

# Spatial ecology of jaguars in Mexico: implications for conservation

**Gerardo Ceballos**

National Autonomous University of Mexico

**Carlos Cruz González** (✉ [carloscga72@hotmail.com](mailto:carloscga72@hotmail.com))

Universidad de Alicante

**Vicente Urios**

Universidad de Alicante

**Daniela Medellín**

Universidad de Alicante

**Heliot Zarza Villanueva**

Universidad Autónoma Metropolitana

**Sara Morollón**

Universidad de Alicante

**Victor H. Luja**

Universidad Autónoma de Nayarit

---

## Research Article

**Keywords:** Movement Ecology, GPS, Home range size, Overlapping, Top Predator

**Posted Date:** May 11th, 2022

**DOI:** <https://doi.org/10.21203/rs.3.rs-1617784/v1>

**License:**   This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

---

# Abstract

## Context

Movement ecology contributes valuable information about animal interactions with the environment, and their responses to landscape-level anthropogenic impacts. Big cats are vulnerable to such changes, but the current deficit of information about home range movements, limits the scope of conservation initiatives.

## Objectives

Describe the home range size, interactions, and differences between jaguar populations across its distribution in Mexico

## Methods

We used 41,008 GPS-generated data points obtained from 28 tagged jaguars (*Panthera onca*) in five different states of Mexico over an 18-year period to describe home range size, differences between male and female territories, interactions in overlapping territories, and territory differences among populations.

## Results

Our data shows that jaguar home range is smaller than tiger's but larger than leopard's. Male mean home range size (285.28 km<sup>2</sup>, n=13) tends to be larger than that of females (152.2 km<sup>2</sup>, n = 15), the difference was not statistically significant. While the home range for at least one male was 633.44 km<sup>2</sup>, contrasted with the much smaller 48.89 km<sup>2</sup> for some female jaguars. Data of overlapping ranges showed 34.71% of female territory overlaps male territory, 32.46% of female territory is shared with other females, 18.97% of male territory is shared with other males, and only 16.89% male territory overlaps with female territory.

## Conclusions

The absence of significant differences in home range sizes among the habitats suggest jaguar territory is not highly dependent on the type of habitat it occupies. Our findings of the spatial parameters of jaguar movements can be applied to identifying ecological corridors and the design of protected areas for this species.

# Introduction

Humankind is facing a sixth mass extinction (Ceballos et al. 2015), because of the current acceleration of biodiversity loss and extinction rates. The extinction rates are as high as past mass extinctions episodes and are fueled by unsustainable human population growth and resource exploitation. The global scale defaunation is particularly acute among certain vertebrate groups (e.g., amphibians and some mammals) and geographic regions, especially tropical zones (Dirzo et al. 2014). Human-induced habitat transformations, that alter trophic cascades, increasingly put predators at risk (Dorresteijn et al. 2015), giving as a result in declining populations. While numerous studies of the population loss of the emblematic

genus *Panthera* have been conducted, because of its important socio-ecological connections and implications, there are still many unanswered questions about felid species that when answered, will provide useful guidance in developing conservation initiatives (Brodie 2009; Krafte-Holland et al. 2018).

The jaguar (*Panthera onca*) is the largest felid of America and has a broad distribution, from northern Mexico to southern Argentina (Quigley et al. 2017). Its current distribution is less than half of the historical one, and almost 90% of the total population is inside the Amazonia (De la Torre et al. 2018). Although jaguars are found in different ecosystems due to their ecological plasticity, like xeric shrublands in their northern distribution, they mainly occur in forestry environments and avoid areas adjacent to urban centers (Medellín et al. 2016; Zarza et al. 2007). Current major threats to jaguar include habitat loss and degradation, direct persecution (either for utilization in traditional medicine or as a retaliation for livestock killing), and lack of suitable prey (Medellín et al. 2016; Ripple et al. 2014).

The combination of ecological exogenous and endogenous processes determines spatial characteristics of a species or population, such as, movement and dispersal, resource acquisition, and intra and interspecies interactions (Fletcher and Fortin 2018). Aided by advanced technology and data analysis methodologies, research on the spatial ecology of jaguars has already yielded valuable information on movement and spatial patterns, which are key to arresting habitat loss and, therefore the fragmentation and subsequent decline in biodiversity. Movement ecology focuses on species dispersal which impacts population and community dynamics (Collinge 2010; Nathan 2008). Earlier studies (e.g., Emmons 1987) have identified jaguars as solitary felines that tend to avoid both intra and interspecific interactions with other big cats, and that their territories vary in size (from about 22 km<sup>2</sup> to 690 km<sup>2</sup>), depending on sex, age, body weight, size, seasonal land characteristics, and ecoregion type (González-Borrajo et al. 2017), with males usually associated with larger home ranges than females. Home range size varies temporally within and between years depending on external factors such as dry and wet seasons and prey activity patterns (Cavalcanti and Gese 2009; Emmons 1987) and the amount of overlap with adjacent territories varies with jaguar population dynamics as dominant members die or leave the area and others take their place (Eaton, 2016). While it is not uncommon for female territories to overlap, the absence of this spatial phenomenon may be related to the breeding season (Crawshaw and Quigley 1991), and in contrast, the overlap of two or more male territories is substantially smaller. However, there is few data to suggest mutual avoidance in areas with high density of individuals and prey abundance (Cavalcanti and Gese 2009; Harmsen et al. 2009).

## Materials And Methods

### Study area

Our data was collected across five different states of Mexico (Campeche, Quintana Roo, Yucatán, Chiapas, and Sonora) and reflected a section of ecosystem and habitat types.

*Campeche and Quintana Roo:* The Calakmul region of these two states is a federal protected area of approximately 1,300,000 ha of tropical forest and encompasses the 723,100 ha Calakmul Biosphere Reserve and the Campeche state protected areas of Balamku and Balam´kin (Chávez et al. 2007). The

region, located in the center of the Yucatan Peninsula, has a tropical subhumid climate with a rainy season between June and November, high annual precipitation variability ranging from 552 mm to 1,634 mm, and average annual temperature of 24.6°C (Martínez and Galindo-Leal 2002; INEGI 1996). It consists of extensive conserved forests surrounded by a mosaic of agricultural, cattle grazing, and forestry activities (Briceño-Méndez et al. 2017). Although much of the region has a karst-type topography which causes rainwater to seep rapidly underground, area flooding regularly occurs during the wet season (Martínez and Galindo-Leal 2002). The Calakmul region supports a high biodiversity and the largest jaguar population in Mexico (Ceba-Ilos et al. 2002). *Northern Quintana Roo*, which is covered primarily by semi-deciduous tropical forests, savannah, mangroves, and secondary vegetation, also supports one of the largest jaguar populations in Mexico and is considered a priority area for jaguar conservation (Ceballos et al. 2012; Sanderson et al. 2002).

*Nayarit*. The habitat is a mosaic mostly represented by mangrove forests, but also tropical deciduous forests, secondary forests, agricultural lands, and protected areas. Climate is warm and humid with annual average temperature of 31.7°C (Luja et al. 2017)

*Chiapas*: The habitat is the largest extension of tropical rainforest in México, is considered a priority conservation area, with a high number of threatened species (Medellín, 1994 a; b). The predominant type of vegetation is medium sub-evergreen forests (Castillo and Narave 1992; Sánchez-Gutiérrez et al. 2017). The climate is warm and humid with rains in summer. Average annual precipitation is over 2,500 mm, the average annual temperature is higher than 24 ° C (García-Gil and Lugo-Hupb 1992).

*Sonora*: The 22,000 ha Northern Jaguar Reserve, about 56 km north of the small town of Sahuaripa, Sonora, is home to more than 300 native fauna species, including the remnants of the northern jaguar population. Owned and operated by Naturalia, a nongovernmental environmental organization, the reserve is situated in a mountainous region at elevations ranging between 433 m to 1,396 m and supports primarily thorny scrub and oak woodlands vegetation communities, depending on the altitude. This temperate, subtropical ecotone is a key component for the conservation of the northern jaguar population (Rorabaugh et al. 2011).

