Population density and daily activity patterns of bobcat in its southernmost continental distribution

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Abstract
Population density and daily activity patterns of bobcat in its southernmost continental distribution. Estimating density and activity patterns is useful for management and conservation of species. Data for Mexican bobcat (*Lynx rufus*) populations are scarce. Here we estimated the density of a bobcat population in Oaxaca, southern Mexico, and evaluated its daily activity patterns. We also evaluated macroecological patterns of bobcat density across its distribution range to determine any geographical (latitudinal, longitudinal, elevation, or range centroid) or climatic effects on the population density. Camera–trap data were divided into four 60–day periods (two in the dry season and two in the rainy season). Density was calculated using the random encounter model and daily activity patterns were analyzed fitting a kernel density function. The mean estimated density for the four periods was 17.3 bobcats/100 km^2, with the highest densities occurring during the dry periods. Bobcat daily activity pattern presented two peaks, one after midnight and the other after dawn, with very slight changes between seasons. In the study area, density and activity patterns were associated with anthropogenic perturbation and prey availability. Bobcats increased their population density in the dry season, and showed a preference for activity at night and early morning hours when it is cooler and there are likely fewer competitors but more prey. Across its range, bobcat density was mainly related to annual precipitation and mean temperature of the driest quarter at 100 km radius buffers, and between annual precipitation and longitude on a smaller scale (50 km radius buffers). These findings support their preference for the arid or mesic environments that enabled them to reach southern areas of the Neartic region.

Key words: Camera–trap, *Lynx rufus*, Mesocarnivore, Oaxaca, Random Encounter Model

Resumen
Densidad demográfica y patrones de actividad diaria del gato montés en su área de distribución más meridional del continente. La estimación de la densidad demográfica y de los patrones de actividad diaria es útil para el manejo y la conservación de las especies. Los datos disponibles en relación con las poblaciones mexicanas de gato montés (*Lynx rufus*) son escasos. Los objetivos de este trabajo fueron estimar la densidad de una población de gato montés y evaluar sus patrones de actividad diaria en Oaxaca, al sur de México. Asimismo, evaluamos patrones macroecológicos de la densidad del gato montés a lo largo de su área de distribución para comprobar si existe algún efecto geográfico (latitud, longitud, elevación y centroide de su área de distribución) o climático en la densidad de la población. Los datos recabados mediante fototrampeo se agruparon en cuatro períodos de 60 días (dos en la estación seca y dos en la estación lluviosa). La densidad se calculó mediante un modelo de encuentros aleatorios y los patrones de actividad diaria se analizaron mediante ajustes de modelos Kernel. La densidad media estimada de los cuatro períodos fue de 17,3 gatos montés/100 km^2, con las densidades más altas en las estaciones secas. El patrón de actividad diaria presentó dos picos: uno después de la medianoche y otro después del amanecer, con ligeros cambios entre temporadas. En la zona del estudio, la densidad y los patrones de actividad podrían estar relacionados con la perturbación antropogénica y la disponibilidad de presas. En la estación seca, la población aumentó y los gatos montés prefirieron estar activos durante la noche y la madrugada, cuando la temperatura es más fresca y tienen menos competidores y más presas. En su área de distribución, la densidad del gato montés

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está ligada principalmente a la precipitación anual y a la temperatura media del cuarto trimestre más seco en un radio de 100 km, y entre la precipitación anual y la longitud a una escala menor (radio de 50 km), lo que respalda el hecho de que el gato montés prefiere ambientes áridos o mésicos, que le permitan llegar a las zonas más meridionales de la región neártica.

Palabras clave: Cámara trampa, *Lynx rufus*, Mesocarnívoro, Oaxaca, Modelo de conteo aleatorio

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Introduction

Estimating the number of individuals in an area (population density) is useful to calculate the size of a population, and to promote management and conservation actions (Lawton, 1993; Mills, 2012). Patterns of mammal densities have shown that intrinsic factors, such as body mass and trophic level, can explain the population size of species. For example, large–bodied species, species with strictly carnivorous diets, and species at higher trophic levels occur at lower densities, whereas species with generalist diets and small body size have higher densities (Robinson and Redford, 1986; Fa and Purvis, 1997). In addition, density appears to be correlated with the size of the distribution range (density–range relation; Blackburn et al., 1997; Komonen et al., 2013) as it has been observed that population densities decline gradually toward the range boundaries (centroid distance–abundance relation; Brown, 1984). Among the extrinsic factors explaining density, body size and over–exploitation such as hunting are probably the causes of some small populations, making species more susceptible to local extinction (Lawton, 1994; Cardillo et al., 2005). In association with density estimates, the study of activity patterns sheds light on the circadian rhythms of animals, and the factors influencing them (Ridout and Linkie, 2009; Nouvellet et al., 2012; Rowcliffe et al., 2014; Frey et al., 2017; Sollmann, 2018).

At the intraspecific level, depending on sex and age, individuals use their diurnal and nocturnal time differently (Di Bitetti et al., 2006; Biggerstaff et al., 2017; Stone et al., 2018). The most widely studied temporal segregation has likely been investigated at an interspecific level, that is, for two or more species such as in predator–prey systems (Harmsen et al., 2011; Linkie and Ridout, 2011; Monterroso et al., 2013; Ross et al., 2013; Porfirio et al., 2016) or to evaluate competition between species of the same guild (e.g. Harmsen et al., 2009; Lucherini et al., 2009; Dröge et al., 2017). For management purposes, it is useful to determine species' peaks of activity when planning to monitor a species (Jarnemo et al., 2017; Lavariega et al., 2019).

Camera–traps are a convenient means to record species with minimal interference (O'Connell et al., 2011). Early population studies using this approach focused on naturally marked animals, which in association with capture–recapture models provided the possibility to estimate abundances and densities (Karanth, 1995; Silver et al., 2004; Trolle and Kéry, 2003; Jackson et al., 2006). Nowadays, advances in the technology of camera–traps (e.g. delay time, resolution, and storage capability) have allowed advances in analytical approaches, improving population estimates for a wide range of species (Sollmann, 2018). For example, most recent mathematical models to estimate density have been developed for animals with few or no natural marks (Nakashima et al., 2018; Jimenez et al., 2019; Murphy et al., 2019). The Random Encounter Model (REM) is in the group of models for unmarked individuals calculates population density based on the encounter rate between camera–traps and animals, the velocity of movement of focal species, the sampling effort, and the detection angle of the devices (Rowcliffe et al., 2008). REM has been applied to estimate population density of Harvey's duiker (*Cephalophus harveyi*; Rovero and Marshall, 2009), European pine marten (*Martes martes*; Manzo et al., 2012), and Baird's tapir (*Tapirella bairdii*; Carbajal–Borjes et al., 2014; Lavariega et al., 2016), providing adequate estimates such as capture–recapture methods.

