Received: 21 June 2024 | Revised: 22 October 2024 | Accepted: 5 December 2024

DOI: 10.1111/csp2.13301

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access
WILEY

Jaguar density estimation in Mexico: The conservation importance of considering home range orientation in spatial capture–recapture

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Funding information
Consejo Nacional de Humanidades, Ciencias y Tecnologías (Conahcyt), Grant/Award Number: 3369

Abstract

Accurate estimation of population parameters for imperiled wildlife is crucial for effective conservation decision-making. Population density is commonly used for monitoring imperiled species across space and time, and spatial capture–recapture (SCR) models can produce unbiased density estimates. However, many imperiled species are restricted to fragmented remnant habitats in landscapes severely modified by humans, which can alter animal space use in ways that violate typical SCR model assumptions, possibly cryptically biasing density estimates and misinforming conservation actions. Using data from a two-year camera-trapping survey in the Central Pacific Coast region, Mexico, we demonstrate the potential importance to endangered jaguar (*Panthera onca*) conservation of considering non-circular home ranges when estimating population density with SCR. Strong evidence existed that jaguars had elliptical home ranges wherein movements primarily occurred along linearly arranged coastal habitats that the camera array aligned with. Accounting for this movement with the SCR anisotropic detection function transformation, density estimates were 30%–32% higher than estimates from standard SCR models that assumed circular home ranges. Given much of suitable jaguar habitat in Mexico is fragmented and linearly oriented along coastlines and mountain ranges, accommodating irregular space use in SCR may be critical for obtaining reliable density estimates to inform effective jaguar conservation.

KEYWORDS

abundance, anisotropic detection function, Central Pacific coast, elliptical home range, Felidae, Nayarit, non-circular home range, *Panthera onca*, population density, spatially explicit capture–recapture

1 | INTRODUCTION

Conservation of imperiled species often relies on the implementation of actions that are intended to cause numerical increases of animals in populations. Population density is a commonly used demographic parameter for monitoring spatiotemporal trends of imperiled wildlife populations (Allison & McLuckie, 2018; Satter et al., 2019; Sollmann, Gardner, et al., 2013). Density is particularly useful for comparative evaluations because it reflects the effects of differing ecological, environmental, anthropogenic, and climatic conditions on populations of the same species (Jędrzejewski et al., 2018; Murphy et al., 2022). This is especially the case for imperiled large carnivores, many species of which have declined in number and distribution because of overexploitation and habitat fragmentation and loss (Di Minin et al., 2016; Ripple et al., 2014; Wolf & Ripple, 2017). Multiple concerted national and international large carnivore conservation programs rely on researchers obtaining periodic density estimates for populations (Ceballos, Zarza, et al., 2021; Dupont et al., 2024; Elliot & Gopalaswamy, 2017). However, many large carnivore species are elusive and cryptic, have large home range sizes, and inhabit fragmented habitats in human-modified landscapes at low densities, resulting in low detection rates that can hinder or preclude density estimation (Boitani et al., 2012; Pollock et al., 2012). Consequently, densities for large carnivore populations are often derived from abundance indices or local perceptions of animal abundance, neither of which are reliable surrogates in imperiled species conservation frameworks for empirical, model-based density estimates (Gopalaswamy et al., 2015; Moqanaki et al., 2018; Sollmann, Mohamed, et al., 2013).

Although multiple methods exist for directly estimating wildlife population density, spatial capture–recapture (SCR) models and associated extensions (e.g., spatial mark-resight and spatial partial identity) have emerged as very effective approaches for obtaining accurate and precise density estimates (Augustine et al., 2018; Efford, 2004; Royle et al., 2014; Whittington et al., 2018). These models can produce unbiased density estimates from spatiotemporally replicated detection data obtained using a variety of detection methods and have been shown to outperform other available approaches for estimating densities of numerous taxa (Crum et al., 2021; Obbard et al., 2010; Sutherland et al., 2016; Twining et al., 2022).

There are two notable space use assumptions of standard SCR models: (1) Animals have approximately circular home ranges, and (2) animals exhibit Euclidean movement between their home range (activity) centers and detectors (e.g., camera-traps) deployed across study areas (Efford, 2004; Gopalaswamy et al., 2012; Royle et al., 2014). However, many imperiled species, including multiple large carnivores, are restricted to remnant fragmented habitats, which can alter animal space use such that animal home ranges are non-circular and/or movements are non-Euclidean (Murphy et al., 2016, 2017; Sutherland et al., 2015). For example, if suitable habitats are reduced to dendritic river networks, coastlines, canyons, mountain ranges, or other linear geographic features, animal home ranges may be elliptical and elongated along those features (Gaukler et al., 2020; Murphy et al., 2016, 2021, 2023; Sutherland et al., 2015). Recent research has demonstrated that failure to account for elliptical home ranges in SCR models, particularly if the detector array geographically aligns with the direction of home range elongation, can result in severely biased density estimates (Efford, 2019; Murphy et al., 2016). The standard SCR model that assumes circular home ranges underestimated densities of American black bears (*Ursus americanus*) that had elliptical home ranges in the linearly arranged Appalachian Mountains of the eastern USA and densities of deer mice (*Peromyscus* spp.) that had elliptical home ranges within linear canyons in the arid southwestern USA (Gaukler et al., 2020; Murphy et al., 2016, 2023).

