

SELECTED ECOLOGICAL PATTERNS AND DISTRIBUTION
OF FIVE SYMPATRIC FELIDS IN NORTHEASTERN MEXICO

A Dissertation

by

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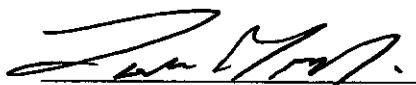
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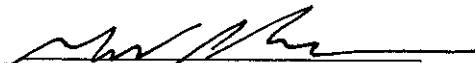
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May 2016

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ABSTRACT

Selected Ecological Patterns and Distribution
of Five Sympatric Felids in Northeastern Mexico
(May 2016)

Sasha Carvajal Villarreal, B.S., UANL; M.S., Instituto Tecnologico de Cd. Victoria

Chairman of Advisory Committee: Dr. Michael E. Tewes

There are few locations where all six species of sympatric felids occur. These species are jaguar (*Panthera onca*), puma (*Puma concolor*), bobcat (*Lynx rufus*), ocelot (*Leopardus pardalis*), jaguarundi (*Puma yaguaroundi*), and margay (*Leopardus wiedii*). In northeastern Tamaulipas, these species occur at their northeastern range, (except puma and bobcat, their distribution extends to Canada); however, little is known about the spatial patterns and interactions among these sympatric felids in this region. This study was conducted on two private ranches, the Caracol and Camotal, in Sierra Tamaulipas, Mexico, from 2009 to 2010.

I estimated the population density and home range of the jaguar and ocelot. I also examined the activity patterns, abundance, coexistence, and distribution of jaguar, ocelot, puma, bobcat, jaguarundi, and margay. Jaguar density estimation using the program CAPTURE was 3.5 jaguars/100 km² using the Maximum Mean Distance Moved radius (MMDM), and 4.2 jaguars/100 km² using the Half Maximum Mean Distance Moved radius (HMMDM). Ocelot density using the program CAPTURE using the MMDM was 9.9 ocelots/100 km² and 14.5 ocelots/100 km² using the HMMDM. Jaguar density using the program SPACECAP was 2.2 jaguars/100 km² (SD=0.6) with a 95% confidence interval of 1.6–3.4 jaguars/100 km². Ocelot

density using program SPACECAP was 21.9 ocelots/100 km² (SD=2.7) with a 95% confidence interval of 16.7–27.3 ocelots/100 km².

Estimated mean home range size using automated remote cameras and radio-telemetry data of 10 ocelots (5 females and 5 males) was 8.6 km² (range 3.1–14.9 km²). Jaguar mean home range using camera data for females was 15.7 km² and 11.9 km² for males. The carnivore community activity pattern was mainly nocturnal. Activity patterns were mainly nocturnal for jaguar and ocelot, cathemeral for puma, crepuscular for bobcat, and diurnal for jaguarundi. The Relative Abundance Index (RAI) was calculated by the number of photographic events/number of camera traps–nights x 1000. The RAI for ocelot was 69%, jaguarundi 11%, jaguar 10%, puma 6%, bobcat 3%, and margay 1%.

To determine the actual and potential distribution of jaguar, ocelot, jaguarundi, and margay, I obtained Class I (photographs, parts of the animal like fur, skull or other physical evidence) and Class II (reports and personal communication from reliable sources) records from 27 survey points for Nuevo Leon and Tamaulipas. Information from literature, scientific collections from universities, and reliable records from personal communications were used for this analysis. I used the Adaptive Kernel Range Estimator for species distribution. For species distribution modeling, I used Maxent 3.3.3K software with maximum entropy analysis. Results indicate that the forest and mountainous regions of northeastern Mexico represent important conservation areas for jaguar, ocelot, jaguarundi, and margay. With the data presented in this study, researchers and government officials will be able to identify new priority areas for conservation. Additionally, the IUCN Red List is currently re-assigning the global distribution ranges for these species and the results of this study will be used to clarify the delineation of these ranges.

DEDICATION

I dedicate this dissertation to my daughters Arusha and Ana Graciela, who have been my inspiration and strength. Arusha supported me during the time that I was not with her. I hope that in the future both girls will read this manuscript and feel proud of me, using this as an example of perseverance for their life. I hope Arusha continues her love of animals.

I also dedicate this thesis to my husband, Arturo Caso Aguilar, who has always believed in me, who has been my example and my inspiration in my personal and professional life, and always supported me and encouraged me to accomplish my goals in this part of my life and to never let me give up. Thank you Arturo, for being a part of my life.

Finally, I would like to dedicate this dissertation to my family. To my parents Mario Joaquin Carvajal Romero and Ana Villarreal Ortega because they were always supportive and let me share this adventure with them. To my two brothers, Mario and Rodrigo, and to my cousin Gilberto Villarreal, who is not with us anymore, but I am sure that if he was here, he would be proud of me.

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This degree took many years to finish and involved many complications and obstacles. However, at the same time, many colleagues, friends, and excellent professors helped and supported me, and overall believed in me. I would like to thank Dr. Michael Tewes for his support and advice during this project. Also, I would like to thank Dr. Lon Grassman who is part of my committee, and also is my friend and encouraged this work. Special thanks to the other members of my dissertation committee, Dr. David Hewitt, Dr. Alan Fedynich, and Dr. La Vonne Fedynich for taking the time to comment and review this dissertation. Special thanks to Dr. Jose Francisco Gonzalez Maya, who helped in this dissertation and for his advice and guidance. Dr. Jose Antonio de la Torre and Dr. Andres Arias Alzate also provided help and support with this work. Sincere thanks are extended to the late Dr. Dave Maehr, whom I consider to be one of the best wildlife scientists I have ever known. I appreciate the ranch access provided by Mr. Barry Putegnat and Mr. Juan Garza where this research occurred.

I also want to thank the Consejo Nacional de Tecnologia (CONACYT) for my scholarship and the Dirección General de Vida Silvestre for the research permits. Appreciation is extended to Mr. Tim Hixon and the Tim and Karen Hixon Foundation for providing the funding for the field research in support of a possible ocelot translocation.

Finally, I would like to thank a special person who helped me since I arrived at the University and always supported me during this difficult journey, Miss Eva De Leon. Special thanks to my friend Dr. Consuelo Donato, who helped and supported me of all the time. Thanks to all my family and friends.

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CHAPTER I

DENSITY AND SPATIAL PATTERNS OF

JAGUAR AND OCELOT IN THE SIERRA TAMAULIPAS, MEXICO

INTRODUCTION

The jaguar (*Panthera onca*) is the largest wild cat in the western hemisphere (Kitchener, 1998) and is a keystone, umbrella, and indicator species (Terborgh *et al.*, 1999). Considered an emblematic species in many countries and by indigenous cultures in the Americas (Redford & Robinson, 1991), the jaguar was formerly distributed from the southwestern USA through the Amazon Basin to the Rio Negro in Argentina (Caso *et al.*, 2008). However, the jaguar has been eliminated from many areas of northern Brazil, and the grasslands of Argentina and Uruguay. It is estimated that this species only occupies about 46% of its historical range (Sanderson *et al.*, 2002). In Mexico, jaguar occur in the Sierra Madre Occidental, along the Pacific Coast and through most of southern Mexico (Caso *et al.*, 2008).

The ocelot (*Leopardus pardalis*) is widely distributed from the southern USA (a small remnant population occurs in south Texas) through Mexico, Central and South America to southern Brazil, Uruguay and northeastern Argentina, excluding Chile (Caso *et al.*, 2008; Hunter, 2011). Ocelot range has been reduced during the last 30 years because of habitat destruction (Sunquist & Sunquist, 2002; Oliveira *et al.*, 2010). In Mexico, commercial trade of ocelot was greatly reduced after Mexican laws listed it as an endangered species in 1986 and after the addition of Mexico to the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES; Nowell & Jackson, 1996).

The jaguar and ocelot are considered endangered species in Mexico (SEMARNAT, 2010)

Style and format of this dissertation chapter follows the *Journal of Zoology*.

and are included in the Red List for the International Union for Conservation of Nature. In the IUCN Red List, jaguar is listed as a near-threatened species and ocelot is listed as a least-concern species (IUCN; Caso *et al.*, 2008). Both species are listed within APPENDIX I of CITES (CITES, 2013).

Recent studies of jaguar and ocelot have used remote sensing cameras which have yielded important population data for these species (Griffiths & Van Schaik, 1993; Carbone *et al.*, 2001). Camera-trapping methods also have been effective in determining tiger and jaguar density (Karanth and Nichols, 1998; Kelly, 2003; Karanth *et al.*, 2004; Maffei *et al.*, 2004; Soisalo & Cavalcanti, 2006), and ocelot population densities (Trolle & Kery, 2003; Maffei *et al.*, 2005; Di Bitetti *et al.*, 2006; Haines *et al.*, 2006). Balme *et al.* (2009) stated that camera-trapping was an effective method to estimate density and abundance of cryptic carnivores using the Half Maximum Mean Distance Moved (HMMDM) radius. However, Dillon & Kelly (2008) caution that using the HMMDM radius may overestimate ocelot density.

In 2006, the National Jaguar Census (CENJAGUAR) in Mexico was planned with the use of camera-trapping (Ceballos *et al.*, 2006). The CENJAGUAR northeastern Mexico survey area included the Sierra Tamaulipas, which was the same area where my study occurred. The Sierra Tamaulipas is considered an important conservation area for wild cats and other species being designated a Terrestrial Priority Area (RTP 91) by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO; Arriaga *et al.*, 2000) and it also is a high priority Jaguar Conservation Unit (JCU, Rabinowitz & Zeller, 2010). Several papers have been published on the results of the CENJAGUAR studies. In Sonora, jaguar density was reported to be 1 individual/100 km² (Gutierrez-

Gonzalez *et al.*, 2012). In Jalisco, jaguar density was 5.3 individuals/100 km² (Nuñez-Perez, 2011), and in Chiapas, jaguar density was reported at 1.7 individuals/100 km² (De la Torre & Medellin, 2011).

There are no published studies on ocelot density in Mexico using camera-trap methods. However, there is information from radio-telemetry studies (Caso, 1994; Caso, 2013), surveys and distribution reports (Arzate *et al.*, 2011; Azuara & Medellin, 2011). Results from my study are important to help evaluate the ocelot population as a source for future translocations from Tamaulipas to Texas.

The objectives of this study were to determine the density and spatial patterns of jaguar and ocelot in northern Sierra Tamaulipas and to compare different software programs to estimate density using remote sensing cameras.

METHODS

Study sites

This study was conducted in the northern region of the Sierra Tamaulipas and included two private ranches, the “Caracol” and “Camotal” ranches, combined as the Caracol and Camotal Ranch Complex. Both ranches occur in Abasolo and Jimenez counties (UTM E 547219–N 2654254), and comprised a study area of 6,320 ha (Figure 1). The main activity of the Caracol Ranch was northern bobwhite (*Colinus virginianus*) and white-winged dove (*Zenaida asiatica*) sport hunting; whereas the Camotal Ranch produced cattle.

The study site supported several habitat types including Tamaulipan thornshrub, low tropical forest, riparian, and secondary vegetation (Stresser-Pean,

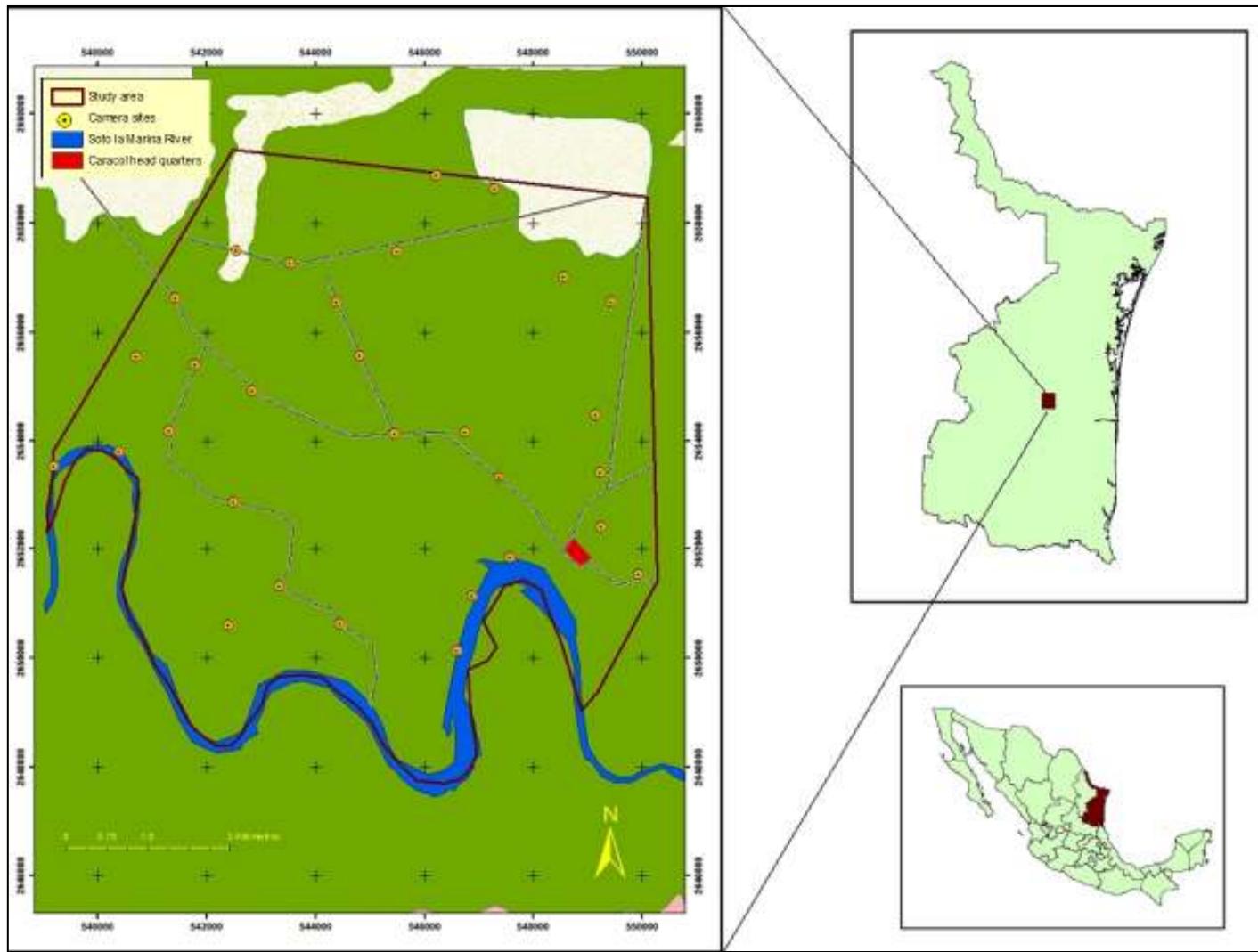


Figure 1. Study area on the Caracol and Camotal Ranch Complex in Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

2000). The dominant vegetation in both ranches was high shrubland, with plant species such as anacahuita (*Cordia boissieri*), barreta (*Helietta parvifolia*), black-brush (*Acacia rigidula*), cenizo (*Leucophyllum frutescens*), guajillo (*Acacia berlandieri*), and skeleton leaf goldeneye (*Viguieria stenoloba*; Cram *et al.*, 2006). Tamaulipan scrubland was also present on both ranches characterized by amargoso (*Castela texana*), brasil (*Condalia hookeri*), honey mesquite (*Prosopis glandulosa*), saffron plum (*Bumelia angustifolia*), spiny hackberry (*Celtis pallida*), and white indigoberry (*Randia aculeata*). The deciduous tropical forest was characterized by ebony (*Pithecellobium ebano*), Berlandier's jopoy (*Esenbeckia runyonii*), gumbo limbo (*Bursera simaruba*), mahuira (*Phoebe tampicensis*), and mauto (*Lysiloma divaricata*; Cram *et al.*, 2006).

Topography in the study area consisted of lowland hills with the highest elevation of about 600 m. The Soto la Marina River represented the southern boundary of the study area. Average annual temperature was 18° C and annual precipitation was 800 mm. Annual precipitation is usually <800 mm in the northern and western regions of the Sierra Tamaulipas, with typically four or five months of rainfall. Dry and wet seasons occur but are not well defined temporally (Stresser-Pean, 2000).

Camera-trapping design

Camera-trapping methods were based primarily on the CENJAGUAR for Mexico (Chavez *et al.*, 2006). I designed a camera grid on the Caracol and Camotal Ranch Complex that contained 10, 9-km² blocks. Each block contained three camera stations, and at least one station had two paired cameras, (double stations are used to obtain both sides of the individual to facilitate and reduce the error of individual identification, reducing the error). Thirty camera stations were used in the survey with 16 double stations. Camera

stations were separated by at least 1 km. Distance between camera stations was based on average home range and daily distances covered by ocelots in Tamaulipas from a previous radio-telemetry study where home range size was 9 km² and average daily distances travelled were 1 km (Caso, 1994; Figure 2).

Four types of remote sensing-camera brands were used: Cuddeback® (Cuddeback Digital, Green Bay Wisconsin), Wildview® (Stealth Cam, LLC, Grand Prairie, Texas), Moultrie® (EBSCO Industries, Inc. Birmingham, Alabama), and Bushnell® (Bushnell Outdoor Products, Kansas City, Missouri). Camera stations were established along roads, existing trails, and near artificial or natural water sources. Camera units were positioned 30–50 cm above the ground in order to be triggered by the body of a passing cat. Cameras were programmed to continuously record diurnal and nocturnal photographs with a 30–second delay used between photographs. Independent photograph events were determined by separation of >30 min between photographs. No attractant was used to avoid bias in the detection of individuals (Gutierrez-González *et al.*, 2012). A camera-trap data form was completed when memory cards and batteries were replaced every 45 days. Each camera-trapping period covered 40–100 days, and the population was assumed to be closed during a camera trapping period (Dillon & Kelly, 2008; Maffei & Noss, 2008). I collected data over 187 days and four sessions, during continuous camera-trapping from December 2009 to June 2010.

Density analysis

Individual jaguars and ocelots were identified by their pelage spotting pattern. Population density was estimated using capture–recapture statistical models in the programs CAPTURE (Otis *et al.*, 1978; Dillon & Kelly 2008; Soria-Díaz *et al.*, 2010) and SPACECAP (Gopalaswamy *et al.*, 2012; Noss *et al.*, 2012; Tobler *et al.*, 2013).

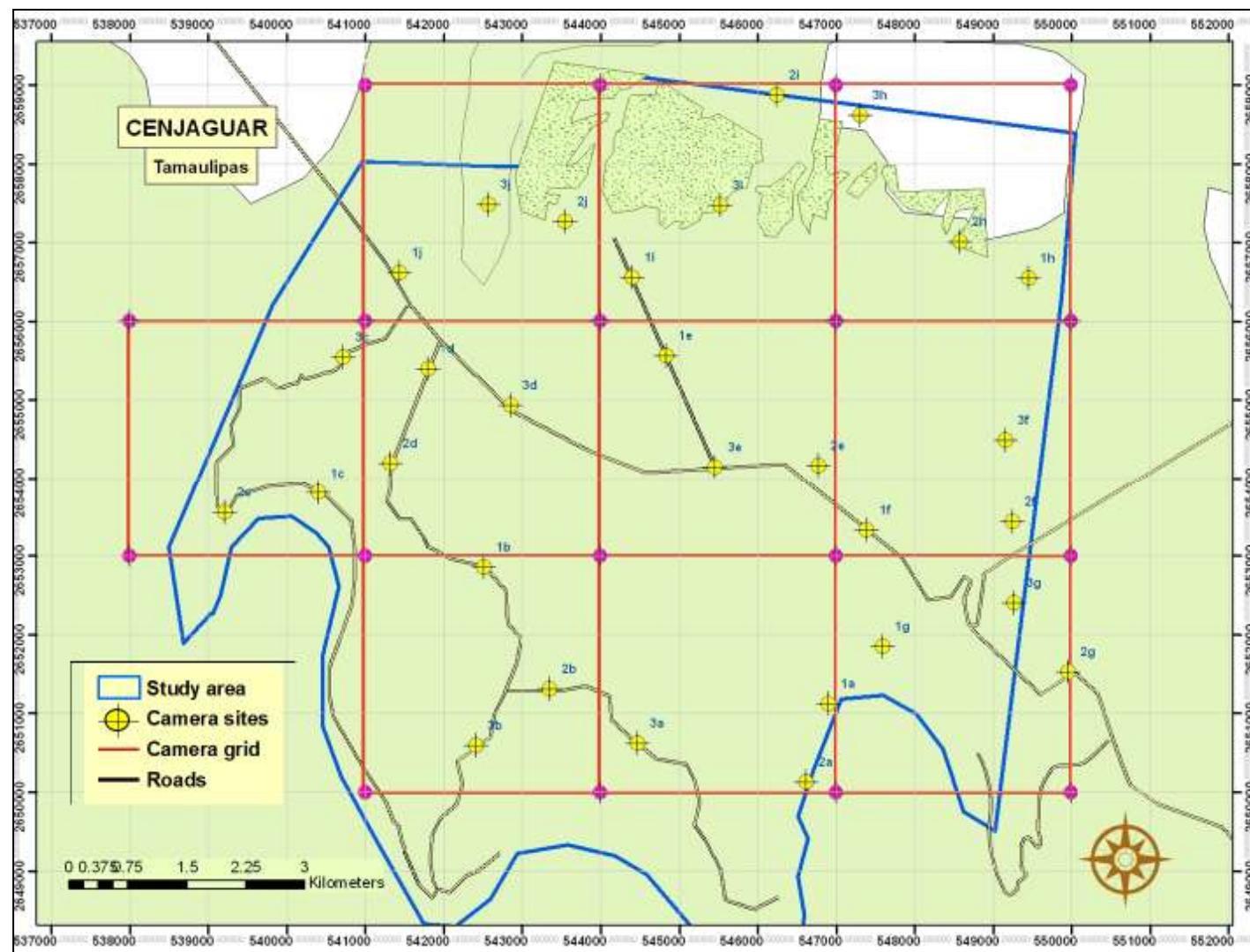


Figure 2. Camera-trapping design for jaguar and ocelot density estimation on the Caracol and Camotal Ranch Complex in Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

For the CAPTURE program, I determinated the effective sampling area by measuring the Maximum Mean Distance Moved (MMDM) of different individuals photographed in the area and the HMMMD of individuals photographed at two or more camera stations (Wilson & Anderson, 1985; Balme *et al.*, 2009).

Population estimators used to estimate density were the jackknife population model (*h*) and null model (*o*). The jackknife model considers the heterogeneity among individuals and that each individual has a unique probability of capture being independent of the other individuals in the same population. This approach is considered the best model based on behavioral differences of individuals and of the species (Otis *et al.*, 1978; Karanth & Nichols, 1998; Silver *et al.*, 2004). I ran the CAPTURE program using four intervals of 45 days and two intervals of 92 days. Survey dates were from 15 December 2009 to 18 June 2010.

The R package SPACECAP program analyzes animal densities using closed capture–recapture model sampling. Photographs from camera–trapping are used with Bayesian spatially explicit capture–recapture models (SECR; Gopalaswamy *et al.*, 2012). To run SPACECAP, it was necessary to create three input files using Microsoft EXCEL: (1) animal capture details, including location number (LOC_ID), animal identification number (ANIMAL_ID) and occasion number (SO); (2) trap details, including the Universal Transverse Mercator (UTM) coordinates of each camera trap, and the trap occasion where “1” represented a trap station that was active during that period of time, and “0” where the station was not active; and (3) potential home range centers, which contained the locations of possible home range centers for all animals which could be detected by camera–traps. These locations were represented by a large number of equally spaced points or pixels in a

grid. This buffer input file was created with ArcMap10® (ESRI industries, Redlands, California).

To create the circular buffer file, radii were calculated for jaguar (8.61 km) and ocelot (4.64 km) based on the maximum distanced moved by all individuals for each species. In the input file, a third column used “1” to identify suitable habitat at the trap location or “0” if there was not suitable habitat available. Because the study area habitat was homogeneous (Stacey, 2012), I set the “1” value for all of the camera stations. The specific area of each pixel (km^2) that represented the potential home range center was 1 km^2 for jaguar and 0.25 km^2 for ocelot (Noss *et al.*, 2012).

To run the SPACECAP model combination definition analysis, I selected the following options indicated for the program: trap response absent, spatial capture–recapture, half–normal detection function, and Bernoulli’s encounter model (Gopalaswamy *et al.*, 2012). For the Markov–Chain Monte Carlo (MCMC) simulations I used 50,000 interactions for ocelot and jaguar, a burn–in period of 10,000 interactions for both species, and data augmentation (5 or 10 times the number of animals captured) of 90 and 350 jaguar or ocelots individuals ($n = 9 \times 10$ was used for jaguar and $n = 35 \times 10$ for ocelot).

Spatial patterns

I determined ocelot home range using data from radio–telemetry and camera–trapping, whereas only information from camera–trapping was used for jaguar home range estimation. Ocelot live–trapping periods were during December 2009 and February 2010. Box trapping periods lasted for 13 nights for a total trapping period of 520 trap nights. Ocelots were captured using Tomahawk® wire box–traps (107 x 50 x 40 cm; Tomahawk Live Trap Company, Tomahawk, Wisconsin) with a rear compartment for live bait (i.e., chickens) (Tewes, 1986; Carvajal *et al.*, 2012; Caso, 2013). Traps were set continuously in

locations with sufficient shade to prevent heat stress of captured cats and checked every morning before 10:00 h.

Captured ocelots were immobilized with an intramuscular injection of tiletamine hydrochloride–zolazepam using a pole syringe (Zoletil® Virbac, Ltd., Carros, France) (Shindle & Tewes, 2000; Caso, 2013). A VHF 120-g radio-collar (148.00–149.99 MHz) with a mortality sensor (Advanced Telemetry Systems. Inc., Isanti, Minnesota) was attached to adult and sub-adult ocelots. Ocelots were placed in a pet carrier during recovery and were released at the capture site. Capture and handling of ocelots were allowed by the Mexican Federal Permit issued by SEMARNAT (SGPA/DGVS/08764/09).

Portable radio-telemetry VHF receivers (Advanced Telemetry Systems®) were used to radio-track ocelots. For each location, at least three bearings were taken with a Suunto® (Sunnto Instruments, Finland; Kenward 1987) compass from fixed receiver stations previously established with a hand-held GPS unit. I obtained one independent location every 24-h and used Locate III ® software (Tatamagouche, NS, Canada) for spatial analysis. Because of limited radio-telemetry data, I combined the radio-tracking data with camera-trapping information to obtain the home range values. I selected ocelot individuals with the greatest number of locations from different camera stations (Maffei *et al.*, 2005; Gil-Sanchez *et al.*, 2011) and added the radio-telemetry locations for that individual. All locations were used to calculate ocelot home ranges using a 100% minimum convex polygon (MCP100) estimator (Mohr, 1947; MacDonald *et al.*, 1980; Oliveira *et al.*, 2010) and to measure home range overlap (Oliveira *et al.*, 2010; Carvajal *et al.*, 2012; Caso, 2013). Home range boundaries and ocelot locations were converted with ArcMap10 to polygon and point shape files (Caso, 2013). Personal safety concerns around the study area resulted in ending the monitoring of ocelot and jaguar populations for a

longer period to exclude summer and autumn seasons in the analyses.

RESULTS

Camera-trapping occurred from 15 December 2009 to 18 June 2010 yielding 5,700 trap-nights. During this period, 9 jaguars (4 females, 4 males, and 1 unknown sex) and 34 ocelots (18 females and 16 males) were identified. Of these 34 ocelots, 11 (6 females and 5 males) individuals also were captured and radio-collared.

Other photographed species during this period were puma (*Puma concolor*), bobcat (*Lynx rufus*), jaguarundi (*Puma yagouaroundi*), margay (*Leopardus wiedii*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), coatimundi (*Nasua narica*), long-tailed weasel (*Mustela frenata*), badger (*Taxidea taxus*), hog-nosed skunk (*Conepatus leuconotus*), striped skunk (*Mephitis mephitis*), spotted skunk (*Spilogale gracilis*), opossum (*Didelphis virginiana*), white-tailed deer (*Odocoileus virginianus*), and collared peccary (*Pecari tajacu*). During the camera-trapping period, 101 jaguar photographs were obtained from 63 independent events, and 400 ocelot photographs were documented from 324 independent events.

Density

The effective sampling area using MMDM was 396.5 km² and using HMMDM was 191 km² for jaguars. Jaguar density was similar during four periods of 45 days, except during the third period when the density increased. Mean density for 45 days using MMDM was 1.6 jaguars/100 km², and the mean density using HMMDM was 3.4 jaguars/100 km² (Table 1).

For the two, 92 day periods, jaguar density decreased slightly during the second period (Table 2). Mean density using MMDM was 2 jaguars/100 km², whereas mean density using HMMDM was 4.2 jaguars/100 km². Jaguar density using the SPACECAP

Table 1. Jaguar density comparisons using CAPTURE during four, 45 day periods on the Caracol and Camotal Ranch Complex in Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

	Period 1 (15 Dec 2009–28 Jan 2010)	Period 2 (29 Jan 2010–14 Mar 2010)	Period 3 (15 Mar 2010–28 Apr 2010)	Period 4 (28 Apr 2010–12 Jun 2010)
	N=5	N=6	N=10	N=5
	95% CI = 4–20	95% CI = 6–13	95% CI = 9–18	95% CI = 5–13
	MMDM	HMMDM	MMDM	HMMDM
12	1.3/100 km ²	2.6/100 km ²	1.5/100 km ²	3.1/100 km ²
	2.52/100 km ²	5.2/100 km ²	1.3/100 km ²	2.6/100 km ²

N = Number of individuals

CI = Confidence interval

MMDM = Maximum Mean Distance Moved

HMMDM = Half Maximum Mean Distance Moved

Table 2. Jaguar density comparisons using CAPTURE during two, 92 day periods on the Caracol and Camotal Ranch Complex in Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

Period 1 (15 Dec 2009–16 Mar 2010)	Period 2 (17 Mar 2010–16 Jun 2010)
N= 9	N= 7
95% CI = 8–20	95% CI = 7–7
MMDM	HMMDM
2.3/100 km ²	4.7/100km ²
MMDM	HMMDM
1.8/100km ²	3.7/100km ²

13

N = Number of individuals

CI = Confidence interval

MMDM = Maximum Mean Distance Moved

HMMDM = Half Maximum Mean Distance Moved

program was 2.2 jaguars/100 km² (SD=0.6; 95% C.I. 1.6–3.4 jaguars/100 km²).

The effective sampling area for ocelots using MMDM was 185 km² and in HMMDM was 126 km². Ocelot density during the 45 day periods revealed that the first 3 periods were constant; however, density decreased during the last period (Table 3). Mean density obtained using MMDM was 9.9 ocelots/100 km², whereas the density using HMMDM was 14.5 ocelots/100 km². Ocelot density results during the 92 day periods was 14.6 ocelots/100 km², whereas during the second period ocelot density decreased (Table 4). Mean density using MMDM was 12.1 ocelots/100 km², whereas density using HMMDM was 17.8 ocelots/100 km². Estimated ocelot density using SPACECAP was 21.9 ocelots/100 km² (SD=2.7; 95% C.I. 16.7–27.3 ocelots/100 km²).

I compared the results of jaguar and ocelot densities using the greatest density for MMDM for the 92–day periods and I assumed that all individuals were recorded. The two techniques produced similar jaguar density, but not for ocelot density. Densities for jaguar using CAPTURE were 2.3 jaguar/100 km² and 2.2 jaguars/100 km² in SPACECAP; however, resulted in a greater density estimate for ocelot using SPACECAP (21.9 ocelots/100 km²; CAPTURE density estimate 14.6 ocelots/100 km²) (Figure 3).

The results of this study compared to other published results for jaguar (Table 5) and ocelots (Table 6) revealed that jaguar and ocelot densities in this study were greater than those cited elsewhere.

Spatial patterns

I obtained a home range size of 5 jaguars (3 males and 2 females) using camera–trapping data (Figure 4). Mean home range size was 15.7 km² for females and 11.9 km² for males. I could not estimate percent overlap among jaguar home ranges because of insufficient sample size.

Table 3. Ocelot density comparisons using CAPTURE during four, 45 day periods on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

Period 1 (15 Dec 2009–28 Jan 2010)	Period 2 (29 Jan 2010–14 Mar 2010)	Period 3 (15 Mar 2010–28 Apr 2010)	Period 4 (28 Apr 2010–12 Jun 2010)
N=20	N=21	N=19	N=13
95% CI = 20–27	95% CI = 20–28	95% CI = 17–30	95% CI = 13–19
MMDM	HMMDM	MMDM	HMMDM
10.8/100 km ²	15.9/100 km ²	11.3/100 km ²	16.7/100 km ²
10.3/100 km ²	15.1/100 km ²	7/100 km ²	10.3/100 km ²

N = Number of individuals

CI = Confidence interval

MMDM = Maximum Mean Distance Moved

HMMDM = Half Maximum Mean Distance Moved

Table 4. Ocelot density comparisons using CAPTURE during two, 92 day periods on the Caracol and Camotal Ranch Complex in Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

Period 1 (15 Dec 2009–16 Mar 2010)	Period 2 (17 Mar 2010–16 June 2010)
N= 27	N= 18
95% CI = 27–33	95% CI = 18–21
MMDM	HMMMDM
14.6/100 km ²	21.4/100km ²
MMDM	HMMMDM
9.7/100km ²	14.3/100km ²

16

N = Number of individuals

CI = Confidence interval

MMDM = Maximum Mean Distance Moved

HMMMDM = Half Maximum Mean Distance Moved

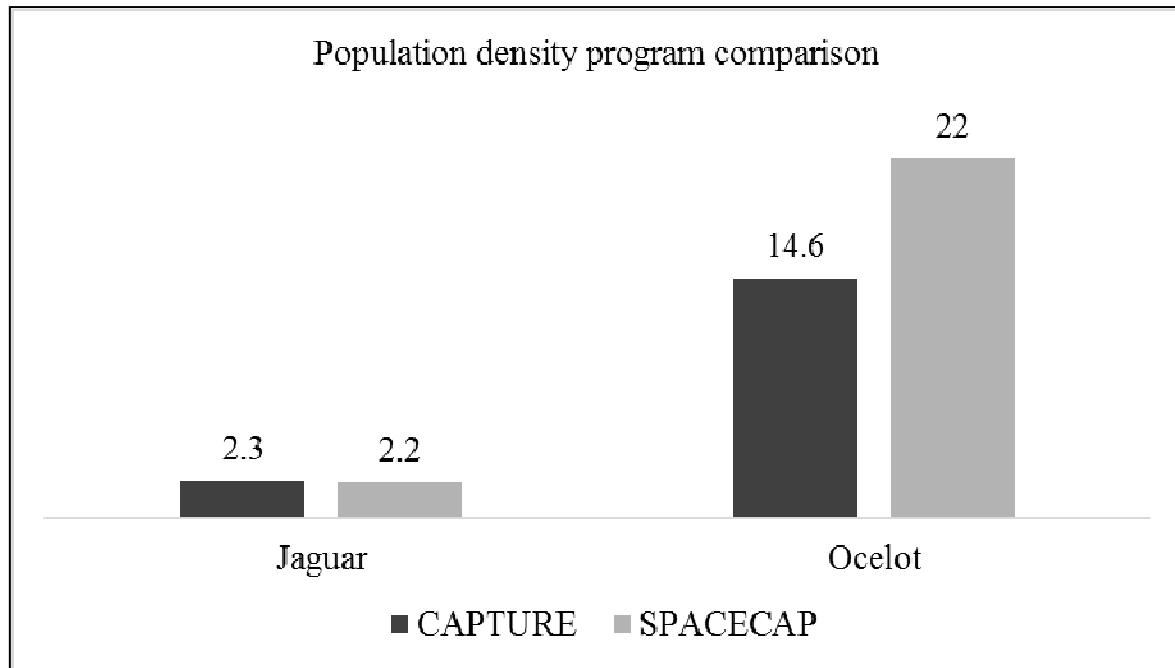


Figure 3. Density comparison of jaguar and ocelot using CAPTURE (HMMDM) and SPACECAP programs on the Caracol and Camotal Ranch Complex Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

Table 5. Comparative jaguar densities from different studies and regions estimated using camera-trapping methods (CAPTURE, SPACECAP and JOLLY).

