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Research paper

Abundance of the northernmost jaguar *Panthera onca* breeding population

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Abstract

Abundance of the northernmost jaguar Panthera onca *breeding population.* Jaguars are the apex predators of tropical and subtropical ecosystems in the Americas but their conservation is threatened due to habitat loss, poaching, and conflicts over predation. The Northern Jaguar Reserve (NJR) was created by Naturalia A.C. as a project to protect the northernmost jaguar population within an area of 59.3 thousand acres (24,400 ha) of private property. The property also includes other protected species. The present study was conducted to verify the status of this jaguar population in order to evaluate the effectiveness of the NJR, and to contribute to knowledge regarding its ecology. We estimated density using mark-resight and spatially explicit capture-recapture (SERC) models, and evaluated home range through a survey with 56 camera-trap stations over 12 bimonthly periods. In total, we obtained a sampling effort of 40,880 camera-days, registering 2.32 records from 1,000 camera-days. Jaguar density, calculated using the capture-recapture models, ranged from 0.3 to 1.44 indiv./100 km^2, while the SERC model estimated a density of between 0.21 and 3.04 indiv./100 km^2. The home range was 78.9 km^2 for males and 45.1 km^2 for females. Long-term population monitoring together with the establishment of Areas Voluntarily Assigned to Conservation, an initiative recently created by the Mexican government, such as the NJR, could be a valid strategy to strengthen jaguar conservation and thereby maintain key ecological processes for other species and their habitat in northwestern Mexico.

Key words: Camera traps, Home range, *Panthera onca*, Neotropical felids, Northern Jaguar Reserve, Spatially explicit mark–recapture

Resumen

Abundancia de la población reproductiva más septentrional de jaguar Panthera onca. El jaguar es el depredador apical de los ecosistemas tropicales y subtropicales en las Américas, pero su conservación está comprometida debido a la pérdida de hábitat, la cacería furtiva y los conflictos por depredación. La Reserva Jaguar del Norte (RJN) fue creada por Naturalia A.C. con la finalidad de proteger la población más norteña de jaguar en una propiedad privada de 24.400 ha, que acoge a otras especies protegidas. Con el propósito de verificar el estado de su población y con ello evaluar el grado de efectividad de la RJN y contribuir al conocimiento de su ecología poblacional, se estimó la densidad mediante modelos tradicionales de marcaje y modelos de captura-recaptura espacialmente explícitos (SERC) y áreas de actividad, mediante un muestreo en 56 estaciones de cámaras-trampa durante 12 periodos bimestrales. En total, se obtuvo un esfuerzo de muestreo de 40.880 días-cámaras y 2,32 reg./1.000 días-cámara para todo el estudio. La densidad de jaguares, calculada con los modelos de captura-recaptura, varió entre 0,30 y 1,44 indiv./100 km^2, mientras que en los modelos SERC se obtuvo una densidad de entre 0,21 y 3,04 indiv./100 km^2. El área de actividad fue de 78,9 y 45,1 km^2 para machos y hembras, respectivamente. El seguimiento de la población a largo plazo y la creación de nuevas Áreas Destinadas Voluntariamente a la Conservación (ADVC), una figura creada recientemente por el Gobierno mexicano, como la RJN, podrían ser una estrategia válida para fortalecer la conservación del jaguar y, con ello, mantener procesos ecológicos clave para otras especies y su hábitat en el noroeste de México.

Palabras clave: Cámaras-trampa, Área de actividad, *Panthera onca*, Felinos neotropicales, Reserva Jaguar del Norte, Modelos de captura-recaptura espacialmente explícitos

Introduction

The jaguar *Panthera onca* is the largest representative of the feline family in the Americas and is considered the top predator of the tropical and subtropical ecosystems, where it thrives. Its geographical distribution previously extended from the southwestern United States of America to northern Patagonia in Argentina (Sanderson et al 2002, Ceballos and Oliva 2005) but today its conservation and persistence are compromised due to habitat loss, poaching, conflicts due to predation on domestic stock, and unsustainable productive activities, all of which have contributed to reductions in distribution ranges, not only for jaguars but for wildlife in general (Bodmer and Robinson 2004, Reyna-Hurtado et al 2009, Ripple et al 2014, Naranjo et al 2015, Thornton et al 2020). Among the most damaging anthropogenic factors are livestock and agriculture activities practiced in unsustainable ways that change forest cover and land use. This translates into fragmentation and loss of habitat and species (Franklin et al 2002, Ceballos and Arroyo-Cabrales 2012, Zarco-González et al 2013, Schank et al 2017, Meyer et al 2019, Ceballos et al 2021). One of the alternatives implemented in Mexico as an instrument for biological conservation is the creation of protected natural areas, both federal and private (Langholz and Krug 2004, Bezaury-Creel and Gutiérrez-Carbonell 2009, Kamal et al 2015, Ceballos et al 2021). The Private Protected Areas proposal emerged from civil society. It was triggered particularly from landowners seeking sustainable productivity, habitat and biodiversity conservation, from among people with high appreciation for the environmental services provided by their land. Although initially not a government project, its role is circumscribed to regulate and certify Areas Voluntarily Designated for Conservation (ADVC). Such areas are considered an ideal strategy for the participation of society in the conservation of natural environments. The ADVC's are a complementary tool to the Natural Protected Areas established by State and Federal offices (Bezaury-Creel and Gutiérrez-Carbonell 2009, Kamal et al 2015). However, in all cases (federal, state and private reserves) constant research and biological monitoring is required to understand and streamline their functionality (Whitacre 1997, Simonetti et al 2002, Hidalgo-Mihart et al 2019).

