Spatial ecology of jaguar (*Panthera onca*) outside protected areas in the Yucatan Peninsula, Mexico

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Abstract

*Spatial ecology of jaguar (*Panthera onca*) outside protected areas in the Yucatan Peninsula*, Mexico. Jaguars (*Panthera onca*) are endangered in several countries and a priority species for conservation action. Despite extensive research efforts in Mexico most studies have been associated with natural protected areas far from human habitation. Because protected areas are too few to conserve the jaguar population over the long–term, a landscape approach that includes both protected and unprotected lands is needed. This is the case in Quintana Roo State where an ecological corridor linking two protected areas (Yum Balam and Sian Ka'an) is at risk of disappearing due to tourism–driven activities. Between 2013 and 2015, four male jaguars were captured and monitored using satellite telemetry inside the corridor. The mean home range size (± SD) was 101.5 km^2 (± 75.9 km^2) for the dry season and 172 km^2 (± 107.29 km^2) for the rainy season. The mean core area size (± SD) was 17.54 km^2 (± 16.21 km^2) for the dry season and 29.07 km^2 (± 16.19 km^2) for the rainy season. No significant seasonal differences were found for home ranges or for core areas. As expected, we observed that jaguars preferred forest or young secondary growth over profusely disturbed areas, using whatever vegetation was available in their home ranges. Although it is not protected, a biological corridor linking Yum Balam and Sian Ka'an still holds its own jaguar population, a population that has learned to coexist with human presence. Conservation actions are recommended at landscape level to maintain what remains of tropical mature forest and to promote the development of long–term secondary growth into close tree canopy.

Key words: Conservation, Corridor, Home range, Habitat use, Non–protected

Resumen

*Ecología espacial del jaguar (*Panthera onca*) fuera de las zonas protegidas de la península de Yucatán, México.* El jaguar (*Panthera onca*) se encuentra en peligro de extinción en países como México y es una especie prioritaria para las medidas de conservación. La mayoría de los esfuerzos de investigación en el país, aunque extensos, se han asociado principalmente a zonas naturales protegidas, alejadas de los asentamientos de población humana. Las zonas protegidas existentes son insuficientes para conservar la población de jaguares a largo plazo, por lo que se debe adoptar un enfoque de paisaje que incluya tanto las tierras protegidas como las no protegidas. Esto es lo que sucede en el estado de Quintana Roo, donde existe un corredor ecológico que une dos zonas protegidas (Yum Balam y Sian Ka'an) que corre el riesgo de desaparecer debido a las actividades impulsadas por el turismo. Entre 2013 y 2015 se capturaron cuatro jaguares machos a los que se siguió mediante telemetría satelital dentro del corredor. La superficie media de la zona de actividad (± DE) fue de 101,5 km^2 (± 75,9 km^2) durante la temporada seca y de 172 km^2 (± 107,29 km^2) durante la temporada de lluvias. La superficie media de la zona central (± DE) fue de 17,54 km^2 (± 16,21 km^2) durante la estación seca y de 29,07 km^2 (± 16,19 km^2) durante la temporada de lluvias. No se encontraron diferencias estacionales significativas con respecto al área de distribución ni con la zona central. Según lo previsto, se encontró que los jaguares prefieren los bosques o las zonas de vegetación joven secundaria a las zonas muy perturbadas de la zona de estudio, mientras que utilizan todos los tipos de vegetación a su alcance dentro de su área de distribución. A pesar de no estar protegido, el corredor biológico que une Yum Balam y Sian Ka'an aún

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alberga una población de jaguares que ha aprendido a convivir con la presencia humana. Se recomienda adoptar medidas de conservación a escala de paisaje para mantener las zonas de bosque tropical maduro que queden y permitir la máxima recuperación posible de las zonas con vegetación secundaria para que se conviertan en bosques densos.

Palabras clave: Conservación, Corredor, Área de distribución, Uso del hábitat, Zonas no protegidas

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Introduction

Understanding how large cats move and use a landscape is important in order to accurately identify priority habitat areas and connectivity corridors, both of which play a key role in the effective design and implementation of conservation strategies (Rodriguez–Soto et al., 2011). Because of their body size, social behavior, prey and habitat requirements, large felids such as jaguar (*Panthera onca*) require large home ranges for their survival and population health, which in turn means their population densities are low (Macdonald et al., 2010).

The home range size of jaguars varies from 10 to 690 km^2, depending on sex, prey availability, and habitat fragmentation level (see González–Borrajo et al., 2016; Morato et al., 2018; de la Torre and Rivero, 2019 for a review). Due to these spatial requirements, protected areas of suitable size are too few to guarantee long–term viability of jaguar as their conservation is hard–pressed to interweave a landscape that includes both protected and unprotected lands (Sanderson et al., 2002; Rabinowitz and Zeller, 2010). Currently, jaguar populations across their distribution range are mostly concentrated in 'Jaguar Conservation Units' (JCUs), that is, in areas that have a stable prey community and are known or believed to contain a resident population of at least 50 breeding individuals (Sanderson et al., 2002). The most important area for jaguar conservation in the northern jaguar range is the Selva Maya, a large region that includes several JCUs in the Yucatan Peninsula in Mexico, northern Guatemala and western Belize. These JCUs are connected by a complex corridor network (Sanderson et al., 2002; Rabinowitz and Zeller, 2010; fig. 1). The region is composed of both protected and unprotected land tracts. Jaguars inhabit a landscape across gradients that include heavily perturbed areas, large tracts of almost intact forests, and areas with intense human disturbance (Mitchell et al., 2013; Ellis et al., 2017). Research on spatial ecology of jaguar in the Selva Maya has mainly been associated with natural protected areas (de la Torre et al., 2017) or areas where large human population settlements are rare (Figueroa, 2013; Cruz et al., 2021). In these preserved areas, such as Calakmul, the jaguar home range varies from 37–436 km^2 for females to 49–633 km^2 for males (Cruz et al., 2021). Further variation has been reported in relation to habitat in areas where the forest is well–preserved and human disturbance is minimal, such as between Selva Maya and the Maya Mountains (Figueroa, 2013), Selva Lacandona, and Selva Maya (de la Torre et al., 2017).

Despite this well–established understanding of the jaguar home range, the only published data on jaguar home ranges from the corridor between Yum Balam and Sian Ka'an is based on the report of a single male (Gonzalez–Gallina et al., 2017a). This individual showed a particularly small seasonal home range (16 km^2) that was attributed to the availability of unintended human subsidies. This male is also included in the present study.

Human population density alone does not account for past extirpations of jaguar or for decreases in populations. Similarly, human population increases will not necessarily determine jaguar declines. Jaguar extirpations, however, are potentially avoidable through the design and implementation of sustainable management and conservation programs (Jędrzejewski et al., 2017). Considering that jaguars will enter some non–protected areas with high human disturbance, it is essential to know how they respond to these mixed territories in order to develop comprehensive and effective conservation plans that consider further urban expansion into jaguar populated areas. One relevant area for jaguar conservation in the Selva Maya lies in the northeastern part of Quintana Roo state in Mexico, in an area popularly referred to as 'The Mayan Riviera'. The urban and touristic development presently being undertaken here is affecting the tropical forest therein (Ellis et al., 2017). Furthermore, the area is characterized by a high frequency of hurricanes followed by forest fires that largely influence the process of forest cover loss and recovery in the region (Whigham et al., 2003; Ellis et al., 2017). Such unprotected regions are well–preserved natural ecosystems and valuable biological corridors that link the JCUs (Salom–Pérez et al., 2010; Foster et al., 2020), as is the case, for example, of the area between Yum Balam (to the north) and Sian Ka´an (to the south) (Rabinowitz and Zeller, 2010; Rodríguez–Soto et al., 2013). A jaguar population with resident males and females has been reported in this region (González–Gallina et al., 2018). However, the continuous and accelerated expansion of the urban areas, and the growing road network crisscrossing the corridor is increasing the number of jaguars killed on roads (González–Gallina and Hidalgo–Mihart, 2018) and intensifying conflict between humans and jaguars (Remolina–Suárez, 2014; Carral–García et al., 2021).