The jaguar (*Panthera onca*) historically ranged from the southwestern USA to central Argentina but has been reduced to approximately 51% of its native range and is internationally listed as Near Threatened, primarily because of declining populations and increasing habitat fragmentation and loss (Quigley et al., 2017). Although jaguars have been documented in a variety of habitat types, the species prefers dense forests that are below 3,000 m elevation and near water sources (Ceballos et al., 2011, 2016; Quigley et al., 2017; Sanderson et al., 2002). Forested wetlands have been identified as keystone habitats for jaguars in landscapes that are fragmented by agriculture (Figel et al., 2019). Deforestation rates throughout jaguar range are among the highest in the world, with most of the forest loss and fragmentation occurring from agricultural expansion (D'Annunzio et al., 2016).

In Mexico, where jaguars are nationally listed as Endangered, suitable habitats have been lost and severely fragmented by agriculture and urbanization, particularly in the northern two-thirds of the country (Ceballos et al., 2016; Rabinowitz & Zeller, 2010; Rodríguez-Soto et al., 2011). Outside of the generally contiguous forests of the Yucatan Peninsula, jaguars in many areas of Mexico have been relegated to remnant forested lowlands and wetlands that are linearly arranged along coastlines, rivers, and the foothills of prominent mountain ranges (Ceballos, de la Torre, et al., 2021; Quigley et al., 2017). A National Jaguar Conservation Strategy was developed to identify multiple critical topics for effective jaguar conservation in Mexico, one of which is to monitor populations by periodically estimating densities to evaluate population trends across suitable habitats through time (Ceballos et al., 2016; Ceballos, Zarza, et al., 2021; CONANP and PACE, 2017).

Despite multiple jaguar densities having been derived or estimated throughout Mexico, few previous studies estimated density using SCR models and no studies considered the potential effects that the geographical arrangement of remaining suitable habitats may have on jaguar space use when estimating density (Amador-Alcalá et al., 2024; Ávila-Nájera et al., 2015; Charre-Medellín et al., 2023; Figel et al., 2016). However, predominantly elliptical jaguar home ranges have been documented in multiple locales based on camera-trapping and radio-collar tracking data (Amador-Alcalá et al., 2024; Nuñez-Perez & Miller, 2019; Sollmann et al., 2011). Ignoring this information when asymmetrical camera-trap arrays are used, which are recommended for jaguar studies (Tobler & Powell, 2013), might lead to inaccurate density estimates that could misinform conservation decisions and jeopardize jaguar recovery efforts. Therefore, we analyzed detection data from a two-year camera-trapping study conducted in suitable coastal jaguar habitats using two variants of SCR models—the standard that assumed circular home ranges and an anisotropic transformation that accommodated elliptical home ranges—to investigate the potential consequences of ignoring space use characteristics in jaguar density estimation in Mexico. Considering results of previous SCR studies on other species (Efford, 2019; Gaukler et al., 2020; Murphy et al., 2016, 2023), we suspected that the standard SCR model would underestimate jaguar density.

2 | METHODS

2.1 | Study area

This study was conducted in the Central Pacific Coast region of Mexico, in the state of Nayarit, approximately 60 km northwest of Tepic, the capital city (Figure 1). The study area was located within the Sinaloa-Central Pacific Jaguar Conservation Unit that was identified as a conservation priority area by Mexico's National Alliance for the Conservation of the Jaguar (Ceballos et al., 2016; Ceballos, de la Torre, et al., 2021). The study area has been heavily impacted by agricultural expansion over the last 20 years, resulting in approximately 50% of the land area being converted to agriculture with a concomitant reduction of suitable jaguar habitats to just 26% of the total land area (Luja et al., 2022). Most of the remaining natural vegetation is in wetlands and comprised primarily of mangroves (*Avicennia germinans*; *Conocarpus erectus*) interspersed with deciduous forest patches. The climate is tropical, with high humidity, warm temperatures (average annual temperature = 31.7°C), and high levels of precipitation (average annual precipitation = 140 cm).

