



# Ocelots thrive in a non-typical habitat of northwestern Mexico

Miguel Ángel Gómez-Ramírez<sup>1,2</sup>, Carmina Elizabeth Gutiérrez-González<sup>1,2</sup>,  
Carlos Alberto López-González<sup>1,\*</sup>

<sup>1</sup>Laboratorio de Zoología, Universidad Autónoma de Querétaro, Campus Juriquilla, Av. de las Ciencias S/N, Delegación Santa Rosa Jáuregui, Querétaro, Querétaro CP 76230, Mexico

<sup>2</sup>Present address: Northern Jaguar Project, 2114 W. Grant Rd., Ste. 121, Tucson, AZ 85745, USA

**ABSTRACT:** Ocelots *Leopardus pardalis* are legally protected in Mexico as an endangered species. The main threats throughout the species' range are habitat loss and fragmentation. The ocelot population that inhabits Sonora, Mexico, is at the northern limit of the species' distribution and knowledge about it is still scarce. We used remote camera data from 2010–2012 and spatially explicit capture-recapture (SECR) models for density estimation, and the Barker robust design mark-recapture model to estimate survival, abundance, and density of ocelots in an arid region in northeastern Sonora. Average apparent survival was 0.65 for females and 0.63 for males; abundance estimates (mean  $\pm$  SE) ranged from  $2.02 \pm 0.13$  to  $7.06 \pm 0.24$  ocelots. Average ( $\pm$  SE) density was  $0.63 \pm 0.06$  females  $100 \text{ km}^{-2}$  and  $0.95 \pm 0.08$  males  $100 \text{ km}^{-2}$  using Barker robust design, and  $0.51 \pm 0.26$  females  $100 \text{ km}^{-2}$  and  $0.77 \pm 0.25$  males  $100 \text{ km}^{-2}$  using the SECR. Our survival and density estimates are the lowest reported. However, due to the low human population density in our study area, we consider that our findings must be associated with natural processes rather than human-caused disturbance, without dismissing an additive factor by the latter. Arid environmental features could have a negative influence on primary productivity and consequently on prey availability, limiting ocelot survival and density in this region. Large tracts of unpopulated wildlands over a non-fragmented landscape favor ocelots in this area, and it is important to maintain current habitat conditions for this Neotropical species to continue thriving in this region of North America.

**KEY WORDS:** *Leopardus pardalis* · Ocelot survival · Density · Sonora · Mexico · Mark-recapture

## INTRODUCTION

Ocelots *Leopardus pardalis* are listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), indicating that it is a species threatened with extinction for which trade is restricted (CITES 2005). The IUCN Red List has catalogued the species as being of Least Concern (IUCN 2012), but in Mexico, ocelots are listed as endangered (Norma Oficial Mexicana 2010). Their main threats are habitat loss, fragmentation,

and illegal hunting (Paviolo et al. 2015). Ocelots are distributed from southern Arizona and Texas in the USA to northern Argentina (Nowell & Jackson 1996, Sunquist & Sunquist 2002). The ocelots that inhabit Sonora, Mexico, are near the northern limit of the species' distribution, where habitat conditions are drier than other locations throughout their range. Ocelots live in a wide variety of habitats, including mangroves, tropical wet forest, tropical dry forest, and temperate montane vegetation (Murray & Gardner 1997, Sunquist & Sunquist 2002). They are also

\*Corresponding author: cats4mex@gmail.com

found in the semi-arid thornscrub and woodlands of Sonora, Chihuahua, and Arizona (López-González et al. 2003, 2014, Grigione et al. 2007). Ocelots are not generalists in any of these habitat types and are usually associated with dense vegetation cover (Harve-son et al. 2004, Horne et al. 2009).

Most published studies about ocelot populations across their distribution are focused on abundance and population densities (Trolle & Kéry 2003, 2005, Maffei et al. 2005, Di Bitetti et al. 2006, 2008, Dillon & Kelly 2007, 2008, Sternberg & Mays 2011, Rodgers et al. 2014, Martínez-Hernández et al. 2015). There are few studies that report other important demographic parameters such as survival rates (but see Haines et al. 2005).

There is a lack of knowledge about the northernmost population of ocelots that inhabit the aridlands of Sonora, Chihuahua, and Arizona. In this region, they face extreme climatic conditions with contrasting seasonal changes, low precipitation, xeric vegetation, and open canopy cover in most of the area (Brown 1994). Our objective was to estimate the survival, abundance, and density of ocelots in a region of Sonora, Mexico, and contribute to the knowledge and understanding of ocelot populations in their

northernmost distribution, as well as to establish a basis for long-term monitoring of this population. This information can be applied to improve the management and conservation of ocelots in the region and other areas with similar environmental conditions.

