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La Portada

Zorrillo espalda blanca (*Conepatus leuconotus*) es una de las ocho especies de zorrillos que se encentran en México. Su distribución incluye gran parte de Norte América, incluyendo mayormente a México. *Conepatus leuconotus* es una especie relativamente abundante y muy conspicua donde se encuentra, la especie es casada constantemente sin razón, aunque en algunos lugares de México consideran que su carne es medicinal. La foto fue tomada en las planicies del istmo de Tehuantepec (Fotografía de Sergio Ticul Álvarez Castañeda).

Nuestro logo "Ozomatli"

El nombre de "Ozomatli" proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimero en la cosmogonía mexica. "Ozomatli" es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. " Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo."

Therya

Volumen 9, número 2 mayo 2018

Contenido

ARTICLES

Notes

fascículo 26 http://www.mastozoologiamexicana.org/doi/10.12933/therya-9_2

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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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Diet and abundance of bobcat (*Lynx rufus*) in the Potosino-Zacatecano Plateau, Mexico

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The Potosino-Zacatecano Plateau (PZP) is characterized by a system of hills surrounded by ridges where the bobcat is the only wild felid; however, there is no information on the basic ecology of this species in this region. The objective of this work was to determine the diet and abundance of the bobcat in Cerro del Peñón Blanco, San Luis Potosí. The diet was inferred from the analysis of prey remains in feces; in addition, the minimum number of bobcats in the study area was estimated by camera traps placed in Cerro del Peñón Blanco, San Luis Potosí. Diet composition was expressed as percentage of occurrence. Individual bobcats were identified by the distinctive morphological characteristics of each. Seventy five scat samples were collected and analyzed. The diet included 14 taxa, with the rabbit *Sylvilagus audubonii* as the species most frequently consumed. The mouse *Peromyscus* spp. was the rodent species with the highest frequency of occurrence; however, no single species was dominant. We identified seven bobcat individuals: three males, three females and one of unknown sex. The bobcat diet allows inferring how this feline uses landscape in the study area, feeding on its main prey in foothills fragmented patches and complementing its diet with prey present in Peñón Blanco. The study area still provides sufficient prey base for the bobcat.

El altiplano Potosino-Zacatecano (APZ) se caracteriza por presentar un sistema de elevaciones rodeadas de lomeríos donde el gato montés es el único felino silvestre, sin embargo, no existe información sobre la ecología básica de esta especie en la región. El objetivo de este trabajo fue determinar la dieta y abundancia del gato montés en el cerro del Peñón Blanco, San Luis Potosí. La dieta se obtuvo del análisis de los restos de presas halladas en excretas y se estimó el número mínimo de gatos monteses en la zona de estudio por medio de trampas-cámara colocadas en el Cerro del Peñón Blanco, San Luis Potosí. La composición de la dieta se expresó como porcentaje de aparición. Los distintos individuos se identificaron por la presencia de características morfológicas distintivas. Se colectaron y analizaron 75 excretas. La dieta estuvo compuesta por 14 taxa, siendo la especie más común el conejo *Sylvilagus audubonii*. El ratón *Peromyscus* spp. fue la especie de roedor con mayor frecuencia de aparición, sin embargo, ninguna especie fue dominante. Se identificaron siete individuos de gato montés, tres machos, tres hembras y uno de sexo desconocido. La dieta del gato montés permite identificar como este felino usa el paisaje en la zona de estudio, alimentándose de su presa principal en las zonas bajas fragmentadas y complementando su dieta con presas presentes en el Peñón Blanco. La zona de estudio aún cuenta con una base de presas adecuada para el gato montés.

Keywords: camera-trapping; diet; feces; fragmentation; lagomorphs.

Introduction

The Chihuahuan Desert is the largest arid zone in North America, and one with the highest biodiversity in the world (Hoyt 2002; Loa-Loza *et al.* 2009; Rzedowski 2005). Its southernmost portion corresponds to the Potosino-Zacatecano Plateau (PZP). This region is characterized by a system of elevations (*e. g.*, ridges and rock outcrops) surrounded by hills and plains (INEGI 1985). Some of the elevations are covered by relicts of oak forest (*Quercus potosina* and *Q. Greggi*; Cabrera-Rodríguez 2015) that provide shelter for priority species for conservation in Mexico, such as the golden eagle (*Aquila chrysaetos*; Loa-Loza *et al.* 2009). However, many of these ridges and flat areas have been modified by anthropogenic activities such as cattle ranching, rainfed agriculture and mining (Martínez-Montoya *et al.* 2012).

The bobcat (*Lynx rufus*) is a felid whose historical distribution in Mexico stretched from the border with the United States south to the state of Oaxaca (Hall 1981). In Mexico, this species is not listed under any risk category (SEMARNAT 2010), although local bobcat populations have become isolated as a result of anthropic fragmentation processes (Lopez-González *et al.* 2015).

Most of the studies about bobcat in Mexico have analyzed their food habits, abundance and density in virtually undisturbed semi-desert and temperate habitats (Lopez-González *et al.* 2015; Medéllín and Bárcenas 2010). These studies reveal that the bobcat diet consists mainly of lagomorphs (Aranda *et al.* 2002; Delibes *et al.* 1997; Luna-Soria and López-González 2005; Medéllín and Bárcenas 2010).

The bobcat is the only wild felid currently inhabiting the PZP (Dalquest 1953, Martínez de la Vega *et al.* 2016). Its presence serves as an indicator of the conservation status of this region, as this feline requires territories with abundant prey base (Butrey 1979; McCord and Cardoza 1982; Sunquist and Sunquist 1989, 2000). In spite of its ecological importance, *L. rufus* is perceived to be a major predator of goats by local communities located in the PZP (Martínez-Montoya *et al.* 2012). However, this claim has not been evaluated and there is a lack of baseline information on the ecology of the bobcat in PZP.

This work determined the diet of the bobcat across an area surrounded by a fragmented landscape, where ridges act as important relicts and shelters for biodiversity, specifically in *El Peñón* and other nearby elevations where the existing vegetation cover provides suitable habitats (Martínez-Montoya *et al.* 2012). This study contributes baseline information on the ecology of bobcat in PZP and its trophic relationship with goats.

Materials and Methods

Study area. The study was carried out in *Cerro del Peñón Blanco*, a mount located in the municipality of Salinas, to the northwest of the state of San Luis Potosi (22° 27′ 44″ N, -10° 43′ 00″ W), with an altitudinal range of 2,120 and 2,750 m. It islocated 13 km southeast of the city of Salinas de Hidalgo, 8 km southwest of highway 57 and on the border between the states of San Luis Potosí and Zacatecas. Two communities are located in the mount foothills. El Alegre and San Juan sin Agua, each with less than 100 inhabitants (INEGI 1997; Figure 1).

The local climate is dry and semi-cold, with summer precipitation (June to September) and occasional drizzles in January; mean annual precipitation is 391 mm. Mean annual temperature ranges between 16 °C and 18 °C (INEGI 2009). The vegetation communities include scrubland ("matorral crasicaule") and relicts of oak forest in the higher elevations (INEGI 1997). The original vegetation in the surrounding area was microphyll xeric shrub, yucca scrub, cardon scrub and cactus shrub (Rzedowski 2005). The dominant species are creosote bush (*Larrea tridentata*), alicoche (*Opuntia bradtiana*), mesquite (*Prosospis laevigata*), and Chinese palmtree (*Yucca filifera*). The local vegetation has been disrupted by excessive grazing by bovine cattle and goats, urbanization, mining operations and the opening up or expansion of terrestrial communication routes (Martínez-Montoya *et al.* 2012).

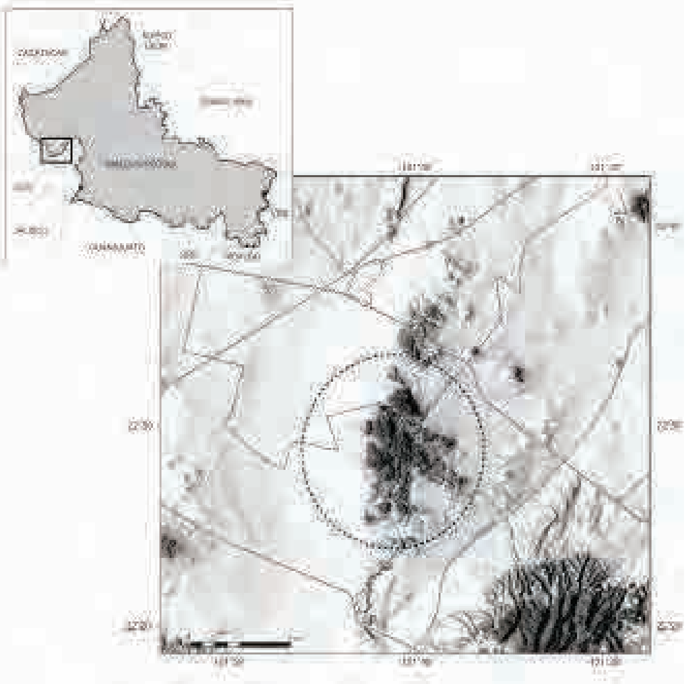

Figure 1. Location of Peñón Blanco in the Potosino-Zacatecano Plateau, Mexico. The dotted line marks the area of study.

Diet Characterization. Diet components were quantified through the location, collection, identification and analysis of feces along dirt roads, livestock paths used by wildlife, and stream beds. Scat samples were collected once a week between June and November 2011 from nine latrines located throughout the study area. One week prior to the start of the field surveys, the area was walked to collect and dispose of all bobcat feces accumulated up to that time, to ensure that any feces analyzed in the study were one week old maximum.

Bobcat feces were differentiated *in-situ* from those of other carnivores also inhabiting the study area (*e. g.*, coyote *Canis latrans*, and gray fox *Urocyon cinereoargenteus*) by comparing their physical characteristics and identifying the respective footprints and associated sign (*sensu* Aranda 2012). Any scats of questionable origin or weathered were discarded. Scat samples were placed in airtight Ziplock^{MR} bags containing water and 10 g of powder detergent, and were soaked for at least 5 days. Afterwards, samples were washed under running water in 6-mm and 3- mm mesh sieves. Once washed, the content was oven-dried at 40 °C for 24 hours.

Bones, feathers and scales were identified by comparison vs. reference collections and identification guides (Elbroch 2006; Scott and McFarland 2014). For the identification of hairs, slides were prepared to examine the medulla and cortical scales using the technique by Williamson (1951). Slides were compared against material from the collection of mammals of the Laboratory of Population Ecology, School of Biology, Benemérita Universidad Autónoma de Puebla. Components in scat samples were identified to the lowest taxonomic level possible.

The frequency and percentage of occurrence of the different species in feces was calculated. The percentage of occurrence was determined as: $PA_i = (FA_i/N) \times 100$. Where: FA_i = Frequency of occurrence of species *i*. N = Total number of components in the scat samples analyzed.

Variations in the frequency of food items were determined by applying a G-test under the null hypothesis that species share the same frequency. In case of significant differences, paired G-tests were conducted for significant differences in the frequency of each item vs. the expected frequency (Zar 2010).

Estimate of the minimum number of individuals. In parallel with the collection of scats, eight simple camera-trap stations were installed (DeerCam®DC200, 35 mm) across

Peñón Blanco following the criteria by Heilbrun *et al.* (2003), distance between stations was 200 to 600 m. Cameras were set to operate 24 hours with 5 minutes between triggers. Due to the lack of trees in the study site, cameras were installed on wooden stakes at 30 cm above the ground. No baits were used in any station.

The minimum number of individuals during the sampling period was determined. The distinctive traits of individual bobcats used in the analysis of photographs included spot pattern, scars, facial ruff shape and color, sex and body size (Heilbrun *et al.* 2003, 2006; Figure 2). The identification and quantification of captures-recaptures were conducted according to the guidelines proposed by Heilbrun *et al.* (2003), namely a) only photographs of an individual bobcat that could not be associated with another captured previously were considered as initial captures; b) recaptures were determined even in cases where there were no photographs of the complete individual, provided its identity could be fully established; c) any poor-quality photographs that could not be classified as an initial capture or a recapture were discarded; d) In all cases, at least three natural characteristics (*e. g.,* tail stripes, scars, face marks, or facial ruff patterns) were used to identify individuals and to determine recaptures; e) the identification of a single different trait was considered as sufficient to consider that two photographs represented different individuals.

Results

A total of 75 scat samples of *L. rufus* were collected and analyzed, from which food items belonging to 14 different taxa were identified. Mammals were the most frequent prey, with 11 spp. To a lesser extent, the diet also included birds, reptiles and invertebrates (Table 1).

Differences were observed in the frequency of occurrence of the various taxa in the diet (G = 114.73; g. l. = 13; $P = 0.001$). The rabbit *S. auduboni* was the species with the highest percentage of occurrence. The frequency of occurrence of this lagomorph in feces was significantly higher relative to any other species ($P < 0.001$). The raccoon (*Procyon lotor*) and invertebrates were consumed with lower-than-expected frequencies ($P < 0.05$). No rodent species was consumed more frequently than any other prey taxa. No goat remains were identified in any of the scat samples analyzed.


LD01 – 30/ago
LH01 – 8/sept
LH01 – 9/oct
LH02 – 20/sept
LH03 – 26/sept
LM01 – 6/oct
LM02 – 9/oct
LM02 – 7/nov
LM03 – 12/oct

Figure 2. Bobcat individuals photographed in the Peñón Blanco in the Potosino-Zacatecano Plateau, Mexico

Table 1. Diet of the bobcat at Peñón Blanco, Potosi-Zacatecas Plateau, Mexico.

Species	Frequency of occurrence	Percentage of occurrence
Mammals		
Rodents		
Chaetodipus nelsoni	13	5.1
Neotoma mexicana	19	7.5
Peromyscus boylii	19	7.5
Peromyscus maniculatus	11	4.3
Peromyscus sp.	28	11.1
Peromyscus truei	23	9.1
Otospermophilus variegatus	21	8.3
Lagomorphs		
Lepus callotis	23	9.1
Sylvilagus audubonii	58	22.9
Carnivores		
Procyon lotor	2	0.8
Unidentified Mammal	11	4.4
Birds		
Unidentified bird	10	4.0
REPTILES		
Sceloporus sp.	8	3.2
Invertebrates		
Invertebrates	7	2.8

Table 2. Photographs of wildlife captured at *Peñón Blanco,* Potosino-Zacatecano Plateau, Mexico.

Species	Independent Photographs	IAR*
Canis latrans	1	0.16
Canis lupus familiaris	1	0.16
Conepatus leuconotus	2	0.32
Geococcyx californianus	3	0.48
Lynx rufus	12	1.90
Procyon lotor	8	1.27
Sciurus sp.	1	0.16
Otospermophilus variegatus	1	0.16
Urocyon cinereoargenteus	3	0.48
Total	32	

* sensu O' Brien *et al*. 2003.

A sampling effort of 630 trap-nights yielded 32 separate photographs (*sensu* O'Brien *et al.* 2003) of nine species of wild animals (Table 2). Twelve of these photographs were of bobcat (Table 2), with nine being useful for the identification of individual specimens. The remaining photographs were excluded due to poor image quality, showing an individual in a position that restrained an accurate observation of its characteristics, or for being partial pictures that hindered a reliable identification. As a minimum, three males, three females and one individual of undetermined sex were identified. All individuals, except for female LH1 and male LM02, were photographed only on one occasion. Recaptures occurred in the same camera-trapping site.

Discussion

The bobcat is the top predator in desert ecosystems where large carnivores (*i. e.*, *Puma concolor*) have been eliminated; hence, its diet is expected to consist of a broad variety of prey types available in the ecosystem (Sergio *et al.* 2006). The results of the diet composition were very similar to observations reported from non-fragmented desert environments in the United States (Fritts and Sealander 1978; Jones and Smith 1979; Koehler and Hornocker 1991) and Mexico (Aranda *et al.* 2002; Delibes *et al.* 1997; Luna and López 2005).

The analysis of the diet makes possible to identify how the bobcat uses the landscape in the study area. In this case, rabbits were the group with the highest percentage of occurrence in the feces analyzed, with *S. auduboni* being best adapted to flat areas and hills (Bond *et al.* 2002). This suggests that the bobcat forages mainly in the lower elevations of Peñón Blanco. Rabbits and hares are species that can tolerate the fragmentation of their habitat; however, this fragmentation increases the risk of being consumed by predators (Villafuerte *et al.* 1997). In this sense, the fragmentation adjacent to Peñón Blanco apparently does not affect the feeding ecology of the bobcat, since the conditions resulting from habitat fragmentation substitute the preferential consumption of lagomorphs.

The consumption of other prey types such as the rock squirrel, *Otospermophilus variegatus,* and lizards of the genus *Sceloporus,* which are abundant in rocky outcrops across Peñón Blanco (Martínez-Montoya *et al.* 2012), demonstrate the importance of this elevation has as a source of secondary prey items for the bobcat. The consumption of rock squirrels has been recorded in sites with rocky outcrops similar to Peñón Blanco, as is the case of Plomito in Sonora (Aranda *et al.* 2002), Sierra del Ajusco (Romero 1993) and La Malinche National Park (Cortés 1998).

As a group, rodents are key components of the diet of the bobcat in the study area. This group is particularly abundant in sites covered by grasslands interspersed with patches of scrub vegetation and rocky outcrops (Mellink 1991), which are located in the foothills of Peñón Blanco (INEGI 1985). The bobcat is an opportunistic hunter that forages on the most abundant prey items in its habitat (Lopez-Vidal *et al.* 2014), such as mice of the genus *Peromyscus*. Altogether, these mice accounted for 32 % of the diet, indicating that they are important prey for the bobcat in this region. These rodents likely serve as alternate prey items in areas where lagomorphs are relatively scarce. This has been reported for central Mexico, an area where rabbits are scarce due to hunting, leading to *Peromyscus* becoming the most important prey of bobcats (Cortés 1998).

The opportunistic behavior of *L. rufus* in the study area is highlighted by the presence of raccoon in its diet. This is the first record of bobcat predating on raccoon across its distribution range. The raccoon is a species strongly associated with water bodies (Valenzuela 2005), so that the presence of temporary streams flowing down from Peñón toward lowlands, where some ponds remain even in the dry season, may favor their presence to the point of being the second most abundant species recorded by camera traps.

This study recorded no evidence of the predation of goats or sheep by bobcat. The predation of livestock by bobcat is poorly documented; therefore, it is considered as a species with low risk of conflict with humans (Inskip and Zimmermann 2009). The absence of livestock items in the diet suggests that anecdotic claims about this species as a predator of livestock may be a misperception of the local inhabitants rather than reflecting a genuine impact. Moreover, this finding also suggests that, in spite of the current fragmentation, the landscape in the study area still provides a sufficient prey abundance that allows maintaining the local bobcat population. However, the increase in grazing intensity by goat herds that roam freely across Peñón Blanco and its surrounding areas could lead to a decline in the abundance of the local populations of rodents and lagomorphs (Vorhies and Taylor 1933), resulting in the possibility of predation on livestock by bobcat.

The presence of seven bobcat individuals during the period of study highlights the importance of Peñón Blanco as a habitat for this species. Peñón Blanco, one of the highest elevations across an area of 2,000 km^2, has features that are preferred by the bobcat to establish burrows and daytime resting sites (*e. g.*, rugged topography and presence of abundant rocky formations; Romero 2005), so it may be the site of confluence of the territories of various individuals. This hypothesis is further supported by the presence of abundant latrines (n = 15) in the highest sites of Peñón, where at least two individuals were photographed while performing territorial marking.

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Annual cycle of the mexican ground squirrel (*Xerospermophilus perotensis*)

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Seasonality and changes in climate and habitat dynamics lead ground squirrels to use resources during the most favorable seasons and avoid less favorable conditions by hibernating. The Perote ground squirrel (*Xerospermophilus perotensis*) is nationally and internationally classified as vulnerable to extinction; however, our knowledge of this species is scant. The aim of this study was to describe and analyze its annual cycle. Temperature and rainfall data (2008 to 2014) for the area were used. Animal frequencies were obtained for seven sites by capture-mark-recapture; captured animals were marked, and their sex, weight, age and reproductive status noted. Population structure was obtained for each site using the male:female sex ratio and age structure. Activity during the annual cycle is statistically associated with temperature. Scrotal males were most abundant while females with signs of pregnancy and those lactating were recorded least often. The number of adults and juveniles differed statistically, with adults more abundant throughout the study. Weight varied throughout the study, and differed between adults and juveniles. The Perote ground squirrel exhibits phenological patterns similar to those of species of the genus *Spermophilus*, which respond to changes in temperature and its activity cycle begins in spring and ends in autumn. The weight of the squirrels was dynamic, probably resulting from reproduction, hibernation and their response to changes in environmental resources. The frequency of this species was low, with few juveniles recorded, indicating that *X. perotensis* is facing serious problems, likely from severe anthropogenic pressure and its own ecological characteristics.

La estacionalidad y dinamismo del clima y hábitat inducen a que las ardillas terrestres exploten los recursos en las mejores estaciones y eviten la menos favorable a través de la hibernación. La ardilla endémica de Perote (*Xerospermophilus perotensis*) se encuentra clasificada a nivel nacional e internacional como vulnerable a la extinción, ya que su hábitat se ha reducido drásticamente por lo que su conservación se ha visto comprometida, a pesar de esto el conocimiento acerca de la especie es escaso. El objetivo de este estudio fue describir y analizar la fenología de la especie. Se obtuvieron las temperaturas y precipitaciones del área de estudio del año 2008 al 2014; la frecuencia de capturas se obtuvo a través del método de captura-marcaje-recaptura. Los animales capturados fueron marcados y se registró el sexo, edad, peso y estado reproductivo en el que se encontraban. La estructura poblacional se obtuvo para cada sitio usando la proporción de sexos, edad y estado reproductivo. Los resultados indicaron que la actividad durante el ciclo anual está relacionada estadísticamente con la temperatura, ya que cuando desciende ocurre la hibernación; así como de las condiciones reproductivas debido a que se presentaron cuando las temperaturas fueron las más altas. En lo que respecta a las características reproductivas, los machos escrotados fueron los más abundantes y las hembras con signos de preñez o lactantes fueron las menos registradas. Para la categoría de edad, el número de adultos y juveniles difirieron estadísticamente, siendo los adultos los más abundantes. Con relación al peso de las ardillas, fue variable a lo largo del estudio y sólo existió diferencia estadística entre el peso de los adultos y juveniles. La ardilla de Perote exhibe patrones fenológicos similares a las del género *Spermophilus*, ya que la especie responde a los cambios de temperatura y la actividad de su ciclo empieza en la primavera y termina en el otoño. El peso de los organismos fue dinámico, probablemente causado por la reproducción, hibernación y por su respuesta a los cambios en los recursos ambientales. En general, las frecuencias de los organismos fueron bajas y con pocos registros de juveniles, lo que indica que la especie está enfrentando serios problemas para persistir debido a las severas presiones antropogénicas a las que se enfrenta y a sus propias características ecológicas.

Key words: ground squirrel; hibernation; phenology; reproductive characteristics; temperature.

Introduction

Climate and habitat conditions are dynamic, so organisms avoid or mitigate the effects of the least favourable times of the year through migration, aestivation or hibernation, taking advantage of the season that favors their development and reproduction (Bradshaw and Holzapfel 2007; Williams and Lane 2014). The timing of these events and their relationship to the different stages of life are induced by abiotic forces such as light, temperature and seasonality (Michener 1983; Williams *et al.* 2014) and by biotic forces such as hormone levels (Bradshaw and Holzapfel 2007).

In ground squirrels, annual cycles are marked and divided into an active and an inactive phase, the durations of which vary by species, sex, age, latitude, climate and habitat (Michener 1983; Williams and Lane 2014; Williams *et al.* 2014). Reproductive cycles, gestation, lactation, emergence of juveniles, fat storage and preparation for hibernation occur during the active phase and hibernation occurs during the inactive phase (Michener 1983). Some annual events are critical for ground squirrels, such as the day that they emerge from hibernation. Males who emerge late have less chance of acquiring territory and a decreased possibility of developing the secondary sex characteristics required for reproduction. Late emergence by females can affect their weight because after reproducing (gestation and lactation), they must accumulate enough fat to hibernate (Williams and Lane 2014).

The reproductive season in Sciuridae, the family to which the ground squirrels belong, coincides with peak food availability. So, if these two events go out of phase, reproductive rates and survival could decrease and cause serious imbalances in the population, and even lead to extinction (Michener 1983; Miller-Rushing *et al.* 2010; Lane *et al.* 2012). Repeated observation of the population structure (sex ratio, age category and reproductive status) allows us to understand the relationship between the annual cycle and demography, since both are sensitive to time and can provide information about the viability and state of the populations. It is generally understood that five to ten years of observations are necessary to obtain sufficient information about these parameters (Van Horne 1983; Caughley 1977; Miller-Rushing *et al.* 2010).

The endemic ground squirrel of Perote (*Xerospermophilus perotensis*) is diurnal, social, terrestrial and mainly herbivorous (Best and Ceballos 1995; Castillo-Castillo and González-Romero 2010). Its reproductive period begins in May and ends in August. Gestation lasts 30 days and females have an average of four kits (Yensen and Sherman 2003). Hibernation occurs from the end of October to March, interrupted by short feeding periods (Valdez and Ceballos 2003; Castillo-Castillo 2009). These animals prefer to live in open treeless, shrubless areas with short grasses (Yensen and Sherman 2003; Hannon *et al.* 2006; Montero-Bagatella *et al.* 2017), though they have also been recorded in areas with shrubs and in crops (Best and Ceballos 1995; Mendoza-Carreón 2009). This species is facing conservation problems resulting from the intense development and extreme transformation of its habitat by humans, which has spared only 30 % of its original habitat (Sánchez-Cordero *et al.* 2005). Currently, this species is classified as threatened in Mexico (Official Mexican Standard NOM-059-SEMARNAT-2010; SEMARNAT, 2010) and as endangered by the International Union for the Conservation of Nature (IUCN; Álvarez-Castañeda *et al.* 2008).

Because the Perote ground squirrel is extremely vulnerable, we decided to describe and analyze its annual cycle and learn about the relationship between climate conditions and the population dynamics of this species. The information obtained will allow us to understand the ecology of this species and provide the tools necessary to understand what is necessary for its protection and conservation. Combined with legal action, this could lead to the preservation of the species.

Materials and Methods

Study Area. The study was done in the Perote Valley, located in the municipality of Perote, Veracruz, Mexico. This valley is located between two mountain ranges, the Sierra Norte of Puebla and the Cofre de Perote, both of which offer unique environmental conditions that have resulted in the presence of several endemic species (Best and Ceballos 1995; Sánchez-Cordero *et al.* 2005). These species are facing severe conservation problems owing to intensive agricultural practices (both crops and livestock) that have fragmented and decreased the limited available habitat in the region (Gerez-Fernández 1985; Arriaga *et al.* 2000). The elevation of the study sites is 2,300 to 2,700 masl. The climate is the most humid of the semiarid climates, with a mean annual temperature of 14 °C and a mean annual precipitation of 500 mm (Gerez-Fernández 1985; Medina and Angulo 1990). The vegetation is diverse: pine-oak forest (*Pinus* spp. and *Quercus* spp.), Juniper forest (*Juniperus deppeana*), scrub (*Yucca periculosa, Nolina parviflora*), natural meadows (*Scleropogon brevifolius, Erioneuron avenaceum*) and induced pastures (*Muhlenbergia quadridentata, Aristida divaricata*), along with halophytic vegetation (*Bouteloua scorpioides, Atriplex linifolia*; Gerez-Fernández 1985; Delgadillo 2011).

Seven sites were sampled, differing mainly in their plant associations and the time they have been protected from livestock management (Figure 1). The composition of the vegetation was obtained from the study of Montero-Bagatella *et al.* (2017). Site 1 was on a basalt flow with short grass pastures and sparse tussocks of *Aristida harvadii* and *Sclerepogon brevifolius*. Site 2 was located 200 m from the Veracruz-Mexico City highway, with native plants like *Jarava ichu* and *Bidens anthemoides* and no agricultural activity. Site 3 was located approximately 500 m from the same highway, furrowed from past agricultural activities, with *Aristida divaricata* as the dominant plant species. Site 4 was close to the Perote-Amozoc highway, with predominantly short tussocks of grasses like *Jarava ichu* (20 cm) and occasional pasturing of goats and sheep. Site 5 was adjacent to Site 4, with irregular soil owing to management practices to prevent erosion; some shrubs interspersed among its moderately long grasses, in dense tussocks, such as *Jarava ichu*. Although this site has been reforested and is to be used for conservation, livestock is still pastured on it. Site 6 is an area where crop farming was abandoned about 14 years ago and has been used as a succession of native pastures with *J. ichu* and *Bouteloua scorpioides*, some succulents and shrubs. It is surrounded by an electric fence and barbed wire and is under surveillance to prevent grazing by intruding domesticated animals. Site 7 has patches of short grass like *Aristida harvadii* and some bunches of other types of grasses such as *Bouteloua scorpioides*, but has not been subjected to any agricultural activities in the last four years and is also under the same type of surveillance as site 6.

Study Design and Data Collection. To capture the squirrels, two plots (1 ha) separated by 100 m were set up in each

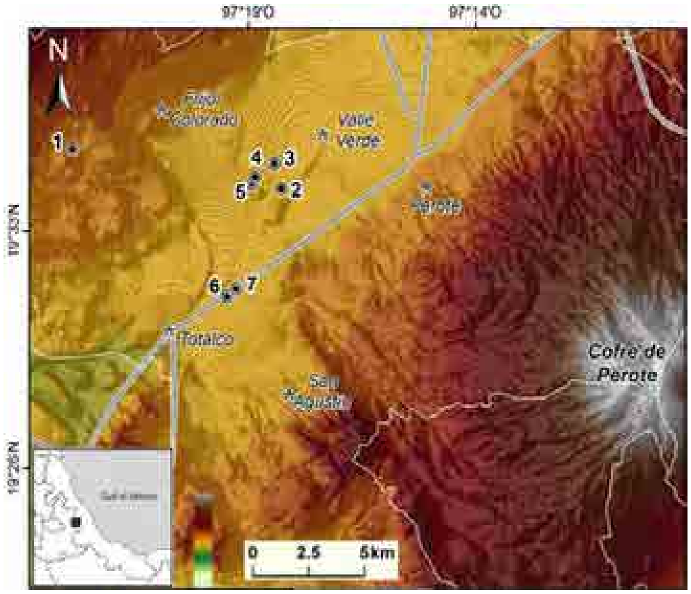

Figure 1. Study area with the sites where sampling was conducted. The seven study sites are shown and main towns are indicated with a star. More intense colors indicate a higher altitude

of the seven study sites. In each plot, 36 Sherman® traps (30 x 10 x 8 cm) were set up in a grid (6 x 6 traps), separated by 20 m. The traps were baited with oat flakes and peanut butter and were active from 0830 to 1500 h (Gurnell and Flowerdew 2006; Castillo-Castillo 2009). Each plot was active for three consecutive days (Jones *et al.* 1996; Castillo-Castillo 2009; Montero-Bagatella and González-Romero 2014) for each month during the ground squirrels' activity cycle from June 2008 to June 2014. The animals captured were marked using magnetic chips (MUSSICC Chips-AVID®), and their sex, weight and reproductive status were noted (*e. g.*, in males scrotal testes and in females mammary glands that indicate pregnancy or lactation; Gurnell and Flowerdew 2006; Castillo-Castillo 2009). The animals were later released *in situ* (Sikes *et al.* 2016). Animals weighing more than 170 g or exhibiting reproductive characteristics were considered as adults (Dimmick and Pelton 1996; Gurnell and Flowerdew 2006; Castillo-Castillo 2009) and those weighing less or without these characteristics were considered juveniles (Castillo-Castillo 2009). Population structure was obtained for each site using sex ratio (males and females) and age (Caughley 1977). Temperature and precipitation data for the study period were provided by the National Water Commission (Comisión Nacional del Agua; CONAGUA).

Statistical Analysis. To carry out the statistical analyses, based on the reported frequencies of the ground squirrels, the years were divided into three periods: pre-reproductive (April and May), reproductive (June to July) and post-reproductive (September, October). Averages of monthly temperature and precipitation data were analyzed using one-way ANOVAs, with *post hoc* Newman-Keuls tests (Zar, 1999). Sex characteristics were analyzed using a chi-squared test (Zar, 1999). All of the analyses were run in Statistica 10.0.

Results

The number of animals captured, monthly precipitation and temperature for 2008 to 2014 are shown in Figure 2. Total sampling effort was 12,528 trap days (Table 1). The highest abundance values mostly coincide with the peaks in temperature and precipitation, decreasing when these variables decreased. The year of 2008 was atypical, it was very rainy and hot, with more than 350 mm of rain and temperatures above 30 °C; 2009 and 2010 were also very rainy. The highest peaks in rainfall are reported from August onward and decreased in October with little rain in the following months. The mean temperature throughout the study was 22.2 °C. The highest temperatures were recorded in March-April, with lower temperatures in August and the lowest from November to January, as low as 13 °C for this period in 2014, which was the coldest year of the study. There were statistically significant differences in temperature during the three periods of the ground squirrel's reproductive cycle (F = 10.70, d. f. = 21, *P* = 0.0006). The *post hoc* test detected differences between the temperatures of the post-reproductive period and those of the pre-reproductive period (*P* = 0.0004) and between the temperatures of the pre-reproductive period (*P* = 0.03). Precipitation did not differ significantly among the different phases of the reproductive period (F = 3.3, d. f. = 21, *P* = 0.05).

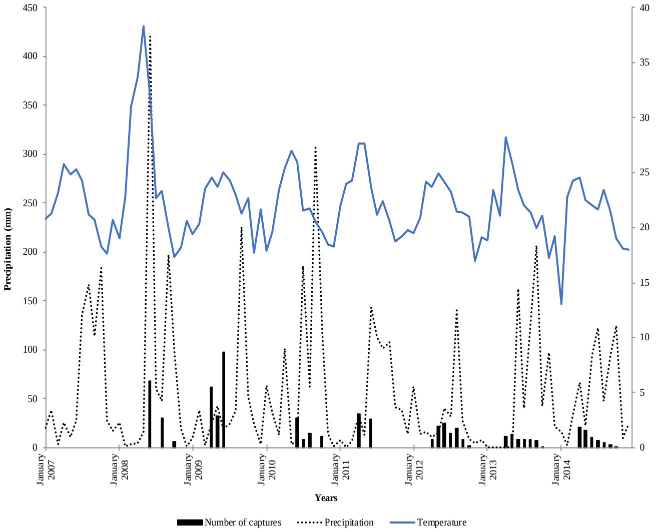

Figure 2. Mean monthly temperature and precipitation for Perote, Veracruz, Mexico 2008 - 2014. The number of captures of the Perote ground squirrel (*Xerospermophilus perotensis*) is also shown. Black bars = number of captures, blue line = temperature, point line = precipitation.

In 2009 the highest number of males and females was caught. In 2009 and 2012 males were caught more frequently (Table 1). Adults were more abundant than juveniles, and there were statistically significant differences in the number of adults and juveniles (F = 5.70, d. f. = 1, *P* = 0.03). Adult males were recorded with greater frequency in the pre-reproductive and reproductive periods (Figure 3). Juveniles were recorded throughout sampling, though their frequency was low. Their abundance was greater and their emergence began in the pre-reproductive period. In 2008 and 2012 the number of juveniles recorded was highest.

Table 1. Total number of *Xerospermophilus perotensis* caught, by sex, age and sampling year.

Year	Female		Male	
	Adult	**Juvenile**	**Adult**	**Juvenile**
2008	39	17	64	18
2009	55	3	134	0
2010	32	8	31	5
2011	16	8	39	0
2012	30	21	71	15
2013	33	3	44	0
2014	23	3	43	3

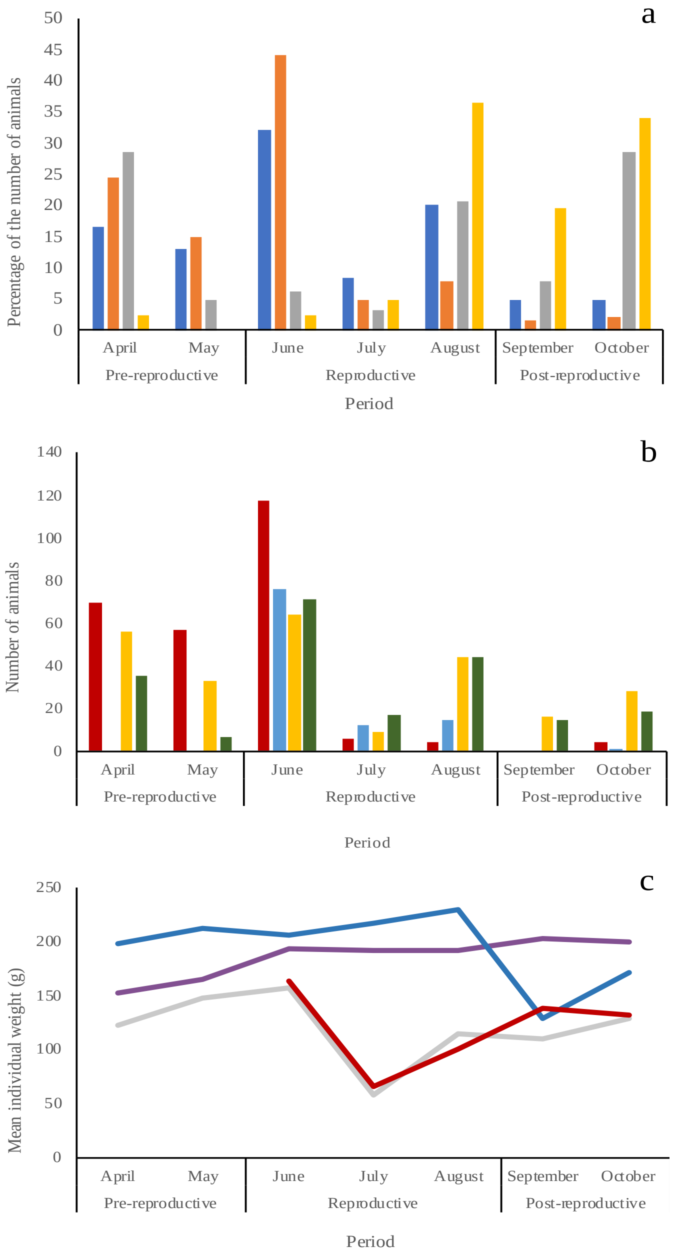

Figure 3. a) Sex and age ratios for the Perote ground squirrel (*Xerospermophilus perotensis*) recorded during its active cycle. Blue bars = adult females, orange bars = adult males, grey bars = juvenile males, yellow bars = juvenile males. b) Secondary sex characteristics of the Perote ground squirrel (*Xerospermophilus perotensis*) recorded during its active cycle. Red bars = scrotal testicles, blue bars = lacting / pregnant, yellow bars = not pregnant, green bars = abdominal testicles. c) Mean weight of the Perote ground squirrel (*Xerospermophilus perotensis*) by sex and age during its active cycle. Blue line = adult males, purple line = adult females, red line = juvenile females, grey line = juvenile males.

Regarding reproductive characteristics, scrotal males were most abundant and females with signs of pregnancy or lactating were recorded least often. Scrotal males were abundant starting in April, reached their maximum in June and decreased in July, when males with abdominal testes were more abundant (Figure 3). Non-pregnant females were recorded in all samples, with those showing signs of pregnancy or lactation appearing in June and through August, with similar values in July (12) and August (15).

The results of the chi-squared test indicate statistically significant differences in the number of adult males exhibiting secondary sex characteristics and those that did not during the three stages of the reproductive period (X^2 = 56.28, d. f. = 2, $P < 0.001$) and in the number of females in different states (pregnant, not pregnant, lactating) over the same period ($X^2 = 28.09$, d. f. = 4, $P < 0.001$). There were differences in the number of females that were not pregnant during the reproductive period (F = 39.5, d. f. = 2, $P < 0.001$), and the post hoc tests indicate differences between the pre- and post-reproductive period and with the reproductive and pre-reproductive period ($P < 0.001$ in both cases). There were differences in the number of pregnant females among study sites ($t = 8.64$, $P < 0.001$), and differences in the number of lactating females between the reproductive and post-reproductive periods ($t = 1.8$, *d. f.* = 21, $P = 0.03$). The number of scrotal males did not differ among periods (pre-, reproductive, post-; F = 0.40, d. f. = 2, $P = 0.66$, nor did the number of males with abdominal testicles (F = 0.37, d. f. = 2, $P = 0.6$).