Within Mexico, most efforts concerning topics related to jaguar have been carried out to analyze their conservation status and ensure long-term permanence (Sanderson et al 2002, Silveira et al 2010, Medellín et al 2016). Geographically, these efforts have focused mainly on central and southern Mexico (Hidalgo-Mihart et al 2019, Lavariega et al 2020, Charre-Medellín et al 2021), but a few have been established in the semi-arid Northwest (Gutiérrez-González et al 2015, Greenspan et al 2020) to identify present distribution, priority areas and natural corridors (Chávez and Ceballos 2006, Rodríguez-Soto et al 2011, 2013, De la Torre et al 2018). Nevertheless, many ecological and conservation issues remain unaddressed, especially in the northernmost areas of the jaguars' distribution (Sanderson et al 2022, Cruz et al 2021).

The Northern Jaguar Reserve (NJR) is a private reserve located in the state of Sonora, in northwestern Mexico. It was created to protect the northernmost population of breeding jaguars on the continent as well as other key species inhabiting its boundaries. One reason why the jaguar was chosen as the NJR flagship animal is that it is a focal species in this conservation process because its wide habitat requirements and high sensitivity to anthropic pressures give it great relevance as an umbrella species and are a key indicator of environmental quality (Dalerum et al 2008, Medellín et al 2016, Thornton et al 2020).

In spite of the NJR's considerable acreage of 24,400 ha (59.3 thousand acres), besides its ecological requirements jaguar conservation requires a multifactorial approach. Social issues score high on such priorities, and are a major challenge that requires intervention through specific management actions based on solid scientific evidence and knowledge and consideration of environmental and regional social conditions (Gibbs 2000, Ceballos et al 2007, Schwartz et al 2015). Carrying out effective conservation strategies requires scientific studies to estimate basic population parameters related to distribution, abundance and ecology (Aranda 1994, Caughley and Sinclair 1994, Ojasti and Dallmeier 2000).

For these reasons, the present study aimed to provide information on jaguar population parameters in a poorly researched region of its distribution. The main objective was to estimate and update jaguar population density within the NJR based on camera traps, traditional mark-resight methods, and spatially explicit capture-recapture models. The home range was calculated using camera-trap records. Generating knowledge about these ecological aspects can contribute greatly to the conservation plans carried out in the area. In addition, it can help validate the importance of the region for the preservation of jaguars and serve as a baseline to detect the dynamics of wild felids. Strategies then put in place could contribute to improving NJR management so as to comply with the function for which it was created and to support the extending jaguar presence in neighboring Chihuahua, Arizona and New Mexico (Sanderson et al 2022).

Material and methods

Study area

The Northern Jaguar Reserve (NJR) is located north of the municipality of Sahuaripa, Sonora, Mexico (fig. 1). The reserve is roughly 244 km^2 (ca. 94.2 miles^2) and is monitored for the protection of jaguars and other protected species. The altitude varies from 370-1,600 m a.s.l. The predominant climate is semi-arid, and semi-warm, and the average annual temperature is between 18-22 °C, with summer temperatures rising to 45 °C. The varied topography accounts for concomitant changes in climate. There may be arid-warm temperatures at the bottom of canyons, yet semi-warm subhumid and even temperate high temperatures in the sierras (CONABIO 2004, Brito-Castillo et al 2010, fig. 1).

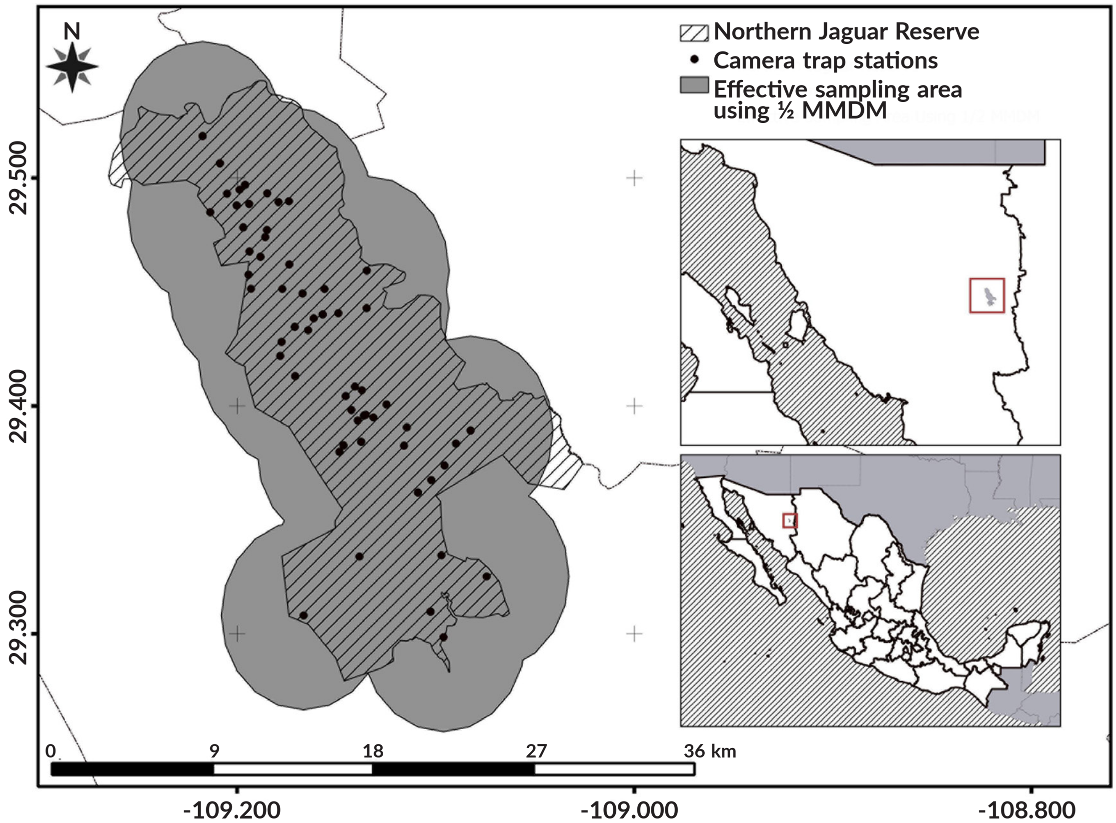

Fig. 1. Location of the Northern Jaguar Reserve, Sahuaripa, Sonora (Mexico).