## MATERIALS AND METHODS

### Study area

The study area is located in the foothills of the Sierra Madre Occidental in northwestern Mexico near Sahuaripa, Sonora, between 29.199° N, 108.983° W and 29.541° N, 109.236° W. It is comprised of protected private land in the Northern Jaguar Reserve (NJR) without cattle, and 10 adjoining cattle ranches with a conservation agreement that includes protection for all wildlife inside their boundaries (Gutiérrez-González et al. 2015). Until 2012, the NJR comprised 220 km<sup>2</sup>, and the neighboring private properties comprised approximately 130 km<sup>2</sup> (Fig. 1). Human activity in this area is scarce. The principal economic activity in the region is extensive cattle ranching,

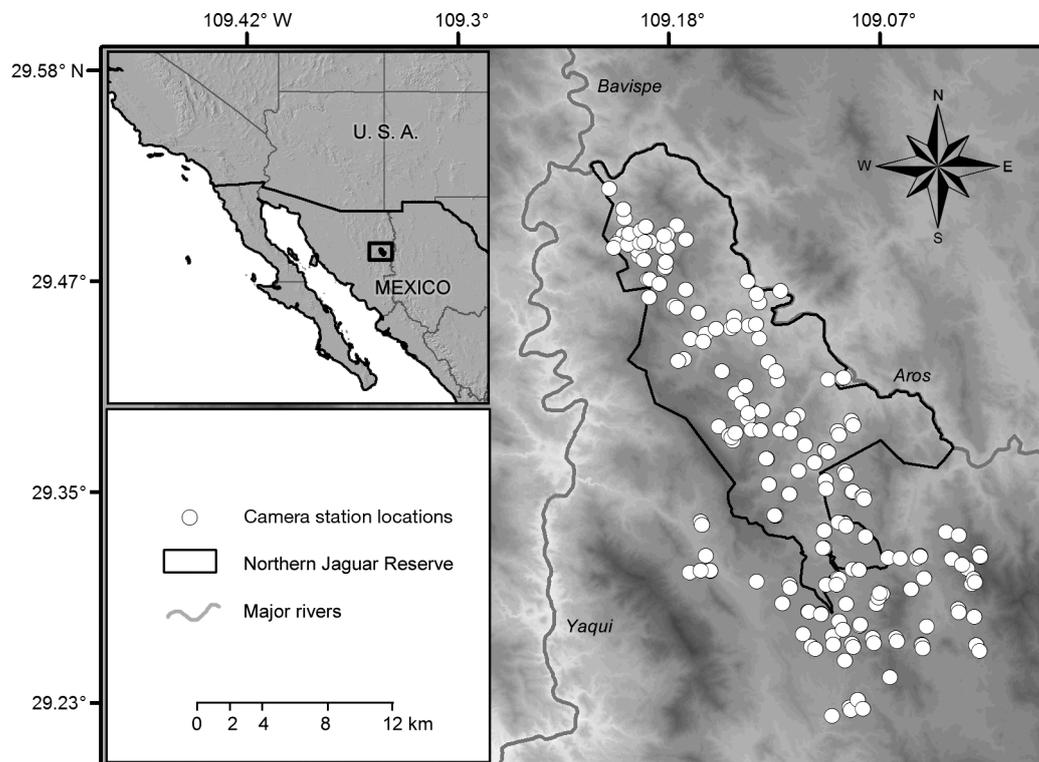


Fig. 1. Study area (inset: location within Mexico) and camera stations, January 2010 to July 2012. Dots inside the polygon are cameras located in the private reserve; dots outside the polygon are cameras at the neighboring cattle ranches

where cattle are free-ranging and without constant supervision. The nearest human settlement, Sahuaripa, is >50 km away and accessed by a dirt road used only by the ranch owners.

The climate in this region is warm and dry with an average annual temperature >18°C. Annual rainfall ranges from 400 to 800 mm (CONABIO 2004, INEGI 2015). Extreme temperatures reported in the area vary between -7 and 46°C during winter and summer, respectively. Altitude ranges from 370 to 1600 m. Therefore, the vegetation is a heterogeneous mosaic comprised of foothills thornscrub (*Acacia cochliacantha*, *Prosopis velutina*, *Stenocereus thurberi*, *Haematoxylum brasiletto*, *Lysiloma divaricatum*, *Fouquieria macdougalii*), relicts of tropical deciduous forest (*Ceiba acuminata*, *Ipomoea arborescens*, *Erythrina flabelliformis*, *Bursera* spp.), oak woodlands (*Quercus chihuahuensis*, *Q. albocincta*, *Q. toumeyii*), and riparian vegetation (*Salix gooddingii*, *Havardia sonora*, *Prosopis velutina*, *Platanus wrightii*, *Ambrosia ambrosioides*) (Brown 1994, Felger et al. 2001).

