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# Habitat availability and connectivity for jaguars (*Panthera onca*) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape

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A B S T R A C T

The jaguar (*Panthera onca*) is the largest felid in the Neotropics, and habitat fragmentation and conversion are severe threats for this species. We used empirical models to identify 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. We used Resource Selection Probability Functions to identify suitable habitat patches that were occupied by jaguars. Then, we used Step Selection Functions to directly measure movement probability given different landscape variables and to generate a resistance matrix to develop a model of habitat connectivity through Circuit Theory approach. Finally, we categorized the habitat patches and corridors to establish conservation and management priorities. Landscape variables that best described habitat use and movements of jaguars were similar. We propose that suitable habitat is maintained in large areas of primary forest, which are located at longer distances from deforested patches with relatively gentle topography. On the other hand, the functional connectivity exists through areas that include forest cover in a surrounding area within 240 m, and through areas with moderate to medium slopes or flat areas. We identified 27 habitat patches and 50 corridors for jaguars in the Southern Mayan Forest. However, we identified some gaps in the protection of these key habitats and corridors. Decision-makers in Mexico and Guatemala should encourage investment in specific sites for conservation, management programs, and habitat restoration to ensure the integrity of the entire Mayan Forest ecosystem.



## 1. Introduction

One of the most vital and urgent challenges in conservation science is the issue of habitat loss and fragmentation of wildlife habitats (Ito et al., 2013; Rathore et al., 2012; Riley et al., 2003; Wang et al., 2014). Habitat fragmentation has been recognized as one of the top threats for many species (Haag et al., 2010; Ito et al., 2013; Ramiadantsoa et al., 2015; Tapia-Armijos et al., 2015; Yumnam et al., 2014). The rapid expansion of human populations and the conversion of natural habitats have transformed areas that used to be continuous into fragmented landscapes, which causes isolation of wildlife populations contained within the fragments (Gaston, 2005; Schipper et al., 2008; Skole and Tucker, 1993). The consequences of isolation in wildlife populations include the disruption of the original patterns of gene flow, drift-induced differentiation among local populations and, after long periods of time, the risk of extinction due to excessive interbreeding (Finger et al., 2014; Haag et al., 2010; Yumnam et al., 2014). Furthermore, small and isolated populations also are more likely to become extinct by stochastic events such as diseases, climate change, or natural disasters (Brown and Kodric-Brown, 1977; Colchero et al., 2009; Uphyrkina et al., 2002).

Habitat fragmentation is particularly relevant in developing countries, where most of the terrestrial biodiversity occurs. Natural ecosystems in developing countries are under unprecedented threats due to excessive population growth, demand by human populations for new lands, and unplanned economic development (Mendoza and Dirzo, 1999; Rosa et al., 2013; Skole and Tucker, 1993; Swenson et al., 2011; Tapia-Armijos et al., 2015). One of the main solutions for mending the negative effects of habitat fragmentation on wildlife populations is to maintain or restore connectivity through wildlife corridors (Rabinowitz and Zeller, 2010; Rathore et al., 2012; Wang et al., 2014). Connectivity is the degree to which the landscape facilitates or impedes movement among habitat patches, and it depends not only on the landscape characteristics, but also on the ability of species to move through habitats and corridors (Crooks and Sanjayan, 2006; Ferreras, 2001; Rudnick et al., 2012; Taylor et al., 1993). Nevertheless, designation of habitats and corridors for protection rarely take into account habitat selection and movement patterns of the species of interest, and they focus instead on the relative integrity of the ecosystem alone (Beier and Noss, 1998; Chetkiewicz et al., 2006; Kertson and Marzluff, 2010; Poor et al., 2012;

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Rathore et al., 2012). Recently, many studies have combined new technologies, such as GPS radio-telemetry and remote sensing, to integrate habitat requirements and behavior of focal species with landscape characteristics (Cagnacci et al., 2010; Chetkiewicz et al., 2006; Poor et al., 2012; Squires et al., 2013; Tomkiewicz et al., 2010; Zeller et al., 2014). This approach has allowed the identification of priority areas to conserve populations of endangered species and to identify corridors to maintain linkages between populations in fragmented landscapes (Colchero et al., 2011; Conde et al., 2010; Lapoint et al., 2013; Squires et al., 2013; Ziółkowska et al., 2016).

The jaguar (*Panthera onca*) is the largest felid in the Neotropics, and the least studied species in the genus *Panthera* (de la Torre and Medellín, 2011). Historically, jaguars occurred from southwestern United States to central Argentina (Sanderson et al., 2002; Seymour, 1989). 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 (Caso et al., 2008; Medellín et al., 2016, 2002; Rabinowitz and Zeller, 2010; Sanderson et al., 2002; Swank and Teer, 1989). The jaguar is listed currently in the IUCN Red List as Near Threatened, and fragmentation and habitat conversion are severe threats for the species (Caso et al., 2008; Haag et al., 2010). Jaguar habitats are being converted to agricultural lands, pastures, and human settlements, and roads and other human infrastructure are destroying jaguar habitat as well (Caso et al., 2008; Haag et al., 2010; Nowell and Jackson, 1996; Sanderson et al., 2002; Swank and Teer, 1989).

One of the largest jaguar populations throughout its range is located in the Mayan Forest region, and this represents one of the few viable populations of the species (Ceballos et al., 2002; de la Torre and Medellín, 2011; Sanderson et al., 2002; Zeller, 2007). Previously, jaguars were distributed throughout the Mayan Forest. However, the accelerated human development in this region has transformed natural habitats into an irregular matrix where human activities dominate the landscape, which affects biodiversity and ecological processes adversely. Under this scenario, most of the jaguars in this region are limited to nature reserves and the largest tracts of conserved forest where human activities have not had a significant impact (Ceballos et al., 2002; Conde et al., 2010). One alternative is to conserve, over the long term, the jaguar populations of the Mayan Forest by maintaining and restoring the connectivity between suitable patches of habitat with wildlife corridors to ensure movement of individuals between these patches (LaRue and Nielsen, 2008; Morato et al., 2014; Rabinowitz and Zeller, 2010; Yumnam et al., 2014).

Understanding how the jaguars use space in the Mayan Forest is essential to develop proper conservation plans and to ensure its persistence in this increasingly human-dominated landscape. Previous studies have shown that jaguars use extensive home range areas and that this species requires vast areas for their survival (Cavalcanti and Gese, 2009; Ceballos et al., 2002; Chávez, 2009; Conde et al., 2010; Quigley and Crawshaw, 1992). Jaguars occupy a great variety of habitats throughout its distribution range, such as tropical rainforest, mangroves, wet grasslands, arid scrub, and pine oak forest (Sanderson et al., 2002). However, previous studies have shown that jaguars prefer primary vegetation types, and human-modified landscapes are usually avoided or used with lower frequency (Conde et al., 2010; Cullen et al., 2013; Foster et al., 2010). Furthermore, human infrastructure also has a negative effect on habitat use by jaguars, because they avoid moving across paved roads or through areas modified by human activity (Colchero et al., 2011; Conde et al., 2010).

