

# Therya

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AMMAC

### La Portada

La musaraña de Los Tuxtlas, *Cryptotis nelsoni*, es una de las especies de mamíferos más amenazadas en México. Esta imagen no solo simboliza uno de las características peculiares de las musarañas, el hocico pronunciado, sino lo muy poco que aun conocemos acerca de este grupo de pequeños mamíferos (Fotografía de Lázaro Guevara)

### Nuestro logo "Ozomatli"

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

### Las musarañas son importantes

“Hay muertos que no hacen ruido, Llorona, y es más grande su penar” versa “La Llorona”, una de las canciones más populares dentro de la cultura mexicana. Nada más parecido a esto es el caso de las musarañas, un grupo altamente amenazado por el cambio global actual, pero más aún por el desconocimiento en torno a ellas. A pesar de su penar, muy pocos son los mastozoólogos interesados en las musarañas.

#### Un poco sobre musarañas

Las musarañas se caracterizan por su tamaño relativamente pequeño, ojos diminutos, hocico largo y delgado, pelaje denso y por su apetito voraz que las obliga a alimentarse constantemente y casi exclusivamente de anélidos y artrópodos, lo cual las convierte en controladores naturales de sus poblaciones (ver imagen de portada). Son parte de uno de los órdenes más diversos y ampliamente distribuidos en el planeta: el orden Eulipotyphla. Además de las musarañas (familia Soricidae), este orden también incluye a los erizos (familia Erinaceidae), topos (familia Talpidae) y solenodones (Solenodontidae). Las musarañas o sorícidos son el grupo más diverso dentro del orden Eulipotyphla (85 %; [Woodman 2018](#)), conteniendo a casi 500 especies repartidas en 25 géneros ([Burgin and He, 2018](#)). Los sorícidos se encuentran entre los linajes de mamíferos más viejos que existen y que se han adaptado a una gran variedad ambientes, desde los desiertos hasta los bosques lluviosos y la tundra.

Las musarañas también pertenecen al grupo de los mamíferos no carismáticos. Su apariencia de ratón casero, la dificultad de observarlas, y los mitos que las rodean, han provocado que la sociedad, los estudiantes e investigadores muy difícilmente se vean interesados en conocerlas y estudiarlas. En Latinoamérica el caso es incluso menos alentador. En esta región ellas se encuentran entre los mamíferos menos representados en colecciones biológicas y entre los menos estudiados. Esto es debido a la dificultad que implica tanto su captura en campo y la identificación taxonómica. En esta región, las musarañas suelen habitar regiones remotas e inhóspitas que hacen muy difícil el trabajo de campo, lo que complica la obtención de la información más básica. Antes del inicio del siglo XXI, la colecta de musarañas en Latinoamérica podría definirse como contingente, debido a su colecta accidental al tratar de muestrear diversas especies de roedores. Hoy en día, algunas especies aún se conocen solo de la localidad tipo

(e. g., *Sorex stizodon*) o no han sido colectadas nuevamente durante varias décadas (e. g., *Sorex sclateri*). En contraparte están las que apenas están siendo descubiertas y descritas, como los casos de *C. lacandonensis*, *C. dinirensis* y *C. monterverdensis*; otras probablemente están en el camino de la extinción debido a actividades humanas. Ante el notable vacío de información sobre su distribución y diversidad actual, no ha sido posible realizar una adecuada valoración del estado de conservación de la mayoría de especies de musarañas en Latinoamérica.

#### Lo que falta

Yo empecé a estudiar musarañas en México hace cerca de 15 años, gracias a la iniciativa del curador de la Colección Nacional de Mamíferos del Instituto de Biología de la UNAM, Fernando A. Cervantes. Con el esfuerzo de estudiantes de licenciatura, maestría y doctorado, durante este tiempo hemos realizado trabajo de campo, revisión de ejemplares en colección, depuración de bases de datos y estudios de taxonomía, sistemática y biogeografía de especies principalmente mexicanas. No tengo duda que se ha avanzado en su conocimiento, pero también debo reconocer con profunda pena que todavía no ha sido lo esperado. Aun existen pocos, muy pocos estudiantes interesados en el estudio de musarañas a largo plazo, lo que se refleja en pocas publicaciones científicas. En los Congresos bianuales que organiza la Asociación Mexicana de Mastozoología A. C., son pocas o a veces nulas las presentaciones que abarcan algún aspecto de las musarañas. Simplemente, no hay un club de “musarañólogos”. Echar a andar este fascículo especial sobre musarañas es un claro ejemplo de lo mucho que aun falta por promover el estudio de estos mamíferos pequeños.

A pesar de todo esto, aquí estamos, intentado dar a conocer un poco más acerca de este grupo fascinante de mamíferos. La intención de este número especial va más allá de generar y compartir este conocimiento, sino para inspirar a las nuevas generaciones de jóvenes mastozoólogos para que inviertan su tiempo, esfuerzo y corazón, en estudiar grupos extraordinariamente diversos pero muy poco atendidos en nuestra región, tal como las musarañas. ¿Oportunidades? Muchas. Por ejemplo, debido a que son altamente vulnerables al cambio global, tal como los efectos asociados con la destrucción del hábitat y por el cambio climático, son un grupo idóneo para evaluar el efecto potencial de las actividades antropogénicas en la biodi-

versidad (Scholss *et al.* 2011; Guevara *et al.* 2015). Por otro lado, la importancia de las musarañas en interacciones hospedero-parásito está aún en pleno desarrollo en la región. Los estudios de anatomía y fisiología son prácticamente nulos, por lo que aun desconocemos el potencial de estas especies para adaptarse a las presiones que ejerce el mundo actual sobre los ecosistemas. El trabajo de campo hacia lugares poco explorados muy probablemente arrojará luz nueva sobre los patrones de distribución, así como sobre la variación genética y fenotípica en poblaciones naturales. Estos son solo algunos ejemplos que, desde mi perspectiva, ofrecen un oportunidad inigualable para estudiar aspectos básicos, pero prioritarios en nuestra región.

## Agradecimientos

Agradezco a todos los autores invitados que están participando con sus contribuciones, ya que ustedes son parte crucial de este esfuerzo noble de dar a conocer un poco más sobre las musarañas. En el plano más personal e íntimo, agradezco a todas personas que viven en la Latinoamérica de hoy y que, a pesar de las dolencias y “carencias”, nos han abierto sus puertas en los lugares más remotos para que podamos pernoctar, dejar nuestro equipo de campo o simplemente pasar a beber un poco de agua o una taza de café mientras hemos estado en busca de musarañas. Todas esas personas nos han ayudado a ver las verdaderas riquezas con las que cuenta nuestra región, más allá de las musarañas.

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# Differentiation pattern in the use of space by males and females of two species of small mammals (*Peromyscus difficilis* and *P. melanotis*) in a temperate forest

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The distribution patterns of individuals together with mechanisms that maintain them have significant implications for population-level processes. Sex-specific differences in home-range may strongly influence the spatial distribution of individuals, while the differential use of space by the sexes can yield insights into the mating system and the life history of the species. Sexual differences in the use of space could be due to different habitat requirements during the breeding season. This is interesting because the males and females likely are interacting with operational sex ratios and mating strategies. Here, we evaluated for ten months of the year 2014, the spatial patterns of ecological distribution in males and females of two species of deer mice (*Peromyscus difficilis* and *P. melanotis*) that coexist in a temperate forest. Also, we assessed the variation in the use of space by males and females in both *Peromyscus* species and we analyze the intensity of positive association or repulsion between males and females. During drought and rain seasons, males and females of both *Peromyscus* were captured. The sex and reproductive status of each were identified. To analyze the spatial patterns of ecological distribution, we used the Nearest Neighbor Analysis. Kernel spatial analysis was performed to evaluate the variation in the use of space of males and females between seasons. The Ripley's K bivariate function was carried out to assess the positive association or repulsion between males and females in each season. We found a different use of space between sexes. Our evidence shed light on the respective life histories of these species and provides information on possible factors that they may be using to coexist successfully among them. We conclude that in this temperate coniferous forest: 1) use of space by *P. difficilis* and *P. melanotis*, is influenced by both sex and by the reproductive season, and that this pattern varies, according to shifts on ecological conditions that promote variation and availability of resources during the two pluvial seasons; 2) there are interspecific differences in the use of space with conspicuous intraspecific differences in females and males of *P. difficilis* (e. g., males are more territorial, and both sexes only become more clustered during the breeding season), while both sexes of *P. melanotis* are more gregarious; and 3) there is a clear differentiation in the reproductive seasons of both species that could be related to resources availability, such as shelters and food.

Los patrones de distribución de los individuos junto con los mecanismos que los mantienen, tienen implicaciones significativas en los procesos que ocurren a nivel poblacional. Las diferencias sexo-específicas en el ámbito hogareño pueden influenciar fuertemente la distribución espacial de los individuos, mientras que el uso diferencial del espacio por los sexos puede ayudar a comprender los sistemas de apareamiento y la historia de vida de las especies. Las diferencias sexuales en el uso del espacio por las especies podría deberse a los distintos requerimientos de hábitat que tienen los individuos durante su época reproductiva, esto es especialmente interesante por que los machos y las hembras probablemente están interactuando con proporciones de sexo operacionales y distintas estrategias de apareamiento. Aquí, evaluamos durante diez meses del año 2014, los patrones espaciales de distribución ecológica en los machos y las hembras de dos especies de "ratones ciegos" (*Peromyscus difficilis* y *P. melanotis*) que coexisten en un bosque templado. También, evaluamos la variación en el uso del espacio por parte de ambos sexos en las dos especies de *Peromyscus* y analizamos la intensidad de asociación positiva o repulsión entre los machos y las hembras. Durante las épocas de secas y lluvias del año 2014, capturamos a individuos machos y hembras de ambos *Peromyscus* así como identificamos el estado reproductivo de cada individuo. Para analizar los patrones espaciales de distribución ecológica, usamos el "análisis del vecino más cercano". El análisis espacial de Kernels fue utilizado para evaluar la variación en el uso del espacio de machos y hembras entre épocas. Mientras que la función bivariada K de Ripley fue usada para evaluar la asociación positiva o repulsión entre machos y hembras en cada época. Los resultados demostraron el uso distintivo del espacio entre los sexos, y mostraron evidencia sobre las respectivas historias de vida de estas especies y brindan información sobre posibles factores que pueden estar usando para convivir exitosamente entre ellas. Concluimos que en este bosque templado de coníferas: 1) el uso del espacio por *P. difficilis* y *P. melanotis*, está influenciado por el sexo de los individuos y por las épocas reproductivas de cada especie, estos patrones varían de acuerdo a los cambios que ocurren en las condiciones ecológicas (i. e., variación en la disponibilidad de recursos) durante las dos épocas (secas y lluvias), 2) hay diferencias interespecíficas así como diferencias intraespecíficas visibles en el uso del espacio entre las hembras y los machos de *P. difficilis* (e. g., los machos son más territoriales y ambos sexos solo se agrupan más durante la temporada de reproducción), mientras que ambos sexos de *P. melanotis* se comportan de manera más gregaria, y finalmente, 3) hay una clara diferenciación en las épocas reproductivas de ambas especies que podría estar relacionada con la disponibilidad de recursos, como refugios y alimentos.

**Keywords:** ecological distribution; *Peromyscus*; spatial analysis; small mammals; use of space.

## Introduction

Spacing patterns of individuals together with mechanisms that maintain them have significant implications for population-level processes (Adler 2011). For instance, sex-specific differences in home-range may strongly influence the spatial distribution of individuals (Blondel *et al.* 2009), while differential use of space by the sexes can yield insights into the mating system, thus improving our comprehension of little-studied species (Ostfeld *et al.* 1985; Gaulin and Fitzgerald 1988; reviewed in Clutton-Brock 1989, 1991; Heske and Ostfeld 1990). Indeed, rodents exhibit intra-sexual differences in home range sizes and spacing patterns, since male home-ranges are more extensive than those of females (Bowers and Smith 1979; Morris 1984; Kamler and Gipson 2003; Blondel *et al.* 2009). Also, spatial partitioning between the sexes (Morris 1984) may result from competitive interactions for habitat-based resources in short supply, such as foraging areas or refuge cover, or from intrinsic differences on reproduction roles (*e. g.*, females select a dense cover for natal care). Although males and females must cooperate for sexual reproduction, their best reproductive strategies to maximize fitness, frequently conflict with one another (Parker 1979; Arnqvist and Rowe 2005; Morris and MacEachern 2010). These differences between the sexes in habitat requirements are especially interesting because they are likely to interact with operational sex ratios and mating strategies (Morris and MacEachern 2010).

The space partition by sexes can become very complex when they have to coexist or compete with their counterparts in another congeneric species, especially if habitat heterogeneity also varies spatiotemporally (De-la-Cruz *et al.* 2018). For instance, temporal fluctuations can stabilize coexistence via storage effect (Chesson 2000), when inter-annual variation in climate or resource availability favors alternatively one group of species over the others (Zavaleta *et al.* 2003). Therefore, in order to document how sexual partition of space is influenced by breeding season and by the presence of another congeneric species, here we studied the differential use of space by males and females of two species of deer mice (*Peromyscus difficilis* and *P. melanotis*) in two seasons (drought and rain) in a temperate coniferous forest in Central Mexico. Hence, our four objectives were: 1) to analyze capture variation in males and females for both species; 2) to identify spatial patterns of ecological distribution (dispersion) of each sex for both species; 3) to assess variation in the use of space by males and females in each species, and 4) to analyze the intensity of association or repulsion within and between the sexes in the two species.

## Methods

**Study system.** Our biological models were two syntopic species of *Peromyscus* in a temperate mountain forest in Central Mexico. *Peromyscus difficilis* (J. A. Allen, 1891) is an endemic species with scansorial to semiarboreal locomotion, which dwells in a wide variety of habitats, from dry and semiarid hills to montane forests (Fernández *et al.* 2010). *P. difficilis*

is considered a medium-sized mouse (total length 180 to 260 mm) with a long tail (91.0 to 145.0 mm). *Peromyscus melanotis* (J. A. Allen and Chapman 1897), is a mostly ground-dwelling (cursorial), quasi-endemic species, whose range overlaps extensively with the former deer mouse (Álvarez-Castañeda 2005). *P. melanotis* is considered a small size mouse (total length 140 to 177 mm) with a small tail (49 to 75 mm). In the Transmexican Neovolcanic Belt, *P. melanotis* is restricted to the mountainous highlands with pine-fir forests (Álvarez-Castañeda 2005) and mixed forests of coniferous and broad-leaved trees (Carleton 1989).

**Study area.** We worked in a temperate forest (conifers and broad-leaved trees) at the National Park Desierto de Los Leones (PNDL; CONANP 2006), Mexico City, within the Transmexican Neovolcanic Range. Temperature averages  $12.6 \pm 6$  °C from April to July, while it descends to  $8.1 \pm 2$  °C from December to February. Rainfalls occur from late spring throughout summer (May to August), with average precipitation of  $235 \pm 30$  mm, though this period can go until mid-fall (October). From winter to early spring (December to March), precipitation average becomes  $12 \pm 4$  mm, introducing dry and cold weather (CONANP 2006). Dominating vegetation by strata includes: canopy, *Abies religiosa*, *Pinus hartwegii*, *P. leiophylla*, *P. montezumae*, *Prunus serotina*, *Garrya laurifolia*, *Salix paradoxa*, and *Buddleia cordata*; understory shrubs, *Baccharis conferta* and *Senecio spp.*, and understory herbs, *Acaena elongata*, *Sigesbeckia jorullensis*, and *Alchemilla procumbens*; ground level, a rich variety of mosses and fungi (CONANP 2006).

**Mice sampling design.** We captured mice along ten months to include either dry season (October 2013 to February 2014) and rain season (March 2014 to July 2014), within a 2,475 m<sup>2</sup> surface plot at an altitude of 2,289 m. The plot was configured as a grid (12 vertical lines, A - L; 10 horizontal lines, 1 - 10) marking intersections each 5 m with buried wood stakes (150 x 2.5 x 2.5 cm) to construct a coordinate system for independent sampling stations, where we set 120 Sherman live traps (Tallahassee, FL 32303, USA), baited with oat flakes and vanilla scent (Ramírez *et al.* 1989). Each independent sampling station was considered as a replicate of each other. Therefore, each month, we set traps for two continuous nights (in total we carried out 20 capture events resulting in 2,400 trap-nights), shortly before dusk, left open overnight, and checked at next day dawn. To avoid bias in the abundance and use of space of both *Peromyscus* during each sampling session, we used a temporal mark (gentian violet applied in the abdomen of the mice) to identify the captures and recaptures. If we saw signals that the gentian violet was disappearing in the abdomen of the mice, we applied it again. This temporal mark enabled us to count the net frequency of the individuals in each microhabitat. We carried out an initial analysis with the recaptures, and we found the same patterns that we obtained with the first frequency (without recaptures). Thus, for the analyses, we used only the first capture data for each of the 120 sampling stations during all trapping sessions. All the

traps were cleaned, and bedding was changed at each trap check event (Brouard et al. 2015). Also, to avoid bias in the frequency quantification due to recurrence behavior or shyness of the mice to the trapping, in all capture sessions the traps were moved within an influence zone of 2.5 m<sup>2</sup> that was assigned to each sampling station (Brouard et al. 2015). Coordinates of all trapped mice were recorded, and the species and sex, and reproductive activity determined through visual inspection.

**Statistical analysis.** To map variations in point density captures of small mammals, and to find density gradients across the plot area, we used the Kernel function. To test for type of ecological dispersion patterns (*i. e.*, clustering or overdispersion) for males and females of both species within the plot, at each season, we used a “Nearest Neighbor Analysis” (Clark and Evans 1954), applying the wrap-around edge effect adjustment, which is only appropriate for rectangular domains, as our plot. In general, the “Nearest Neighbor Analysis” compares the mean distance of each from its nearest conspecific neighbor with the mean distance expected for a set of points randomly dispersed at the same density (Vázquez and Álvarez-Castañeda 2011). The ratio of the observed mean distance to the expected distance ( $R$ ) indicates how the observed distribution deviates from random. Clustered points give  $R < 1$ , Poisson patterns give  $R \sim 1$ , while overdispersed points give  $R > 1$ . We performed these analyses in PAST software (ver. 3.14, Hammer et al. 2001).

To assess whether the sexes were associated or disassociated within and between species, we compared its dispersion patterns using Ripley’s K bivariate function (Ripley 1977), since the method considers all distances among individuals located under a Cartesian scheme (X, Y) in a quadrat plot (Ripley 1977; Dale 1999; Zavala-Hurtado et al. 2000). We used PASSaGE (ver. 2, Rosenberg and Anderson 2011) to carry out Ripley’s bivariate K analysis. We used the option to test the associations conditional on current locations hypothesis in PASSaGE. In this test, the point locations remain fixed, and only the types are randomized (the sexes). The number of each type remains fixed, but the association of each type with a specific, fixed location is randomized. In this case, one is not testing whether the points are themselves random or clustered, but rather whether the association of type A with type B (males vs. females) is what one would expect given the locations of the points as fixed (Rosenberg and Anderson 2011). We assigned coordinates to each sampling stations considering 5 m distance between them. Therefore, because each sampling station had a Cartesian coordinate system, we used as data input for each station where we capture mice. Thereby, our null hypothesis involved independence between females and males (Ripley 1977; Dale 1999), since we were interested in whether points of a specific type (*e. g.*, females) were associated, or disassociated, with points of the other specific type (*e. g.*, males). In other words, Ripley’s  $K_{12}(d)$  allowed us to assess spatial attraction or repulsion between the sexes within and between species, among

the stations of the plot. To evaluate the statistical significance of  $K_{12}(d)$ , we estimated 95 % confidence envelopes (95 % CI), using a Monte Carlo procedure, based on 1000 stochastic relocation simulations of the sampling stations in the plot (Upton and Fingleton 1985; Zavala-Hurtado et al. 2000). When  $L(d)$  was positive and took values over the upper limit of the confidence region, we inferred dissociation or repulsion between the sexes at the corresponding ( $d$ ) scale; whereas a significant negative deviation indicated us a pattern of association or attraction between the two sexes (Dale 1999). If  $L(d)$  remains within the limits of the 95 % CI for a given value of  $d$ , the null hypothesis of independence between the two contrasts cannot be rejected (Dale 1999). The height of the  $L(d)$  function (peak height) indicates the intensity of the association or repulsion. Control for edge effect was carried out for the analysis by rescaling the count based overlap with the study boundary (Rosenberg and Anderson 2011).

## Results

In this study with a capture effort of 2,400 traps-nights, we captured 110 individuals from both species during the dry season, while for the rainy season we captured 168 individuals. In the dry season, we captured 64 individuals of *P. difficilis*. While for *P. melanotis* during the dry season, we captured 46 individuals. In contrast, during the rainy season, the frequency of capture of *P. difficilis* was 87 individuals. While the total captures in this season for *P. melanotis* were 81 individuals. We also captured along the study 16 individuals of *Sorex saussurei*, two *Neotomodon alstoni*, five individuals of *Reithrodontomys chrysopsis* and two individuals of *Cryptotis alticola*. In the dry season (Table 1), the number of adult males was higher than that of females in both species (*P. difficilis*, 47:17; *P. melanotis*, 29:17, respectively), and overall, *P. difficilis* was more abundant than *P. melanotis*. Nonetheless, the number of reproductive males to females was very similar in both species within both seasons (Table 1: *P. difficilis*, 14:13; *P. melanotis*, 9:7). In the rainy season (Table 1), the number of captured adult males was higher than that of adult females in *P. difficilis* (60:27), while this ratio was very similar between the sexes in *P. melanotis* (42:39). Although we documented a significant increase in captures of *P. melanotis*, *P. difficilis* remained as the more abundant species in the rainy season (Table 1).

**Table 1.** Capture variation for the sexes and reproductive individuals in two syntopic species of *Peromyscus*, along two seasons in a temperate forest. Note that there were more captured males than females in both species, more reproductive individuals of *P. difficilis* during the dry season, and more reproductive individuals in *P. melanotis* during the wet season. The values of reproductive individuals belong to the total males and females captured during each season.

	Dry		Rains	
	<i>P. difficilis</i>	<i>P. melanotis</i>	<i>P. difficilis</i>	<i>P. melanotis</i>
Adult males	47	29	60	42
Adult females	17	17	27	39
Reproductive males	14	9	9	16
Reproductive females	13	7	5	14

In overall, the number of captures of reproductive males was twice the captures of reproductive females in *P. difficilis*, and we also detected a decrease in captures of breeding individuals from the dry to the rainy season (Table 1). In contrast, the number of captures of breeding males and females was very similar in *P. melanotis* (16:14). That is, our results supported that the main reproductive period for *P. difficilis* occurred during the dry season, while the same was true during the rainy season for *P. melanotis* (Table 1).

In the dry season, Kernel's maps revealed a different use of space between males and females of *P. difficilis* (Figure 1) with some overlaps in certain capture points, though we detected that males occurred on a broader area along the plot than females. On the contrary, males and females of *P. melanotis* show distribution overlaps in the capture points (Figure 1). In contrast, in the rainy season, we observed a high decrease in the dispersion of females of *P. difficilis* along the plot, while males of this species still expanded its dispersion along the plot (Figure 2), even though both sexes were captured almost in the same sampling stations. On the other hand, both males and females of *P. melanotis* expanded their distribution area within the plot during the rainy season, and we observed more overlaps between sexes of this species at the sampling stations (Figure 2).

In both seasons, the Nearest Neighbor Analysis revealed that males and females of each species showed a significant clustered pattern within the plot with both specific and sex differences (Table 2). Therefore, during the dry season (Table 2), the mean distance was farther among females of *P. difficilis*, and males were more clustered; while males and females were at a similar mean distance in *P. melanotis*. In the rainy season (Table 2), females remained more distant from each other than males, though the mean distance between individuals decreased in *P. difficilis*, while mean distance increased in males of *P. melanotis* and females had a reduction in their occupied area.

In the dry season, Ripley's bivariate K analysis within species (Figure 3) revealed that males and females of *P. difficilis* were mainly positively associated at short distances with the major intensity of association at 2 and 6 m. Similarly, although males and females of *P. melanotis* exhibited higher association than *P. difficilis*, the major intensity of such association also occurred at 6 and 12 m (Figure 3). In the rainy season, males and females of *P. difficilis* were randomly dispersed in almost all the distances showing the major positive association at 2 and 6 m, and little peaks at distances 8 and 12 m. In contrast, males and females of *P. melanotis* showed a negative association at 5 m, followed by high positive associations at all analyzed distances (Figure 3).

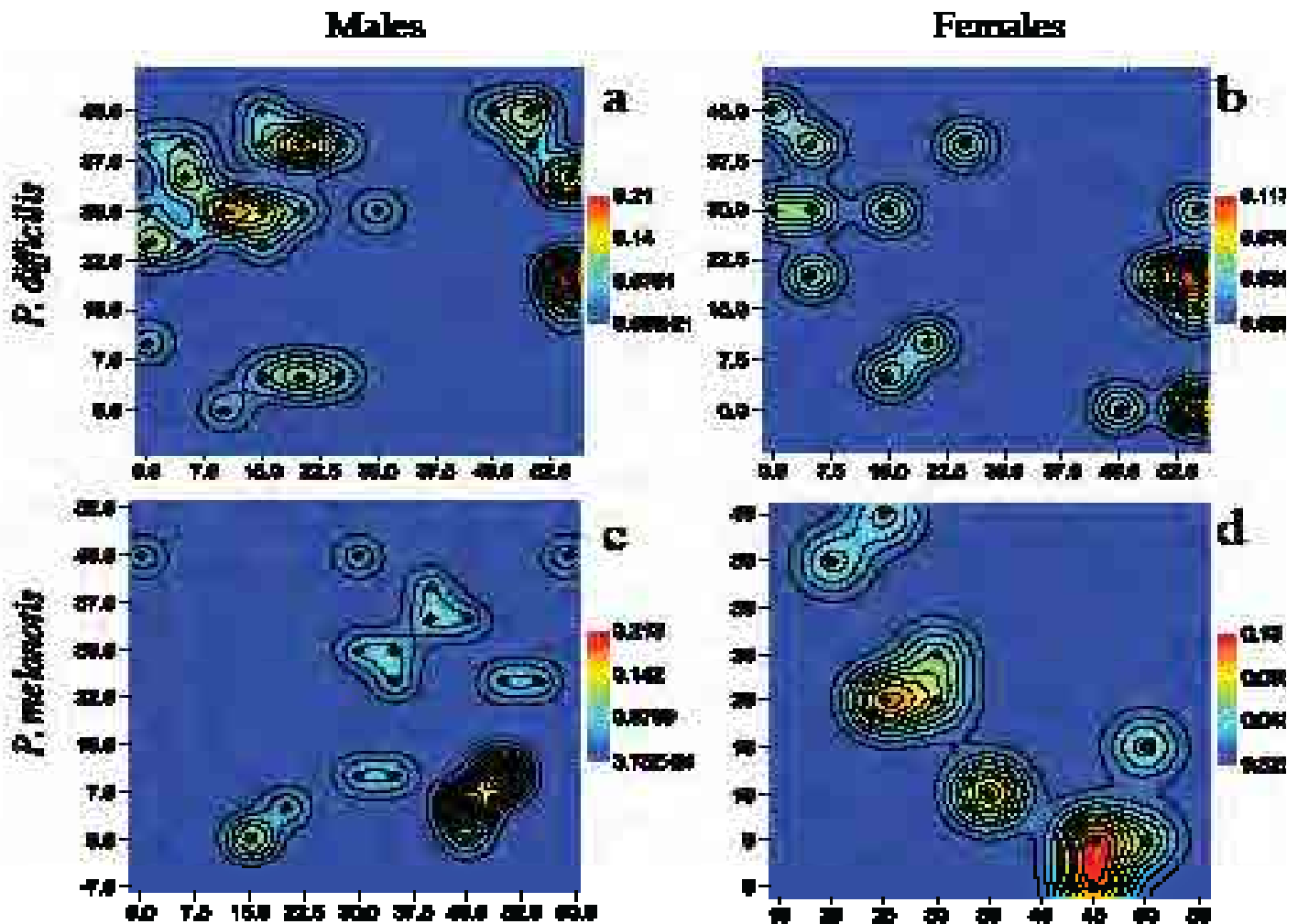
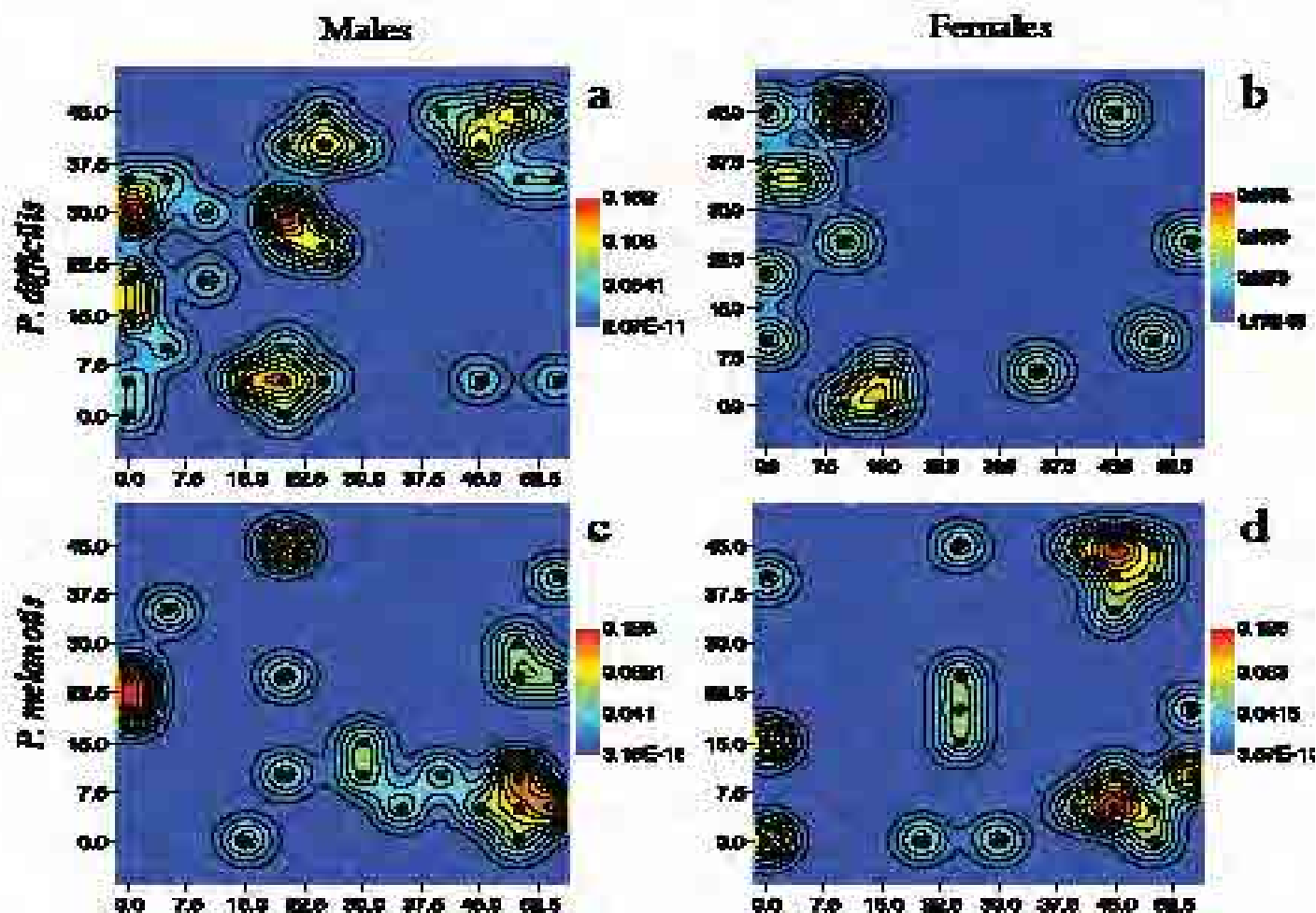


Figure 1. Mapping of point patterns from Kernel Analysis for males and females of both *Peromyscus* species during the dry season, to show segregation and use of space for males (a) and females (b) of *P. difficilis*; males (c) and females (d) of *P. melanotis*. Dots indicate actual capture points; red colors depicts higher density. Scales in both axes are in meters.



