Characteristics of ocelot populations in Tamaulipas, Mexico, using capture–recapture techniques

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ABSTRACT: Although the ocelot *Leopardus pardalis* is listed as endangered in the USA and Mexico, research on the characteristics of ocelot populations in northeastern Mexico has been limited. Effective conservation strategies in this binational region can benefit from additional information on the distribution and status of these populations. We estimated ocelot abundance and density using capture–recapture data from remote cameras at 2 locations in Tamaulipas: 1 inland site near the Sierra Tamaulipas and 1 coastal site along the Laguna Madre. The inland site was sampled in 2013 with 32 camera stations, and estimated densities (mean ± SE ocelots per 100 km^2) using non-spatial and spatial modeling approaches were 17.57 ± 1.10 and 28.19 ± 6.81, respectively. The coastal site was sampled in 2017 with 16 camera stations, and estimated densities using non-spatial and spatial modeling approaches were 59.03 ± 2.32 and 43.24 ± 7.24, respectively. These are the first published ocelot densities for these locations, and these sites represent the closest known populations to those in Texas, USA. The ocelot populations surveyed appear to be robust, with estimated abundances similar to or greater than other areas surveyed within the state of Tamaulipas. Future work should monitor the long-term status and connectivity of these and other nearby populations to inform management actions to ensure their continued existence, as well as to assess whether they could serve as suitable sources for the translocation of individuals into existing populations in need of genetic rescue in Texas.

KEY WORDS: *Leopardus pardalis* · Northeastern Mexico · Camera trap · Spatial capture–recapture · Program MARK · Population density · Translocation

1. INTRODUCTION

The ocelot *Leopardus pardalis* occurs from North to South America, including south Texas and Arizona, USA, and south to Argentina (Paviolo et al. 2015). Ocelots occur across a broad range of vegetation types (Shindle & Tewes 1998, Harveson et al. 2004, Caso 2013, García-Bastida et al. 2016, Gómez-Ramírez et al. 2017, Lombardi et al. 2022), and population densities reported throughout their range vary widely from 1 to 94 ocelots per 100 km^2, with estimates from 1 to 39 ocelots per 100 km^2 in Mexico

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(Fernández 2001, Rocha et al. 2016, Monterrubio-Rico et al. 2018, Greenspan et al. 2020, Lombardi et al. 2022). Although across its range, the ocelot is considered by the IUCN to be a species of 'Least Concern' (Paviolo et al. 2015), it is listed as endangered in the USA (USFWS 1982) and Mexico (SEMARNAT 2010).

Ocelot research in the binational northeastern-most portion of its range has primarily been conducted in the USA. In Texas, ocelots have been the focus of many detailed ecological studies (Harveson et al. 2004, Haines et al. 2005, 2006b, Laack et al. 2005, Janečka et al. 2007, 2011, Sternberg & Mays 2011, Schmidt et al. 2020, Lehnen et al. 2021), the findings of which suggest that in this region, ocelots can be considered fragmentation-intolerant habitat specialists. Literature on the distribution and characteristics of ocelot populations roughly 200 km south in the state of Tamaulipas, Mexico, a neighbor state to Texas, USA, remains scant (Ocañas-García et al. 2018, Lombardi et al. 2022). The ocelot's current range in Mexico includes the northeastern states of Nuevo León and Tamaulipas (Velazco-Macías & Peña-Mondragón 2015, García-Bastida et al. 2016, Caso & Dominguez 2018). Thus far, the goal of research in this part of the ocelot range has been on identifying new locations of ocelot populations. Some studies modeled the potential distribution of ocelots on a regional or national scale for conservation planning (Martínez-Calderas et al. 2015, Monroy-Vilchis et al. 2019). In an evaluation of potential distribution of 4 tropical felid species, including the ocelot, Monroy-Vilchis et al. (2019) identified northeastern Mexico as a region with high habitat suitability for ocelots. Given the knowledge of the distribution and habitat suitability, an important next step is to evaluate population characteristics of ocelot populations in northeastern Mexico, including abundance and density, to determine status and trends.

To date, ocelot population densities have been evaluated at 1 Tamaulipan site on the northern edge of the Sierra Tamaulipas. Carvajal-Villarreal (2016) estimated ocelot densities per 100 km^2 to be 9.90 and 21.9, depending on the estimation method. In that study, ocelots demonstrated a significant preference for tropical deciduous forest relative to open habitats. Lombardi et al. (2022) estimated the density to be 11.69 ocelots per 100 km^2 using spatial capture–recapture (SCR) techniques from the same study area within a similar timeframe to Carvajal-Villarreal (2016). This study found that ocelots preferentially used tropical deciduous forest patches that afforded more interior cover, as measured by patch edge

length relative to total patch area. Given the scarcity of ocelot research in Tamaulipas, more investigation is needed on the distribution and characteristics of ocelot populations in this region to better inform scientists and wildlife managers in guiding binational recovery efforts for this species.

Evaluation of the status of ocelot populations in northeastern Mexico could have implications for binational conservation efforts. Ocelots in Texas represent the last breeding populations in the USA, and habitat loss and fragmentation have led to increased road mortality and genetic isolation, threatening local extinction in this region (USFWS 2016). In some areas of south Texas, 93% of the native habitat has been converted to agriculture, rangeland, or urban development since the 1930s (Tremblay et al. 2005). The Rio Grande delta region in the state of Tamaulipas, Mexico, has seen similar trends in land conversion and habitat loss (Purdy 1983, Sánchez Colón et al. 2009). There is a vast area of mostly unsuitable habitat that separates the historically connected ocelot populations of this binational region in Texas and Tamaulipas. In addition to preservation and restoration of habitat (Haines et al. 2006b), translocation of individuals into south Texas from genetically similar but more robust populations in northern Mexico has been suggested as a potential recovery strategy for at-risk populations in the USA (Haines et al. 2006b, Janečka et al. 2007, 2011), yet to date, suitable ocelot populations have not been identified.