## Data collection

In Campeche and Quintana Roo, southeastern Mexico, we located adult jaguars with the help of trained hounds that cornered or treed them. We immobilized the jaguars using a 1 or 3 cc Pneu-Dart, discharged by a Dan-inject CO2 rifle (model I.M), that contained a combination of 0.06 mg/kg of Medetomidine 20 mg/ml (Medised 20X) and 5–6 mg/ kg of Ketamine 200 mg/ml (Ketamil); 20 mg/ml Atimil was used as the antagonist (Crawshaw and Quigley, 1991; Hoogesteijn et al. 1992; Morato et al. 2001). We followed the ethical standards required by the General Wildlife Office while collecting standard metrics data and attached GPS collars (Telonics® TGW-5477). The collars were programmed to send locations data every two to four hours with the ARGOS system to track the movements once released.

In the state of Nayarit, we captured jaguars by modified Aldrich foot snares (Araujo et al. 2020) and monitored active snare sites every 3 h using VHF trap-site transmitters and receivers (Telonics Inc., Mesa, Arizona). Jaguars were caught during the last week of February in 2019 and 2020. We sedated animals with

either a combination of ketamine (5 mg/kg Ketanilt, 200 mg/mL) and medetomidine (0.08 mg/kg 20 mg/mL), antagonized with atipamezole (0.35 mg/kg 20 mg/mL), or a mix of butorphanol (0.4 mg/kg 30 mg/mL) combined with medetomidine (0.08 mg/kg) and azaperone (0.15 mg/kg 50 mg/mL). We fitted all captured animals with Iridium or Global Star satellite GPS collars programmed to download locations eight times during each 24-hour period. In 2019, two adult jaguars were captured, one female (February 26; weight 49 kg, seven years old) and one male (February 27; weight 73 kg, six years old). Both animals were tagged with Telenax. In 2020, two adult jaguars were captured, the male (recaptured for the previous year was fitted with a Telenax collar) and a new female (February 28, 2020; weight 45 kg, nine years old); this last animal was fitted with a North Star collar. (Luja et al. 2017)

We used the Morato et al. (2018) database for jaguar movement information for the remaining three sites (Sonora, Chiapas, and Northern Quintana Roo). This database is part of an initiative to make information about jaguar movement throughout its distribution range available for research, conservation, and management.

## Data analysis

We obtained information of 28 jaguars (15 females and 13 males) over a period of 18 years (Table 1), from the 41,008 GPS-generated point locations and used this data to describe their home range size, differences in the territories between males and females, interactions between the individuals where overlapping territories occurred, and differences between populations in their territories. The territory overlap was classified into 4 groups: male-male, female-female, male-female, and female-male. Home range areas were estimated using 95%, 75%, and 50% fixed kernels (Worton, 1989), with the Animal Movement extension for ArcView 3.2 (Hooge and Eichenlaub, 1997), and the data layers were also created in that program. Having established a 95% core as the representative area, we calculated the overlap percentage between the home range areas for the different individuals and used R software (R Core Team, 2019) to perform an ANOVA test and a *post hoc* Tukey test to determine if there are differences between males and females, and between populations, with a statistical significance level of  $p < 0.05$ .

Table 1  
Identifying information on the 28 jaguars captured and tracked and the estimated fixed kernels of 95%, 75% and 50%

Jaguar ID	Sex	Total number of locations	Localities	Start track date	Finish track date	Fixed Kernel 50%	Fixed Kernel 75%	Fixed Kernel 95%
43	Female	577	Sonora	02/01/13	01/01/14	21.06	59.55	190.96
64	Male	1616	Sonora	02/01/12	01/03/14	15.60	74.40	440.42
44	Female	104	Chiapas	17/01/12	14/09/13	37.46	83.01	254.53
46	Female	443	Chiapas	25/08/12	10/11/13	25.28	79.31	201.57
47	Male	633	Chiapas	08/01/12	24/02/13	24.27	78.71	234.08
48	Male	72	Chiapas	14/08/12	24/12/12	123.93	291.71	575.12
49	Male	979	Northern Quintana roo	13/10/14	03/12/15	31.77	64.04	163.15
118	Male	468	Nayarit	01/03/19	06/05/19	6.26	23.96	67.76
119	Female	678	Nayarit	02/03/19	26/06/19	13.17	35.06	76.09
630187	Female	1774	Campeche	11/05/13	05/05/14	2.00	21.66	133.16
Dalia	Female	1239	Campeche	23/07/01	02/03/09	32.50	124.41	435.77
Eugenia	Female	318	Campeche	05/06/01	08/03/03	20.98	69.74	278.95
Guillermo	Male	4422	Campeche	16/04/09	30/10/09	2.50	13.92	48.89
José	Male	5064	Campeche	16/04/09	29/10/09	3.86	18.42	90.53
Lico	Male	295	Campeche	08/04/05	24/11/05	34.76	129.82	519.56
Melisa	Female	73	Campeche	26/03/05	06/02/06	2.26	16.05	80.12
Paola	Female	226	Campeche	16/04/01	25/01/02	2.36	6.58	37.27
Patricia	Female	77	Campeche	24/03/03	13/02/04	20.02	38.64	83.35
Sandra	Female	428	Campeche	16/05/09	17/09/09	4.58	16.43	49.17
Tony	Male	362	Campeche	09/06/02	31/05/03	38.83	171.68	633.44
Ulises	Male	5322	Campeche	16/04/09	30/10/09	9.06	38.29	185.96
UNK54	Female	245	Campeche	14/04/08	01/03/09	11.86	45.68	130.18
Verónica	Female	100	Campeche	07/04/05	01/01/08	14.23	59.11	106.67
Carlos	Male	1576	Quintana Roo	08/10/18	27/03/19	6.53	13.51	70.89

Jaguar ID	Sex	Total number of locations	Localities	Start track date	Finish track date	Fixed Kernel 50%	Fixed Kernel 75%	Fixed Kernel 95%
Iris	Female	3952	Quintana Roo	18/01/19	02/06/20	3.50	20.59	126.73
Marcos	Male	4629	Quintana Roo	20/01/19	31/05/20	18.77	70.23	180.82
Pedro	Male	3198	Quintana Roo	16/04/19	30/05/20	5.59	207.07	497.97
Sol	Female	2138	Quintana Roo	02/04/19	17/05/20	4.21	20.21	99.80

## Results

Information about animal interactions with their environment, and their responses to landscape anthropogenic impacts can be obtained with movement ecology studies. One of the most vulnerable groups affected by these changes are big cats like jaguars, but the current lack of information about home range movements severely limits the scope and breadth for taking conservation actions. We analyzed 41,008 GPS-generated data points obtained from 28 tagged jaguars (*Panthera onca*) in five different states of Mexico (Sonora, Chiapas, Nayarit, Campeche, and Quintana Roo) over an 18-year period to describe jaguar home range size, differences between male and female territories, interactions in overlapping territories, and territory differences among populations. Individuals with a tracking period exceeding > 85% of their home range were selected, this means more than two months of tracking for a total of 28 jaguars (Table 2). Only one individual, with 17 days of tracking, was excluded from the initial database.