Camera–trapping studies aiming to obtain information on abundance, density, and activity patterns have been mainly focused on large–sized mammals, whereas medium–sized species have been largely overlooked throughout their range (O'Connell et al., 2011). This is the case of the bobcat (*Lynx rufus*). Bobcat populations have been widely studied in the USA for many years, with estimates ranging from 3 to 48 indiv./100 km^2 (Thornton and Pekins, 2015). The total population size has been estimated at 1,419,333 to 2,638,738 individuals, indicating that the bobcat population is stable in this country (Roberts and Crimmins, 2010). However, data on population size and densities in Mexico are scarce, precluding comparisons of regional variations and trends for the species (CITES, 2009). To date, Medellín and Bárcenas (2010) have evaluated the density of bobcat in six localities across Mexico, with estimates varying from 5 to 53 indiv./100 km^2 in four localities. López–González et al. (2015) estimated a minimum density of 17 indiv./100 km^2 for El Cimatario National Park in central Mexico and suggested that the lower densities found are due to the higher rates of habitat loss and urbanization. More recently, Greenspan et al. (2020) estimated a bobcat density of 16/100 km^2 in a private ranching area in Sonora at north of Mexico, and Vega–Flores and Farías–González (2021) estimated a population density of 15 indiv./100 km^2 in the Tehuacán–Cuicatlán Biosphere Reserve in the state of Puebla in the border with Oaxaca. However, density estimates for the southernmost limit of the bobcat's range in Mexico are lacking.

Regarding the activity patterns of bobcat, many authors report that the species is cathemeral, but activity peaks occur at crepuscule in response to environmental factors (Witmer and Decalesta, 1986; Bradley and Fagre, 1988; Neale and Sacks, 2001; Harrison, 2010; Rockhill et al., 2013; Symmank et al., 2014; Farías et al., 2015; Serna–Lagunes et al., 2019a). Most studies on bobcats in Mexico consist of reports concerning their presence (Bárcenas and Medellín, 2007; Valenzuela–Galván et al., 2013; Elizalde–Arellano et al., 2014; Ramírez–Albores et al., 2014; Sosa–Guerrero et al., 2017; Monterrubio–Rico et al., 2019), whereas studies on their ecology, such as feeding habits (Delibes et al., 1997; Aranda et al., 2002; Islas and Ceballos, 2018), competition (Sánchez–Cordero et al., 2008; Flores–Morales et al., 2019; Serna–Lagunes et al., 2019a), and population estimates (Medellín and Bárcenas, 2010; López–González et al., 2015; Vega–Flores and Farías–González, 2021) are scarce.

This scarcity of general information further limits macroecology analyses. For instance, Thornton and Pekins (2015) found a longitudinal and climatic relation with the densities of bobcat in USA, but they were concerned about the need to include data regarding southern estimates. Using ecological niche modeling with presence data only, Loveless et al. (2016) found that seasonal climatic variables are relevant to predict habitat suitability of bobcat, and Pérez–Irineo et al. (2019) found a positive relation between bobcat densities and distance to the climatic niche centroid rather than a relationship with habitat suitability.

Here we aimed to expand the analyses of Thornton and Perkins (2015) by testing for a latitudinal effect, plus geographic and climatic relations of densities including density estimates for Mexico. It has been observed that bobcat densities are lower in central and southern Mexico than in the north of the country (Kelly et al., 2016). We estimated the population density of bobcat and evaluated its daily activity patterns in the southernmost limit of their current distribution in North America in order to test the latitudinal effect and geographic and climatic relations. We hypothesized that the density and the daily activity patterns could be affected by stochastic climatic variables, with differences between seasons as a response to the changing conditions of the environment (e.g. availability of resources, hours of light, and temperature). Thus, we predicted that bobcat population densities in the southern portion of their distribution would be lower than in the north due to its larger longitudinal space (cone shape effect; Sánchez–Cordero et al., 2008) and because bobcat populations in Mexico are far from the centroid of their range (Brown, 1984). Bobcat subspecies in Mexico are smaller than those in the USA (Loveless et al., 2016), and they consequently have greater densities (Robinson and Redford, 1986; Fa and Purvis, 1997; Vega–Flores and Farías–González, 2021). We considered that their daily activity patterns would be higher in the dry season than in the rainy season because they would spend more time hunting and searching for water.

Material and methods

Study site

The study was performed in the Municipality of Cosoltepec, Oaxaca, Mexico, on the borders with the Puebla State (18º 8' 13.08'' N and 97º 47' 26.16'' W; fig. 1). The area is characterized by mountains with an elevational range from 1,600 to 1,800 m a.s.l., a semi–warm and semi–humid climate, a rainy season in the summer (May–September), and a dry season in the winter (October–April). The average annual precipitation is 800 mm and the annual average temperature is 18–22 ºC (maximum 40 ºC and minimum 4 ºC). The landscape is composed of a matrix of grazing areas, temporary crops, patches of crasicaule scrubland, deciduous forest, and secondary vegetation (INEGI, 2008; Guizar, 2011).

Camera–trap survey

From December 2013 to September 2014 we deployed 14 camera–traps (Cuddeback ® models Capture and Expert) in a grid, covering 19.7 km^2 (fig. 1). The distance between camera–traps was approximately 1.5 km, considering the average home range of a bobcat (11.54 km^2) in Oaxaca, Mexico (Monroy and Briones–Salas, 2012), and consistent with a travel distance of 1.76 ± 0.41 km recorded in Puebla, close to north Oaxaca (Vega–Flores and Farías–González, 2021). Camera–traps were set 30 cm above the ground, programmed to take photographs only, and to function 24 hrs with a minimum delay time (30 sec). The traps were checked monthly to download information and change batteries. We also recorded the presence of other terrestrial vertebrates.