The weight of the squirrels varied throughout the year. Adult males were heaviest during the pre-reproductive and reproductive periods and lightest during the post-reproductive period (Figure 3). Adult females were heaviest during the post-reproductive period and lightest in April. Juveniles weighed less during July, when they emerged, and their weight increased over the subsequent months.

There were no significant differences in weight between adult males and adult females (F = 0.42, d .f. = 1, $P = 0.5$), and no differences in weight between male and female juveniles (F= 0.12, d. f. = 1, $P = 0.7$), though there were differences between adult and juvenile males (F = 11.79, d. f. = 1, $P = 0.005$) and between adult and juvenile females (F = 21.4, d. f. = 1, $P < 0.001$).

Discussion

Our results reveal that the Perote ground squirrel exhibits phenological patterns similar to those described by Schwanz (2006) and by Williams and Lane (2014) for species belonging to the genus *Ictidomys* and *Tamiasciurus* since the species responds to changes in temperature and its activity cycle begins in the spring and ends in autumn. The highest environmental temperatures were recorded during the pre-reproductive period and marked the end of hibernation and the beginning of preparation for reproduction. When the temperature dropped, hibernation began; similar behaviours were reported for the Mexican ground squirrel (Schwanz 2006). Given that there is a statistically significant relationship between the squirrels' cycle and temperature, we infer that temperature is the most important phenological signal for the Perote ground squirrel, as observed with *Urocitellus* by Lane *et al.* (2012). While precipitation was not significantly related to the cycle of the Perote ground squirrel, it may exert some influence given that tropical storms and hurricanes originating in the Gulf of Mexico are a regular occurrence in the region (García 2003), and at times could prevent the animals from leaving their burrows. This could result in a low capture rate, as occurred in Mendoza-Carreón's (2009) study of this species.

The large number of male squirrels captured at the beginning of the year indicates that they were the first to emerge from hibernation. Michener (1983) reported the same pattern and indicates that this behaviour has the objective of obtaining the best territory and resources until the females emerge and reproduction occurs. The low number of captures at the end of the year reveals that the males were the first to enter hibernation, and this coincides with the findings of Holekamp and Sherman (1989), Michener (1983) and Castillo-Castillo (2009).

The results for secondary sex characteristics indicate they are related to temperature since their frequency was higher in April and June when temperatures were hottest and precipitation was not as intense as in other months. The records of these characteristics were lowest in August when the temperature begins to drop and rainfall is regular and heavy. Similar patterns have been reported in other studies (Best and Ceballos 1995; Valdez and Ceballos 1997; Castillo-Castillo 2009). In our study, scrotal males were the most abundant, a result that concurs with the findings of Castillo-Castillo (2009), and Montero-Bagatella and González-Romero (2014); this may result from their greater susceptibility to being captured. Males generally cover larger areas in their search for females to copulate with, as mentioned by Castillo-Castillo and González-Romero (2010). In contrast, females with signs of being pregnant were recorded least frequently, as occurred in the study by Montero-Bagatella and González-Romero (2014). This may result from the females staying in their burrows to attend to their young, allowing them to escape capture (Mendoza-Carreón 2009) or, as reported for other species of squirrel (Descamps *et al.* 2008; Kneip *et al.* 2011), because reproduction was not achieved.

For age category, the number of adults and juveniles differed statistically, with adults being more abundant throughout the study. Juveniles were more abundant during the post-reproductive period, likely because they were emerging from their burrows and beginning to explore the land as reported by Mendoza-Carreón's (2009). Their emergence coincided with the August peak in rainfall and is reflected in the growth of food resources that could benefit the squirrels development (Williams and Lane 2014). At the beginning of the year, juveniles were also recorded more frequently, as also reported by Castillo-Castillo (2009) and Mendoza-Carreón (2009), who mention that these values are the result of squirrels that were born the previous year emerging from their burrows. In general, the number of records of juveniles was low, as observed in the study by Montero-Bagatella and González-Romero (2014), this can indicate that the populations are aging, that they are not being replenished, and are not growing, meaning that the possibilities for the recovery of this species are limited (Caughley and Sinclair 1994, Miller-Rushing *et al.* 2010). Kneip *et al.* (2011) mentioned that it is possible to underestimate juveniles because they disperse as they grow, so these numbers should be interpreted with some caution.

Hoogland (2003) and Schwanz (2006) demonstrated that in ground squirrels hibernation and reproduction require a notable energetic expenditure and this is reflected in the loss of body weight. This could be what happened to *X. perotensis* over the course of the study since, on emerging from hibernation, the animals encounter a change in food, refuge and habitat availability (Humphrey 1962). Reproduction requires a large energetic investment, more so by females that gestate and care for their young (Hoogland 2003; Yensen and Sherman 2003). Disturbances to the environment that occurred in some of the study sites were agricultural fires that get out of control and plowing, which can cause variations in the weight of the squirrels by limiting resource availability and increasing resource competition (Humphrey 1962).

The abundance of the Perote ground squirrel varied with temperature and precipitation. Increases in population may have been a response to heavy annual rains as documented in other studies of rodents (Kneip *et al.* 2011; Williams and Lane 2014; Heisler *et al.* 2014), since heavy rains can increase the yield of the grasses and asters that this species feeds on. If these conditions persist, they could result in an increase in population (Heisler *et al.* 2014). If however, conditions do not favour the ground squirrels, litter size may decrease, as observed in red squirrels (Descamps *et al.* 2008). The resources present in the habitat can therefore explain the frequencies of this squirrel, and limit or favor the population growth of the species.

The highest abundance values were recorded in April when the ground squirrels had come out of hibernation and were in their reproductive phase. In October, there were few captures, possibly because of low temperatures, resource scarcity and because it was the beginning of the hibernation period. Other studies on this species have reported similar results (Valdez and Ceballos 1997; Castillo-Castillo 2009; Montero-Bagatella and González-Romero 2014). The abundance of the endemic Perote ground squirrel was greater in open sites and those with short grass such as sites 1, 2 and 3 (sampling years 2008 and 2009), because the species prefers this type of site, where it is easier for them to detect potential predators, move shorter distances to find refuge and find better resources such as territory and food (Heisler *et al.* 2014). Grass shoots are more nutritious and palatable and are optimal for the growth of these animals (Hannon *et al.* 2006; Yensen and Sherman 2003;

Pasch and Koprowski 2011). These areas contrast with sites 6 and 7 (sampling years 2013 and 2014) where the pasture was dense and abundant, rendering them perhaps not as habitable as the other areas and resulting in a lower population estimate. In spite of the electric fence and surveillance at site 7, in June 2013, seven squirrels were lost; the traps had been moved from their locations and there were traces of blood and fur, suggesting the squirrels had been predated by dogs. This caused the decrease in abundance recorded in the subsequent months. For this species, the study of Castillo-Castillo (2009) reports maximum densities close to 50 ind/ha, but for 2014 maximum density was 20 ind/ha (Montero-Bagatella and González-Romero (2014)). Based on the proposal of Yensen and Sherman (2003) that the minimum viable density for ground squirrels is 20 ind/ha, we infer that the populations of *X. perotensis* have been decreasing and are small. Density indices overestimate values, in contrast to number of captures, which gives a real estimate of the population and is considered a more appropriate value for the purpose of conservation, especially for endangered species (Caughley and Sinclair 1994).

Even though the number of captures and the reported densities have different values, the tendencies of both parameters indicate steady population decreases in recent years; decreases caused by environmental disturbance, anthropogenic pressure and changes in resource availability (Hoffmann *et al.* 2003). Studies such as those of Mendoza-Carreón (2009) and Sánchez-Cordero *et al.* (2005) mention that the Perote ground squirrel has shown a certain degree of plasticity in the face of unfavourable conditions, though recent population studies indicate that it is now reaching its limit (Castillo-Castillo and González-Romero 2010; Montero-Bagatella and González-Romero 2014).

Ground squirrel density and precipitation can be considered demographic predictors for the purpose of conservation (Kneip *et al.* 2011), and precipitation can even be a predictor of survival rate (Bronson 1979). As such, these variables can be used for the proper management of this species, since the results show that its abundance values are low. This, in addition to its limited distribution, low dispersal capacity and the constant transformation and reduction of its habitat, confirms that *X. perotensis* is facing serious problems for survival, as highlighted in other studies of this species (Valdez and Ceballos 1997; Sánchez-Cordero *et al.* 2005; Álvarez-Castañeda *et al.* 2008; Castillo-Castillo 2009; Mendoza-Carreón 2009; Ochoa *et al.* 2012; Montero-Bagatella and González-Romero 2014). Greater knowledge of this species, its population parameters and its ecology, will provide us with the tools required to better understand its protection and conservation needs. This, together with legal actions could save the species.

The conservation efforts of the private company Granjas Carroll de México, on whose land some animals were trapped, have allowed the populations of this species and others to develop. Also, the government of the state of Veracruz recently decreed a State Natural Conservation Area (Gaceta Oficial 2016) that includes a small part of the distribution of this species. The sum of these actions, will benefit some populations of *X. perotensis* and over time could increase their populations. Another conservation strategy, as suggested by Montero Bagatella *et al.* (2017), would involve the local people, and would be based on environmental education plans, which allow the species to establish by preventing induced fires that destroy the resources that *X. perotensis* needs for to survive. Another strategy is to control feral dog populations, since they prey on it. Fences in the sampled areas would also reduce the risk of predation. Continuous anthropocentric development has considerably reduced the habitat available to this species, so *ex situ* conservation could also be considered, as long as the necessary guidelines for the conservation of the specimens are respected. From the results of our study, genetic studies are recommended in order to know how robust the genetic pool of extant populations is, and to effect the translocation of individuals as suggested by Ochoa *et al.* (2012). Based on the results of our study we consider that the status of this species under Mexican Legislation could be changed from "threatened" to "endangered".

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Diet selectivity in relation to food quality and availability by the endemic Perote squirrel (*Xerospermophilus perotensis*)

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Climatic fluctuations have a biogeochemical effect on food availability and quality, resulting in adjustments of the foraging and food selection behavior of animals. Our study aimed to evaluate the influence of seasonal variation on abundance of food resources and its effect on food selection of *Xerospermophilus perotensis*, an endemic species of ground squirrel in the Oriental Basin. Food selection behavior was recorded using focal animal and continuous behavior sampling on a squirrel population inhabiting the grassland of a semi-arid area. The results show that their diet consisted of 6 plant species with significant differences in the time spent feeding on each plant species ($X^2 = 128.96$; $P = 0.01$). The species with the highest feeding times included *Scleropogon brevifolius* (63.6 %), *Verbena bipinnatifida* (10.6 %) and *Erigeron pubescens* (10.5 %). These plant species had the highest percentage of vegetation cover and availability among seasons, but they were of low nutritional quality with regard to their protein/fiber ratio. However, during specific periods, associated either with gestation and lactation or prior to hibernation, the squirrels increased their protein consumption. This suggests that squirrels are opportunistic feeders, and under certain conditions tend to select plant species that provide them with better quality diets.

Las fluctuaciones climáticas tienen un efecto biogeoquímico sobre la calidad y la disponibilidad de los alimentos, lo que resulta en ajustes en la conducta y la selección de los alimentos de los animales. Nuestro objetivo fue evaluar la influencia de la variación estacional en la abundancia de los recursos alimenticios y su efecto sobre la selección de alimentos por *Xerospermophilus perotensis*, una especie de ardilla endémica de la Cuenca Oriental. La conducta de alimentación se registró utilizando un muestreo animal-focal con registro continuo en una población de ardillas que habita en los pastizales de una zona semiárida. Los resultados mostraron que su dieta consistió en 6 especies de plantas con diferencias significativas en el tiempo de alimentación de cada especie ($X^2 = 128.96$; $P = 0.01$). Las especies con los mayores tiempos de alimentación fueron *Scleropogon brevifolius* (63.6 %), *Verbena bipinnatifida* (10.6 %) y *Erigeron pubescens* (10.5 %). Estas especies de plantas tuvieron el mayor porcentaje de cobertura vegetal y disponibilidad entre estaciones, pero fueron de baja calidad nutricional con respecto a su relación proteína / fibra. Sin embargo, durante períodos específicos, asociados con la gestación y la lactancia o antes de la hibernación, las ardillas aumentaron su consumo de proteínas. Esto sugiere que las ardillas son consumidores oportunistas, y bajo ciertas condiciones tienden a seleccionar especies de plantas que les proporcionen dietas de mejor calidad.

Key words: Diet; endemism; ground squirrel; nutritional quality; seasonal variation.

Introduction

Seasonality refers to recurrent climatic variations that tend to occur over an annual period. These variations define the type of vegetation that exists in a place and directly affect the abundance and quality of food resources (Schaik and Brockman 2005). Such seasonal variations in food abundance and quality have been reported to cause concurrent alterations in the abundance and/or dietary habits of herbivorous species (Gutiérrez 1998; Hirsch 2009; García-García and Santos-Moreno 2014; Penezić and Ćirović 2015; Tsindi *et al.* 2016).

Although herbivory is largely determined by external factors that regulate food abundance and availability, dietary flexibility plays an important role as it depends on individual digestive processes that regulate the acquisition of metabolizable energy and nutrients (Karasov *et al.* 1986). In this way, the chemical characteristics of the food directly affect the selection of the diet of the animals, and a preference for certain types of food can be the consequence of its chemical composition (Ulappa *et al.* 2014). In this context, each animal faces the dilemma of having to obtain an adequate food in terms of quantity and quality to meet its nutritional needs, and protein and fiber are considered the chemical constituents that determine this preference (Stephens and Krebs 1986; Grier and Burk 1992; Rezsutek and Cameron 2011).

Within nutritional ecology there are four hypotheses with regard to the aims of diet selection, each of which proposes that dietary selection has a different nutritional primary objective: 1) maximization of energy uptake (Schoener 1971). 2) The maximization of nitrogen uptake (Mattson 1980; White 1993). 3) Toxin evasion (Freeland and Janzen 1974; Dearing *et al.* 2005). 4) The acquisition of a nutritionally balanced diet (Raubenheimer and Simpson 2004, Robbins *et al.* 2007). The quantification of these different nutritional goals is a challenge, especially in studies of wild animals, where research requires detailed data on feeding behavior of animals over continuous periods, adequate analysis of all food consumed, and an analytical framework to address the complex nature of nutritional data (Felton *et al.* 2009).

In fact, the diet of herbivorous mammals is considered one of the most complex in comparison with that of other dietary specialists (Belovsky 1978; Owen-Smith and Novellie 1982). This notion is supported by the fact that herbivores can consume foods in high abundance but of low quality, which often lack essential nutrients, so that they require supplementary intake of different food items to maintain nutritional balance (Westoby 1978).

In semi-arid environments, herbivores must develop even more efficient strategies for harnessing food resources, as the supply of quality vegetation is usually low. These strategies are both behavioral (ability to select proper feeding sites and selection of dietary components) and physiological (development of a digestive system that optimizes food processing; Benítez *et al.* 2006). Ground squirrels that live in semi-arid environments are therefore a good model to study because of the selectivity of their diet in relation to its quality and availability, which varies seasonally (Valdés 2003).

The ground squirrel of Perote (*Xerospermophilus perotensis*) is an endemic species of the semi-arid area of the state of Veracruz, Mexico (Best and Ceballos 1995). It has been classified as threatened in the Official Mexican Standard 059 (SEMARNAT, 2010), and as endangered species on the IUCN Red list (Álvarez-Castañeda *et al.* 2016). During the winter the squirrels encounter low food availability and remain inactive for 2 to 3 months (Valdéz and Ceballos 1997).

Perote's squirrel is adapted to the semi-arid environment, Xerophile shrubland with associations of rosetophilous shrubs, nopaleras, izotal and spiny shrubs with terminal spines. This environment greatly limits the consumption of quality food and adequate nutrient intake. To our knowledge studies on Perote´s squirrel have so far focused on aspects related to their ecology and behavior, however, they have not addressed ecophysiological or nutritional aspects. The aim of this study was therefore to investigate the availability, selection and energetic-nutritional content of the diet of *X. s. perotensis* according to seasonal variations, with the purpose of knowing if there is a relationship between the quality of the diet, its consumption, and the adequacy to cover certain physiological demands, using protein as a measure of nutritional quality.

Materials and methods

Study area. The study was carried out in a semi-arid area in the Valley of Perote, Veracruz, Mexico (19° 34′ 54″ N, -97° 21′ 55″ W). According to the Köppen climate classification, modified by García (1973), the study area has a climate Bs, K'w'(i'), which is the most humid among semi-arid climates, temperate with warm, rainy summers, and little atmospheric temperature range.

A sampling zone was established in a 3.5 ha grassland area. The natural vegetation of the zone is xerophile shrubland (Velázquez *et al.* 2016), where areas covered with different types of vegetation like spiny shrub with lateral spines, cardonales, spineless parvifolia shrub, also identified such as "izotal" (*Nolina parviflora* and *Yucca periculosa*), shrubs (*Agave obscura*), grasslands (*Distichlis spicata*, *Bouteloua hirsuta* and *Suaeda nigra*), nopal fields or "nopalera" (*Opuntia robusta*, *O. tunicata*, *O. huajuapensis* and *Mammillaria discolor*). In addition, herbaceous species such as *Salvia microphylla*, *Dalea alopecuroides*, *Bouvardia ternifolia*, *Tagetes micrantha* and grass of the species *Aristida barbata* (Miranda and Hernández 1963; Sandoval 1984) occur in this region.

Behavioral record. The composition of the squirrels' diet was obtained through field observations, aided by Bushnell binoculars (10 x 50) and a monocular (12 x 50) from a maximum distance of 20 m. The observation schedule began at 8:00 h (time when the squirrels began their activity) until 16:00 h (when activity decreased). We collected data using 5-min focal animal observations (Martin and Bateson 1993) combined with a continuous recording method. Feeding behavior was considered when an individual manipulated and consumed a plant. Although no particular individuals were identified a record sheet was used, recording the duration (seconds) of the feeding and the plant species used as food. Data collection was performed for eight days on a monthly basis, starting in April and ending in November 2010, with a total sampling time of 464 hours.

Collection and identification of the plant species. The plants that the squirrels used as food were collected in the study area and identified in the Herbarium XAL of Instituto de Ecología A. C. Since the squirrels did not do any discrimination between parts of the plant for consumption, all the plant samples (with exception of the fruits of *Yucca periculosa*) were whole plant of each of the identified species. The plant species were cut at ground level, weighed and later kept in paper bags to be taken to the laboratory for chemical analysis.

Determination of food availability. Two squares of 10 x 10 m were established to record plant food availability, and were sampled in May, August and November. Samples were collected and botanized from 20 places of 1 m^2 that were randomly selected. Afterwards, the Braun-Blanquet scale of coverage-abundance was used to evaluate the percent of vegetation coverage for each plant species (Wikum and Shanholtzer 1978). The resulting values were converted to percentages of area for each of the plant species considered.

Analytical methods. The plant species that constituted the squirrels' diet were analyzed through proximate chemical analysis, Dry matter (DM), crude protein (CP, N x 6.25), ether extract (EE; AOAC 1990), neutral detergen fiber (NDF), acid detergent fiber (ADF), cell content (CC), hemicellulose (H), cellulose (C) and lignin (L; Van Soest 1967). Duplicate analyses followed the AOAC (2012) guidelines. The content of dry material was determined by drying the plants in a forced air oven until reaching a constant weight after three measures. We estimated the dry weight by determining the difference of the water content value.

Evaluation of diet quality. The protein-fiber ratio was calculated as an estimate of the nutritional value of the plant species, in which the total percent of crude protein was divided by the value of the acid detergent fiber (ADF; Chapman and Chapman 2000; Table 3). A nutrient intake rate was used, which considers the proportion of plant matter ingested by the squirrels and its corresponding nutritional value. The relative frequency of each of the plant species consumed by the squirrels was used and the nutrient intake rate was calculated as indicated in the following formula: Nutrient intake rate = nutritional value of the plant species (%) * relative frequency consumed. Based on the estimates of the nutrient ingestion rate of each plant species, the total nutrient contribution was calculated per month: Total nutrient intake rate = Σ nutrient intake rates of each plant species per month / total of consumed species.

Statistical Analysis. To determine the feeding time dedicated to each plant species used by *X. perotensis*, as well as for each of the months of data collection, descriptive statistics were used. Afterwards, the difference between the percentage use of each plant species for each month was calculated, and since the data did not comply with the normality and homogeneity of variances test, the Kruskal-Wallis test and Tukey's post hoc tests were applied to verify the statistically significant differences between the analyzed factors. The confidence level was 95 %.

Food availability was measured as percentage of plant cover in May, August and November. To determine the changes in plant species availability across months, a Friedman test was applied.

Results

Behavioral record. In the study area 14 plant species within six families were recorded. *X. perotensis* used six plant species as a food resource. Considering the average time spent on feeding per food item the squirrels spent 63.60 % on the indigenous grass species *Scleropogon brevifolius*, followed by *Verbena bipinnatifida* with 10.60 %, and *Erigeron pubescens* with 10.50 % and *Croton* sp. with 6.69 %. Fruits of *Bouteloua scorpioides* and *Yucca periculosa* were included in the diet during September to November, because the fruiting and flowering occurs during these months of the year, with an average percent of time feeding of 2.3 % and 6.1 % respectively (Figure 1).

There was a significant difference in the time spent feeding on different plant species ($X^2 = 128.96$; $P = 0.01$). Pairwise post hoc test revealed that squirrels spent significantly more time feeding on *S. brevifolius* compared to all other plan species ($P = 0.001$). The foraging time per month varied across the different months of the study. The squirrels devoted a higher percentage of their daily activity budget on feeding during April (22.7 %), May (21 %) and July (21 %), compared to August (17.5 %) and September (17.6 %; Figure 2A).

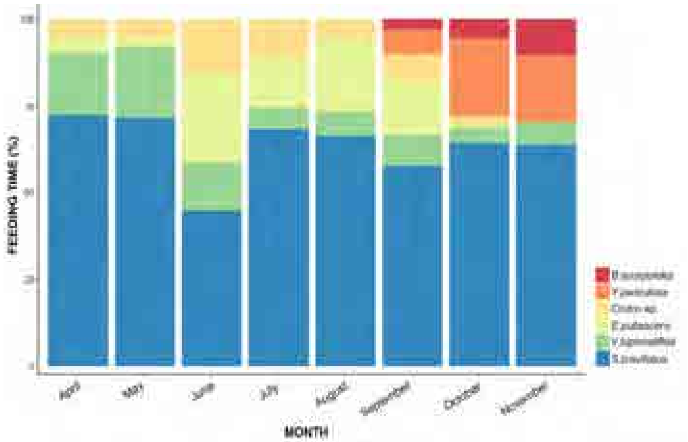

Figure 1. Average percent of time spent on feeding on each of the plant species included in the diet of the squirrels.

Plant species availability and food selection. The plant species with the widest cover were *S. brevifolius*, *E. pubescens*, *Croton* sp. and *V. bipinnatifida*, which were part of the diet of the squirrels (Table 1). The percentage of the vegetation cover of

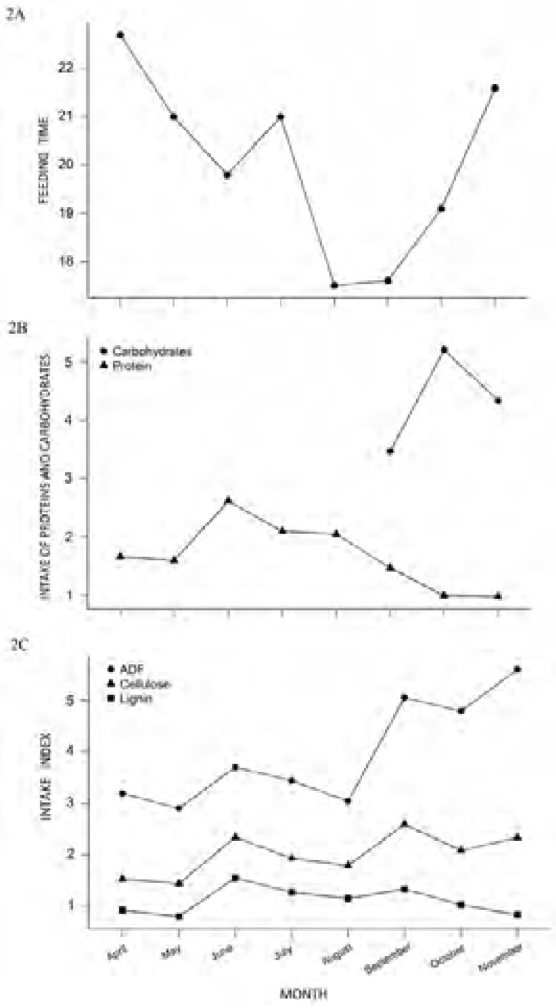

Figure 2. Percentage of feeding time per month considering all plant species used in Perote squirrels diet (A). The protein and carbohydrate index shows that during the recorded period the squirrels ate foods containing mainly protein, while during the months of September, October and November they ingested carbohydrates, due to fruiting and consumption the fruits of Y. periculosa (Carbohydrate data from: Baraza *et al.* 2008) (B). Intake Index of ADF (Acid Detergent Fiber), Cellulose and Lignin for *X. s. perotensis*. The ADF consumption was higher than the others (C).

the species that were part of the squirrels' diet showed significant changes during the months in which this variable was recorded ($X^2 = 6.50$, d. f. = 2, $P = 0.039$), and post hoc comparison revealed significant differences between the months of August and November ($P < 0.05$) but no significant differences between May and August, and May and November.

Evaluation of diet quality. The total nutrient intake rate was calculated per month (Table 2). The protein intake rate varied during the data collection period. During April and May, the protein intake was 1.67 %, increased in June to 2.61 %, July and August (2.10 % and 2.50 %, respectively) and decreased during following months (September to November). For this study, the carbohydrate content of plants was not evaluated, however, the percentage of soluble carbohydrates in the fruits of *Y. periculosa* have been reported previously by Baraza *et al.* (2008) are included in (Figure 2B). According to the consumption of Acid Detergent Fiber, there was an increase during the sampling period, being most notable in the months of September (5.05 %) and November (5.60 %). In the case of cellulose, the percentages remained constant, increasing slightly in the months of June (2.34 %) and September (2.59 %), in the same way it happened for lignin, where an increase was shown for the month of June (1.55 %; Figure 2C).

Table 1. Availability of plant species expressed as percent of cover. The species marked with an asterisk (*) were part of the diet of *X. s. perotensis.*

	% Cover		
Species	May	August	November
	Compositae		
*Erigeron pubescens**	3.9	16.6	6.8
Gnaphalium gracile	0.6	1.5	0.3
Gnaphalium stramineum	0.3	1.1	0.7
Bidens laevis	0.4	0.7	0.1
	Euphorbiaceae		
Croton sp.*	4.9	6.5	3.3
Chamaesyce prostrata	0.8	0.5	1.2
	Leguminosae		
Leguminosa	0	0	0.2
	Poaceae		
*Scleropogon brevifolius**	49.2	54.3	39.3
Bouteloua gracilis	0	0.9	1.1
*Bouteloua scorpioides**	0	0	1.8
Distichlis spicata	0.5	0.4	1.3
Aristida divaricata	0.7	0.3	0.6
	Tetrachondraceae		
Polypremum procumbens	0	0.7	0.5
	Verbenaceae		
*Verbena bipinnatifida**	4.4	5.9	1.6

The plant species consumed by the squirrels was mainly supplied by *E. pubescens*, *Croton* sp. and *V. bipinnatifida*, which contained the highest protein values (13.43 % to 15.06 %). Fiber content differed markedly between plant species and ranged from 18.23 % to 74.96 % for neutral detergent fiber (NDF), and from 6.11 % a 52.35 % for the acid detergent fiber (ADF). Lignin content ranged from 4.33 % to 14.32 %, between plant species, which showed that *E. pubescens* and *Croton* sp. had a high percentage of indigestible materials. The cell content (soluble parts of the plant) ranged from 25.04 % to 81.77 %, and *Y. periculosa* fruits had the highest value for cell content (Table 3).

Table 2. Percentage of nutrient intake rate per month by *X. s. perotensis*

	MONTH							
	April	May	June	July	August	September	October	November
ADF	3.19	2.9	3.7	3.44	3.04	5.05	4.79	5.60
Cellulose	1.53	1.44	2.34	1.93	1.79	2.59	2.08	2.33
Lignin	0.92	0.8	1.55	1.27	1.15	1.33	1.03	0.83
Protein	1.67	1.6	2.61	2.10	2.05	1.47	1.00	0.98
Carbohydrates						3.46	5.19	4.32

Protein/fiber ratio. The protein/fiber ratios of the plant species that the squirrels included in their diet differed significantly from each other (interval: 0.09 to 2.20). The plant species that showed a low protein/fiber ratio, and thus were of low nutritional quality, included *B. scorpioides* (0.09 %) and *S. brevifolius* (0.18 %). The squirrels, however, fed on the latter, most frequently, while *E. pubescens* was the plant species with the highest protein/fiber ratio (2.20 %; Table 4).

Table 3. Approximate chemical value expressed in percentage for each plant species consumed by *X. s. perotensis* (values reported in dry material). Humidity (H), Dry material (DM), Crude protein (CP), Ether extract (EE), Acid detergent fiber (ADF), Neutral detergent fiber (NDF), Cell content (CC), Hemicellulose (H), Cellulose (C), Lignin (L).

SPECIES	H	DM	CP	EE	ADF	NDF	CC	H	C	L
Erigeron pubescens	5.74	94.26	13.43	6.11	6.11	42.16	57.84	8.24	15.24	11.62
Croton sp.	5.46	94.54	13.56	8.92	41.24	50.40	49.60	9.16	21.32	14.32
Scleropogon brevifolius	4.58	95.42	8.75	3.70	48.34	70.75	29.25	22.41	14.54	10.08
Bouteloua scorpioides	3.60	96.40	4.88	3.03	52.35	74.96	25.04	21.71	20.63	5.60
Verbena bipinnatifida	5.17	94.83	15.06	5.96	30.53	40.42	59.58	9.89	17.48	7.65
Yucca periculosa	9.39	90.61	4.37	7.65	11.65	18.23	81.77	6.58	6.97	4.33

Discussion

The goal of our study was to examine the food quality of the dietary items of *X. perotensis* related to seasonal variation. We found that their diet included six plant species. During the period from April to August the diet was conformed by four indigenous grass species, while from September through November the squirrels´ diet included also

Table 4. Protein and fiber content as well as protein/fiber ratios and proportion of time spent feeding on the plant species included in the diet of *X. s. perotensis*.

SPECIES	PROTEIN %	FIBER (ADF) %	PROTEIN/FIBER %	% TIME OF FEEDING
Erigeron pubescens	13.43	6.11	2.20	10.54
Croton sp.	13.56	41.24	0.33	6.69
Scleropogon brevifolius	8.75	48.34	0.18	63.69
Bouteloua scorpioides	4.88	52.35	0.09	2.33
Verbena bipinnatifida	15.06	30.53	0.49	10.61
Yucca periculosa	4.37	11.65	0.38	6.12

fruits of two plants (*B. scorpioides* and *Y. periculosa*). It is likely that the low diversity of plant species in the diet of *X. s. perotensis* is due to the small range of species that are available for consumption in their habitat.

With regard to the food resource availability, *S. brevifolius* had the highest vegetation cover during the sample period (May, August and November), and it was the most consumed item. Several studies performed on rodents showed that the plant species with a high vegetation cover are also the most consumed food items (Cortes *et al.* 2002; Matamoros-Trejo and Cervantes 1992). Our results coincide with those reported by Valdéz and Ceballos (1991), who found that the composition of the diet of the terrestrial squirrel *Spermophilus mexicanus* varied in relation to the phenological changes and the availability of the plants, the same pattern has been shown in meadow vole (*Microtus pennsylvanicus*) and ground squirrels *(Urocitellus beldingi*; Bergeron and Jodoin 1987; Eshelman and Jenkins 1989).

Regarding nutritional quality of the plant species used as food by the Perote´s squirrels expressed as protein/fiber ratio, the species *B. scorpioides* and *S. brevifolius* had the lowest quality (0.09 and 0.18 respectively). In general terms, we considered that with exception of *E. pubescens* and the fruits of *Y. periculosa* the rest of the items that comprise the squirrels'diet are low quality items. A vegetarian diet is considered to be of low quality when it presents high fiber contents (mainly acid detergent fiber), including lignin, which are difficult to digest (Mc Donald *et al.* 1995; Quan-Sheng and De-Hua 2007). However, although *S. brevifolius* was of low dietary quality it was nevertheless both the most abundant and most consumed plant species, suggesting that Perote´s squirrels are opportunistic feeders, as they exploit the most available food resources.

The highest percentage of protein intake was recorded during the summer months from June through September, due to the increased consumption of *E. pubescens*, the plant species with the highest quality, according to the protein/fiber ratio among the six species consumed by the squirrels. Interestingly, *E. pubescens* was consumed most during the period of pregnancy and lactation in the females (Valdéz and Ceballos 1997), and according to literature reports the emergence of young juvenile squirrels (Ceballos and Oliva 2005). The increase in protein consumption is therefore likely to have served to meet the increased nutritional requirements of pregnant and lactating females. Increased protein consumption during pregnancy and lactation has been found to occur in other mammals as well (*e. g.,* Mantled howler monkeys, *Alouatta palliata* Serio-Silva *et al.* 1999; common degu, *Octodon degus*, Veloso and Bozinovic 2000) and thus seems to be a common pattern among mammals (McNab 1986; Pianka 1981). The Perote squirrel has been reported to also consume insects (Valdéz and Ceballos 2005), which serve as a source of protein, however, no insect consumption was observed during this study.

We recorded a higher level of fiber intake during September through November, compared to the period between April and August. During the same time window protein consumption decreased. The high proportion of fiber intake during autumn could be the result of the lower availability of other plant resources in this season. This in turn may 'force' the squirrels to feed on resources with a higher fiber content in their diet. During these months, however, consumption of *Y .periculosa* fruit was recorded. Although yucca fruits do not have high protein contents, they do have high contents of metabolizable energy in the form of carbohydrates, which increases with ripening (Baraza *et al.* 2008). Thus, these fruits may play an important role to meet the energy requirements and prepare the squirrels for hibernation during the low temperatures period from November to February. The mature seeds of *Y. periculosa* also contain high concentrations of non-structural lipids and carbohydrates (García-Villanueva 1986), and this may contribute to the caloric increase of the squirrels before hibernation.

Our results show a connection between plant availability and their consumption by *X. perotensis*, with the plant species having the widest cover and availability during the data collection period being the most consumed one. It appears that Perote´s squirrels were able to adjust their consumption of different plant species to meet certain physiological requirements, across the breeding season and during lactation, which both require a high-energy intake. This may explain the increase in protein intake during this period, and to prepare themselves for hibernation by including high amounts of simple sugars in their diets. Our study contributes relevant information on the diet and feeding behavioral strategies that the Perote squirrels use to adapt to and survive in an environment with limited resources.

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Interactions between bats and floral resources in a premontane forest, Valle del Cauca, Colombia

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The study of interaction networks between species is a subject that has drawn increasing attention in recent decades, especially in investigations involving relationships between plants and pollinators or seed dispersers. In the Neotropics, bats of the subfamily Glossophaginae show morphological modifications for a specialized diet consisting of nectar and pollen, but opportunistic species belonging to other subfamilies that consume floral resources (nectar and pollen) have also been identified. This study describes for the first time the interactions between nectarivorous bats in the Andean region of Colombia from the identification of pollen associated with the bat species inhabiting the protected area "Reserva Forestal Bosque de Yotoco (RFBY)". Bats were captured with mist nets; a pollen sample was collected from each specimen by contact with glycerin gelatin, and pollen samples were mounted on slides. In addition, plant material of the blooming species that displayed the syndrome of chiropterophyly was collected to build a reference pollen collection. For the analysis, we used Levin's standardized niche breadth (B_A), the relative frequency of resources (Fi), and the Resource Importance Value Index (RIVI). The interaction network was built and the NODF nesting algorithm was calculated to establish the degree of coupling within the network. In 44 loads of contact pollen for six species, three belonging to the subfamily Glossophaginae (*Anoura caudifer, Glossophaga soricina* and *Choeroniscus godmani*), we identified six palynomorphs from 7,971 pollen grains. The highest RIVI values correspond to three species of the genus *Inga*. The Levin's standardized niche breadth (B_A) highlights *Anoura caudifer* and *Glossophaga soricina* as generalist species that take advantage of the availability of floral resources for consumption (Tables 2, 3). The interaction network reveals a high nesting degree according to the value of the NODF algorithm of 86.67 (Figure 3). With four bat species, the RFBY has a high diversity of nectarivorous species relative to other localities across the Andean region of Colombia, despite the study area being a fragmented landscape; hence, this area is of critical importance for the local bat species, as it fulfills their food requirements. The bat species using the largest amount of resources in the community is *Anoura caudifer*; this finding differs from the results of other studies, where the genus *Glossophaga* has been reported as the dominant taxon in terms of resource use. Plants of the genus *Inga* and *O. pyramidale* are key resources for the nectarivorous bat species recorded, and this is probably also the case for other animals in the area; therefore, the inclusion of these species in the active restoration process will likely promote the establishment of a larger number of bats.

El estudio de redes de interacciones entre especies es un tema que ha tomado fuerza en las últimas décadas, especialmente en investigaciones que involucran relaciones entre plantas y dispersores de semillas o polinizadores. En el neotrópico, la subfamilia de murciélagos Glossophaginae presenta modificaciones morfológicas para una dieta especializada en el consumo de néctar y polen, aunque también se han identificado especies oportunistas pertenecientes a otras subfamilias que aprovechan recursos florales (néctar y polen). Este estudio describe por primera vez interacciones de murciélagos nectarívoros en la región Andina de Colombia a partir de la identificación del polen asociado a las especies de murciélagos presentes en el área protegida de la "Reserva Forestal Bosque de Yotoco (RFBY)". Se capturaron murciélagos con redes de niebla, a cada uno se le tomó una muestra de polen de contacto con gelatina glicerinada las cuales se montaron en láminas. Adicionalmente se colectó material vegetal de aquellas especies que estuvieran en floración y presentaran el síndrome de quiropterofilia para conformar la colección de polen de referencia. Para el análisis se empleó la amplitud de nicho estandarizada de Levin (B_A), la frecuencia relativa de los recursos (Fi), el índice de valor de importancia del recurso (IVIR). Se construyó la red de interacciones y se calculó el algoritmo de anidamiento NODF para establecer el grado de acoplamiento de la red. En 44 cargas de polen de contacto para seis especies, tres de estas pertenecientes a la subfamilia Glossophaginae (*Anoura caudifer, Glossophaga soricina* y *Choeroniscus godmani*), se identificaron seis palinomorfos a partir de 7,971 granos de polen. Los valores más altos del IVIR corresponden a tres especies del género *Inga*. La amplitud de nicho estandarizada de Levin (B_A), resalta a *Anoura caudifer* y *Glossophaga soricina* como especies generalistas que aprovechan la disponibilidad de recursos florales para su alimentación (Tablas 2, 3). La red de interacciones presenta un grado de anidamiento alto dado por el valor del algoritmo NODF de 86.67 (Figura 3). Con cuatro especies de murciélagos, la RFBY posee una alta diversidad de especies nectarívoras en comparación a las especies encontradas en otras localidades en la región Andina de Colombia pese a que se trata de un área fragmentada, por ello es una zona fundamental para estas especies ya que cubre los requerimientos alimenticios necesarios. La especie que más recursos utiliza en la comunidad es *Anoura caudifer* a diferencia de los resultados de otros estudios, donde el género *Glossophaga* es el que predomina en la utilización de los recursos. Tanto las plantas del género *Inga* como *O. pyramidale*, representan recursos importantes para las especies nectarívoras registradas como para otra fauna presente en la zona y probablemente al incluir estas especies en el proceso de restauración activa se puede promover el establecimiento de mayor cantidad de murciélagos.