Table 2

Comparison of total home range sizes (km<sup>2</sup>) by Fixed Kernel (95%) analysis for a total sample of 28 jaguars during the first two months of tracking GPS data locations

<i>Jaguar ID</i>	<i>Sex</i>	<i>Fixed Kernel 95%</i>	<i>Fixed Kernel 95% in 60 days</i>	<i>Percentage (%)</i>
43	Female	190	143	75
64	Male	440	588	133
44	Female	254	199	78
46	Female	201	178	88
47	Male	234	138	59
48	Male	575	371	64
49	Male	163	117	72
118	Male	67	41	61
119	Female	76	66	86
630187	Female	133	165	123
Dalia	Female	435	312	71
Eugenia	Female	278	139	50
Guillermo	Male	48	48	99
José	Male	90	60	67
Lico	Male	519	462	89
Melisa	Female	80	59	74
Paola	Female	37	24	66
Patricia	Female	83	83	100
Sandra	Female	49	49	100
Tony	Male	633	580	91
Ulises	Male	185	169	91
UNK54	Female	130	157	120
Verónica	Female	106	64	60
Carlos	Male	70	45	64
Iris	Female	126	74	58
Marcos	Male	180	235	130
Pedro	Male	497	453	90

<i>Jaguar ID</i>	<i>Sex</i>	<i>Fixed Kernel 95%</i>	<i>Fixed Kernel 95% in 60 days</i>	<i>Percentage (%)</i>
Sol	Female	99	60	60
Mean				83

## Differences between male and female territories

We compared home range size (Table 2) to determine if male territories are larger than female territories, which is common with all other big cat species except the lion (*Panthera leo*), a social felid in which both sexes of the same pride share the same territory (Schaller, 2009). While the mean home range for males (285.28 km<sup>2</sup>; n = 13) is larger than that for females (152.2 km<sup>2</sup>; n = 15), the difference is not statistically significant (P = 0.3812, F = 0.7724). Data also showed range size varied by geographic area (state) when tabulated by sex and by mean values for both sexes combined (Table 3). The smallest range was recorded for the two jaguars (one male and one female) in Nayarit in contrast to the largest range by both the male and female jaguars in Chiapas.

Table 3  
Mean of home range size by area and sex

<i>Location</i>	<i>Males</i>		<i>Females</i>		<i>Area mean (km<sup>2</sup>)</i>
	<i>Area (km<sup>2</sup>)</i>	<i>Number individuals</i>	<i>Area (km<sup>2</sup>)</i>	<i>Number individuals</i>	
Campeche	295	5	148	9	200.93
Chiapas	404	2	228	2	316.33
Nayarit	67	1	76	1	71.92
Sonora	275	1	152	1	315.69
Southern Quintana Roo	249	3	113	2	195.25
Northern Quintana Roo	163	1			163.15
		13		15	

The jaguar tracking kernels of 50%, 75%, and 95% for Sonora, Nayarit, Campeche, Quintana Roo, and Chiapas are depicted in Fig. 3 through Fig. 8, respectively.

## Territory overlap between jaguars of the same and different sex

Our data showed that jaguar home range territories of both sex overlaps, but the extent is skewed toward females. The overlap percentage of female territory with that of other females and with males is almost twice the described for male territory overlap with females or other male territory (Table 4).

Table 4  
Percentage of area of territory overlap, by sex

<i>Sex variables</i>	<i>Mean percentage of overlap</i>
Male territory overlaps female territory	17%
Female territory overlaps male territory	35%
Male territory overlaps male territory	19%
Female territory overlaps female territory	33%

## Differences in territory size among the 6 populations

The six regions from which we obtained jaguar tracking data represented a suite of latitudinal and altitudinal gradients, habitat types, and ecological and environmental parameters across Mexico. We investigated differences in jaguar home range sizes (Fig. 2), and in order to not exclude any territory, the areas from the different territories were compared independently of the number of individuals in each area with a Tukey test. There was no significant ANOVA difference when each home range size in every of the sampled regions was compared (Table 5).

Table 5  
ANOVA result between the 95% Kernel comparing home range size of each of the six sampled different regions

<i>Regions of comparison</i>	<i>Difference</i>	<i>Lower</i>	<i>Upper</i>	<i>P</i>
Southern Quintana Roo-Nayarit	0.7489	-1.3217	2.8196	0.8650
Northern Quintana Roo-Nayarit	0.8206	-2.2104	3.8518	0.9557
Campeche-Nayarit	0.6391	-1.2317	2.5100	0.8901
Chiapas-Nayarit	1.3899	-0.7533	3.5333	0.3631
Sonora-Nayarit	1.3959	-1.0790	3.8708	0.5114
Northern Quintana Roo-Southern Quintana Roo	0.0717	-2.6394	2.7829	0.9999
Campeche-Southern Quintana Roo	-0.1098	-1.3992	1.1796	0.9997
Chiapas- Southern Quintana Roo	0.6410	-1.0192	2.3012	0.8308
Sonora-Southern Quintana Roo	0.6469	-1.4237	2.7176	0.9215
Campeche-Northern Quintana Roo	-0.1815	-2.7433	2.3802	0.9999
Chiapas-Northern Quintana Roo	0.5692	-2.1977	3.3363	0.9864
Sonora-Northern Quintana Roo	0.5752	-2.4559	3.6064	0.9905
Chiapas-Campeche	0.7508	-0.6523	2.1539	0.5660
Sonora-Campeche	0.7567	-1.1141	2.6276	0.8026
Sonora-Chiapas	0.0059	-2.1374	2.1493	1.0000

## Discussion

The recent and marked growth of interest in the spatial ecology of big cats (e.g., *Panthera leo*, *Panthera tigris*, *Panthera pardus*, *Puma concolor*, and *Panthera onca*) has unleashed innovative research that has already yielded valuable information for population/species protection and conservation initiatives for this taxon. These studies identify the large expanse of the home range territory, inter and intraspecies overlap, and associated ecological dynamics (du P Bothma et al. 1984; Goodrich et al. 2010; Hernández-Blanco et al. 2015; González-Borrajo et al. 2017). Our study did not consider comparisons with lions, because its highly social behavior is in stark contrast to that of the jaguar and other big cats (Mosser and Packer, 2009; Morato et al. 2016 Schaller 2009). We observed that the size of the jaguar home range in Mexico ( $214 \text{ km}^2 \pm 176 \text{ km}^2$ ) tends to correspond to its body size, is smaller than the tiger home range ( $1,385 \text{ km}^2 \pm 539 \text{ km}^2$ ; Goodrich et al. 2010), similar to that of the cougar ( $281.87 \text{ km}^2 \pm 35.76 \text{ km}^2$ ; González-Borrajo et al. 2017) and snow leopard ( $225 \text{ km}^2 \pm 33 \text{ km}^2$ ; Johansson et al. 2018), and larger than that of the leopard ( $77.9 \text{ km}^2$  to  $130.6 \text{ km}^2$ ; González-Borrajo et al. 2017).

Male jaguars in Mexico generally have a larger home range than female jaguars, and while our data did not show a statistical difference, the variability of the small sample size ( $n = 28$ ) may have masked the

differences. For sure, noticeable differences in male jaguar home range size, from 48.89 km<sup>2</sup> to 633.44 km<sup>2</sup>, may represent males occupying one or more female home ranges as depicted in Figs. 5–7. This behavior of male jaguars contrasts with that displayed by some large monogamous predators, such as large birds of prey, in which couples present territories with similar size (Newton, 1979). This occupation (or overlap) with some female home range suggests a heightened degree of aggressiveness and dominance among some males (for example, Lico and Marcos) while other males that are rejected in encounters or fights with other male jaguars are relegated to smaller territories and don't have access to females (for example, Guillermo and Charles). This disparity in range size between males and females has been observed in other big cats including tigers (males: 1,385 km<sup>2</sup> ± 539 km<sup>2</sup>, females: 390 km<sup>2</sup> ± 136 km<sup>2</sup>; Goodrich et al. 2010), cougars (males: 166 km<sup>2</sup> ± 26 km<sup>2</sup>, females: 117 km<sup>2</sup> ± 23 km<sup>2</sup>; Johansson et al. 2018), and snow leopards (males: 225 km<sup>2</sup> ± 33 km<sup>2</sup>, females: 133 km<sup>2</sup> ± 23 km<sup>2</sup>; Johansson et al. 2018).

