Chapter 13
Insights of the Movements of the Jaguar in the Tropical Forests of Southern Mexico

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13.1 Introduction

Movement is a critical animal behavior which reflects the animal response to its current biological needs and to its environment. Movement can maximize probability of survival in animals, because it can ensure access to resources such as food and water, the evasion of predators and competitors, and to find mates in reproduction (Morales et al. 2010). Understanding how and why animals use the available space and the underlying drivers of animal movements is essential to the management and conservation for both the species and the ecosystems where they inhabit (Allen and Singh 2016). The disruption of the natural patterns of animal movement can have important implications for ecosystem dynamics and function, including disturbances to trophic chains and nutrients cycling process (Ning et al. 2016; Tucker et al. 2018). Studies about movement ecology have grown in recent years with the improvement of tracking devices and the analytical tools, and these had provided unprecedented insights to understand where, when, and why the species move across the landscapes (Cagnacci et al. 2010a, b; Tomkiewicz et al. 2010).

Most apex predators in terrestrial ecosystems are facing dramatic population declines and range reduction (Ripple et al. 2014, 2016; Treves and Bruskotter 2014). Understanding the details of how these species move and use the space is essential to develop and implement effective conservation plans to ensure their long-term

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conservation (Chetkiewicz et al. 2006; Lehmann et al. 2008; Marker et al. 2008; de la Torre et al. 2017a; Tucker et al. 2018). The jaguar (*Panthera onca*) is the largest felid in the Neotropics and probably the least studied species of the *Panthera* genus (de la Torre and Medellín 2011). Historically, jaguars ranged from southwestern United States to central Argentina (Seymour 1989; Sanderson et al. 2002). However, this species has been extirpated from more than half of its original range over the last 100 years, and recent conservation assessments have concluded that jaguars are declining in much of its remaining range (Swank and Teer 1989; Rabinowitz and Zeller 2010; Medellín et al. 2016; de la Torre et al. 2018). Though the jaguar is not endangered as the same level of the other species of large felids such as lions, tigers, and snow leopards, the most current evaluations of the conservation status of this species have shown that most of its populations are threatened (de la Torre et al. 2018). The jaguar currently is listed as Near Threatened by the IUCN Red List (Quigley et al. 2017). However, fragmentation, habitat conversion, and poaching in retaliation to cattle predation are severe threats for the species in most of its distribution range (Nowell and Jackson 1996; Sanderson et al. 2002; Haag et al. 2010; Medellín et al. 2016; Quigley et al. 2017).

Diverse factors determine the patterns of movement and space utilization of solitary large felids such as the jaguar. For instance, home range sizes and patterns of space use in these animals are usually determined by their body size (Gittleman and Harvey 1982; Jetz et al. 2004; Carbone et al. 2005, 2007; Macdonald et al. 2010), prey availability across the space and time (Herfindal et al. 2005; Odden and Wegge 2005; Marker et al. 2008; Schmidt 2008), habitat suitability (Spong 2002; Broomhall et al. 2003; Conde et al. 2010), and sociality (Logan and Sweanor 2001; Azevedo and Murray 2007; Cavalcanti and Gese 2009; Goodrich et al. 2010). Furthermore, other factors such as interactions with other large carnivores can influence patterns of space use in large felids (Scognamillo et al. 2003; Harmsen et al. 2009; Odden et al. 2010; Bhattarai and Kindlmann 2012; Noss et al. 2012; Foster et al. 2013). Landscape configuration and connectivity are critical aspects that determine the space use in large felids, as well (Colchero et al. 2009; Conde et al. 2010; de la Torre et al. 2017a).

Due to its natural history and secretive behavior, studying the movements of large felids is expensive and logistically challenging, especially in the tropical forests. Only a few studies aimed at large felids in tropical forests have been able to capture and monitor several individuals to give relevant conclusions (Rabinowitz and Nottingham 1986; Jenny 1996; Karanth and Sunquist 2000; Ceballos et al. 2002; Odden and Wegge 2005; Nuñez 2006; Figueroa 2013; de la Torre et al. 2017b). Most of the former studies focused on evaluating jaguar spatial ecology have tried to describe the home range areas and spatial organization (Schaller and Crawshaw 1980; Rabinowitz and Nottingham Jr. 1986; Crawshaw and Quigley 1991; Ceballos et al. 2002; Cavalcanti and Gese 2009; Chávez 2009; Morato et al. 2016; de la Torre et al. 2017b) and jaguar habitat use (Conde et al. 2010; Cullen et al. 2013; de la Torre et al. 2017a). Other aspects of jaguar movement ecology that have been previously addressed are the assessment of their movement rates with respect to different variables such as time of day, moon phases, sex, etc. (Cavalcanti and Gese 2009; de la Torre et al. 2017b), as well as understanding the movement

decisions of jaguars in order to predict the most appropriate areas to maintain the connectivity between populations or patches of suitable habitat (Colchero et al. 2011; de la Torre et al. 2017).

With the aim to contribute in the knowledge of the spatial ecology of the jaguar in the tropical forests, in this chapter we summarize all information that has been obtained about the movements of this species for the Greater Lacandona Ecosystem, Southern Mexico. This jaguar population is one of the most studied in Mexico (de la Torre and Medellín 2011; de la Torre and Rivero 2017; de la Torre et al. 2017a, b; Towns et al. 2017). Formerly, we published in different sources some information related to movements of these jaguars tracked in this region. We analyzed these data comparing the spatial ecology of jaguars and pumas in our study area with the aim to compare the spatial requirements of these species in the tropical forest of Southern Mexico (de la Torre et al. 2017b). Additionally, we identified the suitable habitat and the functional corridors for jaguars to design a strategy to maintain connectivity in the Southern Mayan Forest, which spans the border of Mexico and Guatemala (de la Torre et al. 2017a). With this analysis we gave recommendations to decision-makers in Mexico and Guatemala to invest in specific sites for conservation, management programs, and habitat restoration to ensure the long-term viability of the jaguar population of the Mayan Forest (de la Torre et al. 2017a).