Key words: *Anoura caudifer*; community; *Glossophaga soricina*; pollen; Yotoco.

Introduction

Mutualistic interactions between plants and their pollinators or dispersers form complex interdependence networks that lead to a dynamic stability in particular habitats (Bascompte 2007; Rohr *et al.* 2014). In studies of different taxonomic groups, heterogeneity and asymmetry have been identified as network features that provide stability to communities. In general terms, generalist plant species are linked to specialist pollinators and vice versa, shaping the physical structure of diversity (Bascompte and Jordano 2007; González *et al.* 2010). Data processing by managing complex networks facilitates the analysis of the coupling between species; this uses various metrics, including the degree of nesting that shows the level of structure for the network according to the number of connections and nodes (Bascompte *et al.* 2003). In this sense, the most common arrangement in a mutualist network involves the majority of species showing few connections and a small number of species with multiple connections, which contribute to maintain the attributes of the community (Bascompte *et al.* 2006; Olesen *et al.* 2008).

Most angiosperms require biological pollination, especially in the tropics, where an estimated 99 % of the species in humid tropical forests are pollinated by animals (Bawa 1990). Only three to 11 % of these pollinators correspond to birds and bats (Devy and Davidar 2003). Overall, approximately 528 species of angiosperms are recognized as being pollinated by bats (Fleming *et al.* 2009); in South America, 140 species have been identified as visited by bats for the consumption of nectar and pollen (Geiselman and Defex 2015). Worldwide, an estimated 7.7 % of bat species visit flowers in search of food resources, including species with specialized morphological traits for the consumption of nectar (4.7 % of the world species) or opportunistic frugivorous species (Fleming *et al.* 2009; Geiselman and Defex 2015). In South America, the subfamilies Glossophaginae and Lonchophyllinae (family Phyllostomidae) show specialized morphological features for the consumption of nectar and pollen, including a long rostrum with reduced teeth and, in many cases, with spaces between them, long canines and long tongues with papillae or lateral grooves (Freeman 1995; Winter and von Helversen 2003). Separately, in the subfamilies Stenodermatinae, Phyllostominae, Rhinophyllinae, Glyphonycterinae and Carolliinae, frugivore and opportunistic omnivorous genera have also been reported that are capable of feeding on nectar and pollen: *Artibeus, Carollia, Chiroderma, Phyllostomus, Platyrrhinus, Rhinophylla, Sturnira, Trinycteris, Uroderma* and *Vampyressa* (Fleming *et al.* 2009).

Compared to the Old World, the Neotropics display a high taxonomic richness of pollinating species associated with the available resources, a fact that has been related to specialized ecological niches (Fleming and Muchhala 2008). The nectarivorous Neotropical bats show a shift in species composition along an altitudinal gradient, mainly due to the specialization of niches related to the morphological adaptations of individual species (higher dietary specialization) and to the complexity of the community structure associated with the closer relationships between species (Owen 1990; Patterson *et al.* 1996; Fleming and Muchhala 2008). In line with the above, in intermediate and high zones of the Andean region (500 to 3,600 meters above sea level), the genus *Anoura* has diversified and specialized in the consumption of nectar and pollen (Koopman 1978; Mantilla-Meluk and Baker 2006; Fleming *et al.* 2009; Mantilla-Meluk *et al.* 2014), in contrast with low areas of the Andean region dominated by the genus *Glossophaga*, a species that inhabits an altitudinal range of 0 to 1,800 masl (Solari *et al.* 2013) that has less specialized morphological traits and diet.

In Colombia, few articles are available on the interactions between nectarivorous bats and the floral resources (nectar and pollen) consumed by them. In low areas (below 1,500 masl) of the Andean region, there is information available on the interactions between *Glossophaga longirostris* and columnar cacti in the Tatacoa desert (Ruiz *et al.* 1997), one study on the pollen carried by *G. soricina* in a suburban area of Cartagena, Bolívar (Lemke 1985), and one study about anthophilous bats of La Macarena, Meta (Muñoz-Saba *et al.* 1997). There is no information available on the potential interactions for the mountainous area of the Andean region, where a replacement of species and a lower species richness of nectarivorous bats occur. This study describes for the first time the interactions between nectarivorous bats in the Andean region of Colombia from the identification of pollen associated with bat species inhabiting the protected area Reserva Forestal Bosque de Yotoco (RFBY), located in Valle del Cauca, Colombia.

Materials and Methods

Study area. The protected area Reserva Forestal Bosque de Yotoco, in the department of Valle del Cauca, is located in the eastern slopes of the Western Cordillera of Colombia and includes the largest patch of premontane forest in this slope. It comprises an area of approximately 559 has spanning across an altitudinal range of 1,200 to 1,700 masl. Mean annual temperature is 20 °C and mean annual precipitation is 1,500 mm; the local climate regime is bimodal, with two rainy seasons (March to May and September to November) alternated with two dry seasons (June to August and December to February; Escobar 2001).

The RFBY is split in two areas by the Buenaventura-Loboguerrero-Buga highway; the zone under active restoration where this study was conducted is located in the high elevation area. The area under active restoration comprises 18 % of the total area of the RFBY and includes a border zone with pastures used for livestock raising and a multi-purpose area that includes gardens and a compost heap (Figure 1). Two field trips were conducted, one in the dry season in June-July, and another in the rainy season in October 2016.

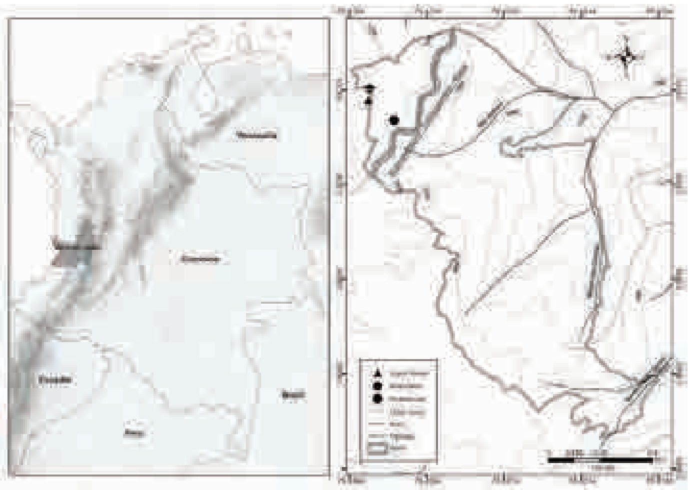

Figure 1. Map of the protected area "Reserva Forestal Bosque de Yotoco (RFBY)", Valle del Cauca, Colombia. The three areas sampled are shown (Upper Border, Restoration and Multiple Use) and the dotted line shows the Buenaventura-Loboguerrero-Buga highway that splits the total area of the RFBY (Perez-Moreno, 2018).

Capture and Sampling of Bat Specimens. Five to ten mist nets measuring 6 m, 9 m and 12 m long were used, keeping them open from 18:30 to 00:00 h. These nets were placed on the border as well as in the interior of the forest, considering the location of the flowering plants. Contact pollen samples were collected from the pelage of each specimen captured using glycerin gelatin prepared according to the technique of Beattie (cited by Voigt *et al.* 2009), sampling the rostrum, dorsum and wings. Samples were stored in tightly closed vials. Samples were mounted directly on slides without processing them through acetolysis to prevent loss of material, although this results in a lower resolution of the pollen wall.

From each specimen, data were recorded on reproductive status, age, weight and standard morphometry: total length (TL), tail length (TL), leg length (LL), ear length (EL), and forearm length (FL). Most specimens were identified in the field, and the rest were collected under the framework of the collection license of wild species of biological diversity for research purposes of the Universidad Nacional de Colombia. These were deposited in the Alberto Cadena Garcia collection of mammals, Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, with catalog numbers ICN 22767, 22792, 22795, 22796, 22798 to 22805, 22809 to 22821, 22829, 22852, 22860, 22861, 22862, 22888, 22896, 22898, 22905 to 22907, 22920 to 22923, 22926 to 22928, for subsequent identification following the keys of Griffiths and Gardner (2008), and the features described by Mantilla-Meluk and Baker (2006).

Collection of Reference Plant Material. The flowers collected were white or greenish with exerted stamens; corolla tubular or tubulose and perianth radially symmetrical or actinomorphic; nocturnal anthesis; rancid and moldy odor; nectar rich in hexoses and may contain sulfuric compounds for attraction following the description of the syndrome of chiropterophyly (Howe and Westley 1988; Von Helversen *et al.* 2000). Three vegetation transects located in different parts of the reserve were walked and flowering plants were identified by comparison with voucher specimens, taking into account those flowers that displayed the morphological traits mentioned above. Two transects were located in the area under active restoration and one at the upper border of the RFBY. In each transect, measuring 100 m long by 20 m wide, the flowering plant species were identified, and the flowering specimens were counted. In addition, trails and the border of the study area were walked to supplement the plant survey.

Palynological Analysis. To facilitate the identification of contact pollen collected from bat pelage, a reference collection was elaborated from flower samples including stamens and whole flowers seeking to have ripe pollen samples; these were preserved in 10 % glacial acetic acid. For purposes of comparison and identification, these pollen samples were processed through acetolysis unlike the samples obtained from contact pollen according to the methodology established by Erdtman (1969), then mounted in slides and sealed with paraffin.

Palynomorphs in contact pollen samples were identified assisted with the reference pollen collection and the palynological atlas of Roubik and Moreno (1991), and the number of pollen grains per sample was determined. Each palynomorph was described including pollen unit, size, polarity, openings, scope, shape and sculpture to facilitate its identification (Punt *et al.* 2007).

Data Analysis. We calculated the sampling effort (hour-meter network), and capture success (number of captures per sampling unit) for each field trip, considering the total number of bats captured. For each bat species, the total number of grains in each sample was recorded, as well as the total number of individuals captured and the total number of palynomorphs found. Levin's stardardized niche breadth (B_A) was used to set any preference in the use of the resources available for each bat species; this measure ranges from 0 to 1 depending on the predilection for resources (Krebs 1999).

We calculated the relative frequency of resources (Fi = ni/n * 100), where: ni = number of samples (slides) containing species i; *n* = total number of pollen slides analyzed. In addition, the Resource Importance Value Index (RIVI) was estimated using the formula by Amaya (1991) that calculates the value of resource use for each species of interest, then individual values are added up to give the importance value.

The degree of coupling and stability of the network was determined by calculating the NODF nesting algorithm (Almeida-Neto *et al.* 2008), whose value ranges from zero to 100, attaining a maximum when the network is completely nested. The species interaction network was constructed with the statistical program R and the RStudio platform, using the Bipartite 2.02 package (Dormann *et al.* 2008); this array uses binary data to facilitate comparisons.

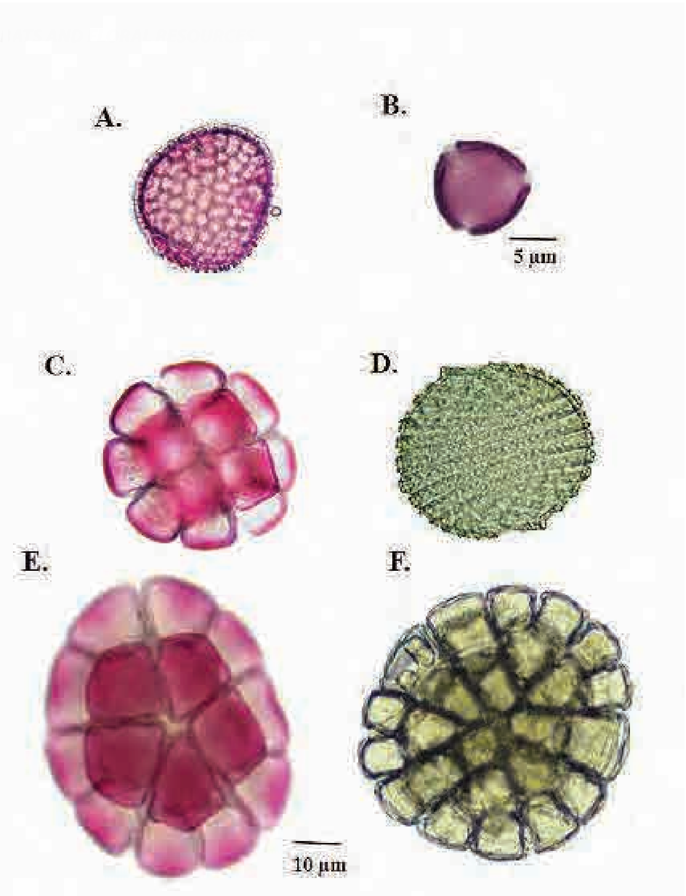

Figure 2. Palynomorphs found in contact pollen samples. **A.** *Ochroma pyramidale*. **B.** Clusiaceae. **C.** *Inga* cf. *marginata*. **D.** Acanthaceae. **E.** *Inga* cf. *punctata*. **F.** *Inga* cf. *densiflora*.

Table 1. Bat species and number of individuals of each species captured in the protected area Reserva Forestal Bosque de Yotoco (RFBY).

Family	Subfamily	Species	Individuals captured
Phyllostomidae	Carolliinae	*Carollia brevicauda**	35
		Carollia castanea	1
		Carollia perspicillata	67
	Desmodontinae	*Desmodus rotundus*	27
	Glossophaginae	*Anoura caudifer**	10
		*Choeroniscus godmani**	2
		*Glossophaga soricina**	33
	Micronycterinae	*Micronycteris hirsuta*	1
	Phyllostominae	*Phyllostomus discolor*	1
	Stenodermatinae	*Artibeus jamaicensis*	7
		*Artibeus lituratus**	11
		Chiroderma salvini	1
		Dermanura phaeotis	18
		Mesophylla macconnelli	4
		Platyrrhinus albericoi	2
		Sturnira bakeri	1
		*Sturnira ludovici**	3
		Sturnira luisi	3
Vespertilionidae		*Eptesicus chiriquinus*	3
		Eptesicus cf. *andinus*	3
		Myotis riparius	5
Total		21	238

* Bat species from which contact pollen samples were collected.

Results

A total of 238 individuals were captured, belonging to 21 bat species (Table 1); of these, 45 individuals (18.9 %) corresponded to nectarivorous species. Ten captured specimens were identified as *Anoura caudifer*, 33 as *Glossophaga soricina* and two as *Choeroniscus godmani*; the latter species represents a new record for the RFBY. A total sampling effort was 5,124-hour-net meter for the first trip, with a capture success of 0.34, and 3,589.5 hours-net meter for the second, with a capture success of 0.26. For nectarivorous species the capture success was 0.035 for the first trip and 0.091 for the second. Contact pollen was found in only 44 individuals (18.5 % of the total capture), with 38 samples (86.4 %) obtained from nectarivorous bat species. The largest number of pollen samples was collected from *G. soricina,* with 28 samples in total, and only a single sample from *S. ludovici* (Table 2). About resource use, the values of Levin's stardardized niche breadth (B_A) ranged from 0.20 for *S. ludovici* to 0.77 for *A. caudifer.*

From 7,971 pollen grains in the samples (Table 2), a total of six palynomorphs were identified in contact pollen (Figure 3), namely *Inga* cf. *densiflora, Inga* cf. *punctata, Inga* cf. *marginata, Ochroma pyramidale*, a single Clusiaceae and a single Acanthaceae. The majority of palynomorphs measure between 80 and 120 µm in diameter; only the pollen of the Clusiaceae was small (10 µm). Except for the pollen of *Inga,* all other grains showed a sculpture with some type of reticle in the exine. The relative resource frequency (Fi) yielded the highest value for the species *I.* cf. *densiflora* (Fi = 0.0069), and the lowest for the Clusiaceae (Fi = 0.0002); these results are consistent with the highest (0.0119) and lowest (0.0003) Resource Importance Value Index (RIVI) for these same species (Table 3). For the Acanthaceae and *O. pyramidale*, although both were resources used by most bat species, their relative frequencies and RIVI are the lowest (Fi = 0.0022; RIVI = 0.0047 and Fi = 0.0020; RIVI = 0.0044, respectively) due to the few samples with pollen from these palynomorphs. The pollen from Clusiaceae was only found in one sample from *A. caudifer*; nonetheless, due to the abundance of grains in the sample (> 100), it is considered as an important resource for the species (Table 3).

In the dry season, two blooming species, *Psychotria brachiata* and *Piper setosum*, and three fruiting species, *Piper augustum, Miconia acuminifera* and *Nectandra macrophylla,* were identified along the vegetation transects. In the rainy season, there was an increase in the number of flowering

Table 2. Bat species that used floral resources (nectar and pollen), with the respective number of total grains (G), number of samples with pollen (N), amount of resources used (R), and Levin's standardized niche breadth (B_A).

Species	G	N	R	B_A
Artibeus lituratus	7	2	3	0.40
Carollia brevicauda	3	3	3	0.40
Sturnira ludovici	5	1	2	0.20
Choeroniscus godmani	7	2	2	0.33
Glossophaga soricina	5,258	28	5	0.54
Anoura caudifer	2,691	8	6	0.77

plants to four species, *Anthurium* sp., *Psychotria brachiata, Cyclanthus* sp. and *Philodendron montanum*; fruiting plants of *Beilschmiedia costaricensis* were also observed. The reference collection included 17 plant species that were found in the transects and surveys in the RFBY. Of this collection, two species match palynomorphs found in contact pollen, *I.* cf. *densiflora* and *I.* cf. *punctata*.

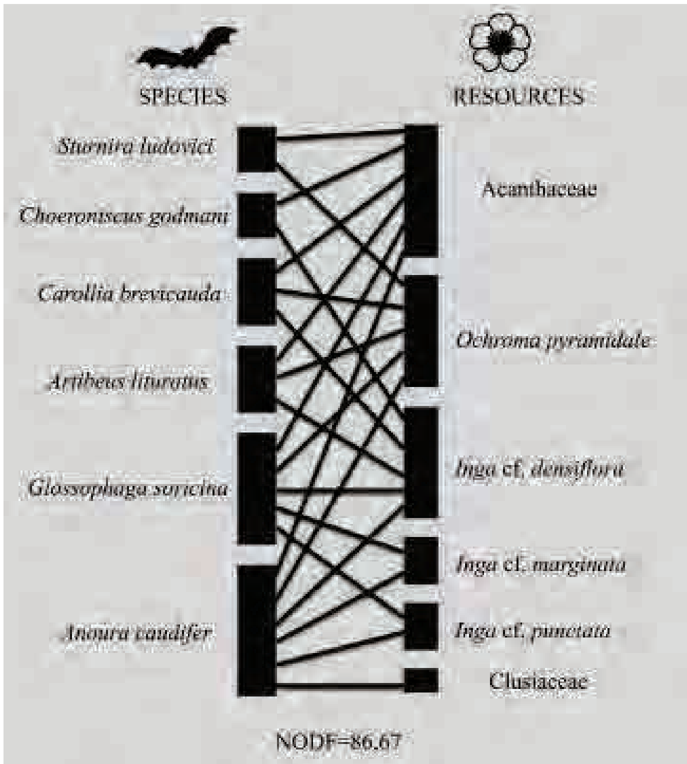

Figure 3. Interaction network between bats and floral resources (nectar and pollen) used in the protected area "Reserva Forestal Bosque de Yotoco (RFBY)", Valle del Cauca, Colombia. The nesting value according to the NODF algorithm is shown.

In the interaction network (Figure 3), the resources with more connections are the most important ones for the community in the season studied correspond to Acanthaceae, *O. pyramidale* and *Inga* species, mainly *I.* cf. *densiflora*, which was used by five bat species. As for bats, *A. caudifer* is the species using the greatest variety of resources, followed by *G. soricina*. *C. godmani* only used two resources, but this finding is inconclusive as it is based on only two samples. The remaining bat species used two or three resources that can be considered as sporadic records (< 10 grains; Table 2). The degree of nesting given by the NODF algorithm is 86.67, reflecting the coupling between the most generalist species in the network and the species that have few connections.

Table 3. Floral resources identified from contact pollen, with the respective number of grains (G), total number of samples with presence of the palynomorph (NM), number of bat species that used the resource (EM), Relative Frequency (Fi), and Resource Importance Value Index (RIVI).

Resource	G	NM	EM	Fi	IVIR
Inga cf. *densiflora*	3,864	34	5	0.0069	0.0119
Inga cf. *punctata*	274	25	2	0.0051	0.0081
Inga cf. *marginata*	510	23	2	0.0047	0.0074
Acanthaceae	85	10	6	0.0022	0.0047
Ochroma pyramidale	2,005	11	5	0.0020	0.0044
Clusiaceae	1,235	1	1	0.0002	0.0003

Discussion

The results described above provide an overview on the interactions between bats and floral resources observed in the RFBY. The degree of nesting in the network (NODF = 86.67) indicates that the nectarivorous species registered, particularly *A. caudifer* as a generalist species, contribute to the stability of interactions, a fact that may have ecological implications as to the pollination of the plants visited (Almeida-Neto *et al.* 2008; González *et al.* 2010). A review of studies conducted on bats in the same area (2011 Moreno-Mosquera; Velasquez-Carrillo 2015) and the catalog of vascular plants of the RFBY (Escobar 2001) identified 22 bat species that include nectar and pollen in the diet, and 25 plant species reported as visited by bats (Fleming *et al.* 2009; Geiselman and Defex 2015). Only three of these bat species are nectarivorous, *Anoura caudifer*, *Anoura latidens* and *Glossophaga soricina*: the rest are either frugivorous or omnivores that occasionally or rarely feed on pollen and nectar; in the case of plants, six genera, *Cordia, Guzmania, Vriesea, Centropogon, Capparis,* and *Inga,* are widely used by bats. In accordance with the above information, further sampling is needed to broaden our information about a larger number of bat species and their resources, in order to identify potential key species in the network, which interact with most species and connect different modules (Bascompte *et al.* 2003; Mello *et al.* 2015).

Although a smaller amount of pollen samples was obtained from *A. caudifer* relative to *G. soricina*, the former was the species using the largest number of resources (six) in the community, being the most generalist bat species in the network. This contrasts with the findings in other studies, where the genus *Glossophaga* has been reported as the dominant species in terms of resource use. In La Tatacoa desert, the bat species that maintains the closest relationship with the available resources, especially with columnar cacti, is *G. longirostris* (Ruiz *et al.* 1997). In Cartagena, Bolivar, *G. soricina* uses five resources in a suburban area (Lemke 1985), and in Serrania de La Macarena the only nectarivorous species reported that consumes nectar and pollen is *G. soricina,* which uses six available resources (Muñoz-Saba *et al.* 1997). The main diet of *A. lituratus*, *S. ludovici* and *C. brevicauda* is based on the consumption of fruits, and in montane forests these species are among the most abundant for this trophic guild (Estrada-Villegas *et al.* 2010; Moreno-Mosquera 2011). Therefore, it is considered that the use of nectar and pollen is occasional, consistent with the small amount of pollen grains found in samples. In the interaction network there is still uncertainty about the resources used by *A. latidens* in the study area, since this bat species was not captured in this study.

In the interaction network, the species of the genus *Inga* was an important resource for the bat community during the two seasons studied. In temperate climates with sufficient moisture, blooming plants of this genus occur throughout the year. Although these species have been reported to be pollinated by insects, especially lepidopterans (Koptur 1983), they are an essential resource for nectarivorous bats in the RFBY for their continued availability, as shown in other studies, particularly in humid tropical forests (Fleming and Muchhala 2008). Likewise, *O. pyramidale* is a generalist species used as a food resource for many species of animals, particularly mammals (Mora *et al.* 1999). The only individual observed in the study area is continuously used by primates and marsupials, although this plant is pollinated by nocturnal insects and mammals. It blooms from September to January in humid tropical forests (Rojas-Rodríguez and Torres-Cordoba 2009), representing a seasonal resource; however, its phenology in Andean ecosystems remains unknown. Although the family Acanthaceae is the resource used by the largest number of species in the study area, its phenological and reproductive characteristics could not be determined in this study because the palynomorph is impossible to identify at the species level.

The abundance of pollen grains with reticulated sculpture is related to their adaptation to be transported by certain groups of animals (Amaya 1991; Stroo 2000). Pollen grains with a reticulated sculpture easily adhere to bat or bird pollinators, and in the case of plants of the genus *Inga*, there is a large production of pollen, hence increasing the probability of an effective pollination, as bats tend to carry a larger amount of pollen that birds (Muchhala and Thomson 2010).

The sampling conducted showed that RFBY has a high diversity of nectarivorous species relative to other localities across the Andean region of Colombia despite this being a fragmented area due to anthropogenic activities (Cantillo and Gómez 2004; Rodríguez *et al.* 2006). To date, four species have been registered in the RFBY, *Anoura caudifer, A. latidens, Glossophaga soricina* and the new record of *C. godmani* found in the present study (Moreno-Mosquera 2011; Velasquez-Carrillo 2015). Chavez-Landazury (2012), in La Mariposa reserve, located in Valle del Cauca, reports only *A. caudifer* in a premontane forest under a restoration process similar to the study area, at an altitude of 1,439 masl. Similarly, in a study on the diversity of bats along an altitudinal transect in the Tolima department, *A. caudifer* is reported as the only nectarívorous species in a strip between 1,000 and 2,000 masl (Bejarano *et al.* 2007). At altitudes above 2,000 masl in the Cordillera Central and the Cordillera Oriental of Colombia, only one species of the genus *Anoura* has been recorded (Rodríguez-Posada 2010; Perez-Torres and Ahumada 2004). These results are consistent with the predominance of the genus *Anoura* in intermediate and high altitudes in the Andean region, due to its diversification by niche specialization, which is related to the morphological adaptations of the species and the complexity of the community structure (Owen 1990; Patterson *et al.* 1996; Fleming and Muchhala 2008).

The increased success in the capture of nectarivorous species from the dry to the rainy season suggests that the species move following resource dynamics and availability; this has been observed mainly in dry tropical forests and arid ecosystems where bats are mobilized according to the availability of temporary resources (Fleming 1982; Cornejo *et al.* 2011). This phenomenon has been demonstrated in other species of nectarivorous bats in seasonal habitats such as dry areas (Ruiz *et al.* 1997; Moreno-Valdez *et al.* 2000). However, there is no clear evidence to date suggesting that the species found in this study and other nectarivorous species of Andean ecosystems do migrate (Rodríguez *et al.* 2012), although in humid tropical forests it is estimated that *A. caudifer* can travel up to 50 km in a single night in search of food (Von Helversen and Reyer 1984).

Conclusions

The RFBY is highly important for nectarivorous bat species, as it provides shelter and food in a fragmented landscape. It is a key area for the settlement of nectarivorous species, particularly *A. caudifer* and *G. soricina*, thus representing a suitable habitat for these species to be established and meet their food requirements.

The network constructed illustrated the interaction between six species of nectarivorous and frugivorous bats with six food resources identified. The species of the genus *Inga* and *O. pyramidale* were the resources most commonly used by the bat community over the season studied. Although *A. caudifer* visited all the plants recorded, it displayed selectivity or preference for some of them, such as *I.* cf. *marginata*, *I.* cf. *punctata* and the Acanthaceae during the study period.

To continue with the active restoration processes in the area, it is recommended to plant species of the genus *Inga* to promote the establishment of a larger number of nectarivorous bats, as these plants would represent a resource available throughout the year; in addition, their fruits are consumed by other mammals and birds. The same is also true for *O. pyramidale*, which represents an important food source for the local fauna despite its low abundance.

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New records and estimation of the potential distribution of the Stump-Tailed Porcupine *Coendou rufescens*

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The stump-tailed porcupine (*Coendou rufescens*) is a medium-sized species that inhabits subtropical, temperate and High-Andean forests of the northern Andes, at 800 to 3,650 m asl. This species is characterized by a short non-prehensile tail and a distinctive reddish color. Here, we report new localities for *Coendou rufescens* in Ecuador based on direct field sightings and the revision of mammal collections. In addition, we conducted a review of literature records of *C. rufescens* throughout its distribution range. A total of 52 georeferenced records were modeled for the potential distribution at the regional level (Colombia, Ecuador, and Peru) based on 19 bioclimatic variables. Finally, we overlaid the layers of vegetation remnants and state protected areas. We report 10 new localities for *Coendou rufescens* in Ecuador; these records are concentrated to southern Ecuador between 1,120 to 4,387 masl. Fifty two records found that the bioclimatic variables Temperature Seasonality (BIO4) and Minimum Temperature of the Coldest Month (BIO6) associated with the type of habitat made the greatest significant contribution to the distribution model of *C. rufescens*. The suitable habitat for the species spans across ~ 448,820 km^2, with 50.4 % in Colombia. These findings indicate that the locality Camino del Inca in Sangay National Park, at 4,387 m asl, is considered the highest-elevation record for *C. rufescens* and the family Erethizontidae. Colombia and Peru include the highest proportion of potential habitat across its range (40.2 % and 32.7 %) based on remnant vegetation; however, Ecuador maintains the largest proportion of the porcupine distribution within protected areas (35.5%), with a larger extent of landscape connectivity, essential for the conservation of *C. rufescens*.

El puerco espín de cola corta (*Coendou rufescens*) es una especie de tamaño mediano que habita los bosques Subtropicales, Templados y Alto-Andinos de los Andes norte, entre los 800 a 3,650 m de elevación. Esta especie se caracteriza principalmente por presentar una cola corta y no prensil, además de su peculiar coloración rojiza. Se reportan nuevas localidades para *Coendou rufescens* sobre la base de avistamientos directos en campo y revisión de colecciones mastozoológicas. Adicionalmente se realizó una revisión de los registros bibliográficos de *C. rufescens* a lo largo de su distribución geográfica. Con un total de 52 registros recopilados y georefenciados, se modeló la distribución potencial a escala regional (Colombia, Ecuador y Perú) utilizando 19 variables bioclimáticas seleccionadas por su nivel de correlación. Finalmente, se superpusieron las capas de vegetación remanente y áreas protegidas estatales. Se adicionan 10 localidades para *Coendou rufescens* en Ecuador, los registros se concentran en el sur del país en un rango altitudinal entre 1,120 a 4,387 m. Con base a los 52 registros se determinó que las variables bioclimáticas que contribuyen más significativamente al modelo de distribución predictiva son BIO4: Temperatura estacional y BIO6: Temperatura mínima del mes más frío, las cuales están asociadas al tipo de hábitat. Se determinó que el hábitat idóneo para la especie es de ~448,820 km^2, donde el 50.4 % de la distribución potencial se concentra en Colombia. La localidad del Camino del Inca en el Parque Nacional Sangay, ubicado a 4,387 m es el registro de mayor elevación para *C. rufescens* y la familia Erethizontidae. Colombia y Perú contienen la proporción más alta de hábitat adecuado para la especie (40.2 y 32.7 %) con base en la vegetación remanente; no obstante, Ecuador mantiene la mayor proporción de la distribución dentro de áreas protegidas (35.5 %), por ende, presentaría mayor conectividad de paisaje, lo cual es esencial para la conservación de *C. rufescens*.

Key words: altitudinal range; distribution model; mammals; protected area; vegetation remnants

Introduction

The genus *Coendou* Lacépède, 1799 (Rodentia: Erethizontidae), distributed only in America, groups together 13 species that live in tropical, subtropical and temperate areas in wet and dry forests, from sea level up to 3,650 masl (Voss *et al.* 2013; Voss 2015; Brito and Ojala-Barbour 2016). The stump-tailed porcupine *Coendou rufescens* Gray, 1865 is distributed in the Andes of Colombia, Ecuador and northwestern Peru (Alberico *et al.* 1999; Voss 2011, 2015; Tirira 2016; Brito and Ojala-Barbour 2016; More and Crespo 2016; Romero *et al.* 2018). An unusual record from northern Bolivia has been recently reported, representing a biogeographical enigma that suggests that some individuals of this species moved to this area (Voss 2011).

Coendou rufescens is characterized mainly by a short non-prehensile tail, unlike other long-tailed porcupines, in addition to its distinctive reddish coloration (Voss 2015). Although the ecological information available for *C. rufescens* is rather limited, it is considered as a species that inhabits only mature and well-preserved forests (Tirira 2017). Some point observations in the Sangay National Park in Ecuador have served to characterize the species as either solitary or gregarious (1 to 4 individuals), diurnal and nocturnal (Brito and Ojala-Barbour 2016). Incidental records have documented that the stump-tailed porcupine is preyed upon by pumas (Tirira 2016) and ocelots (Sanchez *et al.* 2008).

A predictive distribution model can be used to locate suitable or potential habitats outside of the known range of a given species (*e. g.,* Morueta-Holme *et al.* 2010; Chatterjee *et al.* 2012; Ortega-Andrade *et al.* 2015). Some potential-distribution correlation models (Braunisch *et al.* 2008; Peterson *et al.* 2011) use information on the current distribution of the species and assume that the habitat where records are located represents the ideal habitat for the species. However, the distribution of many vertebrates (especially those threatened) has shrunk, and thus these species could be considered as refugee species, that is to say, limited to survive in suboptimal habitats due to anthropogenic pressures (Kerley *et al.* 2012).

One of the methods frequently used for modeling the potential distribution is maximum entropy modeling (*e. g.,* Phillips *et al.* 2006; Phillips and Dudik 2008; Elith *et al.* 2011; Renner *et al.* 2013; Nuchel *et al.* 2018), which has proved to be useful for establishing high-diversity, high-endemism and conservation areas for vertebrates in Neotropical regions (Cuesta *et al.* 2017; Reyes-Puig *et al.* 2017). This method is often better than traditional statistical approaches and other species-distribution modeling methods (Elith *et al.* 2006; Phillips *et al.* 2006). However, several authors suggest using a consensus of models to reduce the uncertainty of predictions derived from individual models (*e. g.,* Marmion *et al.* 2009; Qiao *et al.* 2015; Zhu and Peterson 2017).

This work reports 10 new localities for *Coendou rufescens* in Ecuador. A potential distribution model was developed for Colombia, Ecuador and Peru using the new localities, those available in the literature, and those associated to museum vouchers. In addition, the geographical layers of remnant vegetation in the three countries were overlaid and the proportion of each within the potential distribution range was calculated. The information on the extension of the distribution range may be valuable for further taxonomic, phylogenetic and ecological studies, while contributing relevant data for the protection of this poorly known species.

Materials and Methods

Records of living and road killed individuals were obtained through direct field observations during various faunal surveys conducted as part of environmental studies for mining and power companies between years 2007 and 2017. In addition, two specimens of *C. rufescens* (MEPN 3260 and 10433) deposited in the mammal collection of the Escuela Politécnica Nacional (MEPN), Quito-Ecuador, were also examined. Each encounter was georeferenced and photographed, recording the behavior of each living specimen. In addition, informal interviews were carried out to residents living in the study area to determine the extent of the local knowledge about the species.

*Potential Distribution Model***.** In order to estimate the potential distribution of *C. rufescens,* records were obtained from the published literature (Gray, 1865; Williams 2008; Ramírez-Chávez *et al.* 2008; Tirira and Boada 2009; Fernández de Cordoba-Torres and Nivelo 2016; More and Crespo 2016; Brito and Ojala-Barbour 2016; Romero *et al.* 2018), along with the new records from this study (Appendix 1). Presence coordinates were transformed to the decimal degree coordinate system, Datum WGS84 and Universal Transverse Mercator projection (UTM), zones 17S and 18S. Duplicate coordinates and those that were less than 2 km away from each other were discarded, thus avoiding oversampling presence records while preserving the independence between localities and bioclimatic variables.

The potential-distribution exploratory model was developed based on the 19 bioclimatic variables of WorldClim 19 1.4 (http://www.worldclim.org; Table 1), which are geo-environmental layers derived from monthly temperature and precipitation data with a resolution of ca. 1 km^2 (Hijmans *et al.* 2005). The model was developed with the software MaxEnt v3.3.3 (Phillips *et al.* 2006) based on the maximum entropy principle and the convergence of environmental variables covering an area of suitable habi-

Table 1. Contribution of 19 bioclimatic variables to the predictive model of *Coendou rufescens.*

Code	Contribution	Variable
BIO4	28.15	Seasonal temperature
BIO6	16.89	Minimum temperature of the coldest month
BIO18	15.04	Precipitation of the warmest annual quarter
BIO8	10.94	Mean temperature of the wettest annual quarter
BIO19	4.72	Precipitation of the coldest annual quarter
BIO11	4.64	Mean temperature of the coldest annual quarter
BIO3	3.45	Isothermality
BIO10	3.22	Mean temperature of the warmest annual quarter
BIO1	2.49	Mean annual temperature
BIO14	2.38	Precipitation of the driest month
BIO13	1.89	Precipitation of the wettest month
BIO7	1.64	Annual temperature range (BIO5-BIO6)
BIO16	1.32	Precipitation of the wettest annual quarter
BIO17	1.25	Precipitation of the drieest annual quarter
BIO15	0.52	Seasonal precipitation
BIO12	0.45	Annual precipitation
BIO2	0.45	Diurnal mean range (monthly average (max temp-min temp)
BIO5	0.29	Maximum temperature of the warmest month
BIO9	0.18	Mean temperature of the driest annual quarter

tat (Elith *et al.* 2006; Phillips *et al.* 2006; Ortega-Andrade *et al.* 2015). The maximum entropy model uses a confusion matrix that combines the predicted presence/absence with pseudo-absence and true-presence data, producing commission and omission rates. In addition, the probability distributions estimated by the software should be consistent with the known environmental conditions of the species (Peterson *et al.* 2011).

A total of 52 validated presence records and the 19 bioclimatic variables were entered in MaxEnt. Fifty replicates were run with a Jackknife test to measure the percent contribution of the variables to the model (Phillips *et al.* 2006; Lizcaino *et al.* 2015; Ortega-Andrade *et al.* 2015). A correlation matrix was elaborated with the key variables; highly correlated variables were eliminated by means of a correlation chart ($r > 0.8$). To build the model, we established a convergence threshold of 0.00001, a maximum of 1000 interactions, and a regularization parameter of 1. The model was tested and calibrated with 50 additional replicates using non-correlated climatic variables; data were split into 25 % as test and 75 % as training data (Menendez-Guerrero and Graham 2013). The "Equal training sensitivity and specificity" cohort threshold was selected, as it reflects a lower omission rate (Liu *et al.* 2005).

The predictive capacity of the model was evaluated by ROC (Receiver Operating Characteristic) curves and AUC (Area under the Curve) curves (Hanley and Mc Neil 1982; Lobo *et al.* 2008). In addition, we used the partial area under the ROC curve test (Lobo *et al.* 2008), thereby avoiding the improper calculation of the weight in AUC commission and omission rates (Lobo *et al.* 2008; Peterson *et al.* 2008). Partial AUCs were calculated using the ToolBox developed by Osorio-Olvera (2018). The statistical significance of AUC was tested by bootstrapping and comparisons vs. null hypotheses (*i. e.*, Ho = difference between model-predicted AUC and random AUC is ≤ 0). We used 50 % of presence data at random for the resampling, with 500 iterations. Significance was evaluated using the calculated AUC values and the values of pseudo-replicates following the proposal of Peterson *et al.* (2008). All distribution, normality and correlation statistical analyzes of variables were run in the statistical program R (R Core Team 2016). Once the model was calibrated, a final model was constructed with 100 % of the presence data and non-correlated bioclimatic variables in order to obtain the distribution predictive model.

The total potential distribution area was calculated for Colombia, Ecuador and Peru (Datum WGS84 and Universal Transverse Mercator (UTM) projection, zones 17S and 18S). In addition, the layers of remnant vegetation (*i. e.*, plant cover of natural ecosystems) and protected areas for the three countries were overlaid to assess the reduction in the distribution of *C. rufescens* in non-protected areas with no vegetation cover. Maps and calculations of geographic layers were elaborated in ArcMap 10.5.1 (ESRI 2017). The layers of remnant vegetation for Ecuador were obtained from the Sistema Nacional de Información (National Information System) website (SIN 2017); for Colombia, from the Sistema de Información Ambiental de Colombia (Environmental Information System, SIAC 2017); and for Peru, from the Ministry of the Environment´s official website (MINAM 2017).

