Therya

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La Portada

Mono verde (*Chlorocebus sabaeus*) de la isla de barbados. La especie es originaria de África tropical que ha sido domesticada y considerada como mascota. Los Monos verdes fueron introducidos en diferentes islas del caribe principalmente por las embarcaciones de esclavos provenientes de África, en la actualidad se encuentra presentes en las islas de San Cristóbal, Nieves, San Martín y Barbados a finales del Siglo XVII (fotografía: 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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EDITORIAL

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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

COVID-19: posibles efectos en la educación mastozoológica y otras disciplinas biológicas

La enfermedad COVID-19 (**CO**rona**VI**rus **D**isease 20**19**) se encuentra clasificada dentro de las enfermedades denominadas como síndrome respiratorio agudo grave (*Severe Acute Respiratory Syndrome,* SARS) y es producida por un virus de la familia de los coronavirus llamado SARS-Cov-2. La COVID-19 ha ocasionado, en la mayoría de los países donde ha emergido, la implementación del distanciamiento social como estrategia para reducir el riesgo de contagio. Esta acción ha modificado la dinámica social en el mundo, afectando de manera directa las actividades cotidianas en prácticamente todos los sectores de la sociedad. En cada sector productivo existe el reto de volver a funcionar, pero ahora bajo un esquema cauteloso ante la posibilidad de rebrotes, y de una forma distinta a la previamente existente, tomando en cuenta las lecciones que deja esta pandemia. Es evidente que tendrá que existir un cambio de actitud, percepción y visión después de COVID-19, y deseable que haya una evaluación de las prioridades tanto a nivel individual como de comunidad.

En el caso específico de la educación, la investigación y el desarrollo tecnológico, debe haber un cambio hacia un nuevo paradigma. En particular, el proceso de docencia debe conllevar acciones que deban impactar positivamente la formación de los recursos humanos en todos los niveles educativos. A partir del proceso de aislamiento social, implementado en unas cuantas semanas, el sector académico ha sido uno de los más activos en el desarrollo, aprovechamiento y utilización de herramientas digitales e informáticas. Acciones que han permitido al profesorado de diferentes niveles educativos continuar con el proceso de enseñanza de manera virtual y a distancia. La efectividad de estas acciones para el sistema educativo general se basa en que la educación a distancia ha sido impulsada desde hace más de dos décadas, para lograr avances en la enseñanza y capacitación a todos los niveles de profesionalización, incluyendo licenciaturas, diplomados, especializaciones y posgrados.

Las instituciones de educación superior en México han hecho esfuerzos por transformarse en esta dirección; sin embargo, los resultados no han sido del todo satisfactorios, principalmente al incorporar las tecnologías de la información y comunicación (TIC) a la enseñanza, centradas más hacia el uso de tecnologías que en la innovación de la educación. La educación a distancia se caracteriza porque el profesor deja de ser el centro del escenario y en su lugar se ubica al estudiante, quien asume la responsabilidad de su propio proceso de aprendizaje, se hace más independiente y creativo. Este es un esquema difícil de alcanzar sin un entrenamiento que vaya más allá del uso de las herramientas tecnológicas correspondientes. La problemática más importante ha sido la deficiente capacitación de los docentes en el uso eficiente de las herramientas, los usos y costumbres de las clases presenciales, el desconocimiento, indiferencia y falta de motivación en el docente para capacitarse e incorporarse a una nueva visión en la educación, aunado a la marcada brecha generacional informática, la cual implica actualización constante. A la brecha generacional se le suma la brecha socioeconómica que ha puesto en evidencia que muchos sectores de la población tienen acceso muy limitado o nulo a estos recursos digitales (hardware, software y servicios de internet de calidad), complicando aún más el proceso de educación a distancia. En México, se ha observado la falta de servicios en zonas aisladas y marginadas que impiden la comunicación. Hasta antes del surgimiento de la COVID-19, las TIC se utilizaban principalmente para apoyar las clases presenciales, mejorando el proceso de enseñanza-aprendizaje y promoviendo la participación, comunicación e interacción de quien la utiliza. La implementación de las TIC en este proceso ayuda a que los estudiantes, que muchas veces de manera presencial no participan o expresan sus dudas, lo realicen en el ámbito virtual. Favorece el trabajo en equipo, debido a que cada uno puede trabajar desde el lugar que prefiera, no invirtiendo tiempo y recursos en trasladarse a algún sitio específico, pero reduce las interacciones sociales y fomenta el individualismo. Las generaciones Y "milennials" y Z "centúrica" han sido denominadas como nativos digitales; adquieren y usan la información en muy corto tiempo por medio de redes de comunicación y estaciones multimedia. Son alumnos jóvenes multitareas que han crecido en un mundo digital, acostumbrados a la comunicación a través de mensajes de texto, videollamadas, correo electrónico, redes sociales, entre otros. Estas capacidades no necesariamente son signo de mejor desempeño para muchos estudiantes, y por lo mismo, no les es fácil escribir textos que expresen sus ideas.

Ante esta situación emergente en la educación, parece obvio plantear las siguientes preguntas: ¿Qué cambiará en los procesos de enseñanza-aprendizaje, particularmente en ciencias como la Biología, donde además de las actividades presenciales, se deben llevar a cabo prácticas en los laboratorios y en el desarrollo de habilidades manuales en el trabajo de campo? ¿Qué cambiará particularmente en el caso del estudio de los mamíferos, ecología, y sistemática entre otros?

¿Cómo se debe impulsar el estudio de la naturaleza en las nuevas generaciones por vía remota? Estas preguntas tienen cabida aquí, si se considera que entre los cambios que se deben asumir en el regreso a la nueva cotidianidad está una nueva forma de relación con el ambiente para evitar otras pandemias.

La enseñanza de las ciencias biológicas y sus áreas de conocimiento, como la mastozoología, ecología, entre otros, se aborda bajo el esquema de dos componentes centrales. El primero se refiere a los aspectos teóricos-conceptuales, impartidos mediante la cátedra, el análisis y discusión de lecturas, ensayos y la realización de análisis epistemológico. Sin duda, este componente puede ser abordado en la educación a distancia con menores limitaciones. El segundo es el aspecto práctico, sensorial y de desarrollo de habilidades, cubierto con las prácticas de laboratorio y actividades extramuros, donde el proceso de enseñanza debe salir necesariamente del aula para vivir una experiencia biológica.

En el caso particular de la educación de la biología teórica, una de sus principales características es que la variación de los organismos se puede expresar de manera diferencial bajo muchas circunstancias. En las cátedras se pueden dar explicaciones para entender esa variación, además de ampliar en las posibles causas. Los profesores que dictan cátedras saben que lo más interesante y el mayor reto de un docente es explicar con claridad la gran cantidad de excepciones que se presentan a las reglas. Entender que la enseñanza de la biología es un proceso que puede presentar diferentes tonalidades ante las mismas condiciones, factores que convierte a la cátedra presencial en la gran diferencia, respecto a la remota.

Es un hecho que la educación a distancia será el quehacer diario, y una tendencia durante esta pandemia y en ulteriores tiempos. Por ello, se debe buscar una estrategia que permita una discusión abierta sobre los diferentes tópicos, con flexibilidad, adaptabilidad, dinamismo, coherencia y comprensión de las distintas temáticas. Las herramientas de apoyo existen, solo se requiere que la estructura asegure la comprensión de lo que pretendemos se transmita al receptor de información. El entorno virtual de aprendizaje deberá ser adecuado, donde se propongan actividades para alcanzar el aprendizaje. Las actividades deberán ser planteadas pensando en qué es lo que se quiere conseguir, la factibilidad de realizarlas y las habilidades de pensamiento que el estudiante requiere para lograrlas con éxito y así asegurar un mejor aprendizaje.

En este paradigma emergente, las adecuaciones más sustanciales se tendrán en los tópicos relacionados al laboratorio o directamente fuera de las aulas, denominados "extramuros", como es todo el trabajo de campo, indispensable para los mastozoólogos. Las actividades docentes extramuros, por un lado permiten conocer la diversidad biológica, observar de manera directa las interacciones entre las especies y estar físicamente en las situaciones reales de los ambientes para entender la historia natural de las especies. Se aprende a manipular a los organismos, así se tiene una visión tridimensional, y por otro lado, en muchos casos el contacto físico o el uso de los cinco sentidos que crean una imagen mental multidimensional, integral y holística. A pesar de que algunas de estas condiciones se pueden replicar mediante el uso de la realidad virtual o de simulaciones computarizadas, los procesos de aprendizaje más profundos que se llevan a cabo en actividades extramuros, estarán ausentes. La ausencia de este tipo de actividades tendrá un fuerte efecto en la formación de futuros biólogos. El simple hecho de asistir a ellas va mucho más allá de la actividad académica que se va a realizar en sí. El proceso implica interacciones sociales, logística, planeación, organización, relaciones interpersonales y el trabajo en equipo. En la mayoría de los casos permite experimentar la adaptabilidad a condiciones no óptimas y con diversas carencias. Todos aquellos profesionistas que han realizado actividades extramuros mantienen el recuerdo de ellas, incluso por encima de las actividades intramuros, y en muchos casos han definido el quehacer de muchos profesionistas, sobre todo si consideramos a los mastozoólogos. El entorno del campo permite al docente enseñar procesos que de otra manera, son muy difíciles o imposibles de obtener en un salón de clases, y menos con la educación a distancia en la cual solamente se percibe en un plano, siendo un gran inconveniente al limitar el uso de todos los sentidos para lograr una comprensión satisfactoria. Estas actividades en donde el alumno puede aprender de la experiencia del catedrático y enfrentarse a la naturaleza son muy valiosas.

La educación a distancia es una estrategia educativa que llegó para quedarse, sustituyendo en algún grado y complementando a la docencia como la conocíamos hasta principios del siglo XXI. En diversos campos de la Biología, entre otras ciencias, se debe de trabajar para atender sus particularidades y reestructurarse a fin de adecuarse a las necesidades particulares de la biología. Sin duda, las diferentes asignaturas de las ciencias biológicas van a cambiar, y aunque no sabemos de qué manera, seguramente sí lo harán en una medida aún no dimensionada, sobre todo aquellas relacionadas con la práctica y el conocimiento sensorial de la Biología.

La pregunta inevitable es ¿cómo van a ser los próximos especialistas en diferentes áreas de la Biología? Probablemente muy activos en la teoría. Sin embargo, se debe evitar que su formación sea sin la base "manual" y ajena a la realidad de los ambientes, impedir sustentar sus estudios solamente sobre la base teórica, que pueden o no, reflejar la situación actual de los biomas. La gran incógnita que se debe de resolver es que México por su biodiversidad, fisiografía, climas y ambientes, lo que más necesita son profesionistas de campo, que atiendan las necesidades y demandas de los sectores ambiental y social del país. Las interacciones naturaleza-humano, desarrollo tecnológico-preservación del ambiente, creación de infraestructura-conservación de las especies, uso de recursos sustentablemente, entre otros. El gran reto que tendrá que superar este nuevo sistema de educación a distancia es cómo introducir al estudiante en el conocimiento del medio natural, más aún si tienen un origen urbano. Se hace indispensable diseñar las estrategias para brindar los elementos de formación para que los nuevos profesionistas puedan conocer y entender de manera integral la compleja dinámica de los ambientes y tengan la capacidad de solucionar los requerimientos de los sistemas humanos-biológicos y los procesos para conservar y manejar la biodiversidad.

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Activity of the Russian desman *Desmana moschata* (Talpidae, Insectivora) in its burrow

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A new method of studying for activity of a semi-aquatic mammal Russian desman *Desmana moschata* (Linnaeus, 1758) with use of digital portable voice recorders is developed. To identify the burrows in which the recorders were to be installed, the burrows were probed. A probe is a pole pointed at one end with a T-shaped handle at the other end. The researcher's task was to detect the entrance to the burrow, usually under water. The direction of the underground passage is determined by means of the probe. For this purpose, the ground is pierced to detect the hollows in the burrow with the probe starting from the burrow entrance (the probe falls through unevenly). At a distance of 2 to 3 meters from the burrow, in some cases largely depending on the burrow length, the ground is dug up above the burrow in the form of a small well, 10 to 15 cm in diameter. A digital voice recorder was placed vertically in this well, so that the microphone was directed down towards the burrow. Desman noises can be characterized as short series formed as a sequence of contiguous short peaks of 15 to 25 seconds with five second interruptions formed by regular waves of breathing and its movement noises. As a rule, the noise audibility ranges from 1 to 3 minutes.

Se desarrolla un nuevo método de estudio para la actividad del Desman ruso *Desmana moschata*, mamífero semiacuático, por medio del uso de grabadoras portátiles digitales. Para identificar las madrigueras en las que se iban a instalar las grabadoras, se sondearon las madrigueras. Se utilizó una sonda, adjunta en un extremo a un poste con un mango en forma de T en el otro extremo. La tarea del investigador era detectar la entrada a la madriguera, generalmente bajo el agua. La dirección del tunel subterráneo se determina por medio de la sonda. Para este propósito, se perfora en el suelo huecos en la madriguera con la sonda, comenzando desde la entrada de la madriguera (la sonda cae de manera desigual). A una distancia de dos a tres metros de la madriguera, en algunos casos dependiendo en gran medida de la longitud de la madriguera, el suelo se excava sobre la madriguera en forma de un pequeño pozo, de 10 a 15 cm de diámetro. Se colocó una grabadora de voz digital verticalmente en este pozo, de modo que el micrófono se dirigió hacia la madriguera. Los ruidos de Desman se pueden caracterizar como series cortas formadas como una secuencia de picos cortos contiguos de 15 a 25 segundos con interrupciones de cinco segundos, formadas por ondas regulares de respiración y los ruidos del movimiento. Como regla general, la audibilidad del ruido varía de uno a tres minutos.

Keywords: burrow; daily activity; day-night activity; desman; voice recorder.

Introduction

The study of the Russian desman in the Republic of Mordovia was initiated by well-known mammalogist Borodin (1963, 1970). In his monograph and articles (Borodin 1963, 1970), stated the following habitat areas of the desman within the territory of Mordovia: Zubovo-Polyansky, Temnikovsky, Tengushevsky, Kochkurovsky, Bolshebereznikovsky, and Dubensky Districts. He noted that the desman was found in the Sura, Moksha, Vad, Vysha, Yuzga, Partsa Rivers and their tributaries.

Our research on the desman in Mordovia has been intensified since 2009 until 2018. We aimed at identifying the current distribution of the species within the region and their populations status. In the course of expeditionary work on accounting for desmans in remote areas, we had the idea of checking whether the desman's burrow is residential or non-residential. On the first (transparent) ice, finding out whether a burrow is inhabited or uninhabited is not difficult. However, clear ice is not always; moreover, it is problematic to have time to examine a large number of reservoirs in the short-term period of clear ice. Therefore, we have developed a technique that allows studying the desman's activity in a hole and determining whether a burrow is inhabited or uninhabited in the ice-free period. The method for identifying the activity of underground excavation is taken as the basis (Andreychev and Zhalilov 2017; Andreychev 2018, 2019a). The method could be adapted and improved for other semi-aquatic mammals (*e. g.* muskrat or beaver; Andreychev 2019).

The sudy of the day-night rhythm of the Russian desman in the wild was carried out in the Khopersky Nature Reserve on Lake Kresty using an actograph. Serdyuk (1969) the device was installed in inhabited and fodder burrows from 2:00 pm on October 31 to 2:00 pm on November 2. The device recorded the entry of animals into the burrows. By the number of into or exits of desman from the burrow, their activity was determined. Two peaks of the desmans' day-night activity were identified. They are associated with the periods of sunrise and sunset (Serdyuk 1969). Similar results using a night vision device were obtained in Ryazan region in July 1967 (Khakhin and Ivanov 1990).

In the Seltsov hunting estate, Vladimir region, the number of burrow entries was recorded by an actograph for 51 days from November 1972 to April 1973. Three seasonal periods of desmans' activity associated with changes in external conditions were identified. The first period is associated with the beginning of freeze-up (November–December) and it is characterized by high activity. The second period is associated with strong freeze-up (January–February). The activity of animals decreases during this period. They spend most of their time in burrows. The third period is associated with the end of freeze-up (end of March – beginning of April). It is characterized by increased activity, but less than during the freeze-up period (Khakhin and Ivanov 1990). There are three peaks of day-night activity during freeze-up: morning (5:30 to 7:30), afternoon (12:30 to 14:30), and evening (19:30 to 21:30; Barabash-Nikiforov *et al.* 1964; Sokolov *et al.* 1984; Sukhov 1984); in some cases, the fourth peak is recorded (23.00 to 0:00; Khakhin and Ivanov 1990).

With the use of actographs and a night vision device, only activity at the entry to the burrow was recorded. With regard to identifying the burrow activity of semiaquatic inhabitants, in particular, the Russian desman, both of the above methods are largely unsuitable. Since the animal can use another entrance or be active inside the burrow.

Detailed studies of the daily and seasonal activity of the Russian desman have been conducted by Onufrenya and Onufrenya (2016). They noted that the duration of the continuous stay of the desman in water, regardless of the season of the year, rarely exceeds four to five minutes. The maximum values of this indicator, noted in different individuals for all the time of observation, lie within 18.8 to 65.7 min (Onufrenya and Onufrenya 2016). A detailed discussion of their results is given below in comparison with our data.

The majority of researches on activity of the Russian desmans have been conducted in experimental captive conditions (Barabash-Nikiforov *et al.* 1964; Nazyrova and Karpov 2000; Rutovskaya and Kulikov 2013). In 1994 to 1995 in the vivarium of the Khopersky Reserve, it was revealed that desmans spent more time in artificial burrows, and less time in the water. Sukhov (1984) *in vivo* showed that is, muskrats spend more time in water than on land. The authors of experimental studies in vivarium conditions recognize that the activity of animals' changes depending on the conditions created by them, in particular the feeding conditions. In vivarium conditions distinguish five types of Russian desman activity can be distinguished: activity on the ground, activity in the water, feeding, brushing wool, rest (day and night; Nazyrova and Karpov 2000).

This article describes the method that can be used to study the activity of the Russian desman *Desmana moschata*, with potential implications on other semiaquatic species (*e. g.* beaver, muskrat, and others). The principle of this method is based on recording the noise of animals while they are moving along burrows.

Materials and methods

Study region. The Republic of Mordovia is located in the centre of the European part of Russia. It is extreme points are defined by geographical coordinates 53º 38′ 64″, –55º 11′ 41″ N and 42º 11′ 53″, –46º 45′ 16″ E. Features of the geological structure of Mordovia are determined by its location in the central part of the Russian Platform and the north-western slopes of the Volga Upland. In the western part of the Republic of Mordovia, the Volga Upland reaches the Oka-Don Lowlands.

The climate of the region is moderate with pronounced seasons throughout the year. The influx of direct solar radiation in Mordovia varies from 5.0 in December to 58.6 kJ / cm^2 in June. Total radiation throughout the year is 363.8 kJ / cm^2; the radiation balance is 92.1 kJ / cm^2. The average annual air temperature varies from 3.5 to 4.0 °C. The average temperature of the coldest month (January) is in the range of –11.5 to –12.3 °C. Temperature drops down to –47 °C occur. The average temperature of the warmest month, i.e. July, is in the range of 18.9 to 19.8 °C. Extreme temperatures in the summer reach 37 °C. The average annual precipitation in the territory of Mordovia is 480 mm. Over the course of observation lasting many years, periods of more and less humidification were noted, ranging between the minimum and maximum values of 120 to 180 mm. Distribution of precipitation across the territory is not very diverse. The average long-term value of evaporation is calculated to be in the range of 390 to 460 mm (Yamashkin 1998).

Surveys were carried out on the possible habitats of the Russian desman in areas of the Republic of Mordovia in order to find its holes for subsequent study of activity (Figure 1). In the course of the field work, we used burrows to a greater extent, which are known to us from of expeditionary work of 2009 to 2012 in the Tengushevsky region (Andreychev *et al.* 2012). As a result, we also found desman burrows in the European beaver's burrows and passages, which was consistent with the literature data on the desman and beaver symbiotic relationships (Barabash-Nikiforov 1959). The high population density of European beaver population is favorable for the desman in Mordovia in this respect (Andreychev 2017).

Since there is no information on animal noise in burrows in the literature, some explanations are required. According to G. Tembrock's classification (Tembrock 1963), acoustic signals of mammals are divided into two groups: own voice sounds, and non-voice noises not related to the vocal apparatus itself. The second group includes, in particular, the noise generated by the air stream during inhalation and exhalation, mainly by means of nasal cavities (Ilyichyov *et al.* 1975). In addition, they are overlapped by noises of the animal movements. The method proposed is based on the registration of these noises as a whole.

A description of the method for studying the activity of semiaquatic mammals in burrows should be given, since it has not been previously mentioned in the literature. Habitat areas should be identified at the preparatory stage. Difficulties in identifying the burrowing systems of most species of semi-aquatic mammals are due to the absence of land emissions from the burrows, as is the case with under-

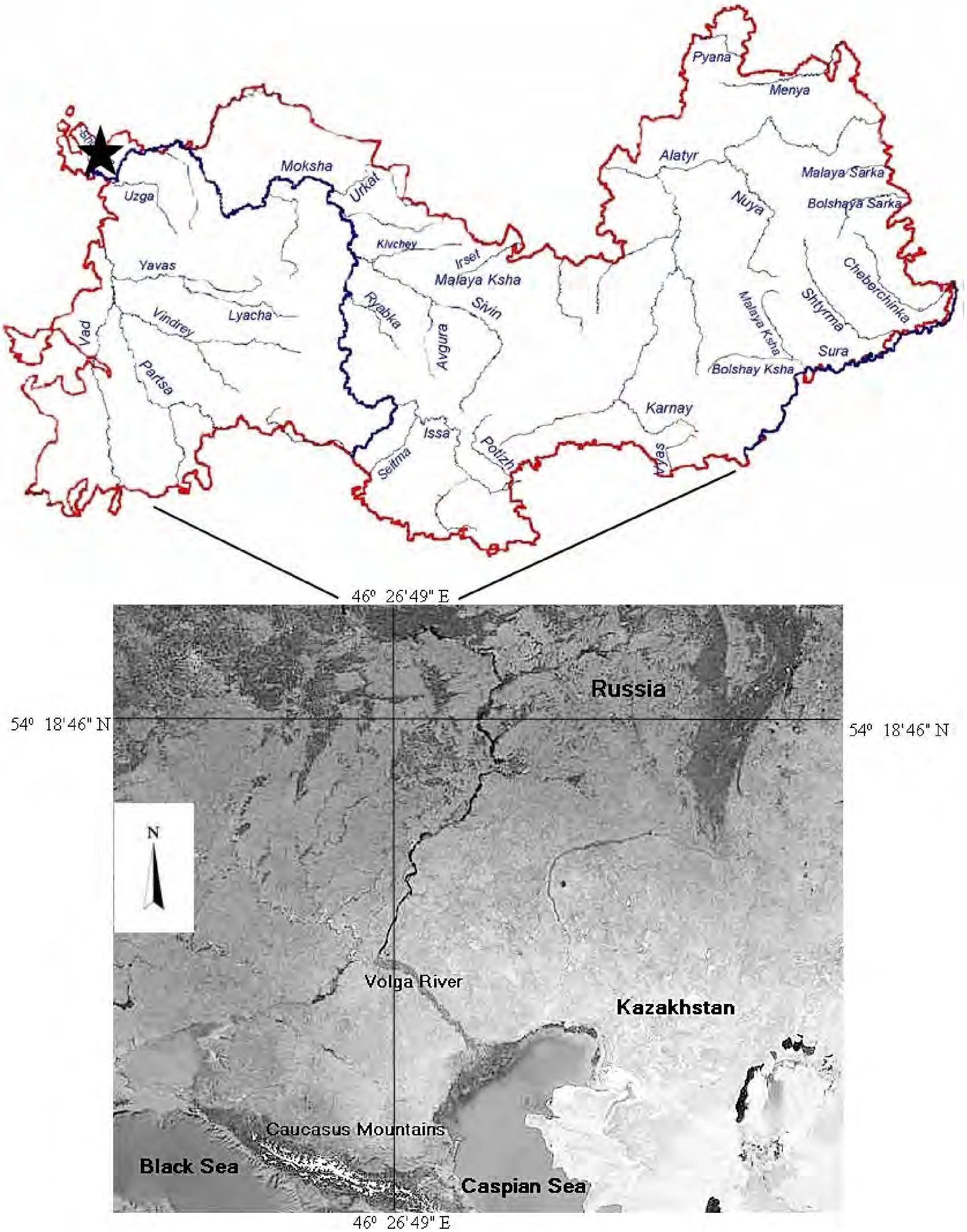

Figure 1. Geographic location of the Russian desman populations studied in Tengushevsky District, Russia.

ground burrowing animals (*e. g.,* mole rats and moles). Therefore, to identify the burrows in which the recorders were to be installed, the burrows were probed (Figure 2). A probe (5) is a pole pointed at one end with a T-shaped handle at the other end. The researcher's task is to detect the entrance to the burrow, usually under water. And then the direction of the underground passage is determined by means of the probe. For this purpose, the ground is pierced to detect the hollows (1) in the burrow with the probe starting from the burrow entrance (the probe falls through unevenly). At a distance range of 2 to 3 meters from the burrow, in some cases largely depending on the burrow length, the ground is dug up above the burrow in the form of a small well (depression), 10 to 15 cm in diameter approximately. A digital voice recorder (4) was placed vertically in this well, so that the microphone was directed down towards the burrow. The recorder was placed in a 0.5 liter water plastic bottle which was used as a container. Pre-cuts were made in the bottle to place the recorder as well as two through cross holes for the spacer bar on which the bottle itself was fastened in the ground. Plastic bottles were used for moisture insulation of voice recorders. The bottles were preliminary cleared of labels and poured with boiled water to eliminate all suspicious odors. After placing the switched-on voice recorders into the wells, they were covered with plates (3) and covered with soil and turf (2).

Olympus VN-416PC, VN-712PC voice recorders were successfully used. Other alternative models that are similar in technical characteristics may also be used. Voice recorders were powered by alkaline or zinc-carbon AAA batteries, or by an external battery unit, which extended the recording time of the voice recorder. On average, one set of batteries was enough for 80 to 100 h of continuous recording. Batteries were replaced at the end of the battery life.

The activity of animals should be monitored using voice recorders in different parts of the reservoir. The choice of installation locations for recording devices was determined using the OziExplorer software. To check the sensitivity of microphones to record the noise of animals, several recorders were placed in one burrow. In this case, one recorder was placed directly at the burrow entrance and the rest were placed a few meters away from the burrow entrance. For convenience of the further processing of audio recordings obtained from voice recorders from one burrow system, the recorders were switched on simultaneously. This made it possible to clearly identify the time intervals in which the animal moved past each recorder. Practice showed that the noises of animals were heard on all voice recorders. However, the recorders that were placed farther from the entrance recorded only the noises of the animals themselves, excluding extraneous noises, such as the wind noise. Therefore, it has been concluded that it is better to place a voice recorder not at the burrow entrance, but directly in the burrow system at some distance from the entrance. For easy re-detection of previously placed voice recorders in the field, a GPS navigator was used. Diurnal time was set between dawn and dusk, and nocturnal time between dusk and dawn.

Office processing of the audio recordings obtained should be carried out using AIMP 1.75 (2007) and AUDACITY 2.1.1 (2015). This software allows for identification and subsequent listening to the noises of moving mammals along the burrow by frequency characteristics in visual mode. Alternative software, in particular, Sony sound forge audio studio 7.0 (2003), can be used to convert audio files from WMA to WAV and divide them into short sections for easy analysis in AUDACITY. During the study period, we listened to more than 2000 hours of recordings.

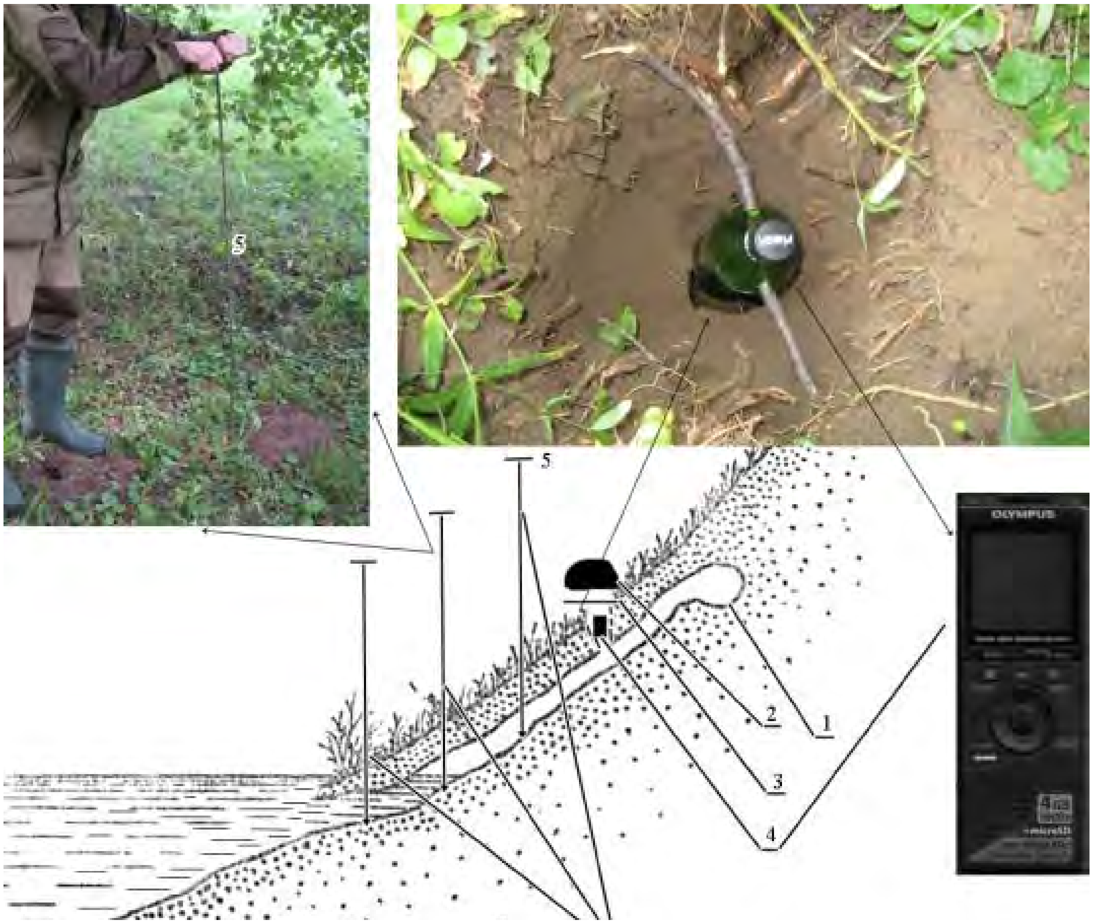

Figure 2. Diagram of installation of a voice recorders of the Russian desman in their burrow:1) hollows, 2) soil, 3) plates, 4) voice recorder, 5) probe.

Results

Desman noises can be characterized as short series formed as a sequence of contiguous short peaks of 15 to 25 seconds with five second interruptions formed by regular waves of breathing and its movement noises. Desman noises differ by mean amplitude and duration on oscillograms. As a rule, the noise audibility ranges from one to three minutes.

According to the results of radiotelemetric observations of Onufrenya and Onufrenya (2016) on average flow Oka is known that the type of daily activity of Russian desman remains unchanged throughout the entire annual cycle (Onufrenya and Onufrenya 2016). Our results using digital voice recorders confirm the results of radiotelemetric observations on the polyphase activity of the animal. The desman's activity in the hole is unevenly distributed in time of day. The greatest activity in the burrow was noted from 13:00 to 15:00 h. Somewhat inferior activity was in the period from 1:00 to 03:00 h and from 19:00 to 22:00 h. Four periods of rest in the hole were noted: from 6:00 to 7:00 h, from 11:00 to 13:00 h, from 15:00 to 16:00 h, from 22:00 to 1:00 h (Figure 3). During these hours there was no desman passage along the course. This indicates that the animal was at this time either in a nest or in water. In this regard, the effectiveness of radio telemetry observations is more promising than the use of digital voice recorders, since the data obtained are more informative. However, the information obtained from digital voice recorders is important for assessing the internal activity. In the remaining periods, stable low activity in the burrow was observed. Thus, it is possible to distinguish the four phases type of activity of the Russian desman in the burrow.

Discussion

The results of works in the aviary of Rutovskaya and Kulikov (2013) can explain the high frequency of noise of the Russian desman in the burrow. Their observations in the experimental tunnel showed that every ten steps the desman 10 to 30 times touches the walls of the tunnel with the tip of the proboscis, with 45.4 % of touches falling on the ceiling. Almost half as many touches (27.9 %) are on the floor. The walls of the tunnel account for about 10 % of contacts (Rutovskaya and Kulikov 2013).

According to Onufrenya and Onufrenya (2016) Russian desmans marked with radio transmitters were active for a considerable part of the day. In all seasons of the year, they were out of shelters for at least 10 to 11 hours. On average, different animals are active from 11.4 to 15.5 hours. Or 48 to 65 % of the total time of day. The averaged duration of the activity phase of all observed animals was 12.5 hours of the day (Onufrenya and Onufrenya 2016). According to our averaged data, the desmans in the hole are not active seven hours a day, and seventeen hours are active in the hole. Moreover, a large proportion of activity in the hole falls at night.

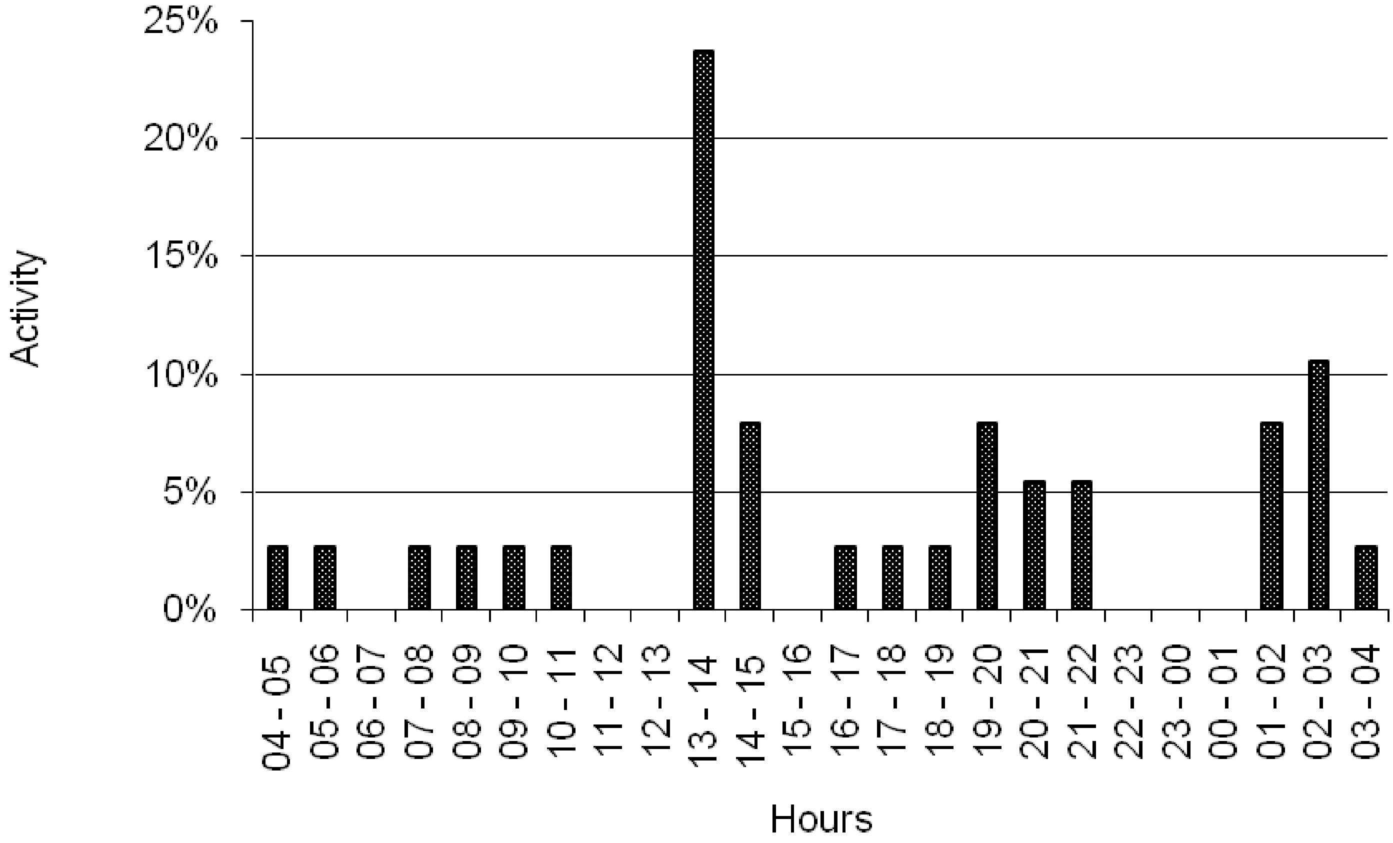

Figure 3. The daily activity of the Russian desman in summer months.

Directly in water, of the Russian desman can be from 3.2 to 11.6 hours a day. On average, for different animals, this indicator is 5.3 to 9.0 h (Onufrenya and Onufrenya 2016). Studies of the activity of the Pyrenean desman (*Galemys pyrenaicus*) to detect habitat or absence in the French Pyrenees were carried out using an automatic radio tracking system (Stone and Gorman 1985; Stone 1987). For the Pyrenean desman obtained two separate periods of activity for the period May-July. The day period of activity is short, the night period is longer. Every day the beginning and termination of activity for all desman was highly synchronized. This can be explained from the point of view of ecological resources of production and social ecology of the species.

Some others were the results of studies of the Pyrenean desman in the work of Melero *et al.* (2014). On average, individuals spent more time inactive than active, with 36.51 % of active radiolocations, and 9 to 10 h of activity per day. In general, the activity of desman was mainly nocturnal, although the activity pattern differed between autumn and spring. During autumn, individuals presented two nocturnal, or exceptionally three, activity bouts with an average duration of five hours each, separated by one (exceptionality 2) inactive period of 100 min average duration that commonly happened at 14:00 approximately, and a single diurnal activity bout of 73.75 min on average without any inactive period, but diurnal activity was longer (Melero *et al.* 2014).

Thus, summing up our own data and data of other researchers on the activity of the Russian and Pyrenean desmans, we can conclude that both species have a polyphasic rhythm. We realize that with the help of voice recorders we could not characterize the full rhythm of desman activity, as it was done by other researchers using radio telemetry. However, undoubtedly our data supplement and expand information about desman's activity in the hole. Therefore, digital voice recorders are indispensable in studies of normal activity and determining the employment of a hole. This method is expensive for the rapid identification of residential burrows, which is valuable for accounting work. With the help of the proposed method, in perspective, results can be obtained for the phases of the activity of difficult-to-investigate semi-aquatic mammals, which will be of undoubted significance in comparative terms.