In order to explore other aspects of the movement ecology of jaguars in tropical forests, this chapter had the following objectives: (1) to evaluate jaguar home range sizes and movement rates in the tropical rainforests of Southern Mexico using new methods; (2) to evaluate the periodicity of jaguar movement, analyzing the frequency and the intensity with which they visit certain sites within their home range; and (3) to evaluate movement decisions of jaguars across different landscape features. The questions that we intended to answer are: (1) How do the jaguars use the space within their home range area in the Southern Mexico? and (2) Does the landscape configuration influence the behavior and movement patterns of jaguars? We expect that this analysis help to improve the understanding of the movement ecology of jaguars in tropical forests and increase the knowledge of this species to advance in its conservation throughout the tropical forest of Central America.

13.2 Methods

13.2.1 Study Area

Our study area was located in the Greater Lacandona Ecosystem in southeastern Mexico. This region contains the largest remaining portion of tropical humid rainforest in Mexico and is considered one of the most biodiverse regions of the country. The Greater Lacandona Ecosystem is part of what is called the "Mayan Forest," a trinational forest shared by Mexico, Guatemala, and Belize that holds important cultural and natural associations (Medellín 1994; de la Torre and Medellín 2011). The Mayan Forest is crucial for the conservation of different species of large

wildlife, because it is one of the few landscapes in Mesoamerica that is large enough to maintain viable populations of large mammals such as jaguars, white-lipped peccaries (*Tayassu pecari*), and Baird's tapirs (*Tapirus bairdii*) (March 1993; Medellín 1994; Matola et al. 1997; Sanderson et al. 2002; Naranjo et al. 2015; Reyna-Hurtado et al. 2017). Despite its importance for the conservation of numerous species, the Greater Lacandona Ecosystem continues to be subjected to anthropogenic destruction. Of its original 1,500,000 ha of rainforest, 2/3 has been lost due to human impact in the past 40 years (Mendoza and Dirzo 1999; Jong et al. 2000). The main threats for this ecosystem are the rapid growth of human populations, deforestation, unregulated extraction of flora and fauna, and the illegal use and extraction of natural resources from nature reserves (Medellín 1994; Davis et al. 1997; Mendoza and Dirzo 1999).

There are seven natural protected areas within the Greater Lacandona Ecosystem. These cover the largest forested areas of this region: Montes Azules (3312 km^2), Lacantún (619 km^2), Bonampak (48 km^2), Yaxchilán (26 km^2), Chan-kin (122 km^2), Naha (38 km^2), and Metzabok (33 km^2). Our study area was located in the north of Greater Lacandona Ecosystem and covered approximately 2500 km^2, including Yaxchilán (Usumacinta River as the border with Guatemala on the north), Bonampak, Lacantún, and Montes Azules Natural Protected Areas (Fig. 13.1). The study area also encompassed the Sierra la Cojolita, a tract of natural habitat in the
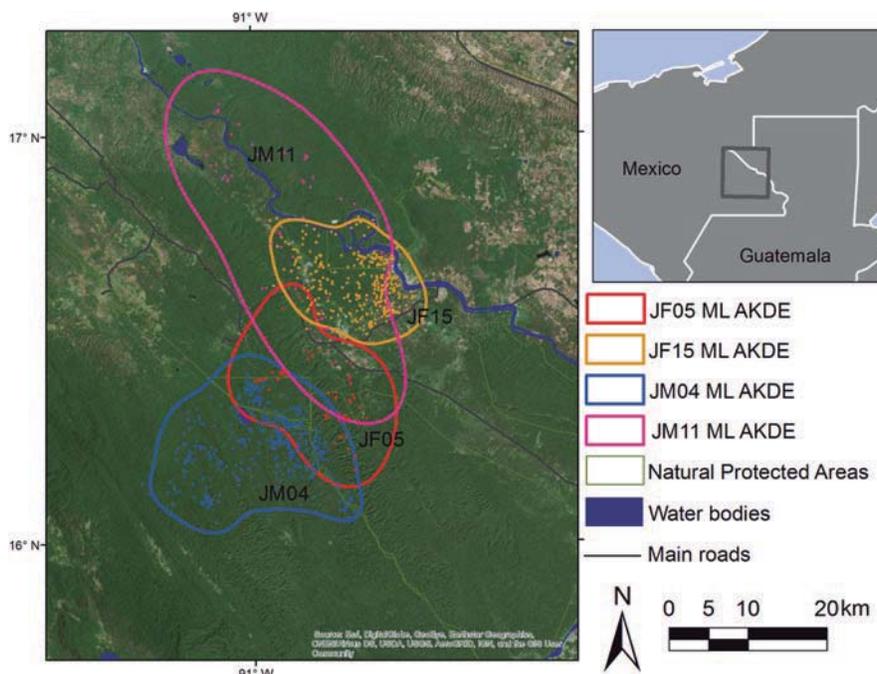

Fig. 13.1 Location of our study area and home ranges of jaguars in Southern Mexico using the autocorrelated kernel density estimation

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north of Greater Lacandona Ecosystem that is protected by local communities. Three indigenous communities inhabit the Mexican part of our study area: Lacanja Chansayab (~1000 people), Nueva Palestina (~20,000), and Frontera Corozal (~15,000). The main economic activities in this region include ranching, farming, and ecological and archeological tourism. Thus, the landscape outside the protected areas is composed of a matrix of primary forest surrounded by secondary forest, agricultural fields, and managed grasslands for livestock. The climate is hot (mean of 25 °C), and the mean rainfall per year is 2800 mm, with the greatest concentration in June–September and the lowest in March–April (reviewed by O'Brien 1998).

Among the species that potentially are important prey for jaguars in the area are collared peccary (*Pecari tajacu*), white-lipped peccary, the brocket deer (*Mazama temama*), white-tailed deer (*Odocoileus virginianus*), agouti (*Cuniculus paca*), paca (*Dasyprocta punctata*), and the nine-banded armadillo (*Dasypus novemcinctus*). Our field base camps to implement this study were located in the community of Lacanja Chansayab and in the CONANP (National Commission of Natural Protected Areas) field station at Yaxchilán Natural Protected Area.