Results

New localities. In addition to the Ecuadorian localities previously reported in the literature (Appendix 1), the following are the new localities where the species has been spotted.

1) Road in the vicinity of the Chaguarpamba, province of Loja: The record corresponds to a road killed individual (Figure 1a) photographed on 28 June 2007. The area is a secondary forest (Figure 2a) in a piedmont deciduous forest ecosystem, foothills of the Western Cordillera, southern subregion (Cerón *et al.* 1999), subtropical western zoogeographical area (Albuja *et al.* 2012).

2) Quilanga, province of Loja: Individual kept as a pet, photographed (Figure 1b) on 23 June 2011. This specimen was captured in a forest with secondary vegetation adjacent to agricultural land (Figure 2b), montane cloud forest ecosystem, southern sector of the Western Cordillera, southern subregion (Valencia *et al.* 1999), Temperate zoogeographical area (Albuja *et al.* 2012).

3) Olmedo, province of Loja: Individual photographed (Figure 1c) on 18 February 2012. The area corresponds to an agricultural area (Figure 2c) located in a piedmont decid-

Figure 1. New records of *Coendou rufescens* in Ecuador: a = Road in the vicinity of Chaguarpamba, b = Quilanga, c = Olmedo, d = vicinity of the Villonaco Wind Project, e = Barrio Zamora Huayco, f = Vicinity of Gonzanama, G = Camino del Inca, and h = 5 km of Saraguro. a-f and h = province of Loja; h = province of Chimborazo.

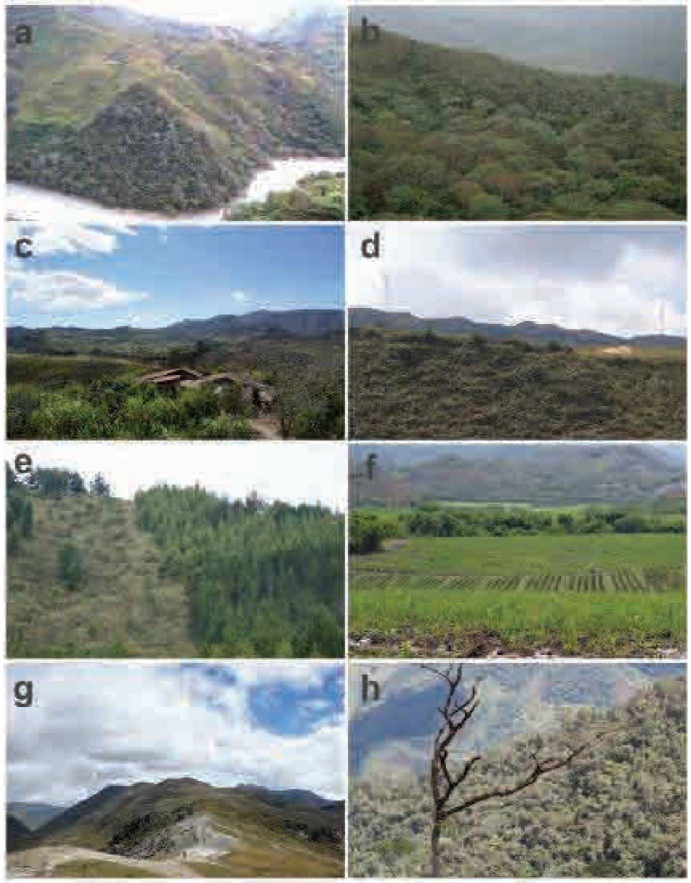

Figure 2. Localities of new records of *Coendou rufescens* in Ecuador*:* a = Road in the vicinity of Chaguarpamba, b = Quilanga, c = Olmedo, d = Vicinity of the Villonaco Wind Project, e = Barrio Zamora Huayco, f = Vicinity of Gonzanama, g = Camino del Inca, and h = 5 km of Saraguro. a-f and h = province of Loja; h = province of Chimborazo.

uous forest ecosystem, foothills of the Western Cordillera, southern subregion (Cerón *et al.* 1999), subtropical western zoogeographical area (Albuja *et al.* 2012).

4) Vicinity of the Villonaco Wind Project (Figure 1d), Sucre, province of Loja: Individual photographed on 17 March 2012. The site of the finding corresponds to a rural zone with secondary vegetation and agricultural fields (Figure 2d) pertaining to a mountain cloud forest, southern sector of the Western Cordillera, southern subregion (Valencia *et al.* 1999), western Andean high zoogeographical area (Albuja *et al.* 2012).

5) Zamora Huayco neighborhood in El Sagrario, province of Loja: The record corresponds to an individual (Figure 1e) photographed on 7 September 2012. This was observed in a planted conifer forest (*Pinus sylvestris*) adjacent to the boundary of the Podocarpus National Park (Figure 2e), montane cloud forest ecosystem, southern sector of the Western Cordillera, southern subregion (Valencia *et al.* 1999), Temperate zoogeographical area (Albuja *et al.* 2012).

6) Vicinity of the Gonzanamá, province of Loja: Road-killed individual photographed on 28 September 2012 (Figure 1f). The area corresponds to an agricultural zone with small remnant patches of native vegetation (Figure 2f) pertaining to a mountain cloud forest, southern sector of the Western Cordillera, southern subregion (Valencia *et al.* 1999), Temperate zoogeographical area (Albuja *et al.* 2012).

7) Inner zone of the Sangay National Park, province of Morona Santiago: Individual (Figure 1g) photographed on 12 June 2015 in a high Andean moorland in the Camino del Inca sector (Figure 2g). Andean High zoogeographical area (Albuja *et al.* 2012).

8) 5 km from Saraguro, province of Loja: Specimen (Figure 1h) photographed on 17 June 2017 in the Huashapamba forest, in an area between shrub vegetation and a pasture located in the western part crossed by the Pan-American Highway. The area is located inside a protected natural forest (Figure 2h) pertaining to a mountain cloud forest, southern sector of the Western Cordillera, southern subregion (Valencia *et al.* 1999), Andean High zoogeographical area (Albuja *et al.* 2012).

9) El Tuni, province of Azuay: MEPN 10433.

10) San Francisco Scientific Station, province of Zamora Chinchipe: MEPN 3260.

The individuals observed and photographed displayed morphological traits consistent with the description for the species (Voss 2015), namely short, blackish, non-prehensile tail measuring about 40% of the head-body length. Chin, throat and abdomen of pale brown color.

Potential Distribution. An AUC of 0.969 (min = 0.945, max = 0.98, σ = 0.007, n = 50) and a AUC ratio of 1.89 ± 0.04 ($P < 0.05$) were obtained. Fourteen variables with a significant contribution to the model were identified (Table 1); however, variables BIO1, BIO3, BIO7, BIO8, BIO10, BIO11, BIO13, BIO16 and BIO17 were eliminated for being highly correlated (Figure 3). Five non-correlated bioclimatic variables made a significant contribution to the model; seasonal temperature (BIO4) and minimum temperature of the coldest month (BIO6) accounted for 82.7 %, whereas precipitation of the fourth warmer quarter (BIO18), precipitation of

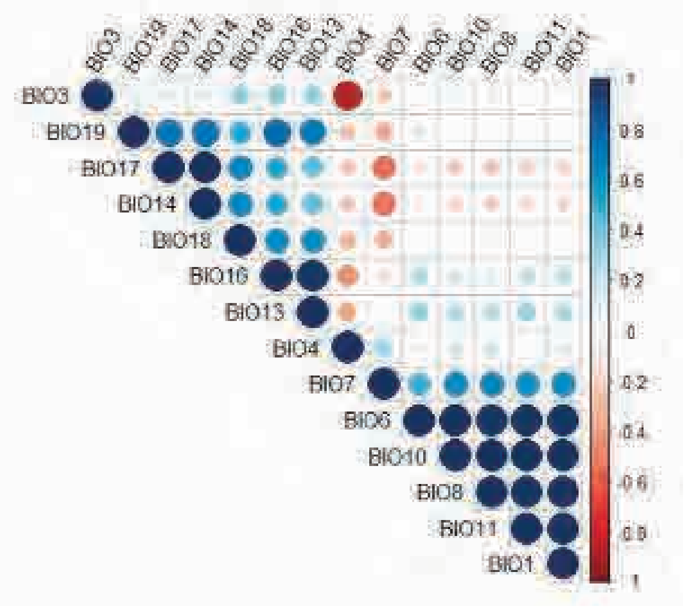

Figure 3. Correlation chart of the bioclimatic variables that make a significant contribution to the predictive model of the distribution of *Coendou rufescens.*

the fourth annual quarter (BIO19), and precipitation of the driest month (BIO14) contributed 17.3 %.

The area of suitable habitat predicted by the model for *C. rufescens* was ~448.820 km², which in Colombia spans from the north end of the Eastern Cordillera, crossing the Central and Western Cordillera and Nudo de los Pastos; in Ecuador, this species is distributed in the Andean foothills and moorlands throughout the territory. In Peru, it stretches across the northern and central Andes in Western, Central and Eastern Cordilleras (Figure 4). Colombia has 50.4 % of the suitable distribution of the species, while Peru and Ecuador show 28.5 % and 21.1 %, respectively (Table 2). The potential distribution of *C. rufescens* in relation to remnant vegetation is reduced in 50.6 % (Table 2, Figure 4), with Peru and Colombia keeping 73 % (40.2 % vs 32.8 %) of remnant vegetation within the potential distribution range of the species (Figure 5). The potential distribution coinciding with the borders of protected areas in the three countries is 14 %, with Ecuador and Colombia keeping 10 % (Table 2, Figure 5).

Table 2. Percentage of potential distribution and remnant vegetation of the predictive model for *Coendou rufescens.*

Country	Potential Distribution km² (%)	Remnant vegetation km² (%)	Potential distribution within protected areas (%)
Colombia	226,146 (50.4)	72,675 (32.7)	21,931 (34.9)
Peru	128,104 (28.5)	89,252 (40.2)	18,522 (29.5)
Ecuador	94,570 (21.1)	59,665 (26.9)	22,279 (35.5)
Total	448,820 (100)	221,592 (100)	62,732 (100)

Discussion

In Ecuador, the distribution range of *C. rufescens* was known by few and scattered records along the Eastern Cordillera, with a single record from the Western Cordillera (Orcés and Albuja 2004; Voss 2015; Vallejo and Boada 2017; Romero *et al.* 2018). The localities reported in this study broaden the distribution range of the species to the south and southwest areas of the Eastern and Western Cordillera across an altitudinal range of 1.120-4.387 m. The Camino del Inca locality in the Sangay National Park at 4,387 masl is the highest-elevation record for the species (Appendix 1) and for the family Erethizontidae (Voss 2015; Barthelmess 2016). High elevations are characterized by extreme weather conditions, where only the best-adapted species are able to thrive (Monge and León-Velarde 1991); thus, mammals that inhabit ecosystems above 4,300 m asl are currently scarce in Ecuador (< 10 spp.) (Tirira 2017; Brito *et al.* 2018).

Observations by the authors and references provided by local residents indicate that *C. rufescens* inhabiting southwest areas move at ground level and climb easily, being tolerant to anthropic areas such as villages and farming land; a similar behavior has been documented for Peruvian (More

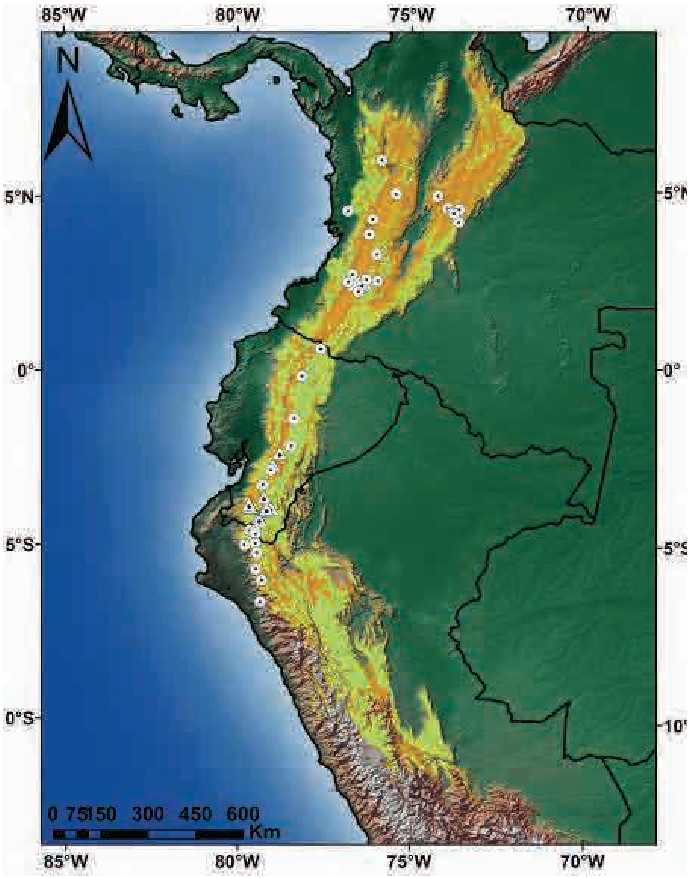

Figure 4. Records and potential distribution of *Coendou rufescens* (orange), potential range of *C. rufescens* in relation to remnant vegetation in Colombia, Ecuador and Peru (light green). Circles represent records from the literature review; triangles, the new locations reported in this study.

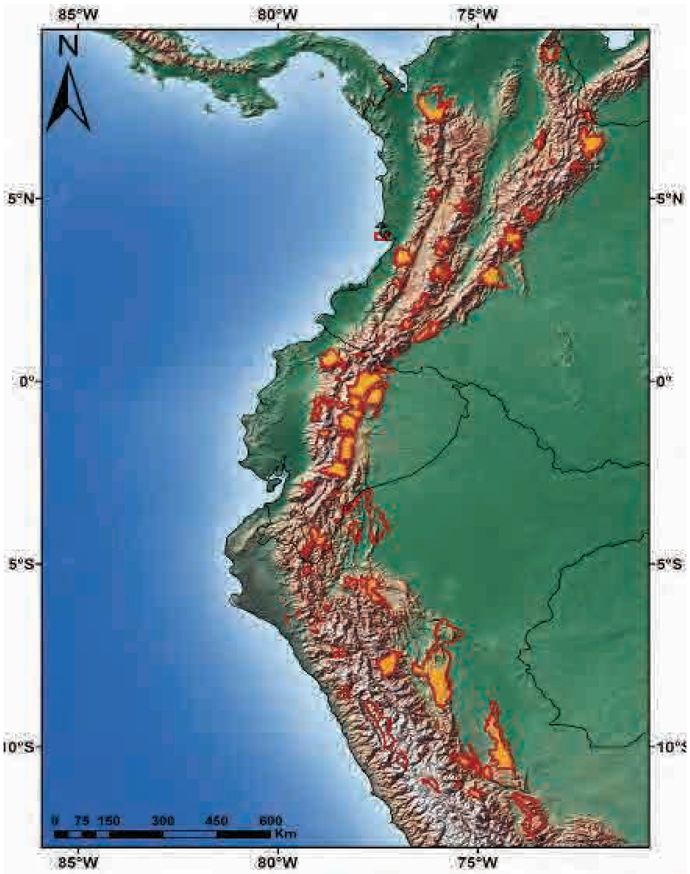

Figure 5. Potential distribution range of *Coendou rufescens* (orange) in relation to protected areas in Colombia, Ecuador and Peru (red boundaries).

and Crespo 2016) and Ecuadorian populations (Brito and Ojala-Barbour 2016). Similar to other related species (Voss 2015), the specimens of *C. rufescens* observed in this study showed a quiet temperament and adopted a still position, hiding the head and ruffling up the spines when perceiving danger. In the province of Loja, local peasants frequently capture specimens of *C. rufescens* resting on tree branches to keep them as pets and/or for consumption as bush meat. Rhodas *et al.* (2007) report this as one of the species most commonly marketed in southern Ecuador.

The distribution of *Coendou rufescens* predicted by the model yielded a high AUC, and the AUC ratio in the analysis of partial ROC curves showed that the predictive capability of the model is significantly better than the one produced by a random model (Hanley and McNeil 1982; Lobo *et al.* 2008; Peterson *et al.* 2008) and may be a similar representation to the distribution range of the species. The results of this study are consistent with the distribution reported elsewhere (Alberico *et al.* 1999; Orcés and Albuja 2004; Voss 2011; Brito and Ojala-Barbour 2016; More and Crespo 2016; Romero *et al.* 2018), although the suitable habitat that may be occupied by the stump-tailed porcupine was maximized; thus, the maximum entropy principle allowed us to model the convergence of environmental variables (Phillips *et al.* 2006) in a total area of ~448.820 km^2. However, our map — predictive model — does not display the actual geographical distribution of the species, as the existence of a suitable habitat is no guarantee that the species indeed inhabits the whole habitat. However, the absence of *C. rufescens* in an area of suitable habitat could be the result of biotic interactions (*e. g.* competition with other species, presence of predators) or the inability of the species to move across geographical barriers (*e. g.* rivers, canyons, mountains, etc.) to colonize that habitat.

It is considered that the two bioclimatic variables that made a significant contribution to the predictive distribution model of *C. rufescens* — seasonal temperature (BIO4) and minimum temperature of the coldest month (BIO6) — are associated to the habitat occupied by the species (Ministerio del Ambiente del Ecuador 2013; Voss 2015; Brito and Ojala-Barbour 2016; More and Crespo 2016). The relationship between the Andean mountain ranges and these variables is displayed in the case study for small vertebrates; Muñoz-Ortiz *et al.* (2015) report that the localities of *Rheobates* (Anura) at the Central Cordillera are related to seasonal temperature (BIO4), whereas the localities at the Eastern Cordillera relate to the minimum temperature of the coldest month (BIO6). *Coendou rufescens* are distributed along the Western, Central and Eastern Cordillera, which explains a > 80 % contribution by the two variables.

In a number of studies, the maximum entropy model (MaxEnt) has yielded a better performance vs. other species-distribution models (Elith *et al.* 2006; Phillips *et al.* 2006; Aguirre-Gutiérrez *et al.* 2013), and some studies support that the ability of the algorithm to model the predictive distribution of the species is superior to that of other algorithms; however, these authors suggest that consensus models may be used in order to reduce the uncertainty in the predictions of individual models (Marmion *et al.* 2009; Qiao *et al.* 2015; Zhu and Peterson 2017). However, irrespective of the model — or a consensus of models — used, caution should be exercised when extrapolating data from the model, as it will depend on the objectives of the research.

Although Colombia is the country with the greatest portion of the potential distribution of the stump-tailed porcupine, when evaluating the proportion related to remnant vegetation, Peru comprises 20 % of the remaining distribution with respect to this variable, being the country with greatest coverage for the species. For its part, Colombia shows highly fragmented habitats in the western, central and eastern foothills (SIAC 2017), similar to Ecuador, which also faces threats related to habitat fragmentation in the Andes (Ministerio del Ambiente del Ecuador 2013; Lozano *et al.* 2006). However, the presence of continuous protected areas in Ecuador — mostly in the eastern slope — may ensure the mid-to-long-term permanence of the species.

Finally, the fact that several of our records correspond to road killed individuals evidences the need to implement measures to reduce the impact of roads on natural populations of this and other wild species, such as the construction of structural crossing tunnels/bridges (at least in the vicinity of National Park), in addition to implementing adequate signaling (Bank *et al.* 2002; Grillo *et al.* 2010).

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Appendix 1.

Localities of records of *Coendou rufescens* throughout its distribution range.

Country/ Department/ Province	Locality	Latitude	Longitude	Altitude	Reference
		Colombia			
Antioquía	Concordia	6.0333	-75.9000	-	Ramírez-Chaves *et al*. (2016)
Caldas	Manizales	5.0666	-75.5166	-	Ramírez-Chaves *et al*. (2016)
Cundinamarca	La Vega	4.9833	-74.3333	-	Ramírez-Chaves *et al*. (2016)
Cundinamarca	La Aguadita	4.6333	-74.0500	-	Ramírez-Chaves *et al*. (2016)
Cundinamarca	Chingaza	4.6000	-73.7333	-	Ramírez-Chaves *et al*. (2016)
Cundinamarca	Choachí	4.5166	-73.9166	-	Ramírez-Chaves *et al*. (2016)
Cundinamarca	Fómeque	4.4833	-73.8833	-	Ramírez-Chaves *et al*. (2016)
Cundinamarca	Quétame, quebrada Susumuco	4.2166	-73.7500	800	Gray (1865)
Meta	Puerto López	4.0833	-72.9500	-	Ramírez-Chaves *et al*. (2016)
Cauca	San Antonio	4.5833	-76.8833	-	Ramírez-Chaves *et al*. (2016)
Cauca	Bolívar	4.3333	-76.1833	-	Ramírez-Chaves *et al*. (2016)
Cauca	Buga	3.9000	-76.2833	-	Ramírez-Chaves *et al*. (2016)
Cauca	Hato Viejo Natural Reserve	3.3166	-76.0666	-	Ramírez-Chaves *et al*. (2016)
Cauca	Munchique	2.7333	-76.7666	-	Ramírez-Chaves *et al*. (2016)
Cauca	Charguayaco	2.4333	-76.8000	-	Ramírez-Chaves *et al*. (2016)
Cauca	Sabanetas	2.5333	-76.8833	-	Ramírez-Chaves *et al*. (2016)
Cauca	Silvia	2.6000	-76.3666	2,040	Ramírez-Chaves *et al*. (2016)
Cauca	Road to Inzá	2.5500	-76.0500	-	Ramírez-Chaves *et al*. (2016)
Cauca	Road to Sotará	2.2500	-76.6000	-	Ramírez-Chaves *et al*. (2016)
Cauca	Vereda Las Guacas	2.5000	-76.5833	1,800	Ramírez-Chaves *et al*. (2016)
Cauca	Vereda Clarete	2.5166	-76.5333	-	Alberico *et al*. (1999)
Cauca	Vereda Aguas Claras, Quebrada La Parada, La Tupía	2.4000	-76.4166	2,590	Ramírez-Chaves *et al*. (2008)
Cauca	Vereda Santa Teresa	2.4166	-76.3833	3,535	Ramírez-Chaves *et al*. (2008)
Cauca	Vereda Santa Bárbara	2.3833	-76.5500	1,900	Ramírez-Chaves *et al*. (2008)
Cauca	Vereda Julumito, Río Saté	2.4500	-76.6500	1,700	Ramírez-Chaves *et al*. (2008)
Cauca	Vereda Pisojé	2.4166	-76.5000	1,800	Ramírez-Chaves *et al*. (2008)
		Ecuador			
Carchi	RB Guandera	-0.6000	-77.6666	3,405-3,405	Tirira and Boada (2009)
Imbabura	Pimampiro	-0.1768	-78.1940	2,900	Romero *et al*. (2018)
Morona Santiago	Sangay National Park	-2.1917	-78.4974	3,650	Brito and Ojala-Barbour (2016)
Morona Santiago	Sangay National Park	-2.3889	-78.3016	2,500	Brito and Ojala-Barbour (2016)
Tungurahua	Baños	-1.3956	-78.4249	1,855	Voss (2015)
Chimborazo	Camino del Inca	-2.3894	-78.8193	4,387	This study
Azuay	Balcón del Azuay	-2.8830	-79.0797	2,800	Fernandez de Cordoba-Torres and Nivelo (2016)
Azuay	El Tuni	-2.7520	-79.0110	3,200	MEPN 10433 Este Estudio
Zamora Chinchipe	Estación San Francisco	-3.9675	-79.0741	1,900	MEPN 3260 Este Estudio
Azuay	Valle de Yunguilla	-3.3000	-79.3000	1,650	Voss (2015)
Loja	Vicinity of Gonzanama	-4.2349	-79.4300	2,092	This study
Loja	Olmedo	-3.9354	-79.6464	1,284	This study
Loja	Vicinity of the Villonaco Wind Project	-4.0139	-79.2439	2,401	This study
Loja	Quilanga	-4.2972	-79.4011	1,897	This study
Loja	Chaguarpamba	-3.8720	-79.6938	1,120	This study
Loja	Barrio Zamora Huayco	-4.0058	-79.1845	2,195	This study
Loja	5 km from Saraguro	-3.6615	-79.2688	2,938	This study
		Perú			
Chongoyape	RE Chaparrí	-6.6784	-79.3788	-	Williams (2008)

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Piura	Socchabamba	-4.6158	-79.6786	2,485	More and Crespo (2016)
Piura	Samanguilla	-4.6250	-79.5191	2,335	More and Crespo (2016)
Piura	Toronche	-4.7114	-79.5877	2,269-2,308	More and Crespo (2016)
Piura	Totora	-4.9852	-79.5152	2,570	More and Crespo (2016)
Piura	Ñoma	-5.0344	-79.8311	1,715	More and Crespo (2016)
Piura	Santa Rosa de Congona	-5.2538	-79.4747	2,490	More and Crespo (2016)
Piura	San Juan de Palomataz	-5.7300	-79.5022	2,700	More and Crespo (2016)
Kañaris-Lambayeque	Congoña	-6.0541	-79.3355	2,800	More and Crespo (2016)

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A Review of Road-killed Felids in Mexico

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Six species of felids are distributed across Mexico and all are affected to a greater or lesser extent by the national highway network (377,660 km in length), but the magnitude of its impact on these species is unknown. Part of the issue is the scarce information available spread across the scientific literature, mammal collections records, environmental consultancies, and the local press. This work compiled the information available on road-killed felids in Mexico and organizes it systematically to identify potential data trends. We conducted a systematic search for records of verified felid roadkill events across Mexico reported in the scientific literature, mammal collections, online news and emails addressed to mammal -- particularly wild cat -- management/conservation specialists. First, felid roadkill records were entered and classified according to origin, *i.e.* source of information, and then classified according to the state where the event occurred. This information was used to explore the potential correlation between felid roadkill frequency and road density per state. Roadkill events were reported for all felid species, with a total of 115 records in 25 states: *Herpailurus yagouaroundi*, 21; *Leopardus pardalis,* 20; *L. wiedii*, 11; *Lynx rufus*, 50; *Puma concolor*, 5; and *Panthera onca,* 8. Most of the information came from mammal collections (40 records), followed by personal communications (25), and publications in local media (19), citizen science websites (10), peer-reviewed journals (9), non-governmental organizations (7), and government agencies (5). We found a significant correlation between road density and number of roadkill events recorded per state. Road density alone is insufficient to explain some geographic bias in felid roadkill data, which might instead be related to the appeal of a species, and to being recorded by people (scientists or otherwise) interested in this issue in a particular location. Acknowledging road mortality as an issue for felids in our country might contribute to identify and apply methods to improve data collection (citizen science) to develop preventive measures in our highways (wildlife crossing structures), particularly in wildlife high-risk areas.

En México se distribuyen seis especies de félidos y todos están afectados en mayor o menor medida por la presencia de una red carretera nacional con una longitud aproximada de 377,660 km; pero se desconoce qué tan importante resulta este impacto sobre este grupo. Parte del problema es la poca información disponible publicada en artículos científicos, registros de colecciones mastozoológicas, consultorías ambientales y prensa local. En este trabajo se realizó una revisión histórica de atropellamientos de félidos en México ordenándola de manera sistemática para observar tendencias en fuentes de información. Se realizó la búsqueda sistemática de registros verificados de félidos atropellados en México en literatura científica, colecciones mastozoológicas, medios de comunicación disponibles en Internet y a través de cadenas de correos electrónicos dirigidas a especialistas en conservación y manejo de mamíferos, especialmente félidos. Los registros fueron volcados en una base de datos por especie en orden filogenético y clasificados primeramente por su origen de acuerdo a la fuente de información de la que provenían. Luego se clasificaron según el estado en el que ocurrió el evento de atropellamiento y se determinó si existe correlación entre los atropellamientos y la densidad de carreteras por entidad federativa. Se encontraron 115 registros de atropellamientos los cuales ocurrieron en 25 estados de México. Se registraron 21atropellamientos de *Herpailurus yagouaroundi*, 20 de *Leopardus pardalis*, 11 de *L. wiedii*, 50 de *Lynx rufus*, cinco de *Puma concolor*, y ocho de *Panthera onca*. La mayoría de los registros se obtuvieron en colecciones científicas (40 registros), seguidos por comunicaciones con expertos (25), registros en prensa local (19), portales de ciencia ciudadana (10), publicaciones arbitradas (9) organizaciones no gubernamentales (7) y finalmente agencias gubernamentales (5). Se encontró correlación significativa entre densidad de carreteras por estado con el número de atropellados registrados en el estado. En México la mortalidad de félidos en las carreteras representa un problema, el cual debe ser atendido en primera instancia mejorando la colecta de información y difusión de la misma, por ejemplo, con el uso de portales de ciencia ciudadana. El trabajo demostró que, a pesar de que existe una relación entre la densidad de carreteras y el número de félidos atropellados, la densidad de carreteras no explica los sesgos geográficos en la distribución de registros de félidos atropellados, el cual se encuentra probablemente relacionado a otros factores como el interés que las especies de félidos podrían tener para diferentes grupos (*e. g.*, academia o prensa local). La sistematización y registro de atropellamientos de felinos en México podrá apoyar la toma de decisiones para el adecuado establecimiento de obras de mitigación en carreteras en México.

Key words: Felines; highways; mortality; roads.

Introduction

The quantity and quality of the road infrastructure are key economic growth drivers, facilitating access of inhabitants to health and education services, besides contributing to reduce poverty (Bird *et al.* 2011). In Mexico, investment in road infrastructure is considered a strategic issue, since it fosters economic growth and development. It is one of the cornerstones of competitiveness and social well-being, supporting economic growth and regional development, and reducing transportation costs (Gobierno de los Estados Unidos Mexicanos, 2014). However, roads involve multiple negative environmental effects, including pollution, habitat fragmentation, and deforestation, as well as wildlife mortality from roadkill events (Forman *et al.* 2003).

In particular, wild cats are affected to a large extent by roads (Kerley *et al.* 2002; Ngoprasert *et al.* 2007; Ford *et al.* 2010; Jansen *et al.* 2010; McGuire 2012; Basille *et al.* 2013), as these mammals typically have large home ranges and roam long distances (Macdonald *et al.* 2010b), in addition to being low tolerant to human disturbance (Macdonald *et al.* 2010a). These attributes increase the vulnerability of these species to the effects of roads and traffic (Grilo *et al.* 2015). Mortality associated to road collisions has been reported for several felids [*e.g.* tiger (*Panthera tigris*) Gruisen 1998a, b; lion (*Panthera leo*) Drews 1995; Iberian lynx (*Lynx pardinus*) Simon *et al.* 2012], leading to significant effects on the conservation of some species such as the Iberian lynx and subspecies as the Florida puma (*Puma concolor coryi:* Taylor *et al.* 2002).

Mexico is home to six felid species: *Herpailurus yagouaroundi* (jaguarundi), *Leopardus pardalis* (ocelot), *L. wiedii* (margay), *Lynx rufus* (bobcat), *Puma concolor* (puma) and *Panthera onca* (jaguar; Ramírez-Pulido *et al.* 2014). The effect of roads on felids has focused on the jaguar, both in Mexico and throughout its distribution range, finding that these negatively affect its mobility and dispersal (Ortega-Huerta and Medley 1999; Conde 2007; Conde *et al.* 2010; Colchero *et al.* 2011; Pallares *et al.* 2015; Stoner *et al.* 2015; Cullen *et al.* 2016; Ceia-Hasse *et al.* 2017). At the continental level and particularly in Mexico, *P. concolor* and *H. yagouaroundi* are considered to be species exposed to high road densities, and hence to their negative effects, including death by vehicle collision (Ceia-Hasse *et al.* 2017). For *L. pardalis*, *L. wiedii* and *L. rufus* there are no specific data on the potential effect of roads on their populations in Mexico.

There are literature reports of roadkill events outside of Mexico involving the six felid species (*e. g., H. yagouaroundi,* Cunha *et al.* 2010; Hegel *et al.* 2012; Arias-Alzate *et al.* 2013; Giordano 2015; *L. pardalis*, Cáceres *et al.* 2010; *L. wiedii*, Carvalho *et al.* 2014; *P. concolor*, Maehr *et al.* 1991; Cáceres *et al.* 2010; *P. onca*, Srbek-Araujo *et al.* 2015). However, in Mexico no felids have been reported in publications addressing road-killed wildlife (see González-Gallina and Benítez-Badillo 2013); the few sporadic records come from studies on the distribution of species rather than the effect of roads as such (*e. g.*, Meraz *et al.* 2010; Almazan-Catalan *et al.* 2013).

At the global level, a large amount of information on road-killed wildlife is available in informal information sources including news in the local press, anecdotal evidence or records in informal unpublished technical reports (Smith and van der Ree 2015), and more recently also in social websites (Shilling *et al.* 2015). No studies have been conducted to date to gather information from informal media such as citizen science websites to assess felid roadkill events in Mexican roads. In addition, despite the fact that information systems have been put in place in Mexico for the systematic recording of wildlife road kills (*e. g.*, Naturalista by CONABIO http://www.naturalista.mx/ and Observatorio de Movilidad y Mortalidad de Fauna (Wildlife Mobility and Mortality Observatory) by SCT/IMT http://watch.imt.mx), these have not been fully developed, unlike other countries (*e. g.,* URUBU System in Brazil http://sistemaurubu.com.br/es/; California Roadkill Regitration System in USA http://www.wildlifecrossing.net/california/; Shilling *et al.* 2015).

The collection of information on the number of road-killed felids and the regions where these are killed in Mexico is of great importance for the conservation of these species, as four of the six felid species are listed in one of the protection categories established in the Mexican regulations (NOM-059-SEMARNAT-2010), and roadkill mortality adds to other anthropogenic causes (*e .g.*, hunting, loss of habitat, human-carnivore conflicts, etc: CONANP 2009). From the above, the objective of this work was to carry out a review of the records regarding felid roadkill events in Mexico, from formal and informal sources, sorting them systematically according to their origin (time and place of occurrence).

Materials and Methods

Study Area. The survey of felid roadkill records comprised all mexican territory. The country has a road network of approximately 156,797 km (141,545 km of two-lane roads and 15,252 km of highways with more than two lanes; SCT 2016) traveled by a fleet of 27,500,000 vehicles (INEGI 2017). The distribution range of the six species of wild cats living in Mexico is very broad (Hall 1981), so that *P. concolor* is potentially found throughout the country, while *P. onca*, *L. pardalis, L. wiedii* and *H. yagouaroundi* are distributed in tropical areas, and *L. rufus* in mostly temperate areas.

Methods. Information on felid roadkill events in Mexico was obtained through a systematic search of confirmed records of wild cats killed by cars in Mexico in the scientific literature, mammal collection records, online news, and emails addressed to specialists in conservation and management of mammals, especially wild cats. The information gathered from each of the records of road-killed felids included species, road or town closest to the collision site, state of Mexico where the incident occurred, year, type of information source, and reference. The survey aimed at obtaining an annual overview of the sources of these records, discarding those with uncertain date. Two types of information sources were surveyed, *i. e.* published and non-published; the first can be consulted and the second has added reliability through consultation with specialists. Within these two categories, the following media were searched:

Scientific literature. The survey included published articles and theses using specialized webpages like Google Scholar (http://scholar.google.com.mx) and Web of Science (https://www.webofknowledge.com/). In each of these sites, the search criteria used were the felid species (common and scientific name) and the word *hit/struck/road-killed* in both English and Spanish. Once a record was identified, this was reviewed to determine the type of record. A felid roadkill record was deemed valid if it explicitly referred to the record of a hit animal, in addition to providing specific information on place and date. In the case of bachelors or graduate theses, the record was determined as valid only when a photograph of the struck specimen was included, provided the author could confirm the cause of death.

Mammal Collections and Citizen Science websites. Information was requested from curators of 28 collections listed in the Asociación Mexicana de Mastozoología A. C. (Lorenzo *et al.* 2006), particularly regarding collection site and year of recording, about any of the six Mexican wild cat species that were collected and deposited in the collection after being hit. Also, each field record in the NaturaLista webpage (http://www.naturalista.mx/) was reviewed to identify the road-killed specimens.

Internet media. The Google web browser (http://www.google.com) was extensively surveyed for informal published records of road-killed felids (*e. g.*, news about specific roadkill events mentioned in national or local news media, personal web pages or social networks, and reports from the web pages of non-governmental organizations). The search was conducted using the following key words: common name + road-killed, species + road-killed, common name + Mexico, species + Mexico, species + road, common name + road, in both Spanish and English. Once a record was identified, the original source was reviewed, and the quality of the information assessed based on the presence/absence of photographs of the event, as well as its geographic location.

Emails addressed to specialists (personal communications). Through e-mails sent to specialists in wild cats and wildlife conservation in Mexico working in Non-Governmental Organizations (NGOs), universities and government authorities, information was requested on specific events involving struck felids that these specialists witnessed or on which they had specific information. Once the specialist was contacted, specific data were requested regarding species, year and location of the roadkill event, as well as any photograph of it, if available. These records were classified into personal communications or obtained from a NGO.

Data Analysis. The records of road-killed felids were entered into a database by species in phylogenetic order (Prevosti *et al.* 2010) and classified first by origin, in accordance with the source of information (scientific literature, collections, online news or specialists). From the geographical standpoint, records were classified according to the state where the roadkill event occurred. It was decided that the analysis would be conducted by state, since many of the observations (from published and unpublished sources) had no precise data of the specific locality or road segment where the event occurred.

The first stage of the analysis compared roadkill data (dates and sites) obtained from the various sources of information, in order to identify potential duplicate records. Subsequently, it was investigated whether the felid roadkill sites matched the distribution range of the species in Mexico. To this end, the presence/absence of felid roadkill events obtained from all information sources in each state of the country was determined by species and compared in a Geographical Information System versus the range reported for the respective species (Hall 1981) from the Digital Distribution Maps of the Mammals of the Western Hemisphere v. 3.0 (Patterson *et al.* 2007).

The next stage of the analysis was to determine whether felid roadkill events are related to road density. A positive relationship between road density in a region and the number of medium-sized mammal roadkill events has been observed (Saeki and Macdonald 2004). In Mexico, the national road network is not evenly distributed; instead, important regional differences occur in the density of roads across the different states of the country (Deichmann *et al.* 2004). The surface area in km^2 (INEGI 2015) and the length of roads (km) in state were obtained (SCT 2016). Road density per state was calculated by dividing the total number of km of roads by the surface area of each state. The relationship between road density and the number of felid roadkill records per state was investigated through a Spearman's rank correlation (Siegel and Castellan 1988); road density per state was associated with the number of felid roadkill events for each state considering all the sources of information used.

We analyze the data on an annual basis according to the source of information, to identify any changes in the trends in data recording during the period covered by the study. We excluded from the analysis those years were information was not available.

Results

The review revealed the existence of records of road killed-felids dating back to 1982. A total of 115 records of roadkill events was found for the six felid species living in Mexico (Supplementary Material 1, Figure 1). The number of roadkill records found were: *H. yagouaroundi*, 21; *L. pardalis*, 20; *L. wiedii*, 11; *L. rufus*, 50; *P. concolor*, 5; and *P. onca*, 8 (Figure 2). Of all records, 90 came from publications (academic and news, 78.2 %) and 25 were obtained through personal communications (21.7 %). Within published news (online or printed), 40 (34.8 %) came from scientific collections, 9 (16.5 %) from the local press, 10 from citizen science through CONABIO's Naturalista webpage (8.7 %), nine (7.8 %) from peer-reviewed publications, seven (6.1 %) from NGOs, and five (4.3 %) from government agencies (Table 1).

