); 8: Lopes and De Freitas (2012); 9: Mapelli *et al.* (2012); 10: Kittlein and Gaggiotti (2008); 11: Gómez Fernández *et al.* (2016); 12: Flores-Manzanero *et al.* (2019); 13: Cosentino *et al.* (2015); 14: Byrne *et al.* (2015); 15: Walker *et al.* (2007); 16: Garrido-Garduño *et al.* (2016); 17: Adams and Hadly (2010); 18: Laurence *et al.* (2013); 19: Munshi-South (2012); 20: Marrotte *et al.* (2014); 21: Gardner-Santana *et al.* (2009); 22: Combs *et al.* (2018); 23: Chambers and Garant (2010); 24: Anderson *et al.* (2015); 25: Vignieri (2005); 26: Lonsinger *et al.* (2015); 27: Cullingham *et al.* (2016); 28: Hapeman *et al.* (2011); 29: Wultsch *et al.* (2016); 30: Atwood *et al.* (2011); 31: Draheim *et al.* (2018); 32: Fraser *et al.* (2019); 33: Epps *et al.* (2007); 34: Creech *et al.* (2014a); 35: Creech *et al.* (2014b); 36: Creech *et al.* (2017)

2010; Garrido-Garduño and Vázquez-Domínguez 2013; Dyer 2015), where the development of tools, like geographic information systems (GIS), has allowed a more real representation of terrestrial landscapes (Waits *et al.* 2015). In this review, we found that one of the LG questions most frequently addressed globally (America) was the connectivity between populations, and all studies evaluating this topic used GISs to represent the landscape. These studies also used different analytical methods to relate the landscape with the genetic structure of populations, including the correlation between genetic distances and different geographic distances, since just the linear (Euclidean) distance does not represent the true distance between populations (Vignieri 2005). The so-called effective distance or functional distance represent ecological measures of distance commonly used in LG studies, the most used being the least-cost path and the resistance distance (Storfer *et al.* 2007; McRae *et al.* 2008). Also, the Mantel and partial Mantel tests were the approaches most frequently used to evaluate the correlation between these distances. Although the use of Mantel tests has been questioned (see Guillot and Rousset 2013), they are considered appropriate methods when setting hypotheses that explicitly involve distance (Legendre and Fortin 2010; Legendre *et al.* 2015), while also favoured as models that are easy to interpret and serve as starting points for the parameterization of resistance matrices (Storfer *et al.* 2010). For example, Munshi-South (2012) evaluated the connectivity between populations of the white-footed mouse (*Peromyscus leucopus)* in an urban area using estimates of migration rates and correlating these with cost and resistance distances, supported on the resolving power of GISs and Mantel and partial Mantel tests. Also, in an environment with anthropogenic impact, Amaral *et al.* (2016) assessed the connectivity between populations of the gray rabbit (*Sylvilagus transitionalis*) from cost and resistance distances, which were optimized using correlations through partial Mantel tests. Likewise, Draheim *et al.* (2018) implemented simple and partial Mantel tests to correlate genetic distances between paired individuals with geographic (linear) and resistance distances, to evaluate whether changes in the landscape over time influenced the spatial genetic structure of the black bear (*Ursus americanus*).

An aspect worth mentioning is the development of additional methods to assess connectivity in terms of the relationship between effective and genetic distances, like the generalized linear models, which prevailed in studies with rodents (Kittlein and Gaggiotti 2008; Mapelli *et al.* 2012; Marrotte *et al.* 2014; Cosentino *et al.* 2015). We should also highlight the use of species distribution models for the construction of connectivity hypotheses in landscape genetics, as these combine presence data (localities where the species has been recorded) and climate data associated with that locality, also considering vegetation cover, topography, and other environmental variables (Rolland *et al.* 2015). For instance, Gómez Fernández *et al.* (2016) modeled the distribution of the tuco-tuco (*Ctenomys* sp.), taking into consideration the environmental variables available for the flooded area where it thrives, which allowed determining that permeable sandy soils and temperature are the factors significantly associated with its population genetic structure. Notably, the use of species distribution models in LG studies is restrained by the geographic scale, since most of the variables used for constructing these models are available at large scales (for example, the WorldClim layers have 1 km^2 resolution; Hijmans *et al.* 2005) and, therefore, their use is restricted to considering large areas.

Finally, we highlight the construction of genetic and demographic networks from resistance matrices. As an example, Creech *et al.* (2014a) combined resistance models with the network theory and evaluated their correlation with partial Mantel tests to identify patches and corridors that facilitate the connectivity between populations of the bighorn sheep (*Ovis canadensis nelsoni*). Thus, this analytical approach can be useful for identifying corridors, particularly in conservation studies.

Not surprisingly, connectivity is one of the topics most commonly addressed in landscape genetics, particularly under the current context of global changes that currently affect (and will continue to affect) the habitat of multiple species (Manel and Holderegger 2013).

Genomics, gene flow, and local adaptation. The work in landscape genetics has been based largely on the use of neutral genetic markers, such as microsatellite loci. However, given the accelerated transformation of natural environments, it is increasingly important to be able to assess the patterns derived from adaptive genetic variation, especially because there lies the potential of species to respond to these changes (Manel *et al.* 2003; Balkenhol *et al.* 2015). In this sense, the use of molecular markers such as SNPs (Single Nucleotide Polymorphisms) has made it possible to multiply the number of loci by the thousands, increasing the statistical power of landscape genetic analyses (Combs *et al.* 2018). Also, since these markers are distributed throughout the genome, it is feasible to identify those that correspond to genes subject to selection. Therefore, the movement of these variants through gene flow between individuals and populations is largely determined by the characteristics of the landscape (Creech *et al.* 2017). In this review we found that Combs *et al.* (2018) used thousands of markers (61,400 SNPs) to explore the patterns of spatial genetic structure of the Norway rat (*Rattus norvegicus*) in New York. The authors proved the existence of genetic structure at a fine spatial scale, attributed to the elements of the urban matrix and the ecological characteristics of the species. Also, these authors mention that previous studies, with the same species and using microsatellites, did not detect genetic structure patterns, highlighting the resolving power of SNPs in LG studies. On the other hand, Creech *et al.* (2017) explored the effects of landscape elements in gene flow from the optimization of resistance models, using simulations in populations of the bighorn sheep (a species that inhabits desert environments). Their results from simulations based on loci subject to selection show a higher gene flow of variants (loci) with adaptive potential in habitats with a continuous distribution of vegetation cover, among other variables. The above is particularly relevant in the context of the vulnerability of desert ecosystems (Bachelet *et al.* 2016; WWF 2019) and, therefore, the species that inhabit these systems, because their persistance will depend on the movement of genes with adaptive potential through an environment with scarce vegetation.

Remote sensing. One of the most powerful tools that has contributed to the generation of spatially explicit predictive variables is the information obtained from satellites, *i. e.*, remote sensing (He *et al.* 2015). With our revision we evidence that one of the most innovative aspects in landscape genetics studies is the use of remote sensing information to achieve a more realistic interpretation of the landscape studied. For instance, Mapelli *et al.* (2012) used Landsat ETM+ sensor images to identify habitat patches in their study area and extract reflectance values of each, which were used to generate predictive variables. Thereby, the distance between good-quality patches was determined to be the most significant factor associated with the genetic structure patterns in *Ctenomys porteousi*. An additional sensor used to obtain satellite images is LiDAR, which has a higher resolution than Landsat, particularly for retrieving information on vegetation (Lefsky *et al.* 2002). Thus, Amaral *et al.* (2016) used LiDAR images to generate resistance layers used to assess the connectivity across populations of the rabbit *Sylvilagus transitionalis* and showed that patches of shrub vegetation facilitate gene flow in this species. As to its use in desert environments, Creech *et al.* (2014b) used MODIS (Moderate Resolution Imaging Spectroradiometer) images to extract reflectance values for vegetation and to estimate the NDVI, which is significantly associated with genetic diversity values in *Ovis canadensis nelsoni*; that is, vegetation determines the functional connectivity in this species. Flores-Manzanero *et al.* (2019), using Landsat 8 images, also calculated the NDVI for detecting the vegetation cover at a fine spatial scale, which produced various resistance models; the NDVI turned out to be the best predictor of gene flow for *Dipodomys merriami*. This strongly supports the conclusion that remote sensing is an excellent tool for landscape genetics studies, particularly in deserts, where the fine-scale definition of the various aspects of the landscape may be a complex issue.

Factors that determine genetic structure and diversity in mammals. The theoretical and methodological framework of population genetics is useful for inferring the patterns that govern the genetic structure and diversity of populations (Freeman and Herron 2002). Landscape genetics allows testing these inferences through hypothesis in a spatially explicit context (Manel *et al.* 2003; Holderegger and Wagner 2006; Balkenhol *et al.* 2015). The studies reviewed tested different environmental and landscape variables associated with genetic patterns in mammals. Geographic distance was the most significant variable and was best represented in rodents (California vole, *Microtus californicus*, Adams and Hadly 2010; pygmy rabbit, *Brachylagus idahoensis*, Thimmayya and Buskirk 2012; tuco tuco, *Ctenomys lami*, Lopes and De Freitas 2012; Córdoba vesper mouse, *Calomys venustus*, Chiappero *et al.* 2016), and in one carnivore (*Panthera onca*, Wultsch *et al.* 2016). Although in most studies anthropogenic impacts (fragmentation associated with agricultural land or roads) and low dispersal ability of species were identified as the drivers of the genetic patterns, we emphasize the importance of considering the greatest amount of environmental or ecological variables possible.

Also, most studies evaluated the effective distance from variables like topography (Vignieri 2005; Epps *et al.* 2007), vegetation cover (Munshi-South *2012*; Lonsinger *et al.* 2015; Cullingham *et al.* 2016), precipitation and water bodies (Chambers and Garant 2010; Hapeman *et al.* 2011; Garrido-Garduño *et al.* 2016), available habitat, extent of fragmentation (Mapelli *et al.* 2012; Balkenhol *et al.* 2013), and anthropogenic impact (Gardner-Santana *et al.* 2009; Atwood *et al.* 2011; Amaral *et al.* 2016). Interestingly, some studies identify the ecological characteristics of species, in addition to environmental variables,as those that govern genetic diversity and structure patterns, particularly dispersal. For example, Chambers and Garant (2010) showed in the eastern chipmunk *Tamias striatus* that male-biased dispersal produces the structure pattern. Dispersal capability was also key in deserts, particularly for small mammals like *Dipodomys spectabilis*, since by incorporating population density data allowed detection of patterns that otherwise could have beeb attributed to geographic distance alone (Cosentino *et al.* 2015). In addition, one of the most significant factors for the bighorn sheep was maximum dispersal distance (i.e., effective distance), in addition to topography and food quality (estimated from the NDVI; Epps *et al.* 2007; Creech *et al.* 2014b). In fact, considering the maximum dispersal distance significantly improved the connectivity models, thus highlighting the importance of considering this little-used variable (Creech *et al.* 2014a). Finally, for large carnivores such as *Ursus americanus*, anthropogenic impact is the most important factor; for instance, the wall along the Mexico and USA border, is a significant barrier to dispersal and gene flow across populations (Atwood *et al.* 2011). Among medium-sized mammals like cacomixtle (*Bassariscus astutus*), the environment is the primary driver represented by the combination of vegetation type, slope, and elevation (Lonsinger *et al.* 2015).

North America… without Mexico? North America is the geographic region with the largest number of landscape genetics studies (Storfer *et al.* 2010). However, when Mexico was considered separately in our review, our analysis revealed the scarcity of studies despite its status as a megadiverse country that hosts a great variety of ecosystems (Mittermeier *et al.* 1997) and a high mammal richness, amounting to 496 species (Ramírez-Pulido *et al.* 2014). Although studies about genetics of the mammals of Mexico have been previously evaluated (Vázquez-Domínguez and Vega 2006), such assessment has not been done for landscape genetics. In this regard, it is important to mention that Rico (2019) recently published a review of landscape genetics studies conducted in Mexico to 2017, including 20 studies, with plants as the most studied taxonomic group (65%), while only two studies focused on mammals. This finding is consistent with our results, since we identified three studies for Mexico, two on rodents; of these, only one was conducted in a desert area. Garrido-Garduño *et al.* (2016) evaluated the effect of the landscape elements on the genetic structure and gene flow of *Liomys pictus* in a tropical deciduous forest, while Flores-Manzanero *et al.* (2019) determined the landscape features that influence gene flow of *Dipodomys merriami* in a region of the Chihuahuan desert. In Mexico, the tropical deciduous forest occupies 11.26 % of the national territory, mainly along the Pacific coast, while deserts represent 40% of the territory, distributed to the north and northwest (Challenger and Soberón 2008). Both ecosystems contain high levels of biodiversity and endemisms, particularly of animals (CONANP 2006; Ceballos *et al.* 2010); this, together with spatial and temporal heterogeneity, makes them suitable systems for hypothesis testing in a landscape genetics context.

Prospects for landscape genetics studies: the case of Mexico. From our review outlined here, we can assert that it is imperative in Mexico to conduct research addressing the effects of landscape and the environment on the distribution of genetic variation and structure of wild populations, through a spatially explicit approach. However, since rodents were the order of mammals most represented in this review, highlighting the studies conducted in Mexico, we believe landscape genetics studies with rodents will likely increase in the near future. This is based on the diversity of studies conducted with rodents in different environments in Mexico focused on aspects of genetic structure and diversity (Vega *et al.* 2007; Castañeda-Rico *et al.* 2011; Espindola *et al.* 2014), taxonomy and systematics (Arellano *et al.* 2006; Álvarez-Castañeda *et al.* 2009; Fernández *et al.* 2012), phylogeography (Espinoza-Medinilla *et al.* 2006; Gutiérrez-García and Vázquez-Domínguez 2012; Álvarez-Castañeda and Murphy 2014), diversification and speciation (Castañeda-Rico *et al.* 2013; Pérez-Consuegra and Vázquez-Domínguez 2015), and even the development of molecular markers (Munguía-Vega *et al.* 2007; Vázquez-Domínguez and Espindola 2013), to mention a few. In addition, the development of environmental and climatic layers with better resolution for Mexico (Téllez-Valdés *et al.* 2010; Cuervo-Robayo *et al.* 2014) will be key for the development of these studies in the country, in combination with remote sensing data that are currently freely accessible (Landsat 8; http://landsat.usgs.gov/). Finally, deserts cover a large part of the national territory (*ca.* 70 million hectares; Challenger and Soberón 2008) and in some cases, as in the Chihuahuan desert, vegetation is patchily distributed (Grünberger 2004). It is worth highlighting that, although deserts can be thought of as relatively homogeneous systems, in reality the spatial distribution of the elements of the desert landscape renders a heterogeneous matrix that allows evaluating the structural and functional connectivity (Manel and Holderegger 2013), making deserts ideal ecosystems to conduct landscape genetics studies.

Some of the most significant advances for the study of landscape genetics in Mexico and elsewhere are worth mentioning, including the use of remote sensing data and species distribution models, which yield a better representation of the landscape and help to set hypotheses considering structure and connectivity within a spatially explicit context. The use of genomic tools (markers, bioinformatics methods, and analyses) and adaptive approaches will allow addressing questions not only regarding the effect of the landscape on genetic patterns but also about how individuals respond in terms of adaptation and selection.

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Literature cited

Adams, R. I., and E. A. Hadly. 2010. High levels of gene flow in the California vole (*Microtus californicus*) are consistent across spatial scales. Western North American Naturalist 70:296-311.

Álvarez-Castañeda, S. T., and R. W. Murphy. 2014. The endemic insular and peninsular species *Chaetodipus spinatus* (Mammalia, Heteromyidae) breaks patterns for Baja California. PLoS ONE 9: e116146.