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Baseline for monitoring and habitat use of medium to large non-volant mammals in Gran Sabana, Venezuela

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The Gran Sabana is a region of great biogeographical and conservation value that has been recently threatened due to increasing overexploitation of natural resources and illegal mining. Systematic survey methods are required in order to study species responses to landscape transformation. The main objectives of this study were: 1) to test the relationship between habitat types and mammal species presence in the Gran Sabana and Canaima National Park (NP), and 2) establish baseline methodology that can set guidelines for future, considering sampling limitations, conservation opportunities and increasing threats to biodiversity in this region. We implemented a stratified sampling design using camera traps for monitoring medium and large mammals in two previously under-sampled regions in the Gran Sabana, south-east Venezuela. We analysed time-series of remotely sensed vegetation indices to classify habitat types and summarized relative abundance of mammals, naïve occupancy, and habitat fidelity for each type. With a sampling effort of 5,523 camera*days, 29 species of mammals were recorded, including endangered *Priodontes maximus*, and vulnerable: *Speothos venaticus*, *Tapirus terrestris*, and *Panthera onca*. *Cuniculus paca* and *Dasyprocta leporina* were the most frequently registered, while *Hydrochoeris hydrochaeris*, *Leopardus wiedii*, and *Leopardus tigrinus* had few records. Most of the species were associated with forest (13), fewer with transitional shrub (7) and savanna (5) habitats, but only some of these were statistically significant. *Cerdocyon thous* show significant association with savanna ($P < 0.01$), whereas *Leopardus pardalis* ($P < 0.05$) and *Cuniculus paca* ($P < 0.05$) with shrub-intermediate habitat. As many as seven species: *Dasypus kappleri*, *Dasyprocta leporine*, *Mazama americana*, *M. gouazoubira*, *Nasua nasua*, *Priodontes maximus*, and *Tapirus terrestris* have statistically significant association to forest habitat ($P < 0.05$). We present the first record *Myoprocta pratti* for Canaima NP. We found higher species richness of large- and medium-sized mammals comparable to lowland Guianas and Amazon sites. Four species remained undetected, probably due to low abundance or detectability, but *Sylvilagus brasiliensis* seems to be truly absent from the Gran Sabana. Uncontrolled development of Orinoco Mining Arc on the border of Canaima NP and the Gran Sabana raised new ecological and social concerns.

La Gran Sabana es una región de gran importancia biogeográfica y valor para la conservación que se encuentra crecientemente amenazada debido a la sobre-explotación de los recursos naturales y la minería ilegal. Para estudiar las respuestas de las especies a la transformación del paisaje es necesario un programa de seguimiento sistemático. Los objetivos principales de este estudio fueron: 1) evaluar la relación entre los tipos de hábitat y la presencia de especies de mamíferos en la Gran Sabana y el Parque Nacional (PN) Canaima, y 2) establecer un método de referencia para el monitoreo a largo plazo considerando las limitaciones de muestreo, oportunidades para la conservación y amenazas crecientes para la biodiversidad en esta región. Se implementó un diseño de muestreo estratificado basado en cámaras trampas para monitorear mamíferos medianos y grandes en dos regiones previamente sub-muestreadas en la Gran Sabana, sureste de Venezuela. Analizamos series de tiempo temporales de índices de vegetación con sensores remotos para clasificar los tipos de hábitat y resumimos la abundancia relativa de mamíferos, la ocupación *naïve* y la fidelidad para cada tipo de hábitat. Con un esfuerzo de muestreo de 5,523 cámara*días, se registraron 29 especies de mamíferos, incluidas cuatro especies amenazadas: *Priodontes maximus*, categoría En Peligro, el *Speothos venaticus*, *Tapirus terrestris* y *Panthera onca*, estos tres en categoría Vulnerables. *Cuniculus paca* y *Dasyprocta leporina* tuvieron mayor cantidad de registros, mientras que *Hydrochoerus hydrochaeris*, *Leopardus wiedii* y *Leopardus tigrinus* tuvieron pocos registros. La mayoría de las especies están asociadas con el bosque (13) y en menor medida con hábitats de arbustos (de transición; 7) y de sabana (5), pero sólo algunas tuvieron asociaciones estadísticamente significativas. *Cerdocyon thous* muestra una asociación significativa con la sabana ($P < 0.01$), mientras que el *Leopardus pardalis* ($P < 0.05$) y *Cuniculus paca* ($P < 0.05$) con el hábitat intermedio. Hasta siete especies: *Dasypus kappleri*, *Dasyprocta leporina*, *Mazama americana*, *Mazama gouazoubira*, *Nasua nasua*, *Priodontes maximus* y *Tapirus terrestris* tienen una asociación estadísticamente significativa con el hábitat forestal ($P < 0.05$). Se presenta el primer registro de *Myoprocta pratti* para PN Canaima. Se registró una mayor riqueza de especies de mamíferos grandes y medianos en comparación con las tierras bajas de las Guayanas y Amazonia. Cuatro especies permanecieron sin ser detectadas, probablemente debido a la baja abundancia o detectabilidad, pero *Sylvilagus brasiliensis* parece estar ausente de la Gran Sabana. El desarrollo incontrolado del Arco Minero del Orinoco en la frontera del PN Canaima y la Gran Sabana genera nuevas preocupaciones ecológicas y sociales.

Keywords: camera trap; Canaima National Park; Guiana Shield; Orinoco Mining Arc; *Priodontes maximus; Speothos venaticus:* Venezuelan Guayana.

Introduction

The Gran Sabana (GS) has been considered an international conservation priority due to its high biodiversity and endemism of fauna and flora (Huber and Foster 2003). Historically low levels of human population, with low pressure and exploitation contrast with the rapid development in the last two decades. The Canaima National Park (NP), covering significant part of the GS, is among the UNESCO Natural World Heritage Sites with the highest deforestation rate in the South America (Allan *et al.* 2016) and illegal mining activities have increased drastically, especially since the declaration of the Orinoco Mining Arc (OMA, Zona de Desarrollo Estratégico Nacional Arco Minero del Orinoco) in 2016. This situation has aggravated threats to medium and large sized mammals that play key roles in sustaining native vegetation, and are sensitive to the effects of land cover change. Moreover, the profound economic crisis in Venezuela also makes bush meat an important source of protein (Rodríguez 2000) especially for indigenous Pemón communities in this region.

Mammals represent a rich but understudied animal group in the Gran Sabana. The earliest known and documented records of mammals collected in Venezuelan part of Guiana Shield were made by Alexander von Humboldt at the beginning of the 19th century. Subsequently, during the 1960's the Smithsonian Venezuelan Project, Handley (1978) carried out expeditions that documented presence of mammals particularly in three location and their surroundings in GS: Kavanayen, El Pauji, and Roraima Mountain. Recently, other inventories of mammals have been conducted in this region but have been focused on bats and small rodents (Ochoa *et al.* 1993; Ochoa 2001; Lim *et al.* 2005; Lew *et al.* 2009), as opposed to medium-sized species of mammals. The 151 species documented in the Canaima NP represent 40 % of mammal species of Venezuela and 61 % of the Guayana region (Lew *et al.* 2009). This mammal assemblage is dominated by bats (74 species) and rodents (29 species), but has an important component of carnivores represented by 16 species (Lew *et al.* 2009). Most studies have focused in basic inventory (Handley 1978; Ochoa *et al.* 1993; Ochoa 2001; Lew *et al.* 2009), but preliminary ecological categorization suggest that most species can be classified into two main groups defined by habitat (Ochoa *et al.* 1993; Huber *et al.* 2001). The first group is represented by frugivorous, omnivorous, and large predatory species mostly associated with forest and shrubland environments, and includes *Panthera onca*, *Nasua nasua*, and edentates such as *Tamandua tetradactyla* and *Priodontes maximus*. The second group consists of herbivores, omnivores, and small vertebrate predators inhabiting herbaceous high-tepui and savanna ecosystem, and includes *Cerdocyon thous*, *Puma yagouaroundi* and edentates such as *Myrmecophaga tridactyla* and *Dasypus novemcinctus*.

Long term monitoring of medium and large size mammals allows a deeper understanding of the ecological consequences of changes in land cover change, and the hidden threat of over-exploitation (Hoppe-Dominik *et al.* 2001). The use of camera trap for ecological studies has become a valuable tool for the observation and recording of large and medium mammals. It is especially a cost-effective method for studying the presence and behavior of rare and elusive species (Lyra-Jorge *et al.* 2008; Cove *et al.* 2013; Morán *et al.* 2018). In this study, we present the results of a first survey of medium and large size mammals in previously under-sampled regions of GS, located on the north and north-east of the Canaima NP (Figure 1). The main objectives of this study were: 1) to test the relationship between broad habitat types and mammal species in GS and Canaima NP, and 2) establish baseline methodology that can set guidelines for future, long-term monitoring. First, we characterized habitat types according to time series of remotely sensed data and used information about presence and frequency of common and elusive medium and large mammals from camera-traps, tracks records and interviews, in order to assess the strength of perceived ecological categorizations. Then, we summarize the base line results considering the sampling efficiency and drawbacks of camera trapping in open habitats like savanna, the observed discrepancies between expected and detected species lists, conservation opportunities and increasing threats to the fauna and ecosystems found in the Canaima NP and surroundings.

Materials and Methods

Study area. GS holds anomalous vegetation – treeless savannas and forest–savanna mosaics and is characterized by a complex relief that varies in elevation from 500 m to 1,450 m and covers ca. 18,000 km^2 of extension (Huber *et al.* 2001). The study area covers 1,442 km^2 with elevations ranging from 700 to 1,400 masl of the sector 5, on the north of GS. We conducted our studies in two sampling areas. The first area was sampled between September 2015 - April 2016, situated close to the Venezuela-Guyana international border and was delimitated by three indigenous Pemón communities: Kawi (5.451° N, -61.243°W, 1,100 masl), Uroy-Uaray (5.442° N, -61.232° W, 1,093 masl), and Wuarapta (5.512° N, -61.157° W, 896 masl; Figure 1). The second area was sampled between May – July 2018 located on the west part of sector 5 in the vicinity of communities Kavanayen (5.594° N, -61.761° W, 1,222 masl), Liworibo (5.559° N, -61.490° W, 1,255 masl) and research station Parupa (5.5677 ° N, -61.544 ° W, 1,267 masl). Vegetation in this sector of Gran Sabana is characterized by shrubs dominated by *Clusia* spp. and *Gongylolepis* spp., broadleaf grasslands and savannas of *Axonopus* spp. interrupted by gallery forest patches and continuous evergreen montane forest near to the Ilú - Tramén-tepui massif and Ptari tepui (Huber *et al.* 2001). The climate is submesothermic ombrophilous characterized by annual average temperatures between 18 and 24 °C and 2,000 to 3,000 mm of total annual rainfall with a weak dry season (< 60 mm / month) from December to March (Rull *et al.* 2013).

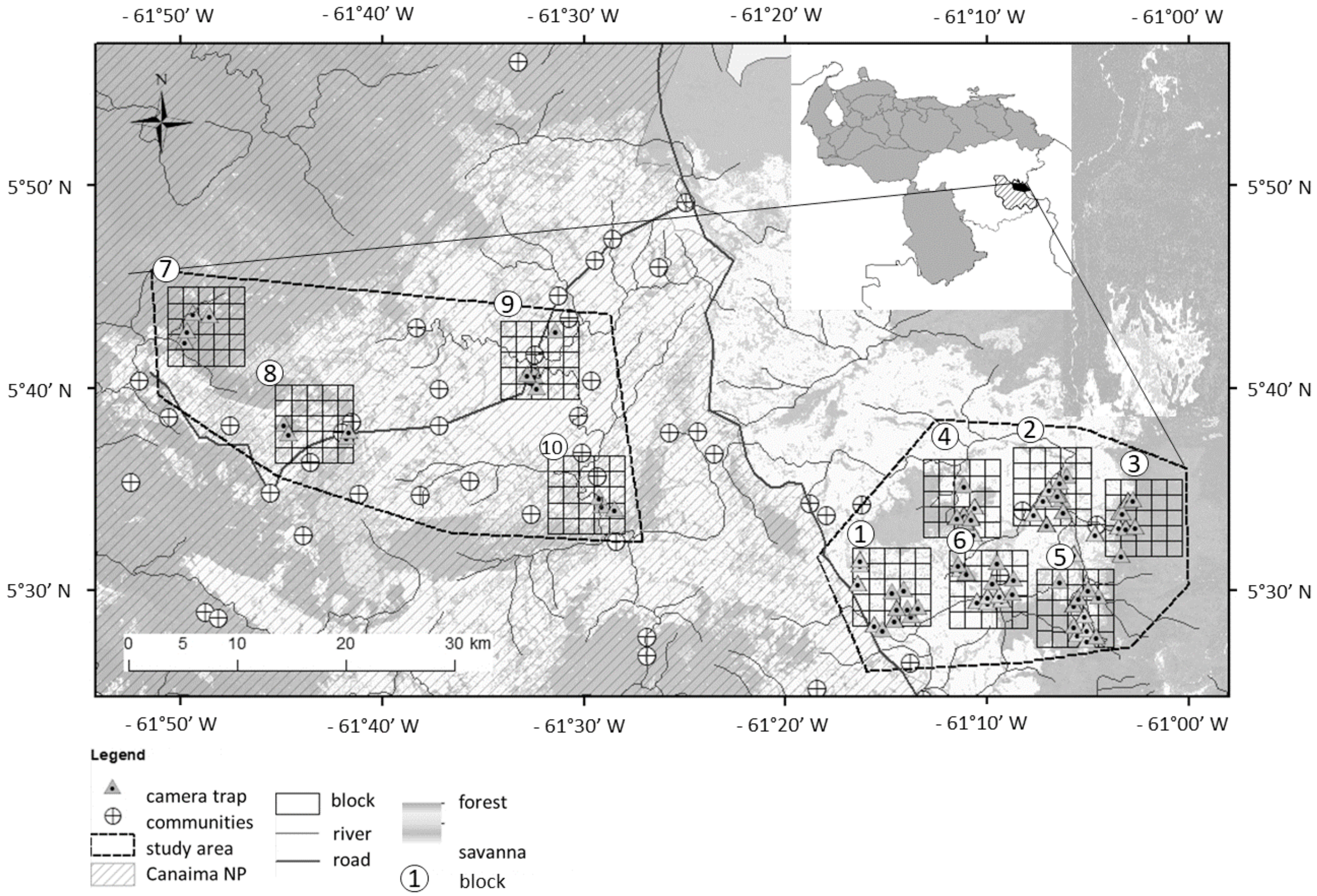

Figure 1. Location of study area in the Gran Sabana, outside (blocks 1 to 6) and inside (blocks 7 to 10) Canaima National Park, Venezuela.

Sampling procedure. In order to cover a large area and a diversity of habitats we selected ten blocks (each covering an area of 50 km^2) representing different landscape configurations. We used series of Landsat satellite images from 2000 to 2016 to estimate forest cover (Sexton *et al.* 2013). Each block was divided in 25 sampling units of 2 km2 that were tentatively classified in four levels based on forest cover: continuous forest (F), fragmented with predominance of forest (f), fragmented with predominance of savanna (s) and savanna (S). ArcGIS 10.1 (ESRI 2012) and R version 1.0.153 (R Core Team 2013) were used for spatial analyses.

Because sampling effort was limited by the number of available cameras (30), we used one camera per sampling unit. Each sampling period lasted 60 days. On the first period we sampled five sampling units (five cameras) with different vegetation characteristics in each of blocks. For the remaining three periods (four in total) we moved the position of the cameras between different sampling units within each block. The rotation of cameras in the blocks assured a balanced representation of different landscape configurations and local conditions. Minimal distance between cameras was 1 km. In continuous savanna (S) and habitat with predominance of savanna (s) we located 39 cameras, in continuous forest (B) 36 cameras and 26 cameras in fragmented with predominance of forest (b) or fragmented with predominance of savanna (s).

We used camera traps of three different brands (Cuddeback, Bushnell, and Moultrie), with similar settings for all cameras: series of three photos with minimum interval between them (max.1 sec), videos 10 sec length, middle LED adjust and maximum sensor of movement activity (Rovero *et al.* 2013). Cameras were placed on the trees at 60-70 cm above ground level, with a plastic roof to protect camera from rain. The survey was complemented with opportunistic track records (scratches, caves, excrements, and bones) and interviews conducted in Spanish with the aid of translators among indigenous Pemón people from the local communities. Participation was voluntary and there was no remuneration. Direct and semi-structured interview was used, which have been widely used in investigations of this type (Carvalho *et al.* 2014). An interviewee was considered reliable if he/she could differentiate local from foreign animals (*e. g*., *Tremarctos ornatus*) shown in pictures and drawings (plates of Linares 1998) and if the person has been living in the community on the Gran Sabana for most of his/her life. During the interviews we registered the local names in Arekuna Pemón's dialect.

We identified the species from camera traps and tracks using reference works from Venezuelan (Linares 1998) and the Neotropics (Eisenberg 1989). In addition, mammalogists from the Instituto Venezolano de Investigaciones Científicas were consulted to confirm the identification of doubtful records registered by cameras. A representative subset of photos of mammals from this study was deposited on iNaturalist (https://www.inaturalist.org/observations/izolinia).

Basic data analysis. For all species two basic parameters were calculated: an index of frequency of detection (number of detection events for species per 100 days of camera trapping, O'Brien 2011) and *naïve* occupancy (proportion of all sampling unit with at least one detection of a species, Rovero *et al.* 2014) in order to have available information to compare with similar studies in Latin America.

Vegetation categorization. For the location of each camera in the sampling unit, we downloaded the time series of Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices (MOD13Q1) Version 6 with a temporal resolution of 16 days and a spatial resolution of 250 meter (Data source: *https://lpdaac.usgs.gov/products/mod13q1v006/*). We used the Normalized Difference Vegetation Index (NDVI) measurements from 2010 to 2018. The time series has 215 total measurements per camera, but we considered only those with good reliability and production quality (approx. 53.6 %) of the observations (see product user manual in https://lpdaac.usgs.gov/documents/103/MOD13_User_Guide_V6.pdf).

As a next step we classified the habitat around each camera using the irregular time series data of reliable NDVI measurements between 2015 and 2018. We performed an unsupervised classification using the partition around medoids method proposed by Kaufman and Rousseeuw (1990). This method uses a mathematical algorithm to identify a subset of observations or "medoids" that represent different combinations of values of the time series, and then calculates the dissimilarity or multivariate distance from all other observations to their closest medoid, these steps are repeated until the algorithm finds the optimal solution with minimum differences within groups and maximum differences between groups. The silhouette width (s_i) is a relative measure of the reliability of the classification for each observation. With this analysis we discriminated three main types of habitat corresponding to "savanna", "forest" and an intermediate "shrub" or "transitional" group (Figure 2).

Analysis of habitat association. We applied the indicator value analysis proposed by Dufrêne and Legendre (1997), which is based on the calculation of fidelity (see definition below) and relative abundance indices for each combination of species and habitat types. In order to apply this analysis, we assumed that species detections are related to abundance and/or activity of individuals and these are in turn indicators of species association with the habitat types identified above. Under these assumption these indices directly assess positive predictive values and sensitivity of the species as bioindicator of particular habitat types in biodiversity monitoring, and is a robust alternative to correlative measures of association (De Cáceres and Legendre 2009).

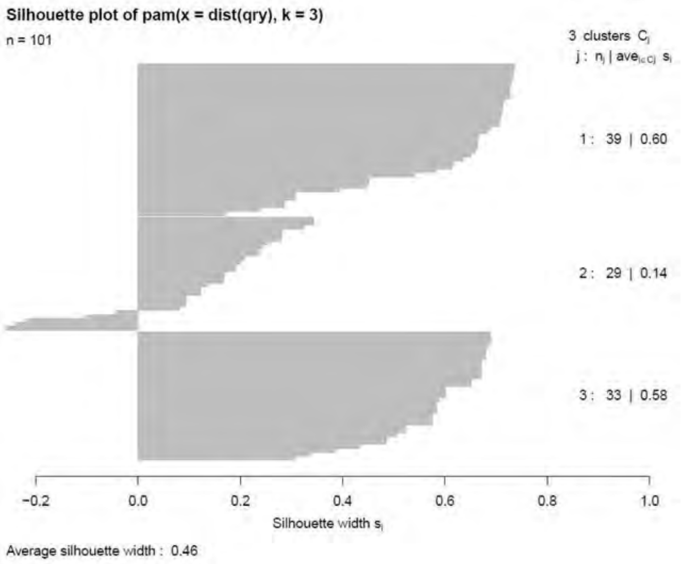

Figure 2. Silhouette plot of the habitat classification.

Here, we consider a detection event as any sequence with less than five minutes difference between consecutive photographs. "Fidelity" is defined as the prevalence of the species in each habitat type (number of different cameras with detection / total number of cameras in the habitat type). Relative abundance (or frequency) is defined as the relative number of detections of each species in each habitat type (number of detections in one habitat type / total number of detections). The "indicator value" (IV) is then calculated for each species/habitat combination as the product of fidelity and relative abundance and can be interpreted as a measure of the strength of the association of one species to a given habitat type. An IV value "0" means there is no record of species activity for that habitat type, while and IV value "1" indicates both extensive and exclusive use of the habitat (*i. e.,* it is detected in all cameras in that habitat and never in any other habitat). High values of IV in one habitat mean it must have low IV values in other habitats, thus only the highest IV value is informative for species associations. The significance of the highest IV value is tested by a random permutation procedure of the sites among the habitat types with a bonferroni correction for multiple testing (Legendre and Legendre 2012).

Results

Effectiveness of camera trapping. Most mammal detections were recorded in blocks with higher forest cover (blocks 3, 5, 6, 7 and 8, Figure 1). Cameras were installed in 101 sampling unit/period combinations (72 unique cells), achieving a total sampling effort of 5,523 camera*day with 7,569 events. There were 1,010 events with presence of mammal, 351 events with birds and reptiles, and 6,082 empty frames or false positives (camera misfiring, likely. due to vegetation movement or heat, among others, Table 1).

Presence of mammals. We detected 29 species of mammals which belong to eight orders (Table 2). Among the species with the highest values of frequency of detection index and *naïve* occupancy we found: *Cuniculus paca*, *Dasyprocta leporine*, and *Cerdocyon thous* (Table 2). Species with lowest values were *Leopardus wiedii*, *Tayassu pecari,* and *Leopardus tigrinus*. One of the rarest species detected was *Speothus venaticus*, with one record. Additional evidence of mammal presence was recorded from scratches, caves, tracks, excrements and bones, with a total of 193 records of 20 species (Table 2). *Cerdocyon thous* were more frequent, with 37 records. During semi-structured interviews with 29 local dwellers (three women and 26 men, with average familiar nucleus 6.5 person) from the Pemón communities, the majority of species from camera trap were recognized (Table 2), but *P. maximus* and *S. venaticus* were only recognized by older interviewees.

Habitat categorization. The categorization of vegetation group of savanna (group 1) and forest (group 3) is well differentiated (the average sillhoutte width is large, all $s_i > 0$), while for shrub-intermediate vegetation (group 2) some observations lay between different groups and might have been misclassified (the average sillhoutte width is low and, some $s_i < 0$, Figure 2).

We show the NDVI values for the camera locations classified for each vegetation group (Figure 3). The NDVI value for savanna group is mostly between 0.4 and 0.7, with some seasonal observations below 0.4 (beginning of 2015 and 2016, but not evident in 2017, Figure 3a) and forest is above 0.8 for most of the year with some isolated observation are below this value (Figure 3c). The shrub – transitional habitat has intermediate (values of NDVI (0.5 to 0.9; Figure 3b), but they are frequently below 0.8 (value for forest group). In some localities the NDVI values might be closer to the forest habitat (localities with negative silhouette width in Figure 2).

Habitat association. We found significant associations for 10 species out of 25 species analysed (Table 3): seven species in forest two in intermediate/shrub habitat and one in savanna. Thirteen species have high relative frequency in forest (values equal or above 0.5), but fidelity was highly variable (ranging from 0.064 to 0.645). Combining both indices leaves only seven species with statistical significant association to forest (indicator value equal or above 0.161 and $P < 0.05$): *Dasypus kappleri, D. leporina, Mazama americana, Mazama gouazoubira, N. nasua, P.maximus*, and *T. terrestris*.

Table 1. Effectiveness of camera trapping. Continuous forest (F), fragmented with predominance of forest (f), fragmented with predominance of savanna (s) and savanna (S), transitional (trans.)

			Number of species register in each habitat			Number of cameras in each habitat		
Block	**No. of events**	**Average no. events/period**	**Forest**	**Trans.**	**Savanna**	**Forest**	**Trans.**	**Savanna**
1	19	6	-	1	7	-	1	14
2	39	13	-	7	7	-	4	9
3	208	69	18	13	-	13	1	-
4	154	51	13	15	-	11	4	-
5	197	66	6	18	2	4	7	4
6	205	68	8	13	6	4	6	4
7	89	89	10	5	-	3	1	-
8	88	88	-	10	-	-	4	-
9	4	4	-	3	1	-	1	3
10	7	7	-	2	1		1	2
Total	1010					35	30	36

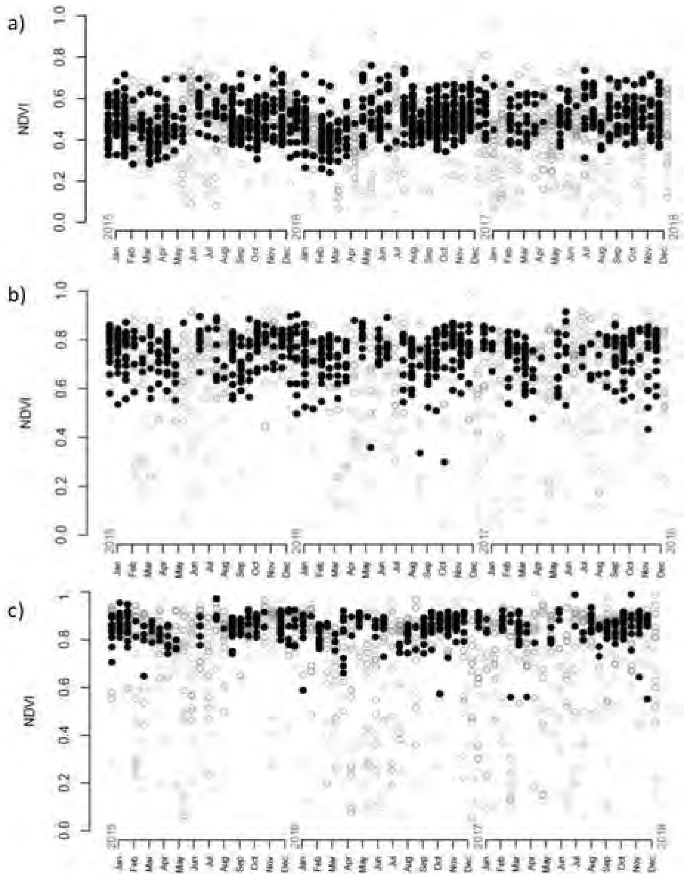

Figure 3. NDVI values for habitat type a) savanna b) intermediate/shrub habitat type c) forest. Dark filled dots represent reliable, good quality measurements used in the analysis, and grey circles represent unreliable or low quality measurements.

Discussion and Conclusions

Savanna vs. forest species. Existing data on species presence on GS is mostly based on non-systematic survey, while our study provides for the first time quantitative data to test common assumptions on animal habitat preference in this region (Ochoa *et al.* 1993; Table 3). *Cerdocyon thous* is present in different types of vegetation from forest to marshland and savanna, but has preference for savanna (Lucherini 2015) and 49 % of specimens collected by the Smithsonian Venezuelan Project were sampled in savanna habitat. In our sample, this was the only species not detected in forest habitat and showing a significant preference for savanna habitat (Table 3). *Odocoileus virginianus* and *Tamandua tetradactyla* have been recorded in a range of habitats (Ochoa *et al.* 1993), but our data suggested a strong (but not significant) association with savanna (Table 3). *Nasua nasua, P. maximus*, and *D. marsupialis* showed a strict preference

Table 2. Nonvolant medium and large mammal species recorded in the present report including its names in Arekuna (Pemón dialect), detection frequency, *naïve* occupancy, status of Red List (RL) following Rodríguez and Rojas-Suárez (2008) and survey method: CT: camera trapping, TRK: tracking, INT: interviews with local Pemón communities.

Species	Name in Arekuna	No. events	No. tracks	Detection frequency	Naïve occupancy	RL	Survey method
ARTIODACTYLA							
Cervidae							
Mazama americana	kutsari	32	10	0.32	0.30	DD	CT,TRK, INT
Mazama gouazoubira	kariyawku	69	18	0.08	0.19	LC	CT,TRK, INT
Odocoileus virginianus	waikín	5	1	0.02	0.05	LC	CT,TRK, INT
Tayassuidae							
Pecari tajacu	poyinke	4	2	0.01	0.04	LC	CT,TRK, INT
Tayassu pecari	pakirá	2	0	0.02	0.04	VU	CT, INT
CARNIVORA							
Felidae							
Leopardus wiedii	-	2		0.02	0.04	VU	CT
Leopardus tigrinus	kaukau	1		0.08		VU	CT, INT
Leopardus pardalis	kaukan	24	3	0.07	0.18	LC	CT, TRK, INT
Panthera onca	temenen	27	4	0.07	0.16	VU	CT, TRK, INT
Puma concolor	kusariwara	32	7	0.07	0.12	LC	CT, TRK, INT
Canidae							
Cerdocyon thous	maikan	94	37	0.24	0.21	LC	CT, TRK, INT
Speothos venaticus	daiyai	1		0.08		VU	CT, INT
Mustelidae							
Eira barbara	yeruena	22		0.11	0.25	LC	CT, INT
Nasua nasua	kuachi	8		0.04	0.07	LC	CT, INT
CINGULATA							
Dasypodidae							
Dasypus kappleri	-	56	18	0.24	0.23	LC	CT, TRK
Dasypus novemcinctus	muruk	47	23	0.18	0.21	LC	CT, TRK, INT
Cabassous unicinctus	-	4	2	0.02	0.04	LC	CT
Priodontes maximus	mauraimu	9	1	0.02	0.11	EN	CT, TRK, INT
PERISSODACYLA							
Tapiridae							
Tapirus terrestris	maikuri	35	21	0.04	0.11	VU	CT, TRK, INT
DIDELPHIMORPHIA							
Didelphidae							
Didelphis imperfecta	-	14		0.09	0.11	LC	CT
Didelphis marsupialis	awaré	3		0.01	0.04	LC	CT, INT
PILOSA							
Myrmecophagidae							
Tamandua tetradactyla	woiwo	6		0.03	0.11	LC	CT, INT
Myrmecophaga tridactyla	wareme	23	8	0.08	0.19	VU	CT, TRK, INT
RODENTIA							
Cuniculidae							
Cuniculus paca	uraná	343	7	1.84	0.42	LC	CT, TRK, INT
Dasyproctidae							
Dasyprocta leporina	akuri	236	4	1.02	0.39	LC	CT, TRK, INT
Myoprocta pratti		2				LC	CT, INT
Hydrochoerinae							
Hydrochoerus hydrochaeris	parwena	10	7	0.03	0.04	LC	CT, TRK, INT
PRIMATES							
Cebidae							
Cebus olivaceus	ibarakao	8		0.07	0.09	LC	CT, TRK, INT
Atelidae							
*Alouatta macconnelli**	arauta			-	-	LC	TRK, INT

* species documented only by vocalization and interviews with local communities.

to forest habitat, and were not found in savanna or shrub – intermediate habitat. *Nasua nasua* and *P. maximus* have decreasing population trends due to loss of undisturbed primary rain forest habitats (Anacleto *et al.* 2014; Emmons and Helgen 2016), moreover *P. maximus* is considered an endangered species in Venezuela (Rodríguez and Rojas-Suárez 2008). Among all mammal species associated to forest group of vegetation (13 species), *D. imperfecta*, *D. leporia*, *D. novemcinctus*, and *M. tridactyla* were also found in savanna. The importance of shrub-intermediate habitat needs to be recognized as the majority of species (21) were detected in this habitat with exception of three forest and one savanna species. Two unexpected results might be related to artefacts of not considering the effect of imperfect detectability. *Didelphis marsupialis* was only detected on three occasions in forest habitat in the study area, but this species is usually tolerant to a wide variety of habitats (Astúa de Moraes *et al.* 2019). On the other hand, *C. paca* is known to occur in a wide range of forest types in moist areas (Emmons 2016) but showed strong association to shrub-intermediate habitat in our study area. The large number of detections of this species (343 records) might result from high abundance (number of individuals) and/or high activity of a limited number of individual due to seasonal availability of resources, but in either case, this results indicate the relative regional importance of this habitat for this species.

A baseline for long term monitoring in GS. Our study represents the first large scale quantitative effort to sample the medium and large mammal fauna in the GS, confirming that camera traps play an important role in monitoring biodiversity. We were able to detect 90 % of expected species of medium and large mammals (Lew *et al.* 2009) and propose new approach to calculate habitat preferences that can be successfully replicate in other parts of GS and among mammals and other animals. The main challenges are related to the detection in open areas such as savanna and undetected or real absences of rare or elusive species. Although shorter monitoring periods are cheaper and easier, they also have lower probability of detecting all the species present in an area (Si *et al.* 2014), especially considering seasonal activity patterns. Here, we established a base line for long term monitoring in the Gran Sabana confirming the sampling effort and study design required to reach monitoring long-term goals. Finally, we have highlighted the importance of this baseline given the expected intensification of threats in the South of Venezuela. Human encroachment has already marked significant deforestation in Canaima NP being one of the most important threat for biodiversity. This study represents a good opportunity to describe effective and exhausting survey in changing vegetation conditions that is transformed into the base line for monitoring.

Inventory of large and medium mammals in the Gran Sabana. Our results demonstrate high effectiveness of camera traps for the inventory of large and medium-sized terrestrial mammals in GS. Earlier camera trap studies in South America were limited by logistic (cost of deployment) or low efficiency (few records per sampling effort; Tobler *et al.* 2008), but notable advances have been made and camera trapping has now become a preferred technique for the efficient survey of medium and large mammals in long term and large scale research. While some regions have been studied extensively with impressive results (Lima *et al.* 2017), many areas remain under-sampled. Our sampling design showed good performance when compared with other South America studies with similar sampling effort and study area size (Table 4), including two published camera-trap studies of mammal communities in Venezuela (Perera-Romero *et al.* 2015; Morán *et al.* 2018). Although camera traps studies are often complemented by other methods, in our case almost all target species detected by tracks and interviews were also detected by cameras, except for *Alouatta macconnelli*. Also, during interviews members of Pemón community have not recognized different species of opossum, Armadillo (except *P. maximus*), and small felids like *Leopardus wiedii*. In other cases, they mentioned in the interviews that in the 60s and 70s *S. venaticus* were commonly observed in the area, while currently they are not observed, probably due to forest cover change. This canid is an elusive species with few records in Venezuela, probably due to low abundance or local extinction (Rodríguez and Rojas-Suárez 2008). The reference results of this first sampling effort can serve as a guide for optimizing future sampling. For example, in similar studies, species accumulation curves (Ferrer Paris *et al.* 2013; Si *et al.* 2014) suggests that sampling could be more effective with larger number of traps and shorter duration rather than with fewer traps and larger duration of sampling (due to low turnover between sampling periods), this would require a larger investment in equipment, but reduced costs of field work.

Drawback from the present sampling need to be considered when designing improved future monitoring programs. Special attention must be given to the lack of detection of expected species, which might reflect either limitations of sampling or real ecological patterns, or limitations of this technique in areas of open vegetation.

Challenge of camera trapping in open areas. The success of camera trapping in the open habitats like savannas is limited. In Thaba Tholo Wilderness Reserve, South Africa cameras took photos of large carnivores (jackal, brown hyena or leopard), but underestimated the presence of small carnivores, for which tracking was a more appropriate technique (Pirie *et al.* 2016). During this study, despite of intense sampling effort on savanna (Table 1), false positives were most frequently recorded in savanna than in forest, which may be caused by the movement of grasses in open areas, exposed to wind. Additionally, rocks heated up by solar radiation can activate the camera sensors. Savanna cameras seemed less effective than cameras in forests, as fewer records of mammals' species were obtained in savanna and some species occupying typically herbaceous and savanna ecosystem like *P. yagouaroundi* and *Cavia aperea* were not detected at all. On the other hand, not sampling savanna habitats with camera traps can generate gaps of knowledge. Other sampling techniques should be considered as well, such as observation with drones, genetic tagging, or more traditional tracks stations and marks studies.

Table 3. Habitat association of mammals in the study in comparison with Ochoa et al. (1993): Fl (lowland forest), Fm (montane forest), B (bush), Sa (savannas) and habitat presence: - savanna, I – shrub-intermediate habitat and F- forest.

Habitat	**Fidelity**	**Relative freq.**	**Indicator value**	**p-value**	**Ochoa *et al.* 1993**	**Habitat association**
Sabana						
Cebus olivaceus	0.11	0.43	0.05	0.91	Fl, Fm	S, I, F
Cerdocyon thous	0.56	0.65	0.36	0.00*	Fl, Fm, B, Sa	S, I
Hydrochoerus hydrohaeris	0.06	0.68	0.04	0.66	Fl, Sa	S, I
Odocoileus virginianus	0.11	0.84	0.09	0.18	Fl, Fm, B, Sa	S
Tamandua tetradactyla	0.11	0.43	0.05	0.76	Fl, Fm, B, Sa	S, I, F
Forest						
Didelphis. imperfecta	0.16	0.60	0.10	0.47	Fl, Fm, B	S, I, F
Dasypus kappleri	0.42	0.91	0.38	**0.00***	Fl	I, F
Dasyprocta. leporina	0.65	0.57	0.37	**0.02***	Fl, Fm, B	S, I, F
Didelphis. marsupialis	0.06	1.00	0.06	0.35	Fl, Fm, B	F
Dasypus novemcinctus	0.26	0.57	0.15	0.29	Fl, Fm, B	S, I, F
Eira barbara	0.29	0.50	0.14	0.30	Fl, Fm	I, F
Mazama americana	0.32	0.78	0.25	**0.03***	Fl, Fm, B	I, F
Mazama gouazoubira	0.61	0.84	0.52	0.00*	Fl, Fm, B	I, F
Myrmecophaga tridactyla	0.26	0.55	0.14	0.33	Fl, Fm, B, Sa	S, I, F
Nasua nasua	0.16	1.00	0.16	**0.05***	Fl, Fm, B, Sa	F
Priodontes maximus	0.19	1.00	0.19	**0.01***	Fl, Fm	F
Pantera onca	0.23	0.52	0.12	0.30	Fl, Fm	I, F
Tapirus terrestris	0.23	0.89	0.20	**0.03***	Fl, Fm, B	I, F
Shrub/intermediate						
Cuniculus paca	0.63	0.63	0.40	**0.03***	Fl, Fm	S, I, F
Cabassous unicinctus	0.05	0.62	0.03	0.84	Fl, Fm, B, Sa	I, F
Leopardus pardalis	0.37	0.61	0.22	**0.05***	Fl, Fm	S, I, F
Leopardus wiedii	0.05	0.62	0.03	0.85	Fl, Fm	I, F
Puma concolor	0.26	0.58	0.15	0.10	Fl, Fm, B, Sa	S, I, F
Pecari tajacu	0.05	0.62	0.03	0.86	Fl, Fm, B, Sa	I, F
Tayassu pecari	0.05	0.62	0.03	0.86	Fl	I, F

Undetected species or real absences? Our study detected a great number of species, when compared with other camera trap studies in South America, yet it did not record all

Table 4. Surveys of non-volant mammals in South America and their respective number of recorded species, study area, sampling efforts, survey method (CT: camera trapping, TRN: transect, TRK: tracking, INT: interviews and references, LT: literature).