13.2.2   Data Collection

We captured jaguars using foot snares (Frank et al. 2003). To respond immediately to any animal capture, we also placed a VHF radio transmitter at the site of each snare trap to monitor if traps were triggered (Halstead et al. 1995). We checked the traps 4 h throughout the night and, depending on weather conditions, several times during the day. We conducted three trapping seasons, one in Bonampak (November 2011 to January 2012) and two in Yaxchilán (July to September 2012 and February to April 2013). In Bonampak, we covered an area of approximately 60 km^2 with foot snares, and in Yaxchilán we covered an area of 25 km^2. We used 8–15 foot snares during each trapping day. All capture and handling protocols followed the Institutional Animal Care and Use Committees guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Upon capture, we immobilized jaguars using medetomidine (0.08 mg/kg) combined with ketamine (5 mg/kg) using a dart fired from a CO_2 pistol or rifle. While immobilized, we examined individual body condition and determined sex. We estimated age based on coat color, tooth wear (Stander 1997), and gum-line recession (Laundré et al. 2000). Body mass and linear measurements were recorded (de la Torre and Rivero 2017). Weight was recorded using a portable scale.

Captured jaguars were fitted with a satellite GPS collar (Telonics®, GEN IV, model TGW-4580). This model included a component for sending information through the ARGOS satellite system. We programmed the global positioning system collars to acquire a location every 4.8 h (four locations/day) and to send data packets through the ARGOS system every 4 days. All collars included a programmable release mechanism (model CR-2a, Telonics®), and we scheduled the release of the collars 12–14 months after jaguars were captured. The collars were recov-

ered, when possible, using the locations obtained after their release through the ARGOS system and searching the VHF pulses using a receiver (model TR4, Telonics®) and antennas of two and three elements (models RA23K and RA3, Telonics®). For all analyses, we used only the 3D GPS fixes that we obtained from collared animals that were calculated from four or more GPS satellites that provided a location estimate with a typical accuracy of 2–10 m.

Our trapping capture rate of jaguars was 2.5 captures per 1000 trap night (total trapping effort = 1,934 trap nights). We captured three females and two males. The female jaguars weighted in average 34.3 ± 1.5 kg and the males 52.5 ± 3.5 kg (de la Torre and Rivero 2017). We successfully deployed satellite global positioning system collars on these five jaguars. A total of 1134 3D GPS fixes were obtained from the collared animals and mean horizontal error was 5.01 ± 4.61 m. However, the fix success of the GPS collars was very low for most of the jaguars probably due to the closed forest canopy, since other studies (Gitzen et al. 2013; Camp et al. 2016) have shown that the performance of the GPS radio collars devices diminishes in tropical forests with multiple canopy layers or in areas with steep terrain. Furthermore, we only recovered three of the collars deployed (JF12, JF15, and JM04), and we could not recover one collar (JF05), because after the release mechanisms were activated, we did not obtain fixes through the ARGOS satellite system to search for this collar. We also never found it using the VHF signal in the field to search for this collar after the release mechanism was activated. Additionally, we lost the signal of jaguar male JM11 after 5 months of tracking through the ARGOS satellite system. Thus, data shown for animals JF05 and JM11 corresponded only to data recovered through the ARGOS satellite system (Table 13.1). We obtained a very few data of the female jaguar JF12, because she was shot 20 days after the capture (Table 13.1).

Table 13.1 Movement parameters and home range sizes for the jaguars tracked in the Greater Lacandona Ecosystem, southern Mexico

Animal ID	Sex	Age class	Weight	Number days/ fixes	Home range crossing time (day)	Velocity autocorrelation time scale (h)	Average distance traveled (km/day)	95% KDE (km²)	AKDE (km²) (95% CI)
JF05	♀	Adult	34	331/88	9.9 (3.6–27.2)	1.65 (0.31–8.5)	7.2 (5.1–9.3)	211.6	297.2 (163.4–470.4)
JF15	♀	Adult	33	350/395	4.6 (3.1–6.7)	2.7 (2.0–3.6)	6.9 (6.3–7.5)	198.8	203.4 (151.0–263.4)
JM04	♂	Adult	50	367/578	4.4 (3.2–5.9)	4.2 (3.4–5.1)	8.1 (7.6–8.5)	322.8	375.7 (294.8–466.4)
JM11	♂	Adult	55	133/72	4.7 (1.8–12.2)	5.2 (2.9–9.2)	9.6 (8.2–11.0)	581.9	714.1 (412.3–1097.4)

Home ranges were estimated using 95% kernel density estimator (KDE) and autocorrelated kernel density estimator (AKDE)

13.3   Analysis

13.3.1   *Home Range Sizes and Movement Rates of Jaguars in Southern Mexico*

One of the basic issues in the study of movement patterns of the wild animals is to define the area used by individuals in its normal activities for food acquisition, mating, and rearing progeny. This area is known as "home range" and generally is estimated aggregating the telemetry locations to evaluate the total use of the space by an animal (Powell and Mitchell 2012). To estimate home range sizes of jaguars in the Greater Lacandona Ecosystem, we used continuous-time stochastic movement models and the autocorrelated kernel density estimation (AKDE), which allows more accurate home range estimation, even if the data are strongly correlated. We calculated variograms, movement models, and estimated home range sizes using the *ctmm* package of the statistical software R (R Core Team 2016). Using the command *variogram*, we plotted the estimated semi-variance function for each animal to visually inspect the autocorrelation structure. We also evaluate the residence of the individuals tracked using the variograms. We expected that resident individuals reached an asymptote on timescale that roughly corresponds to the home range crossing time, and individuals whose plotted semi-variance did not reach an asymptote were not assumed to be home range residents (Morato et al. 2016).

The *ctmm* package allows to fit several movement models and select the best that describe the movement patterns of the individual studied. The *ctmm* package includes four basic movement models: (1) Brown motion (BM), which is based on the regular diffusion, where the velocities are uncorrelated and the space use is not limited. This model is used for data where the time between locations is very broad so it cannot reveal the autocorrelation velocity and too brief to show the residency areas. (2) Ornstein-Uhlenbeck (OU) movement model is a combination between the BM, but in this case the movement tends to remain in a certain area. The OU model fit to data that has no evidence of directional persistence; nevertheless the use of space is restricted. (3) Integrated OU (IOU) model is similar to BM in that it is a process that diffuses continuously, but it has autocorrelated velocities in short time scales. This model is better for data that show directional persistence, but the time is not enough to show a range residency. Finally, the Ornstein-Uhlenbeck Foraging (OUF) model is a combination between the OU and the IOU; this means that the movement tends to have correlated velocities and restricted use of space. This model is appropriated for data that has a very detail information to show velocity autocorrelation and long enough to show range residency (Calabrese et al. 2016).