In this study, we determine the factors that promote habitat use and movements by jaguars in the Southern Mayan Forest, with the aim of identifying areas of suitable habitat and critical areas necessary to maintain connectivity for the species within this landscape. In our analysis, we assumed that habitat use and movement behavior were two independent processes (Chetkiewicz et al., 2006; Squires et al., 2013; Zeller et al., 2014; Ziółkowska et al., 2016). First, we used Resource Selection Probability Functions (RSPFs) to identify suitable habitat patches occupied by jaguars in the region. Second, we used Step Selection Functions (SSFs) to measure movement probability directly given different landscape variables and to generate a resistance matrix to develop a model of habitat connectivity using Circuit Theory. Finally, we categorized the habitat patches and corridors identified to establish conservation and management priorities in the Southern Mayan Forest to establish a conservation strategy for the species in this region. With this approach we modelled jaguar habitat and corridors with a more realistic and detailed scheme than previous studies, which were based exclusively on expert opinion or on presence points for creating the resistance surface (Morato et al., 2014; Rabinowitz and Zeller, 2010; Rodríguez-Soto et al., 2011). Because, jaguars generally prefer areas with natural cover as main habitat and avoided areas with high human occupation (Ceballos et al., 2002; Colchero et al., 2011; Conde et al., 2010; Cullen et al., 2013; Foster et al., 2010), we predicted that jaguars would use primary forest and sites further removed from human activities preferentially. Given that jaguars avoid moving close to roads and sites with human occupation (Colchero et al., 2011), we predicted that jaguar movement would be facilitated by primary forest and by sites further removed from human activities. Because jaguar movements in other landscapes are facilitated by mountain ridges, especially if the flat areas had been cleared of suitable habitat (Morato et al., 2014), we predicted that jaguar movement would be facilitated by the rugged terrain of our study area (Dickson et al., 2005).

## 2. Material and methods

### 2.1. Study area

This study was conducted in the Southern Mayan Forest. The Mayan Forest region holds the largest jaguar population and the largest tract of tropical forest in Mesoamerica (Conde et al., 2010, 2007). The Mayan Forest is crucial for conservation, 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; Matola et al., 1997; Medellín, 1994; Sanderson et al., 2002). 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 (Conde et al., 2007; de la Torre and Medellín, 2011; García-Anleu et al., 2016; Medellín, 1994; Mendoza and Dirzo, 1999).

Our study area is located in south-eastern Mexico and north-western Guatemala between the coordinates 91°40′W/17°35′N and 90°07′W/15°45′N. This region encompasses part of the Mexican States of Chiapas and Tabasco, and a large portion of the Departments of Petén, Quiche, and Alta Verapaz in Guatemala, and covers an area of approximately 45,000 $km^2$ (Fig. 1). The Mexican section of our study area comprises the Greater Lacandona Ecosystem (GLE) and includes two strictly protected areas (IUCN categories I-IV) according to the IUCN classification (UNEP-WCMC, 2015): Bonampak (48 $km^2$) and Yaxchilán (26 $km^2$); our study area also includes six protected areas with sustainable use of natural resources (IUCN categories V-VI): Montes Azules (3312 $km^2$), Lacantún (619 $km^2$), Chan-kin (122 $km^2$), Naha (38 $km^2$), Metzabok (33 $km^2$), and Cañon del Usumacinta (461 $km^2$). The Guatemalan section includes a large portion of the Mayan Biosphere Reserve, and includes seven strictly protected areas: Laguna del Tigre National Park (2899 $km^2$), Rio Escondido Biotopo (451 $km^2$), Sierra del Lacandón National Park (2028 $km^2$), San Román Biological Reserve (608 $km^2$), El Rosario National Park (110 $km^2$), Dos Pilas Cultural Monument (31 $km^2$), and Laguna Lechuá National Park (143 $km^2$). Additionally, it includes two protected areas with sustainable use of natural resources: the Wildlife Refuges Petexbatún (404 $km^2$) and El Pucté (167 $km^2$).

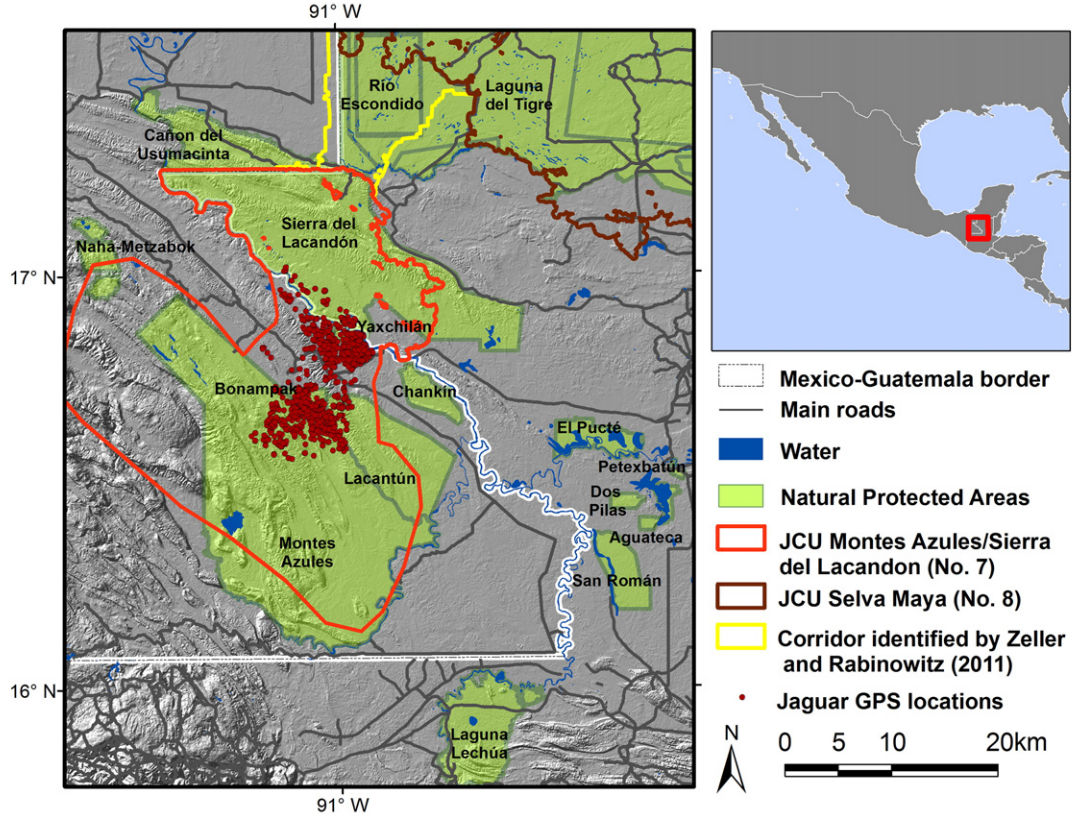


**Fig. 1.** Location of our study area in the Southern Mayan Forest in southern Mexico and northwestern Guatemala. The red points represent the locations of the jaguars tracked in this study.

Our study area encompassed the Selva Maya Jaguar Conservation Unit (No. 155) defined by Sanderson et al. (2002), and the Montes Azules/Sierra del Lacandon (No. 7) and Selva Maya (No. 8) Jaguar Conservation Units defined by Zeller (2007). The dominant vegetation type of this area is tropical rainforest, but flooded forest, flooded savannas, and wetlands are present as well (de la Torre and Medellín, 2011; García-Anleu et al., 2016; Mendoza and Dirzo, 1999). 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.

## 2.2. Research design and data collection

### 2.2.1. Data telemetry

We captured five jaguars using foot snares (see Frank et al., 2003). All capture and handling protocols followed the American Society of Mammalogists' IACUC guidelines (Sikes et al., 2011). Our fieldwork was based in Yaxchilán on the border with Guatemala, and in Bonampak (Fig. 1). 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 ft snares during each trapping day. 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 (4 locations/day), and to send data packets through the ARGOS system every four 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 recovered, when possible, using the locations obtained after their release through the ARGOS system and searching the VHF pulses using a receiver. 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. Mean horizontal error was 5.01 $\pm$ 4.61 m for all the 3D jaguar localizations that we obtained.