Location	Study area (km^2)	Sampling effort	No. mammals species	Survey method	Reference
Cerrado, Brazil	87	2,340 camera day	17	CT	Cabral *et al.* (2017)
Cerrado, Brazil	17	450 camera day	14 from CT (18 in total)	CT,TRK, TRN, INT	Trolle (2007)
Central Surinam	324	1,905*	28	CT	Ahumada *et al.* (2011)
Amazonas, Peru	50	3780 camera day**	28	CT	Tobler *et al.* (2008)
Pantanal, Brazil	20	450 camera day	18 with CT (30 in total)	CT, TRK, TRN, INT	Trolle (2003a)
Rio Negro, Brazil	1,500	750 records	14 with CT(42 in total)	CT, TRK, TRN	Trolle (2003b)
Atlantic forest, Brazil	170	25,512 hours of camera trap	16 with CT (58 in total)	CT, TRK, TRN, LT	Rocha-Mendes *et al.* (2015)
Rio Caura, Venezuela	821	5,661 camera day	20	CT, INT	Perera-Romero *et al.* (2015)
Burro Negro, Venezuela	54	1,799 camera day	20 with CT (40 in total)	CT, TRK, INT	Morán *et al.* (2018)
Gran Sabana, Venezuela	1,442	5,523 camera day	29	CT, TRK, INT	This study

* Number of sampling days for each camera summed for all the cameras at the site

** 1,440 (2005) and 2,340 (2006) camera day

species expected in the area (Table 2; Ochoa 2001; Lew *et al.* 2009). This difference can be due to (a) low detection probability of elusive species, (b) low abundance or local extinction; or (c) real absence of the species. Among the six species of the family Felidae in Venezuela, only the *P. yagouaroundi* remains undetected, possibly due to low detectability, as it is much less common than previously suspected, having overall negative population trends (Caso *et al.* 2015). From the family Mustelidae, *Galictis vittata* and *Mustela frenata* were expected, but not detected in the study. Confirmed records of *G. vittata* are scarce across its distribution, therefore no current accurate estimates of its distribution are available (Cuarón *et al.* 2016). *M. frenata* favoured habitats include brushland and open woodlands, field edges, riparian grasslands, swamps, and marshes (Helgen and Reid 2016) that were not particularly sampled in this study. Also, *Marmosops parvidens* (Didelphidae) was not detected, either due to its preference for humid habitats in primary and secondary tropical forests, including well drained and swampy forests that were not sampled, or due to low detection probability (Martin 2016). Among the rodents, *C. aperea* was not detected, despite of extensive sampling effort on savanna that is its allegedly preferred habitat. We also provide a new confirmed record for *Myoprocta pratii* inside Canaima NP at the limits of its distribution range (previously only known from park surroundings; Lew *et al.* 2009).

Interestingly, there were no camera or track observation of *Sylvilagus brasiliensis*, which is usually a common species within its range and should be recorded by camera traps. Interviewed Pemón do not recognize this species for their region, but they do know it from other regions of Venezuela. Traditionally, *S. brasiliensis* has been considered a widely distributed species, with large information gaps in the Amazon region (Chapman and Hockman 1980). Its presence in GS is disputed because of the lack of collection or museum records (Eisenberg 1989; Ochoa *et al.* 1993; Linares 1998; Lord 1999; Huber *et al.* 2001; Lew *et al.* 2009). Recent publications (Ruedas *et al.* 2017) question the identity of the different populations of *S. brasiliensis*, suggesting that instead of a species with great ecological adaptability, there may be more than 37 different taxa, for which distribution or ecology are not yet fully understood. Thus, the records of the lagomorphs in GS can have important biogeographic and ecological implications. Additional interviews in other parts of GS and the Canaima community inside Canaima NP (I. Stachowicz, personal observation), seem to confirm that the species is not found in GS. Therefore, we suggest that *S. brasiliensis* is the only real absence and should be removed from the list of species of GS and Canaima NP.

Challenges and opportunities for conservation. The timing of our study coincided with a complex socio-economic context, which represents a great challenge for conservation in the country. Sampling in the Kavanayen region was limited to a single period in 2018 because the deterioration of general conditions in Venezuela, lack of fuel or food supply, mining encroachment and thus elevated military presence in the region, increased sampling cost and compromised personal security. Yet this situation makes this first sampling even more valuable as a reference of the conditions close to the onset of one of the largest mining development plans in South America.

The development plans of the OMA have raised serious concern about the future of different forest formations and its fauna along the Orinoco River, the Guiana Shield ecosystems and National Parks like Canaima that historically had low exposure to threats. During interviews, the leaders of Pemón communities expressed interest in rescuing traditional knowledge that might be at risk due to changing livelihoods in the region. Young people are migrating to work in profitable, yet mostly illegal, economic activities like mining and timber extraction, and altering their relationship with their natural heritage (Herrera and Rodríguez 2015). The Canaima National Park, as a UNESCO Heritage site generates important income opportunities for indigenous people, however international tourism has been declining in recent years (I. Stachowicz, per. Obs.).

Lack of proactive management plans for OMA, regulation and enforcement to mitigate and restore impacts on ecosystems and society under severe stress from OMA result in uncontrolled deforestation and erosion degrading watersheds in the Orinoco and Yuruani basins. Management of protected areas within the OMA will play a key role in determining how these threats will affect the different forest formations in southern Venezuela (Ferrer-Paris *et al.* 2019). Therefore, effective and concrete conservation action is needed, even large "paper parks" will not be enough.

Moreover, the presence of six endangered species in the study area represents a good opportunity for conservation action (Table 2). In Venezuela, *P. maximus* has been classified as Endangered (Rodríguez and Rojas-Suárez 2008) and is considered an emblematic native species. *P. maximus* can play an important role as an ecosystem engineer through their excavation activity that may be of high value to the community of vertebrates (Desbiez and Kluyber 2013) but has been little studied due to its fossorial and highly cryptic nature (Silveira *et al.* 2009). During this study, *P. maximus* was detected eight times in six different localities and we suggest using this data to design specific surveys for abundance estimation including a combination of techniques such as radio-tagging, burrow surveys and camera-trapping.

Conservation programs in the region need to combine educational and social action that consider natural resources management and alternative, non-extractive livelihoods. Non-consumptive recreation combined with citizen science monitoring could support long-term monitoring of protected and unprotected area that is useful for park authorities for more detailed surveys of local fauna (Kays *et al.* 2017). Undoubtedly, this strategy needs to be adjusted to Venezuelan conditions but could offer new, possible income for local communities from tourism and better opportunities for monitoring illegal activities.

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First record of *Urotrema scabridum* (Platyhelminthes), and new records of helminths of *Tadarida brasiliensis* from Mexican Plateau

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The Mexican free-tailed bat (*Tadarida brasiliensis*) is an abundant, widely distributed species in Mexico, except for most of the Yucatán peninsula. We studied the helminth fauna of *T. b. mexicana* at seven localities in the State of Zacatecas in order to advance the knowledge of helminth parasites of wild vertebrates in northern-central Mexico. Eighty-four bat specimens were examined for the presence of helminth parasites following standard procedures; helminths found were identified and infections were characterized. Of the specimens examined, 65.47 % were parasitized. The helminth fauna comprises five taxa: three digeneans (*Dicrocoelium rileyi*, *Ochoterenatrema labda*, and *Urotrema scabridum*); one cestode (*Vampirolepis* sp.); and one nematode (*Tadaridanema delicatus*). We present a brief morphological description of *Urotrema scabridum*. *D. rileyi* was the most prevalent and abundant helminth species. The intestine was the habitat most parasitized, with four species. Indirect life cycles predominate, and are related to the insectivorous habits of this host. Further studies on this host-parasite system are necessary to contribute to population monitoring and conservation; biogeographic patterns of helminth parasites of bats should also be studied to explore their origins and evolution in the region. *U. scabridum* is reported for the first time from Zacatecas. All species are new locality records.

El murciélago de cola libre mexicano (*Tadarida brasiliensis*), es una especie abundante y ampliamente distribuida en México, excepto en la mayor parte de la península de Yucatán. Para contribuir al conocimiento de los helmintos parásitos de vertebrados de vida silvestre en el centro-norte de México, la fauna helmíntica de *T. b. mexicana* se estudió en siete localidades del estado de Zacatecas. Se analizaron ochenta y cuatro especímenes de murciélagos de siete localidades dentro de Zacatecas. Los huéspedes fueron examinados para detectar helmintos parásitos siguiendo los procedimientos estándar de revisión, identificación taxonómica y se carcaterizaron las infecciones. El 65.47 % de los huéspedes examinados fueron parasitados. La fauna de helmintos consistió en cinco taxones: tres digéneos (*Dicrocoelium rileyi*, *Ochoterenatrema labda,* y *Urotrema scabridum*); un céstodo (*Vampirolepis* sp.) y un nemátodo (*Tadaridanema delicatus*). Se presenta una breve descripción morfológica de *Urotrema scabridum. D. rileyi* es la especie de helminto más prevalente y abundante. El intestino es el hábitat más parasitado con cuatro especies. El ciclo de vida indirecto es predominante y está relacionado con los hábitos alimentarios insectívoros de este huésped. Es necesario aumentar el número de estudios sobre este sistema huésped-parásito para contribuir al monitoreo de las poblaciones y la conservación, así como realizar estudios sobre patrones biogeográficos de helmintos parásitos de murciélagos que permitan explorar su origen y evolución en la región. *U. scabridum* se reporta por primera vez de Zacatecas, México. Todas las especies son registros nuevos de localidad.

Key words: Cestoda; Helminth parasites; Mexican free-tailed bat; Mexican Plateau; Nematoda; Trematoda.

Introduction

Chiroptera is the second most diverse and abundant order of mammals, it is widely distributed worldwide and is most abundant in tropical regions (Hutson *et al.* 2001). The Mexican free-tailed bat, *Tadarida brasiliensis* (Molossidae), is abundant in the Western Hemisphere, from the United States of America and southward into Central and South America (Russell *et al.* 2005). Its distribution range encompasses most of Mexico, except for most of the Yucatan peninsula (Wilkins 1989; Schmidly 1991; Álvarez-Castañeda *et al.* 2015). This bat species comprises nine valid subspecies (Simmons 2005), one of them is *T. b. mexicana*. This insectivorous species may occupy different habitats, including urban zones, deserts, and pine-oak forests, where it can often be found in caves, under bridges, abandoned mines, tunnels, tree holes and wall cracks (Tuttle 1994).

Although the Mexican free-tailed bat is a widely distributed species, its helminth fauna has been seldom studied in Mexico (reported in all cases as *T. brasiliensis*); studies have been carried out in Mexico City and the states of Mexico, Durango, Morelos, Nuevo Leon, Puebla, and Zacatecas (Tuttle 1994, 1942, 1943; Caballero y Caballero and Caballero-Rodríguez 1969; Guzmán-Cornejo *et al.* 2003; Falcón-Ordaz *et al.* 2006; García-Prieto *et al.* 2012; Caspeta-Mandujano *et al.* 2017; Jiménez *et al.* 2017; Falcón-Ordaz *et al.* 2019; Table 1). Sixteen helminth taxa have been recorded parasitizing this bat species in Mexico (Table 1): nine trematodes, two cestodes, four nematodes, and two nematodes. To the best of our knowledge, only four helminth species had been previously recorded in Zacatecas: three platyhelminth species [two digeneans (*D. rileyi* and *O. labda*) and one cestode (*Vampirolepsis* sp.), and one nematode species (*T. delicatus*).

As part of a research program aimed to compile an inventory of invertebrate parasites of wildlife in Northern-Central Mexico, with emphasis in the Mexican Plateau, the helminth fauna of *T. brasiliensis mexicana* was studied. The trematode species *Urotrema scabridum* was recorded for the first time. The aim of this paper is to report on the presence of this trematode in Mexico and expand the known distribution range of the helminth parasite fauna of *T. b. mexicana*.

Material and Methods

Eighty-four bat specimens were collected from seven localities in the State of Zacatecas between November 2011 and September 2013 (Table 2, Figure 1). The specimens were euthanized with an intraperitoneal overdose of sodic pentobarbital, following the guidelines of the American Society of Mammologists (Sikes *et al.* 2016; scientific collecting license FAUT-268 to EAMS), and examined for the presence of helminth parasites. The body cavity was exposed by means of

Table 1. Summary of helminth fauna of *Tadarida brasiliensis* in Mexico. G = gall bladder and hepatic conduits; I = Intestine; S = Stomach.

Helminths	Locality/State	Reference
Platyhelminthes		
Trematoda		
Dicrocoeliidae		
Dicrocoelium sp.^{G}	Cueva San Bartolo (Santa Catarina), Nuevo León.	García-Prieto *et al*. 2002
Dicrocoelium rileyi ^{G}	Campus Chamilpa (UAEM), Morelos; Concepción del Oro, Zacatecas; Cueva de La Boca (Santiago), Nuevo León; Cueva del Guano (Santa Catarina), Nuevo León; Cueva San Bartolo (Santa Catarina), Nuevo León; Nombre de Dios, Durango; Río Salado (Zapotitlán), Puebla; Tequixquiac, State of Mexico.	Caballero y Caballero, and Caballero-Rodríguez 1969; García-Prieto *et al.* 2002; Guzmán-Cornejo *et al.* 2003; Caspeta-Mandujano *et al.* 2017; Falcón-Órdaz *et al.* 2019
Platynosomum beltrani ^{I}	Monterrey, Nuevo León.	Caballero y Caballero and Caballero-Rodríguez 1969
Lecithodendriidae		
Limatulum limatulum ^{I}	Campus Chamilpa (UAEM), Morelos; Cuicatlán, Morelos.	Caballero y Caballero and Bravo 1950; Caspeta-Mandujano *et al.* 2017
Limatulum oklahomense ^{I}	Zoológico de Chapultepec, México City.	García-Prieto et al. 2012
Ochoterenatrema labda ^{I}	Bosque de Chapultepec, México City; Concepción del Oro, Zacatecas; Cueva de La Boca (Santiago), Nuevo León; Cueva San Bartolo (Santa Catarina), Nuevo León; Nombre de Dios, Durango; Río Salado (Zapotitlán), Puebla; State of México; Campus Chamilpa Campus Chamilpa (UAEM), Morelos.	Caballero y Caballero 1940; Caballero y Caballero 1943; García-Prieto *et al.* 2002; Guzmán-Cornejo *et al*. 2003; Caspeta-Mandujano *et al.* 2017
Paralecithodendrium naviculum ^{I}	Azcapotzalco, México City.	Caballero y Caballero, 1940
Plagiorchiidae		
Plagiorchis vespertilionis ^{I}	Azcapotzalco, México City; Bosque de Chapultepec, México City; Locality unknown, Morelos.	Caballero y Caballero 1940; Caballero y Caballero 1943; Caspeta-Mandujano *et al.* 2017
Pleurogenidae		
Urotrema scabridum ^{I}	Acolman, State of México; Cueva de La Boca (Santiago), Nuevo León; Cueva San Bartolo (Santa Catarina), Nuevo León; Nombre de Dios, Durango; Río Salado (Zapotitlán), Puebla; Locality unknown, Morelos.	Caballero y Caballero 1942; García-Prieto *et al.* 2002; Guzmán-Cornejo *et al*. 2003; Caspeta-Mandujano *et al.* 2017
Cestoda		
Vampirolepis decipiens ^{I}	Campus Chamilpa (UAEM), Morelos.	Jiménez *et al.* 2017; Caspeta-Mandujano *et al.* 2017
Vampirolepsis sp.^{I}	Concepción del Oro, Zacatecas; Cueva de La Boca (Santiago), Nuevo León; Río Salado (Zapotitlán), Puebla.	Guzmán-Cornejo *et al.* 2003
Nematoda		
Acuaridae		
Acuaridae gen. sp.^{S}	Campus Chamilpa (UAEM), Morelos.	Jiménez *et al.* 2017; Caspeta-Mandujano *et al.* 2017
Capillaridae		
Aonchotheca speciosa ^{S}	Campus Chamilpa (UAEM), Morelos.	Jiménez *et al*. 2017; Caspeta-Mandujano *et al.* 2017
Capillaria palmata ^{S}	Campus Chamilpa (UAEM), Morelos.	Jiménez *et al.* 2017; Caspeta-Mandujano *et al.* 2017
Ornithostrongylidae		
Allintoshius tadaridae ^{I}	Alcoman, State of México; Bosque de Chapultepec, México City; Cueva El Salitre, Morelos.	Caballero y Caballero 1942; Caspeta-Mandujano *et al.* 2017
Molineidae		
Tadaridanema delicatus ^{I}	Campus Chamilpa (UAEM), Morelos; Concepción del Oro, Zacatecas; Cueva de La Boca (Santiago), Nuevo León; Nombre de Dios, Durango; Río Salado (Zapotitlán), Puebla	Guzmán-Cornejo *et al.* 2003; Falcón-Ordaz *et al.* 2006; data in Jiménez *et al.* 2017; Caspeta-Mandujano *et al.* 2017
Nematoda gen. sp.^{I}	Campus Chamilpa (UAEM), Morelos.	Jiménez *et al.* 2017; Caspeta-Mandujano *et al.* 2017

Table 2. Localities surveyed in Zacatecas, Mexico for helminth parasites. Locality codes are used in Figure 1 and Table 3.

Code	Locality, municipality	Geographic coordinates (elevation)	Sample size (number of host infected)	Collection date (month/year)
1	Tepechitlán, Tepechitlán	21° 40′ 13.4″ N; -103° 19′ 42″ W (1,788 masl)	*n* = 18 (8)	5/2012 10/2012
2	Guadalupe, Zacatecas	22° 44′ 38.1″ N; -102° 30′ 53.6″ W (2,479 masl)	*n* = 35 (27)	11/2011 05/2012 06/2012
3	Zacatecas, Zacatecas	22°46′28.63″ N; -102° 32′ 39.66″ W 2,379 masl)	*n* = 1 (1)	06/2013
4	Sombrerete, Sombrerete	23° 38′ 4.47″ N; -103° 38′ 29.51″ W (2,307 masl)	*n* = 7 (5)	08/2012
5	San José de la Parada, Sombrerete	23° 31′ 52.7″ N; -103° 36′ 16.6″ W (2,163 masl)	*n* = 1 (0)	08/2013
6	Susticacán Dam, Susticacán	22° 36′ 38.42″ N; -103° 8′ 40.01″ W (2,081 masl)	*n* = 1 (0)	09/2013
7	San Felipe Nuevo Mercurio, Mazapil	24° 13′ 35.08″ N; -102° 9′ 16.48″ W (1,731 masl)	*n* = 21 (12)	04/2012

a longitudinal incision; all the organs were removed and examined separately under a dissecting stereoscope. Parasites found were first placed in a 0.85 % w/v saline solution, then fixed by sudden immersion in hot (steaming) 70 % ethanol and stored in 70 % ethanol to preserve morphological traits for identification. Nematodes were cleared for morphological study with Ammans's lactophenol and with a 2:8 ethanol–glycerin mixture. Cestodes were stained with Mayer's hydrochloric carmine, and whole-mounted in Canada balsam (Hycel de México, Jalisco). Techniques used are fully described elsewhere (Lamothe-Argumedo 1997).

Some of the specimens were photographed with a Leica ICC50HD camera fitted to a Leica DM750 microscope (Leica Microsystems, Wetzlar, Germany). For the new record specimens, morphometric characteristics were measured in micrometers (µm) unless otherwise stated (total body length and width in millimeters, mm). Minimum and maximum values are reported, along with the mean and standard deviation (SD) in parentheses.

Two specimens of the species newly recorded in Zacatecas and one of the dicrocoeliid species were further examined with scanning electron microscopy (SEM) and environmental scanning electron microscope (ESEM), respectively. The former were stored in 4 % formalin, dehydrated through a series of baths of gradually increasing ethanol concentrations, and critical-point dried. Specimens were coated with a gold–palladium mixture and examined under a Hitachi S-2460N (Hitachi, Tokyo, Japan) SEM at 15 kV. The second specimen was observed directly under an ESEM Quanta 250 FEG (Thermo Fisher Scientific Inc., Brno, Czech Republic) operating in low vacuum mode (p between 100 and 130 Pa).

Taxonomic identification was carried out by examining morphological traits and comparing them with taxonomic keys and descriptions in the specialized literature (Macy 1931;Macy 1931 Caballero y Caballero 1942, 1943; Travassos 1944; Bray *et al.* 1999; Anderson 2000; Lunaschi 2002; Falcón-Ordaz *et al.* 2006; Lunaschi and Notarnicola 2010). Helminth parasites were identified, counted and their sites of infection recorded. Infection parameters of prevalence (P), mean abundance (MA), mean intensity (MI) and intensity range (IR), were calculated according to Bush *et al.* (1997; Table 3).

Voucher specimens were deposited into the reference collection of the Colección de Invertebrados no Artrópodos (CINZ) and Colección de Vertebrados (CVZM), Laboratorio de Colecciones Biológicas y Sistemática Molecular, Unidad Académica de Ciencias Biológicas, Universidad Autónoma de Zacatecas. Additional vouchers specimens were entered into the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.

Results

Eighty-four bat specimens were collected from seven localities in the State of Zacatecas and examined for the presence

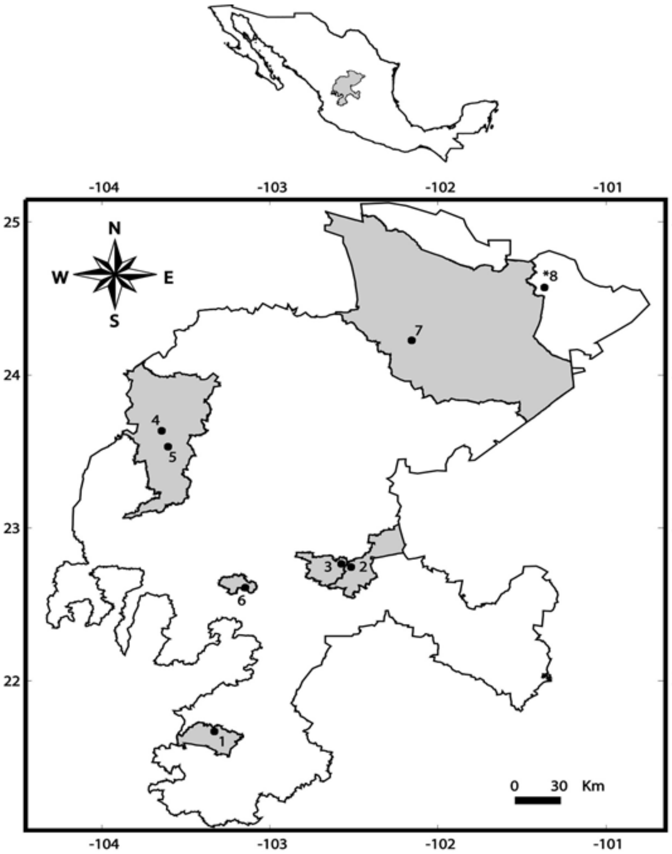

Figure 1. Sampling localities in Zacatecas, Mexico. Municipalities: 1= Tepechitlán; 2 and 3 = Zacatecas; 4 and 5 = Sombrerete; 6 = Susticacán; 7= Nuevo Mercurio. *8 = Concepción del Oro. Previous records are shown in Table I. Codes for localities are shown in Table 2.

of parasites; 65.47 % of the specimens were parasitized. The helminth fauna comprises five species in five different families (Figure 2, 3) the first group, Platyhelminthes, the trematodes *Dicrocoelium rileyi* (Dicrocoeliidae), *Ochoterenatrema labda* (Lecithodendriidae), and *Urotrema scabridum* (Pleurogenidae), and one cestode, *Vampirolepis* sp. (Hymenolepididae; the second group, Nematoda, *Tadaridanema delicatus* (Molineidae). Most of the helminth parasites had been previously recorded in Zacatecas, except for the trematode *Urotrema scabridum* (Table 1; Figure 2) which inhabits the gall bladder and hepatic conduits. A brief morphological description follows.

Class Trematoda

Orden Strigeidida

Family Pleurogenidae (Syn. Urotrematidae Ponche, 1926 according to Tkach *et al.* 2019).

Urotrema scabridum

Characterization (based on 14 specimens, 12 measured and 2 SEM, Figure 2 and Table 4): body elongated, posterior end truncated, yellow color *in vivo* and whitish post fixing, total body length (TBL) 2.012 - 3.580 mm (2.944 ± 0.498) by 0.339 - 0.497 mm (0.433 ± 0.049) wide (W). Tegument covered with small spines (a SEM microphotograph shows collapse of the tegument and spines shape). Oral sucker subterminal, 78 - 132 (109 ± 18) long (OSL) by 75 - 146 (119 ± 24) wide (OSW). Ratio of oral sucker width to ventral sucker width 1:1.21 - 1.49. Pre-pharynx short. Pharynx 33 - 58 (49 ± 8) long by 37 - 61 (51 ± 8) wide. Esophagus 176 - 397 (230 ± 60) long by 17 - 29 (23 ± 4) wide. Ventral sucker on the first third of the body, 107 - 178 (143 ± 21) long (VSL) by 112 - 178 (144 ± 19) wide (VSW). Intestine bifurcation pre-acetabular and narrow, extending to the posterior region of the body to the posterior testis. Ovary intercecal, anterior to testes, 115 - 210 (155 ± 29) long (OL) by 127 - 184 (153 ± 21) wide (OW). Testes tandem; anterior testis 181-334 (247 ± 41) long (ATL) by 160 - 390 (262 ± 60) wide (ATW), posterior testis 207 - 332 (265 ± 41) long (PTL) by 156 - 339 (253 ± 53) wide (PTW). Cirrus sac fusiform, located in the posterior end of the body, 164 - 291 (221 ± 40) long. Genital pore ventral. Vitelline follicles in two lateral fields wrapped around the ceca, both extracecal, several clusters of vitelline glands dorsally situated between ventral sucker and ovary, extending anteriorly to ventral sucker from the anterior testis. Uterus mainly intercecal, the uterine loops descending to posterior end of the body. Eggs 18 - 24 (24 ± 2, *n* = 60) long (EL) by 10 - 12 (11 ± 1, *n* = 60) wide (EW).

Table 3. Infection parameters of helminth parasites of the free-tailed bat, *Tadarida brasiliensis mexicana* in seven localities from Zacatecas, Mexico. L = Locality (codes as in Figure 1 and Table 2). Abbreviations: 1) Infection sites: I = Intestine, G = gall bladder and hepatic conduits. 2) Life cycle: CD = Direct, CI= Indirect. 3) Ecological parameters: *n* = Total number of parasites collected, HIP = Host infected by parasite, P (%) = Prevalence, MA = Mean abundance, MI = Mean intensity, IR = Intensity range. * = Accession numbers in the CINZ and CNHE collections.

Helminth species	L	n	P (%) (HIP)	MA	MI	IR	Accession Number*
Platyhelminthes:							
Trematoda							
Dicrocoeliidae							
Dicrocoelium riley$^{iG, CI}$	1	60	44.44 (8)	3.33	7.50	1 - 23	CINZ158; CNHE 11103
	2	95	42.86 (15)	2.71	6.33	1 - 40	CINZ150; CINZ155; CNHE 11104
	4	85	57.14 (4)	12.14	21.25	2 - 48	CINZ09; CNHE 11105
	7	101	33.33 (7)	4.81	14.43	1 - 52	CINZ 10; CNHE 11106
Lecithodendriidae							
Ochoterenatrema labda$^{I, CI}$	2	22	11.43 (4)	0.63	5.50	1 -15	CINZ151; CINZ154; CNHE 11107
	4	1	14.29 (1)	0.14	1	1	CINZ 11
	7	3	4.76 (1)	0.14	3	3	CINZ 12
Pleurogenidae							
Urotrema scabridum$^{I, CI}$	2	40	11.43 (4)	1.14	10	4 - 27	CINZ156; CNHE 11108
Cestoda							
Hymenolepididae							
Vampirolepis sp.$^{I, CI}$	2	6	14.29 (5)	0.17	1.20	1 - 2	CINZ148; CINZ153; CNHE 11109
	4	1	14.29 (1)	0.14	1	1	CINZ 13
Nematoda							
Molineidae							
Tadaridanema delicatus$^{I, CD}$	1	2	11.11 (2)	0.11	1	2	CINZ159
	2	67	40.00 (27)	1.91	4.79	1 - 12	CINZ149; CINZ152; CINZ157 CNHE 11110
	3	3	100 (1)	3.00	3	3	CINZ 14; CNHE 11111
	4	9	28.57 (9)	1.29	4.50	3 - 6	CINZ 15; CNHE 11112
	7	18	33.33 (7)	0.86	2.57	1 - 6	CINZ 16; CNHE 11113

Taxonomic remarks: The genus *Urotrema* was first described from specimens collected in the intestine of the greater bulldog bat *Noctilio leporinus* (originally recorded as *Noctilio macropus*) and included in *Urotrema scabridum* as the type species. This species mainly parasitizes insectivorous bats and is widely distributed from North to South America and Africa (Zamparo *et al.* 2005). It has also been reported in polychrotid lizards (anoles) from Florida and Louisiana (Sellers and Graham 1987; Goldberg *et al.* 1994), the Caribbean and Central America (Goldberg *et al.* 1994, Goldberg *et al.* 1996; Goldberg *et al.* 1998).

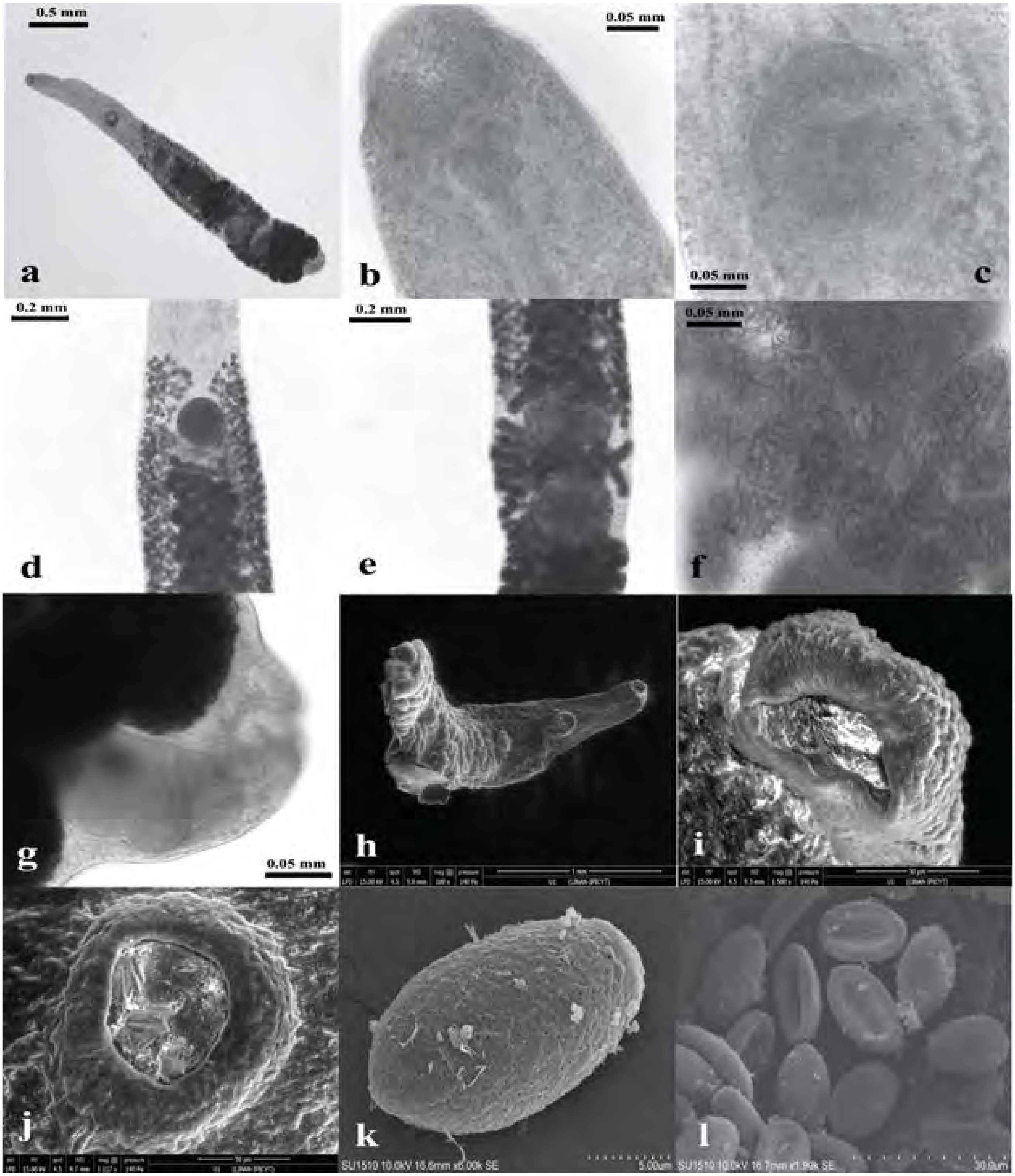

Figure 2. General morphology and ESEM-SEM photomicrographs of *Urotrema scabridum* from Zacatecas, Mexico. Optical microscopy: a) Whole body, ventral view; b) Oral sucker, ventral view; c) Ventral sucker, ventral view; d) Ovary, vitelline follicles arranged in two lateral fields and anterior end of the uterus, ventral view; e) Testis in tandem, ventral view; f) Uterine loops with eggs between testes, ventral view; g) Cirrus sac located in the posterior end of the body, ventral view. ESEM: h) Whole body, ventral view; i) Oral sucker, ventral view; j) Ventral sucker, ventral view. SEM: k and l) Eggs, ventral view. Scale bars are shown in each microphotograph.

Through the taxonomic history of the genus *Urotrema*, eight nominal species have been described parasitizing various mammal and lizard species (Zamparo *et al.* 2005): *U. scabridum*, *U. shillingeri*, *U. lasiurensis*, *U. minuta*, *U. wardi*, *U. aelleni* Baer, 1957, *U. macrotestis*, and *U. shirleyae*. However, the validity of some of the species has been questioned (Caballero y Caballero 1942; Caballero and Grocott 1960; Yamaguti 1971; Bray *et al.* 1999; Tkach *et al.* 2019). Caballero y Caballero (1942) considered *U. scabridum* and *U. wardi* as valid species, and synonymized *U. lasiurensis*, *U. minuta* and *U. shillingeri*. Later on, Caballero and Grocott (1960) synonymized *U. aelleni* with *U. scabridum*. Bray *et al.* (1999) suggested that *U. scabridum* is a species complex showing intraspecific variation (= *U. aelleni*, *U. lasiurensis*, *U. macrotestis,* and *U. shillingeri*). At least three species are currently considered valid: "*U. scabridum* complex", *U. minuta* and *U. shirleyae.* Recently, the phylogenetic position of the genus *Urotrema* within Digenea was clarified by Tkach *et al.* (2019) based on the partial sequence of 28S rDNA; they transferred the genus to the Pleurogenidae and showed that the clade of *U. scabridum* + *U minuta* + *U. shirleyae* is phylogenetically closest to *Parabascus* spp. Our specimens are smaller than those described by Caballero y Caballero (1942) but bigger than the specimens measured by Lunaschi and Notarnicola (2010). Morphological characteristics of the specimens analyzed are shown in Table 4.

Infection parameters: The prevalence, mean abundance, mean intensity, intensity range, site of infection, hosts and localities are shown in Table 3. No helminth parasites were found in the San José de la Parada (Sombrerete) and Susticacán Dam (Susticacán) localities. Platyhelminthes (Trematoda) were the species-richest group. Four of the five helminth taxa inhabit the intestine (*O. labda, U. scabridum, Vampirolepis* sp. and *T. delicatus*), with a general intensity from 1 to 101 helminths per infected free-tailed bat. The highest number of parasite species was recorded in the Guadalupe locality, with four helminth species, three trematodes (*D. rileyi, O. labda,* and *U. scabridum*), one cestode (*Vampirolepis* sp.) and one nematode (*T. delicatus*). Indirect life cycles are predominant in the helminth fauna found. *Dricocoelium rileyi* was the most prevalent helminth in four localities (Table 3): Guadalupe (42.86 %), Nuevo Mercurio (33.33 %), Sombrerete (57.14 %), and Tepechtitlán (44.44%). *Tadaridanema delicatus* was the only parasite found in the Zacatecas locality, with 100 % prevalence in three individuals examined. The species *D. rileyi* and *T. delicatus* from Nuevo Mercurio showed the same prevalence, mean intensity, and intensity range (Table 3).

Discussion

The helminth fauna of the order Chiroptera in Mexico, has been poorly studied compared to the diversity of Mexican bats (144 spp.; helminths: *e. g.* García-Prieto *et al.* 2012; Caspeta-Mandujano *et al.* 2017; Clarke-Crespo *et al.* 2017; Jiménez *et al.* 2017; Salinas-Ramos *et al.* 2017; Luviano-Hernández *et al.* 2018; Falcón-Ordaz *et al.* 2019; bats: Sánchez-Cordero *et al.* 2014). To the best of our knowledge, only 28 bats species in the families Emballonuridae (one species), Molossidae (two species), Mormoopidae (four species), Natalidae (one species), Phyllostomidae (15 species) and Vespertilionidae (five species) have been examined for helminths (see García-Prieto *et al.* 2012; Clarke-Crespo *et al.* 2017; Caspeta-Mandujano *et al.* 2017; Jiménez *et al.* 2017; Salinas-Ramos *et al.* 2017; Luviano-Hernández *et al.* 2018; Falcón-Ordaz *et al.* 2019), only 19.44 % of the bat species occurring in Mexico. Mexican insectivorous bats are one of the groups bearing the highest diversity of parasitic helminths. The species bearing the highest richness is the ghost-face bat, *Mormoops megalophylla*, with 23 helminth species; followed by the Davy´s naked-backed bat, *Pteronotus davyi*, with 15 helminth species; the Mexican greater funnel-eared bat, *Natalus stramineus,* with 14 species; and the Mexican free-tailed bat, *T. brasiliensis* with 17 species (Guzmán-Cornejo *et al.* 2003; Falcón-Ordaz *et al.* 2006; García-Prieto *et al.* 2012; Caspeta-Mandujano *et al.* 2017; Jiménez *et al.* 2017; Table 1).

Previous studies had reported four species parasitizing the Mexican free-tailed bat in Concepción del Oro, Zacatecas: Two digeneans (*D. rileyi* and *O. labda*), one cestode (*Vampirolepis* sp.) and one nematode (*T. delicatus*) (Guzmán-Cornejo *et al.* 2003; Falcón-Ordaz *et al.* 2006). The trematodes were recovered in their adult form; this is the group with the highest number of species parasitizing *T. brasiliensis mexicana* from Zacatecas, compared to cestodes and nematodes which together account for 40 % of the species diversity.

Table 4. Morphometric comparison of *Urotrema scabridum* with some previous records.