OU models are described by two parameters, which are home range crossing time (days) and variance (km^2), and it allows to estimate the home range and home range crossing time, while the OUF models are described by three parameters which are home range crossing time, velocity autocorrelation (hours), and variance (km^2) and allow to estimate home range, home range crossing time, velocity autocorrela-

tion time scale, and average distance traveled for each individual. We fitted the models using the function *ctmm.fit*, which use maximum likelihood, and we ranked the models based on AICc using the function *ctmm.select*. We estimated the home range based on the best fitted model for each individual using the function *akde*.

For comparative proposes, we estimated home ranges using conventional kernel density estimators at 95% for each animal (Worton 1989). For this we also fit in the *ctmm* the independent identically distributed (IID) model, which by definition ignores autocorrelation in the data, and then we adjusted the fitted model to the *akde* function. We compared our jaguar home range estimations with those obtained in other studies. To compare the movement rates between female and male jaguars, we used the distance average traveled by each individual estimated using the OUF models (Morato et al. 2016).

13.4 Frequency and Intensity of Visits of Jaguars to Certain Sites Within Home Ranges

Traditionally, the space use has been studied through classical kernel methods for estimating the utilization distribution within an animal home range (Worton 1989). These methods consider locations as static and independent points rather than a movement process. However, the use of GPS radio tracking devices on wild animals provides information of sequential and correlated localizations that can be used to have a more dynamic approach to describe the space use and habitat selection. The movement-based kernel approach incorporates movement information and considers the time spent between successive relocations to analyze the trajectories of the individuals. This approach seeks to describe the intensity in which the individual actively uses the habitat patches within its home range, rather than the simple area occupied (Benhamou 2011; Benhamou and Riotte-Lambert 2012). Therefore, the movement-based kernel approach is focused in estimating the utilization distribution (UD) and additionally considers that the intensity of the space use is proportional to the activity time spent by unit area (Benhamou and Cornélis 2010).

The movement-based kernel approach can be analyzed under the biased random bridge (BRB) model. This BRB method is based on the biased random walk model, and its main characteristic is that it not only considers the diffusive movement but also includes the advection component; this means that the model considers the drift between successive relocations in the trajectory analysis (Benhamou 2011). Additionally, the BRB model decomposes the use of space in two components, since it identifies the areas that the animal might visit only once but stays for a long time, the intensity distribution (ID), and the areas that the animal visits repeatedly, the recursion distribution (RD), inside their home range. These components can be very helpful to understand how the animals select and make use of space within their home range areas (Benhamou and Cornélis 2010; Benhamou 2011; Benhamou and Riotte-Lambert 2012).

Using the BRB approach, we estimated the space use of two individuals of jaguar (JF15 and JM04) for our study area. We only used these individuals because

they were the ones which we obtained a larger number of fixes. The analysis was conducted using adehabitatHR (Calenge 2013a) of the statistical software R (R Core Team 2016). To calculate the UD, ID, and RD, we first estimated the diffusion coefficient (*D*) (Benhamou 2011). The *D* determines the smallest distance below which we consider that the animal is not moving; for our data we used a maximum time (T_{max}) = 24 h and a minimum distance (L_{min}) = 200 m to calculate *D*. The minimum smoothing parameter h_{min} was set to 100 m, and the radius of circle (radius) of the resident time and the number of visit used for the model was set to 1000 m (for more description regarding the model, see Calenge 2013a). We defined up to 95% cumulative frequency isopleths for UD, because it is better for analyzing the global home range area use, and 30% of isopleth for the ID and RD, because we were interested in identifying the highest density values for these distributions (intensively exploited/repeatedly visited; Benhamou and Riotte-Lambert 2012).

13.5   Movement Decisions of Jaguars Across Different Landscape Features

To understand how the landscape structure of our study area affects jaguar movements, we analyzed the sequential locations obtained from the jaguars tracked in our study using step selection functions (Fortin et al. 2005; Thurfjell et al. 2014; Ziółkowska et al. 2016). Step selection functions are relative new useful models for studying resource selection by animals moving through the landscape, and these compare environmental attributes of observed steps (the linear segment of two consecutives fixes) with alternative random steps taken from the same starting point. This approach has been used to study habitat selection, human wildlife interactions, movement corridors, and dispersal behaviors in carnivore and ungulate species (Thurfjell et al. 2014). With the aim to evaluate how the landscape configuration of the Greater Lacandona Ecosystem affects the movement decision of jaguars, we compiled a geospatial dataset using a suite of environmental and anthropogenic variables for our study area (Table 13.2). Then, for each observed step, we calculated its length (*d*) and turning angle (*α*) using the package "adehabitatLT" (Calenge 2013b) from R 3.1.1 (R Core Team 2016). Steps were divided into "active" and "passive," based on step length (Ziółkowska et al. 2016), with all steps ≥500 m constituting active steps. We only used the active steps for implementing the step selection function analysis.

Each active step was paired with 100 control steps that shared the same starting point but differed either in length, direction, or both. The length and turning angles of control steps of a given individual jaguar were sampled from those observed of the other individuals to avoid problems of circularity (Fortin et al. 2005). We used the command "movement.ssfsamples" of the "Geospatial Modelling Environment" package to generate the control steps (Beyer 2012). For each observed and control

Table 13.2 Landscape variables used to evaluate the potential habitat for jaguars in the Greater Lacandona Ecosystem through resource selection probability functions