### Remote camera survey

The ocelot (*Leopardus pardalis*) camera survey was derived from a long-term jaguar (*Panthera onca*) study in the same area (Gutiérrez-González et al. 2015). We selected information from January 2010 to July 2012 for analysis because of database availability. During these years, cameras were set up with a minimum distance of 1 km between each station (Fig. 1). There was no systematic survey design, as the number of cameras and camera locations changed based on personal observations across the years to maximize detections. Cameras were attached to trees in front of areas used by wildlife (pathways, stream bottoms, and dirt roads). In select locations, and depending on camera availability, we placed cameras in paired stations (31.94% of stations in 2010, 28.12% in 2011, and 45.36% in 2012). The digital remote camera models we used were Cuddeback® Capture, Capture IR, Attack, and Attack IR (Non Typical); Wildview® Xtreme 2 and Xtreme 5 (GSM Outdoors); as well as a CamTrakker® 35 mm film camera model (CamTrakker) (Table 1). All cameras were set to be active 24 h a day with a 5 min delay between capture events, recording 1 picture per event. All cameras were active year-round and checked monthly to download images, change batteries, and make sure they were functioning properly. No bait or lure was used to attract animals.

Table 1. Number of cameras used (by camera model) during the study. Number of different camera stations included in parentheses (number of stations is higher than number of cameras in some years because camera locations changed through the year)

Camera model	2010	2011	2012
Cuddeback® (digital models)	54	64	73
Wildview® (digital models)	28	17	22
CamTrakker® (35 mm film)	12	0	0
Total	94 (95)	81 (112)	95 (83)

### Ocelot identification

Ocelots were individually identified by their unique spot patterns in the photographs (Karanth 1995, Trolle & Kéry 2003). An individual code was assigned to each ocelot. Males were differentiated from females by the presence of testicles (Trolle & Kéry 2003). Photographs which were not clear enough to enable individual identification were discarded. Only adult ocelots whose sex was identified were selected for analysis.

### Data analysis

Barker robust design (Kendall et al. 2013)

We designed our ocelot encounter history with 3 primary periods: January to April of 2010, 2011, 2012, respectively. The primary periods each had 8 secondary periods that consisted of 15 d pooled detections. The pooling of daily data reduced the number of zeros (no detections) in the encounter history (Otis et al. 1978). We selected the months between January and April as the primary periods to meet the assumption of demographic closure, supported by our field observations as we documented 3 ocelot births that occurred during the summer. Havlanová & Gardiánová (2013) observed that, in captivity, a higher number of litters occurred during the summer, which was corroborated by Laack et al. (2005), who found that ocelot births in Texas occurred between mid-April and late December.

We considered each sex as a different group. Estimates of abundance can be negatively biased if sex is not included in the models (Efford & Mowat 2014). Individual detection histories were recorded, with live detections designated as '1' and no detections designated as '0'. Resightings outside of the primary periods (remainder of the year) were denoted by a '2'

in the corresponding column (Kendall et al. 2013). The lack of dead ocelot records precluded us from including them in the analysis.

The Barker robust design includes 9 parameters to model: (1) survival probability ( $S$ ) between 2 primary periods (due to the lack of deceased records, we referred to this as apparent survival probability,  $\phi$ ); (2) capture/detection probability ( $p$ ) and (3) recapture probability ( $c$ ); (4) fidelity to the area ( $F$ ), which is the probability of an individual remaining in the studied population between 2 primary periods; availability probability of individuals being detected between 2 primary periods, given that in the previous period those individuals were (5) available ( $a''$ ), (6) or not ( $a'$ ); (7) dead recovery probability ( $r$ ); resighting probability between 2 primary periods, given that individuals (8) survived ( $R$ ), (9) or not ( $R'$ ) in the previous period. Abundance ( $N$ ), the portion of the population that is available in the study area for a specific primary period is a derived parameter (Kendall et al. 2013). This model and the previous Barker (1997) model were developed to include data from individual dead recoveries, but these models have been previously applied to live-capture data by setting the dead recovery-related parameters to zero (e.g. Collins & Doherty 2006, Ruiz-Gutiérrez et al. 2012, Gutiérrez-González et al. 2015). We followed this approach for our data analysis and set the  $r$  and  $R'$  parameters to 0.

Model construction was performed in the program MARK (White & Burnham 1999). We first explored the relationship between  $p$  and  $c$ , and possible variation among years. Apparent survival ( $\phi$ ) was then modeled in 3 ways: constant for all years; with variation among years; and including an uncommon intense freeze that occurred in February 2011. Availability probabilities ( $a''$  and  $a'$ ) were tested as either constant or time-variant (years), and with a model that precluded temporal emigration with fixed values ( $a'' = 1$  and  $a' = 0$ ). Fidelity probability was modeled as constant and as varying among years. We considered resight probability ( $R$ ) as constant, as ocelots exhibit territorial behavior (Sunquist & Sunquist 2002), and because the sampling effort remained the same each primary period. All parameters were modeled considering differences or not between sexes. Finally, model selection was based on Akaike's information criteria corrected for small samples (AICc), and model average was used due to model uncertainty (Burnham & Anderson 2002). All parameter estimates were reported according to model average results. Comparisons between estimates were made based on their standard error.

