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Ocelot density and habitat use in Tamaulipan thornshrub and tropical deciduous forests in Northeastern México

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Northeastern México is one of the most diverse regions in the country with high mammal richness. This region also sits on the northern periphery of the geographic distribution of ocelots (*Leopardus pardalis*), which are listed as endangered in México. Ocelot ecology in northeastern México is poorly known at local and landscape levels, especially in the ecologically rich temperate sierras, a perceived stronghold for ocelots. We used an occupancy approach to estimate ocelot-habitat use in Tamaulipan thornshrub and tropical deciduous forests and a spatially explicit capture–recapture (SECR) framework to estimate density of ocelots in the northern edge of the Sierra Tamaulipas, México. From May to December 2009, we conducted two camera trap surveys (summer: 20 camera stations; fall: 58 camera stations) on Rancho Caracol and Rancho Camotal, north of the Rio Soto de La Marina. We found ocelot detections were higher in areas with increasing patch density of tropical deciduous forest and habitat use was greater in Tamaulipan thornshrub and tropical deciduous forests with lower edge densities. Ocelot densities varied by sex, with females achieving greater densities (7.88 ocelots/100 km^2 [95% CI: 4.85–12.81]) than males (3.81 ocelots/100 km^2 [95% CI: 1.96–7.43]). Ocelots were averse to areas with high densities of edge cover in each woody community, supporting the notion of a forest patch interior species. Despite the study occurring 11 years ago, population densities were also among the highest reported in México using spatially explicit capture–recapture methods, The high ecological integrity of the habitat within the Sierra de Tamaulipas, recent protection as a Biosphere Reserve, and remote rugged terrain suggest long-term security of the ocelot population in this region.

Key words: edge density, *Leopardus pardalis*, population monitoring, spatially explicit capture–recapture models, Tamaulipas, Tamaulipan Matorral, Tamaulipan Mezquital

El noreste de México es una de las regiones más diversas del país y una zona con alta diversidad de mamíferos. Esta región también se encuentra en la periferia norte del rango de distribución del ocelote (*Leopardus pardalis*), el cual está catalogado como en peligro de extinción en México. La ecología de los ocelotes en el noreste de México es poco conocida a escala local y de paisaje, especialmente en las sierras templadas, de alto valor ecológico y consideradas como un bastión para los ocelotes. Empleamos un enfoque de ocupación para estimar el uso del hábitat del ocelote en los bosques caducifolios de Tamaulipas y en los bosques tropicales de hoja caduca, así como un marco SECR para estimar la densidad de los ocelotes en el límite norte de la Sierra de Tamaulipas, México. Entre mayo y diciembre de 2009, realizamos dos sondeos mediante cámaras trampa (verano: 20 localizaciones con cámara; otoño: 58 localizaciones con cámara) en Rancho Caracol y Rancho Catamol, al norte del Río Soto de La Marina. Encontramos que las detecciones de ocelote fueron mayores a mayor densidad de parche en los bosques tropicales de hoja caduca y que el uso del hábitat fue mayor en los bosques caducifolios de Tamaulipas y en los bosques tropicales a densidades de borde más bajas. Las densidades de ocelote variaron según el sexo, con las hembras alcanzando mayores densidades [7,88 ocelotes/100 km^2 (95% CI: 4,85–12,81)] que los machos [3,81 ocelotes/100 km^2 (95% CI: 1,96–7,43)]. Los ocelotes evitaron aquellas áreas con altas densidades de cobertura de borde en cada comunidad leñosa, apoyando la idea del ocelote como especie de interior de parche forestal. Las densidades de población también estuvieron entre las más altas reportadas en México utilizando métodos de captura-recaptura espacialmente explícitos. A pesar de que el estudio fue realizado hace 11 años, la alta integridad ecológica del hábitat dentro de la Sierra de Tamaulipas, su reciente protección como Reserva de la Biosfera y el terreno accidentado y aislado sugieren que la población de ocelote en esta región se encuentra asegurada a largo plazo.

Palabras clave: densidad de borde, espacialmente explícitos, *Leopardus pardalis*, matorral de Tamaulipas, mezquital de Tamaulipas, modelos de captura-recaptura, seguimiento poblacional, Tamaulipas

Human-mediated changes in natural landscapes represent one of the main causes of biodiversity loss worldwide (Seto et al. 2011). In North America, México is considered a megadiverse country that contains 12% of the world's biodiversity but has been affected by high rates of deforestation and ecological loss (Ortega-Huerta and Peterson 2004; Vázquez-Reyes et al. 2019). From 1970 to 2000, this loss of woody cover has been attributed to agricultural and urban expansion, with urbanization rapidly increasing over the last two decades (Bonilla-Moheno et al. 2012). The country contains a rich mammal diversity; the fifth-highest mammal richness worldwide (Ceballos 2014).

Northeastern México (Tamaulipas and Nuevo Leon) is one of the most diverse regions in the country and is considered a major biodiversity hotspot for species richness, endemism, and threatened and endangered species (Ortega-Huerta 2004; Ceballos 2014; Vázquez-Reyes et al. 2019). This region spans multiple climatic zones and eco-regions but historically was not immune to landscape change (Ortega-Huerta and Peterson 2004; Treviño-Carreón and Valiente-Banuet 2005; Grigione et al. 2009). Areas along the Rio Bravo (*sic*: Rio Grande) experienced extensive clearing of native Tamaulipan thornshrub on each side of the border, which has contributed to reductions in local mammal populations, especially carnivores (Leslie 2016; Bonilla-Moheno and Aide 2020; Lombardi et al. 2020a).