Roadkill events were recorded in 25 of the 32 states of Mexico (Table 2, Figure 1). The comparison of the distribution area with the location of roadkill records for a given species reveals that there are states with no roadkill reports in spite of being included in the distribution range of the species (Figure 4). Roadkill events reported are as follows: *H. yagouaroundi*, 10 of the 15 states where it lives (10/15; 45 %); *L. pardalis*, 10/25 states (40 %); *L. wiedii*, 7/20 (35 %); and

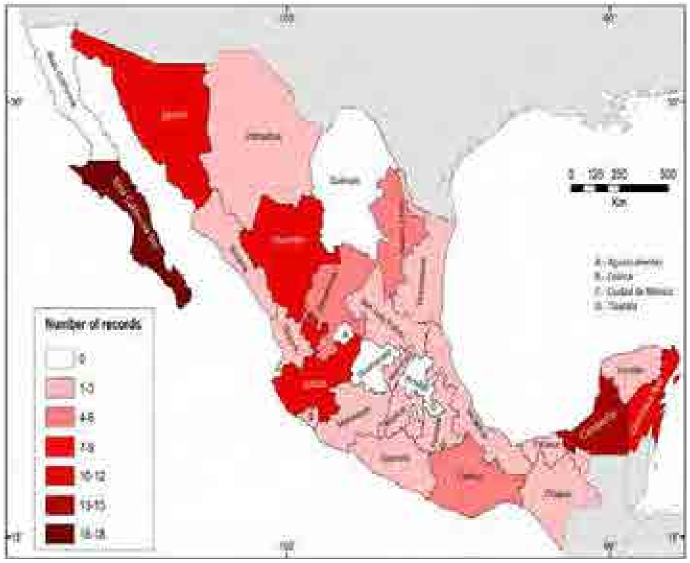

Figure 1. Total number of records of felid roadkill events in Mexico by state. The figure includes the sum of records of *Herpailurus yagouaroundi*, *Leopardus pardalis*, *L. wiedii*, *Lynx rufus*, *Puma concolor* and *Panthera onca* obtained from published (mammal collections, scientific literature, government, citizen science web page, NGOs, digital news) and unpublished sources (personal communication with experts in wild cat conservation) from 1982 to 2017.

L. rufus, 11/27 (41 %). In the case of *P. concolor*, although this species is distributed throughout all of Mexico, roadkill events are recorded in three states only (Jalisco, Durango and Sonora, 9.4 %). Events involving *P. onca* are reported in four (Quintana Roo, Campeche, Veracruz, and Jalisco) of the 27 states where the species is distributed (15 %).

An inverse relationship was observed between road density by state and number of felid roadkill events registered (Rho=-0.35658, $P = 0.04515$). *I. e.* a lower road density is apparently associated with more events. Examples are Baja California Sur, with a road density of 0.8 km/km^2 and 18 records; and Tlaxcala, with a high road density of 0.73 km/km^2 and no roadkill records. Not all states show this same behavior, such as Chihuahua, with the lowest road density (0.05 km/km^2) and no roadkill records, or Jalisco, with a road density of 0.36 km/km^2 and 10 roadkill records.

The analysis of roadkill records and their sources (Figure 4) was conducted with 109 accurately dated records (6 records with no date were excluded). The period 1982-2017, comprising 35 years, included 21 years with roadkill records. The period 1982-2006 reported 25 felid roadkill records, 88 % from collections and scientific literature and the rest from personal communications. From 2007 to date 84 records were reported, 27.4 % from a collection or the scientific literature, and 72.6 % from other sources (22.6 %, online news; 26.2 %, personal communications).

Discussion

Among mammals, carnivores are the group most adversely affected by roadkill events (Rytwinski and Fahrig 2015; Ceia-Hasse *et al.* 2017), with well-documented cases, particularly in wild cats (*e. g.*, Ferreras *et al.* 1992; Taylor *et al.* 2002). In Mexico, up until this report, no estimates of the number of roadkill events involving wild cats in the country was available to document the potential impact of this phenomenon on the conservation of the species. However, we now know that at least 115 individuals of the six species were killed by vehicle collision events between 1982 and 2017.

No records involving wild cats are reported in specific works on the quantification of roadkill events in Mexico (González-Gallina and Benítez-Badillo 2013), suggesting sporadic collision of these species by vehicles. However, despite the important efforts carried out in studies about animals killed on mexican roads, these have focused on a few road stretches and involving short periods of time (*e.g.*, Morales-Mavil *et al.* 1997; Grosselet *et al.* 2008; González-Gallina *et al.* 2013; Pacheco-Figueroa *et al.* 2013), hence limiting its impact when seeking to understand the dynamics of this phenomenon at the national level (González-Gallina and Benítez-Badillo 2013). The information survey in different media allowed to establish the incidence of this phenomenon despite the absence of reports specifically mentioning felids in formal road surveys. This work points to the states where this type of studies should be conducted to gather further information.

It has been proposed that the vulnerability of wildlife species such as felids increases directly with road density (Cullen *et al.* 2016). Particularly for Mexico, the northeast and south-southeast regions of the country were identified as areas where several species of wild cats are exposed to high road densities (Ceia-Hasse *et al.* 2017). Despite the above, there are states for which just a few roadkill events, if any, have been reported, despite the fact that extensive

Table 1. Number of records of the six wild cat species struck in Mexico, classified according to the source of the record. Mammal Collection (MC), scientific literature (SL), citizen science web page (CSW), report in government media (RGM), digital news (DN), non-governmental organization (NGO), personal communication (PC).

	Source of the record							
Species	**MC**	**SL**	**CSW**	**RGM**	**DN**	**NGO**	**PC**	**Total**
Herpaiulurus yagouaroundi	3	6	2	2	1	0	7	21
Leopardus pardalis	4	2	2	1	6	1	4	20
Leopardus wiedii	5	0	1	1	3	0	1	11
Lynx rufus	28	0	5	0	2	6	9	50
Puma concolor	0	0	0	1	2	0	2	5
Panthera onca	0	1	0	0	5	0	2	8
Total (% of total)	40 (34.78 %)	9 (7.83 %)	10 (8.70 %)	5 (4.35 %)	19 (16.52 %)	7 (6.09 %)	25 (21.74 %)	115

Table 2. Roadkill records by species and distribution range of the respective species in each state of Mexico. Roadkill records for each species were obtained from published (90) and unpublished sources (25). The presence of the species in each state was obtained from overlapping Hall's distribution polygons (Hall 1981) for each species on the political division map of the Mexican Republic. The letter "P" indicates that the species is present in the state. "A" indicates that there are roadkill records for the species in the state. As regards the number of species per state, the first column corresponds to the presence and the second to records of struck species.

State	*Herpailurus yagouaroundi*		*Leopardus pardalis*		*Leopardus wiedii*		*Lynx rufus*		*Puma concolor*		*Panthera onca*		Number of species per state	
Aguascalientes							P		P				2	0
Baja California							P		P		P		3	0
Baja California Sur							P	A	P				2	1
Campeche	P	A	P	A	P	A			P		P	A	5	4
Chiapas	P	A	P		P				P		P		5	1
Chihuahua	P		P				P	A	P		P		5	1
Coahuila			P				P		P		P		4	0
Colima	P		P		P	A	P		P		P		6	1
Ciudad de México							P		P				2	0
Durango			P		P		P	A	P	A	P		5	2
Estado de México	P	A	P				P		P		P		5	1
Guanajuato							P		P				2	0
Guerrero	P	A	P		P		P		P		P		6	1
Hidalgo			P		P		P		P		P		5	0
Jalisco	P	A	P	A	P	A	P	A	P	A	P	A	6	6
Michoacán	P	A	P		P		P	A	P		P		6	3
Morelos	P				P		P	A	P		P		5	1
Nayarit	P		P		P	A	P		P		P		6	1
Nuevo León	P	A	P	A			P		P		P		5	2
Oaxaca	P	A	P	A	P		P	A	P		P		6	3
Puebla	P		P		P		P	A	P		P		6	1
Querétaro			P		P	A	P	A	P		P		5	2
Quintana Roo	P		P	A	P	A			P		P	A	5	3
San Luis Potosí	P		P	A	P		P		P		P		6	1
Sinaloa	P		P	A	P		P		P		P		6	1
Sonora	P		P				P	A	P	A	P		5	2
Tabasco	P	A	P		P				P		P		6	1
Tamaulipas	P		P	A	P		P		P		P		6	1
Tlaxcala	P		P				P		P				4	0
Veracruz	P		P	A	P	A	P		P		P	A	6	3
Yucatán	P	A	P	A	P				P		P		5	2
Zacatecas							P	A	P		P		3	1
Total	22	10	25	10	20	7	27	11	32	3	27	4		

Figure 2. a) Specimen of *Herpailurus yagouaroundi* recorded on La Ventosa road, Oaxaca. Photograph: Alejandro Tepatlán Vargas. b) Specimen of *Herpailurus yagouaroundi* recorded on the Tizimín road, Yucatán. Photograph: Diana F. Zamora Bárcenas. c) Specimen of *Leopardus pardalis* recorded near the Federal Highway 85, Ejido Miguel Hidalgo, Tamaulipas. Photograph: Milton Gildardo Ruiz-Bautista. d) Specimen of *Leopardus pardalis* in the Puerto Morelos - Playa del Carmen road. Photograph: Victor Castelazo-Calva. e) Specimen of *Leopardus wiedii* recorded near the Federal Highway 74 in Nayarit. Photograph: Mark Stackhouse. f) Specimen of *Lynx rufus* on a road in the border between the states of Queretaro and Guanajuato. Photograph: Diana F. Zamora Bárcenas. g) Specimen of *Lynx rufus* in the Federal Highway 7D El Sueco, Chihuahua. Photograph: Mircea Hidalgo Mihart. h) Runover specimen of *Panthera onca* near the Sabancuy-Champoton road, Campeche. Photograph: Marco Sánchez (CONANP, Laguna de Términos).

areas of their territories are part of the distribution range of several species (*e. g.,* Coahuila and Baja California), while others report a high number of struck specimens (*i. e.,* Baja California Sur) in spite of the low road density (0.08 km/km^2). This parameter alone does not entirely explain the distribution of roadkill records. Another factor affecting this distribution relates to the existence of professionals or institutions interested in keeping records of roadkill events. Mammal collections were the main source of felid roadkill records (34.8 % of the total number of records), the states with the highest number of records being those associated with a scientific collection, mostly when it focuses on the study of the local or regional fauna. This is the case of the comparison between the records in Baja California Sur (road density 0.08 km/km^2) and Baja California (0.17 km/km^2). Baja California Sur reports the largest number of wild cat roadkill events, with all records coming from the mammal collection of the Centro de Investigaciones del Noroeste (CIBNOR), while Baja California, in spite of sharing many of the ecological and environmental conditions with the neighboring state (Morrone and Márquez 2003), has no records of struck felids, probably because there are no groups of professionals interested in the subject.

Our results showed that 72.2 % of the records came from published sources available for consultation through formal searches (mammal collections or scientific publications); this finding strengthens the proposal that as regards roadkill events, information surveys should always involve information from non-formal sources (Smith and van der Ree 2015). However, although many of the records of road-killed felids

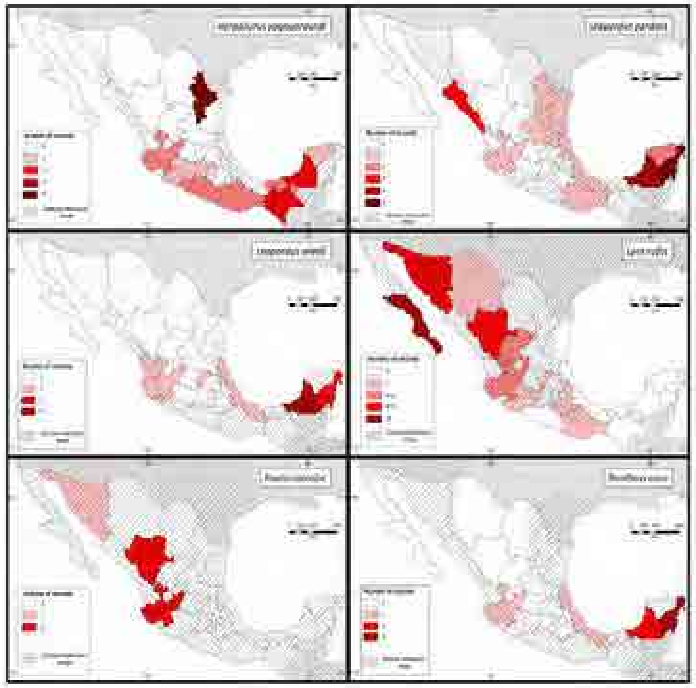

Figure 3. Records of each of the road-killed felid species in Mexico by state, showing the distribution range of each species from Hall (1981; in gray). Sum of records for each species obtained from published (scientific literature, mammal collections, digital news, government, citizen science portal or NGO websites) and unpublished sources (personal communication with experts in wild cat conservation) from 1982 to 2017. a) *Herpailurus yagouaroundi*, b) *Leopardus pardalis*, c) *Leopardus wiedii*, d) *Lynx rufus*, e) *Puma concolor*, and f) *Panthera onca*.

in Mexico referred to *H. yagouaroundi, L. rufus* and *P. concolor* (65.2 % of records), in less formal media — particularly online media — a high percentage of the records (73.7 %) are related to *L. pardalis*, *L. wiedii*, and *P. onca*. This can be explained by the fact that there are animal species that capture the attention of the public (Clucas *et al.* 2008). This is the case of wild cats with stripped or spotted fur (*e. g., L. pardalis, L. wiedii* and *P. onca*), which are conspicuous and are part of the Mexican culture and traditions (Saunders 2005), added to the fact that governmental and non-governmental organizations have disseminated their importance and conservation status (SEMARNAT 2009). This is the case of the jaguar, a species that recorded five roadkill records in the state of Quintana Roo (Supplementary Material 1) from news media and that has been followed up for being a species with public appeal, *i. e.* a news target.

The growth of electronic and online media, as well as the use of smartphones, has facilitated the spreading of news on wildlife roadkill events (Shilling *et al.* 2015). In this work, we observed a steady increase in the number of felid roadkill records over the past 10 years, with the largest growth in records in digital news. The growth in the number of smartphone users (from 50.6 million users in 2015 to 60.6 million in 2016; INEGI 2016), coupled with the creation of specific platforms for the recording of roadkill incidents — such as Fauna Silvestre Atropellada y Fauna Atropellada del Noreste (Road-killed Wildlife and Northeastern Road-killed Wildlife) available in the NaturaLista platform, or the Observatorio de Movilidad y Mortalidad de Fauna (Observatory of Wildlife Mobility and Mortality) —, promote the recording of a growing number of reports, as has happened in other countries (Olson *et al.* 2014; Vercayie and Herremans 2015; Shilling *et al.* 2015). In this work, only 8.7 % of the records of road-killed cats came from citizen science projects. The advancement of information systems through these projects would facilitate the registration on roadkill events, not only of felids but also of other wild mammal species at the country level. The ease of communication by electronic means may potentially improve data quality in the monitoring of roadkill events by professionals (Olson 2014), provided the analyses consider the limitations that are intrinsic to the type of information collected (*e. g.,* variable sampling effort, bias toward larger and more visible species, among others; Sarda-Palomera *et al.* 2012).

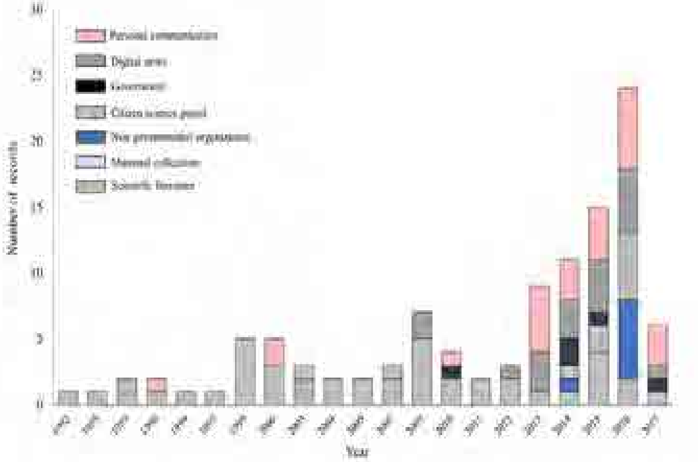

Figure 4. Number of records of road-killed felids according to their origin as obtained from published (scientific literature, mammal collections, digital news, government, citizen science portal or NGO websites) and unpublished sources (personal communication with experts in wild cat conservation).

This work shows that data on road-killed wild cats is an underestimation, since a large number of these events are not recorded. It is therefore imperative to determine whether this type of events affects the different wild cat species at the population level to the extent that may threaten their long-term survival. The majority of wild cat species are listed in a risk category (NOM-059-SEMARNAT-2010), and several are considered as in danger of extinction (*L. pardalis*, *L. wiedii* and *P. onca*). Collisions with vehicles add to other mortality factors such those coming from habitat loss or conflicts with livestock (CONANP 2009), and could be even more important (Simon *et al.* 2012, Taylor *et al.* 2002). The surveillance of roadkill events through systematic long-term monitoring may lead to more effective mitigation measures (Grilo *et al.* 2015). This work should serve as a forewarning to stimulate the development of monitoring efforts and appropriate mitigation measures for these animals at the national level.

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Supplementary material 1.

Records of road-killed felids in Mexico grouped by species. Each record includes the road or locality where the collision occurred, year of recording, name of the state, the source type of the record and origin of the record. Source types are: Mammal Collection (MC), scientific literature (SL), citizen science web page (CSW), report in government media (RGM), digital news (DN), non-governmental organization (NGO), personal communication (PC).

Site	Year	State	Source type	Source
Herpailurus yagouaroundi				
Escárcega	1982	Campeche	MC	DP
Pablillo Galeana	1989	Nuevo León	SL	Peña-Mondragón (2004)
Camino al Parque Funeral Guadalupe	2003	Nuevo León	SL	Peña-Mondragón (2004)
Acapulco - Zihuatanejo 2.5km E de Zihuatanejo	2007	Guerrero	SL	Almazan-Catalan *et al*. (2013)
México-Acapulco 3km NO Tierra Colorada	2007	Guerrero	SL	Almazan-Catalan *et al*. (2013)
Valentín Gómez Farías	2009	Campeche	MC	VER-MAM IIB-UV[1]
Carretera Federal Escárcega-Chetumal Km 7	2010	Campeche	MC	VER-MAM IIB-UV[1]
Arriaga-Ocozocoautla	2010	Chiapas	NGO	http://www.profepa.gob.mx/innovaportal/v/5398/1/mx.wap/rescata__profepa_3_felinos_salvajes__catalogados_como_especies_amenazadas.html
La Huerta-Melaque	2010	Jalisco	PC	Núñez R.
Nueva Alemania cerca de puente Mal paso	2013	Chiapas	DN	http://www.oem.com.mx/diariodelsur/notas/n3038422.htm
Melaque-Tomatlán	2013	Jalisco	PC	Núñez R.
La Ventosa	2013	Oaxaca	PC	Tepatlán-Vargas A.
La Huacana-Lázaro Cárdenas	2014	Michoacán	PC	Núñez R.
El Despoblado	2015	Estado de México	CSW	Conabio, Naturalista http://naturalista.conabio.gob.mx/
Carretera La Ventosa	2015	Oaxaca	PC	McAndrews A.
Tzimin	2015	Yucatán	PC	Zamora Bárcenas D. F.
Carretera Jititol-Tuxtla Gutiérrez	2016	Chiapas	PC	Hidalgo Mihart M.
Jolochero	2016	Tabasco	CSW	Conabio, Naturalista http://naturalista.conabio.gob.mx/
Carretera Coatzacoalcos-Cárdenas	2017	Tabasco	DN	http://www.jornada.unam.mx/ultimas/2017/03/04/rescatan-en-tabasco-a-jaguarundi-presuntamente-atropellado
Parque Ecológico Chipinque A.C.	?	Nuevo León	SL	Peña-Mondragón (2004)
Rancho Lomas Bonito, Montemorelos	?	Nuevo León	SL	Peña-Mondragón (2004)
Leopardus pardalis				
Carretera 9, Rosario	1989	Sinaloa	SL	Brown y López-González (2001)
Pochutla-Huatulco	2003	Oaxaca	SL	Meraz *et al*. (2010)
Parque Ecológico Jaguarundi, La Cangrejera, Coatzacoalcos	2011	Veracruz	MC	CNMA[1]
Carretera Escarcega-Chetumal, Ejido Nuevo Conhuas	2012	Campeche	MC	CM-UAC[1]
El Roble	2012	Sinaloa	DN	http://www.nnc.mx/movil/articulos/?idarticulo=80533
Bacalar-Altos de Sevilla	2013	Quintana Roo	DN	SIPSE, Novedades de Quintana Roo http://sipse.com/novedades/atropellan-un-ejemplar-de-jaguar-huia-de-incendio-forestal-24441.html
Calakmul	2014	Campeche	NGO	http://pronatura-ppy.blogspot.mx/2014/11/efectos-de-la-infraestructura-sobre-la.html
Calakmul, Ejido Constitución	2014	Campeche	MC	CM-UAC[1]
Puerto Vallarta-El Tuito (Conchas Chinas)	2015	Jalisco	NGO	http://www.profepa.gob.mx/innovaportal/v/7850/1/mx/atiende_profepa__denuncias_ciudadanas_y_captura__dos_ejemplares_de_vida_silvestre_en_sinaloa.html
San Juan-Tacuitapa	2015	Sinaloa	DN	El Debate, Mazatlán http://www.debate.com.mx/mazatlan/Video-Ocelote-muere-atropellado-en-San-Ignacio-20150705-0045.html
Cozumel carretera costera	2016	Quintana Roo	DN	SIPSE, Novedades de Quintana Roo http://sipse.com/novedades/atropellan-a-ocelote-en-cozumel-fauna-endemica-197373.html
Abratanchipa	2016	San Luis Potosi	CSW	Conabio, Naturalista http://naturalista.conabio.gob.mx/
Carretera Federal 85 límites entre Linares y Montemorelos	2016	Nuevo León	PC	Ruiz Bautista M.G.
Carretera Federal 85 Mpio. Villagrán	2016	Tamaulipas	CSW	Conabio, Naturalista http://naturalista.conabio.gob.mx/
Carretera Federal 307, entre Puerto Morelos y Playa del Carmen	2016	Quintana Roo	PC	Castelazo Calva V.

Carretera Tixméhuac	2016	Yucatán	DN	http://surcaribenoticias.com/index.php/2016/09/28/muere-otro-jaguar-es-atropellado-en-carretera-de-yucatan/
Tzucacab	2016	Yucatán	PC	Zamora Bárcenas D. F.
Carretera Federal 207 entre Puerto Morelos y Playa del Carmen	2017	Quintana Roo	DN	http://www.miCancún.mx/2017/02/23/atropellan-jaguar-en-la-carretera-Cancún-playa-del-carmen/
Carretera Leona Vicario-Puerto Morelos	2017	Quintana Roo	PC	Castelazo Calva V.
Carretera desconocida	2017	Campeche	MC	CM-UAC[1]
Leopardus wiedii				
Poblado de Lerma Mpio. Campeche	2007	Campeche	MC	CM-UAC[1]
Carretera a 5 Palos	2013	Veracruz	MC	VER-MAM IIB-UV[1]
Trapichillos	2014	Colima	RGM	http://www.profepa.gob.mx/innovaportal/v/6628/1/mx.wap/rescata_profepa_ejemplar_de_tigrillo_en_colima.html
Melaque-Tomatlán	2014	Jalisco	PC	Nuñez R.
km 30 Autopista Campeche-Champotón, Villamadero	2015	Campeche	MC	CM-UAC[1]
Carretera Edzna-Campeche, Mpio. Campeche	2015	Campeche	MC	CM-UAC[1]
Avenida Universidad, Othon P. Blanco	2015	Quintana Roo	DN	Diario Respuesta http://www.diariorespuesta.com.mx/policiaco/atropella-acelerado-conductor-a-tigrillo/
Carretera federal 74	2016	Nayarit	CSW	Conabio, Naturalista http://naturalista.conabio.gob.mx/
Chankana-Cozumel	2016	Quintana Roo	DN	Impctonoticias.mx http://impactonoticias.mx/video-ocelote-muere-atropellado-cuando-buscaba-agua/
Xilitla	2016	Querétaro	DN	Opinión Pública http://opinionpublicaslp.com/index.php/zona-huasteca/xilitla/3669-matan-un-tigre-en-xilitla
Carretera Federal Campeche-Mérida, Kobén	200?	Campeche	MC	CM-UAC[1]
Lynx rufus				
4.5 km S, 2.8 km E San Atenógenes	1985	Durango	MC	CRD[1]
1 Km E Emilio Portes Gil Pue	1990	Puebla	PC	González Christen A.
12.2 km N, 20.0 km W Sombrerete	1990	Zacatecas	MC	CRD[1]
Vicente Guerrero	1994	Durango	MC	CRD[1]
El Centenario, 14.5 km W La Paz	1997	Baja California Sur	MC	CIBNOR[1]
El Centenario, 14.5 km W La Paz	1999[2]	Baja California Sur	MC	CIBNOR[1]
El Centenario, 14.5 km W La Paz	1999[2]	Baja California Sur	MC	CIBNOR[1]
El Comitán, 17.5 km W La Paz	1999[2]	Baja California Sur	MC	CIBNOR[1]
El Comitán, 17.5 km W La Paz	1999[2]	Baja California Sur	MC	CIBNOR[1]
11 km NE Súchil	1999	Durango	MC	CRD[1]
17.5 km N La Paz	2000	Baja California Sur	MC	CIBNOR[1]
El Comitán, 17.5 km W La Paz	2000	Baja California Sur	MC	CIBNOR[1]
El Centenario, 14.5 km W La Paz	2000	Baja California Sur	MC	CIBNOR[1]
Pátzcuaro-Uruapan	2000	Michoacán	PC	Nuñez R.
km 53 carr. Durango-Canatlán, cerca J. Guadalupe Aguilera	2003	Durango	MC	CRD[1]
La Paz	2004	Baja California Sur	MC	CIBNOR[1]
km 37 carr. Durango-Mezquital	2004	Durango	MC	CRD[1]
El Triunfo	2005	Baja California Sur	MC	CIBNOR[1]
6.8 km S, 1.3 km W La Zarca	2005	Durango	MC	CRD[1]
Santa Anita	2009[2]	Baja California Sur	MC	CIBNOR[1]
Santa Anita	2009[2]	Baja California Sur	MC	CIBNOR[1]
Balneario Acatita	2009	Durango	MC	CRD[1]
3.73 km NE Villa Ocampo	2009	Durango	MC	CRD[1]
Huejuquilla-Tenzompa	2009	Jalisco	DN	http://verdebandera.com.mx/mueren-linces-en-carreteras-de-jalisco/
Huejuquilla-Bolaños	2009	Jalisco	DN	http://verdebandera.com.mx/mueren-linces-en-carreteras-de-jalisco/
1.7 km S, 0.5 km W 5 de Mayo	2010	Durango	MC	CRD[1]
Ciudad Constitucion	2011	Baja California Sur	MC	CIBNOR[1]

32 km S, 11 km W Santa Rosalia	2012	Baja California Sur	MC	CIBNOR[1]
Carretera Federal 7D El Sueco	2013	Chihuahua	PC	Hidalgo Mihart M.
Límites Querétaro-Guanajuato	2013	Querétaro	PC	Zamora Bárcenas D. F.
Carr. Guadalajara-Ameca,	2014	Jalisco	CSW	Conabio, Naturalista, Fauna Silvestre Atropellada http://naturalista.conabio.gob.mx/
Carretera Federal 160 Pasando Entronque Jaltetelco-Oaxtepec	2014	Morelos	PC	González Gallina A.
13 km N Jesus Maria	2015	Baja California Sur	MC	CIBNOR[1]
5 km S, La Paz	2015	Baja California Sur	MC	CIBNOR[1]
Carretera Federal 40 Durango-Gómez Palacio	2015	Durango	CSW	Conabio, Naturalista, Fauna Silvestre Atropellada http://naturalista.conabio.gob.mx/
Carretera Federal 190	2015	Oaxaca	CSW	Conabio, Naturalista, Fauna Silvestre Atropellada http://naturalista.conabio.gob.mx/
Carretera Federal 45 Villa Insurgentes	2015	Zacatecas	CSW	Conabio, Naturalista, Fauna Silvestre Atropellada http://naturalista.conabio.gob.mx/
La Paz	2016	Baja California Sur	MC	CIBNOR[1]
Los Planes	2016	Baja California Sur	MC	CIBNOR[1]
Nogales-La Escondida	2016	Sonora	CSW	Conabio, Naturalista, Fauna Silvestre Atropellada http://naturalista.conabio.gob.mx/
Carretera Federal 2 Agua Prieta-Imuris	2016[2]	Sonora	NGO	Sky Island Alliance
Carretera Federal 2 Agua Prieta-Imuris	2016[2]	Sonora	NGO	Sky Island Alliance
Carretera Federal 2 Agua Prieta-Imuris	2016[2]	Sonora	NGO	Sky Island Alliance
Carretera Federal 2 Agua Prieta-Imuris	2016[2]	Sonora	NGO	Sky Island Alliance
Carretera Federal 2 Ciudad Juárez-Agua Prieta	2016[2]	Sonora	NGO	Sky Island Alliance
Carretera Federal 2 Ciudad Juárez-Agua Prieta	2016[2]	Sonora	NGO	Sky Island Alliance
Mazapil, Ejido Mahoma	2016[2]	Zacatecas	PC	Martínez Hernández A. reportados por Ing. A.I. Rangel Galicia
Mazapil, Ejido Mahoma	2016[2]	Zacatecas	PC	Martínez Hernández A. reportados por Ing. A.I. Rangel Galicia
Carretera Federal 15, Hermosillo-Tucson, km 92	2017[2]	Sonora	PC	Juan Carlos Bravo
Carretera Federal 15, Hermosillo-Tucson, km 138	2017[2]	Sonora	PC	Juan Carlos Bravo
Puma concolor				
Minatitlán-Manzanillo	2013	Jalisco	PC	Nuñez R.
Durango-Gómez Palacio	2013	Durango	DN	AM Léon http://www.am.com.mx/leon/mexico/desaparece-cuerpo-de-puma-atropellado-en-durango-57086.html
Durango-Mazatlan	2014	Durango	RGM	http://www.profepa.gob.mx/innovaportal/v/6298/1/mx/atiende_profepa_muerte_de_puma_en_durango.html
Lagos de Moreno-San Luis	2014	Jalisco	DN	Zacatecas On line http://zacatecasonline.com.mx/noticias/policia/40450-atropellan-a-un-puma-en-autopista-de-lagos-de-moreno.html
Carretera Federal 2 Ciudad Juárez-Agua Prieta	2015	Sonora	PC	Bravo J.C. registro de Pérez-Cantú J.M.
Panthera onca				
Melaque-Tomatlán	2000	Jalisco	PC	Nuñez R.
Poblado de Cobá	2014	Quintana Roo	DN	SIPSE- Novedades de Quintana Roo http://sipse.com/novedades/un-jaguar-menos-automovil-a-exceso-de-velocidad-lo-mata-101266.html
Cd. Mendoza-Córdoba	2014	Veracruz	DN	El Mundo de Orizaba http://www.elmundodeorizaba.com/noticias/expediente/181-principal/1493314
Sabancuy-Champotón	2015	Campeche	PC	Sánchez M. (CONANP Laguna de Términos)
Sian Kaán Carretera 307	2015	Quintana Roo	DN	El Universal, Union, Cancún Qroo. http://www.unionCancún.mx/articulo/2015/07/01/RGM/el-tierno-jaguar-que-murio-atropellado
Tulum-Playa del Carmen	2015	Quintana Roo	DN	Enfoque Radio http://enfoqueradio.com.mx/hallan-atropellado-y-muerto-a-un-jaguar-en-la-carretera-federal-tulum-playa-del-carmen/
Tulum-Playa del Carmen	2016	Quintana Roo	DN	Reverso Revista http://reversomx.com/muere-jaguar-arrollado-en-carretera/
Escárcega-Xpujil	**?**	Campeche	SL	Colchero *et al.* (2011)

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[1] Acronyms of the Mammal Collections: mentioned in the table.- CIBNOR .- Colección de Mamíferos del Centro de Investigaciones Biológicas del Noroeste; CM-UAC.- Colección Mastozoológica de la Universidad Autónoma de Campeche; CNMA.- Colección Nacional de Mamíferos CRD.- Colección Científica de Fauna Silvestre Instituto Politécnico Nacional; DP.- Colección Osteológica del Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano" del Instituto

Nacional de Antropología e Historia; VER-MAM IIB-UV.- Colección de Vertebrados de Investigaciones Biológicas de la Universidad Veracruzana. [2] The records corresponded to various specimens collected in the same year, from the same site, and come from the same source.

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Effects of anthropogenic stress on the presence of parasites in a threatened population of black howler monkeys (*Alouatta pigra*)

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Habitat disturbance disrupts the ecological interactions of mammals, leading to negative consequences for biodiversity. In particular, it is suggested that parasite-host interactions are affected in tropical ecosystems, with parasite diversity reduced as environmental perturbations take place. In this study, we examined whether the disruption of tropical forests affects the presence of parasites in a population of endangered black howler monkeys (*Alouatta pigra*) that inhabits a highly fragmented landscape in Balancán, Tabasco, Mexico. Our working hypothesis was that increased forest perturbation would negatively affect the incidence of parasitic infections (parasite presence and richness) in black howler monkeys. We conducted a parasitological study and collected stool samples from 65 adult individuals living in 30 forest fragments across a disturbance gradient. We recovered parasite eggs from stool samples using flotation and sedimentation techniques. We selected fragment size and distance from each forest fragment to the nearest village as measures of forest perturbation. We analyzed the effects of forest perturbation on parasite presence and richness using generalized linear models. Other driving factors such as seasonality, host density, and sex were also considered in the models. Gastrointestinal parasite infection was positively related to distance between forest fragments and the nearest human settlement ($\beta = 0.55 \pm SE\ 0.28$, $z = 2.0$, $P = 0.05$). No effects of fragment size or any other variable considered in the model on the presence of parasite infection were observed. Parasite richness was not affected by any of the measures of forest perturbation, nor by any other variables considered in the analysis. Our findings suggest that an increase in forest perturbation may negatively affect the probability of parasite infection in black howler monkeys, as individuals living in close proximity to human settlements showed a lower presence of parasites. We proposed that the low parasite infection rates recorded in this monkey population reflect synergistic effects associated with both the alteration of the parasite-primate network, as well as the low resilience of parasites to thrive in a disrupted ecosystem.

Los disturbios de hábitat alteran las interacciones ecológicas de los mamíferos con consecuencias negativas para la biodiversidad. En particular, se ha observado que en los ecosistemas tropicales las interacciones entre parásitos y primates son afectadas, y la riqueza de parásitos es reducida conforme aumenta el grado de perturbación ambiental. En este estudio exploramos los efectos de la presión antrópica sobre la presencia y riqueza de parásitos gastrointestinales de una población de monos aulladores negros (*Alouatta pigra*) que habitan un paisaje altamente fragmentado en Balancán, Tabasco, México. Predecimos que un incremento en la perturbación del bosque afectará negativamente medidas de infección parasitaria (presencia y riqueza de parásitos) en monos aulladores negros. Llevamos a cabo un estudio coproparasitológico y colectamos muestras fecales de 65 individuos adultos que habitan 30 fragmentos de bosque a lo largo de un gradiente de perturbación. A través de técnicas de concentración por flotación y sedimentación recuperamos huevos de parásitos. Seleccionamos el tamaño de los fragmentos habitados por monos y la distancia que existe entre un fragmento y el poblado más próximo como medidas de perturbación del bosque. Analizamos los efectos de la perturbación del bosque sobre medidas de infección parasitaria usando modelos lineales generalizados. Otras variables como la estacionalidad, la densidad de hospederos y el sexo de individuos también fueron consideradas en los modelos. Encontramos que la distancia entre un fragmento de bosque y el poblado más cercano predice positivamente la presencia de infección parasitaria ($\beta = 0.55 \pm EE\ 0.28$, $z = 2.0$, $P = 0.05$). Ninguna otra variable tuvo efectos significativos sobre la presencia de parásitos. Las medidas de perturbación del bosque y otras variables consideradas no tuvieron efectos significativos sobre la riqueza de parásitos. Nuestros resultados indican que la presencia de parásitos gastrointestinales disminuye en hospederos que habitan fragmentos que se encuentran en cercanía a asentamientos humanos, lo cual sugiere que un incremento en el grado de perturbación del bosque reduce el parasitismo en monos aulladores negros. Proponemos que las bajas tasas de parasitismo observadas en esta población de monos aulladores reflejan una sinergia derivada de la reducción en la conectividad entre parásitos y hospederos, y de la poca resiliencia de los parásitos para sobrevivir en un ecosistema altamente transformado.

Key words: Habitat perturbation; Mexico; parasites; primates; species loss; tropical forest.

Introduction

Human activities such as agriculture and extensive cattle ranching, extraction of fossil fuels, overexploitation of resources and urbanization have all significantly impacted ecosystems worldwide (Hosonuma *et al.* 2012). Anthropic impact has affected the diversity and abundance of species, endangering the survival of their populations (Haddad *et al.* 2015; Ribeiro *et al.* 2015). In fact, organizations such as the International Union for the Conservation of Nature, as well as various authors, recognize that the accelerated loss of species and drastic ecosystem alterations have set off a global biodiversity crisis (IUCN 2017; Johnson *et al.* 2017). Conservation efforts and strategies to understand and/or reverse extinction trends generally focus on species that are either appealing or of interest to man (Donaldson *et al.* 2016). However, extinction processes associated with organisms perceived as harmful or associated with a negative condition, such as parasites, are poorly documented (Strona 2015).

Ecosystem disturbance (*e. g.*, deforestation), defined by Rykiel (1985) as the set of processes that cause environmental disturbance (*e. g.*, fragmentation and loss of habitat), disrupt ecological interactions at various levels, for instance, by changing food webs and mutualistic interactions (Morris 2010). The documented ecological changes between organisms involving several mammals species have shown that the host-parasite dynamics is one of the aspects affected in disturbed systems (*e. g.*, marsupials, Puttker *et al.* 2008; rodents, Bordes *et al.* 2015). For example, it has been found that in colonization processes, transmission rates and the maintenance of parasitic infections decrease in hosts whose populations have been fragmented and isolated (Bush *et al.* 2013; Bordes *et al.* 2015). Therefore, a prevalent hypothesis in parasite ecology theory is that the diversity and abundance of parasites decrease as environmental disruption increases (Lafferty and Kuris 2005; Lafferty 2012).

The loss of parasite diversity may be aggravated in populations of hosts that are threatened to some extent (Farrell *et al.* 2015). Conwell *et al.* (2012) suggest that organisms such as parasites may undergo co-extinction along with their hosts, since the transmission of parasites is harder to sustain in isolated populations with low host density. In support of this hypothesis, Altizer *et al.* (2007) found in a meta-analysis that several species of threatened primates have a lower richness of parasite species versus unthreatened populations. The order Primates represents an excellent model to explore the effects of habitat disturbance on parasitism patterns in endangered hosts, since over 60 % of the species of primates are under some category of threat (Estrada *et al.* 2017), and most are habitat specialists. Therefore, assessing parasitic infection patterns in endangered primates provides valuable information for the conservation of hosts and their ecological interactions.

The black howler monkey (*Alouatta pigra*) is a Neotropical primate currently threatened of extinction due to habitat loss and the conversion with tropical forests into farming land (Estrada 2015; IUCN 2017). This species is endemic to Mesoamerica (Mexico, Guatemala and Belize) and 80 % of its distribution range is estimated to be located in southeastern Mexico in the states of Tabasco, Campeche, Quintana Roo, and northern Chiapas (Estrada 2015). The municipality of Balancán, Tabasco, is home to one of the populations of black howler monkey most severely affected by changes of land use (Pozo-Montuy *et al.* 2011). Between 1960 and 1975, the federal government promoted colonization programs coupled with extensive livestock raising and agriculture, which resulted in the loss of 115,000 hectares of forest and the conversion of both rainforests and the so-called *tintales* (vegetation dominated by *Haematoxylum campechianum*) into pastures and cropland (Isaac-Márquez *et al.* 2008). This municipality currently includes fragments of the original vegetation of different sizes not covered by government protection (Pozo-Montuy *et al.* 2008); for this reason, the populations of howler monkeys in this region have been proposed as a priority for preserving the species (Pozo-Montuy *et al.* 2008; Tobón *et al.* 2012). A parasitological investigation of this population may illustrate how habitat disturbance has affected ecological interactions between wild primates and other organisms.