Study	Country	Study year	Method	Individuals/100km ²
Paviolo <i>et al.</i> , 2008	Argentina	2006	CAPTURE MMDM	0.1–1.7
Maffei <i>et al.</i> , 2004	Bolivia	2001–2003	CAPTURE HMMDM	2.3–5.4
Wallace <i>et al.</i> , 2003	Bolivia	2002	CAPTURE HMMDM	1.6
Soisalo & Cavalcanti, 2006	Brazil	2003–2004	CAPTURE MMDM	11
Silveira <i>et al.</i> , 2009	Brazil	2007	CAPTURE MMDM	2.8
Sollmann <i>et al.</i> , 2011	Brazil	2008	SPACECAP	0.3
Salom <i>et al.</i> , 2007	Costa Rica	2002–2003	CAPTURE HMMDM	6.9
Nuñez-Perez, 2011	Mexico (Jalisco)	2008	CAPTURE HMMDM	5.4

MMDM = Maximum Mean Distance Moved

HMMDM = Half Maximum Mean Distance Moved.

Table 5. Continued

Study	Country	Study year	Method	Individuals/100km ²
De la Torre & Medellin, 2011	Mexico (Chiapas)	2007–2008	CAPTURE HMMDM	4.6
Rosas–Rosas, 2006	Mexico (Sonora)	2005	CAPTURE HMMDM	1.0
Faller, 2011	Mexico (Yucatan)	2008	CAPTURE MMDM	1.8
Gutierrez–Gonzalez <i>et al.</i> , 2012	Mexico (Sonora)	2009–2010	JOLLY	0.4
Avila–Najera, 2015	Mexico (Quintana Roo)	2008, 2010–2012	SPACECAP	1.9
Present study, 2015	Mexico (Tamaulipas)	2009–2010	CAPTURE MMDM	2.3
Present study, 2015	Mexico (Tamaulipas)	2009–2010	CAPTURE HMMDM	4.7
Present study, 2015	Mexico (Tamaulipas)	2009–2010	SPACECAP	2.19

Table 6. Comparative ocelot densities estimated from different studies and regions using camera-trapping methods (CAPTURE, SPACECAP and JOLLY).

Study	Country	Study year	Method	Individuals/100 km ²
Dillon & Kelly, 2007	Belize	2002–2004	CAPTURE HMMDM	25.8
Di Bitetti <i>et al.</i> , 2006	Argentina	2003–2004	CAPTURE HMMDM	19.9
Di Bitetti <i>et al.</i> , 2006	Argentina	2003–2004	CAPTURE MMDM	12.8
Maffei <i>et al.</i> , 2005	Bolivia	2002–2004	CAPTURE HMMDM	30
Haines <i>et al.</i> , 2006	United States	2003–2004	CAPTURE HMMDM	30
Goulart <i>et al.</i> , 2009	Brazil	2006	CAPTURE HMMDM	4
Trolle & Kery, 2003	Brazil	—	CAPTURE HMMDM	56
Gonzalez–Maya & Cardenal Porras, 2011	Costa Rica	2009	CAPTURE MMDM	5.6–7.2

MMMD = Maximum Mean Distance Moved

HMMDM = Half maximum Mean Distance Moved

Table 6. Continued.

Study	Country	Study year	Method	Individuals/100 km ²
Kolowski & Alonso, 2010	Peru	2008	CAPTURE HMMDM	75.2
Kolowski & Alonso, 2010	Peru	2008	CAPTURE MMDM	43.5
Avila-Najera, 2015	Mexico (Quintana Roo)	2008, 2010–2012	SPACECAP	1.7–13.9
Avila-Najera, 2015	Mexico	2008, 2010–2012	CAPTURE HMMDM	2.9–26
21 Stasey, 2012	Mexico (Tamaulipas)	2009	CAPTURE MMDM	19.2
Noss <i>et al.</i> , 2012	Bolivia	2001 and 2007	CAPTURE HMMDM	10–77
Noss <i>et al.</i> , 2012	Bolivia	2001 and 2007	SPACECAP	5–77
Present study, 2015	Mexico (Tamaulipas)	2009–2010	CAPTURE MMDM	14.6
Present study, 2015	Mexico	2009–2010	CAPTURE HMMDM	21.4
Present study, 2015	Mexico	2009–2010	SPACECAP	21.9

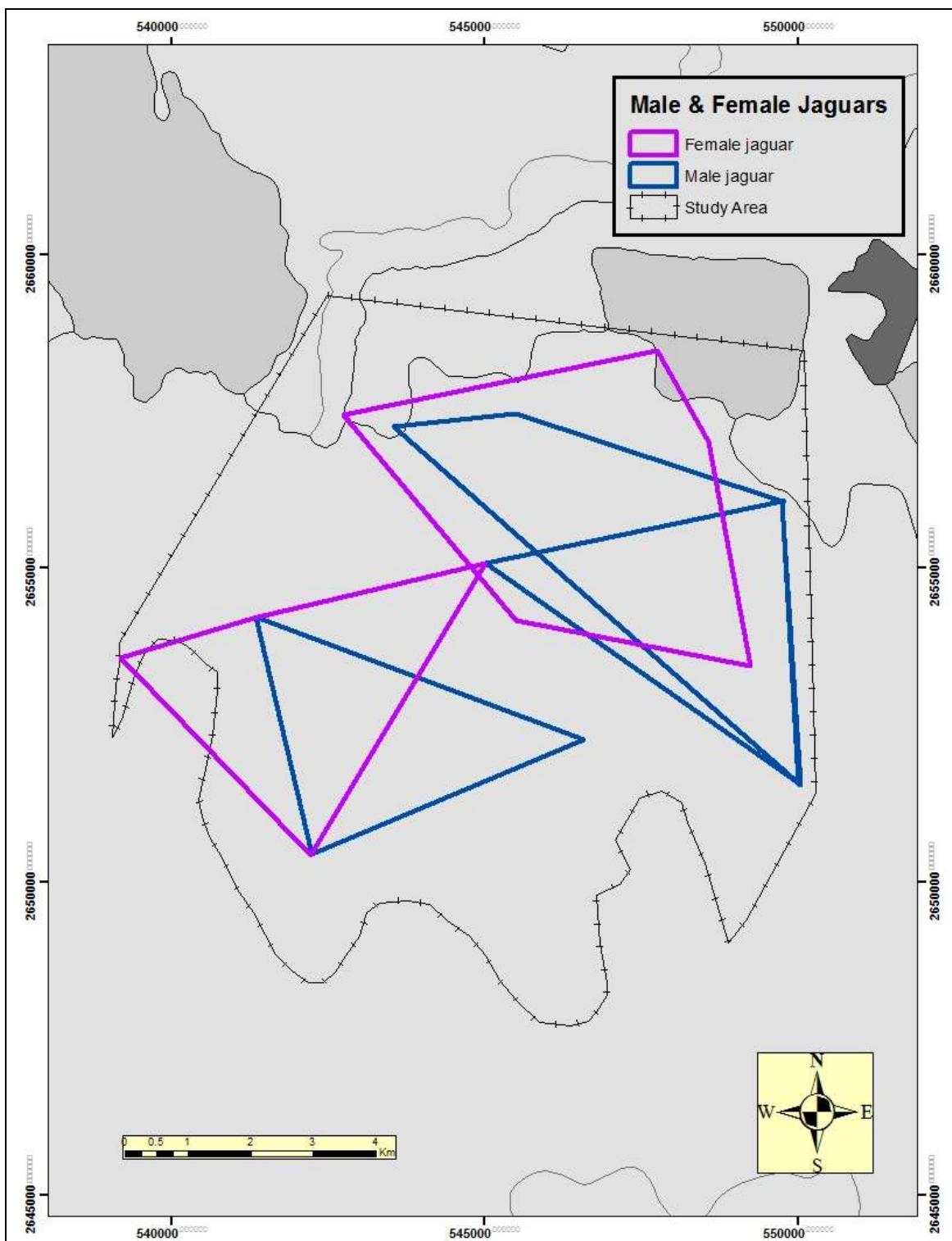


Figure 4. Selected jaguar home ranges on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

I estimated home range size of ocelots using radio-telemetry and camera-trapping data from 10 ocelots (5 males and 5 females). The home range size for male ocelots was from 8.2 to 14.9 km², and the mean was 11.3 km². The home range size for female ocelots was 3.1 to 9.8 km², and the mean was 6.4 km². Male ocelots (n= 4) overlapped 11.5% (Figure 5), whereas females overlapped 16.6% (Figure 6). Overlap between males and females was 15.6% and was not significant (*t*-test, *p*=0.390) (Figure 7).

DISCUSSION

Density estimation for many species has been obtained with the use of remote sensing cameras. The software needed to analyze camera data has been evolving and is now more specialized. Initially, the most popular software to analyze camera data was CAPTURE (Otis *et al.*, 1978; White *et al.*, 1978; Rexstad & Burnham, 1991), and many studies used this program (Maffei *et al.*, 2004; Dillon & Kelly, 2008; Paviolo *et al.*, 2009; De la Torre & Medellin 2011; Anile *et al.*, 2012). However, CAPTURE has limitations that may over or under estimate density, one of the limitations of the program is that the program does not exceed 98 days because this program is based on the assumption of a closed population no deaths, births or immigrants in the population (White *et al.*, 1978; Rexstad & Burnham, 1991). This constraint could be a disadvantage for species (e.g., jaguars) in which the capture and recapture of individuals is difficult (Harmsen *et al.*, 2011). However, CAPTURE is used widely in many studies; therefore, results from CAPTURE should be compared with other programs and models to determine if there are important density differences (Tobler *et al.*, 2013).

The program SPACECAP is based on a SECR model, which has fewer limitations than CAPTURE. In addition, it estimates other parameters such as activity center points, distance moved and abundance in a pre-defined area (Royle & Young, 2008; Royle &

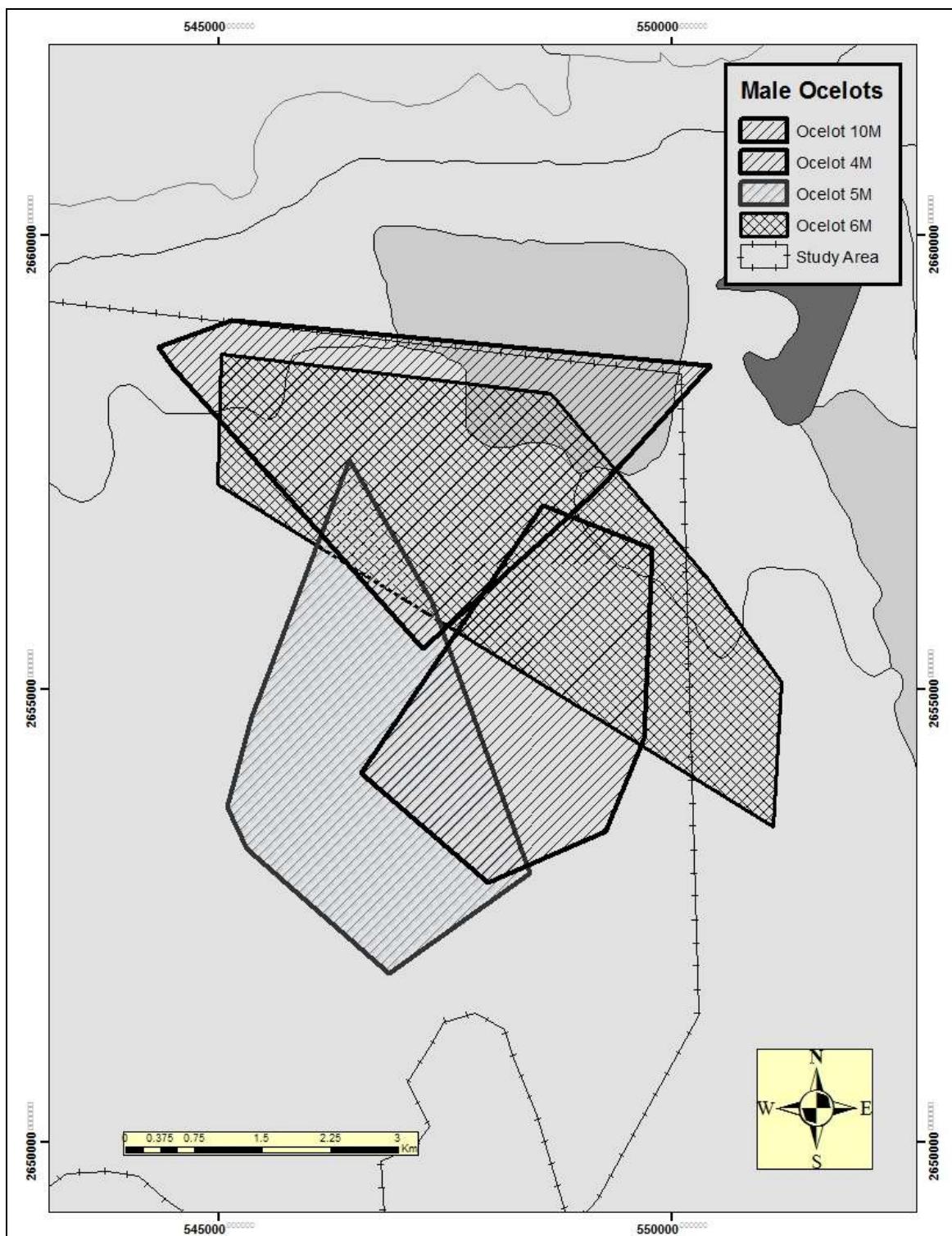


Figure 5. Selected overlapping male ocelot home ranges on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

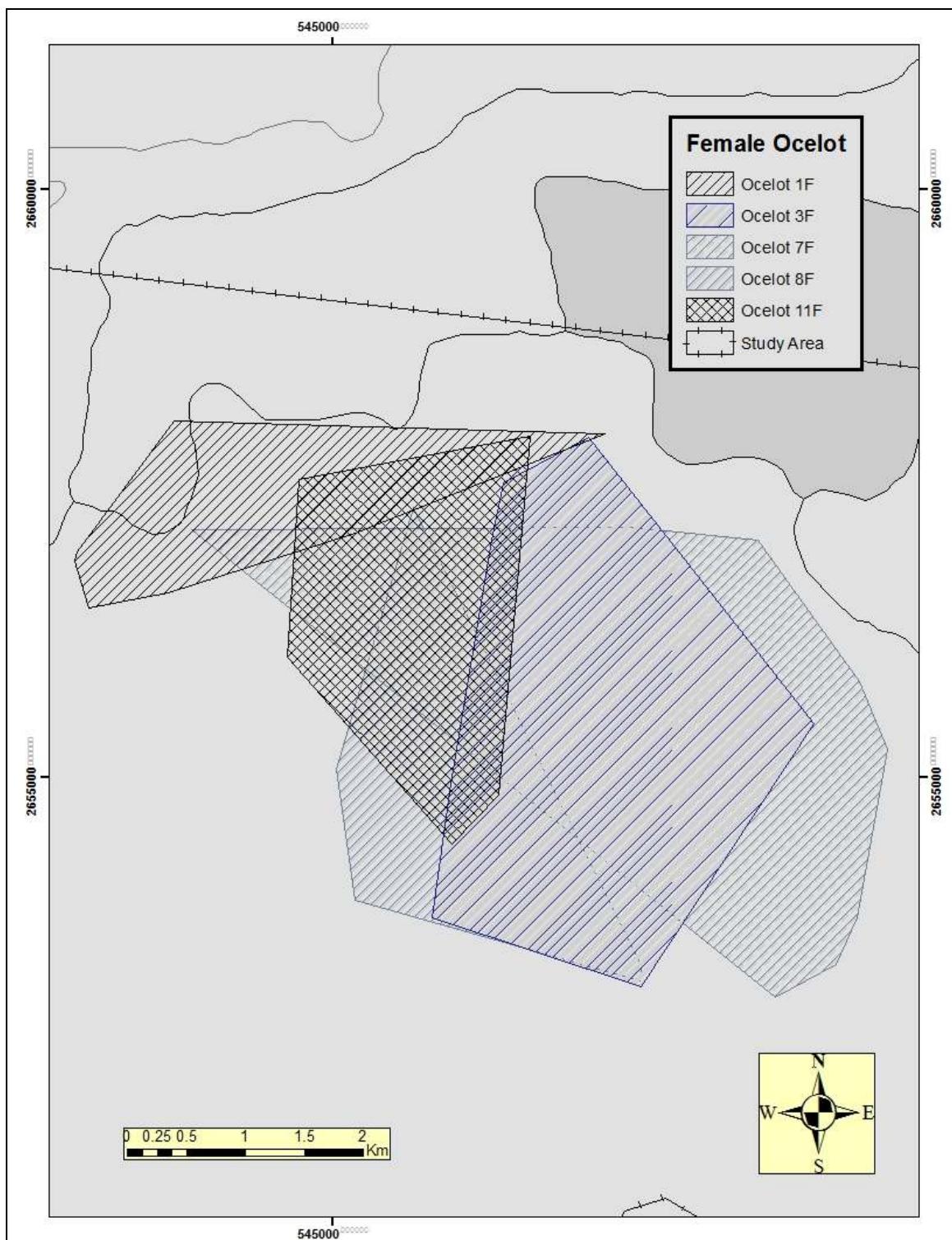


Figure 6. Selected overlapping female ocelot home ranges on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

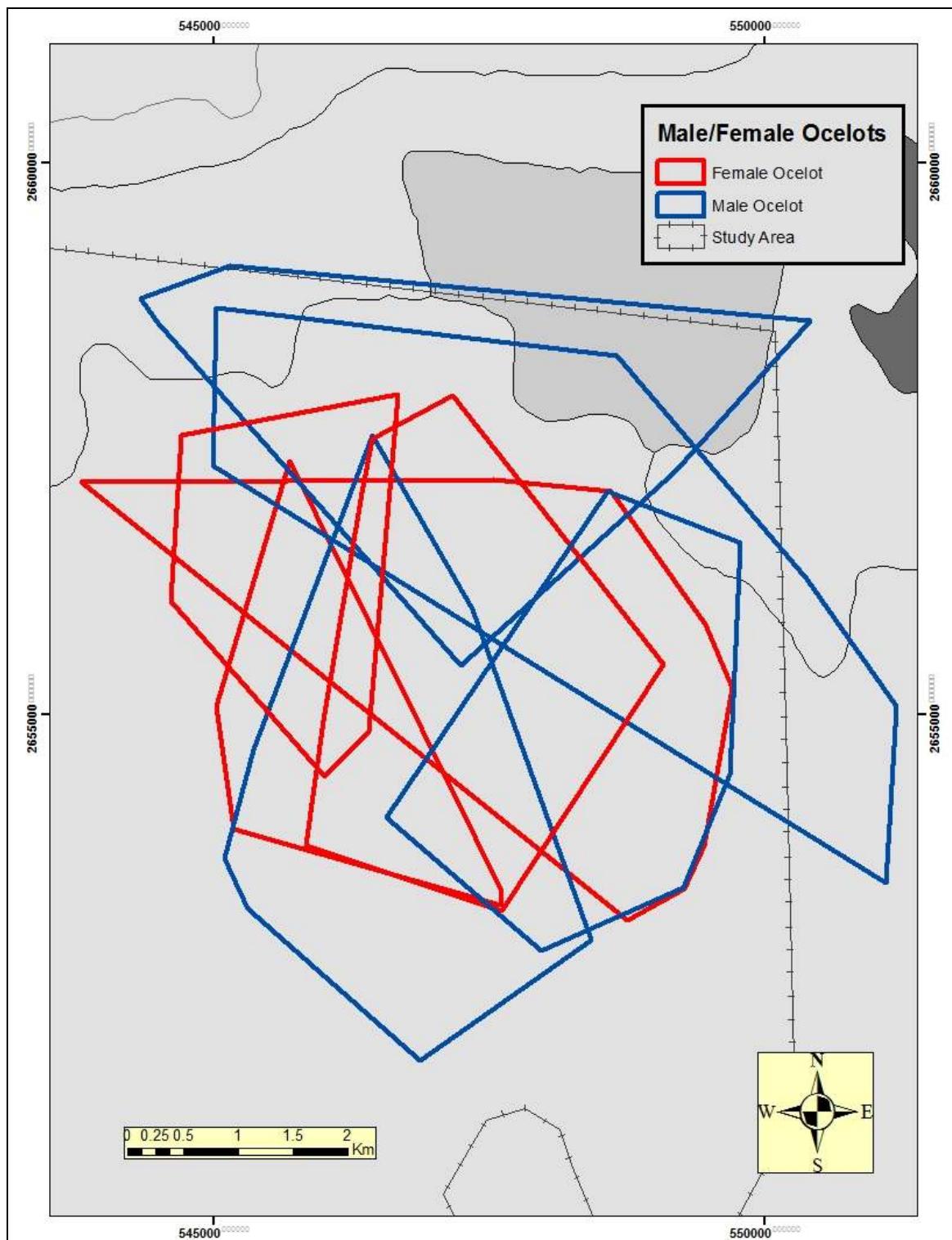


Figure 7. Male and female ocelot overlapping home ranges on the Caracol and Camotal Ranch, Complex Tamaulipas, Mexico, from 15 December 2009 to 18 June 2010.

Gardner, 2011). Density estimation for ocelots and jaguars was estimated with both methods, but I concluded that the results obtained with SPACECAP were more reliable because it used the entire trapping period (187 days) whereas the CAPTURE analysis only used 98 days. This conclusion is based on a closed population thus reducing bias. Another reason SPACECAP is a better method, is because it considers the cameras that were active during the camera trapping period, while CAPTURE did not. These two considerations reduce the possible error that could affect the density estimation.

The camera design for this study was based on one developed for CENJAGUAR; (Ceballos *et al.*, 2006). This design was used for ocelot and jaguar population density estimation (Noss *et al.*, 2011).

Tobler *et al.*, (2013) conducted an analysis of 74 publications on density estimation of jaguars using remote sensing cameras and found that CAPTURE and SECR were the most reliable; but they also suggested some considerations on sampling designs. Tobler *et al.*, (2013) suggested that the camera area polygon should be at least the size of a male jaguar home range. In some areas Tobler *et al.*, (2013) suggested that the home range of a male jaguar is as large as 200–300 km² (Cavalcanti & Gese, 2009). Jaguar home ranges in the Pantanal of Brazil have may be 1,000 km² (McBride, 2007; Conde, 2008). However, the polygon size varies by site depending on the jaguar density. For example, in areas with high jaguar density (3–4 jaguars/100 km²) the polygon may be as small as half the home range size of a male jaguar, but in sites with low jaguar density (e.g., <2 jaguars/100 km²) the polygon would need to encompass many home ranges. Of the 74 publications that Tobler *et al.*, (2013) reviewed, 54% used polygons with a range from 51–100 km², 17% used polygons < 51 km², and 8% used polygons >250 km².

In Mexico, the recommended camera trap design for CENJAGUAR, considering the size of the home range of a male jaguar reported for Mexico, is 36.6 km² for Jalisco (Nuñez, 2006) and 56 km² for Campeche (Chavez *et al.*, 2011); if is consider the jaguar density a polygon from 64–200 km² for areas with high jaguar density is enough (7–9 jaguars/100 km²; Maffei *et al.*, 2004; Chavez *et al.*, 2006; Medellin *et al.*, 2006) and 400–500 km² for areas with lower densities (< 1 jaguar/100 km²; Paviolo *et al.*, 2008). In my study, I used a 90 km² polygon that was within the range established by the CENJAGUAR design and within recommendations by Tobler *et al.*, (2013).

Limitations for determining home range polygon sizes include site conditions, such as accessibility, topography, ownership, and other factors (Medellin *et al.*, 2006). Therefore, it is recommended that an evaluation of the site be conducted before attempting to implement a camera design. For future studies, polygon size should be increased to determine if density results are affected. Tobler *et al.*, (2013) recommend 60 days as a minimum survey period if the density value or number of captures are high, or if a block design will be used. Tobler *et al.*, (2013) state that the survey period could range from 90–120 days but longer periods may affect the closed population status. However, shorter periods (e.g., < 30 days) may not be long enough to estimate density. Of the 74 publications that Tobler *et al.*, (2013) analyzed, 44.7% used a survey range of 60–69 days.

I used the same methodology and design for ocelots as for jaguars (Di Bitetti *et al.*, 2006). This design was more appropriate for ocelots because their home ranges are smaller than jaguars. In Tamaulipas, ocelot home ranges have been reported as 15.09 ± 8.10 km² for males (Caso *et al.*, 2013); therefore, the distance between cameras was 1 km (Dillon & Kelly, 2008) and the survey time of 45–90 days was appropriate for the species. Another factor that supported the design used to obtain ocelot density was the methodology used in

a previous study by Stasey (2012) in Tamaulipas. Stasey (2012) estimated 19.2 ocelots/100 km² and compared these results to other studies such as the Atlantic Forest of Brazil with 4 ocelots/100 km² (Goulart *et al.*, 2009) and in Costa Rica where density was reported as 5.9–7.3 ocelots/100 km² (Gonzalez–Maya & Cardenal Porras, 2011).

Many studies recommend using CAPTURE with MMDM to avoid overestimating density when calculating the buffer ratio for the effective area (Dillon, 2005; Di Bitetti *et al.*, 2006; Soisalo & Cavalcanti, 2006; Tobler *et al.*, 2013); however, some studies prefer to use HMMDM (Silver *et al.*, 2004; Harmsen, 2006; Romero–Muñoz *et al.*, 2006; Payan, 2009). Balme *et al.*, (2009) compared various methods (i.e., tracks, cameras, and GPS collars) to estimate density in leopards (*Panthera pardus*). The GPS information suggested that using HMMDM was the best method to estimate density using cameras.

It is difficult to determine which method is best to analyze the density of a species using CAPTURE; however, I believe that MMDM is better because it is more conservative, and is not likely to overestimate the density of endangered species such as the jaguar and ocelot. Overestimation of a population may affect decisions that could negatively undermine the conservation of these species (Tobler *et al.*, 2013).

Jaguar density estimation using CAPTURE with MMDM resulted in minor differences depending on the length of the survey period (mean of 1.6 jaguars/100 km² using 45 days and a mean of 2 jaguars/100 km² using 92 days). However, these results could not be tested statistically because sample size was too small. The four periods of 45 days were similar (Table 1), as were the two periods of 92 days (Table 2).

The density variation observed may be attributed to change in ambient temperatures between winter and spring seasons, which may have affected jaguar activity, and thus the number of captures. During this project, mean ambient temperature for December (2009)

to February (2010) was 15.6° C; however, the temperature increased to 29.4° C during June when the field project ended. During the 92–day periods the spring season resulted in decreased jaguar density values. This density change may have been related to a lower capture rate caused by decreased activity of jaguars. Laack (1991) reported ocelot captures (box traps) in Texas were lower during summer and Tewes (1986) found that ocelot home ranges were reduced during the same season. Temperature and humidity increases during the summer may have caused less activity that resulted in lower capture success. This pattern may have occurred in my study area (using camera traps) because temperatures and humidity were similar to Texas. Crawshaw & Quigley (1991) reported that decreased jaguar home ranges during the wet season in the Pantanal of Brazil coincided with high temperatures.

Ocelot densities obtained with CAPTURE were constant during the first 3, 45–day periods (10.8, 11.3 and 10.3 ocelots/100 km²) and decreased during the last period with 7 ocelots/100 km² (Table 3). This density decrease coincides with temperature increases in late spring. Density values decreased during the 92–day periods for jaguars; however, ocelot change during this period was more dramatic from 14.6 ocelots/100 km² to 9.7 ocelots/100 km². This pattern suggests that climatic factors may influence the population dynamics of wild cats in the study area.

According to Tobler *et al.*, (2013) <2 jaguars/100 km² were considered low densities and any value over 3 jaguars/100 km² high; conversely, Chavez *et al.*, (2006) considered <1 jaguar/100 km² low and 7 jaguars/100 km² high. The lowest jaguar densities reported using CAPTURE were in Argentina (Paviolo *et al.*, 2008), Brazil (Silveira *et al.*, 2009), Guatemala (Moreira *et al.*, 2005), and Bolivia (Romero–Muñoz *et al.*, 2006; Table 5). Highest jaguar densities reported with the same methods were in Brazil with 5.8

jaguars/100 km² (Soisalo & Cavalcanti, 2006) and Guatemala with 7 jaguars/100 km² (Moreira *et al.*, 2008). In Mexico, there have been six jaguar field studies, yielding the lowest densities in the states of Sonora, Yucatan and Quintana Roo, and the highest densities in the states of Jalisco, Chiapas and in the present study (Table 5).

Comparison of ocelot and jaguar mean densities using MMDM from other studies with my estimated jaguar density of 2.3 jaguars/100 km² is interesting. Biologist often believe that the jaguar and ocelot densities are higher in tropical areas than other vegetation types. However, this is not always accurate because, the jaguar and ocelot densities are high and in the study area dominated with Tamaulipan thornshrub, low tropical forest, riparian, and secondary vegetation (Stresser-Pean, 2000).

Jaguar density with SPACECAP and CAPTURE were similar with 2.2 jaguars/100 km² for SPACECAP and 2.3 jaguars/100 km² for CAPTURE. This similarity suggests that density estimated with MMDM was probably accurate. Few studies have compared the same results using SPACECAP and CAPTURE. Sollmann *et al.*, (2011) and other studies used SPACECAP to estimate a jaguar density of 0.29 jaguars/100 km² in Brazil, whereas Tobler *et al.*, (2013) obtained densities of 4.4 jaguars/100 km² in Peru and 1.95 jaguars/100 km² in Quintana Roo, Mexico.

Ocelot densities obtained with CAPTURE were similar to other field studies in Argentina (Di Bitetti *et al.*, 2006), Belize (Dillon & Kelly, 2007) Bolivia (Noss *et al.*, 2012), and the USA (Hanes *et al.*, 2006). Studies in Peru had the highest densities, with the lowest densities reported in the Atlantic Forest of Brazil (Goulart, 2009) and Costa Rica (Gonzalez-Maya & Cardenal-Porras, 2009; Table 6). In México, Avila-Najera (2015) reported lower ocelot densities compared to this study. This result was unexpected as the study by Avila-Najera (2015) was done in the Mayan rain forest where the habitat is

considered more productive (Table 6). The previous survey in my study area by Stacey (2012) reported an ocelot density using MMDM of 19.23 ocelots/100 km². I obtained 14.59 ocelots/100 km²; however, this variation may be related to a different camera grid design or changes in weather conditions and prey availability (Table 6).

Two studies compared SPACECAP and CAPTURE ocelot density results (Avila-Najera, 2015; Noss *et al.*, 2012). Both studies reported lower densities with the SPACECAP program. However, in my study I obtained similar densities with both programs with 21.95 ocelots/100 km² with SPACECAP, and 21.42 ocelots/100 km² with CAPTURE (Figure 3).

Few studies have estimated home range size using camera-trap data as this analysis is not applicable for all species (Gil-Sánchez *et al.*, 2011). Home range estimation with camera-traps for species with large home ranges such as jaguars may be inaccurate (Soisalo & Cavalcanti, 2006) because the MMDM to calculate the effective area likely would not represent the maximum distance covered by a jaguar. Soisalo & Cavalcanti (2006) conclude that home ranges obtained with camera traps during a short period are not comparable to those obtained with radio-telemetry. However, this technique may be appropriate for species that cover shorter distances, as seen in an Iberian lynx (*Lynx pardinus*) study by Gil-Sánchez *et al.*, (2011), that used camera-traps to successfully obtain home range values.

Home range size for jaguars in Brazil range from 38.20 km² in the Pantanal (Caselli & Murray, 2007) to 262.9 km² in other areas (Cavalcanti & Gese, 2009). In Mexico, Chavez *et al.*, (2011) reported a home range size for jaguars of 56 km², but one male showed a home range of >1,000 km². In this study, home range size for females was larger than for males, which was unexpected because home ranges for males are typically

larger than for females (Cavalcanti & Gese, 2009; Cascelli & Murray, 2007; Soisali & Cavalcanti, 2006; Scognamillo *et al.*, 2003). Although it was not possible to calculate home range overlap between jaguars, graphically it could be observed that overlap did occur (Figure 4). Jaguar home range size analysis would likely be more homogenous if the number of survey days and camera stations were increased (Gil-Sánchez *et al.*, 2011); however, a cost–benefit analysis should determine if the use of GPS collars may be a better option.

Home ranges for ocelots in my study area were similar to other studies. Martínez–Meyer & Lopez–Gonzalez (1999) in Chamela, Jalisco, Mexico reported a mean home range size of 5.2 km^2 for males and 5.7 km^2 for females. In Texas, Tewes (1986) reported a home range size of 12.3 km^2 for males and 7 km^2 for females. In my study area, I estimated a mean home range size for 5 males of 11.3 km^2 and 6.4 km^2 for 5 females. Caso (2013) obtained home ranges (95% minimum convex polygon estimator) of $11.56 \pm 4.51 \text{ km}^2$ for males and $9.47 \pm 5.21 \text{ km}^2$ for females on the Tamaulipan Coast. The percentage of overlap for males (11.5%) was lower compared to females (16.6%), and this percentage of overlap was similar to results (15.5%) obtained by Caso (2013).

In conclusion, the methods used to determine jaguar and ocelot density were similar to results found in the literature. However, the distance between stations should be modified by increasing the distance to 3–5 km for more accurate jaguar density estimates, and the number of stations should be increased. For ocelot, both methods seemed adequate using the closed population capture–recapture model and SPACECAP, particularly when compared with previous studies (Table 5 and Table 6).

Both CAPTURE and SPACECAP have advantages and disadvantages. Some studies consider the SECR method that SPACECAP uses as most appropriate (Avila, 2015;

Tobler *et al.*, 2013). They consider the number of individual captures and recaptures as the most important factor. I obtained similar results for ocelots applying both programs, with a slight increase in density using SPACECAP. This result may be related to SPACECAP being used for 187 days, whereas CAPTURE was used for 92 days, because of constraints imposed by the CAPTURE program. However, remote sensing camera analysis for home range estimation should be used only for small to medium-size species because it is difficult to cover the complete range of larger animals, (e.g., jaguars) (Gil-Sanchez *et al.*, 2011).

The density values in this study for jaguar and ocelot were generally higher compared to other areas. These results indicate that the Sierra Tamaulipas should have a high level of conservation value since species that require a large amount of suitable habitat (e.g., jaguar and ocelots) occur in relatively high numbers. The ocelot density found in this study, and in Stacey (2012), provides support that the ocelot population in this area is robust enough to serve as a source population for ocelot translocation between Tamaulipas and Texas.

It is essential to consider this region of the Sierra Tamaulipas as an important core area for the protection of endangered species such as jaguar, ocelot and other sensitive species. Studies and monitoring programs should be encouraged to track variations in these cat populations and to expand the information base.

This is the first study in the Sierra Tamaulipas to examine the population dynamics of jaguar and ocelot. This study should be used as a tool for the Federal Government Comision de Areas Protegidas (CONANP) to designate the Sierra Tamaulipas as a protected area for Mexico.