Individual jaguars have shown differential use of space in relation to the degree of human disturbances (Morato et al., 2016). One study showed that jaguars can survive in areas with a relatively high degree of human presence (Morato et al., 2016; Boron et al., 2016; Hidalgo–Mihart et al., 2019). It has also been observed that seasonality plays a role in the size of the home range as animals adapt to changes such as the availability of cover and of resources (Núñez and Miller, 2019). In the present study, our main objectives were to assess the seasonal home range and core area sizes and analyze habitat use in a non–protected area with high human densities between the JCUs of Yum Balam and Sian Ka'an in the state of Quintana Roo, Mexico. The aim of this study was based on our interest to preserve the high ecological value of the area as much as possible despite the lack of formal protection. As the area not only contains jaguars but also plays a role in connecting JCUs it is necessary to promote management practices that will allow jaguars to persist in this increasingly disturbed area.

Material and methods

Study area

This study took place in the municipality of Solidaridad in the state of Quintana Roo, México (fig. 1), between the city of Playa del Carmen and the 180D Highway (Merida–Cancun; 87º 15' W, 20º 45' N´) in the vegetation corridor linking the protected areas of Yum–Balam (north) and Sian Ka´an (south) JCUs (Rabinowitz and Zeller, 2010). Average elevations in the area are between 5 and 10 m a.s.l. The climate is warm and sub–humid with average annual temperatures between 26 ºC and 33 ºC. Mean annual rainfall is 1,300 mm, mainly occurring from June to November. The dry season is well–defined (December to May) (INEGI, 2013). The original vegetation is tropical semi–deciduous forest with tree height around 12m and a well–defined understory (Rzedowski, 2006). Although this vegetation covers about 57 % of the state´s surface (The Nature Conservancy, 2006), due to the regular presence of hurricanes and agricultural–related fires, secondary growth in a patchwork of succession stages now occurs in most of the area. At the time of the study, the most extensive land cover was the old secondary–growth forests (regenerating for approximately 25 years after the fires that followed Hurricane Gilbert, 1988), characterized by trees of 8–10 m in height and a luxuriant understory. The second most extensive type is young secondary–growth forest (15 years or less of regeneration following recent fires, hurricanes, or human interventions), dominated by shrub and herbaceous strata. Amid these vegetation types there are small open areas used for slash–and–burn agriculture. To date, cattle farming is limited to only a few areas where people have cleared the forest and established pastures. Human presence in the study area is associated with the suburbs of the city of Playa del Carmen (population 149,923) (INEGI, 2010), with some 10 small towns of 100 to 500 inhabitants) and several outlying ranches. There are also a few illegal settlements scattered throughout, each with 5 to 10 inhabitants. The road network in the area is complex with numerous roads close to the Caribbean coast and the tourist areas. Inland, a few roads cut through the Sian Ka'an–Yum Balam corridor. These include the 305D Highway (Nuevo Xcan–Playa del Carmen), the 180D Highway, and some secondary paved and dirt roads.

Capture and telemetry

The jaguars were captured using Aldrich type foot–hold snare traps (Frank et al., 2003) set along trails with evidence of jaguar presence (e.g. scats, tracks, photos). Each trap was equipped with a VHF radio transmitter to monitor the triggering of traps (Halstead et al., 1995). Traps were set from January to April in 2013 and from April to May in 2014. They were checked using hand–held equipment with two antennae every four hours, except in the hottest months (March to April) when they were checked every two hours and turned off after the morning check (9:00) to prevent the animals' exposure to heat. They were reopened in the afternoon (17:00) so as to avoid the hottest hours of the day. Once a jaguar was captured, it was immobilized with a mixture of ketamine/medetomidine for processing. Age, weight, and sex were estimated and each animal was fitted with a Vectronic GPS Plus Pro satellite collar with a Globalstar system and a drop–off device (Vectronic Aerospace GmbH, Berlin, Germany). Once the animal recovered from the anesthetic it was immediately released at the place it was captured. The whole process complied with the guidelines of the American Society of Mammalogists (Sikes et al., 2011) under collection permit SGPA/DGVS/9611/12 (15 X 2012) and SGPA/DGVS/975/14 (6 II 2014) granted to Mircea Gabriel Hidalgo Mihart by the Dirección General de Vida Silvestre–SEMARNAT–México.

The collars were programmed to record and send a GPS location every 6 hours, and the drop–off mechanism was set to release the collar approximately one year after activation. VHF telemetry was used to locate the collars after drop–off. Jaguar location data were classified for each animal seasonally, considering a dry season (January–May) and a rainy season (June–December). Jaguar 1 records were included even though some had been published previously (González–Gallina et al., 2017a). There were two reasons for this; first, to keep the variance of seasonality and habitat use of jaguars in the area in the current scenario and to increase the number of captured individuals, and second, because the previous analysis was focused on the home–range and core area size in relation to a distance to a landfill.

Home range and core areas

We calculated the home range so as to determine the space used by the jaguar over a given period. We calculated core areas because they indicate the most important areas. From this information we assessed landscapes where resources appeared to be clustered and hence important to the animal. These data were more likely to provide relevant clues on the specific life requirements of the animal rather than simply delimiting the peripheral areas (Harris et al., 1990; Powell, 2000). The home range of individual jaguars was calculated independently for each season as defined above, using only validated GPS locations (locations obtained with five or more satellites and with a dilution of precision of less than 10 meters). We estimated the seasonal home–range size and boundaries using the adaptive kernel method (Worton, 1989) at 90 % and seasonal core areas at 50 %. All home range and core areas were calculated using the Home Range Tools extension for ArcGis (Rodgers et al., 2007). The smoothing parameter (h) for each estimate was obtained using the least squares cross–validation method (Kernohan et al., 2001). To compare the jaguar home range with that of other studies (Gula and Theuerkauf, 2013), we also calculated the seasonal home range size of each jaguar using the Minimum Convex Polygon (MCP) estimator, applying the Animal Movement extension for 100 % of the locations (Hooge et al., 2001; table 1s in supplementary material).

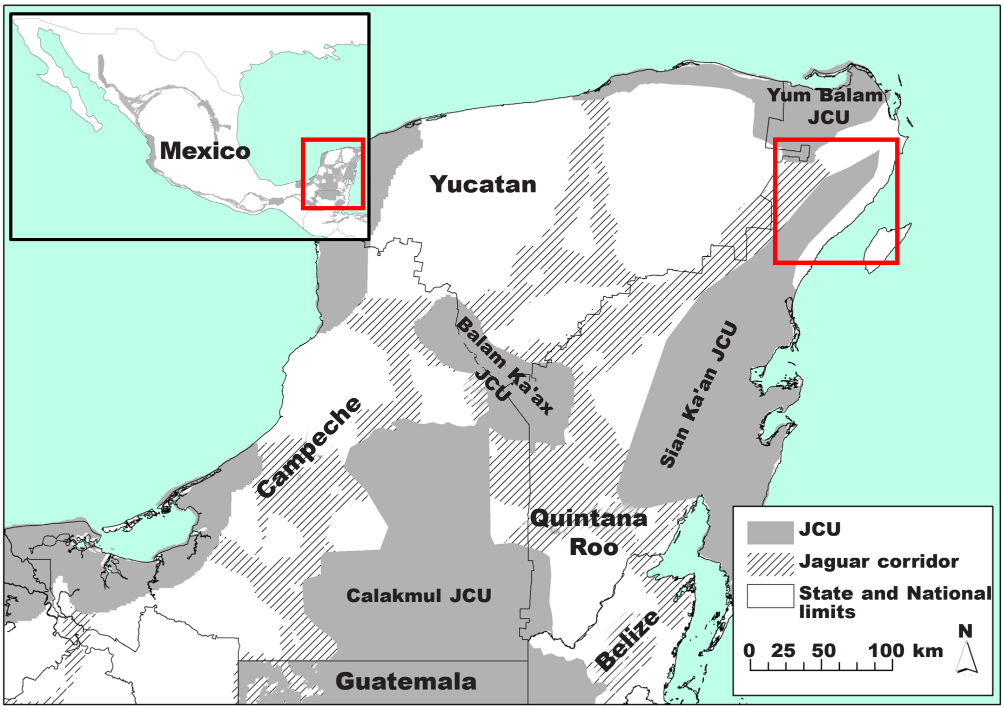

Fig. 1. Location of the study area in the north–eastern portion of the Yucatan Peninsula in relation to the Jaguar Conservation Units (JCU) and jaguar corridors of the 'Selva Maya' region. (JCUs and jaguar corridors according to Rabinowitz and Zeller, 2010).