***Fig. 1.** Ubicación de la Reserva Jaguar del Norte, en Sahuaripa, Sonora (México).*

Plant communities in the NJR are dominated by thorny scrubs with species such as tepehuaje *Lysiloma watsonii* and mesquite *Prosopis velutina*. Tropical subdeciduous forests are covered by torotes *Bursera* spp., palo santo *Ipomea arborescens* and ceiba *Ceiba acuminata*, while in the mountains, oak forests *Quercus arizonica* and *Q. emorii* are the dominant species (Pennington and Sarukhan 2005, Van Devender et al 2010). Wildlife species recorded comprehend 10 amphibians, 31 reptiles, 241 birds and 59 mammals (Rorabaugh et al 2011, Gutiérrez et al 2012, Flesch et al 2015). There are 14 species of potential prey in the study area, including white-tailed deer *Odocoileus virginianus*, collared peccary *Pecari tajacu*, white-nosed coati *Nasua narica*, opossum *Didelphis virginiana*, lagomorphs *Lepus* spp., wild turkey *Meleagris gallopavo* and three species of skunk (Rosas-Rosas et al 2008, Cassaigne et al 2016).

Sampling design

Systematic sampling was carried out using camera-traps that included Cuddeback® (Digital and Attack) and Stealth Cam® (StealthCam LLC, Grand Prairie, USA) equipment. The design of the National Jaguar Census (CENJAGUAR) proposed by Chávez et al (2013) was followed. Twelve sampling periods (every two months) were carried out from January 2014 to December 2015. Each survey period ranged from 59 to 62 days. Although this is a short period in relation to the jaguar life cycle, it is similar to methods used in previous feline studies (Karanth and Nichols 1998, Trolle and Kéry 2003, Silver et al 2004, Di Bitetti et al 2006, Dillon and Kelly 2007, Soria-Díaz et al 2010, Maffei et al 2011), and is a reasonable time to fulfill demographic closure assumption for jaguars (Maffei et al 2004, Silver et al 2004, Soisalo and Cavalcanti 2006). Each period was considered a sampling event and a demographically-closed population assuming no recruitment, death, or migration during that period (Seymour 1989, Karanth and Nichols 1998).

Throughout the survey periods, the study area was sampled simultaneously using a grid design that included 56 stations. In 35 of these stations, we used paired cameras spaced at a mean of 1.5 km (1-3 km), a method recommended by CENJAGUAR (Chávez et al 2013). This approach ensures that within the sampled area, camera-trap coverage left no gaps greater than 10 km^2. This value is based on the smallest home range recorded for jaguars and is used to attempt to ensure that all individuals are potentially exposed to camera-traps (Silver et al 2004, Chávez et al 2013). The area covered in this survey by camera traps was calculated using the method of minimum convex polygon (fig. 1). Cameras were placed following the method proposed by Karanth and Nichols (1998) and Chávez et al (2013) at sites with potential for jaguar crossings, such as paths, streams, roads and ravines. Nevertheless, not all camera-trap stations were placed evenly throughout the sampled area due to the rugged topography and the inaccessibility of some sites. The camera-trap stations were installed at a height of approximately 50 cm from the ground, attached to tree trunks or stakes. They were programmed to remain active 24 hours a day and were checked approximately every 30 days to replace batteries, collect data, and maintain equipment.

Using photographic records, we identified individuals from the unique pattern of their rosettes. Each specimen was assigned a name and given a unique code, and gender was identified by the presence/absence of testicular sacks. We excluded distorted pictures and those that lacked clarity for individual identification. A matrix of capture history was elaborated for each individual photographed, thus generating a detection (1)-no detection (0) base, according to sampling periods (MacKenzie et al 2002, Trolle and Kéry 2003). Therefore, only individuals identified on both flanks, or those whose identity was unquestionable, were taken into account.

Estimate of abundance

The relative abundance index (RAI) was calculated according to Maffei et al (2002) and Sanderson (2004) using the following algorithm:

$$RAI = (C/EM) \times 1{,}000 \text{ days/trap}$$

where C are the captures or independent events photographed; EM is the total sampling effort (number of camera traps multiplied by days of sampling) and 1,000 days/trap (frequency of capture, standardizing at 1,000 days/trap).

To avoid overestimations, the analyses considered only those records that were independent within a 24-hour gap between each event. The independent records were considered as: i) consecutive photographic records, when individual identification was not possible; ii) consecutive photographic records of totally identifiable individuals; and iii) consecutive photographic records of different individuals.

Density estimation

To obtain jaguar density, we used the MARK® program in its CAPTURE® mode. This program analyzes data (captures-recaptures) and determines which model achieves the best fit. In addition, CAPTURE generates a capture probability for a closed population (p) to make population estimates, under two assumptions: the population must be closed, and all individuals have the same capture probability, greater than zero (Noss et al 2013, Mackenzie et al 2018). To select the best fit, values obtained varied from 0 to 1, and the highest value indicated the best fit. Subsequently, density was estimated by dividing the abundance obtained by CAPTURE by the effective sampling area (ESA). This was constructed from the convex minimum polygon method (Kernohan et al 2001) which included all the sampling stations that were at the border. A buffer area was added to this. This buffer area corresponds to half the maximum mean distance (½ MMDM) traveled by jaguars and captured by two or more camera-traps. Density estimation using the previous method and the probability of capture, associated with the animal location with respect to the camera-trap, can introduce sources of variability in addition to not incorporating the spatial structure, both regarding the ecological process and the sampling process (Efford 2011, Foster and Harmsen 2012). Therefore, in order to improve density estimates of individuals in the study area, we also determuned the density based on the spatially explicit capture-recapture model (SERC) in the Density program 5.0 (University of Otago, New Zealand). Density uses SERC models of the locations of each animal detected and the number of detections of individuals already identified (or recaptured) on one or more occasion (detection histories or captures matrix) to fit a spatial model of the detection process. In this way, population density estimates generated were unbiased by border effects and incomplete detections (Efford et al 2004, Borchers and Efford 2008). We calculated density using SERC models with a maximum likelihood approximation (MLE) (Efford 2011), assuming a Poisson distribution. We used a buffer distance corresponding to the ½ MMDM calculated in this study during each period. Three half-normal, negative exponential and hazard detection functions were contrasted with three models: $g_0(.)\sigma(.)$, where all individuals have the same capture probability; $g_0(b)\sigma(.)$, individuals show behavioral response after the first capture; and $g_0(h2)\sigma(.)$, individuals show heterogeneity in the probability of capture. The choice of the best models was based on the Akaike selection criteria adjusted for small samples (AICc) (Burnham and Anderson 2002).