Due to its rich biodiversity, the region has designated many protected areas, biosphere reserves, and priority regions for conservation (Arriaga et al. 2000; Vázquez-Reyes et al. 2019). Many of the protected areas and regions occur in remote and remnant temperate forests of the Sierra Madre Oriental, and sky islands of the Sierra San Carlos and Sierra Tamaulipas in Nuevo Leon and southern Tamaulipas (Ortega-Huerta and Peterson 2004; Monroy-Vilchis et al. 2019; Vázquez-Reyes et al. 2019). These extensive mountainous areas have also retained high ecological integrity, biodiversity, naturalness, and landscape heterogeneity (Ortega-Huerta and Medley 1999; Ortega-Huerta and Peterson 2004; Mora 2017, 2019). Protected and priority regions of northeastern México are thought to have retained larger populations of carnivores, as compared to areas along the border (Mora 2017).

This region sits on the northern geographic periphery of a variety of neotropical carnivores such as jaguar (*Panthera onca*), white-nosed coatimundi (*Nasua narica*), jaguarundi (*Puma yagourundi*), margay (*Leopardus weidii*), and ocelot (*Leopardus pardalis*; Ceballos 2014; Hunter 2015). Compared to elsewhere in their geographic range, these species may be threatened or rare; thus, protection of these peripheral populations is of important conservation value (Grigione et al. 2009; Mora 2017, 2019). Peripheral population protections or lack thereof can differ by species, conservation value, and distribution within each country. For instance, in Texas, the white-nosed coatimundi is considered rare and threatened, with limited distribution in the borderlands, but in Tamaulipas and Nuevo Leon, they are common mesocarnivores. Regardless of conservation status, ecological evaluation of population-level processes and habitat use is important for conservation and recovery action of threatened and endangered species (Monroy-Vilchis et al. 2019).

Ocelots are medium-sized neotropical felids and are listed as endangered in the United States and México (Ceballos 2014; Hunter 2015). Populations in Tamaulipas, Nuevo Leon, and southern Texas are considered genetically similar but have remained genetically isolated for more than 80 years (Janeĉka et al. 2007; Caso et al. 2008). Threats in each country impacting ocelot populations include habitat loss and fragmentation, environmental stochasticity, road mortality, illegal hunting, and loss of genetic diversity (López-González et al. 2003; Janečka et al. 2007; Martinez-Hernandez et al. 2015; Blackburn et al. 2020). Populations in southern Texas (<80 individuals) face a >33% probability of extirpation by 2055 without population augmentation or mitigation measures (Haines et al. 2005). Compared to Texas, ocelot populations in México are considered more stable occurring along the Sierra Madre Occidentalis in the west, throughout central and southern México, and into the Sierra Madre Oriental and Tamaulipan Mezquital in northeastern México (Ceballos 2014). Consequently, ocelots occur in a variety of dense vegetation types ranging from moist broadleaf forests (Pérez-Irineo and Santos-Moreno 2014; Martínez-Hernández et al. 2015), tropical deciduous and sub-deciduous forests (De Villa Meza et al. 2002; Caso 2013), pine-oak woodlands (Barcenas and Medellin 2010), and semi-arid scrubland (Velazco-Macías and Peña-Mondragón 2015). Additionally, ocelots continue to be documented in nontypical habitats across México (see Gómez-Ramírez et al. 2017).

Less than 10 studies have undertaken ecological research on ocelot populations in northeastern México at local (Caso 1994, 2013; Martínez-Hernández et al. 2015; Velazco-Macías and Peña-Mondragón 2015; Carvajal-Villarreal 2016) and landscape levels (Ortega-Huerta and Peterson 2004; Martínez-Calderas et al. 2015; Mora 2017). Ecological evaluations of ocelot population strongholds in this region, especially in the remote and ecologically rich temperate sierras are important for informing bi-national and regional conservation strategies of ocelots. Information on biological processes such as population density and landscape structure (e.g., patch density, edge density, shape index) that influence habitat use and quality can be used to manifest information about ocelots and infer high productivity of protected areas and vegetation classes (Jackson et al. 2005; Mora 2017; Lombardi et al. 2020b). Furthermore, the inclusion of sex-specific variations in local population estimates and sex ratios can help further refine management and conservation efforts (Satter et al. 2019).

We designed the study in the northern Sierra Tamaulipas to use an occupancy approach to identify habitat use patterns of ocelots in Tamaulipan thornshrub and tropical deciduous forests and use a spatially explicit capture–recapture (SECR) framework to estimate population size and density. This information will allow us to gain a better understanding of the population dynamics of the central Tamaulipas metapopulation located in the foothills of the northern Sierra Tamaulipas. We predicted (i) spatial structure and pattern of woody communities would reflect ocelot use of larger areas with lower edge densities of thornshrub and deciduous forest; (ii) ocelot densities and encounter probabilities would vary by sex, with females having greater densities, and (iii) densities may reflect a potential stronghold for ocelots in northeastern México.

Materials and Methods

Study area.—Our study occurred on Rancho Caracol and Rancho Camotal in the northern edge of the Sierra Tamaulipas of central Tamaulipas, México (125.3 km^2) (Fig. 1). Annual climate included 40–86 cm precipitation (Leopold 1959), and temperatures of 19°C in the dry (November to April) and 26°C in the wet (May to October) seasons (Comisión Nacional de Áreas Naturales Protegidas 2005). The area occurred within the confluence of the Tamaulipan Mezquital, Tamaulipan Matorral, and northern edge of the Veracruz moist forests eco-regions (Ricketts et al. 1999). The Rio Soto La Marina formed the southern border of the study area. Elevations ranged from 100 to