With the present study, we add information on characteristics of ocelot populations in northeastern Mexico with the intention of identifying populations that could serve as sources for recovery of the ocelot in this binational region. We estimate ocelot abundance and density using traditional (non-spatial) and spatially explicit capture–recapture techniques at 2 ecologically different study areas, an inland site and a coastal site in northeastern Mexico. We use multiple methods to facilitate comparisons to other studies of ocelot abundance and density in Mexico that have used a variety of density estimation methods. Informed by previous research on tropical felids in northeastern Mexico (Caso 2013, Martínez-Calderas et al. 2015, Carvajal-Villarreal 2016, Monroy-Vilchis et al. 2019, Lombardi et al. 2022), we expected that ocelot density would be higher at the inland site, which is characterized by relatively intact habitat around the Sierra of Tamaulipas, relative to the human-induced fragmented state of the habitat along the coast.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in the state of Tamaulipas, Mexico, within the Northern Gulf Coastal Plains Province, and more specifically in the Tamaulipas Coastal Plains, and the Plains and Hills Sub-provinces (Instituto Nacional de Estadística y Geografía 2005; Fig. 1). The natural landscape is comprised of relatively flat terrain to rolling hills covered with tropical forests and xeric scrub (Commission for Environmental Cooperation 1997, Rzedowski 2006, Challenger & Soberón 2008), with several mountains nearby, such as the Sierra Tamaulipas, and coastal lagoons that are recognized for their significant wildlife conservation value (Comisión Nacional de Áreas Naturales Protegidas [CONANP] 2005).

Two camera surveys were undertaken, including the survey of an inland site in 2013, and a coastal site in 2017 (Fig. 2). Both study sites are within the legally defined 'Area of Influence' of the federally recognized protected area (SEMARNAT 2005) known in English as the Laguna Madre and Rio Grande Delta. This restricted-use area is a 5728 km^2 biosphere reserve recognized by UNESCO. Study sites were chosen based on landowner permission, reports of ocelot presence, presence of forested habitat anticipated to be of high quality for ocelots, staff safety, and reliability of access.

The inland study site was located 22 km east-southeast of Soto la Marina, Tamaulipas, located in the Sierra San José de las Rusias, an area characterized by deciduous forests at lower elevations, and deciduous and semi-deciduous thorny woodlands (Instituto Nacional de Estadística y Geografía 2005, Rzedowski 2006) on rocky hills at higher elevations, as well as some small, improved pastures for livestock. All cameras at the inland site were no higher than 300 m above mean sea level.

The coastal study site was located 60 km northeast of the inland site, along the Laguna Madre near the San José de los Leones community of Tamaulipas, Mexico. This site was located on a peninsula covered with lowland semi-deciduous forest and thorn forests and an understory of shrubs and native grasses, as well as some small, improved pastures for livestock fragmenting the forest patches. All cameras at the coastal site were no higher than 10 m above mean sea level.

2.2. Data collection and formatting

Using ArcGIS 9.3 (ESRI), a grid design of 700 × 700 m blocks was overlaid on each study site (Medellín et al. 2006), overlapping stands of forest and thorny woodland habitats due to their documented preferential use by
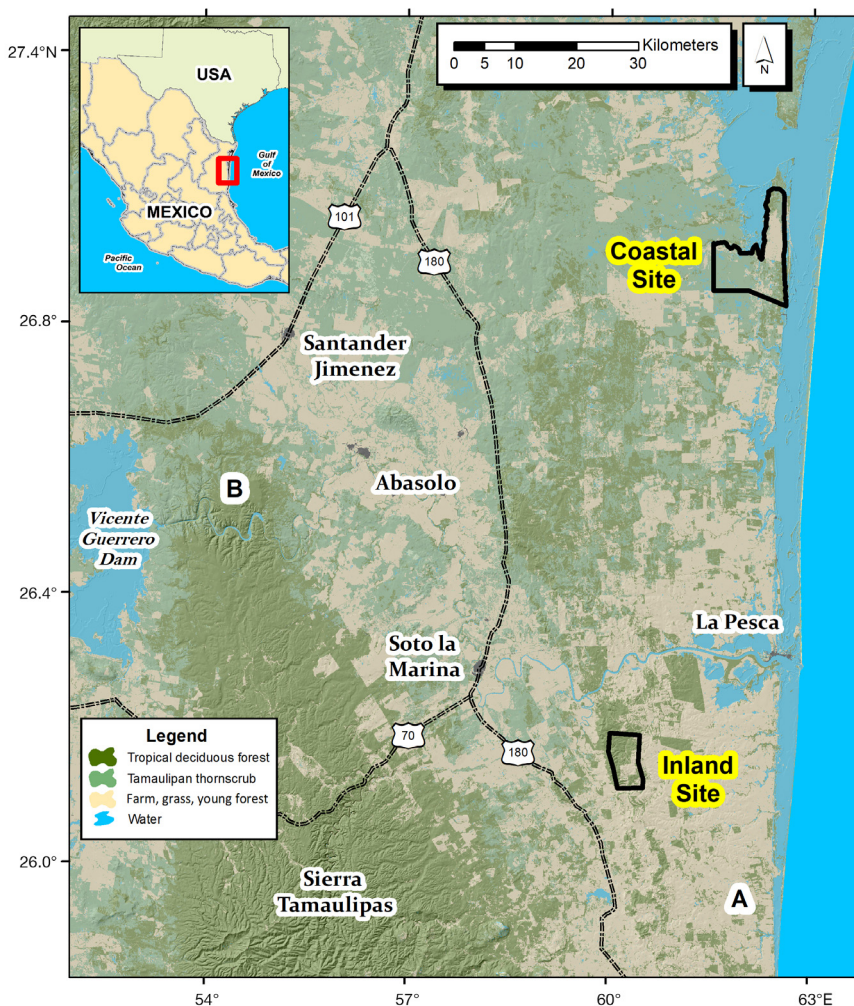