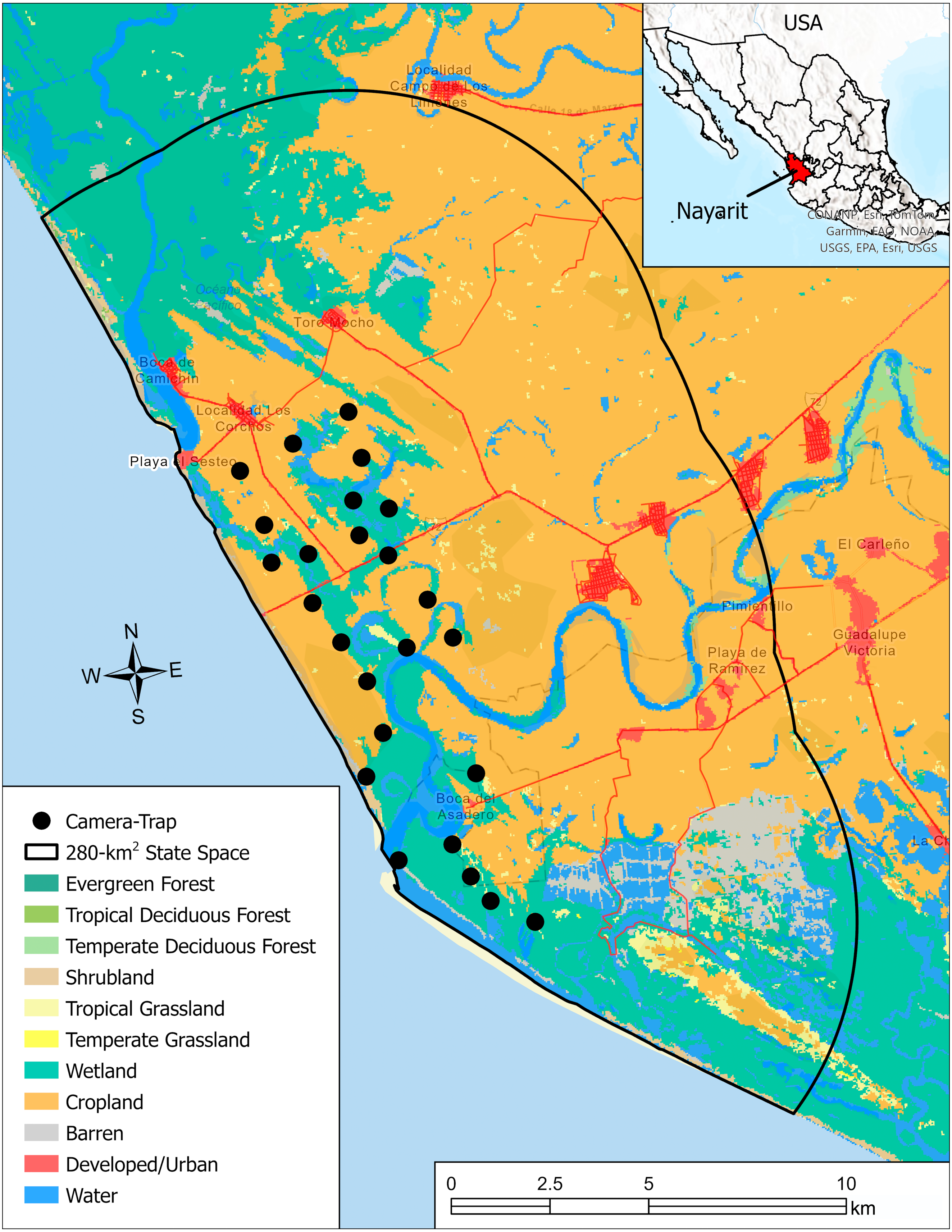
2.2 | Data collection

Noninvasive camera-trap surveys were conducted for 65 and 62 days during January–March of 2019 and 2020, respectively, to obtain jaguar detection data in a capture–recapture design (Luja et al., 2022). The survey design adhered to the National Jaguar Census (*Cenjaguar*) protocol that was developed to standardize jaguar camera-trapping studies conducted in Mexico (Chávez et al., 2007). A total of 25 camera-trap stations were operated during both years; cameras were deployed along wildlife trails at locations where jaguar sign (e.g., tracks, scrapes, and scat) was present to maximize detection rates, with 1-km average spacing among sites, resulting in a 38-km^2 minimum convex polygon around all stations (Harmsen et al., 2010; Sollmann et al., 2011; Tobler & Powell, 2013). All cameras were Cuddeback Color X-Change models (Cuddeback, De Pere, USA), which were attached to trees 40–50 cm above the ground, faced perpendicular to trails, and programmed to take one photo per trigger with a 0.5-sec trigger speed. Most camera-trap stations were comprised of two cameras facing each other, but because of financial limitations, some stations were comprised of a single camera.

2.3 | Statistical analysis

All photograph detections were manually reviewed by jaguar experts who identified individual jaguars and their respective sex based on individually unique face and rosette patterns and observed genitalia, respectively (Ceballos, Zarza, et al., 2021; Luja et al., 2022; Silver et al., 2004; Tobler & Powell, 2013). Additionally, three individual jaguars (one male: two females) had been live-captured and artificially marked in the area as part of a separate study (Ceballos et al., 2022), which assisted individual identification in photographs. We constructed three-dimensional spatially explicit detection histories comprised of individual × occasion × trap location, where an occasion represented a single day, and included sex as an individual-level categorical covariate. We then fit multi-session, closed-population SCR models using the full-likelihood approach available in the package secr in the R statistical computing environment to estimate year-specific jaguar densities (Efford, 2024; R Core Team, 2024; Royle & Converse, 2014).

Camera-traps produce count detections because the same individual can be detected at the same camera-trap or multiple camera-traps multiple times during a single sampling occasion; therefore, we specified camera-traps as "count" detectors and used a Poisson observation model via the hazard half-normal detection function



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(Efford, 2024; Royle & Gardner, 2011). This detection function relates exposure to detection for an individual to the distance between its home range center (activity center) and a camera-trap, and is comprised of two estimated parameters: the baseline detection rate at an activity center (λ_0) and the spatial scale of detection (σ; Royle & Gardner, 2011; Royle et al., 2014). To account for spatiotemporal variation in sampling effort, which often arises when a camera-trap is rendered non-operational due to theft, vandalism, or battery expiration, we specified a binary hazard-based effort adjustment in all models that represented whether a camera-trap was operational or not during each day (Efford et al., 2013). To define the geographical area to which density applied, which is often referred to as the area of integration or state space (S) in SCR, we first buffered the camera-trap array by 4× estimated σ and then manually truncated the western boundary to the coastline because the ocean represents unsuitable habitat that could not ecologically support jaguar home range centers (Borchers & Efford, 2008; Efford, 2004, 2023a; Royle et al., 2014). We then generated a discrete mesh of latent points across the entirety of S with a spacing of $0.5 \times \sigma$ to create potential locations for individual activity centers (Efford, 2023a; Royle et al., 2014; Sutherland et al., 2019).