Data analyses

The camera–trapping survey was divided into four 60–day periods, two in the dry seasons (period one: 31 January to 31 March; period two: 1 April to 30 May) and two in the rainy seasons (period three: 31 May to 29 July; period four: 30 July to 27 September). Periods of 60 days allowed us to comply with the assumption of population closure. We calculated the camera–trap capture rate (CR) for bobcat and for their potential prey for the whole study and for each camera–trap period using the quotient of independent event (IE) and the effort survey (ES) per 1,000 (CR = IE/ES x 1,000; Lira–Torres and Briones–Salas, 2012). An event was considered independent: a) when consecutive photographs of different identifiable individuals appeared; b) when a period of 24 hours passed between photographs, even if it was the same species or individual; and c) when photographs of the same species at the same place were not consecutive (Monroy–Vilchis et al., 2011; Lira–Torres and Briones–Salas, 2012).

To test the variations between dry and rainy seasons in the capture rate, we applied a two–sample test for equality of proportions with continuity correction in R program v. 2.15.0 (R Development Core Team, 2019). To estimate the bobcat density, we used the equation of Rowcliffe et al. (2008):

$$D = (y/t)\ (\pi/vr\ (2+\theta)$$

where D is the density, y/t is the number of photographs per unit time, v is the animal movement, r is the radial distance and θ the angle of detection of cameras. Values of r and θ were taken directly from camera–traps with trials of passing in front of them. We then used the means of 9 m for r and 19° for θ. For v, we used the value of 0.3 km/hr, which was the mean velocity of bobcats recorded throughout GPS radio–tracking in a desert of Chihuahua, northern Mexico (Elizalde–Arellano et al., 2012). To calculate density we used the RandEM package (Caravaggi, 2017) in the R program. According to the photographic records, bobcats were active day and night, so bobcat activity parameters over 24 hrs were used.

Bobcat daily activity was analyzed fitting a kernel density function to quantify overall levels of activity. Using the package Overlap (Meredith and Ridout, 2018) in R program, we used a circular kernel to calculate data. A smoothing parameter of h = 1 was

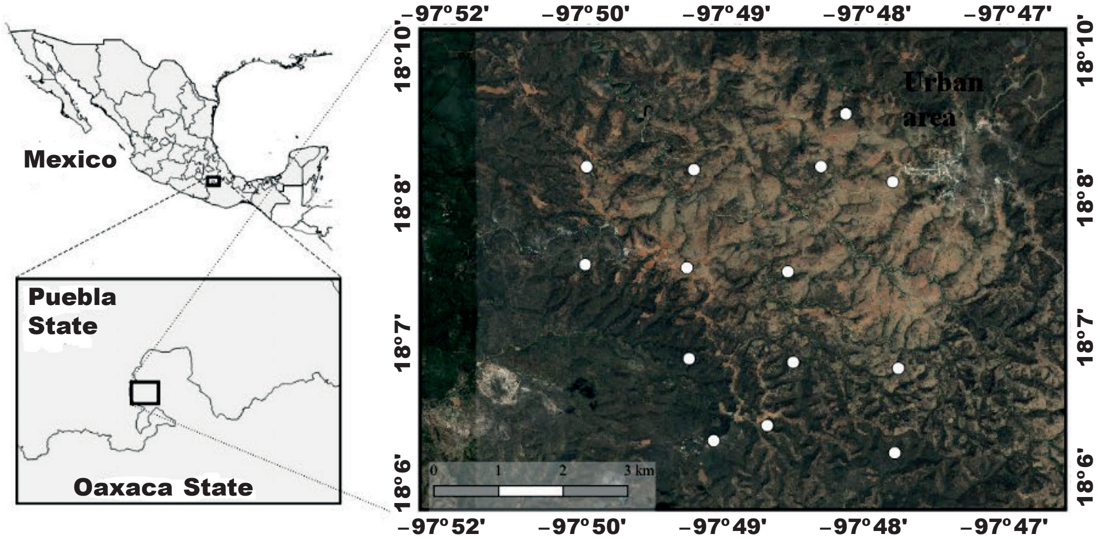

Fig. 1. Study area for the estimate of density of bobcat (*Lynx rufus*) in the Mixteca region, Oaxaca, southern Mexico: the location of camera–trap stations is indicated in white dots.

*Fig. 1. Área de estudio para la estimación de la densidad del gato montés (*Lynx rufus*) en la región Mixteca, en Oaxaca, en el sur de México: las estaciones de cámaras–trampa se indican con círculos blancos.*

selected following the Ridout and Linkie (2009) recommendations for small samples. To compare activity level estimates of bobcat between the dry and rainy seasons, we applied a Wald test on a χ^2 distribution with 1 degree of freedom, in the package Activity (Rowcliffe, 2015) in R program.

Wide range density patterns

Using regression linear models we followed procedures of Thornton and Pekins (2015) to test the relationship of bobcat population density estimates with latitude, longitude, elevation, and bioclimatic variables. To test for a density–range centroid relationship, we used the distance between density studies and range centroid as covariables.

First, we compiled information on methods, locations, and bobcat density estimates from studies cited by Thornton and Pekins (2015). To add estimates from recent studies (> 2015) and to include studies in Mexico, we performed a search in Google Scholar (https://scholar.google.com/), using as keywords: density, bobcat, and *Lynx rufus*, in both Spanish and English. In all cases, for the study areas, we estimated a centroid according to geographic coordinates or maps provided by authors using Google Earth. From every centroid, we obtained the latitude, longitude, and elevation, and applied two buffers to characterize the surroundings, with a radius of 50 km and 100 km, similarly to Thornton and Pekins (2015). Climatic data was retrieved from the WorldClim project (www.worldclim.org; Hijmans et al., 2005), including 19 bioclimatic variables with 30 arcseconds of resolution (~1 km) generated from precipitation and temperature covering a time span of 1950 to 2000. In QGIS (2012), we cut the bioclimatic variables with both buffer polygons 50 km and 100 km. We then calculated the average values of the clipped variables. To test the relationship between density and range centroid, we downloaded a map of geographic distribution of the bobcat from the International Union for Conservation of Nature (IUCN; Kelly et al., 2016). In QGIS (2012), we calculated the geographic centroid, and estimated the distance between density studies centroids and the bobcat geographic centroid (fig. 2).

A Pearson correlation test revealed some variables were correlated (r > 0.7). In these cases, we maintained the variable most ecologically significant for bobcats (Loveless et al., 2016). Linear regression models were tested with log–transformed density estimates as response variable. Latitude, longitude, elevation, annual mean temperature (Bio1), mean diurnal range (Bio2), mean temperature of wettest quarter (Bio8), mean temperature of the dries quarter (Bio9; only for 100 km buffers), annual precipitation (Bio12), precipitation of wettest month (Bio13), precipitation seasonality (Bio15), distance to bobcat geographic centroid, and method used to obtain data (invasive for radio–tracked individuals, and noninvasive when fecal DNA sampling or camera–trapping) were used as explanatory variables. We tested the models with up to two variables in order to avoid overfitting. The best model was selected using the Akaike Information Criteria (AICc) adjusted to small samples (Burnham and Anderson, 2002). All analyses were performed in the R program (R Development Core Team, 2019).