### 2.2.2. Landscape variables

We compiled a geospatial dataset using a suite of environmental and anthropogenic variables for our study area (Table 1). Jaguars in the Mayan Forest are restricted mostly to areas of primary forest where they find their natural prey and refuge (Ceballos et al., 2002; Conde et al., 2010; Rabinowitz and Nottingham, 1986). To appraise habitat quality, we used the results from time-series analysis of Landsat images to characterize forest cover with different tree cover density, which ranged from primary forest cover to sites that have been modified by human activity. Specifically, a High Resolution Global Forest map was used (Hansen et al., 2013). This dataset includes the extent of global tree cover, and its loss and gain from 2000 to 2012 at a spatial resolution of 30 m. For forest cover in 2012, tree cover density was related to forest loss and gain to obtain forest cover as a percentage per output grid cell at the Landsat pixel scale. Tree cover density is defined as vegetation higher than 5 m and is expressed as a percentage. Forest loss was defined as a stand-replacement disturbance or the complete removal of tree cover, and forest gain was defined as the inverse of loss, or the establishment of tree canopy from a non-forest state (Hansen et al., 2013).

Given that habitat use and movement by jaguars would 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 pixel using the Focal Statistic tool of ArcGIS 10.2 (ESRI, 2013). This allowed us to obtain an output raster where the value for each output cell was a mean function of the values of all the input cells that were

**Table 1**
Variables used to quantify resource selection of jaguars in response to the heterogeneity of the Southern Mayan Forest landscape.

| Type | Variable name | Abbreviation | Description | Resolution (m) | Units | Data range |
|---|---|---|---|---|---|---|
| Forest cover | Forest Cover 30 m | FCov-30 | Percentage of forest coverage in each pixel of 30 m | 30 | % | 0–0.999 |
| | Forest Cover 240 m | FCov-240 | Percentage of forest coverage 240 m around the pixel | 30 | % | 0–0.999 |
| | Forest Cover 510 m | FCov-510 | Percentage of forest coverage 510 m around the pixel | 30 | % | 0–0.999 |
| Water Runoffs | Distance to water courses | DistW | The minimum distance to the nearest water runoff | 30 | km | 0–9.3 |
| Terrain | Topographic Position Index | TPI | Classification of landscape according the slope position | 30 | – | −116.4–163.7 |
| | Elevation | ELEV | Elevation | 30 | m.a.s.l. | 0–3320 |
| | Shannon | SHANN | Differences of ranges of elevation values within a radius of 8 pixels | 30 | – | 0–5.17 |
| Human | Distance to towns | DistT | The minimum distance to the nearest town | 30 | km | 0–23.3 |
| | Distance to paved roads | DistR | The minimum distance to the nearest paved roads | 30 | km | 0–43.3 |
| | Distance to deforestation edge | DistD | The nearest distance to the deforested patch >1 $km^2$ | 30 | km | 0–29.3 |

in a specified neighborhood around that location. For creating the maps FCov-240 and FCov-510, the original FCov-30 pixel values were used with the focal mean in the 8 × 8 and 17 × 17 windows, respectively, around each sample location.

Because, jaguars are known to use riparian habitats to move through landscapes and use sites with permanent water more frequently (Emmons, 1987; Núñez et al., 2002; Rabinowitz and Nottingham, 1986; Schaller and Crawshaw, 1980), we constructed a raster with the minimum distance to all the main water runoffs (DistW) of our study area using a layer of the hydrological drainage system of the entire study area (Tapia and Nuñez, 2008). Jaguar habitat use and movements are affected by different terrain conditions. For instance, 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 Zeller, 2010; Sunquist and Sunquist, 2009; Zeller et al., 2011). For these reasons, we considered three terrain variables. Using a 30 m digital elevation model, we obtained elevation ranges (ELEV). We created a layer called a topographic position index (TPI) to characterize the slope's position in the terrain and landform (TPI). We estimated the Shannon Index in a neighborhood of eight pixels to evaluate differences in heterogeneity for ruggedness (SHANN). This index incorporated richness and evenness into a single measure, and to calculate it we used three landform classes that we expressed as canyons, slopes, and ridges. In general, higher values reflected more diversity and better balance among unique landform values. Thus, a high index value was achieved by maximizing the number of landforms within the neighborhood and by balancing representation of those landforms (Riley et al., 1999).

Because human activity affects habitat use by jaguars negatively due to disturbance and persecution (Colchero et al., 2011; Conde et al., 2010; Espinosa et al., 2014), we also generated raster layers with minimum distances to towns (DistT) and paved roads (DistR), which we obtained from INEGI (Instituto Nacional de Estadistica e Informatica) for Mexico and IGN-SEGLAPAN (Instituto Geográfico-Secretaria de Planificación y Programación de la Presidencia) for Guatemala. Given that 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), we additionally constructed a raster layer with the minimum distance to the nearest deforested patches >1 $km^2$ (DistD) to evaluate the distances that jaguars use from the boundaries that separated the forest from open modified areas. For all these explanatory variables, we generated raster layers of 30 m of resolution (Table 1).

### 2.3. Analytical methods

#### 2.3.1. Resource selection probability functions (RSPF)

To define jaguar habitat, we calculated RSPFs using the use vs. availability design (Boyce, 2006; Boyce et al., 2002; Lele and Keim, 2006; Manly et al., 2002). RSPFs quantified landscape characteristics used by jaguars relative to those landscape characteristics that were available across the study area (second order of habitat selection - Johnson, 1980). RSPFs were estimated using design II of Manly et al. (2002), and they were constructed through conditional logistic regressions using the logit link (Lele and Keim, 2006). We defined resource units from telemetry data as those used by tracked individuals, and available resource units were identified from random points that we obtained from the minimum convex polygon that enclosed all GPS locations obtained that were buffered by 5 km (Conde et al., 2010). We used the Hawths tools extension for ArcGis 9.3 to generate random points. We tested several used:availability ratios (1:2, 1:4, 1:6, 1:8, 1:10, 1:20, 1:40, and 1:50) to ensure that logistic regression approximated the point process model and that the coefficients converged (Benson, 2013; Northrup et al., 2013). We tested all explanatory variables for multicollinearity using the Pearson's correlation matrix (Dormann et al., 2013). We used the package R 3.1.1 to implement the correlation analysis (R Core Team, 2016). We did not include variables in the same candidate model that were correlated at >0.5. We tested 46 RSPFs with different combinations of explanatory variables (Table A.1), and we tested these models using the log and the logit links to ensure that the exponential model did not outperform the logistic model (Lele, 2009; Lele et al., 2013; Watson et al., 2014). Finally, we tested the number of bootstrap samples needed to ensure stable results, from 99 to 5000 bootstrap samples. For the best RSPF models, we considered independent variables with confidence intervals that did not include 0 to be informative predictors of resource selection. We used the package "ResourceSelection" (Lele et al., 2014) from *R*3.1.1 (R Core Team, 2016) to estimate RSPFs. Then, we used the Akaike Information Criterion (AIC) to identify the best RSPF models based on model parsimony (Burnham and Anderson, 2002). We considered models comparable if ΔAIC was <2.0, and we compared the AIC weights (*wi*) to determine the most appropriate models that described jaguar habitat.

We evaluated the predictive performance of the best RSPF model by dividing the GPS locations randomly into two groups before model development: 80% of the data comprised a "model training" group and the remaining 20% comprised a "model testing" group for validation (Johnson et al., 2006). Additionally, we used 70 different locations where we and other researchers have documented jaguar presence through camera traps within the study area. This database included information on at least 25 jaguars (10 ♀ and 15 ♂) that were recorded from 2007 to 2015. We applied our best model to ArcGIS10.2 using the Raster Calculator Tool (ESRI, 2013) to calculate the probability of selection for each resource unit (30 m pixel). We classified probabilities of selection for each resource unit into 10 bins that ranged from 1 = low to 10 = high. We counted our jaguar evaluation fixes and camera trap locations in each bin to evaluate our model on the assumption that we would find a larger number of jaguar locations in higher probability bins that were normalized by area. We used Spearman correlation coefficients to test the relationship between the bin rank and jaguar locations that were normalized by bin area (Boyce et al., 2002).

