Therya

Volumen 8 Número 3 Septiembre 2017

AMMAC

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La Portada

Mapaches (*Procyon lotor grinnelli)* es uno de los carnívoros más abundantes en Norte América, pero sobre todo se puede encontrar con frecuencia asociado a asentamientos humanos. En este caso son tres juveniles de que descansan durante un día de verano en una palmera de dátiles. La palmera les ofrece protección, sombra y alimento. Por estar en la parte alta hay buena circulación de aire que ayuda a amortiguar las altas temperaturas. Está es una subespecie endémica del sur de la Península de Baja California. Fotografía tomada en una palmera en la explanada central del Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California, México (Fotografía de Sergio Ticul Álvarez Castañeda).

Nuestro logo "Ozomatli"

El nombre de "Ozomatli" proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo 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."

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DERECHOS DE AUTOR Y DERECHOS CONEXOS, año 8, No. 3, Septiembre-Diciembre del 2017, 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 2017.

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

THERYA y sus perspectivas

THERYA surgió como el órgano de difusión académica de la Asociación Mexicana de Mastozoología A. C. (AMMAC) en un formato de revista electrónica, pero con estructuración de una revista impresa. La evolución de la revista ha sido notable a través de éstos cinco años de desarrollo, debido en gran medida al acelerado desarrollo de la tecnología y a que se busca que THERYA en que cada publicación se distinga por el contenido y calidad logrando una difusión exitosa en el conocimiento de la mastozoología.

Acorde a la tendencia internacional de las revistas con formato electrónico, a partir de 2018, el volumen 9 de la revista THERYA será completamente electrónico, desde el planteamiento hasta la ejecución, éste cambio será trasparente para los autores y los editores asociados. Con esta estrategia se pretende que las contribuciones efectuados por los distintos autores se procesen de forma continua, en lugar de que sea a intervalos cuatrimestrales, como es el caso actual. A partir de éste volumen los diferentes artículos se publicarán en el momento en que estén terminados, eliminándose la separación actual entre artículos, notas y revisiones. Para conservar la legalidad en el ISSN cada cuatro meses se compilaran los artículos publicados en un fascículo. Con esta iniciativa se pretende que los artículos sean publicados lo más pronto posible y con ello se incremente el tiempo de vida de los artículos para la indexación de los mismos.

Otro cambio sustancial que sufrirá nuestra revista es la incorporación al formato XML +JATS (Journal Article Tag Suites) [DTD, Document Type Definition], que es un metalenguaje genérico que tiene como resultado un texto plano, de fácil indexación de la información y rápida extracción. En esencia es un archivo sin formato con claves de programación que puede ser utilizado por diferentes visualizadores. Por lo que la revista presentará los artículos en los formatos XML, HTML y PDF. Los tres formatos estarán disponibles a partir de las publicaciones 2015, tratando que en el trascurso del 2018 se tengan los tres formatos para todas las contribuciones. El formato XML permite ingresar de manera más rápida a la "Web of Science", sobre todo en relación a las citas cruzadas, aspecto importante para la determinación de los índices bibliométricos.

Con relación al Identificador de objeto digital, comúnmente citado como DOI (Digital Object Identifier), a partir del 2018 se asignará al artículo y a cada una de las figuras. Por lo que la información de las figuras será por sí misma citable y utilizable, así como registrada. Este avance también implica una serie de cambios e incrementos en los costos de DOI, pero el resultado final muy bien vale el esfuerzo.

Se espera que próximamente sea liberada una versión más reciente de la plataforma OJS 2.4, la cual es complicada y en cierto momento difícil de utilizar. La nueva plataforma (OJS 3.0) promete un uso más amigable, que en conjunto con la plataforma "Lents" hará la página más interactiva rápida y compatible con las necesidades internacionales de intercambio de información, así como la operación de programas tipo "software/spiders" que rastrean automáticamente el contenido de la revista (también conocido como minería de texto). En este momento estamos trabajando en coordinación con Scielo México, en dos aspectos importantes: capacitación al menos una persona en la generación de los archivos XML (debido a que los costos con las empresas privadas son elevados), y localización de un proveedor certificado que instale y diseñe las nuevas plataformas. Por lo que se deberá tener próximamente algunos cursos de capacitación y vinculación, para hacer la trasferencia de información de THERYA más ágil hacia Scielo y la "Web of Sciences".

La denominación de minería de datos es un tema de importancia en el ámbito de la publicación, ya que se están generando cambios significativos en el manejo de las revistas, por lo que THERYA, debe migrara a esas nuevas plataformas y con ello ser una mejor revista científica. En el ámbito de la publicación internacional, cada vez es más fuerte el domino de la editorial Elsevier, en todos los aspectos asociados a la elaboración, publicación y difusión de los contenidos científicos, es probable que las licencias actualmente utilizadas en edición y publicación tengan costos que puedan repercutir directamente en el costo de producción y difusión de las revistas, lo que impactará negativamente el presupuesto asignado a THERYA.

En el aspecto de distribución, el directorio de socios 2017 se ha incrementado de manera significativa. Por diferentes medios se han conseguido direcciones de investigadores asociados a la mastozoología del mundo, por lo que la lista de lectores de la revista cerrará en poco más de 3,000 de todos los continentes. Se pretende incrementar el número de lectores en al menos un 50% más en el 2018, aunado a la publicación de los artículos en inglés debe de catapultar la difusión de THERYA y sobre todo las contribuciones que produce.

El programa de traducción implementado en THERYA ha sido utilizado además para la revisión y apoyo de los artículos que son enviados en inglés, con la finalidad de que sean más fluidos y comprensibles, durante 2017 todos los artículos fueron publicados en idioma inglés, lo que ha sido un éxito. Esto es porque los autores escriben en este idioma o por el programa de becas a la traducción que la AMMAC a través de THERYA ha implementado. Este programa también recibe fondos del Consejo Nacional de Ciencia y Tecnología, pero sobre todo se destaca el apoyo de los autores, que en varias ocasiones ellos mismos pagan el costo de traducción para que el fondo de becas se destine a estudiantes o quién lo requiera.

THERYA es uno de los proyectos bandera de la Asociación Mexicana de Mastozoología A. C. y en sus ejes rectores esta la difusión del conocimiento de los mamíferos y el posicionamiento de la asociación como punto de referencia internacional. THERYA ha crecido significativamente desde su origen y ha tratado de incorporar los avances tecnológicos posibles. En estos años y en los próximos van a existir fuertes modificaciones en el área de las publicaciones científicas y más en las digitales, es por ello que estamos trabajando en mantenernos actualizados y a la vanguardia técnica, sin descuidar la calidad académica.

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Editorial

Holotypes of recently described species of Mexican mammals: where should they be?

Contrary to conventional perception, hundreds of mammalian species continue to be discovered and described around the world (Patterson 2000; Reeder *et al.* 2007). Many newly discovered species have been found by field biologists in previously poorly surveyed areas (Ceballos and Ehrlich 2009). Hence, fieldwork and scientific collecting are responsible for many discoveries, especially in tropical and semitropical regions (Patterson 2002; Reeder *et al.* 2007; Ceballos and Ehrlich 2009). Given that evidence indicates that this trend will continue (Patterson 2002), mammalogists must have knowledge of all laws and regulations that pertain to scientific collecting of mammals (Sikes *et al.* 2016), including those cases where specimens collected in the field are subsequently recognized as new species.

In Mexico, activities of scientific collecting of specimens of wild flora and fauna (not only mammals) have been regulated particularly by the *Norma Oficial Mexicana* NOM-126-ECOL-2000. This regulation establishes, for example, specifications to obtain permits issued by the Mexican government for scientific collecting in the country. In addition, the NOM-126-ECOL-2000 also regulates cases where specimens collected in Mexico are later designated as the name-bearing type of a nominal species (*i. e.,* the holotype):

"5.11. *En caso de que el titular de una autorización de colecta científica identifique que el material biológico colectado incluye una nueva especie depositará al menos el holotipo en alguna institución mexicana o colección científica registrada mexicana y dará aviso de ello a la Secretaría [de Medio Ambiente y Recursos Naturales, SEMARNAT]".*

"5.11. In case the holder of a scientific collecting permit identifies that the biological material collected includes a new species, it shall deposit at least the holotype in a Mexican institution or Mexican scientific collection and shall notify the Secretary thereof."

It should be noted that NOM-126-ECOL-2000 is mandatory for all those persons who carry out activities of scientific collecting in Mexican territory and entered into force in April 2001 (*i. e.,* 60 days after the publication of this regulation). Consequently, all specimens collected in Mexico after April 2001 (using collecting permits provided by the Secretary), which are later designated as holotypes of a new species, should be housed in Mexican institutions. As an example, I describe the case of a species of rodent recently described from Nayarit, Mexico. In 2011, some individuals of pocket gophers were collected in Sierra del Nayar. Later, genetic analyses revealed that those individuals represent a previously unrecognized species, *Thomomys nayarensis*. An adult male was designated as the holotype (Louisiana State University Museum of Natural Science, LSUMZ 36794, Mathis *et al.* 2013). Given that pocket gophers were collected using a collecting permit issued by the Secretary, the holotype of *T. nayarensis* was properly sent from LSUMZ to a Mexican institution (Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México, CNMA 45745).

Here, I specifically highlight the specification 5.11 in the NOM-126-ECOL-2000 because fieldwork is far from over and many more mammalian species await discovery in Mexico (Sánchez-Cordero *et al.* 2014). The discovery of at least four species of Mexican mammals whose holotypes were collected during this century support this idea. Unfortunately, this regulation is unclear in the case of someone other than the holder of the collecting permit can later designate as holotype a specimen, which should be clarified in future modifications of this regulation. Despite this, I hope that this letter serves as an invitation to students, investigators, and field technicians to become familiar with Mexican official regulations regarding the discovery and description of new species in the country.

Lázaro Guevara

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Availability of two species of fruits and their influence on the social structure of *Tayassu pecari* and Dicotyles *tajacu*

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The white-lipped peccary (*Tayassu peccari*) and the collared peccary (*Dicotyles tajacu*) are social ungulates that contribute to tropical forest maintenance, molding the composition of tree species through herbivory and seed dispersal and predation. The fruits of zapote (*Manilkara zapota*) and ramon (*Brosimum alicastrum*) trees are important items in the diet of both peccary species. The objective of this study was to assess the relationship between the abundance of fruits of *Manilkara zapota* and *Brosimum alicastrum* and its relationship with the number of newborns in groups of both peccary species during the rainy and dry season in a tropical forest in the Yucatan Peninsula, Mexico. Peccary groups were monitored with ten camera trap stations and through direct observations during the dry season of 2014 (February-May) and the rainy season of 2015 (June - September). To estimate fruit availability, five transects (2 km long) were set at random in forested areas. Several 2-m^2 tree plots were established in each transect to obtain a fruit abundance index. Peccary group size and number of newborns in each season were correlated with fruit abundance. In both species, group size was significantly larger in the dry vs. rainy season ($P < 0.001$). Offspring were proportionally more abundant during the dry season ($P < 0.001$). Fruits of *M. zapota* were more abundant in the dry season and reached the peak availability in May ($P < 0.001$). Fruits of *B. alicastrum* were more abundant in the rainy season, reaching the peak availability in September ($P < 0.001$). For both peccary species, the highest numbers of newborns in individual groups may be attributable, although not specifically, to the abundance of *M. zapota* fruits during the dry season. In this sense, the groups of both peccary species may depend on the seasonal availability of food of key species, such as the fruits of *M. zapota* during the dry season. Based on these results, preserving areas in good conservation status is deemed important, as well as reducing tree clearing of species such as zapote and ramon at the study site.

El pecarí de labios blancos (*Tayassu pecari*) y el pecarí de collar (*Dicotyles tajacu*) son especies de ungulados sociales que contribuyen en al mantenimiento y composición arbórea de los bosques del trópico a través de los procesos de herbivoría, dispersión y depredación de semillas. Los frutos del zapote (*Manilkara zapota*) y ramón (*Brosimum alicastrum*) son especies arbóreas importantes en la dieta de ambas especies. El objetivo de este estudio fue evaluar la relación entre la abundancia de frutos de *Manilkara zapota* y *Brosimum alicastrum* y su relación con el número de crías en grupos de pecarí de ambas especies durante la estación seca y húmeda de una selva tropical en la Península de Yucatán, México. Se realizó un monitoreo con 10 estaciones de cámaras trampa y observaciones directas de grupos de pecaríes durante la estación seca de 2014 (febrero-mayo) y la estación de lluvias de 2015 (Junio-Septiembre). Para estimar la disponibilidad de frutos, se recorrieron cinco transectos de 2 km de longitud establecidos al azar en la zona forestal. En cada uno de los transectos se establecieron 15 parcelas de 2 m^2 para obtener un índice de abundancia de frutos. El tamaño de grupo y número de crías en ambas estaciones se correlacionó con la abundancia de frutos. En ambas especies el tamaño de grupos fue mayor significativamente en la estación seca que lluvias ($P < 0.001$). La proporción del número de crías fue mayor significativamente durante los meses de la estación seca ($P < 0.\ 001$). Los frutos de *M. zapota* fueron también más abundantes en la época de secas alcanzado su mayor disponibilidad en mayo ($P < 0.\ 001$). Los frutos de *B. alicastrum* fueron más abundantes en los meses de la estación lluviosa alcanzando su mayor disponibilidad en septiembre ($P < 0.001$). Para ambas especies de pecaríes, el mayor número de crías presentes en los grupos puede ser atribuible a la abundancia de frutos de *M. zapota* durante la estación seca. En este sentido, los grupos de ambas especies de pecaríes podrían llegar a depender de la disponibilidad de alimento estacional de especies clave como los frutos de *M. zapota* durante la estación seca. Con base a estos resultados se considera importante conservar áreas en buen estado de conservación, y reducir la tala de especies como el zapote y el ramón en el sitio de estudio.

Key words: *Brosimum alicastrum*; Calakmul; fruit index availability; *Manilkara zapota*; ramon; newborns; peccary; zapote.

Introduction

Frugivorous or omnivorous mammals are a key component in tropical forest ecosystems, since they serve as seed dispersers or predators (O' Farrill *et al.* 2006, 2011; Peres *et al.* 2016). This contributes to the regeneration of forests, by structuring their composition (Peres *et al.* 2016). However, the reduction of tropical forests through changes in land use affects the diversity and availability of fruits and prolongs the natural periods of scarcity (Tabarelli *et al.* 2004; Keuroghlian and Eaton 2008). As a result, some mammal species migrate to other areas in search of fruits, while others are able to make adjustments to their diets (Altricher et al. 2001; Keuroghlian 2003; Keuroghlian and Eaton 2008). In peccary species (*Tayassu pecari* and *Dicotyles tajacu*), it has been pointed out that the breeding, gestation and birth periods are related to the nutritional quality of food resources and the primary productivity of key fruit species available in the environment (Altricher *et al.* 2001; Keuroghlian *et al.* 2004; López *et al.* 2006).

The white-lipped peccary (*T. pecari*) and the collared peccary (*D. tajacu*), belonging to the Family Tayassuidae, are important social ungulate species in tropical ecosystems. Both species contribute to the maintenance and composition of trees in forests through herbivory and seed dispersal and predation (Bodmer 1991; March 1993; Beck 2005, 2006; Keuroghlian and Eaton 2009; Beck *et al.* 2010). Peccaries are an essential food resource for the inhabitants of rural and indigenous communities throughout their distribution range (Weber 2000; Altrichter and Boaglio 2004; Desbiez *et al.* 2009; Reyna-Hurtado *et al.* 2010; Briceño-Méndez *et al.* 2011; Keuroghlian *et al.* 2013; Naranjo *et al.* 2015). Wild populations of both species are currently under an intense pressure by hunting and loss of habitat (Reyna-Hurtado 2009; Góngora *et al.* 2011; Altrichter *et al.* 2012; Keuroghlian *et al.* 2013; Naranjo *et al.* 2015; Briceño-Méndez *et al.* 2016).

The Calakmul region, in the state of Campeche, is one of the main remnants of tropical forest in Mexico and includes the Calakmul Biosphere Reserve (RBC; 7,231 km^2). Various activities such as the production of charcoal and the use of natural resources have led the accelerated deforestation and fragmentation of the primary vegetation, in addition to poaching of wild species. A site adjacent to this reserve is the ejido Nuevo Becal, stretching across 520 km^2, where the loss of habitat and poaching of wild species prevail (Briceño-Méndez *et al.* 2016). The forests of the Calakmul region include two tree species that are key in the diet of peccaries (Reyna-Hurtado 2007; Perez-Cortez and Reyna-Hurtado 2008): the ramon, *Brosimum alicastrum,* and the zapote, *Manilkara zapota*. These species account for 57.10 % of the total species producing fruits consumed by peccaries on the ground (Briceño-Méndez *et al.* 2014). Given the importance of their fruits as a source of food, these species have also been described as part of the diet of primates such as the spider monkey, *Ateles geoffroyi,* and the howler monkey, *Alouatta pigra* (Hernández-Sarabia 2013), as well as of other ungulates such as the tapir, *Tapirus bairdii* (O' Farrill *et al.* 2006, 2011) and the temazates deer, *Mazama temama* and *M. pandora* (Weber 2008; González-Zamora *et al.* 2009).

An investigation conducted in RBC has revealed that the availability of ramon is related to the surface area used by *T. pecari* (Reyna-Hurtado 2007). However, it is unknown whether the proportion of newborns in groups of peccaries varies according to the season. This could be related to the availability of *M. zapota* and *B. alicastrum* fruits, documented as essential seasonal food items in the peccary diet (Reyna-Hurtado 2007, Perez-Cortez and Reyna-Hurtado 2008). Unveiling the relationship between the availability of key fruit species such as ramón and zapote and the composition in the social structure of peccaries is essential for management and conservation plans. The objectives of this study were two. Quantify the seasonal availability and variations of *M. zapota* and *B. alicastrum* fruits in ejido Nuevo Becal. Evaluate the social structure of *T. pecari* and *D. tajacu.* Specifically, it was assessed whether there are fluctuations in the number of newborns of the two peccary species according to the rainy and dry seasons matching the availability of *M. zapota* and *B. alicastrum* fruits.

Materials and Methods

Area of study. The site is located in the southeastern portion of the Calakmul region, at ejido Nuevo Becal (18.6920° N, -89.2511° W; 20.9450° N, -89.6433° N; 21.2811° N, -89.6650° W; 21.0161° N, -89.8772° W), in the municipality of Calakmul, Campeche, Mexico. This area is adjacent to RBC, a protected area of tropical forest in Mexico with an extension of 7,231 km^2 (Figure 1).

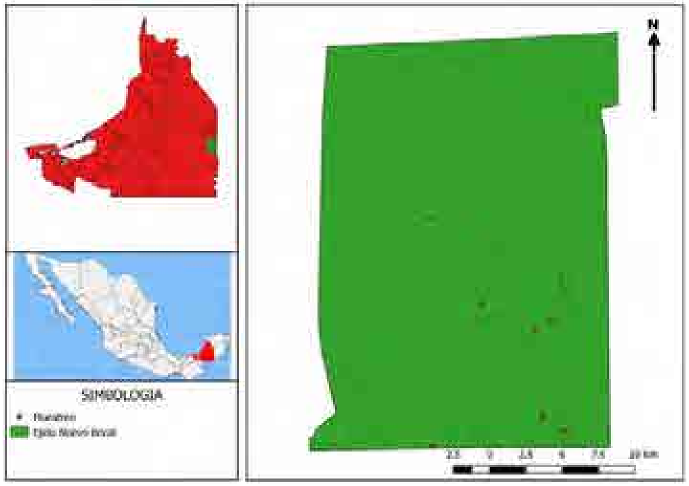

Figure 1. Location of the study area and sampling points at ejido Nuevo Becal, Calakmul, Campeche Mexico.

The ejido comprises an area of 520 km^2. The types of vegetation include subdeciduous forest, floodplain forests, dry forests, and secondary vegetation (Pennington and Sarukhan 1998). Elevation ranges between 100 to 380 masl. The predominant climate is warm sub-humid with summer rainfall and with less than 60 mm of precipitation in the driest month; the mean annual temperature is 25 °C (García-Gil 2003).

Social structure. During the 2014 dry season (February-May) and the 2015 rainy season (June-September) peccary groups were monitored in 10 camera-trap stations (Reconyx PC800 Hyperfire Professional IRTM y PC600 Hyperfire Pro White FlashTM; Reconyx, Inc., Holmen, Wisconsin, USA) on a permanent basis in sites near water bodies, roads and trails selected at random in the ejido section covered by natural vegetation. Camera traps were placed at a height not exceeding 50 cm from ground level and with a separation of 1.5 km, covering an area of approximately 112 km^2 delimited by the external location of traps (Figure 1). The period of photographic records was set to operate 24 hours with trigger intervals of one second. This interval allows counting all individuals passing in a line or grouped (Maffei *et al.* 2002; Figure 2). Records were considered independent after 24 hours between one record and another, or when more than one individual appeared in the photograph. The position of each station was georeferenced with a Garmin 62s® GPS. For each picture obtained, the time and date was recorded (Lira Torres *et al.* 2014). The age structure of each group was examined and evaluated by obtaining the individuals into three categories, adults, juveniles, and young, according to size and pelage coloration; then, the percentage of each category was calculated (Reyna-Hurtado *et al.* 2010). The average number of hatchlings was estimated and counted during the month of birth, either in the February-May dry season or in the June-September rainy season (Figure 2).

Figure 2. Group of white-lipped peccaries (*Tayassu pecari*) photographed with camera traps. Blue arrows indicate five newborns of white-lipped peccaries in ejido Nuevo Becal, Calakmul, Campeche, Mexico. © Marcos Briceño-Méndez.

Fruit Availability. To estimate fruit abundance, five 2 km-long transects were established, which were determined randomly in forested areas, avoiding a radius of at least 7 km from the village. Transects were visited once a month in order to derive a fruit abundance index (Altrichter *et al.* 2001). The method consists in finding a fruit on the ground, then locating the source tree where the fruit came from, provided it is located at a perpendicular distance not exceeding 5 m from the center line of the transect. Once the source tree was located, all the fruits found within a quadrat of 2 m^2 under the canopy were recorded.

Data Analysis. To evaluate the differences in the size of the groups of both species between the dry and rainy seasons, and the proportion newborns, Mann-Whitney tests were conducted. We used the availability index of each fruit species and the monthly variation was evaluated using a Pearson's Chi^2 non-parametric test. In all cases, statistical tests considered a significance level of $P < 0.05$. The variables analyzed were the proportion of newborns per group, species, fruit availability index, dry season and rainy season. A simple correlation analysis was conducted between fruit availability index values and number of newborns. The statistical analyzes were performed in SPSS v. 17.0.

Results

The sampling effort was 2,420 trap-nights (302.5 trap-nights per month) and a total of 86 records of *Tayassu pecari* were obtained, resulting in a total of 1,026 individuals counted. For *Dicotyles tajacu,* 76 records were obtained, leading to a total of 33 individuals counted.

A higher number of groups and individuals of both species were observed in the dry season (*T. pecari* 53.8; *D. tajacu* 46.2) versus the rainy season (*T. Pecari* 33.1; *D. tajacu* 30.1). Similarly, the average size (mean ± SD) of groups for both species was significantly higher in the dry season (*T. pecari* 23 ± 5.3, $n = 53$; *D. tajacu* 4.9 ± 2.6, $n = 46$; $U = 0.01$).

Social structure. The age structure of *T. pecari* in the dry season was determined based on 886 individuals, with the following proportions: adults, 76.3 %; sub-adults, 9.4 %; and newborns 14.3 %. In the rainy season, the age structure on the basis of 140 adult individuals was 66.6 %, sub-adults 26.2 % and 7.2 % newborns. The age structure of *D. tajacu* in the dry season ($n = 46$) was: adults, 76.0 %; sub-adults, 7.7 %; and newborns, 16.3 %; the percentages of these age classes for the rainy season ($n = 17$) are 93.0 %, 6.0 % and 1.0 %, respectively. In both species, the proportion of offspring was significantly higher during the months of the dry season *T. pecari* ($X^2 = 27.14$, d. f. = 7, $P < 0.001$) and *D. tajacu* ($X^2 = 34.0$, d. f. = 5, $P < 0.001$, Figure 3, 4).

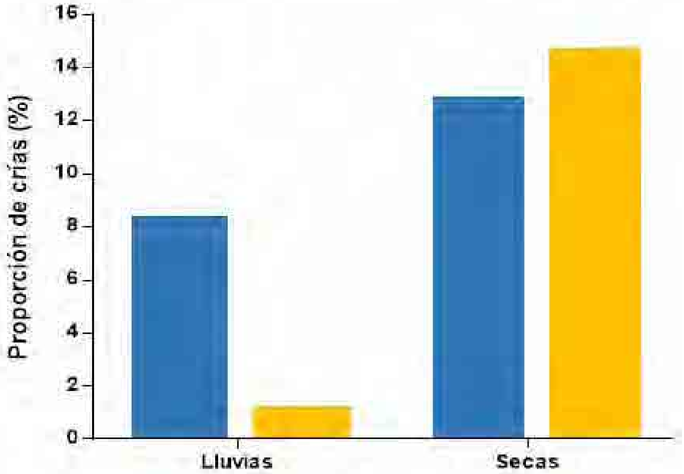

Figure 3. Proportion of the number of newborns in groups of white-lipped peccary (*Tayassu pecari*) (blue bars), and collared peccary (*Dicotyles tajacu)* (yellow bars) recorded during the 2014 dry season and 2015 rainy season in ejido Nuevo Becal, Calakmul, Campeche, Mexico.

Fruit Availability. The walkthrough of 80 km of transects ($n = 5$) in 15 plots per season (dry and rainy seasons) yielded a total of 329 fruits of *B. alicastrum* and 267 of *M. zapota*. The fruit availability index for ramon was variable, peaking in September ($X^2 = 39.00$, d. f. = 3, $P < 0.001$, Figure 4). The availability of *M. zapota* fruits was significantly higher in the dry season and varied throughout this season, reaching its peak availability in May ($X^2 = 33.14$, d. f. = 7, $P < 0.001$, Figure 4). The proportion of offspring in both peccary species was significantly correlated with the availability of *M. zapota* fruits during the dry season (*T. pecari*, $r^2 = 0.43$; *D. tajacu*, $r^2 = 0.46$).

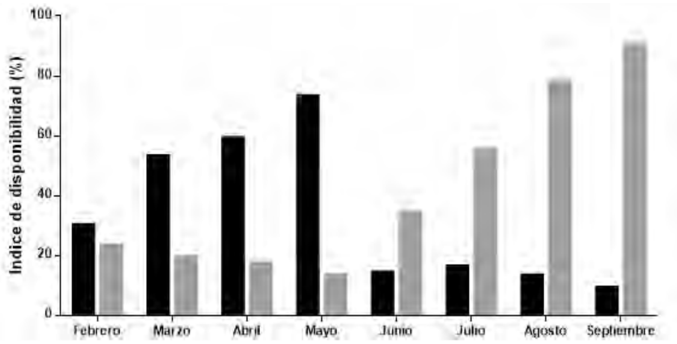

Figure 4. Availability of fruits of zapote *Manilkara zapota* (black bars) and ramon *Brosimun alicastrum* (gray bars) during the dry season (Feb-May 2014) and rainy season (June-Sept 2015) in ejido Nuevo Becal, Calakmul, Campeche, Mexico.

Discussion and Conclusions

Social Structure and Fruit Availability. In both species, the social structure within groups showed a higher proportion of adults. This is consistent with the findings reported in the Calakmul Biosphere Reserve (Reyna-Hurtado *et al.* 2010), in areas subjected to hunting pressure in ejido Nuevo Becal for the white-lipped peccary (Briceño-Méndez *et al.* 2016), and for the collared peccary in the Chimalapas, Oaxaca (Pérez Irineo and Santos Moreno 2016).

The proportion of offspring was higher in the dry season than in the rainy season for both species; this is consistent with the findings reported for white-lipped peccaries in the Calakmul Biosphere Reserve (Reyna-Hurtado *et al.* 2010). However, for the collared peccary these findings are contrary to those reported in French Guiana, where the proportion of offspring is higher in the rainy season (Henry 1994).

Although there are no data on the nutritional value of the fruit species for peccaries, it has been reported that both ramon and zapote play a key role in the seasonal diet of both species (Perez-Cortez and Reyna-Hurtado 2008). This fact may explain the relationship between the presence of a higher number of offspring of both species during the dry season and the fruit abundance index for zapote fruits. Two plant species (*Ficus* spp. and *Licania operculipetata*) have been mentoned as fructifying during periods of shortage of other food items, and are related to the breeding season and number of offspring, which affects the size and composition of groups in both peccary species, although not necessarily being the factor that could be driving the increase in group size in both species (Altricher *et al.* 2001; Keuroghlian 2004). Another possible explanation in relation to the number of offspring during the greater availability of fruits, is that these may be providing postpartum mothers nutrient needs for young infants (Lopez *et al.* 2006).

The fruits of *Pouteria campechiana*, *Ampelocera hottlei, Cratavea tapia*, *Byrsonima crassifolia*, *Citrullus vulgaris*, *Talisia olivaeformis* and *Metopium brownei* are identified as potential food items for peccaries in the region, being a supplement to their diet (Perez-Cortez and Reyna-Hurtado 2008). The production of these fruits is variable; they are usually available for very short periods of time (Reyna-Hurtado 2007; Briceño-Méndez *et al.* 2014), contrary to the zapote and ramon fruits, which are available throught a season. For example, zapote can reach peak fruit availability in the dry season during May, while ramon reaches its highest fruit abundance index values in the rainy season (Reyna-Hurtado 2007; Briceño-Méndez *et al.* 2014).

Both peccary species are benefited by the availability and search for these important dietary resources in heterogeneous environments during well-marked seasons of the year in the study site. In addition, peccaries can consume a wide variety of food types available in the landscape, and even modify their diet (Keuroghlian 2004; Beck 2005; Keuroghlian and Eaton 2008; Fernandes *et al.* 2013).

Our results reveal the relationship between the primary productivity of fruit species and the size and social composition in groups of both peccary species in the tropics (Altrichter *et al.* 2001). There are other factors related to group composition and size; for example, it has been documented that in the rainy season white-lipped peccaries consume small amounts of animal food items, including invertebrates and some fish species (Fernandes *et al.* 2013; Reyna-Hurtado 2007). Water availability, the state of conservation of the habitat and the hunting pressure have been considered as factors that strongly influence group size in peccaries inhabiting the Calakmul region (Reyna-Hurtado *et al.* 2015).

Conservation Perspectives. An important factor for the conservation of peccaries is the reduction and/or control of zapote tree logging, which is an important resource in the study site. The plant species consumed by peccaries are also relevant for other endangered species such as the spider monkey (*Ateles geoffroyi*), howler monkey (*Alouatta pigra*), tapir (*Tapirus bairdii*), temazate deer (*Mazama temama* and *Mazama pandora*), all of which depend to a large extent on these fruit species to supplement their diet (O' Farrill *et al.* 2006, 2011; Weber 2008; González-Zamora *et al.* 2009).

The ejido Nuevo Becal is home to endangered species and includes habitats in good state of conservation (Briceño Méndez *et al.* 2017). However, human activities such as hunting and loss of habitat still prevail (Escamilla *et al.* 2000; Santos Fita *et al.* 2012; Briceño-Méndez *et al.* 2014). Therefore, it is imperative to introduce feasible subsistence strategies to the local community (Montiel *et al.* 1999), particularly for being a rural community that is connected to the Calakmul Biosphere Reserve.

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Abundance, density and habitat use of lowland paca (*Cuniculus paca*, Rodentia: Cuniculidae) in the Lacandon Rainforest, Chiapas, Mexico

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In this study, the effect of relevant variables (availability of food and cavities, competition, predation, and hunting pressure) on the relative abundance and population density of the spotted lowland paca (*Cuniculus paca*) was assessed. In addition, habitat use of this species at three sites with different land use regime (Montes Azules Biosphere Reserve, community reserves, and anthropic sites) in the Lacandon Rainforest, Chiapas, Mexico was analysed. From the perspective of the source-sink systems, it was predicted that pacas selectively would use the habitat with higher food and cavity availability (source habitats), where higher densities were expected. Twelve transects were located in three sites with different land use regimes, where food availability and potential cavities used by pacas were assessed. Along these transects, 4 camera-traps were deployed every 200 meters to estimate the relative abundance of pacas and their potential competitors and predators. Photo-captured individuals were identified to estimate population density and seasonal variation in habitat use. Generalized linear models (GLM) were constructed to analyse the effects of several variables on paca abundance and density. A relative abundance of 0.05 and 0.08 paca photographs/100 camera-days were recorded in the dry and the rainy season, respectively. A density of 54 pacas/km^2 was estimated in both seasons. The availability of cavities was the only variable that showed a significant effect on paca density ($P = 0.04$ for the dry season, and $P = 0.006$ for the rainy season). Community reserves were used in the dry season more than expected from their availability in the study area ($x^2 = 28.8$; $P = 0.0001$). In the rainy season, all three sites were used by paca in proportion to their availability. Our results suggest that the cavities used as refuges by pacas drive their population dynamics, and constitute a key habitat resource for them in the study area. We propose that the Ejidal Reserve and Montes Azules Biosphere Reserve may be source habitats supporting higher paca densities and greater availability of adequate cavities to protect adults and their offspring. On the other hand, areas transformed into croplands and grasslands for livestock production would represent sink habitats with lower paca densities, less availability of adequate cavities, and absence of offspring. The long-term conservation and habitat management of pacas in transformed landscapes will probably rely on the distribution and connectivity between and within the different habitat types available in the study area.

En este estudio, se evaluó el efecto de variables (disponibilidad de alimento y cavidades, competencia, depredación y presión de cacería) sobre la abundancia y densidad poblacional de *Cuniculus paca*. Se determinó el uso de hábitat de esta especie en tres sitios con distinto uso de suelo (Reserva de la Biosfera Montes Azules, reservas ejidales y sitios antrópicos) en la Selva Lacandona, Chiapas, México. Desde la perspectiva de los sistemas fuente-sumidero, se propuso que *C. paca* utilizaría selectivamente el hábitat con mayor disponibilidad de alimento y cavidades (hábitats fuente), donde presentaría mayor densidad poblacional. Se realizaron 12 transectos en tres sitios con diferente uso de suelo, donde se estimó la disponibilidad de alimento y cavidades potenciales para *C. paca*. A lo largo de éstos, se colocaron 4 trampas-cámara (cada 200 m) para determinar la abundancia relativa del tepezcuintle, sus competidores potenciales y depredadores. Por medio de la identificación de individuos a través de las foto capturas, se obtuvo la densidad, misma con la que se determinó el uso de hábitat por medio de pruebas de chi-cuadrada e intervalos de Bonferroni. Se construyeron modelos lineales generalizados para analizar el efecto de diversas variables sobre la abundancia y densidad de *C. paca*. En temporada seca se registraron 0.05 fotografías/100 días-cámara y en la de lluvias 0.08 fotografías/100 días-cámara, además de una densidad de 54 individuos/km^2 en ambas temporadas. La disponibilidad de cavidades fue la única variable que mostró efecto significativo sobre las densidades del tepezcuintle ($P = 0.04$ temporada seca, $P = 0.006$ temporada de lluvias). Las reservas ejidales en temporada seca, se utilizaron más de lo esperado con base en su disponibilidad ($X^2 = 28.8$; $P = 0.0001$). En la temporada lluviosa, los tres hábitats fueron utilizados en proporción a su disponibilidad. Los resultados sugieren que las cavidades utilizadas como refugio estarían direccionando las dinámicas poblacionales del tepezcuintle y son un recurso clave dentro de los requerimientos de hábitat de esta especie en la zona de estudio. Se propone que la Reserva Ejidal y la Reserva de la Biósfera Montes Azules podrían considerarse hábitat fuente, ya que ambos contaron con mayor disponibilidad de cavidades adecuadas para la protección de los adultos y sus crías, mayores densidades, además de la presencia de crías tomada como indicador del éxito reproductivo. Por su parte, el hábitat antrópico sería sumidero, por tener menor disponibilidad de cavidades adecuadas, menor densidad poblacional y ausencia de crías. La conservación a largo plazo y manejo de hábitat del tepezcuintle en paisajes transformados, dependerán en gran parte de la distribución y conectividad entre y dentro de los diferentes tipos de hábitats.

Keywords: cavities; food; hunting pressure; rodent; source-sink.

Introduction

Natural and man-made disturbance often result in discontinuous landscapes and shifts in land cover (Cuarón 2000) representing habitat loss and habitat fragmentation for many wildlife species. These are among the primary drivers of population declines and species extinctions (Caughley *et al.* 1996). Once a habitat gets fragmented, its resource availability shifts, producing variations in animal population densities and distributions (Pulliam and Danielson 1991). This situation may be analyzed using the source-sink system approach, where source fragments provide most of the essential resources for the survival and reproductive success of wildlife species. Therefore, natality rates usually are higher than mortality rates in source habitat, which may get to the point of reaching carrying capacity in such fragments. Surplus individuals may migrate into lower quality (sink) fragments, where mortality overcomes natality. Consequently, local populations in sink habitats rarely persist in the long term without immigration from source fragments (Pulliam and Danielson 1991; Hanski and Simberloff 1997).

A population may be distributed across source and sink fragments, giving place to subpopulations with different growth, natality, and mortality rates depending on available resources (*e.g.* food and shelter; Pulliam and Danielson 1991). When the resources within a habitat are used with higher frequency in relation to their availability, selectivity is inferred (Johnson 1980). The use of resources and their importance for a particular species vary as function of a series of factors that should be recognized to better evaluate the habitat requirements of animal species (Chalfoun and Martin 2007), especially those affected by habitat loss and unregulated hunting, as it happens to the spotted lowland paca *Cuniculus paca* (Cuarón 2000; Urquiza-Haas *et al.* 2009). The paca is a solitary and nocturnal Neotropical rodent. Pacas rest during the day inside underground cavities where their newborns are raised and kept apart from both predators and adverse weather conditions. This mammal occurs in a wide array of ecosystems such as different kinds of tropical forests, montane forests, mangroves, and riverine vegetation (Pérez 1992). Pacas feed mainly on fruit, contributing to seed dispersal and seed predation of many tropical tree species (Pérez 1992; Dubost and Henry 2006). Pacas are also important food items for predators such as jaguars (*Panthera onca*), pumas (*Puma concolor*), and ocelots (*Leopardus pardalis*; Pérez 1992; Eisenberg and Redford 2000). Besides, the paca has always been a primary prey for Neotropical subsistence hunters, who regard this species as very relevant in cultural and nutritional terms (Weitlaner 1997; Corona and Enríquez 2011). Currently, this mammal is heavily pursued by hunters in every place it can be found, particularly in southern Mexico, where it is often the most hunted and consumed wild mammal due to the relative easiness of its capture and the excellent taste of its meat (Naranjo *et al.* 2004; Centeno and Arriaga 2010).