We implemented a three-stage SCR model fitting approach. First, we fit typical homogeneous Poisson SCR models with the standard isotropic detection function that assumed Euclidean animal movement, circular home ranges, and spatially random distribution of home range centers, but allowed density and both detection function parameters to differ between years while also accounting for sex-specific differences in detection and movement via a categorical sex covariate (i.e., sex × year interaction effects on λ_0 and σ; Sollmann et al., 2011; Tobler & Powell, 2013). That approach facilitated estimation of year-specific densities while testing whether detection function parameters could be shared between years to improve parameter estimates (Royle & Converse, 2014). Second, we fit inhomogeneous Poisson SCR models, which also assumed circular home ranges, that included sex effects on detection function parameters, as well as interactions with year if supported by the first stage, but allowed the spatial distribution and intensity of home range centers to vary as a log-linear function of habitat and landscape covariates (described in subsequent paragraph) to attempt to identify important effects of local ecological and anthropogenic conditions on jaguar density (Devlin et al., 2023). Third, we repeated said analyses with the same parameter effects described for both stages above but specified an anisotropic detection function, which accommodated elliptical home ranges by transforming space such that home range shape becomes approximately circular (Efford, 2019; Murphy et al., 2016). We implemented the anisotropic transformation following the methods described by Murphy et al. (2016), using the package geoR to define the anisotropy angle parameter (Φ_A) as 152° based on the northwest to southeast orientation of the camera-trap array, coastline, and natural habitats, and estimated the anisotropy ratio parameter (Φ_R) via maximum likelihood (Diggle & Ribeiro, 2004; Efford, 2019; Gaukler et al., 2020; Murphy et al., 2016). This approach directly accommodated jaguar movement and elliptical home range elongation occurring predominantly along the direction of the asymmetrical camera-trap array and orientation of natural habitats.

We considered the following five spatial covariates in the inhomogeneous Poisson SCR models as effects on the density parameter, based on the findings of previous range-wide jaguar density and spatial ecology studies (Devlin et al., 2023; Jędrzejewski et al., 2018; Thompson et al., 2021). A two-class categorical habitat covariate that represented natural versus unnatural habitats, which we created from 30-m resolution 2020 land cover raster data produced by the North American Land Change Monitoring System (CEC, 2023) by reclassifying forests, grasslands, and wetlands as natural, whereas agriculture, human development, and bare ground were reclassified as unnatural. Using the natural versus unnatural habitat raster, we also created a percentage natural cover raster by applying the Focal Statistics tool in ArcGIS Pro (ESRI, Redlands, USA) with a circular moving window with 50-m radius. We again reclassified the 2020 land cover raster data into two layers, wetlands and agriculture, and applied the Focal Statistics tool with a 50-m radius circular moving window to each layer to create percentage wetland and percentage agriculture rasters, respectively. We obtained shapefiles of all roads in the area (HOT, 2023) and applied the Distance tool in ArcGIS Pro to create a distance from roads raster that represented the Euclidean distances (meters) from roads. We then combined the roads data with the human development classification in the 2020 land cover raster data and applied the Distance tool to create a distance from development raster of the Euclidean distances (meters) from all human

FIGURE 1 Study area in the state of Nayarit, Mexico, where 25 camera-traps were deployed during 2019 and 2020, respectively, to obtain individual detections for estimating spatially explicit densities of endangered jaguars (*Panthera onca*). Land cover classes are shown at 30-meter resolution. Inset map depicts the location of Nayarit along the Central Pacific Coast of Mexico.

development and related infrastructure. We standardized all spatial covariate rasters to 30-m resolution and rescaled each raster's values to the 0–1 interval before fitting the inhomogeneous Poisson SCR models.

We conducted information-theoretic model selection based on Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham & Anderson, 2002). All models that were ≤4 ΔAIC_c units from the top-ranked model were considered competing (Burnham et al., 2011). If multiple models were competing, then we produced parameter estimates via model-averaging (Arnold, 2010; Burnham et al., 2011; Burnham & Anderson, 2002); otherwise, estimates were produced from the top-ranked, most parsimonious model.

3 | RESULTS

3.1 | Data collection

Jaguars were detected at 18 and 13 of the 25 camera-traps during the 2019 and 2020 survey periods, respectively. A total of 82 and 83 unique detection events of five (3F:2M) and six (4F:2M) individual jaguars were obtained during 2019 and 2020, respectively. The total number of spatial recaptures (detection of an individual at >1 camera-trap) ranged from 33 to 46 (40%–56% of all detection events) in 2020 and 2019, respectively. In 89% and 85% of those spatial recapture events during 2019 and 2020, respectively, jaguar movements between camera-trap detections occurred along the *y*-axis in the northwest-southeast direction (Figure 2a).

3.2 | Statistical analysis

Models with anisotropic transformation of the detection function, which accommodated elliptical home ranges, were substantially supported over models with the standard isotropic detection function that assumed circular home ranges ($\Delta AIC_c = 31.19$; Table S1). We found no evidence that λ_0 or σ differed between years for either sex (Table S2); therefore, we shared both parameters between years but retained sex-specific parameter estimation in subsequent models. One model received all the support, which included a spatially random distribution