Fig. 1. Ubicación de la zona del estudio en el noreste de la península de Yucatán, en relación con las Unidades de Conservación de Jaguar (JCU, por sus siglas en inglés) y los corredores de jaguares de la región "Selva Maya". (Los corredores y las JCU para el jaguar se recabaron de Rabinowitz y Zeller, 2010).

To quantify the jaguars'degree of seasonal fidelity to their home range, we calculated the seasonal home range and core area overlap proposed by Kernohan et al. (2001). This method involves superimposing two–dimensional home range maps (HR_1 and HR_2). The measure of shared space use is the percent area overlap between the seasonal Kernel 90 % home ranges computed as:

$$SFI_{i,j} = \frac{HR_i \cap HR_j}{HR_i}$$

where $SFI_{i,j}$ is the Seasonal Fidelity index between animals *i* and *j*, resulting from the intersection of both animals in respect to seasonal home ranges (HR) relative to animal *i* seasonal home range.

A similar calculation was performed for seasonal core areas (CA); the resulting index was labeled CFI as Core Area Fidelity index:

$$CFI_{i,j} = \frac{CA_i \cap CA_j}{CA_i}$$

We analyzed the overlap of the seasonal home range for each individual because a simultaneous comparison between several individuals was marginal between seasons.

Jaguar habitat use

We characterized land use of the study regions from a mosaic of two ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) satellite scenes (pixel size 15 x 15 m) acquired in 2011. We performed a supervised classification of the mosaic image from 200 verification points distributed throughout the study area where the land cover was known and could be reliably assumed to be the same at the time the scenes were acquired. We classified the image based on the reflectance captured and stored by the ASTER sensor (visible and infrared) using the MaxLike algorithm in ENVI 4.5 (Exelis Visual Information Solutions, Boulder, USA). Four land cover categories were identified in the study area: tropical forest (including areas covered by tropical deciduous forest and old secondary growth forests with over 20 years' regeneration), young secondary growth forest

Table 1. Number of verified GPS locations (Loc), home range (HR) and core areas (CA) of four male jaguars that were radio–collared from 2013 to 2015 in a non–protected area in northeastern Quintana Roo, México. Home range and core area size (km^2) were calculated using Kernel adaptive method at 90 % and 50 % respectively: J, jaguar number; W/A, weight (kg) and estimated age; T, total locations (Data from jaguar 1 was previously reported in González–Gallina et al., 2017a).

Tabla 1. Número de ubicaciones GPS verificadas (Loc), tamaño del ámbito hogareño (HR) y superficie de las zonas centrales (CA) de cuatro jaguares macho seguidos con collares satelitales entre 2013 y 2015 en una zona no protegida del noreste de Quintana Roo (México). El área de distribución y la superficie de la zona central (km^2) se calcularon utilizando el método adaptativo Kernel al 90 % y 50 %, respectivamente: J, Jaguar; W/A, peso (kg) y edad estimada; T, ubicaciones totales. (Los datos del jaguar 1 se habían reportado previamente en González–Gallina et al., 2017a).

		Dry season			Rainy season			Dry season			Rainy season			Dry season			
J	W/A																T
		Loc	HR	CA	Loc	HR	CA	Loc	HR	CA	Loc	HR	CA	Loc	HR	CA	
1	50 (adult)																
		466	16.22	2.5	561	97.46	2.55	508	82.38	2.51							1,535
2	48 (adult)																
		101	135.62	17.88	51	228.61	56.88										152
3	52 (adult)																
		239	129.98	18.22	854	318.04	38.29	304	218.1	43.61	95	170.27	35.22				1,492
4	48 (adult)																
											438	45.69	12.42	94	26.69	5.53	438

(under 10 years' regeneration), induced grasslands/agriculture and urban areas. Despite its influence on jaguar behavior, we omitted the category 'water bodies'. It was not possible to identify this category because the karst landscapes in the Yucatan Peninsula of Mexico lacks flowing rivers or extensive water bodies on the surface (García–Gil et al., 2002). Surface water is either in 'aguadas' (topographic depressions in sparse tree cover that accumulate rainfall that usually dries out during the dry season) or in 'cenotes' (permanent water holes where the karst breaks, exposing underground water currents). Only a few are large enough and sufficiently exposed to be detected from above, and smaller ones are always hidden by the canopy (Delgado–Martínez et al., 2018) as is the case with 'sartenejas', that is, rock crevices that accumulate water (Delgado–Martínez et al., 2018). In our case, no reliable GIS layer showed either 'cenotes' or 'sartenejas'. We also included a null category (less than 3 % of the study area) for areas where we were unable to identify any land use due to cloud cover.

We investigated habitat selection following the framework developed by Johnson (1980) and Aebischer et al. (1993), under the assumption that animals make decisions about use at hierarchical stages, namely selection of home range within a study area (second–order selection) and selection of patches within the home range (third–order selection). To determine second–order selection (hereafter called study–area selection), we defined habitat use as the percentage of total area occupied by each habitat type within the boundaries of the seasonal home range of each jaguar, obtained with the adaptive kernel method (ADK) at 90, and habitat availability as the total area occupied by each habitat type within the boundaries of the study area. For each season, we defined our study area as the boundaries of the home range obtained from all the GPS locations of all jaguars present during that season, estimated by the MCP method with 100 % utilization distribution. We used the MCP at 100 % because it is the smallest convex polygon that contains all locations (including those considered to be exploratory movements) and has been successfully used to determine the extension of a second order resource selection study (Horne et al., 2009). For the third–order selection (hereafter called home–range selection), we defined habitat use as the number of seasonal GPS locations of each jaguar in each land use type, and habitat availability as the percentage of the total area occupied by each habitat type within the boundaries of the seasonal ADK 90 % home range polygon of each jaguar (see table 2s in supplementary material for first, second and third order selection percentages).

We used compositional analysis (Aebisher et al., 1993) to examine seasonal habitat selection. We tested for differences of log–ratio habitat use and