Type	Variable name	Abbreviation	Description	Units	Justification
Forest cover	Forest cover 30 m	FCov-30	Percentage of forest coverage around the pixel	%	Jaguars in tropical forest are restricted mostly to areas of primary forest where they find their natural prey and refuge (Rabinowitz and Nottingham 1986; Conde et al. 2010; Cullen et al. 2013). To appraise
	Forest cover 240 m	FCov-240	Percentage of forest coverage 240 m around the pixel	%	habitat quality, we used the high-resolution global forest map (Hansen et al. 2013). This dataset includes the extent of global tree cover density, which is defined as vegetation higher than 5 m and is
	Forest cover 510 m	FCov-240	Percentage of forest coverage 510 m around the pixel	%	expressed as a percentage (Hansen et al. 2013). Given that habitat use and movement by jaguars might be limited by the amount of surrounding forest, as it is by other large predator species (Beier 1995; Dickson et al. 2005), we estimated forest cover in a neighborhood of 240 m (FCov-240) and 510 m (FCov-510) around each raster pixel
Terrain	Topographic position index	TPI	Classification of landscape according to the slope position within a different radius. This index incorporated richness and evenness into a single measure	–	Jaguar habitat use and movement are affected by different terrain conditions. Jaguar mobility would be facilitated in areas of high topographic complexity, especially if the flat areas of suitable habitat have been cleared (Dickson et al. 2005; Morato et al. 2014). However, jaguars are frequently associated with lowland areas, and jaguar occupancy and movements would be hampered by the mountain ranges at higher altitudes (Rabinowitz and Nottingham 1986;
	Elevation	ELE	Elevation	m.a.s.l.	Rabinowitz and Zeller 2010; Zeller et al. 2011). Topographic position index was used to characterize the slope's position in the terrain and
	Shannon topographic index	SHAN	Differences of ranges of elevation values within a different radius	–	landform. This index incorporated richness and evenness into a single measure. Using a 30 m digital elevation model, we obtained elevation ranges. Shannon index was used to evaluate differences in heterogeneity for ruggedness. In general, higher values reflected more diversity and a better balance among unique landform values (Riley et al. 1999)

Water runoffs	Distance to water courses	DistW	The minimum distance to the nearest water runoff	km	Jaguars are known to use riparian habitats to move through landscapes and use sites with permanent water more frequently (Schaller and Vasconcelos 1978; Rabinowitz and Nottingham 1986; Emmons 1987; Nuñez 2006). We constructed this raster using a layer of the hydrological drainage system of the entire study area (Tapia and Nuñez 2008)
Human	Distance to towns	DistT	The minimum distance to the nearest town	km	Human activity affects habitat use by jaguars negatively due to disturbance and persecution (Conde et al. 2010; Colchero et al. 2011;
	Distance to paved roads	DistR	The minimum distance to the nearest paved roads	km	Espinosa et al. 2018). Information of towns and roads was obtained from INEGI (Instituto Nacional de Estadística e Informatica) for Mexico and IGN-SEGLAPAN (Instituto Geográfico-Secretaria de
	Distance to deforestation edge	DistD	The nearest distance to the deforested patch >1 km^2	km	Planificación y Programación de la Presidencia) for Guatemala. To evaluate the distances that jaguars use from the boundaries that separated the forest from open modified areas, we used a raster layer with the minimum distance to the nearest deforested patches <1 km^2 since the average size of the cleared areas transformed to create grassland for livestock is 1 km^2 in our study area (equivalent to 100 ha)

step, we calculated the exact values of the predictors covariables at the endpoint of steps (Thurfjell et al. 2014).

We constructed step selection function models with the package "ResourceSelection" (Lele et al. 2014) from R 3.1.1 (R Core Team 2016) using a conditional regression with log link, which is adequate to construct this kind of models (Thurfjell et al. 2014). The step selection functions were fit using the observed steps matched to their respective control steps (Lele and Keim 2006; Northrup et al. 2013). We tested 54 step selection function models with different combinations of explanatory variables (Table 13.5). Then, we used the Akaike information criterion (AIC) to identify the best step selection function models (Burnham and Anderson 2002). We considered models comparable if ∆AIC was <2.0, and we compared the AIC weights (wi) to determine the most appropriate models that described jaguar movements.

13.6 Results

13.6.1 Home Range Sizes and Movement Rates of Jaguars in Southern Mexico

After the preliminary analysis with the variograms, we only calculated the home ranges of four jaguars tracked (2 ♀, 2 ♂), because the variogram of the female jaguar JF12 did not reach the asymptote. The best movement model, for the four jaguars that we estimated the home ranges, was the OUF. The examination of our home range estimations showed that jaguars use vast annual areas in the tropical forests in Southern Mexico. Mean annual home range for female ranges from 203 to 297 km^2 and for male jaguars from 375 to 714 km^2 (Fig. 13.1 and Table 13.1). Home range sizes of jaguars in Southern Mexico were similar to other studies carried on in tropical rainforests, which ranged from 10 to 268 km^2 for females and from 34 to 624 km^2 for males (Table 13.3). However, some of these estimations were obtained using VHF tracking technique and conventional tools to estimate home ranges such as minimum convex polygons and kernel density estimator which suggest that some of these were underestimated (Morato et al. 2016).

13.6.2 Frequency and Intensity of Visits of Jaguars to Certain Sites Within Home Ranges

The results of the BRB model allowed identifying the areas more intensively used and the areas more frequently visited within the home range areas of the female jaguar JF15 and the male jaguar JM04. It is plausible that areas intensively used by both jaguars were areas associated with a killing of large prey event, since jaguars

Table 13.3 Jaguar home range estimates (in km²) obtained from different studies using VHF and GPS tracking techniques and the autocorrelated kernel density estimation (AKDE), kernel density estimator (KDE), and minimum convex polygon (MCP). Also are included the countries, regions, and habitat types