Jaguar home range in the NJR

Jaguar home range was determined from camera-traps data recorded within the NJR. A hotspot test was applied to these data using the least convex polygon technique to determine the highest concentration of activity. This analysis was based on the estimate of individuals analyzed per unit area (km^2). This approach determines the sites with the highest and lowest concentration of individuals (Pfeiffer et al 2008). The home range is considered the area inhabited by an individual for its normal activities, such as mating, food gathering, and rearing of cubs (Burt 1943, Maffei and Taber 2003).

The home range was estimated for two individuals recorded by more than two camera trap stations, according to the following selection criteria: i) the individual male whose locations generated the largest special overlap over other jaguars of either sex; ii) an estimate of home range size of a potentially breeding male for mating, so the female with the largest home range extension detected in the study area was considered. Home range size was estimated using the minimum convex polygon (MCP) technique, suggested for use in other large mammals (Kernohan et al 2001, Fashing et al 2007, Kumbhojkar et al

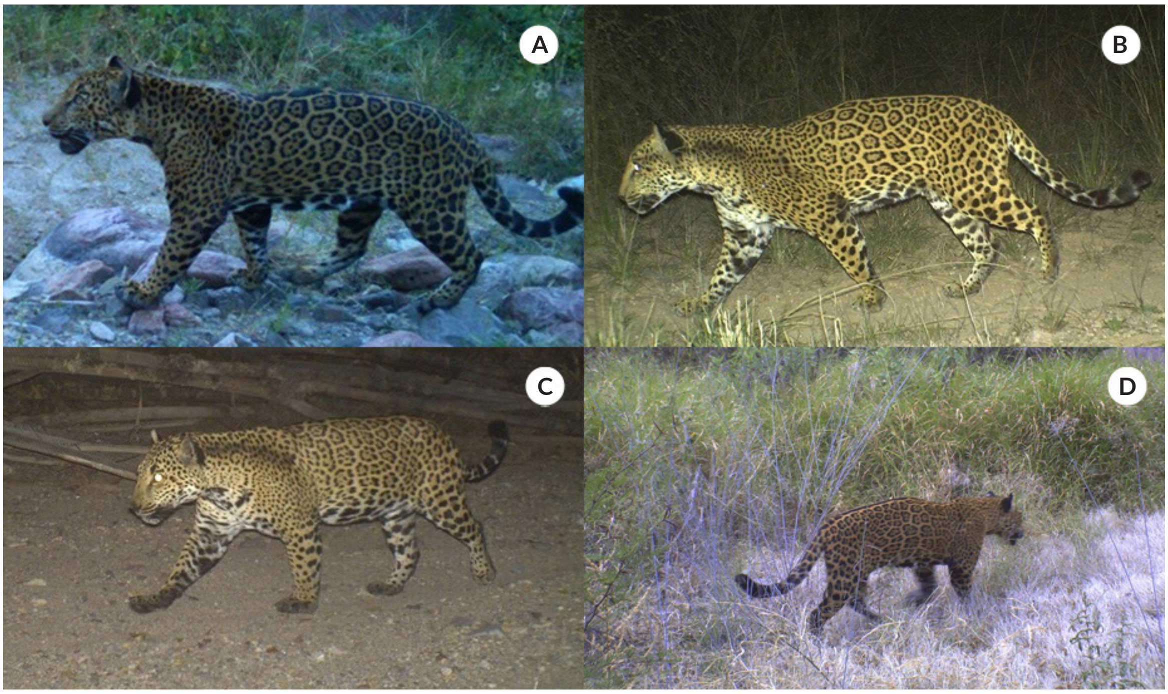

Fig. 2. Camera trap photographs of three jaguars *Panthera onca*: Female 4 (A), Male 1 (C), Female 1 (B and D) recording during period January 2014-December 2015 in the Northern Jaguar Reserve, Sonora (Mexico).

Fig. 2. *Fotografías de tres ejemplares de jaguar* Panthera onca: *Hembra 4 (A), Macho 1 (C), Hembra 1 (B y D) registrados durante el período enero 2014-diciembre 2015 en la Reserva Jaguar del Norte, Sonora (México).*

2020). The MCP analysis consisted of creating the smallest possible polygon formed by internal angles ≤ 180° that encompassed all locations where focal individuals were recorded.

Results

We obtained 95 photographic records for identification. Nine individuals were identified: four males, four females, and one for whom sex was not determined (fig. 2). We obtained a total sampling effort of 40,880 camera trap-days, with periods of highest effort reaching 3,472 camera trap-days, and periods with the lowest effort being 3,304 camera trap-days. The effective sampled area (including a ½ MMDM buffer around the camera-traps) varied significantly across surveys, from 290.2 km to 770.6 km^2. The study comprised an area of 182 km^2, calculated through the method of convex minimum polygon and considering the area covered by camera traps used for this research without buffer.

Abundances

In the twelve bimonthly sampling periods the sampling effort resulted in the 40,880 camera trap-days mentioned above. Highest sampling was achieved in July-August 2015, reaching 3,472 camera trap-days. As for the estimated RAIs for the entire study, we calculated 32 rec./1,000 camera trap-days. The months with the highest RAI were November-December 2014 with 6.14 rec./1,000 camera trap-days (fig. 3).