Álvarez-Castañeda, S. T., W. Z., Jr. Lidicker, and E. Ríos. 2009. Revision of the *Dipodomys merriami* complex in the Baja California Peninsula, Mexico. Journal of Mammalogy 90:992-1008.

Amaral, K. E., M. Palace, K. M. O'Brien, L. E. Fenderson, and A. I. Kovach. 2016. Anthropogenic habitats facilitate dispersal of an early successional obligate: implications for restoration of an endangered ecosystem. PLOS ONE DOI:10.1371/journal.pone.0148842.

Anderson, S. J., E. M. Kierepka, R. K. Swihart, E. K. Latch, and O. Rhodes. 2015. Assessing the Permeability of Landscape Features to Animal Movement: Using Genetic Structure to Infer Functional Connectivity. PLoS ONE 10:e0117500. doi:10.1371/journal.pone.0117500.

Anderson, C. D., B. K. Epperson, M-J. Fortin, R. Holderegger, P. M. A. James, M. S. Rosenberg, K. T. Scribner, and S. Spear. 2010. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular Ecology 19:3565-3575.

Arellano, E., D. S. Rogers, and F. X. González-Cózatl. 2006. Sistemática molecular del género *Reithrodontomys* (Rodentia: Muridae). Pp. 27-35 *in* Genética y mamíferos mexicanos: presente y futuro (Vázquez-Domínguez, E., and D. J. Hafner, eds.). New Mexico Museum of Natural History and Science. Albuquerque, U.S.A.

Atwood, T. C., J. K. Young, J. P. Beckmann, S. W. Breck, J. Fike, O. E., Jr. Rhodes, and K. D. Bristow. 2011. Modeling connectivity of black bears in a desert sky island archipielago. Biological Conservation 144:2851-2862.

Bachelet, D., K. Ferschweiler, T. Sheehan, and J. Strittholt. 2016. Climate change effects on southern California deserts. Journal of Arid Environments 127:17-29.

Balkenhol, N., L. P. Waits, and R. J. Dezzani. 2009a. Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. Ecography 3:818-830.

Balkenhol, N., S. A. Cushman, A. Storfer, and L. P. Waits. 2015. Introduction to Landscape Genetics – Concepts, Methods, Applications. Pp. 1-7 *in* Landscape Genetics: Concepts, Methods, Applications (Balkenhol, N., S. A. Cushman, A. T. Storfer, and L. P. Waits, eds.). John Wiley & Sons, Ltd. The Atrium, Chichester, U.K.

Balkenhol, N., R. Pardini, C. Cornelius, F. Fernandes, and S. Sommer. 2013. Landscape-level comparison of genetic diversity and differentiation in a small mammal inhabiting different fragmented landscapes of the Brazilian Atlantic Forest. Conservation Genetics 14:355-367.

Balkenhol, N., F. Gugerli, S. A. Cushman, L. P. Waits, A. Coulon, J. W. Arntzen, R. Holderegger, H. H. Wagner, and Participants of the Landscape Genetics Research Agenda Workshop 2007 World Congress. 2009b. Identifying future research needs in landscape genetics: where to from here? Landscape Ecology 24:455-463.

Burgin, C. J., J. P. Colella, P. L. Kahn, and N. S. Upham. 2018. How many species of mammals are there? Journal of Mammalogy 99:1-14.

Byrne, M. S., R. D. Quintana, M. L. Bolkovic, M. H. Cassini, and J. I. Túnez. 2015. The role of river drainages in shaping the genetic structure of capibara populations. Genetica 143:645-656.

Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M. Mace. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biol 2: e197.

Castañeda-Rico, S., L. León-Paniagua, L. A. Ruedas, and E. Vázquez-Domínguez. 2011. High genetic diversity and extreme differentiation in the two remaining populations of *Habromys simulatus*. Journal of Mammalogy 92:963-973.

Castañeda-Rico, S., L. León-Paniagua, E. Vázquez-Domínguez, and A. G. Navarro-Sigüenza. 2013. Evolutionary diversification and speciation in rodents of the Mexican lowlands: The *Peromyscus melanophrys* species group. Molecular Phylogenetics and Evolution 70:454-463.

Castillo, J. A., C. W. Epps, A. R. Davis, and S. A. Cushman. 2014. Landscape effects on gene flow for climate-sensitive montane species, the American pika. Molecular Ecology 23:843–856.

Ceballos, G., L. Martínez, A. García, E. Espinoza, C. J. Bezaury, and R. Dirzo. 2010. Diversidad, amenazas y regiones prioritarias para la conservación de las selvas secas del Pacífico de México. FCE, Conabio, Conanp. México.

Challenger, A., and J. Soberón. 2008. Los ecosistemas terrestres. Pp. 87-108 *in* Capital natural de México, Vol. I: Conocimiento actual de la biodiversidad. Conabio. México.

Chambers, J. L., and D. Garant. 2010. Determinants of population genetic structure in Eastern chipmunks (*Tamias striatus*): the role of landscape barriers and sex-biased dispersal. Journal of Heredity 101:413-422.

Chiappero, M. B., L. V. Sommaro, J. W. Priotto, M. P. Wiernes, A. R. Steinmann, and C. N. Gardenal. 2016. Spatio-temporal genetic structure of the rodent *Calomys venustus* in linear, fragmented habitats. Journal of Mammalogy 97:424-435.

Combs, M., E. E. Puckett, J. Richardson, D. Mims, and J. Munshi-South. 2018. Spatial population genomics of the brown rat (*Rattus norvegicus*) in New York City. Molecular Ecology 27:83-98.

Conanp. 2006. Programa de conservación y manejo Reserva de la Biosfera Mapimí, México. Comisión Nacional de Áreas Naturales Protegidas. Secretaría del Medio Ambiente y Recursos Naturales, México.

Cosentino, B. J., R. L. Schooley, B. T. Bestelmeyer, A. J. McCarthy, and K. Sierzega. 2015. Rapid genetic restoration of a keystone species exhibiting delayed demographic response. Molecular Ecology 24:6120-6133.

Creech, T. G., C. W. Epps, R. J. Monello, and J. D. Wehausen. 2014a. Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology 29:605-619.

Creech, T. G., C. W. Epps, R. J. Monello, and J. D. Wehausen. 2014b. Predicting diet quality and genetic diversity of a desert-adapted ungulate with NDVI. Journal of Arid Environments 127:160-170.

Creech, T. G., C. W. Epps, E. L. Landguth, J. D. Wehausen, R. S. Crowhurst, B. Holton, and R. J. Monello. 2017. Simulating the spread of selection-driven genotypes using landscape resistance models for desert bighorn sheep. PLoS ONE 12:e0176960. https://doi.org/10.1371/journal.pone.0176960

Cuervo-Robayo, A. P., O. Téllez-Valdés, M. A. Gómez-Albores, C. S. Venegas-Barrera, J. Manjarres, and E. Martínez-Meyer. 2014. An update of high-resolution monthly climate surfaces for Mexico. International Journal of Climatology 34:2427-2437.

Cullingham, C. I., C. D. Thiessen, A. E. Derocher, P. C. Paquet, J. M. Miller, J. A. Hamilton, and D. W. Coltman. 2016. Population structure and dispersal of wolves in the Canadian Rocky Mountains. Journal of Mammalogy 7:839-851.

Draheim, H. M., J. A. Moore, M-J. Fortin, and K. T. Scribner. 2018. Beyond the snapshot: Landscape genetic analysis of time series data reveal responses of American black bears to landscape change. Evolutionary Applications 11:1219–1230.

Dyer, R. J. 2015. Is there such a thing as landscape genetics? Molecular Ecology 24:3518-3528.

Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal corridor models using landscape genetics. Journal of Applied Ecology 44:714-724.

Espindola, S., A. D. Cuarón, O. E. Gaggiotti, and E. Vázquez-Domínguez. 2014. High genetic structure of the Cozumel Harvest mice, a critically endangered island endemic: conservation implications. Conservation Genetics 15:1393-1402.

Espinoza-Medinilla, E., I. Sánchez, M. García, and C. Lorenzo-Monterrubio. 2006. Análisis de la distribución de roedores de la familia Muridae en el sur de México. Pp. 47-54 *in* Genética y mamíferos mexicanos: presente y futuro (Vázquez-Domínguez, E. and D. J. Hafner, eds.). New Mexico Museum of Natural History and Science. Albuquerque, U.S.A.

Fernández, J. A., F. A. Cervantes, and M. S. Hafner. 2012. Molecular systematics and biogeography of the Mexican endemic kangaroo rat, *Dipodomys phillipsii* (Rodentia: Heteromyidae). Journal of Mammalogy 93:560-571.

Flores-Manzanero, A., M. A. Luna-Bárcenas, R. J. Dyer, and E. Vázquez-Domínguez. 2019. Functional connectivity and home range inferred at a microgeographic landscape genetics scale in a desert-dwelling rodent. Ecology and Evolution 9:437–453.

Fraser, D. L., K. Ironside, R. K. Wayne, and E. E. Boydston. 2019. Connectivity of mule deer (*Odocoileus hemionus*) populations in a highly fragmented urban landscape. Landscape Ecology https://doi.org/10.1007/s10980-019-00824-9(0123456789

Frankel, O. H. 1974. Genetic conservation: our evolutionary responsibility. Genetics 78:53-65.

Frankham, R., J. D. Ballou, and D. A. Briscoe. 2010. Introduction to Conservation Genetics, Second edition. Cambridge University Press. New York, U.S.A.

Freeman, S. and J. C. Herron. 2002. Análisis evolutivo. Prentice Hall. España.

Gardner-Santana, L. C., D. E. Norris, C. M. Fornadel, E. R. Hinson, S. L. Klein, and G. E. Glass. 2009. Commensal ecology, urban landscapes, and their influence on the genetic characteristics of city-dwelling Norway rats (*Rattus norvegicus*). Molecular Ecology 18:2766-2778.

Garrido-Garduño, T., and E. Vázquez-Domínguez. 2013. Métodos de análisis genéticos, espaciales y de conectividad en genética del paisaje. Revista Mexicana de Biodiversidad 84:1031-1054.

Garrido-Garduño, T., O. Téllez-Valdés, S. Manel, and E. Vázquez-Domínguez. 2016. Role of habitat heterogeneity and landscape connectivity in shaping gene flow and spatial population structure of a dominant rodent species in a tropical dry forest. Journal of Zoology 298:293-302.

Gómez-Fernández, M. J., E. S. M. Boston, O. E. Gaggiotti, M. J. Kittlein, and P. M. Mirol. 2016. Influence of environmental heterogeneity on the distribution and persistence of a subterranean rodent in a highly unstable landscape. Genetica 144:711-722.

Grünberger, O. 2004. Características esenciales de la Reserva de la Biosfera. Pp. 41-55 *in* Las playas del desierto chihuahuense (parte mexicana): Influencia de las sales en ambiente árido y semiárido (Grünberger, O., V. M. Reyes-Gómez, and J. L. Janeau, eds.). Institut de Recherche pour le Développement. Instituto de Ecología, A. C., México.

Guillot, G., and F. Rousset, F. 2013. Dismantling the Mantel tests. Methods in Ecology and Evolution 4:336-344.

Guillot, G., R. Leblios, A. Coulon, and A. C. Frantz. 2009. Statistical methods in spatial genetics. Molecular Ecology 18:4734-4756.

Gutiérrez-García, T. A., and E. Vázquez-Domínguez. 2012. Biogeographically dynamic genetic structure bridging two continents in the monotypic Central American rodent *Ototylomys phyllotis*. Biological Journal of the Linnean Society 107:593-610.

Hall, L. A. and S. R. Beissinger. 2014. A practical toolbox for design and analysis of landscape genetics studies. Landscape Ecology 29:1487-1504.

Hapeman, P., E. K. Latch, J. A. Fike, O. E. Rhodes, and C. W. Kilpatrick .2011. Landscape genetics of fishers (*Martes pennanti*) in the Northeast: dispersal barriers and historical influences. Journal of Heredity 102:251-259.

He, K. S., B. A. Bradley, A. F. Cord, D. Rocchini, M-N. Tuanmu, S. Schmidtlein, W. Turner, M. Wegmann, and N. Pettorelli. 2015. Will remote sensing shape the next generation of species distribution models? Remote Sensing in Ecology and Conservation 1:4-18.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Holderegger, R., and H. H. Wagner. 2006. A brief guide to Landscape Genetics. Landscape Ecology 21:793-796.

Kittlein, M. J., and O. E. Gaggiotti. 2008. Interactions between environmental factors can hide isolation by distance patterns: a case study of *Ctenomys rionegrensis* in Uruguay. Procedings of the Royal Society B 275:2633-2638.

Landguth, E. L., B. C. Fedy, S. J. Oyler-McCance, A. L. Garey, S. L. Emel, M. Mumma, H. H. Wagner, M-J. Fortin, and S. A. Cushman. 2012. Effects of sample size, number of markers, and allelic richness on the detection of spatial genetic pattern. Molecular Ecology Resources 12:276-284.

Laurence, S., M. J. Smith, and A. I. Schulte-Hostedde. 2013. Effects of structural connectivity on fine scale population genetic structure of muskrat, *Ondatra zibethicus*. Ecology and Evolution 3:3524-3535.

Lefsky, M. A., W. B. Cohen, G. G. Parker, and D. J. Harding. 2002. Lidar remote sensing for ecosystem studies. BioScience 1:19-30.

Legendre, P., and M-J. Fortin. 2010. Comparison of Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. Molecular Ecology Resources 10:831–844.

Legendre, P., M-J. Fortin, and D. Borcard. 2015. Should the Mantel test be used in spatial analysis? Methods in Ecology and Evolution 6:1239-1247.

Lonsinger, R. C., R. M. Schweizer, J. P. Pollinger, R. K. Wayne, and G. W. Roemer. 2015. Fine-scale genetic structure of the ringtail (*Bassariscus astutus*) in a Sky Island mountain range. Journal of Mammalogy 96:257-268.

Lopes, C. M., and T. R. O. De Freitas. 2012. Human impact in naturally patched small populations: genetic structure and conservation of the burrowing rodent, tuco-tuco (*Ctenomys lami*). Journal of Heredity 103:672-681.

Ludwig, J. A., B. P. Wilcox, D. D. Breshears, D. J. Tongway, and A. C. Imeson. 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology 86:288-297.

Manel, S., and R. Holderegger. 2013. Ten years of landscape genetics. TRENDS in Ecology and Evolution 28:614-621.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. TRENDS in Ecology and Evolution 4:189-197

Mapelli, F. J., M. S. Mora, P. M. Mirol, and M. J. Kittlein. 2012. Population structure and landscape genetics in the endangered subterranean rodent *Ctenomys porteousi*. Conservation Genetics 13:165-181.

Marrotte, R. R., A. Gonzalez, and V. Millien. 2014. Landscape resistance and habitat combine to provide an optimal model of genetic structure and connectivity at the range margin of a small mammal. Molecular Ecology 23:3983-3998.

McNeely, J. A., K.R. Miller, W. Reid, R. Mittermeier, and T. B. Werner. 1990. Conserving the World's Biological Diversity. IUCN, World Resources Institute, Conservation International, WWF, and the World Bank. Washington, DC. EE.UU.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712-2724.

Mittermeier, R. A., P. Robles-Gil, and C. G. Mittermeier. 1997. Megadiversidad: Los países biológicamente más ricos del mundo. Cemex-Agrupación Sierra Madre, México.

Mittermeier, R. A., C. G. Mittermeier, T. M. Brooks, J. D. Pilgrim, W. R. Konstant, G. A. B. da Fonseca, and C. Kormos. 2003. Wilderness and biodiversity conservation. Proceedings of the National Academy of Sciences USA 100:10309-10313.

Montgelard, C., S. Zenboudji, A-L. Ferchaud, V. Arnal, and B. J. Van Vuuren. 2014. Landscape genetics in mammals. Mammalia 78:139-157.