Study area	Country	Habitat type	Tracking technique	Estimation method	Males	Females	♂/♀	References
Mexican Pacific	Mexico	Tropical dry forest	VHF	MCP 100%	92.7 (2)	38.0 (4)	2.4	Nuñez (2006)
Calakmul	Mexico	Tropical rainforest	VHF	MCP 100%	36.9 (2)	45.5 (2)	0.8	Ceballos et al. (2002)
Calakmul	Mexico	Tropical rainforest	GPS	Kernel 95%	624.95 (3)	155.42 (7)	4.0	Chávez (2009)
Lacandona	Mexico	Tropical rainforest	GPS	AKDE	544 (2)	250 (2)	2.3	This study
Center of Belize	Belize	Tropical rainforest	GPS	Kernel 95%	264.3 (6)	169.3 (1)	1.5	Figueroa (2016)
Cockscomb	Belize	Tropical rainforest	VHF	MCP	34.4 (4)	10 (2)	3.4	Rabinowitz and Nottingham (1986)
Los Llanos	Venezuela	Tropical savannas	VHF	MCP	130 (1)	49 (2)	2.6	Scognamillo et al. (2003)
Dry Chaco	Paraguay	Tropical dry forest	GPS	AKDE	727(5)	255 (2)	2.8	McBride and Thompson (2018)
Humid Chaco	Paraguay	Tropical savannas	GPS	AKDE	818(4)	237 (8)	3.4	McBride and Thompson (2018)
Amazon	Brazil	Tropical rainforest	GPS	AKDE	211 (4)	68 (6)	3.1	Morato et al. (2016)
Cerrado	Brazil	Tropical savannas	GPS	AKDE	1268	–	–	Morato et al. (2016)
Cerrado	Brazil	Tropical savannas	VHF	MCP 80%	265 (1)	228 (1)	1.1	Silveira (2004)
Atlantic Forest	Brazil	Tropical rainforest	GPS	AKDE	462 (5)	268 (5)	1.7	Morato et al. (2016)
Pantanal	Brazil	Tropical savannas	GPS	AKDE	144 (6)	52 (10)	2.7	Morato et al. (2016)
Pantanal	Brazil	Tropical savannas	GPS	Kernel 95%	154 (6)	62.5 (4)	2.4	Cavalcanti and Gese (2009)
Pantanal	Brazil	Tropical savannas	VHF	Kernel 95%	67.3 (3)	38.2 (5)	1.7	Azevedo and Murray (2007)
Pantanal	Brazil	Tropical savannas	VHF	MCP 100%	152.4 (1)	139.5 (4)	1.1	Crawshaw and Quigley (1991)
Pantanal	Brazil	Tropical savannas	VHF	MCP 100%	80 (1)	31.5 (2)	2.5	Schaller and Crawshaw (1980)

can spend several days feeding of a carcass of a large prey and they can stay around killing sites from 1 to 21 days (Cavalcanti and Gese 2010). In Figs. 13.2 and 13.3 is shown the intensity distribution of both animals using an isopleth of 30%. This intensity distribution at 30% of isopleth covered 23 km^2 for the female jaguar JF15 and 40 km^2 in the male jaguar JM04.

On the other hand, areas frequently visited might be associated with refuge areas or areas used frequently as foraging sites. Contrasting the recursion utilization at 30% of isopleth with the core areas estimated through 50% fixed kernel (utilization distribution), we observed that these areas were very similar in both individuals.
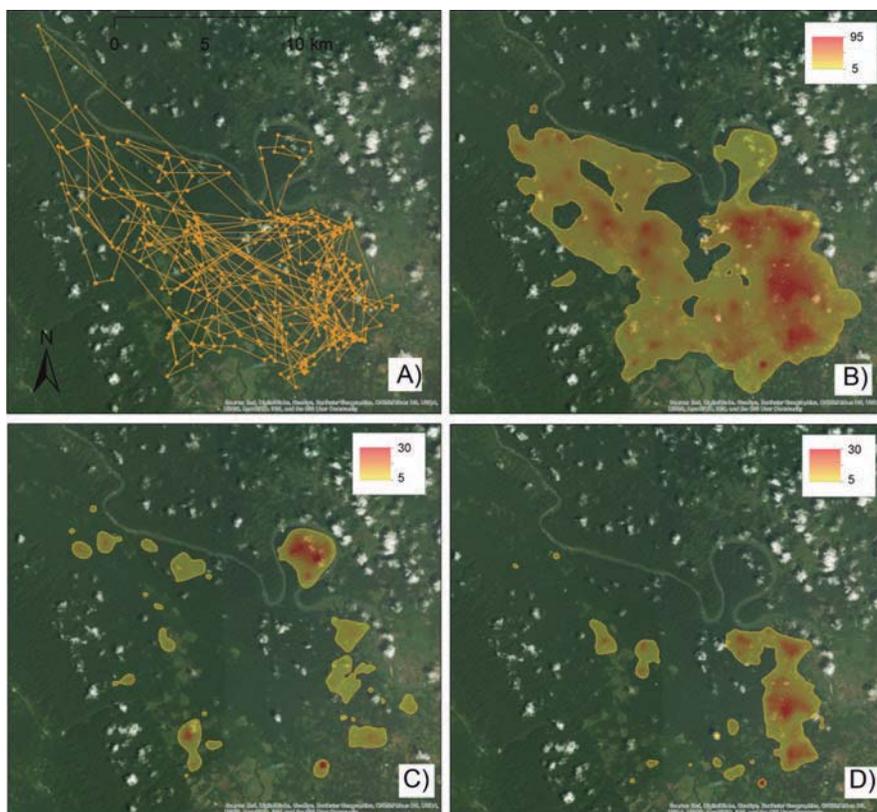
Fig. 13.2 Home range polygons obtained using the biased random bridge model for the jaguar female JH15. (**a**) Locations and trajectories obtained from the individual followed by the GPS collar. (**b**) Utilization distribution using an isopleth of 95%. (**c**) Intensity distribution using an isopleth of 30%. (**d**) Recursion distribution using an isopleth of 30%
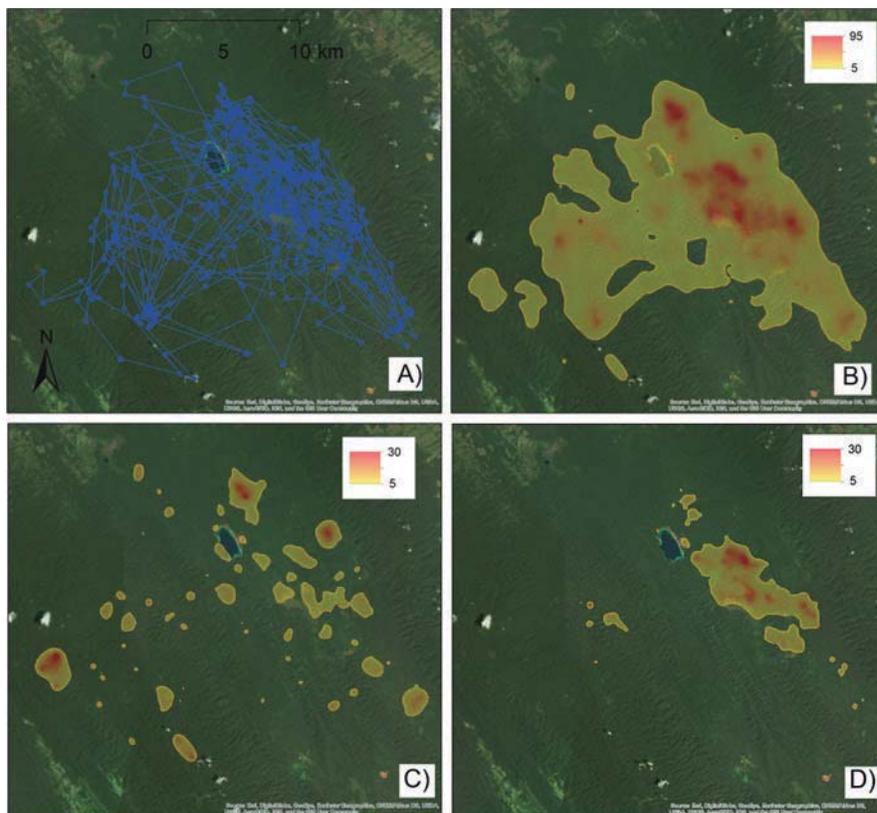
Fig. 13.3 Home range polygons obtained using the biased random bridge model for the jaguar male JM04. (**a**) Locations and trajectories obtained from the individual followed by the GPS collar. (**b**) Utilization distribution using an isopleth of 95%. (**c**) Intensity distribution using an isopleth of 30%. (**d**) Recursion distribution using an isopleth of 30%