*2.3.2. Patches occupied by jaguars*

To identify patches that jaguars occupied in the Southern Mayan Forest, we identified the optimal threshold at which to discriminate habitat from non-habitat by calculating the Receiver Operating Characteristic (ROC) of our best RSPF model (Pearce and Ferrier, 2000). ROC analysis tests a range of probabilities at which each observed localization was assigned correctly and incorrectly over and continuous range of thresholds levels. It then compares these predictive probabilities of the true presences to a data set of pseudo-absences and calculates the proportion of true positives and false positives. The probability at which the proportion of true positives is maximized and the false positives are minimized is selected as the threshold for habitat and non-habitat (Pearce and Ferrier, 2000). We implemented the ROC analysis using the package "pROC" (Robin et al., 2013) from R 3.1.1 (R Core Team, 2016).

We converted the raster data set of habitat suitability into polygons using the ArcGIS10.2, and we calculated the area, perimeter, surface area, perimeter ratios, and the center of each polygon. Given that the minimum forest patch size where jaguars have been recorded by camera traps is 5 $km^2$ in our study area (at GLE), we identified all the patches >5 $km^2$ using a radius of 15 km where jaguar presence has been recorded in articles, theses, technical reports, or book chapters within the last 10 years. We assumed that these polygons were occupied by jaguars, and these polygons were then treated as source habitat patches in our analysis of connectivity.

*2.3.3. Estimating movement models*

To understand how the landscape structure affects jaguar movements, we used step selection functions combined with conditional logistic regression (Fortin et al., 2005; Thurfjell et al., 2014; Ziółkowska et al., 2016). For this analysis, we used only the sequential locations that we obtained every 4.8 h, and for each observed step we calculated its length ($d$) and turning angle ($\alpha$) using the package "adehabitatLT" (Calenge, 2013) 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.

Each observed 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 (Beyer, 2012) to generate the control steps. For each observed and control steps we calculated the exact values of the predictors covariables at the endpoint of steps (Thurfjell et al., 2014; Ziółkowska et al., 2016).

We constructed our movement model with the package "ResourceSelection" (Lele et al., 2014) from R 3.1.1 (R Core Team, 2016) using the log link, which is applicable for step selection functions (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. 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 ΔAIC was <2.0, and we compared the AIC weights ($wi$) to determine the most appropriate models that described jaguar movements. We then mapped the jaguar movement surface by spatially applying our best step selection function across the study area using the Raster Calculator Tool (ESRI, 2013).

*2.3.4. Mapping connectivity among patches*

We integrated our movement model with Circuit Theory to assess the connectivity across the species' occurrence in the Southern Mayan Forest (McRae et al., 2008). Circuit Theory models the dispersal movements that identify high connectivity in areas that have a higher probability of being crossed by random walkers moving from a source to a destination, and several studies have proven that the Circuit Theory approach is a more realistic approximation of dispersal movements than other analysis (Lapoint et al., 2013; McClure et al., 2016). We used the inverse of the movement model that we created through the step selection function surface to generate a resistance surface for the Circuit Theory analysis using reciprocal probability values. With this transformation, we assumed that pixels with higher probability values for step selection afforded lower costs to movement than those pixels with low probability values for step selection (Beier et al., 2008; Zeller et al., 2012). We used Circuitscape version 4.0 to model the connectivity between the habitat patches using the pairwise scenario in which the analysis iterated all pairs in a focal node (McRae et al., 2013).

We generated a cumulative current map between each habitat patch (focal nodes) to identify the areas of high connectivity for jaguars in our study area landscape. Each current map are continuous grid cell values of current flow, where current values are indicative of predicted movement of random walkers. Current maps are useful for visualizing bottleneck movements, barriers, and connectivity across the landscape, but they can be difficult to interpret objectively (Lapoint et al., 2013; Rudnick et al., 2012). Therefore, we identified potential corridors visually from current maps and extracted the cells with higher current values, which suggested funneled jaguar movements. Because, very little is known about the dispersal ability of jaguars (Quigley and Crawshaw, 2002), we only considered as potential corridors those that connected habitat patches (focal nodes) that did not exceed the distance threshold of 15 km between them (Euclidian distance). This threshold value was established on the basis of the maximum distance traveled by the jaguars tracked within their home range (Euclidian distance) in a time lapse interval of 72 h (15,710 m).

*2.3.5. Categorization of habitat patches and corridors*

We used the following variables to categorize habitat patches: 1) patch size, 2) protection status, and 3) isolation. We classified habitat patches according to their size as patches that could maintain a viable population, as breeding patches, and as stepping-stone patches (Beier et al., 2008). We calculated the smallest continuous area to maintain a viable population of 50 individuals (Morato et al., 2014; Rodríguez-Soto et al., 2011). If we assume a mean density of three jaguars for each 100 $km^2$ in GLE (de la Torre and Medellín, 2011), the minimum continuous area to maintain 50 individuals would be 1666 $km^2$. We assumed that breeding patches were areas sufficiently large enough to support a breeding event, and the minimum size of breeding patches was determined by the mean annual home range area of female jaguars in the study area. The mean home range size for female jaguars that were tracked for one year at GLE estimated using the 95% fixed kernel was $181.4 \pm 4.0$ $km^2$ (de la Torre et al., under review). Habitat patches smaller than 180 $km^2$, which cannot hold resident female jaguars but which are important for jaguar movements throughout the landscape, were classified as stepping-stone patches. The level of protection of each habitat patch was determined by the percentage of protected area within each habitat patch; this percentage was estimated using the WDPA database of protected areas of the world including the strictly protected areas and the sustainable use protected areas according to the IUCN categories of protected areas (UNEP-WCMC, 2015). Additionally, we estimated the area protected by Payments for Ecosystem Services (PES) in each habitat patch. The PES is a conservation scheme used by the Mexican Government that provides economic compensation to local communities for conserving their land with natural forest. Habitat patches were classified according to their percentage of protection as *protected* (>75%), *partially protected* (>25% to <75%), and *unprotected* (<25%). Additionally, we estimated the total minimum distance from each habitat patch to each of the nearest five habitat patches to evaluate their isolation, and we classified them as *low isolation* (3.9 km), *medium isolation* (>3.9 km to <10 km), or *high isolation* (>10 km). These thresholds distance values were defined according with the maximum Euclidian distances traveled by jaguars between the time lapse intervals of 4.8 h (3960 m) and 24 h (10,095 m).

We used the following variables to categorize corridors: 1) total area of jaguar habitat that was connected by a corridor; 2) protection status; 3) percentage of primary forest within each corridor's boundary; and 4) number of paved roads crossed by corridors. Corridors that connected areas >1666 km$^2$ were classified as connecting viable populations, corridors that connected a total area between >180 km$^2$ and <1666 km$^2$ were classified as connecting breeding patch, and corridors that connected a total area < 180 km$^2$ were classified as connecting stepping stone patches. We estimated the percentage of area of each corridor that was included within the protected areas in Mexico and Guatemala, and in PES. Corridors with >75% of their total area protected were designated as *protected*, corridors with 25–75% of their total area protected were designated as *medium protected*, and corridors with <25% of their total area protected were designated as *unprotected*. We classified the priority management actions for each corridor according to the total percentage of primary forest included within the corridor's boundary. Corridors that retained >75% of primary forest were designated as *conservation*, corridors that retained >25 and <75% of primary forest were designated as *conservation and habitat restoration*, and corridors that retained <25% primary forest were designated as *restoration*. Because large felids avoid areas near paved roads (Colchero et al., 2011; Conde et al., 2010; Dickson and Beier, 2006; White et al., 2015), and individuals may be killed in vehicle collisions (Gubbi et al., 2014; Kerley et al., 2002; Schwab and Zandbergen, 2011), we counted the number of putative corridors that crossed segments of paved roads in the Southern Mayan Forest landscape to evaluate where the paved roads potentially interrupted connectivity.