**Figure 2.** Mapping of point patterns from Kernel Analysis for males and females of both *Peromyscus* species, during the rainy season, to show segregation and use of space for males (a) and females (b) of *P. difficilis*; males (c) and females (d) of *P. melanotis*. Dots, red colors, and axes scales as in figure 1.

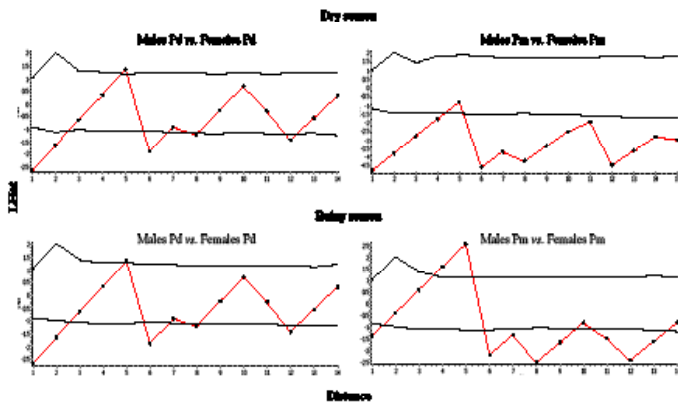
In the dry season, Ripley's bivariate K analysis between sexes of the species (Figure 4) revealed a clear negative association at all distances between males of *P. difficilis* vs. males of *P. melanotis* (Figure 4). Nevertheless, the females of *P. difficilis* vs. females of *P. melanotis* exhibited a random pattern of distribution. Therefore, we cannot reject the null hypothesis (Figure 4). In contrast, in the rainy season, males of *P. difficilis* vs. males *P. melanotis* revealed a positive association in different distances and repulsion at 5 m. While females of *P. difficilis* vs. females of *P. melanotis* also showed an association at different distances (Figure 4).

## Discussion

As expected from a relatively common pattern in studies conducted with *Peromyscus* species, we captured more males than females in both species. In general, females have smaller daily home ranges (DHRs) and lowest movements above ground than males, especially during the dry seasons (Trivers 1972; Gittleman and Thompson 1988). Thus, differences in captures between the sexes and smaller female's DHRs in both species of *Peromyscus*, could be a consequence of reproductive roles, since females need to allocate more energy than males into mating, and especially

**Table 2.** Nearest Neighbor Analysis for the sexes in each species of *Peromyscus*, showing mean distance between males or females. R-values indicate deviation of observed distribution from random as follows: Clustered points =  $R < 1$ ; Poisson patterns =  $R \sim 1$ ; overdispersed points =  $R > 1$ .

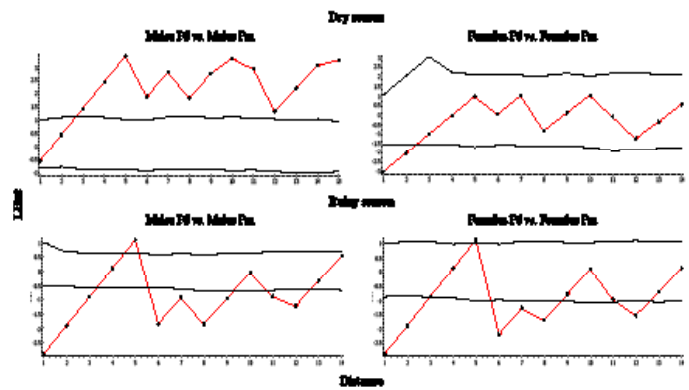
	Dry season				Rain season			
	<i>P. difficilis</i>		<i>P. melanotis</i>		<i>P. difficilis</i>		<i>P. melanotis</i>	
	Males	Females	Males	Females	Males	Females	Males	Females
Points	47	17	29	17	60	27	42	39
Mean distance	2.04	4.43	2.72	2.59	1.33	2.66	3.06	1.86
R	0.56	0.73	0.59	0.57	0.41	0.55	0.70	0.43
P value	1.6763x10 <sup>-8</sup>	0.036409	2.4924x10 <sup>-5</sup>	0.00074115	4.4812x10 <sup>-18</sup>	1.094x10 <sup>-5</sup>	0.001336	9.2124x10 <sup>-11</sup>
Point pattern	clustering	clustering	clustering	clustering	clustering	clustering	clustering	clustering



**Figure 3.** Shifts in interaction patterns (attraction-repulsion) between the sexes of each *Peromyscus* in dry and wet seasons, according to Ripley's bivariate K Analysis. The solid blue line represents Ripley's K bivariate pattern, while red dashed lines depict the area of a 95 % confidence interval (CI). Thus, if blue lines fell within the 95 % CI area, the null hypothesis of random interaction cannot be rejected; while if blue lines fell either below or above this area, the sexes were either attracted or repulsed, respectively. In *P. difficilis* (Pd), there was a high positive association between both sexes at all analyzed distances during the dry season, while both sexes had random segregation along the plot at rains, but still with attraction patterns at 1 - 3, 6, 8, and 12 m. *P. melanotis* (Pm) had a more stable pattern of positive association between the sexes in both pluvial seasons: the sexes were highly attracted to each other in all analyzed distances during the dry season, and there was only a negative association (repulsion) at 5 m of distance between them during the rainy season, remaining associated in all other distances.

into gestation, delivery, nursing, and raising of pups, which would occur at the expense of energy invested in displacements (Gittleman and Thompson 1988). Availability of food resources has been considered as one of the most critical factors influencing the use of space in mammals (Dimitri et al. 2009; Adler 2011; Adrian and Sachser 2011; Maher and Burger 2011). Therefore, in order to maximize their fitness, the distribution of females could be profoundly influenced by the distribution of food resources (Adler 2011), mainly if food resources are scattered and with lower renewal rates, while the males are distributed according to the distribution of the females (Ostfeld et al. 1985). Here, we found that males and females of both species showed a clustered pattern of dispersion. However, males of *P. difficilis* displayed a more segregated pattern of distribution in the reproductive season (dry season), when they became highly associated with the females.

In contrast, males of *P. melanotis* showed a similar use of space as females along the plot, or at least they were captured in nearby stations in both seasons; indeed, such positive association pattern between sexes increased throughout the reproductive season (rainy season) in this species. Therefore, intraspecific temporal changes in mean distances between the sexes, as well as temporal patterns of association, showed us that the distribution of females could influence the distribution of the males. Moreover, when we compare the positive association or repulsion of the sexes between species (*i. e.*, males of *P. difficilis* vs. males of *P. melanotis* and females of *P. difficilis* vs. females of *P. melanotis*), we observed that in the dry season, the males of both species were associated negatively, while the females did not show an association. In contrast, in the rainy season, males and females showed a positive association at different distances analyzed. This support that the distribution of males



**Figure 4.** Shifts in interaction patterns (attraction-repulsion) between males of *P. difficilis* (Pd) vs. males of *P. melanotis* (Pm) and between females of *P. difficilis* (Pd) vs. females of *P. melanotis* (Pm) in dry and wet seasons, according to Ripley's bivariate K Analysis. The solid red line represents Ripley's K bivariate pattern, while dark dashed lines depict the area of a 95 % confidence interval (CI). Thus, if red lines fell within the 95 % CI area, the null hypothesis of random interaction cannot be rejected; while if red lines fell either below or above this area, the sexes were either attracted or repulsed, respectively. In the dry season, males of both species are negatively associated at all distances, while females of both species had random segregation along the plot. In the rainy season, males of both sexes were positively associated at different distances with a little peak of repulsion at 5 m. This last pattern also was observed for females of both species.

is profoundly influenced by the use of space of the females. We also believe that the repulsion pattern in the dry season between males of both species occurs due to resources availability are more scarce during this season. Therefore, the competition for the resources is more intense.

Furthermore, the primary breeding season of *P. difficilis* occurs in the dry season and thus, is probably that territoriality behavior can occur in the males that are searching for mating. Conversely, the intensity of such repulsion decreased substantially during the rainy season; indeed, at some analyzed distances, the two deer mice showed an association pattern. Holding our results that the increase of resources during the rainy season can allow that the species can share the habitat and coexist (De-la-Cruz et al. 2018). Thus, our results indicate that in these two syntopic *Peromyscus*, both microhabitat use and spatial organization are seasonally variable depending on the breeding season of both small mammals (Pianka 1973; Schoener 1974; Brown and Zeng 1989; Cramer and Willig 2002; De-la-Cruz et al. 2018).

Sexual differences in use of space by each species could be due to different habitat requirements by females and males during the breeding season (Morris 1984). Females must select safe nesting sites for their young (*e. g.*, against predation), and must spend considerable time at or near those sites, nurturing young. Thus, small female home ranges may be more a constraint of their reproductive role than an adaptation for enabling foraging at resource-rich habitats. Although males also require nest sites, their parental responsibilities give them greater freedom and opportunity to select microhabitats by resource levels or mate availability (Morris 1984).

We confirmed that the reproductive season of *P. difficilis* occurs mainly during the dry season, while that for *P. melanotis* arises in the rainy season. In consensus, Salame-Méndez et al. (2003a, b; 2004a, b) documented highest intrago-



nadal contents of testosterone and other sex steroids in females of *P. melanotis* during the rainy season, while [Castro-Campillo et al. \(2008\)](#), found that *P. difficilis* had its reproductive optimum during the dry season at the PNDL. The excluding and shifted breeding patterns in this two syntopic *Peromyscus* are followed by population increases ([Castro-Campillo et al. \(2008\)](#)), thus allowing their coexistence in their mixed forest at this midlatitude study area.

In summary, we conclude that in our, temperate forest: 1) use of space by *P. difficilis* and *P. melanotis*, is influenced by both sex of the individuals and by reproductive season, and that this pattern varies, according to shifts on ecological conditions that promote variation and availability of resources during dry and wet seasons; 2) there are interspecific differences in the use of space with conspicuous intraspecific differences in females and males of *P. difficilis* (e.g., males are more territorial, and both sexes only become more clustered during the breeding season), while both sexes behave very similar in *P. melanotis*, indicating a much more gregarious behavior; and 3) there is a clear differentiation in the reproductive seasons of both species that could be related to resources available, such as shelters and food (see [De-la-Cruz et al. 2018](#)).

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# Spatial distribution of bat richness in Mexico at different taxonomic levels: biogeographical and conservation implications

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Due to the potential of bats to travel long distances, the great diversity of habitats in which they are found, and their biological peculiarities, bats typically have been excluded in biogeographic analyses. However, like other mammals, bats show common distributional patterns strongly influenced by their biotic and abiotic interactions, aspects that have been poorly analyzed mainly due to technical and methodological limitations. Such occurrence data are limited to a subset of a species' range, the scale of occurrence records, characteristics of the life history (e. g., territory size, vagility) of the taxa being studied, and issues of environmental variable selection and, therefore, the modeling methods and the evaluation of them. In this work, the objectives were to: 1) Evaluate the spatial variation in bat richness in Mexico, both for the order as a whole and at the family taxonomic level. 2) Quantify overlapping species occurrences and corresponding richness values in order to statistically model and generate bat richness maps at different taxonomic levels. 3) Explore the relationship of bat richness with environmental factors and with the biogeographic regions proposed for Mexico. 4) Identify areas of interest with high richness. The information available on the Global Biodiversity Information Facility database for bat species with distribution in Mexico was downloaded, and clearly erroneous records deleted. Using the Kriging Ordinary utility (KO), inside the QGIS software, a geostatistical analysis interpolation data was used to determine patterns of richness. The relationship of bat richness to climate, vegetation, and the biotic provinces proposed for Mexico was also explored. Spatial variation in richness was evaluated at the taxonomic levels of order and family. Based on this determination, areas of interest were identified for their high richness. When considering all species of bats the highest diversity is in the central part of the West, the Northeast zone and on both sides of the Isthmus of Tehuantepec. However, there are differences present at the family level. Deciduous tropical forest vegetation type presents high bat richness, followed by pine-oak forest and evergreen tropical forest. Temperate sub-humid, warm sub-humid and warm-humid climate types correspond to the highest bat richness of both order and family. Collection localities are not uniformly distributed over the country, most of them being concentrated in the west, east and south of the country, while there are very few records in the north and central plateau, and this is reflected in the richness concentration per cell (values from 0 to 52 species per cell). Protection of the four areas with an overall high concentration of bat richness detected in this analysis should be a priority during the development of conservation strategies.

Debido a su amplia capacidad de desplazamiento, la gran diversidad de hábitats en los que se les encuentra y a sus peculiaridades biológicas, los murciélagos han sido excluidos o marginados en muchos análisis biogeográficos. No obstante, se puede esperar que presenten patrones comunes que caractericen su distribución y que exista una regionalización fuertemente influenciada por sus interacciones bióticas y abióticas, aspectos que han sido poco abordados, principalmente por limitaciones técnicas y metodológicas. En este trabajo los objetivos fueron: 1) Evaluar la variación espacial de la riqueza de murciélagos en México, tanto a nivel general como a nivel de familias. 2) Cuantificar las ocurrencias de especies superpuestas y los valores de riqueza correspondientes con el fin de modelar estadísticamente y generar mapas de riqueza de murciélagos a diferentes niveles taxonómicos. 3) Explorar la relación de la riqueza de murciélagos con diferentes factores ambientales y con las regiones biogeográficas propuestas para México. 4) Identificar áreas de interés con alta diversidad. La información disponible en la base de datos Global Biodiversity Information Facility para las especies de murciélagos con distribución en México fue depurada, y mediante la utilidad de "kriging ordinario (KO)", del programa QGIS, se sometió a un análisis geoestadístico de interpolación de datos para determinar sus patrones de riqueza y la generación de mapas que resaltan este aspecto. La variación espacial de riqueza se evaluó en los niveles taxonómicos de orden y familia. Las áreas con mayor riqueza para la totalidad de especies de murciélagos se localizan en la parte central del Occidente, la zona Nororiental y a ambos lados del Istmo de Tehuantepec. Sin embargo, hay diferencias a nivel de familia. El tipo de vegetación de bosque tropical caducifolio presenta una gran riqueza de murciélagos, seguido del bosque de pino y encino y el bosque tropical perennifolio. Los climas templado subhúmedo, cálido subhúmedo y cálido húmedo corresponden a la mayor riqueza de murciélagos. Los registros de las localidades colectadas no se encuentran distribuidas de manera uniforme en el país, la mayoría de ellas están concentradas en el oeste, este y sur del país, mientras que hay muy pocos registros en la meseta norte y central, sesgo que se refleja en la concentración de riqueza por celda (valores de 0 a 52 especies por celda). La protección de las cuatro áreas con una alta concentración general de la riqueza de murciélagos detectada en este análisis debe ser una prioridad durante el desarrollo de las estrategias de conservación.

**Keywords:** biogeographic regions; environmental factors; geostatistical method; kriging; Mexican bats; richness maps.

## Introduction

The majority of studies on bat richness have focused on the roles of spatial scales and sampling methods ([Bergallo et al. 2003](#); [Meyer et al. 2011](#); [Skalak et al. 2012](#)) as well as the relationships between richness and different environmental parameters ([McCain 2007](#); [Tello and Stevens 2010](#); [López-González et al. 2012](#); [Schoeman et al. 2013](#); [López-González et al. 2015](#)). Other studies have evaluated the effects of habitat deterioration on richness at the local, regional or global level ([Estrada et al. 1993](#); [Estrada and Coates-Estrada 2001](#); [Mehner et al. 2011](#); [Frey-Ehrenbold et al. 2013](#)). In recent years, the study of biological richness has acquired greater relevance as a means for evaluating the impacts of global environmental changes and human activities, wherein more robust and reliable estimates using new approaches are required in order to improve analyses ([Henry et al. 2010](#); [Bellamy et al. 2013](#)). Also, in the last two decades greater attention has been placed on the adaptive responses of bats to habitat heterogeneity in addition to the effects of habitat modification on functional and phylogenetic diversity ([Soriano 2000](#); [Stevens et al. 2003](#); [Roncancio and Estevés 2007](#); [Cisneros et al. 2014](#); [Melo et al. 2014](#); [Aguirre et al. 2016](#); [Scheiner et al. 2016](#)).

The systematics and the anatomy of bats have been widely studied as well as different aspects of their behavior, physiology and ecology ([Altringham 1997](#); [Crichton and Krutzsch 2000](#); [Neuweiler 2000](#); [Kunz and Fenton 2003](#); [Simmons 2005](#); [Fenton and Simmons 2015](#)). Compared with other mammals, bats are small in size and have great longevity, a relatively long gestation period and a low reproductive rate ([Brunet-Rossini and Austad 2004](#)). Bats occupy a wide variety of habitats and roost in both natural and manmade structures and are adapted to living in specialized or somewhat uncommon environments and are highly responsive to environmental variables. Finally, bats can perform long-distance movements of various kilometers on a daily basis and are capable of extensive migrations ([Findley 1993](#)). Notwithstanding the biological distinctiveness of bats and their great capacity of displacement, it is expected that bats present common patterns in their distributions that are regionalized and influenced by biotic and abiotic interactions.

Bat distribution patterns have been little studied, mainly due to logistical and methodological limitations. One of the most recurrent problems was the limited occurrence records to characterize the species' range. Others more complex, were to scale the occurrence data to the characteristics of the life history (e. g., vagility), the issues of environmental variable selection and the lack of models to analyze them jointly ([Phillips et al. 2006](#); [Rondinini et al. 2006](#); [Segura-Trujillo and Navarro-Pérez 2010](#)).

Mexico is considered a megadiverse country due to the large number of plant and animal species that inhabit its territory ([Arita 1997](#); [Ceballos et al., 1998](#); [Sarukhán et al. 2014](#)). This diversity results from the geographical position, geological history and the rugged topography of Mexico,

which create a diverse mosaic of environmental and micro-environmental conditions. In Mexico, 512 species of terrestrial mammals have been recorded ([Álvarez-Castañeda et al. 2017](#)), and their general distribution at the species level has been largely mapped since the last half of the past century ([Hall and Kelson 1959](#)), enabling richness patterns to be studied. Such information has also been used to propose various biogeographical regions for the country, the majority of which are predominantly based on the distributions of terrestrial mammals ([Ramírez-Pulido and Castro-Campillo 1990, 1993](#); [Arita 1993, 1997](#); [Arriaga et al. 1997](#); [Escalante et al. 2002](#); [Escalante et al. 2003](#); [Escalante et al. 2007](#)). Unquestionably, these studies have contributed towards increasing knowledge of the country's biogeography but have often excluded or marginalized bats based on their biological differences, the size of their distribution areas and their capacity for widespread movement.

Biogeographical works carried out specifically on Mexican bats are scarce: [Arita and Ortega \(1998\)](#) have proposed that the richness and diversity of bats responds to a latitudinal gradient; [Wang et al. \(2003\)](#) made a species richness prediction map for the chiroptera in the state of Michoacán using temperature, precipitation, soil and vegetation environmental data. [López-González et al. \(2012\)](#) proposed that the distribution of bats along environmental gradients is determined by characteristics of the species group present in a site and not for the study areas defined arbitrarily which confine them. [Grimshaw and Higgins \(2017\)](#) analyzed the correlation of the phylogenetic structure in Mexican bat communities with environmental factors as temperature, precipitation, latitude, and longitude.

In this context, the distribution of bat richness at taxonomic levels not previously evaluated is important for understanding how bats relate to the biogeographical regions proposed for Mexico. In addition, more in-depth analyses are needed on the influence of important environmental variables (latitude, climate and vegetation) on the structuring of bat richness patterns. Bats are particularly sensitive to habitat destruction and to environmental changes, although it also has been reported that the response of bats to change in land use is varied and depends on the taxonomic group ([García-Morales et al. 2013](#)). A precise map of their species richness patterns will enable the variation in such patterns to be better understood and aid in the design of effective regional conservation schemes.

The development of Geographic Information Systems (GIS) along with geostatistical methods and the wide availability of species occurrence records in online databases enable the in-depth analysis of spatial correlations among variables using diverse functions that estimate or predict the values and the distribution of a property across space and time. The Kriging method facilitates the interpolation of different variables, allows spatial estimation for prediction of values in areas where data is not available, based on a limited number of points obtained from a sample, useful for the analysis of species patterns distributions ([Fortin et](#)

al. 2005; ESRI 2006; Tittensor et al. 2010; Hortal and Lobo 2011; Henríquez et al. 2013; Tapia-Silva et al. 2015). Kriging appears to be appropriate for the creation of thematic maps for visualizing zones of greatest species richness under the combined effect of some variables.

The present study had the following objectives: 1) evaluate the spatial variation in bat richness in Mexico, both overall and at the family level. 2) Quantify overlapping species occurrences and corresponding richness values in order to statistically model and generate bat richness maps at different taxonomical levels. 3) Explore the relationship of bat richness with different environmental factors and with the complex biogeographic regions proposed for Mexico. 4) Identify areas of interest with high diversity.

## Material and Methods

**Databases.** Locality records for bats in Mexico were obtained from the online database of the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org> accessed in January 2016). Only georeferenced distribution records supported with specimens deposited in scientific collections, either national or foreign, were considered. The data were reviewed with respect to their geographical distribution and nomenclatural status according to [Medellín et al. \(2008\)](#) and [Álvarez-Castañeda et al. \(2015\)](#). Island records were eliminated as well as reports outside the known geographic distribution of species. Species sampled in less than five localities were not included under the assumption that such records were not sufficient for representing the overall distribution of a species. The edited data set was exported to a database constructed in MS Excel 2011. The database was composed of 6,979 presence records corresponding to 97 species belonging to eight families of Chiroptera distributed throughout Mexico (Table 1), which represents 70.3 % of the 138 species registered for the country ([Álvarez-Castañeda et al. 2017](#)). The 39 species omitted from the analysis is due to that for some of them there are no records in GBIF, others have fewer than five records and also the families represented by a single species cannot be considered in the geostatistical method used.

**Study area.** The area of continental Mexico (32° 43' 06" N, -114° 45' W; 14° 32' 27" N, -92° 13' 0" W), which covers an area of 1,964,375 km<sup>2</sup>, was considered in the analysis. The Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), based on [Rzedowski \(1990\)](#), has proposed nine main vegetation types for Mexico, of which eight were used in our analysis, because the aquatic and sub-aquatic vegetation type was excluded. Also, we employed the 13 main climatic types recognized by [García \(1998\)](#). For the biogeographic regionalization we used the map of [Morrone \(2005\)](#) which depicted 14 biotic provinces according to their ecology and ecological history, and supported by the overlapping distributions of different groups of species.