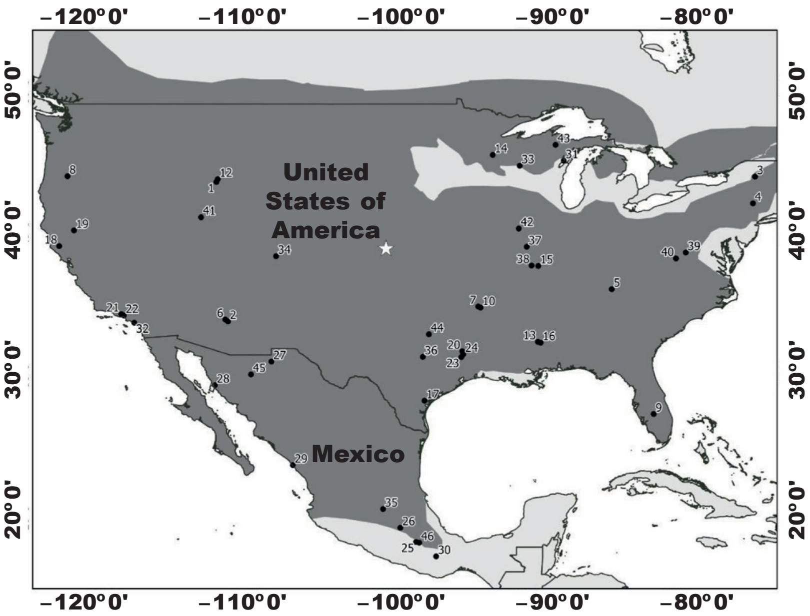

Fig. 2. Locations of bobcat (*Lynx rufus)* density estimates in USA and Mexico. The dark grey area depicts the distribution range of the bobcat according to International Union for Conservation of Nature (IUCN; Kelly et al., 2016). The white star represents the total range–centroid for North America, and the black dots, are the local centroids of the study areas. Numbers correspond to the studies in table 1s in supplementary material

*Fig. 2. Localidades de estimación de densidad poblacional de gato montés (*Lynx rufus*) en Estados Unidos de América y México. El área gris oscuro demuestra la distribución de acuerdo con la Unión Internacional para la Conservación de la Naturaleza (IUCN por sus siglas en inglés; Kelly et al., 2016). La estrella blanca representa el centroide obtenido de la distribución total para América del Norte y los puntos negros son los centroides de cada una de las áreas de estudio referidas y documentadas. Los números son los mismos que se muestran en la tabla 1s en material suplementario.*

Results

The overall sampling effort (eight months) was 3,360 camera–traps/days. We recorded a total of 559 independent events (photographs of the same species separated by 24 hrs) of wild animals, 199 of which corresponded to carnivore mammals (tables 2s and 3s in supplementary material). Bobcats' potential prey were also recorded: Order Lagomorpha, *Lepus* spp. (n = 185), Order Didelphimorphia, Virginia opussum (*Didelphis virginiana*; n = 8), and Order Cingulata, nine–banded armadillo (*Dasypus novemcinctus*; n = 9). We also recorded 127 independent records of bird species, mainly lesser roadrunner (*Geococcyx velox*), plain chachalaca (*Ortalis vetula*), and white–tipped dove (*Leptotila verreauxi*).

We obtained 32 photographic records of bobcats (fig. 3), 28 of which were independent events, giving a capture rate of 8.33 captures per 1,000 days camera–trap. The number of independent events and the capture rate were higher in the two dry periods than in the rainy periods (table 1). However, we did not find differences between seasons regarding the capture rate (χ^2 = 3.2749; df = 1; *p*–value = 0.0703). The mean estimated population density for the entire sampling period was 17.3 indiv./100 km. Considering a mean speed of bobcat movement of 0.30 km/H, the estimated density was higher during the dry seasons than during the rainy seasons (table 1).

Daily activity patterns

The bobcat had two peaks of activity, the first around 2:00 hrs and the second around 09:00 hrs (fig. 4). The pattern of activity was similar between the dry and rainy seasons (kernel density in dry season = 0.228, confidence interval = 0.18–0.28; kernel density in rainy season = 0.412, confidence interval = 0.21–0.44). There was no statistically significant difference between seasons, possibly due to the small sample size (Wald test = 3.88; *p*–value = 0.050).

Wide range analyses

We compiled 47 bobcat density estimates, including nine for Mexico (fig. 2; table 1s in supplementary ma-

Fig. 3. A bobcat (*Lynx rufus*) photographed in this study using camera–traps in the Mixteca region, Oaxaca, southern Mexico.

*Fig. 3. Un gato montés (*Lynx rufus*) fotografiado en este estudio con cámaras–trampa en la región Mixteca, en Oaxaca, en el sur de México.*

terial). Overall, from a total of 56 models, the model that best explained the variation in density estimates was the one containing annual precipitation and the mean temperature of driest quarter in buffers of 100 km radius (AICc = 11.88; table 2). In buffers of 50 km radius, the best model included annual mean temperature and longitude (AICc = 12.77; table 3). The best model with 100 km buffers explained 53 % of the variation on log–transformed bobcat densities (model weight 0.35, AICc = 11.88), similarly to 52 % with 50 km buffer (model weight 0.94, AICc = 12.77). At 100 km radius buffers, we found that annual precipitation (Bio12) had a negative relation with densities, whereas the relation was positive for the mean temperature in the driest quarter (Bio 9). At 50 km radius buffers, we found a positive relation of densities with the annual mean temperature, and a negative relation with longitude.