We defined three levels of scores to prioritize the corridors according to these four variables. The highest level for each criterion was assigned the score of "3", the medium level was assigned the score of "2", and the lowest level was assigned the score of "1". Therefore, each corridor could get a maximum score of "12" and a minimum score of "4" (Table 2). Corridors with a high priority (HP) were defined as those with a final score ≥ 10, which is equivalent to having more than three variables with the highest level score. Corridors with a medium priority (MP) were defined as those that obtained a final score ≥ 7 to ≤9, which is equivalent to having more than one variable with the highest level score. Corridors with final scores ≤6, which is equivalent to having only one variable with the maximum, were defined as those with a low priority (LP).

## 3. Results

### 3.1. Jaguar habitat

A total of 1288 GPS fixes that were obtained from five jaguars (2 ♂ and 3 ♀) was used to develop the habitat model for jaguars in the Southern Mayan Forest. Sensitivity analysis indicated that our results stabilized prior to the 1:50 use:availability ratio with 5000 bootstrapped samples. Examination of the likelihoods and AIC values for our 46 models indicated that our best model included the percentage of forest cover (FCov-30 m), the nearest distance to deforested patches that were >1 km$^2$ (DistD), the TPI and elevation (ELEV) as the variables associated most strongly with resource selection by jaguars (Table 2). This model had a ΔAIC value of 15.63 from the second best ranked model ($wi$ = 1), all the variables were informative, and the 95% CI did not overlap 0 (Table 3; Appendix A).

**Table 3**
Estimated coefficients (β), standard errors (SE), 95% confidence intervals (95% CI), z values (z), and *P* values (P) for the best Resource Selection Probability Function for habitat use of jaguars in the Southern Mayan Forest. We estimated the coefficients and the standard errors for percentage of forest cover (FCov-30), minimum distance to deforested patches >100 ha (Dist-D), the Topographic Position Index (TPI), and the Elevation (ELEV) by bootstrapping (B = 5000).

| Covariate | β | SE | 95% CI | z | P |
|---|---|---|---|---|---|
| Intercept | −0.8474 | 0.3044 | −1.4630 to −0.2749 | −2.784 | <0.001** |
| FCov-30 | 0.0160 | 0.0031 | 0.0110 to 0.0228 | 5.075 | <0.0001*** |
| DistD | 0.4025 | 0.0577 | 0.3244 to 0.5435 | 6.971 | <0.0001*** |
| TPI | 0.0582 | 0.0115 | 0.0397 to 0.0857 | 5.028 | <0.0001*** |
| ELEV | −0.0074 | 0.0006 | −0.0091 to −0.0065 | −10.829 | <0.0001*** |

Area-adjusted frequencies displayed positive rank values across the RSPF bins (Appendix B), and predictive accuracy of our model was very precise using our "model testing" data ($R^2 = 0.93$, $P < 0.0001$), the data for the 70 localities with camera traps that corresponded to the 25 individuals recorded in the study area ($R^2 = 0.94$, $P < 0.0001$), and the combined data ($R^2 = 0.94$, $P < 0.0001$).

Area under the ROC curve was 0.79 (±0.68, 0.89) for true positives and 0.47 (±0.36, 0.57) for false positives, which indicated a reasonable discrimination at a probability threshold of occurrence of 0.65 (±0.54, 0.72). Suitable habitat for jaguars in the Southern Mayan Forest region encompassed 11,650 km$^2$ (the upper 0.65 probability of resource selection). However, we only identified 27 polygons >5 km$^2$ where jaguar presence had been recorded recently (Table 4, Fig. 2). These polygons encompassed an area of 9983 km$^2$ and were situated in seven different sub-regions (Table 4).

### 3.2. Jaguar corridors

We analyzed a total of 452 movement steps, of which 43.5% were classified as active. Our analysis revealed that the best step selection functions included the forest cover in a neighborhood of 240 m (FCov-240), and that the TPI and elevation (ELEV) were the variables associated most strongly with movement probability by jaguars (Table 5). All the variables were informative, and the 95% CI did not overlap 0 (Table 5). However, this model only had a ΔAIC value of 0.54 for the second best ranked model ($wi$ = 0.35) (Appendix C). The second ranked model included the variables forest cover in a neighborhood of 240 m (FCov-240), the nearest distance to deforested patches that were >1 km$^2$ (DistD), TPI, and elevation (ELEV), but the variable nearest distance to deforested patches was not informative because the 95% CI overlapped 0 ($wi$ = 0.35). The third best ranked model was very similar to our best model ($wi$ = 0.24), and included the forest cover in

**Table 2**
Variables considered for prioritizing the corridors. We defined three thresholds for the four variables according to different thresholds values. In the corridors with higher level of a particular variable, we assigned the value of 4, to the medium levels the value of 3, and to the lowest level the value of 2. Corridors that had higher total scores were designed as higher priority, according to our classification.

| Variable | Units | Maximum (3) | Medium (2) | Low (1) |
|---|---|---|---|---|
| 1) Total area of jaguar habitat that was linked | km$^2$ | >1666 | 180 to <1666 | <180 |
| 2) Protection status | % protected within each corridor | <25 | 25 to75 | >75 |
| 3) Primary forest within each corridor's boundary | Percentage of primary forest in each corridor | >75 | 25 to75 | <25 |
| 4) Paved roads that interrupt the connectivity. | Number of paved roads crossed by each corridor | >2 | 1 | 0 |

**Table 4**
Jaguar habitat patches in the Southern Mayan Forest and aspects considered for their categorization: 1) Patch size (V = viable habitat patch; B = breeding habitat patch; S = stepping-stone habitat patch); 2) protection status (PR = protected; PP = partially protected; UN = unprotected); and 3) isolation (H = high; M = medium; L = low). Additionally, for each habitat patch we included the references for jaguar occupancy.