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CHAPTER II

ACTIVITY PATTERNS AND INTERACTION OF FIVE SYMPATRIC FELIDS IN THE SIERRA TAMAULIPAS, MEXICO

Introduction

Different organisms of related taxons are able to coexist in geographic regions and share resources including food, space and cover. Coexistence is possible because some species assemblages may express differences in habitat use and activity patterns (Di Bitetti et al. 2010, Caso 2013) which may allow species coexistence. Fauth et al. (1996) mentioned that some researchers (Gould 1977, Janzen 1980, Mills et al. 1993) have classified species according to the area they occupy biogeographically, according to their taxonomic group or by their use of natural resources. Fauth et al. (1996) simplify ecological community definitions, and they suggest that food resources and space use among interspecific and intraspecific species should be included. Fauth et al. (1996) considered overlap of geography, phylogeny, and resources, and defined three classifications, where (A) is taxa (phylogeny), (B) is community (geography), and (C) is guild (resources). Species with overlapping phylogeny and geography are considered “assemblages,” species with overlapping geography and resources are considered “local guilds,” and species with overlapping phylogeny, geography, and resources are considered “ensembles.” I consider these definitions in discussing the mechanisms that enable coexistence among species, and how this process through time can influence the survival or extinction of species.

Little is known about how coexistence mechanisms operate and how different species with the same food habits can share the same area. In ecology, the presence of species that live in different ecosystems is the result of a long evolutionary history that is oriented or directed

Style and format of this dissertation chapter follows *Mammalia*.

mainly by competition, and at the same time competitive success is determined by genetic differences influenced by biotic and abiotic factors (Bolen and Robinson 2003). From these processes, species occupy different roles in an ecosystem and form an ecological niche (Bolen and Robinson 2003).

Niche differentiation refers to the “process by which natural selection drives competing species into different patterns of resource use or different niche dimensions” (Sahney et al. 2010). This mechanism may enable some species to coexist by means of the differentiation of their realized ecological niches. However, niche differentiation may not occur if there is sufficient or abundant resources for all the species (Sahney et al. 2010). Niche differentiation can occur in several different ways and on multiple temporal and spatial scales. This complexity may create a possible relationship between two species where competition is small or does not exist. Also, it could make it difficult to confirm or refute niche differentiation.

Interspecific competition is considered one of the most important mechanisms that limits the number of species that inhabit the same ecosystem as a result of similarity in their ecological niches (Jaksic and Marone 2007). After Hutchinson’s seminal paper on species niche (1959), controversy followed about how closely related species with similar morphologies and diets could coexist, or how species belonging to different ecological guilds could coexist in the same community (Tokeshi 1999).

In previous studies, carnivores have been used to understand the effects of competition in community structure (Di Bitetti et al. 2010). Dayan and Simberloff (2005) concluded that two sympatric carnivores species with similar diets cannot coexist because of food competition, and, therefore, one species is excluded from the community unless they coevolve and their morphology changes. However, interference caused by intra-guild competition and direct depredation between carnivores may be important factors that segregate species (Carothers and

Jaksic 1984, Palomares and Caro 1999).

In tropical areas, studies have examined coexistence of sympatric large feline species including jaguar (*Panthera onca*) and puma (*Puma concolor*) (Harmsen et al. 2009, Romero–Muñoz et al. 2010). However, interactions among small wild cats have been poorly studied. Kiltie (1984) suggested that two species that are morphologically similar (e.g., jaguarundi [*Puma yaguaroundi*] and margay [*Leopardus wiedii*]) may coexist in the same area because of differences in habitat use. Di Bitteti et al. (2010) studied coexistence among six species of wild cats (jaguar, puma, ocelot [*Leopardus pardalis*], jaguarundi, margay, and oncilla [*Leopardus tigrinus*]) in Argentina. Caso (2013) studied spatial coexistence and interaction between ocelot and jaguarundi with radio-telemetry near my study area in Tamaulipas, Mexico.

There are few areas in Mexico where six wild cat species are sympatric. It is important to determine the ecological mechanisms that allow felid coexistence in these areas. Activity patterns are often used to determine coexistence or niche partitioning in a carnivore community (Chen et al. 2009, Gonzalez–Maya et al. 2009, Di Bitetti et al. 2010, Blake et al. 2012). Consequently, I explored the potential role of this niche dimension (i.e., activity) in allowing felid coexistence in northeastern Mexico.

Material and Methods

Study area

The Sierra Tamaulipas is one of the most important areas for wildlife conservation in northeastern Mexico. This area is a Priority Terrestrial Region (RTP 91) by the Comision Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO; Arriaga et al. 2000), and was proposed as a biosphere reserve by the Comision Nacional de Areas Naturales Protegidas (CONANP) in 2005 (CONANP 2005).

My fieldwork was conducted in the northern region of the Sierra Tamaulipas on two private ranches: Caracol and Camotal (UTM E 547219–N 2654254) located in Abasolo and Jimenez counties. Both ranches comprised the study area of 120 km². The main land-use for Caracol Ranch was sport hunting for northern bobwhite (*Colinus virginianus*) and white-winged dove (*Zenaida asiatica*) whereas Camotal Ranch was a cattle ranch.

The study site supported several habitat types including Tamaulipan thornshrub, low tropical forest, riparian, and secondary vegetation in the Tamaulipas Biotic Province (Stresser-Pean 2000). The dominant vegetation types included anacahuita (*Cordia boissieri*), barreta (*Helietta parvifolia*), black-brush (*Acacia rigidula*), cenizo (*Leucophyllum frutescens*), guajillo (*Acacia berlandieri*), and skeleton leaf goldeneye (*Viguieria stenoloba*) (Cram et al. 2006). Tamaulipan thornshrub was present on both ranches, included amargoso (*Castela texana*), brasil (*Condalia hookeri*), honey mesquite (*Prosopis glandulosa*), saffron plum (*Bumelia angustifolia*), spiny hackberry (*Celtis pallida*), and white indigoberry (*Randia aculeata*). The deciduous tropical forest was characterized by ebony (*Pithecellobium ebano*), Berlandier's jopoy (*Esenbeckia runyonii*), gumbo limbo (*Bursera simaruba*), mahuira (*Phoebe tampicensis*), and mauto (*Lysiloma divaricata*) (Cramn et al. 2006).

Topography in the study area included lowland hills up to 600 m elevation. The Soto la Marina River represented the southern boundary of the study area. Average annual temperature was 18° C and annual precipitation was 800 mm. However, the annual precipitation was often < 800 mm in the northern and western Sierra Tamaulipas with 4 or 5 months of rainfall (Stresser-Pean 2000) (Figure 8).

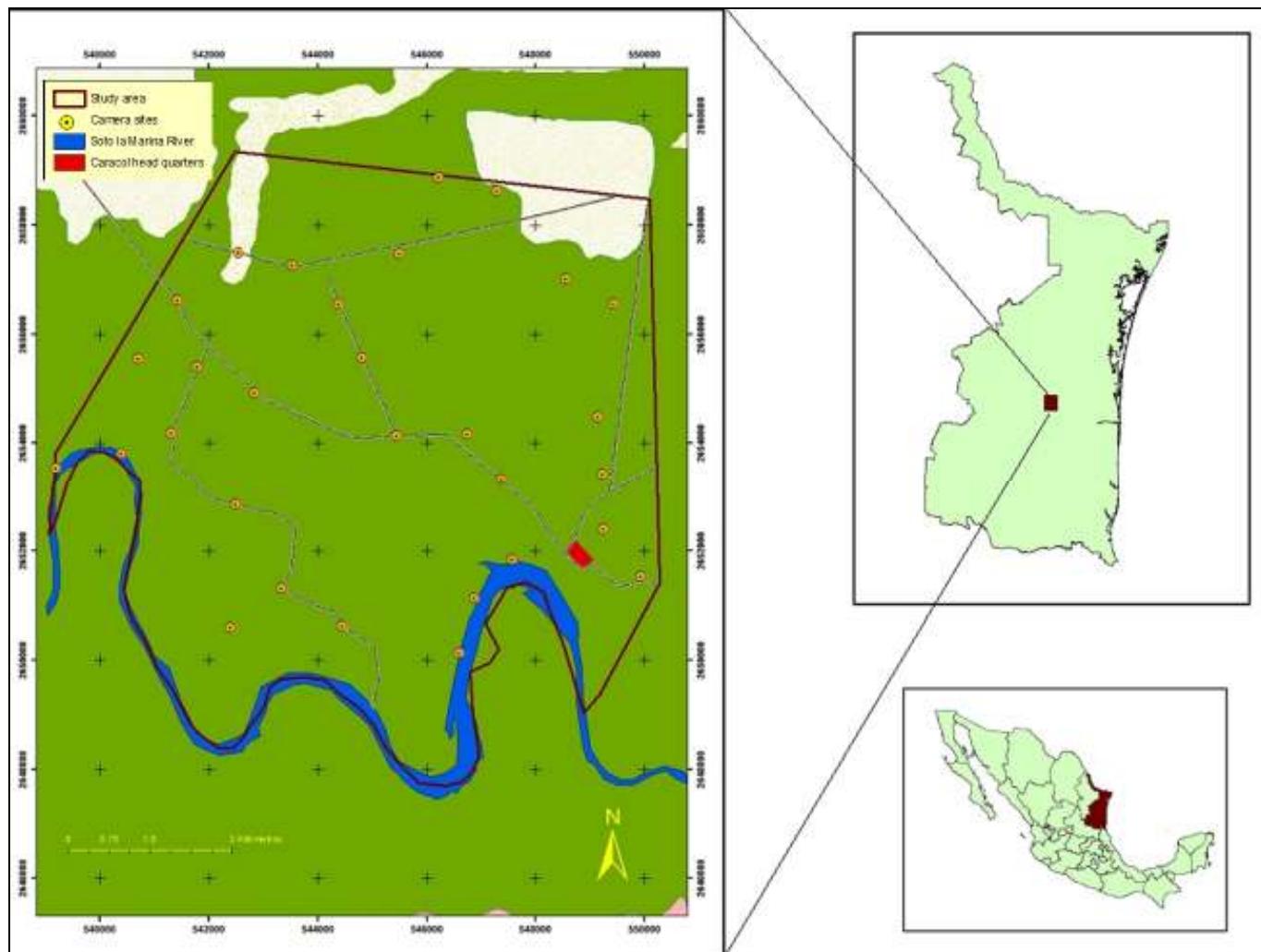


Figure 8. Study area on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

Camera-trapping

I collected continuous camera-trapping data over 15 months (509 days) from February 2009 to June 2010. I used four camera-trapping grids, one grid was used for density estimation over 90 km², and the other three grids covered 163 km² (Stasey 2012) (Figure 9). The cameras were programmed to operate continuously during diurnal and nocturnal periods and were placed along roads, existing trails, near artificial or natural water sources, but no bait or scent attractants were used. Data from photographs included the time and date. Five types of remote sensing cameras were used: Cuddeback Capture®, Cuddeback Excite®, Wildview®, Moultrie®, and Bushnell®. CENJAGUAR camera sites were separated by ≥ 1.5 km, the other three grids the camera stations were set according at site and not at the distance. Cameras were checked at about 40-day intervals to replace batteries and download data.

Activity patterns

To determine the activity patterns of the carnivore community, I standardized the data using relative frequency to reduce the effects of species abundance (Gonzalez–Maya et al. 2009). Additionally, I recorded photographs of white-tailed deer (*Odocoileus virginianus*) and collared peccary (*Peccari tajacu*), which are prey for jaguar and puma (Rabionowitz 1986, Aranda 1996, Rosas–Rosas and Valdez 2010). Independence of observation was set at 30 minutes between photographs (Davis et al. 2011, Blake et al. 2011, 2012).

To determine the activity patterns of each species, I used the time indicated on each photograph and grouped the records into 24, 1-hour intervals with the number of events of each species/hour multiplied by 100 and then divided by the total number of events to obtain an activity index. For activity comparisons between species, I used the Chao–Jaccard Similarity Index with the objective to minimize the negative bias of a traditional similarity index, and to determine confidence intervals for comparisons (Chao et al. 2005). Program Infosat (InfoStat

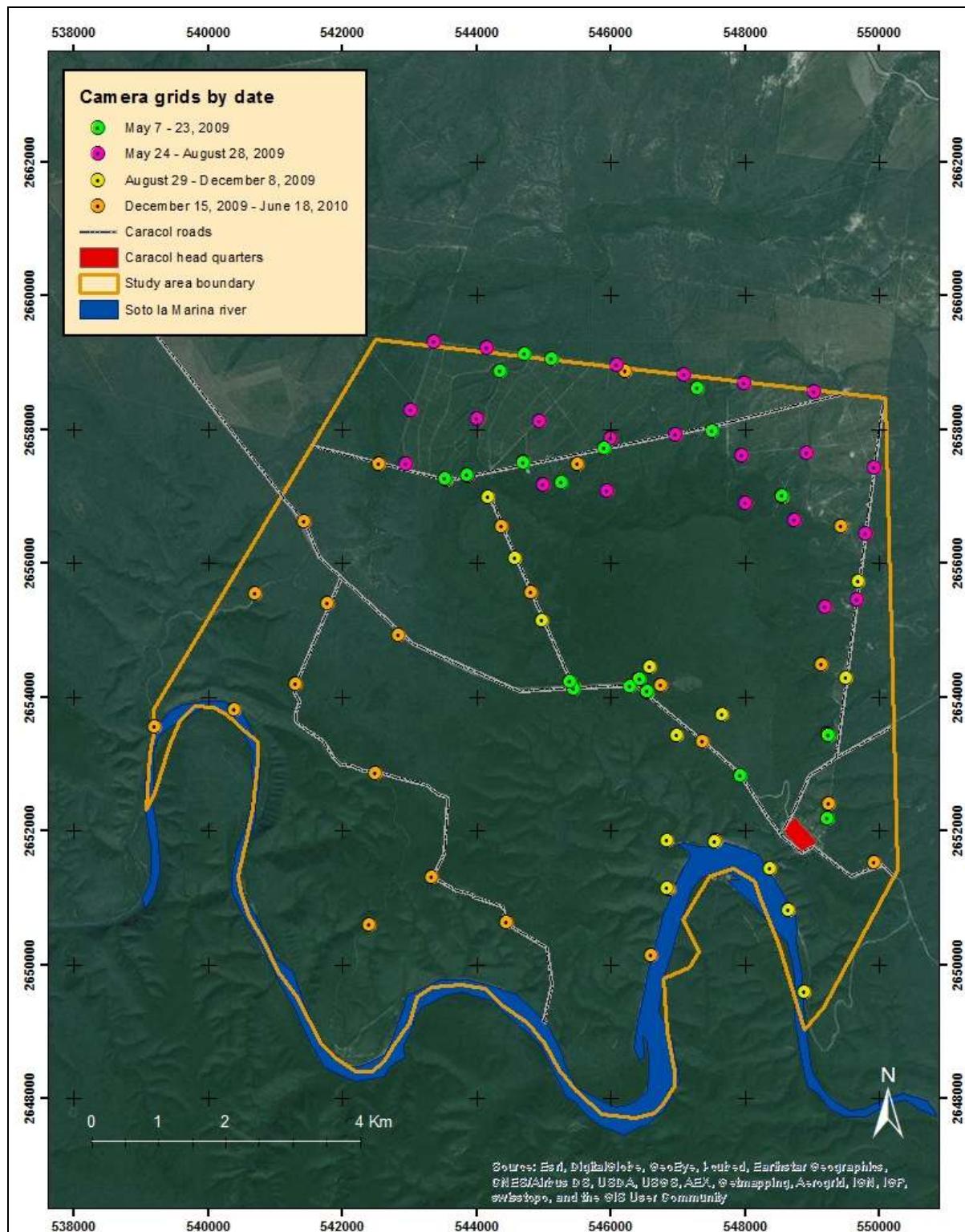


Figure 9. Camera-trap distribution on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

2007) and EstimateS (Colwell 2005) were used to analyze the data.

I paired five wild cat species (e.g., jaguar, puma, bobcat, ocelot and jaguarundi) and large wild cat prey (i.e., deer and peccary) with the Chao–Jaccard Similarity Index. Other carnivores that were considered competitors or prey were used for comparisons including coyote (*Canis latrans*), coatiundi (*Nasua narica*), gray fox (*Urocyon cinereoargenteus*), and raccoon (*Procyon lotor*). I used four categories to determine the activity patterns: diurnal, nocturnal, crepuscular (i.e., during sunset and dawn), or cathemeral (irregular or arbitrary activity during day or night) (Emmons and Feer 1990, Van Schaik and Griffiths 1996).

Abundance

I used the Relative Abundance Index (RAI) to compare the abundance of all species recorded and related the RAI with paired interactions, to determine if the abundance of one species limited or benefited the presence of another. This was calculated with the formula $RAI = \frac{\text{number of events}}{\text{number of traps–nights}} \times 1000$ (Mathew et al. 2006).

Spatial–temporal comparisons

To evaluate spatial–temporal comparisons between cat species, I compared the time interval between photographs of one species (e.g., jaguar) at a station with the next individual of a different species at the same camera station. If the lapse between one individual and the other was >48 hours, this was not included in the analyses.

Results

Camera–trapping

I obtained 15,368 trap–nights during all surveys (Table 7). From 9 February 2009 to 18 June 2010, a range of 20–38 camera stations with a mean of 29 camera stations were operational

Table 7. Capture periods and trap-nights on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

Session	Period	Number of Stations	Number of Nights	Number of Trap-nights
1	9 February 2009 to 6 March 2009	20	26	520
2	6 March 2009 to 3 April 2009	20	29	580
3	3 April 2009 to 24 May 2009	20	52	1,040
4	24 May 2009 to 28 June 2009	34	35	1,190
5	28 June 2009 to 26 July 2009	34	30	1,020
6	26 July 2009 to 28 August 2009	34	35	1,190
7	28 August 2009 to 28 September 2009	25	30	750
8	28 September 2009 to 4 November 2009	27	38	1,026
9	4 November 2009 to 9 December 2009	25	44	1,100
10	9 December 2009 to 23 January 2010	38	40	1,520
11	23 January 2010 to 5 March 2010	37	43	1,591
12	3 March 2010 to 7 April 2010	33	45	1,485
13	7 April 2010 to 18 June 2010	38	62	2,356
Total		—	509	15,368

over 509 nights and 13 sessions during a continuous camera-trapping period. Number of camera stations varied for several reasons including camera failures, stolen cameras and floods. Six species of wild cats were documented: jaguar, puma, ocelot, jaguarundi, bobcat, and margay.

Other carnivores photographed included two canids (coyote and gray fox), two procyonids (raccoon and coatiundi), five mustelids including long-tailed weasel (*Mustela frenata*), badger (*Taxidea taxus*), and three species of skunks: hog-nosed skunk (*Conepatus leuconotus*), striped skunk (*Mephitis mephitis*), and spotted skunk (*Spilogale gracilis*). Two prey species for jaguar and puma, white-tailed deer and collared peccary, were also frequently documented (Table 8).

The species with the most capture events was collared peccary (n=1,768), and for carnivores gray fox (n=1,247) and ocelot (n=594) were photographed most often. Margay was documented once (Table 8).

Activity patterns

For activity patterns, I analyzed felid species that had more than 26 independent capture events (Oliveira-Santos et al. 2008). Margay was excluded from the analysis because only one photograph was obtained during the camera sessions. The collective activity pattern for the carnivore community (all carnivore species combined) was primarily nocturnal with the greatest activity at 05:00 h, followed by peaks at 03:00 h and 04:00 h and another peak at 20:00 h (Figure 10). The activity pattern of the carnivore community started to decrease at 07:00 h and increased again at 17:00 h.

I obtained daily activity patterns for five species of wild cats. Jaguars and ocelots were primarily nocturnal (Figures 11 and 12), pumas showed cathemeral activity (Figure 13), bobcats exhibited a crepuscular activity pattern (Figure 14), and the only diurnal wild cat was jaguarundi (Figure 15).

Table 8. Species recorded and number of capture events on the Caracol and Camotal Ranch Complex, from 9 February 2009 to 18 June 2010.

Species	Number of events	Number of photographs
Jaguar	89	144
Puma	55	186
Bobcat	26	26
Ocelot	594	804
Jaguarundi	96	122
Margay	1	1
Coyote	137	188
Gray fox	1,247	2,190
Raccoon	35	35
Coatimundi	152	218
Hog-nosed skunk	39	45
Striped skunk	25	28
Spotted skunk	10	10
Badger	2	2
Long-tailed weasel	1	1
Collared peccary	1,768	15,135
White-tailed deer	1,304	4,601

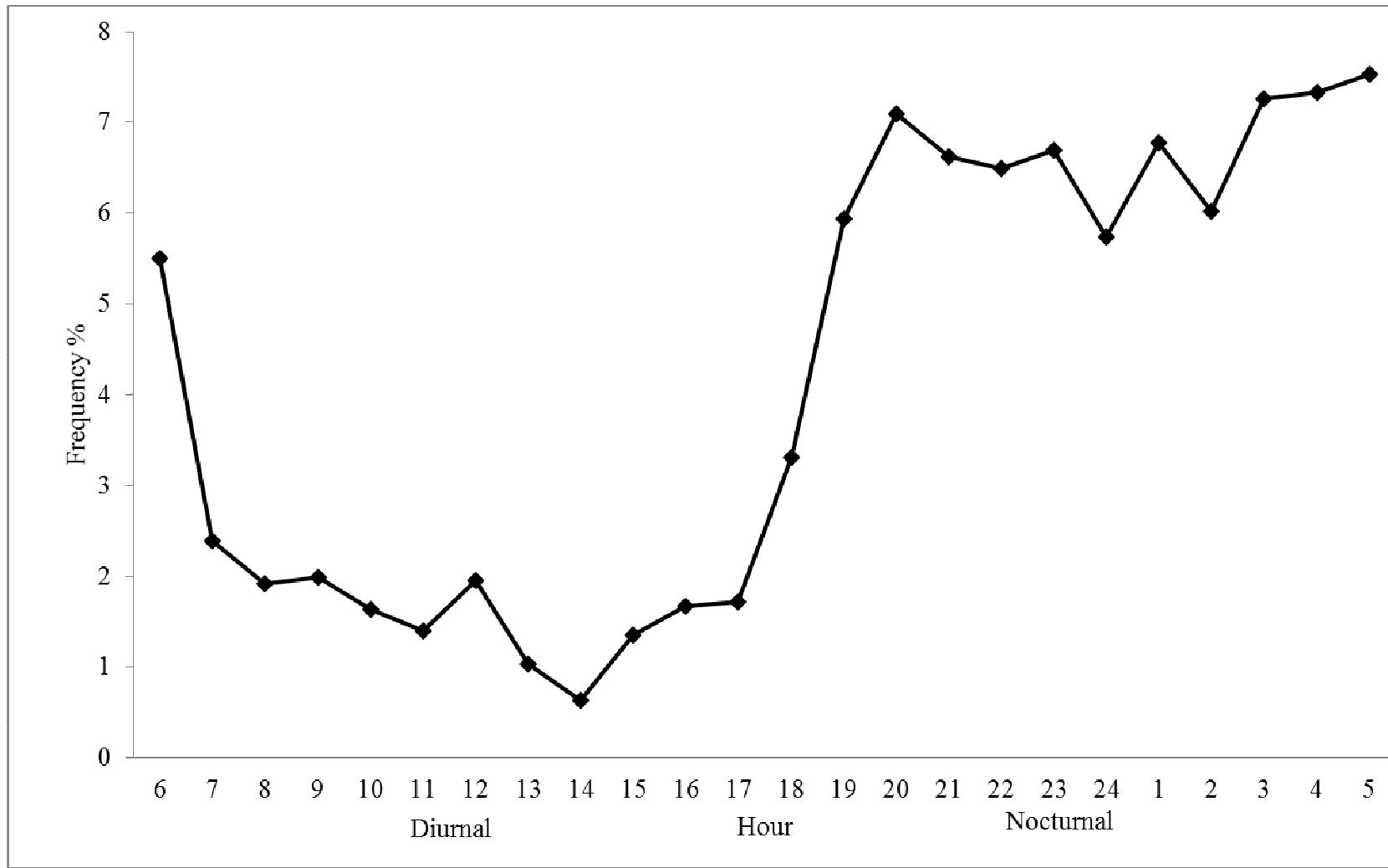


Figure 10. Activity patterns for the collective carnivore community on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

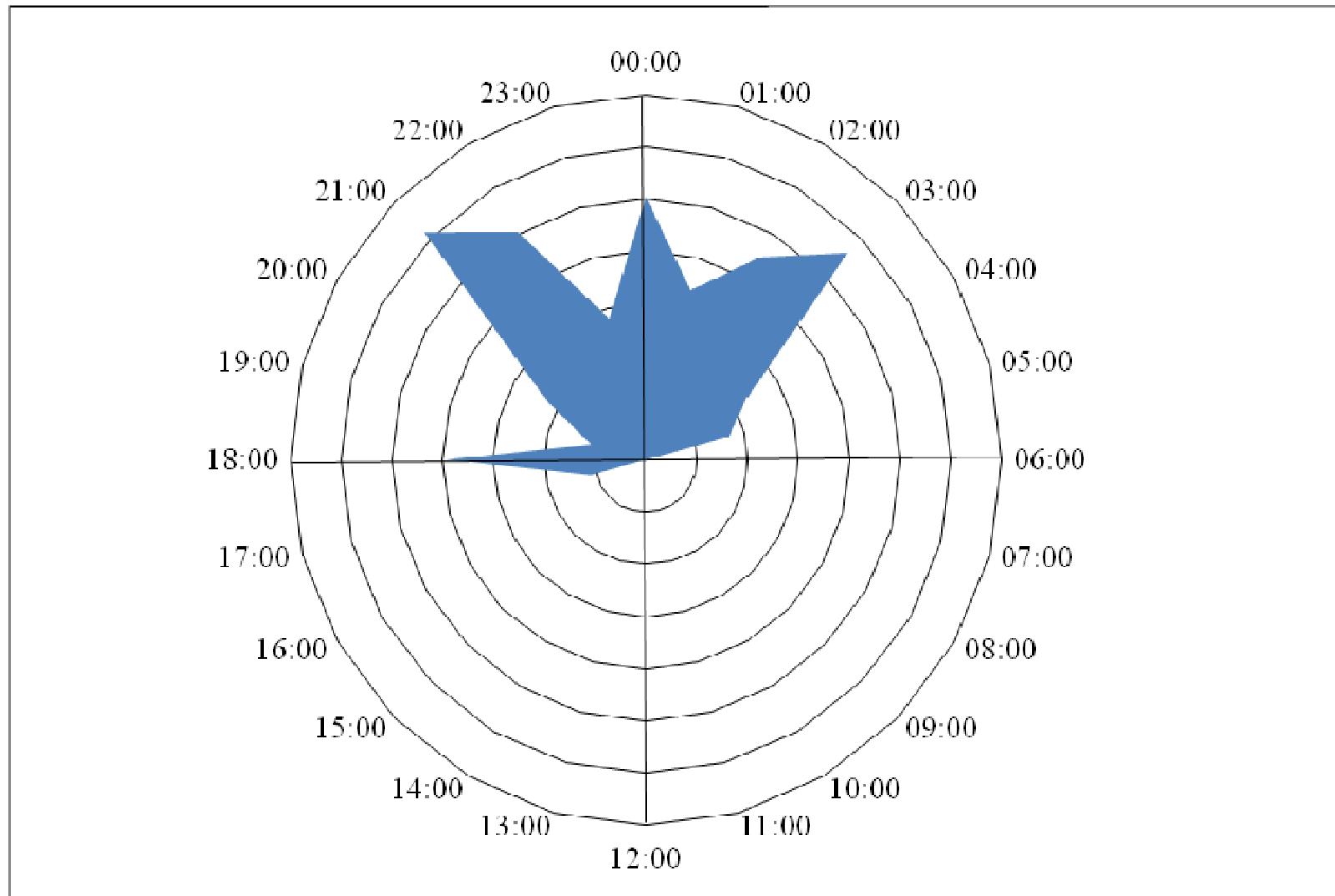


Figure 11. Activity pattern for jaguar on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

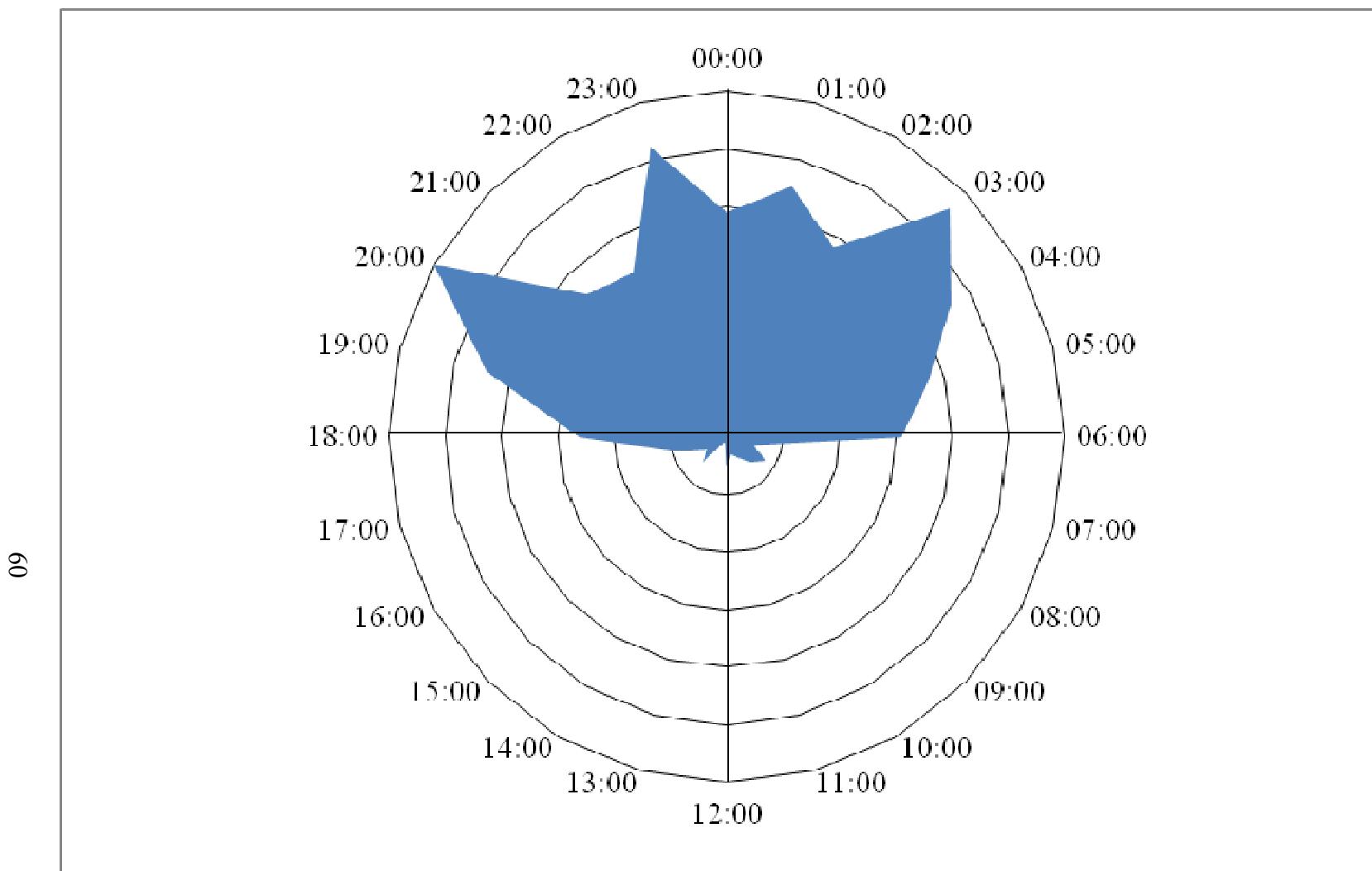


Figure 12. Activity pattern for ocelot on the Caracol and Camotal Ranch Complex in Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

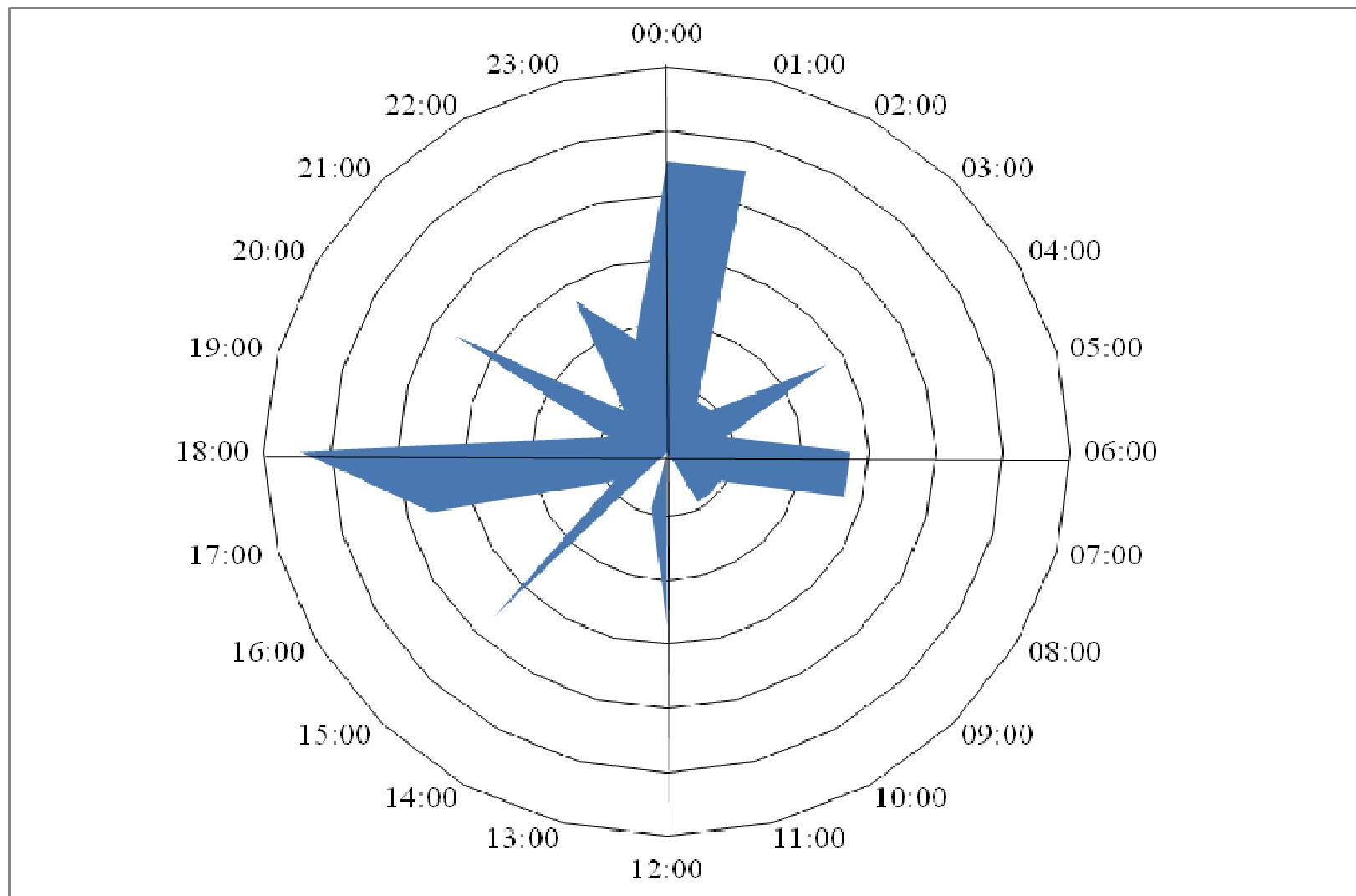


Figure 13. Activity pattern for puma on the Caracol and Camotal Ranch Complex in Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