Characteristic[1]	**Present work**	**Caballero y Caballero (1942)**[2]	**Caballero y Caballero and Grocott (1960)**[3]	**Lunaschi and Notarnicola (2010)**[4]
Distribution	Mexico	Mexico	Panama	Argentina
TBL (mm)	2.01 - 3.58	4.53 - 5.29	2.08 - 2.30	1.70 - 2.50
OSL	78 - 132	102 - 143	91 - 137	133 - 142
OSW	75 - 146	123 - 163	108 - 125	123 - 142
VSL	107 - 178	175 - 245	121 - 125	128 - 144
VSW	112 - 1782	135 - 233	125 - 133	134 - 152
OL	115 - 210	208 - 237	166 - 175	154 - 218
OW	127 - 184	155 - 163	158 - 187	112 - 209
ATL	181 - 334	300 - 350	133 - 141	128 - 323
ATW	160 - 390	200	146 - 162	134 - 285
PTL	207 - 332	310 - 380	133 - 187	112 -351
PTW	156 - 339	200 - 220	154 - 183	122 - 323
EL	18 - 24	22 - 24	21	21 - 22
EW	10 - 12	12 - 14	12	10 - 13

[1] Acronyms as listed in the description of *U. scabridum* in the main text.

[2] Host: *Natalus stramineus* and *T. brasiliensis*.

[3] Host: *Phyllostomus hastatus panamensis* Allen 1904

[4] Hosts: *Myotis levis*; *Molossops temminckii*; *Eumops bonariensis*; and *T. brasiliensis*.

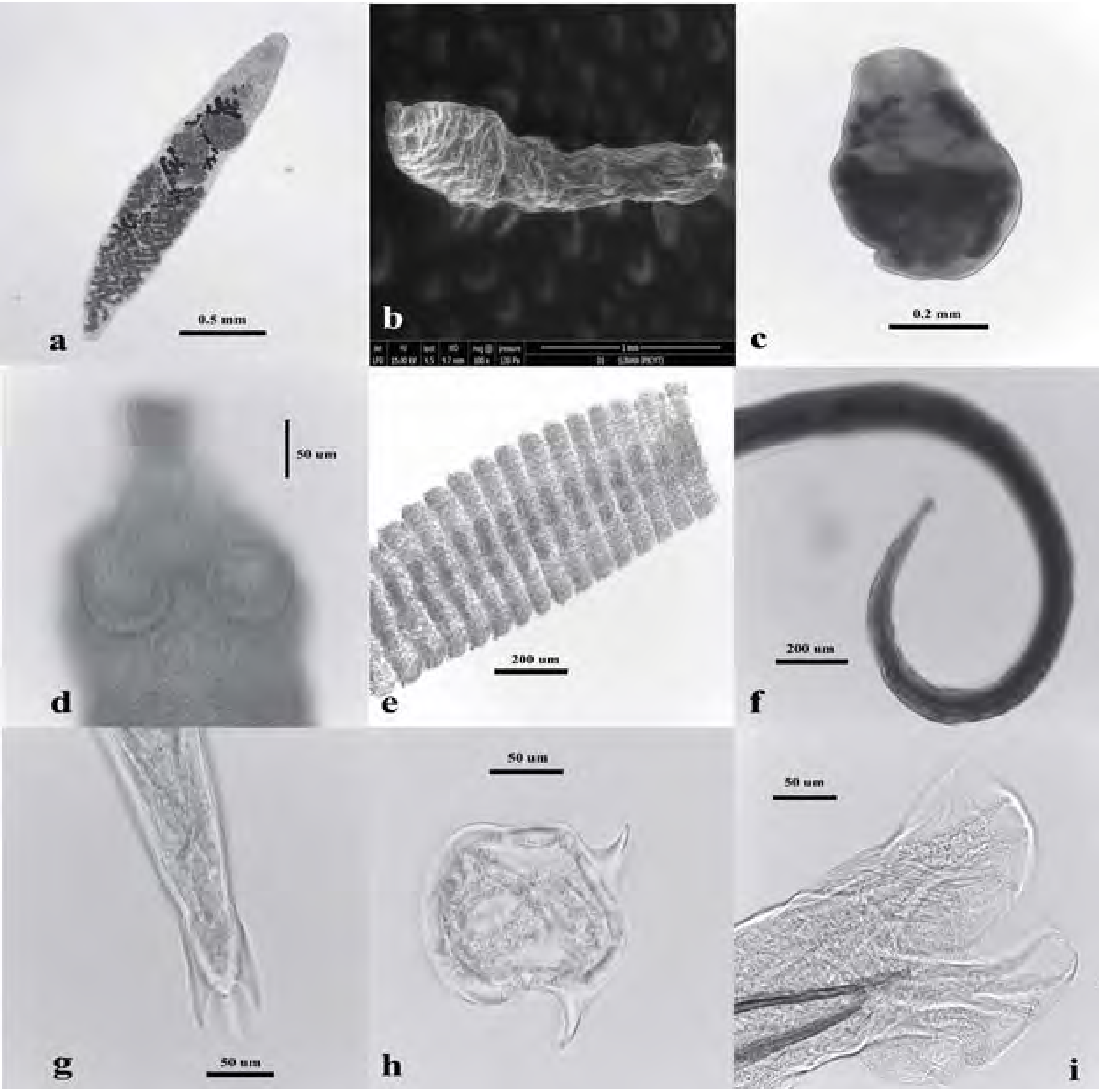

Figure 3. Helminth parasites of the free-tailed bat from Zacatecas, Mexico (excluding the new record). Platyhelminthes: Trematoda: a) *Dicrocoelium rileyi*, full body, ventral view; b) ESEM of *Dicrocoelium rileyi*, full body, ventral view; c) *Ochoterenatrema labda*, full body, ventral view. Cestoda: *Vampirolepis* sp.: d) Anterior end, ventral view; e) Immature proglottids, ventral view. Nematoda: *Tadaridanema delicatus:* f) Female anterior end, ventral view; g) Female posterior end, ventral view; h) Synlophe at midbody level, apical view; i) Male, posterior end, ventral view. Scale bars are shown in each microphotograph.

The trematode *D. rileyi* was the most important helminth in terms of infection parameters, showing the highest prevalence, mean abundance, mean intensity and intensity range in five localities: Tepechitlán (examined in October 2012, not found in May 2011; Medina-Rodríguez pers. obs.), Guadalupe (Zacatecas, October 2011, May and June 2012), Sombrerete (August 2012), San Felipe Nuevo Mercurio (Mazapil, April 2012; see Table 3; Martínez-Salazar, *Pers. Obs.*). In addition, Guzmán-Cornejo *et al.* (2003) also reported infections by this species in Concepción del Oro, Zacatecas (*n* = 3 of the 28 hosts examined in October 1997 and April 1988).

Although the life cycles of the majority of the helminth fauna of bats are still unknown, we can infer some information from their occurrence and their host species; most of the information available in the literature is for the supraspecific level (Yamaguti 1975; Schmidt 1986; Olsen 1986; Anderson 2000). The life cycle of *D. rileyi* is completely unknown; however, the life cycle of *Dicrocoelium dendriticum* has been described as infecting wild and domestic mammals (typically ruminants, not reported in bats) and, very occasionally, humans; its intermediate hosts are terrestrial snails (*i.e. Zebrina* sp., and *Cionella* sp.) and ants (*i.e. Formica* sp.). Pojmańska (2008) suggests that, in general, the Dicrocoeliid-type life cycle involves two intermediate hosts (a terrestrial snail and an arthropod): The xiphidiocercaria leaves the first intermediate host (snail) and becomes encysted in the second intermediate host (an arthropod), which is finally ingested by the definitive host. In Mexico, *D. rileyi* exclusively parasitizes *T. brasiliensis* as definitive host (Caballero y Caballero-Rodríguez 1969; Guzmán-Cornejo *et al.* 2003; García-Prieto *et al.* 2012; Jiménez *et al.* 2017; Falcón-Ordaz *et al.* 2019), but it has also been reported in *T. brasiliensis cyanocephala* and *Vespertilio humeralis* from the United

States (Macy 1931). There are published reports on the presence of *D. rileyi* in four species of terrestrial snails from Zacatecas (Naranjo-García 2014) including *Holospira* (*Holospira*) *temeroso* and *Humboldtiana* (*Humboldtiana*) *chrysogona* in Concepción del Oro; *Humboldtiana* (*Humboldtiana*) *bicincta* in Sierra de Mascarón, Mazapil; and *Humboldtiana* (*Humboldtiana*) *tescola* in San Tiburcio, Mazapil (Thompson 2011). The presence of *D. rileyi* in these five localities in Zacatecas suggests that its intermediate host on which the Mexican free-tailed bat feeds could be present at least from May to October. It is necessary to further examine the genera *Holospira* and *Humboldtiana* in Concepción del Oro; as well as *Humboldtiana* in Mazapil to confirm their role as intermediate hosts of this trematode species in Zacatecas. On the other hand, some 14 Formicidae species have been recorded in Zacatecas (Vásquez-Bolaños 2011) but their helminth fauna has not yet been examined as a possible intermediate host. Further studies on the diversity of terrestrial snails and arthropods (ants) in Guadalupe, Mazapil, Sombrerete and Tepechitlán would help to understand the life cycle of *D. rileyi* in Zacatecas, as well as those of other helminth parasites of wild vertebrates.

Ochoterenatrema labda is an intestinal parasite that has bats as the only known definitive host; it parasitizes bats from United States, Mexico, Panama, Chile and Argentina. Originally described from *T. brasiliensis* from Bosque de Chapultepec, Mexico City and *Natalus stramineus* from Tlalpan, Mexico City (Caballero y Caballero 1943; Caballero y Caballero 1964; Cain 1966; Guzmán-Cornejo *et al.* 2003; Lunaschi and Notarnicola 2010; García-Prieto *et al.* 2012; Jiménez *et al.* 2017), it is the only species that has been reported parasitizing several bat species in Mexico (*Balantiopteryx plicata, Mormoops megalophylla*, *Myotis velifer*, *Natalus mexicanus*, *Pteronotus davyi*, and *T. brasiliensis*; García-Prieto *et al.* 2012; Caspeta-Mandujano *et al.* 2017; Jiménez *et al.* 2017). Guzmán-Cornejo *et al.* (2003) reported this species of digenetic trematode as the most prevalent and abundant helminth in *T. brasiliensis* from Concepción del Oro, Zacatecas. By contrast, our data showed *D. rileyi* as the species with highest infection parameters (Table 3). The taxonomic status of this genus has been questioned; Yamaguti (1958) suggested that it is a synonym of *Prosthodendrium*. However, Cain (1966) and later Yamaguti (1971) considered the genus as valid. Lunashi (2002) provided a redescription of *O. labda* and considered both genera as valid, as *Ochoterenatrema* can be distinguished mainly by the presence of a pseudogonotyl to the left of the ventral sucker. A taxonomic revision of this genus was published by Tkach *et al.* (2003), but a molecular analysis of *Ochoterenatrema* and *Prosthodendrium* is necessary to clarify this issue. The life cycle of this intestinal trematode has not been elucidated and little is known of its intermediate hosts; however, the family Lecithodendriidae requires three hosts: a mollusk, an arthropod, and a vertebrate (Bray *et al.* 2008; Lord *et al.* 2012). In general, the xiphidiocercaria (the first developmental stage) occurs in prosobranch mollusks; larvae of aquatic insects are the intermediate hosts for metacercariae (encysted stage; Yamaguti 1971); chiropterans become infected when they consume infected adult insects, and the adult parasite develops (Lord *et al.* 2012).

In our study we found the trematode *U. scabridum*, which had not been previously recorded in Zacatecas, even though this species ranges from North America to South America (Font and Lotz 2008). To the best of our knowledge, only one species of the genus *Urotrema* has been reported parasitizing Mexican bats: *U. scabridum*. This is a parasite of the Mexican free-tailed bat, and has been recorded in several localities in Mexico, including Acolman, State of Mexico; Cueva de la Boca (Santiago) and Cueva San Bartolo (Santa Catarina), Nuevo León; Nombre de Dios, Durango; and Río Salado (Zapotitlán), Puebla (Caballero y Caballero 1942; García-Prieto *et al.* 2002; Guzmán-Cornejo *et al.* 2003), and an unspecified locality in the State of Morelos (Caspeta-Mandujano *et al.* 2017). It has also been found in *N. stramineus* from Tlalpan, Mexico City (Caballero y Caballero 1942). This is the first time this species has been recorded in the State of Zacatecas; the nearest locality where this species had been previously recorded is in the State of Nuevo León (Guzmán-Cornejo *et al.* 2003). A study on the morphological and molecular variation of this species throughout its distribution range would help to confirm whether or not this is a species complex, as its taxonomic history suggests (*e. g.*, Caballero y Caballero 1942; Caballero and Grocott 1960; Bray *et al.* 1999; Table 4). Life cycles and larval morphology of the Urotrematidae are still completely unknown. Bats acquire this urotrematid parasite by ingesting insects that act as intermediate hosts and harbor encysted metacercariae (Bray *et al.* 2008).

The taxonomic history of the genera *Vampirolepis* and *Rodentolepis* has been controversial. Both genera parasitize chiropterans and share several morphological characteristics, particularly in their body structure. However, the distinguishing difference between these two genera is the number of ovaries, two in *Rodentolepis* and one in *Vampirolepis* (Khalil *et al.* 1994), a characteristic that we confirmed in our study. We were not able to identify all of our specimens to the species level because some of them could not be mounted adequately for morphological study. Nevertheless, we were able to observe some diagnostic characteristics (*e. g.*, presence of an armed rosette endowed with 32 hooks; Medina-Rodríguez, *pers. obs.*) that allowed identification at the genus level as *Vampirolepis* sp. Distinctive features of this genus include between 18 and 50 hooks; linear disposition of the testicles, divided into two groups by the ovary; and transversely elongated proglottids. Only *V. decipiens* has been reported parasitizing *T. brasiliensis* in Mexico (García-Prieto *et al.* 2012); collecting more specimens of *Vampirolepis* would help to clarify the identity of the species present in Zacatecas. Hymenolepididae generally exhibit an indirect life cycle (insects are the intermediate host that is ingested by the vertebrate host) and parasitize insectivorous bats (Bray *et al.* 2008; Roberts and Janovy 2009).

Tadaridanema delicatus is widely distributed across North and South America (Falcón-Ordaz *et al.* 2006; Cheuiche *et al.* 2015); in the State of Zacatecas it is the species with the widest known geographic distribution, having been recorded in six localities (Table 2, Figure 1): Tepechitlán (Tepechitlán), Guadalupe (Zacatecas), Zacatecas (Zacatecas), Sombrerete (Sombrerete), and San Felipe Nuevo Mercurio (Mazapil); it was also previously reported from Concepción del Oro, Zacatecas by Guzmán-Cornejo *et al.* (2003) and Falcón-Ordaz *et al.* (2006). It occurs in simpatry with *D. rileyi* in four localities (Table 2, 3), with exception of Zacatecas (Zacatecas), where we examined only one bat and found three individuals of *T. delicatus*. Additionally, *T. delicatus* has been recorded parasitizing *T. brasiliensis mexicana* from the States of Durango, Nuevo León, and Puebla (Falcón-Ordaz *et al.* 2006), as well as *Molossus ater* from the State of Sinaloa (unspecified locality; Cain and Studier 1974).

The life cycle of *Tadaridanema* spp. is unknown. However, it has been suggested that members of the family Molineidae have a direct life cycle in which the females release numerous eggs into the intestine of the vertebrate definitive host. The eggs are afterwards released to the external medium through the feces, where the first-stage starts developing; later on, they develop into infective third-stage larvae (Roberts and Janovy 2009). It has also been suggested that Molineidae can utilize insects as paratenic hosts (Bush *et al.* 2001), which could increase the possibility of bats being parasitized by nematodes. However, this hypothesis must be tested in *T. delicatus.*

The parasites' infection mechanism can be related to the host's life style and habitat use (Kunz *et al.* 1995; McWilliams 2005). This bat species lives in colonies numbering up to millions of individuals (McCracken *et al.* 1994); this favours infection through their grooming habits and the accumulation of guano in humid environments that harbour a unique ecosystem, including parasites and hosts (Kerth 2008; Altringham 2011). That bats usually host only one parasite taxon is to be expected since some bats are dietary specialists. Parasites are obtained from what bats eat and, being dietary specialists, bats may be predisposed to become parasitized only by the helminth that uses its prey items as intermediate host. Although many species of insectivorous bats have a diversified diet including insects from different orders and families, some species selectively feed on only one type of prey and show foraging habitat specificity. Thus, mayfly and beetle specialists such as *Myotis lucifugus*, and moth specialists such as *Lasiurus borealis* and *T. brasiliensis* are less likely to have multiparasitism than species showing generalist feeding habits (Hilton and Best 2000). These bats roost in a variety of places, including caves, rock crevices, bridges, culverts, highway overpasses and other structures in urban areas (Scales and Wilkins 2007). Infection of insectivorous bats by indirect life cycle parasites occurs outside urban areas as insects are attracted by the city lights (Rydell 2006), and bats prey on them. On the other hand, when bats return to overnight in the colony, the high humidity and feces accumulation in the place, together with the bats' self-cleaning or cleaning between colony members habits, allow the bats to acquire direct life cycle parasites either by autoinfection, by contact between the colony members or by the site's humidity that favours the development of direct life cycle helminths (Bray *et al.* 2008; Bush *et al.* 2001; Roberts and Janovy 2009; Lord *et al.* 2012).

No easily discernable pattern could be found in the diversity of helminths recorded in this bat species in urban areas (localities as Tepechitán, Guadalupe, Zacatecas or Sombrerete) versus those recorded in natural environments (as San Felipe Nuevo Mercurio). Five helminth species were recorded in Guadalupe, four in Sombrerete and three in San Felipe Nuevo Mercurio, and most of them were Platyhelminthes (indirect life cycle). These results might be related to the asymmetric sampling effort (Table 2, 3).

Trematodes showed the highest species richness, and some six helminth species have been reported parasitizing *T. brasiliensis* in Mexico. This pattern had been previously observed in insectivorous bats in North America (Table 1): *D. rileyi*, *P. beltrani*, *O. labda*, *P. vespertilionis*, and *U. scabridum* (Guzmán-Cornejo *et al.* 2003; in García-Prieto *et al.* 2012; Jiménez *et al.* 2017). Two of these indirect life cycle species, *D. rileyi* and *O. labda,* and the nematode *T. delicatus* (considered as a direct life cycle parasite) have been reported as typical helminth fauna of *T. brasiliensis* in Zacatecas and occur in sympatry in the localities of Guadalupe, Sombrerete and San Felipe Nuevo Mercurio. These species had been previously reported in the same condition in Nuevo León and Puebla (Table 1; Guzmán-Cornejo *et al.* 2003).

Tadarida brasiliensis is an opportunistic, generalist, insectivorous bat species (Kunz *et al.* 1995). Food items forming its diet have been generally identified to the order level and, in some cases, to the family level. This bat mainly consumes insects in the orders Lepidoptera (moths), Coleoptera (beetles) and, occasionally, Diptera (true flies), Hemiptera (stinkbugs), Homoptera (leafhoppers), Hymenoptera (wasps), Neuroptera (lacewings) and Odonata (dragon flies, damselflies; Fabián *et al.* 1990; Kunz *et al.* 1995; Whitaker *et al.* 1996; McWilliams 2005; Armstrong 2008). In the United States and Brazil, Coleoptera and Lepidoptera are consumed with higher frequency and volume during the summertime (Fabián *et al.* 1990; McWilliams 2005). Studies on the bat's diet and monitoring the populations in those localities could help to elucidate the indirect life cycles of the helminth fauna of the Mexican free-tailed bat.

The diversity of invertebrates in Zacatecas is almost unknown; studies on the diversity of terrestrial snails and arthropods are necessary to better understand parasite life cycles in wild vertebrates. Monitoring wildlife and their parasites is crucial for conservation and for understanding biogeographic patterns and the evolution of host-parasite interactions. It is, therefore, necessary to further study the helminth parasites of bats to explore their origin and evolution in this region. In this paper, we present the first record of *U. scabridum* in Zacatecas and new locality records for all the helminth taxa recorded.

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Morphological variation in the skull of *Nephelomys meridensis* (Rodentia, Cricetidae): evidence for cryptic species in andean populations from northern South America

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The genus *Nephelomys* comprises at least 13 taxa with altitudinal distribution ranging from 900 to 4,000 meters above sea level. Three species are currently known to occur in Venezuela, but some authors suggest that two additional taxa are present in Venezuelan Andes populations and consider *N. meridensis* as a species complex. We conducted geometric morphometric analyses of skulls and jaws from populations assignable to the monotypic species *N. meridensis* from the Venezuelan Andes, in order to examine and compare morphological variations in this species. We compared four localities (including the type locality of *N. meridensis*) situated in northern, central, and western portions of Cordillera de Mérida and the Tamá páramo. We created morphological landmarks on dorsal, ventral, lateral, and jaw views of each skull using the tpsDIG software. Significant differences were found in skull shape and isometric size in most of the populations examined. The discrimination and morphological differentiation of some of these groups with respect to the population from the type locality (Mérida) were aligned with the results from multivariate and cytogenetic analyses carried out previously by other authors. Our data support recognizing *N. meridensis* as a species complex, comprising at least three still undescribed taxa from the Yacambú National Park (cordillera de Mérida), La Trampita (cordillera de Mérida) and the Tamá páramo (Tamá massif). A more detailed taxonomic study of *Nephelomys* from Venezuela, molecular and linear morphometric analyses, and revision of morphological characters, are necessary to describe potential new taxa and determine the geographical distribution of the species in this genus.

El género *Nephelomys* contiene al menos 13 taxa con distribuciones altitudinales desde los 900 metros sobre el nivel del mar hasta 4,000. Actualmente, tres especies ocurren en Venezuela, pero algunos autores sugieren la existencia de dos taxa adicionales en los Andes venezolanos, considerando a la especie monotípica, *N. meridensis* como un complejo de especies. En este estudio, se usó morfometría geométrica para comparar la forma y tamaño del cráneo en poblaciones de roedores andinos de Venezuela, asignables a la especie monotípica, *N. meridensis*. Se compararon cuatro localidades de *N. meridensis* (incluyendo la localidad tipo), ubicadas en el norte, centro y oeste de la Cordillera de Mérida y en el Páramo El Tamá. Se colocaron hitos morfológicos en las vistas dorsal, ventral, lateral y mandíbula, empleando el programa tpsDIG. Nuestros datos mostraron diferencias significativas en el tamaño isométrico (tamaño centroide) y en la forma del cráneo para la mayoría de las poblaciones evaluadas, resaltando que para algunas, su discriminación y diferenciación morfológica con la población de la localidad tipo (Mérida), coincidió con resultados multivariados y citogenéticos previamente realizados por otros autores. El presente estudio corrobora que *N. meridensis* tiene que ser tratado como un complejo de especies, incluyendo al menos tres taxa no descritos, ubicados geográficamente en el Parque Nacional Yacambú (Cordillera de Mérida), La Trampita (Cordillera de Mérida) y Páramo El Tamá (Macizo El Tamá). Se plantea la necesidad de hacer un estudio taxonómico más detallado para *Nephelomys* de Venezuela en combinación con técnicas moleculares, morfometría lineal y revisión de caracteres morfológicos, entre otros; todo esto con el propósito de describir posiblemente nuevos taxa y delimitar la distribución geográfica de las especies del género.

Key words: cranial morphology; geometric morphometrics; *Nephelomys albigularis* group; Oryzomyini; species complex.

Introduction

The genus *Nephelomys* had been previously included in the genus *Oryzomys* and has been subject to taxonomic, systematic, and molecular studies in recent years, leading to the delimitation of species and new hypotheses about their phylogenetic relationships (*e. g.*, Musser *et al.* 1998; Bonvicino *et al.* 2001; Percequillo 2003; Weksler 2003, 2006; Weksler *et al.* 2006).

Nephelomys comprises at least 13 taxa whose altitudinal distribution ranges from 900 to 4,000 masl (Weksler *et al.* 2006; Percequillo 2015). These rodents inhabit humid montane and cloudy forests in the Andes mountain range, from Bolivia to Colombia. They can also be found along the mountain ranges of northern Venezuela and in the Central American mountain ranges in Panama and Costa Rica (Aguilera *et al.* 1995; Percequillo 2003, 2015; Weksler *et al.* 2006; Anderson *et al.* 2012).

Three species, all included in the *Nephelomys albigularis* group (*sensu* Weksler *et al.* 2006), are currently known to occur in Venezuela, one being endemic to the country (García *et al.* 2019). Their geographical distribution is as follows: *N. caracolus* (endemic) has been recorded in the central and western portions of Cordillera de la Costa (Aguilera *et al.* 1995; Márquez *et al.* 2000; Percequillo 2003, 2015; Anderson and Raza 2010) and in the Lara-Falcón hill systems (Anderson *et al.* 2012); *N. meridensis* is found in the Andes at Cordillera de

Mérida and the Tamá massif (Aguilera *et al.* 1995; Soriano *et al.* 1999; Márquez *et al.* 2000; Percequillo 2003, 2015; Anderson and Raza 2010); *N. maculiventer* was recently recorded in Sierra de Perijá (García *et al.* 2019). However, some authors recognize *N. meridensis* as a species complex, suggesting the existence of two additional taxa in the populations from the Venezuelan Andes (Aguilera *et al.* 1995; Rivas and Péfaur 1999a; Márquez *et al.* 2000; Percequillo 2003).

The use of geometric morphometrics on bony structures (mainly skulls) of cricetid rodents has increased lately as a means to examine intra- and interspecific morphological variation, and to identify and diagnose cryptic species within the group (Cordeiro-Estrela *et al.* 2006, 2008; García and Sánchez-González 2013; Astúa *et al.* 2015; Boroni *et al.* 2017; García *et al.* 2018). Geometric morphometrics is a biologically based statistical analysis method that decomposes variations in size and shape in a two- or three-dimensional space (Bookstein 1991).

Since the Andean populations of *N. meridensis* are considered as taxonomically unstable, we deemed appropriate to collect further evidence that might help to discriminate the species or subspecies currently clustered together into *N. meridensis*. In this work, skulls from Andean populations of this rodent were morphologically characterized and compared using geometric morphometrics techniques. Our objective was to contribute to the delimitation of potentially different taxa currently included within the *N. meridensis* complex of Venezuela.

Materials and Methods

We examined a total of 65 adult specimens (age class 3, as per the classification based on the molar wear pattern; Percequillo 2003) (Appendix 1). These specimens are deposited in the following Venezuelan collections: Museo de la Estación Biológica de Rancho Grande (EBRG, Aragua State), Museo de Historia Natural La Salle (MHNLS, Capital District) and the Colección de Vertebrados de la Universidad de los Andes (CVULA, Merida State).

Given the lack of sexual dimorphism, male and female specimens were pooled together for analyses (Rivas and Péfaur 1999a, b; Percequillo 2003). The specimens were then sorted into groups or morphotypes, according to their geographic distribution (Figure 1): *N. meridensis* (Mérida and adjacent areas), Cordillera de Mérida, Mérida State; *N. meridensis* A (Yacambú National Park), Cordillera de Mérida, Lara State; *N. meridensis* B (La Trampita), Uribante, Cordillera de Mérida, Táchira State; *N. meridensis* C (El Tamá), El Tamá massif, Táchira State; and *N. meridensis* D (Dinira National Park), Cordillera de Mérida, Lara and Trujillo States.

Dorsal, ventral, and lateral views of each skull, as well as the labial view of the jaw, were selected for digitization. All photographs were captured by the same person using a digital camera Nikon D3000 16MP 24X and a tripod; a ruler graduated in millimetres was placed next to each skull as reference. Type-I and -II bidimensional homologous morphological landmarks were digitized (Bookstein 1991; Figure 2) using the software tpsDig (Rohlf 2006); the total number of landmarks digitized on each view were as follows: dorsal (12), ventral (15), lateral (11), and jaw (10). Landmark locations were selected to encompass the skull zones that have taxonomic diagnostic value for this group (Rivas and Péfaur 1999a, b; Márquez *et al.* 2000; Percequillo 2003). Landmark names correspond to those documented by Astúa et al. (2015).

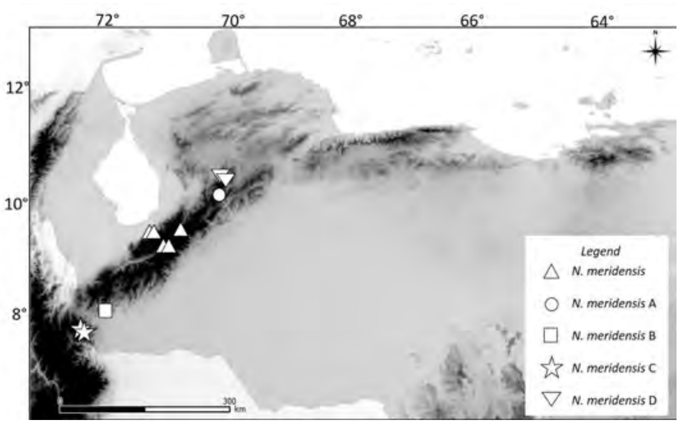

Figure 1. Geographic distribution of the Andean populations of the rodent *Nephelomys* in Venezuela. A darker coloration indicates an elevation higher than 1000 m above sea level.

Morphological landmarks were associated with Cartesian coordinates (x, y) that represent the geometric configuration of each skull. The coordinates were subject to a Procrustes adjustment, using the MorphoJ program, which removes the variations in size due to the position, orientation, and scale of each image (Klingenber 2011). Additionally, to detect a potential allometric correlation between the structures analysed, a Multivariate Regression Analysis (based on Goodall's F statistic) was carried out, using the Regress7a program implemented in the series IMP7 (Sheets 2010). The independent variable was the centroid size and the dependent variables were the shape variables (Meloro *et al.* 2008).

The Procustes residuals produced two matrices; the partial deviations matrix was used for exploratory analyses (Canonical Variable and Discriminant Function analyses) aimed to identify correlations between the different

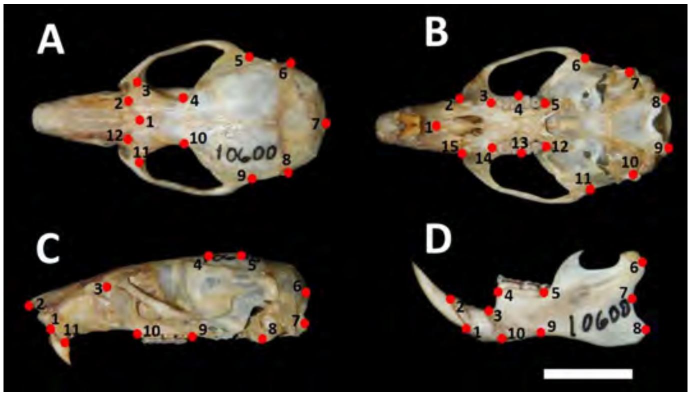

Figure 2. Position of the morphological landmarks selected in the different views of skulls from Andean populations of *Nephelomys* in Venezuela. A Dorsal view. B Ventral view. C Lateral view, and C Mandible. The reference scale is 10 mm.

groups in the morphospace, as well as their shape-related differences. These analyses were conducted using the IMP7 and MorphoJ programs. The groups formed based on the geographic distribution of specimens were used as *a-priori* groups for these analyses. The results from these analyses were estimates of Wilks' λ and Mahalanobis and Procrustes distances, with their statistical significance evaluated by permutations tests with $\alpha \leq 0.05$; the *a-priori* groups were reclassified as per the Discriminant Function Analysis (in percentages) and evaluated with a cross-validation test (*post hoc* classification, also in percentages).

The second matrix was used to document isometric size by the centroid size, using the Past program (Hammer and Happer 2011). Centroid sizes in the different views were compared using a non-parametric Kruskal-Wallis test with the Bonferroni correction ($P \leq 0.05$), as implemented in Past. Finally, MorphoJ (Klingenber 2011) was used to examine changes in shape in the different skull regions, by comparing the average shape superimposed on the groups.

Results

No significant correlation between centroid size and the shape variables was found in any of the skull views: dorsal ($F_{20, 1220} = 2.235$, $P < 0.002$, explained variation = 3.53 %); ventral ($F_{26, 1482} = 4.091$, $P < 0.002$, explained variation = 6.69 %); lateral ($F_{18, 1098} = 3.339$, $P < 0.006$, explained variation = 5.19 %); jaw ($F_{16, 960} = 3.154$, $P < 0.002$, explained variation = 3.53 %).

There were significant differences in the centroid size of some groups in the following views: Dorsal: *N. meridensis* - *N. meridensis* A, and *N. meridensis* A - *N. meridensis* B; Ventral: *N. meridensis* - *N. meridensis* A; *N. meridensis* - *N. meridensis* B; *N. meridensis* - *N. meridensis* C, and *N. meridensis* A - *N. meridensis* C; Jaw: *N. meridensis* A - *N. meridensis* B. These comparisons are detailed in in Table 1.

Figure 3 shows the separation of the groups in the morphospace, with the groups that are significantly different from each other in each view. In all views, the first two axes account for over 50% of the total variation: Dorsal view (variation = 73.01 %; Wilks' λ = 0.2542; $X^2 = 68.0873$; d. f. = 38; $P = 0.0002$); ventral (variation = 76.59 %; Wilks' λ = 0.1732; $X^2 = 76.2631$; d. f. = 52; $P = 0.015$); lateral (variation = 79.79 %; Wilks' λ = 0.2241; $X^2 = 77.0203$ d. f. = 36; $P = 0.0001$) and jaw (variation = 79.18 %; Wilks' λ = 0.2786; $X^2 = 65.8128$; d. f. = 32; $P = 0.0003$).

Table 1. Significant differences in the values of the centroid size estimator for Andean populations of *Nephelomys meridensis* in Venezuela. Descriptive statistics were tested with a probability value less than or equal to 0.05 ($P \leq 0.05$). = Arithmetic mean, σ = standard deviation. Values expressed in millimeters.

Views of the Skull	x̄	σ	*P*
Dorsal			
N. meridensis - *N. meridensis* A	31.95–30.33	2.23–1.37	0.032
N. meridensis A - *N. meridensis* B	30.33–32.18	1.37–2.87	0.019
Ventral			
N. meridensis - *N. meridensis* A	37.03–32.28	4.35–1.14	0.001
N. meridensis - *N. meridensis* B	37.03–33.52	4.35–1. 04	0.001
N. meridensis - *N. meridensis* C	37.03–33.71	4.35–1.04	0.005
N. meridensis A - *N. meridensis* C	32.28–33.71	1.14–1.04	0.037
Mandible lateral wiew			
N. meridensis A - *N. meridensis* B	18.99–19.84	1.26–1.27	0.049

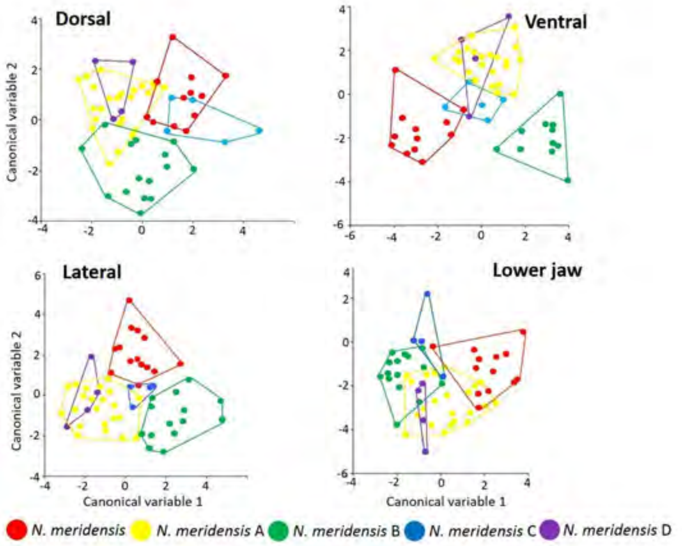

Figure 3. Factorial diagram of the Canonical Variable Analysis showing the spatial distribution and correlation between the different groups identified in the Andean populations of *Nephelomys meridensis* in Venezuela.

There were statistically significant differences in skull configuration between *N. meridensis* - *N. meridensis* A and *N. meridensis* A - *N. meridensis* B in all views (Table 2). The *post hoc* reclassification percentages of these groups were high, with *N. meridensis* A being better classified after the validation tests (Table 2). In addition, there were significant differences between *N. meridensis* and *N. meridensis* B in the ventral, lateral and jaw views; between *N. meridensis* A and *N. meridensis* C in the dorsal and lateral views; and between *N. meridensis* and *N. meridensis* C in the labial view of the jaw (Table 2). Figures 4 to 7 show the separation between these groups.

Regarding cranial morphology by view, the *N. meridensis* population from Mérida and adjacent areas differs from *N. meridensis* A by having a skull slightly longer in the posterior region (morphological landmarks 6 and 7; Figures 4C and 6C, respectively), with nasal bones slightly longer (landmark 2; Figure 6C). Maxillary toothrow slightly shorter (landmarks 9 and 10; Figure 6C); and palate wide between the incisive foramen (landmarks 2 and 15), narrow between the anterior base of the first molar (landmarks 3 and 14), the outer margin of the second molar (landmarks 4 and 13), and the posterior base of the last molar (landmarks 5 and 12; Figure 5C). Basicranium slightly wider at the posterior part of the zygomatic bones (landmarks 6 and 11) and the tympanic bullae (landmarks 7 and 10; Figure 5C). Jaw narrow and more extended, both on the anterior end (landmarks 1, 2 and 3), and by the coronoid and angular processes (landmarks 6 and 8; Figure 7C).

Nephelomys meridensis differs from *N. meridensis* B in that the skull is lower in the parietal-interparietal region

Table 2. Statistical comparison and subsequent differentiation between the different Andean populations of the genus *Nephelomys* (class 3) from Venezuela. Procrustes and Mahalanobis distances were tested with a value of $P \leq 0.05$. The subsequent reclassification was tested with a cross-validation test, also with a value of $P \leq 0.05$. The asterisk indicates statistically significant differences between groups.