Discussion

Our findings contribute to current knowledge of bobcats in the southernmost limit of their distribution range, adding data concerning capture rates, population density, and daily activity patterns. The bobcat capture rate in all periods of the dry and rainy seasons in the Mixteca region of Oaxaca was similar to or higher than rates reported previously for camera–trapping surveys in Mexico (table 4). Higher capture rates (> 12.0) were observed in coniferous forests and meadows in southern Mexico City, and in pasturelands and scrubs in northwestern Chihuahua (Medellín and Bárcenas, 2010). In contrast, capture rates were low (< 2.0) in areas of submontane scrub and pine–oak forests in northwestern Guanajuato (Charre–Medellín et al., 2016), and also in areas with scrublands in western Zacatecas (Sánchez–González et al., 2018). Low capture rates could be explained by the highly disturbed habitats, likely associated with consequent low prey abundance. The lower capture rate in the rainy season in our study contrasts with findings from other studies with similar capture rates along seasons (Cruz–Jácome et al., 2015; Serna–Lagunes et al., 2019b). However, no studies have reported statistical differences between seasons. This suggests that the bobcat has a Nearctic affinity, which could explain the low capture rates in Neotropical latitudes and ecosystems, in addition to the great anthropogenic influence.

The mean bobcat density estimated in this study (17.32 indiv./100 km^2) corresponds to one–third of the range recorded for populations in the USA and Mexico (0.05 to 53 indiv./100 km^2; Medellín and Bárcenas, 2010; Thornton and Pekins, 2015). Particularly for Mexico, our estimates are lower than those reported by Medellín and Bárcenas (2010) in the Sierra Seri, Sonora (17.4–31.9 indiv./100 km^2), San Ignacio, Sinaloa (31.8–47.8 indiv./100 km^2) and Janos, Chihuahua (30.9–53.6 indiv./100 km^2), but slightly higher than those recorded in Acatlán de Osorio, Puebla (6.5–12.2 indiv./100 km^2), and San Miguel Topilejo, Mexico City (5.3–12.4 indiv./100 km^2). They

Table 1. Photographic sightings and density of bobcat (*Lynx rufus*) in four sampling periods over two seasons in their southern–most continental distribution range, in the Mixteca region, Oaxaca, southern Mexico: N, number of independent detections.

*Tabla 1. Detecciones fotográficas y densidad del gato montés (*Lynx rufus*) en cuatro periodos de muestreo en dos estacionalidades en la región Mixteca, en Oaxaca, en el sur de México, su distribución continental más sureña: N, número de detecciones independientes.*

Period	Season	N	Capture rate	Capture rate prey	Density (indiv./100 km^2)
Period 1	Dry	9	10.7	53.6	22.2
Period 2	Dry	10	11.9	84.5	24.7
Period 3	Rainy	5	5.9	58.3	12.4
Period 4	Rainy	4	4.8	30.9	9.9

are similar to the estimates of López–González et al. (2015) in the National Park El Cimatario, Querétaro (17 indiv./100 km^2), and also to those of Greenspan et al. (2020) in Sonora (15.88 indiv./100 km^2) and Vega–Flores and Farías–González (2021) in the Puebla portion of the Cuicatlán–Tehuacán Biosphere Reserve (15.4 ± 3.5 indiv./100 km^2; table 1s in material supplementary). Medellín and Bárcenas (2010) found low bobcat densities in the more disturbed habitats, possibly as a consequence of habitat and refuge loss, and low availability of prey such as leporids. In contrast, intermediate and high densities have been reported in sites with moderate or low perturbation, such as in Sierra Seri, Sonora, San Ignacio, Sinaloa, and Janos, Chihuahua.

Considering climate only, for populations in the USA, Thornton and Pekins (2015) found that bobcat density increased linearly with the mean temperature in the study area (i.e., bobcats were more abundant at higher temperatures) and the more western the localities. However, they did not exclude the possibility that other variables, such as human disturbance, suitable habitat, or the presence of competitors and predators, have a negative effect on population size. Although the bobcat is a species with the ability to use landscapes with some level of anthropic disturbance (Zanin et al., 2015), forested habitat seems to be play a role in maintaining healthy populations.

Another factor that possibly plays an important role in the abundance of bobcats is prey availability.

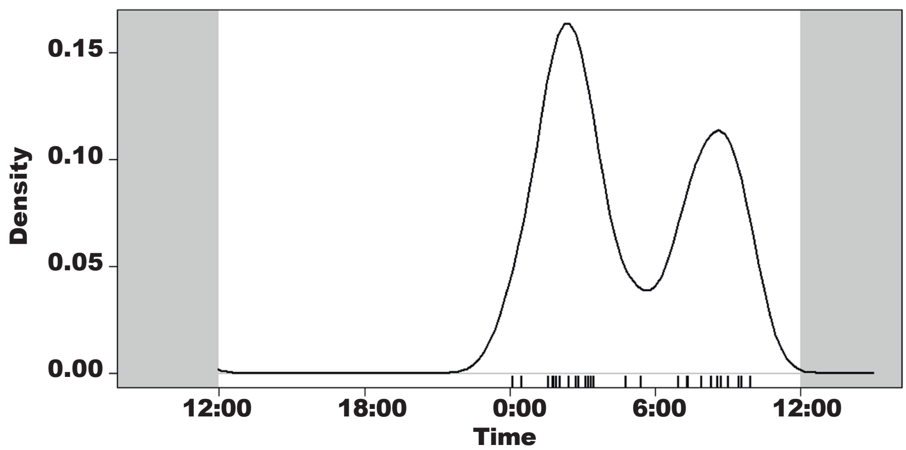

Fig. 4. Daily activity pattern of bobcat (*Lynx rufus*) in the Mixteca region, Oaxaca, southern Mexico.

*Fig. 4. Patrón diario de actividad del gato montés (*Lynx rufus*) en la región Mixteca, en Oaxaca, en el sur de México.*

Table 2. Linear regression analysis of range–wide density estimates for bobcats (*Lynx rufus*) with 100 km radius buffers. Only the best 10 models are presented, and in order. The first corresponds to the best model. Covariables are: Bio1, annual mean temperature; Bio2, mean diurnal range, Bio8: mean temperature of wettest quarter; Bio9, mean temperature of the dries quarter; Bio12, annual precipitation; Bio13, precipitation of wettest month; Centroid, distance to the range centroid; and Method, type of method used to record bobcats (invasive versus no–invasive methods); Mw, model weight.