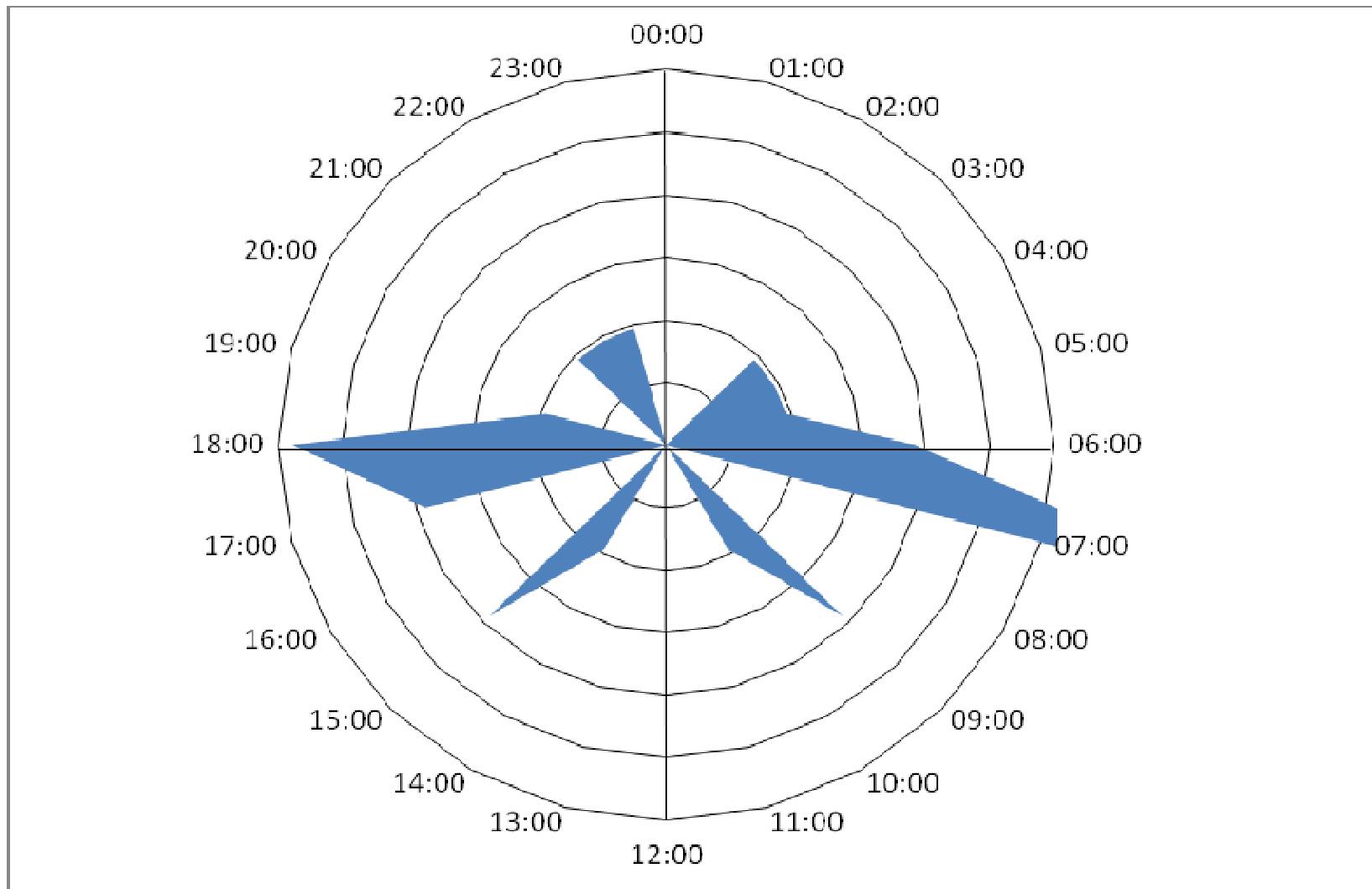


Figure 14. Activity pattern for bobcat on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

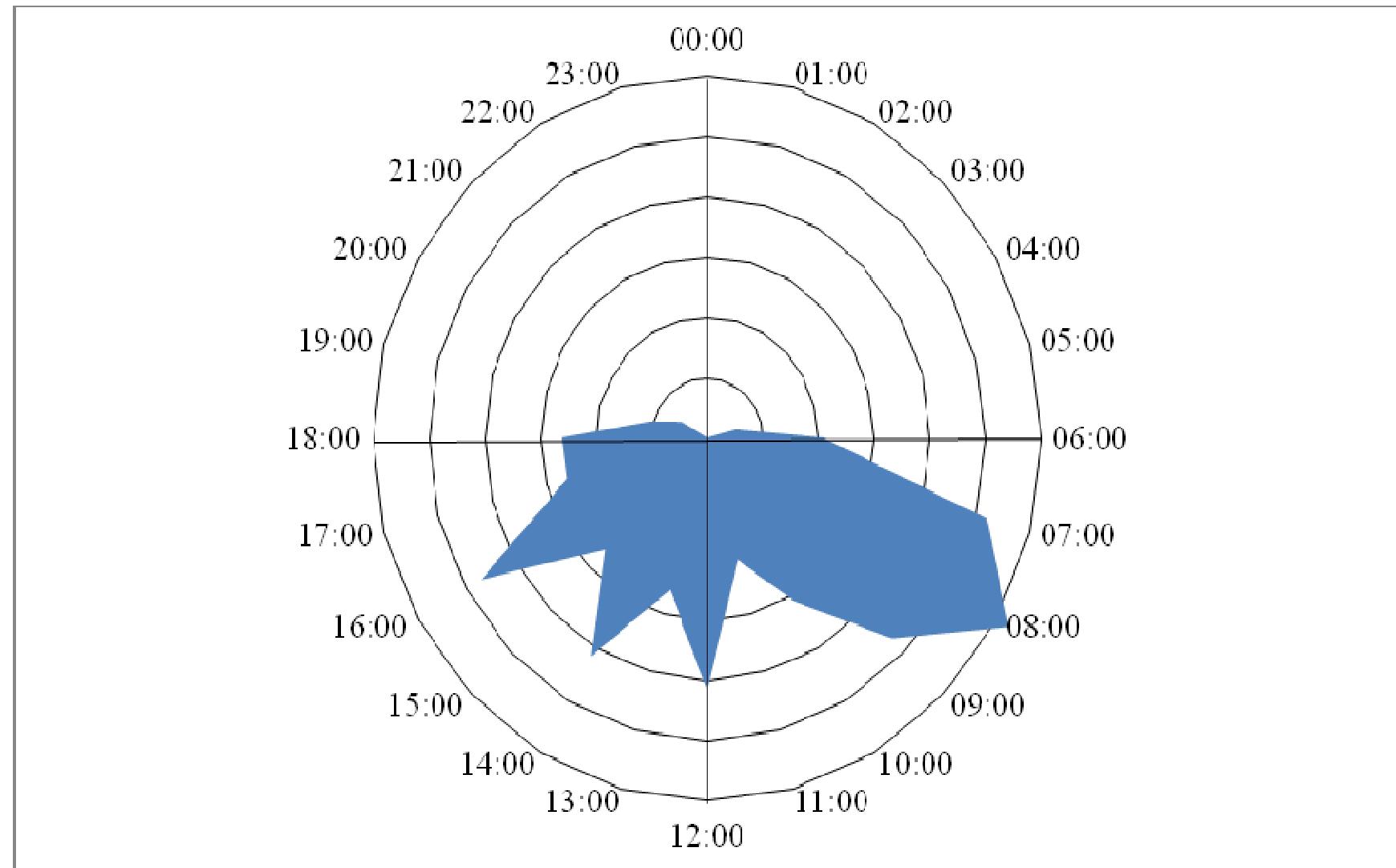


Figure 15. Activity pattern for jaguarundi on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

The largest activity peak for jaguar was at 21:00 h, with other peaks at 03:00 h, 22:00 h, and 24:00 h (Figure 11).

Puma had several activity peaks during the diel with the greatest peak at 18:00 h, and other peaks throughout the diel (i.e., 01:00 h, 15:00 h, 17:00 h, 20:00 h and 24:00 h (Figure 13). The greatest activity peak for bobcat was at 07:00 h, followed by 18:00 h, with less activity at 06:00 h, 09:00 h, 15:00 h, and 17:00 h (Figure 14). Ocelot exhibited four activity peaks at 01:00 h, 03:00 h, 20:00 h, and 23:00 h (Figure 12). Jaguarundi was the only wild cat that showed mostly diurnal activity with peak activity at 08:00 h, and other activity peaks at 07:00 h, 09:00 h, and 16:00 h (Figure 15).

All other carnivores were primarily nocturnal except for the diurnal coatimundi, with diurnal activity peaks at 12:00 h and 16:00 h. Gray fox, raccoon, and the three species of skunks were nocturnal. Coyotes were active throughout the diel except at 13:00 h and 14:00 h, with an activity peak occurring at 06:00 h. Collared peccary and white-tailed deer were active during all periods with greater movements throughout diurnal periods.

Activity pattern comparisons

Activity comparisons between jaguar and two potential prey species indicated activity overlap with collared peccary, but not with white-tailed deer (Figure 16). Puma also overlapped activity with collared peccary but not with white-tailed deer (Figure 17). Activity comparisons for the three species of small wild cats (bobcat, ocelot and jaguarundi) indicated different activity patterns, and only bobcat showed some overlap with ocelot and jaguarundi (Figure 18).

The Chao-Jaccard Similarity Index showed the greatest similarity of activity patterns between ocelot-puma, ocelot-jaguar, and jaguar-puma. A lower but similar proportion was found between ocelot-bobcat, puma-bobcat, jaguar-bobcat, and puma-jaguarundi. A lower proportion of similarity was expressed between bobcat, ocelot, and jaguarundi, and the lowest

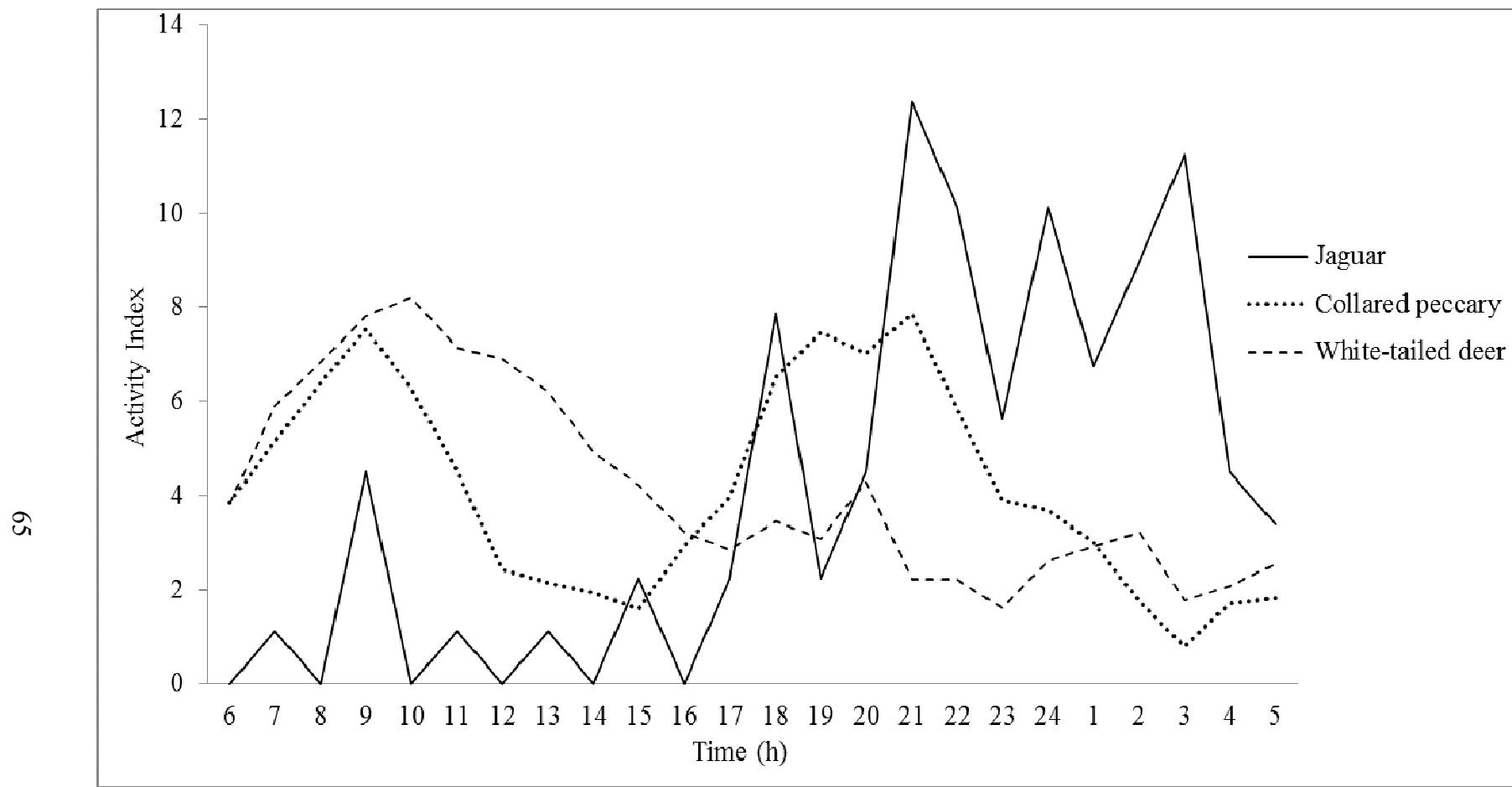


Figure 16. Comparison of activity index for jaguar and prey (white-tailed deer and collared peccary) on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

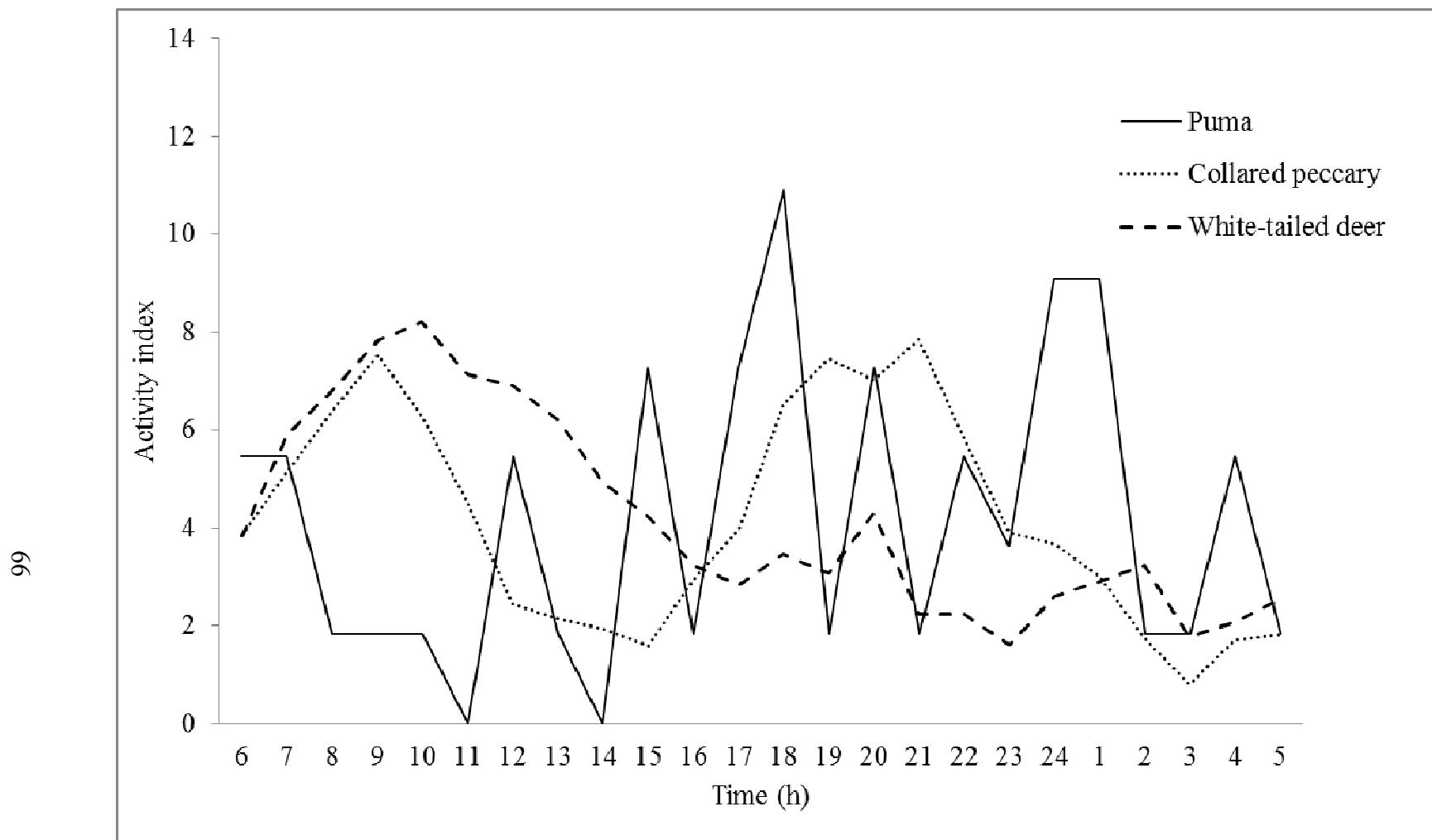


Figure 17. Comparison of activity index for puma and main prey (white-tailed deer and collared peccary) on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

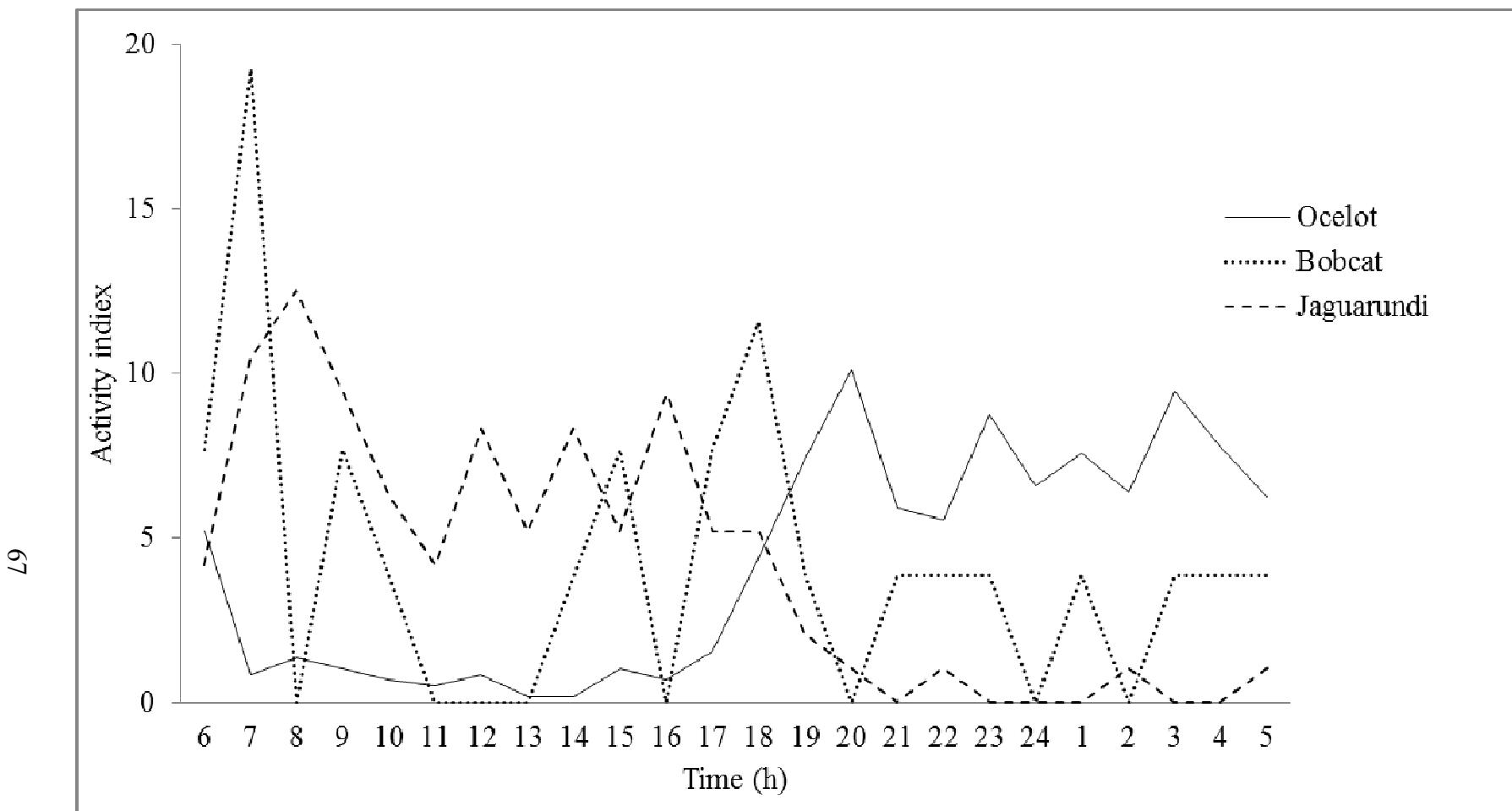


Figure 18. Comparison of activity index for ocelot, bobcat and jaguarundi on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

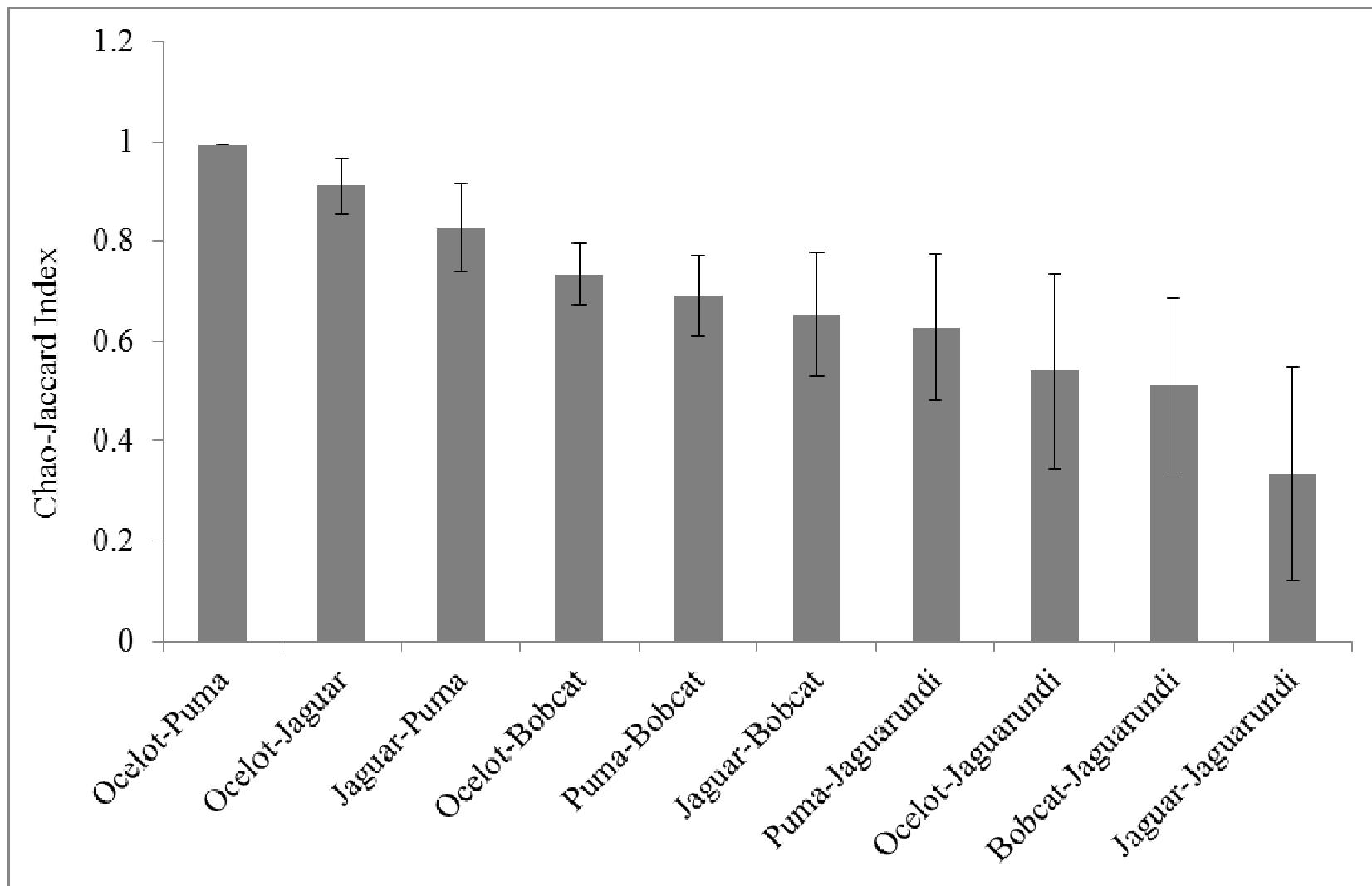


Figure 19. Chao-Jaccard Similarity Index for activity patterns of every wild cat pair on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

similarity was registered among the jaguar–jaguarundi combination (Figure. 19).

Pair comparisons were examined between each wild cat species and other carnivore species. The greatest similarity pattern of activity occurred between jaguar–gray fox and jaguar–raccoon, with the lowest between jaguar–coatiundi. Jaguar–coyote and jaguar–hog–nosed skunk were similar but less than jaguar–gray fox (Figure 20).

The highest pair similarity pattern for puma was between puma–gray fox, followed by puma–coyote, puma–raccoon, and puma–coatiundi. The lowest similarity was with hog–nosed skunk (Figure 21). Bobcat showed a strong similarity proportion with gray fox and was similar to coyote; whereas the lowest similarity was with hog–nosed skunk (Figure 22). The pair comparisons between ocelot and other carnivores showed the greatest similarity between activity patterns with ocelot–gray fox and ocelot–coyote; whereas raccoon and hog–nosed skunk were in less proportion, and the lowest similarity occurred between with coatiundi (Figure 23).

Pair activity comparisons for jaguarundi and other carnivores were markedly different compared to other wild cats and carnivore species. However, jaguarundi showed similar patterns with coatiundi and had a low similarity with raccoon and hog–nosed skunk (Figure 24).

Pair comparisons between jaguar and puma and their potential prey indicated that puma–peccary showed the highest similarity pattern and the next similar pair was puma–deer. Jaguar–peccary showed some similarity, and the jaguar–coatiundi pair had the lowest similarity (Figure 25).

Abundance

For abundance comparison of all species, collared peccary showed the highest abundance percentage (31.6%), followed by white–tailed deer (23.3%), and then gray fox (22.3%). The species with the lowest abundance was margay and long–tailed weasel, both with 0.017% (Figure 26). The percent abundance among carnivore species was dominated by gray fox at

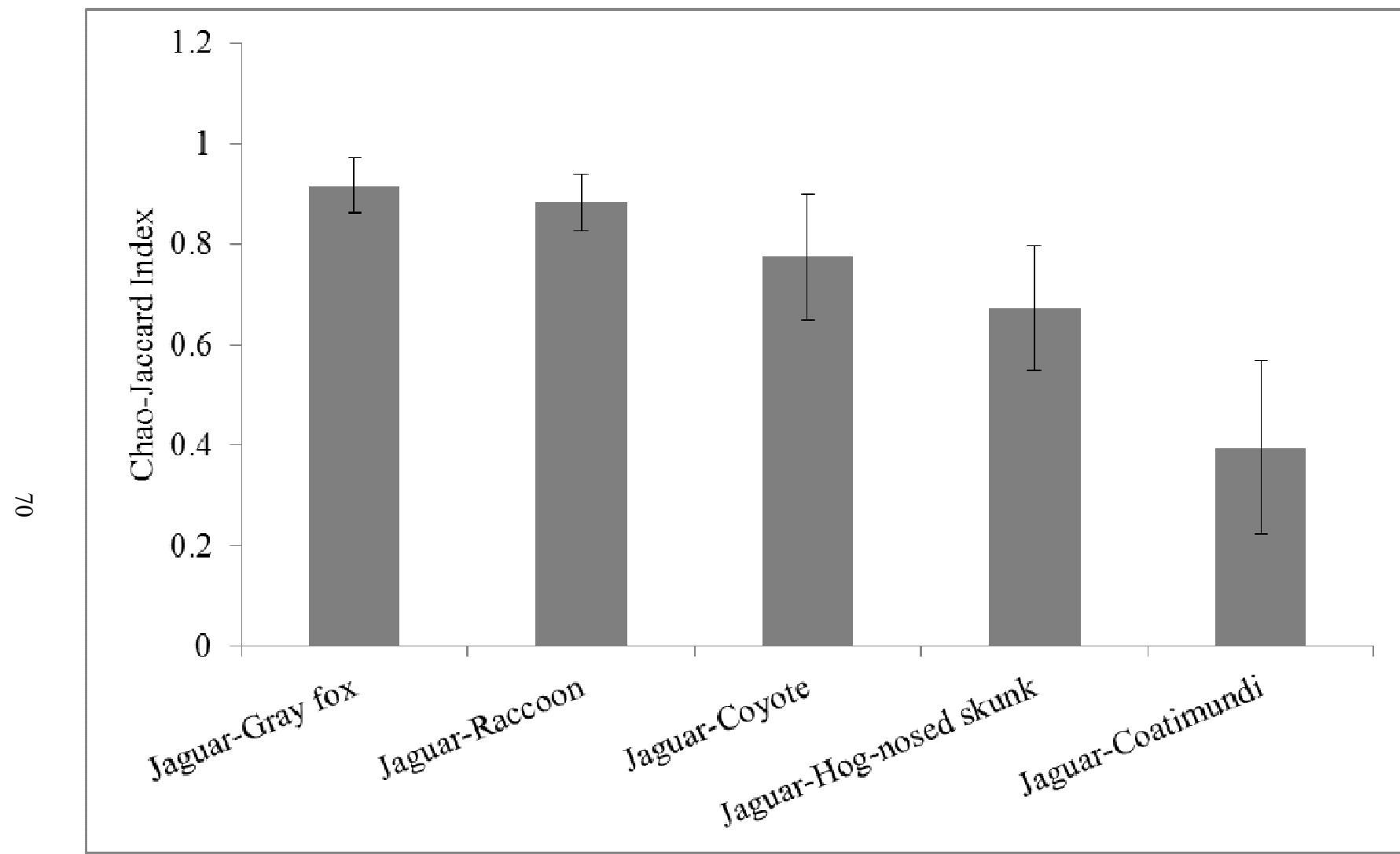


Figure 20. Chao-Jaccard Similarity Index for activity patterns between jaguar and other carnivores on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

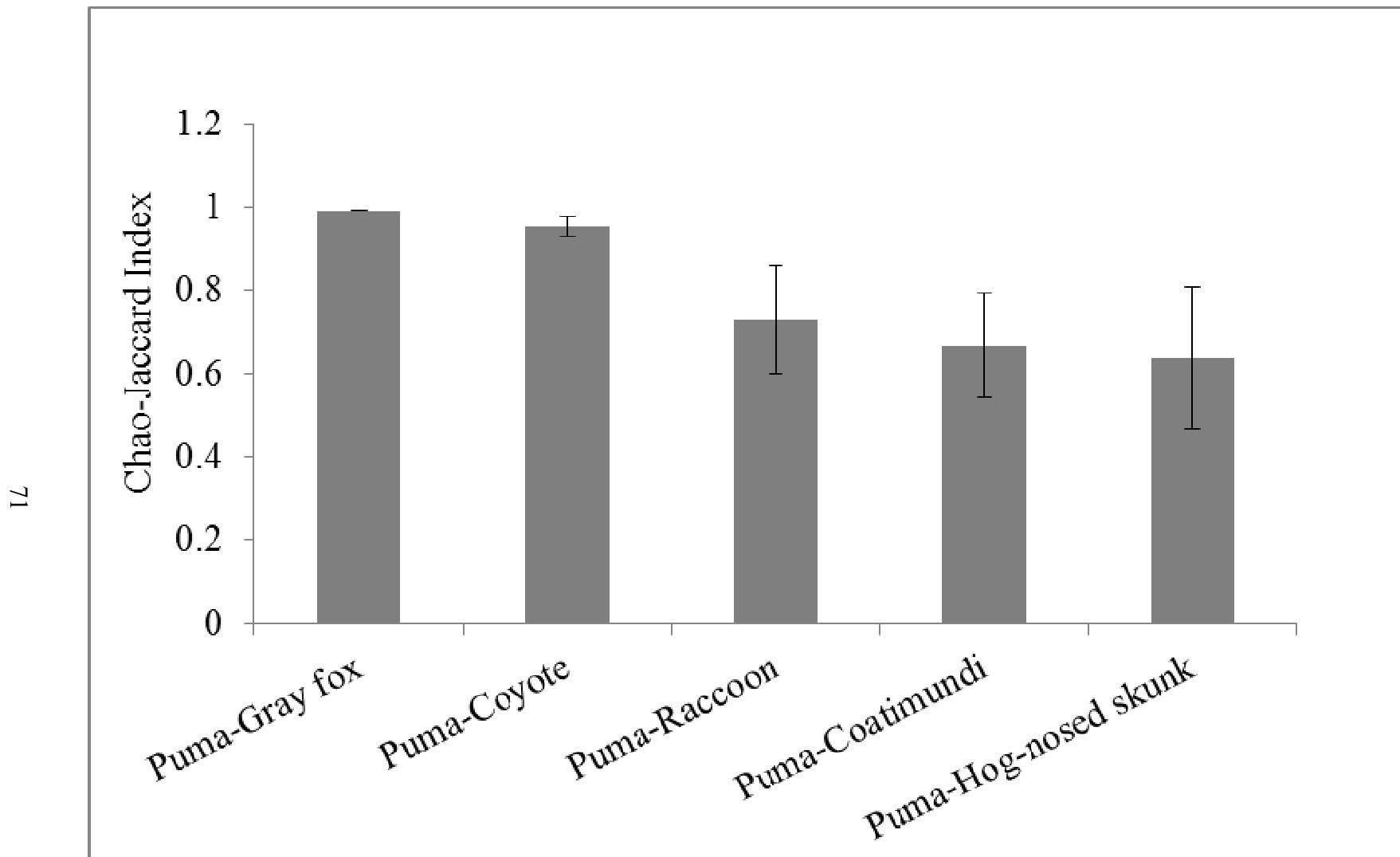


Figure 21. Chao-Jaccard Similarity Index for activity patterns between puma and other carnivores on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