Views of the Skull	Procrustes distances	Mahalanobis distances	Reclassification discriminant function	Reclassification cross validation
Dorsal				
N. meridensis - *N. meridensis* A*	0.02339096*	3.7598*	100 % – 100 %	64 % – 75 %
N. meridensis - *N. meridensis* B	0.02022337	5.7221	100 % – 100 %	41 % – 73 %
N. meridensis - *N. meridensis* C	0.02210766	5.0693	100 % – 100 %	83 % – 40 %
N. meridensis - *N. meridensis* D	0.01950156	1.8399	83 % – 100 %	33 % – 33 %
N. meridensis A - *N. meridensis* B*	0.01595765*	3.1648*	90 % – 94 %	79 % – 63 %
N. meridensis A - *N. meridensis* C*	0.01670396*	3.1271*	90 % – 87 %	78 % – 66 %
N. meridensis A - *N. meridensis* D	0.01166001	5.2342	100 % – 100 %	67 % – 0 %
N. meridensis B - *N. meridensis* C	0.02665050	7.1853	100 % – 100 %	60 % – 86 %
N. meridensis B - *N. meridensis* D	0.02479904	1.5076	80 % – 100 %	80 % – 33 %
Ventral				
N. meridensis - *N. meridensis* A*	0.02199053*	8.2665*	100 % – 100 %	58 % – 93 %
N. meridensis - *N. meridensis* B*	0.02218107*	11.8822*	100 % – 100 %	75 % – 83 %
N. meridensis - *N. meridensis* C	0.03218275	3.2676	91 % – 80 %	91 % – 60 %
N. meridensis - *N. meridensis* D	0.02115735	1.9478	83 % – 100 %	58 % – 33 %
N. meridensis A - *N. meridensis* B*	0.01669937*	5.7588*	100 % – 100 %	82 % – 67 %
N. meridensis A - *N. meridensis* C	0.02193730	4.5667	96 % – 100 %	62 % – 0 %
N. meridensis A - *N. meridensis* D	0.02081512	16.8012	100 % – 100 %	74 % – 33 %
N. meridensis B - *N. meridensis* C	0.02193730	4.5667	100 % – 91 %	20 % – 58 %
N. meridensis B - *N. meridensis* D	0.03506906	2.2241	100 % – 66 %	100 % – 66 %
Lateral				
N. meridensis - *N. meridensis* A*	0.02243218*	5.1764*	100 % – 100 %	86 % – 93 %
N. meridensis - *N. meridensis* B*	0.04068574*	4.6594*	100 % – 100 %	50 % – 72 %
N. meridensis - *N. meridensis* C	0.03906102	23.6338	100 % – 100 %	50 % – 80 %
N. meridensis - *N. meridensis* D	0.01788145	5.0564	100 % – 100 %	50 % – 0 %
N. meridensis - *N. meridensis* B*	0.03523493*	4.1682*	100 % – 100 %	82 % – 72 %
N. meridensis A - *N. meridensis* C*	0.03335329*	6.4908*	100 % – 100 %	85 % – 80 %
N. meridensis A - *N. meridensis* D	0.01985321	4.4808	100 % – 100 %	70 % – 33 %
N. meridensis B - *N. meridensis* C	0.01769165	31.2413	100 % – 100 %	60 % – 78 %
N. meridensis B - *N. meridensis* D	0.03622074	3.6542	100 % – 100 %	80 % – 33 %
Mandible lateral wiew				
N. meridensis - *N. meridensis* A*	0.02952130*	2.6267*	92 % – 85 %	58 % – 70 %
N. meridensis - *N. meridensis* B*	0.03814583*	4.7765*	100 % – 100 %	75 % – 73 %
N. meridensis - *N. meridensis* C*	0.03675974*	48.3824*	100 % – 100 %	58 % – 80 %
N. meridensis - *N. meridensis* D	0.03746015	11.8451	100 % – 100 %	83 % – 33 %
N. meridensis A - *N. meridensis* B*	0.02030497*	3.2410*	96 % – 93 %	85 % – 67 %
N. meridensis A - *N. meridensis* C	0.02402845	4.4597	100 % – 100 %	85 % – 40 %
N. meridensis A - *N. meridensis* D	0.02343556	2.3998	88 % – 75 %	70 % – 33 %
N. meridensis B - *N. meridensis* C	0.02817338	8.8376	100 % – 100 %	80 % – 66 %
N. meridensis B - *N. meridensis* C	0.03109383	2.5269	100 % – 75 %	80 % – 50 %

(landmarks 5, 6, 7 and 8) and has a longer nasal and premaxillae (landmarks 1, 2, and 11; Figure 6C). Maxillary toothrow (landmarks 9 and 10) slightly shorter (Figure 6C) and palate somewhat narrower between the first and second molars (landmarks 3, 14 and 4, 13; Figure 5C). Basicranium wide between the posterior bases of the zygomatic arches (landmarks 6 and 11) and narrow between the tympanic bullae (landmarks 7 and 10; Figure 5C). Jaw narrow and extended, both anteriorly (landmarks 2, 3 and 4) and in the posterior region by the coronoid and angular processes (landmarks 6 and 8; Figure 7C).

Nephelomys meridensis differs from *N. meridensis* C only in its jaw (Figure 7C), which is narrower in the posterior region of the diastema (landmarks 3 and 4) and has extended angular processes aligned with the coronoid processes (landmarks 6 and 8).

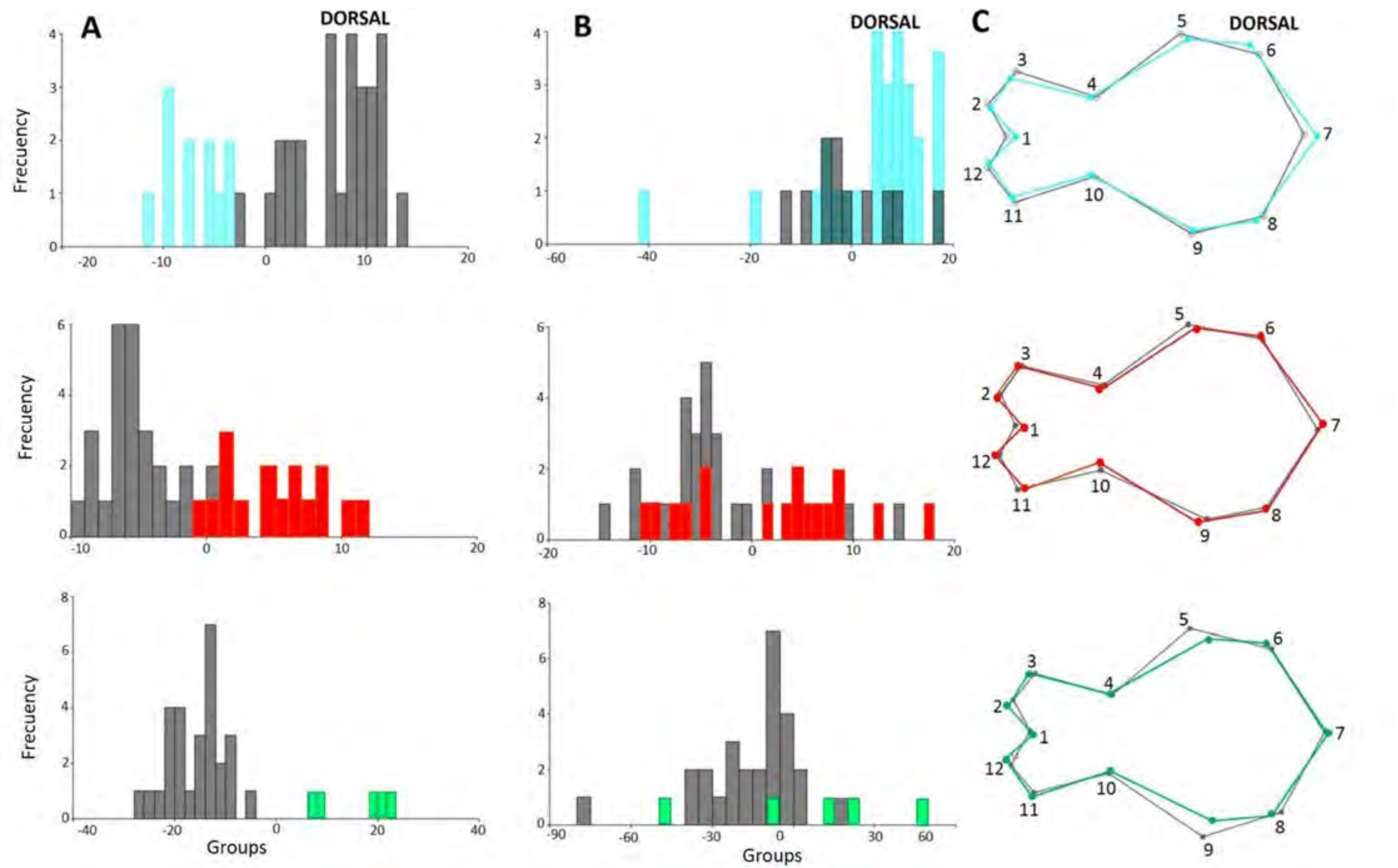

Figure 4. Visual representation of the skull differentiation (dorsal view) in Andean populations of the genus *Nephelomys* in Venezuela. A Histogram resulting from the Discriminant Function Analysis. B Histogram resulting from the cross-validation. C Between-group comparison of the average shape.

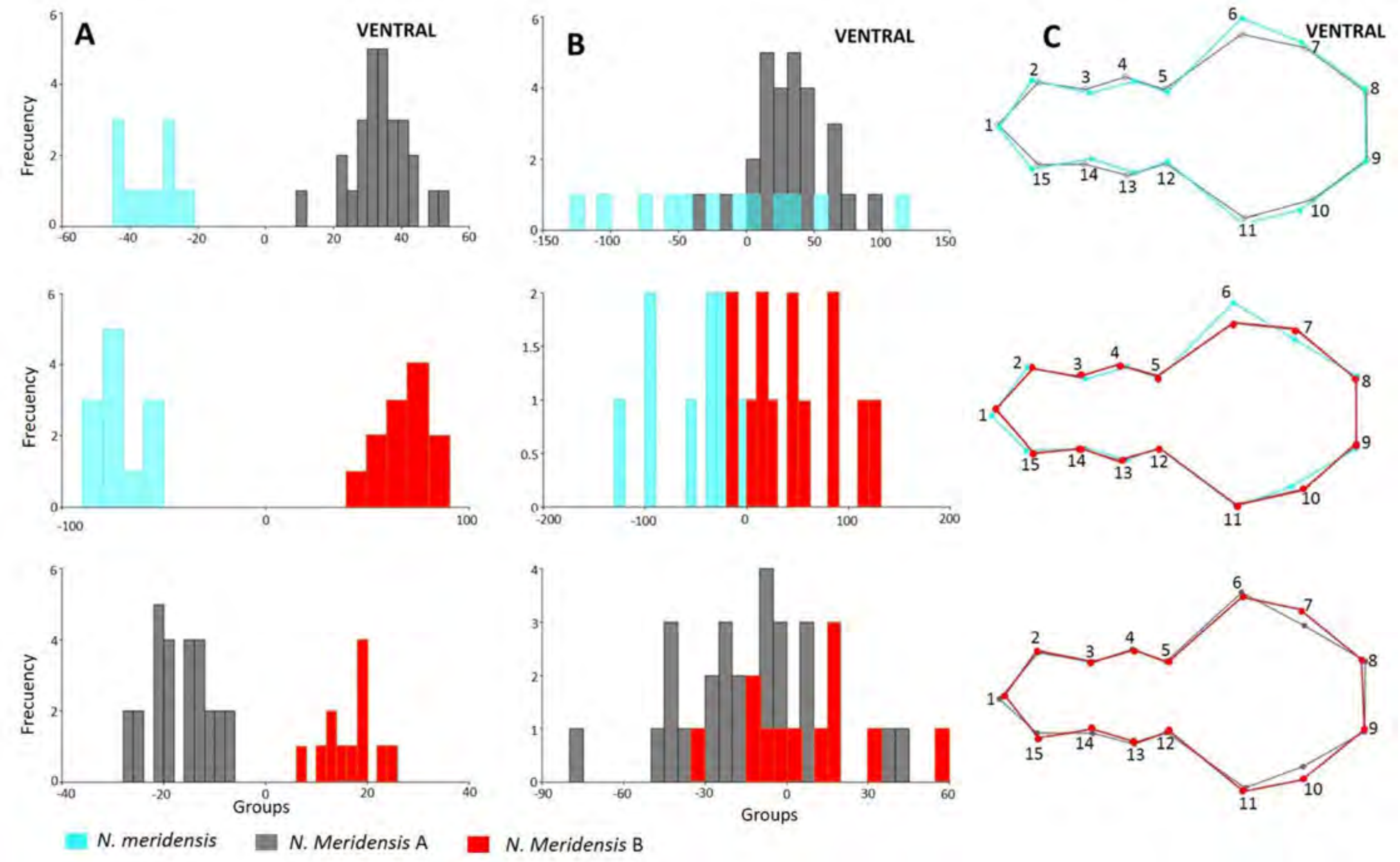

Figure 5. Visual representation of the skull differentiation (ventral view) in Andean populations of the genus *Nephelomys* in Venezuela. A Histogram resulting from the Discriminant Function Analysis. B Histogram resulting from the cross-validation. C Between-group comparison of the average shape.

The frontal bones of *Nephelomys meridensis* A are slightly wider (landmarks 1, 3 and 11) than those of *N. meridensis* B towards the anterior region (Figure 4C). Interorbital region (landmarks 4 and 10) slightly wider in *N. meridensis* A (Figure 4C). Posterior part of the skull in the interparietal region (landmarks 5, 6, 7 and 8) higher in *Nephelomys meridensis* B than in *N. meridensis* A (Figure 6C). Both groups share a maxillary toothrow (landmarks 9 and 10) of similar length (Figure 6C) and a similar morphology in the posterior part of the palate (between the incisive foramen and between the anterior base of the first molar and the posterior base of the last molar; landmarks 2, 3, 4, 5, 12, 13, 14 and 15, Figure 5C). Basicranium of *N. meridensis* A narrower between the bullae (landmarks 7 and 10; Figure 5C) and jaw similar in both groups in the anterior region (in the incisors alveoli), but a little higher at the toothrow base (landmarks 4 and 5) and narrow towards the posterior part, with the coronoid processes (landmark 6) more extended in *N. meridensis* A (Figure 7C).

Nephelomys meridensis A and *N. meridensis* C differed from each other in skull metrics; skull of *N. meridensis* A wider in the posterior part of the zygomatic arches (landmarks 5 and 9; Figure 4C), with longer nasal bones (landmark 2), and posterior part of the skull narrower (landmarks 5, 6, 7 and 8; Figure 6C).

Discussion

Our results show that specimens from the type locality of *Nephelomys meridensis* exhibit a cranial conformation different from that of other populations of the Venezuelan Andes (Yacambú National Park [Cordillera de Mérida, Lara State]), La Trampita [Cordillera de Mérida, Mérida State] and El Tamá massif, Táchira State, respectively). The population herein referred to as *N. meridensis* D (Dinira National Park) was not different, in any of the views, from the other groups compared, contrary to the results obtained by Rivas and Péfaur (1999a) using morphometrics based on linear distances.

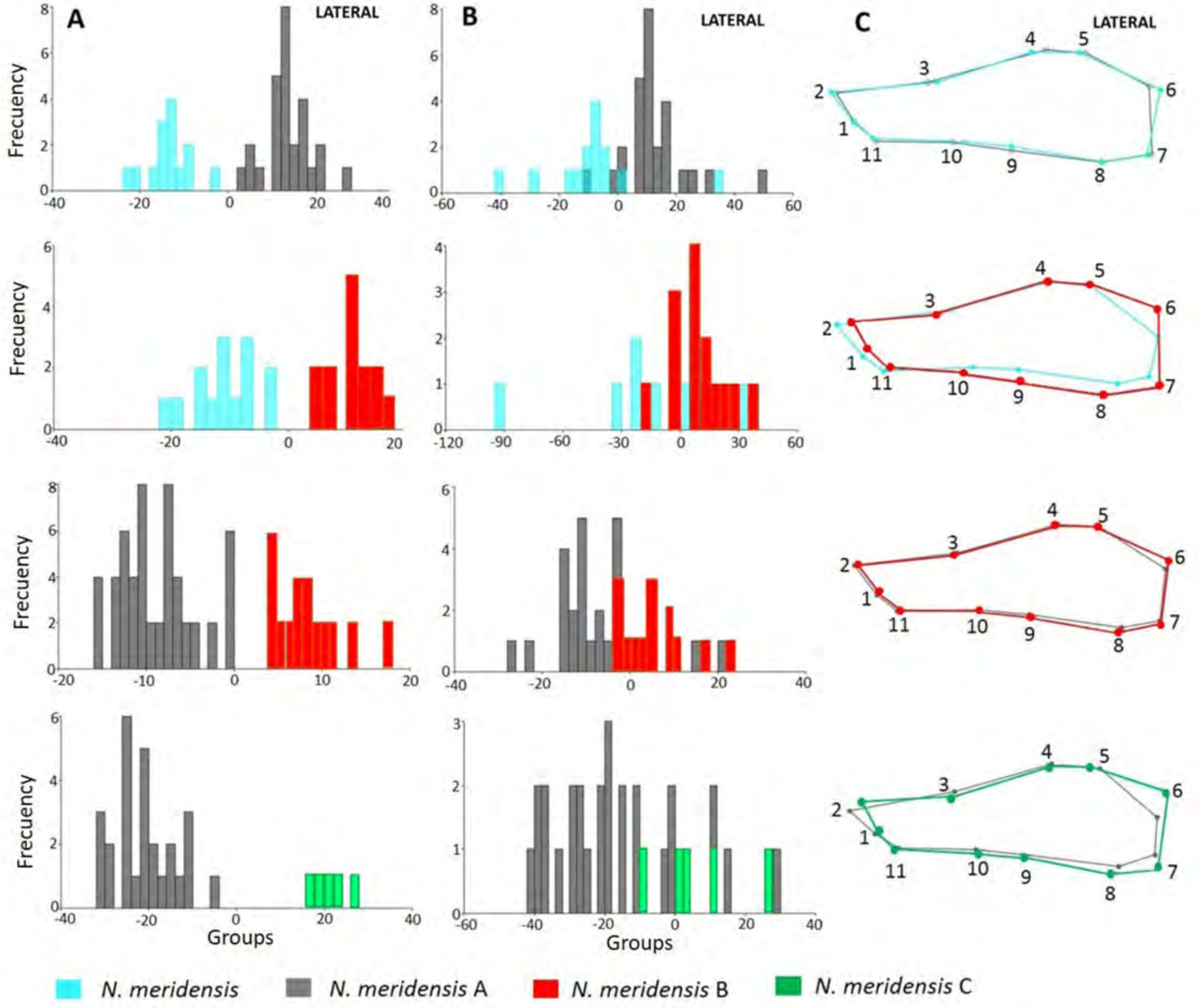

Figure 6. Visual representation of the skull differentiation (lateral view) in Andean populations of the genus *Nephelomys* in Venezuela. A Histogram resulting from the Discriminant Function Analysis. B Histogram resulting from the cross-validation. C.Between-group comparison of the average shape.

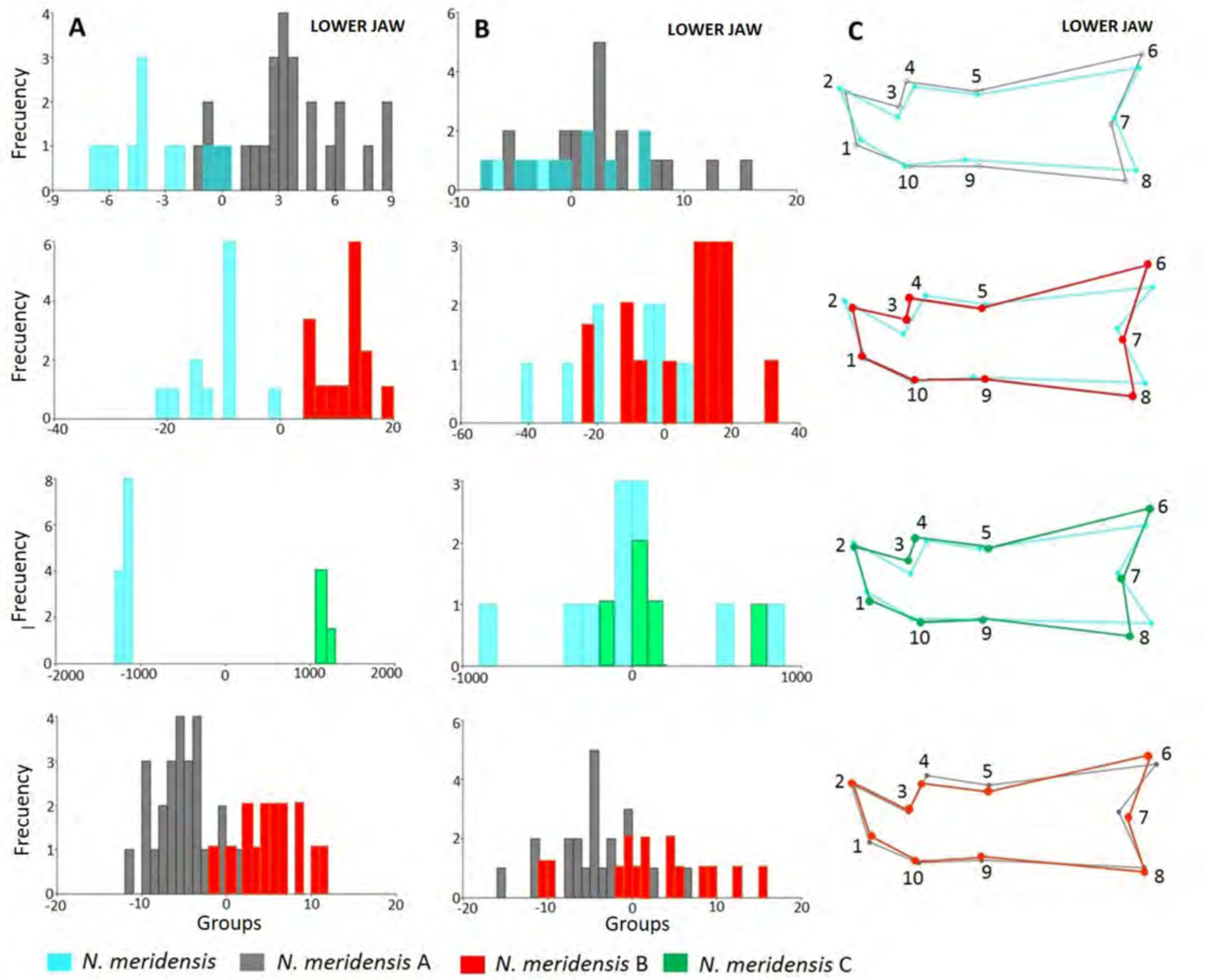

Figure 7. Visual representation of the skull differentiation (jaw view) in Andean populations of the genus *Nephelomys* in Venezuela. A. Histogram resulting from the Discriminant Function Analysis. B. Histogram resulting from the cross-validation. C. Between-group comparison of the average shape.

The clear separation and differentiation of the cranial model in most populations currently recognized as monotypic within *N. meridensis* provides further evidence supporting the hypothesis that this taxon should be treated as a species complex (Rivas and Péfaur 1999a; Soriano *et al.* 1999; Márquez *et al.* 2000). In its current delimitation, *N. meridensis* could include at least one species (karyotype 2n = 66, FN = 92, occurring in the La Trampita and El Tamá localities in Venezuela and Colombia; Aguilera *et al.* 1995; Márquez *et al.* 2000; Percequillo 2003, 2015) and two new subspecies (one from Yacambú National Park, with the same karyotype that the Mérida populations: 2n = 66, FN = 104; Aguilera *et al.* 1995; Rivas and Péfaur 1999a; Márquez *et al.* 2000 and another in the Tamá populations, as per the morphological differences described in this work).

Our morphogeometric data are consistent with morphometrics studies based on linear distances on skulls of *Nephelomys* rodents (Rivas and Péfaur 1999a; Percequillo 2003). Percequillo (2003) studied the systematics of the *Nephelomys albigularis* group and suggested that the El Tamá population should correspond taxonomically to the La Trampita population (although he did not examine specimens from the latter locality). Rivas and Péfaur (1999a) explored the geographic variation in skulls of specimens of the genus *Nephelomys* from Venezuela using multivariate analyses; their results supported the differentiation of the populations from Yacambú National Park and Mérida. Our results using geometric morphometrics demonstrate the validity of this tool for taxonomic studies and for the identification or detection of cryptic species (Cordeiro-Estrela *et al.* 2006, 2008; Astúa *et al.* 2015; Boroni *et al.* 2017).

From a biogeographic viewpoint, the Andes is considered a mega-diverse region that harbors a high species richness and a high level of endemisms of flora and fauna (Josse *et al.* 2009). The Venezuelan Andean system encompasses three mountain ranges: Sierra de Perijá, El Tamá massif (which are part of the eastern Andes of Colombia), and Cordillera de Mérida (Soriano *et al.* 1999). Cordillera de Mérida is the main mountain range of the Venezuelan Andean system; it is approximately 400 km long by 80 km wide and runs in a southwest-northeast direction starting at the Táchira depression and ending at the Barquisimeto depression (La Marca 1997). The Táchira depression separates Cordillera de Mérida from the Colombian Andes; its particular conditions of low elevation (< 1,000 m above sea level), high temperature, and arid (deciduous and xerophytic) vegetation likely function as ecological and geographic barriers that may foster isolation and speciation of some mammalian taxa (*e.g.*, shrews of the genus *Cryptotis*; Woodman 2002). However, it has been reported that the Táchira depression does not act as a natural barrier restraining gene flow in other mammals (Gutiérrez *et al.* 2015).

Cordillera de Mérida encompasses various mountain formations and branches, the most important being Sierra Nevada de Mérida, Sierra de La Culata, Cordillera de Trujillo, Guaramacal massif, Sierra de Barbacoas, and Sierra de Portuguesa (La Marca 1997). These branches are separated by valleys or depressions that may also act as natural barriers (as is the case of the Táchira depression), thus preventing the dispersal and promoting vicariant speciation of rodents of the genus *Nephelomys*. The recent description of the species *Aepeomys reigi* (Rodentia: Cricetidae), which had been previously included in *Aepeomys lugens* (Ochoa *et al.* 2001), and *Cryptotis dinirensis* (Eulipotyphla: Soricidae), previously included in *Cryptotis meridensis* (Quiroga-Carmona and Do Nascimiento 2016), are clear examples of evolutionary processes in small non-flying mammals that took place in Cordillera de Mérida.

Finally, our work highlights the need to gather complete wildlife inventories in biogeographically important zones of the Venezuelan Andes, such as Sierra de Perijá, where the presence of *N. maculiventer* was recently reported (García *et al.* 2019); the protected areas of the Venezuelan System of National Parks located in Cordillera de Mérida (*e.g.*, Dinira National Park, Guache, Páramo Batallón and la Negra, etc.); as well as other areas within the distribution range of the non-Andean species *N. caracolus* in Cordillera de la Costa and the Lara-Falcón hill systems in northern Venezuela. This would allow obtaining a more representative sample that could be used for comprehensive taxonomic reviews using a combination of (geometric and linear) morphometrics techniques, analyses of morphological characters, cytogenetics and DNA sequencing, as well as biogeographic and niche-modeling studies (Anderson and Raza 2010).

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Appendix 1

Specimens used in the geometric morphometrics analyses in this study

Nephelomys meridensis: Mérida and adjacent areas: Mérida, La Azulita (8° 41′ 05″N, -71° 25′ 33″O; 2,000 msnm), CVULA –I - 6350, 1074; Mérida, La Carbonera (San Eusebio) (8° 38′ 39″N, -71° 24′ 57″O; 2,500 msnm), CVULA – I - 1070, 1077; Mérida, Monte Zerpa (8° 38′ 16″N, -71° 09′ 47″ O; 2,000 – 2,200 msnm), CVULA – I - 1093, 1098, 1255, 1257, 1258, 2965, EBRG-28403, 28404; Mérida, Santa Rosa (8° 37′ 40″N, -71° 09′ 15″ O; 2,100 msnm), EBRG - 14885; Mérida, El Baho (8° 50′ 17″N, -70° 43′ 34″O; 3,010 msnm), CVULA – I - 6178. *Nephelomys meridensis* A: Parque Nacional Yacambú, El Blanquito (9° 38′ 30″N, -69° 30′ 47″O; 1,500 msnm), 17 Km de Sanare, Estado Lara: EBRG - 10297, 10298, 10300, 10594, 10595, 10599, 10600, 10601, 10603, 10605, 10606, 10607, 10608, 10609, 10619, 10620, 10956, 10986, 21464, 21465, 21466, 21468, 21469, 21470, 21471, 21474, 21480, 28398. *Nephelomys meridensis* B: La Trampita, campamento Siberia, 12 Km SSE de Pregonero, Uribante, Estado Táchira (7° 35′ 30″N, -72° 04′ 36″O; 1,000 – 1,300 msnm), CVULA – I - 2317, 1528, 1963, 2190, 2307, 2316, 2318, 2471, 3539, 7043, MHNLS - 8749, 8750, 8751, 8753, 8764. *Nephelomys meridensis* C: Páramo El Tamá, Macizo El Tamá, Estado Táchira: 35 Km S, 22 Km O de San Cristobal, Buena Vista (7° 27′ 43″N, -72° 22′ 07″O; 2,460 msnm), EBRG – 14893. Páramo El Tamá (7° 27′ 24″N, -72° 22′ 05″O; 2,400 msnm), MHNLS - 4650, 4652, 4657, 4923. *Nephelomys meridensis* D: Parque Nacional Dinira, carretera La Peña-Carache, sector Las Torres, municipio Las Palmas (9° 41′ 50″N, -70° 04′ 26″O; 2,553 msnm), EBRG - 24669, 24670; Parque Nacional Dinira, sector Buenos Aires (9° 36′ 27″N, -70° 04′ 06″O; 1,900 msnm), EBRG - 24416.

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Using MaxEnt modeling to predict the potential distribution of *Platyrrhinus ismaeli* (Phyllostomidae)

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The broad-nosed bat, *Platyrrhinus ismaeli*, is listed as Near Threatened (NT) by the International Union for the Conservation of Nature, and due to the low number of collected specimens, its geographic distribution is poorly known. This study presents the first documented record of this species in the eastern slope of the Colombian Central range. Herein, museum voucher specimens were used as primary sources for the elaboration of a checklist of *Platyrrhinus ismaeli* from Colombia. In addition, the checklist is supplemented with information on life zones and a potential distribution model for Colombia. This distribution map was used to explore the affinities, in species composition, among Colombian ecoregions as outlined by, and the relationship between associated environmental variables. In total, 15 field-based occurrence points and 20 environmental variables (19 bioclimatic and one topographic) were used to model the potential distribution area. The response curves showed that this species prefers habitats with an annual temperature of 12.0 to 25.5 °C, annual precipitation of 1,000 to 4,000 mm, and an elevation range of 1,200 to 2,850 masl. Most of the current potential suitable conditions were located to the north-center of Colombia. We found that *P. ismaeli* is distributed in Colombia in four main regions, including the Biogeographic Chocó, the Magdalena Valley, the Orinoquia, and the Guianan-Amazon region. The spatial distribution of the species is driven by variables such as temperature, precipitation, and elevation. Changes in these variables affect the normal activities of this species with a narrow geographical niche and dispersal ability may particularly reduce the ability of this species to face global climate change consequences. Therefore, it is imperative to continue exploring the effect of these variables in order to better define the distribution patterns and conservation strategies for this species. Our findings can be used to define high-priority areas for the protection and conservation of *P. ismaeli*.

El murciélago de nariz ancha *Platyrrhinus ismaeli*, está catalogado como Casi Amenazado (NT) por la Unión Internacional para la Conservación de la Naturaleza y, debido a la escasa cantidad de recolectas, su distribución geográfica es poco conocida. Este estudio presenta el primer registro en la vertiente Oriental de los Andes centrales colombianos. Aquí, se utilizaron ejemplares de museo como fuente primaria para generar una lista de verificación de *Platyrrhinus ismaeli* para Colombia. Además, la lista de verificación está acompañada por las zonas de vida, así como el modelo de distribución potencial para Colombia. Este mapa de distribución se utilizó para investigar las afinidades, en la composición de las especies, entre las ecorregiones colombianas como se describe en, y la relación entre las variables ambientales. En total, se utilizaron 15 puntos de ocurrencia y 20 variables ambientales (19 bioclimáticas y una topográfica) para modelar el área de distribución potencial. Las curvas de respuesta mostraron que esta especie prefiere hábitats con una temperatura anual de 12.0 a 25.5 ° C, precipitación anual de 1,000 a 4,000 mm y un rango de elevación de 1,200 a 2,850 m.s.n.m. La mayoría de las posibles condiciones adecuadas actuales se ubicaron en los límites del Centro Norte de Colombia. Descubrimos que *P. ismaeli* se distribuye geográficamente en Colombia en cuatro regiones principales, incluyendo: el Chocó Biogeográfico, el valle del Magdalena, la Orinoquia, y la región de la Guiana-Amazonía. La distribución espacial de la especie depende de variables como la temperatura, la precipitación y la elevación. Estos cambios en estas variables afectan las actividades normales de esta especie con un nicho geográfico estrecho y la capacidad de dispersión puede reducir particularmente la capacidad de esta especie para enfrentar las consecuencias del cambio climático global. Por lo tanto, es importante continuar estudiando el efecto de estas variables para ajustar los patrones de distribución y estrategias de conservación de esta especie. Nuestros hallazgos se pueden usar para definir las áreas de alta prioridad para la protección y conservación de *P. ismaeli*.

Key words: Chiroptera; department of Tolima; distribution; expansion; geographic range; Phyllostomidae.

Introduction

In the Neotropics, bats represent the most diverse group amongst mammals (Vaughan 1997; Medellin *et al.* 2000; Sampaio *et al.* 2003; Bracamonte 2011), showing the greatest variety of dietary habits; this flexibility accounts for the morphological, physiological, and ecological complexity of this group (Altringham 2011). Bats of the genus *Platyrrhinus* (Phyllostomidae) are frugivores that play a key role in seed dispersal and the redistribution of nutrients (Medellin 2003; Velazco and Gardner 2009; Estrada-Villegas *et al.* 2010).

In recent decades, a number of studies have confirmed the role of this genus in forest succession and ecological restoration, because they consume pioneer species and are among the most important seed dispersers in fragmented and early successional ecosystems (Galindo-González *et al.* 2000; Marques and Fisher 2009; Castro-Luna and Galindo-González 2012; García-Herrera *et al.* 2019). Therefore, the species of this genus have the potential to provide functional services to the environment because they disperse large amounts of seeds in Neotropical forests.

The genus *Platyrrhinus* includes 20 recognized species, representing one of the most diverse genera within the family Phyllostomidae (Velazco and Patterson 2008; Velazco and Lim 2014; Velazco *et al.* 2018), only surpassed by the genera *Sturnira* with 24 species (Velazco and Patterson 2019) and *Artibeus* with 23 species grouped into two subgenera (*Artibeus* and *Dermanura*;Cirranello *et al.* 2016; Velazco and Patterson 2019). In Colombia, *Platyrrhinus* is represented by 14 species (Ramírez-Chaves *et al.* 2016), with geographic and altitudinal ranges that vary widely (Velazco and Solari 2003; Gardner 2008; Velazco and Gardner 2009). As part of the most recent IUCN (International Union for Conservation of Nature) Global Mammal Assessment, three species of *Platyrrhinus* are listed as Threatened (*Platyrrhinus chocoensis*, VU, *P. ismaeli* and *P. matapalensis*, NT).

Platyrrhinus ismaeli lives mainly in lowland and montane forests (Tirira 2011). The high rate of habitat destruction throughout the tropical Andes may soon cause *P. ismaeli* to be assigned to the Near Threatened (NT) category (IUCN 2019), thus highlighting the importance of generating in-depth information on the geographic distribution and status of their populations, which is needed to advance conservation actions.

In Colombia, *P. ismaeli* has been recorded in 26 localities along the Andes (Velazco and Gardner 2009); these include eigth localities in the western range (Departments of Risaralda and Valle del Cauca), nine in the central range (Departments of Antioquia, Cauca, Huila, Putumayo, and Quindío), and nine in the eastern range (Departments of Boyacá, Caquetá, Cundinamarca, Norte de Santander and Meta). Records in Colombian collections support that *P. ismaeli* inhabits a wide variety of habitats within an altitudinal gradient of 1,230 to 2,950 m (Muñoz 2001; Solari et al. 2013). Although this species seemingly prefers high-montane forests (Table 1), there are some records of *P. ismaeli* in the foothills of the western range, in the eastern side of the Department of Chocó, suggesting that it also inhabits the premontane very humid forest (Asprilla-Aguilar *et al.* 2016).

The distribution range reported for this species comprises the eastern slope of the central range (Departments of Nariño and Tolima), the eastern range (Departments of Santander and Casanare), and the low montane forest and low montane wet forest of Colombia (according to Holdridge [1987] system, Table 1), which are highly fragile and threatened ecosystems for impacts related to human activities. Accordingly, we analyzed the potential distribution of *P. ismaeli*, provide cranial measurements and information on the life zones for the new localities (Tables 1, 2, Figure 1, 2, Appendix 1), and discuss the scenarios that might determine the distribution of this species in Colombia. Our objectives were: to predict the current potential distribution, and to identify the key environmental factors that are highly correlated with the distribution range of *P. ismaeli*. This information sets the basis for generating data for the conservation of this species, needed to face the current habitat loss and fragmentation issues, and other impacts to the life zones of populations of this species in Colombia.

Materials and Methods

The main sources used for this update included research articles, taxonomic revisions, and direct examination of the zoological collections of the University of Tolima (CZUT-M, Ibagué), Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH-M, Villa de Leyva), Instituto de Ciencias Naturales at Universidad Nacional de Colombia (ICN, Bogotá), and Universidad del Valle (UV, Cali). Secondary sources include records available in the online databases of the National Museum of Natural History, Smithsonian Institution (NMNH; VertNet), and cataloged specimens reported in regional checklists (for example, Asprilla-Aguilar *et al.* 2016; Jimenez-Ortega 2013). For specimens to which we had direct access, we took external and cranial measurements with digital calipers to the nearest 0.1 mm (Table 2). Data on total length (TL) and weight (W) were obtained from specimen labels, recorded at the time of collection.

We reviewed all available specimens housed at the CZUT-M, searching for vouchers of *P. ismaeli*. Based on our review, and because they were suspected of being misidentified, we also included four specimens formerly identified as *Vampyrops aurarius* (Bejarano-Bonilla *et al.* 2007), plus another identified as *P. aurarius* by Galindo-Espinosa *et al.* (2010), and five *Chiroderma salvini* (identified by Galindo-Espinosa *et al.* 2010). To assess the accuracy of their identifications, we compared each specimen with the characters provided by Velazco (2005) and Velazco and Gardner (2009), and described the morphological characters, external, and cranial and dental measures of *P. ismaeli* distributed in Colombia.

Data sources and selection of variables. In order to elaborate the checklist, we reviewed and gathered occurrence data from *P. ismaeli* records in museum collections in Colombia (CZUT-M, ICN, IAvH-M, UV, and NMNH. Including: coordinates, elevation, locality, geographic region, and life zone according to the classification of Holdridge 1987; Table 1), confirmed by reviewing the morphology and taxonomic identification of specimens (Velazco 2005; Velazco and Gardner 2009), as well as from records reported in the scientific literature. Occurrence localities from specimen tag data were then thoroughly georeferenced (*i. e.*, for those lacking field GPS readings; Sánchez-Cordero and Guevara 2016). To reduce issues associated with spatial sampling biases (Merow *et al.* 2013; Boria *et al.* 2014), we spatially thinned our original dataset consisting of 38 localities using the spThin package in R (Aiello-Lammens *et al.* 2015).

Nineteen variables were retrieved as predictors to model the potential environmental niche of *P. ismaeli* based on the current presence dataset in 15 different localities (Velazco and Gardner 2009; Table 1), plus other available records. In particular, 19 bioclimatic layers (Table 3) and one topographic variable (elevation) were obtained from the WorldClim version 2 database (WorldClim: Global Climate Data 2017; Hijmans *et al.* 2005) at a spatial resolution of 30 arc-second (*ca.* 1 × 1 km). Elevation, slope, and aspect data were extracted using ArcGIS 10.4.1. The overall environmental variables are summarized in Table 3. In order to eliminate multicollinearity and select the most fitting predictors that show more contribution power to the model, Variance Inflation Factors (VIFs) of 22 environmental

Table 1. Records of *Platyrrhinus ismaeli* in Colombia used for modeling the potential distribution of the species. Life zones: A) low montane humid forest, B) low montane very humid forest, and C) premontane very humid forest. Regions: Central Range (CR), Eastern Range (ER), and Western Range (WR); Vereda (Ver); Life zone (LZ).