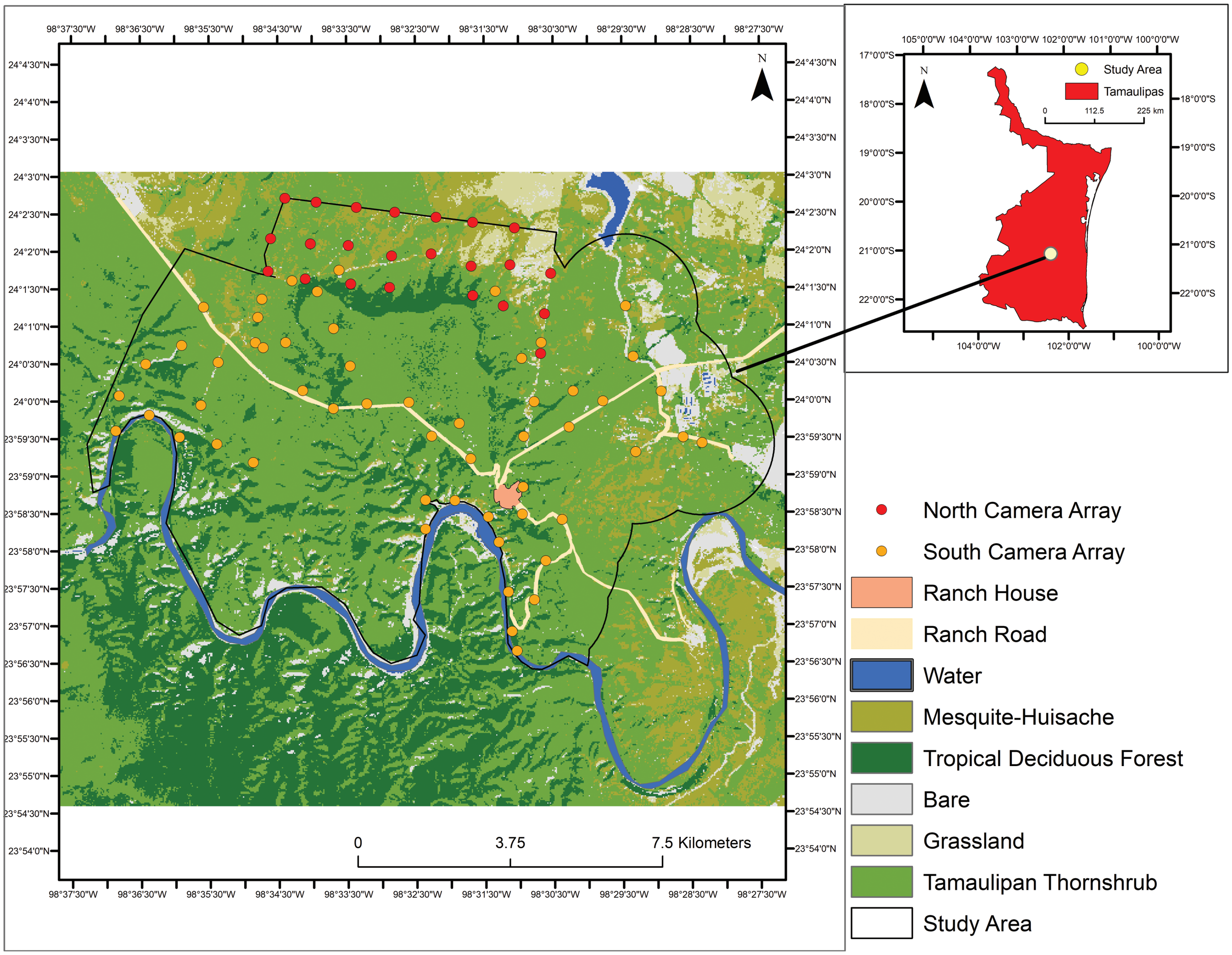

Fig. 1.—Study area on Rancho Caracol and Rancho Camotal in the northern Sierra de Tamaulipas, Tamaulipas, México used for camera trap surveys to estimate ocelot (*Leopardus pardalis*) density and habitat use from 24 May to 9 December 2009.

350 m, across rolling ridgelines, natural drainages, and ravines; elevation changes also were indicative of shifts in the vegetation community. The study area had a diverse plant community made up of Tamaulipan mesquite (*Prosopis glandulosa*)–huisache (*Celtis pallida*) shrubland and dense Tamaulipan thornshrub communities (*sic* Tamaulipan Mezquital) located at lower elevations characterized by cenizo (*Leucophyllum frutescens*), blackbrush (*Acacia rigidula*), and skeleton-leaf goldeneye (*Viguiera stenoloba*; Cram et al. 2006). At higher elevations (>300 m) were patches of closed canopy tropical deciduous forest, located along the ridgelines, ravines, and slopes and were characterized by ebony (*Pithecellobium ebano*), Berlandier's jopoy (*Esenbeckia runyonii*), mahuira (*Phoebe tampicensis*), mauto (*Lysiloma divaricata*), and gumbo-limbo (*Bursera simaruba*; Martin et al. 1954; Cram et al. 2006).

Camera surveys.—We conducted two independent camera surveys in the summer (24 May to 28 August 2009) and fall (29 August to 9 December 2009). Camera spacing was based on earlier recommended spacing (800–1,200 m) for ocelot camera surveys (Dillon and Kelly 2007). During the summer, 23 camera stations were set in the northern edge of the study area, and in the fall 58 camera stations were placed at different sites across the wider southern extent of the study area. Cameras were set along game trails, ranch and pasture roads, and near areas of water in patches of Tamaulipan thornshrub, evergreen forest, and mesquite-huisache woodlands because ocelot occurrence was strongly tied to these vegetation communities in México (Caso 1994, 2013; Martinez-Hernandez et al. 2015). At each camera station, we set one to two Cuddeback Capture 3 (Nontypical Inc., Green Bay, Wisconsin) or WildView Xtreme (Stealth Cam, LLC, Grand Prairie, Texas) camera-traps at each station with a 30-s delay between photographs. Cameras were attached to trees or wooden stakes 0.5 m above the ground and two camera stations (summer: 23; fall: 20) were offset 1–2 m to aid in individual identification of ocelots (Satter et al. 2019). We checked cameras once a month to minimize data loss from dead batteries or malfunctioning cameras.