The objective of this study was to document the effects of habitat disturbance on parasitism in black howler monkeys (*A. pigra*) inhabiting a landscape that has been highly impacted by human activities in the municipality of Balancán, Tabasco, Mexico. As habitat disruption affects the host-parasite interactions, we expected that increased levels of rainforest disturbance would reduce the presence and richness of GI parasites in the black howler monkey. Also, since parasitic infections may follow seasonal patterns and are affected by demographic and intrinsic aspects of hosts (2006), this study also considered seasonality as well as ecological density and sex of individual hosts as potential predictors of parasite presence and richness.

Materials and Methods

Study Area. The study was carried out in a fragmented landscape in the municipality of Balancán, Tabasco, Mexico (17° 40' N, -91° 30' W; Figure 1). The remnants of vegetation (*i.e.*, fragments of howler monkey habitat, *sensu* Pozo-Montuy *et al.* 2013) in this area are located within a matrix of habitats that include livestock pasture, forestry plantations (cedar, *Cedrela odorata*; teak, *Tectona grandis*; melina, *Gmelina arborea*; and eucalyptus, *Eucalyptus* sp.), and cropland (*e. g.*, sorghum, rice, maize). These fragments are scattered in an area of 21,900 hectares bordered by the Usumacinta river and various water bodies (Pozo-Montuy *et al.* 2008). The original vegetation in this area has been described as low and medium subdeciduous forest and *tinto* low thorny tropical forest (*H. campechianum*; López-Mendoza 1980;

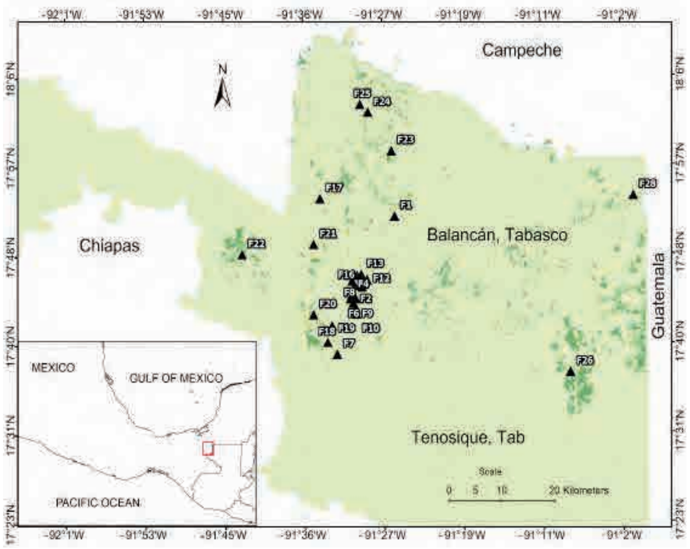

Figure 1. Fragmented landscape in the municipality of Balancán, Tabasco, Mexico. The image shows fragments of remnant forest in the study area, including the fragments sampled and human settlements.

Pozo-Montuy *et al.* 2011). Annual precipitation is 1,976 mm and mean annual temperature is 27.9 °C (CNA 2017).

Sample Collection. As part of a long-term research (2005 - 2018), complete censuses were conducted to record the presence of black howler monkeys, with 264 forest fragments visited during the period 2005-2012 (for further information, refer to Pozo-Montuy *et al.* 2008, 2011). Of these, and based on logistical criteria, a subsample of 30 fragments with confirmed presence of black howler monkeys was selected for the present study (Figure 1). Within the period January-December 2006, in each fragment the size and age-sex structure of howler monkeys was recorded, the ecological density (*i. e.*, number of individuals per fragment size, Rodríguez-Toledo *et al.* 2003) was calculated, and fresh stool samples were collected from 33 males and 32 females of different groups (*n* = 65). Stool samples were collected opportunistically during population surveys and only when individuals could be identified. These samples were preserved in 10 % formaldehyde solution, labeled with the information of origin (*e. g.,* fragment, group, specimen identity), and sent to the Laboratory of Parasitology in the Department of Environmental Sciences at Emory University.

Stool ova and parasite testing. We used the protocol of concentration by flotation and sedimentation ($NaNO_3$ solution), as described in Gillespie (2006), to retrieve helminth eggs and cysts of intestinal protozoa excreted in howler monkey stools. This protocol is highly effective to estimate intestinal parasitic infections using non-invasive methods in various species of wild primates (Gillespie and Chapman 2008). Two slides were systematically examined under a light microscope (Leica® DM500) for each parasite concentration technique. This procedure was carried out for each stool sample. No intestinal protozoan cysts were found in these samples. Parasite eggs (*i. e.*, helminths) were examined at 10× and measured with a micrometer eyepiece (0.1 µm) at 40×. One drop of Lugol's iodine solution was added to highlight egg structures and facilitate the taxonomic identification. In addition, photographs of representative eggs were taken for use in the identification and classification of taxa (Figure 2). The recovery of eggs was used for estimating the presence, prevalence and richness of parasites as a measure of parasitic infection. Parasite richness was defined as the number of different taxa observed per stool sample, while parasite prevalence was defined as the proportion of stool samples infected with at least one taxon.

Figure 2. Parasite eggs found in stools of black howler monkeys that inhabit forest fragments in Balancán, Tabasco, Mexico. A) *Trypanoxyuris* sp., B) *Controrchis* sp., C) unidentified trematode.

Disturbance Measures. The size of each forest fragment occupied by monkeys and the distance from this fragment to the nearest village were considered as landscape measures of habitat disturbance. Both variables were estimated with orthophotos at scale 1:2,000 using the program ArcView 3.3. These data and estimates have been published in greater detail in Pozo-Montuy *et al.* (2008, 2011). Fragment size was included considering that larger vegetation patches can accommodate a larger number of individuals, species and ecological interactions, thus mimicking the conditions found in undisturbed habitats (Collins *et al.* 2017). The distance from each fragment to the closest village was included assuming that fragments in close proximity to human settlements are exposed to greater disturbance (*e. g.*, logging and resource extraction, magnification of the edge effect; Popradit *et al.* 2015).

Data Analysis. The effects of habitat disturbance on parasitic infection patterns were analyzed using generalized linear models. The effects of habitat disturbance on the presence of parasites were explored by constructing a matrix with values 0 and 1 as response variables, where these figures represented non-infected (absence of parasites) and infected (presence of parasites of any taxon) samples, respectively. In this model, we established a canonical logit link function with binomial distribution (Crawley 2007). Fragment size and distance between a fragment and the nearest town were selected as predictors. Also included was ecological host density in each fragment due to a potential density-dependent effect on the parasitic infection (Nunn and Altizer 2006). Since samples were collected in different time points, these models also included seasonality. This was modeled through the sine and cosine of the day of collection, previously transformed into a circular variable (day within the year × 2 × π / 365) (Gillespie *et al.* 2013). The sex of specimens was also considered as a predictor.

In order to investigate the effects of habitat disturbance on parasite richness, we built another model including the number of parasite taxa in each stool sample as the response variable and the same predictors mentioned above. In this model, we established a canonical log link function and used the Poisson distribution (Crawley 2007). All models were run in the program R (version 3.2.4.) using the package MASS (Ripley *et al.* 2017). Taking into account all the predictors, an analysis for the selection of the best model was carried out using the "dredge" function of the package MuMIn (Barton 2017). This produces a series of potential combinations of the predictors previously specified. The best model for both the presence and richness of parasites was chosen according to the Akaike information criterion (Burnham *et al.* 2001). The significance of the best model to explain the data was evaluated with an analysis of deviance, which compares the goodness of fit of the best model vs. a null model that includes only the intercept. A plot of the significant effects of generalized linear models was drawn with the "effects" package (Fox *et al.* 2016) in R. Three stool samples belonging to one group were excluded from these analyses due to missing ecological information about the fragment. Parasitic prevalence values were calculated in the program Quantitative Parasitology 3.0 (Rózsa *et al.* 2000).

Results

This population of black howler monkeys showed a 39.1 % prevalence of intestinal parasites (95% CI: 27.1 to 52.1). On average, howler monkeys were infected by 0.5 ± *SE* 0.08 taxa (range: 0 to 3 taxa). The taxa found were *Trypanoxyuris* sp. (Oxyuridae), *Controrchis* sp. (Dicrocoeliidae), and an unidentified trematode of the family Dicrocoeliidae (Figure 2). *Trypanoxyuris* sp. eggs measured 47.9 µm ± *SD* 4.0 × 23.8 µm ± *SD* 1.4; *Controrchis* sp. eggs measured 43.1 µm ± *SD* 3.3 × 23.5 µm ± *SD* 1.4; and eggs of the unidentified trematode measured 37.7 µm ± *SD* 4.1 × 22.0 µm ± *SD* 1.0. *Controrchis* sp. was the most prevalent parasite (31.6 %), whereas the unidentified trematode and *Trypanoxyuris* sp. showed prevalence rates of 11.7 % and 5.0 %, respectively. Table 1 shows the prevalence of each taxon according to host sex and site of collection. The prevalence of intestinal parasites in black howler monkeys approximately doubled in individuals inhabiting fragments located more than 500 m away from the nearest village (Table 2). Considering fragment size, we found a similar prevalence of intestinal parasites in howler monkeys living in fragments varying from < 1 ha to 50 ha, but this increased by 43 % in larger fragments (>50-1200 ha) (Table 2).

The model found to best predict the presence of GI parasites considers the distance between fragments and closest village, as well as fragment size (Table 3). The analysis of deviance showed that the residual model including these two predictors significantly differed from the null model (χ^2 = 6.4; d.f. = 2; P = 0.04). A generalized linear model indicated that the distance between forest fragments and the closest villages significantly predicted the presence of GI parasites (β = 0.55 ± *SE* 0.28, z = 2.0, P = 0.05). Figure 3 shows that the probability of intestinal parasitic infection increases with the distance between a fragment and the closest village. Although fragment size is an element of the best model, this predictor had no significant effect on the presence of parasites (β = 0.48 ± *SE 0.30*, z = 1.6, P = 0.11). Other predictors considered in this analysis had no significant effects on the presence of intestinal parasites.

Table 2. Prevalence of gastrointestinal parasites in black howler monkeys (*Alouatta pigra*) of Balancán, Tabasco, Mexico, in relation to distance between forest fragments and human settlements, and to fragment size.

Predictive variables	Number of Fragments	Prevalence (%)	n^a
Distance between fragments and the nearest village			
100-250 m	5	29.4	17
>250-250 m	6	26.7	14
>500-1,000 m	8	50.0	12
> 1,000 m	10	56.3	19
Range of fragment sizes			
0.01-10 ha	16	37.9	32
>10-50 ha	9	36.4	22
>50-1200 ha	5	55.6	11

[a] number of stool samples collected

Table 1. Prevalence of three taxa of gastrointestinal parasites associated with the sex of black howler monkeys (*Alouatta pigra*) inhabiting forest fragments in Balancán, Tabasco, Mexico.

			Trypanoxyuris sp.		*Controrchis* sp.		Unidentified trematode		
Fragment	Size (ha)	Distance (m)	Male	Female	Male	Female	Male	Female	n^a
1	0.01	250	0	0	0	20	0	0	5
2	0.01	2,500	0	0	0	0	0	0	2
3	0.2	300	0	0	0	0	0	0	2
4	0.8	NA	0	0	0	0	0	0	3
5	1.4	500	0	0	0	0	0	0	1
6	1.5	950	0	0	100	0	0	0	1
7	1.9	600	0	0	50.0	0	0	0	2
8	2.1	870	0	0	0	100	0	0	1
9	2.5	1,580	0	0	0	100	0	100	1
10	2.8	120	0	33.3	0	33.3	0	0	3
11	3.8	1,019	0	0	100	0	0	0	1
12	4.1	200	0	0	0	0	0	0	1
13	4.5	670	0	0	0	0	100	0	1
14	4.7	1,214	0	0	0	0	0	0	1
15	4.9	2,400	0	0	100	0	0	0	2
16	6.7	400	0	0	20.0	0	0	0	5
17	11.2	2,500	50.0	0	50.0	0	0	0	2
18	14.5	708	0	0	0	50.0	0	0	2
19	17.0	780	0	0	0	0	0	0	1
20	21.9	2,408	0	0	0	0	0	50.0	2
21	24.4	100	0	0	14.2	28.5	14.2	14.2	7
22	25.0	400	0	0	0	0	0	0	1
23	26.6	1,381	0	0	33.3	33.3	33.3	0	3
24	30.0	400	0	0	0	0	0	0	1
25	39.0	560	0	0	0	0	0	0	3
26	76.9	250	0	0	0	0	0	0	1
27	166.0	1,235	0	0	0	0	0	100	1
28	200.0	1,200	0	0	0	0	0	0	4
29	288.5	950	0	0	0	0	0	0	1
30	1,200.0	455	0	0.25	0	50	0	0	4

[a] number of stool samples collected

NA: Information not available

Ecological density was the best predictor of parasite richness in the model selection analysis; however, this model had no significant effects (analysis of deviance: χ^2 = 2.4; d. f. = 1; P = 0.12). The other predictors considered also showed no significant effects on parasite richness.

Discussion

In the present investigation, we conducted an ova and parasite stool study to assess the effects tropical forest disturbance on parasitic infection patterns of in black howler monkeys threatened with extinction. We found that as the extent of disturbance increases — estimated through the proximity of human settlements to forest fragments — the presence of parasites in this population of primates

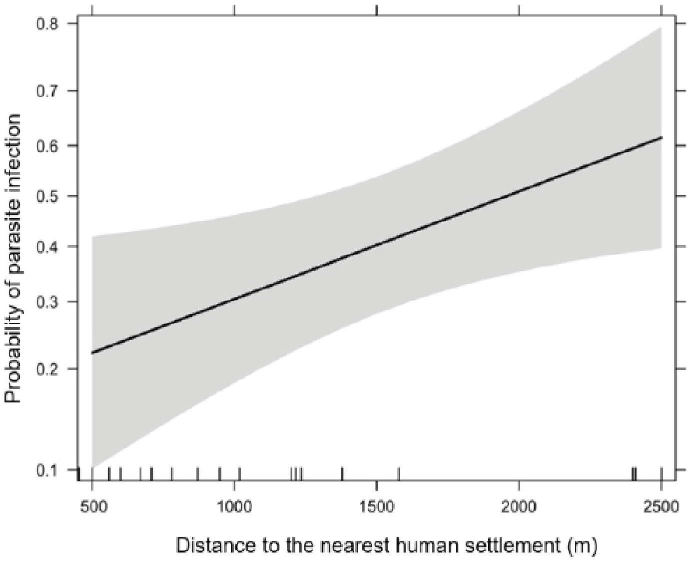

Figure 3. Relationship between distance (m) from forest fragments to the nearest village and likelihood of intestinal parasitic infection in black howler monkeys living in Balancán, Tabasco, Mexico. The shaded area represents 95 % confidence intervals.

decreases. Also, a higher prevalence of parasites was observed in monkeys inhabiting fragments further away from villages. These findings suggest that infection rates, and probably also the transmission processes of parasites infecting black howler monkeys, are disrupted as anthropogenic activities are intensified in the proximity of fragments.

In this population of primates, we also found that parasite richness (*n* = 3 taxa) is low relative to the one reported for howler monkey populations living in undisturbed environments (Table 4). In these populations, individual monkeys carry a higher number of parasite species, ranging from 4 to 9 taxa. In contrast to our results, a study carried out in forest fragments in the southern region of the municipality of Balancán, Tabasco, reported 13 taxa of parasites, 11 of which showed a prevalence of 2 to 10 % (Alvarado-Villalobos 2015). Despite the higher number of taxa found at that site, the low prevalence indicates that infections involving multiple taxa are rare in the area. It is possible that the variability observed in the recovery of parasite species partly resulted from the different parasitological techniques used in other investigations (Alvarado-Villalobos *et al.* 2017); however, our results are consistent with the richness reported for other monkey populations inhabiting fragmented areas (Table 4).

The low probability of occurrence of parasites in the proximity to human settlements and the low richness recorded may be associated to the high degree of ecosystem disturbance and changes of land use in the municipality of Balancán, Tabasco. In particular, this area is recurrently affected by fires associated to pasture burning and practices such slash-and-burn in cropland areas surrounding forest fragments (Manjarrez Muñoz *et al.* 2007). These activities alter the microclimate of the forest floor, considerably reducing soil moisture and increasing desiccation (Laurance 2004). These changes have been reported to reduce the survival of infectious stages of parasites (Bloemers *et al.* 1997). The low probability of occurrence of parasites in this population of howler monkeys likely reflects the synergy resulting from the reduction in the parasite-host encounter rates (Bordes *et al.* 2015) and the low resilience of parasites to survive in a highly disturbed ecosystem.

The parasites reported in this research are considered to be specialists, as they have been found specifically in a monophyletic group of Neotropical arboreal primates (family Atelidae; Solórzano-Garcia and Pérez-Ponce de León 2017). It has been proposed that host-specialized parasites tend to be more susceptible to extinction compared with generalist parasites, which manage to persist in the environment by parasitizing a greater variety of hosts belonging to different evolutionary lineages (Farrell *et al.* 2015). In this context, the decline of howler monkey populations may also lead to the loss of parasites that infect only this endemic primate species. For instance, Solórzano-García *et al.* (2016) have recently described the species *Trypanoxyuris pigrae*, a nematode that parasitizes specifically *A. pigra* and that may be threatened of extinction along with its host.

On the other hand, the high discontinuity of the canopy in some forest fragments in this area forces howler monkeys to descend to the ground to move across treeslocated either within fragments or in the matrix of fragmented landscapes (Pozo-Montuy and Serio-Silva 2007). It has been proposed that this shift in behavior increases the likelihood of contact between primates and infectious stages of parasites deposited in soil and whose primary hosts are humans or livestock (Rwego *et al.* 2008; Zommers *et al.* 2013). However, in this study we found none of the parasite species reported in humans or domestic animals. In a recent research, Helenbrook *et al.* (2015) explored the possibility of cross-transmission of the parasite *Blastocystis* sp. between mantled howler monkeys (*A. palliata aequatoria-*

Table 3. Results of the analysis for the selection of models that predict the presence of gastrointestinal parasites in black howler monkeys (*Alouatta pigra*) in Balancán, Tabasco, Mexico.

Model	D. F.	Log-likelihood	AICc	ΔAICc	Weight
Distance + Size	3	-37.178	80.8	0.00	0.058
Distance + Density + Sex	4	-36.206	81.1	0.36	0.048
Distance + Size + Density	4	-36.354	81.4	0.65	0.042
Distance	2	-38.679	81.6	0.78	0.039
Distance + Density	3	-37.592	81.6	0.83	0.038
Distance + Sex	3	-37.651	81.7	0.95	0.036
Distance + Size + Sex	4	-36.662	82.1	1.27	0.031
Distance + Size + Density + Sex	5	-35.547	82.2	1.42	0.028
Distance + Density + Seasonality (sine) + Sex	5	-35.564	82.2	1.45	0.028
Distance + Seasonality (cosine)	3	-37.971	82.4	1.59	0.026
Distance + Density + Seasonality (sine)	4	-36.954	82.6	1.85	0.023
Density + Seasonality (sine)	3	-38.103	82.6	1.85	0.023
Distance + Size + Seasonality (sine)	4	-36.956	82.6	1.86	0.023
Size	2	-39.219	82.6	1.87	0.023
Distance + Seasonality (sine)	3	-38.139	82.7	1.92	0.022
Seasonality (sine)	2	-39.289	82.8	2.00	0.021

Models are listed from lowest to highest value of the Akaike Information criterion (AICc)

Table 4. Richness and prevalence of gastrointestinal parasites in different populations of black howler monkeys (*Alouatta pigra*)

Habitat	Site[a]	Number of individuals	Number of stool samples	Richness	Range of prevalence	Taxa[b]	Reference
Undisturbed	LAR, CBS	167	167	6	2.0 - 80.8	1, 12, 20, 30, 31, 32	Eckert *et al.* 2006
	CBS, CBWS, PA, CK	50	283	4	27.0 – 81.0	6, 12, 18, 28	Vitazkova and Wade 2006
	MA	15	151	8	25.0 – 35.0	3, 12, 13, 17, 21,24, 25, 33	Stoner and González Di Pierro 2006
	CK, ES, PA, MA	137	137	4	2.5 – 17.0	6, 23, 27, 37	Trejo-Macías *et al.* 2007
	PT, TG	8	8	9	12.5 – 50.0	2, 7, 8, 9, 11, 13, 15, 16, 18	Bonilla Moheno 2002
Fragmented	MR	17	221	5	11.1 - 88.9	1, 5, 26, 27, 36	Behie *et al.* 2014
	MC	22	22	3	7.7 – 50.0	23, 24, 35	Trejo-Macías *et al.* 2007
	PC	43	218	3	9.1 – 73.0	6, 9, 27	Alvarado-Villalobos 2010
	ES	15	258	5	0.7 – 49.0	6, 13, 22, 27, 34	Martínez-Mota *et al.* 2017
	PL, PH	3	3	6	33.3 - 100	2, 7, 11, 13, 16, 18,	Bonilla Moheno 2002
	SB	41	492	13	2.4 – 83.0	1, 3, 4, 5, 9, 10, 12, 14, 17, 19, 24, 27, 30	Alvarado-Villalobos 2015
	T, C	10	46	4	2.2 - 23.9	24, 27, 28, 29	Solórzano-García and Pérez-Ponce de León 2017
	MB	65	65	3	5.0 - 31.6	5, 27, 34	This study

[a] LAR: Lamanai Archaeological Reserve, Belize; CBS: Community Baboon Sanctuary, Belice; CBWS: Cockscomb Basin Wildlife Sanctuary, Belice; PA: Palenque, Chiapas; CK: Calakmul, Campeche; MA: Montes Azules, Chiapas; ES: Escárcega, Campeche; PT: Petcacab, Quintana Roo; TG: Tres Garantías, Quintana Roo; MR: Monkey River, Belice; MC: Marqués de Comillas, Chiapas; PC: Playas de Catazajá, Chiapas; PL: Punta Laguna, Quintana Roo; PH: Pacchen, Quintana Roo; SB: Sur de Balancán, Tabasco; MB: Municipio Balancán, Tabasco; T: Tabasco; C: Chiapas.

[b] 1 *Ascaris* sp.; 2 *Balantidium coli*; 3 *Blastocystis* sp.; 4 *Chilomastix* sp.; 5 *Controrchis* sp.; 6 *C. biliophilus*; 7 *Cryptosporidium* sp.; 8 *Cyclospora* sp.; 9 *Eimeria* sp.; 10 *Endolimax* sp.; 11 *E. nana*; 12 *Entamoeba* sp.; 13 *E. coli*; 14 *E. histolytica*; 15 *E. hartmanni*; 16 *E. poleki*; 17 *Enterobius* sp.; 18 *Giardia* sp.; 19 *Hymenolepis nana*; 20 *Iodamoeba butschlii*; 21 *Isospora* sp.; 22 *Parabronema* sp.; 23 *Raillietina* sp.; 24 *Strongyloides* sp.; 25 *Trichostrongyloides* sp.; 26 *Trichuris* sp.; 27 *Trypanoxyuris* sp.; 28 *T. minutus*; 29 *T. pigrae*; 30 Reported as oxyurid; 31 Nematode larvae; 32 Unidentified trematode; 33 Unidentified trematode; 34 Unidentified trematode; 35 Unidentified trematode; 36 Reported as Trichostrongylidae; 37 Unidentified parasite.

lis) and humans coexisting in close proximity, but found no evidence of transmission between species. Pedersen and Davies (2009) suggest that the transmission of parasites between host species is more likely to occur in phylogenetically closer taxa. As the evolutionary relationship between monkeys and either humans or domestic animals is distant (Perelman *et al.* 2011), this could explain the absence of parasites shared between monkeys and humans/livestock despite the frequent contact of this population of primates with human settlements and farming activities in the area. Further stool ova and parasite studies using molecular techniques may provide compelling information concerning the parasite transmission processes between black howler monkeys and other species.

Our results contrast with those obtained in other studies that have investigated the parasite ecology of wild primates. For example, in colobus (*Procolobus rufomitratus*) and macaque (*Macaca silenus*) monkeys, it has been found that individuals who live in highly disturbed forests show higher rates of GI parasitism (Gillespie and Chapman 2008; Hussain *et al.* 2013). These shifts in susceptibility to parasitic infections are seemingly related to nutritional stress (Chapman *et al.* 2015). However, recent studies on black howler monkeys show that these primates are able to prevent nutritional stress by consuming food items of different nutritional quality and energy content, supplementing the diet with food gathered across the landscape matrix (Pozo-Montuy *et al.* 2013; Martinez-Mota *et al.* 2016). An alternative hypothesis is that the intake of secondary metabolites from plants through the diet might reduce parasitic infections (Forbey *et al.* 2009). *Tinto* (*H. campechianum*) is a plant frequently consumed by howler monkeys in the study area, which contains secondary compounds such as phenols, flavonoids and gallotannins (Kandil *et al.* 1999). These compounds may negatively affect the viability of parasites, as previously reported in experimental studies (Athanasiadou and Kyriazakis 2004). This hypothesis deserves further investigation. The trend observed in our study indicates that changes in host-parasite dynamics in relation to habitat disturbance are specific for each biological system (Salkeld *et al.* 2013).

Despite the fact that parasitic infections are often associated with a negative or poor health condition in animals, parasites are members of healthy ecosystems, functioning as a link in food webs, and making a significant contribution to global biodiversity (Marcogliese 2005; Shea *et al.* 2012; Sukhdeo 2012). Our study suggests that habitat disruption affects not only populations of appealing species, but also the persistence of parasite communities, which is reflected on the patterns of gastrointestinal parasite infections in wild primates that depend strictly on tropical forests.

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Ectoparasites (Polyctenidae, Streblidae, Nycteribiidae) of bats (Mammalia: Chiroptera) from the Caribbean region of Colombia

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Bats are hosts of a high taxonomic diversity of ectoparasites. Six hundred eighty seven insect species have been reported as bat ectoparasites, belonging to orders Dermaptera, Lepidoptera, Diptera and Siphonaptera (Marshall 1982). This study lists an inventory of bat ectoparasites found in fragments of Tropical Dry Forest on the Caribbean coast of Colombia. The study was conducted in the Department of Cordoba in four farms with fragments of Tropical Dry Forest. Bats were captured using mist nets and were collected and stored in plastic bags for subsequent examination in the laboratory. Ectoparasites were stored in alcohol and identified using a stereomicroscope and taxonomic keys. Two hundred fifty one bats belonging to 21 species were captured. The most abundant family was Phyllostomidae, followed by Emballonuridae, Noctilionidae, Vespertilionidae and Molossidae. Twelve genera of ectoparasites were found, belonging to families Streblidae, Nycteribiidae and Polyctenidae. Streblidae was the most abundant family and included the largest number of species. Thirty five percent of bats examined were hosts to at least one ectoparasite species. In this study, carried out in fragments of tropical dry forest in Cordoba, Colombia, we recorded dipterans in 17 out of 21 bat species. Hemypteran ectoparasites of the family Polyctenidae were found in *Molossus molossus* only. Eighty seven individual dipterans were found among 51 *Carollia perspicillata* specimens, which is consistent with the high parasitism levels previously reported. The bat species *C. brevicauda, P. discolor, U. bilobatum* and *C. perspicillata* carried the highest number of ectoparasite species.

Los murciélagos son hospederos de numerosas especies de ectoparásitos pertenecientes a diversos grupos taxonómicos. Se conocen 687 especies de insectos ectoparásitos de murciélagos pertenecientes a los órdenes Dermaptera, Hemiptera, Diptera y Siphonaptera. El objetivo de esta investigación fue realizar un inventario de los ectoparásitos de murciélagos presentes en fragmentos de Bosque Seco Tropical (BST) en la costa Caribe Colombiana (Córdoba, Colombia). El estudio se realizó en el departamento de Córdoba en cuatro fincas con fragmentos de BST. Los murciélagos fueron capturados utilizando redes de niebla, y posteriormente colectados y almacenados en bolsas de plástico para su posterior revisión en el laboratorio; los ectoparásitos fueron almacenados en alcohol e identificados utilizando un microscopio estereoscópico y claves taxonómicas. Se capturaron 251 murciélagos, distribuidos en 21 especies. La familia más abundante fue Phyllostomidae, seguida de las familias Emballonuridae, Noctilionidae, Vespertilionidae y Molossidae. Se encontraron 12 géneros de ectoparásitos, distribuidos en las familias Streblidae, Nycteribiidae y Polyctenidae. La familia Streblidae fue la más abundante y presentó la mayor riqueza de especies. El 35 % de los murciélagos estudiados presentaron al menos un ectoparásito. En la presente investigación se encontró que de 21 especies, 17 presentaban dípteros. La especie *Molossus molossus* fue la única encontrada con ectoparásitos hemípteros de la familia Polyctenidae. En 51 individuos revisados de *Carollia perspicillata* se encontraron 87 dípteros, lo que coincide con los altos valores de parasitismo por moscas previamente reportados para esta especie. Las especies *C. brevicauda*, *P. discolor*, *U. bilobatum* y *C. perspicillata* presentaron el mayor número de especies de ectoparásitos asociados.

Key words: Caribbean region; Colombia; Cordoba; ectoparasitism; extensive livestock; Phyllostomidae; silvopastoral system; tropical dry forest.

Introduction

Parasites play a key role in the life of the host and often exert a significant selection pressure on them (Hart 1990; Zhang *et al.* 2010). By restraining resource investment in their host, parasites may affect its growth, survival or reproduction (Hart 1990; Mooring *et al.* 2002; ter Hofstede and Fenton 2005; Zhang *et al.* 2010).

The knowledge about external parasites (ectoparasites) of bats provides key information for understanding the biology, systematics and phylogeny of the host (Fritz 1983). In addition, this allows clarifying epidemiological aspects of the transmission of some diseases among bats and is essential for gaining a deeper insight on the ecology and behavior of bats in their shelters (Aguiar *et al.* 2006; Aguiar and Antonini 2011). A total of 687 bat ectoparasite insect species are known for bats, belonging to orders Dermaptera, Lepidoptera, Diptera, and Siphonaptera (Marshall 1982; Schuh and Slater 1995). Six families of these orders are unique to bats (Berlota *et al.* 2005), of which Nycteribiidae, Streblidae and Polyctenidae are those most studied and best known worldwide.

The family Nycteribiidae, which contains approximately 275 species distributed in 12 genera, includes ectoparasites that are exclusive of bats. These are highly-specialized obligated blood-feeding true flies that are wingless and show a spider-like appearance; their legs and small head protrude above the thoracic dorsal surface (Theodor 1967; Whitaker *et al.* 2009). This family is divided into three subfamilies: Archinycteribiinae (1 genus, 3 species); Cyclopodiinae (4 genera, 2 species), which are unique to the eastern hemisphere and are associated with bats of the taxa Pteropodidae; and Nycteribiinae (7 genera, 191 species), which are cosmopolitan. The family Streblidae is distributed worldwide and includes five subfamilies, 32 genera and 227 species described. The majority of streblid flies have wings, but in some genera these are vestigial, while some fully winged forms are poor flyers. Streblids are cosmopolitan flies with a well-established specificity for a host, and the largest number of species thrive in the western hemisphere (Kunz 1976; ter Hofstede *et al.* 2004; Dick and Gettinger 2005; Whitaker *et al.* 2009).

The family Polyctenidae includes bat bugs. These are rarely collected permanent ectoparasites of bats in tropical and subtropical regions around the world (Maa 1964; Marshall 1991; Esberard *et al.* 2005). Little is known about the taxonomy of this family, in which 32 species in five genera have been described (Maa 1964; Marshall 1991). The genus *Hesperoctenes* (16 species) is restricted to the western hemisphere, while the four remaining genera are unique to the Old World, which is apparently the center of origin of this group (Ueshima 1972; Esberard *et al.* 2005). Polyctenid bugs are exclusive parasites of microchiropterans, feeding on their blood (Maa 1964; Ueshima 1972; Marshall 1991), and are highly host-specific (Ryckman and Casdin 1977; Whitaker *et al.* 2009).

In Colombia, between the decades of 1940 and 1970, some descriptions and inventories of parasite species and their hosts were carried out (Boshell and Kerr 1942; Marinkelle 1967; Clark 1967; Machado-Allison and Antequera 1969; Marinkelle and Grose 1981). Tasmitt and Fox (1970) elaborated a list of ectoparasites of bats for Colombia and Puerto Rico, recording 28 species parasitizing 18 bat species for Colombia. The study of ectoparasites of bats in the country was subsequently abandoned. In 2012, Calonge-Camargo evaluated the ectoparasites of bats in fragments of tropical dry forest subjected to conventional livestock and silvopastoral management in the Department of Córdoba, and observed changes in the species composition of ectoparasites and their degree of specificity. Herrera-Sepúlveda (2013) compared the ectoparasite load in harems and mixed groups of a *Carollia perspicillata* population in Cueva Macaregua (Santander), finding higher diversity and richness of ectoparasites in harems versus mixed groups. Tarquino-Carbonell *et al.* (2015) elaborated an inventory of ectoparasites of bats in a gallery forest in Vereda El Chorrillo (Tolima), and reported 24 species of ectoparasites associated with 14 bat species. Dick *et al.* (2016) developed a catalog of parasites of the family Streblidae in Colombia, including 73 species distributed in 19 genera and 3 subfamilies. Duran *et al.* (2017) recorded 17 species belonging to 8 genera of Streblidae that parasitize 19 bat species of five families in the Department of Sucre. Despite the recent interest in the study of bat ectoparasites in Colombia, no studies are currently available for environments subjected to extensive livestock farming in the Caribbean zone of Colombia. This paper lists the ectoparasites of bats found in fragments of tropical dry forest (BST) in the Caribbean region of Colombia (Cordoba, Colombia).

Materials and Methods

Study area. Sampling was conducted in four BST fragments located in the Department of Cordoba, northern Colombia, between 9° 26′ 16″ - 7° 22′ 05″ N and 74°47′43″ -76°30′01″ W. The main vegetation types are tropical dry forest (BST) in the low zone, and tropical moist forest (BHT) in higher elevations (Racero-Casarrubia *et al.* 2015). The climate is tropical warm humid, with mean temperature of 28 °C and mean annual precipitation of 1200 mm with unimodal distribution, showing a dry season from December to March, and a rainy season from April to November (Racero-Casarrubia *et al.* 2017). Two of the fragments were located in extensive livestock farms subjected to silvopastoral management (tree planting for timber production; Las Palmeras: fragment area ~45 ha, and San Lorenzo: fragment area ~90 ha), and two in extensive livestock farms subjected to conventional management (pastures with scarce shrub or tree cover; Guacamayas: fragment area ~34 ha, and Chimborazo: fragment area ~55 ha; Figure 1).

Collection of Bats and Ectoparasites. Sampling was carried out from August 2011 to January 2012. Bats were captured using 14 mist nets. Ten nets were placed inside of each fragment; in order to broaden the sampling coverage in each production system, four nets were placed in the matrix adjacent to each fragment, at a distance of 20 meters maximum. For three consecutive nights, nets were opened from 6:00 p.m. to 6:00 a.m., reviewed at half-hour intervals, and relocated occasionally within the forest frag-

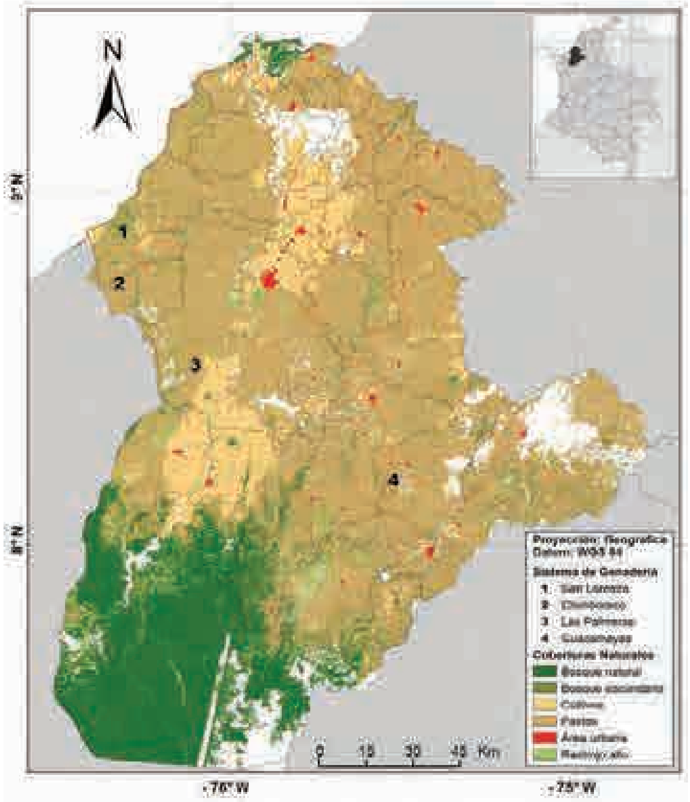

Figure 1. Map of natural cover and localities in the study area: San Lorenzo (Los Córdobas), Chimborazo (Canalete), Las Palmeras (Montería) and Guacamayas (Buenavista), in the Department of Córdoba, Colombia (modified from Ballesteros-Correa, 2015).

ment. Seven field trips were conducted to each farm, for a total of 21 sampling nights/farm. Cumulative species curves were drawn and fitted to the Clench model to obtain an estimate of the expected number of bat and ectoparasite species (Figure 2), taking the number of specimens collected as a unit of effort (Figure 3).

Bats were killed directly on the mist net by craniocervical dislocation using forceps (Sikes 2016), and were deposited in double plastic bags, avoiding direct contact to minimize the loss of ectoparasites (Whitaker *et al.* 2009). Subsequently, bats were injected with 70 % alcohol (through the bag) in the abdomen to prevent decomposition. The preserved specimens were transported to the Laboratory of Functional Ecology at Pontificia Universidad Javeriana, where each individual specimen was examined under a Krüss stereomicroscope (240V AC 12V/20W) To this end, specimens were placed on a white sheet and examined using fine tweezers and a dissecting needle to sort ectoparasites into separate containers. Each bat specimen was reviewed twice to maximize the detection of the ectoparasites. Ectoparasites collected were preserved in 70 % alcohol (Wenzel *et al.* 1966; Whitaker *et al.* 2009). Bats and ectoparasites were deposited in the collection of mammals of the Museo Javeriano de Historia Natural (MPUJ-MAMM:1911-2162) at Pontificia Universidad Javeriana, Bogotá.

Identification of Parasites and Bats. Dipterans and hemipterans were preserved in alcohol and some were cleared with glycerin for identification. Specimens were identified using the keys of Wenzel (1976), Guerrero (1993), and Graciolli and Carvalho (2001), with the assistance of Dr. Ricardo Guerrero (Universidad Central de Venezuela; Guerrero 1997). Bats were identified using the keys of Fernández *et al.* (1988), Emmons and Feer (1997), Tim and LaVal (1998), Linares (1998), Laval and Rodríguez-H. (2002), and Gardner (2007).

Data Analysis. For the purposes of this work, bat parasitism patterns were evaluated at the regional level for the BST in the Colombian Caribbean, so data from the four farms were pooled together. The parasite-host association was evaluated by estimating the rates of prevalence and mean intensity (Bush *et al.* 1997). Prevalence was calculated as the number of bats parasitized with one or more individuals of a given species of parasite, divided by the number of hosts examined for that parasite species, then multiplying the resulting figure by 100 (Bush *et al.* 1997). Intensity was calculated as the number of parasites per bat (Christie *et al.* 2003), and mean intensity as the mean intensity of a parasite species relative to the total number of infected individuals of a particular bat species (Bush *et al.* 1997).