Mora, M. S., F. J. Mapelli, A. López, M. J. Gómez Fernández, P. M. Mirol, and M. J. Kittlein. 2017. Landscape genetics in the subterranean rodent *Ctenomys "chasiquensis"* associated with highly disturbed habitats from the southeastern Pampas region, Argentina. Genetica 145:575-591.

Moraes, A. M., C. R. Ruiz-Miranda, P. M., Jr. Galetti, B. B. Niebuhr, B. R. Alexandre, R. L. Muylaert, A. D. Grativol, J. W. Ribeiro, A. N. Ferreira, and M. C. Ribeiro. 2018. Landscape resistance influences effective dispersal of endangered golden lion tamarins within the Atlantic Forest. Biological Conservation 224:178-187.

Munguía-Vega, A., R. Rodríguez-Estrella, and M. C. Blázquez. 2007. Characterization of nine microsatellite loci on endemic kangaroo rats *Dipodomys simulans peninsularis* from southern Baja California Peninsula. Molecular Ecology Notes 7:127-129.

Munshi-South, J. 2012. Urban landscape genetics: canopy cover predicts gene flow between white-footed mouse (*Peromyscus leucopus*) populations in New York City. Molecular Ecology 21:1360-1378.

Pérez-Consuegra, S. G., and E. Vázquez-Domínguez. 2015. Mitochondrial diversification of the *Peromyscus mexicanus* species group in Nuclear Central America: biogeographic and taxonomic implications. Journal of Zoological Systematics and Evolutionary Research 53: 300-311.

Polis, G. A. 1991. Desert communities: an overview of patterns and processes. Pp. 1-26 *in* The Ecology of Desert Communities (Polis, G. A., ed.). The University of Arizona Press. Tucson, U.S.A.

Ramírez-Pulido, J., N. González-Ruiz, A. L. Gardner, and J. Arroyo-Cabrales. 2014. List of recent land mammals from Mexico, 2014. Special Publications, Museum of Texas Tech University 63:1-69.

Reding, D. M., S. A. Cushman, T. E. Gosselink, and W. R. Clark. 2013. Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (*Lynx rufus*). Landscape Ecology 28:471–486.

Richardson, J. L., S. P. Brady, I. J. Wang, and S. F. Spear. 2016. Navigating the pitfalls and promise of landscape genetics. Molecular Ecology 25:849-863.

Rico, Y. 2019. Landscape genetics of Mexican biodiversity: a review. Acta Universitaria 29, e1894. doi. http://doi.org/10.15174/au.2019.1894

Rolland, J., S. Lavergne, and S. Manel. 2015. Combining niche modelling and landscape genetics to study local adaptation: A novel approach illustrated using alpine plants. Perspectives in Plant Ecology, Evolution and Systematics 17:491–499.

Schimel, D. D. 2010. Drylands in the Earth system. Science 327:418-419.

Scribner, K. T., J. A. Blanchong, D. J. Bruggeman, B. K. Epperson, C-Y. Lee, Y-W. Pan, R. I. Shorey, H. H. Prince, S. R. Wintersterin, and D. R. Luukkonen. 2005. Geographical Genetics: Conceptual Foundations and Empirical Applications of Spatial Genetic Data in Wildlife Management. The Journal of Wildlife Management, 69:1434–1453.

Storfer, A., M. A. Murphy, S. F. Spear, R. Holderegger, and L. P. Waits. 2010. Landscape genetics: where are we now? Molecular Ecology 19:3496-3514.

Storfer, A., M. A. Murphy, J. S. Evans, C. S. Goldberg, S. Robinson, S. F. Spear, R. Dezzani, E. Delmelle, L. Vierling, and L. P. Waits. 2007. Putting the "landscape" in landscape genetics. Heredity 98:128-142.

Téllez-Valdés, O., V. Farías, P. Dávila, J. L. Stein, R. Lira, and F. J. Botello. 2010. Mammalian diversity in climatic domains for Tehuacán-Cuicatlán Biosphere Reserve, Mexico. Revista Mexicana de Biodiversidad 81:863-874.

Thimmayya, A. C., and S. W. Buskirk. 2012. Genetic connectivity and diversity of pygmy rabbits (*Brachylagus idahoensis*) in southern Wyoming. Journal of Mammalogy 93:29-37.

Turner, M. G. 2005. Landscape Ecology: What is the state of the science? Annual Review of Ecology, Evolution, and Systematics 36:319-344.

Vázquez-Domínguez, E., and R. Vega. 2006. ¿Dónde estamos y hacia dónde vamos en el conocimiento genético de los mamíferos mexicanos? Pp. 67-73 *in* Genética y mamíferos mexicanos: presente y futuro (Vázquez-Domínguez, E., and D. J. Hafner, eds.). New Mexico Museum of Natural History and Science. Albuquerque, U.S.A.

Vázquez-Domínguez, E., and S. Espindola. 2013. Characterization of ten new microsatellite loci from the endangered endemic rodent, *Reithrodontomys spectabilis*. Conservation Genetics Resources 5:251-253.

Vega, R., E. Vázquez-Domínguez, A. Mejía-Puente, and A. D. Cuarón. 2007. Unexpected high levels of genetic variability and the population structure of an island endemic rodent (*Oryzomys couesi cozumelae*). Biological Conservation 37:210-222.

Vignieri, S. N. 2005. Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*). Molecular Ecology 14:1925-1937.

Waits, L. P., S. A. Cushman, and S. F. Spear. 2015. Applications of landscape genetics to connectivity research in terrestrial animals. Pp. 199-219 *in* Landscape Genetics: Concepts, Methods, Applications (Balkenhol, N., S. A. Cushman, A. T. Storfer, and L. P. Waits, eds.). John Wiley & Sons, Ltd. The Atrium, Chichester, U.K.

Walker, R. S., A. J. Novaro, and L. C. Branch. 2007. Functional connectivity defined through cost-distance and genetic analyses: a case study for the rock-dwelling mountain vizcacha (*Lagidium viscacia*) in Patagonia, Argentina. Landscape Ecology 22:1303-1314.

Whitford, W. 2002. Ecology of Desert Systems. Academic Press, an Elsevier Science Imprint. San Diego, California. U.S.A.

Wilson, D. E., R. A. Mittermeier and T. E. Lacher. 2017. Handbook of the Mammals of the World, Vol 7: Rodents II. Lynx Editions. Barcelona, España.

Wultsch, C., A. Caragiulo, I. Dias-Freedman, H. Quigley, S. Rabinowitz, and G. Amato. 2016. Genetic Diversity and Population Structure of Mesoamerican Jaguars (*Panthera onca*): Implications for Conservation and Management. PLoS ONE 11:e0162377. doi:10.1371/journal.pone.0162377

WWF (World Wildlife Fund). 2019. Deserts and xeric shrublands. Recuperado de https://www.worldwildlife.org/biomes/deserts-and-xeric-shrublands el 21 de mayo de 2019.

Zeng, N., and J. Yoon. 2009. Expansion of the world's deserts due to vegetation-albedo feedback under global warming. Geophysical Research Letters 36:17-20.

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Synthesis and perspectives of bibliographic information on *Tapirella bairdii* in Mexico

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Tapirella bairdii participates in the dynamics of tropical forests through herbivory and seed dispersal. The objective of the present study was to review and analyze the literature published on *T. bairdii* in México between 1865 and 2018 aiming to identify information gaps and advances in knowledge and propose future research perspectives. The literature references on *T. bairdii* in México published in periodic scientific journals between 1865 (year of description of the species) and 2018 were organized in the software Endnote Plus. Articles were arranged into 5-year periods to identify publication trends. Articles were grouped according to 1) the 11 main topics, 2) the Mexican state where the study was carried out, 3) country of origin (national or foreign) of the first author, and 4) country of origin of the journal (national or foreign). A total of 136 published articles were recorded, more than eighty-eight percent between 1995 and 2018. Eighty-one percent of studies were carried out by Mexican researchers. These articles were published in 43 foreign and 11 national journals. Seventy-three percent of the studies were carried out in Chiapas, Oaxaca, and Campeche. A total of 233 records of occurrence of *T. bairdii* in México have been documented. The topics most frequently addressed include ecology, taxonomy and phylogeny, and distribution. No research has been published on physiology and ethology. The most productive years of research (1995-2018) can be explained by the increase in the number of Mexican researchers, with more funds allocated to research projects, information dissemination about the tapir, and the greater economic, scientific, and technological developments in different areas. The participation of national researchers is highlighted, with most articles published in foreign journals. The compilation of published information highlights the need to continue preserving Natural Protected Areas (NPAs), the Mesoamerican Biological Corridor, and unprotected regions that are home to tapir populations. Also, the connectivity between tapir populations should be improved, and the availability of tapir habitats in the country should be warranted. Research is needed to cover information gaps on basic aspects of the biology of the species, including physiology, ethology, diseases and parasitism, genetics, anatomy, reproduction, and evolutionary history, among others. Our findings reveal that no research on the physiology and ethology of tapirs has been conducted. Finally, the formation of a collaborative network to define and prioritize efforts and set guidelines is a priority.

Tapirella bairdii participa en la dinámica de los bosques tropicales al realizar procesos de herbivoría y dispersión de semillas. La finalidad de este trabajo fue revisar y analizar la bibliografía publicada entre 1865 y 2018 sobre *T. bairdii* en México para identificar los avances y sesgos en su conocimiento, y proponer perspectivas de investigación hacia el futuro. La bibliografía sobre *T. bairdii* en México publicada en revistas científicas entre 1865 (año de la descripción de la especie) y 2018 se organizó en el programa Endnote Plus. Se elaboraron archivos por lustros para identificar tendencias en la producción. Los trabajos se agruparon de acuerdo a: 1) 11 temas principales, 2) las entidades federativas donde se desarrolló el estudio, 3) el país de origen (nacional o extranjero) del primer autor, y 4) el origen de la revista (nacional o extranjera). Se registraron 136 publicaciones, con más del 88 % entre 1995-2018. El 81.6 % se realizaron por autores mexicanos. Se publicaron en 43 revistas extranjeras y 11 nacionales. El 73 % de los trabajos se desarrollaron en Chiapas, Oaxaca y Campeche. Se cuantificaron 233 registros de ocurrencia de *T. bairdii* en México. Los temas más abordados fueron sobre ecología, taxonomía y filogenia, y distribución. Hay nula investigación sobre fisiología y etología. Los años más productivos (1995-2018) pueden ser explicados por un incremento de investigadores mexicanos, del financiamiento de proyectos de investigación, de la divulgación sobre el tapir y por un mayor desarrollo económico, científico y tecnológico. Resalta la participación de investigadores nacionales con la mayoría de las publicaciones en revistas de origen foráneo. La síntesis de información indicó que es necesario continuar con la protección de las Áreas Naturales Protegidas (NPAs), del Corredor Biológico Mesoamericano, y de las regiones no protegidas que alberguen poblaciones del tapir; también se debe mejorar la conectividad entre ellas, para garantizar la disponibilidad de sus hábitats en el país. Se requieren incrementar los estudios sobre enfermedades y parasitismo y cubrir huecos de información sobre aspectos básicos de la biología de la especie como la fisiología, genética, anatomía, reproducción, historia evolutiva, entre otros. Se deben iniciar esfuerzos para estudiar la fisiología y la etología donde hay nula investigación. Finalmente, es prioritaria la formación de una red de colaboración para definir, priorizar esfuerzos y plantear directrices.

Keywords: bibliography; database; history; journals; México; Tapiridae; ungulate.

Introduction

Tapirella bairdii is the largest terrestrial ungulate in the Neotropics, being one of the four species in the family Tapiridae and the only species of tapir in Mesoamerica, endemic to a region stretching from southern México to northern Colombia (García *et al.* 2016). It plays a crucial role in the dynamics of tropical forests through herbivory and seed dispersal, contributing to the regeneration of tropical forests (Camargo-Sanabria and Mendoza 2016).

Tapirella bairdii is listed as endangered by the International Union for the Conservation of Nature (IUCN, García *et al.* 2016), included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2018), and listed as endangered of extinction by the Secretariat of the Environment and Natural Resources (NOM-059-SEMARNAT-2010; SEMARNAT 2010). It is also considered a priority species for conservation. The major threats to the conservation of the tapir are deforestation and habitat fragmentation, poaching, forest fires, drought, incidental encounters with humans, and disease transmission (Cruz-Aldán *et al.* 2006; Contreras-Moreno *et al.* 2013; Naranjo *et al.* 2015). A 50 % reduction in tapir populations has been estimated for the past 30 years (García *et al.* 2016). Its current geographic distribution in México includes the states of Campeche, Chiapas, Oaxaca, Quintana Roo, and southwest Veracruz (Mendoza *et al.* 2013; Botello *et al.* 2014; Naranjo *et al.* 2015); although there is no current evidence, large tapir populations may also thrive in Yucatan and Tabasco (March and Naranjo 2005; Naranjo *et al.* 2015).

The biology and ecology of the tapir are essential in forest environments; however, a single literature review is currently available (March 1994). This points to the need of an updated review and analysis of the published literature to identify the approaches and prospects in Mexico, as well as the biases and advances in knowledge, to propose the perspectives for future research. The objective of this work was to review and analyze the bibliographic references on *Tapirella bairdii* in Mexico, using the literature published in scientific journals over 153 years (1865-2018).

Materials and Methods

Information gathering, selection, and organization. The bibliography concerning *Tapirella bairdii* in México and published between 1865-2018 was gathered based on publications by Ramírez-Pulido *et al.* (1986), Ramírez-Pulido and Castro-Campillo (1990), Ramírez-Pulido and Castro-Campillo (1994), Ramírez-Pulido *et al.* (2000), and Ramírez-Pulido *et al.* (2017a), which include lists of the published literature on mammals of Mexico. In addition, we conducted a comprehensive search of electronic literature through the Google Scholar and the following databases: Biological Abstract, BioOne 1 Journals, BioOne 2 Journals, Current Contents Connect, ELSEVIER Science Direct – Journals, SciELO Mexico, Wiley-Blackwell Current Protocols, and Wiley-Blackwell Full Collection. The search was carried out considering the entire text (including the title), using specific and combined keywords including "tapir", "Tapirus", "Tapirella", "bairdii", "Tapiridae", and "Mexico". We reviewed the literature cited in each article on the subject. The only publications included were formal contributions published in scientific journals, expressly referring to the tapir in Mexico, excluding references of this species in other countries. The studies included date back to the year 1865 when the species was first described. For practical reasons, the year 2018 was selected as the last year, considering that the 153-year period adequately reflects the work conducted on this mammal.

The information contained in the references was analyzed and organized for incorporation into a database including several files produced using the literature management program Endnote Plus for PC version X 7.5 (Niles & Associates, Inc.). The fields used were the following: Author, year, title, journal name, volume, pages, main theme, state of Mexico, country of publication (Mexico, foreign), and nationality of the first author (Mexican or foreign).

Information Analysis. To explore the trend in the production of scientific articles, these were grouped considering 5-year intervals, except for the most recent one, which covered four years. This pooling allowed the identification of production trends and topics addressed in the publications over the 153 years of the study.

Published works were classified in one of the 11 main themes (Feeding, Anatomy and Morphology, Behavior, Conservation, Distribution, Ecology, Diseases and Parasitism, Physiology, Miscellaneous, Reproduction, Taxonomy and Phylogeny; Table 1), following the proposal of Guevara-Chumacero *et al.* (2001). The 11 themes in this proposal contain 100 biological topics as used by Carleton *et al.* (1993). Ethnozoology was incorporated into the Miscellaneous category. Publications were grouped according to the state of México where each study was conducted. Author nationality (Mexican or foreign) was assigned considering the first author of each publication.

A database of records of occurrence of *T. bairdii* in México was built in Excel based on data from the Global Biodiversity Information Facility (GBIF, http://data.gbif.org, accessed in June 2018); georeferences were reviewed and validated through geographic information. This information was mapped using the software ArcView 3.2.