**Determination of richness patterns.** A map was created for Mexico (INEGI, scale 1:1,000,000) using the WGS 84

**Table 1.** Families of Mexican bats considered in this study with their number of species and localities. The data were obtained from an analysis of the information deposited in the online database Global Biodiversity Information Facility (GBIF <http://www.gbif.org/> - Accessed January 2016)

<b>Emballonuridae: Species 7 Localities 373</b>			
<i>Balantiopteryx io</i>	25	<i>Peropteryx macrotis</i>	30
<i>Balantiopteryx plicata</i>	201	<i>Rhynchonycteris naso</i>	17
<i>Diclidurus albus</i>	9	<i>Saccopteryx bilineata</i>	84
<i>Peropteryx kappleri</i>	7		
<b>Molossidae: Species 12 Localities 27</b>			
<i>Eumops ferrox</i>	11	<i>Nyctinomops aurispinosus</i>	14
<i>Eumops perotis</i>	6	<i>Nyctinomops femorosaccus</i>	36
<i>Eumops underwoodi</i>	13	<i>Nyctinomops laticaudatus</i>	27
<i>Molossus molossus</i>	24	<i>Nyctinomops macrotis</i>	16
<i>Molossus rufus</i>	25	<i>Promops centralis</i>	7
<i>Molossus sinaloae</i>	20	<i>Tadarida brasiliensis</i>	226
<b>Mormoopidae: Species 4 Localities 778</b>			
<i>Mormoops megalophylla</i>	330	<i>Pteronotus parnellii</i>	232
<i>Pteronotus davyi</i>	139	<i>Pteronotus personatus</i>	77
<b>Natalidae: Species 1 Localities 172</b>			
<i>Natalus mexicanus</i>	172		
<b>Noctilionidae: Species 1 Localities 41</b>			
<i>Noctilio leporinus</i>	41		
<b>Phyllostomidae: Species 38 Localities 3960</b>			
<i>Dermanura azteca</i>	34	<i>Glossophaga leachii</i>	69
<i>Dermanura phaeotis</i>	189	<i>Glossophaga morenoi</i>	18
<i>Dermanura tolteca</i>	176	<i>Glossophaga soricina</i>	543
<i>Anoura geoffroyi</i>	100	<i>Glyphonycteris sylvestris</i>	9
<i>Artibeus hirsutus</i>	61	<i>Hylonycteris underwoodi</i>	15
<i>Artibeus jamaicensis</i>	442	<i>Leptonycteris nivalis</i>	51
<i>Artibeus lituratus</i>	347	<i>Leptonycteris yerbabuenae</i>	110
<i>Chrotopterus auritus</i>	11	<i>Macrotus californicus</i>	73
<i>Choeroniscus godmani</i>	14	<i>Mimon cozumelae</i>	16
<i>Choeronycteris mexicana</i>	114	<i>Musonycteris harrisoni</i>	13
<i>Carollia perspicillata</i>	90	<i>Micronycteris microtis</i>	32
<i>Carollia subrufa</i>	90	<i>Macrotus waterhousii</i>	73
<i>Chiroderma salvini</i>	45	<i>Phyllostomus discolor</i>	32
<i>Chiroderma villosum</i>	32	<i>Platyrrhinus helleri</i>	24
<i>Centurio senex</i>	59	<i>Sturnira parvidens</i>	333
<i>Diphylla ecaudata</i>	35	<i>Sturnira hondurensis</i>	123
<i>Desmodus rotundus</i>	420	<i>Trachops cirrhosus</i>	24
<i>Enchisthenes hartii</i>	13	<i>Uroderma bilobatum</i>	47
<i>Glossophaga commissarisi</i>	76	<i>Vampyroides caraccioli</i>	7
<b>Thyropteridae: Species 1 Localities 5</b>			
<i>Thyroptera tricolor</i>	5		
<b>Vespertilionidae: Species 33 Localities 1623</b>			
<i>Antrozous pallidus</i>	86	<i>Myotis keaysi</i>	30
<i>Corynorhinus mexicanus</i>	17	<i>Myotis nigricans</i>	39
<i>Corynorhinus townsendii</i>	10	<i>Myotis peninsularis</i>	8
<i>Eptesicus furinalis</i>	44	<i>Myotis planiceps</i>	6
<i>Eptesicus fuscus</i>	186	<i>Myotis thysanodes</i>	32
<i>Idionycteris phyllotis</i>	7	<i>Myotis velifer</i>	191
<i>Lasiurus blossevillii</i>	22	<i>Myotis vivesi</i>	42
<i>Lasiurus borealis</i>	50	<i>Myotis volans</i>	29
<i>Lasiurus cinereus</i>	57	<i>Myotis yumanensis</i>	60
<i>Lasiurus ega</i>	75	<i>Nycticeius humeralis</i>	20
<i>Lasiurus intermedius</i>	43	<i>Pipistrellus hesperus</i>	170
<i>Lasiurus xanthinus</i>	14	<i>Pipistrellus subflavus</i>	9
<i>Myotis auriculus</i>	21	<i>Rhogeessa aeneus</i>	5
<i>Myotis californicus</i>	127	<i>Rhogeessa bickhami</i>	5
<i>Myotis elegans</i>	11	<i>Rhogeessa parvula</i>	78
<i>Myotis evotis</i>	10	<i>Rhogeessa tumida</i>	59
<i>Myotis fortidens</i>	60		

(World Geodetic System 84) datum and was divided into quadrants of 1°x1°, resulting in 253 cells with their respective identification according to Hansen (1997). Bat records were assigned to a cell based on their georeferenced coordinates, and this was also performed independently for each family of bats, regardless of the number of specimens or the date of collection. These records were overlapped with the following data layers: vegetation types, scale 1:250,000; climate types, scale 1:1,000,000; and biotic provinces, scale 1:4,000,000. The layer of biotic provinces was built by digitizing the map of Morrone (2005); the vegetation and climate layers were obtained from the CONABIO portal (<http://www.conabio.gob.mx/informacion/gis/>).

Geostatistical interpolations of the spatial data were performed with Surfer 11 (Golden Software, Golden, CO, USA) and exported into QGIS software v. 2.12.2 ([www.qgis.org](http://www.qgis.org)) to obtain bat richness values and to generate the corresponding maps for the 96 species and independently for members of the families Emballonuridae, Molossidae, Mormoopidae, Phyllostomidae and Vespertilionidae. The families Natalidae, Noctilionidae and Thyropteridae were included only in the overall richness assessment because each is represented by only one species in Mexico.

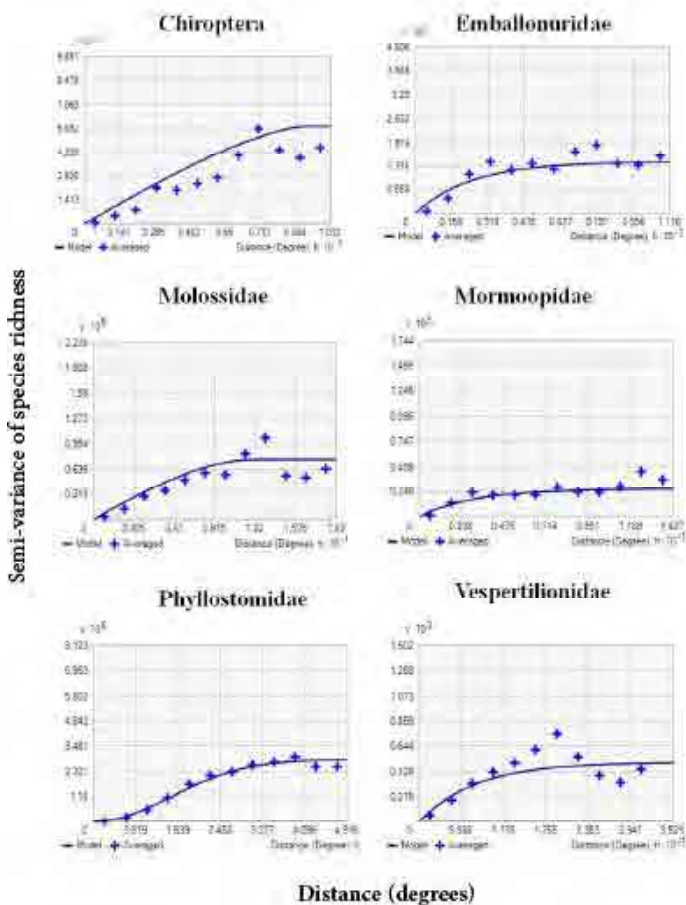
To determine the best model to apply for each family and for the group as a whole, a cross-validation analysis was performed for each semivariogram model generated by the OK tool. Because the best model is that whose error measure is closest to zero (Díaz 2002), the selected model for the Order Chiroptera (all species together) was circular (error = 0.0001), while a spherical model was selected for the family Mormoopidae (error = 0.037) and an exponential model for the families Emballonuridae, Molossidae, Phyllostomidae and Vespertilionidae (error = 0.034; 0.038; 0.000 and 0.006 respectively; Figure 1).

We selected the OK method because it is mainly based on the geographical distance of points to those in neighboring cells, more than the size of cells, which enables geographical units that are not necessarily adjacent or that are spaced at regular intervals to be compared. The spatial structure of the data is usually described in an experimental variogram, which is basically a graph of the semivariance between observation pairs (in this case cells) with respect to distance in a geographic space; descriptions of the requirements for the use of OK can be found in Díaz (2002), Hengl (2009) and Cruz-Cárdenas et al. (2013). Based on the quantitative results, areas with a richness greater than 50 % of species were considered to be high in richness, or 'rich', while areas with less than 10 % of species were considered low in richness, or 'poor'.

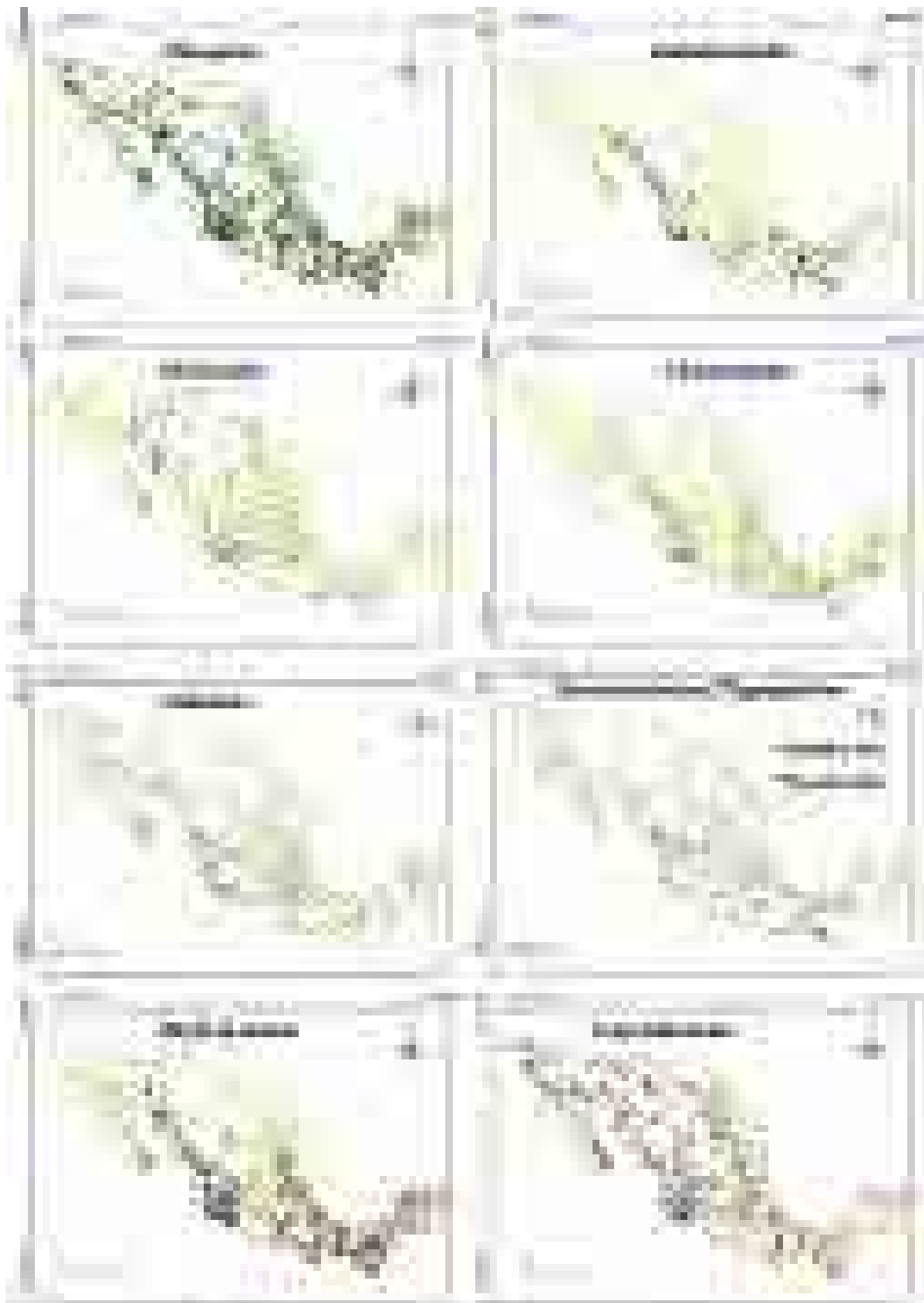
### Results

The distribution of presence records for the 97 species and eight families considered in the present study is shown in Figure 2. When all species of the order Chiroptera are considered the sample localities are dispersed throughout the country. However, at the family level, the distributions follow distinct patterns. Only the families Vespertilionidae and Molossidae are widely distributed. Meanwhile, records for the families Phyllostomidae, Mormoopidae and Natalidae are concentrated in the Pacific and Gulf of Mexico coastal plains, as well as in the central and southern portions, and are scarce or absent in the Central Mexican Plateau and in the northern-central areas of the country. Records for the families Emballonuridae, Noctilionidae and Thyropteridae were found along the Pacific Coastal Plains and in the south and south-eastern areas of the country, and notably missing in the central, northern and eastern areas of the territory.

**Species richness per cell.** Of the 253 cells into which Mexico was divided, 48 cells did not have bat records (19%). These mostly are located in the north of the country. Thus, bat records were found in the remaining 205 cells. The cells had an average of 12 species per cell, with a minimum of one species and a maximum of 52 species (Table 2). Overall, 75 % of cells presented richness values ranging from one to 17 species, 20 % from 18 to 25 species and the remaining 5 % from 36 to 51 species. The highest richness value was encountered in only one cell with 52 species, which was located in western Mexico on the border between the states of Colima and Jalisco.



**Figure 1.** Cross-validation for selecting each semivariogram model generated by ordinary kriging. A circular model was selected for the Chiroptera order (error = 0.000), spherical for the family Mormoopidae (error = 0.037) and exponential for the families Emballonuridae, Molossidae, Phyllostomidae and Vespertilionidae (error = 0.034; 0.038; 10 0.000 and 0.006, respectively).



**Figure 2.** Maps showing the distribution of the 6,979 localities with presence records for the 97 species considered in this study and also their distribution at the family level.

**Table 2.** Clades of Mexican bats with their species number, localities with bats records, number of cells with collecting records and average and maximum values of bat species richness recorded by cell.

Taxonomic group	Species	Localities	Cells with records	Bat richness by cell	
				average	maximum
Chiroptera	97	6,979	205	12	52
Phyllostomidae	38	3,960	149	8	25
Vespertilionidae	33	1,623	184	3	18
Molossidae	12	27	133	2	9
Emballonuridae	7	373	64	2	6
Mormoopidae	4	778	87	3	4
Natalidae	1	172	56	1	1
Noctilionidae	1	41	21	1	1
Thyropteridae	1	5	3	1	1

The number of cells with collecting records, and the average and maximum values of bat species richness recorded by cell for each bat family is show in Table 2.

**Analysis of the spatial distribution of species richness.**

*Order and families.* Considering the 97 bat species together, the greatest richness was found in the Mexican Pacific Coast biotic province, the deciduous tropical forest vegetation type and the temperate sub-humid climate. For the family Emballonuridae the greatest richness was found in the Gulf of Mexico biotic province, the evergreen tropical forest vegetation type and the warm-humid climate. The family Molossidae presented the greatest richness in the Mexican Pacific Coast biotic province, the deciduous tropical forest vegetation type and the warm-humid climate. For each bat family the highest richness values in the biotic provinces, vegetation types as well as climates are presented in Tables 3 to 5.

*Biotic provinces.* The results obtained for the interpolation of the distribution of the species richness and the biotic provinces are shown in Table 3 and Figure 3. The Mexican Pacific Coast and Gulf of Mexico provinces have the greatest richness of bats and the provinces of California and Tamaulipas contain the lowest numbers of species. All provinces contain vespertilionid bats, with generally high percentages of richness, wherein the Mexican Pacific Coast, Sierra Madre Oriental, Gulf of Mexico, and Transmexican Volcanic Belt provinces have high values. The majority of provinces have the presence of phyllostomids but the Mexican Pacific Coast and Gulf of Mexico provinces have notable richness value for this family, and only the California province was lacking in species for this family. With respect to mormoopids, 10 provinces can be highlighted for their high richness values, and the California province is the only one without mormoopids. The greatest molossid and emballonurid richness occurred in the Mexican Pacific Coast and Gulf of Mexico provinces. Bat records are absent in some portions of the following biotic provinces: Mexican Plateau (23 cells), Tamaulipas (9 cells), Sonora (8 cells), Baja California (4 cells), California (2 cells) and Yucatán Peninsula (2 cells).

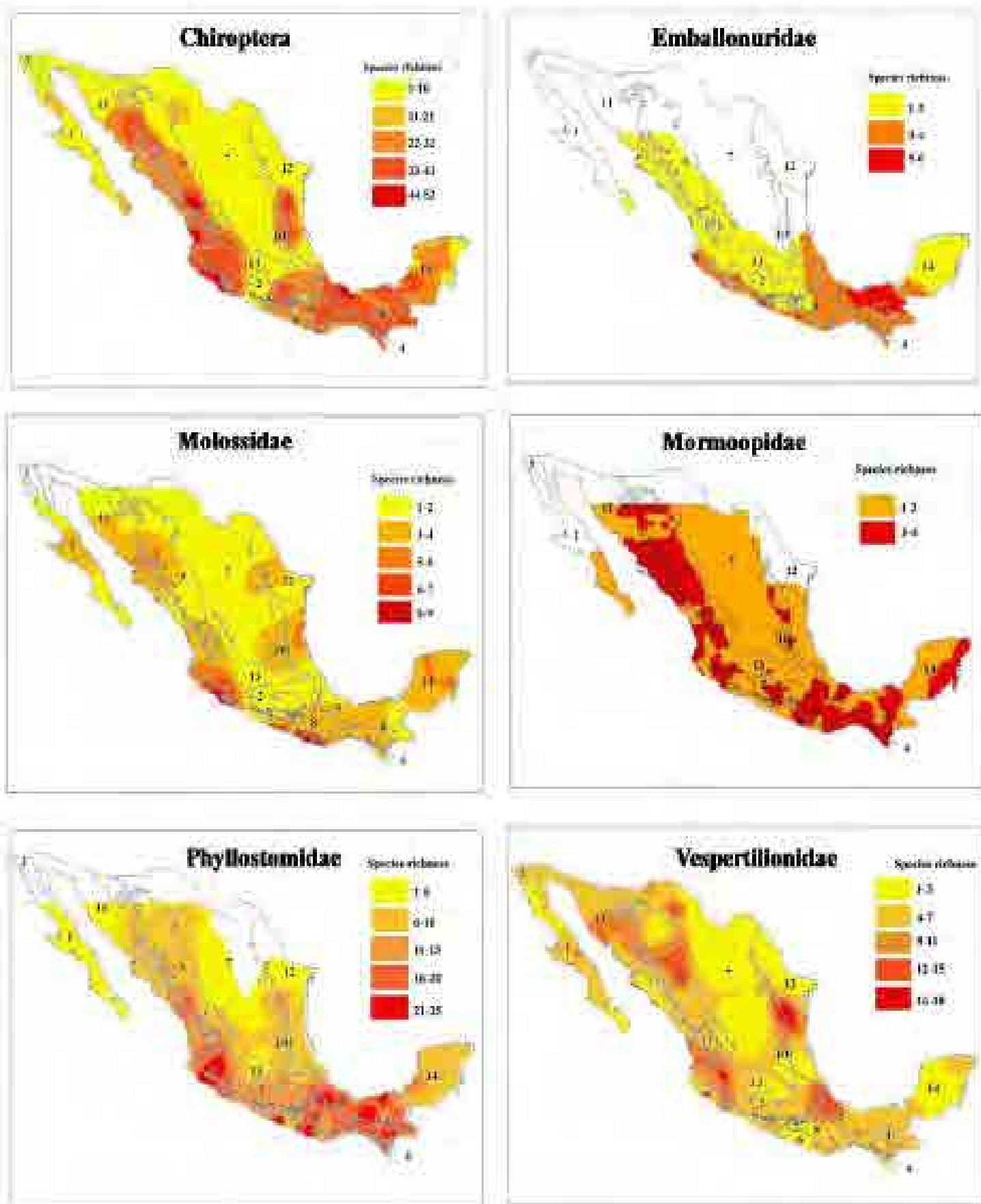
**Table 3.** Percentages of richness for each bat taxonomic group in Mexico's different biotic provinces proposed by Morrone (2005): Baja California (BC), Balsas Basin (BB), California (CAL), Chiapas (CHI), Gulf of Mexico (GM), Mexican Pacific Coast (MPC), Mexican Plateau (MP), Sierra Madre del Sur (SMS), Sierra Madre Occidental (SMW), Sierra Madre Oriental (SME), Sonora (SON), Tamaulipas (TAM), Transmexican Volcanic Belt (TVB), Yucatán Peninsula (YP). Province/Group (P/G), Chiroptera (CH), Emballonuridae (EM), Molossidae (ML), Mormoopidae (MR), Phyllostomidae (PH), and Vespertilionidae (VE).

P/G	CH	EM	ML	MR	PH	VE
MPC	87	71	93	100	95	63
GM	74	86	43	100	87	53
TBV	59	14	57	75	59	53
BB	54	43	36	75	56	45
SMS	52	29	36	75	69	32
SMW	52	14	36	75	51	50
SME	51	0	50	75	44	55
YP	45	29	50	75	54	26
CHI	43	43	14	75	59	26
SON	43	14	43	75	33	45
MP	41	14	29	25	31	58
BC	33	14	29	25	15	47
TAM	14	0	7	25	13	13
CAL	7	0	0	0	0	18

*Vegetation types.* Chiropteran richness is notable in the deciduous tropical forest, followed by pine and oak forest and evergreen tropical forest (Table 4). The vegetation type with poorest bat richness is grassland where only a few records for molossid, phyllostomid and vespertilionid bats are found. At the family level, Mormoopidae exhibits high richness values in six vegetation types: deciduous tropical forest, evergreen tropical forest, pine and oak forest, xerophile shrubland, tropical sub-deciduous and thorn forest. Phyllostomidae presents high richness values in pine and oak forest, evergreen tropical forest and deciduous tropical forest vegetation types. The maximum richness of Molossidae is in deciduous tropical forest, of Emballonuridae in evergreen tropical forest and of Vespertilionidae in xerophile shrubland. Bats were not present in 44 cells located in xerophile shrubland and in four cells of thorn forest.

*Climate.* The richness values for the Order Chiroptera are broadly distributed across diverse climate types (Table 5). The temperate sub-humid, warm sub-humid and warm-humid climate types presented the highest values for bat richness for both order and family levels. Emballonuridae presented high richness values in the warm-humid and warm sub-humid but in nine climate types their richness is zero. For the Molossidae and Phyllostomidae the climates warm sub-humid and temperate sub-humid have high richness values. Meanwhile, the richness values for the family Mormoopidae are high in nine climate types but were zero in another six climates, while the majority of climates have the presence of vespertilionids but not in high numbers. No bat records were found in 35 cells of semi-dry temperate climate, in six of semi-cold sub-humid, in five of very dry-very warm and in two of temperate-humid. For the climates cold, semi-warm humid, semi-dry semi-cold





**Figure 3.** Maps showing the bat richness patterns for different taxonomic groups in the biotic provinces proposed for Mexico following Morrone (2005). Baja California (1), Balsas Basin (2), California (3), Chiapas (4), Gulf of Mexico (5), Mexican Pacific Coast (6), Mexican Plateau (7), Sierra Madre del Sur (8), Sierra Madre Occidental (9), Sierra Madre Oriental (10), Sonora (11), Tamaulipas (12), Transmexican Volcanic Belt (13), Yucatán Peninsula (14).

**Table 4.** Percentages of richness for each bat taxonomic group in Mexico's different vegetation types proposed by Rzedowski (1990): Deciduous tropical forest (DTF), Evergreen tropical forest (ETF), Grassland (G), Pine-Oak forest (POF), Thorn forest (TF), Tropical sub-deciduous forest (TSDF), Xerophile shrubland (XS). Vegetation Type (VT), Chiroptera (CH), Emballonuridae (EM), Molossidae (ML), Mormoopidae (MR), Phyllostomidae (PH), and Vespertilionidae (VE).

VT	CH	EM	ML	MR	PH	VE
DTF	94	50	100	100	95	79
POF	85	38	64	75	90	79
ETF	82	88	50	100	92	63
XS	65	13	64	75	49	82
TSDF	48	50	50	75	59	21
TF	45	13	43	75	41	45
G	28	0	7	0	26	42

and temperate-humid, an estimated richness value was not obtained.

**Modelling overlapping richness values (Maps)**

The maps resulting from the use of ordinary kriging do not show richness patterns that are concordant for the biotic provinces. There is not a biotic province in which there is a predominance or a clear concentration of the bat richness (Figure 3). Maps highlight different patterns of bat richness for each family, not concordant with biotic provinces. For the family Emballonuridae the richness is concentrated towards the coastal plains of the Pacific and Gulf of Mexico and generally in the southeast of the country. Bats of the family Molossidae are present throughout the country, but richness is especially concentrated in five hotspots, three in the western regions of Sonora-Sinaloa, Jalisco-Colima and Oaxaca, one in the south of Chiapas and other in the Yucatan peninsula. In Mormoopidae richness is broadly distributed over the country, but decreases in the center, north and east. For Phyllostomidae richness is high over the country, more concentrated in the coastal plains of the Pacific and Gulf of Mexico and towards the southern portion but decreasing in the center and in the north. For the Vespertilionidae family, bat richness extends throughout the country, with several areas of high species richness located in the northwest and northeast, the central plateau, the isthmus of Tehuantepec and the Yucatan Peninsula (Figure 3).

**Discussion**

The collecting localities for bats are not uniformly distributed over the country, with most of them concentrated in the west, east and south, while there are a very few records in the north and central plateau. This reflects that there are fewer species in those parts of the country and also a bias in the efforts for collecting (Figure 2 Chiroptera map).

The use of GBIF has limitations due that there are only 97 species (70.3 %) of the 138 species registered for the country. The families Natalidae, Noctilionidae and Thyropteridae are poorly represented, have few records, and

**Table 5.** Percentages of richness for each bat taxonomic group in Mexico's climate types proposed by García (1998): Temperate sub-humid (Tsh), Warm sub-humid (Wsh), Warm-humid (Wh), Semi-dry very warm (Sdvw), Semi-cold sub-humid (Scsh), Semi-cold subhumid (Scs), Warm-dry (Wd), Very dry semi-warm (Vdsw), Dry very warm (Dvw), Semi-dry temperate (Sdt), Semi-warm dry (Swd), Semi-dry warm (Sdw), Semi-dry semi-warm (Sdsw), Dry temperate (Dt), Very dry temperate (Vdt), Very dry-warm (Vdw), and Very dry-very warm (Vdvw). Climate/Group (C/G), Chiroptera (CH), Emballonuridae (EM), Molossidae (ML), Mormoopidae (MR), Phyllostomidae (PH), and Vespertilionidae (VE).

C/G	CH	EM	ML	MR	PH	VE
Tsh	94	38	86	100	87	79
Wsh	69	75	100	100	100	63
Wh	34	88	50	75	85	45
Sdvw	34	38	21	75	36	16
Scsh	32	0	14	0	0	34
Scs	32	0	0	0	18	0
Wd	29	13	7	75	33	34
Vdsw	28	0	29	25	10	47
Dvw	25	0	0	50	18	8
Sdt	20	13	21	25	31	34
Swd	20	0	7	0	8	5
Sdw	16	0	29	50	13	39
Sdsw	13	0	14	50	10	37
Dt	8	0	14	0	5	42
Vdt	7	0	21	0	5	37
Vdw	3	13	36	75	18	39
Vdvw	0	13	7	0	0	3

because they are monospecific families they cannot be included in the kriging analysis.

In our maps the comparisons among the richness patterns of bats demonstrate that the pattern of the order level can differ from the patterns of the constitutive families, as well as the richness patterns differing to a substantial extent among families.

Biogeographical approaches are used to examine the cause of the bat distribution patterns, as well as to trace the circumstances of the past that may have influenced to generate such patterns. Various environmental factors such as latitude, temperature, precipitation and topography have been proposed to explain the richness and diversity of bats in the New World. One of the most considered is the effect of the latitudinal gradient for which several studies have proposed that the number of species increases as the latitude decreases (Wilson 1974; Willig and Lyons 1998; McCoy and Connor 1980; Fa and Morales 1991; Kaufman 1995; Arita and Ortega 1998; Willig et al. 2003), even at the local level (Stevens and Willig 2002). But according to Patten (2004) annual precipitation, temperature, and topography are better predictors of species richness in Chiroptera than vegetative cover, which explained little variation, and latitude which explained an insignificant amount of residual variation in species richness. Also, Stevens (2004) stated that ecological and evolutionary differences among higher taxonomic units, those involving life-history traits, predispose taxa to exhibit different patterns of diversity along environmental gradients.

Our results are more in agreement with [Patten \(2004\)](#) and [Stevens \(2004\)](#), but we only include a part of the area analyzed by these authors, which does not allow us to appreciate the extremes on the distribution of the bat families in North America or the Neotropics.

Some authors considered that climatic factors have a profound effect on bat distribution and richness ([Patten 2004](#); [Stevens 2004](#); [Pereira and Palmeirim 2013](#); [Peixoto et al. 2017](#)) because higher richness accumulates in environments resembling the ancestral niche, thus supporting phylogenetic niche conservatism as the mechanism driving the bat diversity gradient; but because niches are phylogenetically conserved within clades, and clades differ in climatic origin in general, the relationship between climate and species richness of mammalian clades is not positive ([Buckley et al. 2010](#)). In our analyses the species richness patterns do not respond to environmental gradients (climate). In addition, vegetation types can be an indicator of the productivity and availability of food in a specific area and the richness patterns of a given group, but in our analyses of the bat richness patterns they also do not respond to vegetation types (Tables 4 and 5). For both climate and vegetation, at the familial level richness is distributed throughout the country, but the greatest richness is concentrated in areas where there is high climatic diversity and the confluence of diverse vegetation types (Figures 3 and 4).

Great differences exist between the richness patterns displayed for the bat families within the biotic provinces proposed for the country (Table 3). [Willig et al. \(2003\)](#) point out that for North American mammals the larger biotic provinces contain more taxa (species, genera and families) than their smaller counterparts, but in our study this is not observed for Mexican bats. These differences are associated with the criteria used for the establishment of the biotic provinces, in which priority is given to ecosystems, their functioning and only the presence or absence of some organisms, rather than put the priorities at the origin, radiation processes, phylogeny and habitats of such organisms that are sharing a certain area. For this reason the biotic provinces cannot explain the richness patterns followed by the Mexican bats either as a whole or the taxonomic level of the family.