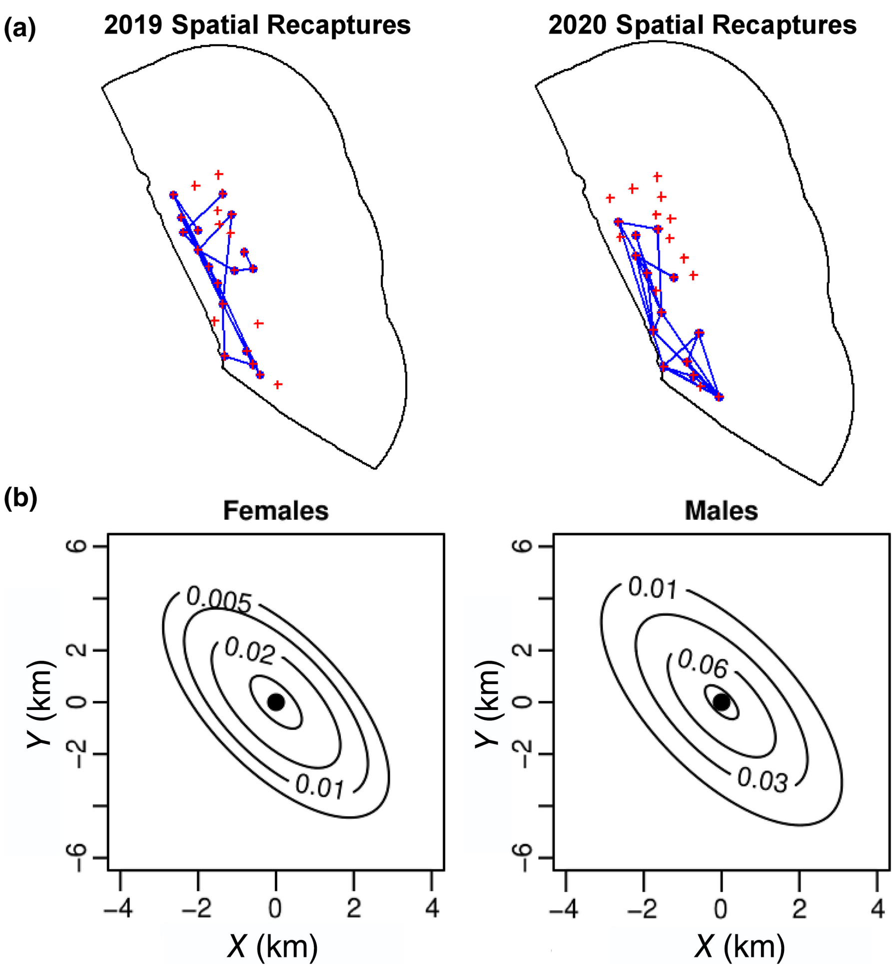

FIGURE 2 (a) Individual jaguar (*Panthera onca*) movements (blue lines) among spatial recaptures at 25 camera-traps (red crosses) deployed in the state of Nayarit, Mexico, during 2019–2020. (b) Elliptical detection functions around home range (activity) centers (black dots) for female and male jaguars, estimated by the top-ranked spatial capture–recapture model that included anisotropic transformation. Values presented for each contour are the estimated detection rate (λ_0) as a function of increasing distance from the home range center.

TABLE 1 Information-theoretic model selection results of fitted multi-session spatial capture–recapture models with anisotropic transformation of the detection function, which accommodated elliptical home ranges that were aligned with the camera-trap array and suitable habitats, for estimating jaguar density in Nayarit, Mexico, during 2019–2020.

Model	K[a]	LL[b]	AIC_c[c]	ΔAIC_c[d]	w[e]
$D \sim$ Year $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	7	−834.47	1720.26	0.00	1.00
$D \sim$ Year + D-Road $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	8	−831.87	1751.73	31.47	0.00
$D \sim$ Year + D-Develop $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	8	−832.61	1753.23	32.97	0.00
$D \sim$ Year + P-Wetland $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	8	−834.29	1756.59	36.33	0.00
$D \sim$ Year + Habitat $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	8	−834.39	1756.78	36.52	0.00
$D \sim$ Year + P-Agriculture $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	8	−834.43	1756.87	36.61	0.00
$D \sim$ Year + P-Habitat $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	8	−834.44	1756.87	36.61	0.00
$D \sim$ Year × D-Road $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	9	−830.76	1859.61	139.25	0.00
$D \sim$ Year × D-Develop $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	9	−832.55	1863.09	142.83	0.00
$D \sim$ Year × P-Wetland $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	9	−834.09	1866.17	145.91	0.00
$D \sim$ Year × Habitat $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	9	−834.23	1866.45	146.19	0.00
$D \sim$ Year × P-Agriculture $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	9	−834.30	1866.61	146.35	0.00
$D \sim$ Year × P-Habitat $\lambda_0 \sim$ Sex $\sigma \sim$ Sex $\Phi_R \sim 1$	9	−834.40	1866.80	146.54	0.00

Note: Estimated model parameters were density (D), baseline detection rate (λ_0), spatial scale of detection (σ), and anisotropy ratio (Φ_R). Models were considered in which jaguar density was spatially random (homogeneous Poisson process) or spatially varied (inhomogeneous Poisson process) as a log-linear function of natural versus unnatural habitats (Habitat), percentage natural habitat cover (P-Habitat), percentage wetland cover (P-Wetland), percentage agriculture cover (P-Agriculture), distance from roads (D-Road), or distance from human development and infrastructure (D-Develop). Models estimated sex-specific (Sex) λ_0 and σ while sharing both parameters between years, and estimated year-specific densities (Year).

[a]Number of model parameters.

[b]Log-likelihood of model.

[c]Akaike's Information Criterion corrected for small sample size.

[d]Difference between AIC_c of model and AIC_c of top-ranked model.

[e]Model weight.