Voucher	Latitude	Longitude	Elev.	Municipality	Department	Region	LZ
ICN 16503	5.5882	-75.9294	2,010	Andes,Ver. La Soledad	Antioquia	CR	A
ICN 17165	6.1654	-74.3173	1,860	Santa María, Ver. Caño Negro	Boyacá	ER	C
ICN 15066	4.9667	-73.3440	1,269	Santa María, Margen izquierda río Batá	Boyacá	ER	C
ICN 16352	4.9443	-73.3252	1,259	Santa María, Sitio Represa Chivor.	Boyacá	ER	C
ICN 5441	5.3066	-72.7138	1,970	Pajarito, Hacienda Camijoque.	Boyacá	ER	C
ICN 19320	5.4166	-71.2750	1,085	Trinidad, Banco de la Cañada	Casanare	ER	C
MHNUC 1467, 1501; USNM 483575	2.4010	-76.1306	2,638	Moscopas, 1 Mi N Moscopas	Cauca	CR	A
ICN 8467, 8468	2.5518	-76.0912	2,253	Inza, Ver. Tierras Blancas, Km. 78 carril Popayan	Cauca	CR	A
CMCH 1136	5.8982	-76.1487	2,950	El Carmen de Atrato	Chocó	WR	A
ICN 5293, 5295	4.6830	-74.3894	1,870	Tena, Laguna de Pedro Pablo	Cundinamarca	ER	C
FMNH 58732, 58733, 58734, 58735, 58736, 58737, 58738.	2.0178	-75.7459	1,100	Parque Natural Nacional "Cueva de los Guacharos"	Huila	CR	C
IAvH-M 1930, 1932, 1934, 1990,1992, 1994, 1996.	1.6000	-76.1301	2,800	Parque Natural Nacional "Cueva de los Guacharos". Puente superior en Río Suaza	Huila	CR	A
ICN 13087	11.1430	-73.8282	1,050	Sierra Nevada de Santa Marta, Alto de Mira, 3 Km W Río Buritaca.	Magdalena		C
ICN 14372	4.2749	-73.5874	1,090	Restrepo, Salinas de Upin	Meta	ER	C
ICN 14800	3.8262	-73.8435	1,000	Cubarral, Ver. Aguas Claras	Meta	ER	C
Jiménez Ortega	1.6812	-78.1417	1,004	Barbacoas	Nariño	WR	C
IAvH-M 6681, 6682	7.2584	-72.2259	1,608	Toledo, Ver. San Isidro	Norte de Santander	ER	C
ICN 21022	1.1336	-76.6328	2,000	Mocoa, El Mirador	Putumayo	CR	A
IAvH-M 6818, 6823	1.0715	-76.7353	1,922	Mocoa, El Mirador	Putumayo	CR	C
ICN 12476	4.6706	-75.6179	1,975	Finlandia, Ver. El Roble	Quindío	CR	C
ICN 12448	4.6834	-75.5244	2,634	Salento, Reserva Natural Cañon Quindio, frente de reforestación Monte Loro	Quindío	CR	A
UV 12694	4.7299	-75.5766	2,250	Quimbaya, Ver. La Suiza	Risaralda	ER	A
ICN 8150, 8972, 8973	6.0967	-73.2036	1,790	Charalá, Margen derecho del Río Guillermo	Santander	ER	C
ICN 17585, 17586, 17587	6.4535	-72.8266	2,013	Encino, Vereda Río Negro, Las Tapias, finca El Aserradero.	Santander	ER	A
ICN 16660, 16661	7.1333	-72.9941	2,150	Tona, Ver. Guarumales, finca El Pajal.	Santander	ER	A
ICN 12448	7.1334	-72.9832	1,800	Tona, Sitio El Mortiño, carretera Bucaramanga-Cúcuta Km 18.	Santander	ER	C
CZUT-M 58.	4.4258	-75.3697	1,557	Cajamarca, Ver. Peñaranda parte Baja	Tolima	CR	C
CZUT-M 83, 84, 144, 145.	4.4830	-75.4532	2,055	Cajamarca, Ver. Planadas	Tolima	CR	A
CZUT-M 208, 317.	4.3865	-75.3417	2,084	Cajamarca, Ver. El salitre	Tolima	CR	A
CZUT-M 57.	4.5440	-75.4204	2,398	Ibagué, Ver. Toche	Tolima	CR	B
CZUT-M 206, 207	4.5000	-75.3000	1,777	Ibagué, Quebrada La Plata	Tolima	CR	C
UV 12402, 12403, 12405, 12407, 13022, 13023.	3.8920	-76.2800	1,124	Buga, Ver. El Janeiro	Valle del Cauca	WR	C

variables were tested. VIFs are based on correlation coefficients (R^2) estimated from regressions for all predictors, implemented through the 'sdm' package in R (version 3.1.1). As a result, 14 variables with VIFs > 5 were excluded (Chatterjee and Hadi 2006) and only eight variables were kept to establish the distribution model of *P. ismaeli* under the current conditions (Table 4).

MaxEnt model. In our study, the model was run using the MaxEnt algorithm (version 3.4.1 k; Guisan and Thuiller 2005; Jarvis *et al.* 2005; Phillips *et al.* 2006) with default settings. We analyzed the presence of the species in the different geographic regions, and the distribution along the Colombian Andes (Table 2) as proposed by Morrone (2014). We employed 10 replicates and the average of probability maps for habitat suitability (Hoveka *et al.* 2016). The training and test data points were 80 % and 20 %, respectively. The relative importance of each environmental predictor for the models of *P. ismaeli* was assessed using the percent contribution of the Jackknife test (Phillips *et al.* 2006), which is the best index for small sample sizes (Pearson *et al.* 2007).

To determine the accuracy of the resulting models, we computed the Area Under the Curve (AUC) of the Receiver Operating characteristic Curve (ROC). AUC is the dominant tool to measure model performance, mainly due to its independence from threshold choices (Bosso *et al.* 2013; Fois *et al.* 2018; Yi *et al.* 2016). Higher AUC values (closer to 1) indicate better model performance (Fielding and Bell 1997; Phillips *et al.* 2006). The AUC graph was obtained by plotting true positive predictions (sensitivity) versus false positive predictions (1-specificity; Fielding and Bell 1997).

In addition, the minimum difference between training and testing AUC data (AUC_{Diff}) was also considered; a smaller difference indicates lesser overfitting in the model (Fois *et al.* 2018; Warren and Seifert 2011).

The logistic output of MaxEnt application is a map, indexing the environmental suitability of *P. ismaeli* with values ranging from 0 (unsuitable) to 1 (optimal). For further analysis, the MaxEnt results were imported into ArcGIS 10.4.1, and four classes of potential habitats were grouped as follows: unsuitable (≤ 0.10), low potential (0.11–0.30), moderate potential (0.31 – 0.70), and high potential (≥ 0.71; Yang *et al.* 2013; Choudhury *et al.* 2016; Qin *et al.* 2017).

Results

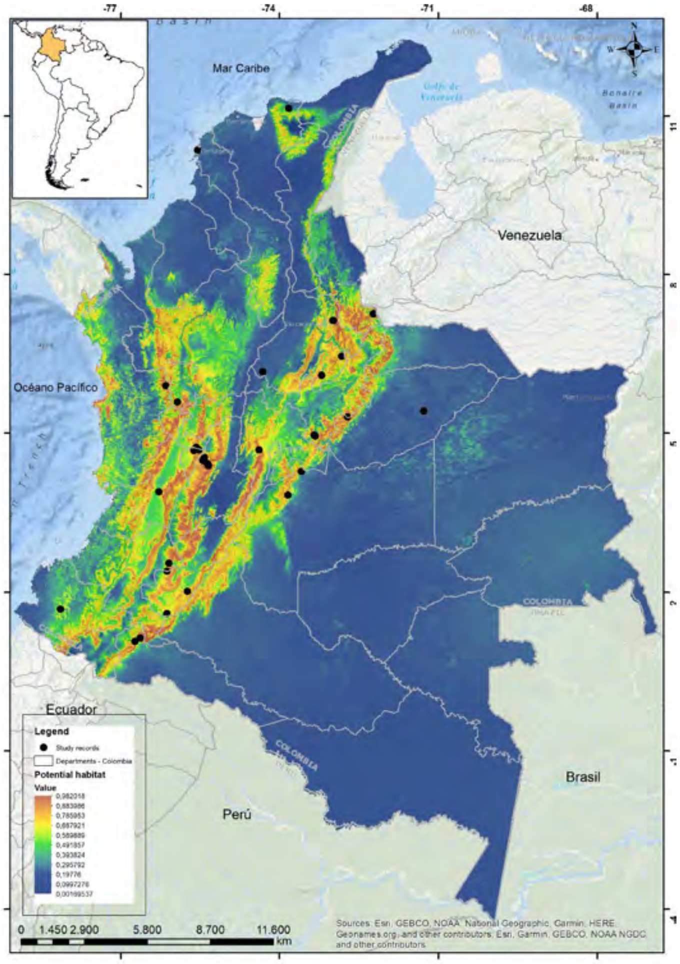
The re-examination of the 10 specimens reported by Bejarano-Bonilla *et al.* (2007; CZUT-M 206 to 208, 0317) and Galindo-Espinosa *et al.* (2010; CZUT-M 57, 58, 83, 84, 144, 145), as *P. aurarius* or *Ch. salvini*, revealed the presence of *P. ismaeli* on the foothills of the eastern slope of the central Andes of Colombia, reported herein for the first time. These records expand the known distribution of *P. ismaeli* to approximately 328 km southeast of the nearest known locality in the Department of Huila, in the Parque Nacional Nevado del Huila, "Cueva de los Guacharos" on the Acevedo trail (FMNH 58732, 58736, 58733 to 58735, 58737, 58738, Figure 1).

These new localities correspond to low montane forest and low montane wet forest, located in the Andean mountains, bordered by the dry tropical valleys of the Magdalena River. These landscapes are characterized by slopes with trees measuring approximately 12 m high and vegetation that includes plant species such as *Pseudobomba septenatum*, *Calophyllum lucidum*, *Maclura tinctoria*, *Poulsenia armata*, and *Virola sebifera*. These life zones are located primarily in areas subjected to intense agricultural and urban development, where the original forest has been cleared and replaced by plantations of coffee, fruit trees, vegetables, and other monocultures.

The diagnostic characters of the *P. ismaeli* specimens collected match the original description of the species (Velazco 2005; Diaz *et al.* 2016). The key features to recognize our specimens were: dorsal and ventral hairs with three bands; dense long hairs on the edge of the uropatagium; a medium forearm, less than 55 mm; upper central incisors with one or two cusps, but not cylindrical; presence of nasals; lingual cingulum not continuous from paracone to metacone (sulcus not continuous between paracone and metacone) of M1 (Figure 2); and cranial measurements (Table 2).

Potential habitat suitability of P. ismaeli over current conditions. Our models showed high levels of predictive performances with values of AUC (training, 0.974 ± 0.001; test, 0.957 ± 0.009) and AUC_{Diff} (0.010 ± 0.007) indicating a good performance with low levels of errors and correctly identifying all the localities where the species has been reported (Figure 1). The results of the contribution of variables using the Jackknife test in distribution modeling of *P. ismaeli* are showed in Table 2. Environmental predictors that exhibited the highest mean contributions are annual precipitation (Bio12), annual mean temperature (Bio1), and elevation (Elev). At the same time, Bio1, Bio12, Bio9, Elev, and Bio5 provided high gains (> 2) to the model when used individually, indicating that each of these variables separately contribute the most useful information than the rest of variables. Considering the permutation importance, Bio1, Bio12, and Elev were the main environmental variables that have influenced the potential distribution of *P. ismaeli* (Table 2). The model predicts a continuous distribution range in the Colombian Andean region, spreading across the three cordilleras, *i. e.*, western, central, and eastern, from the south in Nudo de los Pastos up to the Catatumbo subregion in the Department of Norte de Santander, including the Choco-Magdalena, Orinoquia, and North-Andean biogeographic provinces.

Figure 1. Map for potential current habitat suitability for *Platyrrhinus ismaeli* in Colombia from records in the various Colombian collections. Habitat suitability classes include: unsuitable, low potential, moderate potential, and high potential.



The response curves of eight variables related to *P. ismaeli* habitat suitability are shown in Figure 3. While considering temperature probabilities, the mean annual temperature range (Bio1) of *P. ismaeli* was 12.0 to 25.5 °C, whereas the mean diurnal temperature (Bio2) ranged from 16.5 to 20.15 °C. In addition, the range of isothermality (Bio3) varied from 43.1 to 46.3, whereas the mean temperature of the driest quarter (Bio9) varied from 28.0 to 32.0 °C. On

Table 2. Selection of external and cranial measurements of *P. ismaeli* specimens collected in the central Andes eastern slope, Colombia. The measurements of the holotype and paratype of *P. ismaeli* were taken from Velazco (2005).

Characteristics	This study CZUT-M 0058,0084		Holotype MUSM 4946	Paratypes FMNH 129134, 129136	
Sex	Male	Female	Male	Female	Male
Weight	32.00	39.00	35.00	40.00	38.00
Total length	88.32	80.40	84.00	82.00	87.00
Hind foot length	17.89	13.35	18.00	13.00	18.00
Ear length	22.75	21.03	10.00	21.00	22.00
Forearm length	52.65	53.25	52.00	53.00	54.00
Tibia length	21.35	19.75	21.68	19.52	21.68
Greatest length of skull	28.20	27.08	27.94	27.77	28.15
Condyloincisive length	27.30	26.59	27.10	26.57	27.47
Condylocanine length	26.92	26.07	26.22	26.07	26.88
Postorbital breadth	6.40	6.15	6.54	6.27	6.57
Zygomatic breadth	17.90	16.8	17.13	16.93	18.21
Braincase breadth	12.18	11.5	12.00	11.57	12.29
Mastoid breadth	13.69	12.5	13.99	13.63	14.72
Maxillaty tooth row length	11.78	11.05	11.35	11.43	11.66
Breadth across maxilla	20.71	20.56	12.63	12.65	23.81
Palatal length	15.94	14.9	–	–	–
Molariform teeth row length	12.04	11.14	–	–	–
Width across first upper molars	13.67	21.67	–	–	–
Width across second upper molars	13.89	21.97	–	–	–
Dentary length	24.60	28.00	–	–	–
Length of mandible toothrow	15.70	21.56	–	–	–
Coranoid height	7.07	14.96	–	–	–
Width at mandible condyles	8.36	15.59	–	–	–
Breadth across molars	15.42	22.83	–	–	–

the other hand, the range of annual precipitation (Bio12) was 1,000 to 4,000 mm per year while the suitable habitat occurs under a precipitation seasonality of 1,400 to 4,000, with a peak at 1,658 mm.

Furthermore, there is a positive relationship between habitat suitability for *P. ismaeli* and precipitation of the driest month. The elevation range suitable for *P. ismaeli* was 1,200 to 2,850 masl, with an optimal elevation at around 2,500 masl. Indeed, the conditions of highest suitability for *P. ismaeli* were an annual temperature of 21 °C, annual precipitation of 4,000 mm, and an elevation of 2,500 masl. By contrast, areas with an elevation above 3,000 masl or below 1,200 masl, and with an annual temperature above 30 °C were the least suitable for *P. ismaeli*.

The potential distribution map of *P. ismaeli* in Colombia is shown in Figure 3. Out of the total area of 1,141,748 km^2, some 5,103 km^2 were potentially suitable for *P. ismaeli*. This area was divided into 1,793 km^2 with a low potential, 1,758 km^2 with a moderate potential, and only 1,551 km^2 with a high probability of suitable ecological conditions. The majority of suitable habitats (≥ 0.71) were located in areas located in the mid-north of Colombia.

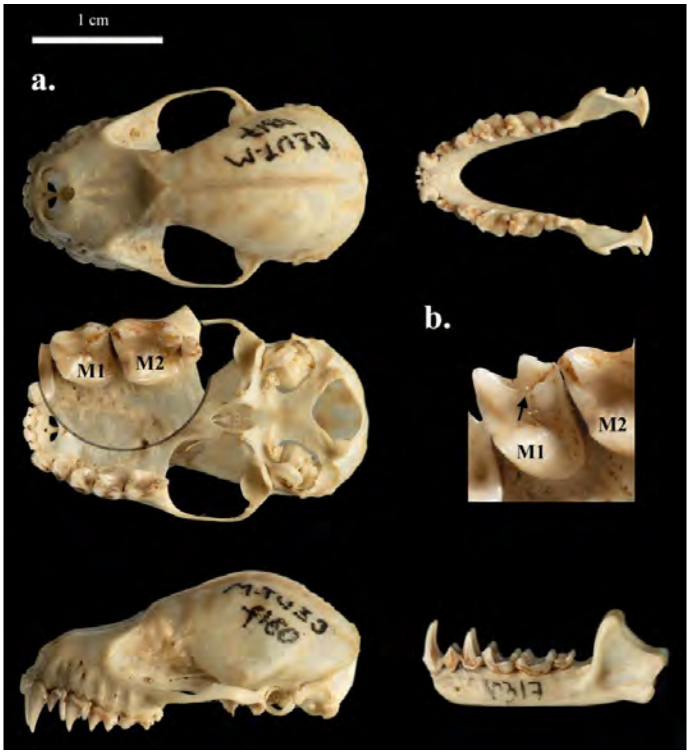
Discussion

Our results update and show a wider distribution range of *P. ismaeli* in Colombia (Table 1). This work is the first record of this species in the eastern slope of central range of Colombia. The existing records of the species correspond to the life zones low montane forest, low montane wet forest and premontane very humid forest. These life zones in Colombia are subjected to an increasing destruction and degradation of habitats, primarily due to agriculture, forestry, illegal crops, and mining, which altogether have resulted in a decline of more than 30 % of the populations of *P. ismaeli* (Ramírez-Chaves and Suárez-Castro 2014; Solari 2016); thus, the species is currently listed as Near Threatened (NT).

The records reported here also represent an extension of the ecological range of *P. ismaeli*. The life zone represented by low montane very humid forest has environmental and climatic characteristics that differ from others previously reported for the species, with precipitation between 2,000 to 4, 000 mm and temperature between 12 to 18 °C. Natural forests in this area were characterized by broad extensions, several arboreal strata, many epiphytes, and fertile soils; however, today most of the forest has been transformed into pastures for agriculture and cattle raising, which causes overgrazing and excessive clearing (Guzmán-González 1996).

Our results show that under the current climatic conditions, the areas with the best environmental suitability for *P. ismaeli* are located in the north-center regions of Colombia. This finding is consistent with the records in Colom-

Figure 2. a) Dorsal, ventral, and occlusal views of the skull and jaw of a male of *Platyrrhinus ismaeli* (CZUT-M 317) captured in El Salitre trail, municipality of Cajamarca, Department of Tolima, Colombia, in July 2003. **b)** Occlusal views of the left first upper molar (M1) and second upper molar (M2). Lingual cingulum not continuous from paracone to metacone of first upper molar.



bian collections and the known distribution reported in the literature (Solari *et al.* 2013), and suggests that the current distribution represents the optimum climatic conditions for the species, in sites of high altitude (2,500 masl) and near steep slopes, with riparian vegetation ecosystems.

The results of the model show that all the current and predicted sites fulfill suitable conditions for *P. ismaeli*, *i. e.*, high elevation (1,200 to 2,850 masl), low temperature (12.0 to 25.5 °C), and annual precipitation range of 1,000 to 4,000 mm. Consequently, warm sites with elevation < 1,200 masl are less suitable for the species. These results are in line with those from Solari *et al.* (2013), which report that *P. ismaeli* mainly lives in wet habitats with a narrow elevation range from 1,230 to 2,950 masl.

However, some studies also report the presence of *P. ismaeli* in premontane forests in mountain ranges (Asprilla-Aguilar *et al.* 2016). In fact, this species prefers secondary forests with abundant vegetation cover, rather than pastures and monocultures or moderately fragmented areas (Tirira 2011), to the extent that it is considered endemic to Yungas in Perú, the ecoregion with the largest number of endemic species (Pacheco *et al.* 2009). The distribution of *P. ismaeli* covers the driest forests of the western slopes of the Andes in northern Perú (Rengifo *et al.* 2011).

Table 3. Environmental variables used for modeling the potential distribution of *P. ismaeli*. Issues related to collinearity were avoided by removing variables with variance inflation factor (VIF) values > 5. Variables highlighted in bold were selected through a multi-collinearity test and were used in modeling. All the variables were obain from the WorldClim.

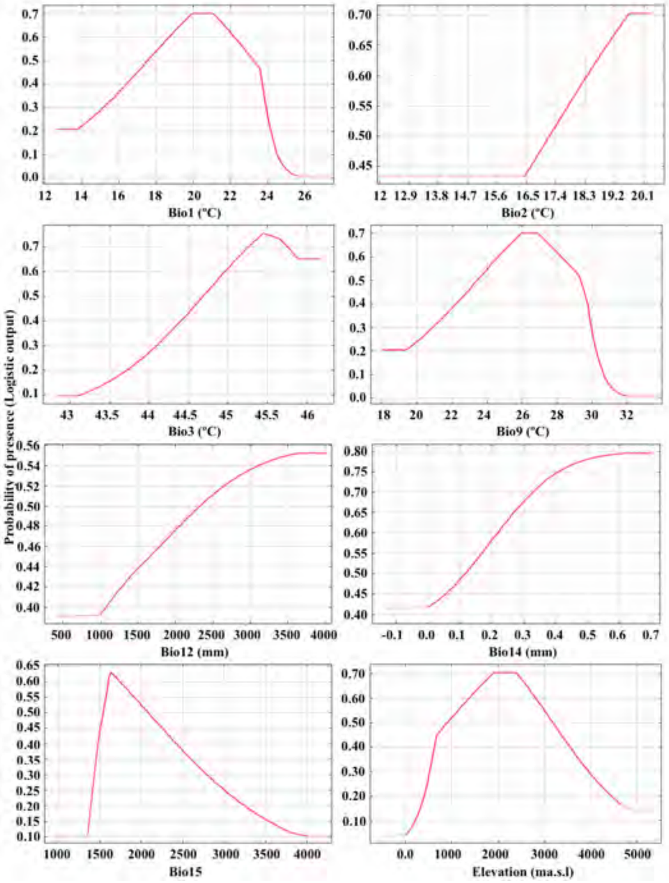
Variable	Code/Unit	VIF
Mean Annual Temperature	Bio1 (ºC)	1.74
Mean Diurnal Range (Mean of monthly (max temp - min temp)	Bio2 (ºC)	2.68
Isothermality (BIO2/BIO7) (* 100)	Bio3	1.10
Temperature Seasonality (Standard deviation *100)	Bio4 (ºC)	8.53
Max. Temp. Warmest Month	Bio5 (ºC)	12.90
Min. Temp. Coldest Month	Bio6 (ºC)	14.20
Temperature Annual Range (BIO5-BIO6)	Bio7 (ºC)	13.40
Mean Temp. of the Wettest Quarter	Bio8 (ºC)	9.20
Mean Temp. of the Driest Quarter	Bio9 (ºC)	3.14
Mean Temp. of the Warmest Quarter	Bio10 (ºC)	9.15
Mean Temp. of the Coldest Quarter	Bio11 (ºC)	9.23
Annual Precipitation	Bio12 (mm)	2.51
Precipitation of the Wettest Month	Bio13 (mm)	8.93
Precipitation of the Driest Month	Bio14 (mm)	3.39
Precipitation Seasonality (Coefficient of Variation)	Bio15	1.85
Precipitation of the Wettest Quarter	Bio16 (mm)	12.86
Precipitation of the Driest Quarter	Bio17 (mm)	6.60
Precipitation of the Warmest Quarter	Bio18 (mm)	9.90
Precipitation of the Coldest Quarter	Bio19 (mm)	12.30
Elevation	Elev (m)	3.65

Table 4. Estimates of average contribution and permutation importance of the environmental variables used in the MaxEnt modeling for *P. ismaeli*.

Variable	Percent contribution	Permutation importance
Bio1	13.6	29.5
Bio2	0.6	2.3
Bio3	3.6	7.4
Bio9	1.5	3.6
Bio12	33.6	8.0
Bio14	1.5	1.4
Bio15	0.3	1.1
Elev	12.5	5.3

Our analysis revealed that the highest probability of occurrence of *P. ismaeli* is recorded in the center of the North Andean Province in the Departments of Antioquia, Caldas, Cundinamarca, Huila, Tolima, Quindío, and Valle del Cauca. The model also predicts a high probability of occurrence in the Choco--Magdalena region and the east of the Orinoquia region. Altogether, this suggests that the distribution of *P. ismaeli* is governed by the ecological association between the Chocó biogeographic region and the valleys of the Magdalena and Cauca rivers, an exchange zone of the biological elements of these areas with those of the cis-Andean and Magdalena valleys, moving through the foothills of the Orinoquia, the Burbua depression, and the Catatumbo basin. This pattern has

Figure 3. Response curves of eight environmental predictors used in the ecological niche model for *P. ismaeli*. For abbreviations, see Table 3.



been documented for different groups of animals, including bats (Hernández-Camacho *et al.* 1992; Mantilla-Meluk *et al.* 2009; García- Herrera *et al.* 2018).

In addition, MaxEnt outputs under the current conditions indicate that the distribution range of *P. ismaeli* is influenced primarily by annual temperature, annual precipitation, and elevation. This is consistent with factors affecting the suitable habitats of several groups of vertebrates such as amphibians, non-volant mammals, bats, and birds (Moura *et al.* 2016), where climatic factors and elevation resulted core drivers of the distribution of vertebrate species (Ferro Muñoz *et al.* 2018).

This study provides ecological information about the habitats occupied by this species, as well as a detailed geographic distribution in the Andean region. This information can be used to support the development of scientifically sound conservation plans, as well as detailed and reliable distribution maps for Colombia, thus allowing the identification of areas that are suitable for the conservation of this species in the country. However, further studies are required addressing the distribution of species in the Central range of Colombia, a region that maintains some high-biodiversity areas in spite of the recent anthropogenic impacts.

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Appendix 1

Specimens analyzed: For each specimen, the collection acronym and museum number are provided, and the localities are listed by country, Department, and specific locality.

Platyrrhinus ismaeli **—Colombia**. **Antioquia:** Andes, Vereda La Soledad (ICN 16503). **Boyacá:** Santa María, Vereda Caño Negro, camino entre las fincas Santa Rosita y El Tesoro, ruta a Palo Negro (ICN 17165). **Casanare:** Trinidad, Banco de la Cañada (ICN 19320). **Cauca:** Moscopas, 1 Mi N Moscopas (MHNUC 1467, 1501; USNM 483575). **Choc***ó:* El Carmen de Atrato (CMCH 001136). **Cundinamarca:** Tena, alrededor de la laguna de Pedro Pablo (ICN 5293, 5295). **Huila:** Parque Natural Nacional "Cueva de los Guacharos". Puente superior en Río Suaza (FMNH 58732 to 58738;IAvH-M 1930, 1932, 1934, 1990,1992, 1994, 1996). **Meta:** Restrepo, Salinas de Upin (ICN 14372). Cubarral, Vereda Aguas Claras, Escuela Santa Clara, finca La Reforma (ICN 14800). **Nariño:** Barbacoas (Jiménez Ortega). **Norte de Santander:** Toledo, Vereda San Isidro (IAvH-M 6681, 6682). **Putumayo:** Mocoa, El Mirador (ICN 21022; IAvH-M 6818, 6823). **Quindio:** Filandia, Vereda El Roble (ICN 12476). **Risaralda:** Quimbaya, Vereda La Suiza (UV 12694). **Santander:** Charalá, Margen derecha del Río Guillermo, inspección de policía Virolín (ICN 8150). **Tolima:** Cajamarca, Vereda Peñaranda parte Baja (CZUT-M 58). Vereda Planadas (CZUT-M 83, 84, 144, 145). Vereda El salitre (CZUT-M 208, 317). Ibagué, Vereda Toche (CZUT-M 57). Quebrada La Plata (CZUT-M 206, 207). **Valle del Cauca:** Buga, Vereda El Janeiro (UV 12402 to 12405, 12407, 13022, 13023).

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Peccaries and their relationship with water availability and their predators in Calakmul, México

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A reduction in the frequency of rainfall and an increase in drought periods, as a consequence of climatic change, has caused the desiccation of water ponds (locally known as "aguadas") in the Calakmul region. The objective of this study was to determine if the abundance and distribution of the white-lipped peccary, *Tayassu pecari,* and the collared peccary, *Pecari tajacu,* in the ponds of the Calakmul Biosphere Reserve, a tropical forest in Southern México, are related to water availability and to the presence of their predators throughout five years of study. Using photo-trapping technique, 12 aguadas were monitored. The index of abundance of photographic records and the activity patterns were estimated, and the presence of both species of peccaries was related through linear and logarithmic regressions with the availability of water and their predators (pumas and jaguars). The abundance and presence of the white-lipped peccary and the jaguar were directly related to decreasing water availability, while water was not a determining factor for the presence of the collared peccary and the puma. The decrease in the availability of water in the aguadas of the reserve has become a serious threat to the white-lipped peccary, one that, when coupled with other threats such as hunting and fragmentation of their habitat in the communities surrounding the reserve, will increase the risk of extinction of these populations, that at least for the white-lipped peccary, is the most important in Mesoamerica.

La reducción en la precipitación y el aumento de los periodos de sequía, como consecuencia del cambio climático, ha ocasionado la desecación de las aguadas en la región de Calakmul. El objetivo de este estudio consistió en determinar cómo la abundancia y la distribución del pecarí de labio blanco *Tayassu pecari* y el pecarí de collar *Pecari tajacu* en las aguadas de la Reserva de la Biosfera Calakmul se relacionan con la disponibilidad de agua y con la presencia de sus depredadores a lo largo de cinco años de estudio. A través de la técnica de fototrampeo 12 aguadas fueron monitoreadas. Se estimó el índice de abundancia de registros fotográficos, los patrones de actividad y se relacionó a través de regresiones lineales y logarítmicas la presencia de ambas especies de pecaríes con la disponibilidad de agua y con sus depredadores (pumas y jaguares). La abundancia y presencia del pecarí de labio blanco y del jaguar, se relacionaron directamente con la disminución de la disponibilidad de agua, mientras que, para el pecarí de collar y el puma, el agua no fue un factor determinante para su presencia. La disminución en la disponibilidad de agua en las aguadas de la Reserva se ha convertido en una fuerte amenaza para el pecarí de labio blanco, aunado a otras amenazas como la cacería y la fragmentación de su hábitat en las comunidades aledañas a la reserva, que ponen en riesgo a esta población considerada la más importante de Mesoamérica.

Key words: climatic change; jaguars; photo-trapping; pumas; Tayassuidae.

Introduction

Calakmul Biosphere Reserve (CBR) located in southern México is the largest protected tropical forest in México (Garcia-Gil *et al.* 1999) and conserves a great diversity of wildlife, including more than 250 species of birds, 150 species of mammals, and 30 species of reptiles and amphibians (Galindo-Leal 1999). In the CBR there are not major water bodies, and all the water that falls by precipitation accumulates in some specific sites known locally as "aguadas." These sites are the only source of water for wildlife and human communities during the dry season (Reyna-Hurtado *et al.* 2010). In the last years, and as a consequence of climate change, the precipitation has reduced and the dry periods have extended, which has caused the desiccation and disappearing of several of these water bodies, especially in the south part of the CBR (Mardero *et al.* 2012; Zúñiga-Morales and Sima-Panti 2015).

This phenomenon may possibly be causing changes in the spatial and temporal patterns of the species associated with the ponds (Reyna-Hurtado *et al.* 2012). O'Farrill *et al.* (2014) estimated that a possible response of the animals to the pond disappearing phenomenon would be the migration to more humid areas, such as the communal forest adjacent to the protected area, which would reduce the conservation value of the CBR.

In the CBR there are two species of peccaries, the white-lipped peccary (*Tayassu pecari)* and the collared peccary (*Pecari tajacu*). For these species, the presence of water is an essential component of their habitat as they drink water and wallow in the mud as a heat refreshing strategy and to avoid ectoparasites (Sowls 1997; Reyna-Hurtado *et al.* 2014; Beck *et al.* 2017; Reyna-Hurtado *et al.* 2017). Water availability has been described as the most important element of the landscape for white-lipped peccary and is the axis of the group's movements in sites where water is not uniformly distributed in time and space (Reyna-Hurtado *et al.* 2009, 2012).

The collared peccary is different than white-lipped peccary as it can also inhabit dry areas and has developed ecological strategies to cope with water scarcity (Sowls 1997; Reyna-Hurtado *et al.* 2014). However, in tropical forests, both collared peccary density and distribution have been related to the presence of water bodies, indicating the importance of these pieces of the landscape for peccary survival (Hernández 2013; García-Marmolejo *et al.* 2015).

Water is an essential component of the peccary habitat and is associated with their presence and abundance. It is probable that the reduction and disappearance of these water bodies in the CBR is having an impact on the distribution patterns of both species, as well as their relationships (increase in competition) and their interaction with predators. Peccaries are two of the more important preys species in the diet of jaguars (*Panthera onca*) and pumas (*Puma concolor*; Aranda 1994; Amín 2004; Moreno 2008). Therefore, the abundance of peccaries in ponds may also affect the presence and use of ponds by these felines.

Climate change scenarios for the Calakmul region predict an even larger reduction in precipitation in the coming years (Magrin *et al.* 2007). Therefore, to describe and understand the preset relationships among species in tropical forests and how they adapt to changes in the environment is essential to promote management of conservation actions. The objective of this study consisted of determining, over five years, the relationships among the abundance and spatial distribution of the two species of peccaries with variation in water availability in the ponds of the CBR and with the presence and abundance of their two main predators species. It is predicted that the white-lipped peccary will be more associated with the ponds than the collared peccary, and that a reduction of water availability will affect the abundance and visitation rate of the white-lipped peccary. It is also expected that white-lipped peccary will co-occur more frequently with jaguars than with pumas; while at the same time, puma and collared peccary will co-occur more often than jaguar – collared peccary (Aranda 1994; Aranda and Sanchez Cordero 1996; Foster *et al.* 2010).

Methods and Materials

Study Site. Calakmul Biosphere Reserve is located in the Calakmul municipality in Campeche State, Southern México. It is located between 18° 40' 7.7" N, -89° 12' 34.3" W (Figure 1). It was established in 1989 and protects the largest tropical forest in México with an area of 7,231 km^2 (Morales and Magaña 2001). The climate is calid sub-humid with an annual temperature of 24.6 °C and with an annual precipitation average between 1,200 to 2,000 mm (García 1988). In the last 50 years the annual precipitation has decreased 16 % and 30 % during the dry and wet season with respect to the average from 1980 to 1999 (Bárcena *et al.* 2010). In addition to this, the number of days without rain is longer in the region each time; since 1986 the rainy and very rainy years have become less frequent and the dry periods have increased in recent years (Mardero *et al.* 2012).

The area is flat with rolling hills and altitude is between 250 to 340 masl. The predominant vegetation type is tropical humid forest classified in 1) Medium sub-perennial forest, 2) Low-flooded forest, 3) Low-tropical forest, and 4) Secondary vegetation. (Pennington and Sarukhán 1998).

Data collection. From January 2014 to December 2018, 12 ponds were monitored with the technique of photo-trapping in the Southern zone of the CBR (Figure 1). Of these ponds only nine were monitored in 2014, 10 in 2015, and 12 from 2016 to 2018. The name of the ponds were: Aguada2, Aguada4, Baños, Bonfil, Calakmul, Corriente, Dos Aguadas, Griselda, Km20, Km46, Nico, and Verde. The distance among ponds varied between 0.7 to 3.7 km and in each pond a single camera was set (Reconyx PC600 and PC800). The cameras were attached to a tree near to the pond, at approximately 50 cm from the ground facing the ponds and they were active 24 hours. The cameras stayed there all year long and were only visited to change memory cards and batteries. The records were entered in a database where the following information was recorded: site, date, hour, time that the recording lasted (in minutes), and the number of individuals.

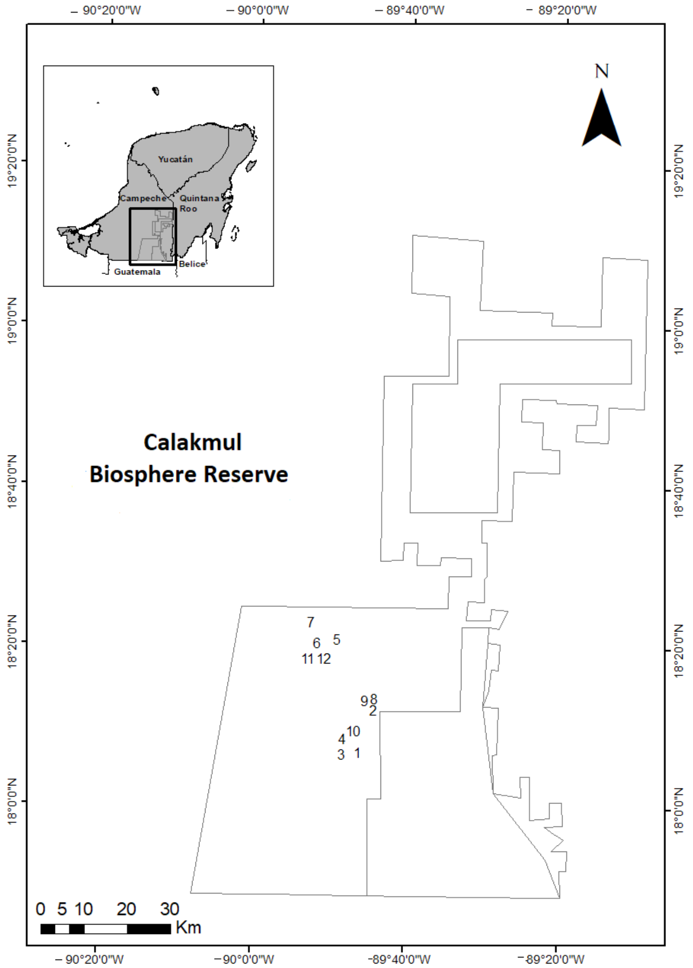

Figure 1. Map of ponds monitored in Calakmul Biosphere Reserve: 1. Baños; 2. Bonfil; 3. Calakmul; 4. Corriente; 5. Dos Aguadas; 6. Griselda; 7. Km 20; 8. Km 46; 9. Nico; 10. Verde; 11. Aguada4 y 12. Aguada2.

Pond visitation records. An abundance index (AI) of photographic records was estimated for the two species with the following equation: AI = N / SE * 1000 trap-days. Where N = Records number, SE = Sampling efforts (number of cameras deployed by the days the cameras were working in the field) multiplied by 1,000 (standard units). Given that peccaries visited and spent time in the ponds (Reyna-Hurtado *et al.* 2009), a one-hour filter was considered among consecutive sequences of photos of a group of peccaries to consider a record independent. This index was used to compare frequency of visits between the two species and among years, seasons (rainy and dry), and ponds.

For each species we ran non-parametric Kruskal Wallis tests followed by a Dunn post-hoc test to compare AI among ponds and years. Mann-Whitney non-parametric tests were also applied to compare abundance between the two seasons (Rohlf and Sokal 1981).

Activity patterns. To estimate activity patterns (AP) of the white-lipped peccary and collared peccary, the records were grouped per species and per two-hour intervals. These intervals were represented in a circular scale where the average angle and the dispersion of the values were estimated through the software Oriana 4.01 (Kovach 1994). Using Kernel estimators the proportion of overlap of activity patterns between the two species was also estimated (overlap coefficient) for the five year period with the tool "Overlap" in R (R Core Team 2018, R Studio ver. 1.1.463). The estimator *Δ4* was used as it is recommend for samples > 75 (Meredith and Rideout 2016). The interval of confidence (CI) between the upper and lower 95 % limit of the overlap estimation of the activity of the two species was calculated through percentages based in 1000 samples (Ridout and Linkie 2009).