We identified individual ocelots photographed by their unique asymmetrical pelage patterns. We compared rosette and spotting patterns on the flanks, head, tail, and legs to identify individual ocelots (Haines et al. 2006; Satter et al. 2019; Greenspan et al. 2020; Nipko et al. 2020). A team of three observers was used to confirm the identity of each ocelot (e.g., right and left flanks, and facial markings). We also used the pelage pattern software HotSpotter (Crall et al. 2013) to ensure no individual detections were missed (Nipko et al. 2020). Individuals that were unable to be identified (e.g., oblique angle of animal or obstructed view) and partially identified individuals (*n* = 1; right-only or left-only flanks) were removed from the analyses (Gómez-Ramírez et al. 2017; Greenspan et al. 2020).

Landscape analysis.—Landscape structure is important to study the ways carnivores use or perceive potential changes in the spatial structure and composition complexity of vegetation patches on the landscape. This allows for a better understanding of the effects these landscape patterns can have on population processes or ecological relationships among Carnivora (Zemanova et al. 2017; Lombardi et al. 2020b). Consequently, we quantified landscape metrics to discern the effects of landscape structure, complexity, and composition on ocelot-habitat use and detection.

Following Lombardi et al. (2020a), we conducted an unsupervised vegetation classification of the northern edge of the Sierra Tamaulipas (which includes our study area) using 30 m Landsat 5 imagery from 2009 in ERDAS IMAGINE 2015 (Hexagon Geospatial, Norcross, Georgia) obtained from the USGS Global Visualization Viewer. We classified imagery based on five vegetation communities including Tamaulipan thornshrub, tropical deciduous forest, mesquite-huisache, herbaceous/grassland, and bare-ground. We digitized permanent bodies of water (e.g., Rio Soto La Marina and man-made ponds), human development (e.g., ranch headquarters), and caliche ranch roads. We conducted an accuracy assessment using field-collected ground truth points collected in 2009 and 2010 and a confusion matrix to validate our classified imagery, achieving a 91.5% accuracy (Congalton 1991).

We followed methods described by Lombardi et al. (2020b) to discern the effects of spatial structure of woody vegetation on ocelots. We created 500 m buffers around each camera site (sampling unit) and conducted a landscape class-level metric analysis using the *landscapemetrics* package in R (Hesselbarth et al. 2019). For Tamaulipan thornshrub and tropical deciduous forest cover types, we estimated the size (mean patch area [MPA; ha]), patch density (PD; the number of patches/km^2), and complexity of patches (landscape shape index [LSI]), which yield an index of patch fragmentation. We examined the amount of edge per unit area (edge density [ED; m/ha]) and used the total proportion of cover (PLAND; %) to examine the percentage of area covered by each vegetation community around each sampling unit. These metrics were derived from five a priori hypotheses that we thought influenced ocelot-habitat use and detection based on previous ocelot-habitat studies in its geographic range (Supplementary Data SD1; Jackson et al. 2005; García-R et al. 2019; Lombardi et al. 2020b).

Occupancy habitat analysis.—We used single-season occupancy analyses for each survey season to assess the effect of landscape structure on ocelot-habitat use and detection probability. We also used these analyses as a proxy for identifying habitat features with high to low-density potential because species presence and density are correlated (Claire et al. 2015; Lewis et al. 2015). Following Lombardi et al. (2020b), we interpreted occupancy as habitat use, due to the 800–1,200 m distance between camera stations, which is smaller than an average ocelot activity center (Satter et al. 2019). Consequently, we defined habitat use (ψ) as the probability that an ocelot will use a particular site. Detection (ρ) was defined as the probability of detecting an ocelot at a particular site, at a specified occasion (MacKenzie et al. 2017; Lombardi et al. 2020b). We defined capture histories based on a one-week occasion, which was chosen to ensure we did not violate assumptions of independence. The first ocelot photographed within the defined seven-day occasion at a specific camera station was marked as detection for each day.

We conducted our analyses using Program PRESENCE v10.9 (Presence v10.9, http://www.mbr-pwrc.usgs.gov/software/presence.html, accessed on 6 June 2021). Due to the small size of the dataset, we built models using only one covariate in each model to ensure model convergence. We defined 12 biologically relevant candidate models to be fit, based on seven total a priori hypotheses thought to influence ocelot detection and habitat use (Supplementary Data SD1). Before model selection, we scaled all continuous variables in PRESENCE to ensure comparability across models. A hierarchal modeling process was used following Lombardi et al. (2020b) where we first modeled detection and then used the top-performing variable for our habitat use models. We considered two detection models based on a within-season trend and the linear distance from each camera station to the nearest permanent water source (i.e., ponds, water guzzler, streams, and river). Using the top detection model, we fit 11 biologically relevant models for habitat use. We assessed model fit and removed models that did not converge from the analyses. The most significant models were when ΔAICc < 2.00 (Burnham and Anderson 2002; MacKenzie et al. 2017) and model averaging was used if the same variable was identified in multiple competitive models. We defined 95% confidence intervals and considered beta-coefficients in competitive models that overlapped zero to be informative but not supportive.

Population density.—A single-season SECR model was used to estimate the population density of ocelots (summer: north grid, fall: south grid), and based on these estimates, we estimated population size across the defined state-space area. We created a capture history based on each unique identifier of an ocelot, stations where detected, and the number of detections. The sex of each ocelot was identified in the capture history based on evidence of external testes in males during image processing (Satter et al. 2019). We built a camera station matrix that indicated the spatial coordinates of each station and the operational status of each camera throughout the survey period.