The overlap of home range is an important social and ecological dynamic that may be related to resource acquisition and/or reproduction. The largest percentage of home range overlap (34.71%) occurs with female incursion on male home range, followed by a slightly smaller percentage (32.46%) where two female home ranges overlap, and then, the overlap of two male home ranges (18.79%). The smallest percentage of overlap (16.89%), which occurs with male home range overlapping that of females, may reflect an extension of the male range. Our observations of jaguar home range overlap contribute to a better understanding of how members of a jaguar population partition space and how these boundaries shift based on social structure, biology, and habitat type. Spatial ecology research on other big cats has revealed trends of overlapping boundaries like what we observed with jaguars. For the snow leopard, the overlap between males was smaller (21%) than between females (25%), and the overlap of cougar home range between males was smaller (11%) than the overlap with females (26%; Goodrich et al. 2010).

Finally, we did not identify significant differences in home range size among the six different locations despite the unique environmental characteristics of each one, from the arid conditions of the Sonora desert to the varied tropical ecosystems of the other five sampling sites (Table 5). While the small sampling size may be a factor in this assessment, we also suggest that jaguar territory is not exclusively dependent on habitat type and other factors, such as density of prey. A more complete understanding of the relationship between habitat type and home range size will emerge from additional future studies.

### **Implications for jaguar conservation**

Patterns described by the spatial ecology of jaguar populations can provide useful information about naturally occurring and human-induced factors that affect their behavior, and potentially risk their survival. Deviations from documented established patterns, such as home range size and overlaps, may signal behavior changes in the population and be an early indicator of ecological and environmental stressors such as inadequate supply of prey, accelerated rates of mortality, disease, climate change, habitat degradation, hunting, and persecution. These indicators can facilitate research to identify the causes and efforts to intervene before the populations are seriously threatened. Information about the spatial patterns of jaguars, which appears to be independent of habitat type, is critical for the planning and design of protected areas and ecological corridors for this species. Our data, and other research on jaguars and other

big cats, support the need to preserve larger areas that incorporate multiple habitat types rather than smaller areas of a specific type (de la Torre and Medellín 2011). For example, the most ecologically beneficial connector corridor between two tropical forest areas for jaguars may not be tropical forest, but a landscape, which confirms other advantages such as proximity to the two areas or absence of disturbances and other threats. Understanding the spatial ecology of jaguars is a key element in the preservation of this unique dominant member of the Mexican landscape.

## Declarations

Funding (information that explains whether and by whom the research was supported)

Alianza WWF - Fundacion Telmex/Telcel, the Universidad Nacional Autónoma de México, Amigos de Calakmul A.C., and the BBVA Foundation Award for the Conservation of Biodiversity (2017)

Conflicts of interest/Competing interests (include appropriate disclosures)

Not applicable

Ethics approval (include appropriate approvals or waivers)

We followed ethical and security standards required by the General Wildlife Office during the capture and handling procedures

Consent to participate (include appropriate statements)

All authors participated freely in this research

Consent for publication (include appropriate statements)

All authors have given their consent for publication of this research

Availability of data and material (data transparency)

Not applicable

Code availability (software application or custom code)

Not applicable

Authors' contributions

Gerardo Ceballos designed the study, collected the data, and wrote the manuscript; Heliot Zarza collected the data; Carlos Cruz led the organization of the manuscript, organize the data, and wrote the manuscript, Daniela Medellín, Victor H. Luja and Vicente Urios organized and analyzed the data, and made comments on the manuscript. All authors reviewed all drafts of the manuscript and gave their final approval for publication

## References

1. Araujo G, Deco-Souza T, Morato R, Crawshaw P, Silva L, Jorge-Neto PN, Csermak-Jr A, Bergo L, Kantek D, Miyazaki S, Beisiegel B, Tortato F, May-Júnior J, Silva M, Leuzinger L, Salomão J, Paula, T (2020) Use of foot snares to capture large felids. *Methods in Ecology and Evolution* 12:322-327. 10.1111/2041-210X.13516.mo
2. Briceño-Méndez M, Naranjo E, Pérez-Irineo G, Contreras-Perera Y, Sandoval-Serés E, Hidago-Mihart, MG (2017) Richness and trophic guilds of carnivorous mammals in ejido Nuevo Becal, Calakmul, Campeche, Mexico. *Therya* 8:145-150.
3. Brodie JF (2009) Is research effort allocated efficiently for conservation? Felidae as a global case study. *Biodiversity and Conservation* 18:2927-2939.
4. Castillo G, Narave H (1992) Contribución al Estudio de la Vegetación de la Reserva de la Biósfera Montes Azules, Selva, Lacandona, Chiapas. In: Vázquez-Sánchez M y Ramos MA (eds). *Reserva de la Biosfera Montes Azules, Selva Lacandona: Investigación para su Conservación*. Publicaciones especiales, Ecósfera, Mexico, pp 51-86.
5. Cavalcanti SM, Gese EM (2009). Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, 90:935-945.
6. Ceballos G, Chávez C, Zarza H (2012) Censo Nacional del Jaguar y sus Presas (1ª Etapa). CONANP, IE-UNAM, ALIANZA WWF-TELCEL, TELMEX y CONABIO. Informe Final SNIB-CONABIO.
7. Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer, TM (2015) Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science advances* 1(5):e1400253.
8. Chávez C, Ceballos G, Amín M (2007) Ecología poblacional del jaguar y sus implicaciones para la conservación en la Península de Yucatán. *Conservación y manejo del jaguar en México, estudios de caso y perspectivas*, 91-100.
9. Collinge SK (2010) Spatial ecology and conservation. *Nature* 1(69):00201-9.
10. Crawshaw Jr PG, Quigley HB (1991) Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology* 223(3):357-370.
11. de la Torre, J. A., & Medellín, R. A. (2011). Jaguars *Panthera onca* in the Greater Lacandona Ecosystem, Chiapas, Mexico: population estimates and future prospects. *Oryx*, 45(4), 546-553.
12. de la Torre JA, González-Maya JF, Zarza H, Ceballos G, Medellín RA (2018) The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar *Panthera onca*. *Oryx* 52(2):300-315.
13. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B (2014) Defaunation in the Anthropocene. *science*, 345(6195):401-406.
14. Dorresteijn I, Schultner J, Nimmo DG, Fischer J, Hanspach J, Kuemmerle T, et al (2015) Incorporating anthropogenic effects into trophic ecology: predator-prey interactions in a human-dominated landscape. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814):20151602.
15. du P Bothma J, Le Riche EN (1984) Aspects of the ecology and the behaviour of the leopard *Panthera pardus* in the Kalahari Desert. *Koedoe* 27(2):259-279. e02371.

16. Eaton TS (2016) Abundance and Activity Patterns of the Jaguar (*Panthera onca*) in the Mountain Pine Ridge, Belize (Doctoral dissertation, Northeastern State University). *Ecology* 70(1):164-168.
17. Emmons LH (1987) Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral ecology and sociobiology*, 20(4):271-283.
18. Fletcher R, Fortin MJ (2018) Introduction to Spatial Ecology and Its Relevance for Conservation. In *Spatial Ecology and Conservation Modeling*, Springer, Cham, pp. 1-13, [https://doi.org/10.1007/978-3-030-01989-1\\_1](https://doi.org/10.1007/978-3-030-01989-1_1)
19. García-Gil JG, Lugo-Hupb J (1992) Las formas del relieve y los tipos de vegetación en la selva lacandona. In: M.A. Vásquez-Sánchez y M.A. Ramos (eds.), *reserva de la biósfera Montes Azules, selva lacandona: Investigación para su conservación*. Publ. Esp. Ecosfera, pp. 39-49.
20. González-Borrajo N, López-Bao JV, Palomares F (2017) Spatial ecology of jaguars, pumas, and ocelots: a review of the state of knowledge. *Mammal Review* 47(1):62-75.
21. Goodrich JM, Miquelle DG, Smirnov EN, Kerley LL, Quigley HB, Hornocker MG (2010) Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapoved- nik, Russia. *Journal of Mammalogy* 91(3):737-748.
22. Harmsen BJ, Foster RJ, Silver SC, Ostro LE, Doncaster CP (2009) Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. *Journal of mammalogy*, 90(3):612-620.
23. Hernández-Blanco JA, Naidenko SV, Chistopolova MD, Lukarevskiy VS, Kostyrya A, Rybin A, et al (2015) Social structure and space use of Amur tigers (*Panthera tigris altaica*) in Southern Russian Far East based on GPS telemetry data. *Integrative Zoology*, 10(4):365-375.
24. Hooge PN, Eichenlaub B (1997) Animal movement extension to ArcView (version 1.1). Alaska Biological Science Center, United States Geological Survey, Anchorage.
25. Hoogesteijn R, Hoogesteijn A, Mondolfi E (1992) El dilema 'depredación vs. conservación' del Jaguar y análisis de la mortalidad de bovinos causada por felinos en tres hatos del Llano Venezolano. In *Proceedings of the Symposium: Felids of Venezuela: Biology, Ecology and Conservation*, Caracas, Venezuela, p. 129-169.
26. INEGI (Instituto Nacional de Geografía y Estadística) (1996). *Anuario Estadístico del Estado de Campeche*. México.
27. Johansson Ö, Koehler G, Rauset GR, Samelius G, Andrén H, Mishra C, et al (2018) Sex specific seasonal variation in puma and snow leopard home range utilization. *Ecosphere*, 9(8):e02371.
28. Krafte-Holland K, Larson, LR, Powell RB (2018). Characterizing conflict between humans and big cats *Panthera* spp: A systematic review of research trends and management opportunities. *PLoS one*, 13(9):e0203877.
29. Luja VH, Navarro CJ, Torres-Covarrubias LA, Cortés-Hernández M, Vallarta-Chan IL (2017) Small protected areas as stepping-stones for jaguars in western Mexico. *Tropical Conservation Science*, 10:1940082917717051.
30. Martínez E, Galindo-Leal C (2002) La vegetación de Calakmul, Campeche, México: clasificación, descripción y distribución. *Botanical Sciences*, (71):7-32.