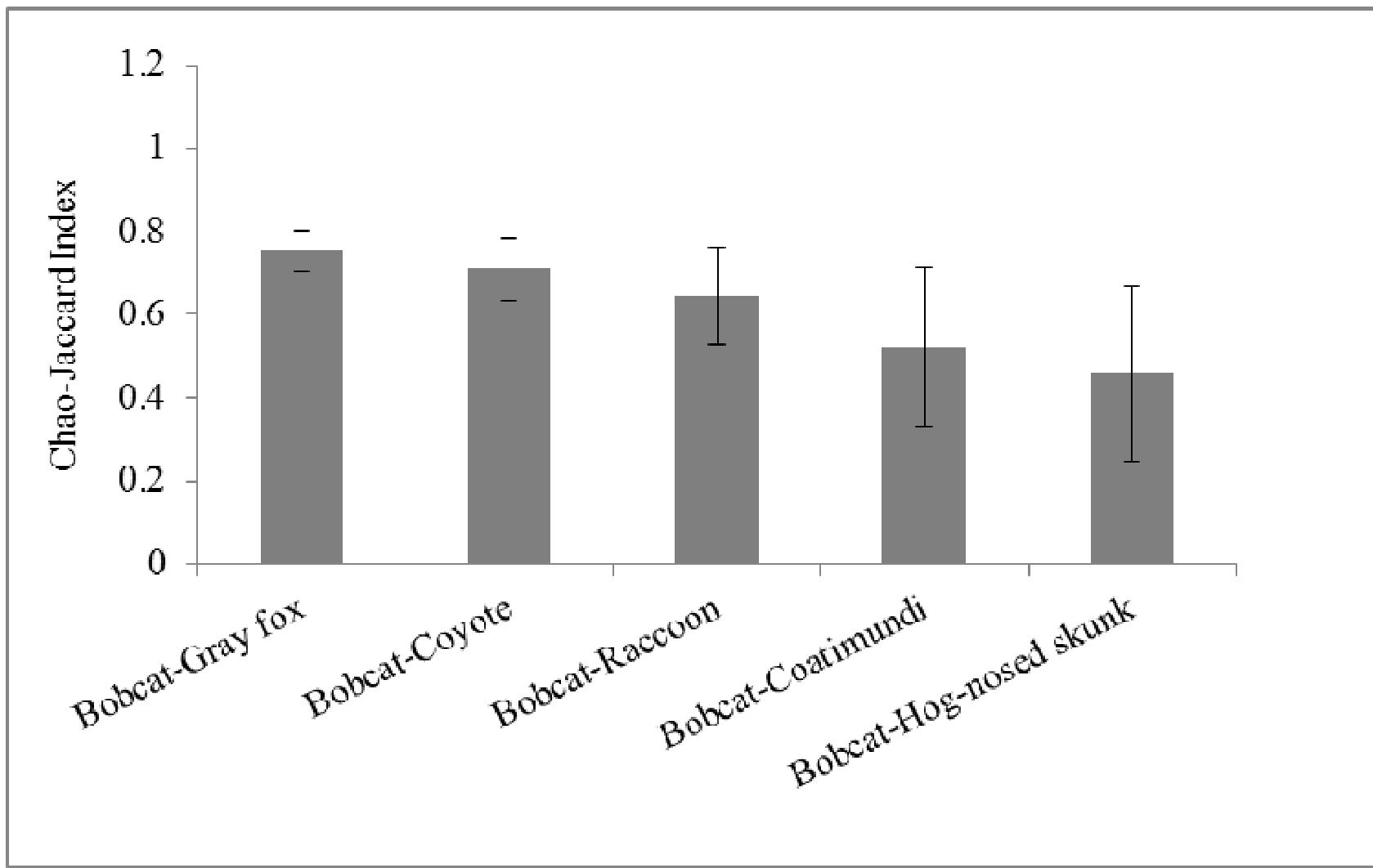


Figure 22. Chao-Jaccard Similarity Index for activity patterns between bobcat and other carnivores on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

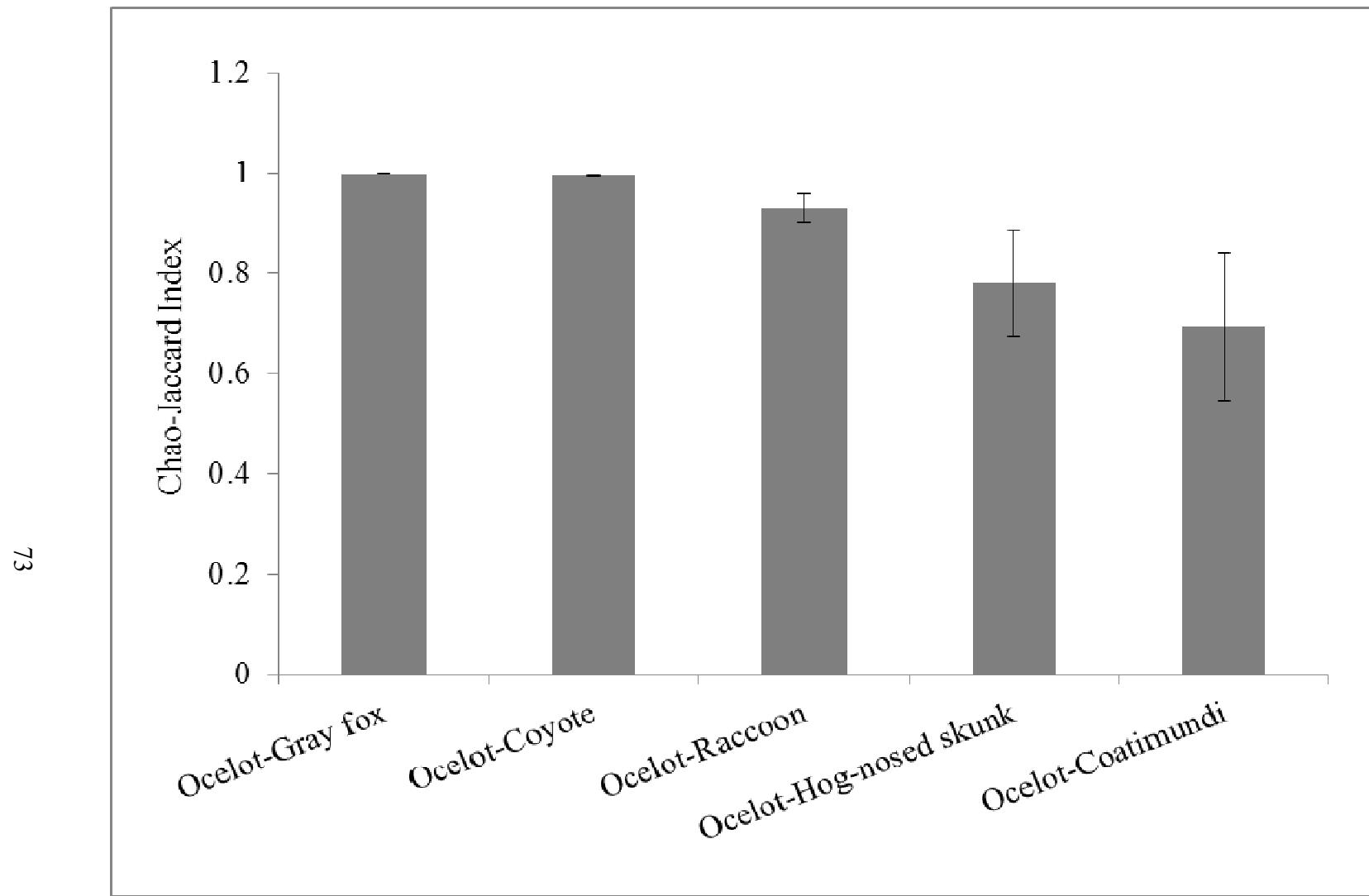


Figure 23. Chao-Jaccard Similarity Index for activity patterns between ocelot and other carnivores on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

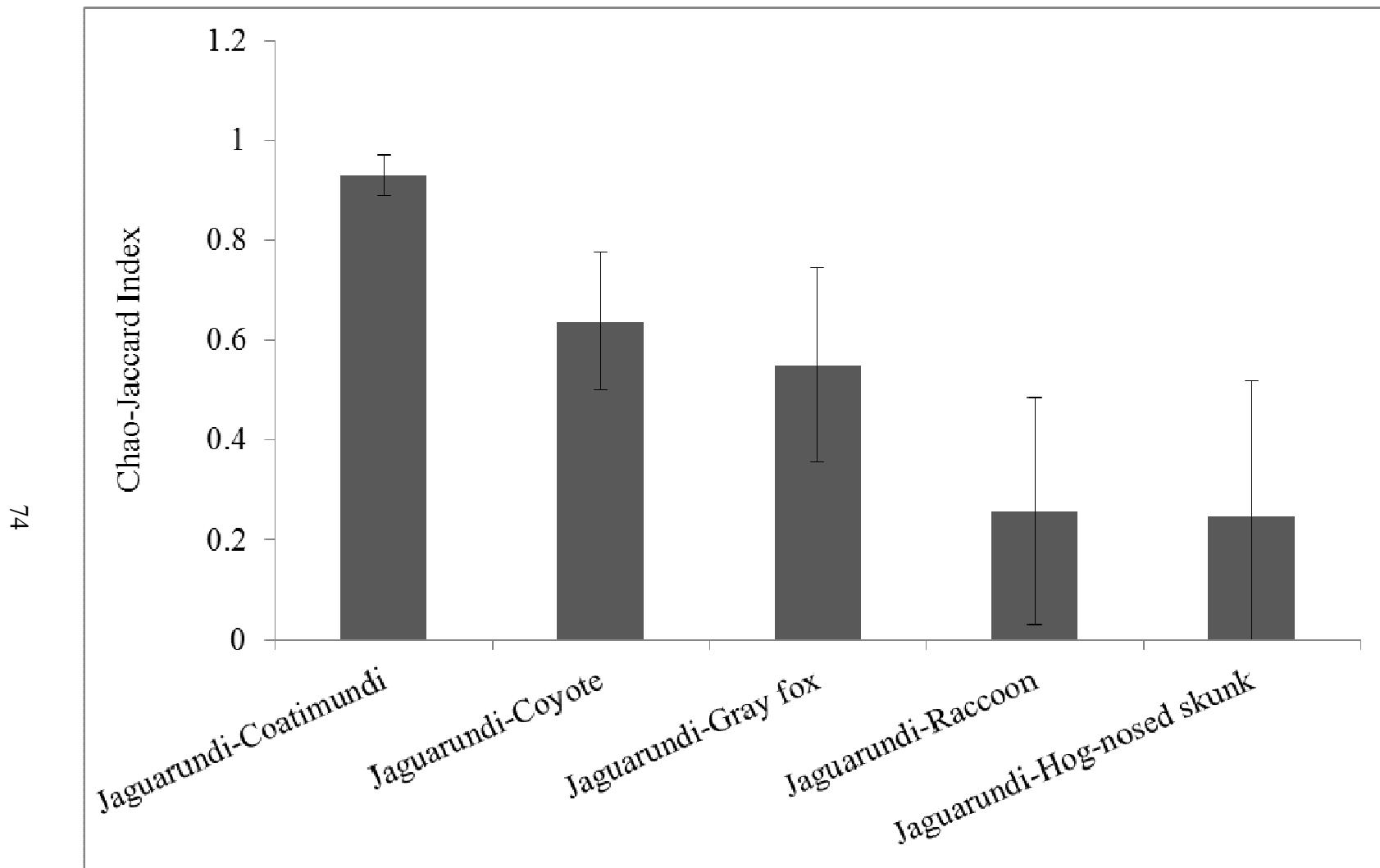


Figure 24. Chao–Jaccard Similarity Index for activity patterns between jaguarundi and other carnivores on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

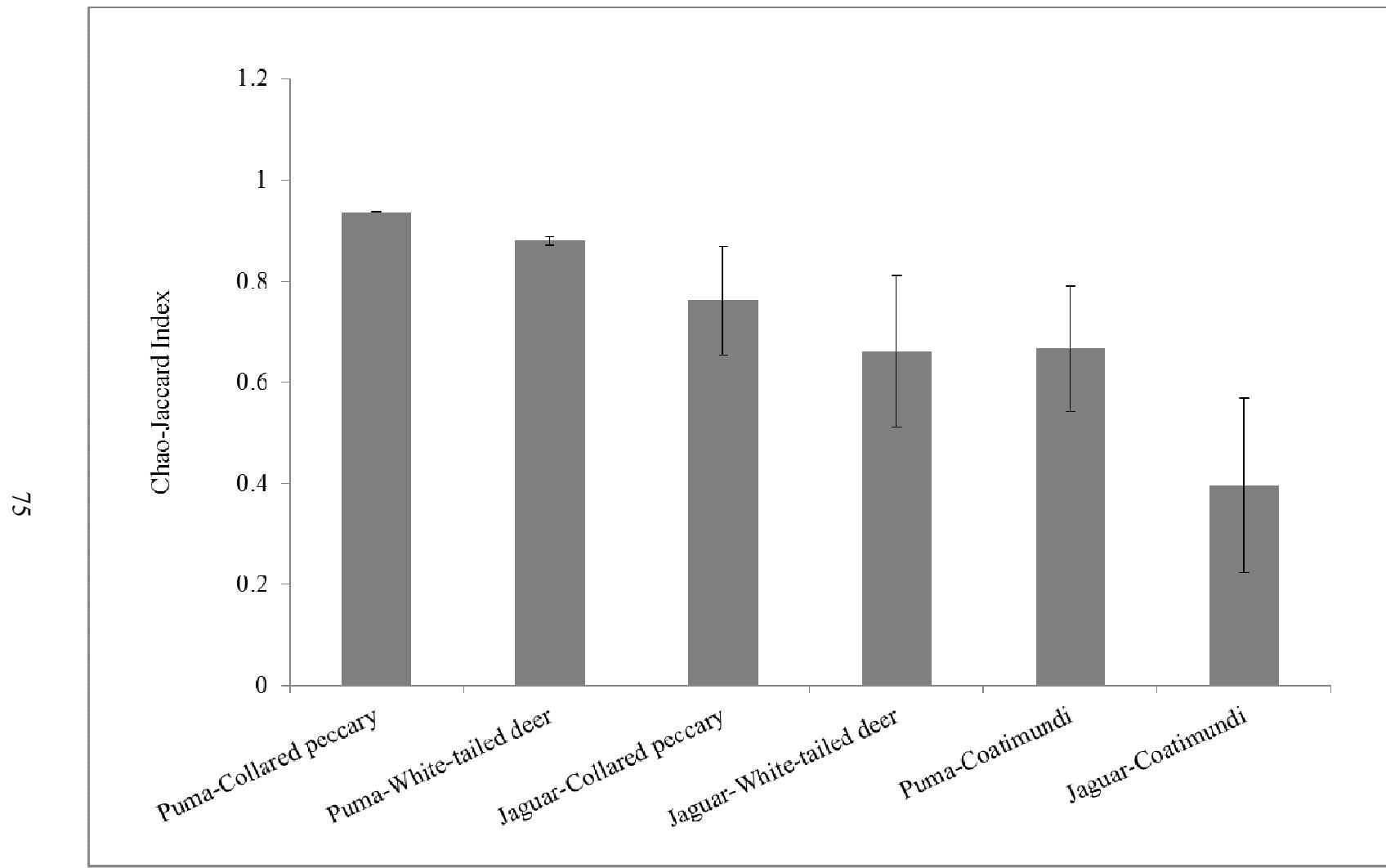


Figure 25. Chao-Jaccard Similarity Index for activity patterns between puma, jaguar and prey on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

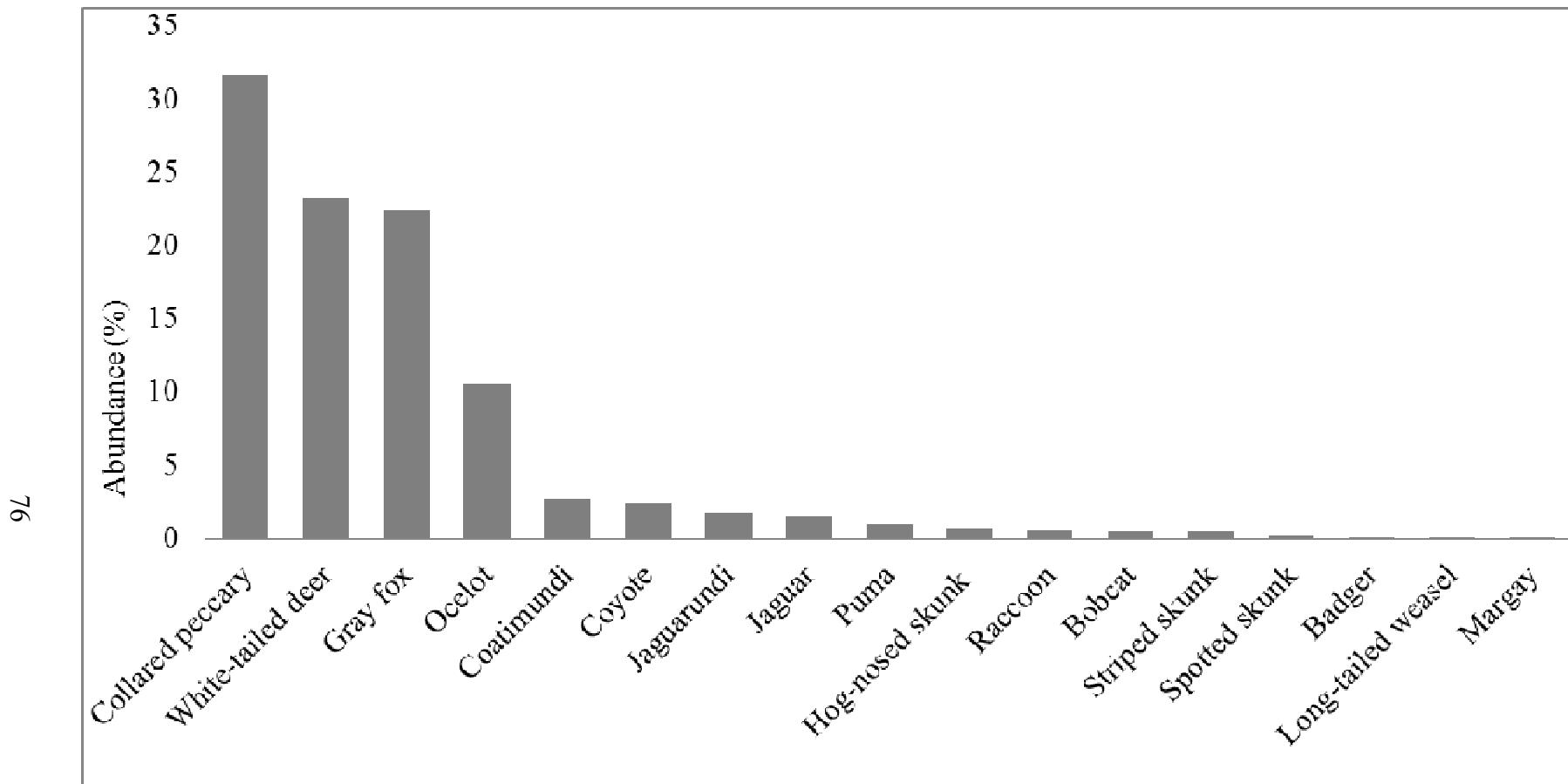


Figure 26. Percentage of abundance of mammalian species photographed on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

49.7%; whereas the lowest was long-tailed weasel and margay (Figure 27).

Comparing abundance between wild cat species, ocelot was the most abundant at 69%, followed by jaguarundi at 11%, jaguar at 10%, puma at 6%, bobcat at 3%, and margay at 0.1% (Figure 28). Among prey species for jaguar and puma, collared peccary was the most abundant at 54%, followed by white-tailed deer at 40% and coatimundi at 4.7% (Figure 29).

Spatial-temporal comparisons

Felid pairs that had the greatest number of encounters at the same camera station within 48 hours were ocelot–jaguarundi (n=32) and ocelot–jaguar (n=10). Less frequent pairs were jaguar–jaguarundi (n=6), ocelot–puma (n=4), ocelot–bobcat (n=7), jaguar–puma (n=2) bobcat–jaguarundi (n=2) bobcat–puma (n=1), and jaguar–bobcat (n=1). No encounters were documented between puma and jaguarundi. Mean number of hours between wild cat photographs at the same station were ocelot–jaguarundi (18 h), ocelot–jaguar (21 h), ocelot–puma (22 h), jaguar–jaguarundi (22 h), ocelot–bobcat (12 h), jaguar–bobcat (9 h), jaguar–puma (37 h), bobcat–jaguarundi (35 h) and bobcat–puma (36 h) (Figure 30). However, a paired *t*-test showed no significant differences ($P > 0.05$) in time comparison between photographs of cat species at the same camera station.

Discussion

Species patterns

Camera-trapping method has allowed researchers to obtain various ecological parameters to study wildlife. This method provides information on the coexistence of species in areas with high biodiversity such as carnivores with similar morphologies that share food, habitat or space. The relationships between several sympatric carnivores have been examined with camera-traps and mechanisms have been proposed to understand coexistence between species that share

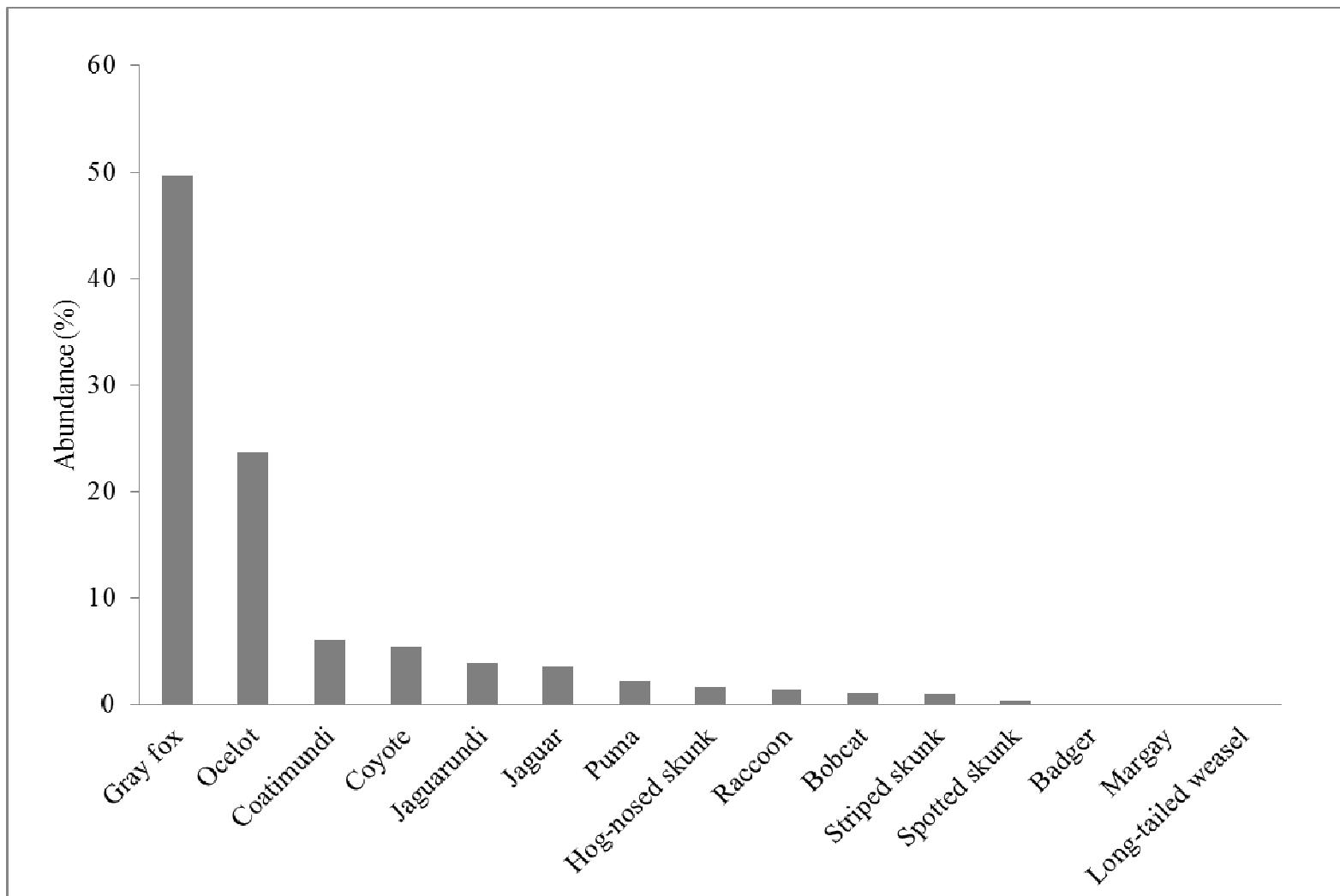


Figure 27. Percentage abundance of carnivore species photographed on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010

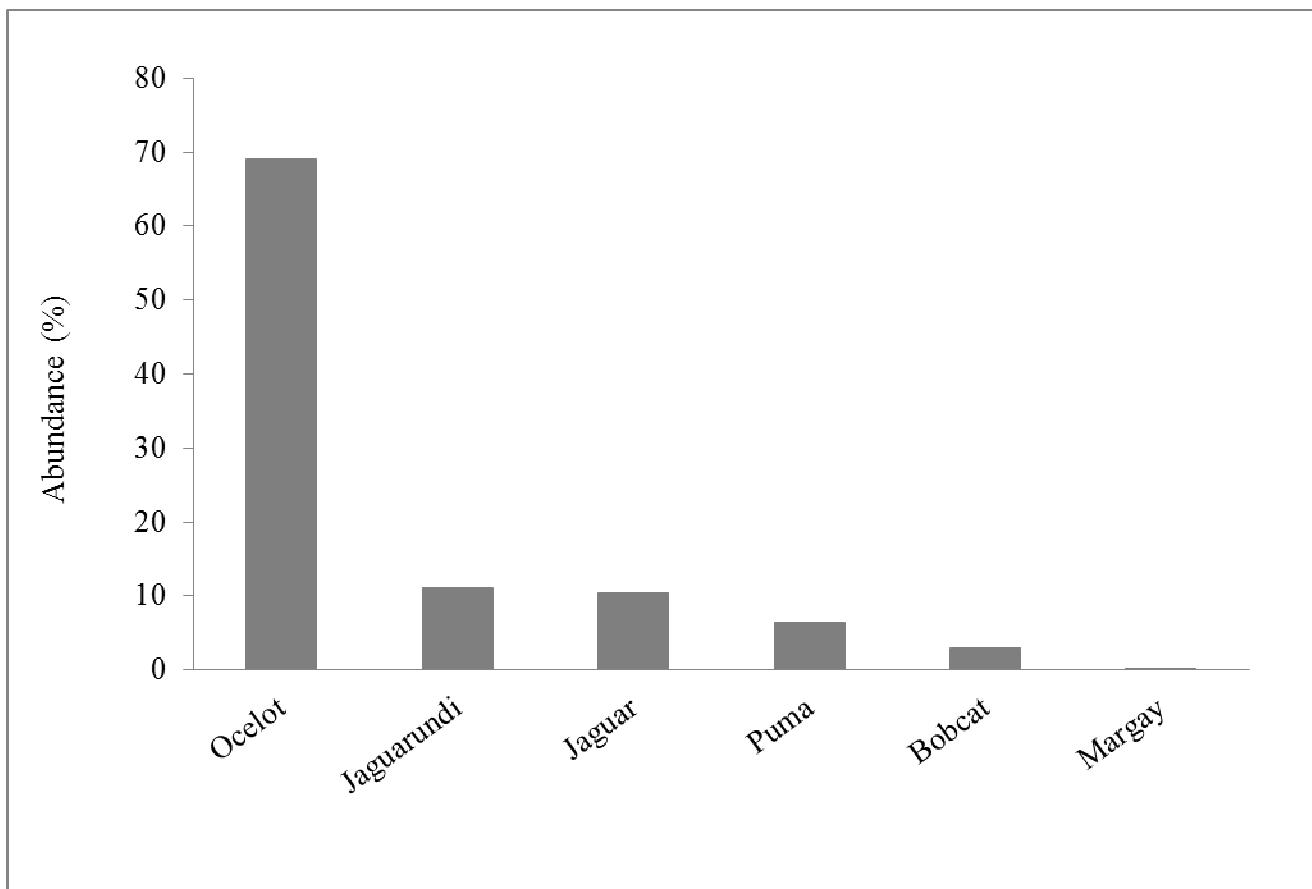


Figure 28. Percentage of abundance of wild cat species photographed on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

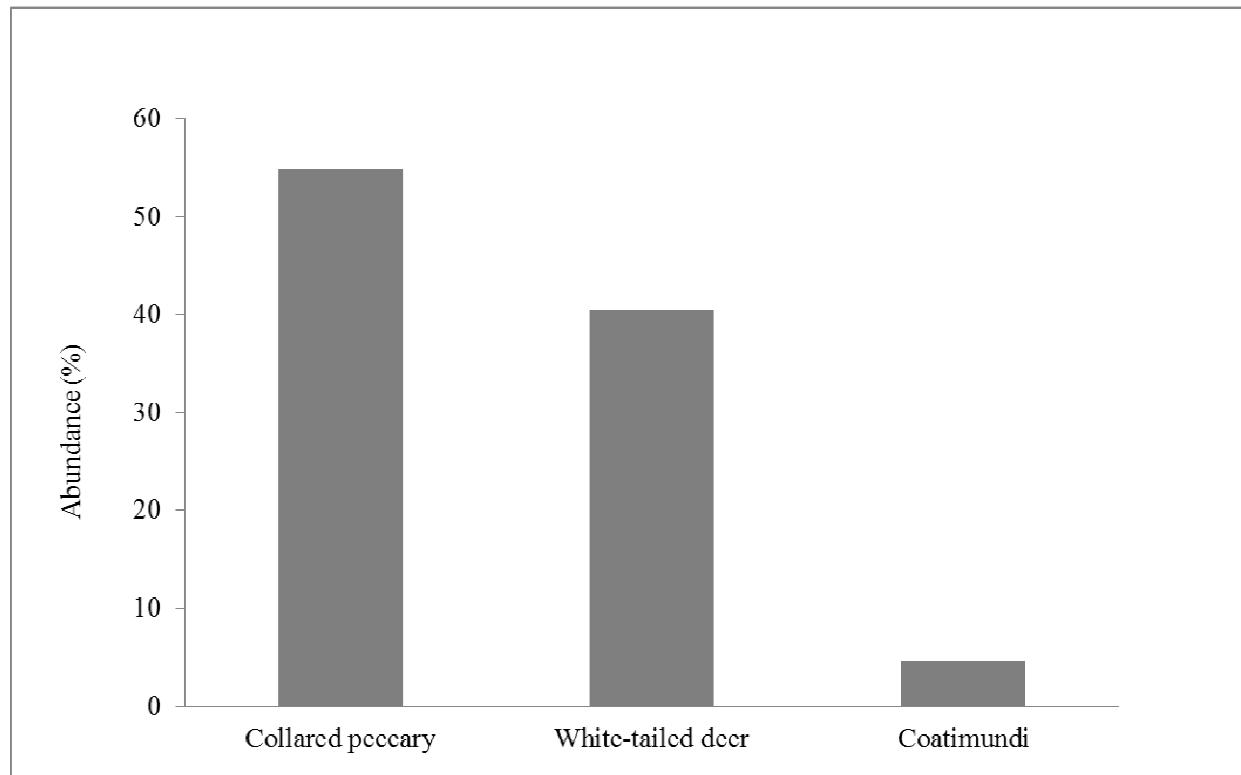


Figure 29. Percentage of abundance of prey species photographed on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009 to 18 June 2010.

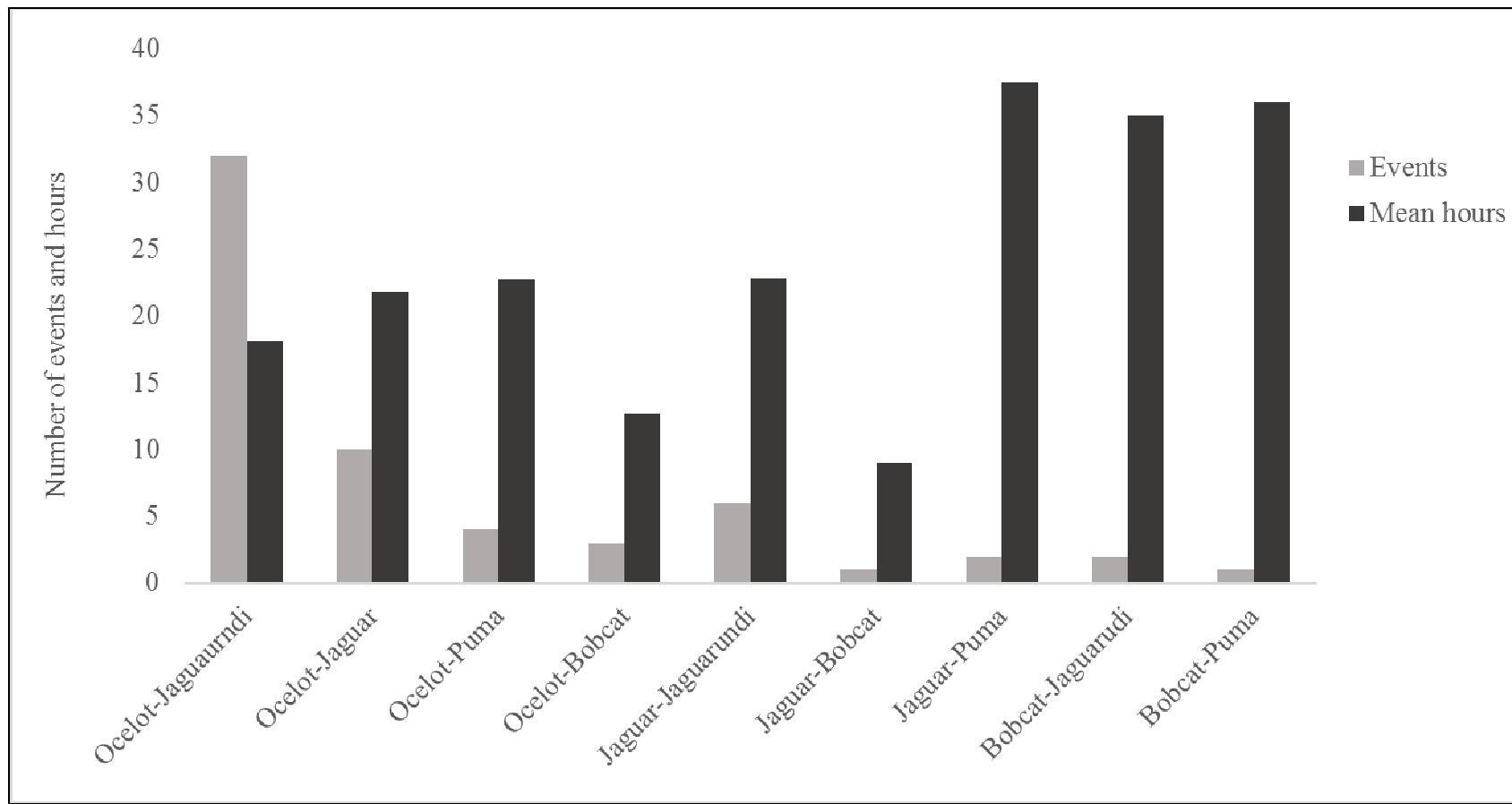


Figure 30. Mean number of paired felid encounters at the same camera–trap site and mean number of hours between felid appearance within 48 hour periods on the Caracol and Camotal Ranch Complex, Tamaulipas, Mexico, from 9 February 2009–18 June 2010..

resources. Other studies have used camera-traps to determine activity patterns of neotropical cats in Central and South America (Gonzalez-Maya et al. 2009, Davis et al. 2011, Di Bitetti et al. 2010); however, in Mexico there has been only one study on habitat use and activity patterns of jaguar and puma (Monroy-Vilchis et al. 2009). This contributes to understanding the interactions among several wild cat species and other carnivore species.

Species biodiversity in my study area is comparable to tropical areas of southern Mexico. The southern states of Chiapas, Campeche, Veracruz, and Yucatan are known for their high biodiversity (Ceballos and Oliva 2005). In my study area, I documented 21 mammal species using camera-traps including 15 carnivores (including six wild cats) indicating high carnivore biodiversity for the area.

The activity patterns of the carnivore community in this area was primarily nocturnal. Nocturnal activity is typical for carnivore species in tropical forests (Van Schaik and Griffiths 1996); however, in some tropical areas carnivore communities express diurnal activity patterns (Gonzalez-Maya et al. 2009). Each area has different conditions and species, so it is possible that other factors such as food availability, presence of other predators, and exploitative competition could also affect the activity patterns of the carnivore community in different areas (Monteiro-Vieira and Baumgarten 1995).