The package *secr* in Program R (Efford 2021) was used to estimate the population density of ocelots (ocelots per 100 km^2) for each camera grid with a half-normal detection function and proximity detectors, which reflected a Bernoulli independent encounter model (Efford 2011; Satter et al. 2019). We followed the methods described by Greenspan et al. (2020) to determine the proper size of the state space to ensure it encompassed every detected animal in the area near the camera grids. It has been previously suggested that a minimum of >3 times the estimated value for the spatial-scale movement parameter (σ) be used (M. Efford, [University of Otago, Dundein, New Zealand], personal communication, [July, 2014]). We defined an initial buffer size for the state space using the *suggest.buffer* tool in *secr* and then generated five competing models with buffers that extended from the trapping array until density stabilized. Following this exploratory analysis, we determined a state-space buffer of 6 km was sufficient for ocelots in this study.

For density models, we assumed a constant trend (D ~ 1) and a sex-variation in density (D ~ sex) because ocelot reproductive strategies suggest there may be multiple female activity centers within a single male activity center (Laack et al. 2005; Hunter 2015; USFWS 2016), so we hypothesized density would vary across sexes. For the encounter probabilities (g0) and σ, we fit all combinations of the default variables and modeled each as a function of a constant fixed baseline encounter rate across occasions and individuals (g0 ~ 1) and constant spatial scale across individuals (σ ~ 1). The effect of sex on individual encounter probability (g0 ~ sex) was modeled and the spatial-scale parameter was sex-specific (σ ~ sex). We considered whether the encounter probability changed occasion to occasion for individuals based on the previous detection at that camera station (i.e., a trap-specific behavioral response; g0 ~ bk), and an additive sex response (g0 ~ bk + sex). AIC_c for model selection was used and top competing models were considered to be ≤2.00 (Burnham and Anderson 2002). We calculated 95% confidence intervals (CI) for all beta-coefficients for each parameter (D, g0, σ) and if the 95% CI crossed zero, we considered effects on parameters to be informative but not supported. To remove uncertainty in model selection, we averaged the model parameter estimates for models that were considered to have substantial support given the data and reported estimates based on these averages. We then used the *pop.regN* tool in package *secr* and the top-performing density model to estimate population size of ocelots across the defined state-space area surrounding the southern trap array.

RESULTS

Habitat use.—In the northern camera survey (May–August 2009) we had 15 ocelot detections over 2,020 trap nights and in the southern camera array (August–December 2009) we had 129 ocelot detections over 5,534 trap nights. We observed similar naïve occupancy estimates: north = 0.40; south = 0.37. In the northern grid, we were more likely to detect ($\rho_{\text{top model}} = 0.25$, 95% CI: 0.19–0.33) ocelots that occurred in areas of increasing patch densities of tropical deciduous forest (β = 1.03; 95% CI: 0.15–1.91; Table 1, Fig. 2). However, each top variable for habitat use, Euclidean distance to nearest patch (β = –5.05; 95% CI: –11.88 to 1.78), and patch density (β = –1.44; 95% CI: –1.93 to 0.44) of tropical deciduous were informative, but not supportive (Table 1). In the southern grid, patch density of tropical deciduous forests (β = 0.12; –95% CI: 0.02–0.26) was found to be informative for ocelot detectability but not supportive. Habitat use ($\Psi_{\text{top model}}$ = 0.39; 95 CI: 0.25–0.55) of ocelots in the southern grid decreased as edge densities of Tamaulipan thornshrub (β = –0.04; 95% CI: –0.07 to –0.01) and tropical deciduous forest (β = –0.05; 95% CI: –0.09 to –0.02) increased (Table 1, Fig. 3).

Density.—Based on unique spotting patterns, we identified 34 different individuals (10 males and 24 females) during the study. In the northern camera array, we identified nine individuals (four male and five females) and in the south, we identified 29 individuals (10 males and 19 females) with four individuals identified in both camera arrays. Due to the lack of spatial recaptures at more than one camera station in the northern camera array, we did not estimate density for that survey period. In

Table 1.—Results of model selection based on the difference of AICc between a model and the model with the smallest AICc (ΔAICc), model weights (ω), and the number of model parameters (*k*) used to estimate habitat use (φ) and detection (ρ) in Tamaulipan thornshrub (TT) and tropical deciduous forests (TDF) at Rancho Caracol and Rancho Camotal in the northern edge of the Sierra de Tamaulipas, México, from 24 May to 28 August 2009 (north) and 29 August to 9 December 2009 (south). Edge density refers to total density of edge (m/ha) of a vegetation community within each sampling unit; Euclidean nearest neighbor refers to the linear distance between two similar patches of a vegetation community within each sampling unit, and patch density refers to the density of patches per km^2 within each sampling unit.

Grid	Model	ΔAICc	ω	Σω	k
north	φ (TDF Euclidean Nearest Neighbor), ρ (TDF Patch Density)	0.00	0. 47	0.47	4
	φ (TDF Patch Density), ρ (TDF Patch Density)	1.18	0.15	0.62	
south	φ (TT Edge Density), ρ (TDF Patch Density)	0.00	0.52	0.52	4
	φ (TDF Edge Density), ρ (TDF Patch Density)	1.76	0.22	0.74	4