*Tabla 2. Análisis de regresión linear en una estimación de amplio rango de densidad para gato montés (*Lynx rufus*) en buffers de 100 km de radio. Solo los 10 mejores modelos se presentan en orden, el primero corresponde al mejor. Las covariables son: Bio1, temperatura promedio anual; Bio2, promedio del rango diurno; Bio8, temperatura promedio en el cuarto trimestre más húmedo; Bio9, temperatura promedio del cuarto trimestre más seco; Bio12, precipitación anual; Bio13, precipitación del mes más húmedo; Centroid, distancia al centroide de la distribución del gato montés; y Method, método usado para registrar a los gatos montés (invasivo y no–invasivo.); Mw, peso modelo.*

Model	AICc	δAICc	Mw
Bio12 + Bio9	11.886	0	0.350
Centroid + Bio8	14.144	2.258	0.113
Bio9	14.511	2.625	0.094
Bio1 + Longitude	15.113	3.227	0.070
Method + Bio13	15.490	3.605	0.058
Longitude + Elevation	15.509	3.623	0.057
Method + Bio2	15.628	3.742	0.054
Bio1 + Bio9	15.638	3.752	0.054
Method + Bio8	15.980	4.094	0.045
Latitude + Bio9	16.551	4.665	0.034

Table 3. Linear regression analysis of range–wide density estimates for bobcat (*Lynx rufus*) 50 km radius buffers. Only the best 10 models are presented, in order. The first corresponds to the best model. Covariables are: Bio1, annual mean temperature; Bio2, mean diurnal range; Bio8, mean temperature of wettest quarter; Bio13, precipitation of wettest month; Bio15, precipitation seasonality; and Centroid, distance to the range centroid; Ww, Model weight.

*Tabla 3. Análisis de regresión linear en una estimación de amplio rango de densidad para gato montés (*Lynx rufus*) en buffers de 50 km de radio. Solo los 10 mejores modelos se presentan en orden, el primer corresponde al mejor. Las covariables son: Bio1, temperatura promedio anual; Bio2, promedio del rango diurno; Bio8, temperatura promedio en el cuarto trimestre más húmedo; Bio13, precipitación del mes más húmedo; Bio15, estacionalidad de la precipitación; y Centroid, distancia al centroide de la distribución del gato motés; Mw, peso modelo.*

Model	AICc	δAICc	Mw
Bio1 + Longitude	12.777	0	0.939
Bio1 + Bio2	20.442	7.665	0.020
Bio1 + Bio8	21.706	8.929	0.011
Bio1 + Bio13	22.571	9.794	0.007
Bio1 + Bio15	22.964	10.187	0.006
Latitude + Longitude	23.389	10.612	0.005
Bio1	23.537	10.760	0.004
Bio1 + Elevation	23.942	11.166	0.004
Bio1 + Centroid	25.594	12.817	0.002
Bio1 + Latitude	25.619	12.842	0.002

Medellín and Bárcenas (2010) and López–González et al. (2015) did not discuss prey availability but it is feasibly lower in crowded central Mexico than in the northern wilderness areas such as Sonora and Chihuahua. In the Mixteca region, we found that the main prey recorded, the cottontail (*Sylvilagus* sp.), presented a higher capture rate (55.06 independent events per 1,000 day/camera) than in many sites in Mexico (Cortés–Marcial and Briones–Salas, 2014; Martínez–Hernández et al., 2017; Hernández et al., 2018; Serna–Lagunes et al., 2019a), and it was only surpassed by a site in the Tehuacán–Cuicatlán Biosphere Reserve in southern Mexico (Cruz–Jácome et al., 2015), but further north of our study area. Other potential prey were not as frequent as *Sylvilagus* sp. (table 2s in material supplementary).

In our study area the weather is predominantly warm throughout the year. Although it is being heavily deforested, it is composed of fragments of crasicaule scrub and deciduous forest mixed with patches of grassland for cattle, and maize crops, providing bobcat with habitat cover to forage. In addition, prey availability is high. The area supports mesocarnivores such as coyote, gray fox, and white–nosed coati, although others, such as ocelot (*Leopardus pardalis*; Cervantes and Riveros, 2012) and large carnivores such as mountain lions (*Puma concolor*) and jaguars (*Panthera onca*; Briones–Salas et al., 2015; Padilla–Gómez et al., 2018) are absent. These characteristics could help explaining the high capture rate and density of bobcats in our study site.

Comparing densities between seasons in the Mixteca region, in accordance with our prediction, we found densities were higher in the dry season than in the rainy season. Similar results were observed by Medellín and Bárcenas (2010) in the Sierra Seri, Sonora, whereas for Janos, Chihuahua, the authors found that densities between seasons were similar (Medellín and Bárcenas, 2010).

We found that bobcats had a daily activity pattern with two peaks. The first peak began at night, reached the highest point around midnight, and then decreased until the sunrise. The second peak began mid–morning and decreased abruptly at noon. Our results are similar to those from other studies in Mexico, with two peaks of activity and the notoriously low activity after noon (Elizalde–Arellano et al., 2012). The temperature at our study area does not present such a wide variation as in some other areas. The maximum temperature range is 26 to 32 ºC, and the minimum temperature is 8 to 15 ºC). Daytime temperatures are predominately warm, contrasting with the extreme temperatures that occur in the deserts in the north of the country. Nevertheless, our results show that activity decreases at noon –when temperatures reach their maximum– and increases around midnight, when temperatures are lowest. Our results are similar to those concerning bobcats in the Chihuahuan desert where they show a significant negative correlation between temperature and daily activity patterns (Elizalde–Arellano et al., 2012). The highest temperatures occur during daylight, resulting in an increase in their nocturnal activity (George and Crooks, 2006; Wang et al., 2015; Lendrum et al., 2017; Flores–Morales et al., 2019). Harrison (2010) showed that bobcats avoid extremely high temperatures. Elizalde–Arellano et al. (2012) mention that distance traveled and the daily activity patterns of bobcats are positively related to energy requirements, prey availability and behavior.

Other potential explanations for concentrating activity at night could be competition with other mesocarnivores in the region, such as gray fox, coyote, and white–nosed coati (Cervantes and Riveros, 2012). These competitors are an important factor for the bobcat in its southernmost limit of the distribution range because of the cone–shape of this Mexican region; as the territory and/or extension of suitable habitat is smaller than that in the north, the species are closer and are more prone to compete. The bobcat share preys with other felids, such as ocelot (*Leopardus pardalis*) and margay (*Leopardus wiedii*; Sánchez–Cordero et al., 2008), and with other carnivores such as coyote and gray fox. It has been observed that the coyote and the bobcat also share activity patterns (Monroy–Gamboa, 2007; Serna–Lagunes et al., 2019). In the Mixteca region they share activity at dawn, but the coyote is more active in the evening and early night hours. In contrast, gray fox and bobcat share activity peaks after midnight, but the gray fox is active in the evening and early night hours. It is therefore possible that the competition could explain the difference between activity patterns in Oaxaca and other places in northern Mexico.