Fig. 1. Study sites from the present study: inland and coastal study sites (black polygons) along the coast of the state of Tamaulipas, Mexico; A: location of the study by Caso (2013); and B: the area of the studies by Carvajal-Villarreal (2016) and Lombardi et al. (2022). Land coverages adapted from Copernicus Sentinel 2 data (2016–18) processed by ESA–CCI Land Cover Project/UC Louvain/Brockmann Consult
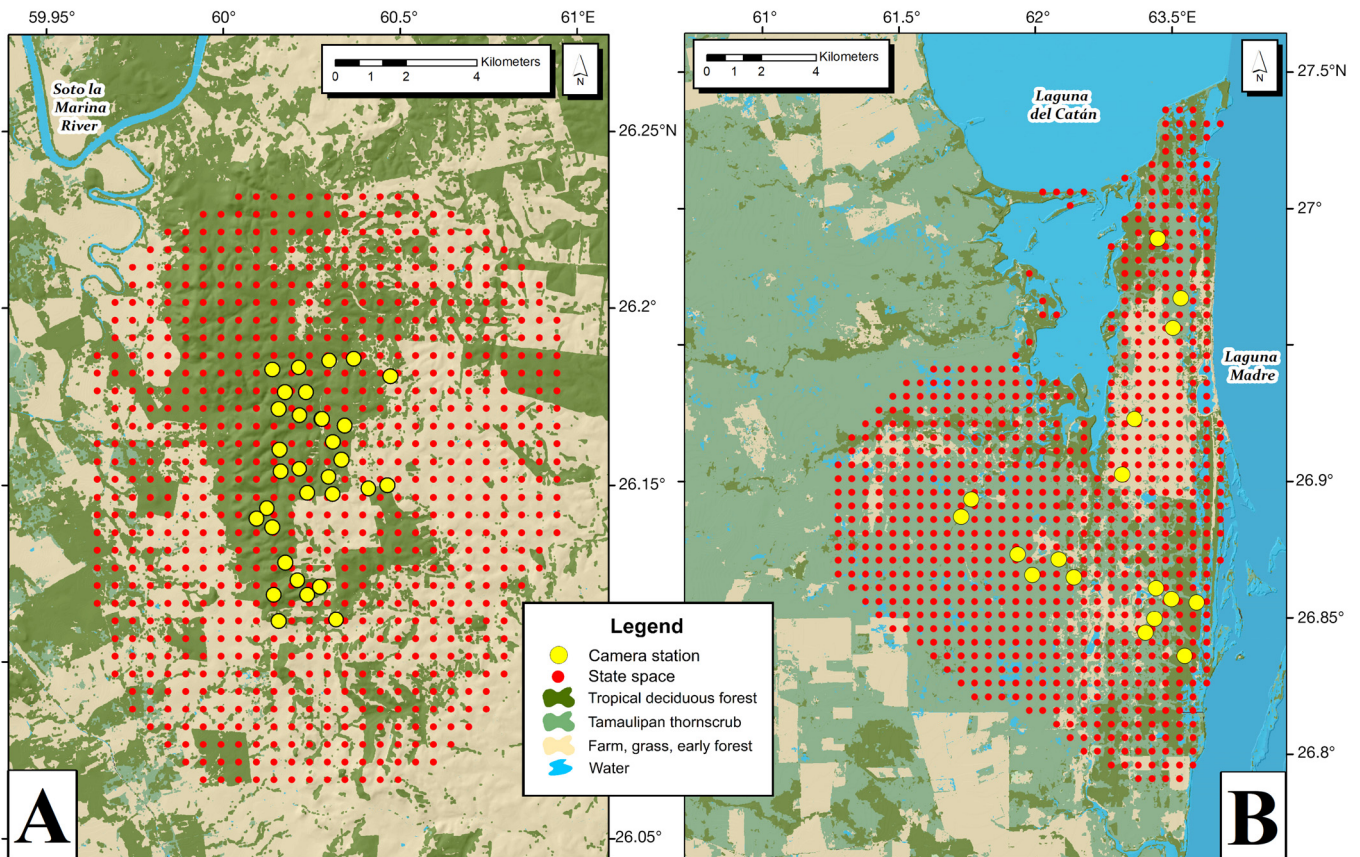
Fig. 2. (A) Inland study site and (B) coastal study site in Tamaulipas, Mexico. Each state space dot represents a pixel in which ocelot density is estimated. Land coverages adapted from Copernicus Sentinel 2 data (2016–18) processed by ESA–CCI Land Cover Project/UC Louvain/Brockmann Consult

ocelots *Leopardus pardalis* (Harveson et al. 2004, Horne et al. 2009, Caso 2013). Previous density analyses suggest that 2 to 4 traps per home range are required for precise, accurate estimates (Otis et al. 1978, Sun et al. 2014). The grid design resulted in several camera stations within the home range size reported from telemetry studies of ocelots in these habitat types, i.e. 8.5 to 9.5 km^2 for females and 11.6 to 15.1 km^2 for males (Caso 2013, Carvajal-Villarreal 2016). Cameras in the current study were placed in the field as close as possible to achieve 1 monitoring site per block, and preferentially along the edge of game trails or unimproved roads. Using cotton or nylon cord, cameras were attached to metal or wooden stakes, with the cameras being about 30 to 50 cm above the ground. The cameras at the coastal site were placed inside of security boxes for added safety from damage or theft.

Cameras were placed at 32 locations at the inland site and 16 locations at the coastal site. Ultimately, the camera configuration at the coastal site was clustered, while cameras were more evenly spaced across the sampling area at the inland site (Fig. 2). At the inland

site, the mean pairwise distance between all camera-trap stations was 3061 m (range: 418 to 7713 m). At the coastal site, the mean pairwise distance between all camera-trap stations was 6540 m (607 to 15 316 m).

We used multiple camera models (Reconyx®, Cuddeback® [Cuddeback Digital], HCO Scoutguard® [HCO Outdoor Products], or Bushnell® [Bushnell Outdoor Products]). Two cameras were placed at each location, and each camera pair, with cameras no more than 20 m apart, was set on opposite sides of the road or trail facing each other to capture both left and right profile patterns to effectively identify individuals (Trolle & Kéry 2003, Dillon & Kelly 2007, Sternberg & Mays 2011). We do not explicitly account for heterogeneity in camera performance in our modeling approach, in part because this was not considered during the design of the study, but we proceed with the assumption that the use of 2 cameras at each site compensates for this potential source of heterogeneity.

Cameras were active at the inland site from August 5 to December 8 in 2013, and at the coastal site from January 3 to October 22 in 2017. Cameras were oper-

ational 24 h d^{-1} throughout the sampling periods and checked every 7 to 14 d. Cameras used medium heat-sensitivity levels. Cameras took 1 to 3 photos when triggered by an animal, and the interval between photos was programmed to be 1 to 60 s, depending on settings of the respective camera.

Scent lures were used at the inland site to encourage ocelots to pause and inspect scents, thus allowing for higher-quality photos of both sides to be obtained to improve chances for individual identification. However, scent was only used intermittently both in time and space at the inland site. Scents included bobcat urine (Harmon Scents®), Wildcat Lure No. 2 (S. Stanley Hawbaker & Sons), and Obsession for Men (Calvin Klein®), and all scents were believed to be hormone-based, not food-based. Scent lures were added to a small section (ca. 9 cm by 9 cm) of carpet nailed to a log, or to a cotton ball inside a partially buried plastic tube (polyvinyl chloride tube; 7.6 cm long by 1.3 cm diameter). We acknowledge that adding scent attractant can potentially induce a 'trap-happy' behavioral response that can affect density estimates if this source of heterogeneity is not modeled (Yang & Chao 2005, Schmidt et al. 2022), and we discuss how we dealt with this in Section 2.4.