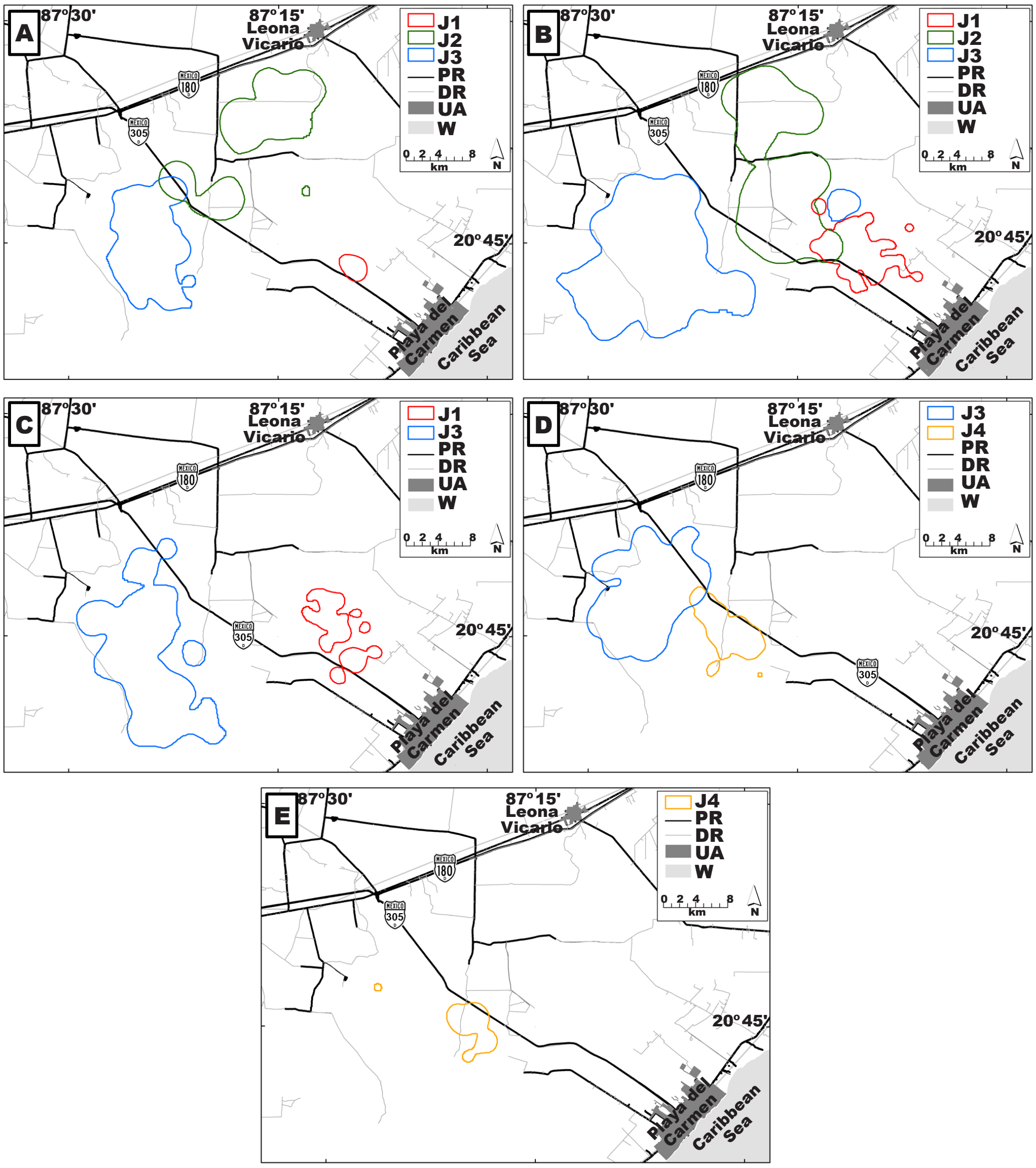

Fig. 2. Seasonal home range configuration of the jaguars tracked by satellite in the north–eastern region of the Yucatan Peninsula, Mexico, obtained with the adaptive Kernel method (90 %): A, dry season of 2013; B, rainy season of 2013; C, dry season of 2014; D, rainy season of 2014; E, dry season of 2015; PR, pavement road; DR, dirt road; UA, urban area; W, water.

Fig. 2. Configuración del área de distribución estacional de los jaguares seguidos con collares satelitales en el noreste de la península de Yucatán (México) obtenida con el método adaptativo Kernel (90 %): A, temporada seca de 2013; B, temporada de lluvias de 2013; C, temporada seca de 2014; D, temporada de lluvias de 2014; E, temporada seca de 2015; PR, carretera pavimentada; DR, camino de tierra; UA, área urbana; W, agua.

availability across seasons at each habitat–selection order with a repeated measure multivariate analysis of variance (MANOVA). The small sample size precluded us from only using data of jaguars present in consecutive seasons. We thus combined data from jaguars that were present in different study years.

When habitat use was significantly non–random ($P < 0.05$), we calculated the mean and standard deviation for all log–ratio differences and constructed a matrix, ranking habitat types in their order of use (Aebischer et al., 1993) using 'adehabitat' HR version 0.3.15 in R (Calenge, 2006). If seasonal differences

Table 2. Seasonal fidelity index (based on Kernohan et al.'s overlap index, 2001) of four male jaguars radio collared from year 2013 to 2015 in a non–protected area in northeastern Quintana Roo, México. Home range and core area size were calculated using Kernel adaptive method at 90 % and 50 % respectively: HR, home range overlap; CA, Core area overlap. (Data from jaguar 1 were previously reported in González–Gallina et al., 2017a).

Tabla 2. Índice de fidelidad estacional (basado en el índice de superposición de Kernohan et al., 2001) entre cuatro jaguares macho seguidos con collares satelitales entre 2013 y 2015 en un zona no protegida del noreste de Quintana Roo (México). La configuración del área de distribución y de la zona central se obtuvieron utilizando el método adaptativo Kernel al 90 % y 50 %, respectivamente: HR, superposición del área de distribución; CA, superposición de la zona central. (Los datos del jaguar 1 se habían reportado previamente en González–Gallina et al., 2017a).

		Jaguar 1		Jaguar 2		Jaguar 3		Jaguar 4	
Season 1	Season 2	HR	CA	HR	CA	HR	CA	HR	CA
Dry 2013	Rain 2013	0.99	0.96	0.53	0.00	0.97	0.02		
Rainy 2013	Dry 2013	0.13	0.94	0.31	0.00	0.40	0.01		
Dry 2013	Dry 2014	0.89	0.87			0.79	0.42		
Dry 2014	Dry 2013	0.18	0.88			0.47	0.18		
Rainy 2013	Dry 2014	0.44	0.88			0.50	0.03		
Dry 2014	Rainy 2013	0.66	0.90			0.73	0.03		
Dry 2013	Rainy 2014					0.49	0.18		
Rainy 2014	Dry 2013					0.37	0.10		
Rainy 2013	Rainy 2014					0.34	0.38		
Rainy 2014	Rainy 2013					0.49	0.34		
Dry 2014	Rainy 2014					0.41	0.02		
Rainy 2014	Dry 2014					0.52	0.03		
Rainy 2014	Dry 2015							0.81	0.34
Dry 2015	Rainy 2014							0.47	0.77

in habitat selection were not detected by MANOVA, we pooled all GPS locations for each jaguar to determine a single–ranking matrix of habitat use and habitat availability.

Results

With a trapping effort of 1267 trap–nights, we captured four male jaguars (table 1) and later recaptured one of the four. Three of the animals were captured during the 2013 trapping season. One new capture and the recapture occurred during the 2014 trapping season. We retrieved the location data directly from two GPS collars that were recovered (jaguar 1 after drop–off and jaguar 3 after recapture). The data from the other three radio collars (jaguars 2 and 4, and the second year of data from jaguar 3) were retrieved from 'cloud data' stored at the Globalstar repository. We obtained 3617 GPS verified fixes from all the radio collared jaguars, with a maximum of 1,492 and a minimum of 152 per individual (table 1). A maximum of three individuals were monitored simultaneously per season.

Home range and core area size

The mean home range size (± SD) across the study period in the dry season for all the jaguars was 101.5 km^2 (± 75.9 km^2) and 172 km^2 (± 107.29 km^2) for the rainy season (table 1). We did not find statistically significant differences between seasonal home range sizes ($F_{1,8}$ = 2.87, P = 0.12).

The mean core area size (± SD) for the four jaguars was 17.54 km^2 (± 16.21 km^2) for the dry season and 29.07 km^2 (± 16.19 km^2) for the rainy season (table 1). We found no statistically significant differences between seasonal core area sizes ($F_{1,8}$ = 1.93, P = 0.20).

Individual site fidelity indexes for both SFI (for HR) and CFI (for CA) values varied from 0.99 to 0.01 (table 2). Variation between individuals was wide. We recorded near complete site fidelity for both HR and CA for jaguar 1 between the dry and rainy seasons of 2013, and for both dry seasons (2013–2014), and almost no site fidelity for jaguar 2 in 2013. HR fidelity did not imply CA fidelity as we can see with jaguar 3 in 2013, or the other way around jaguar 1 comparing the dry season in 2013 and the rainy season in 2014 (fig. 2).

Table 3. Mean habitat–selection ranks (Mean) and relation of use between four habitat types (Relation) at the study area level for jaguars in a non–protected area in northeastern Quintana Roo, México. Values for mean rank of habitat selection go from 0 (least–selected habitat type) to 3 (most–selected habitat type). The relation column indicates how jaguars use habitat type A compared to habitat type B. Each relation was replaced by its sign; a triple sign represents significant deviation from random at $p < 0.05$.

Tabla 3. Rango medio de la selección de hábitat (Mean) y la relación de uso de cuatro tipos de hábitat (Relation) presentes en la zona del estudio en una zona no protegida en el noreste de Quintana Roo (México). Los valores del rango medio de selección de hábitat van de 0 (tipo de hábitat menos seleccionado) a 3 (tipo de hábitat más seleccionado). En la columna de la relación (Relation) se indica cómo los jaguares usan el hábitat de tipo A en comparación con el hábitat de tipo B. Cada relación fue reemplazada por su signo; un signo triple representa una desviación significativa del azar a p < 0,05.