### Spatially explicit capture-recapture (SECR) models

For a second ocelot density estimation, we used the program SPACECAP (Gopaldaswamy et al. 2012) with 3 different input data files: (1) capture information for individuals with each capture associated with its geographical location (WGS 84 UTM coordinates) and the sampling occasion when capture occurred — for sampling occasions, we used the same period as for the Barker robust design (January–April) and each of the 120 days was considered a sampling occasion; (2) trap deployment details with the geographical location of each camera station and the period it was active (1) or not (0); (3) the potential home range or centers of activity areas covering a total area of 3600 km<sup>2</sup>, with 899 potential activity centers equally distributed across this area.

Analyses were performed in the program R (R Core Team 2015) using the package SPACECAP version 1.1.0 (Gopaldaswamy et al. 2014). We performed 1 analysis per sex per year (giving a total of 6), all of them with 50 000 iterations, 2000 iterations as burn-in period, thinning rate set to 10, and a data augmentation value of 50 individuals.

### Effective sampling area (ESA) and density estimation

Annual maximum mean distances moved (MMDM) were calculated by averaging the maximum distance moved by each individual that was detected at >1 camera station (Karanth & Nichols 1998, Silver et al. 2004). According to Maffei & Noss (2008) and O'Brien (2011), if the sampling area is at least 4 times the known home range of the species, then the MMDM can be considered equivalent to the diameter of the home range. Half MMDM throughout the study was considered the radius of a circular area around each camera station. The sum of the overlapped areas constituted the ESA and was calculated by year and by sex (Karanth et al. 2004, Silver et al. 2004).

Density was obtained by dividing the annual abundance estimates by the annual ESA (Karanth et al. 2004, Silver et al. 2004), and thus we were able to obtain a density estimate per year and sex.

## RESULTS

From January 2010 to July 2012, we accumulated 88 508 camera-days. We obtained 381 ocelot (*Leopardus pardalis*) photographs, from which we identified

33 ind. (8 females, 16 males, and 9 ind. with unidentified sex). Due to Barker robust design constraints, the months selected to establish the primary and secondary periods, and sex as a group, only 18 ocelots (5 females, 13 males) were included in the encounter history.

For the Barker robust design, 18 models were built and tested, and the 4 best-supported models based on the AICc are presented in Table 2.

The annual estimate of apparent survival probability was similar among years and between sexes, ranging from (mean  $\pm$  SE)  $0.63 \pm 0.10$  to  $0.65 \pm 0.12$ , and its average value across the 3 years was  $\phi = 0.64 \pm 0.003$ . Male survival decreased from 2011 to 2012; however, based on the overlap of the standard error, this decrease was not significant (Table 3). Fidelity probability was constant among years but different by sex ( $F = 0.67 \pm 0.19$  for females and  $0.58 \pm 0.15$  for males). Resight probability among primary periods was  $R = 0.82 \pm 0.17$  for females and  $0.91 \pm 0.11$  for males. Detection probability did not vary between sexes, but it did vary between the 2010 primary period ( $0.23 \pm 0.06$ ) and the 2011–2012 primary periods ( $0.45 \pm 0.04$ ) (Table 3).

Abundance estimates ranged from  $2.02 \pm 0.13$  to  $3.31 \pm 0.74$  for females and from  $5.04 \pm 0.20$  to  $7.06 \pm 0.24$  for males (Table 4). Average MMDM values for all years were  $8.51 \pm 1.97$  km for females and  $7.06 \pm 1.74$  for males (Table 4). Maximum distance for a single individual over 1 year was 22.67 km for a female and 24.44 km for a male. The average ESA for the 3 years using half MMDM as a buffer distance was  $471.66 \pm 112.14$  km<sup>2</sup> for females and  $668.50 \pm 53.10$  km<sup>2</sup> for males (Table 4).

Ocelot density estimates in the region varied from  $0.49 \pm 0.10$  to  $0.82 \pm 0.04$  ind. 100 km<sup>-2</sup> for females and from  $0.78 \pm 0.03$  to  $1.16 \pm 0.19$  ind. 100 km<sup>-2</sup> for males (Table 4).

According to the SECR models, sigma ( $\sigma$ ; range parameter of the species) values ranged from  $1.76 \pm 0.45$  to  $6.25 \pm 2.08$  km for females and  $2.67 \pm 0.31$  to  $5.01 \pm 1.49$  km for males. Density estimates were lower than Barker robust design estimates (Table 4), with ranges from  $0.24 \pm 0.14$  to  $0.68 \pm 0.31$  ind. 100 km<sup>-2</sup> for females and from  $0.45 \pm 0.19$  to  $1.15 \pm 0.27$  ind. 100 km<sup>-2</sup> for males (Table 4).