Photos of ocelots were classified by age and sex (Emmons 1988, Laack 1991, Haines et al. 2005, Lombardi et al. 2022, C. A. López González & M. A. Sternberg unpubl.). Ocelots were classified as kittens, subadults, or adults based on relative size, and reproductive characteristics such as a bare scrotum for adult males, and obvious swollen teats signifying lactation or lack of bare scrotum for adult females (C. A. López González & M. A. Sternberg unpubl.). The unique patterns of ocelots were used to identify individuals (Trolle & Kéry 2003, Sternberg & Mays 2011), and individual ocelots were given a unique alphanumeric code (Sternberg & Swarts 2021) to record individual capture histories.

Data were formatted into binomial capture histories divided into 14 d consecutive sampling periods. If an individual was photographed at a site in a sampling period, it was recorded as 1, and when it was not photographed, it was recorded as 0. The data from the inland and coastal sites consisted of 9 and 21 consecutive sampling periods, respectively. Due to a lack of obtaining simultaneous right and left profiles for some ocelots, rather than discard these detections, we created 2 datasets: a dataset of ocelots photographed from both profiles and the right side only (hereinafter, right-side), and another dataset of ocelots photographed from both profiles and the left side only (hereinafter, left-side) for both study sites.

2.3. Non-spatial capture–recapture analysis

A non-spatial capture–recapture modeling framework was used to estimate ocelot *Leopardus pardalis* abundance and density at each study site. Program CAPTURE was used to assess the capture histories for closure at each study site and to provide abundance and density estimates with which to compare to other studies (Otis et al. 1978, Rexstad & Burnham 1992).

Population size ($\hat{N}$) was estimated at both study sites with the Jolly-Seber model using the POPAN formulation (Schwarz & Arnason 1996) within Program MARK (White & Burnham 1999). POPAN assumes that a studied population is part of a super-population (N) in which unmarked animals have the same probability of capture as marked animals in the studied population (assumption of equal catchability), survival rates are homogeneous for marked and unmarked animals, the sampled area does not change, and there is no loss of marks during the study. The super-population size is defined as the total number of individuals forming part of the sampled population (Crosbie & Manly 1985).

The following parameters were used in POPAN: p_i as the probability of capture of marked and unmarked individuals on occasion i, $\square_i$ as the probability of survival (*phi*) of marked and unmarked individuals from occasion i to $i + 1$, and b_i as the probability of a new animal entering the population (*p ent*) between occasions i and $i + 1$ from the super-populations into the study site as a result of immigration and/or birth. A sin link function was used to estimate survival and recapture parameters in cases of a singular b_i parameter. A multinomial logit link function was used for b_i parameters to constrain the sum of these values to 1.00. A log link function was used to ensure convergence of the abundance parameter (Cooch & White 2019). The survival, recapture, and probabilities of entry parameters were marked as constant (·) or time-dependent (*t*) for the different models. Temporal variation was used for all 3 parameters. The number of estimable parameters was adjusted as necessary based on model output (Cooch & White 2019).

Goodness-of-fit (GOF) tests implemented in the Program Unified CApture-REcapture, also known as U-CARE (Choquet et al. 2005, 2009), can be used to assess the fit of a fully time-dependent model to data. U-CARE was used to identify variance in the survival or recapture probabilities of cohorts, and to assess transiency (Pradel et al. 1997) and trap-dependence (i.e. trap-happiness or trap-shyness; Pradel 1993), and can be useful in identifying whether particular

cohorts might be having significant influence on the overall fit of the data to the fully time-dependent Cormack-Jolly-Seber (CJS) model (Cooch & White 2019).

A variance inflation factor ($\hat{c}$) was used to correct for overdispersion in abundance model selection and final parameter estimation. Because U-CARE does not support GOF tests of POPAN models, a CJS model was used in Program RELEASE (Burnham et al. 1987) within MARK to derive values for $\hat{c}$ for each model. A second value for $\hat{c}$ was calculated by dividing the deviance of the general model by the mean deviance derived from 1000 parametric bootstrap simulations in MARK (Anderson et al. 1994, Cooch & White 2019). To be conservative, the highest value of $\hat{c}$ was used to adjust values for abundance model comparisons, whether from RELEASE or the second value as a result from the bootstrapping simulations (Cooch & White 2019).

Models were ranked using the Akaike information criterion adjusted for small population sizes (AICc; Anderson et al. 1994). AICc values were adjusted for over-dispersion from GOF testing to provide quasi-likelihood adjusted Akaike information criterion values (QAICc) (Anderson & Burnham 2002). The model with the lowest QAICc value was considered to offer the best balance in bias and precision (White & Burnham 1999, Cooch & White 2019).

Using the Minimum Bounding Geometry tool in ArcMap 10.8.1 (ESRI), we plotted the minimum convex polygon (MCP) as the boundary of the outer locations of cameras. We used the traditional ad hoc buffering approach of calculating mean maximum distance moved (MMDM) for all ocelots photographed at 2 or more camera locations as a proxy to estimate home range radius (Wilson & Anderson 1985, Karanth & Nichols 1998). We buffered the MCP around each study site's camera array by their MMDM to obtain the estimated sampling area (ESA) (Karanth & Nichols 1998, Maffei et al. 2005, Dillon & Kelly 2007, Pérez-Irineo & Santos-Moreno 2014). Abundance was estimated within defined ESAs. Density estimates were derived by dividing the abundance estimate from the model selected in MARK by the size of the ESA. Conditional standard error (SE) and 95% confidence intervals (CIs) for the MMDM density estimates were estimated with the delta method (Nichols & Karanth 2002) using the deltaMethod() function in the 'car' package (Fox & Weisberg 2019) in R version 4.2.2 (R Core Team 2021). We also estimated density using the half-MMDM and present these results in Section S4 in the Supplement (www.int-res.com/articles/suppl/n052p113_suppl.pdf).

2.4. Spatial capture–recapture

Ocelot density was estimated at both study sites using a multi-session SCR approach. SCR is an established update to non-spatial capture–recapture methods that overcomes assumptions of geographic closure by incorporating spatial heterogeneity in individual detection probability (Royle et al. 2013). Spatial relocations of unique individuals at multiple detector locations are used to estimate latent animal activity centers, commonly equated with home ranges or centralized space use of individuals, and detection probability is modeled as a function of distance between the detector and animal activity center (Royle & Young 2008). The spatial component of the hierarchical model also allows for an intrinsic definition of the sampling area, or state space, providing explicit estimates of density that can be homogeneous or vary spatially.