Table 1. Topics included in this study. From Guevara-Chumacero *et al.* (2001).

Main topics	Topics used by Carleton *et al.* (1993)
Feeding	Diet, digestion, feeding habits, and nutrition.
Anatomy and Morphology	Determination of age, allometry, dentition, growth changes locomotion, molting, morphometry, sexual dimorphism size, weight.
Behavior	Activity, communication, territoriality, movement, shelters, pheromones, odor marks, social structure, vocalization.
Conservation	Cinegetic species, endangered, threatened, rare, hunting, status.
Distribution	Biogeography, zoogeography, ecogeography.
Ecology	Activity patterns, population censuses, demography, density, dispersal, habitat, home range, territoriality, migration, mortality, photoperiod, Predation, radiotelemetry, sex ratio.
Diseases and Parasitism	Parasites, injuries, pathology.
Physiology	Development, energy, function, immunology, metabolism, thermoregulation, hibernation, torpor.
Miscellaneous	Longevity, histology, orientation, echolocation, synopsis of works in congresses, ethnozoology.
Reproduction	Breeding, gestation, lactation, reproductive patterns, litter size, parturition, sexual maturity.
Taxonomy and Phylogeny	Chromosomes, cladistics, classification, cytogenetics, description, electrophoresis, evolution, fossils, genetics, geographic variation, heterozygosis, hybridization, karyotype, systematics.

Results

A total of 136 works on *T. bairdii* were recorded for Mexico, published between 1865 and 2018 (Appendix I). A low productivity was observed between 1865 and 1994, with just 15 scientific articles (Figure 1). From 1995, scientific production increased, peaking between 2010-2018. Of the total number of publications, 111 (81.6 %) were conducted by Mexican scientists and 25 (18.4 %) by foreigners. In the period of low productivity for the species (1865-1994), Mexican and foreign researchers contributed to the same extent. However, between 1995 and 2018, the ratio between Mexican and foreign authors was 5:1.

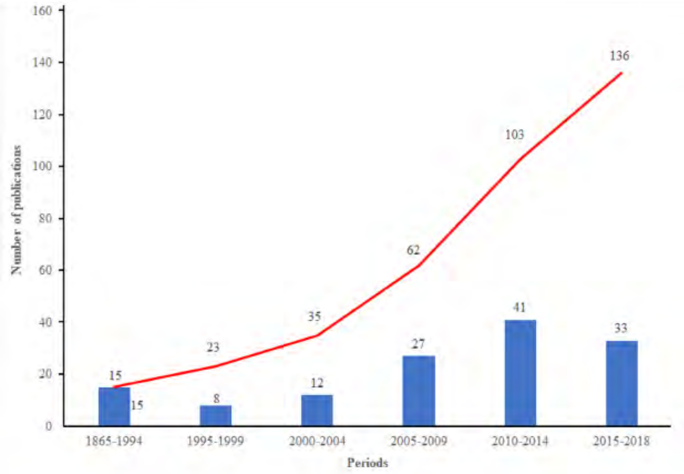

Figure 1. Number of publications on *Tapirella bairdii* in México between the years 1865-2018. Blue bars represent the number of publications per five year-intervals, while the red line marks the cumulative number of publications.

Articles on *T. bairdii* were published in 54 different journals, 43 foreign (53.3 %) and 11 Mexican journals (46.6 %). Although articles were published in a greater diversity of foreign journals, the 3 with the highest number of publications were Mexican journals (Acta Zoológica Mexicana, Revista Mexicana de Biodiversidad, and Revista Mexicana de Mastozoología). The most important national and foreign journals in terms of the number of studies published on the tapir in México are shown in Table 2. Seventy-three percent of the works were conducted in three states: Chiapas (32.4 %), Oaxaca (21.8 %), and Campeche (18.8 %). The states with the lowest number of studies were Tabasco (2.3 %) and Guerrero (1.2 %; Figure 2a).

Table 2. List of the main Mexican and foreign journals based on the number of articles published. Number of publications (NP)

	Mexican journals	NP	%		Foreign journals	NP	%
1.	Acta Zoológica Mexicana	16	11.8 %	1.	Tapir Conservation	8	5.9 %
2.	Revista Mexicana de Biodiversidad	13	9.6 %	2.	Revista de Biología Tropical	5	3.7 %
3.	Revista Mexicana de Mastozoología	12	8.8 %	3.	Tropical Conservation Science	5	3.7 %
4.	Therya	8	5.9 %	4.	Conservation Biology	3	2.2 %

The topics addressed more frequently were Ecology (29.9 %), Taxonomy and Phylogeny (20.4 %), and Distribution (15.3 %). Some subjects were either scarcely addressed, including Feeding (1.5 %), Anatomy/Morphology (0.7 %), and Reproduction (0.7 %), or were not addressed as main themes (Physiology and Ethology; Table 3).

Table 3. Number of papers published according to the main topic. Main topic (MT); number of works (NW).

MT	NW (%)	MT	NW (%)
Ecology	41 (29.9 %)	Diseases and Parasitism	9 (6.6 %)
Taxonomy and Phylogeny	28 (20.4 %)	Feeding	2 (1.5 %)
Distribution	21 (15.3 %)	Anatomy and Morphology	1 (0.7 %)
Miscellaneous	20 (14.6 %)	Reproduction	1 (0.7 %)
Conservation	14 (10.2 %)	Behavior	□
		Physiology	□

For the period 1884-2018, 233 records of occurrence of *T. bairdii* in México were obtained from the GBIF, corresponding to seven states (Oaxaca, Veracruz, Campeche, Tabasco, Chiapas, Yucatan, and Quintana Roo). Of these, 126 (54.5 %) records were observations, 59 (25.1 %) are of unknown origin, and 48 (20.4 %) were collections. Chiapas is the state with the largest number of records (106; 45.5 %), followed by Campeche (34; 14.6 %), and Oaxaca (31; 13.3 %), while Yucatan and Tabasco each reported two occurrence records.

Discussion

This study is the first work that compiles and assesses the current knowledge on *Tapirella bairdii*, a species that had been scarcely studied in México since its description (Gill 1865) to 1995, with just 15 scientific works published. Prior to the 20th century and following its description, the early studies where the tapir was mentioned were species listings for Tabasco, Oaxaca, and Chiapas, the aim of which was to record the local distribution of the fauna (Sumichrast 1881; Rovirosa 1885). In the period 1890-1949, the absence of works for this species was evident; only Alvarado (1915) mentioned the tapir in his work entitled "Sinonimia vulgar y científica de los mamíferos mexicanos" (Common and Scientific Synonymy of Mexican Mammals). After 1950 and until the decade of 1970, most of the studies published (n = 7) referring to *T. bairdii* were also taxonomic or distribution listings of mammals. The exception was the study by Álvarez del Toro (1966) that provided data about tapir breeding in the Tuxtla Gutiérrez Zoo, including observations on various reproductive aspects of the tapir in captivity. In the decade of 1980, two works that mentioned the tapir were published: Sánchez-Herrera (1986) included the tapir in the list of new records of mammals for Quintana Roo, and March (1987) mentions the tapir as one of the animals traditionally hunted and consumed as bushmeat by Mayan Lacandons in the state of Chiapas.

More than 88 % of the articles about this species were published in the period 1995-2018, with 2010 to 2018 as the most productive years, concentrating over 55 % of research articles (Figure 1). This productivity pattern can be attributed to various factors including the formation of new Mexican researchers that completed post-graduate programs in México and abroad, plus an increase in communications about the importance of the tapir in Mexico. An additional factor is the increased financing of research projects and the boost in economic, scientific, and technological development, consistent with the trends observed by Ramírez-Pulido *et al.* (2017b) in their analysis of the bibliographic synthesis of the Mexican mammalogy.

The most remarkable increase in the number of published works on the tapir started in 1995, mainly in foreign journals, although not synchronized with the overall pattern for the mammals of Mexico, for which the greatest increase took place from the 1950s (Guevara-Chumacero *et al.* 2001). This lack of synchrony may be due to the historical difficulties that are intrinsic to the study of the tapir in its natural habitat, including low population densities, evasive behavior, and presence restricted to remote and inaccessible areas (Matola *et al.* 1997). It is until recent decades that new observation, population quantification and sampling techniques have emerged (Silveira *et al.* 2003; Lyra-Jorge *et al.* 2008; Tobler *et al.* 2008).

The increase in the number of studies about the tapir in recent decades is also explained by the larger number of specialists and the diversity of projects in institutions such as the Universidad Nacional Autónoma de México (National Autonomous University of Mexico), the Center for Tropical Research at the Universidad Veracruzana, El Colegio de la Frontera Sur, the Africam Safari Zoo, Universidad McGill, the Miguel Álvarez del Toro Zoo, the DGPA Environmental Consultancy, and the Protected Natural Area (NPA) National Commission (Mendoza-Ramírez and Carbajal-Borges 2011).

In recent years, the knowledge about the tapir has focused on three main topics: ecology, taxonomy and phylogeny, and distribution. Investigations on ecology have been a priority in the generation of knowledge, involving a broad range of subjects such as density (*e.g.*, Botello *et al.* 2014), population activity patterns and habitat preference (*e.g.*, Lira-Torres *et al.* 2014), and ecological role in seed dispersal (*e.g.*, O'Farrill *et al.* 2013), among others. However, the main topic addressed has been the relative abundance of the species (*e.g.*, Carrillo-Reyna *et al.* 2015a; Naranjo *et al.* 2015; Pérez-Irineo and Santos 2016; Sandoval *et al.* 2016), which is essential for the development of proper management plans. Photo-trapping is a valuable tool that has played a fundamental role in the conduct of these studies in recent decades, reducing the time and effort of observers in the field (Carbajal-Borges *et al.* 2014; Carrillo-Reyna *et al.* 2015a; Mandujado 2019).

The studies with a focus on taxonomy and phylogeny include updated listings of mammals at national and state levels (*e.g.*, Ceballos and Arroyo-Cabrales 2012; Guzmán-Soriano *et al.* 2013; Rivero and Medellín 2015).

A key taxonomic aspect for this species was the proposal to change the generic name (*Tapirus bairdii*) to *Tapirella*. The genus *Tapirus* was proposed by Brünnich (1772), while *Tapirella* was a new generic name assigned by Palmer (1903) to replace the name *Elasmognathus* coined by Gill (1865) to name a new genus of the family Tapiridae based on two skulls found in the Isthmus of Panama showing morphological differences with specimens from South America (named *Elasmognathus bairdii*). However, this name was changed because the latter generic name had already been used in the order Hemiptera of the class Insecta (Fieber 1844). The generic name *Tapirella bairdii* was recovered by Groves and Grubb (2011), who reviewed the taxonomic relationships of the Perissodactyla and Artiodactyla based on morphological, cytogenetic, and molecular traits.

Information on karyotypes has been produced for other tapir species or geographic areas (*Tapirus terrestris*; Aguilera and Expósito 2009), as well as for phylogenetic relationships (South America; Holanda and Ferrero 2013); no such information is currently available for populations in Mexico. Zavala-Páramo *et al.* (2017) identified a relatively high genetic diversity in populations of southeast Mexico, through the use of microsatellites and the mitochondrial control region; however, most samples were taken from captive individuals in zoos related to wild populations in Mexico. These authors highlight the need to conduct a study across the entire distribution range in Mexico, to identify critical conservation aspects and set the basis for a proper management plan suitable for the species.

Investigations on distribution have focused on recording new locations (*e.g.*, Sánchez-Herrera *et al.* 1986; Peña-Azcona *et al.* 2015) and, recently, on the application of models to determine its potential distribution (*e.g.*, Carrillo-Reyna *et al.* 2015a; Schank *et al.* 2015; Schank *et al.* 2017). It is essential to continue using cameras-traps in locations with documented records through fingerprints, skeletal remains, fur, or direct observations of tapir individuals, to provide evidence about the species in new geographic regions (*e.g.*, Lira-Torres and Briones-Salas 2011; Lavariega *et al.* 2013), and where assessments of the abundance and density would be required subsequently.

The states with the largest number of records of occurrence and where most of the studies have been conducted are Chiapas, Oaxaca, and Campeche, the NPAs of which show the highest population abundances estimated for the species (Naranjo *et al.* 2015). Yucatan, Tabasco, and Guerrero produced low or zero records of occurrence and turned out to be the least studied states (Figure 2b). Historically, the tapir had a continuous distribution throughout southeast Mexico; however, in recent years, the presence of this species in Yucatan and Tabasco is uncertain (Naranjo *et al.* 2015). In the particular case of Guerrero, no records of occurrence are available and only one study includes eight historical records, collected by J. A. Sutter in 1873 in Acapulco (Nolasco *et al.* 2007); this finding supported an extension of the historical distribution of the tapir in the Pacific slope in Mexico.

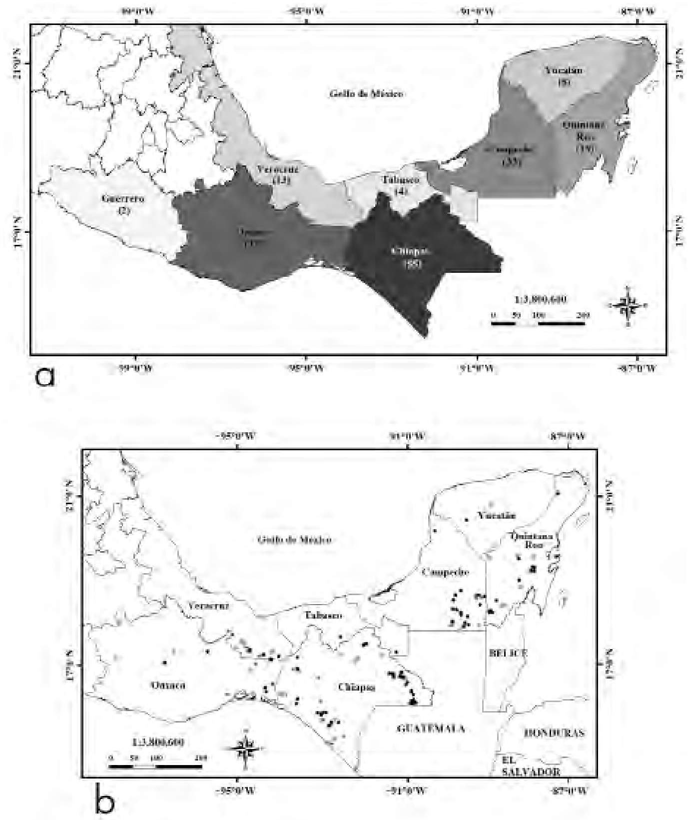

Figure 2. a) Map of the number of published works by state of Mexico. b) Map of records of occurrence of *Tapirella bairdii* in Mexico; black circles mark observed records observed; asterisks, collection records; gray boxes, unconfirmed records.

The importance of the Central American tapir for rural communities of southeastern México has been reflected in the publication of several studies on ethnozoology (13.2 % of the total), showing that the species is hunted for food by different communities in Oaxaca, Chiapas, Campeche, and Quintana Roo (Contreras-Díaz and Pérez-Lustre 2008; Barrasa 2013; Lira-Torres *et al.* 2014). Occasional hunting in a few ejidos in Quintana Roo has also been documented (Reyna-Hurtado and Tanner 2005; Ramírez-Barajas and Naranjo 2007; Santos-Fita *et al.* 2012): this activity has been ruled out definitely because tapirs are usually difficult to locate (Jorgenson 1995). In the Lacandon town of Métzabok in Chiapas, tapir hunting has been ruled out, as there have been no sightings in 15 years (Rodas-Trejo *et al.* 2016).

Zooarchaeological studies indicate that tapir consumption for food was a common practice among the Mayas in the Postclassic period in Yucatan; besides, tapir teeth may have been used as merchandise (Masson and Peraza Lope 2008). A study with strontium isotopes supports the hypothesis that the ancient Mayas traded body parts of the tapir (Kennedy-Thornton 2011).