The paca is relatively tolerant to habitat fragmentation and land use change in the tropical forests of Mexico (Cuarón 2000; Gallina *et al.* 2012). During the second half of the twentieth century, over 50% of the original cover of the Lacandon Rainforest, Chiapas, Mexico has been lost (Vásquez-Sánchez and Ramos 1992). Habitat loss and fragmentation coupled to heavy hunting pressure in southern Mexico (Naranjo *et al.* 2004), may be primary drivers to paca population declines and even local extinctions (Estrada *et al.* 1994). Thus, it is of utmost importance to improve our knowledge on paca populations and their habitat requirements in the wild as well as in transformed landscapes. This information will support sound management plans and actions for sustainable use and conservation of paca populations.

In this study, we evaluated the effect of different variables (availability of food and cavities, interspecific competition, predation, and hunting pressure) on abundance and density of *C. paca*. In addition, we analyzed habitat use by pacas from a source-sink systems perspective in sites with three different land uses: Montes Azules Biosphere Reserve, community reserves, and agricultural landscapes of the Lacandon Rainforest. We expected that paca abundance and density would be positively associated to the availability of food and cavities, and negatively correlated to interspecific competition, predation, and hunting pressure. We predicted that pacas would prefer habitats with more food available, and cavities resistant to predation and hunting, which would favor their survival and reproductive success. Preferred (source) habitat types would show higher paca densities than the others.

Materials and Methods

Study area The study area included a southeastern portion of Montes Azules Biosphere Reserve (MABR) and territories of two neighboring communities (ejidos): Playón de la Gloria (pop = 209), and Reforma Agraria (pop = 145) in the Lacandon Rainforest of Chiapas, Mexico. Both communities are located on the east side of the Lacantun River (INE 2000; INEGI 2010). Three habitat types were considered in this study: 1) Transformed landscapes, including secondary vegetation along rivers and within agricultural and grazing areas, and human settlements. Human presence in this habitat type was continuous; 2) Community reserves, established by local residents for conservation in Reforma Agraria (14.6 km^2) and Playon de la Gloria (2.5 km^2). Both reserves are primarily covered by secondary forest, abandoned plantations, and rainforest fragments. Tourism and research are present in these reserves for relatively short periods (a month or less); 3) Montes Azules Reserve, where undisturbed mature rainforest is predominant. Human activity is negligible in this site, where only a few researches and visitors are allowed (Figure 1).

Fieldwork. Monthly samplings were carried out in the study sites from September 2013 through August 2014. Four line transects were walked in each habitat type for each season (dry = December-May, wet = June-November). Each transect was 1 km long and 50 m wide (Figure 1). A minimum distance of 175 m between transects was set for sampling independence based on the average home range of the paca (1.74 ha; Beck-King *et al.* 1999). Our cri-

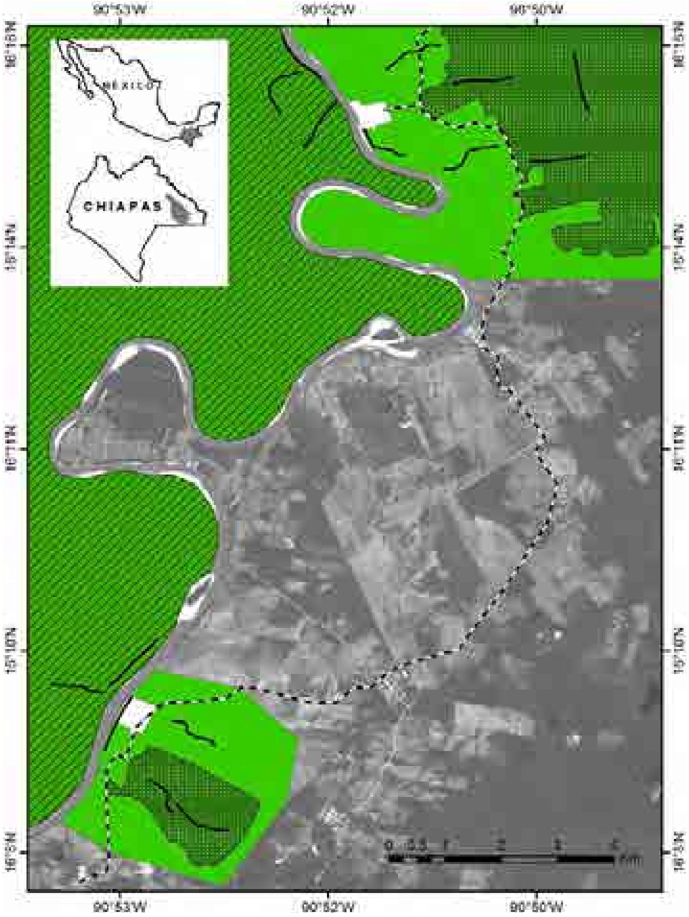

Figure 1. Location of the study site in the Lacandon Rainforest, Chiapas, Mexico. Transects (black lines) and habitat types are shown: Transformed landscape (light plain green), Community reserve (dark dotted green), and Montes Azules Biosphere Reserve (MABR; green with diagonal lines). Human settlements are represented with a white square: Reforma Agraria in the upper part, and Playon de la Gloria in the lower part.

terion to select transect locations was the presence of paca signs (footprints, feeding sites, active burrows, and sights by residents). Four camera-traps were deployed every 200 meters along each transect in order to estimate the relative abundance of pacas and their potential competitors and predators. That distance was considered appropriate for independence of paca records (Karanth and Nichols 1998) and for its competitors of similar or smaller size. For larger competitors and predators such as the white-tailed deer (*Odocoileus virginianus*), red brocket deer (*Mazama temama*), Baird's tapir (*Tapirus bairdii*), collared peccary (*Pecari tajacu*), white-lipped peccary (*Tayassu pecari*), jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), tayra (*Eira barbara*), and dogs (*Canis lupus familiaris*), the minimum distance for independent records was 1 km (Maffei and Noss 2008; Naranjo *et al.* 2015). Camera-traps (models Moultrie D55, Stealth-Cam Q8X, and Bushnell Trophy XLT) were programmed to be active 24 hours for 30 consecutive days each season, taking 3 still pictures and a short video (10 to 20 sec) per event. Records were considered independent if taken in different transects and days, unless individual identification was possible (Monroy-Vilchis *et al.* 2011; Jax *et al.* 2015). Capture rates were estimated by calculating the number of independent records (pictures) of pacas in relation to the total number of effective records of all species per season and habitat type. Effective pictures were those where pacas or their potential competitors and predators appeared (Pérez 1992; Dubost and Henry 2006; Figueroa-de-León *et al.* 2016a).

Relative abundance indices of pacas and other mammals (Appendix 1) were estimated using photo-trapping data (RAI_{ft}). These indices were calculated as follows: RAI_{ftv} = number of independent records (pictures or videos) of *C. paca* / total effective pictures / sampling effort per 100 camera-days (Carbone *et al.* 2001). The density of pacas was assessed by counting the individuals photo-captured along each transect. Individuals recorded during abundance monitoring and photographic records previously obtained in cavities occupied by pacas (Figueroa-de-León *et al.* 2016a) were taken into account for density estimations. Individual identification was based on descriptions of pacas made by Figueroa-de-León *et al.* (2016a). Diffuse pictures were excluded from this analysis.

Food availability for pacas was evaluated by establishing five 1,000 m^2 circular plots along each transect. The distance between centers of two contiguous plots was 200 m (Elzinga *et al.* 2001). All trees and palms within plots producing fruits potentially consumed by pacas (Beck-King *et al.* 1999; Muñoz *et al.* 2002; Zucaratto *et al.* 2010) were counted and marked. Field observations of fruits bitten by pacas and references by local hunters were also helpful for selecting the tree species considered in this analysis. Samples of leaves, flowers and fruits of each tree species were collected for taxonomic determination in the Herbarium at El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas. Fruit production in each habitat type was monitored monthly between September 2013 and August 2014. Mean area under the tree crown and the average number of fallen fruits per tree were counted for each of the 30 tree species recorded. Fallen fruit counts were done monthly in 5-10 circular plots with a radius of 0.5 m (fruits up to 3 cm diameter) and 1 m (fruits over 3 cm diameter). All counted fruits were removed from the plots to avoid double counts in subsequent samplings. Collected fruits were taken to the bromatology lab at El Colegio de la Frontera Sur, where fruit parts were separated to estimate the biomass available as paca food (Beck-King *et al.* 1999; Muñoz *et al.* 2002; Zucaratto *et al.* 2010; Appendix 2). Fruit parts were dehydrated at 60 °C until constant weight (adapted from Wallace and Painter 2003). The numbers of fallen fruits per tree species were multiplied by the average dry weight of all parts consumed by pacas (Ganesh and Davidar 1999). Available food estimates from all tree species were pooled to obtain food availability indices by habitat type and season.

In April (dry season) and September (wet season) 2013 we intensively searched for cavities used as refuges by pacas. This search was done along each transect (1,000 x 50 m) from 7:00 through 16:00. All cavities found were examined, including those under the forest floor, within tree roots or fallen logs. Cavities were considered available for pacas if they were at least 15 cm in diameter, 60 cm deep (Aquino *et al.* 2012), and located at 100 m or less from the nearest water source (Figueroa-de-León *et al.* 2016a,b). Only cavities with indicators of recent activity (fresh tracks, fresh litter around, and clean entrance were considered. A minimum distance of 100 m between cavities was taken as a criterion for spatial independence (Beck–King *et al.* 1999). An index of cavity availability was estimated by dividing the number of available cavities by the total area sampled in each habitat type and season.

Hunting pressure on pacas was estimated by gathering information consisting of hunted paca carcasses found during fieldwork, paca cavities destroyed by hunters, pictures and videos of hunters and their dogs nearby cavities, platforms for hunting built on trees, personal observations of hunting by the authors, and comments by residents about the presence of paca hunters in their communities. A persistently hunted transect was that in which a hunting evidence was detected at least once a month, or when there were 2 to 3 weekly references about paca hunters present. A slightly hunted transect showed no frequent hunting evidence or weekly references. In addition, a hunting pressure index was built by dividing the number of persistently hunted transects by the number of slightly hunted transects in each habitat type and season. Habitat use by pacas was assessed by estimating their densities in the three habitat types and both seasons. The total available habitat was the sum of sampled areas in each transect, habitat type, and season (Morrison *et al.* 2006).

Data analyses. Paca abundance, density, food and cavity availability, and hunting pressure were compared among habitat types and between seasons using Wilcoxon's signed-rank tests, Kruskal-Wallis's analysis of variance on ranks tests, and Pearson's Chi-squared tests of independence with Yates's correction of continuity (Crawley 2005). Durbin and Watson's tests were used to verify independence in our abundance and density data (Crawley 2005). Generalized Linear Models (GLM; McCullagh and Nelder 1989) were built to determine the effect of explaining variables (food and cavity availability, hunting pressure, competition, and predation) on paca density and abundance indices. Because of our limited sample size (13 and 12 transects in dry and wet season, respectively), each model was built with a single explaining variable at a time. A Poisson distribution was assumed in the GLM unless an over-dispersion due to zero predominance in data was present. In such cases, a negative binomial distribution was assumed (Crawley 2005). All statistical procedures were applied using packages MASS (Venables and Ripley 2002), and lmtest (Zeileis and Hothorn 2002) in R platform version 3.3-1 (R Core Team 2016). HABUSE program (Neu *et al.* 1974; Byers *et al.* 1984) was used to assess habitat use based on paca abundance and its habitat availability. By running Chi-squared tests and Bonferroni's confidence intervals in this program, we detected preference or avoidance of each habitat type by pacas in the study area (Neu *et al.* 1974; Byers *et al.* 1984).

Results

A total of 125.3 km were walked and an area of 125 hectares was sampled in the study area. A sampling effort of 2,226 camera-days resulted in 5,745 photographic records of 23 mammal species. Of these records, 1,026 were considered effective photographs and 191 of them corresponded to *C. paca*. Paca relative abundance was slightly lower in the dry season than in the wet season (0.01 versus 0.02 photographs/100 camera-days, respectively). However, no significant differences were found between seasons ($W = 77.5$, $P = 1$) and among habitat types in dry ($X^2 = 0.2$, $P = 0.9$) and wet ($X^2 = 2.8$, $P = 0.2$) seasons. Paca densities were similar between seasons (dry = 0.56 pacas/ha, wet=0.54 pacas/ ha; $W = 77.5$, $P = 0.99$) and among habitat types ($P > 0.05$).

Food availability for pacas was estimated under the crown of 297 trees of 30 species, of which 5 species produced fruit in the dry season, 16 in the wet season, and 8 in both seasons. A lower food availability was found in the dry season compared to the wet season ($W = 125$, $P = 0.009$). Nonetheless, there were no differences among habitat types ($P > 0.05$; Table 1). Cavity availability was similar between seasons ($W = 61.5$, $P = 0.4$), and among habitat types ($P > 0.05$; Table 1). Similarly, we detected no seasonal ($X^2 = 0.04$, $P = 0.8$) or habitat-based ($P > 0.05$; Table 1) differences in the numbers of persistently hunted versus slightly hunted transects in the study area.

Potential paca competitors recorded by photo-trapping in MABR were: Red brocket deer, Baird's tapir, collared peccary, nine-banded armadillo (*Dasypus novemcinctus*), agouti (*Dasyprocta punctata*), opossums (*Didelphis spp., Philander opossum,* and *Metachirus nudicaudatus*), and great curassow (*Crax rubra*). In the community reserve we detected the white-tailed deer, red brocket deer, Baird's tapir, raccoon (*Procyon lotor*), coati (*Nasua narica*), nine-banded armadillo, opossums, great curassow, and green iguana (*Iguana iguana*). In the transformed landscapes, the red brocket deer, Baird's tapir, collared peccary, and great curassow were registered. Potential predators detected through photo-trapping in MABR were the ocelot and tayra; the jaguar, puma, and dogs were recorded in the

Table 1. Relative abundance indices, densities, food and cavity availability indices, and hunting pressure on Cuniculus paca in three habitat types of the Lacandon Rainforest, Chiapas, Mexico (2013-2014). The following units were used: Relative abundance index (RAI): photographs/100 camera-days; density: pacas/ha; food availability index (FAI): kg/ha; cavity availability index (CAI): number of cavities/ ha; hunting pressure index (HPI): number of persistently hunted transects/ number of slightly hunted transects.

[a] Number of transects, [b] Relative abundance index: Number of photographic records of pacas / total effective photographs / days * 100. [c] Biomass (dry weight of edible parts of fallen fruits, kg) / ha of each habitat type. [d] Total cavities available / ha sampled in each habitat type. [e] Persistently hunted transects / slightly hunted transects. [f] MABR: Montes Azules Biosphere Reserve.

Season	Habitat type	n[a]	RAI[b]	Density	FAI[c]	CAI[d]	HPI[e]
Dry	Transformed	4	0.04	0.41	12505	0.40	1
	Comm. Reserve	4	0.08	0.82	5088	0.65	1
	MABR[f]	5	0.02	0.44	9561	0.52	0.6
Wet	Transformed	4	0.08	0.41	20945	0.25	0.3
	Comm. Reserve	4	0.13	0.56	11919	0.45	1
	MABR[f]	4	0.04	0.65	48226	0.50	0.3

community reserve, and no predators were recorded in the transformed landscape.

Paca relative abundance was no significantly affected by food and cavity availability, hunting pressure or abundance of competitors and predators (Appendices 3 and 4). Contrastingly paca density was positively correlated with cavity availability (dry season: $r = 0.15$, $P = 0.04$; wet season: $r = 0.22$, $P = 0.006$). In the dry season, pacas used the transformed landscape in proportion to its availability, the community reserve more than expected, and MABR less than expected. However, during the wet season the three habitat types were used by pacas in proportion to their availability (Table 2).

Table 2. Habitat use and availability of Cuniculus paca in the Lacandon Rainforest, Chiapas, Mexico (2013-2014). HAB=Habitat type. Available habitat in the transformed landscape and the community reserve: 20 ha (dry and wet seasons). Available habitat in Montes Azules Biosphere Reserve (MABR): 25 ha (dry season), 20 ha (wet season). [a]OBS: observed proportion of use. [b]EXP: expected proportion of use. [c]INTERVAL: Bonferroni's confidence intervals. [d]HU: habitat use by paca, where "=": used in proportion to availability; "+": used greater than expected (selected habitat); "-": used lower than expected ($P = 0.05$).

HAB	Dry season $X^2 = 28.8$; $P = 0.0001$				Wet season $X^2 = 4.8$; $P = 0.08$			
	OBS[a]	INTERVAL[b]	EXP[c]	HU[d]	OBS[a]	INTERVAL[b]	EXP[c]	HU[d]
Transformed	0.246	0.166 - 0.325	0.30	=	0.253	0.171 - 0.335	0.33	=
Comm. Reserve	0.491	0.398 - 0.584	0.30	+	0.346	0.256 - 0.435	0.33	=
MABR	0.263	0.182 - 0.345	0.39	-	0.401	0.309 - 0.493	0.34	=

Discussion

Similarities in paca abundances and densities between seasons and among habitat types may have been due to our limited sample sizes (13 and 12 transects in dry and wet seasons, respectively), which make difficult to detect potential differences. In addition, paca abundance indices may be skewed because differences in capture probabilities across seasons and habitat types were not considered. Capture probabilities are conditioned by factors such as individual behavior and physical condition, cover type around camera-traps, and weather, among others (O'Connell *et al.* 2010). These factors may be confounding potential effects of variables explaining paca abundance. Similarly, density estimates could have been subject to problems in distinguishing paca individuals because of low resolution of night pictures, and distance impairing the observation of the spot pattern of some pacas (Figueroa-de-León *et al.* 2016a). In spite of this, cavity availability was the only variable with a significant link with paca densities, which suggests that cavities constitute a key resource driving paca population dynamics in the study area.

Food availability did not show a significant effect on paca density and abundance. This can be partially explained by the methodological limitations mentioned above, or by the opportunistic behavior of pacas (Laska *et al.* 2003), which may adjust their diet following seasonal and spatial variations in fruit availability (Dubost and Henry 2006). Hunting pressure had no effect on paca density and abundance, which may be due to the relatively low frequency of hunting practices in the communities visited in this study. Yet, it is important to encourage multiannual surveys for better understanding the impact of hunting on paca population dynamics and its persistence in transformed landscapes.

The abundance of competitors did not have an effect on paca populations, probably because the ecological and behavioral traits of pacas (nocturnal activity, opportunist diet, and cavity use for avoiding predation; Aquino *et al.* 2009), allow them to reduce the encounter probability with other species. On the other side, the abundance of potential predators was unrelated to paca abundance. A likely explanation to this result is the fact that pacas reduce their predation risk by taking cover inside safe cavities such as those under tree roots or in fallen logs (Figueroa-de-León *et al.* 2016a, b), which are frequently located at strategic sites (*i. e.,* near water courses that can be used as routes for escaping from predators; Aquino *et al.* 2009).

Pacas selectively used the community reserve of Playon de la Gloria during the dry season, probably due to the existence of a rocky area with multiple cavities of the appropriate size to avoid predation and hunting. In contrast, the three habitat types considered in this study were used in proportion to their availability during the wet season. This may be explained by: 1) An increase in paca movements favored by a shortage of cavities produced by seasonal floods or collapse of burrows; 2) food and water abundance. Proximity to permanent water sources has been documented as a key variable for selective use of cavities by pacas (Figueroa-de-León *et al.* 2016a). Similarly, water bodies have proven key habitat elements related to paca defecation (Figueroa-de León *et al.* 2016b) and reproduction (Epigmenio Cruz Aldán, Tuxtla Gutierrez Zoo, Chiapas, Mexico 2016 comm. pers.). Therefore, food and water abundance during the wet season reflects in lack of habitat selectivity by pacas in the study area.

In summary, we found that cavity availability had an effect on paca densities, which highlights the relevance of those habitat components on the population dynamics of this rodent in our study area. Besides, cavities used by pacas as shelters to avoid predation and adverse weather constitute habitat resources of utmost importance for pacas in the Lacandon Rainforest (Figueroa-de-León *et al.* 2016a). Thus, source habitats for pacas such as MABR and the community reserve of Playon de la Gloria have high availability of cavities favoring higher paca densities and reproductive rates inferred from higher frequencies of newborns (Figueroa-de-León *et al.* 2016a). On the contrary, sink habitats for pacas such as the transformed landscape included in this study have lower availability of appropriate cavities, lower densities and absence of newborns (Figueroa-de-León *et al.* 2016a).

Conserving wildlife species tolerant to land use change (*i. e.,* the paca) in transformed landscapes will depend on their habitat requirements as well as the distribution and connectivity of habitat fragments available (Ye *et al.* 2013). Hence, habitat types with continuous, mature cover are as important for paca conservation and management as secondary forest fragments interconnected to the first (Jax *et al.* 2015). Habitat connectivity is fundamental for paca mobility and dispersal, improving the viability of its populations in the long term (Ahumada *et al.* 2003; Gallina *et al.* 2012).

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Appendix 1. Relative abundance indices (RAI) of Cuniculus paca, its potential competitors and predators in three habitat types of the Lacandon Rainforest, Chiapas, Mexico (2013-2014). RAI: photographs/100 camera-days.

	Dry season			Wet season		
	Transformed landscape	**Community reserve**	**MABR[a]**	**Transformed landscape**	**Community reserve**	**MABR[a]**
Camera-days	375	342	409	402	294	404
Photographs analyzed	345	88	244	142	74	133
IAR *Cuniculus paca*	0.04	0.08	0.02	0.08	0.13	0.04
Predators						
IAR *Leopardus pardalis*	0	0	0.01	0	0	0
IAR *Panthera onca*	0	0	0	0	0.01	0
IAR *Puma concolor*	0	0	0	0	0.01	0
IAR *Eira barbara*	0	0	0.002	0	0	0.003
IAR *Canis lupus familiaris*	0	0	0	0	0.01	0
Competitors						
IAR *Dasypus novemcinctus*	0	0.1	0	0	0.01	0.01
IAR *Nasua narica*	0	0.01	0	0	0	0
IAR *Dasyprocta punctata*	0	0	0	0	0	0.01
IAR *Crax rubra*	0.01	0.01	0.02	0.04	0.04	0.05
IAR *Iguana iguana*	0	0.01	0	0	0	0
IAR *Procyon lotor*	0	0.01	0	0	0.01	0
IAR *Pecari tajacu*	0	0	0	0.01	0	0.03
IAR *Tayassu pecari*	0	0	0	0.01	0	0
IAR *Tapirus bairdii*	0	0.01	0.01	0.01	0	0
IAR *Odocoileus virginianus*	0	0	0	0	0.01	0
IAR *Mazama temama*	0	0.01	0.01	0.01	0	0
IAR *Didelphidae*	0	0.01	0	0	0.03	0.01

[a]MABR=Montes Azules Biosphere Reserve.

Appendix 2. Tree species producing fruits potentially consumed by *Cuniculus paca* in the Lacandon Rainforest, Chiapas, Mexico, 2013-2014.

Local name	Species	Family	Fruiting season[a]	Fuit parts consumed[b]	Source[c]
Aguacate silvestre	*Beilschmiedia anay* (Blake) Kosterm.	Lauraceae	2	P, S	OC
Amate	*Ficus insipida Will.*	Moraceae	3	FC	OC, L
Amatillo	*Sapium lateriflorum* Hemsl.	Euphorbiacea	3	FC	L, CL
Anona silvestre	*Annona scleroderma* Saff.	Anonaceae	3	FC	OC, L
Anonillo, Orejuelo	*Cymbopetalum penduliflorum* (Dunal) Baill.	Anonaceae	3	FC	OC, L
Barí	*Calophyllum brasiliense* Cambess.	Guttiferae	2	FC	L
Cedrillo*	*Guarea kunthiana* A.Juss.	Meliaceae	3	FC	OC
Colorado	*Guarea glabra* Vahl.	Meliaceae	1	FC	L, OC
Corozo*	*Attalea butyracea* (Mutis ex L. f.) Wess. Boer	Arecaceae	3	P, C	OC
Espino	*Acacia usumacintensis* Lundell	Fabaceae	1	S	CL
Frijolillo	*Cojoba arborea* (L.) Britton & Rose	Fabaceae	3	FC	L
Guapaque	*Dialium guianense* (Aubl.) Sandwith	Fabaceae	3	FC	L
Guatope de río	*Inga vera* Willd.	Fabaceae	2	P, S	L
Guatopito de rio	*Inga punctata* Willd	Fabaceae	2	P, S	L
Guatopito verde de montaña	*Inga laurina* (sw.) Willd.	Fabaceae	2	P, S	L
Hule	*Castilla elastica* Cerv.	Moraceae	2	P, S	CL
Jaboncillo	*Sapindus saponaria* L.	Sapindaceae	1	FC	CL
Jobo amarillo	*Spondias mombin* L.	Anacardiaceae	2	C, P	OC, L
Jobo verde*	*Spondias radlkoferi* Donn. Sm.	Anacardiaceae	2	C, P	OC
Luín	*Ampelocera hottlei* (Standl.) Standl.	Ulmaceae	3	FC	L
Mamey	*Pouteria sapota* (Jacq.) H.E. Moore y Stearn	Sapotaceae	2	FC	OC, L
Memela	*Bellucia grossularioides* (L.) Triana	Melastomataceae	1	FC	L
Molinillo	*Quararibea funebris* (La Llave) Vischer	Malvaceae	3	FC	OC, L
Mulato	*Bursera simaruba* (L.) Sarg.	Burseraceae	3	FC	L
Paterna	*Inga pavoniana* G.Don	Fabaceae	2	FC	L
Ramon grande	*Brosimum alicastrum* Sw.	Moraceae	2	FC	L
Ramon mediano	*Brosimum lactescens* (S. Moore) C. C. Berg	Moraceae	2	FC	L, CL
Sunzapote	*Licania platypus* (Hemsl.) Fritsch	Chrysobalanaceae	2	P, S	OC, L
Volador	*Virola guatemalensis* (Hemsl.) Warb.	Myristicaceae	2	P, S	L
Zapotillo	*Pouteria durlandii* (Standl.) Baehni	Sapotaceae	2	FC	L

* New record for paca diet; [a] Fruiting season: 1 = dry, 2 = wet, 3 = both. [b] Fruit parts consumed by pacas: C = Shell; P = Pulp; S = Seed; FC = Whole fruit. [c] Source: L = Literature, OC = Bitten fruit observed in the field, CL = Reference by residents of the study area.

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Is *Galea tixiensis* Quintana, 2001 a synonym of *G. leucoblephara* Burmeister, 1861?

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The genus *Galea* (Rodentia, Caviidae) includes five living and two extinct species of terrestrial and herbivorous cavies that inhabit grasslands and rocky scrub areas at both high and low elevations in South America. Fossil samples from the late Pleistocene-Holocene from central-eastern Argentina have been referred to as *Galea* sp., *G musteloides* or G. cf. *musteloides* and finally described as a new species under the name of *G. tixiensis*. However, recent studies based on large series of individuals fail to find qualitative morphological differences between *G. leucoblephara* and *G. tixiensis*. Based on these findings, in this contribution we reviewed the taxonomic status of the fossil species *G. tixiensis*. A total of 110 individuals of the three currently recognized subspecies of *G. leucoblephara* (*i. e*., *G. l. demissa, G. l. leucoblephara* and *G. l. littoralis*) from Argentina Bolivia and Paraguay were examined. Nine craniodental measurements were recorded. Quantitative data were subjected to a principal component analysis (PCA) in order to identify the contribution of each measurement to the total variance. Qualitative characters were evaluated through the comparisons of the diagnostic traits of *G. tixiensis* with the variability derived from the recent samples. PCA showed a high overlap of the multivariate spaces of the three subspecies studied, suggesting that they do not differ significantly in terms of cranial shape. The holotype of *G. tixiensis* was allocated within the morphospace of the recent *G. l. littoralis* samples. Qualitative traits diagnostic of *G. tixiensis* were also recorded in recent samples of *G. leucoblephara*, in particular of *G. l. littoralis*. Based on both qualitative and quantitative cranial traits, we suggest that *G. tixiensis* is a synonym of *G. leucoblephara*. The morphological traits supposedly unique to *G. tixiensis* were also recorded in specimens of living populations of *G. l. littoralis*. The large values of some quantitative cranial traits in fossil samples -- compared to living ones -- are reinterpreted here as an ecophenotypical response to the more severe climatic conditions of the Holocene.

El género *Galea* (Rodentia, Caviidae) incluye cinco especies vivientes y dos extintas de cávidos terrestres y herbívoros, que ocupan pastizales y matorrales rocosos, tanto en áreas altas como bajas de América del Sur. Algunas muestras fósiles del Pleistoceno-Holoceno del centro-este de Argentina han sido referidas como *Galea* sp., *G. musteloides* o *G.* cf. *musteloides* y finalmente se describieron como una nueva especie bajo el nombre de *G. tixiensis*. Sin embargo, estudios recientes basados en series grandes de individuos fallaron en encontrar diferencias morfológicas cualitativas entre *G. lecucoblephara* y *G. tixiensis*. Sobre la base de estos hallazgos, en esta contribución revisamos el estatus taxonómico de la especie extinta *G. tixiensis*. Se examinaron 110 individuos de las tres subespecies actualmente reconocidas de *G. leucoblephara* (i.e., *G. l. demissa*, *G. l. leucoblephara* y *G. l. littoralis*) de Argentina, Bolivia y Paraguay. Se registraron nueve medidas cráneo-dentarias. Los datos cuantitativos se sometieron a un análisis de componentes principales (PCA) con el fin de identificar la contribución de cada medida a la varianza total. Los caracteres cualitativos se evaluaron a través de las comparaciones de los rasgos supuestamente diagnósticos de *G. tixiensis* con la variabilidad representada por las muestras recientes. Los espacios multivariados de las tres subespecies estudiadas se superpusieron ampliamente en el PCA, lo que sugiere que estos taxones no difieren significativamente en la figura del cráneo. El holotipo de *G. tixiensis* se ubicó dentro del morfoespacio correspondiente a muestras recientes de *G. l. littoralis*. Los caracteres cualitativos supuestamente diagnósticos de *G. tixiensis* también se verificaron en muestras recientes de *G. leucoblephara*, en particular de *G. l. littoralis*. Sobre la base de sus rasgos craneanos cualitativos y cuantitativos se sugiere que *G. tixiensis* es un sinónimo de *G. leucoblephara*. Los mayores valores para algunos rasgos craneanos cuantitativos en las muestras fósiles -comparadas con las actuales- son reinterpretados en este trabajo como una respuesta ecofenotipica a las condiciones climáticas más severas durante el Holoceno.

Key words: Caviidae; Cavioidea; Caviomorpha; *Galea leucoblephara littoralis*; Hystricognathi.

Introduction

The genus *Galea* Meyen 1833, with five living and two extinct species, is one of the most diverse genera within the Family Caviidae (Ubilla and Rinderknecht 2014; Dunnun 2015). Its fossil record dates back at least to the Ensenadense (Vucetich *et al.* 2015) and is composed mainly of fragmentary cranio-mandibular remains (Ubilla and Rinderknecht 2014). The only two known extinct species (*i. e*., *G. orthodonta* Ubilla and Rinderknecht 2001 and *G. tixiensis* Quintana 2001) are based on well preserved craniodental and postcranial remains. The former of these species, *G. orthodonta*, has been found in Pleistocene sediments of Uruguay and southern Bolivia (Ubilla and Rinderknecht 2001; Ubilla and Rinderknecht 2014). The second extinct species, *Galea tixiensis*, was established from remains accumulated throughout the Holocene in rocky outcrops in the southeast of Province of Buenos Aires, in east-central Argentina (Quintana 2001). The materials that led to the description of *G. tixiensis* were instead referred to as either *Galea* sp., *G musteloides or G.* cf. *musteloides* (*e. g*., Tonni *et al.* 1988; Quintana and Mazzanti, 1998; Quintana 2001), highlighting its morphological similarity with individuals of the recent populations inhabiting this same region, firstly referred to *G. musteloides* and now allocated within *G. leucoblephara* (Dunnun 2015). Quintana (2001) indicated several diagnostic traits for *Galea tixiensis* (see below), in addition to larger size relative to other species in the same genus. Unfortunately, Quintana (2001) did not document what living specimens were compared against the fossil samples, nor some other relevant aspects that are key for the description of a new species, such as holotype measurements (which were not illustrated either). More recently, a species related to *G. tixiensis*, referred to as *G.* aff. *tixiensis,* was mentioned for the Pleistocene of Province of Corrientes, in northeast Argentina (Francia *et al.* 2012).

The examination of a vast number of specimens as part of a qualitative and quantitative morphologic review of the genus *Galea* allows us to assume that many of the diagnostic traits of *G. tixiensis* are not unique to this species, and neither is the combination of these traits (see also Ubilla and Rinderknecht 2014). The taxonomic status of *G. tixiensis* is relevant for several reasons (*e. g.*, biogeographic, evolutionary), but mainly because, should this be a distinct species, it would be one of the eight species of mammals that became extinct over the past 500 years in mainland South America (cf. Teta *et al.* 2014; Prevosti *et al.* 2015).

The aim of this work is to review the taxonomic status of *Galea tixiensis.* Based on qualitative and quantitative morphological evidence, it is hypothesized that *G. tixiensis* is synonym for *Galea leucoblephara* Burmeister 1861.

Materials and Methods

We studied 110 specimens of *Galea leucoblephara*, including skulls and mandibles, from Argentina, Bolivia and Paraguay. These are deposited in the following collections (for details, see Appendix 1): CFA, Collection of Mammals of Fundación de Historia Natural Félix de Azara (Buenos Aires, Argentina); CMI, Collection of Mammals of Instituto Argentino de Investigación de Zonas Áridas (Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina); CML, Collection of Mammals of Facultad de Ciencias Naturales e Instituto Miguel Lillo (Facultad de Ciencias Naturales e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina); CNP, Collection of Mammals of Centro Nacional Patagónico (Centro Nacional Patagónico, Puerto Madryn, Argentina) MACN-Ma, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina) MNHNP, Collection of Mammals of Museo Nacional de Historia Natural de Paraguay (Asución, Paraguay); UACh, Collection of Mammals of Universidad Austral de Chile (Valdivia, Chile). Samples were grouped into 3 major geographical groups, allocated to subspecies *G. leucoblephara demissa, G. l. leucoblephara* and *G. l. littoralis*, following the taxonomic scheme proposed by Bezerra (2008) and Dunnun (2015). The first of these taxa is distributed across the lowlands of southeastern Bolivia and western Paraguay to the Provinces of Santiago del Estero and Catamarca in Argentina; the second, from southern Catamarca to Córdoba and northern Mendoza and San Luis, in Argentina; and the third, from southern Mendoza, La Pampa and southeastern Buenos Aires to northeastern Santa Cruz, in Argentina.

The following cranial measurements were recorded for each adult specimen (classes 3-5; cf. (*sensu* Bezerra 2008) (using a digital caliper accurate to 0.01 mm): AN = nasal width; CIO = interorbital constriction; FL = frontal length; LD = diastema length; AFI = incisive foramen width; LFI = incisive foramen length; LP = palatilar length; SMS = length of the upper toothrow length (alveolar); APM3 = palate width at the third upper molar. The measurements of the holotype of *G. tixiensis* were estimated using the software tpsdig2 from photographs in Bezerra (2008) and Francia *et al.* (2012), using as reference the scale in the latter.

To summarize the causes of morphometric variation and rank them according to importance, a principal components analysis (PCA) was performed from a variance-covariance matrix of the log-transformed measures. Previously, each individual measurement was corrected by the geometric mean of each individual to avoid the distortion derived from the effect of size (for this methodology, see Meachen-Samuels and Van Valkenburgh 2009). For the purposes of this work, *form* is defined as the appearance, configuration or composition of the traits, including size, whereas *figure* refers to the form excluding size (Vizcaíno *et al.* 2016). This is consistent with the approach of Richtsmeier *et al.* (2002), in his attempt to circumvent the use of these terms in the colloquial sense.

The anatomical terminology corresponds to the one used by Cherem and Ferrigolo (2012). The qualitative and quantitative morphological traits of *Galea tixiensis* were taken from the literature (*i. e.*, Quintana 2001) and discussed from the comparison with recent specimens.

Results

The first two PCA axes accounted for 63.1% of the variation in craniodental measurements (Figure 2; Table 2). The overlap of the polygons corresponding to the three subspecies currently recognized was moderate to high, suggesting that there are no major differences in figure. In this context, the holotype of *G. tixiensis* was allocated with *G. l. littoralis* specimens (Figure 2), toward positive values in PC 1. All the variables were negatively correlated with PC 1, except AFI, which was positively correlated.

The states for morphological traits originally referred to as diagnostic for *G. tixiensis* were also observed in living specimens of *G. leucoblephara*. The morphological variability recorded in different qualitative features of the fossil taxon is well within the variability documented for the living populations of *G. leucoblephara*, but especially of *G. l. littoralis* (for a summary see Table 3).

Discussion

The most striking feature of *G. tixiensis* relative to other species in the same genus is its larger overall size (Quintana

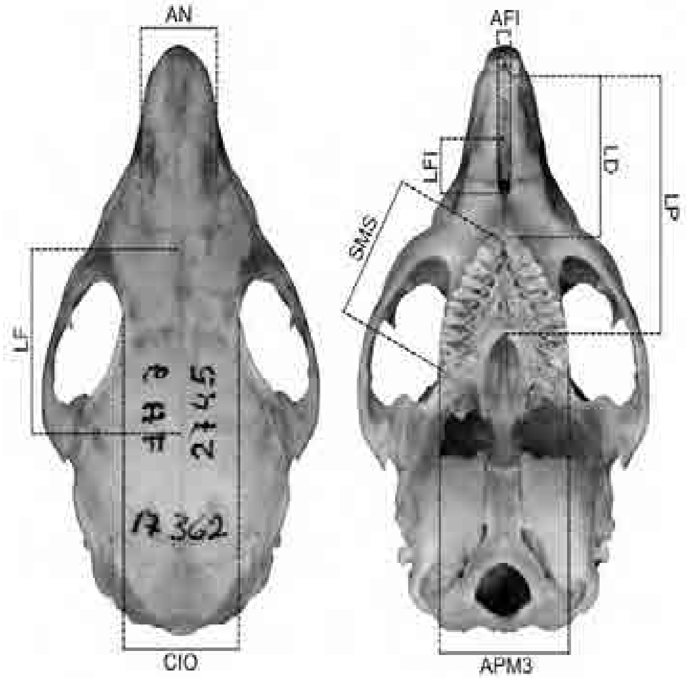

Figure 1. Cranial measurements used in this study, shown on a skull of *Galea leucoblephara* (MACN 17362). For a reference of the abbreviations, see Materials and Methods.