(homogeneous Poisson) of jaguar home range centers within each year and sex-specific detection function parameters (Table 1). Although none of the models with spatial variation in jaguar density as a function of habitat or landscape covariates were competing ($\Delta AIC_c > 4$), the second-ranked model estimated that jaguar density increased with increasing distance from roads ($\beta = 9.49$; 95% confidence interval [CI] = 1.76–17.23).

The estimated anisotropy ratio parameter (Φ_R) from the top-ranked model was 1.49 (95% CI = 1.01–2.23), thereby strongly supporting that jaguar home ranges were elliptical and elongated in the northwest-southeast direction, aligned with the camera-trap array and orientation of suitable habitats (Figure 2b). Estimated densities from the model with the anisotropic detection function were 2.55 (95% CI = 1.14–5.70) and 2.14 (95% CI = 0.89–5.16) jaguars/100 km^2 during 2019 and 2020, respectively (Figure 3a). In contrast, estimated densities from the complementary model with the standard isotropic detection function were 1.95 (95% CI = 0.87–4.38) and 1.62 (95% CI = 0.67–3.91) jaguars/100 km^2 during 2019 and 2020, respectively. Density estimate precision (coefficient of variation) was similar between those two complementary models ($CV_{Aniso} = 0.47$; $CV_{Iso} = 0.48$). Both models estimated that male jaguars had higher λ_0 than females ($\lambda_{0[Male]} = 0.07$–0.09; $\lambda_{0[Female]} = 0.03$–$0.04$; Figure 3b) but that σ was similar between sexes ($\sigma_{Male} = 1010$–2026 m; $\sigma_{Female} = 988$–2021 m); however, σ estimates were significantly smaller from the model with the anisotropic detection function (Figure 3c).

4 | DISCUSSION

Conservation of endangered jaguars in Mexico relies on researchers obtaining periodic estimates of jaguar densities from camera-trapping in multiple locales throughout the country (Ceballos et al., 2016; Ceballos, de la Torre, et al., 2021; Ceballos, Zarza, et al., 2021; Chávez et al., 2007; CONANP and PACE, 2017). For this approach to be effective, density estimates produced across space and time must be accurate and precise, which are qualities largely dictated by the survey design and analytical method used (Borchers et al., 2013; Kowalewski et al., 2015; Thompson, 2004). SCR models have been the recommended approach for estimating jaguar densities across the species' extant range for more than a decade, primarily because SCR can produce