In the most productive research period on the tapir, several themes have been poorly addressed, if at all. An illustrative example is parasitism. The presence of different genera of nematodes, protozoa, mites (Cruz-Aldán *et al.* 2006; Guzmán-Cornejo *et al.* 2006, 2011; Güiris-Andrade *et al.* 2009, 2018), and bacteria (Güiris-Andrade *et al.* 2007) has been reported. It is essential to continue exploring various aspects, as the tapir is susceptible not only to diseases such as enteritis and tuberculosis (Cubas 1996) but also to infectious diseases such as equine infectious anemia from the horse (Cruz-Aldán et *al.* 2006; Lepe-López *et al.* 2018). Only one study addressing the anatomy/morphology of the tapir has been published. The aim was to provide a tool to evaluate the body condition of wild tapirs from the comparison of individuals captured by camera-traps *versus* morphometric measurements and images of anatomical regions of captive tapirs (Pérez-Flores *et al.* 2016). Dumbá *et al.* (2018) support the hypothesis of interspecific variation for different species of living and extinct tapirs using geometric morphometry. Further analyses of intraspecific geometric morphometrics are needed for *T. bairdii*, involving sampling across its geographic range; this information will contribute to advance our knowledge about the evolutionary processes in the tapir. In addition, the possibility of phenotypic variations cannot be ruled out, as is the case of other mammals (Morteo *et al.* 2017; García-Mendoza *et al.* 2018).

Our survey did not find studies addressing ethological or physiological aspects as main research subjects, although behavioral data have been reported as secondary topics. For instance, in the Calakmul Biosphere Reserve, Reyna-Hurtado *et al.* (2016), have reported home-range size estimates from the monitoring of movement patterns of one tapir for over four and a half years; a maximum dispersal distance of 10.5 km and home-range areas from 4 to 24 km^2 have been estimated, which are larger than those reported in previous studies (*e. g.*, Foerster and Vaughan 2002). Sandoval *et al.* (2016), estimated the relative abundance of this species and evaluated the frequency of use of *aguadas* (water bodies formed by rain), concluding that these play a key role to determine the presence and abundance of the tapir in the Calakmul region. On the other hand, it is worth noting that there are no published studies on road-killed tapirs in México (Carrillo-Reyna *et al.* 2015b), and assessing whether it represents a new threat to the species is important, as is the case in Belize (Poot and Clevenger 2018).

The scarce or nil productivity in these areas can be explained by the low number of specialists in these academic fields and has been a general issue in scientific research of mammals (Guevara-Chumacero *et al.* 2001). In addition to the population decline of the tapir (Naranjo 2009; Naranjo *et al.* 2015), its elusive behavior with nocturnal and crepuscular habits, thriving in areas of difficult access (Naranjo and Cruz-Aldán 1998; Lira-Torres and Briones-Salas 2012) have been factors restraining its monitoring, tracking, and capture in the field.

The articles on conservation reviewed conclude that the main human activities with a negative effect on tapir populations are hunting, habitat loss, increasing human density, and extensive livestock (*e.g.*, Escamilla *et al.* 2000; Naranjo and Bodmer 2007; Urquiza-Hass *et al.* 2009; Lira-Torres and Briones-Salas 2011). According to the findings reported by Mendoza *et al.* (2013), the Mesoamerican Biological Corridor, which runs from southeast México (Campeche, Chiapas, Quintana Roo, Yucatan, and Tabasco) to Panama, may potentially play a prominent role in the conservation of the tapir habitat; however, there is an urgent need to implement management plans that reinforce and complement this conservation initiative. Another area also requiring special attention is Selva de Zoque (that stretches from the Sierra Atravesada in Oaxaca to the Sierra Madre de Chiapas), which is home to one of the largest populations of *T. bairdii* in Mesoamerica; however, this could be in danger of local extinction if indiscriminate hunting continues (Lira-Torres *et al.* 2012). The existence of corridors to enable the connectivity between populations of tapirs, like those in the Sierra Madre de Chiapas (De la Torre *et al.* 2018), are essential elements in the conservation strategies for the species. Innovative species distribution models have been recently used for assessing the distribution and conservation status of the tapir throughout its range in the continent (*e. g.*, Schank *et al.* 2017). In the near future, these models will surely involve mobility patterns that will produce increasingly accurate results, necessary for improved conservation management aimed at reducing the loss of species in ecosystems.

The tapir is listed in the NOM-059-SEMARNAT-2010 as "endangered of extinction", being a priority species for conservation (SEMARNAT 2010). The states of Chiapas, Oaxaca, Campeche, and Quintana Roo are the main reservoirs of tapir populations (Schank *et al.* 2015); this geographic region is critical to protect the species since it concentrates nearly 50 % of the total population worldwide (Naranjo 2009). It is essential to continue conducting long-term monitoring in this region, such as the one carried out in the Calakmul Biosphere Reserve, Campeche, which recorded the presence of the tapir in 14 *aguadas* between the years 2008-2010, involving a sampling effort of 3,470 trap-days, and recording 37.57 individuals/1,000 trap-nights (Pérez-Cortez *et al.* 2012).

It has been shown that Protected Areas are effective tools for the conservation of the tapir at regional and local levels (Porras-Murillo *et al.* 2011), as these were addressed in 43.0 % of the studies. Nonetheless, future planning and development of research projects should also include sites where the status of the species remains unknown, or areas where its current presence is uncertain (Veracruz, Tabasco, and Yucatan).

Another key strategy for the conservation of the tapir involves agreements with local communities. In this sense, an agreement was recently signed by 14 communities in Reserva La Frailescana, in the Sierra Madre de Chiapas, that prohibited tapir poaching in this area (De la Torre *et al.* 2018), which will surely contribute to conserving the species in the region.

The most important foreign journals in terms of number of published articles were Tapir Conservation (*n* = 8), Revista de Biología Tropical (*n* = 5), Tropical Conservation Science (*n* = 5), and Conservation Biology (*n* = 3). Most of these journals focus on conservation; the treatment of this topic as a priority is encouraging, given the current threatened status of the tapir (ranking 34 in priority for conservation among more than 4,000 species of mammals, according to the Zoological Society of London – Isaac *et al.* 2007). The preservation of Natural Protected Areas and the Mesoamerican Biological Corridor, together with the conservation of unprotected natural areas that harbor tapir populations, should be considered in conservation programs; in addition, improving the connectivity between these regions is a top priority for ensuring the preservation of tapir habitats in the country.

The information generated to date is essential to develop alternatives for improving the management of the habitat and natural populations of this valuable species. The conservation of the tapir requires awareness raising in rural populations, avoiding poaching and uncontrolled logging to the extent possible, as these factors continue impacting the population size of tapirs. Also evident is the need to increase the number of studies on disease and parasitism, and fill the current information gaps on basic aspects of the biology of the tapir, including physiology, genetics, anatomy, reproduction, and evolutionary history. The formation of a collaboration network and the continued generation of information on this species are essential in order to advance the objectives of the Program of Actions for Conservation (Cruz-Aldán *et al.* 2009), which in general terms aims to achieve the conservation and management of this emblematic species in Mexico.

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Literature cited

Aguilera, M., and A. Expósito, A. 2009. Cariotipos de *Tapirus terrestris* (Perissodactyla, Tapiridae) y *Pecari tajacu* (Artiodactyla, Tayassuidae) presentes en Venezuela. Memoria de la Fundación La Salle de Ciencias Naturales 69:7–18.

Alvarado, R. 1915. Sinonimia vulgar y científica de los mamíferos mexicanos. Boletín de la Dirección de Estudios Biológicos 1:11–41.

Álvarez del Toro, M. A. 1966. A note on the breeding of Baird´s tapir *Tapirus bairdii* at Tuxtla Gutierrez Zoo. International Zoo Yearbook 6:196–197.

Barrasa, G. S. 2013. Conocimiento y usos tradicionales de la fauna en dos comunidades campesinas de la Reserva de la Biósfera de la Encrucijada, Chiapas. Etnobiología 10:16–28.

Botello, F., O. Hernández, D. Reyes, V. Sánchez-Cordero, and J. Sánchez. 2014. Registros notables del tapir centroamericano (*Tapirus bairdii*) en la Sierra Mixe, Oaxaca, México. Revista Mexicana de Biodiversidad 85:995–999.

Brünnich, M. T. 1772. Zoologiae fundamenta praelectionibus academicis accomodata (Lat. et Dan). Transaction of the Linnean Society of London 7:241.

Camargo-Sanabria, A. A., and E. Mendoza. 2016. Interactions between terrestrial mammals and the fruits of two neotropical rainforest tree species. Acta Oecologica 73:45–52.

Carbajal-Borges, J. P., O. Godínez-Gómez, and E. Mendoza. 2014. Density, abundance and activity patterns of the endangered *Tapirus bairdii* in one of its last strongholds in southern Mexico. Tropical Conservation Science 7:100–114.

Carleton, M. D., R. D. Fisher, A. L. Gardner, L. K. Gordon, H. L. Kafka, C. A. Ludwig, and D. F. Schmidt. 1993. Twenty-year index to Journal of Mammalogy volumes 51-70 inclusive, 1970-1989. The American Society of Mammalogists. Allen Press, Lawrence, USA.

Carrillo-Reyna, N. L., R. Reyna-Hurtado, and B. Schmook. 2015a. Abundancia relativa y selección de hábitat de *Tapirus bairdii* en las reservas de Calakmul y Balam Kú, Campeche, México. Revista Mexicana de Biodiversidad 86:202–207.

Carrillo-Reyna, N. L., H. Weissenberger, and R. Reyna-Hurtado. 2015b. Distribución potencial del tapir centroamericano en la península de Yucatán. Therya 6:575–596.

Ceballos, G., and J. Arroyo-Cabrales. 2012. Lista actualizada de los mamíferos de México 2012. Revista Mexicana de Mastozoología 2:27–80.

Convención sobre el Comercio Internacional de Especies Amenazadas de Fauna y Flora Silvestres (CITES). 2018. http://www.cites.org/esp/index.shtml. Accessed April 12, 2018.

Contreras-Díaz, R. G., and M. Pérez-Lustre. 2008. Etnoecología de mamíferos silvestres y los zapotecos del municipio de Santiago, Camotlán, Oaxaca. Etnobiología 6:56–67.

Contreras-Moreno, F. M., M. G. Hidalgo-Mihart, L. A. Pérez-Solano, and Y. A. Vásquez-Maldonado. 2013. Nuevo registro de tapir centroamericano (*Tapirus bairdii*) atropellado en el noroeste del estado de Campeche, México. Tapir Conservation Newsletter 20:22–25.

Cruz-Aldán, E., I. Lira-Torres, D. M. Güiris-Andrade, D. Osorio Sarabia, and T. Quintero. 2006. Parásitos del tapir centroamericano *Tapirus bairdii* (Perissodactyla: Tapiridae) en Chiapas, México. Revista de Biología Tropical 54:445–450.

Cruz-Aldán, E., E. J. Naranjo, D. M. Güiris-Andrade, P. Oropeza, E. Rendón, E., and L. Araujo. 2009. Programa de acción para la conservación de la especie (PACE): tapir centroamericano (*Tapirus bairdii*). Secretaría de Medio Ambiente y Recursos Naturales. Ciudad de México, México.

Cubas, Z. S. 1996. Special challenges of maintaining wild animals in captivity in South America. Scientific Technical Review 15:267–82.

De la Torre, J. A., M. Rivero, G. Camacho, and L. A. Álvarez-Márquez. 2018. Assessing occupancy and habitat connectivity for Baird's tapir to establish conservation priorities in the Sierra Madre de Chiapas, Mexico. Journal for Nature Conservation 41:16–25.

Dumbá, L. C., R. P. Dutra, and M. A. Cozzuol. 2018. Cranial geometric morphometric analysis of the genus *Tapirus* (Mammalia, Perissodactyla). Journal of Mammalian Evolution 1–11.

Escamilla, A., M. Sanvicente, M. Sosa, and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, Mexico. Conservation Biology 14:1592–1601.

Fieber, F. X. 1844. Entomologische Monographien. Abhandlungen der k. böhmischen Gesellschaft der Wissenschaften 3:277–416.

Foerster, C., and C. Vaughan. 2002. Home Range, habitat Use, and activity of Baird's tapir in Costa Rica. Biotropica 34:423–437.

García, M., C. Jordan, G. O'Farril, C. Poot, N. Meyer, N. Estrada, R. Leonardo, E. Naranjo, Á. Simons, A. Herrera, C. Urgilés, C. Schank, L. Boshoff, and M. Ruiz-Galeano. 2016. *Tapirus bairdii*. The IUCN Red List of Threatened Species 2016: e.T21471A45173340. www.iunredlist.org. Accessed on 12 April, 2018.

García-Mendoza, D. F., C. López-González, Y. Hortelano-Moncada, R. López-Wilchis, and J. Ortega. 2018. Geographic cranial variation in *Peromyscus melanotis* (Rodentia: Cricetidae) is related to primary productivity. Journal of Mammalogy 99:898–905.

Gill, T. 1865. On a new generic. type of the family Tapiridae. Proceedings of the Academy of Natural Sciences of Philadelphia 17:183.

Groves, C., and P. Grubb. 2011. Ungulate Taxonomy. The Johns Hopkins University Press, Baltimore, USA.

Guevara-Chumacero, L. M., R. López-Wilchis, and V. Sánchez-Cordero. 2001. 105 años de investigación mastozoológica en México (1890-1995): una revisión de sus enfoques y tendencias. Acta Zoológica Mexicana 83:35–72.

Güiris-Andrade. D. M., A. Oceguera-Figueroa, D. Osorio-Sarabia, and M. E. Pérez-Escobar. 2018. *Tziminema unachi* n. gen., n. sp. (Nematoda: Strongylidae: Strongylinae) parasite of Baird's tapir *Tapirus bairdii* from Mexico. Journal of Helminthology 92:752–759.

Güiris-Andrade, D. M., N. M. Rojas-Hernández, A. V. Berovides, E. Cruz-Aldán, H. C. Chávez, J. A. Moguel-Acuña, M. E. Pérez-Escobar, and G. M. Palacios-Mendoza. 2009. Primer registro de *Probstmayria tapiri* (Nematoda: Atractidae) en *Tapirus bairdii* (Gill 1865) de la sierra madre del estado de Chiapas, México. Acta Zoológica Mexicana 25:83–91.

Güiris-Andrade. D. M., N. M. Rojas-Hernández, A. V. Berovides, E. Cruz-Aldán, H. C. Chávez, J. A. Moguel-Acuña, M. E Pérez-Escobar, and E. R. Pérez. 2007. Análisis de la microbiota bacteriana, aislada en heces de *Tapirus bairdii*, de la Sierra Madre de Chiapas, México. Tapir Conservation 16:15–19.

Guzmán-Cornejo, C., T. María-Pérez, S. Nava, and A. A. Guglielmone. 2006. First records of the ticks *Amblyomma calcaratum* and *A. pacae* (Acari: Ixodidae) parasitizing mammals of Mexico. Revista Mexicana de Biodiversidad 77:123–127.

Guzmán-Cornejo, C., R. G. Robbins, A. A. Guglielmone, G. Montiel-Parra, and T. María-Pérez. 2011. The *Amblyomma* (Acari; Ixodida: Ixodidae) of Mexico: identification Keys, distribution and hosts. Zootaxa 1922:16–38.

Guzmán-Soriano, D., O. G. Retana Guiascón, and J. D. Cú-Vizcarra. 2013. Lista de los mamíferos terrestres del estado de Campeche, México. Acta Zoológica Mexicana 29:105–128.

Holanda, E. C., and B. S. Ferrero. 2013. Revalorización del género *Tapirus* (Perissodactyla, Tapiridae): afinidades sistemáticas y filogenéticas de los tapires sudamericanos. Diario de la evolución de los mamíferos 20:33–44.