2001:404). However, a size-adjusted PCA indicates that, in terms of figure, the *G. tixiensis* holotype does not differ from other individuals referred to as *G. leucoblephara*. This is not a minor issue, as certain quantitative traits are among the phenotypic variables most frequently associated with physiological or environmental changes (*e. g*., Maestri *et al.* 2016). Also, some differences might be magnified by the different sample sizes considered by previous authors. For example, for a set of 35 individuals of *G. leucoblephara*, Quintana (2001) reported a higher mean upper alveolar toothrow length of 11.77 mm, with a range between 10.4 to11.7 mm (*n* = 35; note the contradiction between the mean and maximum values recorded), while for the same species, with a sample three times larger (*n* = 110), we recorded an average of 11.82 mm and a range of 10.1 to 15.54 mm (*n* = 110). This evidences that although the mean value remains clearly lower for *G. leucoblephara*, the range of measurements for this species covers completely the range reported for *G. tixiensis* (mean = 13.18 mm; 12.2-15.1 mm range; n = 107).

Our review of extensive series of specimens indicates that none of the qualitative traits supposedly diagnostics of *G. tixiensis*, nor the combination of them, is unique to this taxon. For example, the morphology of the zygomatic arch and the diastema and its associated foramina does not differ significantly from the one observed in living specimens of *G. l. littoralis* (cf. Figures 3 and 4; Table 3). In this subspecies, the shape of the incisive foramen varies between tapered and diamond-shaped, together with the presence of a conspicuous interpremaxillar foramen, accompanied by accessory foramina with a lateral and posterior arrangement, in a disposition similar to that reported for *G. tixiensis* (Figure 3). This contradicts what has been pointed out by Quintana (2001:402 to 404), who indicated that the diamond shape of the incisive foramen was exclusive to the fossil species and that the accessory foramina were not present in other species, nor did this displayed the overall disposition as *G. tixiensis*. Also, the robustness of the zygomatic arch, as well as the development of the paraorbital apophysis on the ascending branch of the zygomatic portion of the maxilla and the size of the jugal were relatively variable in samples of the living specimens, with some individuals (*e. g*., MACN-Ma 13335; cf. Figure 4B) displaying a disposition similar to the one observed in *G. tixiensis* (cf. Quintana 2001; Fig. 3A). Other traits (*e. g*., shape of the mesopterygoid fossa, shape of the nasolacrimal foramen, appearance of the tympanic bulla, morphology of the mandibular ramus and molars) did not show major differences between *G. tixiensis* and *G. leucoblephara* (cf. Quintana 2001; this work). For all the above mentioned, we consider that there is no qualitative morphological evidence to suggest that G. tixiensis is a different species from *G. leucoblephara*.

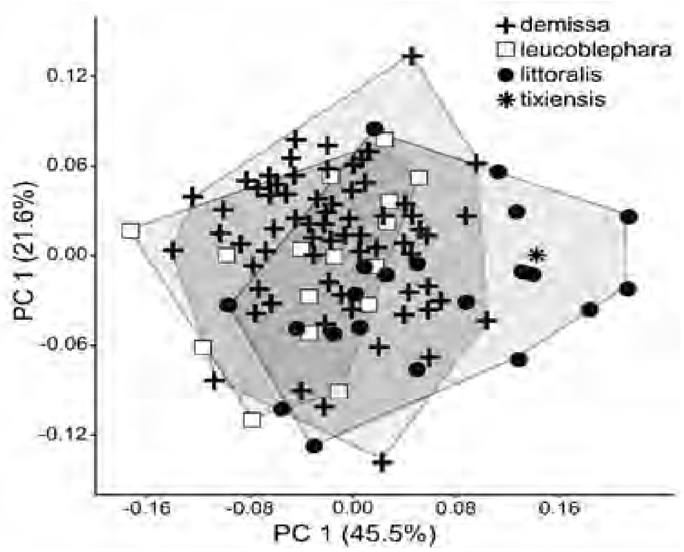

Figure 2. Polygons and individual scores for adult specimens (n = 111) in three subspecies of *Galea leucoblephara* and the holotype of G. *tixiensis* for principal components 1 and 2 (obtained from a variance-covariance matrix on nine craniodental measurements corrected by the geometric mean).

For Quintana (2001), *G. tixiensis* became extinct toward

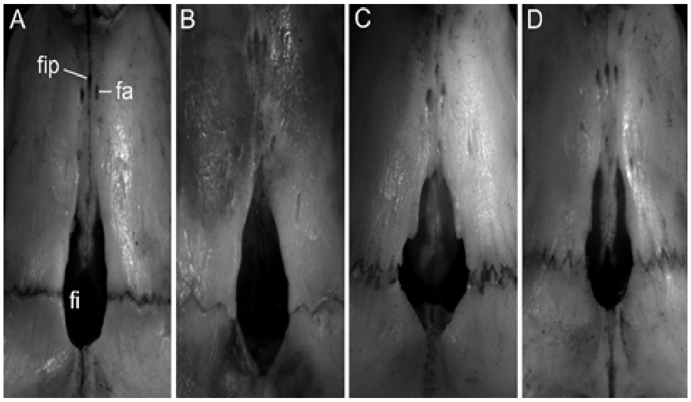

Figure 3. Individual variation in the morphology of incisive foramina and associated structures in specimens of *Galea leucoblephara littoralis* (from left to right: MACN-Ma 13226, 22607, 16405, 13664). Abbreviations: fa = lateral accessory foramina; fip = interpremaxillar foramen.

Table 1. Statistical summary for nine craniodental measurements (in mm; for a reference of the abbreviations, see Materials and Methods) in adult specimens of the genus *Galea*. Other abbreviations: N = number of specimens measured; SD = standard deviation; Min = minimum recorded value; Max. = maximum recorded value.

	G. leucoblephara demissa					*G. leucoblephara leucoblephara*					*G. leucoblephara littoralis*					*G. tixiensis*
	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	
AN	71	7.39	0.56	6.27	8.91	18	7.18	0.42	6.52	8.08	21	6.98	0.44	6.42	8.20	7.83
CIO	71	10.89	0.79	8.89	13.06	18	10.32	0.87	8.55	12.36	21	10.64	0.50	9.47	11.49	11.74
LF	71	16.34	0.90	13.58	18.36	18	16.36	2.13	10.03	19.91	21	17.08	0.90	15.69	19.23	16.86
LD	71	12.93	1.11	10.84	15.25	18	13.55	1.05	11.81	15.25	21	13.27	0.89	11.35	15.13	15.85
AFI	71	1.44	0.22	1.02	2.04	18	1.40	0.21	1.00	1.75	21	1.72	0.38	1.16	2.51	2.39
LFI	71	4.50	0.56	3.14	6.19	18	4.38	0.58	3.02	5.43	21	4.15	0.48	3.16	5.20	5.05
LP	71	11.79	0.92	10.10	15.52	18	11.95	1.22	10.41	15.54	21	11.81	0.72	10.70	13.52	13.96
SMS	71	20.92	1.58	17.72	24.48	18	20.79	2.57	12.20	23.83	21	21.29	1.19	17.83	23.45	15.00
APM3	71	12.60	0.75	10.97	14.22	18	12.77	0.69	11.48	13.88	21	12.90	0.70	11.88	14.56	25.58

the 18th century, in accordance with the earliest records of exotic wildlife in the southeast of the Province of Buenos Aires, during a period of cold and dry climate referred to as the Little Ice Age. If his hypothesis is correct, *G. tixiensis* would have been replaced in those same ecosystems by *G. l. littoralis*, the species currently recorded in the south of the pampas region (Galliari *et al.* 1991). In other words, the colonization of *G. l. littoralis* would have occurred in the last 200 years after the extinction of *G. tixiensis*, since there are no references of both species coexisting in sympatry in any of the sites studied by Quintana (2001; see also Quintana, 2016a, 2016b). This hypothesis is hardly parsimonious, especially in view of the morphological results discussed above. It is more likely that *G. leucoblephara* had experienced changes in size throughout the Holocene, a phenomenon that is well documented for mammals of the Northern Hemisphere (Martin and Barnosky 1993). In fact, the record of Holocene mammals of larger sizes than their living counterparts has already been mentioned for hilly and interhilly areas of Buenos Aires. A number of authors have highlighted the findings in various archaeological and fossils sites, of specimens of the rodent *Dolichotis patagonum* (*e. g*., Lobería; Tonni 1985) and the xenarthran *Zaedyus pichiy* (*e. g*., La Toma, Fortín Necochea, Laguna del Trompa, San Martín; see Vizcaíno *et al.* 1993) based on skeletal remains of larger size vs living specimens. A similar finding has been described for the cervid *Ozotocerus bezoarticus* and the sigmodontine rodent *Holochilus vulpinus* in several sites in the hilly area of Cordoba, central Argentina, for the same period of time (Teta *et al.* 2005; Medina and Merino 2012).

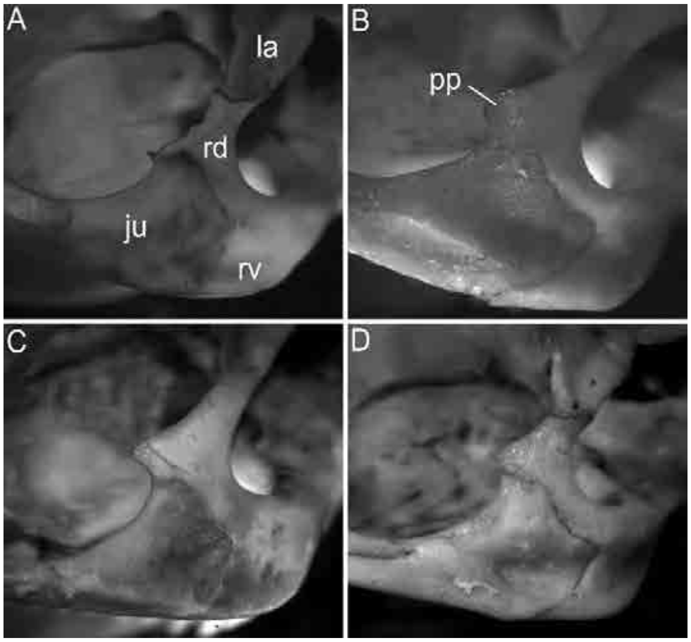

Figure 4. Individual variation in the morphology of the orbit in specimens of *Galea leucoblephara littoralis*: A) MACN-Ma 16405; B) MACN-Ma 13335; C) MACN-Ma 22607; D) MACN-Ma 13226. Abbreviations: ju = jugal; = lacrimal; pp = paraorbital apophyses; rd/rv = dorsal/ventral root of the zygomatic portion of the maxilla.

The climatic conditions for the largest part of the Holocene in the Pampean region were colder and drier than the current climate (cf. Tonni *et al.* 1999). In this context, it would not be unlikely that some mammal lineages likely developed phenotypic and physiological responses consistent with this scenario, including the variation in size, but not necessarily implying speciation events.

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S. Lucero collaborated in the measurement of specimens and facilitated our work in the Museo Argentino de Cien-

Table 2. Results of the principal component analysis performed on adult individuals (n = 111) of three subspecies of *Galea leucoblephara* and the holotype of *G. tixiensis*. For a reference of the abbreviations, see Materials and Methods.

	PC 1	**PC 2**	**PC 3**
AN	-0.14	0.01	0.43
CIO	-0.06	-0.06	0.71
LF	-0.11	-0.13	-0.41
LD	-0.14	-0.26	-0.31
AFI	0.94	0.05	-0.04
LFI	-0.17	0.90	-0.15
LP	-0.12	-0.24	-0.11
SMS	-0.09	-0.13	-0.08
APM3	-0.10	-0.14	-0.05
Autovalues	0.01	0.00	0.00
% Variance	45.14	21.60	10.59

Table 3. Diagnostic traits of *Galea tixiensis* (from Quintana, 2001) and expression of these same traits in a sample of 20 adult specimens of *G. leucoblephara littoralis* (for further details see Appendix 1).

	G. tixiensis	*G. l. littoralis*
Size	Larger than in living populations of *G. l. littoralis*	Smaller than in *G. tixiensis*
Zygomatic arches	Robust	Robust to moderately robust
Jugal	Proportionately short and wide	Proportionately short and wide to short and thinner
Ascending branch of the zygomatic portion of the maxilla	Proportionately short, with a well-defined paraorbital apophysis	Proportionately short, with a moderately to well-defined paraorbital apophysis
Ventral surface of the diastema	Flat in front of the incisive foramina	Flat in front of the incisive foramina
Incisive foramen	Large and diamond-shaped	Large, tapered to diamond-shaped
Interpremaxillar foramen	Large with two accessory foramina located with a lateral and posterior disposition, forming a structure that is connected to the incisive foramen through two open channels that cover the premaxilla on the lower side of the diastema	Large to medium in size, with two accessory foramina located to the sides and back, with the same disposition and connection with the incisive foramen as in *G tixiensis.*

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Appendix 1.

List of the Galea specimens studied in the present work, and their record localities in Argentina, Bolivia and Paraguay. These materials are deposited in the following collections: CFA, Collection of Mammals of Fundación de Historia Natural Félix de Azara (Buenos Aires, Argentina); CMI, Collection of Mammals of Instituto Argentino de Investigación de Zonas Áridas (Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina); CML, Collection of Mammals of Facultad de Ciencias Naturales e Instituto Miguel Lillo (Facultad de Ciencias Naturales e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina); CNP, Collection of Mammals of Centro Nacional Patagónico (Centro Nacional Patagónico, Puerto Madryn, Argentina) MACN-Ma, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina) MNHNP, Collection of Mammals of Museo Nacional de Historia Natural de Paraguay (Asución, Paraguay); UACh, Collection of Mammals of Universidad Austral de Chile (Valdivia, Chile):

Galea leucoblephara demissa (*n* = 77): Argentina: Catamarca: Hualfín, Casa de Piedra (CML 917). Chaco: General Güemes, Misión Nueva Pompeya (MACN-Ma 22589). Formosa: Matacos, Ingeniero Guillermo N. Juárez (MACN-Ma 47.391). Jujuy: San Pedro, Ingenio La Esperanza (CFA 4704). La Rioja: Chilecito, Chilecito (MACN-Ma 34.189, 34.272); Coronel Felipe Varela: Villa Unión (MACN-Ma 34.190, 34.193); Famatina, Las Pirquitas (MACN-Ma 34.194, 34.200); Famatina, Tres Cerros (MACN-Ma 34.196, 34.198). Salta: Anta, Los Colorados, 17 km E Santo Domingo (CML 3052); El Quebrachal (MACN-Ma 36.312, 36.313, 36.314, 36.315, 36.685, 36.752, 36.755, 36.761, 36.764, 36.766, 36.767, 36.771, 36.772, 36.774, 36.775, 36.776, 36.778, 36.779, 36.783, 36.784, 36.785, 36.786, 36.790, 36.791); General José de San Martín, Dragones (MACN-Ma 36.262); Metán, Metán (MACN-Ma 17362); Metán, La Represa, 500 mts. (MACN-Ma 30.363, 30.368); Orán, Orán (MACN-Ma 16227); Río Pescado (CFA 4307); Tabacal (MACN-Ma 16227); Finca San Javier, 8,5 km SE Joaquín V. González (CMI 3021); San Javier-Pozo Largo, 19 km SE Joaquín V. González (CMI 3023); Puesto Yuchán, camino a Salta forestal, 35 km N Joaquín V. Gonzalez (CMI 3022). Santiago del Estero: Banda, Sotelillo (CML 509); Choya, Villa La Punta (CFA 10809); Pellegrini, Santa Isabel (MACN-Ma 17351, 17352); sin localidad precisa (MACN-Ma 35.137, 35.138). Tucumán: km 81 de la R307, Tafí del Valle, 12 km O de Quebradita (CMI 4160); Trancas: Cerro Vipos, 1000 m s.n.m. (MACN-Ma 30.167, 30.169-30.171); Cumbres Calchaquies, cercanas a Vipos (MACN-Ma 30.167); Leales (CFA 111); Villa M. Paz (CFA 4370). Paraguay: Alto Paraguay: Estancia "Tres Marias"(TK 62443); Palmar de Las Islas (TK 65319, 65391). Boquerón: (TK130781, 130786, 130807, 13785); Parque Cué (TK 63298, 63371); Parque Nacional "Teniente Enciso" (TK 65029); Parque Nacional "Teniente Enciso", 3 Km. al Sur del fortín Teniente Enciso (MNHNP 753); Parque Nacional "Teniente Enciso", cerca del Puesto Siracua (TK66471); Rodeo Trebol, 5 Km. al NE de Loma Plata (TK 130764). Parque Nacional "Defensores del Chaco", 500 mts. al Oeste de Madrejón (MNHNP 755); Presidente Hayes, Estancia "Samaklay" (TK 122211, 122212, 122226).

Galea leucoblephara leucoblephara (*n* = 11): Argentina: Córdoba: Pocho, Tala Cañada (MACN-Ma 14745); San Alberto, Pampa de Achala (MACN-Ma 14706); San Javier, La Paz (MACN-Ma 29.10); Santa María, Alta Gracia, Falda del Carmen (MACN-Ma 14705). Mendoza: Mendoza (IZH 17); Santa Rosa, Reserva de Biosfera de Ñacuñan (UACH 6168); Tunuyán, Manzano Histórico (CMI 4160). San Juan: 9 de Julio, Monte de Oro (CMI 7065), San Juan (MACN-Ma 29.876); San Luis: General Pedernera, Villa Mercedes (MACN-Ma 50.49); Merlo, El Rincón (MACN-Ma 29.51).

Galea leucoblephara littoralis (*n* = 22): Argentina: Buenos Aires: Bahía Blanca (MACN-Ma 25281); Balcarce, Napaleofú (MACN-Ma 16405); Benito Juárez, Benito Juárez (MACN-Ma 54.134, 54.135); General Pueyrredón, Sierra de los Padres (MACN-Ma 13064); Necochea, Quequén (MACN-Ma 28.11); Torquinst, Abra de la Ventana (MACN-Ma 14936); Villarino, Algarrobo (MACN-Ma 22607). Chubut: Biedma, Arroyo Valdes (US s/n); Puerto Madryn, Playa Kaiser (CNP s/n, CNP s/n, CNP s/n); Escalante, Valle Hermoso (MACN-Ma 29.927); La Pampa: Caleu Caleu (MACN-Ma 13335, 13336, 15500); Hucal, Laguna Colorada Grande (MACN-Ma 15500); Lihuel Calel, Parque Nacional Lihué-Calel (MACN-Ma 20845); Pichi Mahuida, Estación de Aforos Nº44 (CNP 3619). Neuquén: Collón Curá (CFA 5567). Rio Negro: Avellaneda: Choele Choel (MACN-Ma 28.141). Santa Cruz: Deseado, 20 km al Norte de Caleta Olivia (MACN-Ma 22838).

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Density and activity pattern of *Leopardus wiedii* and *Leopardus pardalis* at Sierra Norte of Oaxaca, Mexico

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The margay, *Leopardus wiedii*, and the ocelot, *L. pardalis*, are sympatric species through their distribution areas. Some studies indicate that *L. pardalis* exerts a strong influence on other smaller felids. Our goal in this study was to estimate the density and activity patterns of these felid species in two vegetation types at Sierra Norte of Oaxaca, southwestern Mexico. We expected that *L. pardalis* had a high density relative to other felids due to its ecological plasticity, as well as segregation in the activity pattern between species. We placed camera traps in 22 sites in the semi-evergreen forest and 22 sites in the cloud forest, from July 2014 to June 2015. We estimated density using the Cormack-Jolly-Seber probabilistic model with the program MARK and assessed the degree of activity overlapping between species by the coefficient of overlapping Δ_1 in the program R. We recorded low abundance of *L. pardalis* (8.3 individuals) and a higher abundance of *L. wiedii* (51.5 individuals). The density of both species was 7.8 individuals /100 km^2 and 81 individuals/100 km^2, respectively. Both species displayed predominantly nocturnal activity. The overlap coefficient between species in the semi-evergreen forest was high ($\Delta_1 = 0.75$, CI = 0.63–0.90). Factors such as differences in vegetation type and the presence of a large number of transient individuals may influence the density of *Leopardus*. The lower density of *L. pardalis* and the high conservation status of the cloud forest may contribute to the higher density of *L. wiedii* in Sierra Norte of Oaxaca. Our results suggested that both species showed a highly overlapping activity pattern, and the activity pattern of the margay is seemingly unaffected by the presence of the ocelot. We provided information about density and activity of medium-sized felids, as well as on the factors that may potentially affect these patterns in mountain tropical forests.

El margay *Leopardus wiedii* y el ocelote *L. pardalis* son simpátricos a través de sus distribuciones. Algunos estudios indican que *L. pardalis* ejerce una influencia fuerte en otros felinos más pequeños. Nuestro objetivo fue estimar la densidad y el patrón de actividad de estos felinos en dos tipos de vegetación en la Sierra Norte de Oaxaca, en el Sureste de México. Esperábamos que *L. pardalis* presentara una densidad alta en comparación con otros félidos, debido a su plasticidad ecológica y también, esperábamos una segregación en el patrón de actividad entre especies. Ubicamos 22 sitios con trampas cámara en la selva mediana y 22 sitios en el bosque mesófilo de julio 2014 a junio 2015. Estimamos la densidad usando el modelo probabilístico de Cormack-Jolly-Seber con el programa MARK y evaluamos el grado de sobreposición de la actividad entre especies por medio del coeficiente de sobreposición Δ_1 en el programa R. Registramos una abundancia poblacional baja de *L. pardalis* (8.3 individuos) y una mayor de *L. wiedii* (51.5 individuos). La densidad poblacional de ambas especies fue 7.8 individuos/100 km^2 y 81 individuos/100 km^2, respectivamente. Ambas especies presentaron un patrón de actividad principalmente nocturna. El coeficiente de sobreposición entre especies en la selva mediana fue alto ($\Delta_1 = 0.75$, CI = 0.63–0.90). Factores como las diferencias en el tipo de vegetación y la presencia de varios individuos transeúntes pueden influir en la densidad de ambas especies de *Leopardus*. La densidad baja de *L. pardalis* y las condiciones favorables en el bosque mesófilo pueden contribuir a la densidad alta de *L. wiedii* en la Sierra Norte de Oaxaca. Nuestros resultados sugieren que ambas especies presentan una sobreposicion alta en el patrón de actividad y la presencia de *L. pardalis* parece no afectar la actividad de *L. wiedii*. Proporcionamos información acerca de la densidad y la actividad de felinos de talla corporal media, así como los posibles factores que pueden afectar estos patrones en ambientes tropicales montañosos.

Key words: capture-recapture; cloud forest; Cormack-Jolly-Seber model; overlap coefficient.

Introduction

The margay (*Leopardus wiedii*) and the ocelot (*L. pardalis*) are two medium-sized felids of the Neotropic. They are sympatric through their distribution ranges and occur in several habitats (Sunquist and Sunquist 2002). *Leopardus pardalis* is 2 to 3 times larger than *L. wiedii* (Sunquist and Sunquist 2002; Wilson and Mittermeier 2009), and shows plasticity in habitat use and feeding habits (Sunquist and Sunquist 2002; de Oliveira *et al.* 2010). *L. pardalis* is relatively common and its habitat use, diet, and activity pattern overlaps with those of other felids such as *Puma concolor* (Cougar) and *Panthera onca* (Jaguar; Moreno *et al.* 2006; Di Bitetti *et al.* 2010; Davis *et al.* 2011; but see Gómez-Ortiz *et al.* 2015). Some studies indicate that *L. pardalis* exerts a strong influence on other smaller felids in the Neotropic (de Oliveira *et al.* 2010). Particularly, *L. pardalis* abundance appears to negatively impact the abundance and activity patterns of other species by aggressive intraguild interactions or resource limitation (Cuellar *et al.* 2006; de Oliveira *et al.* 2010). Negative interactions exert a strong influence on population size, activity patterns and coexistence between species, but may decrease by spatial or temporal segregation (Donadio and Buskirk 2006; Ritchie and Johnson 2009).

Little research has been conducted on these felids in mountain tropical forests. Particularly the Sierra Norte, in southeastern Mexico, is a mosaic of natural vegetation including tropical, subtropical forest, temperate, and cloud forests. There are also areas of human activity such as agroecosystems and conservation areas (Arriaga *et al.* 2000). Several felids inhabit this region: *L. pardalis*, *L. wiedii*, *Puma yagouaroundi* (Yaguarundi) and *Lynx rufus* (Bobcat), as well as two larger felids: *P. concolor* and *Panthera onca*. The population size and activity pattern of these felids are still largely incomplete and their understanding is essential for the development and evaluation of conservation strategies in mountain tropical forests. Our goal was to estimate the density and activity pattern of *L. wiedii* and *L. pardalis* in Sierra Norte of Oaxaca. Specifically, we expected that *L. pardalis* had a high density relative to other felids due to its ecological plasticity (Sunquist and Sunquist 2002; de Oliveira *et al.* 2010). We also expected segregation in the activity patterns between both felids as a mechanism to reduce negative intraguild interactions (Ritchie and Johnson 2009; de Oliveira *et al.* 2010).

Materials and methods

Study area. The study area is located in the Sierra Norte region, Oaxaca, Mexico, in the community of San Isidro Yolox (17° 38′ N, -96° 25′ W; Figure 1). The region is part of the Sierras Norte-Mixe Oaxaca Priority Land Region (Arriaga *et al.* 2000). The climate is warm and humid. Mean annual temperature varies from 16 °C to 26 °C and precipitation ranges from 2500 to 4000 mm (Trejo 2004). The rainy season stretches from July to December, but there is rainfall throughout the year. The dominant vegetation types are semi-evergreen forest and cloud forest. Semi-evergreen forest areas alternate with agriculture land, pastures, open areas and human settlements. Cloud forests show little fragmentation and human intervention, being among the best preserved areas of natural vegetation in Mexico (Arriaga *et al.* 2000).

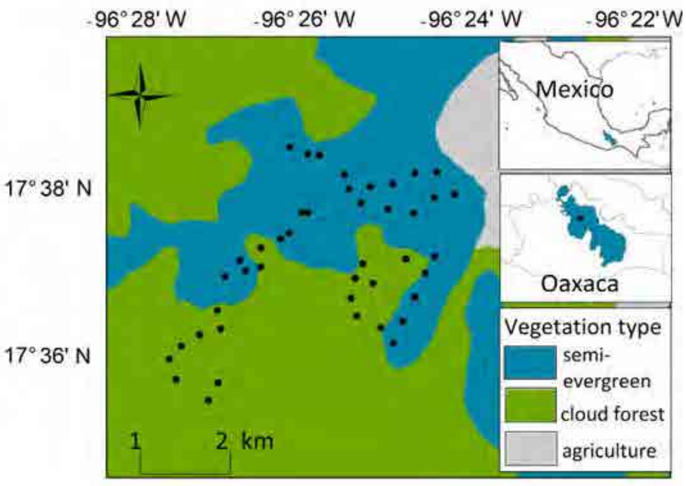

Figure 1. Location of Sierra Norte in southwestern Mexico (A), and study site at Sierra Norte, Oaxaca (B). Black dots indicate the position of camera traps in semi-evergreen and cloud forests (C).

From July 2014 to June 2015, we placed camera traps in 22 sites in the semi-evergreen forest and 22 sites in the cloud forest. The altitude of sites ranged from 480 to 1,050 and from 1,250 to 2000 m, respectively. We placed unbaited traps at 20 to 30 cm above ground and at an average distance of 0.5 ± 0.1 km between them. Camera trap models used were Bushnell Trophy Cam® and 990i Digital Game Camera Moultrie®.

Data analysis. In order to estimate population size, we identified each *Leopardus* individual according to patterns of rosettes, spots and strips on flanks. Males were identified by the presence of testes. We quantified the residence time of each individual as the time from the first to the last record, and considered as a transient individual any individual recorded only in a single month. Because photographs of both sides of the individuals were obtained in different numbers, only the most abundant side were used in the analysis to estimated population size by the Cormack-Jolly-Seber probabilistic model (Lebreton *et al.* 1992). Previously, we determined whether the populations were statistically open or closed with the program CloseTest (Stanley and Richards 2005). The Cormack-Jolly-Seber model estimates only two parameters: survival probability (φ) and capture probability (p). Both parameters can either vary or remain constant over time, so four candidate models emerge: 1) both parameters constant (φp); 2) constant φ and p varies through time (in this case expressed in years: 2014 and 2015; φp_t); 3) φ varies through time and constant p ($\varphi_t p$); and 4) both φ and p vary through time ($\varphi_t p_t$; Lebreton *et al.* 1992; Table 1). We used the program MARK version 8.1 (White and Burnham 1999) for the construction and analysis of the models and used the Akaike Information Criterion modified for small samples to select the best (final) model from the set of four candidate models. We estimated population size (N) as the number of identified organisms divided by the probability of capture of the final model. We extrapolated the population size to an area of 100 km^2. We calculated the effective sampling area as the polygon defined by all trapping stations and a boundary strip. Strip width was defined as the mean maximum distance traveled by an individual that was recorded more than once.

In order to describe activity patterns, we divided the 24-h period into one-hour segments, and classified each independent record within those intervals. We defined an independent record as all photographs belonging to one species taken by each sampling station within a one-hour span. We assessed the level of activity overlapping between species by the coefficient of overlapping Δ_1, a coefficient specially developed for circular data, such as those obtained with camera traps, which ranges from 0 (no overlap) to 1 (complete overlap) (Ridout and Linkie 2009). We also calculated the 95 % confidence intervals for the coefficient from 10, 000 replicates by the bootstraps method. The statistical analysis was performed with the Overlap package in R, version 3.3.1.

Results

With an effort of 12,800 trap-days, we obtained 141 independent records of *L. wiedii* and 68 records of *L. pardalis*, as well as records of another three felid species: *P. concolor* (*n* = 81), *P. onca* (*n* = 11), and *P. yagouaroundi* (*n* = 3). We obtained 86 % of *L. wiedii* records in the cloud forest and 97 % of *L. pardalis* records in the semi-evergreen forest. To estimate the density, we removed 50 % of the total records obtained for both species due to poor photographic quality, and we identified five individuals of *L. pardalis* and 16 individuals of *L. wiedii*. The capture history no fulfilled the assumption of closure (not additions or losses over the period of study) for *L. wiedii* ($\chi^2 = 5.53$, $P = 0.93$) and *L. pardalis* ($\chi^2 = 0.93$, $P = 0.96$). For both species, the best model was φp (*i. e.*, survival and capture probabilities were constant throughout the survey; Table 1). According to this model, the estimated abundance was 51.5 individuals for *L wiedii* and 8.3 individuals for *L. pardalis*, and the density was 81 individuals/100 km^2 and 7.8 individuals/100 km^2, respectively (Table 2).

Of these 16 individuals of *L. wiedii* identified, four were females, four males and eight of indeterminate sex. We recorded two different cubs following the female closely. In the first case (27 January 2015; 05:29), the body size of the cub was about one-third of the body size of the female. In the second (2 February 2015; 05:57), the body size of the cub was similar to that of the female, and perhaps it was one year old. In the case of *L. pardalis*, two were females, two males and one of indeterminate sex. A female with its cub was recorded once (11 July 2014, 23:40 h). The cub followed the female closely, and its body size was about half the body size of the female, so it likely was less than one year old. Fifty six percent of individuals of *L. wiedii* and 40 % of individuals of *L. pardalis* were recorded for a month in the area. One female of *L. wiedii* had the longest residence time (12 months) and the mean residence time was 4.4 ± 1.4 months. One male of *L. pardalis* remained in the zone for 13 months and the mean residence time was 5.17 ± 2.3 months.

Both species were mostly nocturnal (*ca* 82 % of the records; *n* = 68 for *L. pardalis*, *n* = 141 for *L. wiedii*). The period of peak activity of *L. wiedii* occurred around midnight (00:00 h), while *L. pardalis* was most active from 03:00 to 05:00 and from 19:00 to 21:00 (Figure 2). Since *L. pardalis* had fewer records in the cloud forest (*n* = 2), we assessed the overlap between species only in the semi-evergreen forest (*n* = 20 for *L. wiedii*; *n* = 66 for *L. pardalis*). The overlap coefficient was 0.75 (95 % Confidence interval CI = 0.63–0.90). Additionally, we assessed the activity overlapping of *L. wiedii* between cloud forest and semi-evergreen forest, obtaining a high overlap coefficient ($\Delta_1 = 0.77$, CI = 0.63–0.90).

Table 1. Selection of Cormack–Jolly–Seber models for *L. wiedii* and *L. pardalis* in Sierra Norte, southwestern Mexico. The models include time as a covariate to survival probability (φ) and capture probability (p).

Specie	Model	AICc[a]	Δ AICc[b]	AICc Weight[c]	Number of parameters
L. wiedii	φp*	117.98	0	0.48	2
	$\varphi_t p$	119.07	1.09	0.28	3
	φp_t	120.35	2.36	0.14	3
	$\varphi_t p_t$	121.39	3.41	0.08	4
L. pardalis	φp*	54.68	0	0.37	2
	$\varphi_t p$	55.20	0.51	0.29	3
	φp_t	55.61	0.92	0.23	3
	$\varphi_t p_t$	57.30	2.61	0.10	4

[a] Akaike information criterion modified for small samples
[b] Difference between the respective model and the best model
[c] Relative contribution of each model regarding the sum of four models
*Best model selected for each species

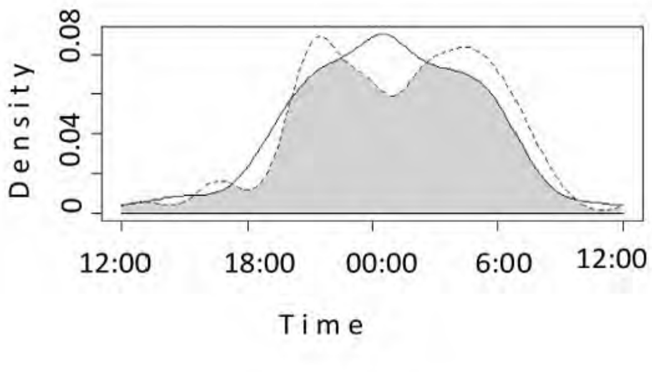

Figure 2. Activity patterns of *Leopardus wiedii* (*n* = 141 records) and *Lepardus pardalis* (*n* = 68 records) at Sierra Norte, Oaxaca, southwestern Mexico. The solid line represents data for *L. wiedii*; the dashed line, for *L. pardalis*.

Discussion

The density of *L. pardalis* was low (7.8 individuals/100 km^2) at Sierra Norte relative to Neotropical regions of Central and South America (3 to 160 individuals/100 km^2; Di Bitetti *et al.* 2008). Density studies for *L. wiedii* were scarce, but the estimated density and number of recorded individuals in our study area were higher (81 individuals/100 km^2) compared to other regions where density has been estimated by capture-recapture with camera trap data, such as Sierra Nanchititla (12 individuals/100 km^2; López-Hernández 2010) or Los Chimalapas (68 individuals/100 km^2; Pérez-Irineo and Santos-Moreno 2016) in the central and southeastern Mexico, respectively.

Several factors may affect the density and activity pattern in felids, such as predators, prey availability, interac-

Table 2. Density and associated data according of the best model (*i. e.,* φp) for *L. wiedii* and *L. pardalis* in Sierra Norte, southwestern Mexico.

	L. wiedii	*L. pardalis*
Number of individuals	16.00	5.00
Abundance	51.50	8.30
Capture probability (standard error)	0.31 (0.06)	0.60 (0.10)
Survival probability (standard error)	0.93 (0.004)	0.91 (0.05)
Density[a]	81.04	7.82
Area (km^2)	63.00	106.00
MMDM (km)[b]	1.90	3.30

[a] Individuals/100 km^2
[b] Mean maximum distance traveled by an individual captured in two or more occasions.

tions between species, human presence, or quality and type of habitat (Di Bitetti *et al.* 2010; de Oliveira *et al.* 2010). In our study area, the presence of large predators may not be a key factor affecting *Leopardus* density, since the record rate of larger predators (*i. e.*, *P. onca* and *P. concolor*) was similar in both vegetation types. Some studies have indicated that large differences in body size minimize the risk of negative interaction between felids (Donadio and Buskirk 2006; Ritchie and Johnson 2009), and other studies did not record evidence of spatial avoidance between *L. wiedii* or *L. pardalis* and larger predators (Hodge 2014). Further studies are required to determine whether the influence of larger felids is similar in the habitat of *L. wiedii* and *L. pardalis*.

Most *L. pardalis* records were obtained in the semi-evergreen forest, and *L. wiedii* was recorded more frequently in the cloud forests. There are few studies in cloud forests for felids; however, the record rate of *L. wiedii* was higher compared to *L. pardalis* in mountain tropical forests or cloud forests (Hodge and Arbogast 2016; Vanderhoff *et al.* 2011). *Leopardus wiedii* inhabits tropical forests, but is also reported in premontane moist forests and cloud forests, and is more strongly associated with dense forests than any other Neotropical felid (Wilson and Mittermeier 2009). In contrast, *L. pardalis* mainly inhabits lowland tropical forests under 2,000 m, including moist and dry forest, swampy savanna and dense thorny chaparral, but is rare in temperate forest (Sunquist and Sunquist 2002; Wilson and Mittermeier 2009). The records of both species may reflect the suitable vegetation types according to their habitat preferences. We also recorded that medium-sized prey of *L. pardalis* had a higher record rate in the semi-evergreen forest, such as *Cuniculus paca* (paca), *Dasyprocta mexicana* (agouti), and *Dasypus novemcinctus* (armadillo). Meanwhile, more small-sized prey (*e. g.,* mice and small birds), common in the diet of *L. wiedii,* were most abundant in the cloud forest compared to the semi-evergreen forest in Sierra Norte.