Mean	Land use A	Relation	Land use B
3	Tropical forest	+	Young secondary–growth forest
		+++	Induced grasslands/Agriculture
		+++	Urban areas
2	Young secondary–growth forest	–	Tropical forest
		+++	Induced grasslands/Agriculture
		+++	Urban areas
1	Induced grasslands/Agriculture	–––	Tropical forest
		–––	Young secondary–growth forest
		+++	Urban areas
0	Urban areas	–––	Tropical forest
		–––	Young secondary–growth forest
		–	Induced grasslands/Agriculture

Habitat use

We did not find any significant differences in the repeated measures MANOVA of the log–ratios between seasons, either at the study–area level (Wilks' λ = 0.69, $F_{3,7}$ = 1.03, P = 0.44) or at the home–range level (Wilks' λ = 0.72, $F_{3,7}$ = 0.92, P = 0.48). Because no seasonal differences were found, we pooled the seasonal data for all jaguars.

At the study area level (which considers all home ranges as a whole) we found that the proportional use of vegetation types was significantly different from availability (Λ = 0.003, d.f. = 3, P < 0.001). In order of relative selection at this level, jaguars selected forest land use, young secondary growth, induced grasslands/agriculture and urban areas (table 3). Because none of the GPS locations of the jaguars were in urban areas, so as to avoid the biases from missing habitat types (Aebisher et al., 1993) we eliminated this land use from the habitat use analysis at the home range level. In contrast, we found that jaguars within their home range level used all the habitats in proportion to their availability (Λ = 0.87, d.f. = 2, P = 0.76).

Discussion

Here we report on the home range of male jaguars and their habitat use in a non–protected area under increasing human influence from urban expansion and a growing road network. We recognize that our results could be biased by the low number of tracked individuals and the lack of information regarding female jaguars in the region.

Home range and core areas

The mean home range size of the jaguars in our study was smaller (128 km^2 dry season and 190 km^2 rainy season) than that of previously published home ranges in the 'Selva Maya' where mean male home ranges obtained with GPS tracking technology varied from 264 km^2 in Belize (Figueroa, 2013), to 296 km^2 in Calakmul (Cruz et al., 2021). The wide variation in the size of jaguar home ranges (González–Borrajo et al., 2016; Morato et al., 2018; de la Torre and Rivero, 2019) can be expected, however, as the geographic distribution of this species extends from southern

North America to the rest of the continent, and within this distribution, jaguars occur in various habitat types (Sanderson et al., 2002), leading to variation in their spatial ecology. When we look at individuals, male home ranges vary from a minimum of 109 km^2 (Figueroa, 2013) to a maximum of 1,016 km^2 (de la Torre et al., 2017). Our results seem unexpected as one could think that protected areas hold better habitat quality than non–protected areas, causing space use to increase as habitat quality decreases. Home range size and shape for a male jaguar is mostly influenced by prey availability (Sunquist and Sunquist, 1989; de Azevedo and Murray, 2007; McBride and Thompson, 2018), water availability (Delgado–Martínez et al., 2018) and the presence of females (Cavalcanti and Gese, 2009; Goodrich et al., 2010). Following this premise and our results, it seems that the Yum Balam–Sian Ka´an corridor holds enough resources to maintain a resident jaguar population with less than average home range sizes. Resource selection behavior varied considerably across individuals. Nevertheless, we noticed that jaguars in heavily forested areas (shift point = 58.4 %) showed a stronger tendency to avoid non–forest than individuals in more open landscapes. Also, a higher human population and livestock density does not appear to increase the strength of resource selection (Morato et al., 2018).

Although we did not find differences between the rainy and dry seasons regarding home ranges and core areas, we observed that those in the rainy season were almost twice the size of those in the dry season (HR 101.5 and 172 km^2; CA 17.54 and 29.07 km^2). Núñez and Miller (2019) found differences in more contrasting seasonal areas in the coast of Jalisco where water appears to be the limiting factor. A different pattern is known for jaguars in Calakmul (Cruz et al., 2021) and Belize (Figueroa, 2013), although the sample size could also be limit detection of such an effect. This lack of change may indicate that the resources for male jaguars in the region do not change greatly across seasons, for jaguars will respond to shifts in the availability of prey by shifting the core areas of seasonal ranges to correspond with these shifts in prey availability (Figueroa, 2013).

In the Yum Balam JCU (a protected area), jaguars feed mostly on brocket deer (*Mazama temama*), collared pecari (*Pecari tajacu*) and armadillo (*Dasypus novemecintus*; Avila–Nájera et al., 2018), but in non–protected habitat there could be important changes in diet, as jaguars frequently prey on domestic dogs (Remolina–Suárez, 2014), and Jaguar 1 commonly visited the Playa del Carmen's landfill, probably searching for prey therein (González–Gallina et al., 2017a), such as black vultures (*Coragyps atratus*; González–Gallina et al., 2017b). We can thus assume that relative seasonal stability in the core area size in our study region could be attributed to the year–long availability not only of wild prey (Cavalcanti, 2008), which could be attracted by easy access to urban disposal zones, but also to prey items such as domestic dogs (Carral–García et al., 2021). Jaguar 1 home range size is the smallest for a male jaguar reported to date, and is considered largely attributable to the availability of human–related prey at the Playa del Carmen landfill (Gallina et al., 2017a). Far from being a desirable situation, this reflects increasing jaguar–human conflict (Carral–García et al., 2021). This shift in prey items between forested areas and more urbanized areas is becoming a more common strategy among jaguars. Further research on the subject is needed. Prey availability and other resources, such as water, should be assessed. There is also the need to determine how widespread human presence is influencing resource availability.

We found the jaguars in our study showed a high degree of spatial overlap on the subsequent seasonal home range and core areas fidelity. The home range fidelity for at least two seasons in the case of jaguars 2 and 4, and for three seasons in jaguar 1 and four in jaguar 3, together with individual age, indicate they were all resident individuals. Long–term occupation of the same area has been used to distinguish resident jaguars from and transient jaguars (de Azevedo and Murray, 2007). As there is evidence of at least a few potentially reproductive females (González–Gallina et al., 2018) we can assume we were documenting a resident population (Karanth et al., 2006; Macdonald et al., 2010; Andersen et al., 2012).

We recommend jaguar conservation status of the area should be reconsidered. It could be incorporated into the region to the Sian Ka´an JCU or developed as a new JCU in the 'Selva Maya' region. This new JCU could consider encompassing the whole region between Cancun (to the north) between Leona Vicario and Puerto Morelos across the study area between Playa del Carmen and Tintal, connecting the natural protected area of Otoch Ma'ax Yetel Kooh, south to the Coba area. This would connect Yum Balam and Sian Ka'an JCUs. This whole area retains valuable jaguar habitat and resident populations, and it is under only minimal pressure of urban expansion.

Habitat use

According to GPS tracking, we found the jaguars were mainly located in tropical forests (defined as areas of tropical deciduous forest and old secondary growth forests with more than 20 years of regeneration), followed by young secondary forests (defined as areas with less than 10 years' regeneration). They were only occasionally located in induced grasslands/agriculture and never in urban areas. At the home range level, they appeared to use the habitat according to availability. At the core area level they preferred well developed tropical forests regardless of availability. Using photo trapping, Ávila–Nájera et al. (2019) observed that jaguars in Yum Balam JCU selected old secondary growth forests over other vegetation types. In general, we observed that jaguars in the study region preferred areas with low disturbance and dense vegetation, avoiding human modified areas as in other parts of the Selva Maya (Chávez, 2010; Conde et al., 2010; Figueroa, 2013; de la Torre et al., 2017)

Our results support previous observations that jaguars use forested areas in the northeastern portion of the Yucatán Peninsula, and highlight the importance of conservation of these habitats throughout the region (Figueroa, 2013; de la Torre et al., 2017; Cruz et al., 2021). We emphasize the conservation value of young secondary growth forests resulting from forest fires. Though this vegetation type is structurally composed of seasonal bushes, thicker undergrowth and sparse tree cover, it represents the largest patches of natural vegetation in northern Quintana Roo. Not only is it the dominant vegetation type but it could become the jaguar's preferred habitat if it is allowed 10 to 15 years to fully recover. Furthermore, this young secondary growth also harbors jaguar prey items such as white–tailed deer *Odocoileus virginianus,* collared peccary, and ocellated turkeys (*Meleagris ocellate*) (Urquiza–Haas et al., 2009).