31. Medellín RA (1994a) Community ecology and conservation of mammals in a Mayan tropical rainforest and abandoned agricultural fields.
32. Medellín RA (1994b) Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico.
33. Medellín RA, de la Torre JA, Chávez C, Zarza H, Ceballos G, (2016) El Jaguar en El Siglo XXI: La Perspectiva Continental. Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Ciudad de México.
34. Morato RG, Conforti VA, Azevedo FC, Jacomo AT, Silveira L, Sana D et al (2001) Comparative analyses of semen and endocrine characteristics of free-living versus captive jaguars (*Panthera onca*). *Reproduction*, 122(5):745-751.
35. Morato, R. G., Stabach, J. A., Fleming, C. H., Calabrese, J. M., De Paula, R. C., Ferraz, K. M., ... & Leimgruber, P. (2016). Space use and movement of a neotropical top predator: the endangered jaguar. *PloS one*, 11(12), e0168176
36. Morato RG, Thompson J, Paviolo A, de la Torre JA, Lima F, Roy Jr, Cunha de Paula R, Laury Jr, Silveira L, Kantek D, Ramalho E, Maranhão L, Haberfeld M, Sana D, Medellín R, Carrilo E, Montalvo V, Monroy-Vilchis O, Cruz P, Ribeiro M (2018) Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. *Ecology* 99(7):1691
37. Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, 78(2), 359-370
38. Nathan R (2008) An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences*, 105(49):19050-19051.
39. Newton I (1979) Population ecology of raptors. Vermillion, South Dakota.
40. Quigley H, Foster R, Petracca L, Payan E, Salom R, Harmsen B (2017) *Panthera onca* (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e. T15953A123791436.
41. R Core Team (2019) A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2012. URL <https://www.R-project.org>
42. Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson M, Schmitz O, Smith D, Wallach A, Wirsing A (2014) Status and ecological effects of the world's largest carnivores. *Science* 343:1241484. 10.1126/science.1241484.
43. Rorabaugh JC, Gómez-Ramírez MA, Gutiérrez-González CE, Wallace JE, Van Devender TR (2011) Amphibians and reptiles of the Northern Jaguar Reserve and vicinity, Sonora, Mexico: a preliminary evaluation. *Sonoran Herpetologist* 24:123-131.
44. Sanderson E, Redford K, Chetkiewicz, CL, Medellín R, Rabinowitz A, Robinson J, Taber A, (2002) Planning to Save a Species: the Jaguar as a Model. *Conservation Biology* 16:58-72. 10.1046/j.1523-1739.2002.00352.x.
45. Sánchez-Gutiérrez, F., Valenzuela-Gómez, A., Valdez-Hernández, J. I., & González-González, C. A. (2017). Estructura y diversidad de especies arbóreas en el sitio arqueológico "El Mirador", Selva Lacandona, Chiapas. *Polibotánica*, (44), 79-94.
46. Schaller, G. B. (2009). *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press.

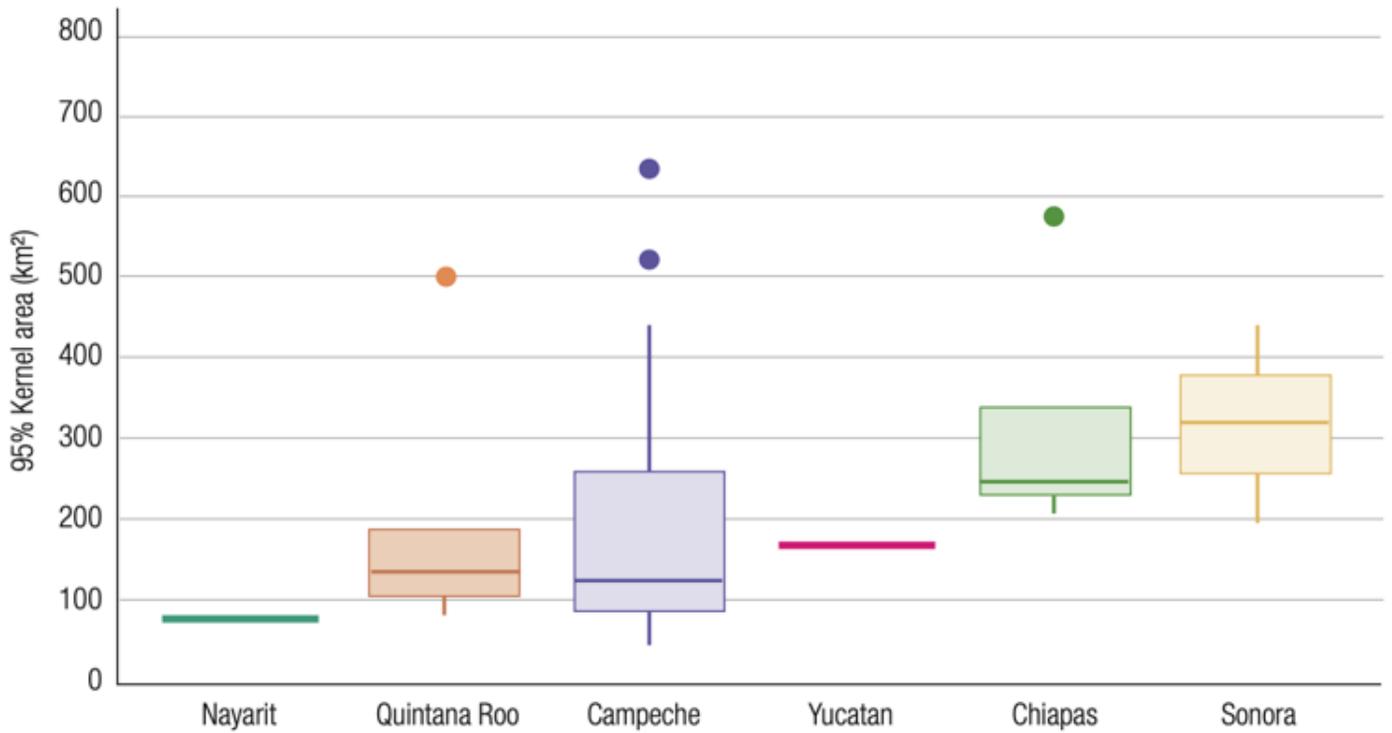
47. Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.
48. Zarza H, Chávez C, Ceballos G (2007) Uso de hábitat del jaguar a escala regional en un paisaje dominado por actividades humanas en el sur de la península de Yucatán. Conservación y manejo del jaguar en México: estudios de caso y perspectivas, 101-110