Densities

During the 12 periods, jaguar density was estimated by the CAPTURE program as an average of 0.7 (± 0.28) indiv./100 km^2, and the average of the maximum mean distances covered was 4,158 m, with a range between 1,522 m for females and 6,879 m for males. According to these results, the models with the best fit for density were the individual heterogeneity *M(h)* and the null *M(o)*. The former assigns various capture probabilities for each individual and these remain the same along each sampling occasion, while *M(o)* assumes that the probability of capture is the same for each animal on any occasion (table 1).

Results estimated through the SERC models in Density 5.0 obtained a density between 0.21-3.04 indiv./100 km^2. The $g_0(.)\sigma(.)$ model using the half-normal and negative exponential detection functions was superior in most cases to the other models used according to the adjusted Akaike information criteria (AICc), and both detection functions were similarly supported (table 2).

Home range

Regarding photo-trapping individuals, we obtained 72 independent records. The analysis considered male 1 (n = 21 records) and female 1 (n = 22 records), these being the individuals that fulfilled the criteria required by the methodology. Hotspot analysis highlighted four sites where high jaguar activity was observed within the

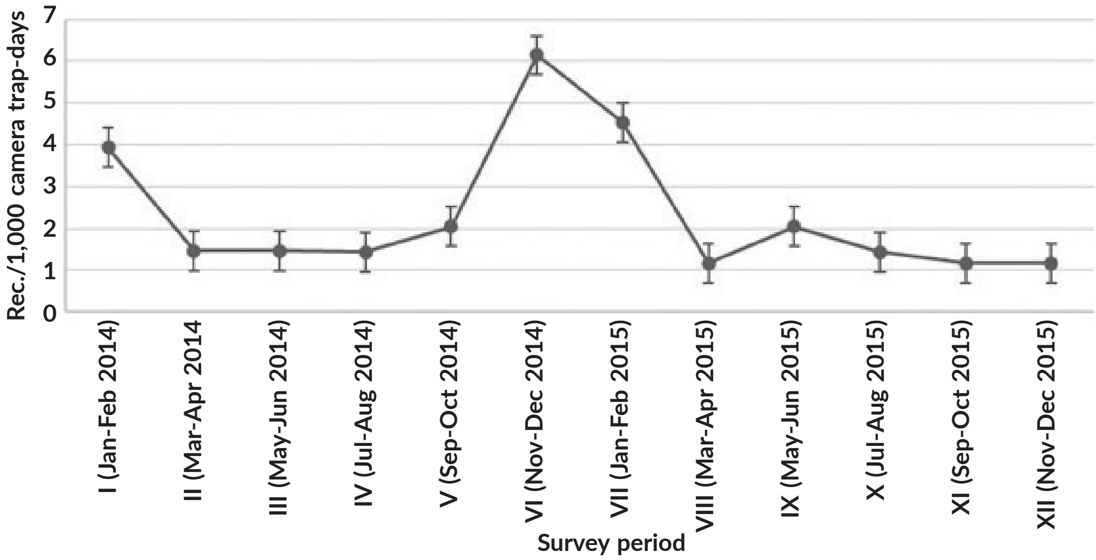

Fig. 3. Jaguar *Panthera onca* relative abundance indexes at the Northern Jaguar Reserve, Sahuaripa, Sonora (Mexico), during 12 sampling periods between 2014-2015.

Fig. 3. *Índices de abundancia relativa del jaguar* Panthera onca *en la Reserva Jaguar del Norte, en Sahuaripa, Sonora (México) durante 12 períodos de muestreo entre 2014-2015.*

reserve. Only one of these was within the limits of the northwestern part of the Reserve, within the properties of Los Pavos and Tres Corrientes (located north in NJR). The rest were generally in the core zone of the reserve (fig. 4). For two individuals, the home range is represented as a proxy of their home range in the study area. One male (M1) presented an area of activity of 78.8 km^2 according to the MCP method, and one female (F1) presented an area of activity of 45.1 km^2.

Discussion

In this study, jaguar density in northwestern Mexico was estimated for the first time using both the spatially explicit models and the classic capture-recapture models, the latter widely used in several studies on relevant issues of ecology and wildlife conservation (O'Connell et al 2011, Meek et al 2014). Through camera-trapping, we were able to estimate the distribution and abundance of this northernmost jaguar population in the NJR. Camera trapping allowed us to generate relevant information about wildlife populations, and is a valuable non-invasive method for monitoring wild feline species and their prey (Maffei et al 2004, Di Bitetti et al 2006, Dillon and Kelly 2007, Martínez-Hernández et al 2014). However, recent debate has questioned the precision of camera-trapping to estimate density. (Dillon and Kelly 2007). One criticism concerns the area covered by the cameras. This area is generally small and less than the real area of action of the species of interest. In this study we covered an area of 182 km^2, which is considerably larger than the minimum 80 km^2 recommended for this species (Silver et al 2004, Azuara and Medellín 2007, Maffei et al 2011, Chávez et al 2013), and also larger than the area covered in other studies reported elsewhere (Kelly 2003, Trolle and Kéry 2003, Salom-Pérez et al 2007, De la Torre and Medellín 2011, Rosas-Rosas and Bender 2012, Ávila-Nájera et al 2015, Briones-Salas et al 2016, Carrera et al 2016). Another concern is that density estimates using traditional capture-recapture models tend to generate an inaccurate assessment of density because they use little information to calculate buffers, especially when studying an activity area that is smaller than that of the target species (Foster and Harmsen 2012). Also, it is important to consider the density of cameras-traps, since the higher the camera density, the greater the number of records (Soria-Díaz et al 2010). Conventional capture-recapture models tend to be dependent on sample size (Gopalaswamy et al 2012). Nonetheless, currently, some studies use SECR models. The results of these are very similar and do not appear to differ statistically from the capture-recapture method (Tobler and Powell 2013, Charre-Medellín et al 2021). In this study, we complemented estimates using both capture-recapture and SERC models. The latter are more robust as they relay in few individuals and fewer recaptures than traditional models, and are therefore less sensitive to small grid size (Gopalaswamy et al 2012, Tobler and Powell 2013, Harmsen et al 2020). In addition, it is a priority to have estimates of both methods in order to favor comparisons with other assessments at national and continental levels, as is the case of the National Jaguar Conservation Censuses (CenJaguar, by its Spanish acronym, De la Torre et al 2018, Ceballos et al 2021).