13.6.3   Movement Decisions of Jaguars Across Different Landscape Features

We analyzed a total of 452 movement steps, of which 43.5% were classified as active. Our best step selection function model included the forest cover in a neighborhood of 240 m (FCov-240), the TPI, and elevation (ELEV) as the variables associated most strongly with movement probability by jaguars in the Greater Lacandona Ecosystem landscape (Table 13.4). For this model all the variables were informative, and the 95% CI did not overlap 0 (Table 13.4). However, this model only had a ΔAIC value of 0.54 for the second best ranked model (Table 13.5). This second ranked model included the same variables than the first ranked one but as well including the nearest distance to deforested patches that were >1 km^2 (DistD)

Table 13.4 Estimated coefficients (β), standard errors (SE), 95% confidence intervals (95% CI), z values (z), and P values (P) for the best step selection functions for movements of jaguars in the Southern Mayan Forest

Covariate	β	SE	95% CI	z	P
FCov-240	0.0335	0.0079	0.0199 to 0.0527	4.241	<0.0001
TPI	0.0379	0.0109	0.0166 to 0.0595	3.475	<0.001
ELEV	−0.0070	0.0015	−0.0103 to −0.0049	−4.680	<0.0001

We estimated the coefficients and the standard errors for percentage of forest cover in a neighborhood of 240 m (FCov-30), the topographic position index (TPI), and the elevation (ELEV) by bootstrapping ($B = 5000$)

Table 13.5 The ten best step selection function models tested to understand how the landscape structure of the Greater Lacandona Ecosystem affects jaguar movements

Model	df	LogLik	AICc	ΔAIC	Weight	Rank
FCov-240 + TPI + ELEV	3	−893.414	1793.00	0	0.355	1
FCov-240 + DistD + TPI + ELEV	4	−892.642	1793.50	0.54	0.271	2
FCov-510 + TPI + ELEV	3	−893.771	1793.70	0.71	0.248	3
FCov-510 + DistT+ TPI+SHANN	4	−894.667	1797.50	4.59	0.036	4
FCov-240 + DistD + DistT + ELEV	4	−895.108	1798.40	5.47	0.023	5
FCov-510 + TPI + SHANN	3	−896.844	1799.80	6.86	0.011	6
FCov-240 + DistT + ELEV	3	−896.919	1800.00	7.01	0.011	7
FCov-510 + DistT + ELEV	3	−897.367	1800.90	7.91	0.007	8
FCov-240 + DistD + ELEV	3	−897.409	1800.90	7.99	0.007	9
FCov-30 + DistD + TPI + ELEV	4	−896.446	1801.10	8.15	0.006	10
Null model	1	−910.457	1822.90	29.98	0	55

variable. However this last variable was not informative because the 95% CI overlapped 0. The third best ranked model was very similar to our best model (wi = 0.24) and included the forest cover in a neighborhood of 510 m, TPI, and elevation (ELEV). Since the three ranked models were very similar, we used the first ranked model to explain the movement decisions of jaguars across the different landscape features of our study area.

13.7 Discussion

13.7.1 Home Range Sizes and Movement Rates of Jaguars in Southern Mexico

Comparing our home range sizes, estimations with other studies where home ranges were estimated using GPS tracking technique suggest that the areas used by the jaguars in the tropical rainforest of Central America are similar (Table 13.3). This demonstrates that jaguars require extensive areas to meet their spatial requirements

in this ecosystem type. On the other hand, it appears that in other kinds of ecosystems such as tropical savannas, such as in the Pantanal, Brazil, jaguars use smaller home ranges than in the tropical rainforests (Table 13.3).

Contrasting the home range sizes between sexes, male jaguars had 2.1 times larger home range than those of female jaguars. Jaguars, as most of the felid species, are solitary except for periods of mating and breeding. Usually, females have smaller home ranges than males, and the home ranges of males include and overlap with the home ranges of several females (Schaller and Crawshaw 1980; Rabinowitz and Nottingham Jr. 1986; Cavalcanti and Gese 2009). Home ranges of females are shaped by the abundance and distribution of prey, which is critical to meet the energetic requirements that raising cubs demands (Eisenberg 1986; Sandell 1989; Logan and Sweanor 2001). Another factor that determines space use in solitary female felids is the availability of safe refuges for offspring (Nuñez 2006; Steyn and Funston 2009). Larger home ranges of males are determined by the spatial distribution of females and have to be large enough to cover several females to increase mating opportunities. Other factor that determines the space in males is defending their territory from other males, which would compete for the mates or would kill their cubs (Eisenberg 1986; Cavalcanti and Gese 2009; Ferguson et al. 2009; Goodrich et al. 2010).

Movement rates also varied between male and female jaguars. Male movement paths, represented by velocity autocorrelation time scale and distance traveled by day, were larger compared with female jaguars (Table 13.1). However, home range crossing time was variable between individuals. These results are similar to previous studies of jaguar movements which have reported that female jaguar movement paths are proportionally more erratic or tortuous with smaller distances traveled per day (Cavalcanti and Gese 2009; Morato et al. 2016).