For the 97 bat species as a whole, the modelled distributions maps show a greater concentration of species richness in three areas of the country: 1) The area in western Mexico where the biotic provinces of the Trans-Mexican Volcanic Belt and the Mexican Pacific Coast converge. 2) Northeastern Mexico, where the biotic provinces of Tamaulipas, the Sierra Madre Oriental and the Coastal Plains of the Gulf of Mexico unite. 3) The Isthmus of Tehuantepec area, where the provinces of the Sierra Madre del Sur, the Coastal Plains of Gulf of Mexico and the Highlands of Chiapas converge (see Chiroptera in Figure 3). The maps also show that each family has a particular pattern of species richness across the country (Figure 3) and the points where

it is concentrated are scattered. This suggests that the bat richness concentration in some areas is probably due to the environmental heterogeneity, areas with a complex topography that give rise to a wide diversity of climates and vegetation types that promote the formation of several habitats within a relatively small territorial extension; this is in accord with [Willig and Presley \(2018\)](#) who postulate that the variation in species composition among local assemblages is typically associated with habitat heterogeneity and contributes to the disparity between biodiversity at local and regional scales.

[Arita et al. \(2014\)](#) proposed that bat richness in Mesoamerica is determined at the generic level by the distinct tendencies of diverse clades and is tightly linked with the origin and the processes of diversification at the family level. For instance, the families Vespertilionidae and Natalidae have a North American origin, while the family Molossidae underwent an early diversification in South America. Meanwhile, the diversification processes for Mormoopidae and Phyllostomidae and probably for Emballonuridae were complex. In the maps obtained by us only the richness pattern observed in Vespertilionidae may be viewed as a reflection of the family's origin.

The richness of bats among biotic provinces is very complex to attribute only to the conjugation of some environmental factors and the types of vegetation existing in them. [López-González et al. \(2012\)](#) proposed that the structure of Mexican bat meta-communities is associated with multiple environmental gradients at different spatial scales and that the distribution of bats along environmental gradients is determined by characteristics of the species group and not the defined study areas that arbitrarily confine them. Our results show a similar behavior for concentrated bat richness.

Bat families differ in their richness patterns, so studies of bat biogeography in Mexico may be misleading if they are examined only at the ordinal level; beside this the results of this study also show that the species richness of bats and their relationship with environmental parameters are more complex than previously reported and that the distribution patterns can differ depending on the taxonomic level or the parameters considered. Likewise, the bat richness is similar for the vegetation and climate types; but due to the complex orography of the country representation of these two factors on a map is very complex (Figures 4a, 4b).

Vegetation and climate, either independently or together, do not completely explain the observed richness patterns, thereby demonstrating the need to examine different dimensions of richness as well as the biological richness of bats in megadiverse ecosystems using new approaches that consider phylogenetic aspects and the evolutionary history of each taxon.

Other authors have already mentioned some of the areas in this study with the greatest species richness. For example, Chamela, Jalisco (western Mexico); Los Tuxtlas,

Veracruz (to the west of the Isthmus of Tehuantepec); and El Triunfo, Chiapas (to the east of the Isthmus of Tehuantepec), are mentioned in the study of [Arita and Ortega \(1998\)](#) as localities with high species richness. In the maps generated in this study, these localities each represent one point within much wider areas of high species richness, wherein the species richness decreases with respect to increasing distance from these points.

Various authors have highlighted the importance of the 'Mexican transition zone', an area where the Nearctic and Neotropical regions converge, for understanding the diversity patterns of mammals ([Ortega and Arita 1998](#); [Fa and Morales 1991](#); [Escalante et al. 2005](#); [Morrone and Escalante 2002](#)). The generated maps also demonstrate the importance of this zone for bat species as a whole and particularly for Phyllostomidae. In addition, the maps show the significance of the Río Balsas Basin and the Trans-Mexican Volcanic Belt, especially for the families Mormoopidae and Vespertilionidae.

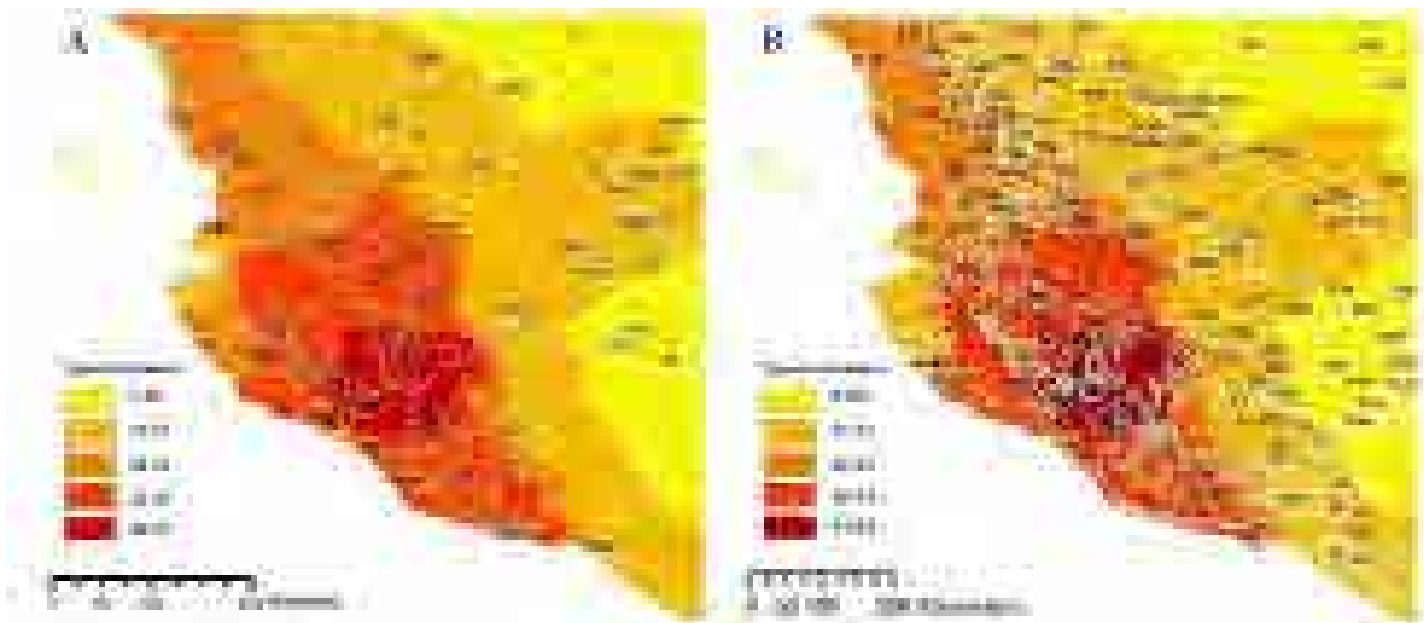
Our results highlight that for Mexican bats, patterns may be dependent on characteristics of spatial scale and taxonomic hierarchy and also point out the need to consider, beside the origin and diversification process, the potential differences in the macroecology and biogeography among families. Additional analyses that consider the patterns of richness presented in this study and that incorporate at the same time other variables (productivity, environmental structure, and landscape heterogeneity) and processes (phylogenetic and functional diversity) could reveal new information about the factors that influence and shape the distribution of bat species richness, both overall and for distinct clades.

Bats are related to the upkeep of ecosystem services that are very important for the maintenance of humid

tropical forests, dry forests, cactus plants, xerophilous thickets and cave environments, in which they perform as pollinators, seed dispersers and regulators of insect populations ([Kunz et al. 2011](#)). The application of conservation plans for bats will make it possible to preserve these ecoservices and others relevant to human beings, such as the control of various insect pests in plants of agricultural interest ([Maine and Boyles 2015](#)), the pollination of plants with commercial interest ([Rocha et al 2006](#); [Valenzuela 2011](#)) as well as in the field of human health, because bats are also controllers of insect populations that can be vectors of important diseases such as malaria, dengue, zika and chikungunya, among others ([Plowright et al. 2015](#)).

The protection of areas with high concentration of bat richness, especially the rich hotspot diversity areas showed in this paper, should be a priority during the development of conservation strategies. The analysis of geographical concentrations of endemic taxa are frequently used to determine priorities for conservation actions; preserving areas with a broader taxonomic focus, such as the one proposed in this study at the family level, would consider phylogenetic relationships (evolutionary history) among taxa. It may therefore provide a better currency for conservation evaluation than only species richness.

Decision makers should consider the richness patterns presented in this study in order to design appropriate strategies for the conservation of bats in Mexico. Their conservation is especially important considering their high ecological value, furthermore, their richness patterns result from the interaction of multiple variables and processes that affect other faunistic groups in addition to bats.



**Figure 4.** Maps showing the bat richness patterns in western Mexico and its complex relationship with vegetation (A) and climate types (B). Vegetation types: Deciduous tropical forest (DTF), Grassland (G), Mountain cloud forest (MCF), Pine-Oak forest (POF), Thorn forest (TF), Tropical sub-deciduous forest (TSDF) and Xerophile shrubland (XS). Climates: Cold (Co), Dry-very warm (Dvw), Semi-cald sub-humid (Scs), Semi-cold sub-humid (Scsh), Semi-dry semi-warm (Sdsw), Semi-dry temperate (Sdt), Semi-dry very warm (Sdvw), Semi-dry warm (Sdw), Semi-warm humid (SwH), Temperate sub-humid (Tsh), Temperate-humid (Th), Very dry semi-warm (Vdsw), Very dry-temperate (Vdt), Warm sub-humid (Wsh), and Warm-humid (Wh).

The results presented here enable a general understanding of the species richness patterns of bats and of the areas where this richness is concentrated and its relationship with diverse biogeographic regions and environmental parameters. Even so, these results are not completely satisfactory, due to methodology problems.

Novel techniques for identifying insectivorous bats have been developed (ultrasonic detectors) do not necessarily involve the capture of individuals, so species records can change, causing possible variations in the maps presented here. The utilized scale of 1:1,000,000 and the use of a 1° X 1° grid functioned well for the biogeographical regions (biotic provinces) but not for environmental factors considered (vegetation and climate). Along the country some climates types had a limited or very fragmented geographical distribution with the utilized scale these climates occupied the same cells dominated by other climate types with a wider geographical distribution; therefore, in the analyses, the relationships of the cold, semi-warm humid, semi-dry semi-cold, and temperate-humid climate types with species richness were excluded from the results. This same phenomenon occurs also with vegetation types and for the Mountain cloud forest the analysis either did not generate results. This highlights the need to investigate the interactions with environmental parameters at different scales in order to have a better understanding of the richness patterns in Mexican bats.

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# Analysis and trends of photo-trapping in Mexico: text mining in R

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This paper gathers published studies that used photo-trapping as the primary or supplementary method to obtain data on mammal and bird species in Mexico. The aim is to determine temporal trends, scientific journals, species, research groups, regions, and key topics investigated using this technology. A secondary objective of this paper was to illustrate the usefulness of text mining tools to analyze and summarize relatively large amounts of information. Papers about photo-trapping in Mexico published in specialized journals and books from 1998 to 2017 were compiled from *Google Scholar* and processed with various packages in R. A total of 188 papers about photo-trapping in Mexico were compiled, with 88.2 % published in 50 journals over the past seven years. The main journals were *Therya*, *Revista Mexicana de Biodiversidad*, *Acta Zoológica Mexicana (New Series)* and *Revista de Biología Tropical*. The articles identified were written by 406 co-authors, 28 of whom contributed with 32.4 % of the papers published. A total of 40 species were reported in the title and abstract of these papers; the most frequent species were *Panthera onca*, *Leopardus pardalis*, *Puma concolor*, *Tapirus bairdii*, *Tayassu pecari*, *Odocoileus virginianus*, and *Cuniculus paca*. Oaxaca, Campeche, Sonora, Chiapas, Guanajuato, and Puebla were the main states where studies were conducted; in particular, most of them were carried out within Biosphere Reserves. Major research topics comprised records that broaden the distribution range, estimates of relative abundance and density, analysis of activity patterns, ecological interactions between species, and use of photo-trapping data as supplementary information to elaborate inventories of species. The analysis of text mining clearly indicates a trend towards an increasing use of photo-trapping in Mexico. Felines, ungulates and various species of the order Carnivora are main subjects of study. Photo-trapping has been used to explore a number of aspects of the biology of animal species. A large number of studies have been carried out in southeastern Mexico. The use of text mining techniques is a practical approach to analyze large volumes of data.

El objetivo del presente trabajo fue recopilar los estudios publicados donde se emplea el foto-trampeo como método principal o complementario para la obtención de datos de mamíferos y aves de talla mediana y grande en México, con la finalidad de conocer la tendencia temporal, revistas donde se publicó, especies, grupos de investigación, regiones y temas principales abordados con esta tecnología. Adicionalmente, como segundo propósito en este trabajo se ejemplifica la utilidad de las herramientas de minería de textos para analizar y sintetizar cantidades relativamente grandes de información. Se recopilaron libros, capítulos y artículos científicos publicados sobre foto-trampeo en México entre 1998 a 2017 en el *Google Académico*, y se procesaron a través de minería de textos con diferentes paquetes en R. Se encontraron 188 artículos sobre foto-trampeo en México de los cuales el 88.2 % fue publicado en los últimos siete años. Los artículos fueron publicados en 50 revistas; destacan *Therya*, *Revista Mexicana de Biodiversidad* y *Acta Zoológica Mexicana (nueva serie)* y *Revista de Biología Tropical*. Los artículos fueron escritos por 406 coautores, de los cuales 28 han contribuido con el 32.4 % de los trabajos publicados. Un total de 40 especies se reporta en el título y resumen de los documentos; de las cuales las más estudiadas fueron: *Panthera onca*, *Leopardus pardalis*, *Puma concolor*, *Tapirus bairdii*, *Tayassu pecari*, *Odocoileus virginianus* y *Cuniculus paca*. Oaxaca, Campeche, Sonora, Chiapas, Guanajuato y Puebla fueron los principales estados estudiados. En particular, destacan Reservas de la Biosfera. Los principales temas de investigación tratan sobre registros notables que amplían el rango de distribución geográfica de varias especies, diversidad, estimaciones de abundancia relativa y de la densidad de población utilizando captura-recaptura, análisis de patrones de actividad entre especies, e interacciones ecológicas. El análisis de minería de texto indica claramente que el foto-trampeo es un método en crecimiento en México. Los felinos, ungulados y varias especies del orden Carnívora, son los más frecuentemente estudiados. El foto-trampeo se ha empleado para conocer variados aspectos de la biología de las especies animales. La región del Sureste del país es donde se ha realizado un mayor número de estudios. El empleo de técnicas de minería de texto es una alternativa práctica para analizar volúmenes grandes de datos.

**Key words:** birds; camera-traps; journals; mammals; R; text mining; topic trend.

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## Introduction

The monitoring of biodiversity, in either different regions or a single region through time, requires collecting data on many species, often across different taxonomic groups and trophic levels, and with different life histories and other parameters that add complexity to the investigation (O'Brien *et al.* 2010). In particular, inventories serve a number of purposes, such as determining the ecological diversity in a given site, making comparisons between sites, refining distribution maps for individual species, obtaining demographic parameters on populations, or assessing the impact of human activities on mammal communities

(Baillie *et al.* 2008). An in-depth knowledge of the fauna supports the development and planning of improved conservation strategies, particularly in protected natural areas (Bruner *et al.* 2001). In this sense, birds and medium-sized and large mammals are considered to be key groups to monitor biodiversity and the state of ecological integrity (Ahumada *et al.* 2011).

One of the most popular techniques to survey the fauna is based on cameras-traps, also called photo-trapping (Meek and Pittet 2012, McCallum 2013, Burton *et al.* 2015, Rowcliffe 2017). This is due, among several factors, to the improvement in technological development and the lower

costs of the equipment involved (Rovero *et al.* 2013). The applications of this technique range from data collection for species inventories, the study of activity patterns, estimates of occupancy, the relative abundance and density of animals, up to more specific aspects such as behavior and interactions between species and their habitat, among other topics (Jenks *et al.* 2011). Photographs provide reliable records about the presence of species, and can be shared for verification by experts (O'Connell *et al.* 2010). The use and development of photo-trapping has been so successful that several books and manuals studies addressing it have been published in just a few years (O'Connell *et al.* 2010, Fleming *et al.* 2014, Rovero and Zimmermann, 2016, Wearn and Glover-Kapfer 2017). In Mexico, the use of camera traps has boomed, mainly in the past decade, being applied to several species with various objectives in different regions and habitats across the country. Hence, the trends and contributions of this technology to the knowledge of the fauna is a topic worth investigating.

One way to measure the overall and particular trends in the use of photo-trapping is data mining (text mining), as this approach facilitates the methodical analysis of large volumes of data. Specifically, text mining is the process of extracting information from a set of texts (Kwartler 2017). The results are displayed as tables and graphs that can be useful for multiple purposes (Silge and Robinson 2017). In a scientific context, for instance, text mining may contribute to a relatively rapid analytical processing of extensive information. Although text mining may not be a fully automated process in itself, the different computation tools currently available enable the processing of large amounts of text over a relatively short time. In particular, several packages have been developed for the R platform that are useful to analyze this type of information (Kwartler 2017, Silge and Robinson 2017).

The main objective of this work was to gather published studies using photo-trapping as a primary or supplementary method to collect data or records on the presence of species in various locations in Mexico. The specific objectives were: 1) Analyze the temporal trend of studies. 2) Identify the species that are either most frequently studied or for which more information is obtained with this method. 3) Identify the main research groups, highlighting the research leaders. 4) Identify the sites, regions, and natural areas studied. 5) Assess whether the data from photo-trapping are being applied to specific management and conservation issues/solutions, in addition to the generation of scientific knowledge. 6) Suggest further topics in the application of photo-trapping in our country.

## Methods

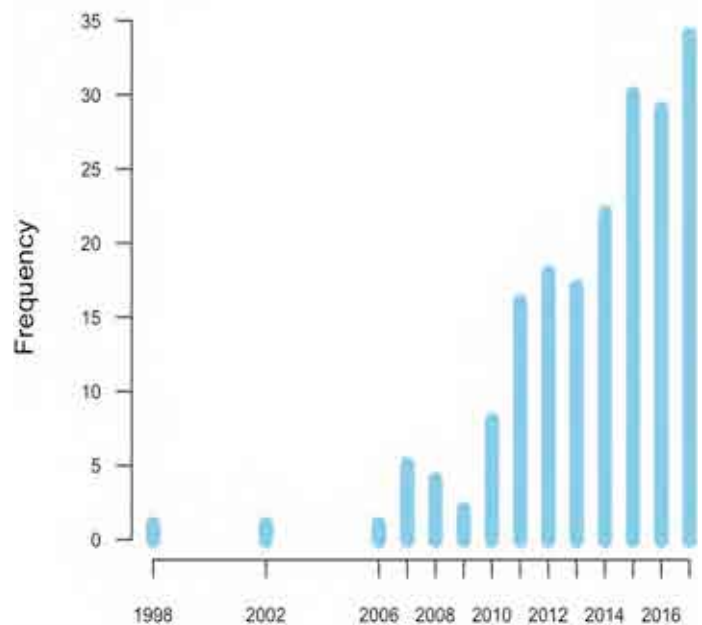
**Information gathering.** Published information was collected on studies reporting the use of camera-traps as the main or supplementary methodology to get information from a number of animal species. To this end, a comprehensive search of articles cited in the *Google Scholar* was conducted spanning from 1990 to late 2017. The search was con-

ducted using the key words photo-trapping, camera-traps, monitoring, Mexico, in both Spanish and English. Excluded sources were technical reports, theses and website news. The respective literature references were saved in *BibTeX* format (Mata-Perez 2014). The RefManageR package was used for managing the bibliography in *BibTeX* format (McLean 2014, 2017). Once all the literature references were compiled, these were saved as files with the extension *.bib* and used as basis for the text mining analysis in R. The quantitative analysis consisted basically in constructing frequency tables for each objective stated in this work using the packages *tidyverse* (Wickham 2017), *tm* (Feinerer and Hornik 2017), and *ggplot2* (Wickham 2009). The work teams and the interactions between them were determined using the *igraph* package (Csardi and Nepusz 2006). All analyzes in this study were carried out using R version 3.3.3 (R Core Team 2017) on the RStudio platform (RStudio Team 2015).

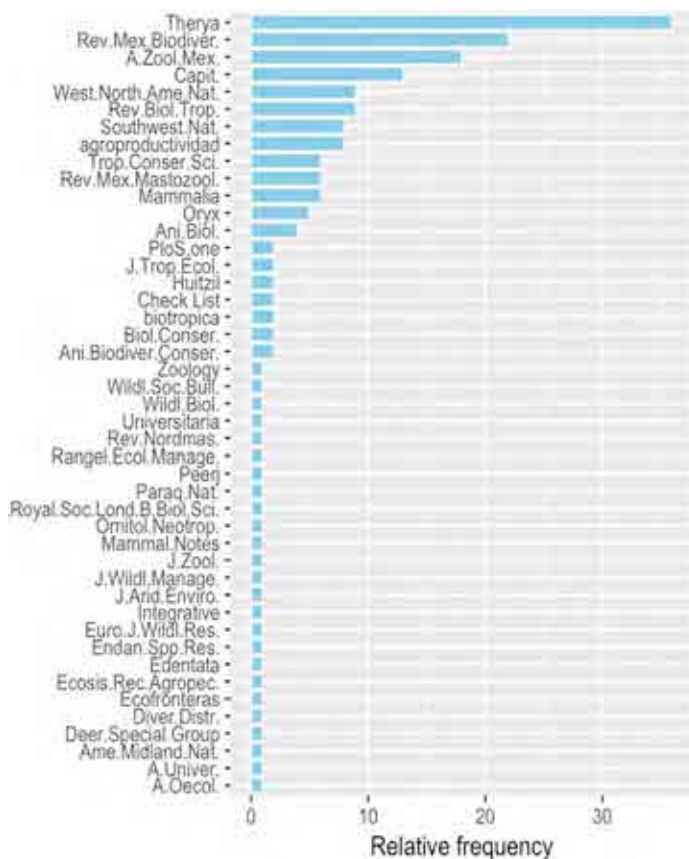
## Results

**Temporal Trend and Journals.** A total of 188 articles were gathered: 1 book, 6 book chapters and 181 articles published between 1998 and 2017; 88.2 % of these were published over the past 7 years (Figure 1). These articles were published in 50 journals: 9 national and 41 international journals; 76.1 % were published in the journals *Therya*, *Revista Mexicana de Biodiversidad*, *Acta Zoológica Mexicana* (new series), *Revista de Biología Tropical*, *Western North American Naturalist*, *The Southwestern Naturalist*, *Agroproductividad*, *Tropical Conservation Science*, *Revista Mexicana de Mastozoología*, *Oryx*, *Mammalia*, and *Animal Biology* (Figure 2).

**Authors.** Articles were written by 406 co-authors from various Mexican and foreign institutions. According to their contribution, 28 authors published 5 or more articles, altogether accounting for 32.4 % of all articles published (Fig-

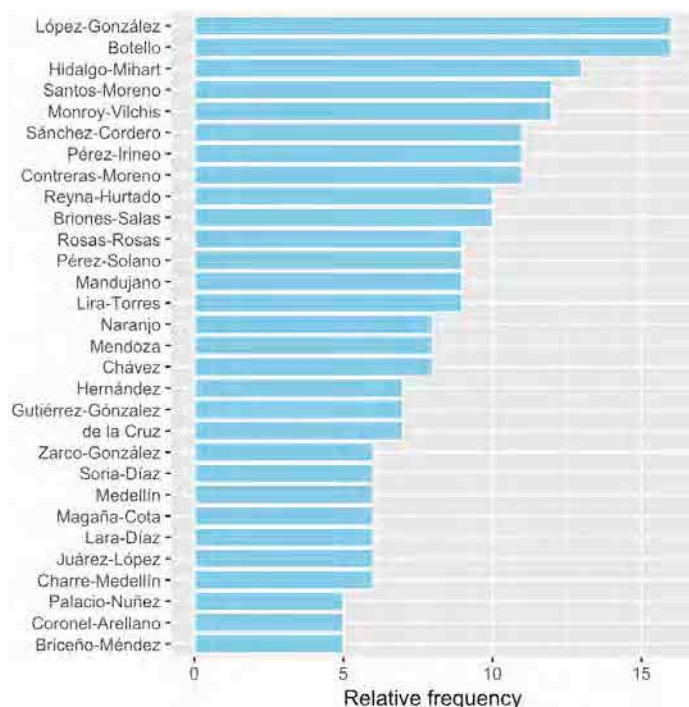


**Figure 1.** Trend in the number of publications involving the use of photo-trapping to gather data about wildlife in Mexico.

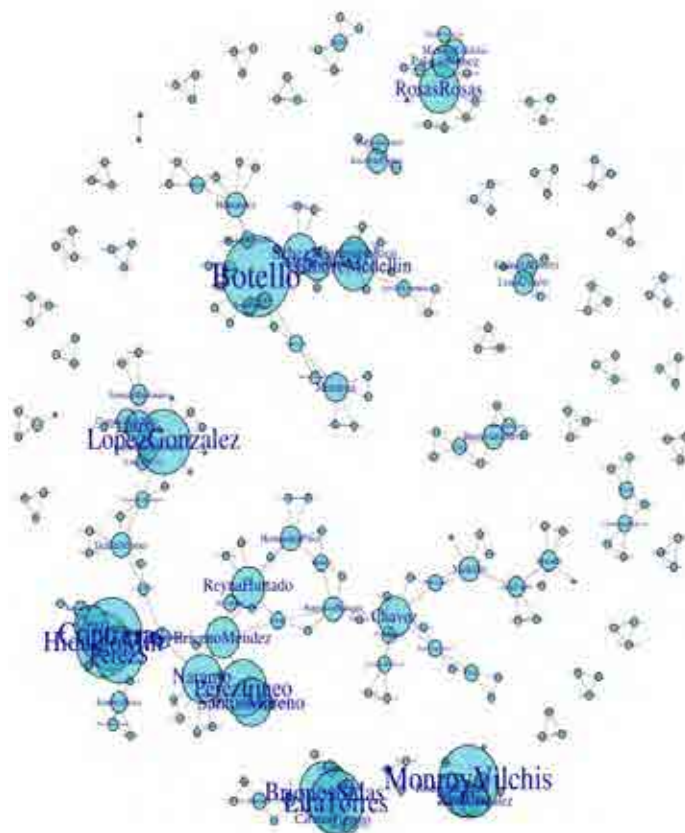


**Figure 2.** Journals that have published studies involving photo-trapping in Mexico. Abbreviations:

ure 3). This analysis yielded a relatively complex network of interactions between researchers (Figure 4). Research groups with some publications and little interaction with the rest are shown at the periphery of the network. In con-



**Figure 3.** Main authors that have contributed a large number of publications involving photo-trapping in Mexico. Authors who have contributed more than two articles are shown.

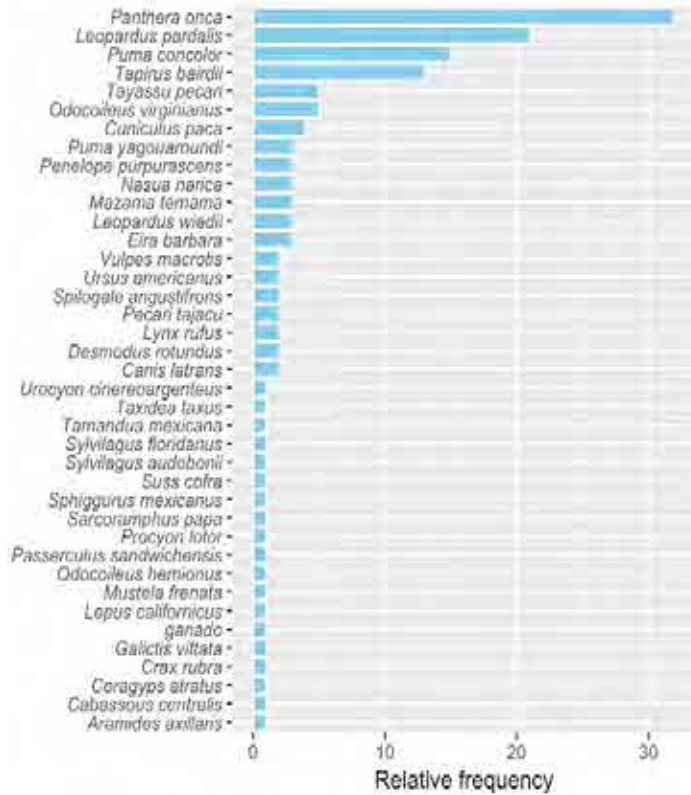


**Figure 4.** Interactions network between scientists who have used and published works involving photo-trapping in Mexico. The size of letters indicates the number of publications by a given author and the extent of his/her interactions with other co-authors.

trast, several clusters of work teams and their interaction with other groups appear to the center of the network. The major teams identified are: 1) Botello, Sánchez-Cordero, Charre-Medellín. 2) López-González, Lara-Díaz, Coronel-Arellano, Gutiérrez-González. 3) Hidalgo-Mirhart, Contreras-Moreno, de la Cruz, Pérez-Solano. 4) Reyna-Hurtado, Briceno-Méndez, Sandoval-Serés, Sanvicente-López. 5) Monroy-Vilchis, Soria-Díaz, Rodríguez-Soto. 6) Rosas-Rosas, Tarango-Arambula, Clemente-Sánchez, Palacio-Núñez, Hernández- SaintMartín. 7) Lira-Torres (r. i. p.), Briones-Salas. 8) Pérez-Irneo, Santos-Moreno. 9) Chávez, Ceballos. 10) Medellín, de la Torre.