Contrary to parts of the Selva Maya where the main threat to forest is the expansion of induced grasslands for cattle grazing (Chávez, 2010; Figueroa, 2013; de la Torre et al., 2017), in our study area the main threats to forest are fires and urban development (Ellis et al., 2017). Regarding the main conflict between jaguars and humans in the area, this is not livestock predation. Conflict is more likely the result of road kill (González–Gallina and Hidalgo–Mihart, 2018), retaliation after dog predation (Remolina–Suárez, 2014; Carral–García et al., 2021), or simply an increasing fear as the urban frontier expands further into the jaguar territory. This trend is likely to increase unless strong conservation actions are undertaken, such as establishing a new protected area in the regions to further protect the forest.

Researchers working with jaguars in cattle ranches (Hoogesteijn et al., 1993; Scognamillo et al., 2002; Polisar et al., 2003; Boron et al., 2016) have suggested that jaguars can live across unprotected human–use areas and co–exist with agricultural landscapes. The conditions conducive to this coexistence are the presence of sufficient natural areas and prohibition of hunting both jaguar and prey (Jedrzejewski et al., 2017). Conservation actions in the area are needed at both patch and corridor levels to maintain what remains of the tropical forest and to allow naturally disturbed patches to properly regenerate. Unless such action is taken, we risk further landscape alterations which, combined with other disturbance factors, will drive local extinctions not only of top predators such as jaguars but also second–growth tolerant mammal species (Urquiza–Haas et al., 2011; Ortiz–Lozada et al., 2017).

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References

Aebischer, N. J. Robertson, P. A., Kenward. R. E., 1993. Compositional analysis of habitat use from animal radio–tracking data. *Ecology*, 74(5): 1313–1325, http://www.jstor.org/stable/1940062

Andersen, L., Everatt, K. T., Somers, M. J., Purchase, G. K., 2012. Evidence for a resident population of cheetah in the Parque Nacional do Limpopo, Mozambique. *African Journal of Wildlife Research*, 42: 144–146

Ávila–Nájera, D. M., Palomares, F., Chávez C. Tigar, B., Mendoza, G. D., 2018. Jaguar (*Panthera onca*) and puma (*Puma concolor*) diets in Quintana Roo, Mexico. *Animal Biodiversity and Conservation*, 41(2): 257–266, Doi: 10.32800/abc.2018.41.0257

Ávila–Nájera, D. M., Lazcano–Barrero, M. A., Chávez, C. Pérez–Elizalde, S., Tigar, B., Mendoza, G. D., 2019. Habitat use of jaguar (*Panthera onca*) in a tropical forest in northern Quintana Roo, Mexico. *Revista Mexicana de Biodiversidad*, 90: e902186, Doi: 10.22201/ib.20078706e.2019.90.2186

Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes–Rodriguez, L., Schaller, G., Payan, E., 2016. Jaguar densities across human–dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. *Plos One*, 11(5): e0153973, Doi: 10.1371/journal.pone.0153973

Calenge, C., 2006. The package 'adehabitat' for the R software: tool for the analysis of space and habitat use by animals. *Ecological Modeling*, 197: 516–519

Carral–García, M., Buenrostro, I., Weissenberger, H., Rosales, V., Pérez–Flores J., 2021. Dog predation by jaguars in a tourist town on the Mexican Caribbean. *Neotropical Biology and Conservation,* 16(4): 461–474, Doi: 10.3897/neotropical.16.e68973

Cavalcanti, S., 2008. Predator–prey relationships and spatial ecology of jaguars in the Southern Pantanal, Brazil: implications for conservation and management. PhD thesis, Utah State University.

Cavalcanti, S. M. C., Gese, E. M., 2009. Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, 90: 935–945, Doi: 10.1644/08-MAMM-A-188.1

Chávez, C., 2010. Ecología y conservación del jaguar (*Panthera onca*) y puma (*Puma concolor*) en la región de Calakmul y sus implicaciones para la conservación de la Peinínsula de Yucatán. PhD thesis, Universidad de Granada.

Conde, D. A., Colchero, F., Zarza, H., Christensen, N. L. Jr, Sexton, J. O., Manterola, C. ,Chávez, C., Rivera, A., Azuara, D., Ceballos, G., 2010. Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biological Conservation*, 143(9): 1980–1988, Doi: 10.1016/j.

biocon.2010.04.049
Cruz, C., Zarza, H., Vidal–Mateo, J. ,Urios, V., Ceballos, G., 2021. Top predator ecology and conservation: Lessons from jaguars in souteastern Mexico. *Conservation Science and Practice* 3(2): e328, Doi: 10.1111/csp2.328
de Azevedo, F. C. C., Murray, D. L., 2007. Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biological Conservation*, 137(3): 391–402, Doi: 10.1016/j.biocon.2007.02.022
de la Torre, J. A. Núñez, J. M., Medellín, R. A., 2017. Spatial requirements of jaguars and pumas in southern Mexico. *Mammalian Biology*, 84: 52–60, Doi: 10.1016/j.mambio.2017.01.006
de la Torre, J. A., Rivero, M., 2019. Insights of the Movements of the Jaguar in the Tropical Forests of Southern Mexico. In: *Movement Ecology of Neotropical Forest Mammals:* 217–241 (C. Chapman, R. Reyna, Eds.). Springer, Cham.
Delgado–Martínez, C. M., Alvarado, F., Mendoza, E., Flores–Hernández, S., Navarrete, A., Navarrete, E., Botello, F., 2018. An ignored role of sartenejas to mitigate water shortage hazards for tropical forest vertebrates. *Ecology,* 99(3): 758–760, Doi: 10.1002/ecy.2078
Ellis, E. A., Romero–Montero, J. A., Hernández–Gómez, I. U., 2017. Deforestation Processes in the State of Quintana Roo, Mexico: The Role of Land Use and Community Forestry. *Tropical Conservation Science,* Doi: 10.1177/1940082917697259
Figueroa, O. A., 2013. The ecology and conservation of jaguars (*Panthera onca*) in central Belize: conservation status, diet, movement patterns and habitat use. PhD thesis, University of Florida.
Frank, L., Simpson, D., Woodroffe, R., 2003. Foot snares: an effective method for capturing African lions. *Wildlife Society Bulletin*, 31(1): 309–314, https://www.jstor.org/stable/3784391
Foster, R. J., Harmsen, B.,J., Urbina, Y.,L., Wooldridge, R. L., Doncaster, C. P., Quigley, H., Figueroa, O. A., 2020. Jaguar (*Panthera onca*) density and tenure in a critical biological corridor. *Journal of Mammalogy,* 101(6): 1622–1637, Doi: 10.1093/jmammal/gyaa134
García–Gil, G., Palacio-Prieto, J. L., Ortiz–Pérez, M. A., 2002. Reconocimiento geomorfológico e hidrográfico de la Reserva de la Biosfera Calakmul, México. *Investigaciones Geográficas*, 48: 7–23, http://www.redalyc.org/articulo.oa?id=56904802
González–Borrajo, N., López–Bao, J. V., Palomares, F., 2016. Spatial ecology of jaguars, pumas, and ocelots: a review of the state of knowledge. *Mammalian Review*, 47(1): 62–75, Doi: 10.1111/mam.12081
González–Gallina, A., Hidalgo–Mihart, M. G., Pérez–Garduza, F., Iglesias–Hernández, J. A., Oliveras de Ita, A., Chacón–Hernández, A., Vazquez–Zuniga, O., 2017a. Home range of a male jaguar spatially associated with the landfill of the city of Playa del Carmen, Mexico. *Mammalia,* 82(1): 1–8, Doi: 10.1515/mammalia-2016-0065
González–Gallina, A., Hidalgo–Mihart, M., 2018. A review of road–killed felids in Mexico. *Therya,* 9(2): 147–159, Doi: 10.12933/therya-18-584
González–Gallina, A., Hidalgo–Mihart, M. G., Castelazo–Calva, V., 2018. Conservation implications for jaguars and other neotropical mammals using highway underpasses. *Plos One*, 13(11): e0206614, Doi: 10.1371/journal.pone.0206614
González–Gallina, A., Pérez–Garduza, F., Iglesias–Hernández, J. A., Oliveras de Ita, A., Chacón–Hernández, A., Vazquez–Zuniga, O., Hidalgo–Mihart, M. G., 2017b. A novel item, black vultures (*Coragyps atratus*) used as food by a jaguar (*Panthera onca*) in Quintana Roo, Mexico. *American Midland Naturalist*, 178(1): 158–164, Doi: 10.1674/0003-0031-178.1.158
Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Kerley, L. L., Quigley, H. B., Hornocker, M. G., 2010. Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote–Alin Biosphere Zapovednik, Russia. *Journal of Mammalogy*, 91(3): 737–748, Doi: 10.1644/09-MAMM-A-293.1
Gula, R., Theuerkauf, J., 2013. The need for standardization in wildlife science: home range estimators as an example. *European Journal of Wildlife Research*, 59: 713–718, Doi: 10.1007/s10344-013-0726-7
Halstead, T. D., Gruver, K. H., Phillips, R. L., Johnson, R. E., 1995. Using telemetry equipment for monitoring traps and snares. In: *Twelfth Great Plains wildlife damage control workshop proceedings:* 121–123 (R. E. Masters, J. G. Huggins, Eds.). Great Plains Agricultural Council, Tulsa.
Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T., Wray, S., 1990. Home–range analysis using radio–tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammalian Review,* 20(2–3): 97–123, Doi: 10.1111/j.1365-2907.1990.tb00106.x
Hidalgo–Mihart, M. G., Jesus–de la Cruz, A., Contreras–Moreno, F. M., Juárez–López. R., Bravata–de la Cruz, Y., Friedeberg, D., Bautista–Ramírez, P., 2019. Jaguar density in a mosaic of disturbed/preserved areas in southeastern Mexico. *Mammalian Biology*, 98: 173–178, Doi: 10.1016/j.mambio.2019.09.009
Hooge, P. N., Eichenlaub, W., Hooge, E. R., 2001. *Animal movement 2.5*. U.S. Geological Survey, Anchorage.
Hoogesteijn, R., Hoogesteijn, A., Mondolfi, X., 1993. Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. In: *Mammals as Predators:* 391–407 (N. Dunstone, R. L. Gorman, Eds.). Zoological Society, London.
Horne, J. S., Tewes, M. E., Haines, A. M., Laack, L. L., 2009. Habitat partitioning of sympatric ocelots and bobcats: implications for ocelot recovery in southern Texas. *Southwestern Naturalist*, 54(2): 119–126, https://www.jstor.org/stable/40263680
INEGI (Instituto Nacional de Estadística y Geografía), 2013. *Anuario estadístico y geográfico de Quintana Roo 2013*. Instituto Nacional de Estadística y Geografía, Aguascalientes.
– 2010. *Censo de Población y Vivienda 2010. Principales resultados por localidad*. Instituto Nacional de Estadística y Geografía, Aguascalientes.
Jędrzejewski, W., Boede, E. O., Abarca, M., Sánchez–Mercado, A., Ferrer–Paris, J. R., Lampo, M., Velásquez, G., Carreño, R., Viloria, A. L., Hooges-