In its southernmost limit, the bobcat distribution range overlaps with the some of its competitors, but it is absent in the south of the Tehuantepec Isthmus despite the suitable habitat (Sánchez–Cordero et al., 2008). The explanation for this is that the Tehuantepec Isthmus is a continental strait with a width of 200 km. On both sides, the elevation is between 200 and 2,000 m a.s.l., resulting in a geographic and ecological barrier for montane species that are unable to move through the lowlands because of the weather and the multiple changes in vegetation (Barrier et al., 1998).

Thornton and Pekins (2015) found temperature and geographic longitude within 50 km radius buffers were the best variables to explain bobcat densities in the USA. This pattern was consistent when they included density estimates from Mexico at 50 km radius buffers. For the 100 km radius buffers, the best model obtained from a total of 56 models tested included annual precipitation and the mean temperature of the driest quarter. In macroecological studies, variations in the relationship between species and environment variables, as observed here, are a common phenomenon, suggesting that species respond to environment in hierarchical ways throughout the buffers (Thornton and Pekins, 2015). However, both buffers offer support for selectivity of bobcat for arid or mesic environments. The northernmost distribution range of the bobcat (*Lynx rufus*) in Mexico occurs in the southernmost limit of the Neartic region. Individuals in this southern area are smaller than those in the north Neartic region, so their prey are also smaller. They are more tolerant and adapted to the tempered weather (coniferous forests with scarce snow precipitations) and also to the warmer conditions (deserts and scrubs). It is in this type of environment where the species mainly occur in Mexico (Bárcenas and Romero, 2014).

Contrary to our expectations, distance to geographic centroid or latitude (fig. 2) did not emerge in the best models to explain bobcat densities, i.e., bobcat densities did not fit the theory of abundance–centroid or a latitudinal pattern (which is also related to a body–size pattern). Through ecological niche modeling, Pérez–Irineo et al. (2019) found a positive relationship between bobcat densities and distance to the climatic niche centroid, which is opposed to the theory of abundance–centroid. Instead, they found that the sites with high bobcat densities were those with high climatic suitability. Climatic variables therefore seem to be related to bobcat densities on a wider scale. However, we do not rule out the possibility that population size at local scales is driven by the interrelation of factors such as habitat availability, productivity, and anthropogenic disturbance. Further studies on bobcat densities in Mexico are needed in order to elucidate the macroecological pattern of the species.

In summary, bobcats of the Mixteca region in Oaxaca, Mexico, increase their population density during the dry season and when there are higher temperatures. They prefer to be active in nocturnal and early morning hours when it is cooler, and when they may have fewer competitors. From a macroecological perspective, bobcat density seems to be

Table 4. Comparison of capture rate of the bobcat (*Lynx rufus*) in camera–trapping studies in the Mixteca region, Oaxaca, southern Mexico.

*Tabla 4. Comparación de la tasa de captura de gato montés (*Lynx rufus*) en estudios usando cámaras–trampa en la región Mixteca, en Oaxaca, en el sur de México.*

Locality	Vegetation type	Capture rate	Bibliographic reference
Northwestern Guanajuato	Pine–oak forests	0.9	Charre–Medellín et al. (2016)
Northwestern Guanajuato	Submontane scrub	1.5	Charre–Medellín et al. (2016)
Western Zacatecas	Scrubland	1.9	Sánchez–González et al. (2018)
Northwestern Sonora	Semi–desert grassland, evergreen woodland, and plain, and great basin grassland	2.0	Coronel–Arellano et al. (2018)
Northwestern Sonora	Montane conifer forest	3.6	Coronel–Arellano et al. (2018)
Northwestern Oaxaca	Tropical deciduous forests and evergreen woodland	4.2	Pérez–Solano et al. (2018)
Northwestern Sonora	Semi–desert grassland, evergreen evergreen woodland, and plain, and great basin grassland	4.3	Coronel–Arellano et al. (2018)
Northeastern Coahuila	Deciduous thorn forest	5.5	Gómez–Naranjo et al. (2017)
Northwestern Sonora	Evergreen woodland and semi–desert grassland	7.3	Coronel–Arellano et al. (2018)
Northwestern Sonora	Evergreen woodland and thorn scrub	7.4	Coronel–Arellano et al. (2018)
Northwestern Sonora	Evergreen woodland, montane conifer forest, and semi–desert grassland	7.5	Coronel–Arellano et al. (2018)
Western Sonora	Sarcocaule scrub and microphilic desert scrub	8.3	Medellín and Bárcenas (2010)
Northwestern Oaxaca	Tropical deciduous forests, crasicaule scrub, pasturelands, and crops	8.3	This study
Central Veracruz	Pine forest, subalpine vegetation, and paramo	9.1	Serna–Lagunes et al. (2019b)
Northwestern Sonora	Semi–desert grassland and evergreen woodland	10.3	Coronel–Arellano et al. (2018)
Northwestern Oaxaca	Tropical deciduous forests, crasicaule scrub, pasturelands, and crops	10.9	Cruz–Jácome et al. (2015)
Southern Mexico City	Coniferous forests and meadows	12.5	Medellín and Bárcenas (2010)
Northwestern Chihuahua	Pasturelands and scrub	12.5	Medellín and Bárcenas (2010)

related to the driest periods and warmer climate, rather than reflect abundance–centroid or latitudinal pattern. However, more population studies throughout Mexico are needed to achieve a balanced sample size. Our findings add further data to our knowledge of the species and may contribute to more efficient management and conservation planning for bobcats in their southernmost distribution range.

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Supplementary material

Table 1s. Studies recovered for macroecological analyses of density across bobcat (*Lynx rufus*) range: ID corresponds to points labeled on the map in figure 4.