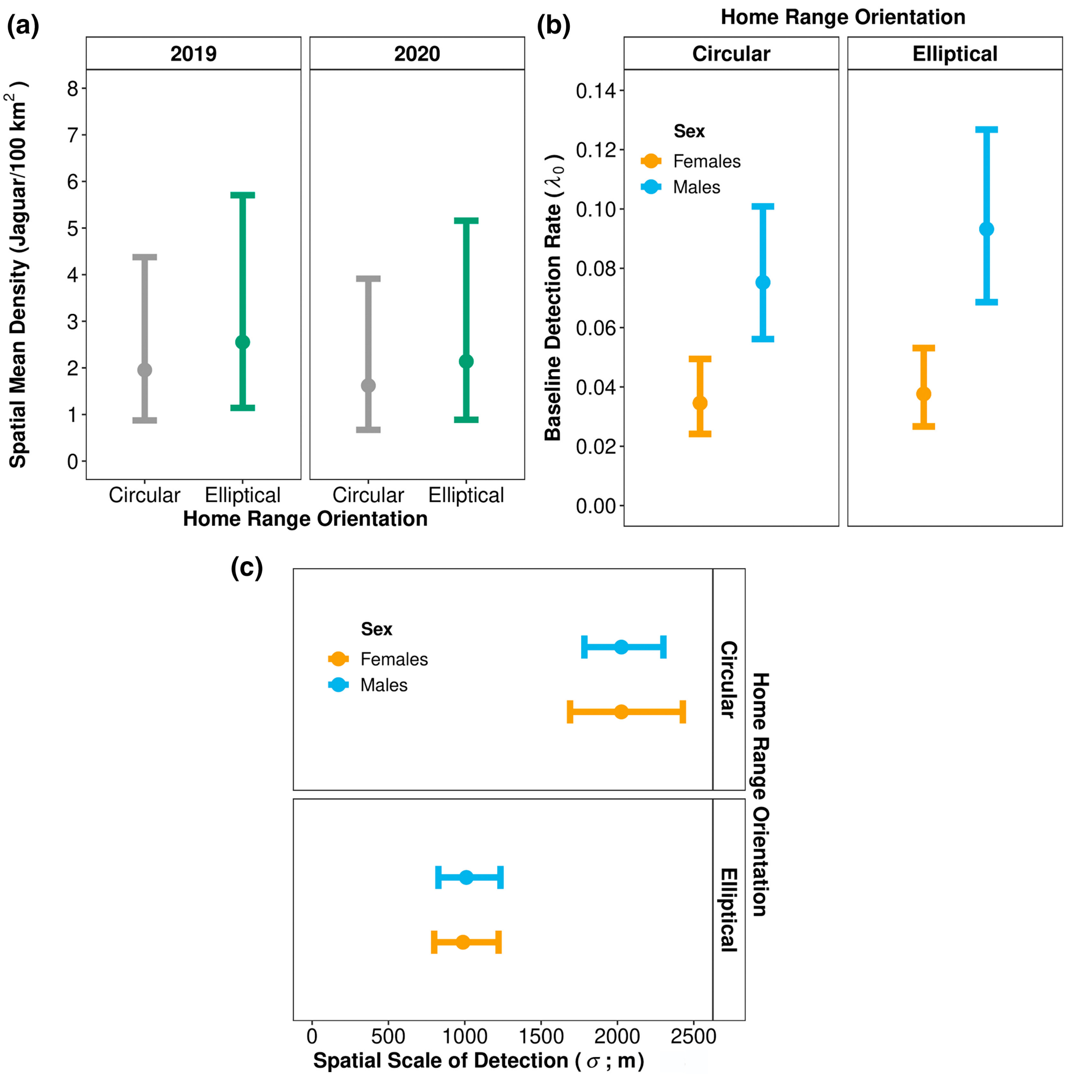

FIGURE 3 Parameter point estimates (dots) with 95% confidence intervals (error bars) from the top-ranked anisotropic spatial capture–recapture model that allowed elliptical jaguar (*Panthera onca*) home ranges versus the complementary default isotropic spatial capture–recapture model that assumed circular home ranges. (a) Year-specific density estimates; (b) sex-specific baseline detection rate estimates; and (c) sex-specific spatial scale of detection estimates. Spatial capture–recapture models were fitted to detection data obtained at 25 camera-traps deployed in Nayarit, Mexico, during 2019–2020.

unbiased (or nominally biased) density estimates for explicitly defined geographical areas (Royle et al., 2014; Sutherland et al., 2016; Tobler & Powell, 2013). However, the results of our analysis indicate that careful consideration of animal space use relative to the orientation of suitable habitats and camera-trap arrays will often be required to obtain reliable jaguar density estimates in Mexico with SCR models. Simply assuming jaguars in all of Mexico's Jaguar Conservation Units have approximately circular home ranges, when much of the available suitable habitats are linearly arranged and camera-trap arrays are typically restricted to those habitats, and producing densities from the corresponding standard SCR model could lead to severely biased estimates. Our findings demonstrate that a primary consequence of that approach can be that densities are underestimated by approximately 30%, which could drastically alter decision-making and result in ineffective conservation actions.

Jaguar densities in Mexico have been produced from different analytical methods and are likely not directly comparable across approaches (Jędrzejewski et al., 2018; Murphy et al., 2022; Tobler & Powell, 2013). Most jaguar densities for Mexico were not directly estimated but were instead derived from abundances estimated with nonspatial capture–recapture (NCR) models and ranged widely from 0.16 to 7.40 jaguars/100 km^2 (Amador-Alcalá et al., 2024; Charre-Medellín et al., 2023). A primary issue with the nonspatial approach is that effective sampling areas, to which abundance estimates are applied to derive densities, are delineated using ad hoc methods and are often too small, resulting in truncation bias (Obbard et al., 2010; Sutherland et al., 2016; Tobler & Powell, 2013). For example, densities derived from abundances estimated by NCR models that were applied to our detection data ranged from 3.00 to 6.36 jaguars/100 km^2, depending on the year and which effective sampling area was used (Supplementary Information S2, Table S2.1, Figure S2.2). Those derived densities are 37%–155% greater than the densities estimated by our SCR models; however, abundance point estimates were identical from the two approaches (N_{NCR} = 6–7 jaguars; N_{SCR} = 6–7 jaguars). The substantial discrepancy in densities but similarity in abundances demonstrates the typical ad hoc delineated effective sampling areas based on mean maximum distance moved (MMDM or ½ MMDM) were too small, which severely inflated the densities derived from abundances estimated by NCR models (Obbard et al., 2010; Sutherland et al., 2016). Consequently, similar to other large felids, including pumas (*Puma concolor*) and snow leopards (*Panthera uncia*), many jaguar densities previously derived in Mexico based on NCR models are likely considerable overestimates (Jędrzejewski et al., 2018; Murphy et al., 2022; Suryawanshi et al., 2019; Tobler & Powell, 2013).

To date, only seven previous studies applied SCR models to estimate jaguar densities in parts of Mexico, producing estimates that ranged from 0.21 to 4.61 jaguars/100 km^2 (Amador-Alcalá et al., 2024; Charre-Medellín et al., 2023; Greenspan et al., 2020), which our density estimates fell within. However, all those previous studies used the standard SCR model that assumed individuals had approximately circular home ranges, despite documenting jaguars having predominately elliptical home ranges that were elongated in the direction of an asymmetrical camera-trap array (e.g., Amador-Alcalá et al., 2024). Geographic restriction of suitable habitats to disjunct networks, such as the coastlines and mountain ranges in much of Mexico (Ceballos, de la Torre, et al., 2021; Quigley et al., 2017), was the impetus for development of SCR models that accommodate non-circular home ranges and/or non-Euclidean movement, including the ecological distance model and the network distance function (Efford, 2023b; Murphy et al., 2021;Royle et al., 2013; Sutherland et al., 2015). Specific to the anisotropic detection function transformation, our study provides another example of the utility of this approach for improving SCR density estimates when animal movement occurs along approximately linearly oriented suitable habitats or landscape features and results in elliptical home ranges that detector arrays align with (Efford, 2019; Murphy et al., 2016). Previous studies that used this approach also found that density estimates were higher compared to estimates from the standard SCR models. This includes an American black bear population that resided within remnant, forested habitats that were fragmented by surface mining and distributed along a linear mountain range (Murphy et al., 2016), and multiple deer mouse populations that were restricted to suitable habitats in the bottoms of linear canyons because of bordering cliffs that were insurmountable (Gaukler et al., 2020; Murphy et al., 2023).