## DISCUSSION

We present the first survival and density study of ocelots *Leopardus pardalis* in the northernmost part of the species' range in Sonora, Mexico. The apparent survival for this population remained constant throughout the study period. Its average value (0.64) is lower in comparison with resident adult ocelots (0.87) in the Laguna Atascosa National Wildlife

Table 3. Model average parameter estimates ( $\pm$ SE) obtained from ocelot (*Leopardus pardalis*) study in Sonora, Mexico from 2010–2012 using Barker robust design (Kendall et al. 2013).  $\phi$ : apparent survival,  $p$ : detection probability,  $R$ : resight probability,  $F$ : fidelity probability

Year	Parameter			
	$\phi$	$p$	$R$	$F$
<b>Females</b>				
2010	$0.65 \pm 0.12$	$0.23 \pm 0.06$	$0.82 \pm 0.17$	$0.67 \pm 0.19$
2011	$0.65 \pm 0.12$	$0.45 \pm 0.04$	$0.82 \pm 0.17$	$0.67 \pm 0.19$
2012	$0.64 \pm 0.12$	$0.45 \pm 0.04$	$0.82 \pm 0.17$	$0.67 \pm 0.19$
<b>Males</b>				
2010	$0.63 \pm 0.10$	$0.23 \pm 0.06$	$0.91 \pm 0.11$	$0.58 \pm 0.15$
2011	$0.63 \pm 0.10$	$0.45 \pm 0.04$	$0.91 \pm 0.11$	$0.58 \pm 0.15$
2012	$0.63 \pm 0.10$	$0.45 \pm 0.04$	$0.91 \pm 0.11$	$0.58 \pm 0.15$

Table 2. Four best-supported models for ocelot (*Leopardus pardalis*) study using Barker robust design for data analysis (Kendall et al. 2013). AICc: corrected Akaike's information criteria, K: number of estimable parameters,  $\phi$ : apparent survival,  $p$ : detection probability,  $R$ : resight probability,  $F$ : fidelity probability,  $a''$ : available,  $a'$ : not available. Dead recovery-related parameters ( $r$  and  $R'$ ) were fixed to 0 for all models. In the parentheses following the parameters, (.): constant among years and between sex, (0): parameter fixed to 0, (1): parameter fixed to 1, (digital): parameter estimate depends on new digital remote camera inclusion, and (sex): parameter estimate depends on sex but is equal among years

Model	AICc	$\Delta$ AICc	AICc weights	Model likelihood	K
$\phi(.), R(.), F(.), p(\text{digital}), a'(0), a''(1)$	345.66	0.00	0.52	1.00	5
$\phi(.), R(.), F(\text{sex}), p(\text{digital}), a'(0), a''(1)$	347.54	1.88	0.20	0.39	6
$\phi(.), R(\text{sex}), F(\text{sex}), p(\text{digital}), a'(0), a''(1)$	347.60	1.93	0.20	0.38	7
$\phi(\text{sex}), R(\text{sex}), F(\text{sex}), p(\text{digital}), a'(0), a''(1)$	349.48	3.82	0.08	0.15	8

Table 4. *Leopardus pardalis* abundance, minimum convex polygon (MCP), maximum mean distances moved (MMDM), range parameter of the species ( $\sigma$ ), effective sampling area (ESA), and ocelot density estimated in Sonora, per year  $\pm$  SE, with Barker robust design (BRD) and spatially explicit capture-recapture model (SECR)

Year	Abundance	MCP (km <sup>2</sup> )	MMDM (km)	$\sigma$ (km)	ESA (km <sup>2</sup> )	Density (ind. 100 km <sup>-2</sup> ) BRD	SECR
<b>Females</b>							
2010	3.41 $\pm$ 0.74	405.32	10.38 $\pm$ 3.53	6.25 $\pm$ 2.08	695.66	0.49 $\pm$ 0.10	0.24 $\pm$ 0.14
2011	2.02 $\pm$ 0.13	428.85	3.58 $\pm$ 1.24	1.76 $\pm$ 0.45	349.85	0.58 $\pm$ 0.03	0.61 $\pm$ 0.31
2012	3.02 $\pm$ 0.16	299.23	4.57 $\pm$ 2.36	2.56 $\pm$ 0.83	369.48	0.82 $\pm$ 0.04	0.68 $\pm$ 0.31
<b>Males</b>							
2010	6.83 $\pm$ 1.12	405.32	8.64 $\pm$ 2.11	5.01 $\pm$ 1.49	588.88	1.16 $\pm$ 0.19	0.70 $\pm$ 0.29
2011	7.06 $\pm$ 0.24	428.85	10.59 $\pm$ 2.45	2.67 $\pm$ 0.31	769.19	0.92 $\pm$ 0.03	1.16 $\pm$ 0.27
2012	5.04 $\pm$ 0.20	299.23	8.96 $\pm$ 2.04	3.58 $\pm$ 0.55	647.43	0.78 $\pm$ 0.03	0.45 $\pm$ 0.19