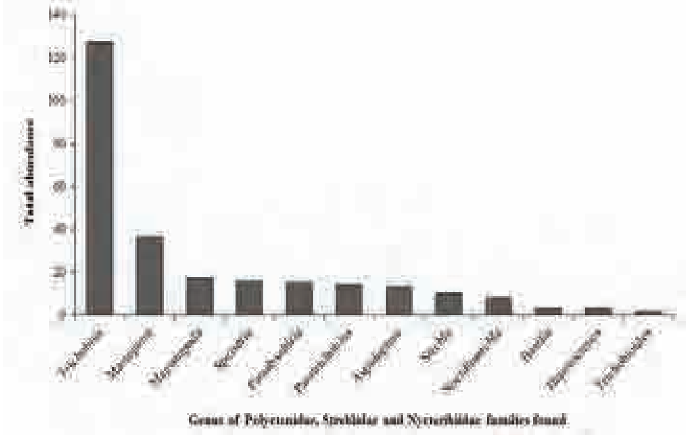

Figure 2. Total abundance of the genera of ectoparasites found in the bats studied.

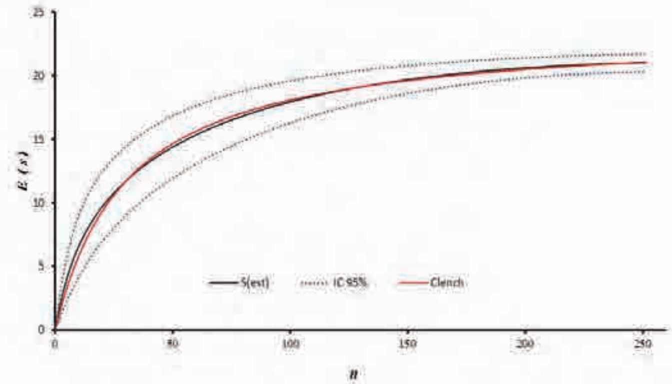

Figure 3. Species accumulation curve S(est) for bats, fitted to the Clench model (red line) for species representativeness. The blue dotted line represents the 95% confidence interval. *E(S)* = Expected Number of species. *n* = Number of specimens.

Results

A total of 251 bats were caught, belonging to 21 species and five families. The most abundant family was Phyllostomidae (94 % of total catch), followed by Emballonuridae (2.3 %), Noctilionidae (0.8 %), Vespertilionidae (0.8 %), and Molossidae (0.8 %). *Carollia perspicillata* was the most abundant species (*n* = 51), followed by *Artibeus planirostris* (*n* = 41), and *Uroderma bilobatum* (*n* = 35; Table 1). The least abundant species were mainly insectivorous bats. Correspondingly,, 12 genera of ectoparasites were recorded, distributed in three families. The family Streblidae showed the highest taxonomic richness (10 genera) and the highest abundance. *Trichobius* was the most abundant genus (49 %), followed by *Mastoptera* (14 %), *Megistopoda* (7 %), and *Speiseria* (6 %) (Figure 2). The six remaining genera, *i.e. Noctiliostrebla, Paradyschiria, Trichobioides, Paratrichobius Strebla,* and *Aspidoptera,* accounted for 24 % of total abundance (Table 1; Figure 2). The sampling representativeness for bats, fitted to the Clench model, was 91 % (Figure 3); for ectoparasites, an 85 % sampling representativeness was estimated (Figure 4).

We found three individuals each of the genera *Basilia* (Nycteribiidae) and *Herperoctenes* (Polyctenidae; Table 1). The bat species *Carollia brevicauda* and *Phyllostomus discolor* showed the largest number of associated ectoparasite species (four species each; *C. brevicauda*: *Speiseria ambigua*, *Strebla guajiro*, *Trichobius joblingi,* and *Trichobius persimilis*; *P. discolor*: *Strebla hertigi*, *Trichobioides perspicillatum*, *Trichobius costalimai* and *Trichobius longipes*), followed by *U. bilobatum* (*Paratrichobius dunni*, *P. salvini* and *P.* sp.) and *C. perspicillata* (*Speiseria ambiguous*, *S. guajiro* and *T. joblingi*), with three species each (Table 1).

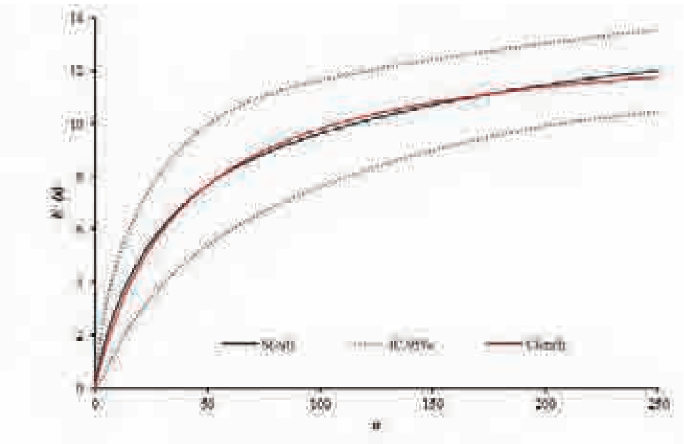

Figure 4. Cumulative curve for ectoparasites S(est) fitted to the Clench model (red line) for species representativeness. The blue dotted line represents the 95% confidence interval. *E(S)*= Expected Number of species. *n* = Number of specimens.

The total number of individuals with ectoparasites was 90, representing a total prevalence of 36 %. The prevalence of the ectoparasites *Noctiliostrebla maai*, *Paradischiria parvuloides*, *Mastoptera minuta*, *Trichobius dugesioides, Mastoptera guimaraesi*, and *T. longipes* in their respective specific hosts was 100 % (Table 1). In contrast, *Strebla guajiro*, *Speiseria ambigua*, *Trichobius dugesii*, *Megistopoda aranea*, *Paratrichobius longicrus,* and *P. dunni* showed a prevalence lower than 20 % in specific hosts (Table 1).

The mean intensity of each ectoparasite species in specific hosts ranged between 0.1 and 10.5. *Mastoptera guimaraesi* and *Trichobius longipes* showed higher values, with a mean intensity of 10.5, while the genus *Paratrichobius* sp. showed the lowest values (Table 1).

Discussion

The bat species with the lowest ectoparasite abundance were mostly insectivorous; this finding is hardly surprising when using mist nets only, as these nets tend to be readily detected by bats and many fly above the canopy (Bergallo *et al.* 2003). Thirty six percent of the bats studied had at least one ectoparasite. In the Department of Tolima, Tarquino *et al.* (2015) found that only 8 (38%) of the 21 bat species captured had dipterans. This study, carried out in fragments of tropical dry forest in Cordoba, found that 17 (81%) of 21 bat species had dipterans. This difference may be due to the sample processing methods used, since dipterans tend to escape readily (Whitaker *et al.* 2009) when the host is manipulated. This indirect disturbance, named "transfer of disturbance" by Wenzel *et al.* (1966), is common among Streblidae parasites of bats captured with mist nets.

Molossus molossus was the only species found with hemipteran ectoparasites of the family Polyctenidae. It has already been reported that the members of this family of ectoparasites are unique to the family Molossidae in the Neotropics (Marshall 1982).

Eighty seven dipterans belonging to three species were found in the 51 specimens of *C. perspicillata* examined. This bat species has been reported to show high parasitism levels, mainly of flies (Komeno and Linhares 1999), although ter Hofstede *et al.* (2004) reported low ectoparasitism levels in this bat species in Belize. The high abundance of ectoparasites typically found in this species could be due to its distinctive social structure (McCracken and Wilkinson 2000). It has been reported that *C. perspicillata* usually shows a harem-type social structure (McCracken and Wilkinson 2000); it has been suggested that harems promote the exchange of ectoparasites between individuals that perch together (McCracken and Wilkinson 2000). In a separate study, Herrera-Sepulveda (2013) found in Macaregua cave (Santander, Colombia) that ectoparasitism was higher (richness and diversity) in individuals living in harems, which show a closer physical contact, relative to individuals living in mixed groups where the extent of physical contact is lower. In addition, species that tend to group together in perching sites may bear a variable number of ectoparasites, depending on the extent of allogrooming within the group (Kerth 2008; Altringham 1996). Separately, Wenzel *et al.* (1966) explained that the high diversity of ectoparasites in *C. perspicillata* results from its high ecological flexibility, that is, from the wide range of ecological conditions where it thrives.

No pattern was evident regarding the bat species showing the greatest infestation level by ectoparasites in Neotropical regions. Some studies have reported that the majority of dipteran species are associated with the genus *Artibeus* (Anderson and Filho 2006; Azevedo and Linardi 2002; Camilotti *et al.* 2010). In Brazil, Berlota *et al.* (2005) and Graciolli *et al.* (2006) reported that *Sturnira lilium* is the species with the highest number of etoparasite individuals and species. In Paraguay, Dick and Gettinger (2005) found that the bat species with the highest number of flies were *S. lilium*, *Noctilio albiventris* and *Desmodus rotundus*.

In this work, *C. brevicauda* showed the highest richness of ectoparasites, with four species. In the work carried out by Duran *et al.* (2017) in a tropical dry forest in Sucre, Colombia, *D. rotundus* and *A. planirostris* showed the greatest richness of ectoparasites, with seven species each. In this study, *P. hastatus*, *N. albiventris*, *S. lilum*, and *L. brasiliense,* respectively, followed *C. perspicillata* in terms of the amount of dipterans (number of individuals). The variation in ectoparasite richness per species may be due to differences in the composition and structure of the local host assemblages studied. According to Rui and Graciolli (2005), differences in ectoparasite assemblages in a given host species may also be attributed to regional differences in the species composition of bats, the biogeographic history of the area, as well as the lack of specificity of ectoparasites. On the other hand, the local environmental conditions, perching behavior of each species, as well as its social structure, may all influence these differences. The feeding habits and foraging pattern may also affect the degree of ectoparasitism, since the blood chemistry changes according to the type of food consumed by the host (Emerson and Roark 2007).

Table 1. List of bats and ectoparasites inhabiting four fragments of BST in the Caribbean region of Colombia. Abbreviations: *n* = Sample size, Nm = Number of parasitized bats, Ne = Number of bats carrying each ectoparasite species, P = Prevalence, Mi = Mean intensity.

Bat				Ectoparasite			
Family and species	**n = 251**	**Nm**	**Ne**	**Species**	**n**	**P(%)**	**Mi**
Emballonuridae							
Saccopteryx leptura	6	0	0				
Noctilionidae							
Noctilio albiventris	2	2	2	*Noctiliostrebla maai*	8	100	4.0
			2	*Paradyschiria parvuloides*	15	100	7.5
Phyllostomidae							
Carollia brevicauda	13	10	3	*Speiseria ambigua*	5	23	0.5
			2	*Strebla guajiro*	2	15	0.2
			7	*Trichobius joblingi*	11	53	1.1
			3	*Trichobius persimilis*	4	23	0.4
Carollia castanea	3	1	1	*Trichobius joblingi*	1	33	1.0
Carollia perspicillata	51	31	9	*Speiseria ambigua*	11	17	0.3
			5	*Strebla guajiro*	7	9	0.2
			28	*Trichobius joblingi*	63	55	2.0
Desmodus rotundus	9	4	4	*Trichobius parasiticus*	6	44	1.5
Glossophaga soricina	8	1	1	*Trichobius dugesii*	1	12	1.0
Lophostoma brasiliense	3	3	3	*Mastoptera minuta*	11	100	3.6
			2	*Trichobius silvicolae*	7	66	2.3
Lophostoma silvicolum	6	3	3	*Mastoptera minuta*	4	50	1.3
Mimon crenulatum	3	2	2	*Basilia sp.*	3	66	1.5
Phyllostomus discolor	2	2	1	*Strebla hertigi*	1	50	0.5
			1	*Trichobioides perspicillatum*	1	50	0.5
			1	*Trichobius costalimai*	6	50	3.0
			1	*Trichobius longipes*	4	50	2.0
Phyllostomus cf. elongatus	1	1	1	*Trichobius dugesioides*	3	100	3.0
Phyllostomus hastatus	2	2	2	*Mastoptera guimaraesi*	21	100	10.5
			2	*Trichobius longipes*	21	100	10.5
Artibeus lituratus	26	2	2	*Megistopoda aranea*	1	8	0.5
Artibeus planirostris	41	5	5	*Megistopoda aranea*	6	12	1.2
			1	*Paratrichobius longicrus*	1	2	0.2
Dermanura phaeotis	6	0	0				
Platyrrhinus helleri	12	0	0				
Sturnira lilium	17	9	6	*Aspidoptera delatorrei*	13	35	1.4
			6	*Megistopoda próxima*	10	35	1.1
Uroderma bilobatum	35	11	2	*Paratrichobius dunni*	4	6	0.3
			7	*Paratrichobius salvini*	7	20	0.6
			2	*Paratrichobius* sp.	2	6	0.1
Vespertilionidae							
Rhogeessa io	2	0	0				
Molossidae							
Molossus molossus	3	1	1	*Hesperoctenes* sp.	3	33	3.0

Further studies should be conducted to analyze this relationship, since given that blood chemistry is sensitive to food type, seasonal variations in the diet may also lead to temporary changes in blood chemistry, thus leading to temporal changes in the type, extent, or prevalence of ectoparasites in bats.

At the regional level, the richness and abundance of ectoparasite species are governed by various factors. Species richness can be explained based on the structure of vegetation, abundance of host shelters, and abundance of host species and individuals (Santos *et al.* 2013). Correspondingly, the abundance of ectoparasites may be related to the characteristics of the host, such as body size, sex, age, and social organization, among others (Moore and Wilson 2002, Dick *et al.* 2003, Morand *et al.* 2004, ter Hofstede and Fenton 2005, Patterson *et al.* 2007). The extent to which each factor determines the abundance of ectoparasites is specific to each parasite-host system (Presley and Willig 2008).

The degree of parasitism by flies per individual was found to be higher in *P. hastatus*. We suggest that this may be due to the size of host individuals (which in turn determines the surface area available to accommodate ectoparasites), or also to socializing in harems (potential increase in ectoparasite transfer through physical contact). These bats often use termite mounds, caves and hollow trees as perching sites (Ochoa 1985; Norman 1970). Each harem may comprise 10 to 100 females and a single male, which would facilitate the exchange of parasites among them (Santos *et al.* 2004). Sex ratio, as well as social structure, are factors that contribute to explain the abundance of parasites in a given species. From a work conducted in Paraguay, Presley and Willig (2008) indicated that since harems are common in the Neotropics, adult females are vectors for host-to-host infection (transferring parasites to offspring), hence skewing the infestation preference toward females vs. males.

The parasitism prevalence and mean intensity values reported in this study contrast the findings reported by Tarquino *et al.* (2015) also in BST fragments in the Andean Region, likely because that study captured different host species and recorded different abundance levels per species. It should also be considered that environmental conditions, the configuration of the landscape, sampling techniques, and climate season differed between our work and that of Tarquino *et al.* (2015). Similar to the findings of Tarquino *et al.* (2015), this work recorded a 100 % prevalence for the association between *P. hastatus* and *T. longipes*, and a 50 % prevalence between *C. brevicauda* and *T. joblingi*, although with a very small sample size (*n* = 2) in this case; therefore, sample size should be increased for these species. Separately, *C. perspicillata* showed a mean intensity of 2 for *T. joblinji* in both studies, while *S. lilium* had a mean intensity of 1 for *Megistopoda proxima*.

In conclusion, the present work recorded ectoparasites of families Streblidae, Nycteribidae, aad Polyctenidae. The bat species *C. brevicauda*, *P. discolor, U. bilobatum,* and *C. perspicillata* showed the largest number of associated ectoparasite species. The species of bats with the highest abundance of ectoparasites (*C. perspicillata*, *P. hastatus*, *N. albiventris*, *S. lilum,* and *L. brasiliense*) showed no evident overall characteristic that would explain this finding.

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Diet of the gray fox *Lycalopex griseus* in an agroecosystem of southern-central Chile

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Lycalopex griseus is a canid distributed in Chile and part of Argentina. Although its food habits have been extensively documented, data for anthropized environments are missing. Understanding the response of this species in these habitats is key, given the progressive modification of the landscape throughout its range. The study area is an agroecosystem of southern-central Chile. Scats were collected throughout the study area and analyzed in the laboratory. Food remains in scats were identified to species and quantified, considering the percentage of the various prey categories in terms of both relative frequency and relative biomass. Thirteen categories were found, with rodents dominating in terms of both relative frequency and percent biomass, followed by birds and arthropods. The presence of exotic species in the food spectrum is highlighted, represented by orders Lagomorpha and Rodentia. Plant material was found to a lesser extent. The diversity of preys evidences that *Lycalopex griseus* is mainly generalist in this type of habitat, as arboreal species were scarce in the diet, an expected finding considering the predominance of herbaceous vegetation in the study area. Lagomorphs were poorly represented compared to other latitudes, suggesting segregation with other species.

Lycalopex griseus es un cánido presente en Chile y parte de Argentina. Aunque sus hábitos alimentarios han sido ampliamente documentados, existen vacíos en lo que respecta al conocimiento de la ecología de esta especie en ambientes antropizados. Comprender la respuesta de esta especie a estos hábitats es relevante debido a la progresiva modificación del paisaje a lo largo de su distribución, siendo el área de estudio un agroecosistema del centro-sur de Chile. Excretas de la especie fueron colectadas a lo largo del área de estudio para su posterior análisis en laboratorio. Los restos de las excretas fueron identificados a nivel de especie y cuantificados, considerando la representación de las distintas categorías de presa tanto en términos de frecuencia relativa como de aporte de biomasa. Se registraron 13 categorías, predominando los roedores tanto en términos de frecuencia relativa como de aporte total de biomasa, seguido por aves y artrópodos. Se destaca la presencia de especies exóticas en este espectro, representados en los órdenes Lagomorpha y Rodentia. En una baja representación se encontró material vegetal. La diversidad de las presas observadas da cuenta de que éstas constituyen principalmente especies generalistas de hábitat, con una mínima representación de especies de hábitos arbóreos, considerando la predominancia de vegetación herbácea en el área de estudio. La representación de lagomorfos es menor en comparación con otras latitudes, por lo que se sugiere su segregación con otras especies.

Keywords: anthropization; lagomorphs; predation; rodents; trophic isoclines.

Introduction

The South American gray fox (*Lycalopex griseus*) is one of the three canids present in Chile, distributed from Arica to Magellan, where it thrives in a variety of habitats (Iriarte and Jaksic 2012). The ecological aspects of this canid species have been extensively studied (Iriarte and Jaksic 2012), but information still remain scarce with regard to research in anthropized areas. The habitats of this fox species are currently under a progressive transformation across a large part of its range, resulting from the conversion of native forests into commercial crops (Echeverria *et al.* 2008). Thus, knowing the ecology of this species in disturbed environments is key. Any alteration of the habitat requires species to display ecological flexibility to exploit the available microhabitats (Crooks 2002), including the existing food resources, leading to various effects in the community where it thrives. The objective of this study was to document the feeding habits of *L. griseus* in an agroecosystem located to the center-south of Chile, characterized by a low biodiversity (Benton *et al.* 2003). In addition, this study compared the relative contribution of the prey species according to their origin (native vs. exotic), as well as in terms of the relative contribution to total biomass consumed.

Materials and Methods

The study area is located 20 km from Mulchén in the center-south of Chile (-37° 49′ 42″ S, -0.72° 14′ 51″ W). This biogeographic zone has a humid climate (Di Castri and Hajek 1974) and was originally covered by deciduous forests (Gajardo 1994); today, this area has been converted into an agroecosystem mainly used to grow lupine (*Lupinus* spp.) and oat (*Avena* spp.).

During the spring (southern hemisphere) of 2016 (November/December), the study area was walked in search of feces through a path (forked in some areas) that runs across crops, covering a total of 4 km. Fox scats were recognized based on gross morphology (Chame 2003) as well as on images from camera traps arranged systematically (separated by 500 m) throughout the study area (Kays and Slauson 2008). These made it possible to identify individuals of the species. Scats were collected in paper bags for subsequent laboratory analysis. In the laboratory, scat samples were dried at 60 °C and then shredded manually to obtain the remains of prey. These remains were identified based on skull morphology (Pearson 1995) and the arrangement of cuticle hairs (Day 1966), in addition to morphotypical comparisons vs. reference vouchers in the collection of Ecology and Biodiversity Laboratory at Universidad Católica de Temuco. Birds were identified based on feathers, culmen and nails. Then, the abundance of each food item relative to the total was quantified, thus obtaining the relative frequency of the different dietary groups (Rau 2000). Dietary diversity was estimated using Levins' index (β; Levins 1968), which allows determining prey diversity from the frequency of prey consumption and the total prey categories observed. The standard deviation of this index was calculated through the Jackknife method (Jaksic and Medel 1987).

The effect of biomass on the dietary preferences of the gray fox was evaluated using the trophic isocline method (Kruuk and DeKock 1980), where the frequency of prey occurrence is graphically incorporated according to the biomass of each relative to the total consumed (Rau 2000). Trophic isoclines are arranged around percentages that allow setting the importance of a particular prey category in the diet of the predator studied (Rau 2000). In addition, we calculated the prey geometric mean based on the sum of the product of the number of individual preys by the log10 transformation of its weight (Muñoz-Pedreros *et al.* 2018). Rodent weight figures were obtained from Muñoz-Pedreros and Gil (2009), as well as from the birds of Norambuena and Riquelme (2014). In the latter group, passeriform birds were considered as a consumption benchmark according to evidence from previous studies (Zúñiga *et al.* 2008). Arthropods and vegetation were excluded from this analysis, the former due to their poor representation relative to the total, and the latter due to the impossibility of identifying the remains collected. In addition, the prey categories observed were compared according to origin (native vs. exotic; Muñoz-Pedreros and Yáñez 2000), in terms of richness and abundance.

Results

A total of 73 scat samples were collected, finding 13 prey categories or items. These were dominated by mammals — mainly rodents of the family Cricetidae (4 species) and Muridae (1 species; Table 1), with a combined relative frequency of nearly 50 % (Figure 1). In addition, the remains (incisors and nails), of an Echimyidae, the coypu (*Myocastor coypus*), which was the prey of largest size. Lagomorphs — an exotic group at this latitude — were also included in this dietary pattern. Birds and arthropods ranked second to mammals in relative frequency of consumption by the gray fox. The trophic diversity was β = 7.43 ± 1.93 (excluding plant materials). Native species (mammals) were represented by five species (62.5 % of total), with an abundance of 54 individuals (79.41 %; non-identified rodents were excluded in both cases).

The evaluation of the effect of prey biomass on trophic isoclines revealed that rodents exceeded the 50 % isocline

Table 1. Dietary consumption of *Lycalopex griseus* in south-central Chile, including frequency (number of preys in each item) and percentage.

Food items	Frequency	Percentage
MAMMALIA		
Rodentia		
Familia Cricetidae		
Abrothrix longipilis	18	14.51
Abrothrix olivaceus	15	12.09
Irenomys tarsalis	4	3.22
Oligoryzomys longicaudatus	16	12.90
Familia Muridae		
Rattus norvegicus	4	3.22
Unidentified rodents	3	2.41
Familia Echimyidae		
Myocastor coypus	1	0.08
Lagomorpha		
Familia Leporidae		
Lepus europaeus	6	4.83
Oryctolagus cuniculus	4	3.22
AVES		
Unidentified passerines	32	25.80
ARTHROPODA		
INSECTA		
Coleoptera		
Brachysternus viridis	2	1.62
Ortoptera		
Cratomelus armatus	5	4.03
Unidentified arthropods	10	8.06
PLANT MATERIAL		
Unidentified remains	4	3.22

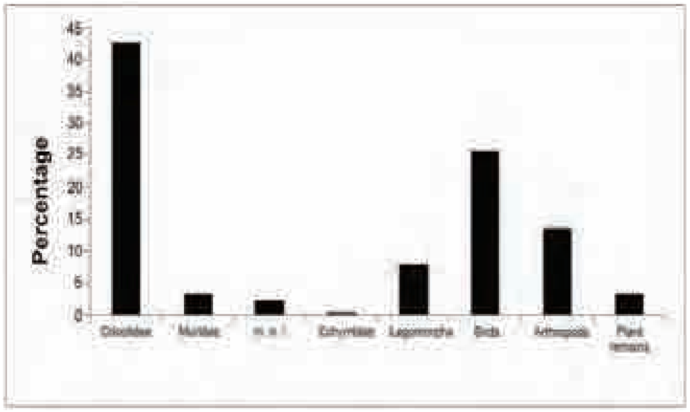

Figure 1. Percentage of prey consumption by *Lycalopex griseus* in south-central Chile. m. n. i.: unidentified murids.

despite representing 40 % of total biomass (Figure 2). The coypu and the hare (*Lepus europaeus*) were assigned to an intermediate isocline (5 %), while the rest of preys analyzed were allocated to the lowest isocline (1 %). The geometric mean for the preys analyzed was 35.35 grams.

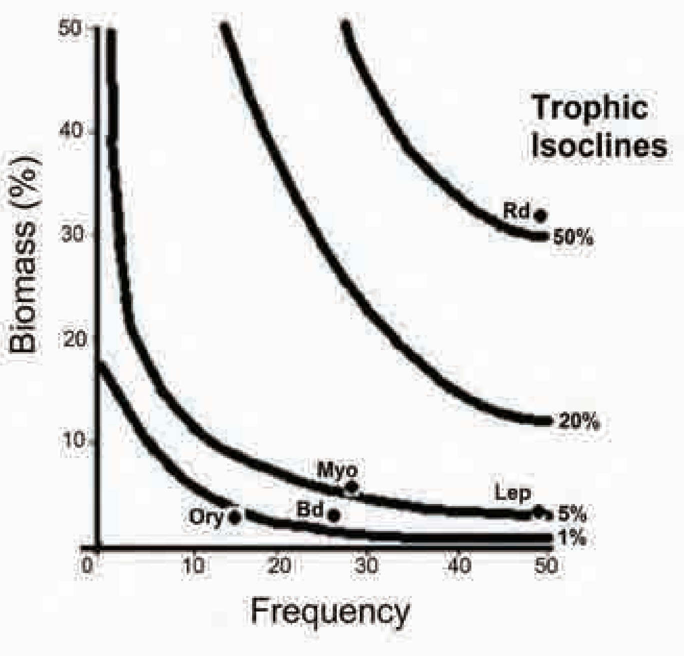

Figure 2. Trophic isoclines of preys consumed by *Lycalopex griseus* in the study area. Bd: Birds; Lep: *Lepus europaeus*, Myo: *Myocastor coypus*; Ory: *Oryctolagus cuniculus*; Rd: Rodents.

Discussion

The results obtained regarding prey diversity are consistent with those reported in other studies conducted in the center-south of Chile (Rau *et al.* 1995; Zúñiga *et al.* 2008), where small mammals — particularly rodents — constituted the core of the gray fox food spectrum. *Abrothrix longipilis*, *A. olivaceus*, *Oligoryzomys longicaudatus*, and, to a lesser extent, *Irenomys tarsalis* constituted the core of the gray fox trophic diversity in the study area. These species are characterized by their flexibility and the use of environments with little plant cover, typical of agroecosystems (Muñoz-Pedreros and Gil 2009). The absence of species sensitive to habitat loss /or with highly restricted distributions was evidenced (Quintana 2008). The diversity of rodents observed in this study partially agrees with the records of rodents for this latitude (Muñoz-Pedreros 1992), where the sampling season coincides with their reproductive period (González and Murua 1983). This allowed recording a significant representation of local prey availability. The presence in feces of an exotic species, *Rattus norvegicus*, which is common in anthropized environments (Fernández and Simonetti 2013), evidences the spatial disruption that characterizes agroecosystems, where this rodent is found in optimum conditions given its ecological versatility (Jaksic *et al.* 2002). The geometric mean obtained is similar to the average weight of rodents, thus highlighting the importance of this group relative to the total observed. The same is interpreted from trophic isoclines: the positioning of rodents on the 50 % isocline suggests that this group is a key food item within the food spectrum (Rau 2000). The presence of a single coypus specimen in the food spectrum, considering the size of this species relative to that of the gray fox (10 kg; Muñoz-Pedreros and Gil 2009), suggests that its consumption may have been due to scavenging rather than hunting, which assumes an incidental consumption. This is based on the fact that the gray fox and the coypu are of similar size (Iriarte and Jaksic 2012), which would make it difficult for the fox to hunt it; additionally, there are no records of this prey in the gray fox diet in areas where both coexist (Zúñiga *et al.* 2008). The higher number of scats collected in this study vs. the figure recorded by Torés (2007) for the culpeo fox (*Lycalopex culpaeus*), where a significant representation of the local prey diversity was reported, suggests that the number of samples in this study was sufficient to achieve representativeness of the dietary analysis.

A noteworthy finding is the absence of marsupials such as the Monito del Monte (*Dromiciops* spp.), in the diet of the gray fox, which contrasts with other studies on this canid in the center-south of Chile (Zúñiga *et al.* 2008). This fact could be explained by the constraints of the study area to be occupied by this marsupial, due the close relationship of the monito del monte with the native forest, as well as its displacement limitations (Fonturbel *et al.* 2010). On the other hand, the broad range of movement of the fox across patches of native forest (Zúñiga *et al.* 2009) would facilitate the consumption of this prey. This suggests a small population size of this marsupial species, which deserves to be further investigated. In this way, the absence of arboreal species in the diet of the gray fox is compensated by the presence of species of terrestrial habits. However, the presence of *Irenomys tarsalis* in the diet of the fox shows the flexibility of this rodent in the use of microhabitats with low vegetation cover, despite its preference for forested areas (Kelt 1993), which would lead to a lower frequency of capture vs. the rest of the cricetids observed.

The low consumption of lagomorphs according to the trophic isoclines contrasts with the observations for *Lycalopex culpaeus*, a canid of larger size than the gray fox that has been reported in other latitudes (Rubio *et al.* 2013; Zúñiga and Fuenzalida 2016), where the frequency of consumption is considerably higher. This finding leads to setting two types of hypothesis: on the one hand, the assumed high abundance of lagomorpha this group is not supported, despite the success experienced as exotic species at this latitude, which has enabled it to spread rapidly across the Chilean territory (Jaksic *et al.* 2002). On the other hand, an interference effect by larger predators, such as the puma, in the study area, leading to a spatial overlap (Zúñiga *et al.* 2009), and ultimately, to competition by exploitation. Both hypotheses should be tested in further studies to investigate which ecological elements affect this canid in anthropized areas, taking into account the variations in prey availability resulting from seasonal effects and changes of land use.

The frequency of bird consumed by *L. griseus* in the study area is consistent with the records from native forests in the same biogeographic zone (Zúñiga *et al.* 2008). However, the impossibility to identify the species consumed has restrained the estimation of the trophic spectrum of this canid (underestimation of the Levins' index; Greene and Jaksic 1983), considering the diversity of birds in this habitat (Zúñiga 2014). Nonetheless, the low contribution of birds to total prey biomass, as reflected by their inclusion in the 1 % isocline, suggests that this group is a minor component of the gray fox diet, in spite of its frequency of consumption. A similar finding was observed for arthropods, *i.e.* the amount of arthropod biomass was negligible in relation to the total, despite their frequency of consumption. This fact is even more significant considering arthropod richness at a regional scale (Peña 1987); hence, it should be interpreted with caution.

The plant remains observed differ from what is documented in localities including native forests, where the presence of seeds of several species has been reported (Zúñiga *et al.* 2008; Morales-Paredes *et al.* 2015), suggesting a potential role of the gray fox in seed dispersal. The scarcity of plant remains may indicate a change in the vegetation pattern as habitat fragmentation continues in the study area. Given this scenario, further studies are required that consider the richness of plant species according to their interaction with the local fauna.

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New records of *Galictis vittata* (Schreber, 1776) for the western slope of the Andes, Pacific region of Colombia

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Galictis vittata (Greater Grison) is distributed from Mexico through Central and South America down to northern Argentina and southern Brazil, from sea level up to 1,500 masl. In Colombia, this species is widely distributed along the Caribbean and Andean regions, and to a lesser extent in the Orinoquia and Pacific regions. Specimens of *G. vittata* were fortuitously captured in the municipality of Quibdó. This finding, along with an observation in the municipality of Rio Quito and a literature survey in international databases and published records of the species, were used to draw a map of current localities of the species in our country. A new record of *G. vittata* is reported for Colombia based on two voucher specimens deposited in the Colección Teriológica del Chocó. These specimens correspond to two females, one adult and one juvenile preserved as skins. This finding is the fourth report of the species from the western Andean zone of Colombia in the Pacific Region and the first for the Department of Chocó. It is a significant addition to the geographical and ecological distribution of *G. vittata* in the Choco, a region currently facing various diversity and conservation issues that threaten its survival, such as loss of habitat and changes of land use.

Galictis vittata (hurón o grisón mayor) se distribuye en la parte norte de América Latina, desde México a través de Centro y Suramérica, hasta el norte de Argentina y el sur de Brasil desde el nivel del mar hasta los 1,500 m, ocurriendo con más frecuencia por debajo de 500 m. En Colombia, esta especie presenta una amplia distribución a lo largo del Caribe, los Andes y, en menor proporción, en las regiones de la Orinoquía y Pacífica. Especímenes de *G. vittata* fueron obtenidos de manera ocasional en el municipio de Quibdó, estos junto a una observación obtenida en el municipio de Río Quito, más la revisión de la información disponible en bases de datos internacionales y registros publicados de la especie en la literatura fueron usados para alimentar un mapa de localidades actual de la especie en nuestro país. Se reporta un nuevo registro de *G. vittata* para Colombia, basado en dos especímenes testigos, depositados en la Colección Teriológica del Chocó. Los especímenes de *G. vittata* corresponden a dos hembras, una adulta y otra juvenil preservados como piel. Este hallazgo, constituye el cuarto reporte de la especie para el occidente de los Andes de Colombia en la Región Pacífica y el primero para el departamento del Chocó, el cual representa una adición significativa en la distribución geográfica y ecológica de este taxón en la región del Chocó, donde su diversidad enfrenta problemas de conservación por factores que amenaza su supervivencia, como la pérdida de hábitat y la transformación en el uso de la tierra.

Keywords: Colombia; greater grison; Pacific region.

Introduction

The genus *Galictis* belongs to the family Mustelidae and groups together a number of species distributed throughout tropical and subtropical areas of North America, including two species: *G. cuja* (Molina 1782) and *G. vittata* (1776) *sensu* Wozencraft Schreber (2005) and Bornholdt *et al.* (2013). *Galictis cuja* (lesser grison) is distributed in southern Latin America, from the southern tip of Peru, southern Bolivia and northeastern Brazil to southern Chile and Argentina (Yensen and Tarifa 2003; Cuaron *et al.* 2008; Bornholdt *et al.* 2013). *G.vittata* (greater grison) thrives across the northern part of Latin America, from Mexico through Central and South America down to northern Argentina and southern Brazil, from sea level up to 1,500 masl, being more abundant at altitudes below 500 masl (Timm *et al.* 1989; Yensen and Tarifa 2003; Cuaron *et al.* 2008; Monjeau *et al.* 2009; Bornholdt *et al.* 2013).

In Colombia, the great grison (*G. vittata*) has been recorded for the Caribbean, the Andes and the Orinoquía (Solari *et al.* 2013); unconfirmed references are also available for the Amazon, such as Alberico *et al.* (2000), and Muñoz-Saba and Alberico (2004). According to current lists of mammals for the country, this species inhabits the Caribbean region in the Departments of Atlántico, Bolívar, Cesar, Córdoba, La Guajira (Jimenez-Alvarado *et al.* 2016), Magdalena and Sucre (Cuervo *et al.* 1986; Alberico *et al.* 2000; Solari *et al.* 2013). In the Andean region, it has been reported in the Departments of Antioquia, Cundinamarca, Caldas and northern Santander (Castaño 2012; Solari *et al.* 2013; Jimenez-Alvarado *et al.* 2016); in Orinoquía, in the Departments of Casanare, Meta and Vichada (Alberico *et al.* 2000; Solari *et al.* 2013). In the Pacific region, in the Departments of Cauca (Alberico *et al.* 2000; Ramírez-Chaves and Perez 2011) and Nariño (Ramírez-Chaves and Noguera-Urbano 2010, Figure 1). However, despite of this broad range, no accurate information is currently available about its ecology, distribution and conservation status (González-Maya *et al.* 2011 Calderon-Capote *et al.* 2015; Jimenez-Alvarado *et al.* 2016).

Jimenez-Alvarado *et al.* (2016) report the existence of 161 documents related to *G. vittata* in Colombia. A detailed revision detected an error in this figure, as according to the information reported by these authors, the total number of references adds up to only 157 documents. Of this, 78 records correspond to the Colombian Caribbean, with 54 new records for this region, which is one of the most important approximations to the distribution of *G. vittata* in northern Colombia. However, besides the references just mentioned, 38 additional mentions for the Colombian territory are available, making a total of 195 recounts. Of these, 58.5 % ($n = 114$) correspond to references in interviews; 27.7 % ($n = 54$), direct observations; 9.2 % ($n = 18$), specimens in scientific collection; and 4.6 % ($n = 9$), photographic records. Of all records, 86.2 % were considered to be poorly reliable (interviews and observations), while the remaining 13.8 % were deemed high reliable, corresponding to photographs and collection specimens. The few mentions for the Colombian Pacific region are reliable, as these refer to geo-referenced evidence on the presence of the species related to collection specimens and photographic records.

Recent studies (Escobar-Lasso and Guzman-Hernández 2014; Jimenez-Alvarado *et al.* 2016) confirm that there are few specimens deposited in Colombian scientific collections. A total of 18 specimens are currently recorded in collections, distributed in the Institute of Natural Sciences at Universidad Nacional de Colombia (ICN), the Museum of Natural History at Universidad del Cauca (MHNC), the Collection of Mammals at Instituto Alexander von Humboldt (IAvH-M), the Collection of Mammals at Universidad del Valle (CM-VC), and the Museum of Natural History at Universidad de Caldas, Manizales-Colombia (MHN-UC), in addition to some international museums in the U.S., including the Field Museum of Natural History, Chicago (FMNH), the National Museum of Natural History, the Smithsonian Institution (USNM), and the American Museum of Natural History (AMNH, Table 1).

From this study, the Collection of Mammals of Chocó at Universidad Tecnológica del Chocó (CMCH) is also included as having specimens of *G. vittata* from the Pacific region of Colombia. Furthermore, data were obtained about the presence of this species in our country from the Global Biodiversity Information Facility database (GBIF; http://data.gbif.org), and from literature records of the species that, together with the records reported herein, were used to elaborate a map of the current distribution of *G. bittata* in Colombia using all record localities; data involving location inconsistencies were excluded. A layer of the national system of natural parks (PNN) was used as an input in this map in order to identify the populations covered by protected areas in our country.

New Records of Great Grison for the Central Biogeographic Chocó: The material reported herein for the western Cordillera of the Andes, specifically in the Department of Chocó, was obtained incidentally in the vicinity of a farm located in the district of Flores de Buenaños, municipality of Quibdó (5° 40′ 55.2″ N, -76° 38′ 27.6″ W 54 masl). Two female specimens of *G. vittata* were hunted by dogs on a farm (apparently in the early morning hours), leading to their immediate death; these specimens were recovered by the farm owner and delivered to S. Mosquera-Mosquera on 6 August 2012 (Figure 1). An additional record refers to an observation on October 2014 (Figure 2) by E. Yair Cuesta-Ríos at the juristiction of La Soledad, municipality of Rio Quito (5° 32′ 17.11″N, -76° 46′ 47.34″ W, 55 masl).

The two Quibdó specimens were prepared and preserved following the protocol of Vargas-Sandoval (1994) and deposited in the Collection of Mammals of Chocó at Universidad Tecnológica del Chocó (CMCH) under collection numbers CMCH003011 and CMCH003012. The specimens collected match the descriptions of the species by Yensen and Tarifa (2003) and Tirira (2007), including short legs, slender body, small and flattened head exhibiting a diagonal stripe that reaches the shoulders, grayish dorsum, short and thick tail, and a long neck. The measurements of the specimens as based on skins are shown in Table 2; the skulls of these specimens are currently missing.

These new records of *G. vittata* confirm the presence of the species in the Pacific region of Colombia, approximately 85 km west from the nearest record in the Department of

Table 1. Complete list of localities of *Galictis vittata* in Colombia, based on data from the literature and international museums. *International collections.