We fit SCR models using maximum likelihood methods in the package 'oSCR' (Sutherland et al. 2019) using R version 4.2.2 (R Core Team 2021). In SCR, the key parameters to be estimated include density, baseline detection probability, and the spatial scale parameter sigma. Baseline detection probability and sigma are parameters in the detection process of the hierarchical model. We used the half-normal model to define the attenuation of detection probability as the distance between the trap and the latent animal activity center increases. As with the non-spatial capture–recapture analysis, models were fit separately for the right-side dataset and the left-side dataset.

To fit the SCR model, density is estimated across a discretized area known as the state space. To avoid positively biased estimates, the state space must encompass a region around the camera trap array that contains all activity centers available for detection by traps. Additionally, the resolution of the state space should be fine enough that a single home range includes multiple discrete state space units, i.e. pixels. Preliminary models were fit by testing a range of state-space buffers to identify the point at which density estimates stabilized, and 5 km was selected as an appropriate state-space buffer for both study sites. Given previous research on ocelot movement distances in the region (2.3 km [females] to 2.4 km [males], Lombardi et al. 2022), state-space pixel resolution was set at 0.25 km^2. At the coastal site, we masked pixels that fell in the Laguna Madre. This yielded a 195.75 km^2 state space of 783 pixels for the inland site and a 199 km^2 state space of 796 pixels for the coastal site.

We employed a multi-session modeling approach, treating the study sites as separate sampling sessions integrated in a single framework in which key SCR parameters could be shared. We chose to hold sigma constant across the 2 study sites to overcome the lack of longer-distance spatial recaptures at the coastal site. We interpreted the absence of longer-distance recaptures as an artifact of the clustered sampling array rather than being reflective of ocelot movement within the coastal study site. We specified a model that allowed density and baseline detection probability to vary across study sites. Sex-specific information was incorporated into our capture histories (male, female, unknown), and therefore we fit all models using the sex-structured likelihood as described in Sutherland et al. (2019) and included an effect of sex on sigma, as males tend to have larger home ranges than females (33.2 vs. 21.3 km^2 [Dillon & Kelly 2008]; 11.6 vs. 9.5 km^2, respectively [Caso 2013]; 11.3 vs. 6.4 km^2, respectively [Carvajal-Villarreal 2016]). To test for the effect of scent on detection, we ran a preliminary model that included a trap-specific behavioral response unique to the inland study site, where scent was deployed, to account for a change in detection probability following the first detection of an individual at a specific trap, often referred to as a 'trap-happy' response. We did not find support for this effect and proceeded to estimate density with a model that did not include a trap-specific behavioral response. We report model results including a trap-specific behavioral effect in the Supplement, as referenced in Section 3. Below, we report model coefficients, estimates of density, abundance, sex ratios, baseline detection, and sigma with accompanying 95 % CIs for the inland and the coastal study sites.

3. RESULTS

3.1. Trapping effort and population demographics

Here we provide results for the right-side datasets. Results from the right-side and left-side datasets were similar. We present most of the results from CAPTURE and from the analyses of the left-side dataset in Sections S1–S5 in the Supplement.

Trapping effort for the inland site covered 3750 trap-nights, yielding a total of 102 ocelot *Leopardus pardalis* detections, including 98 for the right-side dataset. Trapping effort at the coastal site covered 5168 trap-nights, yielding a total of 234 ocelot detections, including 200 for the right-side dataset.

At the inland site, 21 ocelots were identified (13 photographed using both flanks); the right-side dataset consisted of 18 ocelots (7 females, 9 males, 2 sex unknown). At the coastal site, 51 ocelots were identified (25 photographed using both flanks); the right-side dataset consisted of 40 ocelots (16 females, 15 males, 9 sex unknown). Several ocelots were considered possible sub-adults at each site. No ocelots were classified as kittens, although several females exhibited visible signs of pregnancy during our study. Additional summary statistics are provided in Sections S1 & S2.

3.2. Non-spatial capture–recapture

Capture histories for the inland site met the assumption of closure (right-side: $z = 0.83$, p = 0.80), but the coastal site did not meet the assumption of closure (right-side: $z = -1.79$, p = 0.04) (Section S3).

The evaluation of most models with the POPAN formulation in MARK for the ocelot populations suggested the most parsimonious model was that considering ocelot survivorship and recapture probability as constants and probability of entry as time-dependent (Section S4, Table S2). The only exception was the inland site, for which the all-constant model was selected.

The inland site provided an MMDM for males of 3268 m (range: 1145 to 4093 m) and for females of 2191 m (range: 1634 to 2743 m), while the coastal site provided an MMDM for males of 1445 m (740 to 2220 m) and for females of 1177 m (740 to 1670 m). The overall MMDM for ocelots at the inland and coastal sites were 3005 m (SE: 339) and 1301 m (SE: 149), respectively. The ESAs derived using MMDM for the inland and coastal study sites were 108.98 and 76.52 km^2, respectively. For the coastal site, the portion of the ESA that included a large open-water bay, and beaches along the Gulf of Mexico was removed from the calculated area.

Using U-CARE, no significant evidence was found for trap-dependence (i.e. trap-happiness or trap-shyness) in the inland or coastal datasets (p = 0.34 and p = 0.62, respectively), but transiency was evident in the inland and coastal datasets (p = 0.02 and p = 0.04, respectively). Program RELEASE within MARK provided estimates of ĉ for the right-side and left-side datasets for the inland site and the coastal site as 0.93, 0.77, and 0.86, 1.00, respectively, yet parametric bootstrapping of the datasets provided the more conservative values for ĉ (Table 1, Table S2), and therefore these were used for model evaluation.

The ocelot abundance estimate from MARK for each of the inland and coastal study sites (right-side datasets) was 19.15 (SE: 1.44; 95% CI: 16.53 to 22.20) and 45.17 ocelots (SE: 3.14; 95% CI: 39.43 to 51.74), respectively. Using the MMDM, densities of ocelots at the inland and coastal sites were 17.57 per 100 km^2 (SE: 1.10; 95% CI: 15.41 to 19.73) and 59.03 per 100 km^2 (SE: 2.32; 95% CI: 54.49 to 63.57), respectively. See Section S4 & Table S3 for additional results, including densities using half-MMDM.