Regarding the calculation of relative abundance, during the 12 sampling periods, in general we found constant values, except for three periods (I, VI and

Table 1. Jaguar *Panthera onca* densities estimated by means of the Capture-Recapture method using CAPTURE+MMDM (mean maximum distance moved) in the Northern Jaguar Reserve, Sonora in 2014-2015: ESA, effective sampled area; *M(o)*, same capture probability; *M(h)*, heterogeneity of capture probabilities; CP, capture probability; Density (indiv./100 km^2); + no recaptures in this period, abundance from a single individual;

***Tabla 1.** Densidad de jaguar* Panthera onca *estimada a partir del modelo de captura-recaptura por medio de CAPTURE+MMDM en la Reserva Jaguar del Norte, en Sonora en 2014-2015: ESA, área efectiva de muestreo;* M(o), *ninguna diferencia en la probabilidad de captura;* M(h), *probabilidad de captura heterogénea; CP, probabilidad de captura; Density, densidad (indiv./100 km^2); + no hubo recapturas en este período por lo que la abundancia fue de un individuo.*

Bimonthly period 2014–2015	ESA (km^2)	Density (SE)	Selecting model	CP	Closed population test
I (Jan-Feb 2014)	425	0.70 (0.09)	*M(o)*	0.05	*Z* = - 0.407; *P* = 0.342
II (Mar-Apr 2014)	226	1.32 (0.53)	*M(o)*	0.02	*Z* = - 0.810; *P* = 0.208
III (May-Jun 2014)	290	0.74 (0.16)	*M(o)*	0.04	*Z* = - 0.353; *P* = 0.361
IV (Jul-Aug 2014)	381	0.78 (0.39)	*M(h)*	0.02	*Z* = - 1.380; *P* = 0.083
V (Sep-Oct 2014)	539	0.92 (0.48)	*M(h)*	0.02	*Z* = - 1.669; *P* = 0.047
VI (Nov-Dec 2014)	621	0.48 (0.02)	*M(o)*	0.08	*Z* = - 2.273; *P* = 0.011
VII (Jan-Feb 2015)	639	0.62 (0.08)	*M(o)*	0.04	*Z* = - 1.828; *P* = 0.033
VIII (Mar-Apr 2015)	346	1.44 (0.87)	*M(o)*	0.01	*Z* = - 0.398; *P* = 0.345
IX (May-Jun 2015)	539	0.74 (0.27)	*M(o)*	0.02	*Z* = - 1.260; *P* = 0.103
X (Jul-Aug 2015)	330	0.30+	--	--	-- --
XI (Sep-Oct 2015)	770	0.25 (0.12)	*M(o)*	0.02	*Z* = - 1.380; *P* = 0.083
XII (Nov-Dec 2015)	616	0.16 (0.07)	*M(o)*	0.03	*Z* = - 1.309; *P* = 0.095

VII). These temporal variations (dry and wet seasons) have been documented in abundance in other studies (Nuñez et al 2002, Scognamillo et al 2002, De la Torre and Medellin 2011). Although we had the same number of camera traps right throughout survey, such annual changes in individuals from the NJR may occur across time and space. Bruton et al (2015) suggested that detection rates reflect not only population abundance but also relationships between camera settings (e.g., random vs. targeted), spacing, and animal behaviours such as home range size and exclusivity, habitat selection, movement routes, and interspecific interactions.

The estimated average RAI in our study area was 2.43 (1.23-6.49) rec./1,000 camera trap-days. Similar results have been obtained in other regions, such as Arizona, USA (McCain and Childs 2008), Oaxaca, Mexico (Briones-Salas et al 2016) and the Tuichi Valley in Bolivia (Wallace et al 2003), which reported 2.3, 1.55 and 2.67 rec./1,000 camera trap-days, respectively. In contrast, our 2.43 is well below those recorded in south and south-east Mexico, where the RAI range was between 5.2-44.9 rec./1,000 camera trap-days (De la Torre and Medellín 2011, Figel et al 2011, Ávila-Nájera et al 2015), and in the wide range reported in Central and South America with 14-164 rec./1,000 camera trap-days (Kelly 2003, Maffei et al 2004, Soisalo and Cavalcanti 2006, Salom-Pérez et al 2007, Paviolo et al 2008, Silveira et al 2010). One possible explanation for such differences is that most studies reporting high photo-capture rates are in neotropical biogeographic areas, where environmental variables such as precipitation are more abundant and, primary productivity is therefore higher, translating into higher herbivores density and consequently greater prey availability (Carbone and Gittleman 2002, Karanth et al 2004).

Regarding density, the commonly used capture-recapture and SERC models estimated 0.7 (0.16-1.44) and 1.07 (0.36-3) indiv./100 km^2, respectively. Such information is very close to that reported for neighboring Nácori Chico in Sonora, with 1.1-1.54 indiv./100 km^2 (Rosas-Rosas and Bender 2012, Greenspan et al 2020) and 1.59 indiv./100 km^2 in Sinaloa (Coronel et al 2017). These figures are also similar to those of other sites in west-central Mexico, with 1.01 indiv./100 km^2 (Charre-Medellín et al 2021) and in Chinantla (Oaxaca) with 1.16 jaguar/100 km^2 (Lavariega et al 2020). Data from other countries such as Brazil, Paraguay, and Bolivia show ranges of 0.49-1.74 jaguars/100 km^2 (Romero-Muñoz et al 2007, Paviolo et al 2008). In contrast, it is lower than densities reported in some other areas of Mexico that range from 2 to 7 indiv./100 km^2 (Faller et al 2007, Chávez 2009, De la Torre and Medellín 2011, Núñez-Pérez 2011, Ávila-Nájera et al 2015, Carrera et al 2016, Hernández and Bender 2020). It is also lower than the estimated range in other regions of South America that have recorded 2-11 jaguars/100 km^2 (Silver et al 2004, Novack et al 2005, Salom-Pérez et al 2007, Maffei et al 2011). Overall, in Mexico densities average around 3.0 indiv./100 km^2 (Ceballos et al 2021). The low densities at NJR may be because the space to satisfy shelter and feeding needs is greater in an arid habitat of this type (Urness 1981, Rosas-Rosas and Bender 2012). In relation to these factors, studies in various ecosystems argue that carnivorous mammal