Furthermore, the low density of *L. pardalis* may allow *L. wiedii* to attain a higher density in Sierra Norte. This is consistent with observations in other regions: the abundance of *L. wiedii* was higher in regions with absence or low density of ocelots, likely as a result of low interspecific competition (Carvajal-Villarreal *et al.* 2012; Kasper *et al.* 2016; Vanderhoff *et al.* 2011). Other medium-sized felids also showed a similar density pattern in sites with low density of ocelots, such as *L. geoffroyi* in central Argentina and Bolivia (Geoffroy´s cat; Caruso *et al.* 2012; Cuellar *et al.* 2006), and *L. tigrinus* in the Brazilian Atlantic forest (Oncilla; Oliveira-Santos *et al.* 2012).

Leopardus pardalis and *L. wiedii* are primarily nocturnal, and we recorded that the activity of both species was consistent with previous observations in other regions (Pérez-Irineo and Santos-Moreno 2016; Vanderhoff *et al.* 2011). Our results suggest that both species may coexist in the absence of pronounced temporal partitioning in semi-evergreen forests. The activity pattern of *L. wiedii* was similar in both semi-evergreen and cloud forests, seemingly unaffected by the presence of *L. pardalis*. In contrast, other studies indicate that small felids show a different activity pattern in sites where large felids are more abundant relative to sites with lower abundance of large felids (Oliveira-Santos *et al.* 2012).

Separately, the population of both species was breeding and a small part consisted of resident individuals. Transient individuals may use the site as a corridor, as suggested for other regions, with individuals moving from less favorable to more favorable patches (Pérez-Irineo and Santos-Moreno 2016; Vanderhoff *et al.* 2011).

Factors including differences in vegetation type and presence of a large number of transient individuals may influence the density of *Leopardus* in Sierra Norte. In addition, dense vegetation cover and low anthropogenic disturbance of the cloud forest, coupled with the lower abundance of *L. pardalis*, contributed to the higher density of *L. wiedii*. Both species have lost some of their original distribution range and are cataloged as endangered in Mexico (SEMARNAT 2010), but internationally *L. wiedii* is listed by the IUCN as near threatened (De Oliveira *et al.* 2015). We provided information about the density and activity of medium-sized felids, as well as on the factors that potentially affect these patterns in tropical mountain forest environments.

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Genetic diversity of the ghost-faced bat *Mormoops megalophylla* Peters, 1864 (Chiroptera: Mormoopidae) in Ecuador; implications for its conservation

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Mormoops megalophylla is a cave-dwelling bat distributed from southern United States across Central America to northern Peru. Its conservation status at a global level is of Least Concern, according to the IUCN Red List of Threatened Species; in Ecuador, however, it is included under the Vulnerable category due to the threats faced by the only two viable populations known. Individuals from each locality (Carchi and Pichincha) were captured and marked. The D-loop of the mitochondrial control region was obtained from wing membrane tissue samples, in order to analyze the geographic distribution of nucleotide and haplotype diversity of the populations, as well as gene flow between them. The molecular variation within and between populations was evaluated through a molecular variance analysis. A high haplotype diversity and a low nucleotide diversity were observed. The gene-flow estimator revealed that Carchi and Pichincha make up a single population coming from a single lineage. The network of haplotypes indicated that those with the highest frequency are shared in both localities; the largest number of unique haplotypes, however, was observed in Pichincha. The high haplotype diversity and low nucleotide diversity values in Ecuador are due to the fact that the ghost-faced bat populations may have experienced a fast-growing period from a low effective population size, with sufficient time to accumulate haplotype diversity, but insufficient to increase nucleotide diversity. The low genetic variability between both localities indicates the existence of a panmictic population that may have been split by factors such as habitat transformation, leading to isolated colonies. The preservation of this vulnerable species will depend on conservation efforts and studies that seek to supplement the analysis of genetic variability with other molecular markers, a continued monitoring of migratory processes, and inventorying of intermediate sites and localities with historical records.

Mormoops megalophylla es un murciélago cavernícola distribuido desde el sur de Estados Unidos a través de Centroamérica hasta el norte de Perú. Su estado de conservación a nivel mundial es de Preocupación Menor, de acuerdo a la Lista Roja de Especies Amenazadas de la IUCN. Sin embargo, en Ecuador se encuentra en la categoría de Vulnerable debido a las amenazas que se enfrentan las únicas dos poblaciones viables reconocidas. En cada localidad (Carchi y Pichincha) los individuos fueron capturados y marcados. A partir de muestras obtenidas de tejido de la membrana alar, se analizó el *D-Loop* de la región control de la mitocondria, con el fin de analizar cómo se distribuye geográficamente la diversidad nucleotídica y haplotípica de las poblaciones, así como el flujo genético entre las mismas. Se evaluó la variación molecular dentro y entre las poblaciones a través de un análisis de varianza molecular. Se halló una diversidad haplotípica alta y nucleotídica baja. El estimador de flujo génico determinó que Carchi y Pichincha conforman una sola población proveniente de un único linaje. La red de haplotipos indicó que aquellos de mayor frecuencia están compartidos en ambas localidades; sin embargo, se observa mayor número de haplotipos únicos en la localidad de Pichincha. Los valores de diversidad haplotípica alta y nucleotídica baja en Ecuador se deben a que las poblaciones del murciélago rostro de fantasma pudieron haber atravesado un período de crecimiento rápido a partir de un tamaño efectivo poblacional bajo, con suficiente tiempo para acumular diversidad haplotípica, pero insuficiente para aumentar la diversidad nucleotídica. La poca variabilidad genética entre ambas localidades indica la existencia de una población panmíctica que se puede haber visto dividida por efectos como la transformación de hábitat dejando a las colonias aisladas. La preservación de esta especie vulnerable dependerá de esfuerzos de conservación y estudios que busquen complementar el análisis de variabilidad genética mediante otros marcadores moleculares, continuar el monitoreo de procesos migratorios e inventarios de sitios intermedios y en las localidades con registros históricos.

Key words: Control region; D-Loop; genetic variation; haplotypes; *Mormoops megalophylla*.

Introduction

Mitochondrial DNA has been extensively used in studies on phylogeny, demographic processes and intraspecific diversity because of its high nucleotide substitution rate and polymorphism, maternal inheritance, and little recombination (Moritz *et al.* 1987; Brown *et al.* 1992; Melnick and Hoelser 1993; Pesole *et al.* 1999). One of the mitochondrial DNA markers most frequently used for assessing genetic differences and population history in a wide variety of taxa is the control region. This preference derives from its being highly variable with a high level of intra-species polymorphism (Brown *et al.* 1986; Wolfe *et al.* 1989; Billington and Hebert 1991; Pesole *et al.* 1999).

At a geographic scale, landscape affects the habitats, distribution, migration, and genetic structure of populations (Manel *et al.* 2003). The tools used in phylogeography and for the analysis of genetic diversity can be used to assess the effects of landscape in the distribution of species and the geographic patterns of genetic diversity (Avise 2000).

Genetic diversity is defined as the amount of inheritable variations in organisms, both between individuals within a population and between populations of a species, usually quantified with parameters including expected heterozygosity, allelic richness, and haplotype and gene diversity (Beebee and Rowe 2008). Genetic variability analyses contribute to the knowledge of the diversity and evolution of the taxonomic groups studied, the description of species, the differentiation between cryptic groups and their distribution (Frankham *et al.* 2002), and could even explain the spatial distribution of genetic variation in populations (Hartl and Clark 2007).

Ecuador is a megadiverse country. In the specific case of mammals, this country ranks ninth worldwide, despite being up to 31-fold smaller in area relative to higher-ranking countries (Tirira 2017). Currently, a total of 431 species have been recorded, with 170 (39.4 %) belonging to the Order Chiroptera. Despite this richness, there are few studies specifically related to the genetic diversity of bat species.

Given the scarcity of this type of information, this study focused on determining the genetic diversity of the Ecuadorian populations of the ghost-faced bat, *Mormoops megalophylla* (Peters 1864). This is a medium-sized insectivore bat (51 – 60 mm, forearm) characterized by complex skin folds in the rostrum, chin with large concave dermal plates, and small eyes surrounded by short rounded ears connected at the front by a skin fold (Rezsutek and Cameron 1991; Tirira 2017). This species is widely distributed in North America, from southern United States through Central America to northern Peru (Rehn 1902; Simmons 2005). Four subspecies are currently recognized: *M. megalophylla megalophylla, M. m. tumidiceps, M. m. intermedia,* and *M. m. carteri;* the latter being the one reported in Ecuador (Dávalos 2006). At a global level, the species is classified as Least Concern in the IUCN Red List of Threatened Species (Dávalos *et al.* 2008); in Ecuador, however, the species is classified as Vulnerable, since its estimated distribution area is less than 2,000 km^2, having been recorded in less than ten localities, and considering that their populations might experience extreme demographic fluctuations (Boada *et al.* 2011).

Mormoops megalophylla inhabits the northern sierra of Ecuador in temperate and high Andean environments where it has been recorded in seven localities: Gruta de la Paz, Rumichaca, Guandera, and Loma Guagua in the Province of Carchi; and in San Antonio de Pichincha, Lloa, and Jerusalem in the Province of Pichincha (Boada *et al.* 2003, 2011). These localities correspond to dry Interandean forest (MDMQ 2011) and lower montane wet forest (MAE 2012). However, records of the species are recurrent only in Gruta de la Paz and San Antonio de Pichincha. The distance between these two localities suggests the potential exchange of individuals between them or the likely existence of additional caves with important populations not yet identified.

Previous studies, especially in Central America, have shown that when there are geographic barriers between bat populations, these show varying degrees of genetic variability (Guevara-Chumacero 2009; Caraballo 2012; Zárate-Martínez 2013; Ruiz-Ortiz 2014). Thus, it was considered that a study to assess genetic diversity in *Mormoops megalophylla* could provide information on the role of landscape as geographical barrier, since it is composed of an array of agricultural and cattle-raising land with few patches of natural forest within an altitudinal range between 1,800 and 4,020 m. The intraspecific relationships in the species of the family Mormoopidae in Ecuador have not been studied; hence, this first approach will determine the genetic variability patterns between populations that are probably remnants of *Mormoops megalophylla*, characterizing the current geographical distribution of the genetic diversity of populations, and laying the foundation for further studies and proposals related to the conservation of this species.

The research activities proposed in the Action Plan for the Conservation of Bats of Ecuador by Burneo *et al.* (2015) include the design and development of studies that contribute to the knowledge of the species to determine its demographic features and current conservation status. These objectives can be partially achieved with the information derived from the assessments of the genetic status of the main populations of the ghost-faced bat across its distribution range.

The objective of this study is to provide information about the genetic diversity patterns of *Mormoops megalophylla* in Ecuador, through the analysis and description of the geographical distribution of haplotype and nucleotide diversity of populations, in order to infer whether alterations in landscape have become physical barriers that restrain gene flow between them.

Materials and Methods

Study area, marking of individuals and sample collection. Two localities were sampled: Gruta de la Paz (GP, Carchi) 0° 30′ 59.976″ N, -77° 52′ 0.0114″ W, a tunnel-like broad cave, and San Antonio de Pichincha (SAP, Pichincha) 0° 0′ 57.6″ N, -78° 27′ 0″ E, a cave of about 120 m in length (Boada 2003; Figure 1). Individuals were captured and manipulated following the techniques of Kunz *et al.* (2009) using mist nets from 18:30 until 23:30 (5 hours/net/day) at sites close to shelters in the two localities for a total of 12 nights over a period of eight months in each locality, between June and September 2014. Samples of wing membranes were collected and stored in microtubes, preserved in 70 % ethanol and kept at 4 °C until DNA extraction. Bats were marked with aluminum rings (National Band and Tag Company©) in the forearm and with numbered tattoos in the plagiopatagium following the methodology proposed by Kunz and Weise (2009). Bats were released in order to record any displacement of individuals between both areas.

Four voucher specimens were collected, two males and two females from each locality, following the collection,

Figure 1. Sampling and marking localities of *Mormoops megalophylla* in Ecuador. GP (Gruta de la Paz - Province of Carchi) in red; SAP (San Antonio de Pichincha - Province of Pichincha) in green. The map depicts the linear distance between both localities, in kilometers.

preparation, and preservation protocols of Simmons and Voss (2009). The specimens were deposited in the Mammalogy Section of the Zoology Museum at Pontificia Universidad Católica del Ecuador (QCAZ-M). Tissues were frozen at -20 °C.

The sampling and collection of specimens were performed following the ethical guidelines specified in Sikes *et al.* (2016). Field work was conducted with the permission of the Provincial Offices of the Ministry of the Environment in Carchi and Pichincha (Research authorizations MAE-DPAC-UPN-BD-IC-FAU-2014-002 and 09-2014-IC-FAU-DPAP-MA, respectively).

Mitochondrial DNA extraction, amplification, and sequencing. DNA was extracted from 20 individuals from each locality, following the protocol of Lopera-Barrero *et al.* (2008). The D-Loop was amplified following the protocol of Zhong *et al.* (2013) using the primers for the mitochondrial DNA Control region in mammals reported by Fumagalli *et al.* (1996): L16517 (5'-CAT CTG GTT CTT ACT TCA GG-3') and HSC (5'-TGT TTT AGG GGT TTG GCA G-'3), with a modification of primer HSC by Guevara-Chumancero (2010): HSC (5'-TGT TTT AGG GGT TTG GCA G-3') to amplify 700 bp approximately. The thermal profile consisted in an initial denaturation at 94 °C for one minute followed by 35 amplification cycles at 94 °C for one minute, alignment at 50 °C for 45 seconds, extension at 72 °C for 90 seconds, and a final extension step at 72 °C for four minutes.

The amplified products were purified using the commercial kit Amicon Ultra-0.5 mL Centrifugal Filters for DNA Purification and Concentration - UFC503096 (Millipore) according to the manufacturer's protocol. Subsequently, the sequencing reaction of both strings was performed using the Big Dye Terminator Kit (Applied Biosystems) and including the following stages: one run at 96 °C for one minute, 35 cycles at 96 °C for 10 seconds, 50 °C for five seconds, 60 °C for 4 minutes, 60 °C for one second and a final temperature of 10 °C. Samples were sequenced in the ABI PRISM 3130XL analyzer. The extraction, amplification, photodocumentation, purification, and sequencing processes were conducted in the Molecular Biology Divisional Laboratory (LDBM) at Universidad Autónoma Metropolitana, Campus Iztapalapa, Mexico (UAM-I).

Sequences were reviewed, edited, and aligned using the Clustal W algorithm in Geneious v.8.1.3 (Kearse *et al.* 2012), and were analyzed visually. In this process, we worked with a 273 bp fragment because regions of tandem repeats (GTGCACACACCCACGT) with absence of polymorphisms were found from position 274.

Intra-population genetic diversity. The following diversity estimators were determined for each locality: number of polymorphic or segregating sites (S) to represent the number of sites that differ between the aligned sequences; number of haplotypes (k); haplotype diversity (h; Nei 1972) to describe the number and frequency of haplotypes with values between 0 and 1, where < 0.5 and > 0.5 represent low and high diversity, respectively. Also, nucleotide diversity (π; Nei 1978) was determined to reflect the frequency of haplotypes and the divergence of sequences between all haplotypes, by measuring the probability of finding two different homologous nucleotides when these are analyzed in the sequences. This parameter can have values between 0 and 1, and is interpreted in the same way as haplotype diversity (Nei 1972; Frankham *et al.* 2002). These analyzes were run with DNAsp v.5 (Librado and Rozas *et al.* 2009).

The molecular variation within and between populations was determined through an analysis of molecular variance (AMOVA) with Arlequin v.3 (Excoffier *et al.* 1992). The gene flow (*Nm*) between populations was analyzed with DNAsp v.5 (Librado and Rozas *et al.* 2009) based on the Islands Model of Hudson *et al.* (1992).

To estimate genetic distances between populations, the fixation index (F_{ST}) between the two populations was calculated with MEGA v.5 (Tamura *et al.* 2011), using the Tamura-Nei model (Tamura and Nei 1993) which considers the differences in substitution rates (transitions and transversions) as well as the different frequencies of the nucleotide bases.

Generation of the haplotype network. The genealogical relationships between the haplotypes found and their geographical distribution were analyzed through a network of haplotypes following the Median Joining method (Bandelt *et al.* 1999) using PopArt v.5.

Calculation of distances between caves. In addition to the Euclidean distance between the San Antonio de Pichincha cave and the Gruta de la Paz cave, the lowest-cost route between the two localities was calculated based on the minimum difference of altitude in the transition between pixels using the Cost Distance spatial analysis tool from ArcGis v10.3.1, on an elevation layer with a resolution of 30 seconds obtained from the ESRI (Environmental Systems Research Institute) website.

Results

Study area, marking of individuals and sample collection. Over eight months, a total sampling effort of 60 hours/net was conducted in each locality; this led to 473 individuals captured, 93 corresponding to GP (42 males and 51 females) and 380 to SAP (226 males and 154 females). Seventy two of the individuals captured were marked in GP and 338 in SAP. Wing membrane tissue was collected from 53 individuals in GP and 98 in SAP, randomly chosen among the adults captured. During the study, there were no individuals recaptured in a given locality that had been previously marked in the other.

The sampling effort, in hours/net, was similar in the two localities; however, the number of individuals captured in GP represented only 24.5 % of those captured in SAP. This was due to the difficulty of capture in GP, mainly due to the restricted access to the cave through ravines, pasture land, private agricultural plots, and the flooding of Apaqui river between June and September 2014, as well as to the impossibility to capture individuals manually because of the height of the cave roof (about 30 meters).

Mitochondrial DNA extraction, amplification and sequencing. Molecular analyses were run using 20 tissue samples from each locality (GP: 7 males, 13 females; SAP: 16 males, 4 females). Of these tissues, DNA was successfully extracted from 37 individuals: 17 from GP and 19 from SAP. The amplification and sequencing of the selected region produced 33 edited D-Loop sequences with a total length of 700 bp and a final length of 273 bp.

Intra-population genetic diversity. The diversity estimators of the D-Loop region for the study localities are shown in Table 1. The 33 sequences analyzed yielded nine segregating sites (S = 9). The GP population shows lower number of segregating sites, haplotype diversity and nucleotide diversity relative to SAP. However, haplotype diversity was high (> 0.5) and nucleotide diversity was low (< 0.5) in both localities. A total of nine haplotypes (k = 9, encoded as H1 - H9) were identified in both locations. There were eight haplotypes in SAP, four of these being unique (H6, H7, H8, and H9); in GP, five haplotypes were found, with only one being unique (H4; Figure 2). Of these nine haplotypes, three (H1, H2, and H3) showed the highest frequency in the 33 individuals analyzed in both localities. The location of segregating sites in the nine haplotypes identified is shown in Table 2.

Table 1. Diversity estimators of the D-Loop, distribution and frequency of haplotypes within localities. (*n*): sample size; (S): number of segregating sites; (k): number of haplotypes; (h): haplotype diversity; (π): nucleotide diversity.

Population	(*n*)	(S)	(k)	(h)	(π)	Haplotype frequency
SAP	19	9	8	0.854	0.0041	H1(3); H2(4); H3(6); H5(1); H6^u(2); H7^u(1); H8^u(1); H9^u(1)
GP	14	5	5	0.791	0.0034	H1(3); H2(5); H3(4); H4^u(1); H5(1)
TOTAL	33	9	9	0.814	0.0037	

^{u}: unique haplotype for the population

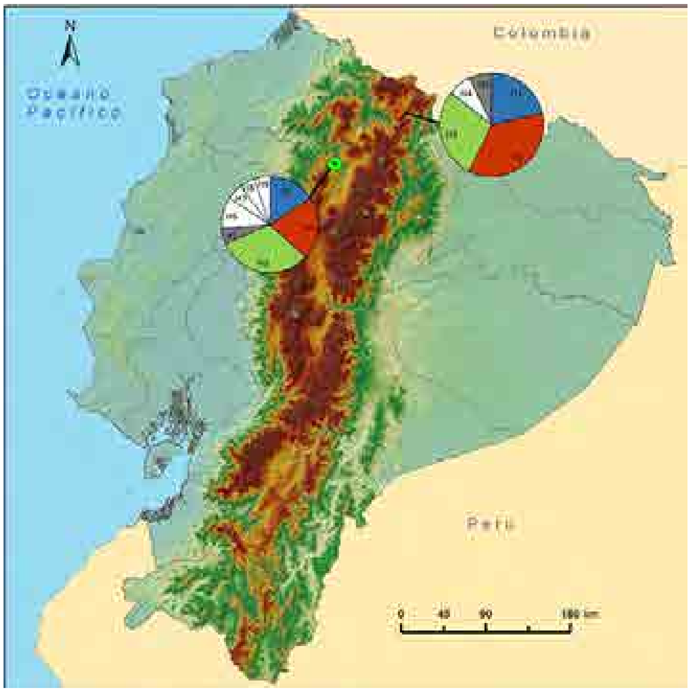

Figure 2. Geographical distribution of D-Loop haplotypes in the two localities. The pie charts show the geographic location of haplotypes and their distribution in the two localities. Colors indicate shared haplotypes; white indicates haplotypes that are unique to each locality. Each haplotype is named with the letter H followed by the respective number.

The AMOVA indicated a low differentiation level between SAP and GP populations ($F_{ST\,(SAP\text{-}GP)} = 0.04$, $P < 0.05$). This analysis showed that this low differentiation level is solely due to differences within populations (103.46 %) rather than to differences between populations (-3.46 %; Table 3).

The gene flow estimated by the number of migrants between both groups using the Islands Model of Hudson et al. (1992) was negative ($Nm_{SAP\text{-}GP} = -15.42$), indicating that this estimator cannot be defined for the sample.

Haplotype network. The configuration of the haplotype network obtained provides further data supporting the lack of differentiation between the populations studied. H1, H2, and H3 are the most frequent haplotypes and are distributed evenly between localities. One unique haplotype was observed for GP and three for SAP (Figure 3).

Calculation of distances between caves. The Euclidean distance between the two bat colonies where large popu-

Table 2. Variable sites and frequency for the nine haplotypes obtained from the D-Loop in the two localities. Dots represent equality based on the first row (H1). Numbers represent the position of the variable base in the sequence. The right side of the table details the frequency of each haplotype by locality.

	131	139	187	197	200	208	220	222	233	SAP	GP
H1	G	G	A	G	T	C	A	C	T	3	3
H2	.	A	.	.	.	.	.	.	C	4	5
H3	.	A	.	.	C	.	.	.	C	6	4
H4	.	A	G	.	C	.	.	.	C	0	1
H5	.	A	.	A	C	.	.	.	C	1	1
H6	.	A	.	.	C	.	.	G	C	2	0
H7	.	A	.	.	C	.	G	.	C	1	0
H8	A	A	.	A	C	.	.	.	C	1	0
H9	.	A	.	.	.	T	.	.	C	1	0

Table 3. Analysis of molecular variance (AMOVA) of the D-Loop in the two populations (*$P < 0.05$).

Source of variation	df	Sum of squares	Variance components	Percentage of Variation	F_{ST} Index
Between populations	1	0.402	-0.02920 Va	-3.46	$F_{ST} = 0.04$*
Within populations	31	27.053	0.87267 Vb	103.46	
TOTAL	32	27.455	0.84346		

lations of the ghost-faced bat have been recorded — San Antonio de Pichincha, in the Province of Pichincha, and Gruta de la Paz, in the Province of Carchi — is 87.6 km (Figure 1). A flight in a straight line following the topography of the land would involve an altitudinal difference of 2,220 m. The calculation of the lowest-cost route indicates that, although the flight distance would increase by 44.6 km (to 132.2 km), the altitudinal difference would be of only 1,090 m (Figure 4).

Discussion

This work is a first approximation to analyzing the genetic diversity between colonies of the vulnerable species *Mormoops megalophylla*, and contributes to the conservation efforts proposed by the Action Plan for the Conservation of Bats of Ecuador (Burneo *et al.* 2015). In spite of living in isolated locations, these bats behave as a single population as evidenced by the little genetic variability between them.

The mitochondrial region analyzed showed a lower genetic diversity in the GP population vs. SAP. This low diversity may be a result of historical reductions in bat population size in GP, leading to bottlenecks with the consequent loss of diversity (Frankham 1995). A pattern of high haplotype diversity coupled with low nucleotide diversity has been observed in the genus *Pteronotus*, as well as in the family Mormoopidae. This pattern arises either because populations underwent bottlenecks followed by accelerated population growth, or because the populations remaining after experiencing bottlenecks have lost their genetic variability (see Guevara-Chumacero 2009; Caraballo 2012; Zárate-Martínez 2013; Ruiz-Ortiz 2014). There were nine segregating sites obtained with the D-Loop (Table 1); this finding is consistent with the expected result, as the D-Loop shows high variation levels for being non-coding (Klicka *et al.* 1999; Milá *et al.* 2007; Beebee and Rowe 2008; McCormack *et al.* 2008). It should be noted, however, that the results of analyzing a mitochondrial marker are associated with females, so that subsequent studies should include markers associated with the Y chromosome in the analysis.

The haplotype diversity found in the control region is low relative to the results obtained in other studies using the same mitochondrial region. In this case, nine haplotypes were observed in 33 samples, contrasting with studies conducted in other bats with long-range flight capabilities: 35 haplotypes in 53 samples of *Leptonycteris curasoae* (Phyllostomidae) (Wilkinson and Fleming 1996); 86 haplotypes in 94 samples of *Tadarida brasiliensis* (Molossidae; Russel *et al.* 2005); and 67 haplotypes in 105 samples of another mormopid bat, *Pteronotus davyi* (Guevara-Chumacero 2009).

Based on the information published by Nei *et al.* (1975) and Avise (2000), it could be inferred that the high haplotype diversity and low nucleotide diversity values in Ecuador suggest that ghost-faced bat populations could have undergone a period of vigorous growth from a low effective population size, with time sufficient to build haplotype diversity but insufficient to increase nucleotide diversity.

The F_{ST} value for the D-Loop is very close to zero (F_{ST} = 0.04), indicating a virtually non-existent population variability. The negative, or infinite, value of *Nm* indicates that in this case the estimator cannot be defined for the sample, which could be due to the fact that the subpopulations analyzed actually belong to a single genetic population (Hudson *et al.* 1992). The AMOVA results show the lack of genetic differentiation between both populations (Table 3); the negative value between populations indicates that there is no variation, while a value above 100 % shows that the total variation occurs within populations (Beebee and Rowe 2008). The poor differentiation between haplotypes is indicative of a panmictic population that has been fragmented recently by habitat loss and transformation, in addition to the direct threats that populations currently face, such as moderate tourism activities in SAP and religious events in GP.

The little differentiation between haplotypes and the shared frequencies between both localities suggest the existence of a single lineage. However, the absence of recaptures of individuals from SAP in GP, and vice versa, in this study, suggests that this population has been split by habitat transformation, leading to isolated colonies.

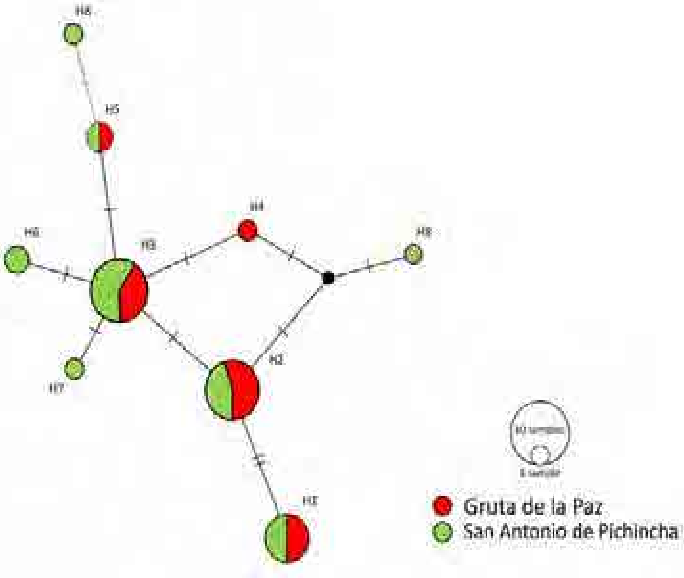

Figure 3. Median-joining haplotype network for *D-Loop* in the populations of *Mormoops megalophylla* studied in Ecuador. Circles represent the nine haplotypes, with GP haplotypes in red and SAP haplotypes in green. Lines on bars that separate haplotypes represent the mutational steps between one haplotype and another. The black dot represents a haplotype that was not sampled.

In spite of this, the absence of genetic differentiation could be due to the high dispersal ability of bats associated with their high and strong flight (Rezsutek and Cameron 1993), although other studies with flying species, including migratory ones, have shown that genetic differences may be a consequence of habitat fragmentation (Bates 2002; Lindsay *et al.* 2008; Oliveras de Ita *et al.* 2011). By avoiding high mountain areas in this potential flight route, individuals would be forced to cross a greater number of fragmented areas, as shown in Figure 4. The species studied is tolerant to fragmented environments, but prefers cave environments (Rezsutek and Cameron 1993); therefore, the lowest-cost route would define future efforts in the search of caves in these intermediate environments where populations of the species could be found, in order to confirm whether there is flow of individuals (and, therefore, gene flow) between the Ecuadorian populations, since non-reproductive males and females of the species often use different caves or different parts of caves than breeding females (Bonaccorso *et al.* 1992).

Endangered species often exist as a few isolated populations (Harrison and Bruna 1999), and this has been the situation observed in the ghost-faced bat populations studied in Ecuador. It is crucial to preserve both populations, as the presence of unique haplotypes suggests the occurrence of an early differentiation event. If this is the case, this variability could be detected in future analysis with the use of markers such as microsatellites or restriction sites associated DNA (RADseq).

Under this assumption, the maintenance of genetic diversity is important for two main reasons: individual differences are important because they are inheritable and, therefore, provide inputs for natural selection; in addition, genetic diversity reduces the inheritability of unfavorable traits, since individuals in isolated populations are forced to mate with relatives (inbreeding), leading to genetic uniformity in offspring (Lacy 1997). Maintaining genetic diversity in endangered species such as *Mormoops megalophylla* is essential for the survival and adaptability of their populations in the face of extreme environmental conditions such habitat fragmentation and pollution.

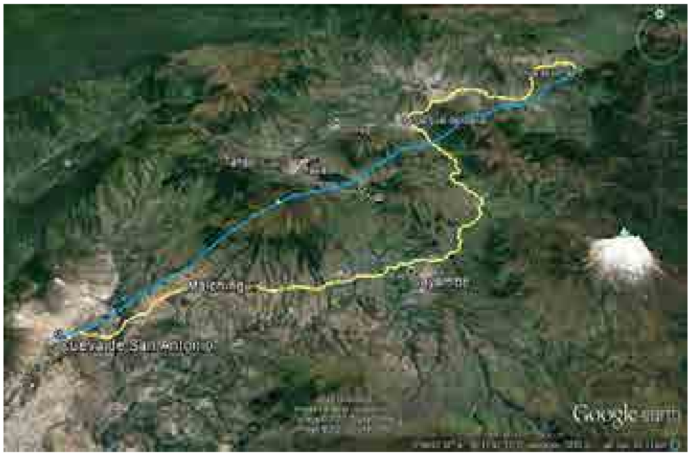

Figure 4. Flight routes between San Antonio de Pichincha and Gruta de la Paz caves. Blue: straight-line route (87.6 km); Yellow: least-cost route (132.0 km).

The San Antonio de Pichincha cave and the Gruta de la Paz cave maintain numerous bat colonies in tourist areas and zones dedicated to the extraction of building materials, making them sensitive to disturbance. Boada *et al.* (2003) estimated that the Pichincha colony would include around 4,800 individuals, while estimates from this study indicate the presence of around 3,260 individuals; which indicates a significant decline in a period of just over a decade. Something similar is likely happening in the Carchi colony. Being a strict insectivore, the ghost-faced bat has a significant bioindicator potential due to its susceptibility to pollutants by having a high bioaccumulation capacity (Jones *et al.* 2009). This is an important trait to be considered in areas that include the last remnants of Andean dry forests in the region.

In order to preserve the genetic variability of this species in Ecuador, a significant effort is needed to inventory possible caves in intermediate localities between San Antonio and Gruta de la Paz, given the genetic flow that may still exist between these populations, as suggested by the results of the gene flow analysis, which could not be confirmed through recaptures. If new colonies of ghost-faced bats are found, local conservation networks should be formed to maintain the integrity of caverns.

In 2011, the cave located in San Antonio de Pichincha was declared an Important Site for the Conservation of Bats (SICOM) by the Latin American and the Caribbean Network for the Conservation of Bats (RELCOM) after having considered this place as a refuge for the species. A similar approach is currently in development for Gruta de la Paz. The information obtained in this study will be one of the inputs to meet the conservation goals for this species, as proposed in the Action Plan for the Conservation of Bats of Ecuador (Burneo *et al.* 2015).

The populations of *Mormoops megalophylla* in Ecuador yielded low estimated diversity values relative to other mormopid bats for the mitochondrial region analyzed. The genetic diversity indicators ($F_{ST,}$ *Nm*, and AMOVA) show that the two populations studied form a single genetic population that, according to the haplotype network, is undergoing an early differentiation stage.

This study and its results, in relation to the information on the molecular marker used, provide early indications of the status of populations based on their genetic variability. These should be supplemented with the use of a marker associated with the Y chromosome, and with information from other markers such as microsatellites.

The disruption of caves has proved to be a significant threat for the conservation of species such as *Mormoops megalophylla* in Ecuador. Although we consider that all caves sheltering bats should be protected and their access restricted whenever possible, we also believe that tourism activities should be carefully planned and monitored.

The conservation of this bat species in the country warrants continued monitoring using marking techniques to determine its migratory processes and evaluate the habitat fragmentation between the two locations studied. Also required are sampling efforts in intermediate sites and localities with historical records, as well as the analysis of other genetic regions as markers of nuclear origin.

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Geographical distribution and niche conservatism in populations of *Orthogeomys dariensis* (Rodentia: Geomyidae) in the Chocó Biogeographical region

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The Chocó biogeographic region is among the richest in terms of natural resources, species richness and number of endemisms. Among the species endemic to this region, the pocket gopher, *Orthogeomys dariensis* (Geomyidae), presents a disjunct distribution on both sides of Serranía Darien-Baudó. These populations have been considered as different species, under the names *O. dariensis s.s.* (northern) and *O. thaeleri* (southérn). This study aims to model the potential distribution of *O. dariensis s.s.* to assess niche divergence between these geographic populations. Using presence records, associated data, and 19 bioclimatic variables, an ecological niche-modeling approach was applied to: 1) estimate the distribution of the northern and southern populations, both separately and as a single species; 2) assess whether each population model predicts the distribution of the other, and analyze their differences through a MESS analysis; and 3) test the overlap and similarity of these niches as a proxy for niche conservatism between *O. dariensis s.s.* and *O. thaeleri*, through the estimation of ecological niche ellipsoids for the fundamental niche (E_A). When considered as separate populations, these show an allopatric distribution, with the Darién-Baudó zone acting as a barrier between them. Also, *O. dariensis* data predicts a large part of the distribution of *O. thaeleri* over the study region, and vice versa. When considered as a single species, it shows a broader and continuous range, including the Darién-Baudó region as part of its potential distribution. The MESS analysis shows similar climatic conditions in general, and few particular conditions that are unique to each zone, which would not represent conditions so unique as to segregate them. Therefore, the apparent disjunction between populations may be due to the lack of records and systematic surveys in this region. This is also reflected in the moderate overlap of their niche ellipsoids, showing the ecological conditions shared between these populations. Our results support the existence of a single species, *O. dariensis* (*sensu* Hafner 2015), with a broad and continuous distribution in the Chocó biogeographic region. This is consistent with recent analyzes of DNA data showing very low genetic divergence between populations north and south of Darién-Baudó (as an intermediate area). Rather than a barrier promoting diversification, this region could represent a dispersal area for these populations.

La región del Chocó Biogeográfico es una de las zonas del mundo con mayor riqueza en recursos naturales, diversidad y endemismo de especies. Entre las especies endémicas de la región se encuentra la tuza *Orthogeomys dariensis* (familia Geomyidae), que presenta una distribución discontinua a ambos lados de la zona Darién-Baudó. Esquemas taxonómicos previos consideraban estas poblaciones disyuntas como especies distintas; *O. dariensis s.s.* al norte y *O. thaeleri* al sur. En este estudio se modela la distribución potencial de *O. dariensis s.s.* y evalúa la diferenciación de nicho de dichas poblaciones. Usando registros de presencia, información asociada, y 19 variables bioclimáticas, 1) se estimaron las distribuciones potenciales para las poblaciones norte y sur y como especie; 2) se evaluó si cada modelo poblacional predice la distribución del otro y mediante el análisis de similitud multivariada ambiental (MESS) se evaluó qué tan diferentes climáticamente son estas áreas con respecto a la de cada grupo; y 3) se realizó una prueba de similitud de nicho ecológico como 'proxy' del conservadurismo de nicho entre *O. dariensis s.s.* y *O. thaeleri* mediante la estimación de los elipsoides del nicho fundamental existente (E_A) en el espacio ecológico. Considerados como poblaciones independientes, estas presentan una distribución alopátrica, con el Darién-Baudó como una barrera entre ellas. Asimismo, *O. dariensis* predice gran parte de la distribución de *O. thaeleri* sobre las áreas evaluadas, y viceversa. Consideradas como una sola especie, ésta presenta una distribución potencial mucho más amplia y continua, incluyendo la zona del Darién-Baudó. El análisis MESS muestra condiciones climáticas similares y algunas particulares entre cada zona evaluada, pero que no representarían condiciones únicas como para separarlas significativamente. Siendo así, esta alopatría podría ser un artificio metodológico por falta de registros y muestreos sistemáticos en la zona. Esto también se refleja en la sobreposición media de sus elipsoides del nicho ecológico, donde estas poblaciones comparten condiciones ecológicas. Nuestros resultados señalan la presencia de una única especie *O. dariensis* (*sensu* Hafner 2015) con una distribución amplia y continua en el Chocó Biogeográfico. Esto es congruente con análisis previos de secuencias de ADN que indican baja o nula divergencia entre poblaciones al norte y sur de la zona Darién-Baudó (área intermedia); ésta, más que una barrera, representaría una potencial zona de dispersión de ambas poblaciones.

Key words: Biogeographic Chocó, niche conservatism, potential distribution, Geomyidae, pocket gophers.