Table 1. Ocelot (*Leopardus pardalis*) abundance models, quasi-likelihood adjusted Akaike's information criterion (QAICc) values, measures of dispersion (ĉ), parameters (i.e. constant or time-dependent survival, recapture, probability of entry), and deviances used to select abundance estimator for inland and coastal study sites in Tamaulipas, Mexico. Includes ocelots photographed from both profiles and right-side only. Models evaluated using POPAN formulation in Jolly-Seber within Program MARK

Area	Model	QAICc	ĉ	Parameters	Deviance
Inland	*Phi*() *p*(.) *PENT*(.) *N*(.)	140.3	1.209	4	50.1
	Phi() *p*(.) *PENT*(t) *N*(.)	145.4		7	47.9
	Phi(t) *p*(t) *PENT*(t) *N*(.)	176.5		20	141.4
	Phi(t) *p*(t) *PENT*(.) *N*(.)	11820.4		13	11705.6
	Phi(t) *p*(.) *PENT*(.) *N*(.)	11836.4		8	11736.3
Coastal	*Phi*(.) *p*(.) *PENT*(t) *N*(.)	619.5	1.080	11	333.9
	Phi(.) *p*(t) *PENT*(.) *N*(.)	633.3		24	315.4
	Phi(t) *p*(t) *PENT*(t) *N*(.)	636.5		22	324.0
	Phi(.) *p*(t) *PENT*(t) *N*(.)	642.6		30	307.9
	Phi(t) *p*(t) *PENT*(t) *N*(.)	657.0		38	297.6
	Phi(t) *p*(.) *PENT*(.) *N*(.)	13562.9		12	14620.0
	Phi(.) *p*(.) *PENT*(.) *N*(.)	20296.1		3	21913.2

3.3. Spatial capture–recapture

Density at the inland site was estimated to be 28.19 ocelots per 100 km^2 (SE: 6.81; 95% CI: 17.56 to 45.25), with a state–space abundance of 46 individuals. Density at the coastal site was estimated to be 43.24 ocelots per 100 km^2 (SE: 7.24; 95% CI: 31.15 to 60.03), with a state-space abundance of 79 individuals. Fig. 3 provides a comparison of the non-spatial and spatial density estimates. Baseline detection probability at the inland site was 0.31 (SE: 0.04; 95% CI: 0.24 to 0.41). Baseline detection probability at the coastal site was 0.43 (SE: 0.05; 95% CI: 0.24 to 0.41). Sigma was held constant across the inland and coastal sites, but varied by sex, and was estimated to be 0.70 km (SE: 0.04; 95% CI: 0.61 to 0.79) for females and 1.18 km (SE: 0.08; 95% CI: 1.03 to 1.36) for males. Probability of being male was 0.35 (SE: 0.07; 95% CI: 0.21 to 0.49) at both sites, indicating a roughly 1:2 ratio of males:females. Previous studies across the ocelot range have found male-biased sex ratios (Belize: Satter et al. 2019), female-biased sex ratios (Argentina: Di Bitetti et al. 2006), and 1:1 sex ratios (Texas, USA: Laack et al. 2005). The sex ratio we report here for the surveyed Tamaulipas populations
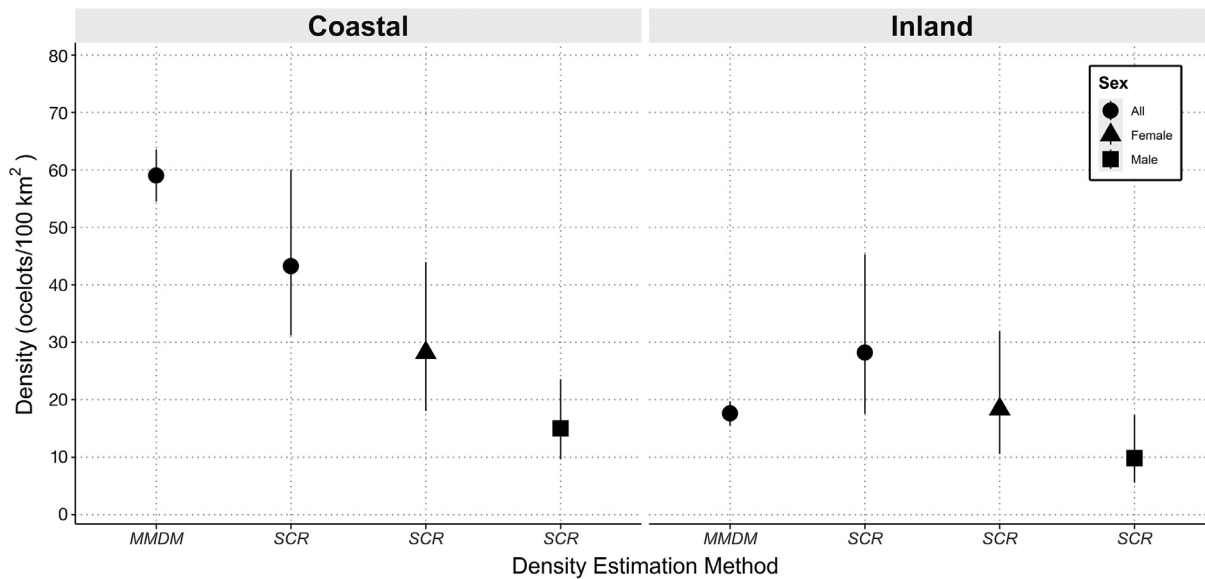

Fig. 3. Density estimates (with error bars representing 95% CI) of ocelots *Leopardus pardalis* across estimation approaches for the coastal and inland study sites from camera trapping in 2017 and 2013, respectively, in Tamaulipas, Mexico. MMDM: Program MARK with mean maximum distance moved; SCR: spatial capture–recapture

is not unexpected for this species. Model coefficients and transformed estimates for density, detection, and sigma for the right-sided models are reported in Table 2. Models were fit separately for the right-side dataset and the left-side dataset, and results from the left-side dataset analyses can be found in Section S5, Tables S4 & S5. As referenced in Section 2.4, to test for the effect of scent on detection, we ran a preliminary model that included a trap-specific behavioral response unique to the inland study site, where scent was deployed; results are presented in Tables S6 & S7 and Fig. S1.

4. DISCUSSION

The ocelot *Leopardus pardalis* is listed as endangered in Mexico (SEMARNAT 2010), though relatively little is published about its status in northeastern Mexico (Caso & Dominguez 2018, Ocañas-García et al. 2018, Monroy-Vilchis et al. 2019, Lombardi et al. 2022). The government of Mexico has stated that the first priorities for ocelot conservation in Mexico are to locate, protect, and monitor ocelot populations (SEMARNAT 2018). The areas of the current study have been highlighted by the Commission for the Knowledge and Use of Biodiversity (CONABIO) in Mexico as being a high priority for conservation efforts (Sarukhán et al. 2017). The current study adds to the body of work on the status and distribution of ocelot populations in northeastern Mexico, where relatively few field studies have been conducted. These are the first published ocelot densities for these locations, and the coastal study site represents the closest known ocelot population to those in Texas ca. 200 km to the north.