| ID | Sub-region | Name | Area ($km^2$) | Patch size | Protected by natural reserves (%) | Protected by PES (%) | Protection | Mean distance to 5 nearest habitat patches (km) | Isolation | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| MF-01 | Mayan Forest | Mayan Forest | 5159.03 | B | 82.8 | 0.00 | PR | 20.94 ± 16.89 | H | a,b |
| SL-01 | Sierra del Lacandón | Sierra del Lacandón | 801.52 | B | 95.9 | 0.00 | PR | 5.21 ± 3.32 | M | a,b |
| TA-01 | Tabasco | Benito Juarez | 100.77 | S | 9.2 | 0.25 | UN | 12.48 ± 9.03 | H | c |
| TA-02 | Tabasco | Niños Heroes | 71.50 | S | 0.9 | 0.00 | UN | 16.48 ± 10.44 | H | c |
| TA-03 | Tabasco | Corregidora | 39.19 | S | 0.6 | 0.00 | UN | 18.09 ± 13.14 | H | c |
| TA-04 | Tabasco | Francisco I. Madero | 102.29 | S | 0.0 | 0.00 | UN | 19.62 ± 14.61 | H | c |
| GLE-01 | Lacandona | Montes Azules | 2389.72 | V | 93.9 | 1.64 | PR | 3.17 ± 1.89 | L | e,f |
| GLE-02 | Lacandona | Yachilán-Cojolita | 299.25 | B | 7.2 | 7.47 | UN | 8.95 ± 10.19 | M | e,f |
| GLE-03 | Lacandona | Chankin | 281.01 | B | 40.8 | 0.00 | PP | 3.14 ± 3.52 | L | d |
| MC-01 | Lacandona | Benito Juarez | 30.55 | S | 0.0 | 8.94 | UN | 8.85 ± 2.27 | M | d,g |
| MC-02 | Lacandona | Emiliano Zapata | 21.95 | S | 0.0 | 11.50 | UN | 12.02 ± 6.14 | H | d,g |
| MC-03 | Lacandona | Quetzalcoaltl | 10.55 | S | 0.0 | 0.03 | UN | 15.08 ± 9.40 | H | d,g |
| MC-04 | Lacandona | Arroyo Delicias | 76.40 | S | 0.0 | 11.86 | UN | 9.93 ± 5.47 | M | d,g |
| MC-05 | Lacandona | Galacia | 19.39 | S | 0.0 | 93.98 | PR | 12.06 ± 7.50 | H | d,g |
| MC-06 | Lacandona | Chajul | 12.08 | S | 0.0 | 66.88 | PP | 10.25 ± 8.06 | H | d,g |
| SR-01 | San Roman | El Chorro | 15.97 | S | 0.0 | 0.00 | UN | 9.17 ± 5.11 | M | a, b |
| SR-02 | San Roman | El Manantial | 7.37 | S | 0.0 | 0.00 | UN | 7.92 ± 3.66 | M | a, b |
| SR-03 | San Roman | Gancho de Fierro | 10.59 | S | 0.0 | 0.00 | UN | 6.54 ± 4.21 | M | d |
| SR-04 | San Roman | El Pucte 1 | 15.67 | S | 79.5 | 0.00 | PR | 6.06 ± 4.32 | M | a, b |
| SR-05 | San Roman | El Pucte 2 | 128.30 | S | 54.0 | 0.00 | PP | 9.27 ± 6.74 | M | a, b |
| SR-06 | San Roman | Petexbatín 1 | 101.26 | S | 22.4 | 0.00 | UN | 5.43 ± 2.92 | M | a, b |
| SR-07 | San Roman | Petexbatún 2 | 8.79 | S | 65.5 | 0.00 | PP | 16.87 ± 9.62 | H | a, b |
| SR-08 | San Roman | San Roman | 37.77 | S | 64.4 | 0.00 | PP | 12.85 ± 4.02 | H | h,i |
| LL-01 | Ixcán | Cuarto Pueblo 1 | 15.15 | S | 0.0 | 0.00 | UN | 11.99 ± 7.90 | H | h,i |
| LL-02 | Ixcán | Cuarto Pueblo 2 | 12.54 | S | 0.0 | 0.00 | UN | 10.71 ± 4.14 | H | h,i |
| LL-03 | Ixcán | Santa Maria Tzeja | 115.36 | S | 0.0 | 0.00 | UN | 17.54 ± 5.66 | H | h,i |
| LL-04 | Ixcán | Laguna Lechúa | 102.38 | S | 96.1 | 0.00 | PR | 21.34 ± 4.30 | H | h,i |

[a]McNab and Polisar (2002); [b]García-Anleu et al. (2016); [c]Hidalgo-Mihart et al. (2015); [d]Unpublised data of the first author; [e]de la Torre (2009); [f]de la Torre and Medellín (2011); [g]Falconi-Briones (2011); [h]Novack et al. (2003); [i]Hermes-Calderón (2004).

a neighborhood of 510 m (FCov-510), TPI, and elevation (ELEV). For these reasons, we used the first ranked model to construct the resistance surface for the connectivity analysis.

We identified 50 potential corridors using Circuit Theory analysis to design a connectivity strategy for jaguar populations in the Southern Mayan Forest (Fig. 3; Table 6; Appendix D). These corridors would

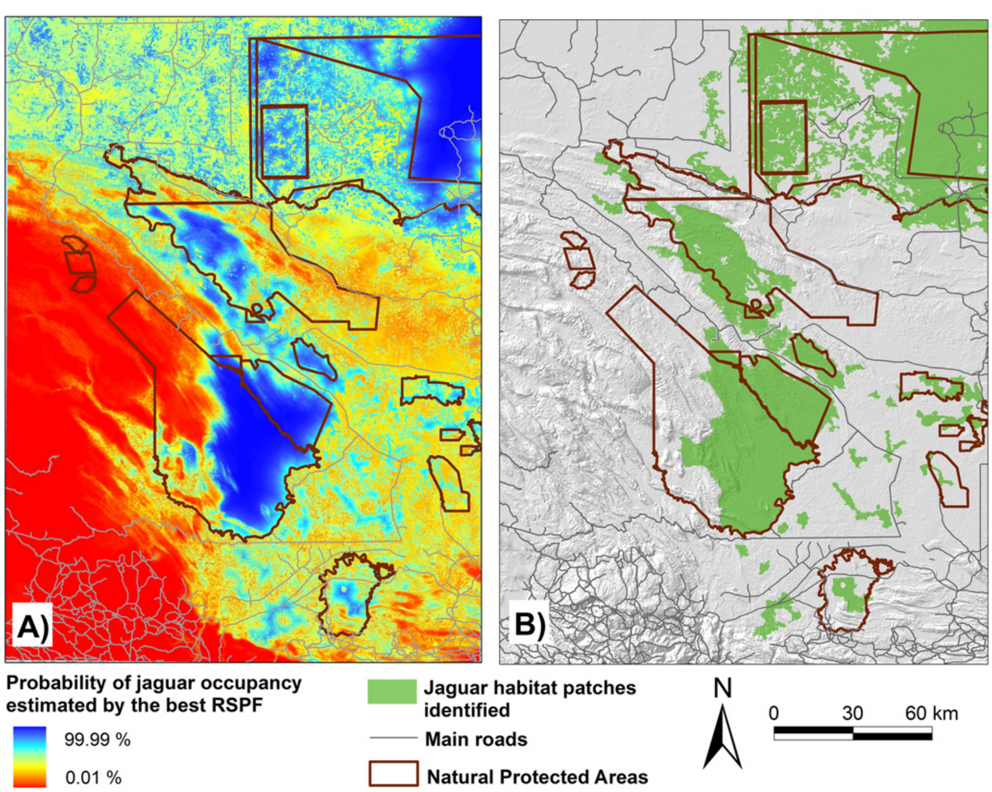


**Fig. 2.** Probability of jaguar occupancy in the Southern Mayan Forest landscape and habitat patches (upper 0.65 of jaguar occupancy probability) identified with occurrence that was documented in the last 10 years.

**Table 5**
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. 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).

| 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*** |

allow for connectivity between the 27 habitats patches identified previously.

### 3.3. Categorization of habitat patches and corridors

We identified only two habitat patches with viable populations, which were the Montes Azules Biosphere Reserve in GLE, Chiapas, Mexico (2389 $km^2$) and the Mayan Biosphere Reserve in Guatemala (5159 $km^2$). We identified three breeding patches with areas that ranged from 281 to 801 $km^2$, and 22 stepping-stone patches with areas that ranged from 7 to 128 $km^2$ (Fig. 4). The total percentage of area that was protected within habitat patches was 77%. Viable population patches were almost completely in protected areas in Mexico and Guatemala, and these habitat patches combined encompassed 65% of the total area protected among all the habitat patches (Table 4). The only breeding patch that was protected was Sierra del Lacandon in Guatemala. Most of the stepping-stones patches were unprotected, with the exception of three habitat patches that were protected and four patches that were partially in protected areas and under PES conservation schemes in the Marques de Colmillas sub-region (Table 4).

Habitat patches with a low degree of isolation were the viable population Montes Azules Biosphere and the breeding patch Chan-kin. Most of the habitat patches that comprised the San Roman sub-region were classified as having a medium degree of isolation. Habitat patches in the Tabasco, Marques de Colmillas, and Ixcán sub-regions were the most isolated patches (Table 4). Additionally, the Mayan Biosphere Reserve viable population was classified as having a high degree of isolation.