Refuge (LANWR) in Texas, but similar to the survival estimate for transients (0.57) in the same area (Haines et al. 2005). In LANWR, human activities (i.e. vehicle collisions, dog attacks, poisoning) are the main threats to ocelot survival (Haines et al. 2005). In South American tropical forests, ocelots are decimated by habitat loss (Massara et al. 2015), which is replacing illegal hunting as the major threat (Sunquist & Sunquist 2002). Human activities and density in our study area and the adjacent mountainous regions of Sonora are limited to cattle ranching and localized mining, producing a non-threatening continuum environment for ocelots, although a certain degree of poaching has been documented elsewhere in the region (López-González et al. 2003). The low survival of ocelots in Sonora is possibly associated with natural causes such as prolonged droughts, intense freezes, or wildfires that directly or indirectly influence dense canopy cover and prey availability.

We modeled 1 year following a hard freeze in 2011, and we found a non-significant decline in male ocelot survival from 2011 to 2012. The freezing event did not explain ocelot survival values in our model selection; however, freeze effects could become apparent in the subsequent years not included in our study. Long-lived species such as ocelots may require long-term research to assess and distinguish any effect of this kind of natural phenomena over population dynamics (Lebreton et al. 1992).

In addition to environmental processes, interspecific and intraspecific killing can contribute to low species survival within the Sonoran ocelot population. Intraspecific killing was documented in LANWR (Haines et al. 2005). Pumas *Puma concolor* are known to kill but not predate on ocelots (Nuñez et al. 2000). Other large carnivores, such as jaguars *Panthera onca* and coyotes *Canis latrans*, that inhabit the same region can represent additional sources of interspe-

cific killing. More research is necessary to identify the specific causes of mortality for ocelots in this area.

The detection probabilities we estimated are among the highest values calculated for ocelot studies with remote cameras (e.g. Sternberg & Mays 2011, Pérez-Irinea & Santos-Moreno 2014). Detection probabilities were almost double in the second and third years (2011–2012) in comparison with the first year (Table 3). This could be due to the use of more cameras with a faster trigger system in the years following 2010 (Table 1). Considering the current range of digital camera models, we encourage the use of those cameras that present the best detection rates without losing good image quality to prevent the loss of information but also to facilitate reliable recognition of individuals.

Despite a growing number of arguments in favor or against the use of traditional capture-recapture models over SECR models (i.e. Foster & Harmsen 2012, de la Torre et al. 2016), our average MMDM value for ocelots (Table 4) is similar to those obtained in Chiquibul, Belize, using radio-telemetry (Dillon & Kelly 2008). We lacked radio-telemetry data for ocelots in this region, but consider that our ESA is large enough for the estimation of an unbiased MMDM.

Regardless of the approach used for density estimation, our calculations are the lowest reported across all of the species' distribution. Other studies that have reported low ocelot population densities were under human pressure: Atlantic Forest in Yabotí, Argentina, where logging occurs (5.8  $\pm$  1.6 ind. 100 km<sup>-2</sup>; Di Bitetti et al. 2008); landscape fragmentation and isolated populations in the Brazilian Atlantic Forest (2  $\pm$  1 ind. 100 km<sup>-2</sup>; Massara et al. 2015); and land conversion for agriculture in northeastern Mexico (3  $\pm$  0.2 ind. 100 km<sup>-2</sup>) (Martínez-Hernández et al. 2015). Because of the low human population density in our study area, we reiterate that our density results must

be associated with natural processes rather than human-caused disturbance, without dismissing an additive factor by the latter.

Contrasting seasonal changes, low precipitation, and xeric vegetation types with open canopy cover in the dry season have a negative influence over primary productivity and consequently on prey availability (Oliveira et al. 2010). Together they may be contributing as limiting factors for ocelot survival and density in this part of the species' range, as has been proposed for coexisting jaguar populations (Gutiérrez-González et al. 2012). The habitat features described above can be considered non-typical or sub-optimal ocelot habitats (Sunquist & Sunquist 2002). However, it seems that large tracts of unpopulated wildlands over a non-fragmented landscape allow ocelots to survive in this area, hence the importance of maintaining current habitat conditions for ocelots in order for this Neotropical species to continue to thrive in this region of North America.