Occurrence and Co-occurrence between peccaries and their predators. To test the occurrence and co-occurrence between the two peccaries and then with their predators, the independent records of the species were used. The percentage of occurrence in each pond and each year of each pair of species were calculated. Then, as a more detailed way to estimate co-occurrence, all records of co-occurrence of any pair of species in intervals of 1, 12, and 24 hours were recorded. Additionally, linear regression analyses were performed between the number of visits of the two species of peccaries and the number of visits of jaguars and pumas to test if the presence of peccaries was related to the presence of predators in the ponds.

Relationships between water availability and peccaries and their predators presence. Logistical regressions were performed to relate water availability (presence/absence) and its variation along the five years with the presence of the four species. Presence/absence of water was recorded using the photographic records and visits to change memories and batteries, and a matrix was built of each pond's water availability and the number of records obtained monthly of each species. The linear simple regression analyses and logistical regression analyses were done in R (R Core Team 2018; R Studio ver. 1.1.463) and were considered significant with a $P < 0.05$.

Results

Pond visitation abundance index. In total, the sampling effort was 13,744 camera-trap days. The AI for white-lipped peccary was 20.51 records/1,000 trap-days. The abundance during the dry season (22.88 records/1,000 trap-days) was higher than in the rainy season (18.35 records/1,000 trap-days) but the difference was not significant (W = 66.5, P = 0.77). However, when comparing AI across years there were statistically significant differences (H = 22.53, $P = < 0.01$). In 2018 there were no records of the species at all, making this year different from the rest of the years (2014, 2015, 2016 and 2017; $P = < 0.05$). The AI of the white-lipped peccary among ponds was also different and the differences were significant (H = 19.35, P = 0.04). The 67.73 % of the records of white-lipped peccary occurred in four ponds: Aguada4, Corriente, Calakmul, and Griselda, and the AI of these were different than the AI from Baños, Bonfil, Dos Aguadas, and Km46 ($P < 0.05$; Figure 2a). The ponds most visited by white-lipped peccary in 2014 were Calakmul and Griselda, in 2015 Corriente and Km20, in 2016 Calakmul and Griselda, and in 2017 Aguada4 and Corriente.

For the collared peccary the AI was 32.15 (records/1,000 trap-days), and in the dry season of 31.27 (records/1,000 trap days) that was very similar to the rainy season AI of 32.96 (records/1,000 trap-days) with no statistically significant differences (W = 64, P = 0.67). Similarly, there were no differences in the AI among years for collared peccary (H = 1.98, P = 0.73). However, when comparing AI of ponds, there were significant differences (H = 29.23, P = 0.002), with 69.45 % of the collared peccary records occurring in the following ponds: Baños, Dos Aguadas, Km20, and Verde, which had a statistically significant difference from Aguada4, Bonfil, Corriente, Calakmul, and Griselda ($P < 0.05$; Figure 2b). The most visited ponds for the collared peccary were Dos Aguadas in 2014; Baños in 2015; Baños and Km20 in 2016; Baños and Km20 in 2017; and Dos Aguadas in 2018.

Activity patterns. The white-lipped peccary and collared peccary were mainly diurnal species when visiting the ponds (6:00 to 18:00 h). The WLP concentrate their activity between 10:00 and 12:00 h (μ: 11.06), while collared peccary were more active from 6:00 to 10:00 h (μ = 9.17) and decrease their activity considerably after midday. However, a great degree of overlap was obtained among the activity patterns between the two species during the five years of study Δ = 0.79 (CI 95 % 0.69 to 0.83; Figure 3).

Occurrence and Co-occurrence among peccaries and their predators. The white-lipped peccary and collared peccary were recorded in all ponds sampled, however, their presence varied with the years, with the CP being higher than the white-lipped peccary in four of the five years of study. The rate of co-occurrence varied among years as well. Considering only the ponds and the times where the white-lipped peccary were present, the co-occurrence was higher than in ponds where the collared peccary was only present (Table 1). Ten records of co-occurrence were obtained between the two species in a period of time less than 24

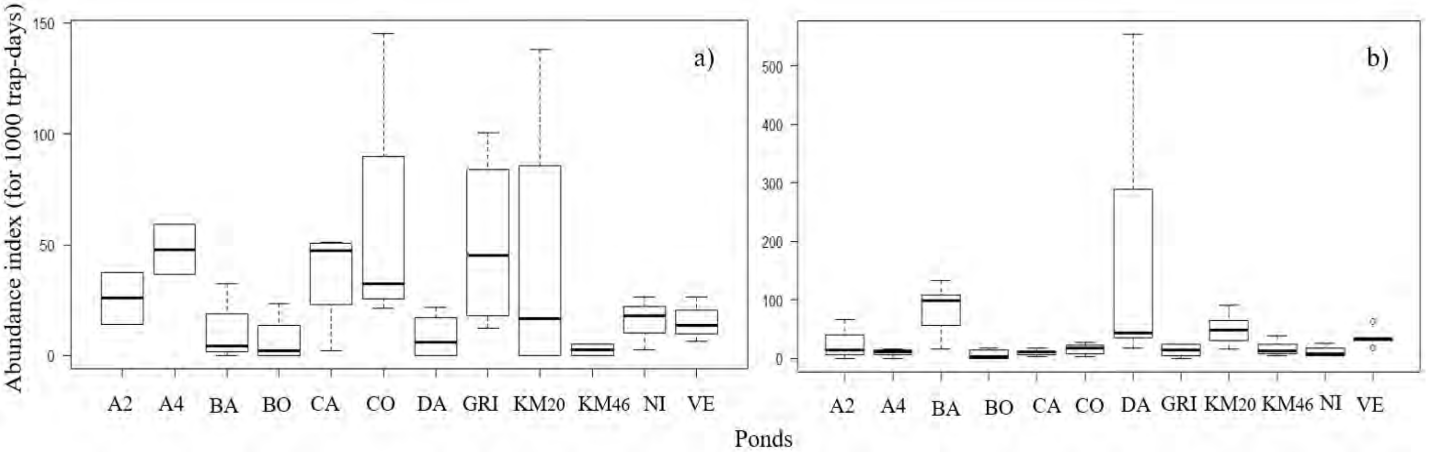

Figure 2. Pond visitation abundance index of *Tayassu pecari* a) and *Pecari tajacu* b) in Calakmul Biosphere Reserve (2014-2018): Baños (Ba); Bonfil (Bo); Calakmul (Ca); Corriente (Co); Dos Aguadas (DA); Griselda (Gri); Km 20; Km 46; Nico (Ni); Verde (Ve); Aguada4 (A4) and Aguada2 (A2).

hours and in all cases the white-lipped peccary preceded the collared peccary.

Peccaries and jaguar. The co-occurrence in ponds between jaguar and white-lipped peccary was higher in general than between jaguar and collared peccary, except for 2018 where there were not records of white-lipped peccary and the co-occurrence between jaguar and collared peccary increased (Table 2). In the same way, the percentage of occurrence in jaguars in ponds with only white-lipped peccary presence were higher in four years of sampling than in ponds with only collared peccary presence. Nineteen records of co-occurrence between jaguar and white-lipped peccary within 24 hours periods were recorded and in 13 of these cases the jaguar preceded white-lipped peccary and in six cases the white-lipped peccary preceded jaguar. The higher numbers of records were obtained in 2014 and 2015. Between jaguar and collared peccary, 12 records of co-occurrence were obtained and in seven of these cases the jaguar preceded collared peccary and in five the collared peccary preceded jaguars. The regression analyses indicated a significant relationship between jaguar and white-lipped peccary along all years ($t = 2.594$, $P = 0.0106$) but not between jaguar and the collared peccary ($t = -0.467$, $P = 0.6451$).

Peccaries-Puma. The percentage of co-occurrence between puma and collared peccary was higher than between puma and white-lipped peccary for all years and the same as in ponds with only records of one species of peccaries (Table 3). Ten records of co-occurrence within 24 hours between puma and white-lipped peccary were obtained and in seven the puma preceded white-lipped peccary and in five white-lipped peccary preceded puma. For 44 records of co-occurrence among puma and collared peccary, in 19 the puma preceded collared peccary and in 25 collared peccary preceded puma. Linear regression analyses showed a significant relationship between CP and puma presence in the ponds ($t = 3.002$, $P = 0.003$), but not between puma and white-lipped peccary ($t = -0.45$, $P = 0.9643$).

Relationship between water availability and peccaries and their predators presence. Water availability varied significantly among the five years of study. In 2014, 90 % of the ponds presented water in the dry season. In 2015 only 30 % of them had water in the dry season and in 2016 and 2017 only 25 % had water. In 2018, 50 % of the ponds had water during the dry season. However, in August 2018 all ponds were dry and remained dry to the end of the study in December 2018.

Table 1. Occurrence and co-occurrence of *Tayassu pecari* (WLP) and *Pecari tajacu* (CP) in the ponds of Calakmul Biosphere Reserve.

Year	WLP Occurrence rate	CP Occurrence rate	Global Co-occurrence	Ponds with WLP presence	Ponds with CP presence
2014	88.9 %	100 %	88.8 %	100 %	88.8 %
2015	88.9 %	100 %	80.0 %	100 %	80.0 %
2016	83.3 %	75 %	58.3 %	70 %	77.7 %
2017	67.0 %	100 %	66.6 %	100 %	66.6 %
2018	0 %	83.3 %	-	-	-

Global co-occurrence (% of ponds where both species were present). Co-occurrence only in ponds where WLP was present. Co-occurrence only in ponds where CP was present.

Table 2. Co-occurrence of *Panthera onca* (jaguar) and *Tayassu pecari* (WLP) / *Pecari tajacu* (CP) on the ponds of Calakmul Biosphere Reserve.

Year	WLP Global Co-occurrence	CP Global Co-occurrence	Ponds only with WLP presence	Ponds only with CP presence
2014	77.7 %	77.7 %	87.5 %	77.7 %
2015	90.0 %	90.0 %	100 %	90.0 %
2016	91.6 %	66.6 %	100 %	88.8 %
2017	83.3 %	66.6 %	87.5 %	66.6 %
2018	-	83.3 %	-	90.0 %

Global co-occurrence (% of co-occurrence in ponds where both species were present). Co-occurrence only in ponds where WLP was present. Co-occurrence only in ponds where CP was present.

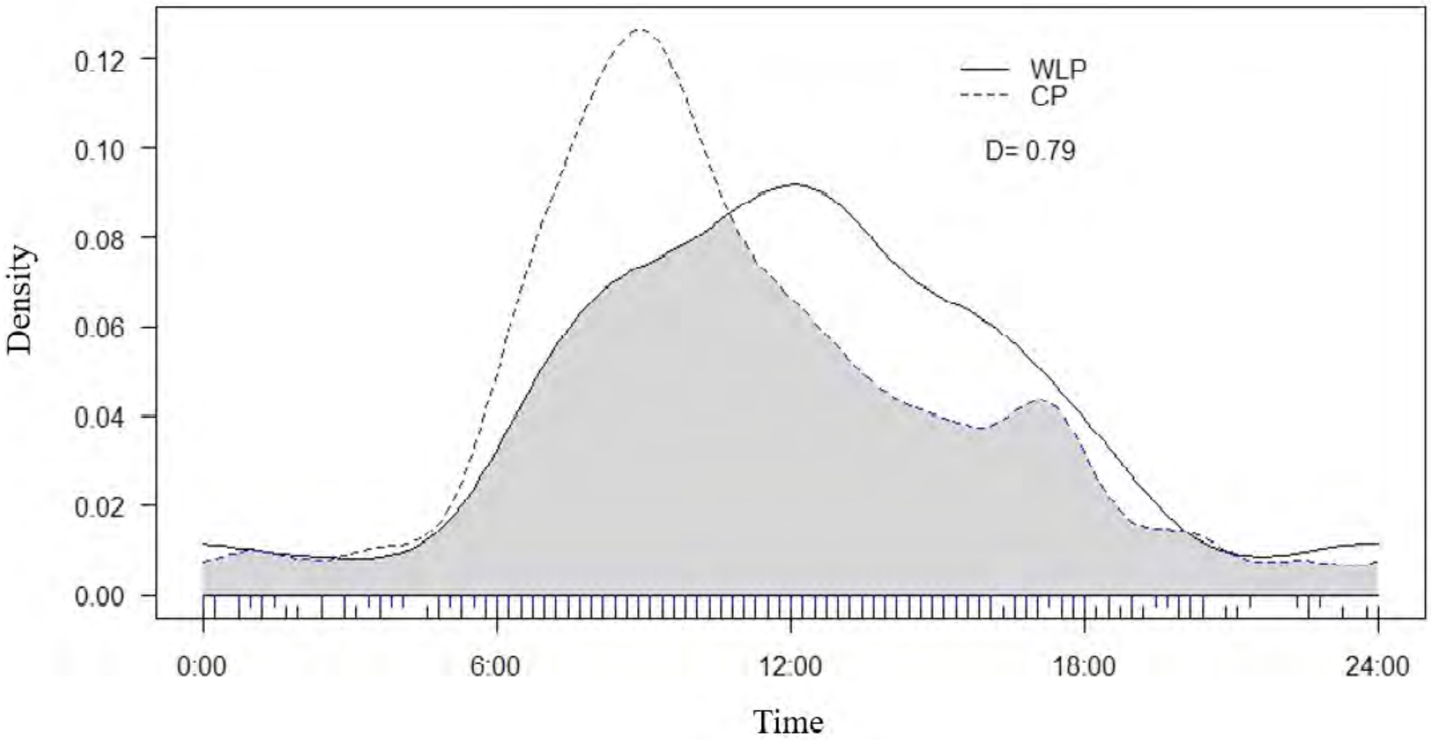

Figure 3. Proportion of overlap (D: overlap coefficient) between the activity patterns of *Tayassu pecari* (WLP, solid line) y *Pecari tajacu* (CP, pointed line) on Calakmul Biosphere Reserve.

Logistic regression analyses indicated a significant relationship between white-lipped peccary and water availability ($z = 2.817$, $P = 0.004$) as well as jaguar and water availability ($z = 2.504$, $P = 0.0123$) while a negative relationship was found among puma and water availability ($z = -3.457$ $P = > 0.001$), and for the collared peccary the water availability was not a factor that determined its presence ($z = 1.152$, $P = 0.249$).

Discussion

Use of ponds. The reduction of water availability and, consequently, desiccation of water bodies in CBR during the five years of study was directly related to the abundance and distribution of white-lipped peccary. In the first year of study the highest abundance of white-lipped peccary was obtained and the activity was centered around the ponds that conserved water. It has been reported through radiotelemetry studies that white-lipped peccary concentrate their home ranges during the dry season around water bodies, while during the rainy season they are more mobile and move long distances (Fragoso 1998; Reyna-Hurtado *et al.* 2009). In 2017 when the rainy season started, all ponds were dry due to a previous bad season, and that was the last time that white-lipped peccary was recorded in ponds. In 2018, there was not a single record of the species in any pond. White-lipped peccary have the ability to move long distances in a single day, making it probable that the species moved to wetter areas looking for water, even leaving the protected areas. This has been described previously for groups followed by radiotelemetry in the same study area (Reyna-Hurtado *et al.* 2009).

Table 3. Co-occurrence of *Puma concolor* (puma) and *Tayassu pecari* (WLP)/ *Pecari tajacu* (CP) on the ponds of Calakmul Biosphere Reserve .

Year	WLP Global Co-occurrence	CP Global Co-occurrence	Ponds with WLP presence	Ponds with CP presence
2014	77.7 %	88.8 %	87.5 %	88.8 %
2015	80.0 %	100 %	100 %	100 %
2016	83.3 %	83.3 %	88.8 %	88.8 %
2017	41.6 %	91.6 %	87.5 %	91.6 %
2018	-	91.6 %	-	100 %

Global co-occurrence (% of ponds where both species were present). Co-occurrence only in ponds where WLP was present. Co-occurrence only in ponds where CP was present.

For the collared peccary, water availability did not have a significant effect on its presence or abundance. This species concentrated its activity in four specific ponds, which remained dry most of the time and were less visited by the white-lipped peccary. The occurrence rate and abundance of the species in these ponds were higher for CP than white-lipped peccary in these ponds. Collared peccary was present in all ponds in three out of five years of study, while the white-lipped peccary showed a decreasing trend through the years. However, the abundance of collared peccary in ponds where the white-lipped peccary was present was very low and most of the visits occurred when white-lipped peccary were absent. In the co-occurrence events that took place within 12 and 24 hours in these ponds the white-lipped peccary always preceded the collared peccary. However, when white-lipped peccary arrived at some ponds, collared peccary did not visit these sites again. In 2017 and 2018 the records of white-lipped peccary decreased or even disappeared, then CP increased its records even in ponds with water that were not used when white-lipped peccary was present. All these facts suggest a possible differentiation in the use of ponds by the two species and a dominance of white-lipped peccary over collared peccary when both species co-occur as it has been described before (Sowls 1997; Fragoso 1999; Keuroghlian *et al.* 2004).

Due to the increase of the dry periods in the Calakmul region and the consequent decrease of water availability, it is highly probable that the competition between the two species of peccaries will increase (Abrams and Chen 2002). Given the large body of the white-lipped peccary and the fact that it forms larger groups than collared peccary, white-lipped peccary it is a dominant species. Therefore, it is probable that the differential use by the two species as described in this study is a behavior to avoid coinciding in the ponds. The CP avoid some ponds, and the white-lipped peccary, as the dominant species, decreased the collared peccary access to the water forcing them to use ponds with less water or no water at all. In a study among elephants and other herbivores, access to water bodies a similar behavior was observed where elephant's presence and distribution affected the presence and distribution of other species (Valeix *et al.* 2007). Despite the strategies that peccaries have developed to coexist, water availability may be a resource that is causing temporal competition among white-lipped peccary and collared peccary (Sowls 1997).

The white-lipped peccary and collared peccary visited the ponds mostly during the day and there were very few nocturnal records. The same pattern has been reported in Mirador-Río Azul National Park in Guatemala (Moreira-Ramírez *et al.* 20155) and Laguna del Tigre National Park (Moreira-Ramírez *et al.* 2016) and in the Calakmul region (Briceño-Méndez *et al.* 2016). A large degree of overlap was detected between the two species, although the activity peak time was not the same (white-lipped peccary: 10:00 to14:00 h; collared peccary: 6:00 to10:00 h). The difference may have occurred because white-lipped peccary used ponds with water during the hottest hour of the day to refresh and drink (Sowls 1997). Conversely, collared peccary visited ponds with less water or no water at all and not during the hottest time of the day. These findings coincide with the fact that collared peccary is a common inhabitant of arid zones such as Texas or New México in the USA and have physiological characteristics that favor the heat dissipation and prevent dehydration as reducing water by evotranspiration or reducing urine disposal (Zervanos and Day 1977; Hellgren and Bissonette 1984; Sowls 1997).

Occurrence and co-occurrence among peccaries and their predators. When the presence of the four species (collared peccary, white-lipped peccary, jaguar and puma) were analyzed, it was found that the jaguar significantly associated with white-lipped peccary, which is considered one of the jaguar's main prey (Aranda 1994; Hernández 2008). It is highly probable that jaguars use these sites as a hunting grounds due to the frequency of visits by white-lipped peccary. Despite these significant relationships, when the co-occurrence events were analyzed, the majority of these occurred within one month and very few within a 24-hour period. Therefore, it is probable that the presence of both species is due to the fact that there is water in the ponds and that there may be more prey diversity and abundance around the ponds, among them the white-lipped peccary (Martínez-Ku *et al.* 2008).

To the contrary, puma presence was associated to collared peccary. Previous studies indicate that in places where jaguars and pumas co-exist there is an evolutionary advantage of jaguars and the two species segregated to co-exist (Foster *et al.* 2013). Puma is a more adaptable species than jaguars and can survive in dry areas. Therefore, water availability is not a determining factor for its presence, rather prey availability and distribution. The ponds where collared peccary distributed are dry ponds that are also visited frequently by deer (Ramírez-Ortiz 2016). The puma presence in these ponds could be also a consequence of deer presence as well as collared peccary in these ponds. Both are highly prized preys of pumas (Aranda and Sanchez Cordero 1996; Hernández 2008).

This study demonstrated that peccaries are sensible to water availability variation, to the presence of the other species, and to the presence of their predators in Calakmul region. The disappearance of white-lipped peccary in the 2017 rainy season and all of 2018 indicate that the groups displaced to wet areas as predicted before by O'Farrill *et al.* (2014), or there was a massive mortality as it was evidenced in 2017 when several individuals of the species were found dead in less than one month in the study site (Reyna-Hurtado pers. obs.). Due to the rapid effects of climate change and the prediction of more dry periods (IPCC 2007) it is possible that species such as white-lipped peccary or jaguar will move to the reserve borders or even leave the protected area. Therefore, it is crucial to continue monitoring the species and its response to elaborate conservation strategies that conserve the two peccaries species and their predators of this changing ecosystem of Calakmul Biosphere Reserve.

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Establishing the availability of the sigmodontine binomen *Geoxus lafkenche* (Rodentia, Supramyomorpha, Cricetidae)

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The sigmodontine species name *Geoxus lafkenche* proposed by Teta and D'Elía (2016) is unavailable, given that the publication where it originally appears did not satisfy the requirements of the International Code of Zoological Nomenclature. In this note we establish the availability of the species name *Geoxus lafkenche*, by fulfilling those requirements.

El nombre de la especie sigmodontina *Geoxus lafkenche*, propuesto por Teta and D'Elía (2016), no está disponible, dado que la publicación donde el mismo fue propuesto no cumplió todos los requisitos del Código Internacional de Nomenclatura Zoológica. En esta nota establecemos la disponibilidad del nombre de la especie *Geoxus lafkenche*, cumpliendo esos requisitos.

Keywords: Abrotrichini; Chile; Taxonomy; Sigmodontinae.

Introduction

In 2016, Teta and D'Elía published a revision of the genus *Geoxus* Thomas 1919, proposing a new species, *Geoxus lafkenche,* for the population from Guafo island, a small Pacific island in the Región de Los Lagos, Chile. The study was published in an electronic only journal. The Fourth Edition of the International Code of Zoological Nomenclature (ICZN 1999) and the Amendment on e-publication (ICZN 2012) establish that to be available, taxonomic names proposed in works that are issued and distributed electronically, must be registered in the Official Register of Zoological Nomenclature (Zoobank) prior to publication, and must include evidence of registration within the work itself. This is most often is done by providing the ZooBank Life Science Identifier (LSID) for the publication. In addition, the ZooBank registration record must include an ISSN for the journal, and an intended online archive. None of these requirements were satisfied in the publication by Teta and D'Elía (2016), where the new binomen *Geoxus lafkenche* was presented. As such, the name is not available. However, all the conclusions reached by Teta and D'Elía (2016) about species limits remain valid.

The objective of this note is to comply with the provisions of The International Code of Zoological Nomenclature (ICZN 1999, 2012) to make the name *Geoxus lafkenche* available. The information provided below was taken from Teta and D'Elía (2016). This published work and the nomenclatural act it contains have been registered in ZooBank. The LSID for this publication is: urn:lsid:zoobank.org:pub:F12E2348-309A-4DE7-A481-1A9D8A46BA77. The online version of this work will be archived and available at Zenodo.

Taxonomy

Rodentia Bowditch 1821
Muroidea Illiger 1811
Cricetidae Fischer 1817
Sigmodontinae Wagner 1843
Abrotrichini D'Elía, Pardiñas, Teta, and Patton 2007
Geoxus lafkenche n. sp.
LSID urn:lsid:zoobank.org:act:db251699-c242-4f5e-abf9-1943343d5647
(Figure 1)

Holotype: UACH 7339 (original number GD 1512 collected by Héctor Pavez in January 2012), an adult female preserved as skull, body in fluid, and tissue sample in alcohol. A partial (785 bp) DNA sequence of the cytochrome-b gene gathered from this specimen was deposited in Genbank with accession number KU904314.

Type locality: Punta Weather, Isla Guafo, Región de Los Lagos, Chile (-43° 34.000', -74° 49.500').

Distribution: only known from the type locality.

Morphological diagnosis: A large species of the genus *Geoxus* (length of head and body ~106 mm, skull length ~29.5 mm), characterized by its small ears (~12 mm), relatively long tail (~66.5 mm), and small molar teeth; pelage somewhat coarse and uniformly dark brown, slightly paler at the venter; skull elongate and fragile, with scarcely flaring zygomata; nasals and premaxillae trumpeted; zygomatic plate inclined with a nearly convex anterior border; upper zygomatic root broad, larger than to a half of the anteropos-

Figure 1. Holotype of *Geoxus lafkenche* n. sp., from Isla Guafo, Chile (UACH 7339): skull in dorsal (left), lateral (middle, above) and ventral (right) views, and left dentary (reversed) in labial view (middle, below). Scale = 5 mm.

terior length of the zygomatic plate; frontal sinus inflated; interorbital region smoothly rounded; toothrow short; palate long, although only exceeding maxillary toothrow by the approximate length of one third of M2; parapterygoid fossa large; middle lacerate foramen broad, bridged by a sharp, well developed stapedial process; length of M3 nearly equal to three quarters of the length of M2.

Etymology: From the mapudungun, the language spoken by Mapuches: lafken (= sea) and che (= people). The specific epithet corresponds to the group of the indigenous people that live along the Pacific coast of south-central Chile.

Measurements of the holotype: external measurements (in mm, taken from specimen tag): total length (TL), 173; tail length (T), 67; hindfoot length (HFL) with and without claw, 15 and 12; ear length (EL), 12.5. Cranial measurements (in mm): skull length (SL), 31.38; condylo-incisive length (CIL), 28.22; zygomatic breadth (ZB), 13.09; braincase breadth (BB), 12.90; palatilar length (PalL), 11.90; incisive foramina length (IL), 5.51; incisive foramina width (IW), 1.69; diastema length (DL), 8.16; maxillary toothrow length (TRL), 3.73; palatal width at M1 (PWM1), 5.12; palatal width at M3 (PWM3), 4.29; zygomatic plate width (ZW), 1.79; nasal length (NL), 11.89; nasal width (NW), 3.49; rostrum width (RW), 4.29; frontal sinus width (FSW), 6.68; interorbital breadth (IB), 5.33; frontal length (FL), 8.90; parietal length (ParL), 6.75; mesopterygoid fossa breadth (MB), 1.45.

Paratype: UACH 7340, an adult female, collected at the same locality of the holotype. A partial (793 bp) DNA sequence of the cytochrome-b gene gathered from this specimen was deposited in Genbank with accession number KU904315.

Measurements of the paratype: External measurements (in mm): TL, -; T, 66; HF (with claw), 14; HF (without claw), 11; E, 12.0. Cranial measurements (in mm): SL, 28.65; CIL, 26.01; ZB, 12.51; BB, 12.75; PalL, 11.47; IL, 5.16; IW, 1.37; DL, 7.27; TRL, 3.80; PWM1, 5.12; PWM3, 4.68; ZW, 1.45; NL, 11.40; NW, 3.16; RW, 4.24; FSW, 6.34; IB, 5.35; FL, 9.07; ParL, 5.73; MB, 1.35.

Final remarks

The morphological comparisons of *Geoxus lafkenche* n. sp. with the other species of the genus *Geoxus* (*i. e., G. annectens*, *G. michaelseni*, and *G. valdivianus*) and their phylogenetic relationships can be found in Teta and D'Elía (2016). The year of availability of *G. lafkenche* n. sp. is 2020 and as such must be referred in future works.

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Activity patterns of arboreal mammals in a tropical rain forest in México

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Studying activity patterns of canopy mammals provides information on the biology of these species. However, the challenges of reaching and sampling the forest canopy restrict the information available on activity patterns. This study aimed to describe the activity patterns of canopy mammals, and analyze their temporal overlap, in the Santa Gertrudis Ecological Reserve, State of Veracruz, Mexico. Camera trap records were obtained from February 2016 to February 2017. Nine camera traps were set in the study area, separated between 300 and 1500 m from each other, along a straight line in the forest canopy (~ 8 to 12 m above the ground). Cameras were affixed to a trunk above a branch that was perpendicular to the line and overlapping a neighboring tree. A total of 12 mammal species that use the tree stratum were recorded, including two diurnal and ten nocturnal species. The five species for which at least ten records were obtained were included in the activity pattern analyses. Four of these are nocturnal species and showed temporal overlap values (Δ_1) ranging from 0.69 to 0.9. Four of the 12 species recorded are listed in an extinctionrisk category as per the Norma Oficial Mexicana NOM. This is one of the first studies providing ecological information on activity patterns of canopy mammals in Mexico.

El estudio del patrón de actividad de los mamíferos del dosel ayuda a complementar la información básica sobre la biología de estas especies. Sin embargo, la dificultad por acceder al dosel para llevar a cabo el muestreo limita la información existente sobre sus patrones de actividad. El objetivo de la presente contribución fue describir el patrón de actividad y analizar el traslape temporal de los mamíferos de dosel en la Reserva Ecológica de Santa Gertrudis, Vega de Alatorre, Veracruz, México. Se obtuvieron los registros mediante cámaras-trampa durante un año de muestreo de febrero 2016 a febrero 2017. En el área se colocaron nueve trampas-cámara con una separación entre 300 m y 1.5 km en línea recta entre el dosel (~8 a 12 m de altura), sujetadas al tronco por encima de una rama en posición perpendicular y con conexión con otro árbol. Se registró un total de 12 mamíferos que hacen uso del estrato arbóreo, de los cuales dos presentaron actividad diurna y 10 actividad nocturna. Únicamente de cinco obtuvimos 10 o más registros que nos permitieron llevar a cabo los análisis de patrones de actividad. Cuatro de estas especies fueron nocturnas y presentaron un coeficiente de traslape temporal de entre Δ_1 = 0.69 a 0.9. De las 12 especies registradas cuatro se encuentran catalogadas bajo alguna categoría de riesgo dentro de la legislación mexicana. Este estudio es uno de los primeros en aportar información ecológica con respecto a los patrones de actividad de un ensamble de mamíferos arborícolas en México.

Keywords: Canopy mammals; diurnal; ecological reserve; nocturnal; tropical forest.

Introduction

The systematic study of daily habits of animals began in 1920 with the work of Szymanski (Halle and Stenseth 2000). Since then, several studies have been conducted on various animal species, mainly in captivity or laboratory conditions (DeCoursy 1990). Photographic cameras were first used by Pearson (1959, 1960) to monitor activity patterns of the California vole (*Microtus californicus*) in the late 1950s. Camera traps have allowed studying the temporal behavior of animals in natural and captivity conditions (*e. g.*, Kachamakova and Zlatanova 2014). The development of more efficient camera traps has now allowed a better approach to the study of activity patterns (Oliveira-Santos *et al.* 2008). The use of camera traps provides a noninvasive research method that, with relatively little effort, yields information on multiple species, including those that are rare, elusive, or little known (Sanderson and Trolle 2005; Jimenez *et al.* 2010; O'Brien and Kinnaird 2011). In addition to their use for recording and documenting species presence, camera traps are also useful for recording their behavior, thus supporting the conduct of community-level analyses (Rowcliffe and Carbone 2008; Whitworth *et al.* 2016).

According to Halle and Stenseth (2000), studies on the temporal behavior of animals can be classified into two fields: 1) activity patterns, in which the activities of animals are examined during two periods of time: the active period, when animals perform activities such as foraging, defense of territory, exploration, and others; and the rest period, when animals carry out "comfort behavior", including sleeping, grooming, social contact, brood care, among others, and 2) time allocated to the various activities carried out by animals during the day.

Much of the knowledge on the activity patterns of mammals has come from studies on terrestrial species at ground level (*e. g.*, Van Schaik and Griffiths 1996; Gómez *et al.* 2005; Gliwicz and Dabrowski 2007; Chen *et al.* 2009), whereas arboreal mammal species have been scarcely studied, mainly due to the technical challenges involved in observing them in the forest canopy. However, the development of technology and affordable sampling techniques have made it possible to make progress in the study of the ecology of the forest canopy fauna (*e. g.*, Charles-Dominique 1975; Van Schaik and Griffiths 1996; Schipper 2007; Bowler *et al.* 2017; Whitworth *et al.* 2016).

The description of activity patterns initially targeted a few rodent species including, for example, the red squirrel (*Sciurus vulgaris*) in coniferous forests and the Panamanian climbing rat (*Tylomys panamensis*) in tropical ecosystems (Wauters 2000; Mendez-Carvajal *et al.* 2015). Fernández-Duque (2003) documented the activity pattern of the Azara's night monkey (*Aotus azarae*) in the western slope of South America, while Shipper (2007) monitored the kinkajou (*Potos flavus*) in Costa Rica. In recent years, similar studies have been carried out in tropical ecosystems around the world, particularly in Latin America, documenting the species richness of forest canopy mammals (Whitworth *et al.* 2016). One of the earliest studies on forest canopy mammals that adopted a community-wide perspective was conducted in Brazil (Oliveira-Santos *et al.* 2008), in which the authors were able to document the presence of at least 11 mammal species in five families. The use of camera traps as a means to gather data on various species has become common in Mexico (Mandujano 2019). However, studies focusing on the community of forest canopy mammals in the Mexican tropics have not yet been carried out or published. For this reason, gathering ecological information on forest canopy mammals is now essential. This study aimed to document the species richness of mammals inhabiting the tree stratum, describing their activity patterns, and evaluating the temporal overlap between them in a tropical forest on the Gulf of Mexico.

Materials and Methods

The study was conducted in the Santa Gertrudis Ecological Reserve (RESG, for its acronym in Spanish), located in the Municipality of Vega de Alatorre, State of Veracruz, Mexico (19º 51′ 49.22″ to 19º 33′ 35.25″ N and -96º 32′ 27.49″ to -96º 36′ 52.41″ W; Figure 1). The RESG is a 1,000-ha private property dedicated to nature conservation and decreed as a federal Zone for Forest and Fauna Protection (SARH 1982). The dominant vegetation is a semideciduous tropical forest in different successional stages located at the northernmost limit of the distribution range of the humid tropical forest in Mexico. The study area also includes riparian forests

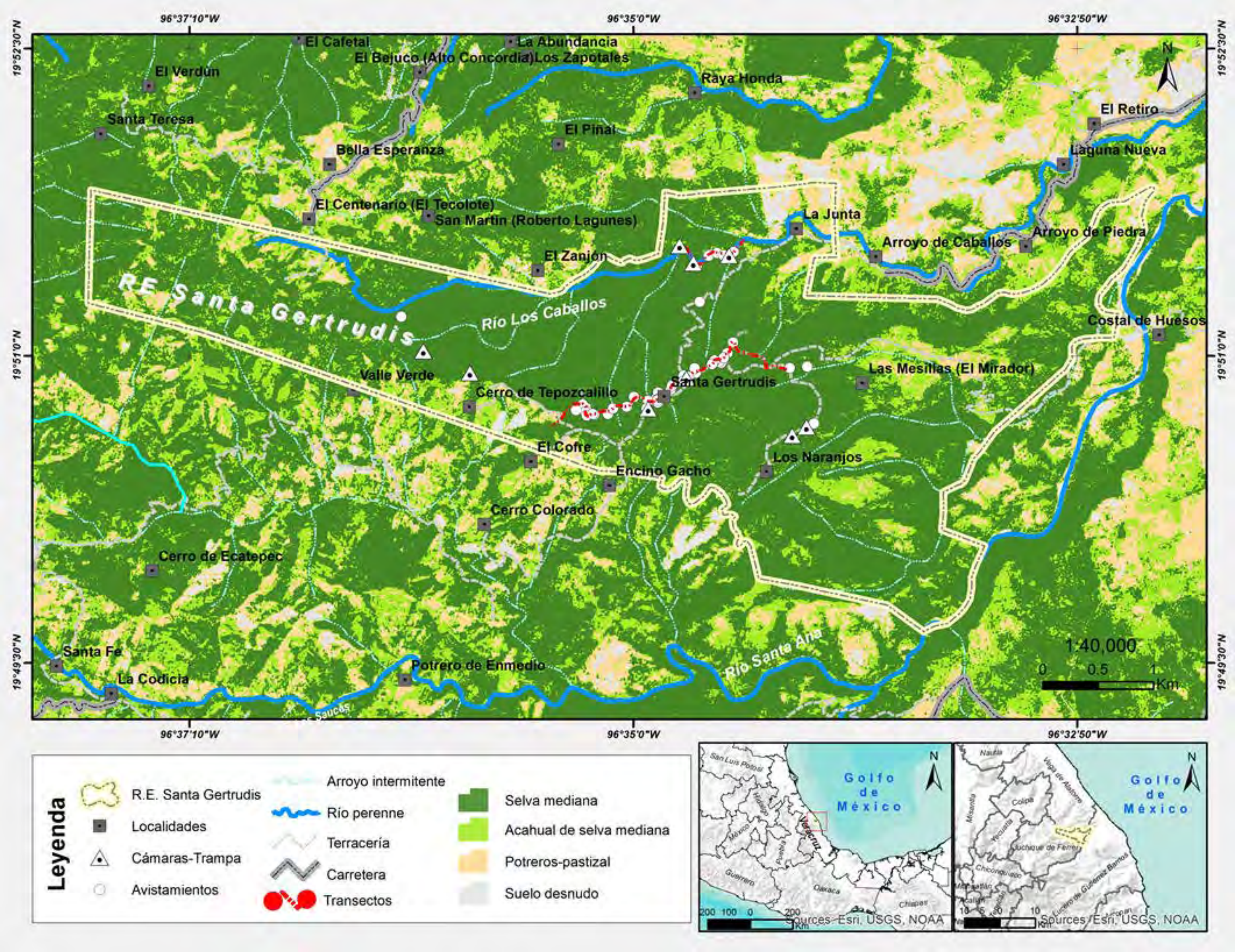


Figure 1. Map showing the location and boundaries of the Santa Gertrudis Ecological Reserve (RESG).

(Godínez-Ibarra and Lopez-Mata 2002), old coffee plantations, remnants of mountain cloud forests, and pastures (B. Vega Hernandez pers. comm). Elevation in the study area ranges between 80 and 940 masl and temperature, between 18.6 and 25.7 °C; the mean annual precipitation is 1,605 mm (CONAGUA 2016).

Data were collected employing camera traps over 12 months, from mid-February 2016 until mid-February 2017. Nine camera traps fitted with infrared motion sensors (Ltl. Acorn, Wild view Tk40, and Cuddeback C2) were installed. The camera traps were placed in the tree canopy (~8 to 12 m above the ground), affixed to the trunk; these cameras were set focusing on a branch overlapping a neighboring tree. These interconnections between trees are known as "canopy highways" that allow mammals to move between trees and increase their probability of detection (Schipper 2007). We used tree climbing gear and techniques to reach the tree canopy. Camera traps were left operating during the entire sampling period and were checked monthly to retrieve the images captured and replace the batteries. The cameras were set to shoot three photographs per event at 1-min intervals.

All consecutive photographs of different species, as well as all photographs of the same species separated by at least one hour, were regarded as independent records. The distance between cameras ranged from 300 to 1,500 m, depending on the terrain accessibility and availability of trees suitable for affixing the cameras. The trees selected had a diameter at breast height (DBH) ≥ 40 cm and at least one branch overlapping those of other trees. The mammals recorded were identified based on specialized guides and literature (*e. g*., Emmons and Feer 1997; Reid 1997, 2004).