**Species.** A total of 40 species are reported in the title or in the abstract of publications involving photo-trapping, with felines and ungulates as the main groups. Particularly, *Panthera onca*, *Leopardus pardalis*, *Puma concolor*, *Tapirus bairdii*, *Tayassu pecari*, *Odocoileus virginianus*, and *Cuniculus paca* account for 55.1 % of articles (Figure 5).

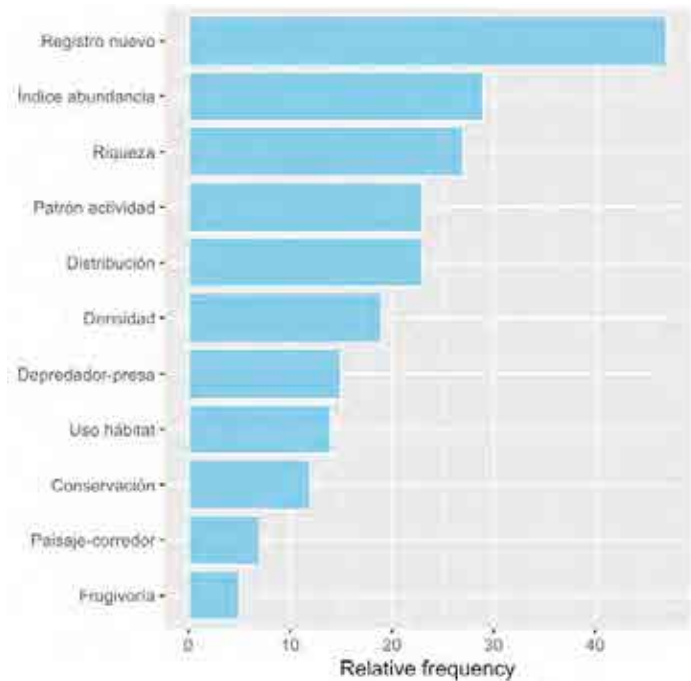
**Main Topics.** Photo-trapping studies cover a diverse range of topics. Most frequently, studies report new records, that is, when a species is recorded photographically in a site for the first time ever (Figure 6). Occasionally, these new records broaden the geographical distribution range. In order of frequency, these are followed by studies that report the number of species (richness) in a particular site or region, and the estimated population size measured as the index of relative abundance (IAR), density, and



**Figure 5.** Species more frequently studied with photo-trapping in Mexico. Abbreviations:

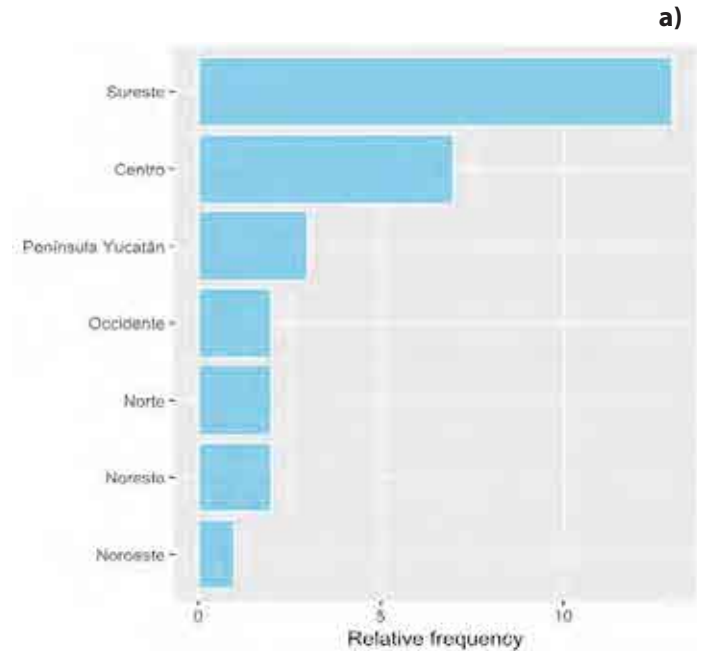
occupancy, activity patterns, and ecological interactions including predator-prey, frugivory, and parasitism. Also, photo-trapping has served to gather presence data for subsequent modeling of the potential geographic distribution.

*Regions, states, and natural areas.* The regions with the largest number of studies using trap-cameras are located in the Southeast, followed by the Center; while fewer investigations have been conducted in the North (Figure 7a). In

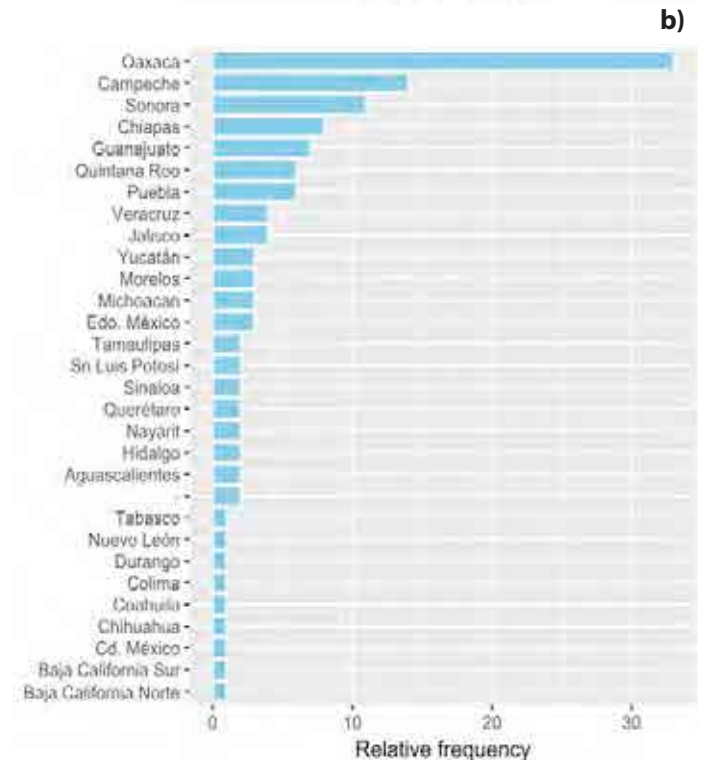


**Figure 6.** Topics most frequently addressed in studies using photo-trapping in Mexico.

particular, Oaxaca is the state where the largest number of studies with this technology have been conducted, followed by Campeche, Sonora, Chiapas, Guanajuato, and Puebla, altogether accounting for 33.1 % of the total number of published articles (Figure 7b). A fact worth mentioning is that many studies have been carried out within or near Biosphere Reserves, reserve areas and similar zones, such as Tehuacán-Cuicatlán, La Lacandona, Calakmul, Los Chimalapas, Sierra Gorda, Laguna de Terminos, Sierra Norte, the so-called Sky Islands, Nanchichitla, El Cielo, and the Chihuahuan Desert (Figure 7c).



**a)**



**b)**

**Figura 7.** Regions (a), and states (b) , most frequently addressed in studies using photo-trapping in Mexico.



2014). Although no published work addressing this issue was identified, a number of field investigations of arboreal mammals involving camera-traps in Mexico are ongoing.

Similar to other countries, photo-trapping has been used in Mexico to investigate a range of aspects about the biology of animal species. In terms of the number of works, the main topic of interest deals with new records of species in sites where their presence had not been previously reported; a topic closely related to new records is the broadening of the geographic range. Likewise, photo-trapping is being used to record the presence of species as supplementary data for modeling the potential distribution range using the ecological niche theory as conceptual framework — a conceptual and methodological approach commonly used today. Another aspect frequently addressed is the study of species richness and diversity. In many cases, photo-trapping is employed as the only method to report species richness, particularly in the case of medium-sized and large species, which are the species most easily detected with this technique. Other studies have applied photo-trapping as a supplementary method along with traps, nets and traces, to elaborate lists of species in certain sites. In other words, photo-trapping is a key method in Mexico for broadening and contributing to the knowledge of biodiversity and distribution of animal species, mainly medium-sized and large mammals which, given their habits and rarity, are often hard to spot and for which data gathering is difficult when other sampling methods are used (Thompson 2013). Finally, some practical aspects worth stressing are, on the one hand, the systematization of images obtained by photo-trapping in record cards filed in Scientific Collections, which are key for the knowledge of diversity; on the other, the development and training in different techniques and methods of analysis associated with photo-trapping (Botello *et al.* 2007).

The study of population size, particularly the use of the so-called indices of relative abundance (IAR), is a topic frequently addressed in photo-trapping studies. Related to population size estimates, some works have focused on density through classical capture-recapture and, more recently, the so-called spatially explicit capture-recapture methods. In contrast, few studies have focused on estimating occupancy. Separately, numerical and statistical methods employed to analyze photo-trapping data have covered various approaches, ranging from the absolute subjective interpretation of the so-called indices of relative abundance (IAR) to very robust methods of analysis (Springer *et al.* 2012). The text mining analysis indicates that the IAR is still extensively used in our country despite its serious limitations (Sollmann *et al.* 2013).

In this respect, users of camera-traps in our country should apply a high statistical rigor in their analysis. Fortunately, the publication of works that estimate population size through capture-recapture and even spatially explicit methods is on the rise (*e. g.*, Carbajal-Borges *et al.* 2014). These models require the recognition of individuals. When

individual identification is not possible, there are several alternatives; one is the use of occupancy models (*e. g.*, Cove *et al.* 2013) and the use of models that estimate density without the need to recognize individuals (*e. g.*, Rowcliffe *et al.* 2014, Cusack *et al.* 2015, Rowcliffe *et al.* 2016). Also, the application of traditional distance-based methods (Thomas *et al.* 2010) for photo-trapping data is increasing (Rowcliffe *et al.* 2011, Howe *et al.* 2017). Another area of opportunity offered by camera-traps is video recording (Delgado-V. *et al.* 2011, McCallum, 2013, Rowcliffe 2017).

Camera-traps can record the time, temperature, moon phase and other data simultaneously with each image. This has the use of this technology to estimate the patterns of activity and the overlap of these patterns between species. In addition, photo-trapping has been used to analyze the use of the habitat. Although this application is not common yet, photo-trapping can be used to gather physiological information, in particular regarding reproduction (*e. g.*, Aranda *et al.* 2012). Ecological interactions is another topic of growing interest, especially for predation-prey interactions, frugivory, and parasitism, through functional ecological (Soria-Díaz *et al.* 2017a, 2017b) and experimental (Camargo-Sanabria *et al.* 2015) approaches. In addition, photo-trapping studies are addressing not only the distribution and abundance of species, but also other aspects related to conservation, such as hunting, habitat fragmentation, and livestock raising, as well as the effect of hurricanes, landscape management and connectivity (*e. g.*, Lara-Díaz *et al.* 2013). In other words, photo-trapping is yielding very interesting findings on a number of topics related to behavior, interactions, and management.

Although camera-traps are being used across the country, data mining clearly evidenced that the majority of studies have been conducted in the Southeast region. In particular, Oaxaca stands out as the state with the largest number of published studies involving photo-trapping. Next in importance are Campeche, Chiapas, Quintana Roo, and Yucatan. In the center of the country, the states that yielded the largest number of publications are Guanajuato, Puebla, Veracruz, Michoacán and Jalisco. In the north, the state of Sonora is worth mentioning. Separately, a significant percentage of studies involving photo-trapping have been conducted in Protected Natural Areas, mainly Biosphere Reserves such as Tehuacán-Cuicatlán, La Lacandona, Calakmul, Los Chimalapas, Sierra Gorda, Laguna de Terminos, and Sierra Norte. The biosphere reserves share a vision of the integration of the various uses of resources consistent with the long-term conservation of biological and cultural diversity, under a land-use scheme based on core, buffer and transition zones. According to Halfpter (2011), some reserves are associated with laboratories or institutions that have been pivotal research centers, producing abundant and important knowledge. In this sense, in addition to their key role in the creation of knowledge and prevention of changes of land use (Figueroa and Sánchez-Cordero 2008), ANPs frequently offer adequate conditions of personal safety and equipment used in photo-trapping studies.

In Mexico, there are initiatives for the application of photograph collection and monitoring protocols at the country level, such as the biological photograph collection of UNAM (Botello *et al.* 2007), as well as programs promoted by the National Forestry Commission (CONAFOR) and the National Commission of Protected Areas (CONANP). There are also local and regional initiatives for the monitoring of wild animals using trap-cameras, such as the Community Monitoring of Biodiversity in Oaxaca, an appealing initiative that includes a user-friendly webpage (<http://dsjm-conanp-monitoreo.org>). Another example is the *Proyecto Guerrero Jaguar* social initiative for the monitoring of wildlife in the state of Guerrero ([www.facebook.com/guerrerojaguar](http://www.facebook.com/guerrerojaguar)). In addition, monitoring programs of key species for conservation have been in place for several years; an example is the jaguar, a species for which photo-trapping has been a core method (Chávez *et al.* 2013). Likewise, meetings such as the *First Meeting of Photo-Trapping Experts in Mexico* organized by the National Commission for the Knowledge and Sustainable Use of Biodiversity (CONABIO) have as a key objective to integrate the information obtained from individual studies and programs involving photo-trapping. As a result, progress has been made in having monitoring protocols in place and, to the extent possible, homogenize data collection to facilitate comparisons between regions.

## Supplementary Material

The complete list of bibliography compiled for the analyses in this article and the detailed text mining procedure in R used in this work are available from the author upon request.

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# Epizoid arthropods of the Mexican Shrew, *Sorex oreopolus* (Mammalia: Soricidae)

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Shrews (Eulipotyphla: Soricidae) are amongst the most diverse and widely distributed groups of small mammals worldwide. In Mexico, more than 40 species of the genera *Sorex*, *Cryptotis*, *Megasorex*, and *Notiosorex* have been documented. There is little knowledge about epizoid arthropods of shrews, with 40 species recorded, 28 corresponding to the subclass Acari, and 12 to Insecta. *Sorex oreopolus* Merriam, 1892, is an endemic species of Mexico, distributed from southwest Jalisco to east Puebla and west Veracruz. This study reports the first records of epizoid arthropods of *S. oreopolus*. Five specimens of *S. oreopolus* were collected during 2016 from four sites at La Malinche National Park, state of Tlaxcala. Epizoid arthropods were removed from the pelage of shrews and processed for identification. For each species found in *S. oreopolus*, ecological parameters of infestation were calculated; for parasitic species, also the degree of host specificity was estimated. A total of 1,194 arthropods were found, corresponding to six mite and one insect taxa. All are new records for this host species. The mites *Orycterxenus soricis* (Oudemans 1915) and *Pygmephorus horridus* Mahunka, 1973 are recorded for the first time in Mexico. The prevalence and abundance of *O. soricis* was high, while *Corrodopsylla lira* Traub, 1950 is less prevalent/abundant (Table 1). Epizoid arthropods comprise commensals (Myobiidae), temporary ectoparasites (Trombiculidae) and (Ctenophthalmidae), and phoretic (Glycyphagidae and Pygmephoridae). Seven taxa of epizoid arthropods recorded in this study represent the first record of association with *S. oreopolus*. The mites *O. soricis* and *P. horridus* had already been documented on shrews of the genus *Sorex*; however, they are recorded for the first time in Mexico, increasing the richness of symbionts of Mexican shrews from 40 to 42 species. Further investigations on the richness of arthropods associated with Mexican shrews are needed, as only seven of 40 species of shrews have been documented, representing 20 % of hosts.

Las musarañas (Eulipotyphla, Soricidae) constituyen uno de los grupos de mamíferos pequeños terrestres más diverso y con mayor distribución en el mundo. En México se encuentran en casi todo el territorio y se han documentado más de 40 especies de los géneros, *Sorex*, *Cryptotis*, *Megasorex* y *Notiosorex*. Es notable la falta de estudios sobre los artrópodos epizoicos de musarañas en el país, se han registrado 40 especies de los cuales 28 corresponden a la Subclase Acari y 12 a la Clase Insecta, asociados a siete especies de musarañas. La musaraña mexicana *Sorex oreopolus* Merriam, 1892 es una especie endémica de México, que se distribuye desde el extremo suroeste de Jalisco hasta el este de Puebla y oeste de Veracruz. Hasta la fecha no se han documentado sus artrópodos epizoicos, por lo que el objetivo de este trabajo es presentar los primeros registros. Durante el 2016 se recolectaron cinco ejemplares de *S. oreopolus* en cuatro sitios del Parque Nacional La Malinche en el estado de Tlaxcala. Los artrópodos epizoicos se extrajeron y procesaron para su identificación. Se calcularon los parámetros ecológicos de infestación: prevalencia, abundancia promedio, intensidad promedio e intervalo de intensidad para cada especie de ácaro. Se recuperaron 1,194 artrópodos epizoicos distribuidos en 6 taxones de ácaros y un taxón de insecto, todos representan nuevos registros para el huésped. El ácaro *Orycterxenus soricis* (Oudemans 1915) presentó los niveles más altos de abundancia y prevalencia, mientras que los valores más bajos de infestación fueron para la pulga *Corrodopsylla lira* Traub, 1950 (Cuadro 1). Por primera vez en México, se registran los ácaros *O. soricis* y *Pygmephorus horridus* Mahunka, 1973. Los simbioses presentaron tres categorías de asociación: comensales (Myobiidae), ectoparásitos temporales (Trombiculidae) y (Ctenophthalmidae) y foréticos (Glycyphagidae y Pygmephoridae). Los siete taxones de artrópodos epizoicos registrados en este estudio representan el primer registro de asociación con *S. oreopolus*. Los ácaros *O. soricis* y *P. horridus*, ya habían sido documentadas sobre las musarañas del género *Sorex*, no obstante, se registran por primera vez en México, incrementando la riqueza de simbioses de musarañas mexicanas de 40 a 42 especies. Se necesitan investigaciones adicionales sobre la riqueza de artrópodos asociados, ya que sólo se han documentado en siete de las más de 40 especies de musarañas mexicanas, lo cual representa cerca del 20 % de los huéspedes.

**Keywords:** Mexico; mites; *Orycterxenus soricis*; parque nacional La Malinche; shrews; symbiosis.

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## Introduction

Shrews (Eulipotyphla, Soricidae) are one of the most diverse and more extensively distributed groups of terrestrial small mammals worldwide. In Mexico, shrews are found across the whole country (Carraway 2007) with more than 40 species of 4 genera documented, grouped in 3 tribes: 1) Soricini, including the genus *Sorex*. 2) Blarinini, with *Cryptotis*. 3) Notiosoricini, grouping together *Megasorex* and *Notiosorex* (Guevara et al. 2014, 2015; Matson and Ordóñez-Garza 2017; Ramírez-Pulido et al. 2014). Shrews consume large

amounts of invertebrates, including worms, crustaceans, and spiders, as well as insects and their larvae (Hope et al. 2016). In addition, they have a diverse and abundant associated fauna (mainly parasites) (Binkienė et al. 2011; Morrone and Acosta 2006). Shrews and their parasites are key indicators to anticipate the consequences of environmental disruption and changes in the interactions between species (Hope et al. 2016).

In Mexico, studies about ectoparasites of shrews are particularly scarce; only 40 species of ectoparasites have

been recorded to date, with 28 corresponding to the Subclass Acari and 12 to the Class Insecta, associated with seven species of shrews: *Cryptotis mexicanus*, *C. magnus*, *Cryptotis* sp., *Notiosorex crawfordi*, *Sorex milleri*, *S. saussurei*, *S. veraepacis*, *S. salvini* (= *S. veraecrucis*), and *Sorex* sp. (Estébanes-González and Cervantes 2005; Fain and Estébanes 1996; Montiel-Parra et al. 2009; Morrone and Acosta 2006; Salceda-Sánchez and Hastriter 2006; Vargas et al. 2009; Whitaker and Morales-Malacara 2005).

The shrew *S. oreopolus* Merriam, 1892, is a endemic species endemic of Mexico, distributed from the southwestern end of Jalisco to east Puebla and west Veracruz; living in mountain forests dominated by conifers and oaks, as well as by sacaton meadow (Castro-Arellano 2005). Ectoparasites or other arthropods associated with this species have not been documented yet; hence, this study reports the first records of epizoic arthropods of *S. oreopolus*.

**Methods**

In 2016, pitfall traps were placed around the area known as La Cañada Grande, located on the eastern slope of La Malinche (Malintzi or Matlalcueyatli) volcano at La Malinche National Park (Lopez-Dominguez and Acosta 2005; Figure

1a-c). Shrews were collected from two habitats representative of the park: pine forest and pine-oak forest (Figure 1d-e). At each site, eight pitfall traps were placed, each consisting of a 1,000 ml plastic container with ethylene glycol as preservative. Traps were left for 72 hours; subsequently, all the specimens captured were collected and deposited in glass bottles with 80 % ethanol. Only five shrews were captured in four sites (Figure 1d-e); these were removed from traps and individually preserved in 96 % ethanol bottles for transportation to the Colección Nacional de Ácaros (CNAC) at Instituto de Biología, Universidad Nacional Autónoma de México (IB-UNAM) in Mexico City. The body surface of each shrew was examined, brushing the pelage over a sheet of paper that was subsequently examined under a stereomicroscope; also, the ethanol where specimens were preserved was examined to obtain any ectoparasites that may have detached from the host. The sampling of shrews was carried out under collection licenses issued by SEMARNAT (FAUT-0309 and FAUT-0002). Shrews were identified and deposited in the Colección Nacional de Mamíferos (CNMA) of IB-UNAM, recorded with the following data: 1 unsexed specimen (UNAM 839/CNMA 49505), 5.4 km road to Estación Científica del Parque Nacional La Malinche, Mpio.



**Figure 1.** Study area: a-b) La Malinche National Park, Tlaxcala, Mexico, c) Sampling sites of specimens of *Sorex oreopolus*, d) View of the pine-fir forest at 3,197 masl, e) view of the pine forest at 3,407 masl.

Ixtenco, Tlaxcala, 1 Abril 2016, 19.25290° N, -97.97917°W, 3,050 msnm, Bosque de Pino, A. Valdez, E. Briones, M. Cortez, A. Juárez, cols.; 1 unsexed specimen (UNAM 840 /CNMA 49511), 1.5 km al oeste de la Estación Científica del Parque Nacional La Malinche, Mpio. Ixtenco, Tlaxcala, 6 mayo 2016, 19.24594° N, -98.00336° W, 3,250 msnm, Bosque de Oyamel-Pino, A. Valdez col.; 1 ♀ (UNAM 858/CNMA 49509), 2.5 km al oeste de la Estación Científica La Malinche, Mpio. Ixtenco, sobre la Cañada Grande, 2 junio 2016, 19.24309° N, -98.01241° W, 3,407 msnm, Bosque de Oyamel-Pino, A. Valdez and E. Briones, cols.; 1 ♀ same data except (UNAM 859/CNMA 49510); and 1 ♀ (UNAM860/CNMA 49508), 800 km al oeste de la Estación Científica La Malinche, 1 diciembre 2016, 19.24565° N, -97.99799° W, 3,197 msnm, Bosque de Oyamel-Pino, A. Valdez, E. Briones and M. Cortez, cols. For the determination, mites were cleared with lactophenol and mounted between microscope slides in Hoyer's medium. The siphonapteran (Insecta) was cleared with KOH and mounted in Canada Balsam. Ectoparasites are deposited in the CNAC. For each mite species, the following ecological infestation parameters were estimated: prevalence, mean abundance, mean intensity, and intensity range (Bush et al. 1997). In the case of parasites, the degree of specificity was determined considering the monoxenous, stenoxenous and oligoxenous (Herrin and Tipton 1975).

## Results

From the five specimens of *S. oreopolus* captured, a total of 1,194 ectoparasites we collected, distributed in seven taxa, six belonging to the subclass Acari, within four families and six genera. One flea *Corrodopsylla lira* Traub, 1950, family Ctenophthalmidae, was found (Table 1). A female of *S. oreopolus* captured in December six of the seven taxa reported in this study.

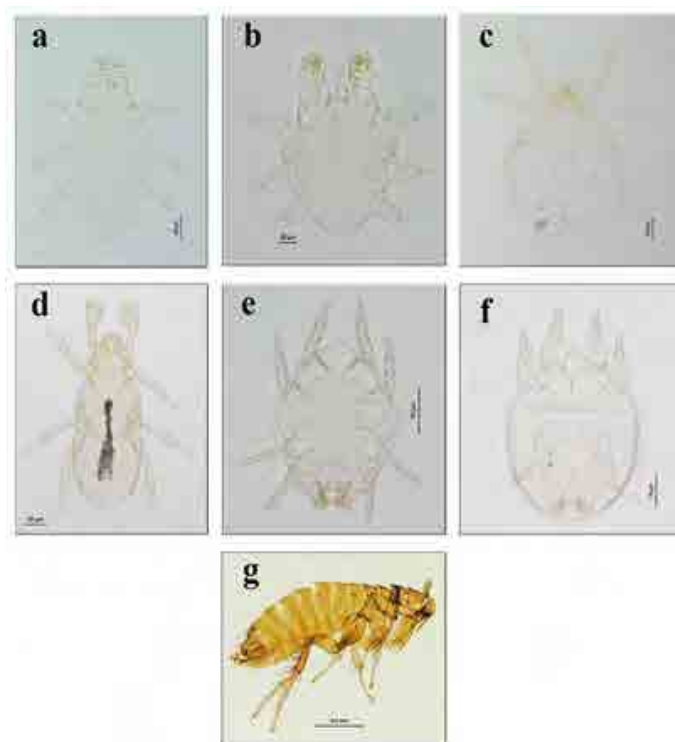
**Table 1.** Species of epizoid arthropods of *Sorex oreopolus* at La Malinche National Park, Tlaxcala, Mexico.

	Host / No. of Arthropods	Total No. of Arthropods	Prevalence (%)	Mean Abundance	Mean Intensity	Intensity range
<b>Class Arachnida</b>						
<b>Subclass Acari</b>						
<b>TROMBIDIFORMES</b>						
<b>Trombiculidae</b>						
<i>Walchioides intrinseca</i>	4	29	80	5.8	7.25	3-15
<b>Pygmephoridae</b>						
<i>Pygmephorus horridus</i>	1	3	20	0.6	3	-
<b>Myobiidae</b>						
<i>Protomyobia</i> sp.	2	3	40	0.6	1.5	1-2
<i>Amorphacarus</i> sp.	1	4	20	0.8	4	-
<b>SARCOPTIFORMES</b>						
<b>Glycyphagidae</b>						
<i>Orycterxenus soricis</i>	5	1,152	100	230.4	230.4	2-466
<i>Xenocyrtis</i> sp.	1	2	20	0.4	2	-
<b>Class Insecta</b>						
<b>SIPHONAPTERA</b>						
<b>Ctenophthalmidae</b>						
<i>Corrodopsylla lira</i>	1	1	20	0.2	1	-

The symbionts found were classified into three association categories: 1) commensals (Myobiidae). 2) temporary ectoparasites (Trombiculidae and Ctenophthalmidae). 3) phoretic (Glycyphagidae and Pygmephoridae).

Mites of the family Myobiidae (Figure 2a, b) showed a high host specificity, supporting the proposed phylogenetic relationships between their hosts. It has been observed that species can be oligoxenous (a parasite associated with two or more species of different genera but belonging to the same subfamily); for instance, the species of *Protomyobia*, *Amorphacarus*, and *Blarinobia* are all parasites specific to the subfamily Soricinae (Jameson 1984; Fain 1979). The specimens of *Protomyobia* sp. and *Amorphacarus* sp. found in *S. oreopolus* could not be identified to species because only an adult was found, the rest being either tritonymphs or protonymphs. Immature stages of this family have been little studied and differ morphologically from adults (Bochkov and Miroslubov 2015).