Our study suggests that ocelot densities in the foothills of the Sierra Tamaulipas and along the coast of central Tamaulipas are comparable to or higher than other densities reported in the state, and the coastal site in this study represents the highest reported in Mexico (i.e. 43.24 per 100 km² using SCR, 59.03 per 100 km² using Program MARK and MMDM). Density estimates were higher at the coastal study site relative to the inland study site, though the magnitude of the difference varied by the estimation method. We expected abundance and density estimates to be higher at the inland site than the coastal site, as the former is closer to the Sierra of Tamaulipas and extensive tracts of suitable ocelot habitat (Caso 1994, Stasey 2012, Lombardi et al. 2022). In contrast, the coastal site was relatively isolated on a peninsula, surrounded by the Laguna Madre and a primarily agricultural landscape to the south and west. We note that a direct comparison between the 2 sites is difficult, as the inland and coastal sites occurred in different geographies affecting the structure of available tropical deciduous forest habitat, the sites were separated by ca. 60 km, and the sites were evaluated across different seasons and different years. Continued monitoring of these populations and others nearby will be essential to understand population trends and inform successful conservation and management of ocelots in this region (Gómez-Ramírez et al. 2017, Amador-Alcalá et al. 2022, Lombardi et al. 2022), as well as any future binational translocation efforts. Long-term monitoring would be needed to ensure that ocelot populations in Tamaulipas would not be negatively impacted by translocation.

The higher ocelot density at the coastal site could also be a result of the heterogeneous landscape of primary and secondary forests and pasture in the general area, and the resulting diverse prey community (Monterrubio-Rico et al. 2018, Moreno-Sosa et al. 2022). The habitat of the coastal site was tropical deciduous forest, similar to habitat used by ocelots in Texas (Shindle & Tewes 1998). Neither the diet of

Table 2. (a) Model results and (b) transformed model results (i.e., transformed from the link scale to the real scale) with associated interpretations for the spatial capture–recapture density analysis of the right-sided dataset of ocelots *Leopardus pardalis* at inland and coastal sites. HR: home range

(a) Model results			(b) Transformed model results	
Parameter	Estimate	SE	Interpretation	Estimate (95% CI)
d0.(Intercept)	−2.65	0.24	Inland site density (ocelots per 100 km²)	28.19 (17.56−45.25)
d.coastal	0.43	0.29	Coastal site density (ocelots per 100 km²)	43.24 (31.15−60.03)
p0.(Intercept)	−0.77	0.20	Inland site baseline detection	0.32 (0.24−0.41)
p0.coastal	0.47	0.29	Coastal site baseline detection	0.42 (0.33−0.53)
sig.(Intercept)	−0.36	0.06	Female HR scaling parameter (km)	0.70 (0.62−0.79)
sig.male	0.53	0.09	Male HR scaling parameter (km)	1.18 (1.02−1.36)
psi.constant	−0.63	0.31	Probability of being male	0.35 (0.21−0.49)

ocelots nor the abundance of ocelot prey was evaluated as part of the current study, but rodents made up the primary prey for ocelots in Tamaulipan thornscrub in Texas (Booth-Binczik et al. 2013). Early successional forests and even brushy pastures can provide higher species richness and biomass of rodents than primary forests (Sternberg & Judd 2006). There were also differences in the occurrence of apex predators, including mountain lions and jaguars, which were detected at the inland site but were very few to absent, respectively, at the coastal site (M. A. Sternberg et al. unpubl.). Some studies have suggested little to no direct negative effect of these predators on ocelots (Oliveira et al. 2010, Davis et al. 2011, Massara et al. 2015, 2018). However, other research has suggested that a lack of pressure from jaguars has a positive effect on the abundance of mesocarnivores such as the ocelot (Moreno et al. 2006, Silva-Magaña & Santos-Moreno 2020); this could be the case in comparing ocelot densities at the inland and coastal study sites.

The density estimates at the 2 study sites are high relative to other ocelot densities reported from Mexico but fall within the range of densities for ocelots reported across their range (Rocha et al. 2016).

Ocelots have been reported in most states of Mexico (USFWS 2016), with population densities ranging from 1 to 38 ocelots per 100 km^2, and as high as 59 ocelots per 100 km^2 with the inclusion of the current study (Table 3). Density estimates from Texas range from 9 ocelots per 100 km^2 (effective sampling area; Sternberg & Mays 2011) to 30 ocelots per 100 km^2 (Half-MMDM; Haines et al. 2006a). For most studies in South America, as summarized by Rocha et al. (2016), densities ranged from 4.0 to 84.8 ocelots per 100 km^2, with an average value of 33.2 ocelots per 100 km^2. Research evaluating large-scale correlates of ocelot abundance suggests that ocelot densities decrease with latitude and increase with rainfall at the continental scale (Di Bitetti et al. 2008). Primary productivity, which can be a driver of prey density, may also play a role. These factors vary across habitats in Mexico, which may affect large-scale patterns in abundance and density (Table 3). Though our research effort was not designed to evaluate species–habitat relationships, we showed that ocelot densities differed across the 2 study sites. Given that the ocelot is widely distributed, additional research exploring spatiotemporal factors affecting ocelot population densities across its range, including those that

Table 3. Estimated densities of ocelots *Leopardus pardalis* reported from camera-trap and telemetry studies in Mexico, listed alphabetically by state and by year of publication. MMDM: mean maximum distance moved; SCR: spatial capture–recapture; RF: rainforest; CF: cloud forest; TDF: tropical deciduous forest; XS: xeric scrub. Density: if a study presents a range of density estimates, the largest estimate is provided