Five species of wild cats were examined in this study. The jaguar was mainly nocturnal with some diurnal activity, a pattern that has also been reported by other studies (Harmsen et al. 2009, Monroy-Vilchis et al. 2009, Chavez et al. 2011). However, some studies consider the jaguar a cathemeral species (Noss et al. 2006, Di Bitetti et al. 2010). The cathemeral activity pattern of jaguars may be related to areas where there is no poaching pressure and ranching is limited or controlled (Maffei et al. 2004, Noss et al. 2006).

In my study area, poaching was rare; however, in recent years some jaguars were poached with hounds and this could be a factor that affects jaguar activity. Another influence on activity may be habitat fragmentation, which occurs when native brush is cleared to create pasturelands.

These two anthropogenic activities may be important factors which caused the nocturnal activity patterns of jaguar in the study area.

In general, the activity patterns of jaguar are variable depending on the site (Harmesn et al. 2011). Puma activity was cathemeral because it has been documented as active during the day and night (Noss et al. 2006, Monroy–Vilchis et al. 2009, Di Bitetti et al. 2010), whereas other studies consider the puma crepuscular (Lucherini et al. 2009, Paviolo et al. 2009). In another study, pumas had the greater activity peaks during the early morning in a protected area, whereas outside the protected area pumas were crepuscular or nocturnal (Paviolo et al. 2009).

These different patterns between sites could be related to illegal hunting pressure or to the activity patterns of prey species (Paviolo et al. 2009). Other variations in activity patterns could be related to season, where pumas were mainly nocturnal during the wet season and cathemeral during the dry season (Romero–Muñoz et al. 2010). Another factor that seems to influence the activity patterns of pumas is the presence of other sympatric carnivores with similar morphology and size such as the jaguar. This relationship between puma and jaguar activity will be discussed later.

The only wild cat species that I consider crepuscular is the bobcat, and this is similar to results from other studies (Leopold 1959, Sunquist and Sunquist 2002, Tigas et al. 2002, Thornton et al. 2004, Elizalde–Arellano et al. 2012, Tewes et al. 2012). However, there are no previous studies of bobcat activity patterns in Mexico.

Ocelots have previously been considered a cathemeral species by some studies; however, activity peaks have been recorded during nocturnal hours (Di Bitetti et al. 2010, Caso 2013).

Goulart et al. (2009) also reported that ocelots were nocturnal, but linked this activity pattern to prey activity (availability) and to an evolutionary adaptation to avoid intraguild predation by big cats. I found that ocelots were strictly nocturnal in my study area. Ocelot nocturnal activity is also supported by other studies (Maffei et al. 2005, Dillon and Kelly 2007, Kolowski and Alonso 2010). In eastern Tamaulipas near my study site, ocelots occurred in denser vegetation and exhibited greater diurnal activity (Caso 2013) compared to my study. Ocelot activity patterns in my study area were likely influenced by prey activity more than exploitative or interference competition with the carnivore community.

The only diurnal cat in this study was jaguarundi with activity peaks similar to patterns found by Di Bitetti et al. (2010) and Caso (2013). Di Bitetti et al. (2010) documented activity peaks at 09:00 h, between 11:00–12:00 h and 13:00–14:00 h. I found activity peaks at 08:00 h, 12:00–13:00 h and 16:00 h (Figure 8). Caso (2013) reported activity peaks between 11:00–14:00 h.

Between species patterns

Carnivore coexistence or avoidance in previous studies has focused on trophic competition, suggesting that this competition could limit or restrict the presence of one species in a specific area (Lomolino et al. 2006, Sanchez–Cordero et al. 2008). However, high overlap of one ecological factor could be balanced by low overlap of other factors (De Oliveira et al. 2010). Consequently, coexistence among sympatric carnivores likely is possible because of differences in activity patterns, habitat use and food selection (Rosenzweig 1966, Kitchener 1991, Thornton et al. 2004). My hypothesis was that the main factors that allowed for coexistence among six wild cats and other carnivores were the differences in activity patterns among species and the spatial avoidance that may occur in species when intraguild predation could be present.

I compared the activity patterns of jaguar and puma with the activity patterns of potential prey species such as collared peccary and white-tailed deer (Novack et al. 2005). There were some differences in activity peaks; however, overlapping activity was clear (index >6) with the Chao-Jaccard Similarity Index (Figure 19). Whereas, jaguar exhibit nocturnal activity, jaguar prey species were active throughout the diel. White-tailed deer were more active during the day and collared peccary activity peaks were in the morning from 08:00–12:00 h and 17:00–23:00 h. Coatiundi were active during the day with three activity peaks at 10:00 h, 12:00 h and 16:00 h. However, puma showed more activity overlap with collared peccary and white-tailed deer because puma was cathemeral that was similar to these prey species.

Although coatiundi are reported as prey for jaguars, they were the only prey species that did not overlap with jaguar activity. Coatiundi may incur predation by jaguar when they are sleeping during the day on the ground or on lower tree branches. These results are different from what was found by Harmsen et al. (2011) that reported that red brocket deer (*Mazama americana*) and white-lipped peccary (*Tayassu pecari*) activity did not overlap with jaguar and puma. Predators and prey may have different activity patterns on different sites (Harmsen et al. 2011). Activity patterns of predators in some sites are similar to their prey patterns, whereas prey species in other areas may change their activity to reduce the risk of being killed from predation (Eccard et al. 2008, Gliwicz and Dabrowsk 2008).

Another factor that may affect carnivore activity patterns is the distribution and activity of prey species in each area. Dominant prey species for jaguar and puma in Brazil are capybara (*Hydrochaeris hydrochaeris*) and caiman (*Caiman yacare*) (Caselli de Azevedo and Murray 2007), whereas eastern cottontail (*Sylvilagus floridanus*) and armadillo (*Dasypus novemcinctus*) are more important prey items in Venezuela (Farrel et al. 2001). The most important prey for jaguars and pumas in Mexico and Mesoamerica are ungulates and coatiundi (Aranda and

Sanchez-Cordero 1996, Nuñez et al. 2000, Scognamillo et al. 2003, Novack et al. 2005, Gomez-Ortiz and Monroy-Vilchis 2013).

I did not analyze the diet of jaguar and puma. However, a food habit study is needed to determine the relationship of diet and activity of sympatric jaguar and puma in northeastern Mexico. This information would be important because diet differences were noted as a probable mechanism that allowed the coexistence of jaguar and puma in previous studies (Harmsen et al. 2009, Foster et al. 2010). Jaguar and puma probably did not compete for food because prey abundance was high in my study area. Collared peccary and white-tailed deer were the most common species recorded by cameras in the area (31% and 23% abundance, respectively). Additionally, other potential prey (i.e., coatiundi and armadillo) occurred throughout the study area. However, I believe temporal partitioning was the most important factor enabling the coexistence of jaguar and puma.

The Chao-Jaccard Similarity Index for activity frequency and activity patterns showed an overlap among jaguar and puma (Nuñez et al. 2000, Harmsen 2009, Monroy-Vilchis et al. 2009, Di Bitetti et al. 2010) (Figure 19). However, there was a difference in the hourly patterns with jaguar being nocturnal and puma being cathemeral. Jaguar exhibited four important activity peaks at 21:00 h, 22:00 h, 24:00, and 03:00 h, and a minor peak in the morning at 09:00 h. Puma showed six activity peaks during the day with the highest at 18:00 h. Separation between jaguar and puma may have been possible because of the differences of use of space and time (Harmsen et al. 2009).

Similarities in activity between jaguar and puma may be related to the activity of their prey. The hunting strategies of these cats is to detect prey primarily by vision and sound (Kitchener 1991, Sunquist and Sunquist 2002), and it is likely easier for predators to detect prey while prey are active (Harmsen et al. 2009).

Puma may coexist with jaguar because it is cathemeral and capable of changing its activity patterns accordingly to environmental conditions. Other factors that could affect jaguar–puma coexistence include predation risk, prey availability, and the presence of other species that may represent competition (Di Bitetti et al. 2010), including jaguar. Jaguar occurred at 10% of abundance among the wild cats, whereas pumas occurred at 6%. In addition, puma appeared to be in poor physical condition in the photographs, whereas jaguar appeared to be in good physical condition. Collectively, this information is consistent with the perspective that jaguars exert a dominant influence over pumas (Paviolo et al. 2009, Di Bitetti et al. 2010).

The Chao–Jaccard Similarity Index showed overlap between ocelot and bobcat. Although, the ocelot is a nocturnal species (Di Bitetti et al. 2006, Di Bitetti et al. 2010, Kolowski and Alonso 2010, Caso 2013) and the bobcat is considered crepuscular there is partial activity overlapping during the late afternoon (Tigas et al. 2002, Thornton et al. 2004, Elizalde–Arellano et al. 2012, Tewes et al. 2012). Few studies have examined the coexistence of ocelot and bobcat. Horne et al. (2009) found that these two species can coexist because of habitat partitioning, where ocelot selected areas with >75% canopy cover and bobcat selected areas with <75% canopy cover. However, Horne et al. (2009) did not compare activity patterns of these felids. Ocelot–jaguarundi and bobcat–jaguarundi showed less overlap because the jaguarundi is diurnal. Temporal segregation likely exists for these sympatric species (Di Bitetti et al. 2010, Caso 2013) (Figure 18).

Another difference among bobcat, ocelot, and jaguarundi was the percentage of relative abundance. Ocelot abundance was 69%, jaguarundi 11%, and bobcat 3%. Previous studies have shown that the ocelot is nocturnal and the jaguarundi is diurnal (Tewes 1986, Konecny 1989, Laack 1991, De Oliveira et al. 2010, Caso 2013), and the relative abundance of ocelots is considerably higher compared with jaguarundi (Konecny 1989, Crawshaw 1995, R. Nuñez pers.).

com. 2010). Nuñez (pers.com.) documented 150 ocelot photographs in a camera-trapping study in coastal Jalisco, Mexico, and recorded one jaguarundi photograph. No jaguarundis were captured in other ocelot studies in Central and South America even though these study sites were within known jaguarundi range (Emmons 1988, Sunquist and Sunquist 2002, Dillon and Kelly 2008). Konecny (1989) captured three jaguarundis, but reported that they were rare in Belize, and Crawshaw (1995) captured 21 ocelots and three jaguarundis in Brazil. There are no recent confirmed reports of jaguarundis in Texas (Caso 2013).

De Oliveira et al. (2010) state that the ocelot plays a dominant role as a mesopredator in the small felid community, with other small cats occurring at lower densities when ocelots were present (i.e., “the ocelot effect”). Although ocelots can coexist with other smaller wild cat species, ocelot density is commonly higher than these other small felids (De Oliveira et al. 2010). Therefore, the “ocelot effect” could be an important factor that reduces the abundance of other smaller wild cats in areas of overlap (De Oliveira et al. 2010). This “ocelot effect” also seems to be evident in other places where ocelots are present (Caso 2013).

One margay photograph was recorded during this study. Margay occur in the El Cielo Biosphere Reserve which is 120 km southwest of my study site (Carvajal et al. 2012). This population is located in the Sierra Madre Oriental and uses a cloud forest in El Cielo Biosphere Reserve.

Bobcat presence is not limited by ocelot presence (Horne et al., 2009); however, the relative abundance of bobcat in my study area was low at 3%. Although environmental conditions are probably adequate for bobcat, its low abundance may be related to the presence of jaguar and puma through interference competition (Hass 2009). However, bobcat are also abundant with puma in other areas. Hass (2009) noted a bobcat was killed and consumed by a puma in Arizona. Two bobcat carcasses with skull punctures were found in Tamaulipas and

track evidence suggested that they were killed by a jaguar but not consumed (A. Caso, pers. comm.). Sanchez-Cordero et al. (2008) found that there was a tendency for bobcat, ocelot, jaguarundi, and margay to avoid jaguar but not puma. This pattern was also reflected in distribution models where bobcat overlapped puma ranges by 97%, but less bobcat overlap occurred with ocelot (44%), margay (46%), jaguar (49%), and jaguarundi (52%) (Sanchez - Corder et al. 2008).

Coatimundi and jaguarundi were diurnal. Other carnivores including coyote, gray fox, raccoon, and the three species of skunk had similar activity patterns as the nocturnal felids. Gray fox was the most abundant species; badger and weasel were the least abundant. Microhabitat segregation may also have contributed to the coexistence of many carnivores.

Some studies mention that differences in diet is the most important factor that allows for ecological coexistence among species, and that spatial and temporal differences do not seem to determine the coexistence of carnivores (Rivera and Rey 1983, Bothma et al. 1984, Sunquist et al. 1989). However, Konecny (1989) did not find significant differences in diet among three sympatric felids (ocelot, jaguarundi, and margay) and one mustelid (tayra; *Eira barbara*) in Belize. However, the ocelot and margay were nocturnal and the tayra and jaguarundi were diurnal.

In another study, small carnivores used areas occupied by larger competitors, and there is no evidence that coexistence is related to habitat partitioning (Davis et al. 2011). In other studies, ocelots and other medium-sized carnivores, (e.g., gray foxes) frequently used areas with high jaguar activity (Donadio and Buskirk 2006, Davis et al. 2011).

In conclusion, most carnivores in my study were primarily nocturnal. I also noted cathemeral patterns by puma and coyote, but these species had activity peaks at night. Even though jaguar and ocelot exhibited some activity during daylight, they were considered nocturnal

because the frequency of peaks of activity were at night. Exclusively nocturnal species included the gray fox, raccoon, and three species of skunk. The bobcat was a crepuscular species. I found a high degree of activity overlap among most carnivores (with the exception of jaguarundi and coatiundi).

Several factors can affect the coexistence of felid species. Initially, I hypothesized that activity was an important factor that influenced species segregation. However, my results indicated substantial overlapping activity patterns among cat species. Coexistence of felids likely involves multiple niche dimensions including dietary, spatial, and temporal elements. However, it seems some species express dominance over others. If ocelot presence in an area affects the presence of smaller cats (e.g., “the ocelot effect”), then this could explain the lower abundance of jaguarundi and margay (De Oliveira et al. 2010, Caso 2013). Ocelot may not have a direct effect on bobcat abundance, because patterns according at the literature, there is not trophic competition, and they have different activity patters, but jaguar presence may affect the densities of bobcat that use more open habitats, and may cause the observed poor body condition of puma.

Diet information of small felids generally consists of small mammals (Tewes and Schmidly 1986). In contrast, large cats (jaguar and cougar) consume large prey including collared peccary and white-tailed deer. Both prey occur at high relative abundances, therefore I believe that food was not a limiting factor that affected the presence or absence of these large cats. Thus, exploitative competition was likely not a dominant mechanism. However, I suspect interference competition operated through differences in spatial temporal patterns and was important for the coexistence of jaguar and puma. The coyote was not an abundant species in the carnivore community, even though it is a generalist species with wide dietary and habitat use patterns.

There were no significant differences ($P>0.05$) in the number of encounters between different cat species at the same camera station. However, I found that the hours separating visits indicated highest avoidance between puma and jaguar.

This study was the first to examine the interactions among six species of wild cats and their spatial–temporal relationship with other carnivores in northeastern Mexico. Future studies should include diet and habitat use analysis for a broader approach in determining the coexistence or avoidance of this diverse felid community.

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CHAPTER III

DISTRIBUTION OF FOUR NEOTROPICAL FELIDS IN NUEVO LEON AND TAMAULIPAS, MEXICO

INTRODUCTION

Some carnivore distributions have been reduced during recent years due to various anthropogenic factors (Ceballos & Ehrlich, 2002). Feline species have been particularly affected since many of them, especially the big cats, require large ranges that have been reduced. These range constrictions have been caused primarily by habitat destruction and poaching (Koford, 1973; Tewes & Schmidly, 1987; Caso, 2007; Caso *et al.*, 2008; Sunquist & Sunquist, 2002). Range maps for felids in Mexico should be refined because of changes caused by human and environmental factors. Additionally, many distribution records in the literature were created from unreliable sources.

Remote sensing cameras and distribution models have been used to assess species richness, hot spots, endemic species range, and reproduction areas (Hay *et al.*, 1998; Osborne *et al.*, 2001; Jetz & Rahbeck, 2002, McPherson *et al.*, 2004). In northeastern Mexico there are six species of wild cats. Four species are considered endangered or threatened including the jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), jaguarundi (*Puma yagouaroundi*), and margay (*Leopardus wiedii*) (SEMARNAT, 2002). Puma (*Puma concolor*) and bobcat (*Lynx rufus texensis*) are not considered endangered or threatened; however, a special permit is necessary to hunt these felids in Mexico (SEMARNAT, 2002). The principal anthropogenic factors that limit the northeastern distribution of these species are illegal hunting (affecting jaguar, jaguarundi, and ocelot) and habitat destruction (affecting margay, ocelot, and jaguar). However, the only recent and reliable information about the distribution of neotropical felids is for the jaguar

Style and format of this dissertation chapter follows the *Journal of Diversity and Distribution*.

(Rabinowitz & Zeller, 2010; Rodríguez-Soto *et al.*, 2011). In Mexico, there is distribution information on jaguar for the states of Jalisco, Nayarit, Colima, Michoacán, and San Luis Potosí (Galvan, 2009; Perez, 2011). Grigione *et al.* (2009) assessed distribution for ocelot, jaguarundi, and jaguar in northeastern Mexico; however, the methodology was flawed. Additional information from Martinez-Calderas (2009) includes a distribution analysis for the ocelot in San Luis Potosí and southern Tamaulipas. The only distribution information for margay is available from the International Union for Conservation of Nature (IUCN) Red List (Payan *et al.*, 2008).

Therefore, it is important to determine reliable distribution ranges for the endangered jaguar, ocelot, jaguarundi, and margay in northeastern Mexico using accurate and recent records. Northeastern Mexico is an important area since these four species find their northeastern distribution range limits in this region (with the exception of southern Texas for ocelot), and any modification or change to these habitats may affect the geographic range of these species (Leopold, 1959). If distributions are not accurately evaluated, future decisions for cat conservation such as designation of protected areas may be ineffective.

The main objective of this study was to determine the recent distributions of four sympatric felids in northeastern Mexico, and to determine which areas should be considered for future conservation efforts. Another objective was to compare the historical ranges with the current ranges of these species to determine differences and to establish hypotheses why these distributions have changed.

METHODS

Study area

The states of Nuevo Leon and Tamaulipas in northeastern Mexico were used in this

analysis. The adjacent state of Coahuila was excluded because only puma and bobcat occur there. Natural vegetation in northeastern Mexico is diverse with a wide array of vegetation types and ecosystems. Habitat types include pine and oak forests, prairie, and deserts. The Sierra Madre Oriental (SMO) is an important ecological area that occurs in both states and is the largest mountain range in northern Mexico. The SMO provides habitat for many important carnivore species such as jaguar and Mexican black bear (*Ursus americanus eremicus*; Ceballos & Ehrlich, 2002) considered endangered species. The climate is diverse with arid, semiarid, subtropical, and temperate zones (Rzedowski, 2006).

Nuevo Leon (N 27°49', S 23°11'; E 98°26', W 101°14'; Instituto Nacional de Estadística Geografía e Informática, INEGI 2000) has extreme climate fluctuations that can reach 47° C during summer with snow accumulation in the higher elevations. Rainfall is typically low with an annual average of 500 mm. Nuevo Leon is 64,924 km² and is divided into three regions based on climate: (a) hot and dry in the northern region, (b) temperate in the mountains, and (c) semiarid in the southern region (Rzedowski, 2006). Natural vegetation in Nuevo Leon includes tropical thornshrub, prairies, and pine oak forests (Rzedowski, 2006). I focused on the central and southern areas of the state for this study.

Tamaulipas (N 27°40', S 22°12'; E 97°08', W 100° 08'; INEGI 2000) is 78,389 km². The climate can be characterized as (1) semi-dry and semi-warm with low annual precipitation in the north-central regions; (2) warm and wet with precipitation during the summer in the south-central and southeastern regions; (3) warm and temperate in the Sierra Madre, and (4) wet to dry in the western region. Tamaulipan vegetation is diverse because of the convergence of the Nearctic and Neotropical bioregions (Leopold, 1959). Vegetation in the southern part of the

state includes tropical and xeric vegetation, whereas the central and northern parts include thornshrub, pine–oak forests, and cloud forest (Rzedowski 2006; Figure 31).

Species records

I reviewed the scientific literature about the distribution and ecology of jaguar, ocelot, jaguarundi, and margay. This literature review included theses, publications, and records from universities. I also conducted interviews with landowners within the study area, and occasionally viewed photographs of specimens. Finally, I gathered personal information during 20 years of field work in Nuevo Leon and Tamaulipas. All reports were considered either Class I records (i.e., photographs, parts of the animal like fur, skull or other physical evidence) or Class II records (reports and personal communication from reliable sources) (Tewes & Everett, 1986). I geo-referenced locations from Nuevo Leon and Tamaulipas and imported them into ArcMap® (ArcGis 9, ESRI 2009) maps to determine the distribution of each species. Only records gathered from the 1980s until present were used in this assessment.

Climatic data

Based on available bio-climatic variables (Hijmans *et al.*, 2005), 1 km² cell grids were generated for the study area. I used five climatic variables: annual mean temperature (Bio 1), temperature seasonality (Bio 4), temperature annual range (Bio 7), annual precipitation (Bio 12), and precipitation seasonality (Bio 15). Additionally, elevation and slope were derived from the Hydro 1k Digital Elevation Model for North America (U.S. Geological Survey 2012).

Species distribution modeling and range estimation

I generated potential distribution maps for each species based on the logistic threshold and the fractional predicted area (Peterson *et al.*, 2011), generating a binary projection of the potential distribution range of the species. These potential distribution maps were performed

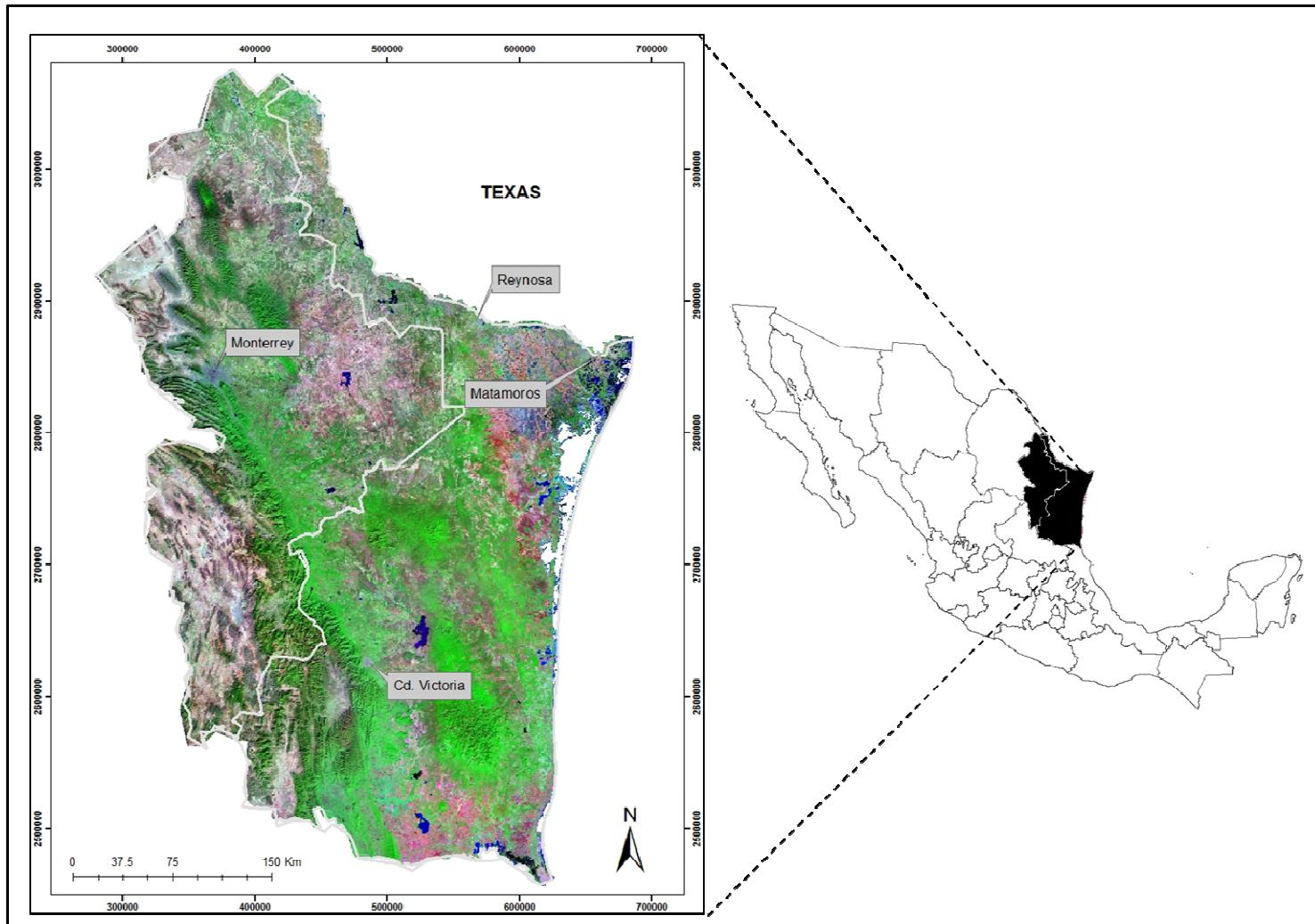


Figure 31. Study area in Nuevo Leon and Tamaulipas, northeastern Mexico.

through the maximum entropy analysis based on ecological niche for potential species distribution modeling (SDM), applying presence–only records and restrictions from environmental variables using Maxent 3.3.3K software (Phillips *et al.*, 2006; Phillips & Dudik, 2008). I used the total number of records in the SDM with 100 replicates in 500 interactions. To test for model fitness and performance I used the Receiver Operating Characteristic (ROC) and the Area Under the Curve (AUC) (Phillips *et al.*, 2006). Although the AUC has been considered a limited measure of model performance (Lobo *et al.*, 2008; Lobo *et al.*, 2011), other studies still consider it a useful measure for ordinal score models (McPherson *et al.*, 2004; Marino *et al.*, 2011; Thuiller *et al.*, 2005; Santika, 2011). All analyses were performed on ArcGIS 9.3® software (ESRI, 2009).

To determine the actual distribution of jaguar, ocelot, jaguarundi, and margay in northeastern Mexico, I used the Adaptive Kernel Range Estimator Model (AKREM). The AKREM is a commonly used home range estimator that is useful in estimating the probability of an individual use of an area based on previous records (Worton 1989, Lopez–Gonzalez 1999, Bader 2000). The AKREM has produced similar results for other distribution analyses such as Genetic Algorithm for Rule Set Prediction analysis (GARP) which generates models based on ecological factors where a species can sustain viable populations (Worton, 1989; Lopez–Gonzalez, 1999; Bader, 2000; Lopez–Gonzalez *et al.*, 2003). I calculated felid distributions based on a 95% probability contour of the AKREM (Lopez–Gonzalez, 1999).

Protected range and available habitats

I estimated the extent of protection for available cover types (i.e., water, forests, mixed cover areas, mosaic shrublands, and grasslands) as related to potential distributions. To accomplish this task, I overlapped distribution polygons with the current protected areas (ESA 2009). Analyses were performed using ArcGIS 9.3® software (ESRI, 2009). To estimate species

richness, I overlapped the distribution polygons of each species and recorded the number of species in each 5 km² grid cell (Safi *et al.*, 2011; Soberon & Ceballos, 2011).

To determine the distribution of jaguar, ocelot, jaguarundi, and margay and their potential distributions, I obtained Class I and II records from 27 survey points, which included private lands, federal protected areas and, rural communities in Nuevo Leon and Tamaulipas (Figure 32).

RESULTS

Jaguar

I obtained 41 jaguar records from 1980 to 2014. These records included remote cameras (n=7), illegally harvested individuals (n=7), private collections (n=3), a museum specimen (n=1), pelages (n=7), a permitted capture (n=1), illegal captures (n=2), tracks and scats (n=5), a photograph (n=1), personal communications (n=5), direct observation (n=3), and a depredated cattle carcass (n=1) (Table 9 and 10). The potential distribution of jaguar was from the mountains in northern Nuevo Leon (Sierra Bustamante, Sierra Picachos and Sierra Papagayos), and south along the SMO in Nuevo Leon to Tamaulipas. Potential jaguar distribution in Tamaulipas occurs in the northern regions where natural vegetation still remains, including the hills of San Fernando and Mendez counties, and the hill region along the southern Gulf Coast.

The Sierra San Carlos is another important area indicated by the potential distribution model, and its border encompasses Nuevo Leon, San Carlos, Cruillas, and San Nicolas counties. Additionally, the Sierra Tamaulipas also was important for jaguar distribution (Figure 33).

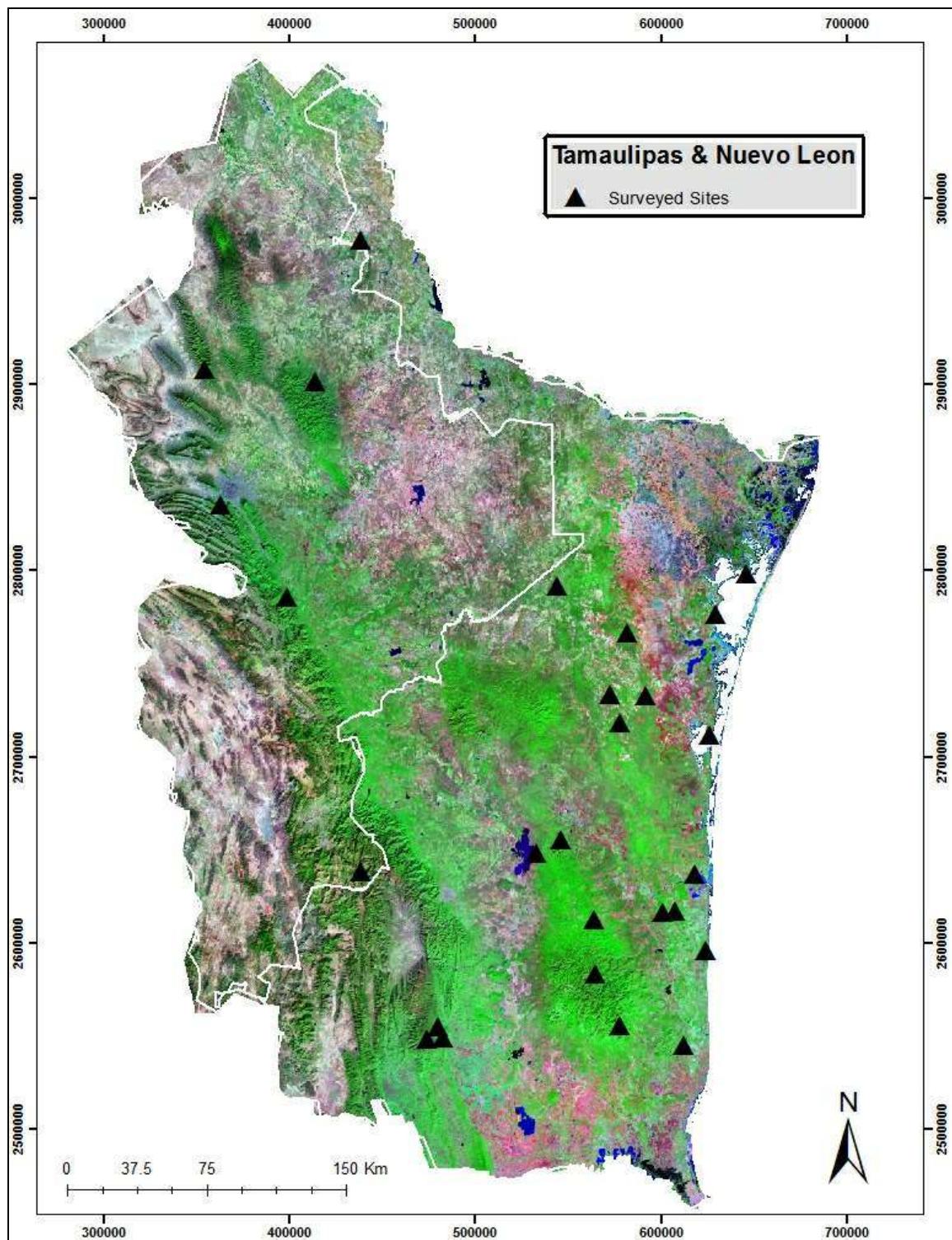


Figure 32. Survey areas in Nuevo Leon and Tamaulipas, northeastern Mexico for detecting the presence of four neotropical wild cats including jaguar, ocelot, jaguarundi, and margay.

Table 9. Jaguar records collected from Nuevo Leon, northeastern Mexico, from 1980 to 2014.

Locality	County	Year	Type record	UTM coordinates	
La Cascara Ranch	Montemorelos	1982	Illegally hunted	399346	2791370
Cañón de Vacas	Aramberri	1991	Private collection	430811	2689271
La Yerbabuena	Montemorelos	1991	Illegally hunted	398331	2788032
Los Fardos	Santiago	1992	Pelage	373802	2805177
Unknown	Allende	1993	Photograph	390880	2795510
Ejido la Ventana	Aramberri	1993	Private collection	434025	2680118
Corral de Piedra Ranch	Iturbide	1993	Museum specimen*	434127	2706049
Cañón de Vacas	Aramberri	1994	Private collection	432358	2689377
Montemorelos	Montemorelos	2003	Personal comm.	422935	2738709

*(UANL # 4311)

Table 9. Continued

Locality	County	Year	Type record	UTM coordinates	
Ejido El Niño	Zaragoza	2006	Remote camera photograph	426693	2647724
Montemorelos	Montemorelos	2007	Personal comm.	412242	2761845
Ejido El Niño	Zaragoza	2007	Remote camera photograph	423252	2650247
Zaragoza	Zaragoza	2008	Personal comm.	438332	2637742
Los Lirios	Montemorelos	2009	Personal comm.	403832	2786311
Unknown	Linares	2013	Illegally hunted	422585	2744235

Table 10. Jaguar records collected from Tamaulipas, northeastern Mexico, from 1980 to 2014.