Specimen	Department	Municipality/Locality	Coordinates	Reference	Quantity
IAvH-M- 5459, 5547	Sucre	Colosó/Ricaurte	9.5 -75.35	Collection of Mammals at Instituto Alexander von Humboldt (IAvH-M)	4
IAvH-M-3111	Magdalena	Santa Marta/PN Tayrona	-		
IAvH-M- 5381	Meta	-	-		
ICN 1423		Villavicencio	4.141 -73.626	Institute of Natural Sciences at Universidad Nacional de Colombia (ICN)	3
ICN1894		Restrepo	4.1584 -73.444		
ICN 9925	Cauca	El Tambo	2.437 -76. 8133		
CM-VC 08105, 08106	Vichada	Puerto Carreño	5.775 -68.184	Collection of Mammals at Universidad del Valle (CM-VC)	2
CMCH 003011	Chocó	Quibdó	6.682 -76.641	Choco Teriologica Collection at Universidad Tecnológica del Chocó (CMCH)	2
CMCH 003012		Rio Quito	5.538 -76.779		
MHN-UC 1156	Caldas	Marquetalia	5.2905 -75.007	Collection of Mammals at the Museum of Natural History, Universidad de Caldas, Manizales - Colombia (MHN-UC)	1
FMNH 68906	Sucre	Colosó/Ricaurte	9.5 -75.35	Field Museum of Natural History, Chicago-EE.UU (FMNH)*	2
USNM 544420	Sucre	Sitio Nuevo /La Trinidad	10.851 -74.6188	National Museum of Natural History, the Smithsonian Institution (USNM)*	2
AMNH-142246	Meta	Villavicencio	-	American Museum of Natural History (AMNH)*	2

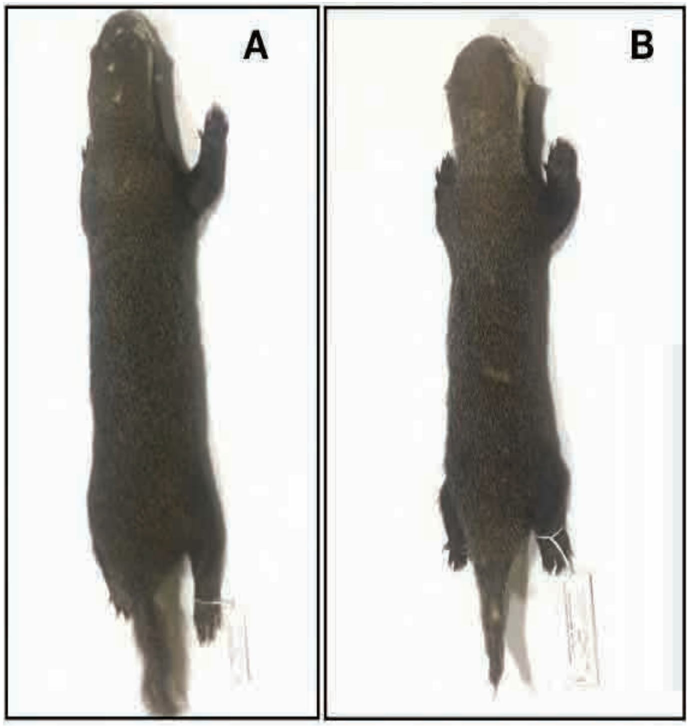

Figure 1. Specimens of *G. vittata* (A=CMCH00301, adult female; B=CMCH003012, juvenile female), collected at Flores de Buenanos, municipality of Quibdó.

Table 2. External measurements of the specimens of *G. vittata* recorded in the municipality of Quibdó, Department of Chocó, Colombia

Measurements	CMCH003011 (mm)	CMCH003012 (Juvenil) (mm)	Yensen and Tarifa (2003)	Tirira (2007)
LT	680	427	600–760	600-747
LC	153	94	135–195	135-195
LCC	525	340	450–600	450–600
LP	80	47	-	66-97
LO	23	16	20–32	20-32

LT: total length; LC: tail length; LCC: head-body length; LP: foot length; LO: ear length.

Antioquia, and 360 km north of the record in the Department of Cauca, in addition to confirming the presence of this species in the Department of Chocó (Figure 3). Nonetheless, its presence in this area was expected, given the ecological continuity of the landscape and the Chocoano tropical forest between southwestern Colombia and northwestern Ecuador (Tirira 2008); in addition, this species has been recorded previously by Handley (1966) as *G. allamandi* in the Darien-Panamá region at the northwest end of the Biogeographic Chocó.

Furthermore, Asprilla-Perea *et al.* (2013) mention the presence of *G.vittata* in the Department of Chocó, based on a lot of specimens confiscated by Corporación Autónoma Regional para el Desarrollo Sostenible del Chocó (Regional Autonomous Corporation for the Sustainable Development of Chocó, CODECHOCO); although the original site of capture of that individual was not established. Thus, the records reported here are remarkable because they fill the information gap in the distribution range of the species, for being located in an area representative of the Chocó-Manabí conservation corridor and the most important strip in terms of the conservation hotspot or the of Tumbes-Chocó Magdalena Priority Terrestrial Ecoregion (ETP). It is worth stressing that this region had not been previously considered within the known distribution of the species, either by Solari *et al.* (2013) or by Jimenez-Alvarado *et al.* (2016), although Muñoz-Saba and Alberico (2004) did mention the presence of the species from observations (without reporting the precise locality) in the municipality of Tumaco, while Ramírez-Chaves and Noguera-Urbano (2010) confirmed its presence at La Cruz, jurisdiction of Plazuelas, Department of Nariño. This record in the region suggests that the tropical rain forest (bp-T) located in the central area of the Biogeographic Choco of Colombia should be included within the habitats of the species, in addition to those already described by other researchers (*e. g.*, Yensen and Tarifa 2003; Tirira 2008; Bornholdt *et al.* 2013).

There is currently scarce information about the biology, ecology and distribution of this rare species (*G. vittata*) in Colombia (Calderon-Capote *et al.* 2015). As it is rarely observed, it has been listed as a priority species in the research of small carnivores in Colombia (González-Maya *et al.* 2011; Suarez-Castro and Ramirez-Chaves 2015). The profound transformation of natural ecosystems in Colombia — particularly in the Pacific region currently under deg-

Figure 2. Photographic record of *G. vittata* in the jurisdiction of La Soledad, municipality of Rio Quito (Photographs: Eric Yair Cuesta Ríos).

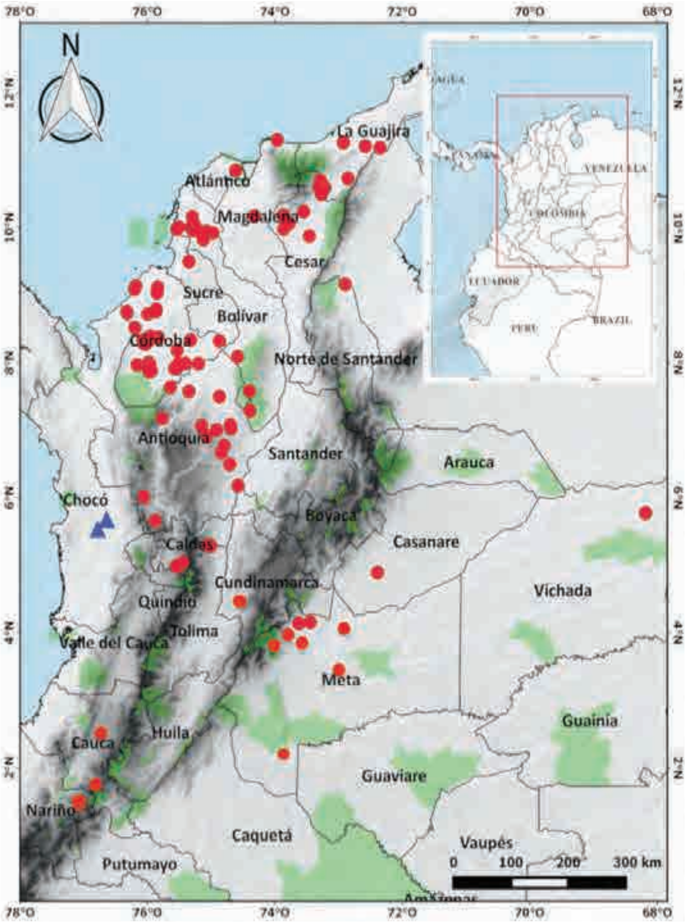

Figure 3. Geographical location of records of *G. vittata* in Colombia: Red circles = records in GBIF (http://data.gbif.org), ICN, MHNC, or in the literature: Escobar-Lasso and Guzmán-Hernández, (2014), Jiménez-Alvarado *et al*. (2016). Blue triangles = New records for the Pacific region of Colombia reported here. Green = System of Natural Parks.

radation processes due to open-pit gold and platinum mining, wood logging, hunting and the Tumbes crop system — have all converted the original forest into a number of landscapes, becoming a factor that affects this species and jeopardizes the viability of its local populations.

According to our map, this species is currently located outside the conservation areas in the National System of National Parks (PNN, Figure 1). Ecological macro-analyses involving mammals of the Biogeographic Chocó (*e. g.*, Mantilla-Meluk and Jimenez-Ortega 2006) suggest the creation of a conservation area in the Chocó central area, a proposal that we support, as it is one of the most suitable areas for the conservation of this and other species. *G. vittata* is likely covered by the protected areas of Colombia; however, further sampling is required to confirm its presence in those areas to preserve its populations. This species is considered as threatened with extinction in Costa Rica (Timm *et al.* 1989) due to the loss of habitats through deforestation; its preservation in this country is regulated by the Law on Wildlife Conservation No. 7317, the Organic Law of the Environment No. 7554, and the Decree No. 26435-MINAE. In Belize, *G. vittata* is protected by the Law of Wildlife Protection, and in Nicaragua, hunting of this species is prohibited (Fuller *et al.* 1987). According to the IUCN Red List, *G. vittata* (greater grison) is listed as Least Concern-LC (Cuarón *et al.* 2016), and is included in Appendix III of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). However, it is not included in the list of threatened species of Colombia (Resol. 1912 of 2017).

Given the huge knowledge gap on *G. vittata* in Colombia, this record for the lowlands in the western Cordillera of the Andes is remarkable, as it broadens its geographic and ecological range in the Pacific region of Colombia, in addition to increasing the number of mammal species recorded for the Department of Chocó. It further highlights the importance of forest conservation in the central area of the Biogeographic Chocó to preserve the diversity of mammals distributed in this portion of the territory.

The information reported here could be used for the development of conservation plans according to data-based analyses on the ecology and conservation status supplemented with distribution maps of this species in the country. This will lead to the identification of priority conservation areas, considering the intensive transformation processes of natural ecosystems in Colombia, particularly in the Colombian Pacific region (Kattan and Naranjo 2008).

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Jaguar in the Tepalcatepec basin in central-western Michoacán, México

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The international conservation status of the jaguar (*Panthera onca*) is Near Threatened, reason to seek priority regions for its conservation. Both national and international geographical distribution models assume that in the Mexican Pacific slope, the jaguar is present from Sonora to Chiapas and constitute a single subpopulation. However, the possible connectivity routes between different distributional areas in the Pacific region of México, are still unknown. In August 2015, it was initiated a community participatory monitoring program in the southwest of the municipality of Tocumbo, Michoacán, in the Tepalcatepec basin. Exploratory sampling consisted of the opportunistic placement of five Cuddeback X-Change camera traps on tracks and roads where inhabitants of the area had identified wildlife activity. The cameras were placed at a distance of between 200 and 1,000 m. With a sampling effort of 1,200 days/camera, on January 5th, 2017 three photographs of a jaguar were obtained at 00:52 h. The record site is a dirt trail located 3.5 km from the state limit with Jalisco, on the edges of an agricultural area surrounded by tropical dry deciduous forest at an elevation of 1,287 masl. In addition, potential prey such as white-tailed deer (*Odocoileus virginianus*), collared peccary (*Dicotyles angulatus*), coati (*Nasua narica*), and predators competitors such as puma (*Puma concolor*) and coyote (*Canis latrans*) were recorded. The jaguar presence in the Tepalcatepec river basin provides valuable baseline information in two aspects. It incorporates an alternative and suitable route with validating a contact area between Jalisco and Michoacán for the mobility of jaguars. In addition, is supporting evidence for the hypothesis that the state contain key regions for the design of a viable conservation corridor on the central Pacific for the jaguar. Knowing in which areas the jaguars maintain activity facilitates the design of more accurate distribution models and potential corridors for Michoacán and neighboring states. Therefore, survey efforts should continue in these regions, where flora and fauna assemblages include several endangered species.

El estado de conservación del jaguar (*Panthera onca*) a nivel internacional es casi amenazado, razón por la cual es importante identificar regiones prioritarias para su conservación. Los modelos de distribución geográfica a nivel nacional e internacional suponen que en la vertiente del Pacífico Mexicano, el jaguar está presente desde Sonora a Chiapas y constituye una sola subpoblación. Sin embargo, aún se desconocen las posibles rutas de conectividad entre las diferentes áreas de distribución en la región del Pacífico de México. En agosto de 2015 se inició un programa de monitoreo participativo comunitario en el suroeste del municipio de Tocumbo, Michoacán, en la cuenca de Tepalcatepec. El muestreo exploratorio consistió en la colocación oportunista de cinco trampas de cámara Cuddeback X Change en veredas y caminos donde los habitantes del área habían identificado actividad de vida silvestre. Las cámaras se colocaron a una distancia de entre 200 y 1,000 m. Con un esfuerzo de muestreo de 1,200 días/cámara, el 5 de enero de 2017 se obtuvieron tres fotografías de un jaguar a las 00:52 h. El sitio de registro es un camino de tierra ubicado a 3.5 km del límite estatal con Jalisco, en los bordes de un área agrícola rodeada de bosque tropical caducifolio a una elevación de 1,287 msnm. Además, se registraron posibles presas como venado de cola blanca (*Odocoileus virginianus*), pecarí de collar (*Dicotyles angulatus*), coatí (*Nasua narica*) y depredadores competidores como el puma (*Puma concolor*) y el coyote (*Canis latrans*). La presencia de jaguar en la cuenca del río Tepalcatepec proporciona información valiosa de referencia en dos aspectos. Por un lado, incorpora una ruta alternativa y adecuada para validar un área de contacto entre Jalisco y Michoacán para la movilidad de los jaguares. Además, se refuerza la hipótesis de que el estado de Michoacán presenta regiones importantes para el establecimiento de un corredor biológico viable en el Pacífico central para la conservación del jaguar. Saber en qué áreas mantienen su actividad los jaguares facilita el diseño de modelos de distribución más precisos y corredores potenciales para Michoacán y los estados vecinos. Por lo tanto, los esfuerzos de muestreo deben continuar en estas regiones, donde los ensambles de flora y fauna incluyen varias especies en peligro de extinción.

Key words: camera trap; community monitoring; connectivity; Felidae.

Introduction

In México, the conservation status of the jaguar (*Panthera onca*) is Endangered and internationally it is Near Threatened, mainly due to the reduction and fragmentation of its habitat in addition to the fact that it is hunted in retaliation for predation of cattle (Caso *et al.* 2008; SEMARNAT 2010; Ceballos *et al.* 2016). In recent years, a consensus among specialists is that long term conservation of jaguar will depend on maintaining a network of suitable habitat corridors allowing the dispersion of individuals among areas that present abundant populations (Rabinowitz and Zeller 2010; Rodríguez-Soto *et al.* 2011; Ceballos *et al.* 2016). Most distributional models designed for México consider that the species occurs into three main geographic areas; the Sierra de Tamaulipas, the Pacific, and the Gulf of México (De la Torre *et al.* 2018). The Mexican Pacific may be considered the most important in the northern hemisphere, as the jaguar is assumed to persist along the Pacific slope, from Sonora to Chiapas as one large sub-population. However, present considerable vulnerability due to fragmentation, a low protected area availability, population reduction and consequent isolation in the central western states like Michoacán and Colima (De la Torre *et al.* 2018).

At national level, the central western states (Nayarit, Jalisco, Colima, Michoacán) have been identified as a single high priority area for jaguar conservation due to habitat availability and the possible existence of ongoing connectivity routes (CONANP 2009; Núñez 2011). For the Michoacán state, a small but resident jaguar population has been confirmed in recent years for the Sierra Madre del Sur and for the lower Balsas River Basin (Charre-Medellín *et al.* 2013; Charre-Medellín *et al.* 2014b).

The location of the areas with actual jaguar presence, habitat availability and the potential distribution models allowed us to hypothesize the most likely contact areas among neighboring states. To the southeast the contact area with the State of México and Guerrero through the Alto Balsas region. Explained by the proximity and location of the records from the Zicuirán-Infiernillo area (Figure 1; (Charre-Medellín *et al.* 2014b). However, the contact areas between Michoacán and the northern populations (Colima-Jalisco) remained unknown. Most published hypothesis considered as the most likely area of contact, somewhere along the coastal areas and/or mountain ranges in the border between Michoacán, and Colima-Jalisco (Núñez 2011; Ceballos *et al.* 2016). However, a total absence of records from coastal areas near Colima state, and from Colima state during the last 50 years (Núñez 2007; Ceballos *et al.* 2016), rejected the hypothesis of the existence of a contact area somewhere along the lowlands and coastlines on the Michoacán-Colima border (Municipalities of Coahuayana and Tecoman respectively). In the absence of evidence, the International Union for Conservation of Nature (IUCN) outlined a potential distributional map showing a gap in the continuity of their distribution (Figure 1). Therefore, until 2016 it was not possible to determine the contact areas between central and northern Pacific jaguar populations, particularly between Michoacán and Jalisco states.

Figure 1. Location of the records of jaguar (*Panthera onca*) in the Tepalcatepec basin. Current records obtained by camera traps in western México: 1 Cuixmala- Chamela, Jalisco (Núñez 2007). 2) Manantlán, Jalisco (Núñez 2007). 3) Arteaga, Michoacán (Charre-Medellín *et al.* 2013). 4) Huetamo, Michoacán (Charre-Medellín *et al.* 2014b). 5) Nanchititla, State of México (Monroy-Vilchos *et al.* 2008). The star is the new photographic record. Triangles are historical photographic records. The crosses are historical anecdotal records. Red polygon Tepalcatepec Basin. Gray polygon is IUCN distribution of jaguar.

In the absence of robust information confirming a specific contact area, the generation of alternate hypothesis initiated. One region was considered as promising, the Jal-Mich Sierra (a bordering mountain range shared by Michoacán and Jalisco state). The region included tropical forest remnants along inaccessible canyons and ravines with the confirmed presence of other endangered species. The area corresponds to the geographic region known as the Tepalcatepec river basin.

Previously, this region was not considered as a potential site for jaguar presence. Neither as a part of a potential corridor, since it is located outside most recognized distributional areas for the species in México (Caso *et al.* 2008; Núñez 2012; Ceballos *et al.* 2016). The only academic analysis considering its potentiality came from Charre-Medellín *et al.* (2014a), suggesting the need to survey such region.

Materials and Methods

Conservation initiatives in the Jalmich mountain range initiated in August 2015. Activities included wildlife surveys by a "Community participatory monitoring program". The activities included the inhabitants of El Palo Bobo, Los Desmontes, El Rodeo and El Santuario localities, in the southwest corner of the municipality of Tocumbo, Michoacán. The area is part of the Jal-mich mountain range, the Cotija cheese region of origin. The regional pride achieved by the international recognition of the cheese brand motivated collective efforts to preserve not only the cheese producing tradition, but also their wildlife heritage, in a "holistic point of view" that included the preservation of cultural and natural heritage (Barragán *et al.* 2007).

Wildlife monitoring by local communities provides the opportunities to gain information by including all their experience in natural resource management (Botello *et al.* 2011). The survey sites in Tocumbo municipalities are located in the northwest portion of the state of Michoacán 19° 32′ 45.03″ N, -102° 40′ 56.26″ W. The area limits with the state of Jalisco and constitute the core of the Tepalcatepec river basin (Figure 1). The entire basin has an approximate area of 17,000 km^2 and is characterized by the presence of warm tropical climates, and a rugged terrain with a broad altitudinal range of 160 to 3,840 m (Mendoza *et al.* 2009). Approximately 41 % of the basin area is dedicated to agriculture, 32 % constitute lowland deciduous forest, and 27 % is temperate forests (INEGI 2010).

Exploratory sampling (without a balanced design), consisted of the opportunistic placement of five Cuddeback X-Change camera traps along trail and dirt roads where footprints reveled intense wildlife activity. The cameras were programmed with a one-minute delay and to obtain three consecutive photographs each triggering event. The cameras were placed at distances between 200 and 1,000 m at a random pattern.

Results

With a sampling cumulative effort of 1,200 days/camera, three photographs of a jaguar (*Panthera onca*) were obtained at 00:52 h, on January 5th, 2017. The record site is a dirt trail located 3.5 km from the state limit with Jalisco, on the edges of an agricultural area surrounded by tropical dry deciduous forest at an elevation of 1,287 masl (Figure 2). The location of the record is 144 km of from the nearest jaguar populations in the Manantlán Reserve in a mountain range. However, is 244 km from the coastal population located in Cuixmala-Chamela, both areas in Jalisco state (Núñez 2007). On the interior of Michoacán to the south, the nearest population is located at 156 km in the Arteaga municipality on the Sierra Madre del Sur, and 164 km from the records in Huetamo municipality on the lower Balsas basin near the Zicuiran Infiernillo Biosphere Reserve (Charre-Medellín *et al.* 2013; Charre-Medellín *et al.* 2014b). The record is located at 240 km from the jaguar record obtained in Nanchititla, State of México (Monroy-Vilchis *et al.* 2008); Figure 1). In addition to the jaguar, the species assemblages included prey species as the white-tailed deer (*Odocoileus virginianus*), collared peccary (*Dicotyles angulatus*), coati (*Nasua narica*), but also a potential competitors such as puma (*Puma concolor*) and coyote (*Canis latrans*).

Figure 2. First photographic record of a jaguar (*Panthera onca*) in the Tepalcatepec basin, municipality of Tocumbo, Michoacán, México.

Discussion

This new record modifies the perception concerning which region constitute the most likely contact area between northern and central jaguar populations (Jalisco-Michoacán). Previous hypothesis considered the Michoacán coast as the potential contact region based on the location of old anecdotal reports proposed by Sanderson *et al.* 2002 and Nuñez (2012, 2011). However, no photographic evidence has been obtained for that region during the last 30 years even though substantial survey effort was allocated (Núñez 2007), therefore such hypothesis should be rejected until updated evidence is provided (Figure 1).

The Tepalcatepec river basin constitute now the most likely area of contact and mobility for the jaguar between Michoacán and Jalisco as previously assumed (Charre-Medellín *et al.* 2014b). Additional supporting evidence comes from the characteristics of the areas with actual jaguar activity in Michoacán. The area where the species present a small but resident population is a rugged mountain range of Arteaga (Sierra Madre del Sur), where canyons and ravines seem to provide cover for the jaguar. Moreover, the second region with jaguar presence is rugged terrain along the higher Balsas basin (Churumuco municipality). Rugged terrain and low human density seem to be the factors found in common for all the areas where jaguar is present in Michoacán (Charre-Medellín *et al.* 2013; Charre-Medellín *et al.* 2014b). Future survey efforts should intensify for the Jalmich Sierra region to determine the jaguar frequency of activity. A buffer area free from land use changes should be designated considering the location of the jaguar record and forest cover in Tepalcatepec river Basin. Restoration programs should initiate to consolidate the long term preservation of the cultural and natural heritage of the region. The Sierra Jalmich constitute now a priority area for jaguar conservation in México, and the official inclusion in national conservation initiatives should be recognized officially. The jaguar site should be combined with nearby localities such as the Ecological Preservation Area of Chorros del Varal, to design a network of wildlife refuge areas connected by corridors, as other endangered species such as military macaws (*Ara militaris*), margay (*Leopardus wiedii*), ocelot *(Leopardus pardalis*), and otter *(Lontra longicaudis*) have been registered in the region (Charre-Medellín *et al.* 2014a).

The surveys for presence, activity and abundance for jaguar should be expanded in this area, including neighboring localities in Jalisco state. An analysis of the primary vegetation actual cover in the region is urgent, and potential routes connecting the distinct jaguar populations among the Sierra Madre del Sur, the Bajo Balsas and the Tepalcatepec basin should be designed and evaluated. Official programs (payment for environmental services) should allocate economic support to land owners. Cattle ranchers must be compensated also if livestock loses caused by predation of wild carnivores occur in areas that are considered of greater value for the jaguar conservation.

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In Memoriam:

Dr. Robert James Baker

(1942-2018)

Robert o Bob, como le conocimos, nació el 8 de abril de 1942 en Warren, Arkansas, en la región sur de los Estados Unidos de América. Sus padres fueron James Simeon Baker, quién falleció durante la II Guerra Mundial, y Laura Cooper, quién se hizo cargo de Robert y seis medios hermanos. Realizó sus estudios de bachillerato en la Ouachita Baptist University con una beca de campo y futbol, así como su licenciatura en Arkansas A&M College en Monticello, situada a unos 30 km de su ciudad natal. En 1965 se matriculó en Oklahoma State University en Stillwater, Oklahoma, para realizar la Maestría en Biología con el Dr. Bryan P. Glass. Dos años más tarde terminó y se inscribió en la University of Arizona en Tucson, donde obtuvo el doctorado bajo la dirección del Dr. E. Lendell Cockrum. En esa universidad fue compañero de otros célebres mastozoólogos, como los Dres. James L. Patton y Alfred L. Gardner. Cabe recalcar que Robert siempre sobresalió y apuntó para cosas grandes, baste señalar que sus dos posgrados los terminó en cuatro años, muy por debajo de la media nacional, además de preparar y publicar durante ese tiempo, varios trabajos y obtener financiamiento para varios de sus proyectos.

Al término de sus estudios en la University of Arizona en 1967, Robert fue reclutado por J. Knox Jones, Jr. para incorporarse a Texas Tech University (TTU) donde pasaría los siguientes 48 años en el Departamento de Ciencias Biológicas. Robert fue reconocido como profesor y científico distinguido por TTU y diversas organizaciones científicas profesionales. Fue miembro activo de numerosas sociedades científicas, incluyendo haber sido el presidente de la American Society of Mammalogists, la Southwestern Association of Naturalists y la Texas Society of Mammalogists. En 1979, solo 12 años después de haberse incorporado a TTU, recibió el premio Paul Whitfield Horn Professorship, la máxima distinción académica para un profesor en esa Universidad.

Robert fue uno de los mastozoólogos más destacados a nivel mundial, tanto por sus hallazgos como por su gran productividad. Con respecto a su investigación, retomo palabras suyas que señalan sus intereses en los últimos años de vida: "Mi investigación se centra en la organización del genoma y la biología evolutiva, así como en los avances recientes en proporcionar datos genéticos para ayudar en el entendimiento de la evolución de los mamíferos". La publicación del Concepto Genético de Especies estuvo en el primer lugar de la lista de trabajos publicados a nivel mundial en 2001 (Baker y Bradley 2006). El trabajo de la filogenia de los murciélagos filostómidos de 2003 (Baker et al. 2003), resolvió un problema (monofilia de Stenodermatinae) que encontró con su tesis doctoral en 1967 (Baker 1967). Una muestra del gusto que le producía su trabajo fue su comentario: "fue un placer lograr desarrollar ese grado de resolución a la filogenia". Otra área de interés fue la evolución cromosómica enfocándose en la hibridación in situ. Su laboratorio tuvo dos objetivos principales: 1) Determinar los efectos biológicos de sobrevivir en los ambientes altamente contaminados por el derretimiento del reactor 4

Fig. 1. Dr. Robert Baker revisando muestras en trabajo de campo.

de Chernobyl (Chesser y Baker 2009) y, 2) estudiar la sistemática de los murciélagos de hoja nasal de la Familia Phyllostomidae (Baker et al. 2003). Cabe resaltar que como muestra de humildad, Robert decidió a mediados de la década de los 1980s que no bastaban los avances que había logrado con sus estudios citogenéticos, sino que debía prepararse para los nuevos retos que implicaban los estudios moleculares y, con ello, tratar de responder a la pregunta pendiente de sus estudios de doctorado. Para lograrlo, realizó una estancia de estudio e investigación durante un año en el laboratorio del Dr. Rodney Honeycutt, uno de sus estudiantes de doctorado, en Harvard University.

Robert desarrolló las teorías y perfeccionó las técnicas citogenéticas y moleculares para utilizarlas como herramientas sólidas para los estudios de taxonomía, sistemática, biogeografía y evolución de uno de sus grupos de mamíferos favorito, los murciélagos, con lo cual realizó importantes avances a las ciencias zoológicas. A diferencia de varios mastozoólogos que trabajan en laboratorio, Robert pasó mucho tiempo en campo. Siempre dispuesto a colocar las redes y trampas para la captura de los especímenes; expectante de las especies que deseaba capturar y conocer; feliz cuando capturaba lo que buscaba; uno de los primeros en levantarse para preparar el material; y de los últimos en acostarse por estar al pendiente de que todo se hubiera procesado y que la información quedara resguardada. Esto le autorizó a declarar el ser uno de los pocos investigadores que han conocido en ejemplares vivos a prácticamente todas las especies de murciélagos del continente. Lo que a su vez, le permitió generar las preguntas adecuadas a los hechos biológicos, y no sólo a aquellas que se refieren a los aspectos metodológicos. Es importante resaltar el énfasis que sus investigaciones han tenido para resolver las preguntas evolutivas que planteó en sus estudios, y que han sido la base para investigaciones de numerosas personas alrededor del mundo.

Robert fue fundador y director del Natural Science Research Laboratory del Museum of Texas Tech University, desde 1976 hasta su retiro en 2015. Con su trabajo, siempre resaltó la importancia de las colecciones científicas e innovó el manejo y preservación de los especímenes de museo (Baker *et al*. 2014; Monk y Baker 1991). Se enfocó no sólo en preservar la piel y el cráneo o esqueleto de los especímenes, como se hacía de manera tradicional, sino además de esto, la mayor parte de los tejidos blandos, muestras de sangre y, cuando era posible, preparaciones de cariotipos y ectoparásitos (Baker y Hafner 1984). Además, el registro de la información no se limitó al etiquetado y catalogado tradicional, sino llegó incluso a la elaboración de etiquetas con códigos de barra para agilizar el procesamiento, catalogación y respaldo de la información en bases de datos electrónicas y su uso en Bioinformática (Baker *et al*. 1998). Su preocupación se centraba en preservar la mayor información posible de las especies, especialmente de aquellas que fueran nuevas para la ciencia; pero también sabía que debido al cambio climático y la fragmentación del ambiente, algunos de los especímenes capturados serían lamentablemente la última evidencia de su existencia. Por lo que dedicó una gran labor a la gestión de recursos y formación de personal con el objeto de equipar y mejorar continuamente la infraestructura física y metodológica de las colecciones del museo.

Su gran capacidad de trabajo le permitió fomentar e incursionar en aspectos administrativos de la ciencia, como la generación de recursos para proyectos, y para lograrlo, sometió con gran éxito, un número importante de solicitudes de recursos económicos en un medio altamente competitivo, tanto en agencias federales como National Science Foundation o el Departamento de Defensa; estatales como Texas Parks & Wildlife Commission; y particulares como Welder Wildlife Foundation. Esto le permitió obtener y encaminar a su Universidad y a sus programas de investigación, recursos por más de cinco millones de dólares, cantidad astronómica, si pensamos que estos recursos se destinaron a investigación básica en el área de la mastozoología. Asimismo, su preocupación por que los resultados de las investigaciones no quedaran inéditos, lo llevó a dedicar un gran esfuerzo para establecer un fideicomiso de un millón de dólares, con la finalidad de dar continuidad a la publicación de las series del Museo, como son los Occasional Papers y Special Publications del Museum of Texas Tech University.

Robert publicó más de 400 contribuciones, la mayoría de ellas en revistas de gran impacto, que lo colocan en el selectísimo grupo de mastozoólogos del Siglo XX que más han publicado (se puede consultar en http://www.nsrl.ttu.edu/personnel/RJBaker/Bakerpubs.htm). En este grupo sólo registramos a C. Hart Merriam, Edward A. Goldman, Oldfield Thomas, Daniel G. Elliott, J. A. Allen, Joseph Grinnell y, más recientemente a E. Raymond Hall y J. Knox Jones, Jr. Una de sus más constantes preocupaciones, fue la de enseñar a sus estudiantes a publicar, al considerar que todo resultado de investigación debe quedar plasmado de manera impresa. En ello demostró ser una persona generosa por compartir sus ideas y llevarlas al papel, junto con la gran cantidad de colegas que lo rodearon y, con quienes en forma por demás sobresaliente formaron su equipo de trabajo. Robert dio a conocer para la ciencia 16 nuevas especies, un género y dos subgéneros nuevos, la mayoría nombradas en honor de investigadores y estudiantes de los quirópteros, muchas de ellas basadas en caracteres diagnósticos, genéticos y moleculares (Tabla 1). Por otro lado, al menos cuatro especies de mamíferos y un artrópodo asociado a mamíferos fueron nombrados en honor de Bob: *Tonatia saurophila bakeri* Williams, Willig y Reid, 1995; *Glossophaga commissarisi bakeri* Webster and Jones, 1987;

Tabla 1. Especies descritas por Robert J. Baker, sólo o con colaboradores.

Especie	Autores	Año
Uroderma bilobatum davisi	Baker y McDaniel	1972
Eptesicus guadeloupensis	Genoways y Baker	1975
Geomys bursarius knoxjonesi	Baker y Genoways	1975
Chiroderma improvisum	Baker y Genoways	1976
Rhogeessa genowaysi	Baker	1984
Rhogeessa hussoni	Genoways y Baker	1996
Carollia sowelli	Baker, Solari y Hoffmann	2002
Notiosorex cockrumi	Baker, O´Neill y McAliley	2003
Lophostoma aequatorialis	Baker *et al.*	2004
Oryzomys andersoni	Brooks y Baker	2004
Anoura cadenai	Mantilla-Meluk y Baker	2006
Carollia benkeithi	Solari y Baker	2006
Micronycteris giovanniae	Baker y Fonseca	2007
Micronycteris (*Leuconycteris*)	Porter *et al.*	2007
Micronycteris (*Schizonycteris*)	Porter *et al.*	2007
Eumops wilsoni	Baker *et al.*	2009
Rhogeessa bickhami	Baird *et al.*	2012
Rhogeessa menchuae	Baird *et al.*	2012
Hsunycteris	Parlos et al.	2014

Fig. 2. Dr. Robert Baker recibiendo el premio de la Asociación Mexicana de Mastozoologia A. C. "Ticul Álvarez Solórzano" por su destacada trayectoria en la mastozoología.

Geomys texensis bakeri Smolen, Pitts y Bickham, 1993; *Reithrodontomys bakeri* Bradley, Mendez-Harclerode, Hamilton y Ceballos, 2004; mientras el artrópodo fue un ácaro, *Parichoronyssus bakeri* Morales-Malacara y Guerrero 2007.

Como docente, impartió diversos cursos de licenciatura y de posgrado, entre estos, un curso de biología para estudiantes que no iban a ser Biólogos, del cual siempre estuvo orgulloso. Robert formó un número considerable de maestros y doctores, la mayoría de los cuales se han convertido en investigadores independientes exitosos. De los numerosos estudiantes de licenciatura que asesoró, al menos 20 de ellos tienen estudios de posgrado y están laborando en instituciones académicas; su experiencia la compartió con más de 60 estudiantes de maestría y alrededor de 50 de doctorado. La mayoría de ellos forman parte del personal académico de prestigiadas universidades que se extienden en todos los Estados Unidos de América, así como diversos países del Continente Americano.

Un aspecto relevante que por lo general olvidamos porque no forma parte de un currículo profesional, son los aspectos humanos de los hombres de ciencia. Desde nuestro punto de vista, eso no debe suceder debido a que estamos inmersos en la sociedad. Por lo tanto, nuestro comportamiento debe estar comprometido con un claro interés para beneficiar a esa sociedad. Robert no fue una excepción a ello. En principio, destacar que fue una persona de trato fácil y amable, siempre dispuesto a ayudar, lo que se reflejaba en su vida profesional, pero también en la personal. Fue gran aficionado a los deportes, principalmente al futbol americano, con el equipo de su universidad, los *Red Raiders*; sabía distraer el tiempo justo para apoyar a su equipo y gozaba los triunfos y sufría las derrotas. También le fascinaba trabajar en su rancho y salir a cazar faisanes y otras aves acuáticas. En su laboratorio, exigió una férrea disciplina, pero a la vez fue cordial y apoyó siempre a los estudiantes que requerían mayor atención, para facilitar que se desarrollaran de manera independiente. El Dr. José Ramírez Pulido nos comentó alguna vez: “Robert con los visitantes era atento; por lo general los

Fig. 3. Robert Baker, colectando mamiferos en Ecuador en el 2004

acompañaba a la recolección de los ejemplares y, posteriormente, les enseñaba las técnicas y los secretos del laboratorio hasta completar el proceso".

Robert fue un gran apoyo a la Asociación Mexicana de Mastozoología y a los estudiantes en general. Siempre fue una persona muy amigable con los mexicanos que asistían a los congresos de la American Society of Mammalogy o congresos internacionales. Llegando a apoyar a varios estudiantes y después investigadores mexicanos en diferentes momentos y espacios. Adicionalmente, sus trabajos de investigación permearon dentro del conocimiento de la mastofauna mexicana y sus investigaciones son un gran adelanto para el conocimiento de la mastodiversidad, en particular el grupo de los quíropteros. Al grado que al revisar temas generales de murciélagos de América se tienen que citar al menos una de sus publicaciones en el campo. La participación de Robert en los estudios mastozoológicos en México y la formación de los especialistas fue reconocida por la AMMAC al entregarle en 2014 el premio a la carrera destacada "Ticul Álvarez Solórzano", el máximo galardón que se entrega por la asociación.

Robert falleció el viernes 30 de marzo de 2018. Le sobrevive su esposa, la Dra. Laura Kyle Baker con quién compartió la vida por 39 años. Asimismo, su hija April Baker-Padilla y su yerno Michael Padilla, ambos viven en Lubbock, Texas, así como sus nietos Jason Baker y Faith Padilla. Tristemente, Robert fue precedido en la muerte por su hijo Robert Kyle Baker.

De manera personal (JAC), considero que Robert nos enseñó que las habilidades que todo investigador requiere para su labor científica, no sólo se aprende en los salones de clases, sino deben desarrollarse desde la etapa de estudiante, entre otras: la capacidad de redactar proyectos o propuestas y someterlas a diversas agencias. La honestidad al participar en las revisiones por pares, ya sea de proyectos o de manuscritos. La redacción de textos en forma que se refleje con fidelidad el producto del trabajo en el laboratorio a partir de los protocolos establecidos. Por ejemplo, una de las recomendaciones que nos hacía más frecuentemente, fue la escribir al menos 15 minutos cada día, ya fuera de la tesis, la disertación, un ensayo o un manuscrito. Por su enseñanza, puedo afirmar que él no creía en la genialidad. Para él, era el trabajo cotidiano, sostenido y constante, el responsable de los logros. Para algunas personas pudo ser alguien controversial, pero para los que lo conocimos fue un humanista que mostró su solidaridad cuando fue requerido, apoyando a sus amigos, colegas y estudiantes más allá de lo exclusivamente académico. Robert fue siempre un verdadero mentor más que sólo un tutor. Lo que demostró al considerarme como su "hijo académico", al igual que todos mis "hermanos" que han pasado por su laboratorio. Fue un referente obligado de lo que es y lo que debe ser un profesor, maestro e investigador, quién además me distinguió con su amistad.

Finalmente, me gustaría honrarlo (CSH) recordando una de las expresiones preferidas por Robert "Cinco mil veces gracias", por todas las preguntas filogenéticas que respondió y por todas las preguntas que nos ayudó a plantear para entender el proceso de evolución de los mamíferos. "Cinco mil veces gracias", por el perfeccionamiento de las técnicas citogenéticas y moleculares, que abrieron nuevos caminos para que los mastozoólogos cimentáramos nuestro trabajo. "Cinco mil veces gracias", por el ejemplo que nos dio para realizar nuestras actividades académicas con honestidad y constancia. Robert, por tu amistad, generosidad y trabajo, "Cinco mil veces gracias".

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