State	Study area	Habitat	Density (per 100 km^2)	Density estimator	Reference
Chiapas	Selva Lacandona	RF	12.9	SCR	De la Torre et al. (2016)
Jalisco	Chamela-Cuixmala Reserve	TDF	39.0	Telemetry	Fernández (2001)
Michoacan	El Naranjal, Playa del Venado	TDF	23.7	MMDM	Monterrubio-Rico et al. (2018)
Oaxaca	Los Chimalapas	RF	38.0	MMDM	Pérez-Irineo & Santos-Moreno (2014)
	Sierra Norte	RF, CF	7.8	MMDM	Pérez-Irineo et al. (2017)
Quintana Roo	Northern area of state	TDF	14.0	MMDM	Torres-Romero et al. (2017)
	El Edén	TDF	5.1	SPACECAP	Ávila-Nájera et al. (2015)
	El Edén	TDF	13.8	MMDM	Ávila-Nájera et al. (2015)
San Luis Potosi	Sierra Abra-Tanchipa	TDF	18.0	SCR	Martínez-Hernández et al. (2015)
Sonora	Northern Jaguar Reserve	XS	1.3	SCR	Gómez-Ramírez et al. (2017)
	Northern Jaguar Reserve	XS	2.9	MMDM	Amador-Alcalá et al. (2022)
	Northern Jaguar Reserve	XS	3.1	SCR	Amador-Alcalá et al. (2022)
Tamaulipas	Sierra of Tamaulipas	TDF	19.2	MMDM	Stasey (2012)
	Sierra of Tamaulipas	TDF	21.9	Telemetry	Carvajal-Villarreal (2016)
	Sierra of Tamaulipas	TDF	11.7[a]	SCR	Lombardi et al. (2022)
	Inland site (2013)	TDF	17.6	MMDM	Current study
	Inland site (2013)	TDF	28.2	SCR	Current study
	Coastal site (2017)	TDF	59.0	MMDM	Current study
	Coastal site (2017)	TDF	43.2	SCR	Current study

[a]A combination of the estimate for females and males from the cited study

field-validate regional and national suitability models (Martínez-Calderas et al. 2015, Monroy-Vilchis et al. 2019), would be valuable.

Using multiple methods of density estimation affords comparability of our results with other studies across the ocelot range. While our intention is not to compare the performance of non-spatial (e.g. Program MARK) with spatial (e.g. SCR) methods, we note that SCR is currently the recognized standard for robust density estimation, particularly for wide-ranging carnivores (Dupont et al. 2021). SCR can explicitly accommodate the assessment of species–habitat relationships, including spatial variation in detection and density, which can be useful for understanding drivers of variability in ocelot population parameters through space and time. Density estimates could also be corroborated or strengthened by data integration, e.g. including assessments of home range using data from GPS collars (Royle et al. 2013), and we encourage researchers to employ spatially explicit methods for ocelot abundance and density estimation (Satter et al. 2019). At the inland site, MARK- and SCR-based density estimates were similar, though SCR estimates incorporated a broader CI, possibly due to the modeled differences in male and female home ranges and densities, which is reflective of ocelot ecology, where males have larger home ranges than females (Dillon & Kelly 2008, Caso 2013, Carvajal-Villarreal 2016). SCR density estimates from the coastal site were lower and with broader CIs than the MARK-based density estimates. Estimates from MARK, because they did not account for individual spatial variation in detection probability and did not incorporate the differences of male–female movements, may be biased or overly precise.

The length of the sampling period at the coastal site (i.e. 10 mo) may have led to the lack of closure in that dataset (Foster & Harmsen 2012). Previous efforts to estimate ocelot density in this region also struggled to obtain sufficient sample sizes for SCR analyses within a short time period (4 mo; Lombardi et al. 2022). Karanth & Nichols (1998) and Silver et al. (2004) conducted studies of jaguars for 2 to 3 mo to reduce the likelihood of violating the assumption of population closure. We used the full 10 mo period to ensure there was sufficient information for the capture–recapture and SCR analyses, while acknowledging that there could be some bias incurred with this larger sampling window. For continued long-term monitoring efforts, we recommend a more intensive sampling effort within 3 or 4 mo periods to obtain sufficient data for analyses.

By using a multi-session framework, we jointly estimated density for the coastal and inland sites, using information from both study sites to inform the home range scaling parameter sigma, which may in part explain the larger differences in density estimates among methods at the coastal site relative to the inland site (Howe et al. 2013, Morin et al. 2018). The multi-session modeling approach used in our SCR analysis was useful to overcome a limitation of the coastal site study design. The distribution of habitat at the coastal site resulted in a clustered camera array, and given resulting ocelot movements, clusters were located too far from each other for sufficient among-cluster recaptures. This resulted in most spatial recaptures (i.e. 1 individual caught at multiple traps) being close together, which can erroneously yield a small home range parameter relative to actual ocelot movement, with implications for overestimating density (Maffei & Noss 2008, Sollmann et al. 2012). Future sampling efforts in coastal Tamaulipas could prioritize a design with a more regular distribution and higher density of cameras that covers the full range of available habitat gradients relevant to ocelots to provide for a larger percentage of recaptures in a shorter time and to better assess density–habitat relationships.

Improved understanding of ocelot populations in northeastern Mexico could have important implications for binational conservation efforts. The relatively high density of ocelot populations in Tamaulipas, and observations of several possible subadults and pregnant ocelots at each study site, speaks to the productivity of these areas and the potential robustness of the 2 populations. Although we did not classify any ocelots as kittens during our survey periods, several females appeared pregnant or were being tracked closely by kittens around the time of our study (M. A. Sternberg et al. unpubl.). Data on population characteristics were of great interest to the federal government of Mexico in their review of the binational translocation plan for ocelots in 2010 (M. A. Sternberg et al. pers. obs.). It is important to have reports of these populations evaluated by the respective agencies to identify whether one or both these populations are suitable sources for translocation of a limited number of ocelots to reduce the threat of local extinction in the USA (Haines et al. 2006b, Janečka et al. 2007, 2011). The benefits of conservation translocation involving ocelots from Mexico and Texas could be similar to the positive results achieved with the genetic rescue of the Florida panther (Hostetler et al. 2010, Johnson et al. 2010, Penfold et al. 2022) or the population recovery of the Sonoran pronghorn (US-FWS 2017, 2021, Hahn & Culver 2021).

The current study is an example of effective collaboration among the government, private sector, and academic institutions from Mexico and the USA, to locate and study ocelot populations as part of the binational recovery effort for ocelots (USFWS 2016, SEMARNAT 2018). The USFWS and its partners on this study welcome collaborative opportunities to continue to monitor, and in this way, assist in managing populations in northeastern Mexico to build upon and leverage efforts towards binational recovery for the ocelot. These population estimates add to knowledge of ocelot distribution and abundance in northeastern Mexico. Future work should implement protocols to continue to monitor the long-term status of ocelot populations in this biodiverse region (Arriaga et al. 2000, Ortega-Huerta & Peterson 2004, Sarukhán et al. 2017), as well as to make a robust assessment of their suitability as source populations for conservation translocation into at-risk populations.

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