Temporary parasites of the family Trombiculidae are associated with the host for a short period of time during a single stage of their life cycle (hexapod larvae); these larvae feed on lymph and can be carriers and transmitters of bacteria or other microorganisms, whereas adults and nymphs are free-living (Hoffmann 1990). The species *Walchioides intrinseca* (Brennan 1960) (Figure 2c) has only been found in central Mexico, associated with *Sorex saussurei* Merriam, 1892 in Mexico City and with *Sorex* sp. in the state of Morelos (Hoffmann 1990). *W. intrinseca* is a stenoxene parasite (*i. e.*, associated with two or more host species of the same genus).



**Figure 2.** Epizoid arthropods of *Sorex oreopolus* at La Malinche National Park, Tlaxcala, Mexico: a) *Amorphacarus* sp. (female); b) *Protomyobia* sp. (protonymph); c) *Walchioides intrinseca* (larva); d) *Pygmephorus horridus* (female); e) *Orycterxenus soricis* (deutonymph); f) *Xenocyrtis* sp. (deutonymph); g) *Corrodopsylla lira* (male)

Dimorphic females of the family Pygmephoridae are characterized by a markedly modified leg I, with large grooved claws used for passive dispersal (phoresia) on small mammals (Eulipotyphla, Rodentia, and Lagomorpha), being less frequent in nests, and rarely found in soil or litter samples; other aspects of the biology of this family are unknown (Dastych *et al.* 1991). In Mexico, *Pygmephorus americanus* Banks 1904, has been previously recorded (Smiley 1978); therefore, *Pygmephorus horridus* Mahunka 1973 (Figure 2d) represents the second species of this family reported in the country, in addition to being the first record in association with soricid mammals. *P. horridus* has been collected in association with *Blarina brevicauda* (Say 1823) and *Scalopus aquaticus* (Linnaeus 1758) in the United States of America (Mahunka 1973).

Several deutonymphs (a post-embryonic development stage of mites between larva and adult) of species of the family Glycyphagidae have been recorded in American shrews. Ninety six per cent of the symbionts found in *S. oreopolus* belong to this family. *Orycteroxenus soricis* (Oudemans 1915; Figure 1e) showed the highest infestation levels (1,152 individuals), a 100 % prevalence, and a mean abundance of 230.4 mites per shrew, with an intensity range of 2 to 466 mites (Table 1). This species has been collected in shrews of the genera *Sorex* and *Blarina* in North America (Whitaker and Richards 2005). In Mexico, the species *Orycteroxenus mexicanus* Lukoschus *et al.* 1977 has been reported associated with shrews of the genera *Cryptotis* and *Sorex*; *Orycteroxenus notiosorex* Lukoschus *et al.* 1977, in *Notiosorex crawfordi* (Coues 1877); and *Orycteroxenus* sp., in *Sorex salvini* Merriam 1897 (Whitaker and Morales-Malacara 2005; Vargas *et al.* 2009). On the other hand, *Xenoryctes* sp. (Figure 2f) has been previously recorded in *S. salvini* (Vargas *et al.* 2009). However, the two deutonymphs found differ from the species already described; therefore, additional specimens of *S. oreopolus* should be examined to confirm whether the specimens found in this study correspond to a new species.

The flea *C. lira* Traub, 1950 (Siphonaptera, Figure 2g) showed the lowest infestation values (Table 1). It has been recorded in *S. saussurei* and *Sorex milleri* from Mexico City, Michoacán, and Nuevo León (Morales-Muciño and Llorante-Bousquets 1986), being considered as a stenoxenous or monoxenous (*i. e.*, exclusive to a single host species) parasite (Morrone and Acosta 2006).

## Discussion

The seven epizoid arthropod taxa documented in this study represent the first record in association with *S. oreopolus*. The mites *O. soricis* and *P. horridus* had been documented previously on shrews of the genus *Sorex* (Fain 1969; Smiley and Whitaker 1984); however, our study is the first record for Mexico, increasing the richness of symbionts of Mexican shrews from 40 to 42 species.

Recent studies on Mexican shrews have contributed to advancing our knowledge about the richness, current distribution, and conservation of these species, as well as on their intra- and interspecies morphological variations (Guevara *et al.* 2015). However, further research is required on their epizoid arthropods, since this aspect has been for only seven of the more than 40 species of shrews, representing about 20% of hosts. For a better estimate the biodiversity of epizoid arthropods of *S. oreopolus*, a larger number of host specimens should be examined in order to obtain adult mites of the family Myobiidae, as well as deutonymphs of Glycyphagidae, seeking to determine the taxa recorded in this study to the species level. Further research should also address biological and ecological aspects of these arthropods to gain a deeper understanding of parasite-host systems, to set the grounds for understanding and documenting ecological changes, as well as other aspects about the biology of the species involved.

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# Review of philopatry and its strategy in xeric environments

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Over recent decades, dispersal and philopatry in natural populations have been addressed together. However, philopatry, or the tendency of an individual to remain in its birthplace, has received little attention, despite the fact that this trait is present in a considerable number of vertebrates. In this paper we discuss hypotheses that state philopatry generators: life-history variables, ecological constraints, benefits of philopatry and agonistic behaviors. Additionally, we propose that genetic microstructure may be an outcome of such behavior. We conducted an analysis based on the above hypotheses in order to explain the presence of philopatry in rodents of arid environments.

En las últimas décadas, la dispersión y la filopatría han sido abordadas en conjunto. La filopatría o la tendencia de un individuo a permanecer en su lugar de nacimiento, es un comportamiento ampliamente observado entre los vertebrados. Aún así, tal comportamiento ha recibido poca atención. En este trabajo, se discuten hipótesis como las variables en las historias de vida, las restricciones ecológicas, los beneficios de la filopatría y los comportamientos agonísticos como generadores del comportamiento filopátrico. Adicionalmente se propone que la microestructura genética puede ser resultado de tal comportamiento. Realizamos un análisis basado en las hipótesis previas para explicar la presencia de filopatría en roedores de ambientes áridos.

**Keywords:** aggressive behavior; desert rodents; dispersal; ecological constraints; genetic microstructure; life-history traits.

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## Introduction

Philopatry is a behavioral trait present in a wide variety of animal populations, principally mammals ([Waser and Jones 1983](#)), birds ([Welty and Baptista 1988](#)), reptiles ([Meylan et al. 1990](#)), and fish ([Gold et al. 1999](#)). Philopatry has been conceived of in different ways depending on the author and the group of organisms studied. The most generalized interpretations refer to an individual's tendency to remain in (mammals), or return to its birthplace (birds, reptiles, and fish). Owing to its various connotations, we will use the idea described by [Waser and Jones \(1983\)](#), which refers to the behavior of an individual remaining in its birthplace even after having reached maturity and independence from progenitors.

Particular patterns of this behavior include natal and sex-specific philopatry ([Hueter et al. 2005](#)). Natal philopatry, or retention of offspring within parental territory, once past the age of dependence from parents, is common among species ([Greenwood 1980](#); [Perrin and Lehmann 2001](#)) because it ensures access to shelter and food sites, among others. Moreover, it is considered of central importance as a method to conform and extend relationships among individuals that share recent ancestry ([Matocq and Lacey 2003](#)), which is a prerequisite of many common phenomena in gregarious species ([Holekamp et al. 2012](#)).

Philopatry is also present in solitary species. It is necessary to mention that the fact that individuals of certain species are considered as solitary does not mean that such individuals are not social. The conditions that have led to the emergence of philopatry in vertebrates are an impor-

tant factor to understand how complex social groups have evolved ([Lacey and Ebensperger 2007](#)).

Most philopatric patterns exhibit sex bias. Such patterns may be related to the mating system of each species itself. The hypothesis of resource defense ([Greenwood 1980](#)) proposes that the philopatric sex—males in birds and female in mammals—is the one that most benefits from being familiar with the area where it lives. The sex less involved in the acquisition of resources should be the one that present dispersal ([Lawson-Handley and Perrin 2007](#)). A common feature in species with philopatric males is their defense of any important resource critical for acquiring mates for breeding. Successful competition among males for females lies in their ability to maintain the resource, rather than defend females ([Greenwood 1980](#)). In species with philopatric females, a widespread characteristic is the need to have access to a resource that allows the female to rear the offspring. Thus, females form stable nuclei and males adopt strategies to maximize their access to these groups ([Schradin and Lindholm 2011](#)). Males do not invest much in their progeny and benefit from dispersal, while females invest significant effort in their progeny and benefit from philopatry ([Lawson-Handley and Perrin 2007](#); [Vázquez and Álvarez-Castañeda 2014](#)). The outstanding plasticity of the mating systems recorded among natural populations, have led to a variety of ideas around such topic. On the other hand, the general idea is that polygyny is the common mating system observed in mammals. Nevertheless, since a great amount of studies have focused on males, the female perspective has often been ignored, resulting in a lack of

information about the mating systems present in mammals ([Shuster and Wade 2003](#); [McEachern et al. 2009](#)).

Philopatry has been studied from different angles. Possibly the one most discussed is that of dispersal, which is understood as the “antipodal” of philopatry. In many vertebrates, juveniles leave home before reaching sexual maturity and move significant distances before settling as breeding individuals ([Waser and Jones 1983](#)). Selection should favor these individuals for several reasons. Among other benefits for those who disperse are a higher frequency of encounters with individuals of the opposite sex, the rearing of a genetically variable brood, and access to free habitats. But what happens to the species in which individuals remain all their lives within the parental home? Inevitably, their philopatric status has an evolutionary reason that has benefited them over time.

An emerging point of view considers that philopatry is influenced by the advantages that an individual has when it remains in a known or familiar habitat, without having to experience the disadvantages of dispersal, such as the risk of being preyed upon or not finding available territory ([Solomon 2003](#); [van Noordwijk et al. 2012](#)). Within this conceptual framework, several elements have been addressed as causing philopatry. Those that have received most attention are: variables in life-histories ([Kokko and Lundberg 2001](#); [Solomon 2003](#)), ecological constraints ([Solomon 2003](#); [Schradin et al. 2010](#)), and benefits of philopatry ([Kokko and Johnstone 1999](#); [Solomon 2003](#)).

#### Variables in life-history traits

Different studies ([Krause and Ruxton 2002](#)) have proposed models that allow the presence of philopatry in species with altricial or slowly developing offspring to be predicted. It is possible that individuals of these species must delay natal dispersal, because they need more parental care in order to survive before reaching adulthood ([Blumstein and Armitage 1999](#)). One fact that may support this hypothesis is that the dispersal of individuals is delayed until they have the ability to contend for the resources that are critical for reproduction, such as mates, breeding sites, or food. The longevity of the individuals is another important factor and has been linked to restricted space or habitat saturation. [Kokko and Lundberg \(2001\)](#) suggest that habitat saturation is not the primary factor causing philopatry, but rather the longevity or lifespan of members of the population, which will define the occupation of vacant sites and the recruitment of new breeding individuals into the group.

#### Ecological constraints

Although philopatry has evolved in species over a long period of time, there are different ways in which the behavior of a species can be affected by the environment. Differences in habitat quality will guide individuals of natural populations to present dispersal or remain philopatric. If optimal habitats are saturated or limited, the answer is the philopatry, which somehow ensures the provision of critical resources such as food or safe nesting sites. Once vacant sites are avail-

able, dispersal will be possible ([Schradin et al. 2010](#)), with the subsequent relaxing of the philopatric response.

Ecological constraints also involve some risk during dispersal, such as that of predation. In this case, an individual stays longer in a suboptimal and no well-known habitat, unlike that encountered were it to stay in its place of origin. Moreover, the need to find available food in unknown sites makes it particularly susceptible to predation.

Additionally, it has been proposed that arid environments promote the formation of groups of individuals and favor philopatry ([Solomon 2003](#); [Sichilima et al. 2008](#)). This hypothesis states that extreme conditions, unpredictable and sporadic rainfall, and the pattern of food resource distribution in such environments may impose severe restrictions on dispersal. Because of this, individuals are forced to stay in their birth area, leading to philopatry and the formation of family groups. It has been documented that after a period of considerable precipitation, both activity and foraging area increase in desert species, which is proposed as an indication of dispersal ([Lacey and Wiczorek 2003](#)).

#### Benefits of philopatry

The benefits of philopatry may be direct or indirect. The direct benefits influence the survival and reproduction of only a single individual. In contrast, the indirect benefits affect the survival and reproduction of offspring or, in a broader sense, the general population. The inheritance of territory is a potential benefit to philopatric populations. Although little is known about optimal territory inheritance ([McGuire et al. 1993](#)), this hypothesis is interesting, as by staying in its home area an individual is subject to inheriting a high quality territory; in addition, it will not need to present dispersal in order to find space. Thus, over time, well-established genealogical groups will form ([Randall and Stevens 1987](#)). One additional advantage of living close to the family is increased tolerance among individuals, thus avoiding clashes and attacks that can have a high cost during times of intense competition for resources ([Holekamp et al. 2012](#)). Group cooperation in obtaining food, in defending refuge and breeding sites, and in caring for offspring are some examples of the ways in which philopatry and the formation of kinship groups benefit different species ([Blumstein and Armitage 1999](#); [Lacey and Sherman 2007](#)).

#### Philopatry in arid environments

A successful way to study mammal behavior has been the comparison of different patterns among closely related species ([Randall 1993](#); [Meshriy et al. 2011](#)). As examples, studies among squirrels (Sciuridae) can be cited. These have helped researchers in developing behavioral models to explain the evolution of social organizations, mating systems, and the presence of philopatry in this taxon ([Michener 1983](#)); another example is mole rats (Bathyergidae). This group presents very complex social characteristics ranging from extremely solitary and aggressive species to possibly the most-studied social mammal, the naked mole rat *Heterocephalus glaber* ([Jarvis and Bennett 1991](#); [Sichilima et al. 2008](#)).



Rodents of the Heteromyidae (kangaroo rats and pocket mice) are another group of mammals for whom comparative studies have yielded a great deal of information about the evolution of different behavior patterns, including philopatry. The heteromyids differ from other mammals by being nocturnal inhabitants of North American arid environments, and communities can be very complex (Vaughan *et al.* 2000). Their presence in open habitats, their rapid familiarization with human observers, and their philopatric tendency are characteristics that make them ideal for behavioral studies *in situ* (Randall 1984). Another advantage of studying the behavior of heteromyids is their rapid adaptation to captivity. Laboratory experiments with controlled variables make it possible to test different hypotheses based on field observations.

The main behavioral studies on desert heteromyids have focused on the kangaroo rat (*Dipodomys spp.*, Randall 1984; Cooper and Randall 2007; Meshriy *et al.* 2011), while for other genera (*Perognathus*, *Microdipodops* and *Chaetodipus*) there is a significant lack of information. Heteromyids are mainly granivorous and live in environments where extreme precipitation cycles alternate with long periods of drought. Because of this, they carry food to their burrows to hoard and subsequently consume. It has been documented that during times of extreme temperatures, pocket mice can enter a state of torpor, using 20 to 30 percent of their energy—unlike kangaroo rats who do not have this capability—so they depend on the accumulated reserves in their burrows to maintain normal energy requirements (MacMillen 1983). This hoarding of food as well as locating safe places for shelter allow them to survive periods of scarcity or extreme environmental conditions (Vander Wall 1990), benefits accrued from their philopatric nature.

Authors such as Randall (1993), have proposed that evolution has favored the clustering of groups of individuals to confront the risk of being preyed upon in open or scarcely vegetated areas. Nevertheless, heteromyids are mostly solitary and cannot rely on the protection of a group. Instead, solitary species depend on morphological strategies such as cryptic coloration and special behaviors (Mares 1983). The heteromyids may be particularly vulnerable to predation during social interactions, since their attention is focused on conspecifics. Such is the case of the kangaroo rat, which devotes considerable time to mating, defending territories, and dispersal. This is how, by maintaining a stable social environment and familiarity with the area it inhabits, an individual can successfully avoid predation (Daly *et al.* 1990).

Although the heteromyids are a group of solitary species, these rodents have established solid social systems and have developed familiarity with closely related individuals (Cooper and Randall 2007). Both males and females reproduce and raise offspring in their home territories, a pattern that imposes significant restrictions on dispersal and promotes connections among individuals (Jones 1989). In addition, the overlapping of individuals' territories is a common phenomenon that contributes to the spatial and social

organization of populations (Vázquez and Álvarez-Castañeda 2014). Furthermore, the relatively long lifespan (1 year to a maximum of 4–6 years, depending on the species) and the fact of remaining in the same burrow over this time, also promote long-term relationships among neighbor individuals. Among *D. spectabilis* females, burrows are shared and even passed on from mothers to daughters (Waser 1988; Vázquez and Álvarez-Castañeda 2014). It has been documented that kangaroo rat juveniles that inherit parental burrows are more likely to survive to reproductive age than individuals who have presented dispersal (Jones 1986).

The kangaroo rat shows high activity around its burrow because it maintains constant interaction with other rodents (Leaver and Daly 2001). The coexistence of up to six different species, including *Dipodomys spp.*, has been documented on deserts (Vaughan *et al.* 2000), which confirms that the defense of burrows between conspecifics and sympatric species is a generalized pattern.

Genetic microstructure studies have shown that there is a wide variety of haplotypes with very restricted distribution in species of the genus *Chaetodipus*. Derived haplotypes are found in optimal habitats, while ancestral ones are found in less optimal ones (s. s. Banks 1964; Aguilera-Miller *et al.* 2018b). These findings led to a study of agonistic behaviors that recorded intense aggression among females, which have the tendency to monopolize food resources and space (Aguilera-Miller *et al.* 2018a). The defense of such resources may be more important among females because they are the sex that requires more energy to maintain costly reproductive activities (Vázquez and Álvarez-Castañeda 2014).

The combination of a clear genetic microstructure and strong female aggression when defending food resources from other individuals regardless of sex indicates marked territoriality. This territoriality is reflected in the control of an area to rear the young (Wolff and Peterson 1998) or to pass it on to their offspring, creating strong philopatry. These results may be related to observations made in other species such as *D. merriami* and *D. heermanni*, in which there is minimal territory overlapping among females (Jones 1989); thus we can infer that low tolerance among females is possibly a widespread pattern in heteromyids.

The fact that unique matrilineal haplotypes occur in areas only 1.7 km apart may indicate little dispersal of females between sites (Aguilera-Miller *et al.* 2018b). Similar results were documented in populations of the desert cricetid *Neotoma micropus*; private matrilineal haplotypes were found among sites separated by 2 km, which suggests a limited effective dispersal among subpopulations (Méndez-Harcloode *et al.* 2005). The geographic restriction of haplotypes with clear spatial segregation may be rooted in the philopatric character of the females (Aguilera-Miller *et al.* 2018b).

For philopatry to be considered an evolutionary advantage, the fitness of philopatric species must be proven. In species where females remain philopatric, the formation of family groups is common. Associating in groups will

promote breeding success and survival (Silk 2007) as well as cooperation in obtaining food and defending breeding sites (Silk 2007). In species with slow maturation rates, philopatry offers an advantage, because if parents remain philopatric, this somehow assures their access to resources needed to feed the young (Blumstein and Armitage 1999). When there are adverse conditions and food is not assured, some species choose philopatry, avoiding dispersal.

For over thirty years efforts have been made to explain the presence and evolutionary significance of philopatry among different species of vertebrates. These studies have been relevant to different areas of biology such as demography, population genetics, and behavioral ecology (Clutton-Brock and Lukas 2012). As we have seen, they have resulted in numerous definitions, which have led to confusing comparisons and complicated conclusions; to this day, little agreement remains as to the importance of the different evolutionary mechanisms that have caused philopatry (Greenwood 1980; Ronce 2007; Clobert *et al.* 2008).

Although the assumptions discussed above differ in importance according to the species in question, it has been proposed that they be unified in a generalized model that can theoretically explain the presence of philopatry in natural populations (Solomon 2003; Doerr and Doerr 2006). To better understand the mechanism of action of the factors involved in philopatry, it is necessary to consider two general ideas. The first has to do with the consistent presence of philopatry in a certain species. In this case, variables in life-history traits are the guiding factors for the existence of this trait. The second idea is related to species in which philopatry occurs when certain ecological conditions do not favor dispersal. An example of this type are the mole rats (Bathyergidae) inhabiting arid regions of Africa. There is a relationship between the distribution of the rats and patches of geophytes, their main source of food. The behavior of these populations is gregarious. In contrast, solitary populations live in mesic environments where their food source is more evenly distributed and, hence, more easily found by individuals who disperse separately (Sichilima *et al.* 2008). Although social populations can be found in both habitats, solitary ones are not present in arid environments. It would be useful to determine whether competition for reproduction among individuals of the same sex increases, or whether groups tend to dissolve when they reach a certain size or composition, owing to the change in conditions that lead to philopatry.

It is possible to conclude that philopatry is a response to the interaction of a number of ecological and biological variables that threaten the reproductive success of individuals. The questions that arise are mainly related to the fact that since each species has very special ecological requirements, as well as a different life history, it benefits from philopatry in a unique way. Many questions remain and much remains to be done to understand the phenomenon of philopatry.

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# New record of *Artibeus aequatorialis* Andersen, 1906 (Chiroptera: Phyllostomidae) for northwestern Colombia

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The Neotropical fruit bats of the genus *Artibeus* are distributed from southern México to northern Argentina occupying a wide array of different habitats. Of the 14 species present in Colombia, 85.7 % ( $n = 12$ ) occur in the department of Chocó. Bat inventories were carried out by the Consejo Comunitario Mayor de Istmina and Medio San Juan (COCOMINSA) and the Universidad Tecnológica del Chocó in the corregimiento de Chiqui Choqui, municipality of Medio San Juan. We present a new record of *A. aequatorialis* for Colombia, that makes an important addition to the bat fauna of Chocóan biogeographic region and is the northernmost record of the species. Our specimen of *A. aequatorialis* was collected in the Chiqui Choqui locality, that belongs to the district of Alto-Atrato San Juan that is a poorly study area, whose diversity is threatened by human activities, like deforestation and mining activities.

Los murciélagos frugívoros Neotropicales del género *Artibeus* extienden su distribución desde el sur de México hasta el norte de Argentina ocupando una gran variedad de hábitats. De las 14 especies registradas para Colombia el 85.7 % ( $n = 12$ ) ocurren en el departamento del Chocó. Muestreos con redes de nieblas fueron llevados a cabo durante un inventario de murciélagos realizado por el Consejo Comunitario Mayor de Istmina y Medio San Juan (COCOMINSA) y la Universidad Tecnológica del Chocó en el corregimiento de Chiqui Choqui, municipio de Medio San Juan. Se presenta un nuevo registro de *Artibeus aequatorialis* para Colombia, el cual constituye una adición significativa en la distribución de este taxón en la región del Chocó Biogeográfico-colombiano y el registro más norte conocido para esta especie en su distribución. El espécimen de *A. aequatorialis* fue colectado en la localidad de Chiqui Choqui, la cual forma parte del distrito Alto-Atrato San Juan que corresponde una zona pobremente muestreada en su fauna y flora, cuya diversidad se encuentra amenazada por presiones antrópicas como la tala selectiva y la minería a cielo abierto.

**Key words:** bat; distribution; diversity; pacific coast; Stenodermatinae.

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## Introduction

The Neotropical fruit bats of the genus *Artibeus* Leach, 1821 are distributed from southern México to northern Argentina and currently includes 23 species grouped into two subgenera: *Artibeus* and *Dermanura* (Hooper *et al.* 2008; Marques-Aguiar 2008; Redondo *et al.* 2008; Solari *et al.* 2009; Cirranello *et al.* 2016). For decades, there has been controversy regarding whether all the “*Artibeus*” species should be grouped into three genera (*Artibeus*, *Dermanura*, and *Koopmania*), two genera (*Artibeus* and *Dermanura*) or only one genus (*Artibeus*). Recently Baker *et al.* (2016) and Cirranello *et al.* (2016) settle this controversy by supporting with molecular and morphological data the recognition of a single genus with two subgenera (*Artibeus* and *Dermanura*).

Out of the 23 species, 14 occur in Colombia, seven of the subgenus *Artibeus*: *A. aequatorialis* Andersen, 1906; *A. amplus* Handley, 1987; *A. concolor* Peters, 1865; *A. jamaicensis* Leach, 1821; *A. lituratus* (Olfers, 1818); *A. obscurus* (Schinz, 1821); *A. planirostris* (Spix, 1823), and seven of the subgenus *Dermanura*: *A. anderseni* Osgood, 1916; *A. bogotensis* (Andersen, 1906); *A. glaucus* Thomas, 1893; *A. gnomus* Handley, 1897; *A. phaeotis* (Miller, 1902); *A. ravus* (Miller,

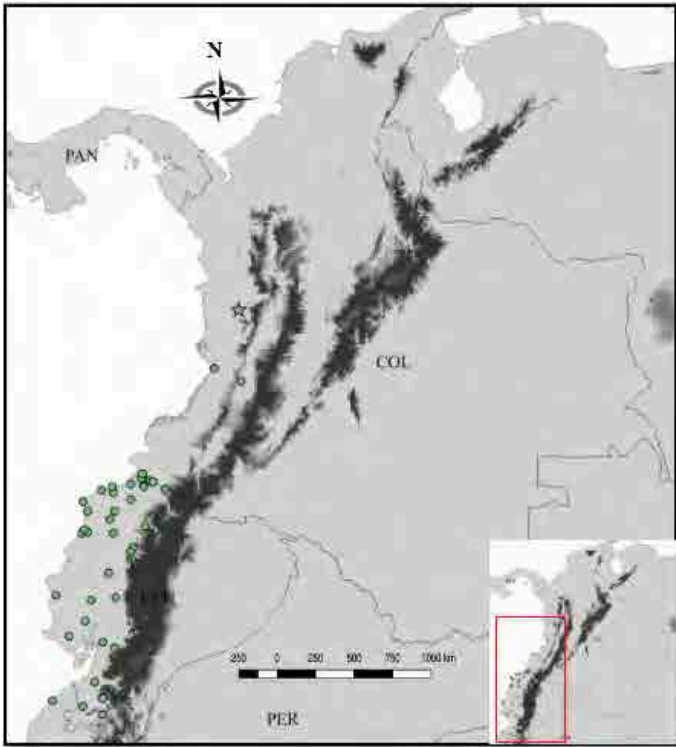
1902); and *A. rosenbergi* Thomas, 1987 (Ramírez-Chaves *et al.* 2016).

*Artibeus aequatorialis* is known from west of the Andes Mountains from northern Perú, northward throughout western Ecuador to Colombia (Larsen *et al.* 2010). The northernmost vouchered record of the species occurs in the department of Valle del Cauca [Rio Raposo 3° 43' N; -77° 08' W] (Larsen *et al.* 2010). Even though *A. aequatorialis* is considered by some authors to occur in the departments of Chocó and Nariño (e. g., Solari *et al.* 2013), there are no vouchered record that support this assertion. Herein, we report the northernmost vouchered record of this species, extending its distribution into the department of Chocó (Figure 1).

## Methods

During a bat inventory carried out by the Consejo Comunitario Mayor de Istmina and Medio San Juan (COCOMINSA) and the Universidad Tecnológica del Chocó along the left bank of the San Juan river (5° 2' 16.26" N, -76° 43' 23.4" W, 45 m), corregimiento de Chiqui Choqui, municipality of Medio San Juan (Figure 1), one adult male specimen of *A. aequatorialis* was collected with a mist-net at a height of 1.60 m

from the ground in a secondary growth habitat that is in the process of recovery after being the subject of intensive gold and platinum mining activities. The specimen was deposited in the Colección Masozoológica del Chocó, Universidad Tecnológica del Choco (CMCH), in Quibdó, Chocó, Colombia. The following species were also captured in this locality: *Artibeus lituratus*, *A. ravenus*, *Carollia castanea*, *C. perspicillata*, and *Uroderma convexum*.



**Figure 1.** Geographic distribution of *Artibeus aequatorialis* and the new record (star) in the department of Chocó, western Colombia.

## Results

Our specimen (CMCH 1410) was captured on 12 October 2011 at 21:48 h and is preserved as a study skin and skull. It was identified based on the characteristics described in [Larsen et al. \(2010\)](#). Standard external measurements (in mm) and weight (in gr) are as follows: total length, 78.3; length of hind foot, 17.1; length of forearm, 64.3; length of ear, 24.0; weight, 45.9. Selected craniodental (in mm) measurements based on [Larsen et al. \(2010\)](#) were taken with a digital caliper (0.01 mm precision) and are provided in Table 1.

Our specimen externally presents the following diagnostic characteristics of *Artibeus aequatorialis*: brown dorsal fur with pale white bands at the base, pale brown ventral fur with whitish tips, almost imperceptible facial lines, white wing tips, broad inter-femoral membrane with V-shaped notch of almost naked appearance, with few short hairs in ventral and dorsal view.