teijn, R., Robinson, H. S., Stachowicz, I., Cerda, H., Weisz, M. M., Barros, T. R., Rivas, G. A., Borges, G., Molinari, J., Lew, D., Takiff, H., Schmidt, K., 2017. Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (*Panthera onca*) in Venezuela. *Biological Conservation,* 206: 132–142, Doi: 10.1016/j.biocon.2016.09.027

Johnson, D. H., 1980. The comparison of usage and availability measurements for evaluation of resource preference. *Ecology,* 61: 65–71.

Karanth, U. K., Nichols, J. D., Kumar, N. S.,Hines, J. E., 2006. Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology,* 87: 2925–2937, Doi: 10.1890/0012-9658(2006)87[2925:atpdup]2.0.co;2

Kernohan, B. J., Gitzen, R. A., Millspaugh, J. J., 2001. Analysis of animal space use and movements. In: *Radio tracking animal populations:* 125–166 (J. J. Millspaugh, J. M. Marzluff, Eds.). Academic Press, San Diego.

Macdonald, D. W., Mosser, A., Gittleman, J. L., 2010. Felid society. In: *Biology and Conservation of Wild Felids*: 125–160 (D. W. Macdonald, A. J. Loveridge, Eds.). Oxford University Press, Oxford.

McBride, R. T., Thompson, J. J., 2018. Space use and movement of jaguar (*Panthera onca*) in western Paraguay. *Mammalia,* 82(6): 540–549, Doi: 10.1515/mammalia-2017-0040

Mitchell, T. A,. Clark, M. L., Grau, H. R., López–Carr, D., Levy, M. A., Redo, D., Bonilla–Moheno, M., Riner, G., Andrade–Núñez, M. J., Muñiz, M., 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica,* 45(2): 262–271, Doi: 10.1111/j.1744-7429.2012.00908.x

Morato, R. G., Connette, G. M., Stabach, J. A., De Paula R. C., Ferraz, K. M. P. M., Kantek, D. L. Z., Miyazaki, S. S., Pereira, T. D. C., Silva, L.C., Paviolo, A., De Angelo, A., Di Bitetti, M. S., Cruz P., Lima, F., Cullen, L., Sana, D. A., Ramalho, E. E., Carvalho, M. M., da Silva, M. X., Moraes, M.,D. F., Vogliotti, A., May Jr, J. A., Haberfeld, M., Rampim, L., Sartorello, L., Araujo, G. R., Wittemyer, G., Riberio, M. C., Leimgruber P., 2018. Resource selection in an apex predator and variation in response to local landscape characteristics. *Biological Conservation*, 228: 233–240, Doi: 10.1016/j.biocon.2018.10.022

Morato, R. G., Stabach, J. A., Fleming, C. H., Calabrese, J. M., De Paula, R. C., Ferraz, K. M. P. M., Kantek, D. L. Z., Miyazaki, S. S., Pereira, T. D. C., Araujo, G. R., De Angelo, A. P. C., Di Bitetti, M. S., Cruz, P., Lima, F., Cullen, L., Sana, D. A., Ramalho, E. E., Carvalho, M. M., Soares, F. H. S., Zimbres, B., Marina, M. X., Silva, X., Moraes, M. D. F., Vogliotti, A., May Jr., J. A., Haberfeld, M., Rampim, L., Sartorello, L., Ribeiro, M. C., Leimgruber, P., 2016. Space use and movement of a Neotropical top predator: The endangered jaguar. *Plos One*, 11(2): e0168176, Doi: 10.1371/journal.pone.0168176

Núñez, R., Miller, B., 2019. Movements and Home Range of Jaguars (*Panthera onca*) and Mountain Lions (*Puma concolor*) in a Tropical Dry Forest of Western Mexico. In: *Movement Ecology of Neotropical Forest Mammals:* 243–262 (C. Chapman, R. Reyna, Eds.). Springer, Cham.

Ortiz–Lozada, L., Pelayo–Martínez, J., Mota–Vargas, C., Demeneghi–Calatayud, A. P., Sosa, V. J., 2017. Absence of large and presence of medium–sized mammal species of conservation concern in a privately protected area of rain forest in southeastern Mexico. *Tropical Conservation Science,* Doi: 10.1177/1940082917738093

Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M. E., Eisenberg J. F., 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation,* 109(2): 297–310, Doi: 10.1016/S0006-3207(02)00157-X

Powell, R. A., 2000. Animal home ranges and territories and home range estimators. In: *Research techniques in animal ecology: controversies and consequences:* 65–110 (L. Boitani, T. Fuller, T, Eds.). Columbia University Press, New York.

Rabinowitz, A., Zeller, K., 2010. A range–wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143(4): 939–945, Doi: 10.1016/j.biocon.2010.01.002

Remolina–Suárez, J. F., 2014. *Reporte de Reubicación de un jaguar que estuvo atacando perros en un asentamiento irregular que invade el territorio de su distribución al Oeste de Playa del Carmen, Quintana Roo*. Technical report for the Comisión Nacional de Áreas Naturales Protegidas, SEMARNAT, Cancún, México.