**Table 6**
Variables considered for categorization and prioritization of corridors and the number of corridors based on their categorization.

| | | | |
|---|---|---|---|
| Area of jaguar habitat linked | Viable population | Breeding patch | Stepping stone patch |
| | 19 | 21 | 16 |
| Level of protection of corridors | Protected | Partially protected | Unprotected |
| | 4 | 10 | 36 |
| Priority managements actions for corridors | Conservation | Conservation & Restoration | Restoration |
| | 3 | 40 | 7 |
| Number of paved roads that corridors cross | ≥2 | 1 | 0 |
| | 12 | 12 | 26 |
| Corridor priority | High | Medium | Low |
| | 6 | 36 | 8 |

According to our evaluation of priorities among corridors, we categorized six corridors of high priority that connected the largest habitat patches, and 36 and eight corridors of medium and low priority, respectively (Table 5; Appendix E). Most of the corridors that we identified were unprotected or only protected partially. Only a few corridors that were located in the GLE and Marques de Comillas sub-regions were protected partially by PES conservation schemes (Table 5). Our analysis revealed that most corridors were not covered completely with forest (Table 5). Finally, we identified 24 corridors that crossed paved roads 1–4 times.

## 4. Discussion

### 4.1. Jaguar habitat use and movements

We used empirical models to identify suitable habitat and functional corridors for jaguars to design a conservation strategy for the species.

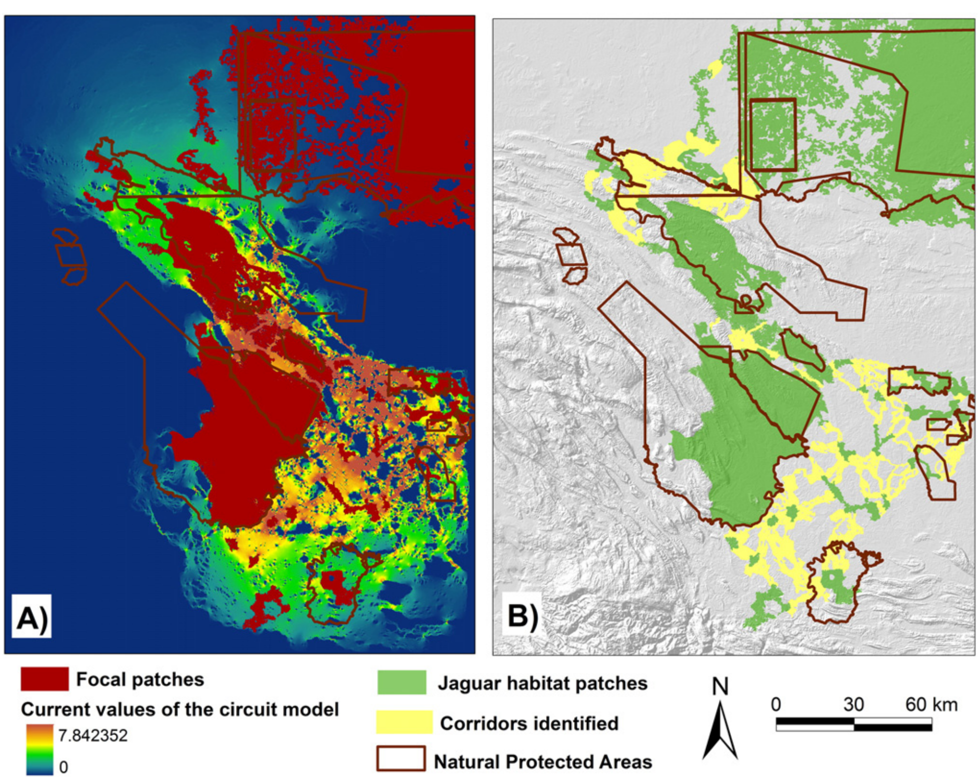


**Fig. 3.** Current map output from Circuit Theory analysis and corridors identified to link all the jaguar habitat patches.

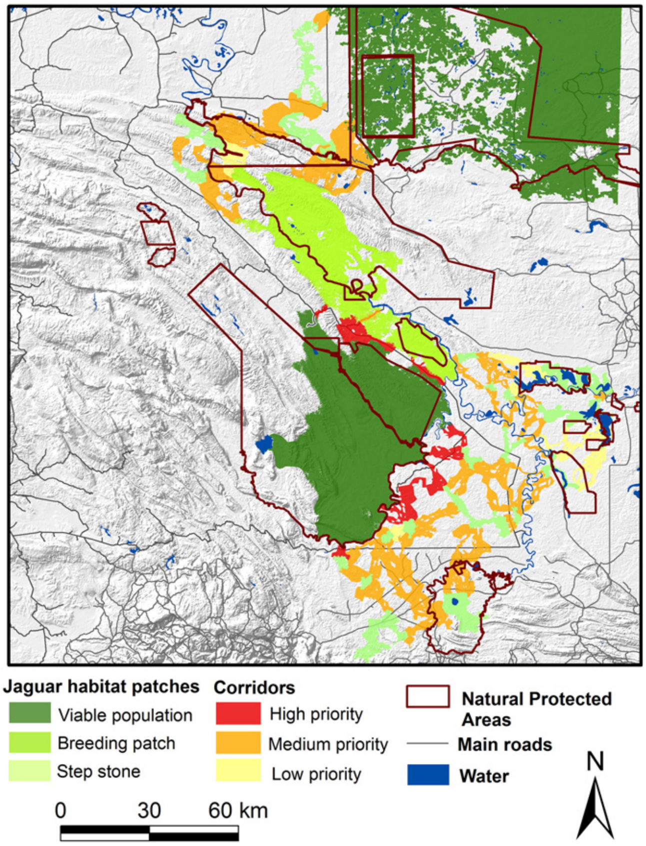


**Fig. 4.** Habitat patches and corridors for jaguars in the Southern Mayan Forest.

This is the first study to propose corridors for jaguars that integrates landscape characteristics with habitat requirements and movement behavior of the species (Morato et al., 2014; Rabinowitz and Zeller, 2010; Rodríguez-Soto et al., 2011). Our results showed that the landscape variables that best describe habitat use and movements of jaguars were similar. We propose that suitable habitat for the species in the Southern Mayan Forest region is maintained in large areas of primary forest, and located at longer distances from deforested patches with relatively gentle topography. On the other hand, functional connectivity for jaguars existed through areas that included forest cover in the surrounding area within 240 m, and through areas with moderate to medium slopes or through flat valleys.

These results supported our predictions that jaguar habitat use is positively associated with the best preserved sites in our study area. Although jaguars do not use primary forest exclusively, they preferred areas with a high percentage of forest cover in contrast to modified environments that were associated with human activities. Large areas with primary forest provide prey availability, forest cover for stalking prey, and refuge for rearing cubs (Ceballos et al., 2002; Conde et al., 2010; Crawshaw and Quigley, 1991; Cullen et al., 2013; Foster et al., 2010; Rabinowitz and Nottingham, 1986). Furthermore, our results indicated an edge effect in habitat use by jaguars. Jaguars avoided using areas that were located at nearby sites of cleared areas, because the probability of use increased as the distance from deforested parches that were >1 km$^2$ increased. All deforested patches >1 km$^2$ in our study area were associated with human activities, and these included cropland, open pastures for livestock, secondary forest, and sites near roads and towns. Theses human activities affected the spatial distribution of jaguars by modifying the surrounding natural landscape, which reduced the abundance of potential prey species and disrupted jaguar hunting in nearby sites (Carroll and Miquelle, 2006; Colchero et al., 2011; Conde et al., 2010; Escamilla et al., 2000; Espinosa et al., 2014; Foster et al., 2010; Linkie et al., 2006; Takahata et al., 2014; Woodroffe, 2000). Human activities not only had an impact at the local scale, but also at the landscape scale, which could limit the range of jaguars in the Southern Mayan Forest (Naves et al., 2003; Woodroffe, 2000).

The TPI and elevation also were included in our best habitat model. Positive values for TPI were associated with mountain ridges and negative values were associated with valleys (Weiss, 2001). This variable had a positive coefficient, which indicated that jaguars were associated with upper and middle slopes of mountain ranges. However, elevation had a negative coefficient, which suggested that jaguars used higher elevation sites infrequently, a result that was similar to other studies where the probability of detection of jaguars was higher in low elevation zones (Zeller et al., 2011). Jaguars have been associated frequently with lowland areas, although there are records of this species at altitudes as high as 2000 m.a.s.l. (Sunquist and Sunquist, 2009). GPS locations of jaguars tracked in this study were 100–950 m.a.s.l., but elevation of the random locations used in the RSPF models were 100–1500 m.a.s.l. This suggested that jaguars avoided sites at higher elevations in the Southern Mayan Forest landscape.