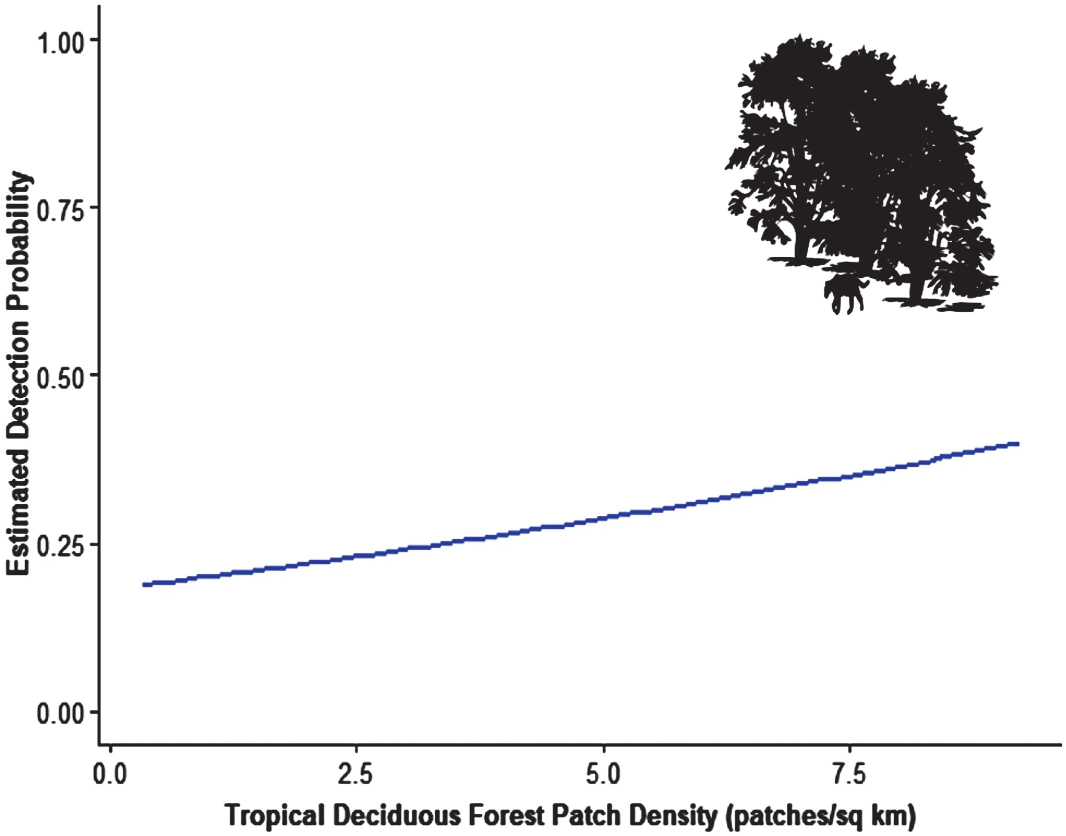

Fig. 2.—Probability of detection of ocelots as a function of increasing patch density of tropical deciduous forests in the northern camera array during May to August 2009 on Rancho Caracol and Rancho Camotal in the northern Sierra de Tamaulipas, Tamaulipas, México.

the south, we detected ocelots at 30 of 58 sites and observed 147 spatial recaptures. Only one "right-only individual" was removed from the analysis.

Model selection indicated support for three top models (Table 2), which were model-averaged. We observed sex differences in each parameter estimate and observed a trap-specific behavioral response, which affected encounter probabilities. Female ocelots had the greatest density (7.88 ocelots/100 km^2; 4.85–12.81), lower encounter probabilities (0.40; 29.62–55.24), and shorter movement distances (2,320 m; 1,973.44–2,727.81). Male densities were more than two times lower than females (3.81 ocelots/100 km^2; 1.96–7.43), with slightly greater encounter probabilities (0.43; 30.77–60.09) and greater movement distances (2,444.14 m; 1,979.12–3,018.41). The estimated population size in the state-space area was estimated to be 42.23 ocelots (26.18–68.13).

DISCUSSION

This study demonstrates the importance of understanding the habitat use patterns and the density of ocelots in a remote mountain range in northeastern México. Ocelot-habitat use in these areas was impacted by increasing edge densities of Tamaulipan thornshrub and evergreen forests. The study, albeit a decade old, indicates a potentially robust population of ocelots occurring at high densities in the northern edge of the Sierra Tamaulipas range, which is important for regional and bi-national conservation efforts of ocelots. These results help describe a potential highly productive and quality thornshrub-tropical deciduous forest system in the northern edge of the temperate Sierra de Tamaulipas. Density estimates reported here are among the greatest ocelot densities documented in México and across their geographic range using SECR models