Isaac, N. J. B., S. T. Turvey, B. Collen, C. Waterman, and J. E. M. Baillie. 2007. Mammals on the EDGE: conservation priorities based on threat and phylogeny. PLOS ONE 2:e296.

Jorgenson, J. P. 1995. Maya subsistence hunters in Quintana Roo, Mexico. Oryx 29:49–57.

Kennedy-Thornton, E. 2011. Reconstructing ancient Maya animal trade through strontium isotope (87Sr /86Sr) analysis. Journal of Archaeological Science 38:3254–3263.

Lavariega, M. C., M. Briones-Salas, and C. Rodríguez. 2013. Registro de tapir centroamericano (*Tapirus bairdii*) con cámaras-trampa en la sierra Madre de Oaxaca, México. Revista Mexicana de Biodiversidad 84:1007–1011.

Lepe-López, M., R. García-Anleu, N. M. Fountain-Jones, G. Ponce, M. Gonzalez, and L. E. Escobar. 2018. Domestic horses within the Maya biosphere reserve: A possible threat to the Central American tapir (*Tapirus bairdii*). Caldasia 40:188–191.

Lira-Torres, I., and M. Briones-Salas. 2011. Impacto de la ganadería extensiva y cacería de subsistencia sobre la abundancia relativa de mamíferos en la selva Zoque, Oaxaca, México. Therya 2:217–244.

Lira-Torres, I., and M. Briones-Salas. 2012. Abundancia relativa y patrones de actividad de los mamíferos de los Chimalapas, Oaxaca, México. Acta Zoológica Mexicana 28:566–585.

Lira-Torres, I., M. Briones-Salas, F. R. Gómez de Anda, D. Ojeda-Ramírez, and A. Peláez-Acero. 2014. Uso y aprovechamiento de la fauna silvestre en la selva Zoque, México. Acta Zoológica Mexicana 30:74–90.

Lira-Torres, I., C. Galindo-Leal, and M. Briones-Salas. 2012. Mamíferos de la selva Zoque, México: riqueza, uso y conservación. Revista de Biología Tropical 60:781–797.

Lyra-Jorge, M. C., G. Ciocheti, V. R. Pivello, and S. T. Meirelles. 2008. Comparing methods for sampling large-and medium-sized mammals: camera traps and track plots. European Journal of Wildlife Research 54:739–744.

Mandujano, S. 2019. Analysis and trends of photo-trapping in Mexico: text mining in R. Therya 10:25–32.

March, I. J. 1987. Los lacandones de México y su relación con los mamíferos silvestres: Un estudio etnozoológico. Biotica 12:43–56.

March I. J. 1994. Situación actual del tapir en México. Centro de Investigaciones Ecológicas del Sureste, Serie Monográfica. San Cristóbal de las Casas, Chiapas, México.

March, I. J., and E. J. Naranjo. 2005. Tapir (*Tapirus bairdii*). Pp. 496–497 *in* Los mamíferos silvestres de México (Ceballos, G., y G. Oliva, eds.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, y Fondo de Cultura Económica. Distrito Federal, México.

Masson, M. A., and C. Peraza Lope. 2008. Animal use at the postclassic Maya center of Mayapan. Quaternary International 191:170–183.

Matola, S., A. D. Cuarón, and H. Rubio-Torgler. 1997. Conservation status and Action Plan of Baird's Tapir (*Tapirus bairdii*). Pp. 29–45 *in* Tapirs - Status Survey and Conservation Action Plan. (Brooks D., R. Bodmer y S. Matola, eds.). Gland, Switzerland and Cambridge, UK.

Mendoza, E., T. Fuller, H. Thomassen, W. Buermann, D. Ramirez, and T. B. Smith. 2013. A preliminary assessment of the effectiveness of the Mesoamerican Biological Corridor for protecting potential Baird's tapir (*Tapirus bairdii*) habitat in southern Mexico. Integrative Zoology 8:35–47.

Mendoza-Ramírez, E., and J. Carbajal-Borges. 2011. Avances y perspectivas para la conservación del tapir centroamericano en México. Biodiversitas 99:12–16.

Morteo, E., A. Rocha-Olivares, R. Morteo, and D. W. Weller. 2017. Phenotypic variation in dorsal fin morphology of coastal bottlenose dolphins (*Tursiops truncatus*) off Mexico. PeerJ 5:e3415.

Naranjo, E. J. 2009. Ecology and Conservation of Baird's tapir in Mexico. Tropical Conservation Science 2:140–158.

Naranjo, E. J., S. A. Amador-Alcalá, F. A. Falconi-Briones, and R. A. Reyna-Hurtado. 2015. Distribución, abundancia y amenazas a las poblaciones de tapir centroamericano (*Tapirus bairdii*) y pecarí de labios blancos (*Tayassu pecari*) en México. Therya 6:227–249.

Naranjo, E. J., and R. E. Bodmer. 2007. Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, México. Biological Conservation 138:412–420.

Naranjo, E. J., and E. Cruz-Aldán. 1998. Ecología del tapir en la Reserva de la Biósfera La Sepultura. Acta Zoológica Mexicana 73:111–125.

Nolasco, A. L., I. Lira-Torres, and G. Ceballos. 2007. Ampliación del área de distribución histórica del tapir (*Tapirus bairdii*) en el pacífico mexicano. Revista Mexicana de Mastozoología 11:91–94.

O´farrill, G., M. Galetti, and A. Campos-Arceiz. 2013. Frugivory and seed dispersal by tapirs: an insight on their ecological role. Integrative Zoology 8:4–17.

Palmer, T. S. 1903. Some new generic names of mammals. Science 17:873.

Peña-Azcona, I., R. M. Gómez-Ugalde, and M. Briones-Salas. 2015. Nuevos registros de tapir centroamericano *Tapirus bairdii* en el distrito de Tehuantepec, Oaxaca, México. Acta Zoológica Mexicana 31:120–122.

Pérez-Cortez, S., P. L. Enríquez, D. Sima-Panti, R. Reyna-Hurtado, and E. J. Naranjo. 2012. Influencia de la disponibilidad de agua en la presencia y abundancia de *Tapirus bairdii* en la selva de Calakmul, Campeche, México. Revista Mexicana de Biodiversidad 83:753–761.

Pérez-Flores, J., S. Calmé, and R. Reyna-Hurtado. 2016. Scoring body condition in wild Baird's tapir (*Tapirus bairdii*) using camera traps and opportunistic photographic material. Tropical Conservation Science 9:1–12.

Pérez-Irineo, G., and M. A. Santos. 2016. Abundance, herd size, activity pattern and occupancy of ungulates in Southeaster Mexico. Animal Biology 66:97–109.

Poot, C., and A. P. Clevenger. 2018. Reducing vehicle collisions with the Central American tapir in Central Belize District, Belize. Tropical Conservation Science 11:1–7.

Porras-Murillo, L. P., R. Sarmiento Aguilar, E. J. Naranjo, and L. Bernardo-Vázquez. 2011. Conservation effectiveness of protected areas in Mexico: effects on medium and large mammals at local and regional scales. International Journal of Biodiversity and Conservation 3:487–496.

Ramírez-Barajas, P. J., and E. J. Naranjo. 2007. La cacería de subsistencia en una comunidad de la zona maya, Quintana Roo, México. Etnobiología 5:65–85.

Ramírez-Pulido, J., M. C. Britton, A. Perdomo, and A. Castro-Campillo. 1986. Guía de los mamíferos de México, referencias hasta 1983. Universidad Autónoma Metropolitana. D. F. México.

Ramírez-Pulido, J., and A. Castro-Campillo. 1990. Bibliografía reciente de los mamíferos de México: 1984/1988. Universidad Autónoma Metropolitana. Ciudad de México, México.

Ramírez-Pulido, J., and A. Castro-Campillo. 1994. Bibliografía reciente de los mamíferos de México: 1989/1993. Universidad Autónoma Metropolitana. Ciudad de México. México.

Ramírez-Pulido, J., A. Castro-Campillo, M. A. Armella, and A. Salame-Méndez. 2000. Bibliografía reciente de los mamíferos de México: 1994-2000. Universidad Autónoma Metropolitana. Distrito Federal, México.

Ramírez-Pulido, J., N. González-Ruiz, G. Ameneyro, A. Castro-Campillo, and A. Salame-Méndez. 2017a. Bibliografía reciente de los mamíferos de México: 2000-2010. Universidad Autónoma Metropolitana. Ciudad de México, México.

Ramírez-Pulido, J., N. Gonzáles-Ruiz, and D. F. García-Mendoza. 2017b. References on mexican mammals: Origin and Impact. Therya 8:151–170.

Reyna-Hurtado, R., M. Sanvicente-López, J. Pérez-Flores, N. Carrillo-Reyna, and S. Calmé. 2016. Insights into the multiannual home range of a Baird's tapir (*Tapirus bairdii*) in the Maya Forest. Therya 7:271–276.

Reyna-Hurtado, R., and G. W. Tanner. 2005. Habitat preferences of an ungulate community in Calakmul Forest, Campeche, Mexico. Biotropica 37:676–685.

Rivero, M., and R. A. Medellín. 2015. Mamíferos de Chiapas. Revista Mexicana de Mastozoología. Nueva Época 5:23–38.

Rodas-Trejo, J., A. Estrada, A. J. Rau, and H. M. Morales. 2016. Uso local de los mamíferos no voladores entre los habitantes de Metzabok, el Tumbo y Laguna Colorada, Selva Lacandona, México. Revista Etnobiología 14:39–50.

Rovirosa, J. N. 1885. Apuntes para la zoología de Tabasco, vertebrados observados en el territorio de Macuspana. La Naturaleza 7:345–389.

Sandoval, S. E., R. Reyna-Hurtado, M. M. Briceño, and V. R. Cerda. 2016. Pond use and relative abundance of *Tapirus bairdii* in the Calakmul region, Campeche, Mexico. Therya 7:39–50.

Sánchez-Herrera, O., G. Téllez-Giron, R. A. Medellín, and G. Urbano-Vidales. 1986. New records of mammals from Quintana Roo, México. Mammalia 50:275–278.

Santos-Fita, D., E. J. Naranjo, and J. L. Rangel-Salazar. 2012. Wildlife uses and hunting patterns in rural communities of the Yucatan Peninsula, México. Journal of Ethnobiology and Ethnomedicine 8:1–17.

Secretaria de Medio ambiente y recursos naturales. 2010. Norma Oficial Mexicana NOM-059-SEMARNAT-2010. Protección ambiental -especies nativas de México de flora y fauna silvestres- categorías de riesgo y especificaciones para su inclusión, exclusión o cambio- lista de especies en riesgo. Secretaría del Medio Ambiente y Recursos Naturales. México. 30 December, 2010.

Schank, C. J., M. V. Cove, M. J. Kelly, E. Mendoza, G. O'Farrill, R. Reyna-Hurtado, N. Meyer, C. A. Jordan, J. F. González-Maya, D. J. Lizcano, R. Moreno, M. T. Dobbins, V. Montalvo, C. Sáenz-Bolaños, E. Carrillo-Jiménez, N. Estrada, J. C. Cruz-Díaz, J. Saenz, M. Spínola, A. Carver, J. Fort, C. K. Nielsen, F. Botello, G. Pozo Montuy, M. Rivero, J. A. de la Torre, E. Brenes-Mora, O. Godínez-Gómez, M. A. Wood, J. Gilbert, and J. A. Miller. 2017. Using a novel model approach to assess the distribution and conservation status of the endangered Baird's tapir. Diversity and Distributions 23:1459–1471.

Schank, C., E. Mendoza, M. J. García-Vettorazzi, M. V. Cove, C. A. Jordan, G. O' Farrill, N. Meyer, D. J. Lizcano, N. Estrada, C. Poot, and R. Leonardo. 2015. Integrating current range-wide occurrence data with species distribution models to map the potential distribution of Baird's Tapir. Tapir Conservation 24:15–25.

Silveira, L., A. T. Jacomo, and J. A. F. Diniz-Filho. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological Conservation 114:351–355.

Sumichrast, F. 1881. Enumeración de las especies de mamíferos, reptiles, batracios observados en la parte central y meridional de la república mexicana. La Naturaleza 5:199–214.

Tobler, M. W., S. E. Carrillo-Percastegui, R. L. Pitman, R. Mares, and G. Powell. 2008. An evaluation of camera traps for inventorying large and medium-sized terrestrial rainforest mammals. Animal Conservation 11:169–178.

Urquiza-Hass, T., C. A. Pérez, and M. P. Dolman. 2009. Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatan, Peninsula Mexico. Biological Conservation 142:134–148.

Zavala-Páramo, A. S., K. Oyama, E. Mendoza, M. G. Zavala-Páramo, J. Pollinger, and T. B. Smith. 2017. Genetic variability in captive individuals of the endangered species *Tapirus bairdii* in Mexico. Revista Mexicana de Biodiversidad 88:480–484.