Table 2. Jaguar *Panthera onca* density estimated using spatially explicit models with the DENSITY program at Jaguar del Norte Reserve, Sonora, in 2014-2015: AICc, Akaike's Information Criteria; AICωi, Akaike weight; Detection function (HN, half normal; EN, negative exponential); model g0(.)σ(.): all individuals have the same capture probability.

Tabla 2. Densidad de jaguares Panthera onca *estimada mediante modelos espacialmente explícitos con el programa DENSITY en la Reserva Jaguar del Norte, en Sonora en 2014-2015: AICc, criterio de información de Akaike; AICωi, peso de Akaike; Funciones de detección (HN, media-normal; EN, exponencial negativa); modelo g0(.)σ(.): todos los individuos tienen la misma probabilidad de captura.*

		Density (indiv./100 km^2)		
Period	Model	AICc	AICωi	Density (SE)
I (Jan-Feb 2014)	HN g_0(.)σ(.)	170.22	0.22	0.81 (0.52)
	EN g_0(.)σ(.)	170.14	0.23	0.79 (0.50)
II (Mar-Apr 2014)	HN g_0(.)σ(.)	91.38	0.06	3.00 (2.43)
	EN g_0(.)σ(.)	91.48	0.05	3.04 (2.48)
III (May-Jun 2014)	HN g_0(.)σ(.)	89.01	0.27	1.08 (0.93)
	EN g_0(.)σ(.)	89.72	0.18	1.06 (0.99)
IV (Jul-Aug 2014)	HN g_0(.)σ(.)	57.91	0.27	1.38 (1.75)
	EN g_0(.)σ(.)	58.2	0.24	1.37 (1.74)
V (Sep-Oct 2014)	HN g_0(.)σ(.)	159.78	0.26	1.34 (0.76)
	EN g_0(.)σ(.)	159.75	0.26	1.39 (0.84)
VI (Nov-Dec 2014)	HN g_0(.)σ(.)	293.5	0.30	0.51 (0.32)
	EN g_0(.)σ(.)	294.08	0.23	0.50 (0.32)
VII (Jan-Feb 2015)	HZ g_0(.)σ(.)	220.74	0.16	0.82 (0.46)
	HZ g_0(b)σ(.)	222.1	0.08	1.00 (0.75)
VIII (Mar-Apr 2015)	HN g_0(.)σ(.)	90.99	0.22	2.04 (1.59)
	EN g_0(.)σ(.)	91.12	0.20	2.00 (1.55)
IX (May-Jun 2015)	HN g_0(.)σ(.)	125.38	0.02	0.78 (0.54)
	EN g_0(.)σ(.)	125.61	0.01	0.77 (0.53)
X (Jul-Aug 2015)	HN g_0(.)σ(.)	42.36	0.29	0.54 (0.73)
	EN g_0(.)σ(.)	42.81	0.23	0.54 (0.75)
XI (Sep-Oct 2015)	HN g_0(.)σ(.)	77.92	0.23	0.36 (0.33)
	EN g_0(.)σ(.)	77.92	0.23	0.36 (0.32)
XII (Nov-Dec 2015)	HN g_0(b)σ(.)	61.88	0.29	0.21 (0.31)
	EN g_0(b)σ(.)	61.97	0.28	0.21 (0.31)

abundance varies according to the type of vegetation, prey availability and hunting pressure (Sunquist and Sunquist 2002, Chapron et al 2008, Di Bitetti et al 2008, Lavariega et al 2020). Jędrzejewski et al (2018) predicted low densities and occurrence of this felid in dry areas, such as the NJR, are the result of extreme climate throughout the year, the type of thorny scrub vegetation, low rainfall (< 500 mm/year), scarcity of areas with dense cover, and low prey density. Another hypothesis is that in this predominantly livestock region, there is a permanent, low-profile lethal control due to depredation on calves. A shortage of wild ungulates may be another contributing factor because local studies have reported that the numbers of the jaguar's main prey, the collared peccary *Pecari tajacu*, have declined because of poaching and disease-caused mortality (Aranda 1994, Rueda et al 2013, Cassaigne et al 2016). As mentioned previously, one of the main causes for the decrease in the jaguar population in the study area is the lethal control exercised by ranchers as a response to predation on both livestock and important game species, such as white-tailed deer *Odocoileus virginianus* (Rosas-Rosas and Núñez-Pérez 2014). In Sonora, it is estimated that at least 0.5-0.6 jaguars/100 km^2 are lost annually for this reason (Rosas-Rosas et al 2008, Cassaigne et al 2016). Similar results have been reported in southeastern Mexico (Amador-Alcalá et al 2013). Another important aspect to consider is that although photo-trapping is considered a non-invasive technique, it has been reports at that wild cats can pass near to or in front of cameras without being detected (Rosas-Rosas and Bender 2012). In certain areas of Mexico, it has also been documented that jaguars occasionally avoid passing through the site where cameras have been placed, and later rejoin the path (Hernández and Bender 2020). Kays and Slauson (2008) suggested that the presence of camera traps can trigger changes in feline behavior, such as trap shy jaguars. This could be happening in NJR, since most of the monitoring stations have remained in the same places for more than three years. However, Brehm and Mortelliti (2018) suggested that trapability could not be used as a proxy for personality as it was not a repeatable measure (animals that were trap happy or trap shy in one session did not necessarily present this behavior throughout the trapping season). It has been recommended that vigorous attempts should be made to eliminate all sources of variation in capture probabilities (Menkens and Anderson 1988).