INTRODUCTION

The Chocó biogeographic region, stretching from southern Panama to northern Ecuador, is one of the regions of greater richness and biological uniqueness worldwide (Hernández-Camacho *et al.* 1992; Morrone 2001), covering the western (Pacific) slope of the Andes, from sea level to

2,000 m (*sensu* Gentry 1982; Olson and Dinerstein 2002). This biological uniqueness is due to the presence of ecosystems as varied as the Chocó trans-Andean rainforests, the Chocó-Darien humid forests, the montane humid forests of Panama and the Chocó-Esmeraldas mangroves (Holdridge *et al.* 1971; Hershkovitz 1982; Hernández-Camacho *et al.* 1992; Arias-Alzate *et al.* 2012). These ecosystems, communicated with the inter-Andean valleys of the northern end of the Western and Central Cordilleras, are dispersal routes for lineages originated in South, North and Central America (Hernández-Camacho *et al.* 1992; Morrone 2001). Therefore, the Chocó is a region of great importance for understanding the systematics and historical biogeography of many vertebrate species (Morrone 2001; Arias-Alzate *et al.* 2012).

A total of 84 rodent species are currently recorded for the Chocó biogeographic region (Méndez 1993; Tirira 2010; Solari *et al.* 2013), many of which display a continuous distribution throughout the region. Groups like the genus *Orthogeomys*, although showing high diversity from southern Mexico to Central America, have a low species richness in the north tip of South America (Goldman 1920; Hall and Kelson 1959; Méndez 1993). In this region, Serranía del Darién, Serranía de los Saltos and Serrania del Baudó form a mountain range that apparently function as a geographical barrier restraining the dispersal of the terrestrial fauna toward southern areas (Alberico 1990; Sudman and Hafner 1992; Valdés-Velásquez 2003; Hafner 2015). However, some authors argue that in the case of fossorial species this mountain range does not represent a definitive biogeographical barrier (Alberico 1990; Monge 2010).

Historically, the presence of *O. dariensis* in the region had been reported in several locations in the eastern end of Panama, near Serranía del Darién between 80 and 750 m on the border with Colombia (Goldman 1920; Handley 1966). For its part, *O. thaeleri* was described by Alberico (1990) and is known from several localities across central Chocó between 30 and 100 m. Until now, these populations had been treated as different species based on differences in pelage and cranial features (Alberico 1990). However, due to the low genetic divergence between individuals assigned to both species, 0.3 % for the cytochrome-b mitochondrial gene (Sudman and Hafner 1992) and 0 % for two nuclear genes (Spradling *et al.* 2016), *O. dariensis* and *O. thaeleri* are currently considered as a single species (Hafner 2015; Spradling *et al.* 2016).

Given the few distributional and ecological studies on these populations (Goldman 1920; Alberico 1990; Correa and Perea 2007), their geographical ranges remain little known. Moreover, the spatial and temporal variability of their niches, which would allow an approximation to the evolutionary history of the species, remain are unknown. In this investigation, stemming from the hypothesis that *O. dariensis s.s.* and *O. thaeleri* are two allopatric populations, we evaluated the degree of ecological segregation between these populations through an approximation of ecological niche models and niche conservatism hypotheses.

METHODOLOGY

Species records. Records of the presence of *O. dariensis* (northern and southern populations) were gathered through a revision of the specimens deposited in biological collections of Universidad Tecnológica de Chocó (Quibdó) and Instituto Alexander von Humboldt (Villa de Leyva); in addition, the relevant information in the scientific literature was reviewed (*e. g.*, Alberico 1990; Reid 2009; Hafner 2015). For each record, the data gathered included locality and geographical coordinates (in decimal degrees), height above sea level and source of the records. The characteristics of soil were described according to the Soil Geographic Databases compendium (www.soilgrids.org).

Climate Information. Given the scarce knowledge on the taxonomy, ecology and distribution of these taxa (Goldman 1920; Alberico 1990; Correa and Perea 2007), and to avoid subjectivities in the selection of the most relevant climate variables that determine the distribution of *O. dariensis*, 19 bioclimatic variables were used from the general circulation model CGCM31 developed by CCMA (Canadian Center for Climate Modeling and Analysis), downloaded from the WorldClim webpage (http://www.worldclim.org, Hijmans *et al.* 2005). All variables were processed with a resolution of 30 arc-seconds (equivalent to 1 km^2 or 0.008333 degrees).

Ecological niche models and potential distribution. Numerous methods for the study of ecological niches and geographic distributions are currently available, which have been compared extensively (Elith and Graham 2009; Elith *et al.* 2011; Peterson *et al.* 2011). For this reason, since our objective focuses mainly on ecological and evolutionary aspects of isolated populations rather than on the comparison of these methods, this study was conducted using the MaxEnt algorithm, a heuristic method that has produced satisfactory results (Elith *et al.* 2011; Santika 2011). The ecological niche modeling with MaxEnt estimates the probability of occurrence of a species through space, by comparing the ecological conditions in which the species has been recorded vs. a sample of background pixels of the study area using a Bayesian adjustment procedure and under the maximum-entropy principle (Phillips *et al.* 2006; Phillips and Dudik 2008). The predictions derived represent hypotheses on conditions similar to those where the species has been observed; the result is often interpreted as the potential distribution of the species (sensu Peterson *et al.* 2011).

From the hypothesis that *O. dariensis* has two populations (corresponding to *O. dariensis s. s.* and *O. thaeleri* as defined by Alberico 1990), two strategies were developed to model the potential distribution ranges. In the first strategy, the geographic distributions are estimated and compared considering two separate populations; in the second strategy, the species is modeled as a single taxon (*O. dariensis s.l.*). These distributions were derived by dividing the total number of records (G_+, *sensu* Peterson *et al.* 2011) in two data sets: a calibration data set (75 % of the data) and an evaluation data set (25 %), the procedure was repeated 100 times (100 replicates, each with 500 iterations; and each data set with different random partitions) using the bootstrap method (Phillips *et al.* 2006; Phillips and Dudik 2008).

As little is known about the ecological features and dispersal ability of this species, two areas (M; *sensu* Peterson *et al.* 2011) of different size (small and large) were produced to explore whether each individual population considered separately predicted the distribution of the other. Given the geographical characteristics of the region between Panama and Colombia, areas of 4,560 km^2 and 25,500 km^2 were generated for the northern population; and areas of 5,700 km^2 and 24,800 km^2, for the southern population. In addition, an analysis of multivariate environmental similarity surfaces (MESS; Elith *et al.* 2011; Saupe *et al.* 2012) explored the extent of the climatic differences between these areas, and whether some variables show values outside of the calibration area (the area where the model was produced) that might be influencing predictions (area where the model was projected) to a significant extent. The fitness, performance and discriminating capacity of the models were evaluated through the ROC (Receiver Operating Characteristic) curve and the AUC (Area Under the ROC curve) value, based on validation data (Phillips *et al.* 2006; Muscarella *et al.* 2014). The AUC$_{TEST}$ has proved to be a useful tool for ordinal scoring models (McPherson 2004; Thuiller *et al.* 2005; Santika 2011; Muscarella *et al.* 2014). The key variables for each population were identified using the Jacknife test (incorporated in MaxEnt).

Subsequently, a climatic characterization of the distributions in terms of temperature and precipitation was carried out for the analysis of the potential climatic segregation between populations, which would effectively validate a bias in terms of the geographical representativeness of populations. These variables have shown a good environmental resolution to interpret the interactions between species and their environment (abiotic factors) (see Tocchio *et al.* 2015; Qiao *et al.* 2016). Likewise, this characterization was performed for the Darién-Baudó, the geographic area in between the two separate distributions (see results), which apparently would function as a geographical barrier restraining the dispersal of these and other populations to southern areas in the region (Alberico 1990; Sudman and Hafner 1992; Valdés-Velásquez 2003; Hafner 2015). All subsequent processing and analyses were carried out in a geographic information system using the software ArcGIS 10.1 (ESRI 2014).

Similarity and conservatism of ecological niches. After exploring and estimating the distribution range for each population separately and for the two populations combined, we conducted an ecological niche similarity test as a proxy for niche conservatism (Wiens and Graham 2005). To this end, both the individual ellipsoids of each separate population and the one of the overall species were estimated in the ecological space using probabilistic models (MaxEnt output) as the hypothesis of the existing fundamental niche (E_A) (Soberon and Nakamura 2009; Peterson *et al.* 2011; Qiao *et al.* 2016). This was conducted by means of the similarity and ecological niche overlap algorithm using the program Niche Analyst (NicheA; Qiao *et al.* 2016). Given the difficulty to estimate and visualize the multi-dimensional ecological space and the subsequent representation of niches in such space, a principal components analysis (PCA) was performed with climatic variables to reduce the dimensionality and hence visualize the ecological space in three dimensions (three principal components, X, Y, Z), in order to depict the ellipsoids. This overlapping analysis was used to calculate the volume of the ellipsoids corresponding to the three ecological niches, with their respective centroids, eigenvectors and percentage of shared volume. The similarity between ecological niches was measured with the Jaccard index, which produces values between 0 and 1, indicating the degree of similarity between niches in the ecological space (Qiao *et al.* 2016).

RESULTS

Ecological niche models and potential distribution. A total of 15 records of the species were recorded, six for the northern population (*O. dariensis s.s.*) and nine for the southern population (*O. thaeleri*), following the nomenclature proposed by Alberico (1990; Table 1). Both estimates of the distributions showed good performance and discriminating capacity (AUC$_{TEST}$ = 0.995 ± 0.005). The variables identified as most important for the two groups were precipitation in the coldest trimester, temperature seasonality, and temperature in the coldest month.

Considering both populations separately, geographical distributions are allopatric and associated with very humid forests with high precipitation and low temperature seasonality, being separated by the Darién-Baudó zone, which appears as an area that delimits the two distributions (Fig-

Table 1. Geographic records of *O. dariensis* and its populations in the Chocó biogeographic region.

Taxon	Country	Department/ Province	Locality	Length	Latitude
Southern population (*Orthogeomys thaeleri*)	Colombia	Chocó	Alto Baudó	-77.3500	6.0000
	Colombia	Chocó	Nuquí	-77.2410	5.7120
	Colombia	Chocó	Bahía Solano	-77.3370	5.9970
	Colombia	Chocó	Bahía Solano	-77.0830	6.0000
	Colombia	Chocó	Bajo Baudó	-77.0500	5.0500
	Colombia	Chocó	Bajo Baudó	-77.0500	5.0501
	Colombia	Chocó	Bajo Baudó	-77.0500	5.0502
	Colombia	Chocó	Juradó	-77.5710	7.1110
	Colombia	Chocó	Nuquí	-77.2333	5.7667
Northern population (*Orthogeomys dariensis s.s.*)	Panama	Darién	N/A	-78.0989	8.3278
	Panama	Darién	N/A	-77.7550	7.8540
	Panama	Darién	N/A	-77.6860	7.7790
	Panama	Darién	N/A	-77.7730	7.9270
	Panama	Darién	N/A	-77.7170	7.9170
	Panama	Darien	N/A	-77.7550	7.8550

ure 1). The approximate distribution of the northern population includes the far south of Panama, mainly in the Province of Darién, which shows heavily leached red and yellow soils, with accumulation of clay, low cation-exchange capacity and low base saturation, stretching up to the northern portion of Serranía del Baudó and the alluvial valleys of Atrato and San Juan rivers, in Colombia. The distribution of the southern population is restricted to lowlands and soft non-alluvial soils in south-central Serranía del Baudó and the southern portion of the alluvial valleys of Atrato and San Juan rivers, from 0 up to 100 m, in the Pacific region of Colombia (Figure 1). For its part, when considered as a single species, it shows a continuous distribution range across an area of approximately 117,233 km^2, and the Darién-Baudó zone is no longer displayed as a splitting area (Figure 1). However, although favorable conditions for the potential distribution of *O. dariensis* occur to the Pacific coastal plains, its southern distribution limit is possibly the San Juan river, which becomes a barrier for the species (Figure 1).

Considering the areas evaluated, both the small and the large area (for each species), the northern population predicts to a large extent the distribution of the southern population, and vice versa (Figure 2). On the other hand, the MESS analysis and the environmental variables associated with each area show that, although these areas share similar climatic conditions, there are some particular environmental characteristics ($P < 0.05$), which apparently do not represent conditions so unique as to separate these populations to any significant extent (Figure 3).

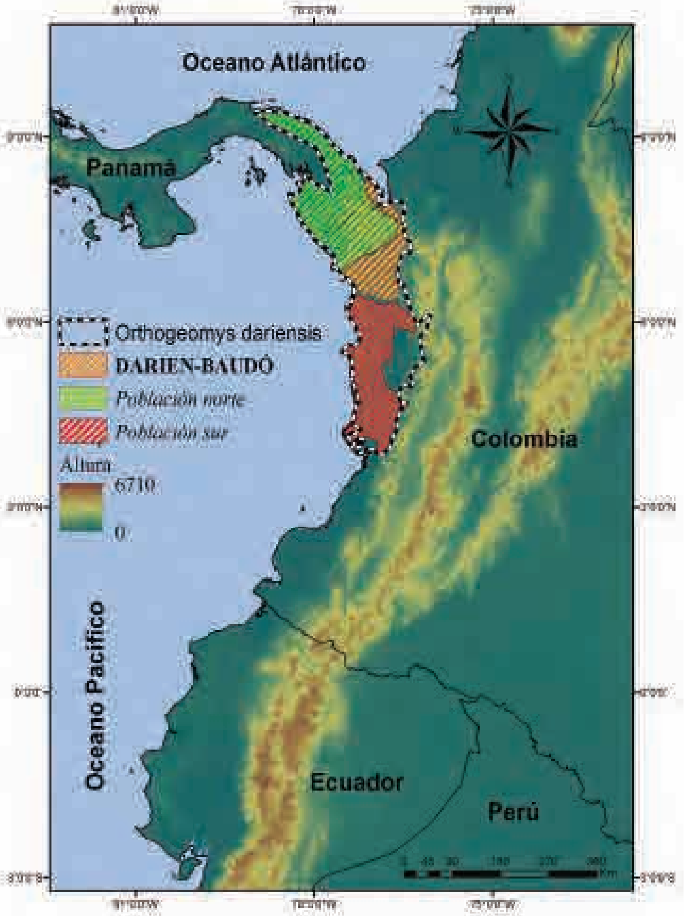

Figure 1. Study area and potential distributions of the northern population (green), southern population (red), and *O. dariensis* (dotted line) in the Chocó biogeographic region.

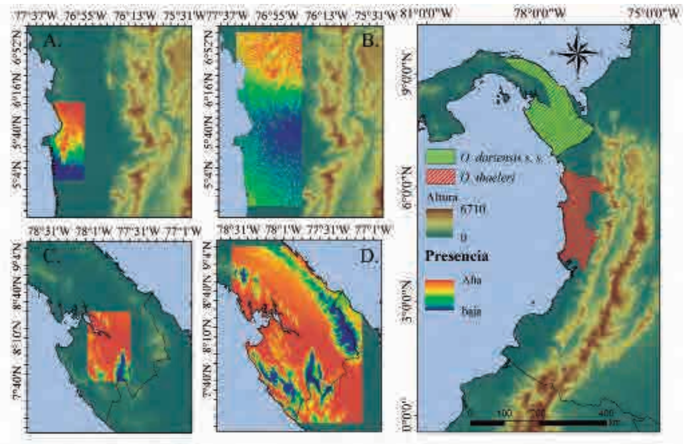

Figure 2. Potential distribution and predictions of the two populations of *Orthogeomys dariensis* in the Chocó biogeographic region. Prediction of the presence (**A.** small area; **B.** large area) of the northern population based on the southern population. Prediction of the presence (**C.** small area; **D.** large area) of the southern population based on the northern population. Note the Darien-Baudo zone as a potential barrier when two allopatric populations are considered.

Similarity and conservatism of the ecological niche. According to the niche similarity analysis in the ecological space, both populations show a slight overlap of their ellipsoids (Jaccard index = 0.30; Figure 4). However, these hyper-volumes are subdivisions of a much larger niche when a single species with a continuous distribution area is considered (Figure 4). In this way, more than niche conservatism or divergence between the two populations, these findings reflect the ecological and environmental conditions associated with each population, one to the north and the other in a location closer to the center of the Chocó biogeographic region.

DISCUSSION

Among the various groups of small non-flying mammals that colonized South America during the Great American Biotic Exchange after the establishment of the Panamanian Bridge (Marshall *et al.* 1982; Cody *et al.* 2010; Almendra and Rogers 2012), apparently the least successful, as evidenced by their limited dispersal in South America (Simpson 1950), are shrews (Woodman and Pefaur 2008) and pocket mice of the genus *Heteromys* (Anderson 2000). However, for fossorial species belonging to the family Geomyidae, this dispersal was seemingly even more restricted, having inhabited and undergone diversification mainly in Central America.

In this region, *O. dariensis* (*sensu* Hafner 2015*)* shows two allopatric populations, with a southern range reaching the San Juan river (4.20° North latitude). These is consistent with the genetic analyses by Spradling *et al.* (2016), which show a very low genetic divergence in mitochondrial and nuclear DNA between these populations (Spradling *et al.* 2016). This is also supported by the morphometric analyses of Hafner (2015) and Spradling *et al.* (2016), who suggest that the morphological variability between the Colombian

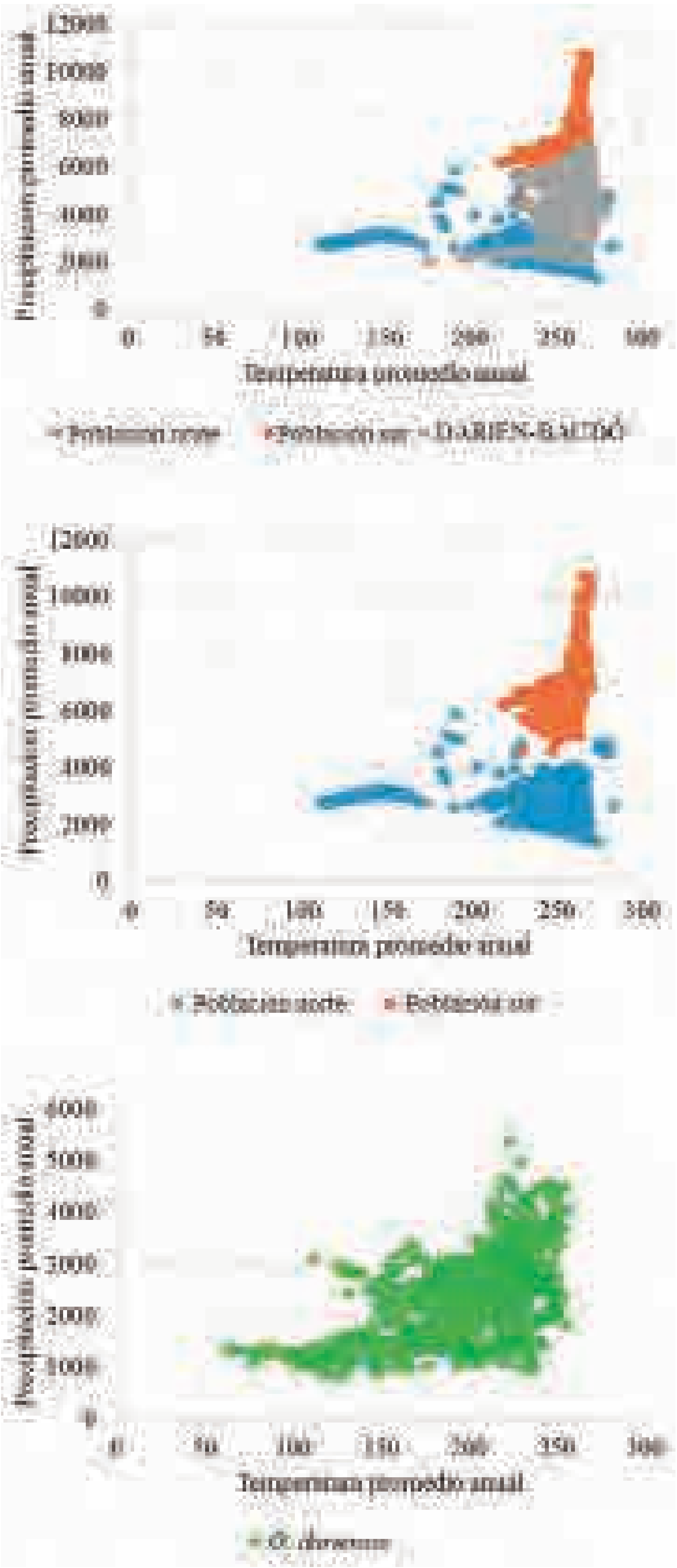

Figure 3. Climate analysis of the distributions of the northern population (blue), southern population (orange), the Darién-Baudo intermediate zone (gray), and *O. dariensis* as a single species (green) in the Chocó biogeographic region.

and Panamanian populations is insufficient to consider them as different species.

Likewise, the slight overlap of the ecological niches of the two populations reflects the particular ecological conditions in the areas they inhabit. Rather than considering the Darién-Baudó zone as a barrier restraining the dispersal and promoting the diversification for these gophers (Alberico 1990; Sudman and Hafner 1992; Valdés-Velásquez 2003), it may represent an area that connects both populations. Furthermore, Correa and Perea (2007) and Alberico (1990) point out that the burrow systems of populations in the Colombian Chocó are built in "inorganic clay" soils, with low-to-medium plasticity, and with scarcely developed profiles due to the continuing input of sediments from the Torreidó river; these characteristics are similar to those found in the Darién-Baudó intermediate zone (mainly in Medio Baudó, Chocó), which would facilitate the mobility and dispersal of populations in the region.

In order to gain a more comprehensive understanding of the evolutionary history and distribution of this geomyid species in the Chocó region, further studies are needed to confirm the presence and gather additional records, mainly for the Darién-Baudó zone, where no records are currently available. However, we believe that the species might be present based on its physical and environmental characteristics (see above). Such studies would contribute to a better understanding of the role of the Darién-Baudó (with an extension of 50 km wide approximately) as a dispersal route for populations of South and Central America. These responses are key to understand geographical and ecological differentiation patterns, not only regarding *O. dariensis*, but also with respect to the biotic and abiotic processes that have taken place in the region.

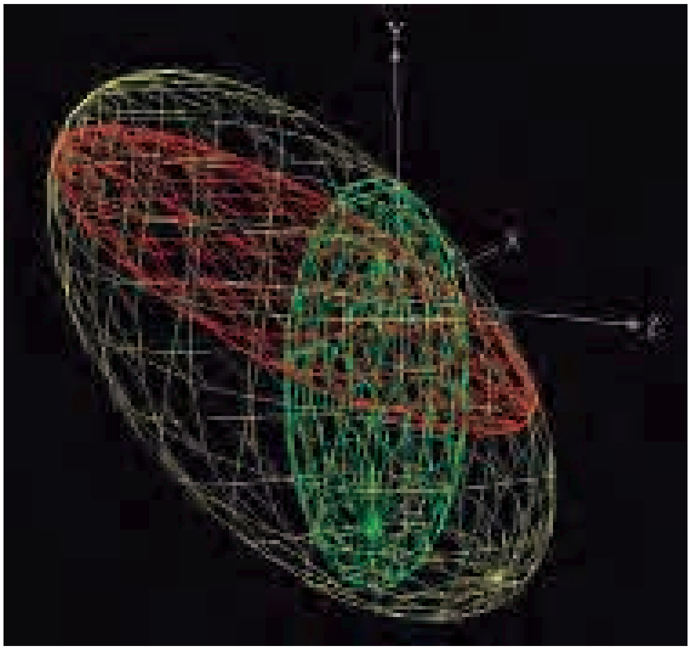

Figure 4. Ecological niches in the ecological space of the northern population (green), southern population (red), and *Orthogeomys dariensis* as a single species (yellow) in the Chocó biogeographic region.

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An annotated checklist of the mammals of Paraguay

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As the center of convergence of some of the major bioregions of South America, Paraguay is a biodiverse country of biogeographic importance. Yet despite a long history of natural history research, basic knowledge of its fauna, including mammals, is still lacking. The last updated list of Paraguayan mammals was published in 2002, but increased research efforts since that time have brought about numerous changes in the taxonomy and known distribution of many species. We present an updated and annotated checklist on the mammals of Paraguay through 2016. Only species records based on the assessment of some type of verifiable voucher are included here. Because the Paraguay River has been considered a significant biogeographic boundary, the distribution of each species (east of the river, west of the river, present on both sides) is tabulated as well. We recorded 181 native species of mammals, 30 more than in 2002, belonging to 10 orders, 33 families, and 116 genera. Chiroptera (58) was the most diverse order, followed by Rodentia (56), Carnivora (20) and Didelphimorphia (18). *Ctenomys pilarensis, C. paraguayensis* y *C. dorsalis* are known only from Paraguay. The inventory is likely incomplete, as well as our knowledge of species distributional limits. Continued collecting of tissues and vouchers, as well as an examination of museum specimens, is necessary to address numerous unsolved questions concerning distribution, taxonomy, ecology, biogeography, population biology and the effects of anthropogenic modification.

Paraguay, localizado en el centro sur de América del Sur, incluye dentro de sus límites algunas de las grandes ecorregiones del continente. A pesar de una larga historia de investigación mastozoológica, el conocimiento básico sobre los mamíferos de Paraguay es aún escaso. El último listado actualizado de especies se publicó en 2002; a partir de entonces se han realizado numerosos cambios taxonómicos y ajustes distribucionales. En este trabajo se presenta una lista de los mamíferos nativos de Paraguay actualizada a 2016 con base en investigación bibliográfica. Sólo se incluyeron en la lista especies nativas cuya ocurrencia en Paraguay fuese respaldada por la evaluación de algun voucher verificable. Dado que el río Paraguay se ha considerado un límite biogeográfico relevante (oriente y occidente del Paraguay), se registró la ocurrencia de las especies en cada una de estas regiones. Se contabilizaron 181 especies nativas (30 más que en 2002) pertenecientes a 10 órdenes, 33 familias y 116 géneros. Chiroptera (58) fue el orden más diverso, seguido por Rodentia (56), Carnivora (20) y Didelphimorphia (18). *Ctenomys pilarensis, C. paraguayensis* y *C. dorsalis* se conocen sólo de Paraguay. El inventario es probablemente aún incompleto, así como las distribuciones de muchas especies son todavía inciertas. Es preciso continuar con la colecta en campo de ejemplares y tejidos, así como el estudio de colecciones de museo, con el fin de abordar vacios de conocimiento sobre distribución, taxonomía, ecología, biogeografía y el efecto de las modificaciones antrópicas sobre la mastrofauna.

Keywords: biogeography; distribution; nomenclature; Paraguay; Mammalia; South America; taxonomy

Introduction

Paraguay is a landlocked country nested among Argentina, Bolivia, and Brazil in the Southern Cone of South America. While its topography is generally flat, a few hills ranging from 50 m to a maximum of 759 m above sea level are located primarily in the eastern portion of the country (Gorham 1973; Bartrina 2007). Because of its geographic position in the middle of South America, several major biomes of the continent (Cerrado, Chaco, Pantanal, and Atlantic Forest) extend into Paraguay, resulting in a more diverse flora and fauna than expected given the country's relatively small area and shallow topographic relief.

Paraguayan borders are delineated mainly by rivers, including the Paraná, Pilcomayo, and Paraguay. The center of the country lies on the Tropic of Capricorn at the interface between temperate and tropical zones. Paraguay's climate is characterized as tropical continental with six regional climates (Fariña 1973) and follows a continuum from semiarid at the northwestern border, where rainfall averages around 400 mm annually, to semitropical in the southeast, where annual rainfall is around 1,800 mm. Average annual temperatures vary from 25.9 °C in the NW to 21.4 °C in the SE

(Fariña 1973). The Paraguay River bisects the country from north to south into eastern and western regions that are distinctive geologically, ecologically, and faunistically (Myers 1982; Hayes 1995; Myers *et al.* 2002; López-González 2004).

Paraguay was the site of some of the earliest explorations of the Americas (Sainz Ollero *et al.* 1989), and it has played an important role in the history of South American mammalogy. The work of Félix de Azara (Azara 1801, 1802) supplied descriptions that are the basis of numerous currently recognized taxa, many of which are widely-distributed mammalian species. A total of six currently recognized marsupial (Gardner 2008a), two armadillo (Gardner 2008a), one felid, two canid (Wozencraft 2005), three primate (Groves 2005), two cervid (Grubb 2005), seven bat (López-González 2005; Simmons 2005), and 17 rodent species (Patton *et al.* 2015) have been described based on Paraguayan specimens.

Despite the long history of mammalogy in Paraguay, the country's mammal assemblage remains among the least studied in South America (Pine 1982; Myers *et al.* 2002). During the past 20 years, however, research on Paraguayan mammals has intensified (see a recent summary in López-González *et al.* 2014). A large number of species has been added recently to the Paraguayan fauna, information on species distributions has improved, and the natural history of some species is better known. In this work we provide an updated list of the mammals of Paraguay that reflects recent taxonomic advances and additions to the fauna.

Methods and Materials

Species list. We used the species list of Myers *et al.* (2002) as the starting point for a revised list of the mammalian fauna of the country. Because there was a delay of several years between the submission of the manuscript of Myers *et al.* (2002) and the actual publication of the work, papers published between 1997 and 2002 were not cited in that publication; therefore, those publications on species occurrences were included in this account. We used the list of Myers *et al.* (2002) instead of that of Rumbo (2010) because the latter is based mostly on a previous list by Gamarra de Fox and Martin (1996) with few additions. Similarly, the list by Neris (1998) only included records to 1993. Annotations to the list published here include new species records for the country (NSRC), taxonomic revisions and or nomenclature clarifications (TXNM), updated species distribution east or west of the Rio Paraguay (DIST), and subspecific status of populations when available (SSP).

A species was included in the list only if it could be traced to a published record associated with museum specimens, sequences, photographs, or other types of verifiable vouchers. Verification of literature records by actual examination of specimens (including photographs) is much needed but far beyond the scope of this report; it is our intent to provide a useful platform for such study. Nomenclature and taxonomic arrangement to subfamily level follows Wilson and Reeder (2005) with the following exceptions: for Cetartiodactyla we follow Agnarsson and May-Collado (2008) and Vislobokova (2013); for Cingulata, Gibb *et al.* (2016); and for Primates, Rylands and Mittermeier (2009). Genera and species are arranged in alphabetical order. Domestic or wild introduced species are not considered in the list.

Results

Updated checklist. Our search retrieved 181 native species of mammals (Table 1) that have been reported for Paraguay, representing 10 orders, 34 families, and 116 genera. The order Chiroptera was the most diverse (58 species), followed by Rodentia (56), Carnivora (20) and Didelphimorphia (18; Figure 1). At the family level, Cricetidae had the highest species richness (34), followed by Phyllostomidae (20), Didelphidae (18), Molossidae (17), Vespertilionidae (16), Dasypodidae (11), Felidae (8), Mustelidae (5), Echimyidae (5), and

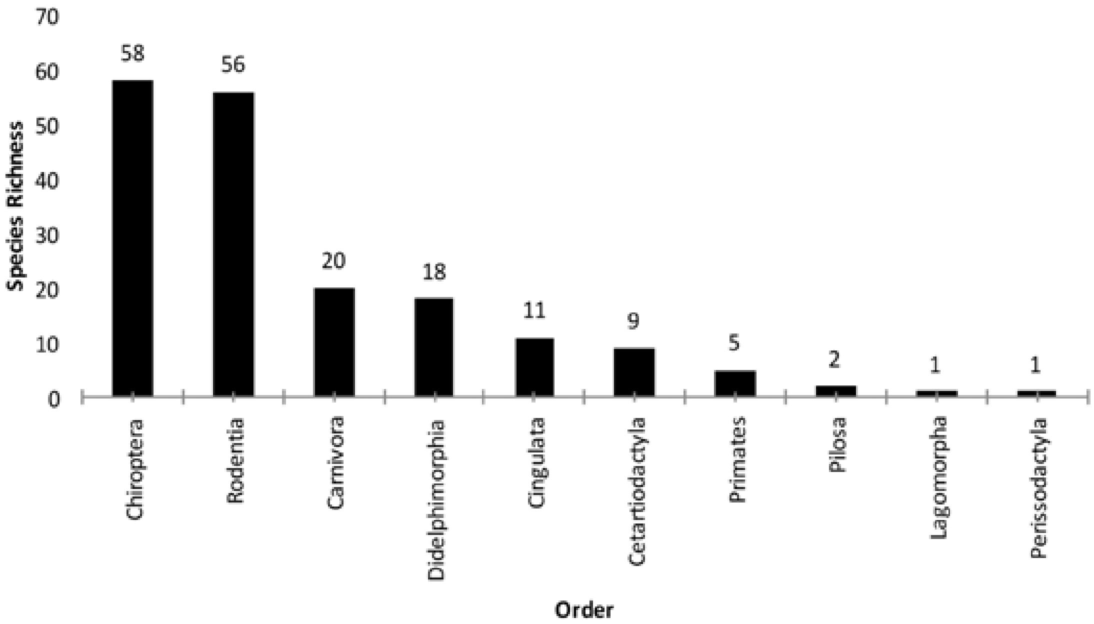

Figure 1. Paraguayan mammal species by order to 2016.

Cervidae (5; Figure 2). All other families were represented by four or fewer species. Three species, *Ctenomys pilarensis*, *C. paraguayensis,* and *C. dorsalis* are known only from Paraguay (Bidau 2015). Subspecific names were available for 69 species. We documented 59 taxonomic or nomenclatural changes at the species level since Myers *et al.* (2002).

Myers *et al.* (2002) reported 156 species in their account, but we could not confirm the presence of *Bradypus variegatus, Monodelphis scalops,* or *Ctenomys boliviensis* in Paraguay. *M. scalops* reported in Myers et al. is a misidentified *M. brevicaudis* = *M. sorex* (de la Sancha *et al.* 2007). *Conepatus humboldti* is now regarded as a synonym of *C. chinga*, both listed by Myers *et al.* (2002) as distinct species. The presence of *Myotis levis* was based on a report that was probably erroneous (Table 1). These changes reduced the list to 151 species. Here we document 30 additional species for the Paraguayan mammalian fauna (Table 1), either as new records or as populations formerly considered as one species but recently split into two, both occurring in Paraguay. Five of the additions are opossums, 10 are bats, 14 are rodents, and 1 is a carnivore. Three additional species, *Anoura caudifer* (López-González 2005), *Dasypus septemcinctus* (Wetzel *et al.* 2008), and *Calomys callidus* (Salazar-Bravo 2015) have been reported for Paraguay but no unambiguous records of their presence are available (Griffiths and Gardner 2008; Salazar-Bravo 2015) and therefore they are not included in our list.

Geographic distribution. We document 27 changes that either expand or restrict the distributions of species in eastern and western Paraguay reported by Myers *et al.* (2002). Of the total 181 species reported (Table 1), 58 (32.0 %) have been found only east of the Río Paraguay, 35 (19.3 %) only west of the river, and 88 (48.6 %) on both sides. Most mammalian Families include more species east of the Rio Paraguay, but one third have more species west of the river (Emballonuridae, Molossidae, Dasypodidae, Sciuridae, Caviidae, Tayassuidae, Camelidae, Callitrichidae, Aotidae, and Pitheciidae), although the difference in numbers between East and West assemblages is small (one or two species) within each of these families.

Discussion

Species richness. The first documentation of the Paraguayan mammal fauna dates to the earliest natural history explorations of South America in the 16th century (reviewed by López-González *et al.* 2014), yet the Paraguayan fauna is still one of the most poorly understood in South America. In recent years, however, investigations focusing on the biology of Paraguayan mammals have accelerated. The 151 species reported by Myers *et al.* (2002); sent to publication in 1997) increased to 167 in the list by Neris (1998), and to 181 in this account, an increase of 19.9 % from Myers *et al.* (2002) in less than 20 years. Species have been added due to new findings in the field, review of museum material, taxonomic revisions, and phylogenetic analyses (*e. g.,* López-González *et al.* 1998; Willig *et al.* 2000; Voss *et al.* 2005, 2009; López-González 2005; Weksler and Bonvincino 2005; de la Sancha *et al.* 2007; D'Elía *et al.* 2008a, 2008b; Percequillo *et al.* 2008; de la Sancha *et al.* 2009; Voss et al. 2009; Stevens *et al.* 2010; de la Sancha *et al.* 2011; Bornholdt *et al.* 2013; de la Sancha 2014; González-Ittig *et al.* 2014; Moratelli and Wilson 2013; Owen *et al.* 2014; de la Sancha and D'Elía 2015; Moratelli *et al.* 2015; Timm *et al.* 2015; Pardiñas *et al.* 2016). The number of nomenclatural and taxonomic changes observed reflects an

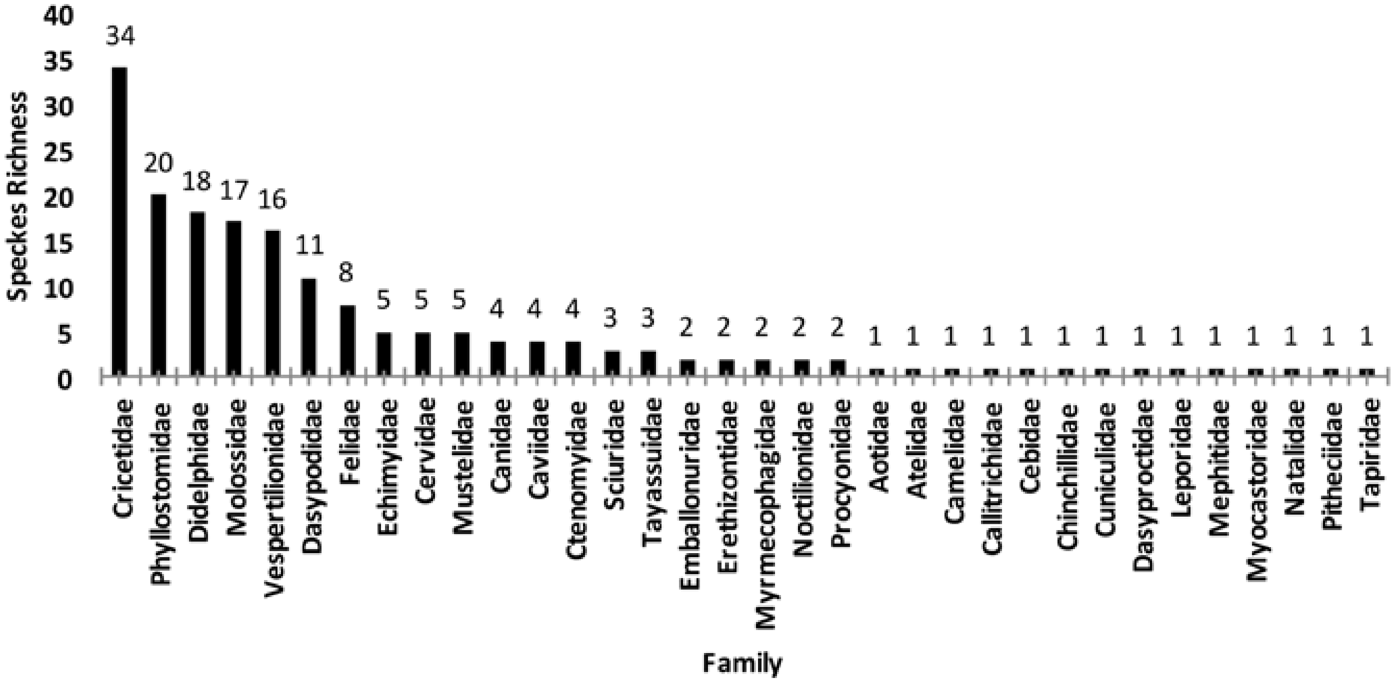

Figure 2. Paraguayan mammal species by family to 2016.

improving understanding of the diversity and phylogenetic relationships of the South American mammalian fauna in general, and the Paraguayan assemblage in particular. This body of work is improving our understanding of distributions at a finer scale for many species, particularly of small mammals, but less has been done on mid-size and large species. Continued field work, museum-based research, DNA barcoding, and raptor pellet examinations (*i. e.,* Torres *et al.* 2014) likely will reveal the presence of undescribed species in the country as well as species currently known from adjacent areas of neighboring countries.