Activity patterns were elucidated using the software Oriana 4.0 (Kovach 2011). As recommended by Ridout and Linkie (2009), only those species with at least ten independent captures were included in these analyses. The times of capture were considered as a random sample taken at any time of the day. The activity pattern of each species was classified based on the hourly records. Data were grouped according to the classification proposed by Van Schaik and Griffiths (1996), as modified by Gómez *et al.* (2005). We identified four periods of activity: 1) diurnal, species with ≥ 70 % of captures during the daytime, 2) nocturnal, species with ≥ 70 % of captures during the night-time, 3) crepuscular, 50-60% of captures during twilight (the period one hour before and one hour after dawn or dusk), and 4) cathemeral, species with captures that showed no distinctive pattern or were randomly distributed along the daily cycle.

We used the package Overlap for R 3.4.1 (R Core Team 2014) to compare the activity patterns and evaluate the overlap between species. The coefficient of overlapping, Δ, is defined as the area under the curve formed by taking the minimum of the two probability density functions at each time point (Ridout and Linkie 2009). The estimator Δ_1 is recommended for analyzing activity patterns when the number of records is less than 25 (Ridout and Linkie 2009). Coefficient values range from 0 to 1, with 0 indicating that the activities of species do not coincide at any time of the day, and ~1 or 1 that their times of activity are the same throughout the day (Ridout and Linkie 2009). We used the bootstrap method with 500 samples to construct 95 % confidence intervals for Δ_1 (Lynam *et al.* 2013).

RESULTS

We invested a total sampling effort of 2,664 camera-nights and collected 176 records of 12 species in seven families and four orders. All the species recorded showed a diurnal or nocturnal activity pattern; no species with crepuscular or cathemeral patterns were registered (Table 1).

Species Records and Abundance. The species most frequently recorded are common in tropical ecosystems (Table 1). However, we also recorded some species that are particularly important by their conservation status; these include the Mexican tree porcupine (*Coendou mexicanus*) and the margay (*Leopardus wiedii*), each with seven records, and the kinkajou (*P. flavus*) with 25records, the latter being one of the species most frequently recorded. It is worth noting that we documented two arboreal rodents: Peters's climbing rat (*Tylomys nudicaudus*), with 20 records, and the vesper rat (*Nyctomys sumichrasti*), with only one register. Our results show that the most abundant species was the Mexican gray squirrel (*Sciurus aureogaster*) with 53 records; the least abundant ones were two species in the family Didelphidae (*Marmosa mexicana* and *Philander opossum*) with one register each.

Daily Activity of Each Species. Only five of the 12 species recorded were included in the activity pattern analysis, due to the insufficient number (< 10) of independent records obtained for the remaining seven species (Table 1). Only one species, *S. aureogaster*, showed a diurnal pattern. The remaining four species were classified as nocturnal; their activity period comprised between 19:00 h and 5:00 h (Figure 2).

The activity of the four nocturnal species peaked between 22:00 h and 2:00 h and dropped towards dawn; they showed similar activity peaks. It should be noted that the activity period of the common opossum (*Didelphis marsupialis)* was more extended than those of the other species (Figure 2) and showed two activity peaks at both ends of the period: around 22:00 h and 4:00 h.

Overlap of Activity Patterns Only the four nocturnal species were included in the analysis of the overlap of daily activity patterns. *S. aureogaster* was excluded because its activity pattern was entirely diurnal, with no overlap with the pattern of other species.

The activity patterns of the four species examined showed a relatively high level of overlap; the overlapping coefficients, Δ_1, ranged from 0.696 to 0.919 (Figure 3). The estimated overall average overlapping of the combinations of the four species is close to 1 ($\Delta_1 = 0.801 \pm 0.065$ D. E.). *D. marsupialis* and *T. nudicaudus* were the species for which activity patterns showed the lowest overlap; the greatest overlap was found between *T. mexicana* and *P. flavus* (Figure 3).

Table 1. Species recorded, common name, number of independent records, abundance index, period of activity, and activity pattern.

Orden	Specie	Common name	Number of records	Abundance index	Time of activity	Activity pattern
Didelphimorphia	*Marmosa mexicana*	Mouse opossum or Tlacuatzin	1	0.375	Nocturnal	0:15
	Didelphis marsupialis	Opposum or Tlacuache	41	15.390	Nocturnal	19:00-5:40
	Philander opossum	Four Eyes Opposum or Tlacuache de cuatro ojos	1	0.375	Nocturnal	22:00
Pilosa	*Tamandua mexicana*	Anteater or Oso hormiguero	11	4.129	Nocturnal	21:50-5:02
Rodentia	*Nyctomys sumichrasti*	Arboreal rodent or Ratón	1	0.375	Nocturnal	00:25
	Tylomys nudicaudus	Arboreal Rat or Rata	20	7.507	Nocturnal	20:30-5:10
	Coendou mexicanus	Porcupine or Puercoespín	7	2.627	Nocturnal	20:00-5:00
	Sciurus aureogaster	Squirrel or Ardilla gris	53	19.894	Diurnal	6:40-18:40
Carnívora	*Leopardus wiedii*	Margay or Tigrillo	6	2.252	Nocturnal	20:10-4:44
	Bassariscus sumichrasti	Ringtail or Sietillo or huiloncha	2	0.750	Nocturnal	21:46-1:00
	Nasua narica	Tejón o Coatí	8	3.003	Diurnal	08:50-21:50
	Potos flavus	Kinkajou or Martucha	25	9.384	Nocturnal	20:30-4:50

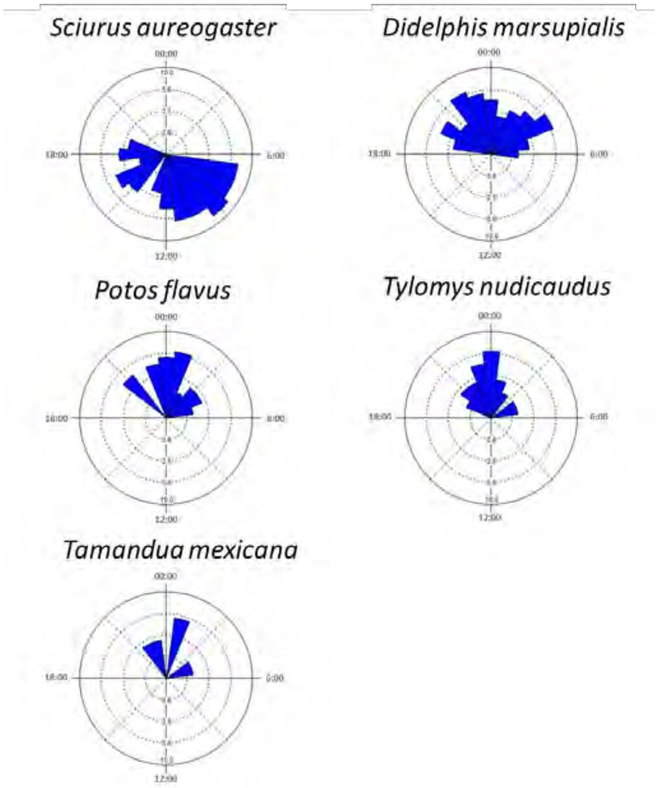
DISCUSSION

We recorded 12 of the 14 arboreal mammal species that have been reported for this region (González-Christen and Delfin-Alfonso 2016). Four of these species are listed in an extinction-risk category as the NOM-059-SEMARNAT-2010 (Diario Oficial de la Federación 2010, vr. 2019): the tropical cacomixtle or ringtail cat (*Bassariscus sumichrasti*) and the kinkajou (*Potos flavus*) are listed as under special protection; the Mexican tree porcupine (*Coendou mexicanus*), as threatened; and the margay (*Leopardus wiedii*), as endangered. Species not recorded in our study were the raccoon (*Procyon lotor*) and the tayra (*Eira barbara*). Gallina and González-Romero (2018) evaluated the diversity of terrestrial mammals in the RESG and recorded only nine species, including *P. lotor*, but did not record *E. barbara* either.

The Mexican gray squirrel (*S. aureogaster*) was active during the daylight period, a result consistent with that reported by Ramos-Lara and López-González (2017) for a pine-oak forest in the Sierra Gorda Biosphere Reserve (RBSG). A similar activity pattern was recorded for the gray squirrel in our study and the one by Ramos-Lara and López-González (2017), although a peak was recorded around 09:00 h in the RBSG, continuous activity was observed throughout the day, with no evident peak, in the RESG. This difference might be because *S. aureogaster* coexists with *S. oculatus* in the RBDG, which might lead to niche segregation. By contrast, no other squirrel that might compete for resources with *S. aureogaster* occurs in the RESG.

The observed activity pattern of *P. flavus* (see Figure 2) is consistent with the one documented in French Guyana (Julien-Laferriere 1993), although the activity peaks also differed. Our results show a unimodal activity pattern in the RESG, whereas it is bimodal in French Guyana (Julien-Laferriere 1993). This difference in activity peaks may be due to two reasons: 1) difference in sampling techniques, as Julien-Laferriere used telemetry to monitor three individuals for 12 days, which allowed him to track their activity 24 hours a day, and 2) difference in the ecological characteristics of the habitat (*e. g.*, climate, the structure of the tropical forest, food availability, presence of predators, among others) that might influence the activity patterns of *P. flavus*.

Our results show that the anteater (*T. mexicana*) had a nocturnal activity pattern (21:50-05:02 h); this is entirely different from what has been reported by other studies in tropical and subtropical ecosystems. For example, Brown


Sciurus aureogaster

Didelphis marsupialis

Potos flavus

Tylomys nudicaudus

Tamandua mexicana

Figure 2. Daily activity patterns of canopy mammals. Blue bars denote the number of records on each hour of the day.

(2011) concluded that the activity pattern of this species in Barro Colorado Island, Panama, can be considered *quasi* cathemeral with a tendency to diurnal (7:00 - 22:00 h) and a peak around 15:00 h. This species has been described as having highly variable habits, as they can be active during the daytime, the nighttime, or both (Montgomery 1985 a, b). The fact that the anteater displays a nocturnal activity pattern in some sites (as in this case) and diurnal in others evidences its ability to adapt to different or unfavorable situations (Montgomery 1985a, b; Brown 2011). One factor that might influence the observed activity pattern is the evasion of predators such as felines, raptors, or snakes (Izor 1985; Aranda 1994), or even poachers who often enter illegally the RESG with dogs (B. Vega Hernandez pers. comm.).

One factor that often limits the study of arboreal mammals is the low register success; a three-dimensional space such as the forest canopy makes detection difficult, as mammals can move along any of the three dimensions of the canopy. This is in clear contrast with ground-level studies in which only two dimensions are relevant, showing capture-success rates usually over 15 % (Tobler *et al.* 2008; Lira-Torres and Briones-Salas 2012). Gallina and González-Romero (2018) attained a 14.5 % capture success in the RESG.

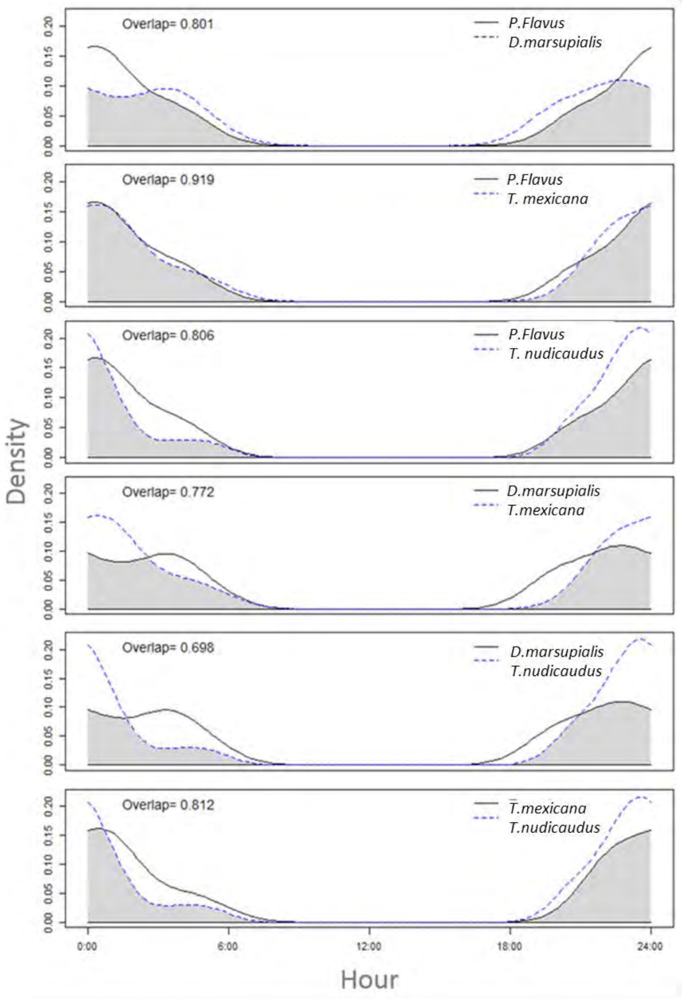


Figure 3. Overlapping between activity patterns of nocturnal species. The overlapping coefficient values range between 0 and 1. The gray area represents the overlap between the species.

Our study is a first effort to document the species richness and activity patterns of mammals in the canopy of a tropical forest in Mexico. We recognize the importance of observing and describing in detail the activity patterns of mammals inhabiting tropical and subtropical ecosystems, although we were somewhat limited in the number of records obtained for some species. In this regard, we suggest carrying out longer-term studies to better understand how assemblages of arboreal mammals are distributed in space and time, allowing species coexistence.

Acknowledgments

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Potential distribution of the Ocelot (*Leopardus pardalis*) in southern Sierra Madre Oriental and Sierra Negra, México

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The ocelot is one of the six species of felids distributed in Mexico. This species is threatened with extinction and thus protected by the Mexican government. Knowledge about the environmental factors that affect its presence is a crucial step in identifying key areas and designing strategies for the conservation of this species. The aim of this study was to document the presence of the ocelot to determine its potential distribution and identify important conservation areas in the southern Sierra Madre Oriental and Sierra Negra of Puebla (as part of the northern Sierra Madre del Sur). We conducted camera-trap surveys from October 2013 through January 2014, placing 63 camera-trap stations distributed in both areas. The overall sampling effort was 2,381 trap-days. The presence of the ocelot was recorded in the Sierra del Abra-Tanchipa Biosphere Reserve, in San Luis Potosi and Sierra Negra in Puebla. An estimated 78 % of the study sites hold suitable environmental conditions for the potential presence of ocelots. The variables that jointly accounted for 65 % of the potential distribution were related to precipitation, namely precipitation of the driest trimester, of the wettest month, and of the warmest trimester. Our potential distribution models suggest the existence of priority regions for ocelot conservation. This research updates the present status of the ocelot in the Sierra Madre Oriental and Sierra Negra in Puebla, sites that have been subject to high habitat encroachment by human settlements.

El ocelote es una de las seis especies de felinos que se distribuyen en México. Está especie se encuentra amenazada y por tanto protegida por el gobierno mexicano. El conocimiento sobre qué factores ambientales afectan su presencia es un paso crucial en el diseño o la propuesta de áreas de conservación para las especies. El objetivo de este trabajo fue documentar la presencia del ocelote para generar una distribución potencial e identificar sitios para su conservación en el sur de la Sierra Madre Oriental y Sierra Negra de Puebla (que es parte del norte de la Sierra Madre del Sur). Para ello, se realizó un muestreo con 63 estaciones de foto-trampeo distribuidas en ambas áreas entre octubre de 2013 y enero de 2014. En total, realizamos un esfuerzo de muestreo de 2,381 días/trampa. La presencia del ocelote se registró en la Reserva de la Biosfera Sierra del Abra-Tanchipa en San Luis Potosí y Sierra Negra en Puebla. Estimamos que el 78 % del área de estudio tiene condiciones ambientales adecuadas para la presencia potencial del ocelote. Las variables que tuvieron una contribución acumulada del 65 % para explicar su distribución potencial estuvieron relacionas con la precipitación y fueron tres: precipitación del trimestre más seco, del mes más lluvioso y del trimestre más cálido. Los modelos de distribución sugieren la existencia de sitios prioritarios para la conservación de ocelotes. Este trabajo representa un avance fundamental en la situación actual del ocelote y su área de distribución en la Sierra Madre Oriental y Sierra Negra en Puebla, sitios que han estado sujetos a presiones humanas.

Keywords: Conservation areas; camera traps; biological corridor; Maxent; ecological niche modeling.

Introduction

The ocelot (*Leopardus pardalis*) is one of six species of felids distributed in Mexico (Aranda 2005). The presence of this species in Mexico has been documented in areas ranging from semi-arid regions with xerophytic scrubs, dry tropical forests, to the coastal plains of the Pacific and Gulf of Mexico, including tropical rain forest, temperate and cloud forests, and mangroves in the Yucatan peninsula (Ahumada-Carrillo *et al.* 2013; Valdez-Jiménez *et al.* 2013; Aranda *et al.* 2014; Martínez-Calderas *et al.* 2011, 2015; Servín *et al.* 2016; Torres-Romero *et al.* 2017). Recent studies in America indicate that the ocelot is a species susceptible to habitat loss, leading to population fragmentation and isolation, producing a low gene flow that ultimately leads to genetic divergence, reduction in population size, and lower dispersal capacity (Janecka *et al.* 2014). For these reasons, it is considered that the current anthropogenic activities in the Sierra Madre Oriental (SMO) may be acting as major barriers restraining the connectivity of wild feline populations (Grigione *et al.* 2009; Villordo-Galván *et al.* 2010; Martínez-Calderas *et al.* 2011, 2015; Dueñas-López *et al.* 2015; Torres-Romero *et al.* 2017).

The Sierra Madre Oriental is considered an important biological corridor that maintains the connection between remnants of primary vegetation in eastern and southeastern Mexico, including those of the Sierra Negra in Oaxaca, Puebla, and Veracruz (Álvarez-Icaza 2013; Grigione *et al.* 2009; Dueñas-López *et al.* 2015). Suitable habitat patches have been found in this region, which can function as corridors for the survival and flow of different species of carnivores (Dueñas-López *et al.* 2015). However, the Sierra Madre Oriental and Sierra Negra in Puebla (SNP) are facing serious conservation problems such as land-use changes, fragmentation, and loss of vegetation cover, related to anthropic factors that could affect the presence of several felid species (Ortega-Huerta and Peterson 2008; Ramirez-Bravo *et al.* 2010; Villordo-Galván *et al.* 2010). In this sense, populations of jaguar, ocelot, cougar, jaguarundi, and their prey have been reported in regions of San Luis Potosi, which have survived given the presence of habitat patches in the region that provide coverage, food, and shelter for these species (Villordo-Galván *et al.* 2010; Martínez-Hernández *et al.* 2014; Dueñas-López *et al.* 2015; Hernández-Saint Marín *et al.* 2015).

In this regard , the generation of basic knowledge about the presence of the ocelot in an area (*L. pardalis*), a species related to landscapes with dense and broad forest coverage and little disturbance, may indicate a relatively low impact in such area and thus potential for its conservation or restoration (Aranda *et al.* 2014). For these reasons, its presence in areas with some degree of human disturbance will provide essential and useful information for the conservation of the species. An example of such areas is the southern Sierra Madre Oriental, a region that can be a biological corridor showing alterations in the landscape due to human impacts. Therefore, the objective of the present work was to record the presence of ocelot and predict, via an ecological niche modeling approach, the potential distribution of ocelot in the southern Sierra Madre Oriental and Sierra Negra in Puebla, seeking to identify and support priority sites for its conservation.

Materials and Methods

Study Area. The Sierra Madre Oriental is a mountain range spanning across 1,350 km with a width of at least 50 km and a maximum elevation of 2,500 m. This mountain complex stretches with a north-west-southeast direction, covering part of the Mexican states of Coahuila, Nuevo León, Tamaulipas, San Luis Potosi, Hidalgo, and north of Puebla (Ruiz-Jiménez *et al.* 2004). It encompasses a broad range of climatic conditions including warm, tropical, humid, temperate, and dry climates; with a mean total annual precipitation ranging from 139 to 3,377 mm (Hernández-Cerda and Carrasco-Anaya 2004). The structure of the landscape is heterogeneous, consisting of livestock and agriculture systems along with important vegetation types, including mountain cloud forests, seasonally dry tropical forests, temperate forests, humid tropical forests, and xeric scrublands. Of these, the xeric scrubland shows the most extensive distribution, while the mountain cloud forest is the most restricted (Contreras-Medina 2004; Suárez-Mota *et al.* 2017).

Sierra Negra in Puebla is a mountain range with a maximum elevation of 3,000 meters; it belongs to the physiographic province of the Sierra Madre del Sur and is located in the southern portion of the state of Puebla, bounded by Sierra Mazateca in Oaxaca and Zongolica in Veracruz (Lugo and Córdova 1992; INEGI 2009). It has a mean annual temperature ranging from 12 to 17 °C and total annual precipitation between 800 to 4,100 mm (INEGI 2009). It is home to a variety of habitats and vegetation types, including rainfed agriculture, cultivated pastures, mountain cloud forest, evergreen tropical forest, and pine forest (INEGI 2009). The study area was located in three regions, specifically the Sierra del Abra-Tanchipa Biosphere Reserve (RBSAT) in San Luis Potosi and Los Mármoles National Park (PNM) in Hidalgo; the Natural Resources Protection Area named Río Necaxa Hydrographic Basin (APRNCHRN) in Puebla; and Sierra Negra in Puebla (Figure 1).

Sampling Design. Sampling was carried out from October 2013 to January 2014 using StealthCam (Delta 8.0 Mpx®) digital camera-traps. Each camera trap was set to record wildlife both day and night during the 24-hour period, with a 3-second delay between photographic records. Each camera also recorded a 90-second video. The sampling design consisted of installing 63 simple photo-trapping stations distributed across the four sampling sites along the main roads, paths, or trails to maximize the likelihood of ocelot capture (Table 1). Trapping stations were spaced 1.5-2.0 km apart, considering the minimum area of activity of an adult female ocelot (Martínez-Meyer 1997; Torres-Romero *et al.* 2017).

Potential Distribution Modeling (MDP). Occurrence records of *L. pardalis* were obtained from fieldwork and from the scientific literature between 1990 and 2015, seeking to gather the highest number of records on the presence of ocelot in recent decades. The literature review was performed using the "ISI web of knowledge" database (https://www.accesowok.fecyt.es/). In addition, we included records of scientific collections such as the Colección de Foto Colectas Biológicas (CFB) of the Instituto de Biología

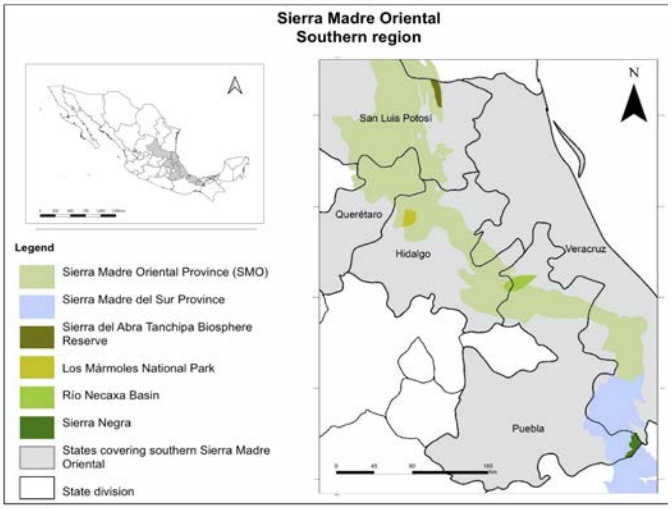

Figure 1. Study area and sampling sites of ocelot in the southern Sierra Madre Oriental.

at the Universidad Autonoma de México (http://unibio.unam.mx/collections/specimens/urn/IBUNAM:CFB:FB) and the databases: Global Biodiversity Information Facility (GBIF, www.gbif.org), Mammal Networked Information System (Manis, www.manisnet.org), Unidad Informática para la Biodiversidad (UNIBIO, www.unibio.unam.mx), and the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO, www.conabio.gob.mx). Then, occurrence records were reviewed for inconsistencies, discarding dubious and duplicate records, retaining 59 locality-unique records for analysis, nine coming from fieldwork and 50 from literature and databases.

We used the 19 digital climatic variables described for Mexico (Cuervo-Robayo *et al.* 2013). Each layer was in raster format at a 1 km^2 spatial resolution and adjusted clipped to the study region (Figure 1). We used presence records and climatic variables for modeling the potential distribution of *L. pardalis* using the maximum entropy algorithm Maxent ver. 3.3.3k (Phillips *et al.* 2006). We chose the following output settings for our models: maximum number of background points = 10,000, regularization multiplier = 1, replicates = 20, type of replication execution= bootstrap, convergence threshold = 0.00001, and maximum number of iterations = 10,000. We built models using 70 % as training data and the remaining 30 % for evaluation using the Area Under the Curve (AUC) generated by the Receiver Operating Characteristic (ROC) technique performed by the same Maxent program (Hanley and McNeil 1983). We assessed the contribution of each environmental variable with the Jackknife method implemented in Maxent. We converted the cumulative Maxent output to a binary map using the 10-percentile threshold value (Figure 2).

Next, we derived the landcover aptitude to support ocelot populations based on an analysis of the number of records of the species in land-use and vegetation classes obtained from INEGI (2011; available at: http://www.inegi.org.mx/geo/contenidos/recnat/usosuelo/; Table 1). To do so, we reclassified the land-use and vegetation classes in four categories based on the ecological requirements of the species (Anderson *et al.* 2002), obtained from the association between the presence of the species and vegetation types, as reported by several authors throughout its distribution range (Martínez-Calderas *et al.* 2011, 2015; Valdez-Jiménez *et al.* 2013; Ahumada-Carrillo *et al.* 2013; Martínez-Hernández *et al.* 2014; Servin *et al.* 2016; Table 2), as follows: optimal (suitable habitat), suboptimal (habitat with minimum environmental conditions for its presence), marginal, and inhospitable; the latter comprises unfavorable zones with no presence of ocelots due to disturbance and anthropic activity.

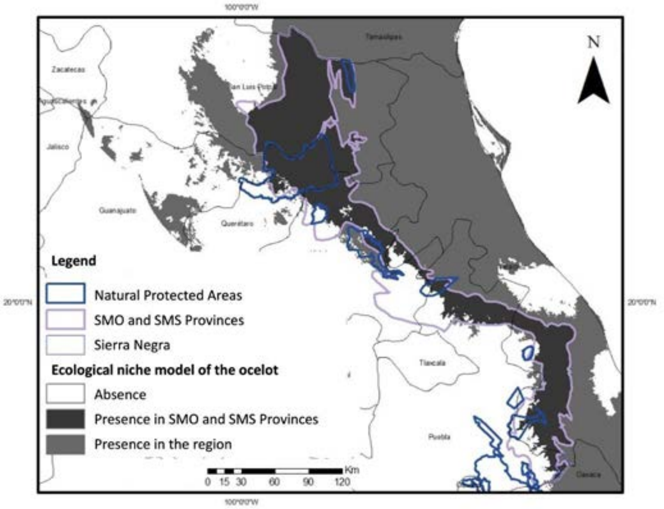

Figure 2. Potential distribution of ocelot for two areas: Study area (dark gray) and for eastern Sierra Madre Oriental (light gray).

Results

Ocelot Records. Photographic records of *L. pardalis* were obtained at two sampling sites: The Sierra del Abra-Tanchipa Biosphere Reserve, in San Luis Potosí, and Sierra Negra, in Puebla, with an overall sampling effort for both areas of 1,258 trap-days. We also recorded ocelot cubs in evergreen and deciduous tropical forests in both sites. By contrast, no ocelot records were obtained in Los Mármoles National Park and the Necaxa River Basin Natural Resources Protection Area with a sampling effort of 1,123 trap-days. Most phtographs (82 %) were captured below 1,000 m, with 260 m as the record at the lowest elevation, corresponding to the Sierra del Abra-Tanchipa; the record at the highest elevation was in Sierra Negra, at 1,117 m. We recorded ocelots in four types of vegetation: deciduous tropical forest (46 %), evergreen tropical forest (36 %), secondary vegetation (9 %), and riparian vegetation (9 %).

Potential Distribution and Suitable Habitat. Seventy-eight percent of the study area presented suitable environmental conditions for the presence of *L. pardalis*, while the remaining 22 % was identified as an unfavorable area (Figure 2). The unfavorable area is in the western portion of the Sierra Madre, bordering the Southern Highlands ("Zacatecano-Potosino") province and the Trans-Mexican Volcanic Belt. The mean AUC value for the *L. pardalis* distribution models was 0.825 (± 0.012). Thirteen environmental variables contributed to account for 100 % of the variation

Table 1. Sampling effort in each study site.

Study sites	Period (2013/2014)	Duration (days)	Photo-trapping stations	Trap-nights
Sierra del Abra-Tanchipa Biosphere Reserve	4 Nov. - 7 Dec. 2013	34	20	680
Los Mármoles National Park	8 Oct. - 23 Nov. 2013	47	17	799
Natural Resources Protection Area named Río Necaxa Hydrographic Basin	13 Dic. 2013 - 17 Jan. 2014	36	9	324
Sierra Negra	14 Dec. 2013 - 16 Jan. 2014	34	17	578
Total			63	2,381

in the potential distribution of ocelot (Precipitation of Driest Quarter; Bio17) , Precipitation of Wettest Month (Bio13), Precipitation of Warmest Quarter (Bio18), Precipitation Seasonality (Bio15), Precipitation of Wettest Quarter (Bio16), Temperature Seasonality (Bio04), Isothermality (BIO2/BIO7; Bio03), Min Temperature of Coldest Month (Bio06), Temperature Annual Range (Bio07), Mean Temperature of Wettest Quarter (Bio08), Precipitation of Driest Month (Bio14), Annual Mean Temperature (Bio01), Max Temperature of Warmest Month (Bio05), but only three explained 65 % of the predicted potential distribution: precipitation of the driest trimester (bio 17), precipitation of the wettest month (bio 13), and precipitation of the warmer trimester (bio 18). We obtained eight vegetation types for optimal zones, 15 for suboptimal zones, 18 for marginal, and 9 for inhospitable (Table 1). Based on this classification, 17 % of the habitat was optimal; 33 % sub-optimal, 19 % marginal, and 31 % inhospitable (Figure 3).

Discussion

*Presence of the Species in the Study Areas***.** In the Sierra del Abra Tanchipa Biosphere Reserve and Sierra Negra, the ocelot was present with males and females, the latter accompanied by offspring. The presence of offspring in a population is worth stressing, mainly because it is indicative of recruitment and turnover of individuals. Most presence records occurred at elevations below 1,000 m (82 %), a finding consistent with Aranda (2005). In previous works, the deciduous and evergreen tropical forests were habitats with the highest incidence of ocelot records (Ramirez-Bravo *et al.* 2010; Martínez-Calderas *et al.* 2011), in agreement with our findings. Interestingly, we recorded no individuals in Los Mármoles National Park or the Necaxa River. However, other studies conducted subsequently reported several carnivorous species, including ocelot, in Los Mármoles (Aguilar-López *et al.* 2016), although the analysis of the records is not specified in detail. Our modeling results suggest that Los Mármoles likely includes suitable habitat to harbor ocelot populations, or at least it can function as a corridor.

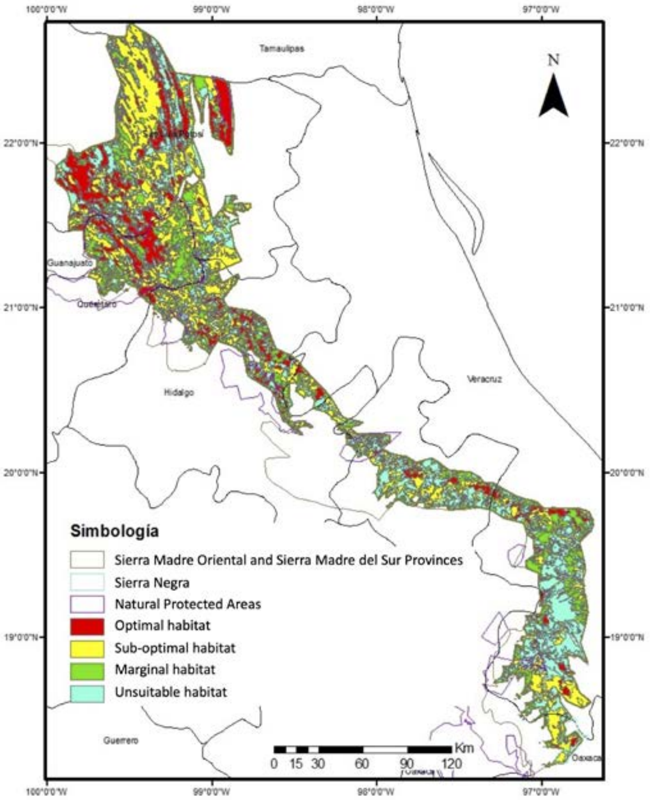

Figure 3. Classification of habitat aptitude for the potential presence of ocelot and landscape connectivity in Sierra Madre Oriental.

In Sierra del Abra Tanchipa Biosphere Reserve, most of the core, buffer, and use areas remain undisturbed; however, the habitat surrounding this reserve to the south is continuously transformed for use in agriculture and livestock raising. The polygon of the Reserve holds a large patch of primary vegetation that is possibly used by ocelots as a transit corridor in SMO (Table 2). It is worth mentioning that, besides the ocelot population located in the Sierra del Abra-Tanchipa (Martínez-Hernández *et al.* 2014), a second population known for eastern Mexico is located in Sierra Negra (Galindo-Aguilar *et al.* 2016). Sierra Negra is an area still covered by patches of primary vegetation and optimal and sub-optimal habitats that favor the presence of ocelots and some potential prey (Galindo-Aguilar *et al.* 2016).

Potential Distribution Models. The potential distribution model of *L. pardalis* is useful for exploring aspects related to its conservation in the study area. The results obtained are consistent with the habitat quality and connectivity models obtained for northeastern Mexico (Martínez-Calderas *et al.* 2011, 2015). Precipitation regimes are important in the distribution of various species of wild mammals such as felids and ungulates in Mexico (Carrillo *et al.* 2015; Martínez-Calderas *et al.* 2011, 2015; Ortíz-García *et al.* 2012), and rodents in Arizona, US (Morrison *et al.* 2002). In addition, tropical environments with high rainfall are usually associated with the presence of various trophic guilds (predators and prey; Di Bitetti *et al.* 2008). These results are consistent with our findings, where the potential distribution model suggests that precipitation of the driest trimester, the wettest month, and the hottest trimester contributed to explaining over 60 % of the potential distribution of ocelot in the southern Sierra Madre and Sierra Negra in Puebla.

*Importance of Sierra Madre Oriental, Sierra Negra, and Human Impac***.** We recorded ocelot offspring in evergreen and deciduous tropical forests, which are the vegetation types with the lowest degree of human disturbance. The presence of offspring is an important attribute indicating that populations are reproductively active and the sites where offspring were recorded hold the ecological requirements for the species to reproduce and persist (Hernández-Huerta 1992; Sunquist and Sunquist 2002). This finding indicates the importance of the remaining deciduous and the evergreen tropical forests patches, as both vegetation types likely function as habitats providing shelter, food, resting sites, and security to protect their offspring from predators. The areas surrounding Sierra del Abra-Tanchipa show a high degree of fragmentation; however, there is a resident population of *L. pardalis* in the Reserve (Martínez-Hernández *et al.* 2014). Probably, ocelots and other felines use patches of vegetation that favor their mobility and dispersal to other vegetation remnants, thus promoting the recolonization of other areas (Espinoza-Medinilla *et al.* 2018).

Our results suggest that the southern portion of the Sierra Madre Oriental, specifically the State of San Luis Potosi and Sierra Negra, still maintain little disturbed areas of vegetation that, as a whole, are likely to function as a priority north-south biological corridor (Grigione *et al.* 2009; Dueñas-López *et al.* 2015). For example, ocelots have been reported in some areas of Hidalgo and Puebla (Hernández-Flores *et al.* 2013; Ramirez-Bravo *et al.* 2010; Aguilar-López *et al.* 2016), which may indicate the mobility of ocelots across the Sierra Madre and Sierra Negra.

Table 2. Habitat aptitude based on the number of records of ocelot presence and the land-use and vegetation variables according to its ecological requirements.

Classification of Habitat Aptitude	**Land Uses and Vegetation Types**	
	Primary Vegetation	**Secondary Vegetation**
Optimal	Evergreen tropical forest Deciduous tropical forest Subdeciduous tropical forest Mountain cloud forest Crassicaule scrubland Microphyll scrubland Rosetophilous Scrubland Submontane scrubland	
Sub-optimal	Oak forest Pine forest Oak-pine forest Pine-oak forest Fir forest Juniper forest	Evergreen tropical forest Deciduous tropical forest Semi-evergreen tropical forest Subdeciduous tropical forest Mountain cloud forest crassicaule scrubland Microphilic desert scrubland Rosetophilous desert scrubland Submontane scrubland
Marginal	Secondary Vegetation	Agroecosystems
	Oak forest Pine forest Oak-pine forest Pine-oak forest Fir forest Juniper forest Mezquite woodland Gallery forest Chaparral Gallery vegetation Gallery tropical forest	Cultivated and induced forest Cultivated and induced pastures Natural and induced palm-dominated forest Xerophilous halophilic vegetation Halophilic grassland Xerophilic mezquital Xerophilous halophilic vegetation
Inhospitable	Agriculture Human settlements Body of water barren land High mountain meadow Tular No apparent vegetation Halophilic hydrophilic vegetation Urban zone	

High levels of anthropogenic habitat disturbance may force individuals to migrate into ecosystems with ecological or biological characteristics that are less suitable for survival (Oliveira 1994). Our results from the potential distribution model suggest that Los Mármoles and the Necaxa River did not present optimum environmental conditions for the presence of ocelots, although these may function as transit areas. In this regard, the subsequent record in Los Mármoles (Aguilar-López *et al.* 2016) suggests that the region may be used as a transit area towards the southern Sierra Madre, indicating that the ocelot is probably tolerant to certain degree of human disturbance (Galindo-Aguilar *et al.* 2016).

Based on our classification of habitat aptitude, the areas that recorded the presence of ocelot exhibited ideal conditions for them to function as biological corridors along the Sierra Madre and Sierra Negra, according to the red and yellow polygons shown in Figure 3. Therefore, we suggest implementing a systematic monitoring in areas adjacent to the study area to determine the extent to which human stressors affect the distribution of ocelots in the Sierra Madre and Sierra Negra. Besides, a molecular study should be conducted to investigate the genetic identity of this population and its relationship with the populations of Oaxaca and southeastern Mexico. Recording ocelots in adjacent areas is deemed relevant information that will enable the development of a more robust habitat connectivity model to advance better knowledge of a possible north-to-south dispersal of ocelot populations. Animal mobility is critical for preserving demographically and genetically healthy populations for conservation (Shepard *et al.* 2008). The fragmentation of the Sierra Madre, in particular, is especially worrying and is a problem that needs to be addressed strategically for the long-term conservation, not only of the ocelot, but of the biodiversity that coexist with it (Escalante *et al.* 2005).

This study contributes with basic, yet indispensable information for the conservation of the ocelot. Our results highlight that precipitation variables are related to the distribution patterns of the ocelot in the Sierra Madre and Sierra Negra.

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