13.7.2   Frequency and Intensity of Visits of Jaguars to Certain Sites Within Home Ranges

The results obtained from the analysis suggest that jaguars exhibited a selective behavior in certain areas within their home ranges, and probably these provide significant habitat component for their survival or reproduction (Samuel et al. 1985; Bingham and Noon 1997; Plowman et al. 1998). For instance, areas frequently used by female jaguar JF15 were associated with rugged terrain across a small mountain range covered with forest, but that has been deforested around it in the flat areas. In the case of female jaguars, rugged terrain would provide den and refuge when they are rearing cubs (Steyn and Funston 2009; White et al. 2015) and could provide protection because these areas maintain more forest cover in contrast with flat areas which are more susceptible to deforestation and other human activities.

Frequently visited areas also might be associated with areas of exclusive use. Other studies have shown that jaguars have little spatial overlap in core areas (Azevedo and Murray 2007; de la Torre et al. 2017b). This spatial segregation

observed in jaguars and other large felids implies territorial behavior because core areas have been frequently associated with regions of resource concentration (Samuel et al. 1985; Plowman et al. 1998; Nuñez 2006; Azevedo and Murray 2007). Spatial segregation of frequently visited areas or core areas could facilitate the coexistence between individuals through resource partitioning (Scognamillo et al. 2003; Azevedo and Murray 2007). Communication between individuals through scent marking using scats, scrapes, or spray urine may provide spatial and temporal information to reduce confrontation and may help to maintain the exclusive territories (Harmsen et al. 2010; Towns et al. 2017).

13.7.3 Movement Decisions of Jaguars Across Different Landscape Features

The step selection function analysis indicates that the probability of movement of jaguars in the Greater Lacandona Ecosystem is positively associated with a high percentage of forest cover in a neighborhood of 240 m. This result suggest that despite the landscape configuration, jaguars prefer to move across forested areas in the tropical forest of south of Mexico. Additionally our model indicates that probability of movement for jaguars was associated with positive values of TPI, which indicated that jaguar movements were facilitated by sites with medium to moderate slopes and flat valleys (Dickson et al. 2005). This is especially plausible if the flat areas had been cleared for cattle pastures or crops, which is a common situation in our study area (Morato et al. 2014). Our best model also indicates that jaguars avoided moving through the ridge tops of mountain ranges, since the probability of movement by jaguars decreased with elevation. Other studies also have suggested that movements of jaguars would be hampered by mountain ranges at higher altitudes (Rabinowitz and Zeller 2010; Zeller et al. 2011); however, it is necessary to track some individuals in forested areas located at higher altitudes to have conclusive results and to improve the knowledge of jaguar movement behavior in areas of higher altitudes and rugged terrain.

13.8 Conclusions

In this study we illustrate that the extensive area requirements of jaguars have crucial implications for the conservation of the species at the landscape scale in the tropical rainforests of Central America; therefore, forest transformation and fragmentation would have severe effects for the species. Although jaguars do not necessarily use areas which are covered completely with forest, several studies have shown that they preferred primary forest in contrast to modified environments associated with human activities (Conde et al. 2010; Foster et al. 2010; Colchero et al. 2011; Cullen et al. 2013; de la Torre et al. 2017a).

Our study demonstrates that to ensure the long-term conservation of jaguars in the tropical rainforest of Central America, large extensions of primary forest should be preserved, for instance, our estimations of jaguar home ranges indicate that it is necessary to conserve connected parches of tropical forest of at least 200 km^2 to guarantee the annual spatial requirements of a single female jaguar in the south of Mexico. This estimation gives an idea of the scale and the magnitude of conservation actions required to preserve jaguar populations in tropical forest areas. Large tropical forest areas provide to jaguars prey availability, dense foliage for stalking prey, and refuge for rearing cubs (Rabinowitz and Nottingham 1986; Crawshaw and Quigley 1991; Conde et al. 2010; Foster et al. 2010; Cullen et al. 2013).

The movement probability model also demonstrates the importance to conserve areas with primary forest to allow the movement of the jaguars across fragmented landscapes, because the probability of movement of jaguars was greater in areas with a forest cover in a neighborhood of 240 m. This outcome has important implications for the design of corridors focused on maintaining the connectivity between suitable habitat patches for the species, because our results suggest that the minimal width at which corridors could be functional for jaguars is 240 m. This result is similar to studies using other species of large felids such as pumas, which indicates that corridors >400 m wide covered with forest or other coverage were functional for dispersal (Beier 1993, 1995).

Our results also showed that BRB model is a new alternative to the traditional home range estimators to study the space use of large carnivores in tropical forests. This model allowed us to decompose the home range of the jaguars into two components, intensity of use and frequency of visit. The results obtained from the estimation of the intensity distribution (ID), which are the areas where the jaguars spend prolonged periods of time, but only visited once, are probably associated with hunting sites. On the other hand, the estimation of the recursion distribution (RD) indicated areas that are frequently visited by jaguars so it can be probably associated with resting or refuge sites. Together, both distributions could represent an approximation of the areas identified by the estimation of the fixed kernel at 50%, considered as the core areas; however, this new approach generated from the BRB model allows us to make a more detailed description of the use of space within the home range by jaguars. Future studies could incorporate this approach combined with an intensive ground tracking of animals to give clearer insights regarding the utilization of certain areas within their home range by jaguars in tropical forests.

We recognize that a caveat in our analyses is that the GPS records used to fit all the models come only from two to five animals tracked, and this sample size probably is not representative of the jaguar population of our study area. Other limitation is that these five animals were tracked in a relatively small area which is mainly represented by lowland areas. However, this effort is the first step to understating jaguar movement in the humid tropical rainforest of Southern Mexico and has opened a window to develop sound conservation actions that ensure the connectivity of this jaguar population across the Greater Lacandona Ecosystem landscape (de la Torre et al. 2017a).

The movement ecology is a discipline that in recent times, with the development of new technologies and analytical tools, has allowed making more precise inferences regarding the space use and movement of wildlife animals. We hope that the growing of this discipline allows in the future a better understanding of the ecology and behavior of the species that inhabit the tropical rainforest to generate the information necessary to implement policy conservation actions that ensure the long-term persistence of the wildlife and these ecosystems.

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