Probable species. Myers *et al.* (2002) reported the occurrence of *Bradypus variegatus* in Paraguay. Although it has been recorded from Misiones, Argentina (Gardner 2008b), and there are unconfirmed reports for Paraguay (Bertoni 1939), we are not aware of unequivocal evidence of its presence, although the species may occur, or may have occurred, in Paraguay. *Anoura caudifer* was included in the Paraguayan fauna by López-González (2005) based on a report by Podtiaguin (1944), but Griffiths and Gardner (2008) questioned this report, and no specimen of *A. caudifer* is available to confirm its presence in Paraguay. Salazar-Bravo (2015) reported *Calomys callidus* for Paraguay; although it is likely to occur in the humid Chaco following a distribution similar to that of several marsupials (de la Sancha and D'Elía 2015), we found no published evidence of its occurrence in Paraguay. *Ctenomys boliviensis* was included in Myers *et al.* (2002), but the only available records for the species are from the area around Santa Cruz, Bolivia (Bidau 2015).

Leopardus guttulus was reported by Johnson *et al.* (1999) and Trigo *et al.* (2008) to occur in the Paraguayan Chaco. However, a closer examination of their specimen lists raises doubts about the distribution of this species. Figure 1 in Johnson *et al.* (1999) includes a locality in the Chaco. In their list of examined material (Appendix 1) these authors report a sample (LTI 37) from Iguazu Paraguay, referring to the source of the sample as "Itaipu Paraguay." They also list a sample (LTI 38) from "Curuguaty, W. Paraguay," referring the source of the sample to "Itaipu Paraguay" as well. Iguazu is not in Paraguay and Curuguaty is not in Western Paraguay, making it impossible to determine where their samples came from. In their Figure 1A, Trigo *et al.* (2008) suggest the species is only found in Eastern Paraguay, but in their Figure 1B they report a site in the Paraguayan Chaco. Furthermore, in their Supporting Material, they state that the geographic origin of their sample is the Paraguayan Chaco. Because of these apparently conflicting reports, we list *L. guttulus* only for Eastern Paraguay but recognize that its distribution is poorly known and may eventually be shown to include Chacoan sites.

Dasypus septemcinctus has been reported to occur in Paraguay (Wetzel *et al.* 2008) but no specimen records were presented by those authors. We were unable to find other published records of this species and thus do not include it in Table 1.

Current knowledge of major mammalian groups

Didelphimorphia. Recent works have incorporated both morphological and genetic evidence to improve our understanding of the distribution and systematics of Paraguayan marsupials (Voss *et al.* 2005; de la Sancha *et al.* 2007; Teta *et al.* 2009; Voss *et al.* 2009; de la Sancha *et al.* 2012; Smith *et al.* 2012; Martínez-Lanfranco *et al.* 2014; Smith and Owen 2015; de la Sancha and D'Elía 2015). Five species of marsupials have been reported for Paraguay for the first time since 2005. Nonetheless, major gaps remain in our understanding of the natural history and ecology of Paraguayan marsupials.

Cingulata. Much of our understanding of the armadillo species present in Paraguay is based on the works of Wetzel (1980, 1985). Only one study has incorporated molecular data from Paraguayan populations (Frutos and Van Den Bussche 2002), and few investigations have addressed geographic distribution or conservation, a pressing concern given that armadillos are hunted for food (Smith *et al.* 2011; Weiler and Núñez 2012). Ecology, phylogenetics, conservation, and management themes provide valuable research opportunities for this group in Paraguay.

Pilosa. To our knowledge, no publication has focused exclusively on Paraguayan anteaters, even though they are common throughout the country. Research on distribution, ecology and natural history is urgently needed because of the extensive habitat conversion and loss currently occurring in Paraguay.

Primates. The taxonomy of Neotropical primates has changed considerably in the past few years, reflecting current research efforts focusing on the group across the South American continent. Although Paraguayan specimens have been used in regional studies including morphology (Arístide *et al.* 2014), genetics (Matayoshi *et al.* 1986; Mudry *et al.* 1987; Pargament and Slavutsky 1987; Martínez *et al.* 2004; Mudry *et al.* 2007; Casado *et al.* 2010), phylogenetics and phylogeography (Hoyos *et al.* 2016), ecology (Boyle 2014) and zoonosis (Díaz *et al.* 2007), little research has been done on this group within Paraguay; the few works available focus on rare or uncommon species such as *Mico melanurus* (Stallings and Mittermeier 1983), *Aotus azarae* (Campos *et al.* 2004), and on the more common *Alouatta caraya* (Giordano and Ballard 2010). Conservation status of primates in Paraguay was assessed by Stallings (1985) and Rumiz and Stallings (1989) and has not been revised since. Given the current rate of habitat loss, this charismatic fauna should be the focus of ecological and conservation studies.

Lagomorpha. Information on Paraguayan lagomorphs is scarce. The taxonomy of the Paraguayan populations is still unclear at best given that *Sylvilagus brasiliensis* is probably a species complex (Bonvicino *et al.* 2015) and is in need of revision. We found no literature focused on the biology of *S. brasiliensis* in Paraguay even though it is a common species throughout the country.

Chiroptera. Bats, with a total of 58 species, are the most species-rich order in Paraguay. López-Gonzalez (2005) summarized knowledge before 2000 of Paraguayan Chiroptera, listing 54 species based on specimens collected and deposited in collections. Since then, *Myotis levis* (Stevens *et al.* 2010)*, M. midastactus* and *Myotis* "simus-like" (Moratelli *et al.* 2015), *Saccopteryx leptura,* and *Gardnerycteris crenulatum* (Owen *et al.* 2014) have been added to Paraguay's fauna, while *Anoura caudifer* has been removed from the list (see above). The inventory of bats is likely to grow as further field and revisionary research is conducted.

Recent non-taxonomic bat research in Paraguay has focused mainly on community ecology (Stevens *et al.* 2004; Gorresen *et al.* 2005; Presley 2007; Stevens *et al.* 2007; Presley *et al.* 2009; Presley 2012; Stevens and Amarilla-Stevens 2012), on relationships of bats with their ectobionts (Durette-Dusset and Vaucher 1999; Dick and Gettinger 2005; Graciolli *et al.* 2006; Heddergott 2008; Presley and Willig 2008), ecological biogeography (López-González 2004; Stevens *et al.* 2007), and conservation issues (Andelman and Willig 2002; Gorresen and Willig 2004). Little has been done on the natural history and ecology of individual species or Paraguayan populations with few exceptions (Stevens 2001; McCulloch and Stevens 2011; McCulloch *et al.* 2013; Stevens *et al.* 2016).

Carnivora. Paraguay is home to 20 species of carnivores, all occurring on both sides of the Rio Paraguay with the possible exceptions of *Leopardus guttulus* (see above) and *Galictis vittata* (see details Table 1). A finer scale analysis is needed to ascertain the specific habitats or bioregions that these organisms occupy. Additionally, their ecology and natural history in Paraguay has not been explored, and a number of taxonomic and nomenclatural issues have yet to be resolved. Considering that many medium and large-sized carnivores are highly charismatic it is surprising to find so little research has been done on them.

Most studies on felids have focused primarily on jaguars and pumas (Taber *et al.* 1997; de Angelo *et al.* 2011a, 2011b; Giordano *et al.* 2014). Studies of other cats include only a few notes on medium sized species (Zuercher *et al.* 2001). For canids, there are few taxon-specific publications. Descriptive and conservation-related work is available for *Chrysocyon brachyurus* (Meritt 1973; Queirolo *et al.* 2011; Cartes et al. 2015). Ironically the most elusive canid in Paraguay, *Speothos venaticus,* is the best studied (Zuercher and Villalba 2002; Zuercher *et al.* 2003, 2005). Nonetheless, basic taxonomic, ecological, and distributional issues are yet to be resolved for Paraguayan populations of the bush dog. Beyond lists or locality records, studies of mustelids, mephitids, and procyonids are essentially non-existent. Carnivores in general represent a major knowledge gap in Paraguay and offer scientists a great opportunity for study.

Cetartiodactyla. Most of the nine species that occur in Paraguay are found on both sides of the Rio Paraguay, with the exception of *Parachoerus wagneri* and *Lama guanicoe*, both restricted to Western Paraguay, and *Mazama nana*, which is restricted to Eastern Paraguay. Until 1975, *Parachoerus wagneri* was known only from the fossil record; the discovery of this "living fossil" (Wetzel *et al.* 1975) precipitated a massive effort to document the biology of this species (Wetzel *et al.* 1975; Mayer and Brandt 1982; Benirschke *et al.* 1985; Mayer and Wetzel 1986; Byrd *et al.* 1988; Benirschke *et al.* 1989a, 1989b; Taber 1990; Handen and Benirschke 1991; Taber 1991; Brooks 1992; Taber 1993; Handen *et al.* 1994; Taber *et al.* 1993, 1994; Yahnke *et al.* 1997; Toone and Wallace 2002; Toone *et al.* 2003; Sutherland-Smith *et al.* 2004; Meritt 2010). Studies of other ungulates in Paraguay, however, have lagged far behind, and those species are known primarily from lists or reports of sightings. Of the five species of Paraguayan deer, only *Mazama gouazoubira* has been studied ecologically (Stallings 1984, 1986) whereas the guanaco (*Lama guanicoe*) is only known from a few sightings (Villalba and Bonacic 2006). Even the taxonomy of populations of common, medium-sized species like *Mazama americana* is uncertain in Paraguay. The name *M. americana* currently applies to populations of northern South America (Groves and Grubb 2011). The names *M. rufa* and *M. jucunda* are available for the Paraguayan populations (Groves and Grubb 2011), but no decision as to which applies is possible without revision of the pertinent materials. Here, we have opted to be conservative and kept the name *Mazama* sp. for Paraguayan populations of this species until such revision is available.

Perissodactyla. The few publications concerning Paraguayan tapirs deal with their use by indigenous people (Hill *et al.* 1997; Hill and Padwe 2000; Hill *et al.* 2003) and the effects that habitat changes are having on this species (Brooks *et al.* 1997). Many habitats in Paraguay have changed considerably since the late 1990s and therefore, this report is likely outdated. Paraguay is a potential contact zone for *T. terrestris terrestris* and *T. t. spegazzinii*; however, to date only *T. t. terrestris* is confirmed for the country (Groves and Grubb 2011). The possible occurrence of *T. t. spegazzinii* is currently an open research opportunity with taxonomic and population genetic implications.

Rodentia. Rodents are the most diverse order of mammals in the world (Carleton and Musser 2005). They comprise close to 50 % of the mammal species in Central and South America (Patton *et al.* 2015), yet in Paraguay they appear to be somewhat less diverse than bats. We suggest that the apparent under-representation of rodents (or over-representation of bats) in the Paraguayan fauna is an artifact of inadequate sampling and lack of taxonomic study. Remarkably, since 2005 a new Family (Sciuridae), three genera (*Sciurus, Bibimys, Juliomys*) and 13 species of rodents (Table 1) have been reported for Paraguay for the first time. Many rodent groups continue to receive scant attention from systematists, and future taxonomic revisions are likely to result in the proportion of rodents in the Paraguayan fauna more closely reflecting proportions in faunas elsewhere.

A better understanding of the rodent fauna of Paraguay is critical. Rodents and other small mammals play important ecological roles, including seed predators, consumers of insects including possible crop pests, and as prey base for a large community of mammalian, avian and reptilian predators. They are valuable in ecological studies, including those concerning anthropogenic disturbance such as landscape and climate change (de la Sancha 2014; de la Sancha *et al.* 2014). Rodents are also important hosts for human pathogens, including hantaviruses, which are known from Paraguay (Yahnke *et al.* 2001; Chu *et al.* 2003, 2006; Goodin *et al.* 2006; Padula *et al.* 2007; Chu *et al.* 2009; Goodin *et al.* 2009). Studies dealing with population dynamics of rodents in Paraguay have been severely handicapped by lack of field identification tools; reliable keys and much more basic work are still needed in Paraguay.

Our review of publications in the preparation of Table 1 revealed the following major trends:

1. Most publications are still fundamentally descriptive works, mostly taxonomic and distributional. Chiroptera, Didelphimorphia, and Rodentia are the most-studied taxa, but research efforts even within these groups have focused on a few species and mostly on distributional, taxonomic, and systematic issues. Other aspects of the Paraguayan mammalian fauna are very poorly studied.

2. The basic taxonomy of many medium-sized and large mammal species is poorly understood at best. Few Paraguayan specimens of most medium-sized and large species are available, and because many of these animals are threatened or endangered, further collection of samples is expected to be limited. However, as new sampling methods are devised and processing costs decrease with the application of new molecular techniques, non-lethal sampling is becoming more effective and affordable. Also, developments in tracking technology and camera trapping make possible new kinds of studies of natural history and distribution. Many opportunities for work on larger mammals exist, and this kind of research is urgently needed.

3. Our inventory of Paraguayan mammals is likely incomplete, as is our knowledge of species distributional limits within Paraguay. Particularly for rodents, no comprehensive review is available, and field identifications are problematic. Considerable collections already exist in several museums across the world, but critical study of many of these specimens, further collection of selected species, and surveys of critical areas remain to be done. DNA barcoding will play a role, but the usefulness of this technique rests on the association of tissue samples with properly identified, well curated, and accessible vouchers.

4. Very few studies at the population, community or metacommunity levels are available. Conservation assessment and management strategies exist only for a handful of species or for restricted protected areas. Conservation-oriented research is urgent given the accelerated rate of environmental modification currently affecting Paraguay.

5. Paraguay is located in the heart of South America and at the intersection of several major South American ecoregions. Yet, for many biological groups, Paraguay represents a knowledge gap between Brazil, Argentina, and Bolivia. Further local and regional research will narrow this gap, thus providing better understanding of large-scale biogeographical and evolutionary processes. For instance, there is still much to understand about the role of the Rio Paraguay as a dispersal filter or barrier between major biomes, not only within Paraguay but at a larger scale.

6. Improved understanding of the Paraguayan fauna is vital to understand the impacts of anthropogenic changes.

Table 1. List of Paraguayan mammals to December 2016. Taxonomic arrangement to subfamily follows Wilson and Reeder (2005), except for Cetartiodactyla we follow Agnarsson and May-Collado (2008) and Vislobokova (2013); for Cingulata, Gibb *et al.* (2016); and for Primates, Rylands and Mittermeier (2009). Genera and species are arranged in alphabetical order within subfamilies. W, western Paraguay, E, Eastern Paraguay. Remarks on taxonomic and nomenclatural changes (TXNM), distributional changes post Myers *et al.* (2002) (DIST), and new species records (NSRC) since Myers *et al.* (2002) are included when applicable. SSP: subspecific epithet and reference of paper where the subspecies is recognized, PY: Paraguay.

Species	W	E	Remarks
Order Didelphimorphia			
Family Didelphidae			
Subfamily Caluromyinae			
Caluromys lanatus (Olfers, 1818)		X	SSP: *lanatus,* Gardner (2008c).
Subfamily Didelphinae			
Chironectes minimus (Zimmermann, 1780)		X	SSP: *paraguensis*, Stein and Patton (2008).
Cryptonanus chacoensis (Tate, 1931)	X	X	NSRC: Voss et al. 2005 DIST: on both sides of PY River (de la Sancha and D'Elía 2015).
Cryptonanus unduaviensis (Tate, 1931)	X		NSRC: de la Sancha and D'Elía (2015).
Didelphis albiventris (Lund 1840)	X	X	SSP: *leucotis,* Cerqueira and Tribe (2008).
Didelphis aurita (Wied-Neuwied, 1826)		X	TXNM: *D. azarae* Temminck 1824 predates current name but Cerqueira and Tribe (2008) retained *aurita* to minimize confusion in literature.
Gracilinanus agilis (Burmeister, 1854)		X	
Lutreolina crassicaudata (Desmarest, 1804)	X	X	SSP: *crassicaudata,* Martínez-Lanfranco *et al.* (2014).
Marmosa constantiae (Thomas, 1904)	X	X	NSRC: Voss *et al.* (2009) DIST: reported for W PY by de la Sancha *et al.* (2012)
Marmosa paraguayana (Tate, 1931)		X	TXNM: as *Micoureus demerarae* in Myers *et al.* (2002), updated by Voss and Jansa (2009).

Metachirus nudicaudatus (É. Geoffroy, 1803)		X	SSP: *modestus*, Gardner and D'Agosto (2008).
Monodelphis brevicaudis (Erxelben, 1777)		X	TXNM: as *Monodelphis sorex* in Myers *et al.* (2002), updated by Solari (2010) and de la Sancha and D'Elía (2015).
Monodelphis domestica (Wagner, 1842)	X	X	
Monodelphis kunsi Pine, 1975	X	X	NSRC: de la Sancha *et al.* (2007).
Philander frenatus (Olfers, 1818)		X	TXNM: as *P. opossum* in Myers *et al.* (2002) DIST: E PY only (Patton and da Silva 2008).
Philander opossum (Linnaeus, 1758)	X	X	NSRC: de la Sancha and D'Elía (2015). TXNM: name applied by Patton and da Silva (1997) to populations of central South America not including PY. SSP: *canus,* Chemisquy and Flores (2012).
Thylamys macrurus (Olfers, 1818)		X	TXNM: as *T. macrura* in Myers *et al.* (2002), updated by Voss *et al.* (2009). DIST: Myers *et al.* (2002) reports it in E and W PY, restricted to E PY by Voss *et al.* (2009).
Thylamys pusillus (Desmarest, 1804)	X		TXNM: as *T. pusilla* in Myers *et al.* (2002), updated by Voss *et al.* (2009) and Teta *et al.* (2009). DIST: Myers *et al*. (2002) reports it for E and W PY, restricted to W PY by Voss *et al.* (2009).
Order Cingulata			
Family Dasypodidae			
Subfamily Dasypodinae			
Dasypus hybridus (Desmarest, 1804)		X	DIST: Myers *et al.* (2002) reports it for E and W, but no western Paraguayan specimens are available (Wetzel *et al.* 2008, Smith 2012).
Dasypus novemcinctus Linnaeus, 1758	X	X	SSP: *novemcinctus*, Wetzel *et al.* (2008).
Subfamily Euphractinae			
Calyptophractus retusus (Burmeister, 1863)	X		TXNM: *Chlamyphorus retusus* in Myers *et al.* (2002), updated by Wetzel *et al*. (2008).
Chaetophractus vellerosus (Gray, 1865)	X		SSP: *vellerosus,* Wetzel *et al.* (2008).
Chaetophractus villosus (Desmarest, 1804)	X		
Euphractus sexcinctus (Linnaeus, 1758)	X	X	SSP: *flavimanus*, Wetzel *et al.* (2008).
Subfamily Tolypeutinae			
Cabassous chacoensis Wetzel, 1980	X		
Cabassous tatouay (Desmarest, 1804)		X	SSP: *tatouay*, Wetzel *et al.* (2008).
Cabassous unicinctus (Linnaeus, 1758)		X	SSP: *squamicaudis*, Wetzel *et al.* (2008).
Priodontes maximus (Kerr, 1792)	X	X	
Tolypeutes matacus (Desmarest, 1804)	X		
Order Pilosa			
Family Myrmecophagidae			
Myrmecophaga tridactyla Linnaeus, 1758	X	X	SSP: *tridactyla*, Gardner (2008b).
Tamandua tetradactyla (Linnaeus, 1758)	X	X	SSP: *straminea*, Gardner (2008b).
Order Primates			
Family Callitrichidae			TXNM: Family clarification by Rylands and Mittermeier (2009).
Mico melanurus (É. Geoffroy, 1812)	X		TXNM: as *Callithrix argentata* in Myers *et al.* (2002), updated by Stallings and Mittermeier (1983) and Rylands *et al.* (2008).
Family Cebidae			
Subfamily Cebinae			TXNM: Subfamily clarification by Rylands and Mittermeier (2009). TXNM: as *Cebus apella* in Myers et al. (2002), updated by Lynch Alfaro *et al.* (2012).
Sapajus cay (Illiger, 1815)		X	
Family Aotidae			TXNM: Family clarification by Rylands and Mittermeier (2009).
Aotus azarae (Humboldt, 1811)	X		TXNM: as *Aotus azarai* in Myers *et al.* (2002), updated by Groves (2005).
Family Pitheciidae			TXNM: Family and subfamily clarification by Rylands and Mittermeier (2009).
Subfamily Callicebinae			
Plecturocebus pallescens Thomas 1907	X		TXNM: as *Callicebus donacophilus* in Myers *et al.* (2002), species clarification updated in Groves (2005), and family and generic clarification updated by Byrne *et al.* (2016).
Family Atelidae			
Subfamily Alouattinae			TXNM: Family and subfamily clarification by Rylands and Mittermeier (2009).
Alouatta caraya (Humboldt, 1812)	X	X	
Order Lagomorpha			
Family Leporidae			

Sylvilagus brasiliensis (Linnaeus, 1758)	X	X	TXNM: very likely a species complex (Bonvicino *et al.* 2015). SSP: *paraguensis*, Bonvicino *et al.* (2015).
Order Chiroptera			
Family Emballonuridae			
Subfamily Emballonurinae			
Peropteryx macrotis (Wagner, 1843)	X	X	
Saccopteryx leptura (Schreber, 1774)	X		NSRC: Owen *et al.* (2014).
Family Phyllostomidae			
Subfamily Desmodontinae			
Desmodus rotundus (É. Geoffroy, 1810)	X	X	SSP: *rotundus*, Kwon and Gardner (2008).
Diaemus youngi (Jentnik, 1893)	X		DIST: reported by Myers *et al.* (2002) on E and W PY, but no specimens available for E PY (López-González 2005).
Subfamily Glossophaginae			
Glossophaga soricina (Pallas, 1776)		X	SSP: *soricina*, Griffiths and Gardner (2008).
Subfamily Phyllostominae			
Chrotopterus auritus (Peters, 1856)	X	X	
Lophostoma brasiliense (Peters, 1866)	X		NSRC: López-González *et al.* (1998) as *Tonatia brasiliense*.
Lophostoma silvicolum D'Orbigny, 1836		X	SSP: *silvicolum*, Williams and Genoways (2008). TXNM: as *Tonatia silvicola* in Myers *et al*. (2002).
Macrophyllum macrophyllum (Schinz, 1821)		X	
Gardnerycteris crenulatum (E. Geoffroy St.-Hilaire 1803)	X		NSRC: Owen *et al.* (2014). TXNM: As *Mimon* in Owen *et al.* (2014), updated by Hurtado and Pacheco (2014).
Phyllostomus discolor (Wagner, 1843)	X		DIST: Reported by Myers *et al.* (2002) for E PY but specimens available for W PY only (López-González 2005).
Phyllostomus hastatus (Pallas, 1767)		X	SSP: *hastatus*, Williams and Genoways (2008).
Tonatia bidens (Spix, 1823)	X	X	
Subfamily Carolliinae			
Carollia perspicillata (Linnaeus, 1758)		X	SSP: *tricolor*, McLellan and Koopman (2008).
Subfamily Stenodermatinae			
Artibeus fimbriatus Gray, 1838		X	
Artibeus lituratus (Olfers, 1818)	X	X	SSP: *lituratus*, Marques-Aguiar (2008).
Artibeus planirostris Spix, 1823	X	X	SSP: *planirostris*, Marques-Aguiar (2008).
Chiroderma doriae Thomas, 1891		X	NSRC: López-González *et al.* (1998).
Platyrrhinus lineatus (É. Geoffroy, 1810)	X	X	
Pygoderma bilabiatum (Wagner, 1843)		X	SSP: *bilabiatum,* Gardner (2008d).
Sturnira lilium (É. Geoffroy, 1810)	X	X	SSP: *lilium,* Gardner (2008e), Velazco and Patterson (2013).
Vampyressa pusilla (Wagner, 1843)		X	
Family Noctilionidae			
Noctilio albiventris Desmarest, 1818	X	X	SSP: *cabrerai*, Gardner (2008f).
Noctilio leporinus (Linnaeus, 1758)	X	X	SSP: *rufescens*, Gardner (2008f).
Family Natalidae			
Natalus macrourus (Gervais, 1856)		X	TXNM: as *Natalus* sp. in Myers *et al*. (2002), updated by Garbino and Tejedor (2013).
Family Molossidae			
Subfamily Molossinae			
Cynomops abrasus (Temminck, 1827)	X	X	TXNM: as *Molossops abrasus* in Myers *et al.* (2002), updated by Eger (2008).
Cynomops planirostris (Peters, 1866)	X	X	TXNM: as *Molossops planirostris* in Myers *et al.* (2002), updated by Eger (2008).
Eumops auripendulus (Shaw, 1800)	X	X	SSP: *major*, Eger (2008).
Eumops bonariensis (Peters, 1874)	X	X	
Eumops dabbenei Thomas, 1914	X	X	
Eumops glaucinus (Wagner, 1843)	X	X	
Eumops patagonicus Thomas, 1924	X	X	NSRC: López-González (2005).
Eumops perotis (Schinz, 1821)	X	X	SSP: *perotis*, Eger (2008).
Molossops temminckii (Burmeister, 1854)	X	X	
Molossus currentium Thomas, 1901	X		NSRC: Willig *et al.* (2000) as *M. bondae.* TXNM: updated by López-González and Presley (2001) and Eger (2008).

Molossus molossus (Pallas, 1766)	X	X	SSP: *crassicaudatus*, Eger (2008).
Molossus rufus É. Geoffroy, 1805	X	X	TXNM: as *Molossus ater* in Myers *et al.* (2002), updated by Eger (2008).
Nyctinomops laticaudatus (E. Geoffroy, 1805)	X	X	SSP: *laticaudatus*, Eger (2008).
Nyctinomops macrotis (Gray, 1840)	X		DIST: Myers *et al.* (2002) reported it from E and W PY; but no evidence of occurrence on E PY is available (López-González 2005).
Promops centralis Thomas, 1915	X	X	SSP: *occultus* (López-González 2005), but revision is pending (Eger 2008).
Promops nasutus (Spix, 1823)	X	X	
Tadarida brasiliensis (I. Geoffroy, 1824)		X	DIST: Myers *et al.* (2002) reported it from E and W PY, but no specimens are available from W PY (López-González 2005). SSP: *brasiliensis*, Eger (2008).
Family Vespertilionidae			
Subfamily Vespertilionidae			
Eptesicus brasiliensis (Desmarest, 1819)		X	DIST: Reported for W PY by Myers *et al.* (2002) and Davis and Gardner (2008), but specimens on which these reports are based are morphologically *E. furinalis* (López-González *et al*. 2005). SSP: *brasiliensis*, Davis and Gardner (2008).
Eptesicus diminutus (Osgood, 1915)	X	X	DIST: Reported for E and W PY by López-González (2005). SSP: *fidelis*, Davis and Gardner (2008).
Eptesicus furinalis (d'Orbigny, 1847)	X	X	SSP: *furinalis,* Davis and Gardner (2008).
Histiotus macrotus (Poeppig, 1835)	X		NSRC: López-González *et al.* (1998).
Histiotus velatus (I. Geoffroy, 1824)		X	DIST: Myers *et al.* (2002) reported it from E and W PY, but no specimens from W PY are available (López-González 2005).
Lasiurus blossevillii (Lesson, 1826)	X	X	SSP: *blossevillii,* Gardner and Handley (2008). TXNM: as *L. borealis* in Myers *et al.* (2002), updated by Gardner and Handley (2008).
Lasiurus cinereus (Palisot de Beauvois, 1796)	X	X	SSP: *villosissimus,* Gardner and Handley (2008).
Lasiurus ega (Gervais, 1856)	X	X	SSP: *argentinus,* Gardner and Handley (2008).
Myotis albescens (E. Geoffroy, 1806)	X	X	
Myotis lavali (Moratelli *et al.* 2011)	X	X	NSRC: Moratelli and Wilson (2013).
Myotis levis (I. Geoffroy, 1824)		X	NSRC: Stevens *et al.* (2010). DIST: included in Myers *et al.* (2002) based on mis-identified specimens (Stevens et al. 2010). SSP: *levis* (Wilson 2008), but Bárquez (2006) elevated subspecies of *M. levis* to species *M. levis* and *M. dinellii* (not in PY).
Myotis midastactus Moratelli and Wilson, 2014	X		NSRC: Moratelli *et al.* (2015) TXNM: as *M. simus* (in part) in Myers *et al*. (2002), updated by Moratelli *et al.* (2015).
Myotis nigricans (Schinz, 1821)	X	X	SSP: *nigricans,* Davis and Gardner (2008).
Myotis riparius Handley, 1960	X	X	
Myotis ruber (E. Geoffroy, 1806)		X	
Myotis "*simus*-like"		X	TXNM: reported in part as *M. simus* (Myers *et al.* 2002, López-González 2005). DIST: Moratelli *et al.* (2015).
Order Carnivora			
Family Felidae			
Subfamily Felinae			
Leopardus braccatus (Cope, 1889)	X	X	TXNM: as *Oncifelis geoffroyi* in Myers *et al.* (2002), updated in Wozencraft (2005). SSP: *braccatus* (Wozencraft 2005 and do Nasimento 2016).
Leopardus geoffroyi (d'Orbigny and Gervais, 1844)	X	X	TXNM: as *Oncifelis geoffroyi* in Myers *et al.* (2002), updated in Wozencraft (2005). SSP: *paraguae* (do Nascimento 2014).
Leopardus guttulus (Hensel, 1872)		X	TXNM: as *L. tigrinus* in Myers *et al.* (2002), updated by Trigo *et al.* (2013). DIST: E PY in Myers *et al.* (2002). Johnson *et al.* (1999) and Trigo *et al.* (2008) report it from W PY, but the information presented is confusing as to the origin of their samples. No clear evidence from W PY is available.
Leopardus pardalis (Linnaeus, 1758)	X	X	SSP: *mitis*, Murray and Gardner (1997).
Leopardus wiedii (Schinz, 1821)	X	X	
Puma concolor (Linnaeus, 1771)	X	X	SSP: *P. c. cabrerae* and *P. c. capricorniensis* occur in PY, but geographic limits are uncertain (Culver *et al.* 2000).
Puma yagouaroundi (É. Geoffroy-Saint-Hilaire, 1803)	X	X	SSP: *eyra*, de Oliveira (1998). TXNM: as *Herpailurus yagouaroundi* in Myers *et al.* (2002), updated in Wozencraft (2005).
Subfamily Pantherinae			
Panthera onca (Linnaeus, 1758)	X	X	SSP: *paraguensis*, Larson (1997).

Family Canidae			
Cerdocyon thous (Linnaeus, 1766)	X	X	SSP: *entrerianus,* Berta (1982).
Chrysocyon brachyurus (Illiger, 1815)	X	X	
Lycalopex gymnocercus (G. Fischer, 1814)	X	X	TXNM: as *Pseudalopex gymnocercus* in Myers *et al.* (2002), updated in Wozencraft (2005). SSP: *gymnocercus,* Wozencraft (2005).
Speothos venaticus (Lund, 1842)	X	X	DIST: reported by Myers *et al.* (2002) for E PY, but Beisiegel and Zuercher (2005) extend the distribution to NW PY. SSP: *wingei,* documented from SE PY (Beisiegel and Zuercher, 2005), another subspecies probably occurring in PY is *venaticus,* but no records are available (Beisiegel and Zuercher, 2005).
Family Mustelidae			
Subfamily Lutrinae			
Lontra longicaudis (Olfers, 1818)	X	X	SSP: *platensis,* Feijó and Langguth (2013).
Pteronura brasiliensis (Gmelin, 1788)	X	X	SSP: *paranensis,* Pickles *et al.* (2011).
Subfamily Mustelinae			
Eira barbara (Linnaeus, 1758)	X	X	SSP: *barbara*, Presley (2000).
Galictis cuja (Molina, 1782)	X	X	TXNM: as *Galictis cuja* in Myers *et al.* (2002), which at that time included both *G. cuja* and *G. vittata*. Taxonomy previously unstable but both are now recognized as separate taxa (Bornholdt *et al*. 2013). DIST: W and E PY (Bornholdt *et al.* 2013)
Galictis vittata (Schreber, 1776)		X	NSRC: Bornholdt *et al.* (2013) reported it for eastern PY. TXNM: as *Galictis cuja* (part) in Myers *et al.* (2002), see above.
Family Mephitidae			
Conepatus chinga (Molina, 1782)	X	X	DIST: Myers *et al.* (2002) reported it from W PY, recently recorded from E PY Velázquez and Ramírez Pinto (2014).
Family Procyonidae			
Nasua nasua (Linnaeus, 1766)	X	X	SSP: *spadicea*, Gompper and Decker (1998), Wozencraft (2005).
Procyon cancrivorus (Cuvier, 1798)	X	X	SSP: *nigripes*, Wozencraft (2005).
Order Perissodactyla			
Family Tapiridae			
Tapirus terrestris (Linnaeus, 1758)	X	X	SSP: *terrestris*, however, *T. terrestris spegazzinii* occurs in N Argentina and Rio Grande do Sul, and potentially in the Paraguayan Chaco (Groves and Grubb 2011), and a revision is needed.
Order Cetartiodactyla			
Family Tayassuidae			
Parachoerus wagneri (Rusconi, 1930)	X		TXNM: as *Catagonus* in Myers *et al.* (2002), updated by Dutra *et al.* (2016).
Pecari tajacu (Linneus 1758)	X	X	TXNM: as *Tayassu tajacu* in Myers *et al.* (2002). Groves and Grubb (2011) suggested more than one taxon may exist in PY populations. SSP: *tajacu* Groves and Grubb (2011).
Tayassu pecari (Link, 1795)	X	X	SSP: *albirostris,* the name *T. p. pecari* (Link 1795), formerly applied to PY populations, was restricted by Hershkovitz (1963) to Cayenne, French Guiana (Groves and Grubb 2011).
Family Camelidae			
Lama guanicoe (Müller, 1776)	X		SSP: *cacsilensis*, Groves and Grubb (2011).
Family Cervidae			
Blastocerus dichotomus (Illiger, 1815)	X	X	
Mazama sp. (Erxleben, 1777)	X	X	TXNM: the name *M. americana* was restricted by Groves and Grubb (2011) to northern South America. PY populations may be ascribed to *M. rufa* or *M. jucunda*, pending revision.
Mazama gouazoubira (G. Fischer von Waldheim, 1814)	X	X	TXNM: as *M. gouazoupira* in Myers *et al.* (2002).
Mazama nana (Hensel, 1872)		X	
Ozotoceros bezoarticus (Linnaeus, 1758)	X	X	SSP: *leucogaster*, Jackson (1987).
Orden Rodentia			
Suborder Sciuromorpha			
Family Sciuridae			
Hadrosciurus spadiceus (Olfers, 1818)	X		NSRC: as *Sciurus urucumus* by D'Elía *et al.* (2008a). SSP: *spadiceus,* de Vivo and Carmignotto (2015).
Hadrosciurus sp.	X		NSRC: specimen of unidentified species reported by D'Elía *et al.* (2008a) from the Chaco, along PY River.
Sciurus ignitus (Gray, 1867)	X	X	NSRC: Timm *et al.* (2015).