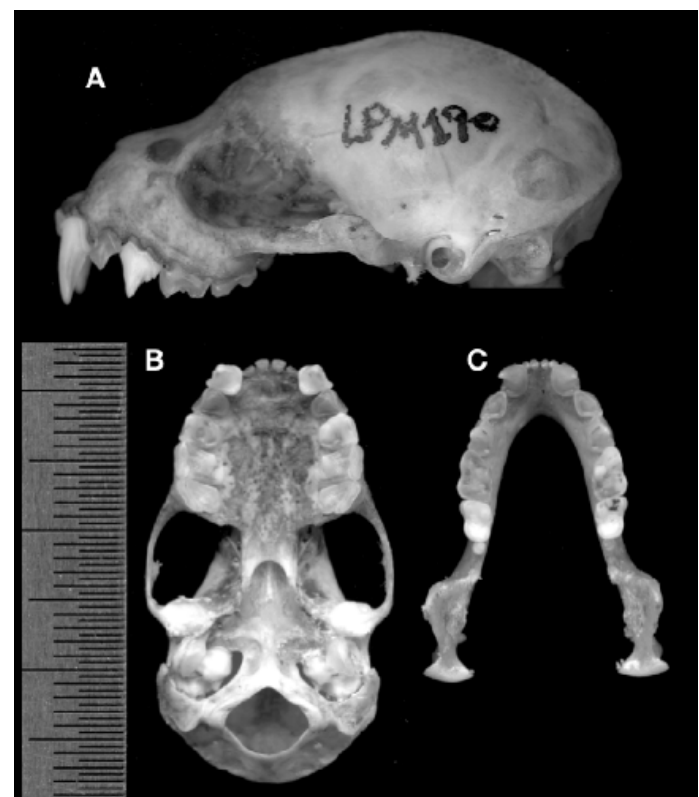
Our specimen has a large skull (GSL = 30.28), a fairly robust dentition. The sagittal crest, as well as the pre- and postorbital processes are slightly developed; the face is relatively short with a slightly arched appearance; and the P4 presents two cusps in the proximal face (Figure 2). Both the protocone and the hypocone of the upper first molar (M1)

**Table 1.** Craniodental measurements of the new record of *Artibeus aequatorialis* from the department of Chocó, Colombia (CMCH 1410). Mean and range of specimens recorded by Larsen et al. (2010).

	CMCH 1410		Larsen et al. (2010)	
	Male	Males (n = 37)	Females (n = 42)	
GSL	30.28	29.43 (27.88 – 30.63)	29.61 (28.54 – 30.84)	
CIL	26.91	26.37 (24.82 – 27.50)	26.54 (25.51 – 27.75)	
SH	12.02	13.12 (12.27 – 13.91)	13.00 (12.29 – 13.96)	
MB	14.41	15.55 (14.32 – 16.60)	15.50 (14.35 – 16.25)	
BRW	13.38	13.96 (12.78 – 14.60)	13.93 (13.28 – 14.61)	
ZB	17.96	17.87 (16.66 – 18.93)	17.97 (16.63 – 18.99)	
POW	7.80	7.35 (6.94 – 7.77)	7.40 (6.85 – 8.01)	
C1C1	8.96	8.64 (7.85 – 9.20)	8.52 (7.92 – 9.05)	
M2M2	13.21	13.40 (12.62 – 14.16)	13.35 (12.83 – 14.22)	
PL	14.53	14.24 (13.15 – 14.89)	14.35 (13.65 – 15.19)	
MXTR	10.91	10.64 (9.88 – 11.39)	10.48 (9.77 – 11.08)	
MIL	19.78	19.38 (18.31 – 20.55)	19.45 (18.54 – 20.36)	
MLT	11.99	11.74 (10.86 – 12.56)	11.62 (10.47 – 12.36)	
c1c1	4.91	4.79 (4.37 – 5.14)	4.73 (4.39 – 5.30)	

are moderately developed, with a broad heel. The upper second molar (M2) is clearly smaller; with its expanded paracone and a well-developed labial cingulum. The M1 and M2 are separated by a diastema (Figure 2B). The third lower molar (m3) is small (Figure 2C). The craniodental measurements obtained for our specimen fall within the range of variation for the species (Table 1; [Larsen et al. 2010](#)).

The habitat at the site of capture is a river bank forest with clay soils and open understory characterized by the



**Figure 2.** Dorsal, ventral, and lateral views of the skull and also dorsal and lateral views of the mandible of *Artibeus aequatorialis* (CMCH 1410). See Table 1 for measurements. Scale bar = 0.05 mm.

presence of *Cyperus luzulae* (L.) Retz., *Scleria secans* (L.) Urb., *Croton killipianus* Croizat, *Isertia pittieri* (Standl.), *Cecropia hispidissima* Cuatrec, *Cecropia peltata* L., *Mimosa pudica* L., *Vismia baccifera* L. Planch. & Triana, *Acacia mangium*, and *Cespedesia spathulata* (Ruiz & Pavon). This site, now under recovery, was subject to intensive gold and platinum mining activities.

## Discussion

Before the revision of [Larsen et al. \(2010\)](#) *Artibeus aequatorialis* was considered one of the five subspecies of *A. jamaicensis*, and because of that its conservation status of is unknown. Neither, IUCN or national red lists include *A. aequatorialis* in their accounts, but there is an urgent need to determine its conservation status since this species has a restricted distribution and many of the populations occur in areas that face many threats, including deforestation, mining activities, etc.

In the last decade, the number of new bat records reported for the Chocó biogeographic region in Colombia has increased exponentially: *Diclidurus ingens*, *Lonchophylla choacoana*, *Lonchophylla orcesi*, *Artibeus rosenbergi*, *Micronycteris giovanniae*, *Platyrrhinus matapalensis*, *P. nitelinea*, among others ([Davalos 2004](#); [Albuja V et al. 2005](#); [Velazco 2005](#); [Fonseca et al. 2007](#); [Hooper et al. 2008](#); [Mantilla-Meluk et al. 2009](#); [Velazco and Gardner 2009](#)). The specimen reported here represents the first record of *A. aequatorialis* in the department of Chocó and extend the known northern limit of the species distribution by more than 153 km (Figure 1).

## Acknowledgements

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# Not eating alone: Andean bear time patterns and potential social scavenging behaviors

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Human-Andean bear (*Tremarctos ornatus*) conflicts are increasing due to the establishment of livestock or crops near to its natural habitats. Here we report scavenging time patterns of Andean bears and the potential social scavenging behaviors in Choachí and Guasca municipalities, Cundinamarca department, buffer zone of Chingaza National Natural Park, Colombia. Between 2013 -2015, we obtained 31 Andean bear scavenging events, allegedly related with human-bear conflict reports; most records occurred in Choachí municipality ( $n = 29$ ). Daily scavenging behaviors showed a heterogeneous pattern, where bears prefer to scavenge in morning hours (6:00 h-10:00 h) with small activity in the afternoon (15:00 h-17:00 h). Furthermore, we report on the first potential record of social activity of three adults scavenging on the same carcass at the same time with no aggressive/antagonistic behaviors between the individuals. Most aspects of Andean bear wild behaviors are still unknown; our observations represent interesting additions to the natural history of the species that could also be included in future programs for the mitigation and reduction of conflicts with human communities in the Andean region of Colombia.

Los conflictos Humano – Oso Andino (*Tremarctos ornatus*) han incrementado debido al establecimiento de sistemas ganaderos o de agricultura cercanos a sus hábitats naturales. Reportamos los patrones temporales de carroñeo de Osos Andinos y comportamientos potenciales de carroñeo social en los municipios de Choachí y Guasca, departamento de Cundinamarca, zona de amortiguamiento del Parque Nacional Natural Chingaza, Colombia. Entre los años 2013-2015, registramos 31 eventos de carroñeo por Oso Andino, reportados como eventos de conflicto Humano – Oso. La mayoría de los eventos ocurrieron en el municipio de Choachí ( $n = 29$ ). Los comportamientos diarios de consumo de carroña mostraron un patrón heterogéneo, donde los osos prefieren carroñar en horas de la mañana (6:00 h -10:00 h) con poca actividad durante las horas de la tarde (15:00 h – 17:00 h). Además, reportamos el primer registro potencial de comportamientos sociales de tres adultos, carroñando en el mismo cadáver a la misma hora, sin presentar comportamientos de agresividad / antagonismo entre los tres individuos. El conocimiento de los comportamientos de oso Andino en vida silvestre aún es incipiente o desconocido. Nuestras observaciones aportan al conocimiento de la historia natural de la especie, los cuales podrían ser incluidos en futuros programas para la mitigación y reducción de los conflictos con comunidades humanas en la zona andina de Colombia.

**Key words:** Andean Range; chingaza Massif; cundinamarca; scavenging; social behavior; spectacled bears; *Tremarctos ornatus*.

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## Introduction

Andean bear (*Tremarctos ornatus*) is one of the largest carnivore species in the American continent; endemic to the tropical Andes, and the only representative of the Ursidae family in South America ([García-Rangel 2012](#)). Lack of substantial ecological information on the species has been one of the main obstacles for constructing long-term conservation and management plans, despite being an emblematic species for most Andean countries and protected areas ([Peyton et al. 1998](#); [Kattan et al. 2004](#), [Vela-Vargas et al. 2011](#); [García-Rangel 2012](#)). Andean bears are being negatively affected by different threats including natural habitat transformation, mostly derived from productive activities expansion (e.g. livestock production and agriculture), and illegal hunting ([Orejuela and Jorgenson 1999](#); [Armenteras et al. 2003](#); [Vela-Vargas et al. 2011](#)). The establishment of

livestock or crops near to Andean bear habitats has considerable contributed to the emergence of conflicts between the species and farmers whom has invested significant economic resources in those activities ([Goldstein et al. 2006](#)).

Andean bears are predominantly herbivores; their diet is mostly composed of bromeliads and palms (e. g., *Puya* spp., *Greigia* spp., *Geonoma* spp.), and some fruits such as *Maclea rupestris* (Uva Camarona) and *Esperomeles goudoutiana* (Mortiño) depending on seasonal availability ([Troya et al. 2004](#)), however, individuals can also consume animal protein either from predation or scavenging ([Goldstein et al. 2006](#); [Rodriguez et al. 2014](#); [Gonzales et al. 2016](#)). In general adults feed solitarily with scarce records of different adults feeding simultaneously and instead maintaining considerable separation distance between individuals ([Castellanos et al. 2005](#), [Goldstein et al. 2006](#)).

Andean bears are known as facultative scavengers: they can predate live animals and consume dead animals opportunistically (Wilson and Wolkovich 2011; García-Rangel 2012), and currently the prevalence of scavenging over predation is debated (Jorgenson and Sandoval 2005; Goldstein et al. 2006; Figueroa 2015). Scavenging behavior records are scarce in literature and normally such records are related with predation and not with opportunistic scavenging events (Figueroa 2015), as it has for other bear species (e. g., brown bears, *Ursus arctos*; Elgmork and Tjorve 1995, Quinn and Buck 2000), where records include small groups of individuals actively searching for dead fish in small creeks without presenting antagonistic behaviors among individuals.

This note aims to describe Andean bears scavenging time patterns and documents that the species might potentially adopt social non-antagonistic behaviors when food availability is concentrated and abundant, as occurs in other bear species. The observations presented herein contribute to the scientific study of Andean bear natural history, enhancing ecological behavioral patterns knowledge potentially applicable to the conservation of this endangered species.

## Materials and Methods

**Study area.** Chingaza National Natural Park (Ch-NNP) is located on the Eastern range of the Colombian Andes (Cordillera Oriental) between 4° 20', 4° 50' N and -73° 30', -73° 55' W. Ch-NNP elevation ranges from 800 to 4,020 masl. and covers an area of 76,000 ha. Main habitats present in the area include Andean forest and paramo ecosystems distributed between Cundinamarca and Meta departments (e.g., states; Parques Nacionales Naturales de Colombia 2016). The field observations presented in this contribution were obtained in Choachí and Guasca municipalities which cover areas both inside and outside Ch-NNP.

**Data collection.** From 2013 to 2015, field surveys were carried out by park rangers in areas where Human-Andean bear interactions events occurred in Andean forest and Paramo on the Ch-NNP buffer zones located in Choachí and Guasca municipalities. When a predation report was informed by the community, park rangers verified the level of decomposition of the domestic animal carcass. If fresh, rangers identified if the predator was a bear or other species such *Puma concolor* or even feral dog groups (*Canis lupus familiaris*; Márquez and Goldstein 2014). For the cases in which the carcasses presented a high degree of decomposition, camera traps (Reconyx®, Wisconsin, USA) were installed to detect individuals that consumed the carcass, to obtain any information regarding the event. Exact location, animal consumed, date, time and the animal's owner name were also recorded to generate a database of events. Each camera was installed during ten days after each conflict event in the area where the domestic animal were reported by local ranchers. All bear pictures were analyzed to estimate the age of the individuals and were validated by Andean bear experts from multiple countries.

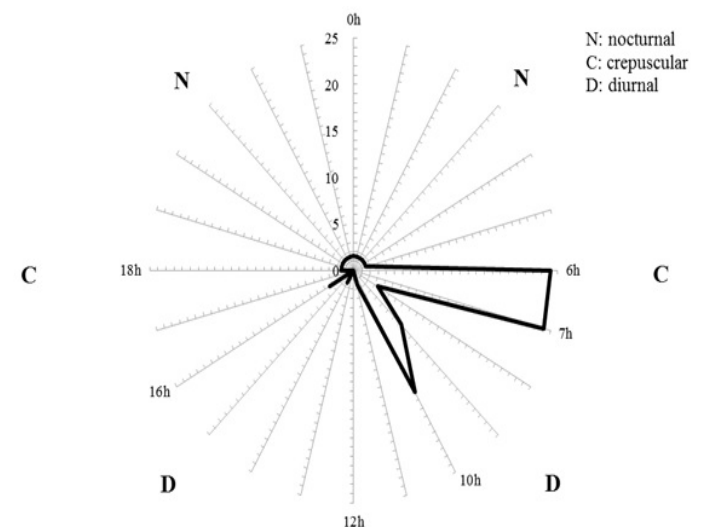
**Data Analysis.** Every record of bears scavenging in front of the camera were considered an independent event; consecutive records over one-hour time-lapses were considered as one capture (Castaño-Urbe et al. 2013, González-Maya et al. 2015). All the records were organized in an hourly-based day-cycle (24 h), in order to evaluate bear scavenging time patterns throughout the day. We used circular statistical analysis to evaluate the uniformity on the distribution of frequencies of the records and identified the activity scavenging patterns of Andean bears (Di Bitteti et al. 2006, González-Maya et al. 2015, Cáceres-Martínez et al. 2016, Zapata-Rios and Branch 2018). Kuiper test for homogeneity were estimated using package Circular for R in R studio version 1.0.153 (R Core Team 2017).

## Results

A total of 31 scavenging records were obtained during field assessments from dead domestic animals reported by local ranchers. All the scavenging events were related with dead domestic animals (e. g., cows) found dead by local communities and reported to Ch-NNP Rangers. Choachí municipality was the locality with the highest number of scavenging events recorded ( $n = 29$ ); in Guasca municipality only two scavenging events were recorded.

We found four events in which more than one individual were scavenging, while 27 events recorded only one individual. In cases where more than one individual were scavenging on a carcass, the average time for each event was 24 minutes, while when solitary bears were recorded, scavenging time was lower (14 minutes). The longest recorded event occurred when three adult bears were scavenging at the same time (45 minutes).

Scavenging activity showed a heterogeneous pattern for Andean Bears along 24-hour day period ( $K = 3.1498$ ,  $P < 0.01$ ). Bears showed preference for diurnal scavenging activities, especially during morning hours (6:00 h to 10:00 h) with 77.4 % of the events (Figure 1).



**Figure 1.** Andean bears scavenging time patterns between 2013 -2015 in Chingaza National Natural Park and buffer zones, Colombia. Distance from the centroid indicates the frequency of records according to 1 - hour intervals.

On October 27, 2014 an individual was recorded scavenging on a cow carcass between 10:50 and 11:00 h in Chatasuga locality, Choachi municipality ( $4^{\circ} 35' 46.79''$  N,  $-73^{\circ} 50' 42.85''$  W; 3,187 masl); the individual was an adult, clearly identified by a small spot in the head and a long chest patch (Figure 2a). Three days after, the same individual was again photographed (October 30, 2014), but this time with two additional individuals, all scavenging simultaneously on the same carcass; all individuals were identified as adults according to their size and the previous photographs of the identified individual (Figure 2b). No antagonistic or aggressive behaviors were recorded between the individuals during the scavenging activity.



**Figure 2.** A) Individual Andean bear recorded on October 27, 2014 in Choachi municipality, Colombia. B) Group of Andean bears scavenging on a single carcass on October 30, 2014, at Choachi municipality, Chingaza National Natural Park, Colombia. From right to left the first individual was recorded feeding alone from the same carcass three days before.

## Discussion

Activity patterns related with scavenging behaviors described herein coincide with the time activity patterns described for the species along its distribution (Paisley and Garshelis 2006, Rodríguez et al. 2016), being more active during the day, with two major activity peaks (morning and evening; Paisley 2001, García-Rangel 2012). Our data showed that Andean bears were scavenging mostly during morning hours (6:00 to 7:00 h and 9:00 to 10:00 h), with almost no scavenging activity during evening (16:00 h). This can be related with the activity pattern of the species, where activity starts around 6:00 h and drops progressively along the day (Castellanos et al. 2005).

Despite the species is commonly classified as predomi-

nantly herbivore (García-Rangel 2012), it seems animal protein can also constitute a significant component of its diet (Paisley 2001; Gonzales et al. 2016). Animal protein can therefore be obtained from wild and domestic animals by active hunting and scavenging. Recent studies have recorded active predation on a wide variety of wild prey from rodents to large species such as Mountain tapirs (*Tapirus pinchaque*) and White tail deer (*Odocoileus virginianus*; Horn et al. 2014; Rodríguez et al. 2014; Gonzales et al. 2016). Our results showed only one case of active predation behaviors, were the Ch-NNP rangers recorded a juvenile Andean bear actively chasing a newborn cow. For the remaining records, local ranchers claimed Andean bears as potential predators, but we only found evidence of scavenging on carcasses.

Generally, predation/scavenging events of bears over cattle are usually categorized as conflicts and is currently considered the main cause of Andean bear illegal hunting across most of its distribution (Peyton et al. 1998; García-Rangel 2012); no surprise, most of these events are recorded in extensive cattle areas adjacent to protected areas (Figueroa 2015). In most areas, inadequate management of domestic species has contributed to the loss and transformation of natural ecosystems, which together with the introduction of exotic species (e. g., feral dogs, cows and cats), has led to changes in the typical time patterns and behaviors of Andean bears and other carnivore species in the tropical Andes (Zapata-Ríos and Branch 2016; Zapata-Ríos and Branch 2018), as supported in our data from adjacent areas of Ch-NNP. Furthermore, two types of predation events have been commonly recorded: local reports of bears feeding from dead domestic animals, usually mis-attributing the predation to the Andean bear but with not confirmed evidence (Goldstein et al. 2006), and direct observations of Andean bears actively hunting domestic animals (Figueroa 2015), all resulting in Human-Andean bear conflicts, as also documented for our study area.

Documented social interactions are mostly unknown for the species and very scarce in the literature, with some observations only described from Peru, and for mating couples and family groups (Figueroa 2015). Andean bear adults are considered in general to be mostly solitary, and couples are only documented during the breeding season (García-Rangel 2012); however, social behaviors have been previously recorded with groups foraging on corn crops (Figueroa 2015). Other bear species commonly show these types of behaviors such *Ursus arctos* foraging for salmon (Quinn and Buck 2000). Social behaviors, such as the one recorded in this paper, have only been recorded in Bolivia (Paisley 2001) and this is the first description of this behavior in Colombia.

Based on our estimations, and validated by a group of experts, the three individuals scavenging in group were confidently identified as adults, however, it is impossible to certainly ensure if they belong or not to the same family group. Nevertheless, one of the three individuals (*i. e.*, the

individual with the spot in the forehead) was recorded foraging alone in other areas close to the carcass during the following days after the scavenging event reported, which allows for a more precise estimation of the adulthood of the individual. Nonetheless, according to Paisley (2001), eventually Andean bears conform rudimentary social groups when food availability is concentrated. Based on this record, multiple individuals could benefit from a scarce but yet likely significant resource, considering its size and the energy required for surviving in this type of ecosystems.

Most aspects of Andean bear natural history, and especially behavior, are still unknown across most of its distribution (Castellanos *et al.* 2005, Vela-Vargas *et al.* 2011) and specially in Colombia. To our knowledge, this is the first record of potential group, none-antagonistic, scavenging behavior for Andean bear and the first report of scavenging activity and time patterns for the species in Colombia. Knowledge on natural history of the species will likely better inform conservation strategies, especially for conflict mitigation, and thus we urge to not only keep documenting records of the species but to make valuable information available for its appropriate use for research and decision-making.

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# Variation in echolocation calls produced by *Myotis velifer* (Chiroptera: Vespertilionidae) during postnatal development

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This work describes the echolocation pulses produced by *Myotis velifer* during postnatal development. The aim was to record the changes of these calls during the development of this bat species and investigate the underlying causes. Bat specimens were sampled in El Salitre cave, Morelos, Mexico, during May and June 2016, where juvenile bats were captured and sorted into five age classes. Forearm length was used as reference for offspring growth. Each juvenile bat was induced to fly and the echolocation calls produced were recorded using an ultrasound detector. Six quantitative characteristics of the echolocation pulses of each call were measured, which served as reference to explore the development of this system during growth through a linear regression. A steady increase in the frequency parameters associated with bat growth was observed, coupled with a decrease in the temporal parameters. The final pulse frequency was the only parameter that remained unchanged during postnatal growth. The major changes in the characteristics of echolocation pulses during postnatal growth in *M. velifer* follow the pattern observed in other species previously studied. These changes are likely related to the development of organs and muscles involved in the emission and reception of sound, and to the learning process involved in the use of this adaptation.

En este trabajo realizamos grabaciones de los sonidos de ecolocalización de *Myotis velifer* con el propósito de describir los cambios que ocurren en las características de los pulsos durante su crecimiento postnatal. Realizamos muestreos en la cueva El Salitre, Morelos, México durante mayo y junio del 2016, donde se capturaron las crías y se clasificaron en cinco clases de edad. La longitud del antebrazo se utilizó como indicador del crecimiento de las crías. Fuera de la cueva, los individuos fueron liberados o forzados a intentar el vuelo para obtener las grabaciones de sus ultrasonidos utilizando un detector ultrasónico. Se midieron seis características cuantitativas de los pulsos de ecolocalización de cada individuo, las cuales sirvieron como referencia para estudiar el desarrollo de este sistema durante el crecimiento por medio de una regresión lineal. Los resultados mostraron un aumento progresivo en los parámetros de frecuencia asociado al crecimiento de las crías, así como una disminución en los parámetros temporales. La frecuencia final fue el único parámetro que no mostró modificaciones significativas durante el crecimiento postnatal. Los cambios notables en las características de los pulsos de ecolocalización durante el crecimiento postnatal de *M. velifer* siguen el patrón observado de especies anteriormente estudiadas. Es posible que estos cambios estén relacionados con el desarrollo de los órganos y músculos involucrados en la emisión y recepción del sonido y el aprendizaje del uso de esta adaptación.

**Key words:** Age; bat; El Salitre cave; ontogeny; ultrasound.

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## Introduction

Most bats rely on the emission of echolocation calls for survival. In aerial insectivorous species, individuals must be capable of producing high-frequency sounds and process spatial information from the echoes produced in order to catch insects successfully during their early flights (Moss *et al.* 1997). Thus, sounds emitted during the first days after birth may be the precursors of echolocation behavior in adult bats (Moss *et al.* 1997; Zhang *et al.* 2005). In most cases, there is a correlation between postnatal development and the type of calls emitted by young bats (Brown and Grinnell 1980). In general, young bats emit long-duration, high-intensity and low-frequency pulses, relative to the sounds emitted by adults (Brown and Grinnell 1980; Rubsamen 1987; Monroy *et al.* 1995; Zhang *et al.* 2005; Liu *et al.* 2007). This differentiation of pulses between bats of different age might make it easier for juveniles to recognize adult individuals and follow them to suitable foraging grounds (Kazial *et al.* 2001).

Works describing the development of vocalizations during postnatal growth, which include species of families Ves-

pertilionidae (Moss *et al.* 1997; Zhang *et al.* 2005), Hipposideridae (Habersetzer and Marimuthu 1986), Rhinolophidae (Rubsamen 1987; Liu *et al.* 2007), Noctilionidae (Brown *et al.* 1983), Mormoopidae (Veter *et al.* 2003) and Phyllostomidae (Carter *et al.* 2013) show a general pattern in the development of echolocation, consisting of a steady increase in frequencies and a reduction of the temporal patterns of pulses. In Mexico, there is virtually no research work addressing the relationship between postnatal growth and the development of echolocation. In this sense, the maternity colony of *M. velifer* that congregates each year at El Salitre cave, Morelos, offers an opportunity to describe in quantitative terms the pulses of echolocation calls produced by *Myotis velifer* (J. A. Allen, 1890), a species widely studied in United States but not in Mexico, during postnatal growth.

## Methods

The study was conducted during June and July, 2016, in El Salitre cave, located in the municipality of Tlaltizapán, Morelos, Mexico (18° 45' 00.3" N, 99° 11' 23.3" W). Individuals (juvenile and adult bats) were captured with a hand net

in the maternity colony that is established each year inside the cave, and were subsequently placed inside cotton cloth bags. After capture, the forearm length (FL) of each individual was measured with a CD-8"CS digital caliper (Mitutoyo Corporation, Japan); additionally, each individual was sexed and sorted into one of 5 age categories (see Results), according to the ossification of phalanges, morphological traits and ability to fly.

A flight simulation experiment was conducted outside of the cave, consisting in rising each individual bat up to a height of two meters, and then dropping it in front of a full-spectrum Echo Meter 3+ ultrasound detector (Wildlife Acoustics, Inc, USA.) set up to record at a sample rate 256 kHz/16-bit resolution and a 1x time expansion (real time). The detector was placed at two meters from the drop point with an inclination of 40° to ensure the capture and recording of echolocation pulses emitted by each bat released. To avoid potential injuries to individuals who were unable to fly, a soft surface was placed on the landing area. This technique has been used in previous studies to record vocalizations of juvenile bats with no reports of apparent harm (e.g. Moss *et al.* 1997). At the end of the sound recordings, juveniles that were unable to fly were returned to the nursery colony by placing them in the same site of capture, while those able to fly entered the cave by themselves.

The recordings were analyzed using the software Bat-Sound Pro 3.30 (Pettersson Elektronik, AB, Sweden). From the acoustic files, high-quality echolocation sequences were selected (those with an energy of at least 20 dB, as measured within the power spectrum) and with more than 10 pulses. By means of an expanded-time spectrogram (10x), a 16-bit resolution, a sample rate of 22,050 kHz, and using a Hanning-type window with 1024 Fourier transformations (FFT) and 95% overlap (Rizo-Aguilar *et al.* 2015), six quantitative characteristics of pulses were measured according to the diagram and description of Rivera-Parra and Burneo (2013): initial frequency, mid-pulse frequency, final frequency, bandwidth, duration, and interval. A sequence involving between 10 and 20 pulses was measured from each individual bat to record variations in each bat evaluated. Statistical analyses were conducted using the average values of each characteristic measured.

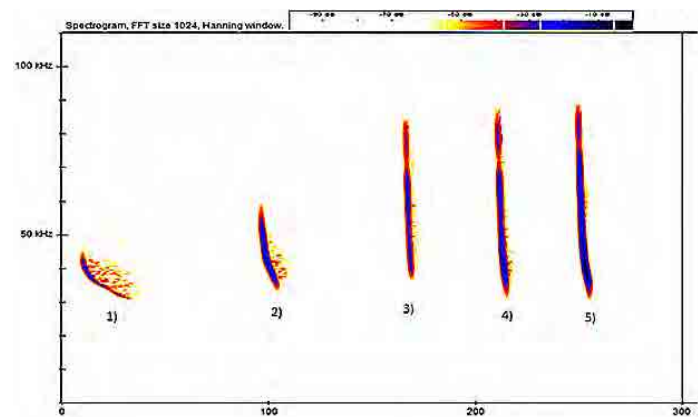
The changes in the variables of echolocation pulses were related to postnatal growth of offspring using forearm length as an indicator of age (Rajan and Marimuthu 1999; Sharifi 2004). The relationship between the changes in the pulse parameters measured and the increase in forearm size was described through a simple linear regression analysis for each variable using the program Statsoft (Statsoft 2001 7); outlier data were previously eliminated through an exploratory data analysis. In order to meet the normality assumption, data were transformed to natural logarithms.