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Appendix I

1. Alvarado, R. 1915. Sinonimia vulgar y científica de los mamíferos mexicanos. Boletín de la Dirección de Estudios Biológicos 1:11–41.
2. Álvarez-Castañeda, S. T., and N. González-Ruiz. 2018. Spanish and english vernacular names of mammals of North America. Therya 9:73–84.
3. Álvarez del Toro, M. A. 1966. A note on the breeding of Baird's tapir *Tapirus bairdii* at Tuxtla Gutierrez Zoo. International Zoo Yearbook 6:196–197.
4. Amador-Alcalá, S., E. J. Naranjo, and G. Jiménez-Ferrer. 2013. Wildlife predation on livestock and poultry: implications for predator conservation in the rainforest of south-east Mexico. Oryx 47:243–250.
5. Araujo-Absolon, B., V. Gallo, and L. S. Ávila. 2016. Distributional patterns of living ungulates (Mammalia: Cetartiodactyla and Perissodactyla) of the Neotropical region the South American transition zone and Andean region. Journal of South American Earth Sciences 71:63–70.
6. Arita, T. H., and G. Ceballos. 1997. Los mamíferos de México: distribución y estado de conservación. Revista Mexicana de Mastozoología 2:33–71.
7. Arita, T. H., F. Figueroa, A. Frisch, P. Rodríguez, and K. Santos del Prado. 1997. Geographical range size and the conservation of mexican mammals. Conservation Biology 11:92–100.
8. Arroyo-Cabrales, J., O. J. Polaco, T. Álvarez, and E. Johnson. 1996. New records of tapir from Northeastern Mexico. Current Research on the Pleistocene 13:93–95.
9. Arroyo-Cabrales, J., O. J. Polaco, E. Johnson, and J. Ferrusquía-Villafranca. 2010. A perspective on mammal biodiversity and zoogeography in the late Pleistocene of Mexico. Quaternary International 212:187–197.
10. Ávila-Nájera, D. M., E. J. Naranjo, B. Tigar, O. Villarreal, and G. D. M. Mendoza. 2018. An evaluation of the contemporary uses and cultural significance of mammals in Mexico. Ethnobiology Letters 9:124–135.
11. Baker, R. H., and J. K. Greer. 1960. Notes in Oaxaca mammals. Journal of Mammalogy 41:413–415.
12. Barrasa, G. S. 2013. Conocimiento -y usos tradicionales de la fauna en dos comunidades campesinas de la Reserva de la Biósfera de la Encrucijada, Chiapas. Etnobiología 10:16–28.
13. Bolaños-Citalán, J. E., and E. J. Naranjo. 2001. Abundancia, densidad y distribución de las poblaciones de ungulados en la cuenca del río Lacantún, Chiapas, México. Revista Mexicana de Mastozoología 5:45–57.
14. Botello, F., O. Hernández, D. Reyes, V. Sánchez-Cordero, and J. Sánchez. 2014. Registros notables del tapir centroamericano (*Tapirus bairdii*) en la Sierra Mixe, Oaxaca, México. Revista Mexicana de Biodiversidad 85:995–999.
15. Botello, F., A. G. Romero-Calderón, J. Sánchez-Hernández, O. Hernández, G. López-Villegas, and V. Sánchez-Cordero. 2017. Densidad poblacional del tapir centroamericano (*Tapirella bairdii*) en bosque mesófilo de montaña en Totontepec Villa de Morelos, Oaxaca, México. Revista Mexicana de Biodiversidad 88:918–923.
16. Briones-Salas, M., M. Cortés-Marcial, and M. C. Lavariega. 2015. Diversidad y distribución geográfica de los mamíferos terrestres del estado de Oaxaca, México. Revista Mexicana de Biodiversidad 86:685–710.
17. Buenrostro-Silva, A., M. Antonio-Gutiérrez, and J. García-Grajales. 2012. Mamíferos del Parque Nacional Lagunas de Chacahua y la tuza de Monroy, Oaxaca, México. Acta Zoológica Mexicana 28:56–72.
18. Camargo-Sanabria, A. A., and E. Mendoza. 2016. Interactions between terrestrial mammals and the fruits of two Neotropical rainforest tree species. Acta Oecologica 73:45–52.
19. Carbajal-Borges, J. P., O. Godínez-Gómez, and E. Mendoza. 2014. Density, abundance and activity patterns of the endangered *Tapirus bairdii* one of its last strongholds in Southern Mexico. Tropical Conservation Science 7:100–114.
20. Carrillo-Reyna, N. L., R. Reyna-Hurtado, and B. Schmook. 2015. Abundancia relativa y selección de hábitat de *Tapirus bairdii* en las reservas de Calakmul y Balam Kú, Campeche, México. Revista Mexicana de Biodiversidad 86:202–207.
21. Carrillo-Reyna, N. L., H. Weissenberger, and R. Reyna-Hurtado. 2015. Distribución potencial del tapir centroamericano en la península de Yucatán. Therya 6:575–596.
22. Ceballos, G., and J. Arroyo-Cabrales. 2012. Lista actualizada de los mamíferos de México 2012. Revista Mexicana de Mastozoología 2:27–80.
23. Ceballos, G., J. Arroyo-Cabrales, R. A. Medellín, and Y. Domínguez-Castellanos. 2005. Lista actualizada de los mamíferos de México. Revista Mexicana de Mastozoología 9:21–71.
24. Cervantes, F. A., A. Castro-Campillo, and J. Ramírez-Pulido. 1994. Mamíferos terrestres nativos de México. Anales del Instituto de Biología, Serie Zoología 65:177–190.
25. Chávez-Hernández, C., J. A. Moguel-Acuña, M. González-Galván, and D. M. Güiris-Andrade. 2011. Abundancia relativa de 3 ungulados en la Reserva de la Biósfera La Sepultura Chiapas, México. Therya 2:111–124.
26. Contreras-Díaz, R. G., and M. Pérez-Lustre. 2008. Etnoecología de mamíferos silvestres y los zapotecos del municipio de Santiago, Camotlán, Oaxaca. Etnobiología 6:56–67.
27. Contreras-Moreno, F. M., M. G. Hidalgo-Mihart, L. A. Pérez-Solano, and Y. A. Vásquez-Maldonado. 2013. Nuevo registro de tapir centroamericano (*Tapirus bairdii*) atropellado en el noroeste del estado de Campeche, México. Tapir Conservation Newsletter 20:22–25.
28. Cristóbal-Azkarate, J., J. C. Dunn, J. M. Day, and C. Amábile-Cuevas. 2014. Resistance to antibiotics of clinical relevance in the fecal microbiata of Mexican wildlife. Plos One 9:e107719.
29. Cruz-Aldán, E., I. Lira-Torres, D. M. Güiris-Andrade, D. Osorio Sarabia, and T. Quintero. 2006. Parásitos del tapir centroamericano *Tapirus bairdii* (Perissodactyla: Tapiridae) en Chiapas, México. Revista de Biología Tropical 54:445–450.
30. De la Torre, J. A., M. Rivero, G. Camacho, and L. A. Álvarez-Márquez. 2018. Assessing occupancy and habitat connectivity for Baird's tapir to establish conservation priorities in the Sierra Madre de Chiapas, Mexico. Journal for Nature Conservation 41:16–25.
31. Delfín-Alfonso, C. A., A. H. Hernández-Huerta, S. Macías-Sánchez, A. González-Gallina, and G. Alducin-Chávez. 2008. Adición a los registros de tapir centroamericano (*Tapirus bairdii*) en Oaxaca, México. Revista Mexicana de Biodiversidad 79:535–538.
32. Desantis, L. G. 2011. Stable isotope ecology of extant tapirs from the Americas. Biotropica 43:746–754.
33. Escalante, T., D. Espinoza, and J. J. Morrone. 2002. Patrones de distribución geográfica de los mamíferos terrestres de México. Acta Zoológica Mexicana 87:47–65.

34. Escamilla, A., M. Sanvicente, M. Sosa, and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, México. Conservation Biology 14:1592–1601.

35. Espinoza-Medinilla, E., A. Anzures-Dadda, and E. Cruz-Aldan. 1998. Mamíferos de la Reserva de la Biósfera El Triunfo, Chiapas. Revista Mexicana de Mastozoología 3:79–94.

36. Espinoza-Medinilla, E., E. Cruz-Aldán, I. Lira-Torres, and I. Sánchez. 2004. Mamíferos de la Reserva de la Biósfera La Sepultura, Chiapas, México. Revista de Biología Tropical 52:249–259.

37. Espinoza-Medinilla, E., E. Cruz-Aldán, I. Lira-Torres, and I. Sánchez. 2004. Mamíferos de la reserva de la Biósfera La Sepultura Chiapas, México. Revista Mexicana de Mastozoología 6:42–59.

38. Espinoza-Medinilla, E. E, E, J. Torres-Romero, and L. A. Tarango-Arámbula. 2018. Registros adicionales de mamíferos silvestres en el área de aprovechamiento forestal: Los Ocotones Chiapas, México. Agrociencia 52:553–562.

39. Ferrusquia-Villafranca, I., J. Arroyo-Cabrales, E. Martínez-Hernández, J. Gama-Castro, J. Ruiz-González, O. J. Polaco, and E. Johnson. 2010. Pleistocene mammals of Mexico: A critical a review of regional chronofaunas climate change response and biogeographic provinciality. Quaternary International 217:53–104.

40. Gallina, S., and S. Mandujano. 2009. Investigaciones sobre ecología, conservación y manejo de ungulados silvestres en México. Tropical Conservation Science 2:128–139.

41. García, M., F. Castillo, and R. Leonardo. 2011. Evaluación preliminar de la conectividad de hábitat para el tapir centroamericano (*Tapirus bairdii*) en Guatemala. Tapir Conservation 20:20–24.

42. García del Valle, G. Y., E. J. Naranjo, J. Caballero, C. Martorell, F. Ruan-Soto, and P. L. Enríquez. 2015. Cultural significance of wild mammals in Mayan and mestizo communities of the Lacandon Rainforest Chiapas, Mexico. Journal of Etnobiology and Ethnomedicine 11:36–41.

43. Garmendia, A., A. Arroyo-Rodríguez, E. Estrada, E. J. Naranjo, and K. E. Stoner. 2013. Landscape and patch attributes impacting medium-and large -sized terrestrial mammals in a fragmented rain forest. Journal of Tropical Ecology 29:331–344.

44. Genoways, H. H., and J. K. Jones. 1975. Annotated cheklist of mammals of the Yucatan Peninsula, Mexico. IV Carnivora, Sirenia, Perissodactyla, Artiodactyla. University of Nebraska State Museum 26:1–22.

45. Goldman, E. A. 1951. Biological investigations in Mexico. Smithsonian Miscellaneous Collections 115:1–476.

46. Goodwin, G. G. 1969. Mammals from the State of Oaxaca, Mexico, in the American Museum of Natural History. Bulletin of the American Museum of Natural History 141:1–269.

47. Guerra-Roa, M. M., E. J. Naranjo, F. Limón-Aguirre, and R. Mariaca-Méndez. 2004. Factores que intervienen en la regulación local de la cacería de subsistencia en dos comunidades de la selva Lacandona, Chiapas, México. Etnobiología 4:1–18.

48. Güiris-Andrade. D. M., A. Oceguera-Figueroa, D. Osorio-Sarabia, M. E. Pérez-Escobar, M. G. Nieto-López, N. M. Rojas-Hernández, and L. García-Prieto. 2018. *Tziminema unachi* n. gen., n. sp. (Nematoda: Strongylidae: Strongylinae) parasite of Baird's tapir *Tapirus bairdii* from México. Journal of Helminthology 92:752–759.

49. Güiris-Andrade, D. M., N. M. Rojas-Hernández, A. V. Berovides, E. Cruz-Aldán, H. C. Chávez, J. A. Moguel-Acuña, M. E. Pérez-Escobar, and G. M. Palacios-Mendoza. 2009. Primer registro de *Probstmayria tapiri* (Nematoda: Atractidae) en *Tapirus bairdii* (Gill 1865) de la Sierra Madre del estado de Chiapas, México. Acta Zoológica Mexicana 25:83–91.

50. Güiris-Andrade. D. M., N. M. Rojas-Hernández, A. V. Berovides, E. Cruz-Aldán, H. C. Chávez, J. A. Moguel-Acuña, M. E Pérez-Escobar, and E. R. Pérez. 2007. Análisis de la microbiota bacteriana, aislada en heces de *Tapirus bairdii*, de la Sierra Madre de Chiapas, México. Tapir Conservation 16:15–19.

51. Guzmán-Cornejo, C., T. María-Pérez, S. Nava, and A. A. Guglielmone. 2006. First records of the ticks *Amblyomma calcaratum* and *A. pacae* (Acari: Ixodidae) parasitizing mammals of México. Revista Mexicana de Biodiversidad 77:123–127.

52. Guzmán-Cornejo, C., R. G. Robbins, A. A. Guglielmone, G. Montiel-Parra, and T. María-Pérez. 2011. The *Amblyomma* (Acari; Ixodida: Ixodidae) of México: identification Keys, distribution and hosts. Zootaxa 1922:16–38.

53. Guzmán-Soriano, D., O. G. Retana Guiascón, and J. D. Cú-Vizcarra. 2013. Lista de los mamíferos terrestres del estado de Campeche, México. Acta Zoológica Mexicana 29:105–128.

54. Hershkovits, P. 1954. Mammals of northern Colombia, preliminary report no. 7: Tapir (Genus *Tapirus*) whit a systematic review of American species. Proceedings of the United States National Museum 103:465–996.

55. Hidalgo-Mihart, M., F. M. Contreras-Moreno, A. Jesús-de la Cruz, R. Juárez-López, y. Bravata de la Cruz, L. A. Pérez-Solano, C. Hernández-Lara, D. Friedeberg, D. Thornton, and J. M. Koller-González. 2017. Inventory of medium-sized and large mammals in the wetlands of Laguna de Términos and Pantanos de Centla, Mexico. Check List 13:711–726.

56. Jorgenson, J. P. 1995. Maya subsistence hunters in Quintana Roo, Mexico. Oryx 29:49–57.

57. Kennedy-Thornton, E. 2011. Reconstructing ancient Maya animal trade through strontium isotope (87Sr /86Sr) analysis. Journal of Archaeological Science 38:3254–3263.

58. Kitty, F. E. 2007. Assessing the impact of ancient Maya animal use. Journal for Nature Conservation 15:184–195.

59. Lavariega, M. C. 2018. An open-access platform for camera-trapping data. Biodiversity Informatics 13:1–10.

60. Lavariega, M. C., M. Briones-Salas, and R. M. Gómez-Ugalde. 2012. Mamíferos medianos y grandes de la sierra de Villa Alta, Oaxaca, México. Mastozoología Neotropical 19:225–241.

61. Lavariega, M. C., M. Briones-Salas, A. Mazas-Teodocio, and E. Duran-Medina. 2016. Ecology and local knowledge of the Baird's tapir (*Tapirella bairdii*) in the Sierra Madre de Oaxaca, Mexico. Integrative Zoology 11:361–374.

62. Lavariega, M. C., M. Briones-Salas, and C. Rodríguez. 2013. Registro de tapir centroamericano (*Tapirus bairdii*) con cámaras-trampa en la sierra Madre de Oaxaca, México. Revista Mexicana de Biodiversidad 84:1007–1011.

63. Lavariega, M. C., N. Martin-Regalado, A. G. Monroy-Gamboa, and M. Briones-Salas. 2017. Estado de conservación de los vertebrados terrestres de Oaxaca, México. Ecosistemas y Recursos Agropecuarios 4:135–146.

64. Lira-Torres, I. 2006. Abundancia, densidad, preferencia de hábitat y uso local de los vertebrados en Tuza de Monroy, Santiago Jimilitepec, Oaxaca. Revista Mexicana de Mastozoología 10:6–31.

65. Lira-Torres, I., and M. Briones-Salas. 2011. Impacto de la ganadería extensiva y cacería de subsistencia sobre la abundancia relativa de mamíferos en la selva Zoque, Oaxaca, México. Therya 2:217–244.

66. Lira-Torres, I., and M. Briones-Salas. 2012. Abundancia relativa y patrones de actividad de los mamíferos de los Chimalapas, Oaxaca, México. Acta Zoológica Mexicana 28:566–585.

67. Lira-Torres, I., M. Briones-Salas, F. R. Gómez de Anda, D. Ojeda-Ramírez, and A. Peláez-Acero. 2014. Uso y aprovechamiento de la fauna silvestre en la selva Zoque, México. Acta Zoológica Mexicana 30:74–90.

68. Lira-Torres, I., M. Briones-Salas, and G. Sánchez-Rojas. 2014. Abundancia relativa, estructura poblacional, preferencia de hábitat y patrones de actividad del tapir centroamericano *Tapirus bairdii* (Perissodactyla: Tapiridae), en la selva de los Chimalapas, Oaxaca, México. Revista de Biología Tropical 62:1407–1419.

69. Lira-Torres, I., C. Galindo-Leal, and M. Briones-Salas. 2012. Mamíferos de la selva Zoque, México: riqueza, uso y conservación. Revista de Biología Tropical 60:781–797.

70. Lira-Torres, I., A. L. Mora, M. A. Camacho-Escobar, and R. E. Galindo-Aguilar. 2005. Mastofauna del cerro de la Tuza, Oaxaca. Revista Mexicana de Mastozoología 9:6–20.

71. Lira-Torres, I., E. J. Naranjo, D. M. Güiris-Andrade, and E. Cruz-Aldán. 2004. Ecología de *Tapirus bairdii* (Perissodactyla: Tapiridae) en la Reserva de la Biósfera el Triunfo (Polígono 1), Chiapas, México. Acta Zoológica Mexicana 20:1–21.

72. Lira-Torres, I., E. J. Naranjo, D. Hilliard, M. A. Camacho-Escobar, M. A. Villa, and M. A. Reyes-Chargoy. 2006. Status and conservation of Baird's tapir in Oaxaca, Mexico. Tapir Conservation 15:21–28.

73. Lira-Torres, I., E. J. Naranjo, and M. A. Reyes-Chargoy. 2005. Ampliación del área de distribución de *Tapirus bairdii*, Gill 1865 (Perissodactyla: Tapiridae) en Oaxaca, México. Acta Zoológica Mexicana 21:107–110.

74. Lorenzo-Monterrubio, C., J. Bolaños-Citalán, E. Sántiz, and D. Navarrete. 2017. Diversidad y conservación de los mamíferos terrestres de Chiapas, México. Revista Mexicana de Biodiversidad 88:735–754.