Nevertheless, the accuracy and precision of SCR density estimates also depends on the quality of the study design relative to biology and ecology of the target species, the distribution of habitats, and landscape characteristics. Even when SCR models are correctly specified to include important sources of heterogeneity in detection function parameters, non-circular home ranges, or non-Euclidean movement, a deficient study design can result in too few individuals being detected and/or too few spatial recaptures being obtained to produce accurate density estimates (Clark, 2019; Efford & Boulanger, 2019; Schmidt et al., 2022; Sun et al., 2014). We used an approximately rectangular array of camera-traps that were operated for 62–65 days each year, both characteristics of which conform to recommendations for SCR-based jaguar camera-trapping studies to produce reliable density estimates (Tobler & Powell, 2013). However, our study used approximately half the recommended minimum number of camera-traps with a 1-km average spacing among camera-traps, the latter of which may have been too close relative to jaguar home range sizes and movement capabilities (Tobler & Powell, 2013). Those two deficiencies of the study design may have caused too few individuals to be detected to accurately estimate the spatial scale parameter (σ), despite obtaining sufficient spatial recaptures (Clark, 2019; Schmidt et al., 2022; Sun et al., 2014; Tobler & Powell, 2013). For instance, our sex-specific σ estimates were within the range of published jaguar σ estimates from studies across the species' extant range but were toward the lower bound (range: 656–5996 m; Amador-Alcalá et al., 2024; Charre-Medellín et al., 2023; Greenspan et al., 2020). Thus, based on established recommendations for jaguar camera-trapping studies and SCR studies in general, ≥40 camera-traps spaced 2–3 × σ, or ≥2–3 km, apart may be required to detect more individual jaguars in our coastal study area to improve estimation of SCR model detection function parameters and therefore density estimates (Clark, 2019; Sun et al., 2014; Tobler & Powell, 2013).

Our study ultimately demonstrates that, although SCR is an effective analytical approach for estimating jaguar densities, the standard SCR model, which assumes circular home ranges and Euclidean movement, may not be appropriate for endangered jaguars in many parts of Mexico. Considering the linear orientation of remaining suitable habitats across much of the country, alternative

SCR models that accommodate elliptical home ranges and/or non-Euclidean animal movement may be required to obtain reliable jaguar density estimates to inform conservation efforts. The anisotropic detection function transformation we used is effective but applicable only when animal home ranges are elliptical and aligned with the directionality of an asymmetrical (e.g., rectangular) camera-trap array that samples unequally along the *x*- or *y*-axis (Efford, 2019; Murphy et al., 2016). In other circumstances, such as when a symmetrical camera-trap array that samples equally along both axes is applied to fragmented and disjunct habitats, the SCR ecological distance model would be more appropriate (Royle et al., 2013; Sutherland et al., 2015).

Considering the mounting evidence for the superiority of SCR models in estimating wildlife densities, particularly of jaguars, camera-trapping study designs likely need to be revised to better conform to the requirements of SCR (Tobler & Powell, 2013). For instance, Mexico's National Jaguar Census (*Cenjaguar*) protocol, which was developed to standardize jaguar camera-trapping studies in Mexico, was created when SCR models were novel. Considerably more knowledge now exists regarding the performance of SCR under a variety of sampling conditions and survey designs (Augustine et al., 2018; Clark, 2019; Sun et al., 2014; Tobler & Powell, 2013). Updating the *Cenjaguar* camera-trapping protocol to the SCR framework via simulation exercises using published parameter estimates may be prudent to ensuring that future studies can produce reliable density estimates for informing effective jaguar conservation in Mexico. We suspect that more efficient range-wide demographic monitoring across space and time could be achieved for jaguars in Mexico by implementing clustered camera-trapping in the SCR framework (Clark, 2019; Murphy et al., 2019; Murphy & Augustine, 2019). Such an approach applied across the country likely would require consolidation of resources and heightened collaboration among university researchers, federal and state governments, and private landowners to maximize effectiveness.

AUTHOR CONTRIBUTIONS

VHL conceived the study design, procured funding for data collection, led data collection, and reviewed and edited the manuscript. SMM analyzed the data, created figures, and tables and led writing of the manuscript.

ACKNOWLEDGMENTS

Mexico National Council of Science and Technology (CONACyT) funded data collection (project #3369). We are grateful for the support from T.C. Esque and the U.S. Geological Survey's Western Ecological Research Center. T.C. Esque, J.M. Guthrie, W.M. Strauss, C. Murcia, and two anonymous referees provided helpful comments that improved this manuscript. We thank R.K. Rowe for assisting with the Graphical/Tweetable Abstract, which was created under license in BioRender (https://biorender.com/d39e686). The authors declare no financial, personal, or other conflicts of interest. Any use of trade, firm, or product names does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no financial, personal, or other conflicts.

FUNDING INFORMATION

Data collection was funded by the Mexico National Council of Science and Technology (CONACyT) via project #3369 to VHL. Institutional support was provided to SMM by the U.S. Geological Survey, Western Ecological Research Center, which also paid the Article Publication Charge.

DATA AVAILABILITY STATEMENT

Jaguars are listed as Endangered in Mexico; therefore, to prevent unnecessary harm, the exact geographic coordinates of individual jaguar detections cannot be publicly shared. However, reasonable requests for research data can be made to the corresponding author (VHL) for consideration.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Murphy, S. M., & Luja, V. H. (2025). Jaguar density estimation in Mexico: The conservation importance of considering home range orientation in spatial capture–recapture. *Conservation Science and Practice*, *7*(2), e13301. https://doi.org/10.1111/csp2.13301