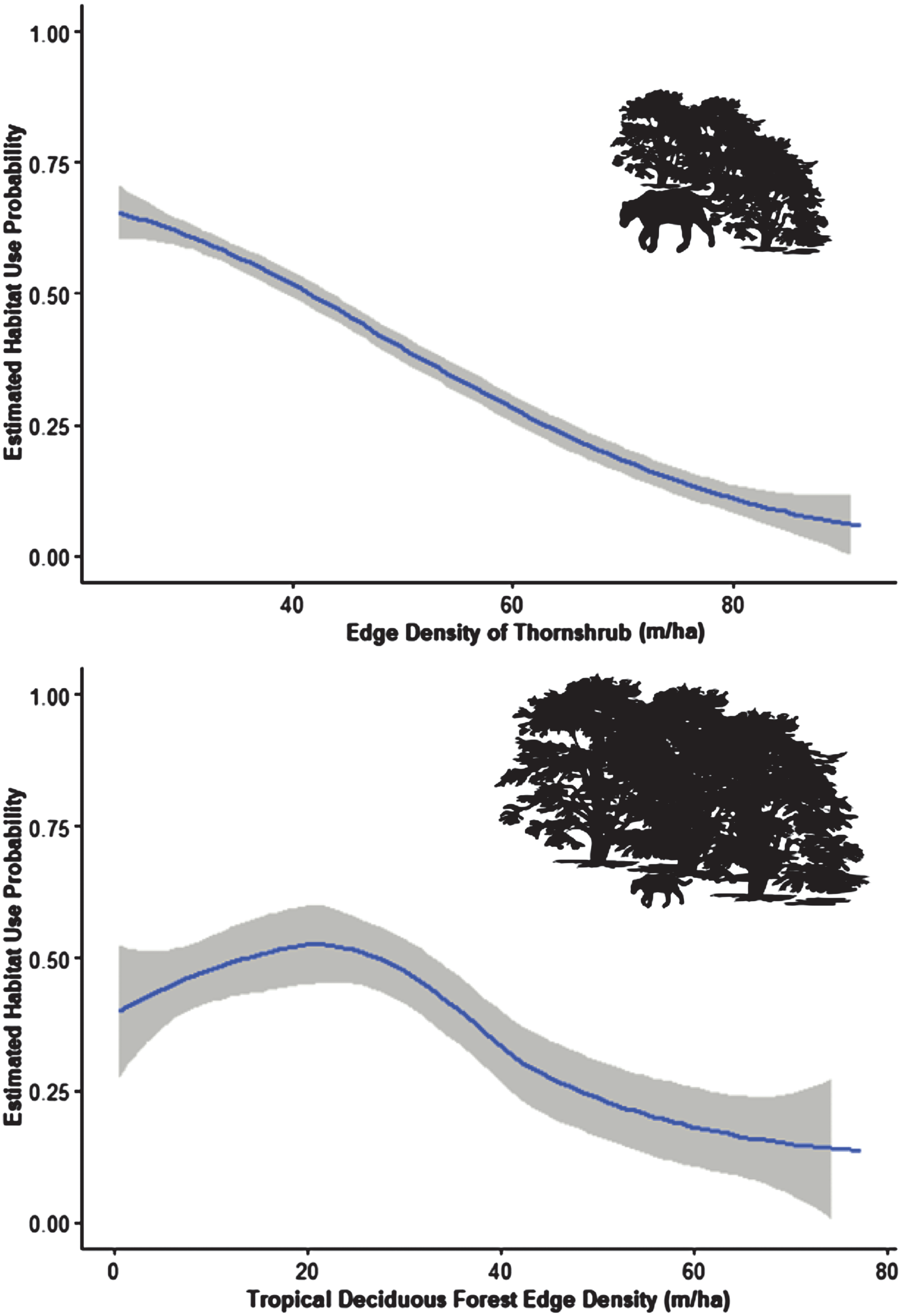

Fig. 3.—Probability of habitat use by ocelots as a function of edge density of Tamaulipan thornshrub (top) and tropical deciduous forests (bottom) in the southern camera array during August to December 2009 on Rancho Caracol and Rancho Camotal in the northern Sierra de Tamaulipas, Tamaulipas México.

Table 2.—Model selection results for maximum likelihood spatially explicit capture–recapture models used to estimate population density (D), encounter probabilities (g0), and spatial-scale movement parameters (σ) for ocelots (*Leopardus pardalis*) from 29 August to 9 December 2009 (fall) using a half-normal detection function in the southern part of the Rancho Caracol and Rancho Camotalstudy areain the northern edge of the Sierra Tamaulipas in Tamaulipas, México. Competitive models were ranked by Akaike's Information Criterion corrected for small sample sizes (AICc) with the most informative models having an AICc <2.00.

Model	AIC	AICc	ΔAICc	ω	Σω	K
D ~ sex g0 ~ Bk σ ~ 1	2,249.50	2,252.11	0.00	0.36	0.36	5
D ~ sex g0 ~ Bk σ ~ sex	2,249.52	2,253.34	1.23	0.19	0.55	6
D ~ sex g0 ~ Bk + sex σ ~ 1	2,250.01	2,253.83	1.72	0.15	0.70	6

(Martinez-Hernandez et al. 2015; Rocha et al. 2016; Gómez-Ramírez et al. 2017; Satter et al. 2019; Greenspan et al. 2020).

Ocelots were averse to using areas with high densities of edge cover and showed similar trends in use in edge densities across the two cover types. Areas of high edge densities occurred near pasture and ranch roads, human-modified areas (e.g., ranch lodging), and in elevation transition zones of tropical deciduous forest and thornshrub. In the study area, Tamaulipan thornshrub was found at lower elevations compared to tropical deciduous forest, which occurred at >300 m elevation in linear patches on ridgelines. Therefore, higher edge densities between the two cover types are likely the result of elevation changes in vegetation, slope, and aspect, rather than human-modified changes. We suggest, however, that these results indicate ocelots, which are strongly tied to forested cover (Wang et al. 2019; Lombardi et al. 2020b), will more likely use interior areas of patches with lower edge densities. These results corroborate a recent study in the northern Andes of Colombia, which demonstrated ocelots were likely to occur in forested areas with higher edge densities of forested cover (García-R et al. 2019). Furthermore, these findings are similar to studies from across their range that link ocelots to interior areas of increasing forested cover (Wang et al. 2019; Lombardi et al. 2020b), and less likely in human-modified areas with greater edge densities (Jackson et al. 2005; Massara et al. 2018; Paolino et al. 2018).

Detection of ocelots also increased with higher patch densities of tropical deciduous forest in the northern camera array and was an informative variable in the southern array. These patches occurring at higher elevations in this area had continuous canopies (>20 m tall) with dense understories of shrubs and cacti. In the northern camera array, tropical deciduous forest is found along a large mesa before descending into lower elevation Tamaulipan thornshrub. Ocelots may be more detectable in these areas due to increased foraging opportunities within this vegetation community, which is one of the most species-rich communities in México (Florez and Gerez 1994). These results also corroborate detections of ocelots in high-elevation tropical deciduous forests in the neighboring Sierra Madre Oriental (Martinez-Meyer and Lopez 1999; Fernandez 2002; De Villa Meza 2002) and coastal tropical deciduous forest (Caso 1994, 2013).