Locality	County	Year	Type of record	UTM coordinates	
EL Gruyo Ranch	Soto La Marina	1985	Pelage	609897	2610819
Ejido Los Caballos	Jaumave	1991	Pelage	447222	2636432
La Lajilla Ranch	Villa de Casas	1992	Tracks and scats	540177	2647381
Miradores Ranch	Soto la Marina	1993	Pelage	556481	2649126
El Porvenir Ranch	Soto la Marina	1993	Tracks and scats	560867	2607789
Ejido Noche Buena	Soto la Marina	1995	Pelage	601113	2625328
Sotolar Ranch	Villa de Casas	1995	Tracks and scats	539871	2631428
Ejido Ricardo Flores Magón I	Ocampo	2001	Pelage	484168	2537650
Ejido San Vicente	Ocampo	2001	Depredated cattle carcass	470826	2522577

Table 10. Continued

Locality	County	Year	Type of record	UTM coordinates	
Gómez Farías	Gómez Farías	2003	Visual observation	485308	2546292
Almagre Ranch	Gonzalez	2003	Pelage	560896	2552677
Los Balcones Ranch	Soto la Marina	2006	Permitted capture	573539	2577892
El Huasteco Ranch	Gomez Farías	2007	Illegally captured	486655	2546292
Particular ranch	Gomez Farias	2007	Illegally captured	486558	2540467
El Amanecer Ranch	Soto la Marina	2007	Remote camera photograph	600124	2616483
La Mision Ranch	Gonzalez	2008	Illegally hunted	600124	2616483
Montecristo Ranch	Gomez Farias	2008	Tracks	503283	2480780
Boasorte Ranch	Llera	2008	Remote camera photograph	495794	2581751

Table 10. Continued

Locality	County	Year	Type of report	UTM coordenates	
Bueno Aires Ranch	Aldama	2009	Illegally hunted	612389	2545007
San Jose de las Cañadas Ranch	Aldama	2010	Personal comm.	577674	2555105
Camotal Ranch	Jimenez	2010	Remote camera photograph	545030	2655075
Caracol Ranch	Jimenez	2010	Remote camera photograph	542490	2652861
114 Sierra Tanchipa	Mante	2013	Remote camera photograph	503283	2480780
Los Ebanos Ranch	Soto la Marina	2013	Visual observation	624194	2595388
Gruyo Ranch	Soto La Marina	2014	Visual observation	607395	2617039
Las Nubes Ranch	Gomez Farias	2014	Tracks	48293	2548718

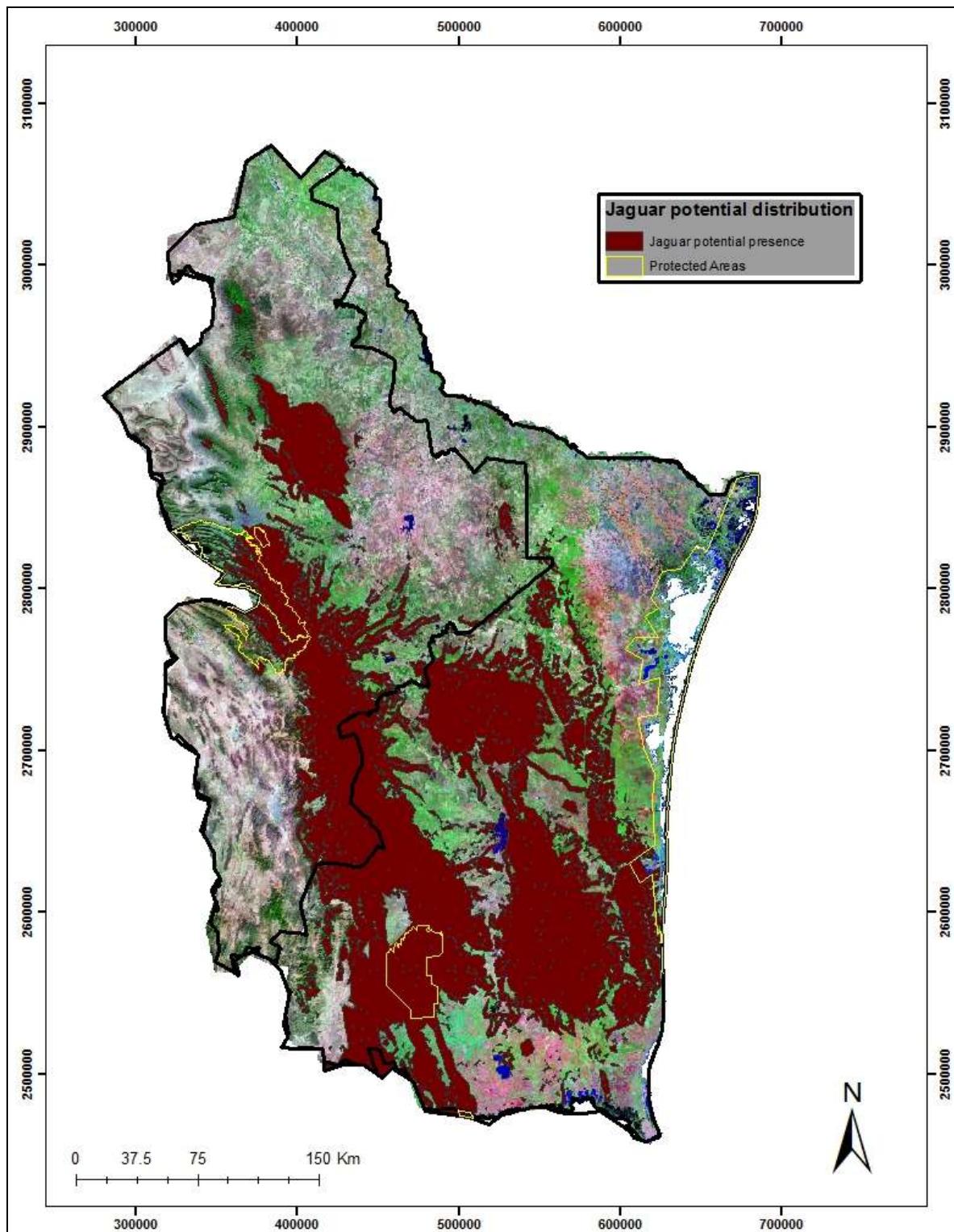


Figure 33. Potential jaguar distribution model in Nuevo León and Tamaulipas, northeastern Mexico.

Of the potential distribution area for jaguar, 44,607 km² was forest, which covered 79% of the jaguar area. Mosaic shrublands and grasslands represent the second largest component with 8,132 km², but only covered 14.5% of the jaguar area. The other two cover types, mixed cover areas (3,242 km²) and water (51 km²), represented 5.7% and 0.09% of the jaguar area, respectively (Table 11). Three federal and one state protected areas comprised an aggregate of 2,663 km², with 4.74% of the jaguar area covered (Table 12).

Jaguar distribution in Nuevo Leon extends from the central portion of the federal protected area Parque Nacional Cumbres of Monterrey (PNCM) into the SMO, continues into Tamaulipas, including the El Cielo Biosphere Reserve (ECBR), and is connected with the Sierra Tamaulipas and the Gulf Coast covering the southern portion of the federal protected area of the Laguna Madre and the Rio Bravo Delta (Figure 34).

Ocelot

I obtained 11 ocelot records from 1980–2010, and 20 additional records after 2014 for a combined 31 records. Records from Tamaulipas were obtained from trapping for research (n=7), remote cameras (n=9), accidental captures (n=3), a legal hunt (n=1), illegal hunts and capture (n=3), observed pelages (n=2), a personal communication (n=1), visual observations (n=2), and road–kills (n=3) (Table 13). Two records from Nuevo Leon were not included in the analyses because they occurred before the years assessed. One record was from an ocelot hunted in 1940 in Santiago County, and the other was a specimen collected in 1946 in General Bravo County, currently held in the museum collection at the Universidad Autonoma de Nuevo Leon (Jimenez & Zuñiga, 1992). Two recent ocelot records occur for Nuevo Leon; one in Montemorelos County (1982) by personal communication (UTM coordinates: 39934–2791370), and one in Allende County (2010) from an accidental capture (UTM coordinates 399030–2791499).

Table 11. Area of potential distribution and percentage of cover types for jaguar in Nuevo Leon and Tamaulipas, northeastern Mexico.

Cover type	Area (km ²)	% Available in the range
Water	51	0.09
Forest	44,607	79.61
Mixed cover types	3,242	5.79
Mosaic shrublands and grasslands	8,132	14.51
Total	56,033	—

Table 12. Area and percentage of the potential distribution of jaguar (56,033 km²) within protected areas of Nuevo Leon and Tamaulipas, northeastern Mexico.

Name	Category	Area protected km ²	Percent of species area
Cerro de la Silla	Natural Monument	60	0.11
Parque Nacional Cumbres of Monterrey	Natural Protected Area	999	1.78
Laguna Madre and Rio Bravo Delta	Flora and Fauna Protected Area	198	0.35
El Cielo	Biosphere Reserve	1,406	2.50
Total	—	2,663	4.74

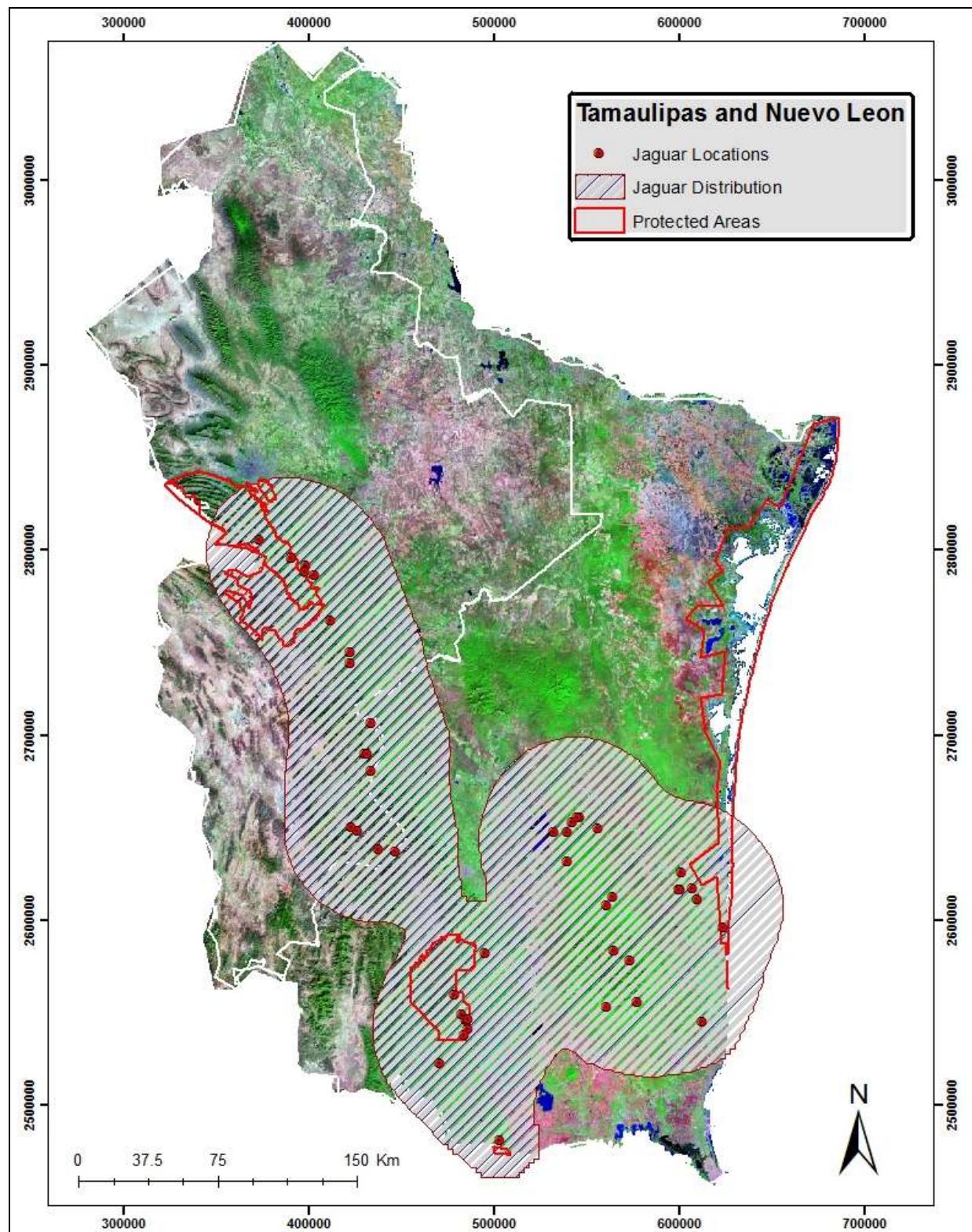


Figure 34. Jaguar distribution using the Adaptive Kernel Range Estimator Model in Nuevo Leon and Tamaulipas, northeastern Mexico.

Table 13. Ocelot records collected from Tamaulipas, northeastern Mexico from 1980 to 2014.

Locality	County	Year	Type of record	UTM coordinates		
El Gruyo Ranch	Soto la Marina	1985	Legally hunted	607395	2617039	
Loma Prieta	Villa de Casas	1991	Illegally hunted	526219	2627086	
La Lajilla Ranch	Villa de Casas	1992	Permitted capture	540177	2647381	
El Porvenir Ranch	Soto la Marina	1993	Permitted capture	560867	2607789	
120	Los Ebanos Ranch	Soto la Marina	1994	Permitted capture	624194	2595388
Miramar Ranch	Soto la Marina	1994	Permitted capture	619313	2605220	
El Tigre Ranch	Aldama	1994	Visual observation	617943	2538589	
San Rafael Ranch	Mendez	1995	Pelage	544474	2791647	
Zoyates Ranch	Villa de Casas	1995	Permitted capture	539871	2631428	
Ejido El Palomo	Gonzalez	1999	Illegally hunted	553459	2541833	

Table 13. Continued.

Locality	County	Year	Type of record	UTM coordinates	
Tampico–Matamoros highway km 135	Soto La Marina	2000	Road kill	593170	2610520
Tampico–Altamira highway	Altamira	2001	Road kill	613332	2485800
Ejido Noche Buena	Soto la Marina	2001	Pelage	611366	2629437
Tangañica Ranch	San Fernando	2006	Remote camera photograph	578171	2717821
Victoria–Soto La Marina highway km 65	Villa de Casas	2006	Road kill	540229	2626073
Ejido Tres Palos	San Fernando	2007	Illegally captured	577231	2715637
Santa Catalina Ranch	San Fernando	2008	Remote camera photograph	591921	2736882
Las Huertas Ranch	Soto La Marina	2008	Remote camera photograph	618090	2636865
Victoria–Mante highway km 103	Llera	2008	Accidental capture	511865	2584220
Las Huertas Ranch	Soto La Marina	2009	Remote camera photograph	621181	2643043

Table 13. Continued.

Locality	County	Year	Type of record	UTM coordinates		
El Amanecer Ranch	Soto La Marina	2009	Remote camera photograph	600111	2616479	
Caracol Ranch	Jimenez	2009	Permitted capture	546586	2654048	
Unknown	Aldama	2009	Accidental capture	582536	2532771	
122	Buenos Aires Ranch	Aldama	2009	Visual observation	612389	2545007
	Caracol Ranch	Jimenez	2010	Remote cameras photograph	546438	2655313
	El Centenario Ranch	Soto La Marina	2012	Remote cameras photograph	624000	2597000
	Zarco Ranch	Soto La Marina	2012	Remote camera photograph	589662	2647054
	Tanchipa	Mante	2013	Remote camera photograph	503283	2480780

The potential distribution for ocelot includes the northern and central regions of Nuevo Leon (excluding the Sierra Bustamante and Sierra Picachos). Ocelot distribution in Tamaulipas includes most of the state, except for a small area near the southwestern border with Nuevo Leon (Figure 35).

The main cover types for ocelots were mosaic shrublands and grassland with 82,226 km², representing 42.7% of the ocelot area, followed by forest with 66,922 km², representing 34.8% of the ocelot area. The remaining cover types were disturbed areas representing 20.9%, and water areas at 1.4% of the ocelot area (Table 14). Protected areas in Nuevo Leon and Tamaulipas covered 4,714 km², or 2.4% of the ocelot area (Table 15).

The distribution model indicates that ocelot are present in Nuevo Leon only in the SMO, and in the central portion of the PNCM through the southern end. Ocelot distribution is widespread in Tamaulipas with the exception of the highly-developed Rio Grande Delta. The northernmost record of ocelot occurred at an isolated point in Mendez County. Ocelot distribution extends from San Fernando and continues into Tampico and Madero counties, excluding most of the SMO (Figure 36).

Jaguarundi

I recorded 32 jaguarundi locations for Nuevo Leon and Tamaulipas, including road-killed jaguarundis (n=5), accidental captures (n=2), personal communications (n=3), one killed by dogs (n=1), visual observations (n=10), permitted captures (n=2), pelage (n=1), remote sensing cameras photographs (n=6), and illegally hunted (n=2) specimens. The jaguarundi reports for Nuevo Leon were from several areas within the SMO.

The northernmost jaguarundi records for Tamaulipas were from San Fernando; two from Soto la Marina to the Gulf Coast, three in the northern part of Sierra Tamaulipas (Jimenez, Abasolo, and Villa de Casas), and the southernmost record occurred in Gonzalez County

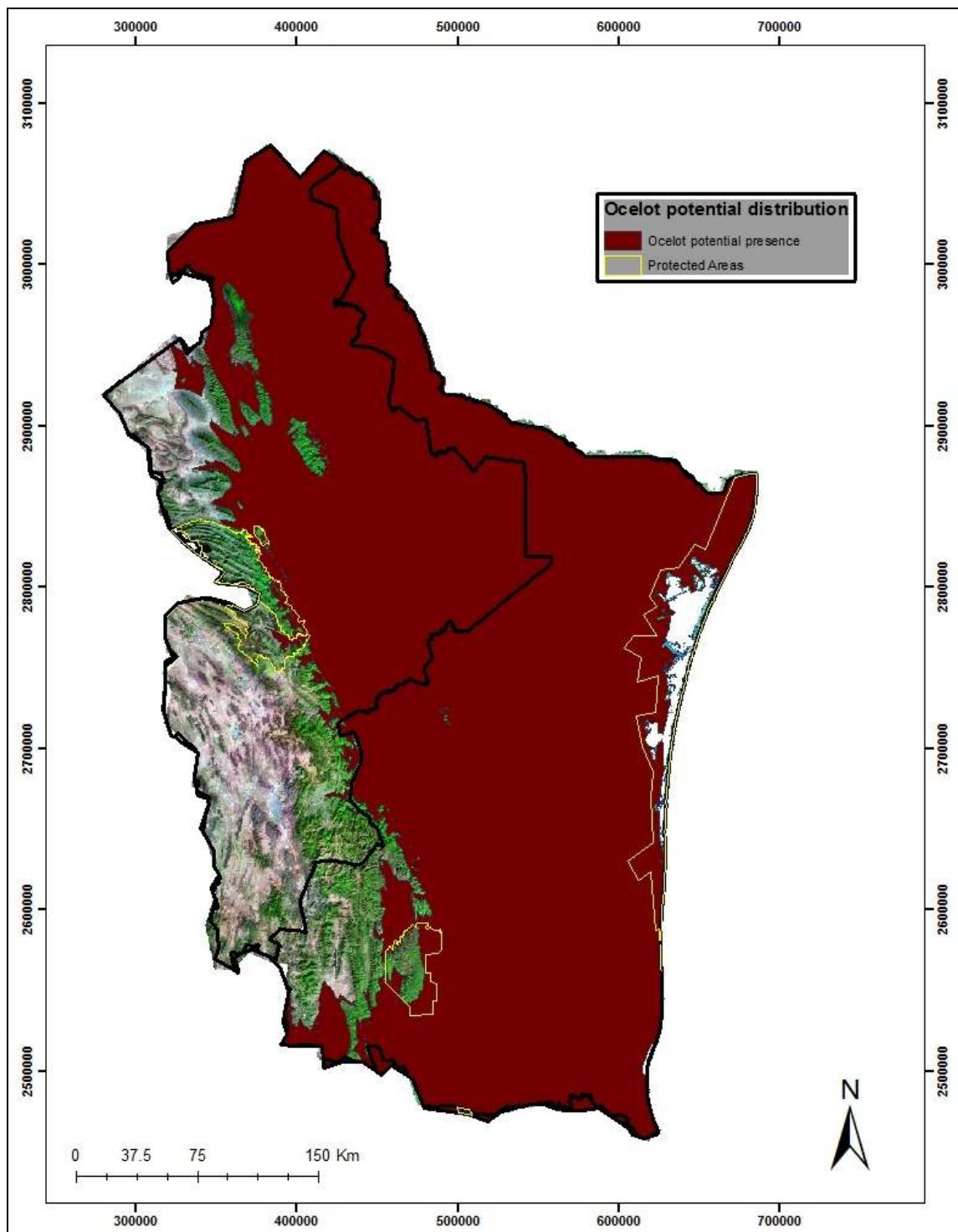


Figure 35. Potential ocelot distribution model in Nuevo León and Tamaulipas, northeastern Mexico.

Table 14. Area of potential distribution and percentage of cover types for ocelot in Nuevo Leon and Tamaulipas, northeastern Mexico.

Cover types	Area (km ²)	Available in the range %
Water	2,687	1.40
Forest	66,922	34.83
Disturbed areas	40,310	20.98
Mosaic shrublands and grasslands	82,226	42.79
Total	192,145	—

Table 15. Area (192,145 km²) and percentage of the potential distribution of ocelot in the protected areas of Nuevo Leon and Tamaulipas, northeastern Mexico.

Name	Category	Area protected km ²	Percent of species area
Cerro de la Silla	Natural Monument	24	0.01
Parque Nacional Cumbres de Monterrey	Natural Protected Area	261	0.14
Laguna Madre and Rio Bravo Delta	Flora and Fauna Protected Area	3,682	1.91
El Cielo	Biosphere Reserve	747	0.39
Total		4,714	2.45

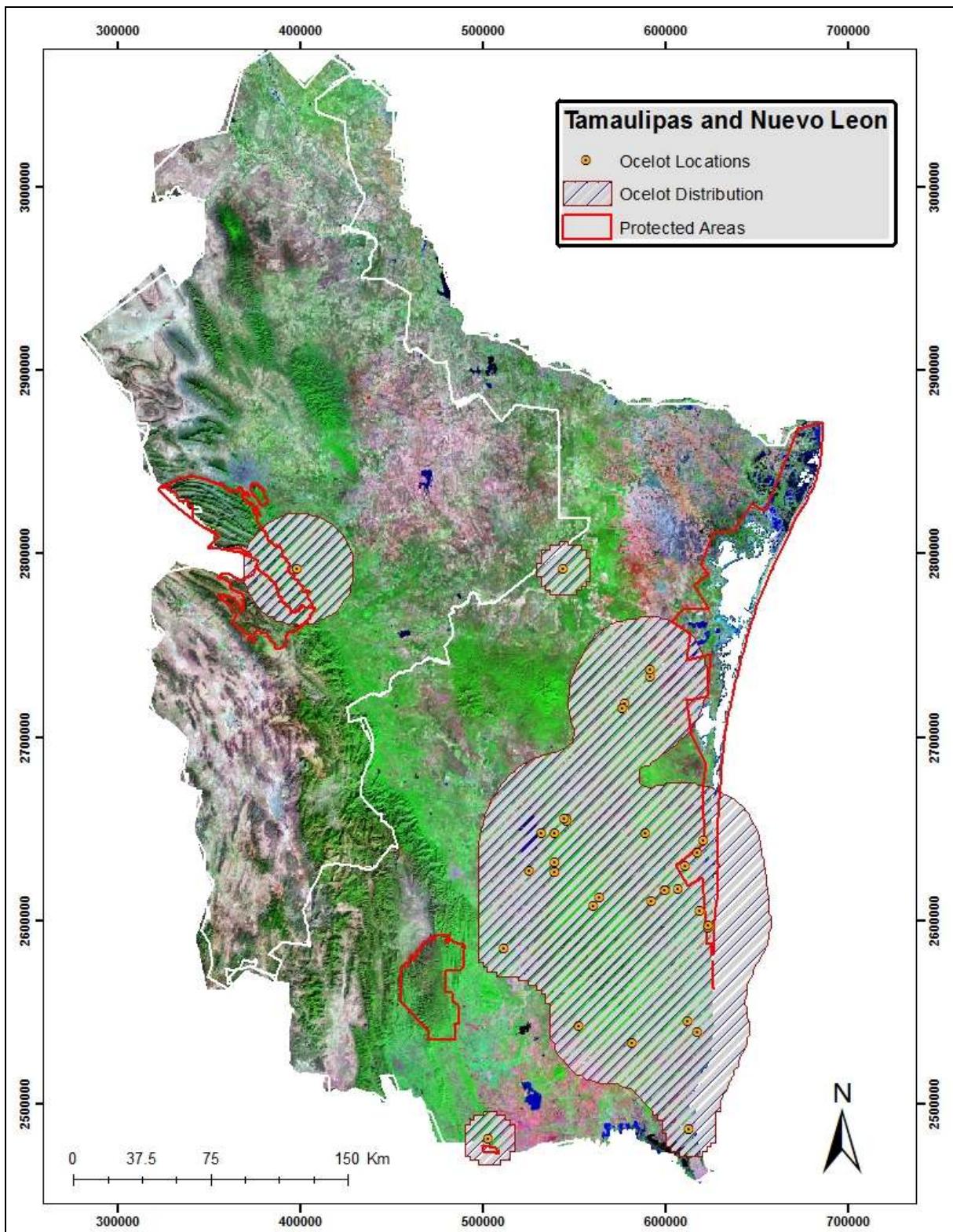


Figure 36. Ocelot distribution using the Adaptive Kernel Range Estimator Model estimator in Nuevo Leon and Tamaulipas, northeastern Mexico.

(Table 16 and 17). Cover types within the potential jaguarundi distribution were dominated by forest with 54,005 km², representing 61% of the jaguarundi area. Mosaic shrublands and grasslands with an area of 23,824 km² represented 26.9%, disturbed areas were 11.4%, and water areas were 0.6% of the distribution area (Table 18). The natural protected reserves covered 3.2% of the jaguarundi area in both states (Table 19).

The potential distribution model for jaguarundi in Nuevo Leon includes the SMO and all of the other mountain ranges of this state, and continues south into Tamaulipas and the Sierra Tamaulipas towards the Gulf Coast. The potential distribution in Tamaulipas only excludes the highly developed Rio Grande Delta of the northern part of the state (Figure 37).

Jaguarundi distribution in Nuevo Leon occurred along the SMO, (except in the southern area) and included two federal protected areas, PNCM and the Natural Monument Cerro de la Silla. However, the SMO in Tamaulipas is completely excluded from jaguarundi distribution. Jaguarundi distribution also includes northern San Fernando County and continues east towards the Gulf Coast (Figure 38).

Margay

Few records (n=8) for margay were obtained for this study, and all were from Tamaulipas (Table 20). Potential margay distribution encompasses most of Tamaulipas, except for a small portion in the northeastern and southwestern area of the state. Only the SMO and a few mountain areas in northwest Nuevo Leon are included as potential distribution (Figure 39).

The cover types within the margay area consisted of forest (57.6%), mosaic shrublands and grasslands (27.7%), disturbed areas (12.9%), and water (1.7%) (Table 21). Protected areas cover 117,428 km² or 5.7% of the margay area in Nuevo Leon and Tamaulipas (Table 22).

Margay distribution using the AKREM method is limited only to Tamaulipas, and is

Table 16. Jaguarundi records collected from Nuevo Leon, northeastern Mexico from 1989 to 2014.

Locality	County	Year	Type of record	UTM coordinates	
Pablillo	Galeana	1989	Road kill	401311	2714139
El Cerrito	Santiago	1998	Personal comm.	378568	2821863
La Puerta del Campo	Santiago	1998	Personal comm.	383915	2809745
Charco San Antonio	Santiago	1998	Personal comm.	386927	2810209
Ecological Park Chipinque	San Pedro Garza Garcia	1999	Road kill	362750	2834883
Camino al Diente	Monterrey	2000	Killed by dogs	373185	2824551
Private property	Monterrey	2001	Remote cameras photographs	370499	2829589
El Barro	Santiago	2002	Accidental capture	378820	2823223

Table 16. Continued.

Locality	County	Year	Type of record	UTM coordinates	
Camino Parque Funeral	Guadalupe	2003	Illegally hunted	371661	2830395
Lomas Bonito Ranch	Montemorelos	No date	Road kill	404407	2773891
Los Pinolillos Ranch	Juarez	No date	Accidental capture	383493	2827701
Montemorelos	La Cascara	No date	Road kill	400087	2790216

Table 17. Jaguarundi records collected from Tamaulipas, northeastern Mexico from 1989 to 2014.

Locality	County	Year	Type of record	UTM coordinates	
La Lajilla Ranch	Villa de Casas	1992	Visual observation	532866	2647592
Porvenir Ranch 2	Soto La Marina	1993	Visual observation	615800	2602685
El Tigre Ranch	Aldama	1994	Visual observation	617943	2538589
Ejido Tepehuajes	Soto La Marina	1994	Visual observation	624000	2597000
Zotolar Ranch	Villa de Casas	1995	Visual observation	526219	2627086
Manuel	Aldama	1995	Visual observation	576953	2506998
Ejido Noche Buena	Soto La Marina	1995	Pelage	611366	2629437
La Mision Ranch	Gonzalez	1998	Visual observation	571610	2512703
Los Pericos Ranch	Soto La Marina	1999	Permitted capture	615686	2589614
Barra de Ostiones	Soto La Marina	2000	Visual observation	625080	2589481

Table 17. Continued.

Locality	County	Year	Type of record	UTM coordinates	
Santa Catalina Ranch	San Fernando	2004	Illegally hunted	589404	2736251
Hgwy Victoria–Soto la Marina	Soto La Marina	2004	Roadkill	542554	2626566
Santa Catalina Ranch	San Fernando	2008	Remote cameras photograph	591996	2732544
Las Huertas Ranch	Soto La Marina	2008	Remote cameras photograph	618090	2636865
132	Los Ebanos Ranch	Soto La Marina	Permitted capture	624194	2595388
	Buenos Aires Ranch	Aldama	Visual observation	612389	2545007
	El Amancer Ranch	Soto La Marina	Remote cameras photograph	600907	2616250
	Caracol Ranch	Jimenez	Remote cameras photograph	546438	2655313
	El Centenario Ranch	Soto La Marina	Remote cameras photograph	589662	2647054
	El Gruyo Ranch	Soto La Marina	Visual observation	607395	2617039

Table 18. Area of potential distribution and percentage of cover types for jaguarundi in Nuevo Leon and Tamaulipas, northeastern Mexico.

Cover type	Area (km ²)	Available in the range %
Water	574	0.65
Forest	54,005	61.00
Disturbed areas	10,129	11.44
Mosaic shrublands and grasslands	23,824	26.91
Total	88,532	—

Table 19. Area and percentage of the potential distribution of jaguarundi (88,532 km²) in the protected areas of Nuevo Leon and Tamaulipas, northeastern Mexico.

Name	Category	Area protected km ²	Percent of species area
Cerro de la Silla	Natural Monument	60	0.07
Parque Nacional Cumbres de Monterrey	Natural Protected Area	849	0.96
Laguna Madre y Delta del Rio Bravo	Flora and Fauna Protected Area	694	0.78
El Cielo	Biosphere Reserve	1,233	1.39
Total	—	2,836	3.20

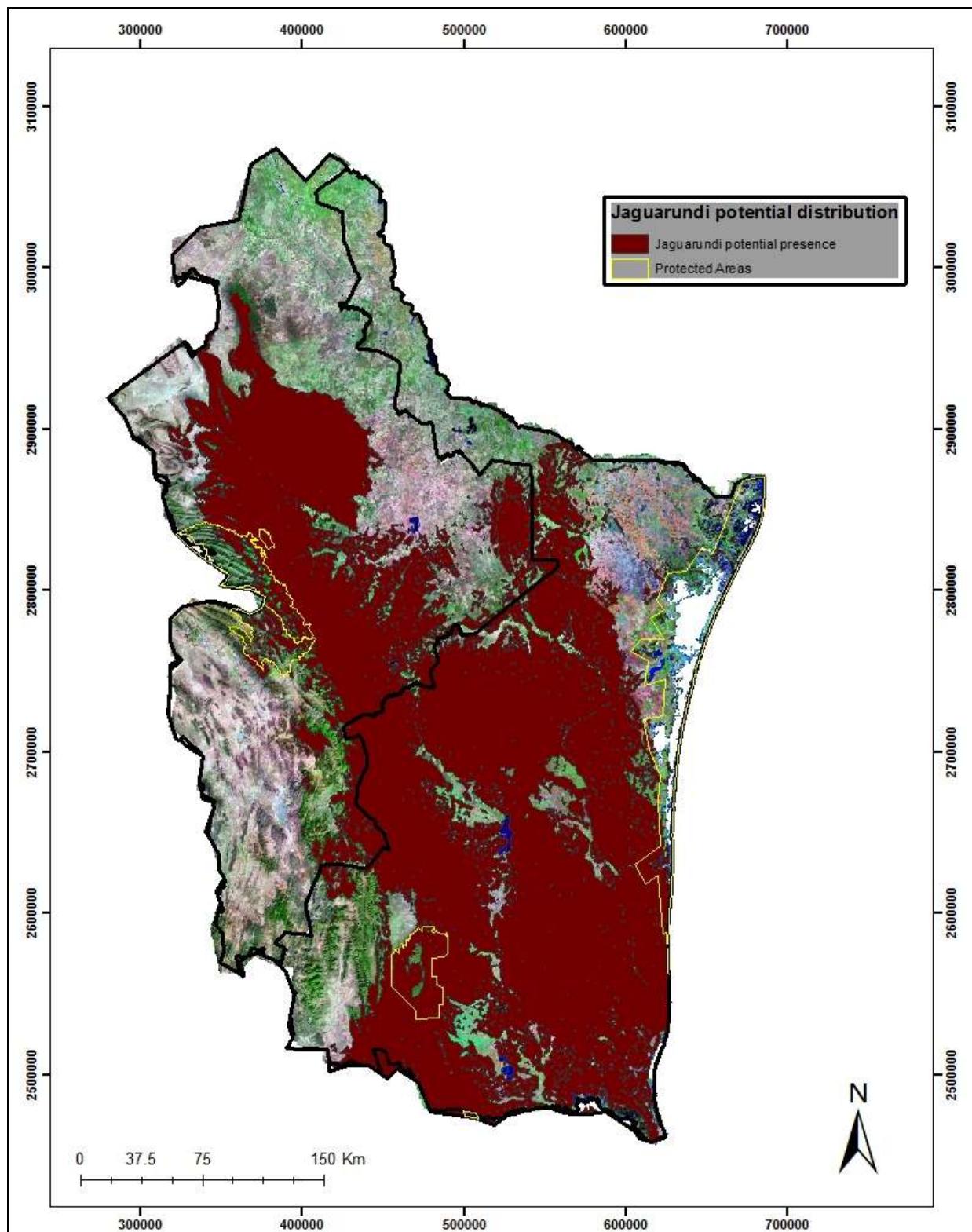


Figure 37. Potential jaguarundi distribution model in Nuevo Leon and Tamaulipas, northeastern Mexico.

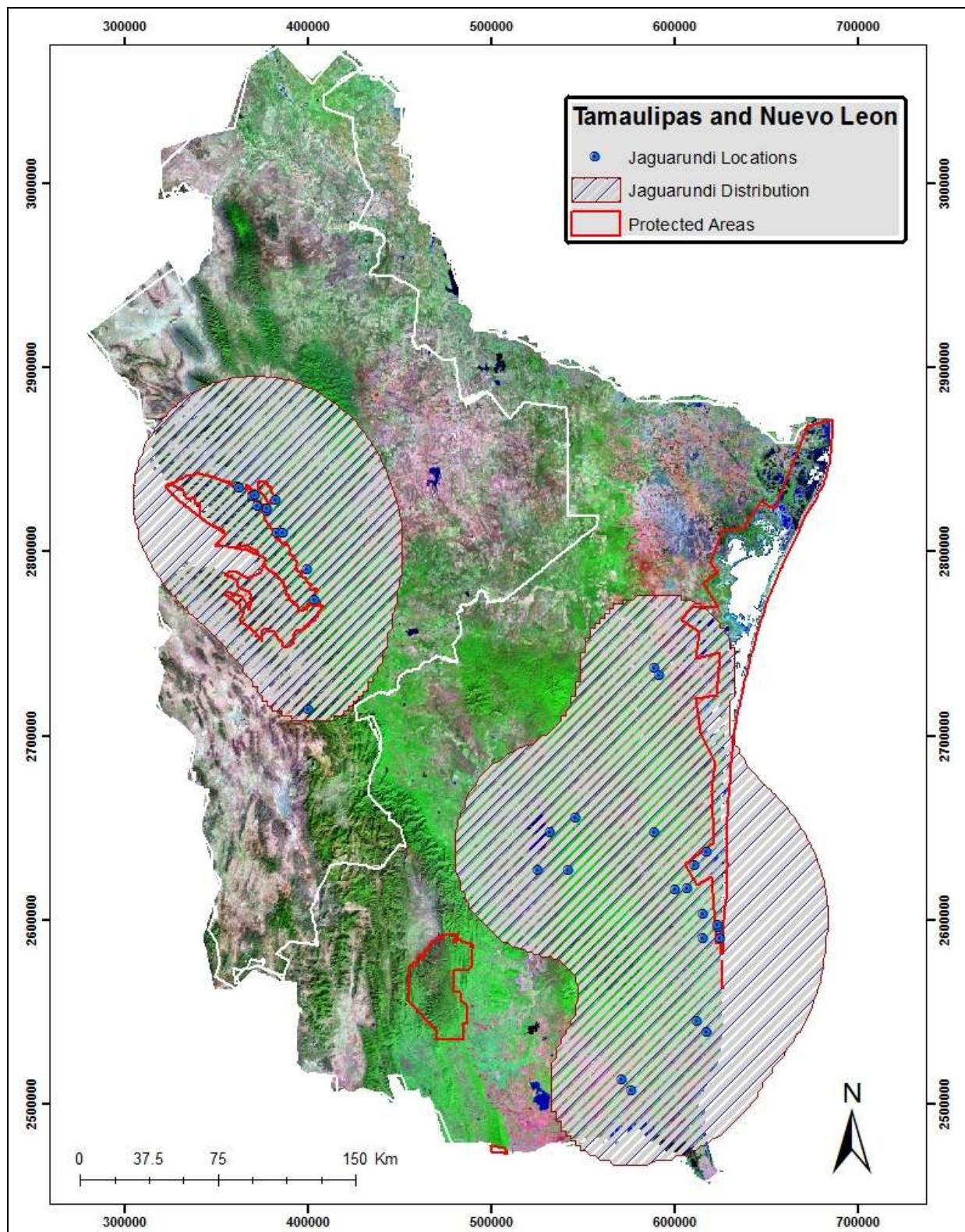


Figure 38. Jaguarundi distribution using the Adaptive Kernel Range Estimator Model in Nuevo Leon and Tamaulipas, northeastern Mexico.