**Acknowledgements.** We are grateful for the support provided by the Northern Jaguar Project and Naturalia for data availability and monitoring permissions on the Northern Jaguar Reserve from 2010 to 2012. We also thank each ranch owner for permission to carry out surveys on their properties. Thanks to the Acacia Conservation Fund, Defenders of Wildlife, Disney Conservation Fund, Jeniam Foundation, Patagonia, Shared Earth Foundation, and the Woodland Park Zoo. CONACYT provided a full scholarship for M.A.G.R. and C.E.G.G. The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. We are grateful to all of the researchers and others who helped us monitor wildlife at the Northern Jaguar Reserve. We also thank Megan 'Turtle' Southern for English and grammar corrections, and anonymous reviewers for comments on this manuscript.

#### LITERATURE CITED

- Barker RJ (1997) Joint modeling live-recapture, tag-resight, and tag-recovery data. *Biometrics* 53:666–667
- Brown DE (1994) *Biotic communities: southwestern United States and northwestern Mexico*. University of Utah Press, Salt Lake City, UT
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference. A practical information-theoretic approach*, 2nd edn. Springer, New York, NY
- CITES (2005) *Convention on International Trade in Endangered Species of Wild Fauna and Flora*. [www.cites.org](http://www.cites.org) (accessed 10 Nov 2013)
- Collins CT, Doherty PF Jr (2006) Survival estimates for royal terns in southern California. *J Field Ornithol* 77:310–314
- CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) (2004) *Climas de México*. Escala 1: 1 000 000. CONABIO, México
- de la Torre JA, Arroyo-Gerala P, Torres-Knoop L (2016) Density and activity patterns of ocelots in the Greater Lacandona Ecosystem. *Therya* 7:257–269
- Di Bitetti MS, Paviolo A, De Angelo C (2006) Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *J Zool* 270: 153–163
- Di Bitetti MS, Paviolo A, De Angelo C, Di Blanco YE (2008) Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*). *J Trop Ecol* 24:189–200
- Dillon A, Kelly MJ (2007) Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx* 41:469–477
- Dillon A, Kelly MJ (2008) Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *J Zool* 275:391–398
- Efford MG, Mowat G (2014) Compensatory heterogeneity in spatially explicit capture-recapture data. *Ecology* 95: 1341–1348
- Felger RS, Johnson MB, Wilson MF (2001) *The trees of Sonora, Mexico*. Oxford University Press, New York, NY
- Foster RJ, Harmsen BJ (2012) A critique of density estimation from camera-trap data. *J Wildl Manag* 76:224–236
- Gopalaswamy AM, Royle JA, Hines JE, Singh P, Jathanna D, Kumar NS, Karanth KU (2012) Program SPACECAP: software for estimating animal density using spatially explicit capture-recapture models. *Methods Ecol Evol* 3: 1067–1072
- Gopalaswamy AM, Royle JA, Meredith ME, Singh P, Jathanna D, Kumar NS, Karanth KU (2014) SPACECAP: an R package for estimating animal density using spatially explicit capture-recapture models. Version 1.1.0. Wildlife Conservation Society, India Program, Centre for Wildlife Studies, Bengaluru
- Grigione MA, Scoville G, Crooks K (2007) Neotropical cats in Southeast Arizona and surrounding areas: past and present status of jaguars, ocelots and jaguarundis. *Mastozool Neotrop* 14:189–199
- Gutiérrez-González CE, Gómez-Ramírez MA, López-González CA (2012) Estimation of the density of near threatened jaguar *Panthera onca*, in Mexico, using camera trapping and an open population model. *Oryx* 46: 431–437
- Gutiérrez-González CE, Gómez-Ramírez MA, López-González CA, Doherty PF Jr (2015) Are private reserves effective for jaguar conservation? *PLOS ONE* 10:e0137541
- Haines AM, Tewes ME, Laack LL (2005) Survival and sources of mortality in ocelots. *J Wildl Manag* 69: 255–263
- Harveson PM, Tewes ME, Anderson GL, Laack LL (2004) Habitat use by ocelots in south Texas: implications for restoration. *Wildl Soc Bull* 32:948–954
- Havlanová D, Gardiánová I (2013) Reproductive characteristics of the ocelot (*Leopardus pardalis*) under captive conditions. *Adv Zool Bot* 1:46–52
- Horne JS, Haines AM, Tewes ME, Laack LL (2009) Habitat partitioning by sympatric ocelots and bobcats: implications for recovery of ocelots in southern Texas. *Southwest Nat* 54:119–126
- INEGI (Instituto Nacional de Estadística Geografía e Informática) (2015) *Mapa digital de México*. <http://gaia.inegi.org.mx>
- IUCN (2012) *IUCN Red List of Threatened Species*, version 2012.2. [www.iucnredlist.org](http://www.iucnredlist.org) (accessed 10 Nov 2013)
- Karanth KU (1995) Estimating tiger *Panthera tigris* populations from camera trap data using capture-recapture models. *Biol Conserv* 71:333–338

- Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862
- Karanth KU, Chundawat RS, Nichols JD, Kumar NS (2004) Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Anim Conserv* 7:285–290
- Kendall WL, Barker RJ, White GC, Lindberg MS, Langtimm CA, Peñaloza CL (2013) Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods Ecol Evol* 4:828–835
- Laack LL, Tewes ME, Haines AM, Rappole JH (2005) Reproductive life history of ocelots *Leopardus pardalis* in southern Texas. *Acta Theriol (Warsz)* 50:505–514
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- López-González CA, Brown DE, Gallo-Reynoso JP (2003) The ocelot *Leopardus pardalis* in northwestern Mexico: ecology, distribution and conservation status. *Oryx* 37:358–364
- López-González CA, Aguilar-Miguel C, Mora-Carrillo F, González ZY (2014) Ocelot (*Leopardus pardalis*): an addition to the mammals of Chihuahua, Mexico. *West N Am Nat* 74:482–484
- Maffei L, Noss AJ (2008) How small is too small? Camera trap survey areas and density estimates for ocelots in Bolivian Chaco. *Biotropica* 40:71–75
- Maffei L, Noss AJ, Cuéllar E, Rumiz DI (2005) Ocelot (*Felis pardalis*) population densities, activity, and ranging in the dry forest of eastern Bolivia: data from camera trapping. *J Trop Ecol* 21:349–353
- Martínez-Hernández A, Rosas-Rosas OC, Clemente-Sánchez F, Tarango-Árambula LA, Palacio-Núñez J, Bender LC, Herrera-Haro JG (2015) Density of threatened ocelot *Leopardus pardalis* in Sierra Abra Tanchipa Biosphere Reserve, San Luis Potosí, Mexico. *Oryx* 49:619–625
- Massara RL, Paschoal AMdO, Doherty PF Jr, Hirsch A, Chiarello AG (2015) Ocelot population status in protected Brazilian Atlantic Forest. *PLOS ONE* 10:e0141333
- Murray JL, Gardner GL (1997) *Leopardus pardalis*. *Mamm Species* 548:1–10
- Norma Oficial Mexicana (2010) NOM-059-SEMARNAT-2010. Protección ambiental. Especies nativas de México de flora y fauna silvestres. Categoría de riesgo y especificaciones para su inclusión, exclusión o cambio. Lista de especies en riesgo. Diario Oficial de la Federación. Distrito Federal, Mexico
- Nowell K, Jackson P (1996) Wild cats: status, survey and conservation action plan. IUCN/SSC Cat Specialist Group, IUCN, Gland
- Nuñez R, Miller B, Lindzey F (2000) Food habits of jaguars and pumas in Jalisco, Mexico. *J Zool* 252:373–379
- O'Brien TG (2011) Abundance, density and relative abundance: a conceptual framework. In: O'Connell AF, Nichols JD, Karanth KU (eds) Camera traps in animal ecology. Springer, New York, NY, p 71–96
- Oliveira TG, Tortato MA, Silveira L, Kasper CB and others (2010) Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. In: MacDonald DW, Loveridge AJ (eds) Biology and conservation of wild felids. Oxford University Press, New York, NY, p 559–581
- Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on closed animal populations. *Wildl Monogr* 62:1–135
- Paviolo A, Crawshaw P, Caso A, de Oliveira T and others (2015) *Leopardus pardalis*. IUCN Red List Threat Species 2015:e.T11509A50653476
- Pérez-Irineo G, Santos-Moreno A (2014) Density, distribution, and activity of the ocelot *Leopardus pardalis* (Carnivora: Felidae) in Southeast Mexican rainforests. *Rev Biol Trop* 62:1421–1432
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Rodgers TW, Giacalone J, Heske EJ, Janečka JE, Phillips CA, Schooley RL (2014) Comparison of noninvasive genetics and camera trapping for estimating population density of ocelots (*Leopardus pardalis*) on Barro Colorado Island, Panama. *Trop Conserv Sci* 7:690–705
- Ruiz-Gutiérrez V, Doherty PF Jr, Santana E, Contreras Martínez S, Schondube J, Verdugo Munguía H, Iñigo-Elias E (2012) Survival of resident Neotropical birds: consideration for sampling and analysis based on 20 years of bird-banding e orts in Mexico. *Auk* 129:500–509
- Silver SC, Ostro LET, Marsh LK, Maffei L and others (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* 38:148–154
- Sternberg MA, Mays JL (2011) Ocelot survey in and around Laguna Atascosa National Wildlife Refuge. US Fish and Wildlife Service, South Texas Refuge Complex, Alamo, TX
- Sunquist M, Sunquist F (2002) Wild cats of the world. University of Chicago Press, Chicago, IL
- Trolle M, Kéry M (2003) Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *J Mammal* 84:607–614
- Trolle M, Kéry M (2005) Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. *Mammalia* 69:405–412
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S138

Editorial responsibility: Matt Hayward, Bangor, UK

Submitted: July 6, 2016; Accepted: March 23, 2017  
Proofs received from author(s): May 21, 2017