Our sex-specific ocelot densities were among the largest reported for ocelots (regardless of sex) in México using SECR models (range 0.51–25 ocelots/100 km^2; Martinez-Hernandez et al. 2015; Rocha et al. 2016; Gómez-Ramírez et al. 2017; Greenspan et al. 2020). Martinez-Hernandez et al. (2015) estimated 3 to 18 ocelots/100 km^2 across three different seasons, 300 km south-southwest of our study area in the Sierra Abra-Tanchipa Biosphere Reserve in eastern San Luis Potosi. However, unlike the studies in San Luis Potosi (Martínez-Hernández et al. 2015) and Sonora (Greenspan et al. 2020), ocelots occurring in our study area were free of intense anthropogenic pressure, indicating ocelots in this area were occurring at natural densities where requisite habitat was available. Furthermore, the sparse number of bobcat (*Lynx rufus*) detections (six), and high ocelot densities may reflect the absence of competition between the two species, thus not limiting ocelot populations (López-González et al. 2003; Greenspan et al. 2020). Comparison to other studies across México and South Texas (Haines et al. 2006; Pérez-Irineo and Santos-Moreno 2014; de la Torre et al. 2016) are difficult due to the use of non-SECR approaches, which often over-inflate estimates (Lewis et al. 2015; Satter et al. 2019).

Density estimates reported in this remote area of the Sierra Tamaulipas are similar to those reported in productive and remote lowland broadleaf rainforest sites in Belize using similar SECR approaches (Satter et al. 2019). Our study is the second ocelot study to date to incorporate sex-specific variation for movement and detection parameters. Accounting for individual heterogeneity (i.e., sex-specific, and behavioral responses) can help biologists avoid negatively biasing their density estimates (Sollman et al. 2011; Abadi et al. 2013; Royale et al. 2013; Satter et al. 2019). However, trap-specific behavioral responses are usually linked to lures or baits used to help increase detection in some studies, which was not the case here. Satter et al. (2019) suggested behavioral responses present in ocelot SECR models are likely due to variation in capture probabilities because of individual heterogeneity. Furthermore, we observed a sex-specific variation in movement, where female ocelot movement parameters were 60% lower than male ocelots. This finding supports the observation that males are more likely to be detected at multiple camera stations because they have larger home ranges than females. Across their geographic range, male ocelots typically have larger movement rates than females, which have been observed in Belize (Satter et al. 2019) and Texas (M. Tewes, unpublished data).

We acknowledge there are limitations to our study, as density only applies to the southern grid from late August to early December. However, we strongly contend the survey duration biased our estimates. Unlike in North American temperate felids (e.g., *Lynx* spp.), there are no data to support seasonal trends in ocelot survival or mortality in the region. Ocelot reproduction in the region also occurs throughout the year, with young staying with their mothers for 18 months, much longer than sympatric bobcats. This makes it unlikely that this survey period was more indicative of dispersing individuals compared to other seasons (Laack et al. 2005; Lombardi et al. 2020b). Another potential limitation is the age of the study, which occurred 11 years ago. We contend these population density estimates are unlikely to have differed over time due to the high ecological integrity, biodiversity, naturalness, and landscape heterogeneity in these temperate sierras (Mora 2017; Monroy-Vilchis et al. 2019). Further, the Sierra Tamaulipas was declared a protected area as the Sierra Tamaulipas Biosphere Reserve, which coupled with its rugged terrain and infertile soils helps provide long-term security to ocelot populations.

Our study suggested the densities and the local population in our study area were large, however, extrapolating population densities to estimate population size across the entire Sierra de Tamaulipas is an informative exercise with major limitations. Our study area was smaller compared to the remainder of the mountain range and we observed varied results in the study area in each camera array. For example, in the northern camera array, we detected and identified fewer ocelots with fewer spatial recaptures. It is plausible that such differences in abundance can vary across topographic gradients and vegetation communities not observed in this study, which makes extrapolation of accurate range-wide population estimates difficult.

Conservation implications.—Long-term, continuous monitoring of this population and surrounding populations should be an integral part of the management of ocelots in northeastern México. Population density estimates provided here are among the highest for México and recent findings indicate there is the potential for more ocelots in other vegetation communities and elevations in the greater region. Since 2010, female ocelots and kittens were observed in lowland valleys 20 km northeast of the study area (Global Biodiversity Information Facility 2021) and Caso and Dominguez (2018) recently documented an ocelot population in the Sierra San Carlos, located 55 km north of our study site. Consequently, there may be potential for this larger metapopulation to serve as a sustainable source population to supplement smaller, more genetically isolated ocelot populations throughout their northeastern range.

Vegetation communities used by ocelots throughout their range are affected by human land-use practices (Hunter, 2015; Massara et al. 2018; Lombardi et al. 2020b). Studies in remote regions of their range (similar to our study) indicate the potential for high population densities in areas with highly productive vegetation communities and free of significant impacts. Throughout northeastern México, more conservation focus is needed for ocelot populations in other vegetation communities across elevation gradients such as high-elevation pine-oak woodlands, low-lying Tamaulipan Mezquital, and tropical deciduous forest, especially outside of protected areas. We also suggest continued protection of tropical deciduous forests in México, which have declined in some areas (Pérez-Vega et al. 2012; Vázquez-Reyes et al. 2019) and serve as important refugia for the six native felid species in México (Florez and Gerez 1994; Monroy-Vilchis et al. 2019).

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Supplementary Material

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—A priori hypotheses for each landscape metric for both Tamaulipan thornshrub and tropical deciduous forests, and detection variables used in occupancy framework to understand habitat use patterns of ocelots (*Leopardus pardalis*) on Ranchos Caracol and Camotal in the northern edge of the Sierra de Tamaulipas, Tamaulipas, Mexico.

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