## Results

A total of 136 individuals were captured (75 females and 61 males). Of these, 21 had no hair and had not opened the

eyes yet (= 23.35 mm, class 1); 35 showed signs of hair and teeth growth, and during the recording experiment these individuals fluttered before and during the fall (LA = 28.99 mm, class 2); 43 had well-defined teeth and pelage, but were unable to fly (LA = 37.63 mm, class 3); 26 showed non-ossified phalanx epiphyses but were able to fly (LA = 64.95 mm, class 4 or subadults); and 11 were considered as adults (= 44.81 mm, class 5).

The echolocation pulses of *M. velifer* during postnatal growth are short-lasting and of modulated frequency (Figure 1). In case of class-1 juvenile bats, the initial frequency was relatively low (= 56.86 kHz) compared with the one used by class-5 individuals = 83.73 kHz). Similarly, the bandwidth changed over time, with a steady increase in the range of frequencies used from class 1 (= 24.33 kHz) to class 5 (= 50.52 kHz). By contrast, the duration of pulses was reduced drastically from class 1 to class 2, shifting from 11.58 to 4.71 ms. From class 2, the duration of pulses showed a slight variation. The mean range shifted from 152.11 ms for class-1 to 93.64 ms for class-5 bats.



**Figure 1.** Spectrogram relating postnatal development of *M. velifer* to the characteristics of echolocation calls in each age class: 1) young bats still lacking hair and teeth (Forearm length, LA = 23.35 mm), 2) young bats showing signs of hair and teeth growth (LA = 28.99 mm), 3) young bats showing well-defined pelage and teeth, but unable to fly (LA = 37.63 mm), sub-adults (LA = 44.32 mm), adults (LA = 44.83 mm).

The statistical analyses (Table 1) showed a significant positive relationship ( $P < 0.001$ ) between forearm length and initial frequency, mid-pulse frequency, and bandwidth, indicating that these variables increased as juvenile bats grew. In addition, there was a significant negative relationship ( $P < 0.001$ ) between forearm length and the duration and interval of pulses, indicating that the time parameters of pulses decreased as juvenile bats grew. However, in the case of the final pulse frequency there was no correlation ( $P = 0.879$ ) with forearm length of juvenile bats; hence, this variable remained virtually unchanged throughout the early growth stages to adulthood.

## Discussion

Our results show that the postnatal development of echolocation in *M. velifer* follows a pattern that resembles the one described for other bat species, consisting in a steady rise in frequencies and a shortening in the temporal patterns of pulses as juvenile bats grow (Brown and Grinnell



**Table 1.** Results of the regression analyses between forearm length (FL) and initial pulse frequency (IF), final pulse frequency (FF), mid-pulse frequency (MF), bandwidth (BW), pulse duration, and interval between pulses. Values corresponding to the (F) statistic, degrees of freedom (*d. f.*), significance value (*P*), and coefficient of determination (*r*<sup>2</sup>).

Regression	F	d. f.	P	r <sup>2</sup>
FL vs IF	64.898	1, 84	<0.001	0.435
FL vs FF	0.231	1, 84	0.879	0.002
FL vs MF	16.357	1, 84	<0.001	0.662
FL vs BW	83.964	1, 84	<0.001	0.599
FL vs Duration	33.244	1, 84	<0.001	0.583
FL vs Interval	90.130	1,84	0.001	0.517

[1980](#); [Brown et al. 1983](#); [Habersetzer and Marimuthu 1986](#); [Rubsamen 1987](#); [Moss et al. 1997](#); [Liu et al. 2007](#)).

The youngest (class 1) bats emitted sounds of relatively low frequencies and long duration, compared to pulses emitted by adults (initial frequency, 44.5-91.6 kHz). These calls may be the precursors of echolocation sounds used by adults, that is, there is likely a gradual learning process in the use and modulation of the high frequencies ([Moss et al. 1997](#); [Zhang et al. 2005](#)). The adjustment of increasing frequencies could also be due to the maturation of the larynx. For instance, it is known that in vespertilionid bats, the frequency and duration of calls are controlled by the contraction and relaxation of the cricothyroid muscles surrounding the larynx and controlling the strain of the vocal cords ([Gould 1975](#); [Moss et al. 1997](#)).

These findings also revealed a steady increase in the bandwidth of echolocation pulses as juvenile bats grow. The modulated frequency and broadband pulses recorded for subadults (class 4) and adults (class 5) allow the precise location of prey and provide information related to its shape and texture ([Schnitzler and Kalko 2001](#); [Altringham 2011](#)). In particular, the increased bandwidth may be related to the development of the echolocation system to capture insects in closed environments as bats grow and feed by themselves.

The drastic reduction in the temporal parameters of pulses throughout the postnatal development of juvenile bats can be attributed to the maturation of the organs involved in sound emission and reception ([Monroy et al. 1995](#); [Moss et al. 1997](#)), or to the learning process to interpret the information transmitted by the echoes of calls emitted, as both pulse duration and the interval between pulses are adjusted according to the distance between the bat and its hunting target ([Neuweiler, 2000](#)).

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# First record of shrews (Eulipotyphla, Soricidae) in the Sierra de Otontepec, an isolated mountain in Veracruz, Mexico

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Knowledge of the diversity and distribution of mammals in tropical and subtropical regions remains incomplete. This is especially true for many small species inhabiting remote areas with limited access. Here we present the first record of small-eared shrews (Soricidae, *Cryptotis*) from the Sierra de Otontepec, Mexico, an isolated mountain in the Gulf Coastal Plain that has remained poorly explored (Figure 1). We conducted a short-term survey in the Sierra de Otontepec using pitfall and Sherman traps during August 2016. Taxonomic identification was based on morphological and molecular analyses (Appendix 1). We collected six shrew specimens from the cloud forests in the Sierra de Otontepec (Figure 2). Morphological and molecular characterization indicated that all specimens collected were small-eared shrews belonging to the *Cryptotis mexicanus* species group (Table 1, Figure 3), a clade which is closely associated with cloud forests. Based on the morphological and molecular evidence, we refer to this population from the Sierra de Otontepec as *C. mexicanus*. Our results corroborate the importance of continued fieldwork in remote tropical areas. Overall, this finding offers relevant information that could be used to better understand the evolution and biogeographic history of this species group and its habitat.

El conocimiento de la diversidad y distribución de los mamíferos en las regiones tropicales y subtropicales sigue siendo incompleto. Esto es particularmente notable para muchas especies pequeñas que habitan en áreas remotas de acceso limitado. Aquí presentamos el primer registro de musarañas (Eulipotyphla, Soricidae) de la Sierra de Otontepec, México, una montaña aislada en la llanura costera del Golfo que ha permanecido escasamente explorada (Figura 1). Nosotros realizamos un estudio a corto plazo en la Sierra de Otontepec utilizando trampas de caída y Sherman durante agosto de 2016. La identificación taxonómica se basó en análisis morfológicos y moleculares (Apéndice 1). Obtuvimos seis especímenes de musarañas en el bosque nuboso de la Sierra de Otontepec (Figura 2). La caracterización morfológica y molecular indicó que todos los especímenes recolectados eran musarañas de orejas pequeñas pertenecientes al grupo de especies de *Cryptotis mexicanus* (Tabla 1, Figura 3), un clado que está estrechamente asociado con los bosques nubosos. Con base en la evidencia morfológica y molecular, nos referimos a esta población de la Sierra de Otontepec como *C. mexicanus*. Nuestros resultados corroboran la importancia de continuar trabajo de campo en áreas tropicales remotas. En general, este hallazgo ofrece información relevante que podría usarse para comprender mejor la evolución y la historia biogeográfica de este grupo de especies y su hábitat.

**Key words:** cloud forests; *Cryptotis*; Mammalia; small-eared shrews.

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## Introduction

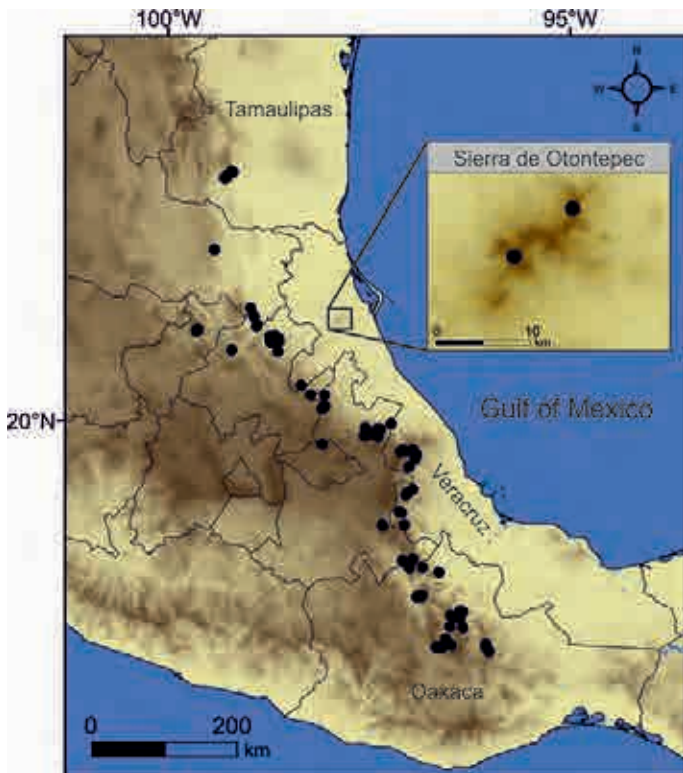
Knowledge of the diversity and geographical distribution of mammals in tropical and subtropical regions remains incomplete (Ceballos and Ehrlich 2009). This is due, in large part, to the fact that many species inhabit remote areas with limited accessibility. This is particularly problematic when collecting small and secretive species that are difficult to find. Small-eared shrews (Eulipotyphla, Soricidae) of the genus *Cryptotis* Pomel, 1848 comprise a group of small- to medium sized species occurring from southeastern Canada to northern South America (Choate 1970). With about 44 species (Zeballos et al. 2013), *Cryptotis* is one of the most diverse genera of small mammals in the Americas. Discovery and description of new species, new distributional records, and range extensions for this genus are not unusual even today (Woodman 2010; Guevara et al. 2014; Guevara and Sánchez-Cordero 2018a).

Recently, while working on mammal inventories, our field team discovered a handful of specimens of small-

eared shrews in the cloud forest of the Sierra de Otontepec (Figure 1), an isolated mountain in Veracruz, Mexico, where biological inventories and research has been scarce (Hall and Dalquest 1963; Secretaría de Desarrollo Social y Medio Ambiente, SEDESMA, 2007). Here we provide morphological, molecular, and ecological information on these specimens that could be used to better understand the evolutionary and biogeographic history of the genus. Because the fauna in the Sierra de Otontepec is poorly known and most of the natural vegetation in the region has already been altered by human activity, we emphasize the biological relevance of this discovery.

## Materials and Methods

**Study area.** The Sierra de Otontepec (also known as Sierra de Tantima) lies on the eastern slope of the Sierra Madre Oriental, Veracruz, Mexico (Figure 1). It is a small, isolated volcanic mountain in the Gulf Coastal Plain that reaches an elevation of nearly 1,300 m, and with an extended range of nearly 20



**Figure 1.** Map showing the known records (black dots) of the small-eared shrew, *Cryptotis mexicanus*, and the new records from the Sierra de Otontepec.

km (SEDESMA 2007). The summit vegetation begins at 900 masl and consists largely of cloud forest, making it one of the northernmost stands of cloud forest in the Neotropics.

**Fieldwork.** The Mexican Ministry of the Environment (SEMARNAT) authorized the capture of mammals under the scientific collector permit SGPA/DGVS/12142/16 issued to LLP. Fieldwork was carried out for 15 consecutive days in August 2016. We used 10 pitfall and 80 Sherman traps, which were placed next to rocks around the bases of the trees and next to fallen trunks. We conducted trapping at two locations covered by dense cloud forest (Site 1: 21.26855278 N, -97.84444 W, 1,080 m; Site 2: 21.24715 N, -97.895 W, 1,020 m), which have not been intensively surveyed for small mammals. We followed standard recommendations on specimen capture, sacrifice and preparation (Sikes et al. 2016). We measured (mm) and weighed (g) voucher specimens in the field and deposited skins, skeletons, and tissues samples at the Mammal Collection of the Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC-M, Mexico City; Appendix 1).

**Taxonomic identification.** We focused morphological and molecular analyses on the comparison with members of *C. mexicanus* species group (*C. magnus*, *C. nelsoni*, *C. mexicanus*, and *C. phillipsii*) because of their greater similarity in pelage coloration, body size, size of forefeet and claws to the specimens from Sierra de Otontepec. We recorded the following cranial measurements for quantitative comparisons: condylobasal length (CBL), cranial breadth (CB), breadth of the palate across the second molars (M2B), and

breadth across the first unicuspid (U1B). All measurements were taken with a Mitutoyo electronic caliper at 0.01 mm precision under a stereomicroscope (Appendix 1). We performed a principal component analysis (PCA) on the matrix correlation of four cranial variables to describe and evaluate the degree of differentiation among the species of the *Cryptotis mexicanus* group.

We also conducted a Bayesian Inference to determine the genetic affinity of the specimens from Sierra de Otontepec within the *Cryptotis mexicanus* group. We amplified the mitochondrial gene *cytochrome b* (*cytb* = 1,140 bp) by a polymerase chain reaction (PCR) using the pair of primers MVZ05 and H15915. The PCR profile included 3 min of initial denaturation at 95° C, followed by 35 cycles of 30 s of denaturation at 95° C, 1 min of annealing at 49° C, and 2 min for extension at 72° C. Finally, we included a step of 5 min of final extension at 72° C. We used the Montage PCR purification kit from Millipore, and the ABI PRISM BigDye Terminator cycle sequencing kit with AmpliTaq DNA polymerase for sequencing the PCR products in an ABI 3730XL sequencer (Applied Biosystems, Seoul, Korea). Both, cleaning of PCR products and sequencing reaction was performed in Macrogen Inc. (Seoul, Korea) following the standard protocols. The sequences generated were deposited in the GenBank database (Accession #'s MK286564-MK286565). We included 21 *cytb* sequences from the *C. mexicanus* species group and one sequence of *C. parvus* (used as outgroup) housed in the GenBank database (see accession numbers



**Figure 2.** A) Specimen of a small-eared shrew collected in Sierra de Otontepec, Mexico. B) Typical cloud forest habitat of the Sierra de Otontepec, where small-eared shrews were collected.

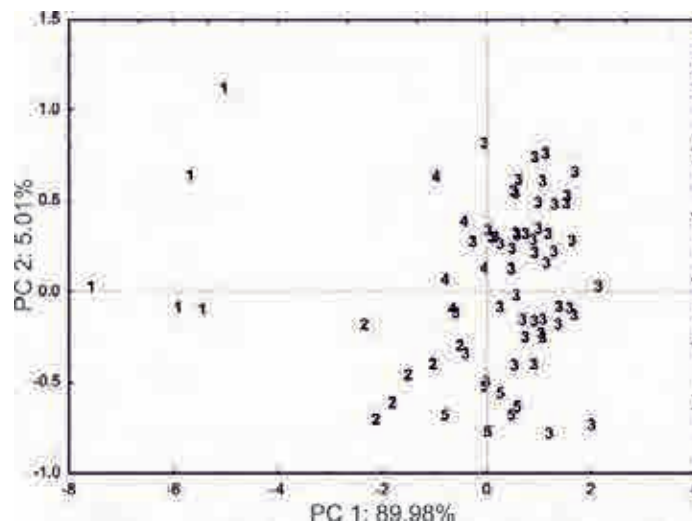
on Figure 4, downloaded on 07 November, 2018). Using PartitionFinder 2 (Lanfear et al. 2017), we selected the best scheme of partition and evolution model ( $cytb_{[1]} = SYM+Γ$ ;  $cytb_{[2]} = F81+I$ ;  $cytb_{[3]} = GTR+I$ ). We then incorporated this partition and evolution model in a phylogenetic analysis using Bayesian inference (MrBayes 3.2.3; Ronquist et al. 2012). We used three hot and one cold chains in two independent runs of 10 million generations, sampling data every 1,000 iterations. The final topology was obtained using a majority tree consensus and considering a burn-in of 25 %. We checked the convergence of our results and a good sampling (ESS > 200) in Tracer 1.6.

### Results

We obtained a total of six shrew specimens in the cloud forests from the Sierra de Otontepec; four were collected with pitfall traps and two with Sherman traps. The sample included three adult males (MZFC-M 16221, 16223-16224) and three adult females (MZFC-M 16219-16220, 16222), one of which was pregnant with five embryos (MZFC-M 16222). Other genera of mammals collected in this short-term survey were *Handleyomys* (rice rat), *Sigmodon* (cotton rat), and *Marmosa* (mouse opossum). The shrew specimens displayed previously reported external diagnostic characters of the *Cryptotis mexicanus* species group (Choate 1970; Guevara and Sánchez-Cordero 2018b). Principal components 1 and 2 explained 95% of the variation in the data (PC 1= 90 % and PC 2 = 5 %). The breadth of the palate across the second molars (M2B) and condylobasal length (CBL) contributed strongly to the first factor axis, providing a measure of overall cranial size. A plot of the two PCs showed that the specimens from Sierra de Otontepec tended to plot among the smaller species within the *C. mexicanus* species group (*C. phillipsii* and *C. mexicanus*) and overlapped partly with previously known specimens of *C. mexicanus* (Table 1; Figure 3). Bayesian Inference indicated that specimens from the Sierra de Otontepec are nested within *C. mexicanus*, which is supported by a high posterior probability (Figure 4). The rest of the relationships within the *C. mexicanus* species group resemble previous phylogenetic hypothesis (Guevara and Cervantes 2014; He et al. 2015).

### Discussion and conclusions

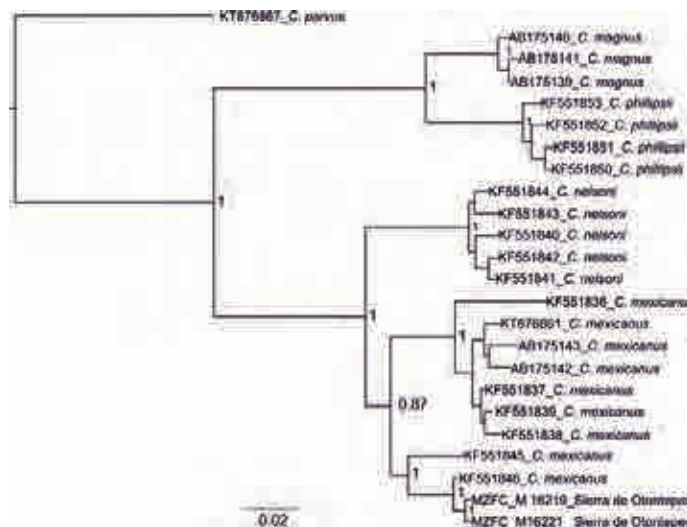
Morphological characterization indicates that the specimens collected in Sierra de Otontepec belong to the *Cryptotis mexicanus* species group, a clade comprising four species highly associated with cloud forests (*C. magnus*, *C.*



**Figure 3.** Plot of the first 2 principal components from a principal component analysis (PCA) of four cranial measurements from *C. magnus* (1), *C. nelsoni* (2), *C. mexicanus* (3), *C. phillipsii* (4), and the specimens from Sierra de Otontepec (5).

*mexicanus*, *C. nelsoni*, and *C. phillipsii*; González-Ruiz et al. 2014; Guevara and Sánchez-Cordero 2018b). The fact that specimens from Sierra de Otontepec are morphological similar and are phylogenetically nested within *C. mexicanus* implies that there is no justification for the recognition of a new species for this new population. Therefore, we refer to the population from the Sierra de Otontepec as *C. mexicanus*. Interestingly, this first record of small-eared shrews in the Sierra de Otontepec is consistent with the potential distribution of the *C. mexicanus* group based on models of its climatic requirements using correlative techniques (Guevara and Sánchez-Cordero 2018b).

Our discovery corroborates the importance of continued surveys in remote tropical areas (Guevara et al. 2014). Very little is known about the biota and biogeographic history of the Sierra de Otontepec (SEDESMA 2007), which has gone largely unnoticed in the study of cloud forest vegetation. Hence, this discovery of small-eared shrews could also be used to better understand the origin and history



**Figure 4.** Majority-rule consensus tree from a Bayesian Inference showing the position of the specimens from Otontepec within the *Cryptotis mexicanus* species group. The numbers on clades indicate the posterior probability for each clade. The accession numbers of GenBank precede the scientific names.

**Table 1.** Loadings of four cranial measurements on the first two axes (PCs 1 and 2) of a principal component analysis of small-eared shrews (*Cryptotis*) from Mexican cloud forests.

	PC 1	PC 2
CBL	-0.955133	0.180397
CB	-0.941390	0.231200
M2B	-0.964130	-0.088268
U1B	-0.933362	-0.326616

of one of the northernmost islands of cloud forest in the Neotropical region. Finally, we highlight the relevance of montane cloud forest fragments like the Sierra de Otontepec because they are important reservoirs of endemic and endangered species that have a critical role in maintaining landscape-level biodiversity in an ecosystem with rapid rates of clearing and global conservation priority (Wilson and Rhemtulla 2018).

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## Appendix 1.

Specimens examined and measurements (CBL-U1B) used for the morphological comparison (see methods for details). Specimens examined are housed in the following collections (followed by their abbreviations): National Collection of Mammals, Mexico City (CNMA); The University of Kansas Natural History Museum, Lawrence, Kansas (KU); Museum of Zoology 'Alfonso L. Herrera', Mexico City (MZFC); Collection of Mammals, Universidad Autónoma Metropolitana, Iztapalapa, Mexico City (UAMI); and National Museum of Natural History, Washington, District of Columbia (USNM).

SPECIES	MUSEUM	CATALOGUE NUMBER	CBL	CB	M2B	U1B							
<i>Cryptotis mexicanus</i>	MZFC	637	18.5	9.7	5.2	2.5							
<i>Cryptotis mexicanus</i>	MZFC	638	18.9	9.6	5.2	2.5	<i>Cryptotis mexicanus</i>	USNM	68525	18.4	10.0	5.2	2.4
<i>Cryptotis mexicanus</i>	MZFC	639	19.1	10.2	5.3	2.5	<i>Cryptotis mexicanus</i>	USNM	68523	18.4	9.8	5.3	2.3
<i>Cryptotis mexicanus</i>	MZFC	640	18.5	9.4	5.3	2.5	<i>Cryptotis mexicanus</i>	USNM	68526	18.4	10.2	5.1	2.4
<i>Cryptotis mexicanus</i>	KU	29548	18.4	10.0	5.6	2.6	<i>Cryptotis mexicanus</i>	USNM	68532	18.5	10.0	5.2	2.4
<i>Cryptotis mexicanus</i>	KU	29561	18.4	10.0	5.3	2.5	<i>Cryptotis mexicanus</i>	USNM	68528	18.7	9.9	5.3	2.3
<i>Cryptotis mexicanus</i>	KU	29552	18.5	9.8	5.3	2.5	<i>Cryptotis mexicanus</i>	UAMI	11169	19.2	10.1	5.4	2.7
<i>Cryptotis mexicanus</i>	KU	29528	18.6	10.3	5.2	2.5	<i>Cryptotis mexicanus</i>	UAMI	11170	19.2	10.2	5.2	2.5
<i>Cryptotis mexicanus</i>	KU	29555	18.7	9.9	5.2	2.5	<i>Cryptotis mexicanus</i>	UAMI	11172	18.8	9.8	5.1	2.4
<i>Cryptotis mexicanus</i>	KU	29554	18.7	10.0	5.3	2.5	<i>Cryptotis mexicanus</i>	UAMI	11176	19.0	10.1	5.2	2.4
<i>Cryptotis mexicanus</i>	CNMA	42741	17.6	9.4	5.1	2.4	<i>Cryptotis mexicanus</i>	UAMI	11177	19.6	10.1	5.4	2.5
<i>Cryptotis mexicanus</i>	CNMA	42733	18.1	9.8	5.1	2.4	Otontepec	MZFC	16224	18.6	9.7	5.3	2.6
<i>Cryptotis mexicanus</i>	CNMA	42748	18.3	9.5	5.2	2.4	Otontepec	MZFC	16223	18.9	10.0	5.4	2.7
<i>Cryptotis mexicanus</i>	CNMA	42756	18.8	9.8	5.1	2.4	Otontepec	MZFC	16222	19.5	10.1	5.4	2.8
<i>Cryptotis mexicanus</i>	CNMA	42744	18.9	10.0	5.3	2.4	Otontepec	MZFC	16221	18.6	9.9	5.4	2.7
<i>Cryptotis mexicanus</i>	MZFC	8354	18.3	10.0	5.2	2.6	Otontepec	MZFC	16220	18.8	9.8	5.3	2.6
<i>Cryptotis mexicanus</i>	MZFC	8332	18.3	9.9	5.0	2.3	Otontepec	MZFC	16219	18.8	9.7	5.3	2.6
<i>Cryptotis mexicanus</i>	MZFC	8386	18.4	10.2	5.3	2.5	<i>Cryptotis nelsoni</i>	CNMA	41961	19.0	10.1	5.6	2.6
<i>Cryptotis mexicanus</i>	MZFC	8400	18.5	9.8	5.0	2.3	<i>Cryptotis nelsoni</i>	CNMA	41993	19.1	10.4	5.5	2.8
<i>Cryptotis mexicanus</i>	USNM	69733	18.4	9.7	5.4	2.4	<i>Cryptotis nelsoni</i>	CNMA	41959	19.4	10.6	5.8	2.9
<i>Cryptotis mexicanus</i>	USNM	69615	18.4	9.7	5.3	2.4	<i>Cryptotis nelsoni</i>	CNMA	41956	19.5	10.3	5.8	2.8
<i>Cryptotis mexicanus</i>	USNM	69609	18.4	9.8	5.3	2.5	<i>Cryptotis nelsoni</i>	CNMA	41992	19.9	10.3	5.7	2.8
<i>Cryptotis mexicanus</i>	USNM	69605	18.6	9.9	5.4	2.4	<i>Cryptotis nelsoni</i>	CNMA	41960	19.9	10.6	5.9	2.8
<i>Cryptotis mexicanus</i>	CNMA	29429	18.9	9.8	5.3	2.4	<i>Cryptotis magnus</i>	CNMA	29468	23.0	11.3	6.3	3.1
<i>Cryptotis mexicanus</i>	CNMA	29431	19.0	10.0	5.3	2.4	<i>Cryptotis magnus</i>	CNMA	29469	22.7	11.3	6.3	2.9
<i>Cryptotis mexicanus</i>	CNMA	29427	19.3	10.4	5.2	2.5	<i>Cryptotis magnus</i>	CNMA	33609	23.3	11.7	6.9	3.3
<i>Cryptotis mexicanus</i>	USNM	68299	18.5	9.5	5.2	2.3	<i>Cryptotis magnus</i>	CNMA	29823	22.4	11.3	6.5	3.2
<i>Cryptotis mexicanus</i>	USNM	68311	18.7	9.9	5.2	2.4	<i>Cryptotis magnus</i>	CNMA	43057	22.2	11.3	6.3	3.2
<i>Cryptotis mexicanus</i>	USNM	68303	18.7	9.6	5.3	2.3	<i>Cryptotis phillipsii</i>	CNMA	44725	19.4	10.0	5.4	2.5
<i>Cryptotis mexicanus</i>	USNM	68305	18.8	9.7	5.0	2.3	<i>Cryptotis phillipsii</i>	CNMA	44727	20.0	9.9	5.8	2.5
<i>Cryptotis mexicanus</i>	CNMA	29989	17.5	9.7	5.0	2.3	<i>Cryptotis phillipsii</i>	CNMA	44728	20.2	10.3	5.5	2.5
<i>Cryptotis mexicanus</i>	CNMA	35261	18.6	10.0	5.1	2.3	<i>Cryptotis phillipsii</i>	CNMA	44729	19.9	10.0	5.5	2.5
<i>Cryptotis mexicanus</i>	CNMA	35260	18.7	10.2	5.1	2.5	<i>Cryptotis phillipsii</i>	CNMA	44730	19.7	10.0	5.6	2.6
<i>Cryptotis mexicanus</i>	CNMA	34859	18.8	10.0	5.2	2.4							
<i>Cryptotis mexicanus</i>	CNMA	29991	19.0	10.1	5.2	2.5							
<i>Cryptotis mexicanus</i>	CNMA	29986	19.0	10.3	5.6	2.6							
<i>Cryptotis mexicanus</i>	CNMA	43060	18.4	9.7	5.1	2.3							
<i>Cryptotis mexicanus</i>	CNMA	43059	18.4	9.6	5.2	2.4							
<i>Cryptotis mexicanus</i>	CNMA	43053	19.1	9.9	5.3	2.5							