Rodgers, A. R., Carr, A. P., Beyer, H. L., Smith, L., Kie, J. G., 2007. *HRT: Home Range Tools for ArcGIS*–Version 1.1. Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada.

Rodríguez–Soto, C., Monroy–Vilchis, O., Maiorano, L., Boitani, L., Faller, J. C., Briones, M. A, Núñez, R., Rosas–Rosas, O., Ceballos, G., Falcucci, A., 2011. Predicting potential distribution of the jaguar in Mexico: identification of priority areas for conservation. *Diversity and Distributions*, 17: 350–361, Doi: 10.1111/j.1472-4642.2010.00740.x

Rodríguez–Soto, C., Monroy–Vilchis, O., Zarco–González, M. M., 2013. Corridors for jaguar (*Panthera onca*) in Mexico: Conservation strategies. *Journal of Natural Conservation*, 21: 438–443, Doi: 10.1016/j.jnc.2013.07.002

Rzedowski, J., 2006. *Vegetación de México Primera Edición digital*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Distrito Federal, Mexico D.F.

Salom–Pérez, R., Polisar, J., Quigley, H., Zeller K., 2010. Jaguar Corridor Initiative: A biological corridor and a long–term commitment to conservation. *Mesoamericana,* 14(3): 25–34.

Sanderson, E. W., Redford, K. H., Chetkiewicz, C. B., Medellin, R. A., Rabinowitz, A. R., Robinson, J. G., Taber, A. B., 2002. Planning to Save a Species: The Jaguar as a Model. *Conservation Biology*, 16: 58–72, Doi: 10.1046/j.1523-1739.2002.00352.x

Scognamillo, D. Maxit, I. Sunquist, M., Farrell, L., 2002. Ecología del jaguar y el problema de la depredación de ganado en un hato de Los Llanos Venezolanos. In: *El Jaguar en el Nuevo Milenio*: 139–150 (R. A. Medellín, C. Equihua, C. Chetkiewicz, P. G. Crawshaw Jr., A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, A. B. Taber, Eds.). Fondo de Cultura Económica, Universidad Autónoma de México y Wildlife Conservation Society. México.

Sikes, R. S. Gannon, W. L., Animal Care and Use Committee of the American Society of Mammalogists, 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy,* 92(1): 235–253, Doi: https://doi.org/10.1644/10-MAMM-F-355.1

Sunquist, M. E., Sunquist, F. C., 1989. Ecological constraints on predation by large felids. In: *Carnivore Behavior, Ecology, and Evolution*: 238–301 (J. L. Gittleman, Ed.). Cornell University Press, Ithaca.

The Nature Conservancy, 2006. *Una visión para el futuro, una agenda para hoy. Plan ecorregional de las selvas mayas, zoque y olmeca*. The Nature Conservancy, San Joé, Costa Rica.

Urquiza–Haas, T., Peres, C. A., Dolman, P. M., 2009. Regional scale effects of human density and forest disturbance on large–bodied vertebrates throughout the Yucatan Peninsula, Mexico. *Biological Conservation*, 42(1): 134–148, Doi: 10.1016/j.biocon.2008.10.007

– 2011. Large vertebrate responses to forest cover and hunting pressure in communal landholdings and protected areas of the Yucatan Peninsula, Mexico. *Animal Conservation*, 14: 271–282, Doi: 10.1111/j.1469-1795.2010.00426.x

Whigham, D. F., Olmsted, I., Cano, E. C., Curtis, A. B., 2003. Impacts of hurricanes on the forests of Quintana Roo, Yucatán Peninsula, Mexico. In: *The lowland Maya: three millennia at the human–wildland interface:* 193–216 (S. Fedick, M. Allen, J. Jiménez–Osorno, A. Gómez–Pompa, Eds.). Haworth Press, Binghamton.

Worton, B. J., 1989 Kernel methods for estimating the utilization distribution in home–range studies. *Ecology,* 70.1: 164–168.

Supplementary material

Table 1s. Seasonal home range size (km^2) of four male jaguar radio–collared from year 2013 to 2015 in a non–protected area in northeastern Quintana Roo, México. Home range and core area size were calculated using the minimum convex polygon at 100 %. (Home range size of jaguar 1 was previously reported in González–Gallina et al., 2017a).

Tabla 1s. Superficie del área de distribución estacional (km^2) de cuatro jaguares macho seguidos con collares satelitales en el noreste de la península de Yucatán entre 2013 y 2015 en una zona no protegida en el noreste de Quintana Roo (México). El área de distribución y la superficie del área central se calcularon utilizando el método del polígono mínimo convexo al 100 %. (La superficie del área de distribución del jaguar 1 se obtuvo de González–Gallina et al., 2017a).

	2013		2014		2015
Jaguar	Dry season	Rainy season	Dry season	Rainy season	Dry season
1	262.20	134.08	167.99		
2	219.25	161.01			
3	153.71	829.13	340.25	192.74	
4				184.35	127.77

Table 2s. Percentages of use and availability of habitat of four male jaguars monitored with satellite collars in the northeastern Yucatan Peninsula from 2013 to 2015 in an unprotected area in northeastern Quintana Roo, Mexico. The percentages of use and availability are shown according to selection of home range within a study area (second–order selection, Model II) and selection of patches within the home range (third–order selection, Model III): TF, tropical forest; YF, young secondary–growth forest; Ig/A, induced grassland/agriculture; U, urban.

Tabla 2s. Porcentajes de uso y disponibilidad de hábitat de cuatro jaguares macho seguidos con collares satelitales en el noreste de la península de Yucatán entre 2013 y 2015 en una zona no protegida en el noreste de Quintana Roo (México). Los porcentajes de uso y disponibilidad se muestran en función de la selección del área de distribución dentro de la zona del estudio (selección de hábitat de segundo orden, Modelo II) y la selección de parcelas en el interior del área de distribución (selección de hábitat de tercer orden, Modelo III): TF, bosque tropical; YF, bosque secundario joven; Ig/A, pastizales inducidos/agricultura; U, urbano.

		Use				Available			
Individual	Year	TF	YF	Ig/A	Y	TF	YF	Ig/A	Y
Model II (selection of home range within a study area)									
Dry season									
Jaguar 1	2013	94.18	5.72	0.10	0.01	80.38	17.17	1.91	0.54
	2014	94.58	5.31	0.11	0.01				
Jaguar 2	2013	81.97	16.60	1.43	0.01				
Jaguar 3	2013	87.94	12.06	0.01	0.01				
	2014	85.76	13.72	0.52	0.01				
Jaguar 4	2015	39.63	58.64	1.73	0.01				
Rainy season						80.87	16.75	1.71	0.67
Jaguar 1	2013	94.43	5.01	0.56	0.01				
Jaguar 2	2013	77.91	19.08	2.78	0.23				
Jaguar 3	2013	85.04	14.55	0.41	0.01				
	2014	81.18	18.24	0.49	0.10				
Jaguar 4	2015	46.34	51.68	1.98	0.01				
Model III (selection of patches within the home range)									
Dry season									
Jaguar 1	2013	94.18	5.72	0.10	0.01	94.76	4.37	0.87	0.01
	2014	94.58	5.31	0.11	0.01	93.64	6.11	0.24	0.01
Jaguar 2	2013	81.97	16.60	1.43	0.01	84.85	15.15	0.01	0.01
Jaguar 3	2013	87.94	12.06	0.01	0.01	89.54	10.46	0.01	0.01
	2014	85.76	13.72	0.52	0.01	83.16	16.50	0.34	0.01
Jaguar 4	2015	39.63	58.64	1.73	0.01	38.30	50.00	11.70	0.01
Rainy season									
Jaguar 1	2013	92.03	6.15	1.82	0.01	94.43	5.01	0.56	0.01
Jaguar 2	2013	86.27	13.73	0.01	0.01	77.91	19.08	2.78	0.23
Jaguar 3	2013	89.61	9.33	1.06	0.01	85.04	14.55	0.41	0.01
	2014	77.89	22.11	0.01	0.01	81.18	18.24	0.49	0.10
Jaguar 4	2015	44.47	53.92	1.61	0.01	46.34	51.68	1.98	0.01