## Figures



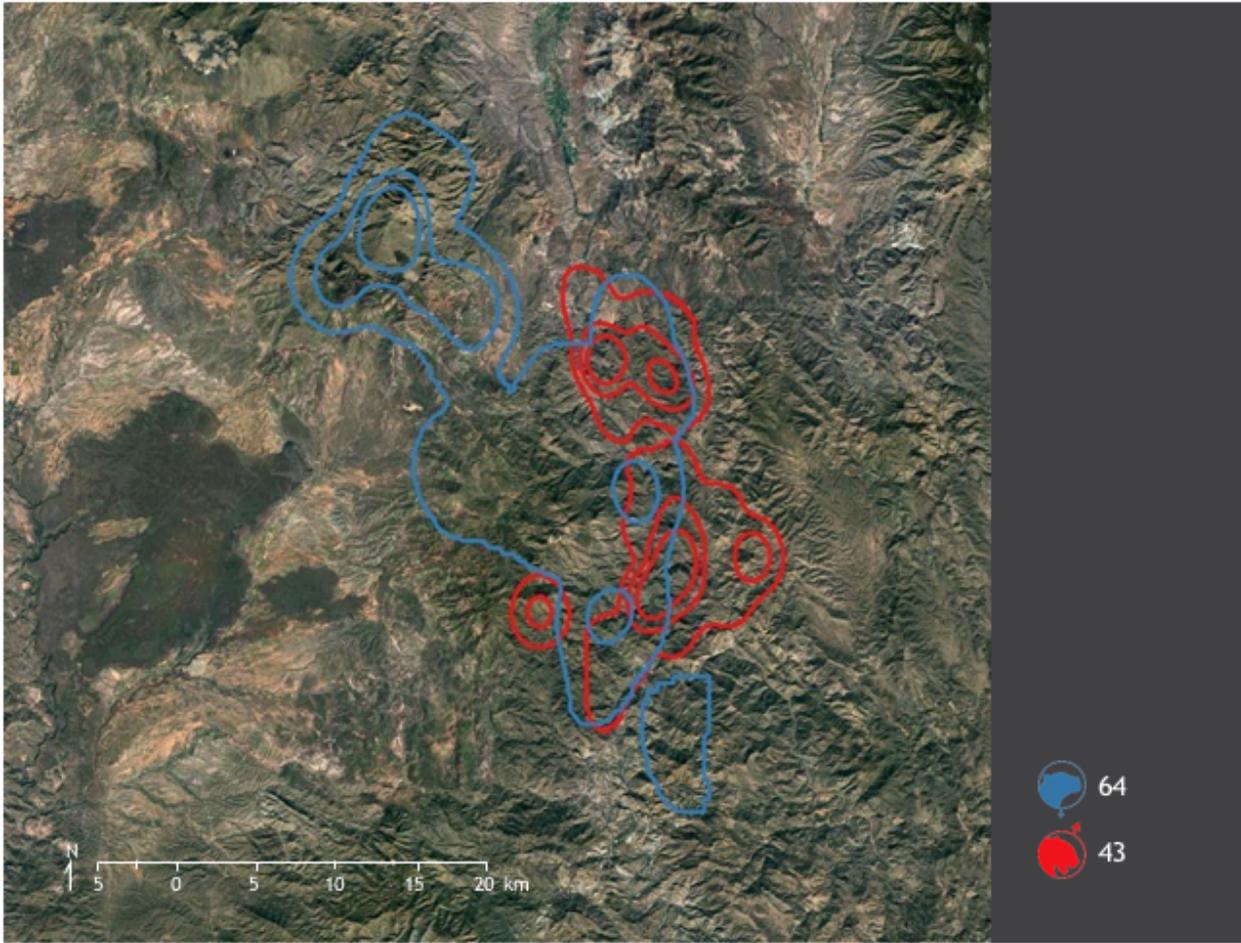
**Figure 1**

Study area of the jaguar spatial ecology in Mexico.



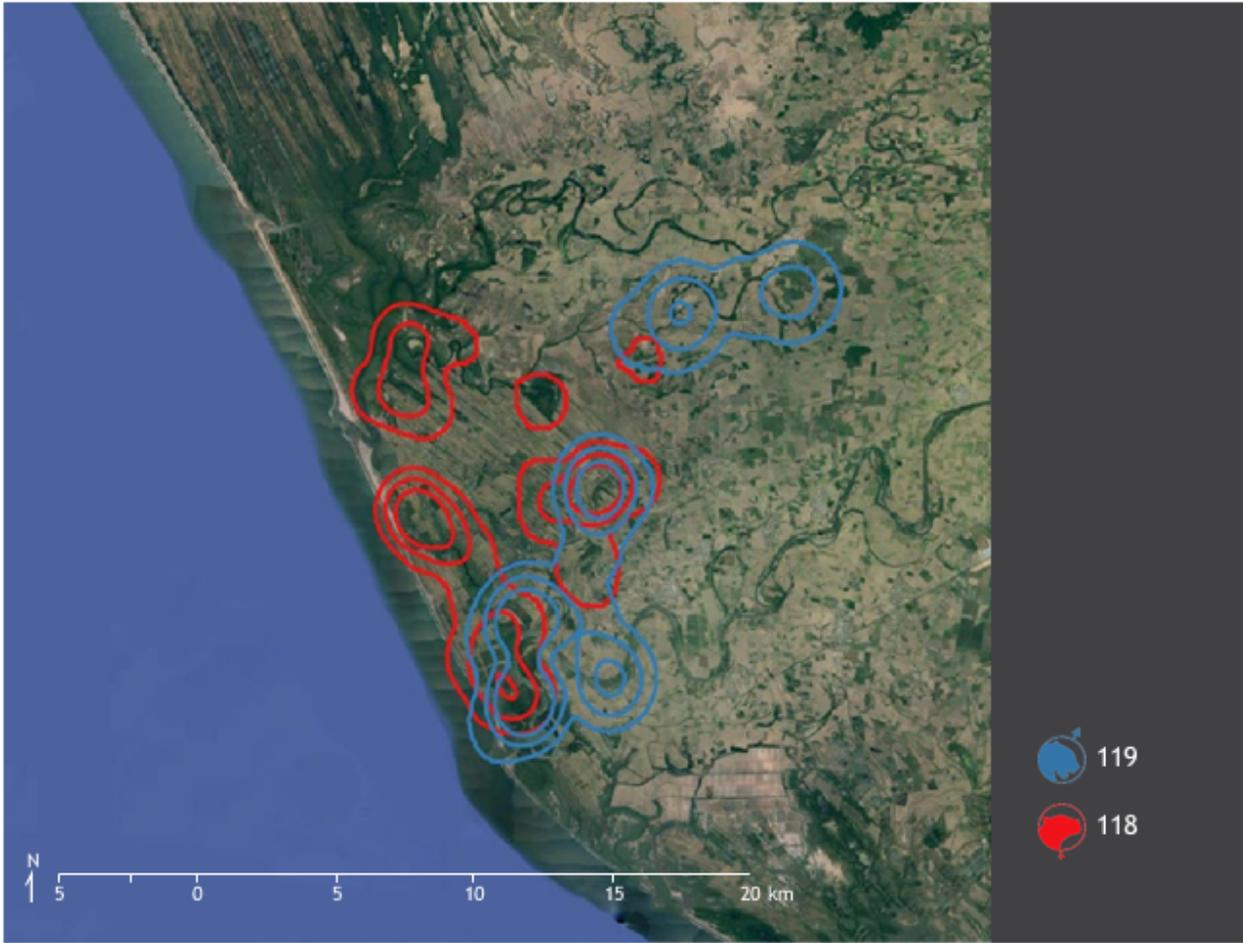
**Figure 2**

This graphical presentation of the 95% Kernel of jaguar home range size tracking data for the six regions sampled shows the area occupied by the tracked jaguars; These data represent only a sample of the whole jaguar populations in each of the regions studied.