Suborder Myomorpha			
Family Cricetidae			
Subfamily Sigmodontinae			
Akodon azarae (Fischer, 1829)	X	X	SSP: *bibianae,* Pardiñas *et al.* (2015).
Akodon montensis Thomas, 1913		X	TXNM: as *A. cursor* in Myers *et al.* (2002), updated by Pardiñas *et al.* (2015).
Akodon paranaensis Christoff et al. 2000		X	NSRC: D'Elía *et al.* (2008).
Akodon toba Thomas, 1921	X		
Andalgalomys pearsoni (Myers, 1977)	X		SPP: *pearsoni*, Braun (2015).
Bibimys chacoensis (Shamel, 1931)		X	NSRC: D'Elía *et al.* (2008).
Calomys callosus (Rengger, 1830)	X	X	
Calomys laucha (Fischer, 1814)	X		DIST: Myers *et al.* (2002) reports it for W PY, Salazar-Bravo (2015) reports it from E PY, but likely based on specimens of *C. tener* (González-Ittig *et al.* 2014).
Calomys musculinus (Thomas, 1913)	X	X	DIST: reported for E PY by Myers *et al.* (2002); Salazar-Bravo (2015) reported specimens from W PY.
Calomys tener (Winge, 1887)		X	NSRC: de la Sancha (2014), González-Ittig *et al.* (2014).
Cerradomys maracajuensis (Langguth and Bonvicino, 2002)		X	TXNM: as *Oryzomys buccinatus* (in part) in Myers *et al.* (2002), updated by Percequillo *et al.* (2008).
Cerradomys scotti (Langguth and Bonvicino, 2002)		X	NSRC: Percequillo *et al.* (2008).
			TXNM: as *Oryzomys buccinatus* (in part) in Myers *et al.* (2002); updated by Percequillo *et al.* (2008).
Euryoryzomys russatus (Wagner, 1848)		X	TXNM: as *Oryzomys intermedius* in Myers *et al.* (2002); updated by Percequillo (2015).
Graomys chacoensis (J. A. Allen, 1901)		X	TXNM: as *G. griseoflavus* in Myers *et al.* (2002); updated by Braun and Patton (2015).
Holochilus vulpinus (Brants, 1827)		X	TXNM: as *H. brasiliensis* (in part) in Myers *et al.* (2002), updated by D'Elía *et al.* (2015). DIST: restricted to E PY in D'Elía *et al.* (2015).
Holochilus chacarius Thomas, 1906	X	X	DIST: E and W PY (D'Elía *et al.* 2015). SSP: *chacarius*, Gonçalves *et al.* (2015).
Hylaeamys megacephalus (G. Fischer, 1814)		X	TXNM: as *Oryzomys capito* in Myers *et al.* (2002), updated by Weksler *et al.* (2006).
Juliomys pictipes (Osgood, 1933)		X	NSRC: de la Sancha *et al.* (2009).
Necromys lasiurus (Lund, 1840)	X	X	TXNM: as *Bolomys lasiurus* (part) in Myers *et al.* (2002), updated by D'Elía *et al.* (2008b).
Necromys lenguarum (Thomas, 1898)	X		NSRC: by D'Elía *et al*. (2008b). TXNM: as *Bolomys lasiurus* (part) in Myers *et al.* (2002), updated by D'Elía *et al*. (2008b).
Nectomys rattus (Pelzeln, 1883)		X	TXNM: as *N. squamipes* in Myers *et al.* (2002), updated by Bonvicino and Weksler (2015).
Oecomys cf. *mamorae* (Thomas, 1906)	X		TXNM: as *O. mamorae* (part) in Myers *et al*. (2002).
Oecomys franciscorum (Pardiñas *et al.* 2016)	X	X	NSRC: Newly described by Pardiñas *et al.* (2016). TXNM: as *O. mamorae* (part) in Myers *et al.* (2002). Described by Pardiñas *et al.* (2016).
Oligoryzomys chacoensis (Myers and Carleton, 1981)	X		DIST: reported for E and W PY by Myers *et al.* (2002). restricted to W PY by Weksler and Bonvicino (2005).
Oligoryzomys flavescens (Waterhouse 1837)	X	X	NSRC: Weksler and Bonvincino (2005) TXNM: as *O. microtis* in Myers *et al.* (2002), updated by Weksler and Bonvicino (2005).
Oligoryzomys mattogrossae (J. A. Allen, 1916)		X	TXNM: as *O. microtis* (part) in Myers *et al.* (2002), restricted to E PY by Weksler and Bonvicino (2015).
Oligoryzomys nigripes (Olfers, 1818)		X	
Oxymycterus delator Thomas, 1903		X	
Oxymycterus quaestor Thomas, 1903		X	NSRC: as *O. misionalis* by D'Elía *et al*. (2008a). TXNM: updated to *O. quaestor* by de Oliveira and Gonçalves (2015).
Pseudoryzomys simplex (Winge, 1887)	X	X	DIST: Myers *et al*. (2002) reported it for W PY only. Recorded in E PY by D'Elía *et al.* (2008a).
Rhipidomys macrurus (Gervais, 1855)		X	NSRC: de la Sancha *et al.* (2011).
Scapteromys aquaticus Thomas, 1920	X	X	TXNM: as *S. tumidus* in Myers *et al.* (2002), PY populations regarded as distinct from *S. tumidus* by D'Elía and Pardiñas (2004).
Sooretamys angouya (Fischer, 1814)	X	X	TXNM: as *Oryzomys ratticeps* in Myers *et al*. (2002), updated by Weksler *et al.* (2006).
Thaptomys nigrita (Lichtenstein, 1829)		X	TXNM: reported by Myers *et al*. (2002) as *Akodon nigrita*, name combination follows Teta *et al.* (2015). SSP: *nigrita* and *subterraneus* (Teta *et al.* 2015), but no limits for each are specified.
Family Erethizontidae			
Subfamily Erethizontinae			
Coendou prehensilis (Linnaeus, 1758)		X	
Coendou spinosus (F. Cuvier, 1823)		X	TXNM: as *Sphiggurus spinosus* in Myers *et al.* (2002), updated by Voss (2015).

Family Chinchillidae			
Lagostomus maximus (Desmarest,1817)	X		SSP: *immolis*, Spotorno and Patton (2015).
Family Caviidae			
Subfamily Caviinae			
Cavia aperea Erxelben, 1777	X	X	SSP: *hypoleuca*, Dunnum (2015).
Galea leucoblephara (Burmeister, 1861)	X		TXNM: as *Galea musteloides* in Myers *et al.* 2002, updated by Dunnum and Salazar-Bravo (2010). SSP: *demissa,* Dunnum (2015).
Subfamily Dolichotinae			
Dolichotis salinicola Burmeister, 1876	X		
Subfamily Hydrochoerinae			
Hydrochoerus hydrochaeris (Linnaeus, 1766)	X	X	TXNM: as *Hydrochaeris hydrochaeris* in Myers *et al.* (2002), updated by Dunnum (2015).
Family Dasyproctidae			
Dasyprocta azarae Lichtenstein,1823		X	DIST: in both regions in Myers *et al.* 2002; Patton and Emmons (2015) placed it in E and W PY, but no records were found for the W.
Family Cuniculidae			
Cuniculus paca (Linnaeus, 1766)	X	X	TXNM: as *Agouti paca* in Myers *et al.* (2002), updated by Patton (2015).
Family Ctenomyidae			
Ctenomys conoveri Osgood, 1946	X		
Ctenomys dorsalis Thomas, 1900	X		
Ctenomys paraguayensis Contreras, 2000		X	TXNM: as *Ctenomys sp.* in Myers *et al.* (2002), described by Contreras (2000).
Ctenomys pilarensis Contreras, 1993		X	NSRC: described by Contreras (1993) from "Pilar, Paraguay". TXNM: validity of name questioned by Bidau (2015). However, because the publication probably does not follow rules of the International Code of Zoological Nomenclature (ICZN, 2012), what is questionable is the availability (not the validity) of the name.
Family Echimyidae			
Subamily Dactylomyinae			
Kannabateomys amblyonyx (Wagner, 1845)		X	SSP: *pallidior*, but revision is needed (Emmons *et al.* 2015).
Subamily Eumysopinae			
Clyomys laticeps (Thomas, 1909)		X	
Euryzygomatomys spinosus (G. Fischer, 1814)		X	
Proechimys longicaudatus (Rengger, 1830)	X		
Thrichomys fosteri Thomas, 1903	X	X	TXNM: as *T. apereoides* in Myers *et al.* (2002), updated by D'Elía and Myers (2014).
Family Myocastoridae			
Myocastor coypus (Molina, 1782)	X	X	SSP: *bonariensis*, but revision of subspecies is needed (Emmons *et al.* 2015).

We conclude that the current status of knowledge on Paraguayan mammals is incomplete and offers a fertile ground for young scientists, offering many valuable and interesting taxonomic, biogeographic, and ecologic questions yet to be resolved.

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Leucism in the three-striped palm squirrel (*Funambulus palmarum*) at Gudalur Forest Division, Tamil Nadu, Southern India

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Leucism is a condition characterized by the reduction of all skin pigmentation, generally observed in animals. In this note we describe the first known cases of the leucism in the three-striped palm squirrel in the fragmented forest habitat of Gudalur forest division, Tamil Nadu, Southern India.

El leucismo es una afección caracterizada por la reducción de toda la pigmentación de la piel, generalmente observada en animales. En esta nota describimos los primeros casos conocidos de leucismo en la ardilla de palmera de tres rayas en el hábitat forestal fragmentado de la división de bosques de Gudalur, Tamil Nadu, sur de la India.

Key Words: Gudalur; Leucism; Southern India; Tamil Nadu; Three-striped palm squirrel.

The observation of color abnormalities in wild mammals is an isolated event because these abnormalities are rare (Robinson 1973; Caro 2005). Inherited color defects, such as albinism and leucism, are well known in several animal species. Leucism is a condition in which there is partial loss of pigmentation in an animal resulting in white, pale, or patchy coloration of the skin, hair, feathers, scales or cuticle, but not the eyes. Unlike albinism, it is caused by a reduction in multiple types of pigments, not just melanin (Rook *et al.* 1998). Leucisitic animals appear white in colour; this condition is controlled by a single recessive allele (Owen and Shimmings 1992). In this note we describe the first known cases of leucism in the threestriped palm squirrel inhabiting the fragmented forest habitat of Gudalur forest division, Tamil Nadu, Southern India.

The three-striped palm squirrel (*Funambulus palmarum*) is a small rodent species that belongs to the family Sciuridae. There are four subspecies of Indian palm squirrels that are native to India and Sri Lanka; the species studied is endemic to southern India and Sri Lanka (Nameer and Molur 2008; Thorington and Hoffmann 2005). It is widely distributed, from sea level up to 2,000 m asl (Nameer and Molur 2008). The three-striped palm squirrel can reach 6 to 7.8 inches in total length and weigh 100 to 120 g (3.5 to 4.2 ounces) (Menon 2003) . It is covered with short fur that is yellowish brown or brown colored on the back and creamy white on the belly (Menon 2003). It has three white stripes on the back that stretch from head to tail. It has dark rounded eyes, small triangular ears, long front teeth and bushy tail (Figure-1a; Prater1971 & 1980; Menon 2003; Pradhan and Talmale 2012). It is an omnivore and its diet is mostly based on fruits and nuts, but it also consumes eggs, small birds, larvae and insects (Prasad *et al.* 1966; Malhi and Kaur 1994; Malhi and Khushrupinder 1995).

On 22 September 2016, at 13:39 hours we observed one leucistic *F. palmarum* specimen in the fragmented forest habitat of Gudalur forest division, Tamil Nadu, Southern India (N 11.493667°, E 76.336977°); it was totally white, with pinkish snout, ears and limbs, but its eyes were normal colored (Figure-1b); it appears to be a case of leucism and not albinism, where the whole body is totally white with reddish eyes (Smielowski 1987). Sayyed *et al.* (2015) reported albinism in jungle palm squirrels (*Funambulus tristriatus*) from Goa, India; in addition, Sayyed and Mahabal (2016) recorded the first known record of leucism in another species of the same genus, the five-striped palm squirrel (*Funambulus pennantii*) from Maharashtra, India. A total of three squirrel species are found in India, namely three-striped palm squirrel, five-striped palm squirrel and jungle palm squirrel; the five-striped palm squirrel is found in northern India, while the jungle and the three-striped palm squirrels are located in southern India, especially in the Western Ghats mountain region (Prater 2005; Menon 2003). The occurrence of leucism is associated with many factors such as pollution, environmental alterations (Moller and Mousseau 2001), low-quality diet (Owen and Shimmings 1992; Peles *et al.* 1995), or follicular damage (Phillips 1954; Hafner and Hafner 1987). Leucism is more frequent in small and isolated populations due to inbreeding, which causes recessive alleles to be expressed (Holyoak 1978; Bensch *et al.* 2000). Leucism reports are relatively rare in small mammals (Robinson 1973; Caro 2005; Steen and Sonerud 2012). Leucistic individuals have lower survival rates than normally colored individuals, because they are more

Figure 1. a) Normal Three striped Palm Squirrel. b) Leucism affected Three Striped Palm Squirrel.

easily detected by predators (Owen and Shimmings 1992). It is worth mentioning that there are probably many animal species from different orders with anomalous coloration; unfortunately, many of these records have not been officially reported, probably due to lack of knowledge. Therefore, we highlight the relevance of photographs as valuable tools for the documentation of natural history as a whole. In conclusion, researchers should be encouraged to report records of leucism in wildlife in order to better understand this phenomenon and the insights into the ecological and physiological implications of this condition, which has a significant effect on animal survival (Fertl *et al.* 2004).

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Morphological description of the glans penis and baculum of *Coendou quichua* (Rodentia: Erethizontidae)

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External morphology of the glans and baculum are important characters for specific delimitation, especially for rodents (Simson et al. 1995). However, for Erethizontidae there are few descriptive works; in fact, for Neotropical porcupines of the genus *Coendou* there is just one brief contribution for an indeterminate species by Pocock in 1922. In this work, the morphology of the glans and baculum of *Coendou quichua* is described. The specimen was collected at the municipality of San Vicente de Chucurí, Santander, Colombia. The penis was dissected and fixed in formaldehyde for one day, and later preserved in ethanol. The baculum was extracted and cleared with potassium hydroxide to be visualized, photographed and measured. The glans and baculum were compared with the description of others porcupines (*Erethizon dorsatum* and *Hystrix brachyura*) available in literature, and three additional Neotropical caviomorph rodents (*Cuniculus paca*, *Dasyprocta punctata* and *Cavia tschudii*). The glans length is almost twice the glans head width (Table 1) and comprises the third part of the total penis length. The penis presents a tenuous dark coloration on the head and small tegumentary protuberances formed by 3-4 small spines (Figure 1A). As in other hystricomorph rodents, the glans exhibits an invagination at its tip (*sacculus urethralis*) which has corrugated walls and presents two conspicuous spikes at the bottom (Figure 1C). Furthermore, the baculum is as large as the *C. quichua* glans, dorsally concave and ventrally convex (Figure 1B). Although the glans and baculum of *C. quichua* and *E. dorsatum* are similar, the latter presents larger glans (Table 1), and the *sacculus urethralis* lacks of corrugated walls and spiny protuberances. When comparing *C. quichua* and *H. brachyura*, the only difference is that the bottom of the *sacculus urethralis*, near to the spikes is smooth, without spiny protuberances. In contrast, the glans of three other Neotropical caviomorphs are remarkable different from *C. quichua*, where they present more complex and densely distributed tegumentary protuberances above the glans. Overall, the baculum is the most varying structure for all species, with marked differences in length and width (Table 1) and the shape of the ends. Although the family Erethizontidae is more closed related to the Cavioidea than to Hystricidae, the glans of individuals of the family Erethizontidae are more similar to the glans of the Hystricidae. In addition, for these species, both glans and baculum present important characters that might be used for taxonomic identification. However, the differences of both structures within *Coendou* are unknown, therefore it is necessary the description of the genitalia of additional species.

La morfología externa del glande y báculo son caracteres importantes para la delimitación de especies, en especial para roedores (Simson et al. 1995). Sin embargo, para Erethizontidae existen pocos trabajos descriptivos; de hecho, para los puercoespines neotropicales del género *Coendou* solo hay una breve contribución publicada por Pocock en 1922. Aquí, se describe la morfología del glande y báculo de *Coendou quichua*. El espécimen se recolectó en el municipio de San Vicente de Chucurí, Santander, Colombia. El pene fue extraído y se fijó en formaldehido por un día, para después ser preservado en etanol. El báculo se extrajo del glande y se transparentó con hidróxido de potasio para ser visualizado, fotografiado y medido. El glande y báculo fueron comparados con la descripción de otros puercoespines (*Erethizon dorsatum* e *Hystrix brachyura*) disponibles en literatura y adicionalmente con tres roedores caviomorfos neotropicales (*Cuniculus paca*, *Dasyprocta punctata* y *Cavia tschudii*). La longitud del glande es cerca de dos veces el ancho de la cabeza del glande (Tabla 1) y comprende la tercera parte de la longitud total del pene. El pene presenta una coloración oscura tenue en la cabeza y protuberancias epiteliales pequeñas formadas por 3-4 espinas (Figure 1A). Al igual que el resto de roedores histricomorfos, el glande presenta una invaginación en la punta (*sacculus urethralis*) la cual tiene paredes corrugadas y presenta dos púas conspicuas en el fondo (Figure 1C). Por otro lado, el báculo es igual de largo al glande de *C. quichua*, cóncavo dorsalmente y convexo ventralmente (Figure 1B). Aunque los glandes y báculos de *C. quichua* y *E. dorsatum* son similares, el último presenta un glande más grande (Tabla 1) y el *sacculus urethralis* no tiene las paredes corrugadas y con protuberancias espinosas. Al comparar *C. quichua* y *H. brachyura*, la única diferencia es que en el fondo del *sacculus urethralis*, cerca de las púas, es liso y sin protuberancias espinosas. En contraste, los glandes de los otros tres caviomorfos neotropicales son bastante distintos del de *C. quichua*, donde los de ellos presentan protuberancias epiteliales más complejas y más densamente distribuidas sobre todo el glande. En general, el báculo es la estructura con mayor variación para todas las especies, con diferencias marcadas en el largo y ancho (Tabla 1) y la forma de cada uno de los extremos. A pesar de que la familia Erethizontidae está más relacionada con Cavioidea que con Hystricidae, el glande de los individuos de la familia Erethizontidae es más similar al glande de Hystricidae. Además, para estas especies, el glande y el báculo presentan importantes caracteres que podrían ser usados en taxonomía. Sin embargo, las diferencias dentro de *Coendou* son desconocidas, por lo cual es necesario la descripción de la genitalia de especies adicionales del género.

Key words: Baculum; Erethizontidae; glans morphology; Quichua porcupine; sacculus urethralis.

Introduction

The external morphology of the glans and the baculum (*os priapi*) contains important characters for specific and subspecific delimitation (Rocha-Barbosa *et al.* 2013), especially in rodents (Lidicker 1968; Bradley and Schmidly 1989; Spotorno 1979; Simson *et al.* 1995; Calderón-Capote *et al.* 2016). However, there are few descriptive studies on the external genitalia morphology of hystricomorph rodents (Tullberg 1899; Pocock 1922; Dathe 1937; Hooper 1961, Atalar and Ceribasi 2006; Adebayo *et al.* 2011), a clade that includes the

New World caviomorphs (*e. g.,* New World porcupines, agoutis, acouchis, pacas and Guinean pigs; *sensu* Upham and Patterson 2015). The New World porcupines of the genus *Coendou* are distributed on Central and South America (Voss 2011) and represents one of the less studied rodent groups in the Neotropics (Alberico *et al.* 2000). Due to the scarcity of specimens available for comparisons, the taxonomic status of many species within the genus is still under discussion (see Voss 2011; Voss *et al.* 2013; Ramírez-Chaves *et al.* 2016). Furthermore, information on *Coendou* genitalia is limited; indeed, there is only one brief published description of the male genitalia of an indeterminate species (reffered as *Coendou novae-hispaniae*) by Pocock (1922). Considering the scarcity of information about these structures in porcupines -and in general in caviomorph rodents- and the possibility to use this information to solve taxonomical problems, in this work we described the morphology of the glans and the baculum of the Quichua porcupine (*Coendou quichua*).

Materials and methods

The description is based on one adult specimen collected at the "Finca el Diviso", vereda La Colorada, municipality of San Vicente de Chucurí, Santander, Colombia (6° 47′ 38.27″ N, -73° 28′ 48.23″ W; 1,400 masl). The specimen was deposited in the mammalian collection of the Universidad Industrial de Santander (UIS-MHN-M-945). The penis was dissected and fixed in 5 % formaldehyde for one day and later preserved in 95 % ethanol. The baculum was extracted from the glans, and cleared in 5 % potassium hydroxide following Wassersug (1976). Both penis and baculum were photographed. Eight measurements were taken using a dial caliper to the nearest 0.001, following Hooper (1961) and Adebayo *et al.* (2011), and include: total glans length (TGL), glans head width (GHW), glans base width (GBW), total bacular length (TBL), baculum head width (BHW), baculum base width (BBW), *sacculus urethralis* spikes length (SusL), and *sacculus urethralis* length (SUL). In addition, the proportion of the total bacular length / total glans length (TBL / TGL), *sacculus urethralis* spikes length / *sacculus urehtralis* length (SusL / SUL) and *sacculus urethralis* length / total glans length (SUL / TGL), were calculated. For the glans, all measurements and photographs were taken before baculum extraction. The nomenclature for the description of both glans and baculum follows previous works (Pocock 1922; Hooper 1961; Adebayo *et al.* 2011).

The glans and baculum were compared with the description of these structures in two others porcupines available in literature (Pocock 1922; Hooper 1961), the North American porcupine, *Erethizon dorsatum*, and the Malayan porcupine, *Hystrix brachyura*, and three additional Neotropical caviomorph rodents (Hooper 1961): *Cuniculus paca*, *Dasyprocta punctata*, and *Cavia tschudii*.

Results

The glans length of *C. quichua* is almost twice the glans head width (Table 1) and comprises the third part of the total penis length (41.2 mm). The glans is cylindrical, with the head wider than the base. The glans exhibits a yellow cream coloration, and as in others hystricomorphs with a notably tenuous dark coloration of the head (Figure 1A), observed pre and post formaldehyde fixation. Another remarkably characteristic of the glans is the presence of small tegumentary protuberances formed by 3-4 small spines (Figure 1D-E). The protuberances are densely distributed in the head of the glans, but scarcely in the base (Figure 1A). At the tip of the glans below to the urethra, there is an invagination called *sacculus urethralis* (SU). This SU has longitudinally corrugated walls and two developed spikes at the bottom, and as the rest of the glans, presents spiny tegumentary protuberances (Figure 1C). The baculum is as large as the *C. quichua* glans (Table 1), dorsally concave and ventrally convex, and have a distal end or head, a medial region or shaft and a proximal end or base. Both ends are wider than the shaft (Table 1), especially the base which is wider than head. Also, the thin shaft becomes wider and robust close to its base (Figure 1B).

Discussion

The glans shape (cylindrical with a round tip and exhibiting tegumentary protuberances) in *C. quichua* is similar to three other Neotropical caviomorphs; however, differences are found in the tegumentary protuberances. In *C. quichua*, *E. dorsatum*, and *Cuniculus paca*, the glans exhibit tegumen-

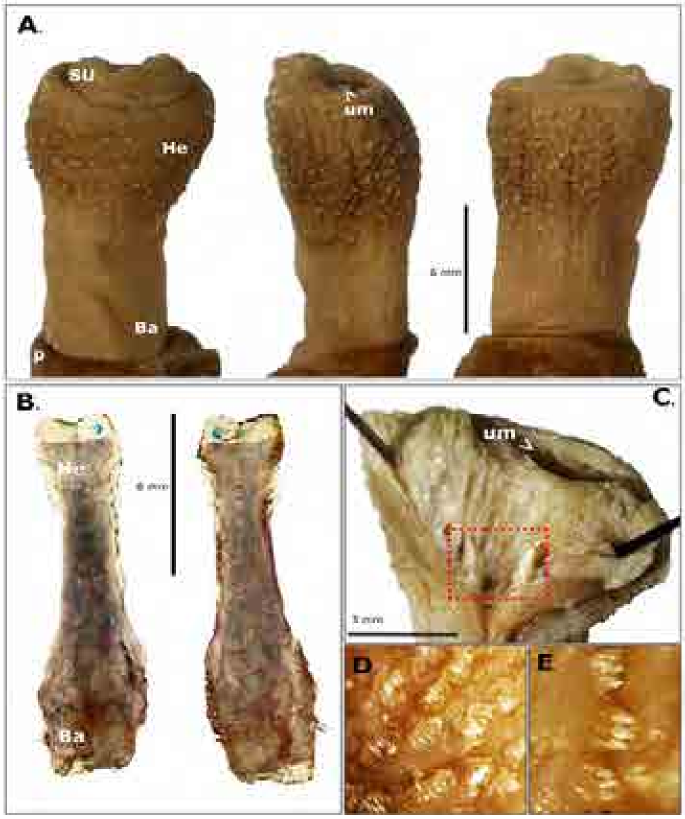

Figure 1. External view of the (A): penis glans, dorsal (left), lateral (middle) and ventral (right) views. SU: *sacculus urethralis*. He: head. Ba: base. p: prepuce. um: urinary meatus. (B): External view of the baculum, dorsal (left) and ventral (right) views. (C): Ventral internal view of the *sacculus urethrlis* and the two spikes (red rectangle). (D-E): Close up of the external tegumentary spiny protuberances.

tary protuberances compound by a single spine (Figure 2A), with variable size in the latter. Furthermore, *Cuniculus paca* presents a notably pair of large dorsolateral multi-toothed rasp (Figure 2D) which are absent in the other species. In *D. punctata* and *Cavia tschudii*, the protuberances are more complex, transversally oriented, and with a blade-like shape, forming a continuous serrate line (Figure 2B-C). In addition, in *Cavia tschudii* those serrate lines are larger than in *D. punctata*, and are distributed only in specific places of the glans (Figure 2B). As in other hystricomorph rodents (Tullberg 1899; Pocock 1922; Dathe 1937; Hooper 1961; Atalar and Ceribasi 2006; Adebayo *et al.* 2011), *C. quichua* presents a *sacculus urethralis* (SU; Figure 1A-C), an invagination at the tip of the glans below to the urethra, that is everted during erection (Layne 1960; Contreras *et al.* 1993). When comparing *E. dorsatum* with *C. quichua*, the SU has smooth and not corrugated walls in the former, lacking of spiny protuberances (Figure 2A). Although the SUL / TGL proportion remains the same for both species, *C. quichua* has longer spikes compared with the length of the SU (Table 1). For the three additional Neotropical caviomorphs compared, the SU is larger when contrasted with the length of the glans, especially for *Cavia tschudii* (Table 1), which differentiate it from *C. quichua*. Also, *C. quichua* and *Cuniculus paca* have similar-sized spikes (compared with the SU length) which are longer than in *Cavia tschudii,* but are shorter than in *D. punctata* (Table 1; Figure 2). Finally, as in *C. quichua*, the walls of the SU in all three Neotropical caviomorph are corrugated with the presence of tegumentary protuberances (Figure 2B-C).

The baculum is one of the most varying structure among mammal species. The general bacular form in *C. quichua* (head and base wider than the shaft, and the base wider than the head; Figure 2C-D), is similar to the one presented in *D. punctata* and *Cuniculus paca*. In contrast, in *E. dorsatum* and *Cavia tschudii*, only the base of the baculum is wider, while the shaft and head are thinner and have the same width (Hooper 1961). The tip of the head is round in *E. dorsatum* and the Neotropical caviomorph (Figure 2), but in *C. quichua* it is flat (Figure 1B). This character seems to be unique for *Coendou*. In contrast, the base of the baculum in *C. quichua* is round (Figure 1B), similar to the one observed in *Cavia tschudii*, whereas for *E. dorsatum*, *D. punctata* and *Cuniculus paca*, the base is flattened with two remarkably lobes at both sides (Hooper 1961; Figure 2).

The comparison of the baculum between *C. quichua* and *H. brachyura* is limited because the brief description of this structure in the latter, which only includes the glans. The glans for both species are similar, being the only difference the bottom of the SU, near to the spikes, which in *H. brachyura* is smooth, without spiny protuberances (see Pocock 1922).

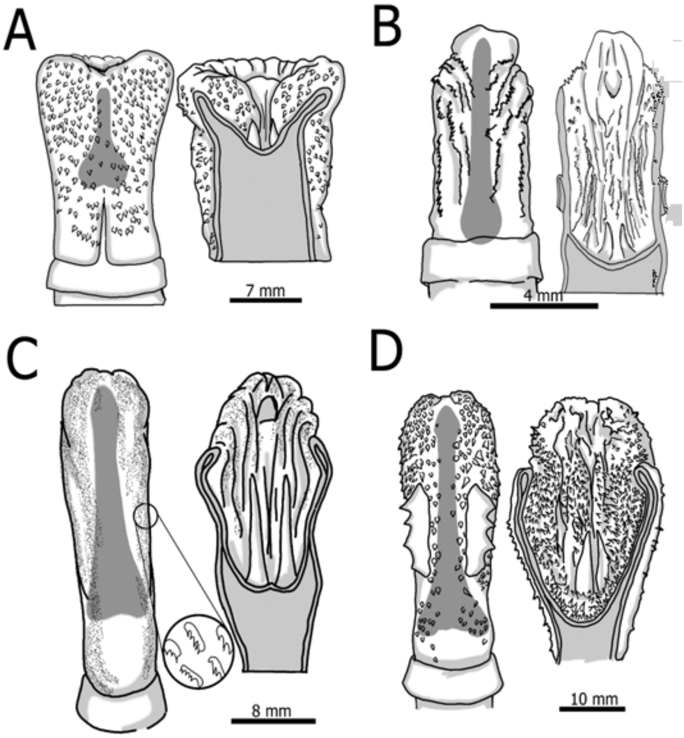

Figure 2. Glans (left), *sacculus urethralis* (right) and baculum (in gray) for the four species compared: *Erethizon dorsatum* (A), *Cavia tschudii* (B), *Dasyprocta punctata* (C) and *Cuniculus paca* (D), modified from Hooper (1961).

Although the family Erethizontidae is more closely related to the Cavioidea than to Hystricidae (Huchon and Douzery 2001; Blanga-Kanfi *et al.* 2009; Antoine *et al.* 2011), the glans of individuals of the family Erethizontidae are more similar to these of Hystricidae. Dathe (1937) suggested that glans with a heavy armature (tegumentary protuberances) and a deep *sacculus urethralis* were characteristics of primitive hystricomorphs; however, Erethizontidae is more basal than the Cavioidea, and Hystricidae is the basal group from the Hystricognathi (see Blanga-Kanfi *et al.* 2009). Due to the similarity in the glans between Erethizontidae and Hystricidae, glans with a slight armature (simply tegumentary protuberances) and a non-deep *sacculus urethalis* (compared with the total glans length) should be characteristics of primitive hystricomorphs. Whereas, for the baculum, this structure shows no general pattern for all species, and it seems to be characteristic for each genus, especially for *C. quichua*. In contrast, the baculum of the Hystricomorpha compared are clearly different from other rodents, such as *Proechymis* (see Hooper 1961), *Marmota* and *Citellus* (see Burt 1960), and several Sigmodontinae rodents (see Calderón-Capote *et al.* 2016). In addition, for these species, both glans and baculum exhibit important characters that might be used for taxonomic identification, such as the tegumentary protuberances, SU depth, or the baculum head shape. However, bacular differences within *Coendou* are still unknown, therefore it is necessary the description of the genitalia of additional species.

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Table 1: Glans and baculum measurements (in mm). TGL: Total glans length, GHW: Glans head width, GBW: Glans base width, TBL: Total bacular length, BHW: Baculum head width, BBW: Baculum base width, SUsL: *Sacculus urethralis* spikes length, SUL: *Sacculus urethralis* Length. There is no information of any measurement for *H. brachyura*. * Proportion (*e. g.* *TBL/ TGL: Proportion of the total bacular length / total glans length). Measurements of additional species taken from Hooper (1961).

	Coendou quichua	*Erethizon dorsatum*	*Cuniculus paca*	*Dasyprocta punctata*	*Cavia tschudii*
TGL	13.1	18.5	38.2	28.7	7.5
GHW	6.3	12	15.3	8	4.7
GBW	5.05	10.3	12.1	7.5	4.9
TBL	12.9	9.2	33.1	20	7.1
BHW	2.15	1.1	4.1	2.1	0.6
BBW	3.6	5.4	12	5.1	1.5
SUsL	2.01	2.1	8.5	9.5	2
SUL	4.2	6.5	18	13.5	8.1
***TBL / TGL**	1 : 1	1 : 2	1 : 1.5	1 : 1.43	1 : 1
***SUsL / SUL**	1 : 2	1 : 3	1 : 2.1	1 : 1.42	1 : 4
***SUL / TGL**	1 : 3	1 : 2.8	1 : 2.1	1 : 2.1	1 : 0.9

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Leucism in *Akodon affinis* (Allen, 1912) (Rodentia: Cricetidae)

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Leucism is a condition where animals show a loss of pigments on certain parts of their skin, without affecting soft tissue, a condition that has been poorly reported for Neotropical rodents. Therefore, our goal was to report leucism for *Akodon affinis*, an endemic species from Colombia, and to analyze the pattern of leucism prevalence in different populations. *A. affinis* specimens deposited in the Mammals Collection of Universidad del Valle (UV) were examined, and any traces of leucism and its prevalence were recorded for 12 different localities where this species was found. These localities were sampled in different years. The association between incidence of leucism and sex was assessed using a Two-tailed Fisher's exact test. A total of 11 individuals from five localities displayed traces of leucism in different parts of their body (Table 1, Appendix 1), including cheeks, dorsum and venter (Figure 1). The analysis revealed that the incidence of leucism was higher in males vs. females. Traces of leucism were most frequent in the dorsum than any other part of their body. Although this species is considered as a Least Concern by the International Union for Conservation of Nature (IUCN), these findings suggest that populations of *A. affinis* might be experiencing inbreeding; however, more information is needed to establish the reproductive and survival consequences of this condition on *A. affinis* populations.

El leucismo es una condición donde los animales presentan una pérdida de pigmentos en ciertas partes de su piel, sin afectar tejido blando, condición que ha sido pobremente reportada para roedores neotropicales. Por lo tanto, nuestro objetivo fue reportar leucismo en *Akodon affinis*, una especie endémica de Colombia, y analizar su patrón de prevalencia en diferentes poblaciones. Una revisión de los individuos de *A. affinis* depositados en la Colección de Mamíferos de la Universidad del Valle (UV) fue llevada a cabo, donde se registró información de leucismo y su prevalencia para 12 localidades diferentes donde esta especie fue encontrada. Estas localidades fueron muestreadas en diferentes años. La asociación entre la incidencia de leucismo y el sexo se evaluó con una prueba exacta de Fisher a dos colas. Un total de 11 individuos de cinco localidades diferentes fueron encontrados con rastros de leucismo en diferentes partes de su cuerpo (Tabla 1, Apéndice 1), incluyendo sus mejillas, dorso y vientre (Figura1). Los resultados indican que la incidencia de leucismo fue mayor en machos que en hembras. Por otro lado, los rastros de leucismo fueron más frecuentes en el dorso en comparación a las otras partes del cuerpo. Aunque esta especie es considerada como Preocupación Menor por la Unión Internacional para la Conservación de la Naturaleza (UICN), estos hallazgos sugieren que las poblaciones de *A. affinis* pueden estar sufriendo de endogamia; sin embargo, es necesaria más información para establecer las consecuencias de esta condición sobre la reproducción y supervivencia de las poblaciones de *A. affinis*.

Key words: Colombia; Colombian grass mouse; conservation; endemism; melanin; population.

Introduction

Leucism is a condition where animals show loss of pigmentation on certain parts of the skin, without affecting soft tissue (Buckley 1982). In mammals, pigmentation results from the synthesis and distribution of melanin (Hearing and Tsukamoto 1991), which depends on several enzymatic factors that modulate pigmentation, especially tyrosinase (Hearing and Tsukamoto 1991; Oetting *et al.* 2003). Melanin plays important roles, including protective coloration, communication, sexual selection, absorption of free radicals and body protection from ionizing radiation (Levine and Krupa 1966; Hearing and Tsukamoto 1991; Caro 2005; Camargo *et al.* 2014). Leucism has been observed in small mammals such as bats (Velandia-Perilla *et al.* 2013) and rodents (Oliveira 2009; Camargo *et al.* 2014; Brito and Valdivieso-Berneo 2016). However, in Neotropical rodents, this condition is barely known, and it has only been reported in a few species (reviewed by Brito and Valdivieso-Berneo 2016).

The Colombian grass mouse, *Akodon affinis* (Allen 1912) (Cricetidae), is a medium-sized Neotropical rodent characterized by uniform dusky brown upper parts with yellowish hair tips, giving an overall olivaceous effect, and dark grayish brown venter with olivaceous hair tips (Pardiñas *et al.* 2015). This species is endemic from the Colombian Andes and is the only representative of the genus in this country (Pardiñas *et al.* 2015; Ramírez-Chaves *et al.* 2016). Considering the limited information on the population and natural history of this species (Pardiñas *et al.* 2015), our main goal was to report leucism in *Akodon affinis* for the first time, and its incidence in populations inhabiting different Andean mountain ranges.

Material and methods

A comprehensive examination of the *Akodon affinis* specimens deposited in the Mammals Collection of Universidad del Valle (UV), Colombia, was carried out. We recorded information on the incidence of traces of leucism for the 12 different localities where this species has been recorded. These localities were sampled across different years, mostly during fieldwork practices of Biology courses at UV, using

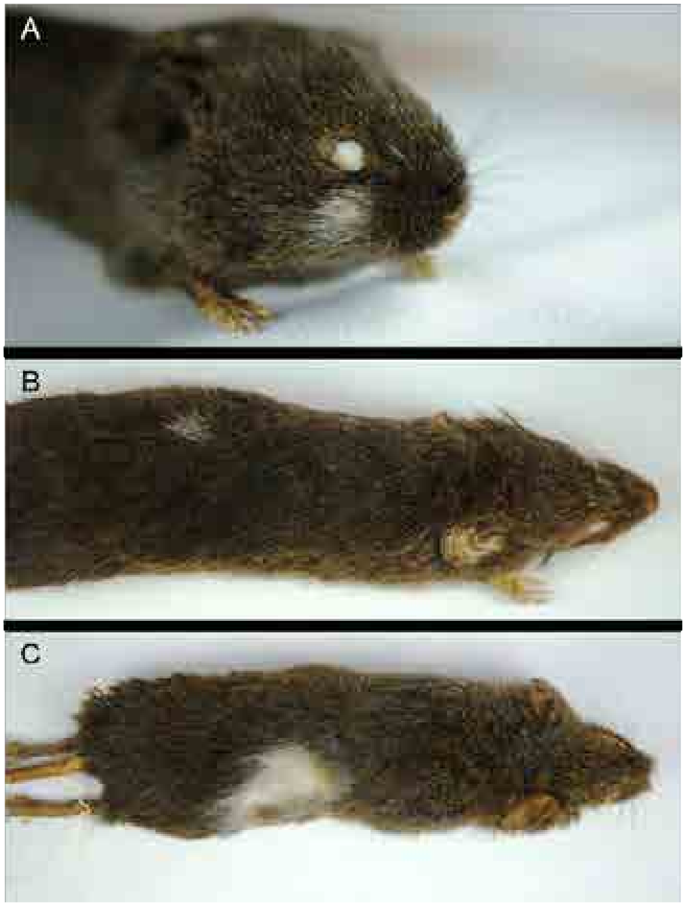

Figure 1. Leucism in individuals of *Akodon affinis* from Colombia: A) Spots on the right cheek and next to the ear (UV 14,440). B) Spot on the dorsum (UV 13,343). C) Wide spot from dorsum to venter (UV 12,025). Photographs by L. Ruano.

100 to 200 Sherman traps (200 in most cases, V. Rojas-Díaz pers. comm.). We used a two-tailed Fischer´s exact test to explore the association between incidence of leucism and sex. For this analysis we only considered the localities (with all the individuals in each) where leucism was detected.

Results

A total of 11 out of 96 (11.46 %) individuals were found to show traces of leucism in different parts of their body (Table 1, Appendix 1), including cheeks, dorsum and venter (Figure 1). The dorsum was the part where most individuals showed traces of leucism ($n = 8$), followed by cheeks ($n = 5$) and venter ($n = 1$). Some individuals presented more than one part of their body with traces of leucism. The analysis showed a significant association between sex and leucism (odds ratio = 8.965, $P = 0.021$), with males having a higher-than-expected incidence of leucism. Leucistic individuals were collected at five different localities (Appendix 1) from the Western and Central Andes of Colombia (Figure 2). The incidence of leucistic individuals per locality was high (Table 2), but fluctuated over time. There were more localities with leucistic individuals in the Central Andes than in the Western Andes (Figure 2).