Estimates of jaguar home range using the PMC method have shown variation between sexes with estimates ranging from 1.7 to 2.53 times higher for males. This corroborates consistent results in many other studies where home ranges of females are lower than those of males (Conde et al 2010, Fragoso et al 2023). De la Torre et al (2017) found similar results in the Lacandon jungle in SE Mexico, with activity areas being 2.3 times larger in males. In contrast, in Jalisco (western Mexico), this variable was only 1.5 times larger (Núñez 2006). In areas where jaguars have been intensively studied, female territories are consistently smaller than those of males, reflecting the pattern of a species with a polygamous breeding system. The home range of females thus depends on the metabolic demand of females and their offspring, while in males it is determined by the distribution of females (Sandell 1989, Morato et al 2016, Astete et al 2017) and competition with other males. Our results are within the ranges reported elsewhere, these being from 10-125 km^2 for females and from 25-625 km^2 for males (Schaller and Crawshaw 1980, Rabinowitz and Nottingham Jr 1986, Crawshaw Jr and Quigley 1991, Ceballos et al 2007, Nuñez 2006, Azevedo and Murray 2007, Cavalcanti and Gese 2009, Chávez 2009, De la Torre et al 2017). Although, large home ranges are attributable to the relatively low productivity of semi-arid ecosystems and high heterogeneity in resource distribution (McBride and Thompson 2018), homes range estimates in NJR are not among the highest reported to date. It is of note that the results from other studies have shown that the distances traveled by radio-collared jaguars can be up to twice those estimated by camera trapping (Maffei et al 2011, Foster and Harmsen 2012).

The range of approaches and methods to research movements and home ranges of jaguar is wide. However, methods such as the use of radio collars may be costly, difficult to set up, or have an impact on animal welfare (Gracanin and Mikac 2022). The high effectiveness of camera traps has been supported in many studies estimating variables related to wild cat spatial distribution (Kumbhojkar et al 2020) such as jaguar home ranges (Socias-Martínez et al 2023). Indeed, the use of photo-trapping-derived MCP can provide greater predictive potential than other home range estimators, such as kernel (KDE) as long as the sample size is representative and has a minimal size of three (Gracanin and Mikac 2022, Socias-Martínez et al 2023) and consider possible bias in the biological interpretation (Nilsen et al 2008, Socias-Martínez et al 2023). It has also been suggested that long-range species such as the jaguar potentially require study areas of over 2,000 km^2, so it is advisable to combine data from both camera-trapping and radiotelemetry for data autocorrelation (Calabrese et al 2016) to ensure more robust rigor (McBride and Thompson 2018).

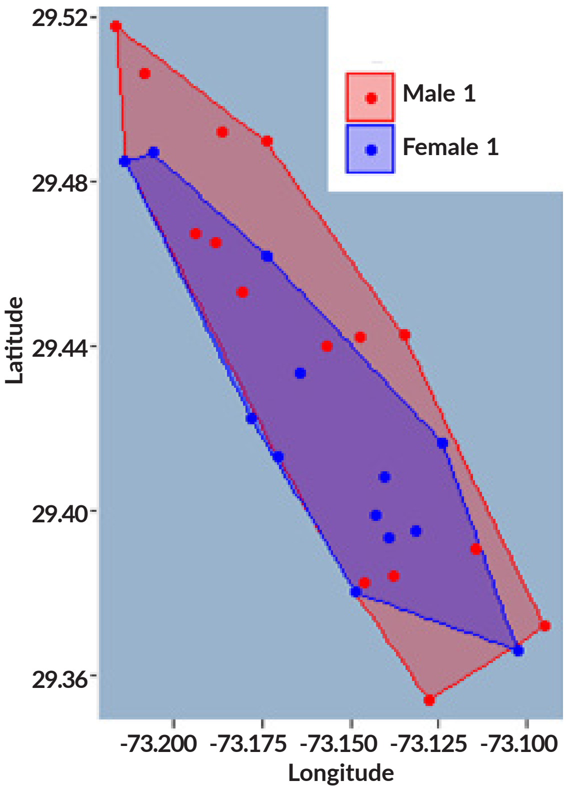

Fig. 4. Home range of a male (M1) and a female (F1), with areas of 78.8 km^2 and 45.1 km^2, respectively, according to the MCP method.

Fig. 4. Área de actividad de un macho (M1) y una hembra (F1), con una superficie de 78,8 km^2 y 45,1 km^2, respectivamente, según el método del polígono mínimo convexo (MPC).

Our study is one of the few in Mexico to follow the most fundamental recommendations to estimate density of large mammals (long sampling periods and areas; Tobler and Powell 2013). It provides useful insight into jaguar abundance and home range in the region and also serves as a baseline for future investigations aiming to evaluate the effectiveness of a reserve. We consider our dataset provides a benchmark for the continuation of long-term monitoring plans on jaguar populations. Our results contribute ecological information for conservation of the northernmost breeding jaguar population, and other emblematic feline species that depend on preserving large wild lands and pristine territory (Jędrzejewski et al 2018, Ceballos et al 2021). We hope these findings contribute to the conservation of wildlife in the region, especially because federal and other authorities base most of their relevant management decisions on density estimates of keystone species such as jaguar. Thus, promoting the creation of ADVC as has been done in the NJR is an important step forward, particularly considering that properties in this region extensive traditional livestock activity and subdividing for mining companies, which already have concessions for their exploitation.

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Author contributions

Saúl Amador, Javier Valenzuela and **Gerardo Carreón** designed the study. **Saúl Amador** and **Javier Valenzuela** collected field data.
Saúl Amador and **Fredy Falconi** analyzed the data. **Carlos Valdez** designed the maps and review edition of paper. **Saúl Amador** wrote the paper with significant input from all co-authors. **Gerardo Carreón** funding acquisition. **Alfonso Gardea** edition and translate review. All authors read and approved the final manuscript.

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No conflicts declared

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