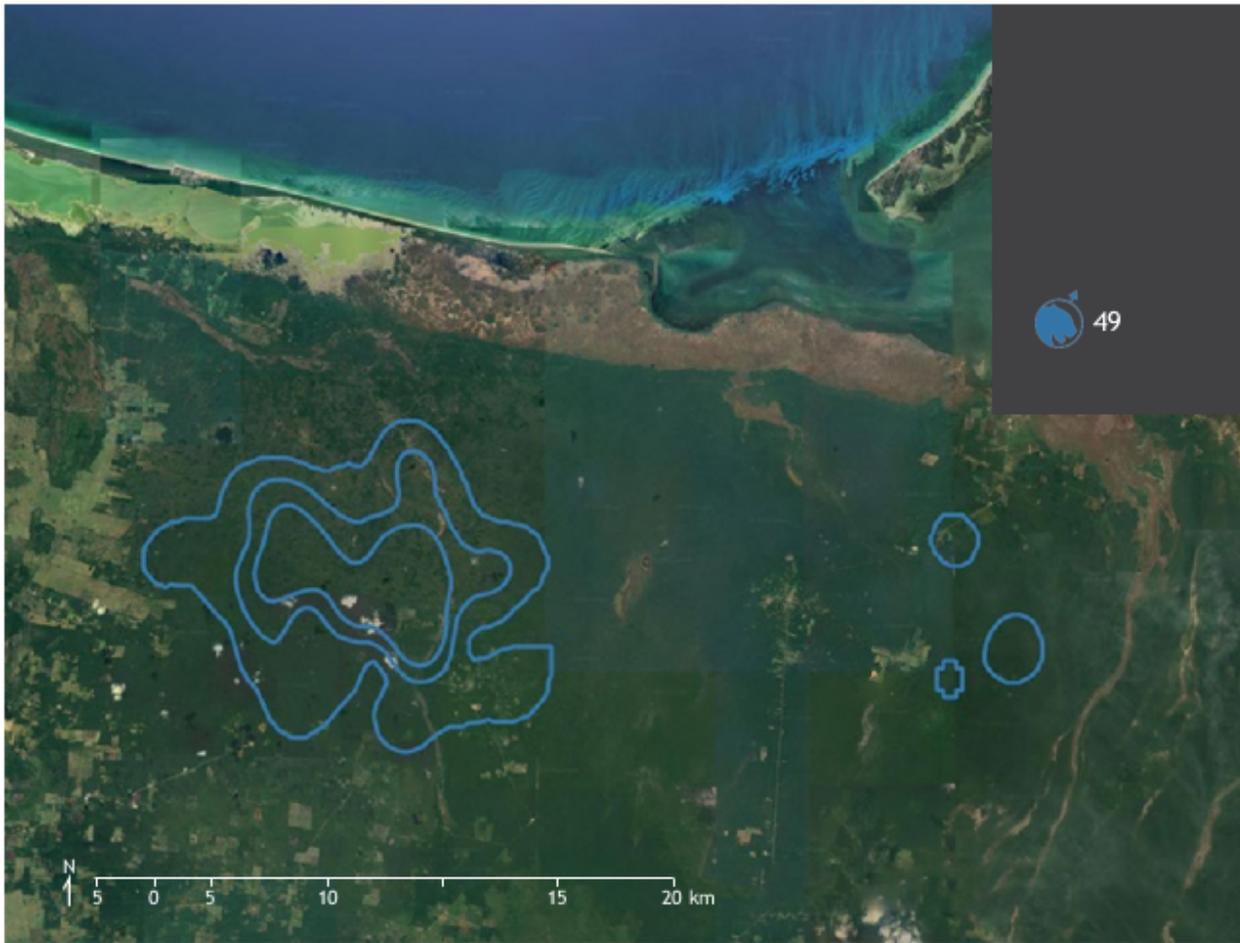
**Figure 3**

Kernel of 50%, 75%, and 95% of the jaguars in Sonora.



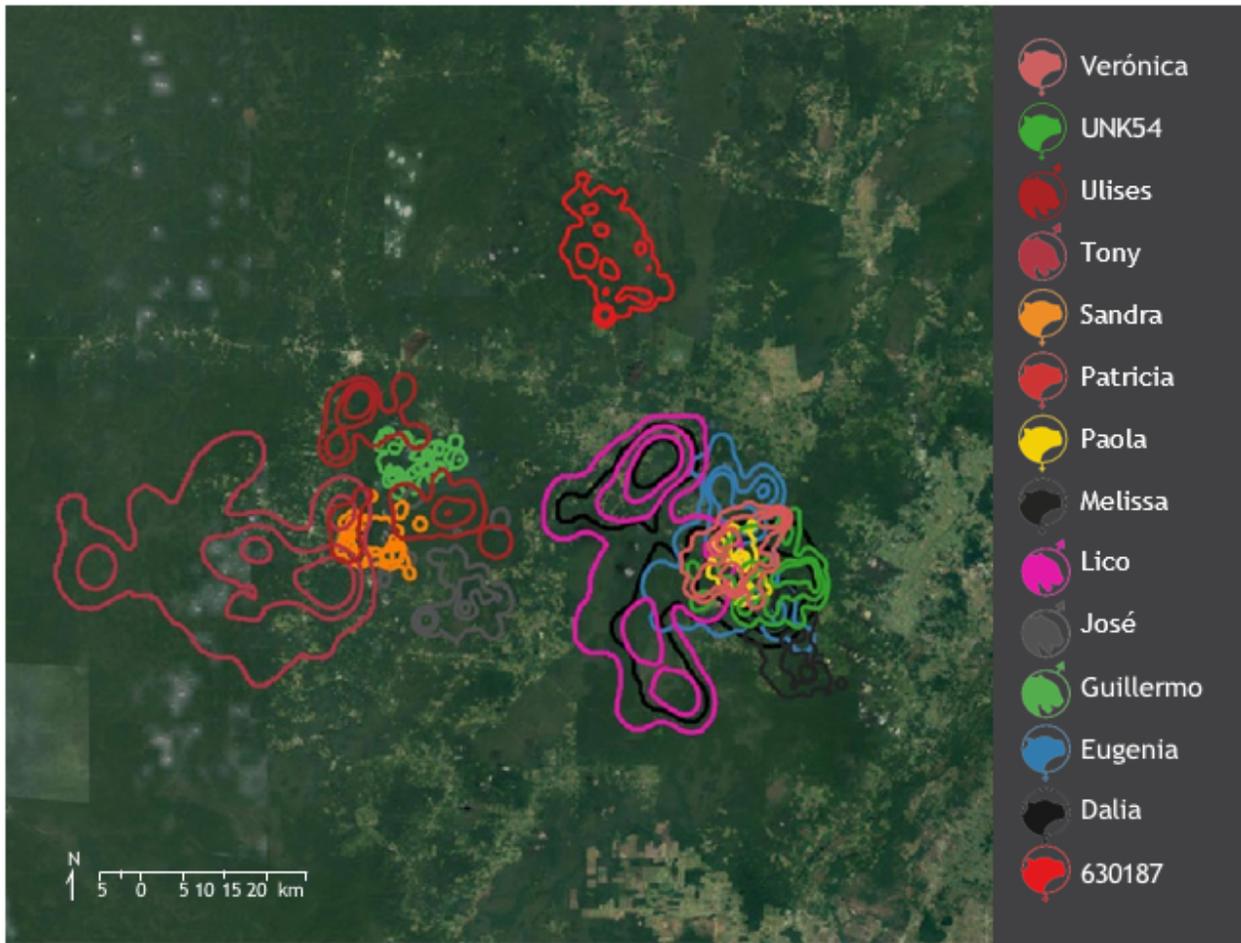
**Figure 4**

Kernel of 50%, 75%, and 95% of the jaguars in Nayarit.