Table 1. Traces of leucism in individuals of *Akodon affinis* (Allen, 1912) from Colombia.

Locality	Specimen	Sex	Traces of leucism
Florida	UV 3570	♂	Multiple spots on dorsum and rostrum
	UV 3571	♂	Multiple spots on dorsum
	UV 3573	♂	Multiple spots on dorsum
	UV 3575	♂	Multiple spots on dorsum and left cheek
	UV 3578	♀	Spot on dorsum
	UV 10867	♂	Spot on left cheek
Palmira	UV 12025	♂	Wide spot from dorsum to venter
Buga	UV 12414	♂	Spot on dorsum
El Cairo	UV 13343	♂	Multiple spots on dorsum
Pereira	UV 14440	♂	Spot on right cheek and next to the ear
	UV 14488	♂	Spot on left cheek

Discussion

This paper reports, for the first time, information on leucism in *Akodon affinis* populations and its incidence over time in several localities. Our results suggest that the presence of leucism in the sampled populations is as high as the incidence found for *Akodon mollis* in Cordillera de Chilla, Ecuador, a highly fragmented habitat (Brito and Valdivieso-Berneo 2016). The incidence of leucism in *A. affinis* is significantly associated with sex, and appears mainly on their dorsum and rostrum. However, there is insufficient information to assess the potential influence of leucism on survival (visibility to a predator) or reproduction (sexual selection).

It has been proposed that leucism can be the result of skin wounds in burrowing rodents of the Family Geomyidae (S. T. Álvarez-Castañeda pers. com.). However, since

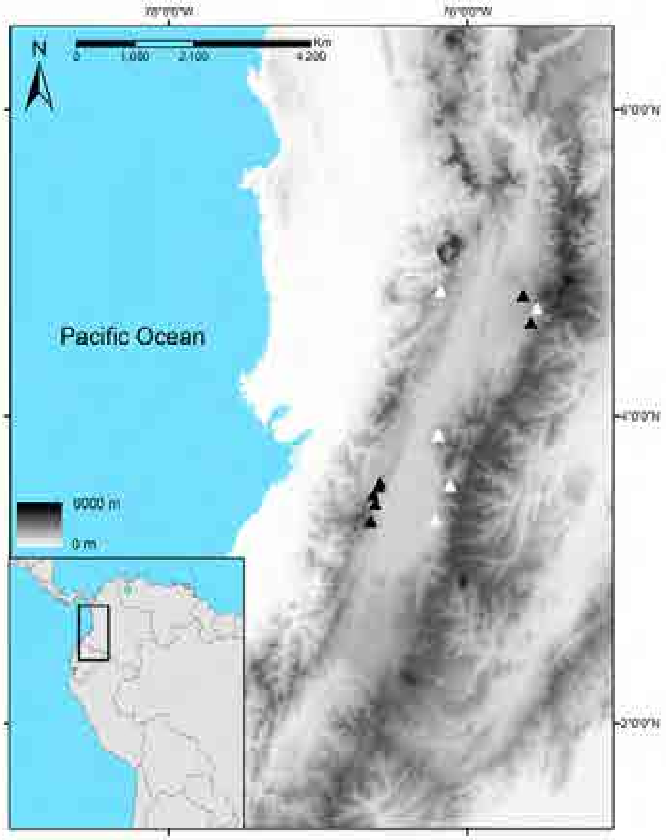

Figure 2. Collection localities of *Akodon affinis* in the Colombian Andes. White and black triangles depict localities where individuals showed traces or no traces of leucism, respectively.

Table 2. Proportion of leucism observed in populations of *Akodon affinis* throughout the years.

Andes	Locality	Year	*n*	Leucistic individuals	Proportion of leucism	Total per locality (n)
Central	Pereira	1989	7	0	0 %	10.53 % (19)
		1990	3	0	0 %	
		2013	9	2	22.22 %	
	Buga	2001	2	1	50.00 %	14.29 % (7)
		2004	5	0	0 %	
	Florida	1983	9	5	55.56 %	23.08 % (26)
		1989	5	0	0 %	
		1992	12	1	8.30 %	
	Palmira	2000	4	1	25.00 %	25.00 % (4)
Western	El Cairo	1984	3	0	0 %	10.00 % (10)
		2001	3	0	0 %	
		2002	4	1	25.00 %	

leucism traits occur with different frequency in both sexes and with different prevalence in the localities we studied, we consider that leucism in *A. affinis* may be due to genetic factors.

Considering the effects of geographic isolation in the emergence of recessive traits (*e. g.*, bottleneck effect; Bensch *et al.* 2000; Lopucki and Mróz 2010), our findings suggest that some populations of *A. affinis* might be experiencing inbreeding due to either the discontinuous distribution of this species (Roach 2016) or to habitat fragmentation in the Colombian Andes (Kattan *et al.* 1994; Kattan and Alvarez-López 1996). According to the International Union for Conservation of Nature (IUCN), *A. affinis* is listed as Least Concern since a large population is presumed from its wide overall distribution range (Roach 2016). Nevertheless, aside from its distribution, there is scarce information about the population ecology of this species (Pardiñas *et al.* 2015). Consequently, information on population dynamics and population genetics is needed to determine the conservation status of *A. affinis*.

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Appendix 1

Specimens of *Akodon affinis*, from the Mammals Collection of Universidad del Valle (UV) examined in this study. Specimens marked with an asterisk (*) show traces of leucism.

Central Andes

Quindío: Reserva Natural La Patasola, Municipality Salento 4° 39′ 32′′ N, -75° 34′ 37′′ W (UV13267, UV13268, UV13458). **Risaralda:** Parque Regional Natural Ucumarí, Municipality Pereira, 4° 42′ 7.4′′ N, -75° 32′ 05.5′′ W, 2,130 m (UV10323 ♂, UV10324 ♂, UV10325 ♂, UV10326 ♂, UV10327 ♂, UV10328 ♂, UV10329 ♀, UV10330 ♀, UV10331 ♀, UV10332 ♀, UV14437 ♂, UV14438 ♀, UV14439 ♂, UV14440 ♂*, UV14466 ♀, UV14467 ♀, UV14468 ♀, UV14487 ♀, UV14488*♂); Finca La Selva, vereda El Cedralito, Municipality Santa Rosa de Cabal, 4° 47′ 18′′ N, -75° 37′ 29′ ‘W (UV3367 ♀, UV13052 ♀, UV13053 ♂).

Valle del Cauca: Finca Venteaderos, Vereda La Nevera, Municipality Palmira, 3° 33′ 02′′ N, -76° 06′ 51′ ‘W, 2,700m (UV12022 ♂, UV12023 ♂, UV12024 ♀, UV12025 ♂*); Finca Santelina, Vereda El Janeiro, Corregimiento La Habana, Municipality Buga, 3° 52′ 37′′ N, -76° 11′ 57′′ W, 1800 m (UV12413 ♂, UV12414 ♂*, UV13027 ♂, UV13028 ♂, UV13029 ♀, UV13030 ♀, UV13031♀); Hacienda Los Alpes, Vereda Las Brisas, Municipality Florida, 3° 19′ 18′′ N, -76° 13′ 07′′ W, 2,400 m (UV3570 ♂*, UV3571 ♂*, UV3572 ♂, UV3573 ♂*, UV3574 ♂, UV3575 ♂*, UV3576 ♂, UV3577 ♀, UV3578 ♀*, UV10335 ♂, UV10336 ♂, UV10337 ♀, UV10338 ♀, UV10339 ♀, UV10343 ♂, UV10344 ♂, UV10345 ♀, UV10346 ♀, UV10347 ♀, UV10512 ♂, UV10513 ♂, UV10514 ♂, UV10515 ♀, UV10867 ♂*, UV10868 ♀, UV10869 ♀).

Western Andes

Valle del Cauca: Campamento Corea, Parque Nacional Natural Farallones de Cali, Municipality Cali, 3° 19′ N, -76° 39′ W (UV2261 ♂, UV2589 ♂, UV2590 ♀, UV2591 ♀, UV4385 ♂); Torre de televisión, Cerro La Horqueta, Municipality Cali, 03° 29′ 25′′ N, -76° 37′ 54′′ W, 2,250 m (UV8162 ♂, UV8163 ♂, UV8164 ♀, UV10333 ♂, UV10334 ♂, UV10517 ♂); Pichindé, Municipality Cali, 3° 25′ 52′′ N, -76° 37′ 6′′ W 1,800 m (UV6621 ♂, UV6622 ♂, UV6623 ♂, UV6624 ♂, UV6631 ♀, UV6632 ♀, UV10613 ♀); Parcelación El Silencio, vereda La Elvira, Municipality Cali, 3° 32′ 43′′ N, -76° 35′ 44′′ W, 2,000 m (UV14645 ♀, UV14652 ♂, UV 14653 ♂); Finca La Minga, Reserva forestal Bitaco, Vereda Chicoral, corregimiento Bitaco, Municipality La Cumbre, 3° 33′ 69′′ N, -76° 35′ 10.1′′ W, 1982 m (UV14774 ♂, UV14775 ♂, UV14780 ♂). Alto Galápagos, Municipality El Cairo, 4° 49′ 00′′ N, -76° 11′ 00′′ W, 2,000 m (UV4171 ♂, UV4172 ♀, UV4173 ♀, UV12334 ♂, UV12335 ♂, UV12336 ♀, UV12583 ♂, UV12584 ♂, UV13343 ♂*, UV13344♂).

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Antillean manatee *Trichechus manatus manatus* (Sirenia: Trichechidae) as a motile ecosystem of epibiont fauna in the Caribbean Sea, Mexico

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The study of epibionts allows inferring ecological, biogeographic and health aspects of the host species (basibiont), and their study on marine mammals is scarce. The aim of this work was to characterize the epibiont fauna associated with the skin of captive individuals of the West Indian manatee in three sites from the Mexican Caribbean. In autumn 2014, 22 dorsal skin scrapings were collected from 11 captive manatees. The biological material was scraped off the skin with a blunt spatula, covering 100 cm^2 of sampled area of the dorsal skin of each manatee. Samples were immediately fixed in 8 % formalin solution and placed in labeled vials for laboratory analysis. We used specialized literature to identify epibionts at the lowest taxonomic level possible. A total of 1,353 individuals from 31 taxa were found, belonging to eight phyla. Twenty nine taxa are new records of epibionts from Sirenians. The nematodes *Monhystera* sp. and *Rabdolaimus* sp., the adult and larvae of copepods from the Order Harpacticoida, the foraminifer *Ammonia* sp. and the rotifer *Lecane* sp. were the dominant epibionts. These new interactions may suggest that in the Caribbean Sea, the manatee skin represents a nutrient-rich substrate for an opportunistic fauna that is more diverse than previously estimated.

Los epibiontes pueden ser estudiados para inferir aspectos ecológicos, biogeográficos y de la salud de la especie que los alberga (basibionte). Su estudio es muy escaso en mamíferos marinos por lo que el objetivo de este trabajo fue caracterizar la fauna epibionte asociada a la piel de individuos cautivos del manatí Antillano en tres localidades del Caribe mexicano. En otoño de 2014 se colectaron 22 muestras de piel de 11 manatíes cautivos. El material biológico se obtuvo por medio de un raspado superficial con una espátula blanda cubriendo un área de 100 cm^2 de la piel del dorso del manatí. Las muestras se fijaron inmediatamente en una solución de formalina al 8 % y fueron colocadas en frascos etiquetados para su análisis en laboratorio. Con el uso de literatura especializada, se realizó la identificación del material al menor nivel taxonómico posible. Se encontraron un total de 1,353 individuos de 31 taxa pertenecientes a ocho fila. De ellos, 29 son nuevos registros de epibiontes para el Orden Sirenia. Los nematodos *Monhystera* sp. y *Rhabdolaimus* sp., las larvas nauplio y adultos de copépodos del Orden Harpacticoida, foraminíferos *Ammonia* sp. y los rotíferos *Lecane* sp. fueron dominantes. Estas nuevas interacciones sugieren que, en el Mar Caribe, la piel de los manatíes representa un sustrato rico en nutrientes para una fauna oportunista que es más diversa de lo previamente estimado.

Keywords: diatom, invertebrates, manatee, marine mammals, Mexican Caribbean, opportunistic fauna, symbiosis.

INTRODUCTION

The manatee *Trichechus manatus* Linnaeus, 1758 is a marine mammal endangered of extinction, characterized by a broad distribution area, that inhabits marine, estuarine, and freshwater systems in tropical America, mainly in the Caribbean Sea (Deutsch *et al.* 2008). In Florida, the manatee subspecies *T. m. latirostris* Harlan, 1824 has been recognized as a basibiont organism that functions as a wandering ecosystem for various epibiont groups of algae and aquatic invertebrates (Bledsoe *et al.* 2006; Franckovich *et al.* 2015), while the Caribbean subspecies *T. m. manatus* Linnaeus, 1758 has been little studied in this regard (Morales-Vela *et al.* 2008; Suárez-Morales *et al.* 2010; Violante-Huerta and Suárez-Morales 2016). Studying epibiont communities in large vertebrates is an indirect method to obtain information on the biogeography, ecology and health of the respective basibiont (Fernández *et al.* 1998; Liria-Loza 2011). The objective of this investigation is to report new evidence on the diversity of epibiont organisms growing on the skin of the manatee in the Mexican Caribbean.

MATERIALS AND METHODS

In the autumn of 2014, a total of 22 samples were collected from the skin of the back of eleven captive manatees, and salinity (salt) was recorded, in three localities of the Mexican Caribbean Sea: four manatees (two adult females, one adult male and one calf) kept in the marine aquarium (27 ppm salt) Dolphin Discovery Puerto Aventuras (20° 30′ 02.13″ N, -87° 13′ 32.25″ W), six (three adult females, one adult male and two calves) living in an estuary (18 ppm salt) at Xcaret eco-archaeological park (20° 34′ 42.50″ N, -87° 07′ 12.91″ W) and one adult male living in the freshwater system (7 ppm salt) at Centro de Atención y Rehabilitación de Mamíferos Acuáticos (Center for Care and Rehabilitation of Aquatic Mammals; CARMA, for its acronym in Spanish), Chetumal Bay (18° 41′ 22.19″ N, -88° 15′ 47.09″ W). The biological material was collected by scrapping off an area of healthy skin on the back of each manatee with a blunt plastic spatula (Suárez-Morales *et al.* 2010; Figure 1) covering 100 cm^2 (10 x 10 cm quadrants). Immediately afterwards, samples were fixed and preserved in a 8 % formalin solution and placed in labeled vials for analysis in the laboratory. The material was identified to the lowest taxonomic level possible assisted with specialized literature.

The complexity of the epibiont community on the skin of manatees, the lack of information on the physical variables of the substrate (skin), the physicochemical variability of water between localities, and the lack of homogeneity in age and sex of the 11 manatees sampled, were all factors that restrained the conduct of robust statistical studies with the data obtained to establish unequivocal relationships. Consequently, only percent total abundance figures were used.

Figure 1. Surface scrape technique used for sampling epibionts found on the West Indian manatee in Mexico. Photograph by Raúl Díaz-Gamboa.

RESULTS AND DISCUSSION

A total of 1,353 specimens of 31 taxa were found, belonging to eight phyla (Table 1). The dominant taxa were nematodes (39 %), harpacticoid copepods in naupliar and adult stages (27.3 %), foraminifera of the genus *Ammonia* (7.6 %) and rotifers of the genus *Lecane* (8.9 %). Large amounts of microalgae directly interacting were also observed (*i. e.*, pennate diatoms) that were neither identified nor quantified.

The interactions of epibiont crustaceans such as harpacticoid and tanaid copepods have been examined in free-living manatees and are recognized as harmless to the health of the specimens studied despite its prevalence and high abundance. The presence of these crustaceans has not been associated with injured skin that could suggest a parasitic interaction (Morales-Vela *et al.* 2008; Suárez-Morales *et al.* 2010). At present, there are three species of harpacticoid copepods (Huys 2016; Violante-Huerta and Suárez-Morales 2016) and two species of tanaid copepods (Bonde 2005; Morales-Vela *et al.* 2008; Ortiz *et al.* 2010) that have been reported as well-established manatee epibionts. In addition to the presence of unidentified harpacticoid copepods and the previously recorded tanaid *Sinelobus stanfordi*, the present study includes five groups of crustaceans that had not been previously found as manatee epibionts: Crypridiidae, Loxoconchidae, *Acartia lilljeborgii*, *Colomastix* and Alpheidae. These groups were unrelated to skin injuries in the manatee individuals sampled.

The species *Acartia lilljeborgii* is considered a strictly planktonic species (Campos and Suárez-Morales 1994); hence, its presence on manatee skin could be an incidental finding. In addition, groups of microinvertebrates were found on healthy skin that had not been previously observed as epibionts of manatees in the Caribbean: fora-

Table 1. Composition of the epibiont community associated with the skin of the West Indian manatee in the Mexican Caribbean. Association record (AR)[2]. Total abundance% (TA%).

Phylum	Taxon	Sampled locality[1]			(AR)[2]	(TA%)
		DD	XCA	CHE		
FORAMINIFERA	*Ammonia*	x	x	x		7.6
	Bolivina		x			0.2
	Epistominidae		x			1.3
	Haplophragmoides		x			1.0
	Massilina		x			0.8
	Textularia		x			0.4
	Trochamina		x			1.3
RADIOZOA	Spongodiscidae		x			0.1
ROTIFERA	Bdelloidea		x	x		0.9
	Lecane		x	x		8.9
NEMATODA	*Archepsilonema*		x			0.2
	Butlerius			x		0.1
	Miconchus		x			0.4
	Mononchoides		x	x		1.7
	Monochromadora	x	x			0.5
	Monhystera	x	x	x		16.4
	Teratocephalus		x	x		2.4
	Tylenchus		x			0.6
	Rabditidae		x	x		1.6
	Rabdolaimus	x	x			15.1
ANNELIDA	Iospilidae	x	x			0.1
	Pilargiidae		x			0.2
PLATYHELMINTHES	Digenia	x	x			0.1
MOLLUSCA	*Limacina*		x			0.4
ARTHROPODA	Cypridiidae	x	x	x		7.4
	Loxoconchidae		x			0.2
	Acartia lilljeborgii			x		0.7
	Harpacticoida (adult, copepodite and naupli)	x	x	x	r	27.3
	Colomastix	x	x			1.1
	Sinelobus stanfordi		x		r	0.6
	Alpheidae			x		0.1

[1] DD= Dolphin Discovery Puerto Aventuras, XCA = Xcaret, CHE = (CARMA) Chetumal bay, x = Presence, [2] r = epibiont interaction previously reported.

miniferans (*n* = 7), radiolarians (*n* = 1), rotifers (*n* = 2), nematodes (*n* = 10, dominant), annelids (*n* = 2), mollusks (*n* = 1), and platyhelminthes (*n* = 1). The findings in this study deepen our knowledge about the external interactions in sirenians, since 29 of the 31 taxa observed in this work are new records of epibionts for the subspecies *T. m. manatus* and for the order Sirenia around the world.

The difference between the diversity of taxa observed in this research and previous reports may have been associated with the captivity status of the specimens sampled. This is due to the hydrologically more stable environments, which facilitate the establishment of colonizing organisms on the available substrate (Railkin 2004). In addition, captivity reduces the exposure of individuals to fluctuations in water salinity and temperature — the primary variables that influence the known load of epibionts in free-living manatees (Bledsoe *et al.* 2006). In addition, captivity favors the retention of nutrients, suspended detritus, bacteria and microflora, which ultimately become part of the biofilm that develops on the skin of manatees. These are likely utilized as food sources for the opportunistic microfauna reported, a common behavior for epibiont organisms (Humes 1964; Bledsoe *et al.* 2006).

Given the complexity associated with the study of epibiont communities and the richness of species associated with the skin of captive and free-living manatees, it is essential to record hydrological variables, assess the influence of the immune status of the manatee (Halvorsen and Keith 2008), correlate the physical composition of the skin (Wahl and Mark 1999; Wahl and Hopper 2002), and analyze the parasitizing potential of opportunistic species, to better understand the ecological niche of manatees as a wandering substrate in the western Caribbean.

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One black bear (*Ursus americanus*) connects the great sierras: Genetic evidence

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The black bear has inhabited North America for three million years. Two clades diverged during this period: coastal and continental; the continental clade includes two subclasses (western and eastern). The contact between both is a recent event. Because there is a high genetic differentiation between subclasses, the genetic flow of populations between Sierra Madre Oriental and Sierra Madre Occidental is considered as restricted to nonexistent; also, desert environments and human settlements act as a barrier. There are no recent records of black bears in Durango, so the capture of an individual from there presents the opportunity to test whether there is a possible connection between the populations of Sierra Madre Occidental and Sierra Madre Oriental. Our objective was to determine the geographic origin of this individual and validate whether there is a likely connection between populations from both mountain ranges. A black bear specimen was captured in Felipe Carrillo Puerto, municipality of Guadalupe Victoria, Durango. This specimen was sedated. Tissue samples from ear, hair and excrement were collected; samples of mtDNA were extracted and amplified, and two 418-bp sequences were obtained. The haplotype was characterized by a neutrality test of the control region. To determine the origin of the specimen, GenBank was searched for matches with haplotypes previously described and geographically characterized. Six 418-bp sequences were successfully amplified. The neutrality test yielded a single haplotype, with a 99.32 % agreement with haplotype C. Haplotype C has been previously described for the Trans-Pecos region in Texas; accordingly, this haplotype belongs to the eastern subclade. The origin of the black bear specimen captured was Sierra Madre Oriental, based on the presence of haplotype C. This bear traveled at least 250 km to reach the municipality of Guadalupe Victoria. This displacement event indicates that connectivity between black bear populations from both Sierras Madres has been maintained. This distance is similar to displacements previously reported in fragmented environments where a suitable habitat is surrounded by arid zones. However, this displacement took place between two large mountain ranges, rather than within a single mountain range. Genetic diversity, frequency of displacement events between the Sierras, time and distance between displacements, dispersal routes and presence of patches of suitable habitat, are all factors that should be evaluated in order to understand the current dispersal and genetic-flow patterns between the subspecies of bears in Mexico.

El oso negro ha estado presente en Norteamérica desde hace tres millones de años; durante este periodo divergieron dos clados: el costero y el continental. Dentro del clado continental existen dos subclados (occidental y oriental), y el contacto entre ambos se considera un evento reciente. Debido a la alta diferenciación genética entre subclados, se considera que el flujo genético de las poblaciones entre la Sierra Madre Oriental y Occidental es de restringido a inexistente; además, ambientes áridos y los poblados humanos actúan como una barrera. En el estado de Durango no se cuentan con registros recientes de osos negros por lo que la captura de un individuo representa la oportunidad para probar si existe una conexión entre las poblaciones de la Sierra Madre Occidental y la Sierra Madre Oriental. Nuestro objetivo fue determinar el origen geográfico de este individuo y validar si existe una probable conexión entre poblaciones de ambas serranías. Se capturó un individuo de oso negro en el poblado Felipe Carrillo Puerto, municipio de Guadalupe Victoria, en Durango. El individuo fue químicamente inmovilizado y se tomaron muestras de tejido de la oreja, pelo y excremento. Se llevó a cabo la extracción de ADN mitocondrial (ADNmt) y se amplificó. Se obtuvieron dos secuencias de 418 pares de bases. Se caracterizó su haplotipo mediante un análisis de neutralidad de la región control. Para asociar la procedencia del individuo, se hizo una búsqueda en GenBank para determinar coincidencias con haplotipos previamente descritos y caracterizados geográficamente. Se amplificaron con éxito seis secuencias de 418 pb. El análisis de neutralidad arrojó un solo haplotipo, con una concordancia del 99.32 % para el haplotipo C. El haplotipo C fue descrito para la región de Trans-Pecos en Texas, EUA; además, pertenece al subclado oriental. De este modo, la procedencia del oso negro capturado fue asociada a la Sierra Madre Oriental, México. El oso capturado, por el haplotipo encontrado, pertenece a la Sierra Madre Oriental, por lo que se desplazó al menos 250 km para llegar al Municipio de Guadalupe Victoria, Durango. Este evento de dispersión indica que la conectividad entre ambas Sierras Madres para los osos negros se mantiene. Esta distancia es similar a dispersiones previamente reportadas en ambientes fragmentados donde el hábitat adecuado está rodeado por zonas áridas. Sin embargo, este desplazamiento fue entre dos grandes sierras, y no sobre el mismo sistema montañoso. La diversidad genética, la frecuencia de eventos de dispersión entre las Sierras, el tiempo y distancia entre desplazamientos, las rutas de dispersión y la presencia de parches de hábitat adecuado, son factores a evaluar para entender los patrones de dispersión actual y el flujo genético entre las subespecies de osos presentes en México.

Key words: Connectivity; control region; dispersal; Durango; haplotype C; mitochondrial DNA; *Ursus americanus*.

Introduction

The black bear (*Ursus americanus*, Pallas 1780) is a species that has inhabited North America for approximately three million years, during which it has extended across a broad geographical range (Kurten and Anderson 1980). This distribution changed significantly during the Pleistocene as a result of the southward shift in the distribution pattern and extent of forests due to glaciation and post-glaciation events (Wooding and Ward 1997). This phenomenon favored the evolution of two clades — coastal and continental — within the species (Pelletier *et al.* 20117). Within the continental clade, the distribution and topology of the diversity of mitochondrial DNA has revealed the existence of two subclades — eastern and western — that diverged in isolation between 1.8 and 0.8 million years ago (Wooding and Ward 1997; Van Den Bussche *et al.* 2009). These subclades have shown disjunct distributions over a long period of time, with refuges associated with forests to the east and west of their distribution range (Wooding and Ward 1997). Contact between both subclades in areas of Texas and New Mexico is considered a recent event (Wooding and Ward 1997).

The difference between these subclades is also evident within the southern limit of the distribution range of this species. The dominant haplotypes found for black bear populations in the Trans-Pecos region, Texas, have been identified as belonging to the eastern subclade (Onorato *et al.* 2004), while haplotypes described for northern Sonora, in western Mexico, belong to the western subclade (Varas *et al.* 2010).

Currently, due to the high genetic differentiation between subclades, it has been postulated that the gene flow between the populations inhabiting Sierra Madre Oriental and Sierra Madre Occidental in Mexico is non-existent (Onorato *et al.* 2004). The above has been proposed due to the existence of desert environments surrounding montane habitats, which act as barriers, in addition to present human activities and presence of towns and/or cities that prevent the displacement of individuals within an array of highly transformed habitats (Atwood *et al.* 2011).

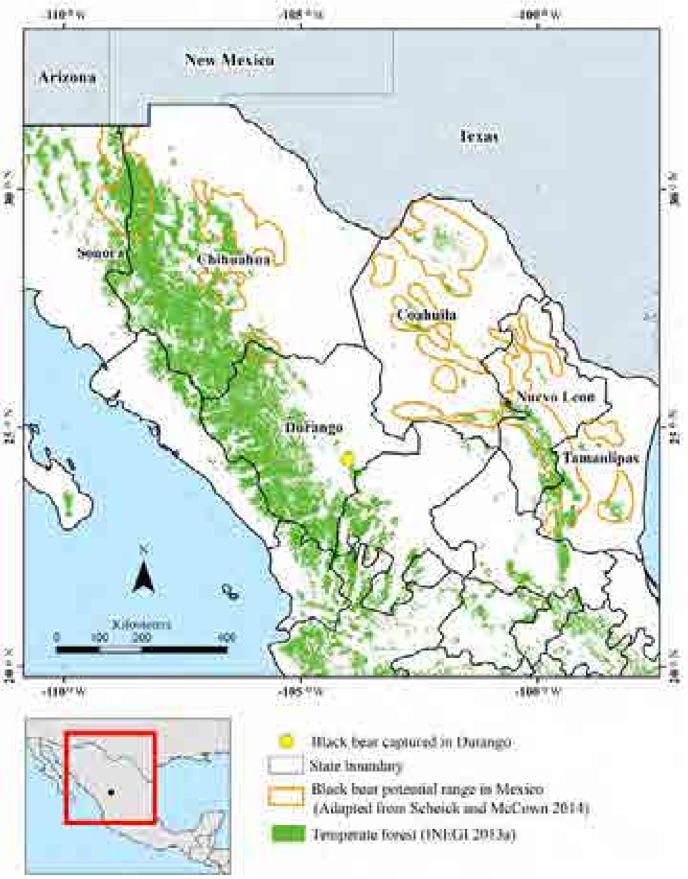

Figure 1. Record of a black bear specimen (*Ursus americanus*) captured in the municipality of Guadalupe Victoria, Durango, compared with the area of distribution of the species in Mexico (Scheick and McCown 2014).

In Mexico, the black bear is considered a species endangered in risk of extinction throughout most of its distribution range (DOF 2015), an area that was significantly reduced largely due to the impact of anthropogenic factors during the twentieth century. The presence of the species in the southern area of its distribution range in Mexico is characterized by a low number of records, and the precise limits of this range are still unknown (Delfín-Alfonso *et al.* 2011; Delfín-Alfonso *et al.* 2012; Scheick and McCown 2014). On April 2014, one black bear specimen was captured by local inhabitants in Felipe Carrillo Puerto, a town located in the municipality of Guadalupe Victoria, state of Durango. Durango is one of the states where there is a high uncertainty about the presence of the black bear (Delfín-Alfonso *et al.* 2012; Juárez-Casillas and Varas 2013); prior to this capture, there had been no recent records of the species in the area (Delfín-Alfonso *et al.* 2011). The presence of the specimen in this locality raise questions about its geographical origin, whether associated with the Sierra Madre Occidental or the Sierra Madre Oriental. This specimen brought the unique opportunity to investigate the possible existence of a recent connectivity event between both regions; accordingly, our aim was to determine the geographic origin of the black bear specimen by characterizing its haplotype.

Materials and Methods

Study area. Felipe Carrillo Puerto (24° 27′ N, -40° 07′ W) is one of the largest urban localities in the municipality of Guadalupe Victoria; it is located to the southeast of the state of Durango, with a population of 2,000 inhabitants. The town is surrounded by rainfed agriculture fields that make up 51 % of the municipality area, while natural grasslands rank second in terms of coberture (28 %), and pine and oak forests comprise less than 4% of the municipality area (INEGI 2013a). Mean annual precipitation ranges between 450 mm and 605 mm per year, and mean annual temperature, between 12.7 °C and 17.4 °C. The elevation within the municipality varies from 1,912 to 2,560 m (INEGI 2013b).

Capture and Maintenance of the Black Bear Specimen. The black bear specimen was captured on 23 April 2014 by two local inhabitants of Felipe Carrillo Puerto using ropes. Once the specimen was securely held, the local inhabitants informed the authorities concerned. On the first veterinary examination at the site of the capture, personnel from PROFEPA Durango and the Sahuatoba Zoo mentioned that the specimen was in good health condition (PROFEPA 2014).

The specimen captured was transferred by PROFEPA Durango to the Sahuatoba Zoo, in the city of Durango, where he was sedated by the local staff (2 mg/kg each of ketamine/xylazine). Once sedated, this specimen was identified as a young male (approximately two years old based on dental wear) and its somatic measurements were recorded (LT = 1.540, LC = 90, LP = 220, 116, W = 81.5);

the specimen was in good physical condition. During the examination, samples of ear tissue, hair and feces (two replicates of each) were collected for processing at *Universidad Autónoma de Queretaro*; afterwards, the specimen was fitted with a radio transmitter collar.

Haplotype Characterization. For DNA extraction, 30 mg of tissue, 0.50 g from the surface of excrement, and three hairs were collected from each sample. For tissue and hair samples, the DNeasy Blood & Tissue mini kit (Qiagen Inc., Valencia, California) was used following the manufacturer's protocols. For stool samples, the QIAmp ®DNA Stool mini kit (Qiagen Inc., Valencia, California) was used following the protocol developed by Varas *et al.* (2010). To confirm the proper operation of the protocol and the amplification and sequencing procedure, we used a negative control (high purity water for PCR) and a positive control (previously identified black bear DNA sample).

Once the mitochondrial DNA was extracted, it was amplified by PCR. Two sequences of 418 base pairs were obtained using a portion of the cytochrome b region and D-loop of mitochondrial DNA, using the primer ADNmtCRf (CTCCACTATCAGCACCCAAAG) and its inverse ADNmtCRr (GGAGCGAGAGGTACACGT) with a volume of 15 ml, where 9 ml were green taq (PROMEGA Corp.), 0.2 ml BSA 7.5 % (Sigma-Aldrich, St. Louis, MO, USA), 0.2 ml MgCl2 (QIAGEN, Inc.), 0.3 ml of each primer, and 5 ml of DNA (Rinkevich 2012).

Initial denaturation was carried out at 95 °C for 10 minutes, followed by 40 denaturation cycles at 94 °C for 45 seconds, hybridization at 54 °C for one minute, extension at 72 °C for two minutes, final extension at 72 °C for 10 minutes, and cooling at 4°C (Short Bull *et al.* 2011). The resulting amplifications were subjected to electrophoresis through 1.5% agarose gel with TBE buffer (Onorato *et al.* 2004) and were visualized through exposure to UV rays. Amplifications were purified using the Wizard PCR Prep DNA Purification System (Promega, Madison, Wisconsin).

The amplified sequences were sent to Macrogen Sequencing Service http://dna.macrogen.com/esp for sequencing. Afterwards, sequences were reviewed and aligned in the program Sequencher 4.6 (Gene Codes Corporation, USA). To determine the haplotypes in the sequences analyzed, ADNmtCR was tested for neutrality using the program dnasp5 (Avin 2012). Finally, GenBank (NCBI http://www.ncbi.nlm.nih.gov/) was searched for potential matches with haplotypes previously described and characterized geographically (Onorato *et al.* 2004; Varas *et al.* 2010, Van Den Bussche *et al.* 2009; Pelletier *et al.* 2011), aiming to associate the origin of the black bear with either the Sierra Madre Oriental or the Sierra Madre Occidental.

Results

The DNA from the six samples of the black bear specimen were successfully amplified (Table 1); thus, all were used in the haplotype characterization analysis**.** The neutrality test yielded a single haplotype. Sequences of 418 base pairs were obtained and the number of base pairs that were not amplified per sample ranged from 1 to 6. Considering these base pairs as unknown, our samples yielded an agreement of 99.32 % ± 0.41 (std dev.) with haplotype C described by Onorato *et al.* (2004) (Table 1).

Based on the above findings, the black bear specimen captured in the municipality of Guadalupe Victoria, Durango, comes from the subclade inhabiting Sierra Madre Oriental.

Discussion

The bear captured in Felipe Carrillo Puerto, Durango, belongs to the eastern subclade representing the populations of Sierra Madre Oriental, since haplotype C has not been recorded in Sierra Madre Occidental (Varas *et al.* 2010). Haplotype C was first described in 2004 from a single specimen inhabiting the Trans-Pecos region, Texas, USA, and has been recently documented in Louisiana (Van Den Bussche *et al.* 2009). It is considered that haplotype B gave rise to haplotypes C and A. Haplotype B is considered the parent haplotype within the eastern subclade, being broadly distributed from Minnesota in northern United States to Mexico. Van Den Bussche *et al.* (2009) consider that colonization by this set of haplotypes (A, B, and C), which are characteristic of the eastern lineages, took place gradually from east to west given the absence of barriers that would restrain gene flow.

The specimen captured in Durango traveled more than 250 km from the area recognized as a part of the known distribution range of the black bear in Coahuila to reach the municipality of Guadalupe Victoria (Scheick and McCown

Table 1. Agreement of base pairs (bp) between samples of the black bear captured in Felipe Carrillo Puerto, Durango, and haplotype C described by Onorato *et al.* (2004). Base pairs 1-3 correspond to the start codon; bp 416-418, to the stop codon.

Sample	Position of non-amplified (-) base pairs																			Agreement (%)
	1	2	3	5	13	17	21	30	39	43	55	104	127	288	405	414	416	417	418	
Tissue	G	A	A	-	A	T	T	-	C	T	C	C	T	A	A	T	G	G	T	99.52
Tissue	G	A	A	A	A	T	T	T	C	T	C	-	T	A	A	T	G	G	T	99.76
Excrement	G	A	A	A	-	T	-	T	-	T	C	C	T	A	A	T	G	G	T	99.28
Excrement	G	A	A	-	A	T	T	T	C	T	-	C	-	A	A	T	G	G	T	99.28
Hair	G	A	-	A	A	-	T	-	C	-	C	C	T	A	-	-	G	G	T	98.56
Hair	G	A	A	-	A	T	T	T	C	T	C	C	T	-	A	T	G	G	T	99.52
Haplotype C	G	A	A	A	A	T	C	G	C	T	C	A	T	A	A	T	G	G	T	

2014). This dispersal event by a relatively young individual strongly supports the fact that the connectivity between the Sierra Madre Occidental and the Sierra Madre Oriental is currently maintained for black bears.

Black bear males are capable of carrying out extensive dispersal events in desert environments within a mountain range. There are reports about the displacement of males covering between 45 and 282.2 km in straight line; these movements have been attributed to a fragmented environment where a suitable habitat is surrounded by grassland or arid areas (Costello *et al.* 2001; Hellgren *et al.* 2005; Liley and Walker 2015). The bear specimen reported herein followed a route similar to the one reported previously. However, this individual extensive displacement connected the two largest mountain ranges of Mexico passing through a landscape matrix dominated by desert conditions, which are considered for the species relative to temperate forests (Costello *et al.* 2001).

Since a single black bear individual — and hence a single haplotype — was available (Van Den Bussche *et al.* 2009), the presence of more individuals in Sierra Madre Occidental coming from Sierra Madre Oriental is currently unknown. Although we cannot be certain that the specimen captured comes from the wild, it showed some features that so indicate. On the one hand, the specimen lacked the calluses on pads and joints that are typical in animals that have spent time in captivity. However, the behavior of the specimen after its release was consistent with the one of a wild animal. The specimen was released by Durango PROFEPA and CONANP staff in La Michilía Biosphere Reserve less than a week after its capture. From the time of release, its displacements were recorded through satellite location over a period of 19 months; it traveled the desert between the two mountain ranges heading to Sierra Madre Oriental (unpublished data).

The genetic diversity, as well as the frequency of dispersal events between the two Sierras Madres, the time and distance between displacement events, the likely dispersal routes and the presence of patches of suitable habitats, are all factors that should be assessed to understand the current dispersal and gene-flow patterns between the subspecies of bears in Mexico.

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