75. Lorenzo-Monterrubio, C., L. Cruz-Lara, E. J. Naranjo, and F. Barragán-Torres. 2007. Uso y conservación de mamíferos silvestres en una comunidad de las cañadas de la selva Lacandona, Chiapas, México. Etnobiología 5:99–107.

76. March, I. J. 1987. Los lacandones de México y su relación con los mamíferos silvestres: Un estudio etnozoológico. Biotica 12:43–56.

77. Martin-Regalado, C. N., M. C. Lavariega, and R. M. Gómez-Ugalde. 2013. Registro histórico del Tapir centroamericano *Tapirus bairdii* en el Istmo de Tehuantepec, Oaxaca, México. Acta Zoológica Mexicana 29:454–557.

78. Masson, M. A., and C. Peraza Lope. 2008. Animal use at the postclassic Maya center of Mayapan. Quaternary International 191:170–183.

79. Medellín, R. A. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, México. Conservation Biology 8:780–799.

80. Medellín, R. A., and M. Equihua. 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, México. Journal of Applied Ecology 35:13–23.

81. Melo, L. P. F., E. Martínez-Salas, J. Benitez-Malvido, and G. Ceballos. 2010. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. Journal of Tropical Ecology 26:35–43.

82. Mendoza, E., T. L. Fuller, H. C. Thomassen, W. Buermann, D. Ramírez-Mejía, and T. B. Smith. 2013. A preliminary assessment of the effectiveness of the Mesoamerican Biological Corridor for protecting potential Baird's Tapir (*Tapirus bairdii*) habitat in Southern Mexico. Integrative Zoology 8:34–46.

83. Naranjo, E. J. 2009. Ecology and conservation of Baird's tapir in México. Tropical Conservation Science 2:140–158.

84. Naranjo, E. J. 2018. Baird's Tapir ecology and conservation in Mexico revisited. Tropical Conservation Science 11:1–4.

85. Naranjo, E. J., S. A. Amador-Alcalá, F. A. Falconi-Briones, and R. A. Reyna-Hurtado. 2015. Distribución, abundancia y amenazas a las poblaciones de tapir centroamericano (*Tapirus bairdii*) y pecarí de labios blancos (*Tayassu pecari*) en México. Therya 6:227–249.

86. Naranjo, E. J., and R. E. Bodmer. 2002. Population ecology and conservation of Baird's tapir (*Tapirus bairdii*) in the Lacandon Forest, Mexico. Tapir Conservation 11:25–33.

87. Naranjo, E. J., and R. E. Bodmer. 2007. Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, México. Biological Conservation 138:412–420.

88. Naranjo, E. J, and E. Cruz-Aldán. 1998. Ecología del Tapir (*Tapirus bairdii*) en la Reserva de la Biósfera La Sepultura, Chiapas, México. Acta Zoológica Mexicana 73:111–125.

89. Naranjo, E. J., M. M. Guerra, R. E. Bodmer, and J. E. Bolaños. 2004. Subsistence hunting by three ethnic groups of the Lacandon forest Mexico. Journal of Ethnobiology 24:233–253.

90. Nolasco, A. L., I. Lira-Torres, and G. Ceballos. 2007. Ampliación del área de distribución histórica del Tapir (*Tapirus bairdii*) en el pacífico mexicano. Revista Mexicana de Mastozoología 11:91–94.

91. Núñez-Antonio, G., M. Mendoza, A. Contreras-Cristán, E. Gutiérrez-Peña, and E. Mendoza. 2018. Bayesian nonparametric inference for the overlap of daily animal activity patterns. Environmental and Ecological Statistics 25:471–494.

92. O'farril, G., S. Calmé, and A. Gonzalez. 2006. *Manikara zapota*: A new record of a species dispersed by tapirs. Tapir Conservation 15:32–35.

93. O'farrill, G., S. Calmé, R. Sengupta, and A. Gonzalez. 2012. Effective dispersal of large seeds by Baird's tapir: a large-scale field experiment. Journal of Tropical Ecology 28:119–122.

94. O'farrill, G., A. C. Chapman, and A. Gonzalez. 2011. Origin and deposition sites influence seed germination and seedling survival of *Manikara zapota*: implications for long-distance, animal-mediated seed dispersal. Seed Science Research 21:305–313.

95. O'farrill, G., M. Galetti, and A. Campos-Arceiz. 2013. Frugivory and seed dispersal by tapirs: an insight on their ecological role. Integrative Zoology 8:4–17.

96. O'farrill, G., S. K. Gauthier, B. Rayfield, O. Bodin, S. Calmé, R. Sengupta, and A. Gonzalez. 2014. The potential connectivity of waterhole networks and the effectiveness of a protected area under various drought scenarios. Plos One 9:e95049.

97. Osorio-López, D., R. Mariaca-Méndez, D. Santos-Fita, D. A. Nazar Beutelspacher, and L. Huicochea Gómez. 2017. Cacería y cosmovisión en una comunidad Ayuuk en San José, el

Paraíso, Oaxaca, México. Revista Etnobiología 15:54–66.

98. Peña-Azcona, I., M. R. Gómez-Ugalde, and M. Briones-Salas. 2015. Nuevos registros de tapir centroamericano *Tapirus bairdii* en el Distrito de Tehuantepec, Oaxaca, México. Acta Zoológica Mexicana 31:120–122.
99. Pérez-Cortez, S., P. L. Enríquez, D. Sima-Panti, R. Reyna-Hurtado, and E. J. Naranjo. 2012. Influencia de la disponibilidad de agua en la presencia y abundancia de *Tapirus bairdii* en la selva de Calakmul, Campeche, México. Revista Mexicana de Biodiversidad 83:753–761.
100. Pérez-Cortez, S., and E. S. Matus-Pérez. 2010. El tapir *Tapirus bairdii* en la región sureste del área de protección de flora y fauna Bala'an Ka'ax, Quintana Roo, México. Therya 1:137–144.
101. Pérez-Flores, J., S. Calmé, and R. Reyna-Hurtado. 2016. Scoring body condition in wild Baird's tapir (*Tapirus bairdii*) using camera traps and opportunistic photographic material. Tropical Conservation Science 9:1–12.
102. Pérez Flores, J., and D. González Solís. 2018. First record of the spinose ear tick (*Otobius megnini*) on the Baird's tapir. International Journal of Acarology 44:189–191.
103. Pérez-Irineo, G., and M. A. Santos. 2016. Abundance, herd size, activity pattern and occupancy of ungulates in Southeaster Mexico. Animal Biology 66:97–109.
104. Porras-Murillo, P. L., L. Bernardo-Vázquez, R. Sarmiento Aguilar, D. Douterlungne, and D. Valenzuela-Galván. 2016. Influence of human activities on some medium and large-sized mammals richness and abundance in the Lacandon Rainforest. Journal for Nature Conservation 34:75–81.
105. Porras-Murillo, P. L., R. Sarmiento Aguilar, E. J. Naranjo, and L. Bernardo-Vázquez. 2011. Conservation effectiveness of protected areas in Mexico: Effects on medium and large mammals at local and regional scales. Journal of Biodiversity and Conservation 3:487–496.
106. Pozo de la Tijera, C., and J. E. Escobedo-Cabrera. 1999. Mamíferos terrestres de la Reserva de la Biósfera de Sian Ka'an, Quintana Roo, México. Revista de Biología Tropical 47:251–262.
107. Ramírez-Barajas, J. P., and E. J. Naranjo. 2007. La cacería de subsistencia en una comunidad de la zona Maya, Quintana Roo, México. Etnobiología 5:65–85.
108. Ramírez-Pulido, J., J. Arroyo-Cabrales, and A. Castro-Campillo. 2005. Estado actual y relación nomenclatural de los mamíferos terrestres de México. Acta Zoológica Mexicana 21:21–82.
109. Reinhard, J. 1872. Et bidrag til Kundskab om aberne i Mexico og centralamerika. Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobenhavn 3:150–158.
110. Retana, G. O., and C. Lorenzo. 2002. Lista de los mamíferos terrestres de Chiapas: endemismo y estado de conservación. Acta Zoológica Mexicana 85:25–49.
111. Reyna-Hurtado, R., L. M. Sanvicente, F. J. Pérez, R. N. Carrillo, and S. Calmé. 2016. Insights into the multiannual home range of a Baird's tapir (*Tapirus bairdii*) in the Maya Forest. Therya 7:271–276.
112. Reyna-Hurtado, R., and W. G. Tanner. 2005. Habitat preferences of ungulates in hunted and non-hunted areas in the Calakmul Forest, Campeche, México. Biotropica 37:676–685.
113. Reyna-Hurtado, R., and W. G. Tanner. 2007. Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (Southern México). Biodiversity and Conservation 16:743–756.
114. Riechers-Pérez, A. 2004. Análisis mastofaunístico de la zona sujeta a conservación ecológica Laguna Bélgica, Chiapas, México. Anales del Instituto de Biología, Serie Zoología 75:363–382.
115. Rivero, M., and R. A. Medellín. 2015. Mamíferos de Chiapas. Revista Mexicana de Mastozoología 5:24–38.
116. Rodas-Trejo, J., A. Estrada, A. J. Rau, and H. M. Morales. 2016. Uso local de los mamíferos no voladores entre los habitantes de Metzabok, el Tumbo y Laguna Colorada, Selva Lacandona, México. Revista Etnobiología 14:39–50.
117. Romero-Castañón, S., B. G. Ferguson, D. Güiris-Andrade, D. González, S. López, A. Paredes, and M. Weber. 2008. Comparative parasitology of wild and domestic ungulates in the Selva Lacandona, Chiapas, México. Comparative Parasitology 75:115–126.
118. Rovirosa, J. N. 1885. Apuntes para la zoología de Tabasco, vertebrados observados en el territorio de Macuspana. La Naturaleza 7:345–389.
119. Sánchez-Cordero, V., F. Botello, J. J. Flores-Martínez, R. A. Gómez-Rodríguez, L. Guevara, G. Gutiérrez-Granados, and A. Rodríguez-Moreno. 2014. Biodiversidad de Chordata (Mammalia) en México. Revista Mexicana de Biodiversidad 85:496–504.
120. Sánchez-Herrera, O., G. Téllez-Girón. R. A. Medellín, and G. Urbano-Vidales. 1986. New records of mammals from Quintana Roo, México. Mammalia 50:275–278.
121. Sánchez-Núñez, E., H. E. Ortiz-Nájera, and E. Arellano-Nicolás. 2011. Abundancia y uso de hábitat del tapir (*Tapirus bairdii*) en Frontera Corozal, Selva Lacandona, Chiapas, México. Tapir Conservation 20:25–29.
122. Sánchez-Trocino, M. 2011. Nuevas recomendaciones para el manejo nutricional del tapir en cautiverio. Tapir Conservation 20:6–13.
123. Sandoval, S. E., R. Reyna-Hurtado, M. M. Briceño, and V. R. Cerda. 2016. Pond use and relative abundance of *Tapirus bairdii* in the Calakmul region, Campeche, Mexico. Therya 7:39–50.
124. Santos-Fita, D., E. J. Naranjo, and J. L. Rangel-Salazar. 2012. Wildlife uses and hunting patterns in rural communities of the Yucatan Peninsula, Mexico. Journal of Ethnobiology and Ethnomedicine 8:1–17.
125. Schank, C. J., M. V. Cove, M. J. Kelly, E. mendoza, G. O'farrill, R. Reyna-Hurtado, N. Meyer, Ch. A. Jordan, J. F. González-Maya, D. J. Lizcano, R. Moreno, M. T. Dobbins, V. Montalvo, C. Sáenz-Bolaños, E. Carillo-Jiménez, N. Estrada, J. C. Cruz Díaz, J. Saenz, M. Spínola, A. Carver, J. Fort, C. K. Nielsen, F. Botello, G. Pozo Montuy, M. Rivero, J. A. de la Torre, E. Brenes-Mora, O. Godínez-Gómez, M A. Wood, J. Gilbert, and J. A. Miller. 2017. Using a novel model approach to assess the distribution and conservation status of the endangered Baird's tapir. Diversity and Distributions 23:1459–1471.
126. Schank, C., E. Mendoza, M. G. Vettorazzi, M. V. Cove, A. Jordan, G. O´ farril, J. D. Lizcano, N. Estrada, C. Poot, and C. Leonardo. 2015. Integrating current range-wid occurrence data with species distribution models to map the potential distribution of Baird's tapir. Tapir Conservation 24:15–25.

127. Sosa-Escalante, J. E., S. Hernández-Betancourt, J. M. Pech-Canché, M. C. MacSwiney, and R. Díaz-Gamboa. 2014. Los mamíferos del estado de Yucatán. Revista Mexicana de Mastozoología 4:40–59.
128. Sosa-Escalante, J. E., J. M. Pech-Canché, M. C. MacSwiney, and S. Hernández-Betancourt. 2013. Mamíferos terrestres de la península de Yucatán, México: riqueza, endemismo y riesgo. Revista Mexicana de Biodiversidad 84:949–969.
129. Sumichrast, F. 1881. Enumeración de las especies de mamíferos, reptiles, batracios observados en la parte central y meridional de la república mexicana. La Naturaleza 5:199–214.
130. Tejeda-Cruz, C., E. J. Naranjo, A. D. Cuarón, H. Perales, and J. L. Cruz-Burguete. 2009. Habitat use of wild ungulates in fragmented landscapes of the Lacandon Forest, Southern Mexico. Mammalia 73:211–219.
131. Urquiza-Haas, T., C. A. Pérez, and M. P. Dolman. 2009. Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatan, Peninsula Mexico. Biological Conservation 142:134–148.
132. Vargas-Contreras, J. A., G. Escalona-Segura, J. Arroyo-Cabrales, M. R. Calderón, I. L. Sosa, and R. Reyna-Hurtado. 2008. Especies prioritarias de vertebrados terrestres en Calakmul, Campeche. Vertebrata Mexicana 16:11–32.
133. Vargas-Contreras, J. A., J. Escalona-Segura, D. Guzmán-Soriano, O. G. Retana-Guiascón, H. Zarza, and G. Ceballos. 2014. Los mamíferos del estado de Campeche. Revista Mexicana de Mastozoología 4:60–74.
134. Vázquez, D. E., and T. A. Arita. 2010. The Yucatan peninsula biogeographical history 65 million years in the making. Ecography 33:212–219.
135. Webb, R., and R. H. Baker. 1969. Vertebrados terrestres del suroeste de Oaxaca. Anales del Instituto de Biología, Serie Zoología 40:139–152.
136. Zavala-Páramo, A. S., K. Oyama, E. Mendoza, M. G. Zavala-Páramo, J. Pollinger, and T. B. Smith. 2017. Variabilidad genética en individuos en cautiverio en México de la especie en peligro de extinción *Tapirus bairdii*. Revista Mexicana de Biodiversidad 88:480–484.

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Corrigendum

The ecological niche of *Echinococcus multilocularis* in North America: understanding biotic and abiotic determinants of parasite distribution with new records in New Mexico and Maryland, United States

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Said:

Results

New records of Echinococcus multilocularis *in the Nearctic*. We include here a new record of a specimen of *E. multilocularis* found in the liver of an individual of ***M. ochrogaster*** collected by Gregory E. Glass in a grassy area in Mount Pleasant Park, Baltimore, Maryland in August, 1985. The parasite cyst in the liver was identified as *E. multilocularis* by Everett L. Schiller (see Methods, above). This represents the first record of *E. multilocularis* for Maryland and the most eastern record for the species in North America.

must said:

Results

New records of Echinococcus multilocularis *in the Nearctic*. We include here a new record of a specimen of *E. multilocularis* found in the liver of an individual of ***M. pennsylvanicus*** collected by Gregory E. Glass in a grassy area in Mount Pleasant Park, Baltimore, Maryland in August, 1985. The parasite cyst in the liver was identified as *E. multilocularis* by Everett L. Schiller (see Methods, above). This represents the first record of *E. multilocularis* for Maryland and the most eastern record for the species in North America.