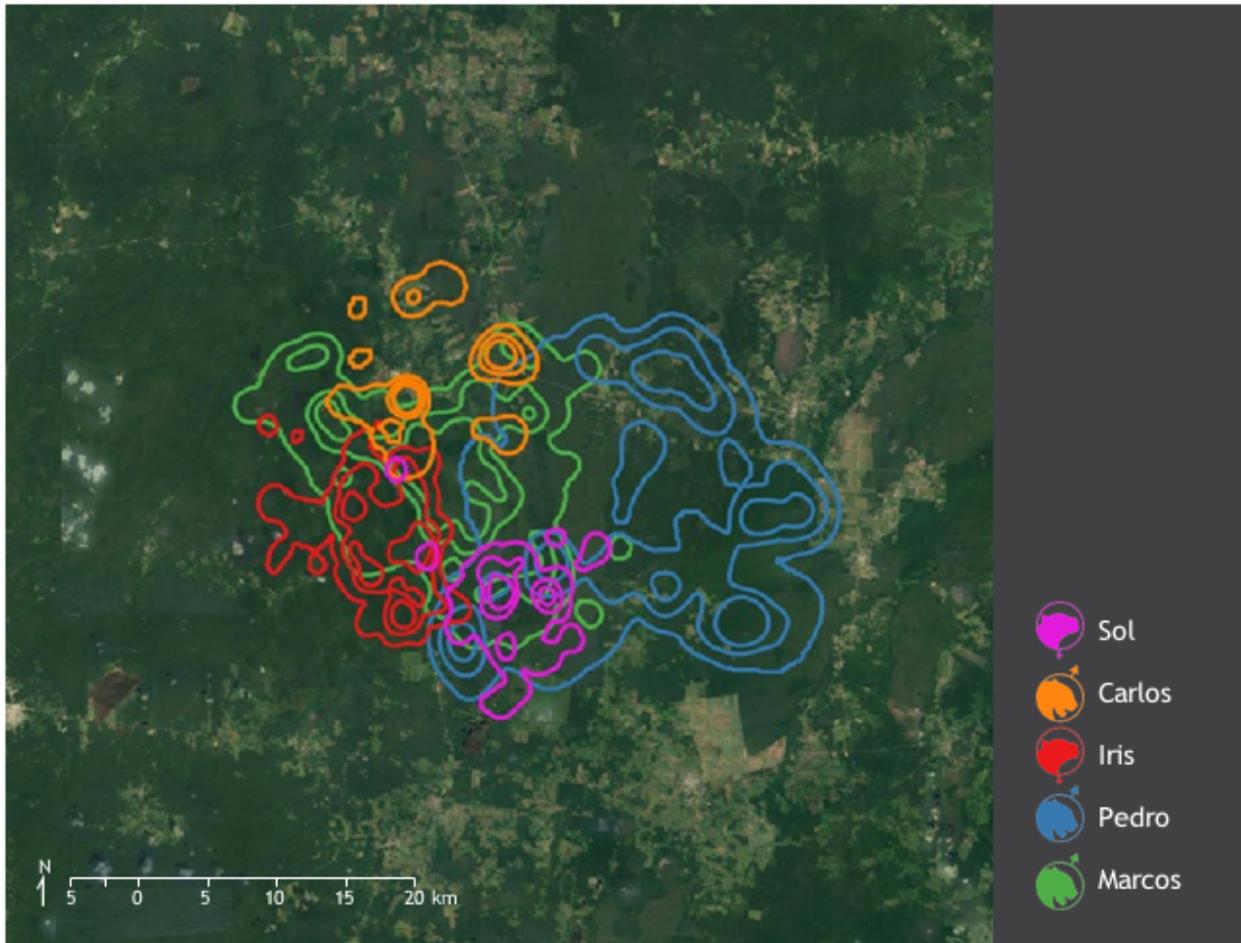
**Figure 5**

Kernel of 50%, 75%, and 95% of the jaguars in Northern Quintana Roo.



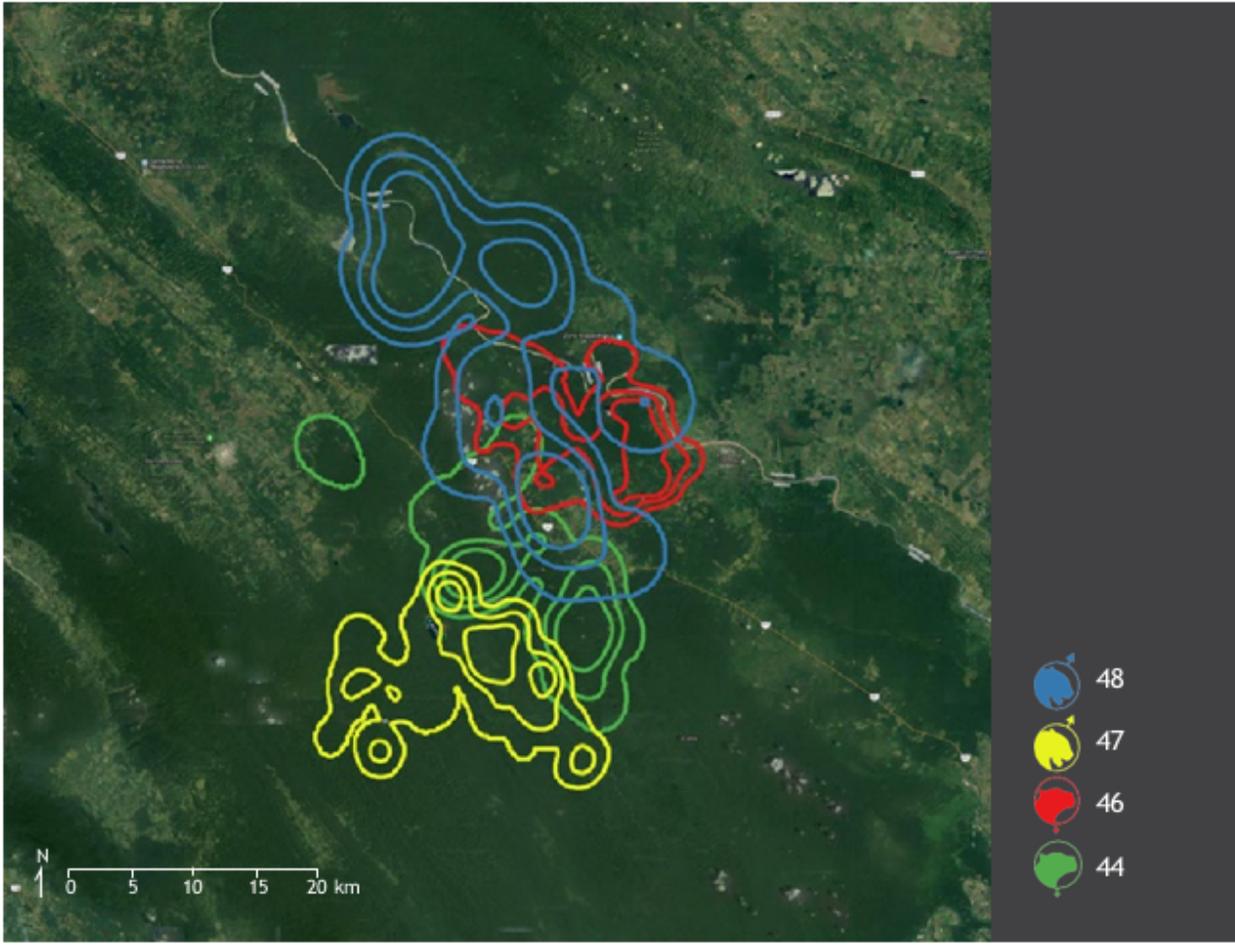
**Figure 6**

Kernel of 50%, 75%, and 95% of the jaguars in Campeche.



**Figure 7**

Kernel of 50%, 75%, and 95% of the jaguars in Quintana Roo.



**Figure 8**

Kernel of 50%, 75%, and 95% of the jaguars in Chiapas.