*Tabla 1s. Estudios recabados para un análisis macroecológico de la densidad del gato montés (*Lynx rufus*) a lo largo de su distribución continental en Norteamérica. ID corresponden a los puntos del mapa en la figura 4.*

ID	Locality	Density (bobcats/100 km^2)	Method	Bibliographic reference
1	Atomic Energy Commission's vast National Reactor Testing Station, Idaho	5.43	Radio–telemetry	Bailey (1974)
2	Three Bar Wildlife Area, Arizona	25.97	Live–capture Minimum number captured	Jones and Smith (1979)
3	Central Adirondack Study Area, New York	1.93	Radio–telemetry	Fox and Brocke (1983)
4	Western Catskill Study Area, New York	6.18	Radio–telemetry	Fox and Brocke (1983)
5	Department of Energy's Oak Ridge Reservation, Tennessee	11.36	Radio–telemetry	Kitching and Story (1984)
6	Three Bar Wildlife Area, Tonto National Forest, Arizona	25.64	Radio–telemetry	Lawhead (1984)
7	Choctaw and Kiamichi districts, Ouachita National Forest, Oklahoma	9.09	Radio–telemetry	Rolley (1985)
8	Willamette National Forest, Oregon	4.00	Radio–telemetry	Toweill (1986)
9	Archbold Biological Station, Florida	26.00	Radio–telemetry	Wassmer et al. (1988)
10	Muddy Creek Wildlife Management Area, Arkansas	10.42	Radio–telemetry	Rucker et al. (1989)
11	Idaho National Engineering Laboratory, Idaho	9.20	Radio–telemetry	Knick (1990)
12	Box Canyon area, Idaho	8.70	Radio–telemetry	Knick (1990)
13	Tallahalla Wildlife Management Area, Mississippi	9.62	Radio–telemetry	Conner et al. (1992)
14	St Croix, Wisconsin	6.90	Radio–telemetry	Lovallo and Anderson (1996)
15	Jackson and Union, Illinois	30.50	Radio–telemetry	Nielsen and Woolf (2001)
16	Tallahalla Wildlife Management Area, Mississippi	9.20	Radio–telemetry	Benson et al. (2006)
17	Welder Wildlife Foundation Refuge, Texas	48.00	Camera–trapping	Heilbrun et al. (2006)
18	Hopland Research and Extension Center, California	39.00	Camera–trapping	Larrucea et al. (2007)
19	Grey Davis Dye Creek Preserve, California	27.00	Camera–trapping	Larrucea et al. (2007)
20	Nacogdoches County, Texas	29.00	Camera–trapping	Symmank et al. (2008)
21	Simi Hills, Santa Monica Mountains National Recreation Area, California	33.00	Fecal DNA samples	Ruell et al. (2009)

Table 1s. (Cont.)

ID	Locality	Density (bobcats/100 km^2)	Method	Bibliographic reference
22	Topanga, Santa Monica Mountains National Recreation Area, California	35.00	Fecal DNA samples	Ruell et al. (2009)
23	Cottingham Hunting Club, Texas	12.00	Camera–trapping	Davis (2010)
24	Winston 8 Ranch, Texas	10.00	Camera–trapping	Davis (2010)
25	Acatlán de Osorio, Puebla	12.20	Camera–trapping	Medellín and Bárcenas (2010)
26	San Miguel Topilejo, Estado de México	12.40	Camera–trapping	Medellín and Bárcenas (2010)
27	Janos, Chihuahua	53.00	Camera–trapping	Medellín and Bárcenas (2010)
28	Sierra Seri, Sonora	23.15	Camera–trapping	Medellín and Bárcenas (2010)
29	Carricitos, San Ignacio, Sinaloa	47.80	Camera–trapping	Medellín and Bárcenas (2010)
30	Santa Catarina Ixtepeji, Oaxaca	8.76	Radio–telemetry	Monroy and Briones–Salas (2012)
31	Delta and Menominee Counties, Michigan	3.00	DNA	Stricker et al. (2012)
32	San Joaquin Hills, Orange County, California.	51.80	Camera–trapping	Alonso et al. (2015)
33	Central Wisconsin	3.33	Camera–trapping	Clare et al. (2015)
34	Uncompahgre Plateau, Montrose and Ridgway, Colorado	19.37	Radio–telemetry	Lewis et al. (2015)
35	National Park El Cimatario, Querétaro	17.00	Live–capture Minimum number captured	López–González et al. (2015)
36	Fort Hood East, Bell and Coryell Counties, Texas	13.20	Camera–trapping	Thornton and Pekins (2015)
37	Godfrey, Illinois	3.32	Camera–trapping	Kaiser (2017)
38	Godfrey, Illinois	12.00	Camera–trapping	Kaiser (2017)
39	Rockingham, Virginia	9.34	DNA	Morin et al. (2018)
40	Bath, Virginia	13.94	DNA	Morin et al. (2018)
41	Utah Test and Training Range, Utah	11.95	Camera–trapping	Muncey (2018)
42	Hancock and Schuyler, Illinois	1.40	Camera–trapping	Jacques et al. (2019)
43	Upper Peninsula of Michigan	3.80	DNA	Kautz et al. (2019)
44	Dallas Fort–Worth Metroplex, Texas	11.00	Camera–trapping	Young et al. (2019)
45	Nácori Chico, Sonora	15.88	Camera–trapping	Greenspan et al. (2020)
46	San José Axuxco, Puebla	15.40	Camera–trapping	Vega–Flores and Farías–González (2021)
47	Cosoltepec, Oaxaca	17.30	Camera–trapping	This study

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Table 2s. Potential competitors and prey of the bobcat cohabiting in the Mixteca region, Oaxaca, southern Mexic, according to camera–trapping.

Tabla 2s. Posibles competidores y presas del gato montés que habitan en la región de Mixteca, en Oaxaca, en el sur de México detectados mediante fototrampeo.

Scientific name	Common name	Independent records	Capture rate
Potential competitors			
Canis latrans	Coyote	20	5.95
Urocyon cinereoargenteus	Gray fox	40	11.90
Conepatus leuconotus	American hog–nosed skunk	34	10.11
Mephitis macroura	Hooded skunk	44	13.09
Spilogale angustifrons	Southern spotted skunk	1	0.29
Bassariscus astutus	Ringtail	13	3.87
Nasua narica	White–nosed coati	3	0.89
Procyon lotor	Raccoon	14	4.17
Potential preys			
Sylvilagus spp.	Cottontail		55.06
Leptotila verreauxi			20.24
Geococcyx velox	Road runner		9.82
Ortalis vetula	Plain chachalaca		4.76
Dasypus novemcinctus	Nine–banded armadillo		2.68
Didelphis virginiana	Virginia opossum		2.38

Competitors / competidores

Canis latrans

Urocyon cinereoargenteus

Conepatus leuconotus

Bassariscus astutus

Nasua narica

Procyon lotor

Prey / presas

***Sylvilagus* spp.**

Dasypus novemcinctus

Didelphis virginiana

Fig. 1s. Camera–trapping images of potential competitors and prey of the bobcat cohabiting in the Mixteca region, Oaxaca, southern Mexico.

Fig. 1s. Imágenes obtenidas mediante fototrampeo de competidores potenciales y presas del gato montés que habitan en la región de Mixteca, en Oaxaca, en el sur de México.