Table 20. Margay records collected from Tamaulipas, northeastern Mexico from 1980 to 2014.

Locality	County	Year	Type of record	UTM coordinates	
Ejido Altacimas	Gomez Farias	2001	Permitted capture	482936	2548718
Ejido El Azteca	Gomez Farías	2001	Permitted capture	477077	2557755
Balcones Ranch	Aldama	2003	Pelage	565006	2582793
Unknown	Llera	2007	Illegally captured	497472	2578625
El Amancer Ranch	Soto La Marina	2008	Remote camera photograph	600907	2616250
Ejido Julilo	Gomez Farias	2009	Remote camera photograph	480217	2554650
Caracol Ranch	Jimenez	2010	Remote camera photograph	546438	2655313
Tanchipa	Mante	2013	Remote camera photograph	503283	2480780

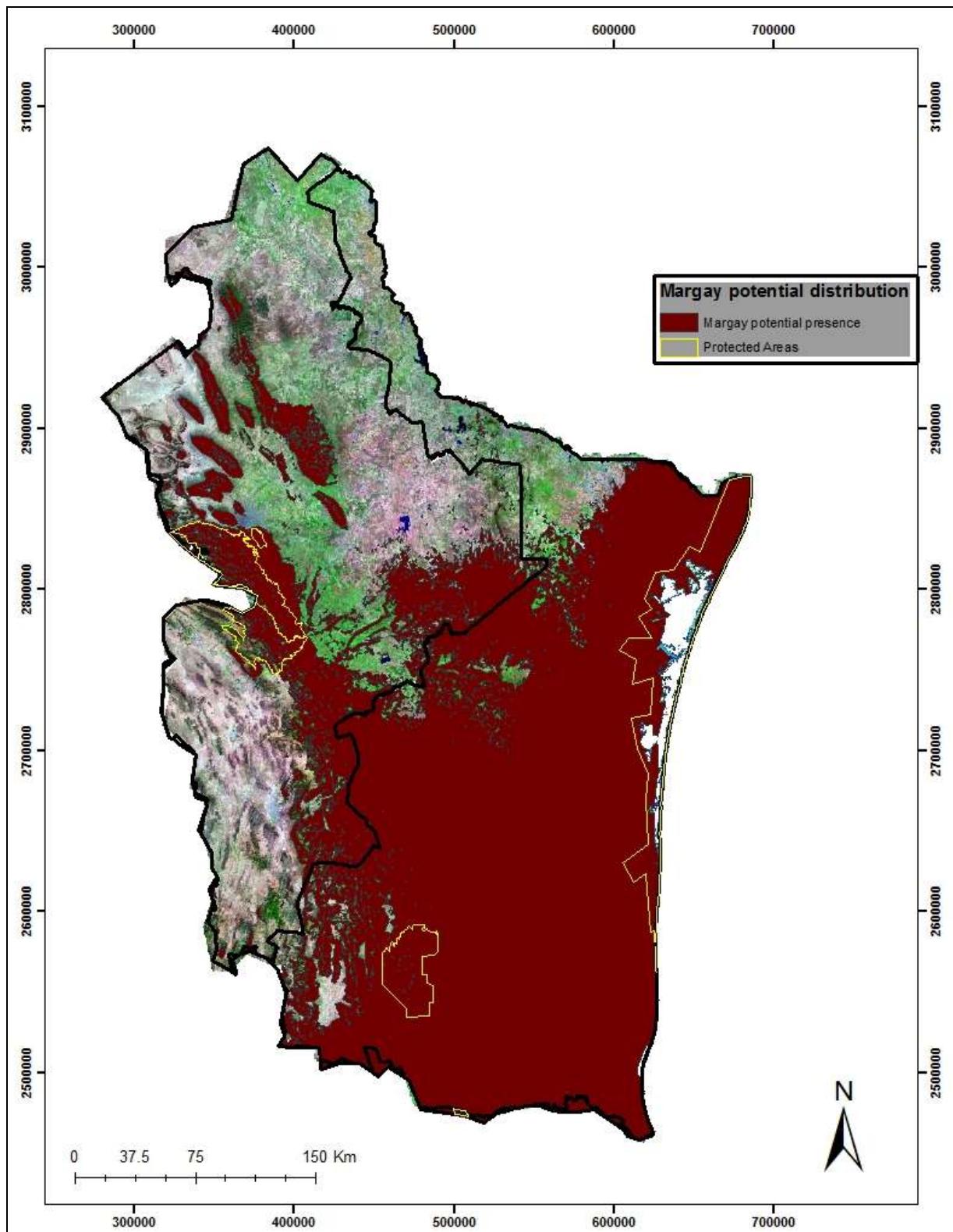


Figure 39. Potential margay distribution model in Nuevo León and Tamaulipas, northeastern Mexico.

Table 21. Area of potential distribution and percentage of cover types for margay in Nuevo Leon and Tamaulipas, northeastern Mexico.

Cover layer	Area of potential distribution (km ²)	% available in the range
Water	2,005	1.71
Forest	67,638	57.60
Disturbed areas	15,229	12.97
Mosaic shrublands and grasslands	32,557	27.73
Total	117,428	—

Table 22. Area and percentage of the potential distribution of margay (117,428 km²) in the protected areas of Nuevo Leon and Tamaulipas, northeastern Mexico.

Name	Category	Protected range km ²	Percent of species area
Cerro de la Silla	Natural Monument	60	0.05
Parque Nacional Cumbres of Monterrey	Natural Protected Area	1,614	1.37
Laguna Madre and Rio Bravo Delta	Flora and Fauna Protection Area	3,682	3.13
El Cielo	Biosphere Reserve	1,412	1.20
Total	—	6,768	5.76

distributed in almost all of the Sierra Tamaulipas, and through the southwest to the SMO. The northern margay distribution begins in El Cielo Biosphere Reserve and continues south following the SMO (Figure 40).

Species Richness Map

The species richness map of wild cats shows that six felids are present along several mountain ranges, in Nuevo Leon and Tamaulipas. Less species richness occurs in southwestern Nuevo Leon and northwestern Tamaulipas where only three wild cat species could be present (Figure 41).

DISCUSSION

A review of the literature indicates that the distribution of jaguar, ocelot, jaguarundi, and margay varies considerably by study. The northern distribution of these species has been reduced during the past 10 years (Sanderson *et al.*, 2002), primarily related to anthropogenic factors (Koford, 1973; Tewes & Schmidly, 1987; Sunquist & Sunquist, 2002; Caso, 2007; Caso *et al.*, 2008). However, details of distribution changes in northeastern Mexico have not been identified.

Jaguar

There is more information about jaguar range and distribution than for any other American felid (Sanderson *et al.*, 2002; Galvan, 2009; Grigione *et al.*, 2009; Rabinowitz & Zeller, 2010; Rodriguez-Soto *et al.*, 2011). Historically, the jaguar in Mexico occupied both coastal lowlands (Leopold, 1959). These ranges converge on the Tehuantepec Isthmus and extend south to Central America (Leopold, 1959). However, previous studies have produced errors. For example, Leopold (1959) excluded Nuevo Leon from the northeastern range, whereas Rosas-Rosas & Lopez-Soto (2002) documented jaguar in this State. Additionally

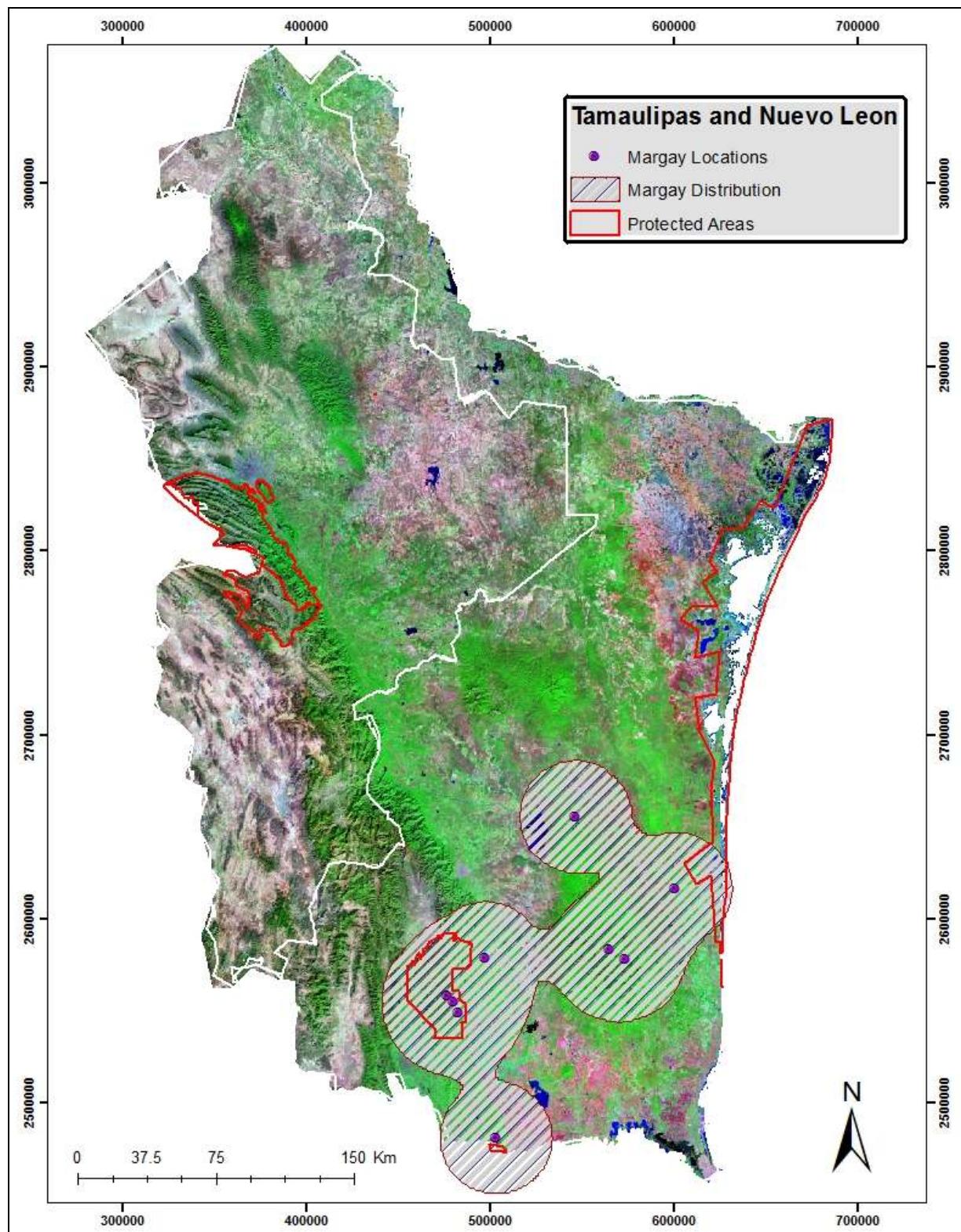


Figure 40. Margay distribution using the Adaptive Kernel Range Estimator Model in Nuevo Leon and Tamaulipas, northeastern Mexico.

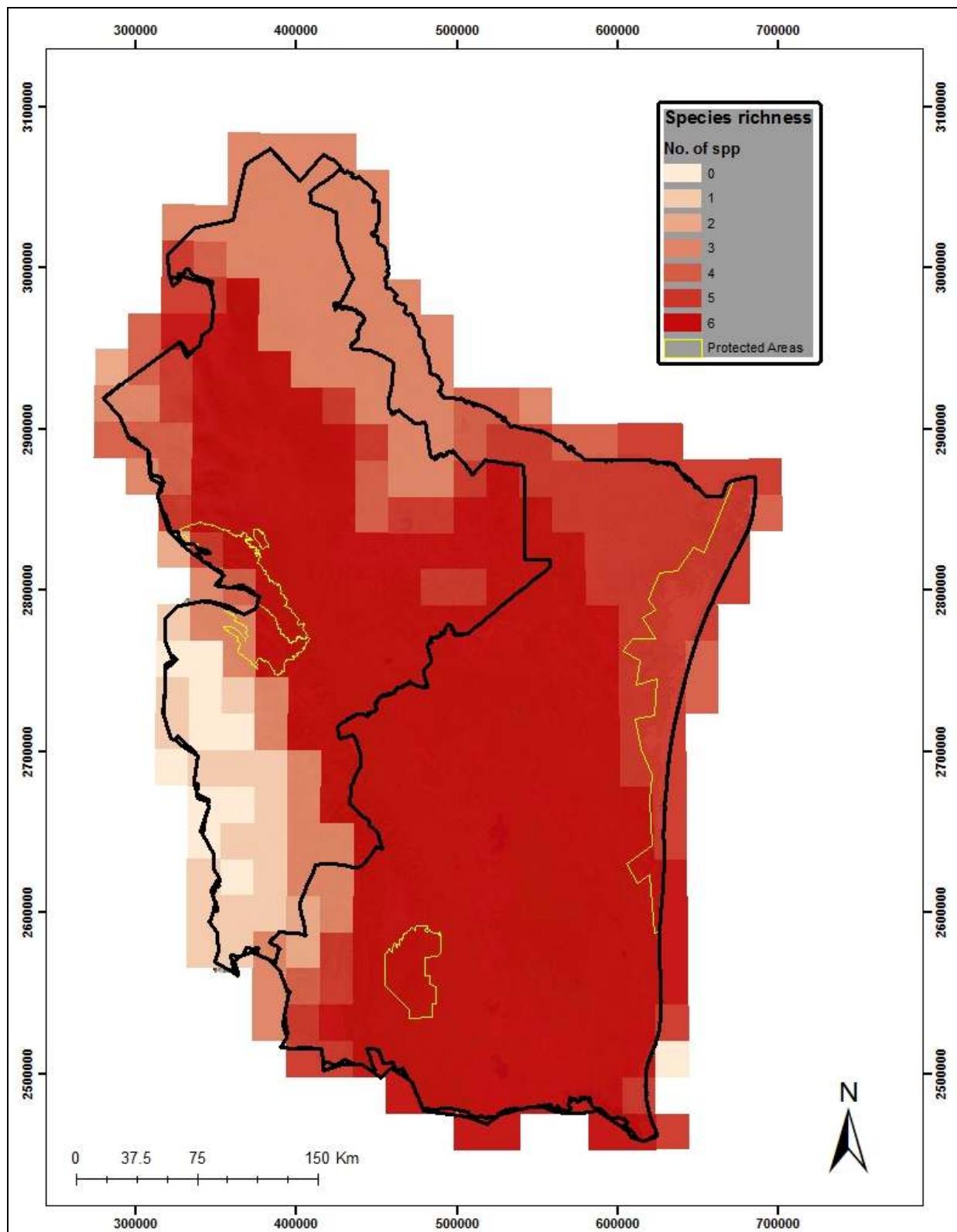


Figure 41. Feline species richness map of 6 wild cats species in Nuevo Leon and Tamaulipas, northeastern Mexico.

Hall (1981) stated that the northeastern jaguar range included Coahuila, Nuevo Leon, and Tamaulipas. Ceballos & Oliva (2005) mentioned jaguar records in Coahuila, Nuevo Leon, and Tamaulipas; however, the date of these records is unknown, which is a similar for observations recorded by Hall (1981) and Villa & Cervantes (2002). Sunquist & Sunquist (2002) recorded the northeastern distribution limited of jaguars in the SMO, including Nuevo Leon and Tamaulipas.

Jaguar distribution is similar to the distribution reported by the IUCN Cat Specialist Working Group (Caso *et al.*, 2008). Grigione *et al.* (2009) recorded six locations for jaguar: five Class I locations, and 1 Class II location. These locations represent a small sample size compared to this study (17 records; 16 Class I and 1 Class II). Grigione *et al.* (2009) also recommended the SMO, the Sierra Maratinez and the Sierra Tamaulipas as priority conservation areas.

This study suggests that the SMO in Nuevo Leon and Tamaulipas is part of the jaguar distribution, similar to conclusions reported by Sunquist & Sunquist (2002) and Rosas–Rosas & Lopez–Soto (2002). Nuevo Leon also was included as part of jaguar distribution by other studies (Caso *et al.*, 2008; Grigione *et al.*, 2009; Figure 34). Additionally, the Sierra Tamaulipas, Sierra Maratinez, and areas south along the Gulf Coast are included within the jaguar distribution, similar to conclusions reported by Caso *et al.* (2008) and Grigione *et al.* (2009). These areas were recommended for jaguar conservation, in addition to the Sierra Picachos in Nuevo Leon where a previous survey failed to document jaguar or ocelot presence (Tewes *et al.*, 2009). I documented 16 jaguar records for Nuevo Leon in the central and southern portions of the SMO (Figure 34). No jaguar records were found in the northern part of Nuevo Leon.

I used the Maxent Model to determine the potential species distribution model (SDM). The Maxnet model was one of several models used by Rodriguez–Soto *et al.* (2011) to determine the potential distribution of jaguar in Mexico. Rodriguez–Soto *et al.* (2011) employed Ecological Niche Factor Analysis, Mahalanobis Distance (MD), and the Ensemble Model (which is a union of the three models). Their results indicate that the Maxent Model was more efficient and conservative than the other models. They consider jaguar presence in Mexico principally associated with tropical rain forests, high prey richness, and non–fragmented vegetation. They also found avoidance of arid vegetation, high elevation, and grasslands.

Other studies note that the jaguar has high ecological plasticity because some individuals occur in semi–desert areas of southwestern Arizona (McCain & Childs, 2008), and at elevations above 1200 m in Arizona and other parts of Mexico (Brown & Lopez–Gonzalez, 2001; Hatten *et al.*, 2005; Monroy–Vilchis *et al.*, 2008). These observations are similar to my results regarding the potential distribution for jaguar in Tamaulipas and Nuevo Leon; however, there is more agreement of my results with the results of Rodriguez–Soto *et al.* (2011) and the conservative Maxenet Model. The discrepancy between distributions may be related to different interpretations between models, as seen in my results for the Sierra Picachos in Nuevo Leon, Sierra San Carlos in Tamaulipas, and other areas of northwestern Tamaulipas. These areas are included as potential areas for jaguar presence; however, previous field surveys have not documented any recent Class I records of jaguars in these areas. These areas have fragmented vegetation, semi–arid habitat, high elevation, and extensive areas with grassland or absence of natural vegetation (i.e., agriculture lands) which jaguars tend to avoid. Consequently, the probability of jaguar presence is low in these areas and there are other areas better suited for jaguar conservation.

Based on the results of this study and jaguar distributions described in the literature (Grigione *et al.*, 2009; Rabinowitz & Zeller 2010; Rodriguez-Soto *et al.*, 2011), I consider the SMO in Nuevo Leon and Tamaulipas, and the Sierra Tamaulipas as part of jaguar distribution. The Sierra Maratinez and the coastal area of Tamaulipas should be priority areas for jaguar conservation. This conclusion is supported by my results in Chapter I where jaguar density seemed to be higher in these areas. Therefore, biologists should monitor changes in the jaguar population and potential threats such as poaching, cattle depredation, and habitat loss.

I also recommend surveying other areas more intensively in northern Nuevo Leon and Tamaulipas. Security problems in northeastern Mexico may have created conditions for increased jaguar occupancy in many areas of Nuevo Leon and Tamaulipas, possibly enhancing jaguar distribution. In the past, the jaguar was common in these areas, but agriculture, cattle production and illegal hunting negatively impacted jaguar. However, many of these rural activities have declined because of the dangerous situation related to the illegal drug cartel. Over recent years there have been multiple jaguar reports in these areas, suggesting jaguar are returning to their original distribution.

Ocelot

Ocelots were not as well studied as jaguar until recent camera-trapping methods became more reliable. In this study, I used Class I reports with camera-trapping, permitted live trapping and other records such as historic photographs. This information about ocelot distribution in northeastern Mexico differs from previous literature.

Historically, the ocelot was reported from eastern and central Texas through Central and South America into northern Argentina (Tewes & Everett 1986; Tewes & Schmidly 1987; Caso, 1994). Leopold (1959) and Sunquist & Sunquist (2002) considered

Tamaulipas as the northeastern range limit for ocelot; however, Nuevo Leon was excluded from this distribution. Conversely, Villa & Cervantes (2002), and Ceballos & Oliva (2005) considered northern Coahuila as the northeastern limit for ocelots and included most of Nuevo Leon and Tamaulipas. Grigione *et al.* (2009) recorded seven Class I records for Tamaulipas and none for Nuevo Leon. Grigione *et al.* (2009) considered the SMO in Nuevo Leon, Sierra Tamaulipas, the Gulf coastal lowlands, and Rio Bravo Delta protected area as priority conservation areas for ocelot. I consider this distribution inaccurate because there is no information that supports an ocelot linkage between Nuevo Leon and Coahuila. This information was based primarily on vegetation analysis without field verification of the habitat types available.

Martinez–Calderas (2009) used 10 ocelot records to determine the northeastern ocelot distribution in Tamaulipas and excluded Nuevo Leon. Martínez–Calderas (2009) included San Luis Potosi; however, this state is not considered geographically part of northeastern Mexico by the Instituto Nacional de Estadística, Geografía e Informática (INEGI, 1999). The INEGI considered northeastern Mexico as consisting of Coahuila, Nuevo Leon, and Tamaulipas. Martínez–Calderas (2009) also used a discriminatory model to evaluate optimal areas for ocelot presence and considered Nuevo Laredo, Guerrero, and Mier counties in Tamaulipas as potential areas for ocelot presence. Caso (2007) evaluated different properties in the area and found bobcat and puma presence but did not document ocelot presence. Martínez–Calderas (2009) mentioned the El Cielo Biosphere Reserve was an optimal area for ocelot presence but did not report any Class I records. In El Cielo Biosphere Reserve where Carvajal *et al.* (2012) studied margay in with box traps and hair traps (Downey *et al.*, 2007), no sign of ocelot were found.

Potential distribution for ocelot in this study includes northeastern Mexico, covering almost all of Nuevo Leon and Tamaulipas, with the exception of central and southwestern Nuevo Leon and northeast Tamaulipas. However, I only obtained one ocelot record (from accidental trapping) in the SMO in Nuevo Leon. Although Grigione *et al.* (2009) proposed the Sierra Picachos and Maderas del Carmen (a protected area in Coahuila) as possible corridors and “hot spots” for ocelot, I do not consider these areas important because of the lack of adequate vegetation for ocelots. Tewes *et al.* (2008) did not document ocelots in the Sierra Picachos of northern Nuevo Leon.

In Coahuila, the only report of ocelot is from Leopold (1959) in Ocampo County, but this information was an isolated record. Leopold (1959) did not include this report in the distribution for the species. For these reasons, the model used for estimating the potential distribution of ocelot could be an overestimation, even though this distribution is similar to the distribution suggested by Ceballos & Oliva (2005). This is further supported by the AKRE method results for ocelot distribution where ocelot occurrence in Nuevo Leon is restricted south of the SMO. The northernmost ocelot record in Tamaulipas is at the same latitude as the northern most record for Nuevo Leon ($25^{\circ} 23' 59.47''$ N), and all of the eastern portions of Tamaulipas, including the Sierra Tamaulipas, Sierra Maratinez, and south of the Laguna Madre and the Rio Bravo Delta Federal Protected Area. Thus, the potential distribution model and actual distribution for ocelot in this study do not completely coincide.

I recommend surveys for potential sites for ocelots such as the southern SMO in Nuevo Leon and Tamaulipas, including the El Cielo Biosphere Reserve, and the southern portion of Tamaulipas. Future models to establish potential ocelot distribution should use detailed maps of vegetation type and cover.

Jaguarundi

The jaguarundi is one of the least ecologically studied wild cats in Mexico and in the Western Hemisphere. Jaguarundi distribution also is largely unknown (Tewes & Everett, 1986). Ecological information on the jaguarundi sub-species (*P. y. cacomitli*) in Nuevo Leon and Tamaulipas is scant, with only Caso (2013) documenting the home range and activity patterns of a population in southeastern Tamaulipas. Distribution reports for this species occur in Nuevo Leon (Moreno-Valdes, 1998), and only three field studies have been conducted in Mexico on jaguarundi (Carvajal *et al.*, 2012; Caso, 2013; Peña J., 2004).

Jaguarundi distribution proposed in this study does not coincide with what has been reported in the literature for northeastern Mexico. Leopold (1959) noted jaguarundi distribution in Mexico from the Tamaulipan coastal lowlands to the Yucatan Peninsula, with some reports along the Pacific Coast within tropical areas. Nuevo Leon was not included in the range reported by Leopold (1959); however, Villa & Cervantes (2002) and Ceballos & Oliva (2005) included all of Tamaulipas and most of Nuevo Leon with the exception of the areas that border Coahuila as jaguarundi distribution. However, records from this study indicate that Nuevo Leon is part of the distribution for this felid. Additionally, the northern distribution limit is located within the SMO, including the protected area Parque Nacional Cumbres de Monterrey and the Cerro de La Silla. These reports do not coincide with the range reported by Leopold (1959).

Villa & Cervantes (2002) show that jaguarundi occur over most of Tamaulipas and Nuevo Leon, contrary to my results. I maintain that jaguarundi distribution for Nuevo Leon is limited to areas within the SMO. In Tamaulipas, jaguarundi distribution is reported (Chapter II, this dissertation) for the Sierra Tamaulipas, the Río Bravo Laguna Madre Natural Protected Area, and part of Sierra San Carlos, but excluding El Cielo Biosphere

Reserve (Figure 8). Results obtained in my study coincide with the IUCN distribution (Caso *et al.*, 2008). However, Caso *et al.* (2008) considered the distribution between Tamaulipas and Nuevo Leon continuous with a corridor along the SMO shared by Tamaulipas and Nuevo Leon.

The distribution model for jaguarundi in this study coincides with the range reported by Tewes & Everett (1986) and Villa & Cervantes (2002). However, the distribution of this study differs partially with the distribution models reported by Grigione *et al.* (2009) that include all of the mountainous areas for both states, such as Sierra Bustamante, Sierra Picachos, and the SMO in Nuevo Leon. In Tamaulipas, the potential jaguarundi distribution includes all of the state with the exception of the northeastern part where the highly developed Rio Bravo occurs. Grigione *et al.* (2009) reported the historical distribution of jaguarundi as Tamaulipas, Nuevo Leon, and Coahuila; however, this conclusion is not supported by other studies (Leopold, 1959; Tewes & Everett, 1986; Ceballos & Oliva, 2005). Grigione *et al.* (2009) proposed conservation areas for jaguarundi throughout the distribution described by the IUCN (Caso *et al.*, 2008), which includes some northwestern areas in Coahuila and Big Bend National Park in western Texas where jaguarundi have never been confirmed. Consequently, I do not consider Coahuila a priority area. Additionally, Grigione *et al.* (2009) used Class III records that have many false reports (Tewes & Everett, 1986).

Margay

The margay is one of the least known wild cat species in the Western Hemisphere (Nowell & Jackson, 1996). No information about the distribution of this felid is found for Mexico, and only two margay ecology studies are available. Konecny (1989) studied one margay in Belize and Carvajal *et al.* (2012) studied eight margays in Tamaulipas, Mexico.

One margay record was recorded from the United States in 1852 near Eagle Pass, Texas; however, the United States is not considered part of margay distribution (Leopold, 1959).

Some studies place the northeastern range limit for margay as the El Cielo Biosphere Reserve (Payan *et al.*, 2008); however, Ceballos & Oliva (2005) include Nuevo Leon and a portion of Coahuila within margay distribution. I disagree with Ceballos & Oliva (2005) because there are no published records of margay in these states. Also, the one record from Texas in 1852 may have been an individual that escaped from captivity or was released in this area (Leopold, 1959). Furthermore, the Class I records that I obtained were located within Tamaulipas. The most reliable margay range is reported by Payan *et al.* (2008) for the IUCN Red List. Payan *et al.* (2008) does not mention margay as part of the carnivore community for Nuevo Leon. In this study, I propose the northern distribution limit for margay is the Sierra Tamaulipas based on one Class I record from camera trapping.

Sanchez-Cordero *et al.* (2008) report margay distribution similar to my results; however, much of the information used by Sanchez-Cordero *et al.* (2008) is old and thus the current distribution may be different because many of the areas that were surveyed do not currently have suitable habitat. A potential area for margay occurrence are the mountainous areas of Nuevo Leon (Figure 39); however, there have been no documented records in this state. Margay potential distribution in Tamaulipas is likely overestimated because the potential distribution model reports most of the state as suitable for margay presence. However, based on recent surveys many areas in northern Tamaulipas have no records of margay and the vegetation is considered unsuitable. Sunquist & Sunquist (2002) reported tropical forest and cloud forests as the most suitable habitats for margays;

however, in northern Tamaulipas margay habitat is considered Tamaulipan thornshrub (Rzedowski, 2006). It is unlikely that margays are found in northern Tamaulipas.

Conservation Importance

The tropical ecosystems and mountainous areas of northeastern Mexico represent important conservation areas for neotropical felids such as jaguar, ocelot, jaguarundi, and margay. The information from this study confirms that northeastern Mexico is the northeastern distribution limit for these species, with the exception of the ocelot that still occurs in southern Texas (Tewes & Everett, 1986; Sunquist & Sunquist, 2000). Thus, northeastern Mexico should be a conservation priority area for many carnivores particularly because some habitat modifications and anthropogenic activities may cause disturbances which can affect the distribution of these species.

Information from this study will assist managers in identifying new priority areas for conservation that were previously considered unimportant. For example, Nuevo Leon was previously considered an unimportant area for jaguar conservation; however, I believe it is an important area for conservation because it represents the northeastern distribution limit, and is linked to a subpopulation that is part of the jaguar metapopulations in Tamaulipas. This study also highlights new occupied areas in coastal Tamaulipas where jaguars were believed extirpated. This coastal area includes recent records in Soto la Marina County.

Although no recent ocelot reports exist for the southern regions of the SMO and in northwestern Tamaulipas, I was able to confirm ocelot distribution in these areas. I identified priority areas such as the Sierra Tamaulipas that should be considered as a potential ocelot source for translocation from Tamaulipas to Texas.

Ocelots also may be present in other areas such as Mendez County. However, there are no recent confirmed reports from this area. If there is a population of ocelots in Mendez, it may suggest connectivity with ocelot populations in San Fernando.

A biologist for the USFWS (Mitch Sternberg pers. com.) suggests that connectivity exists between ocelot populations in Mexico and Texas through the Sierra Picachos of Nuevo Leon; however, a survey completed in 2008 (Tewes *et al.*, 2009) did not find evidence of ocelot presence. Because this survey was for a short period, future surveys should be conducted in this area to clarify ocelot presence or absence.

The most northeastern limit for jaguarundi in this study area was similar to the distribution of other cats, with two Class I reports close to Monterrey, Mexico. However, the AKERM indicates a gap between the jaguarundi population in Tamaulipas and Nuevo Leon, whereas the literature reports the distribution as continuous. This gap may be attributed to inadequate field surveys in the area. I recommend a greater field effort to determine if the jaguarundi population in Nuevo Leon is isolated from the population in Tamaulipas.

Monitoring near the current margay distribution should be conducted to refine margay distribution. Margay populations do not appear to be abundant in northeastern Mexico with the exception of the population at El Cielo Biosphere Reserve. One margay was photographed during 15,368 camera trap–nights on Caracol Ranch. It is difficult to find distribution records for margay because of their low densities, nocturnal and arboreal habits, and the difficulty to identify this species in the wild. Margay are often confused with the similar, yet larger, ocelot.

Distribution maps from this study for jaguar, ocelot, jaguarundi, and margay represent an important tool for understanding the historical and contemporary distribution

for these felids. I have documented records for ocelot and margay outside the previous known distribution for these species. Jaguarundi also may be present in some areas that are included in the potential distribution map.

Jaguars use arid areas such as Sonora and Arizona, which exhibit habitat structure similar to northern Nuevo Leon. Also, there are recent records of jaguars where they were previously believed to be extirpated, such as in coastal Tamaulipas. These new records may be attributed to recent national security problems regarding drug violence in Tamaulipas, where many cattle ranches have been abandoned, habitat and prey have recovered, and dispersing jaguars appear to have reoccupied these areas. If this is a valid interpretation then the security problems in northeastern Mexico have contributed to the expansion the distribution of the jaguar and likely other cat species.

The information gathered in this study should be used by local and federal authorities so that protected areas may be designated and better managed for the conservation of these feline species. Additionally, this information may be shared with the scientific community to guide research for northeastern Mexico. The Red List of the IUCN is currently being update for the global ranges of these species, and these results should contribute to more precise delineation of these ranges.

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- M.S. in Biology Sciences. Instituto Tecnologico de Ciudad Victoria, August 2001 – 2004. Thesis: Home range and activity patterns of the margay (*Leopardus wiedii*) in the Biosphere Reserve “El Cielo”, Tamaulipas, Mexico.
- B.S. Biology. Facultad de Ciencias Biologicas, Universidad Autonoma de Nuevo Leon, August 1993 – 2000. Facultad de Biologia: Thesis: Autumn diet of the coyote (*Canis latrans*) in the San Jose Ranch, Anahuac, Nuevo Leon, Mexico.

WORK EXPERIENCE

- Ecological Park Chipinque A. C. 1999 – 2001. Coordinator of the Dept. Research and Wildlife.
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WORKSHOPS

- Course, SAFE CATURE. Chemical Immobilization of Animals. 16 hours. 8 May 2010.
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GRANTS RECEIVED

- Gladys Porter Zoo. 2004. Margay research at “El Cielo” Biosphere Reserve. 4,000 USD.
- Comisión Nacional de Areas Naturales Protegidas. 2005. Black Bear Survey. 20,000 USD.
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- ALCOA. 2007. Conservation of the bats in the La Boca Cave. 3,000 USD.
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SCIENTIFIC MEETINGS

- Carvajal-Villarreal S., A. Caso and M. E. Tewes. 2012. Ocelot population estimation using remote-sensing cameras in the Sierra of Tamaulipas. 48th Texas Chapter of the Wildlife Society Meetings. Fort Worth, Texas.**

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