The probability of movement of jaguars in the Southern Mayan Forest also was positively associated with a high percentage of forest cover (Colchero et al., 2011). However, our results suggested that jaguar movements were facilitated in areas of surrounding forest in a neighborhood of 240 m. This finding has important implications for the design of corridors focused on jaguars, and suggested that the minimal width at which corridors could be functional for jaguars is 240 m. This result is similar to studies focused on other species of large cats, which suggested that corridors ≥400 m wide were functional for dispersal (Beier, 1995, 1993). Furthermore, 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 (Dickson et al., 2005), especially if the flat areas had been cleared (Morato et al., 2014). However, the probability of movement by jaguars decreased with elevation, which indicated that jaguars avoided moving through the ridge tops of mountain ranges. This suggested that movements of jaguars would be hampered by mountain ranges at higher altitudes (Rabinowitz and Zeller, 2010; Zeller et al., 2011).

We recognize that a caveat in our habitat and movement models is that the GPS records used to fit the RSPFs and the step selection functions come only from 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, and we are inferring habitat availability and connectivity on a much larger scale. But, the extrapolation of these models is justified because the biophysical and socioeconomic conditions are very similar in all the landscapes. For instance, most our study area is represented by lowland areas that used to be covered with tropical rainforest, and the main human activities are similar throughout the landscape (Conde et al., 2010, 2007). However, it is necessary to improve the knowledge of jaguar occupancy in forested areas located at higher altitudes in the Mayan Forest region to improve our models, because our data probably are only limited to the lowland areas of this region. Another caveat is that jaguars, and other species of large cats, are territorial animals, and their movements are not only influenced by environmental variables, but also by their land tenure and the location of their conspecifics territories (Cavalcanti and Gese, 2009; Crawshaw and Quigley, 1991; Rabinowitz and Nottingham, 1986; Seidensticker et al., 1973). Moreover, the movement of jaguars tracked in this study did not necessarily represent the dispersal movement of jaguars, because all animals tracked were mature individuals with established home ranges. For these reasons, the movement pattern of jaguars tracked in this study could be describing only the ordinary movement patterns of jaguars, and not dispersal, when they were moving throughout their home ranges.

### 4.2. Priorities for jaguar habitat and corridors in the Southern Mayan Forest

We identified 27 habitat patches and 50 corridors to establish a conservation strategy for the species in Southern Mayan Forest. Based on the categorization of habitat patches and corridors, we established the priorities for this fragmented landscape. Two habitat patches of the Southern Mayan Forest contained viable jaguar populations, and these habitat patches should be the core for this species' conservation policy and practice in the region. Fortunately, most of the surfaces covered by these habitat patches are protected by nature reserve systems of Mexico and Guatemala. However, there are some gaps in protection of key habitats for jaguars. For instance, habitat patches in Chan-kin and Yaxchilán-Cojolita are only protected partially and unprotected, respectively (Table 4). These two breeding patches jointly provided 580 km$^2$ of suitable habitat for the species and they are crucial for maintaining the linkage across the entire landscape. The Yaxchilán-Cojolita patch is only separated from the Sierra del Lacandón patch by the Usumacinta river, and we documented that two GPS-tracked jaguars repeatedly crossed this river to Guatemala precisely through the forested areas of this unprotected habitat patch. If deforestation and human colonization increase in these areas, connectivity could be compromised.

Habitat patches located in the Tabasco and Ixcan sub-regions are the most threatened, because they are unprotected and isolated (Table 4). Further, potential corridors that potentially link these habitat patches are unprotected as well, and they require habitat restoration to ensure their functionality. Under the accelerated scheme of human development in this region, if these habitat patches are not protected and the corridors for these habitat patches are not implemented, they could disappear in the future along with any resident jaguars, thus further disrupting population connectivity in the region.

Most of the stepping-stone habitat patches that we identified were unprotected completely. The maintenance of these stepping-stone patches is vital and should be integral to achieving the linkage of the jaguar population in the Southern Mayan Forest. Although relatively small patches of habitat might not normally support resident jaguars, these areas are important, because individuals can rest and feed in them, and their existence facilitates the dispersion of jaguars to larger habitat parches (Rabinowitz and Zeller, 2010; Schadt et al., 2002; Söndgerath and Schröder, 2002). Actually, we have recorded several individuals with camera traps in the last five years, including two females with cubs, using the smaller stepping-stone patches (12 km$^2$) in the Marques de Comillas sub-region (unpublished data of the first author). However, reducing the threats to jaguars within the stepping-stone patches is crucial to ensure their functionality and integrity. Most of these habitat patches are surrounded by livestock pastures, and jaguars are poached frequently in these areas by ranchers in retaliation for depredation of domestic cattle (Peña-Mondragón et al., 2016). If jaguar poaching is not eradicated, the stepping-stone patches will continue to act as ecological traps for jaguars (Balme et al., 2010; Delibes et al., 2001).

Between high priority corridors are those that connect Montes Azules habitat patch with Chan-kin and Yaxchilán-Sierra la Cojolita habitat patches (Fig. 4). However, the paved road, MEX-307, interrupts the connectivity between these habitat patches and threatens the integrity of the Southern Mayan landscape. The negative effects of roads on jaguars and other large mammals include increased mortality by collisions, facilitating access to prime jaguar habitat by humans, and accelerating habitat fragmentation (Colchero et al., 2011; Conde et al., 2010; Espinosa et al., 2014; Gaines et al., 2005; Kerley et al., 2002; Linkie et al., 2006; Takahata et al., 2014). In this study, two female jaguars delineated the boundary of their home range areas precisely where road MEX-307 passed, and we documented that two of our jaguars (a male and a female) crossed this road repeatedly. Furthermore, we have documented two jaguar collisions on this road in the last five years.

### 4.3. Conservation and management implications

In this paper we introduced a spatially explicit, specific proposal to maintain connectivity for the jaguar population in the Southern Mayan Forest, and this information should serve as a guide to conservation agencies and decision-makers that are working in this region. Agencies such the National Commission of Protected Areas (CONANP-Mexico), the National Commission for Knowledge and Use of Biodiversity (CONABIO-Mexico) in Mexico, and the National Council of Protected Areas (CONAP-Guatemala), Defensores de la Naturaleza and Wildlife Conservation Society-Guatemala should incorporate this information into their landscape planning for the Mayan Forest to ensure the long-term conservation of jaguar habitat and corridors. By lending this information to programs of sustainable development that is aimed at local communities that share their territory with jaguars, we would be in position to ensure the permanence of the largest jaguar population in Central America.

One urgent action should be to complete and secure the protection of the Chan-kin and Yaxchilán-Cojolita habitat patches. Most of the unprotected jaguar habitat in this area encompassed the Sierra La Cojolita communal reserve. Although this reserve has been set aside by the Lacandon Indigenous Community, significant hunting and incipient deforestation threaten the integrity of this crucial area. This communal reserve should be incorporated into the regional jaguar conservation strategy in the short term as part of a management plan in conjunction with the local communities to guarantee its long-term persistence.

Our analysis suggests that the PES conservation scheme plays a crucial role in protecting jaguar habitat and corridors in the Mayan Forest landscape. The lands owned by local communities that are receiving this compensation are acting as stepping-stones or corridors for jaguars in this landscape. Including more jaguar habitat in the PES scheme would increase the chances of conserving linkage areas for jaguars over the long term, and this tool should be implemented as a conservation alternative across the landscape. This conservation scheme has been implemented only in the Marques de Comillas and GLE sub-regions, but it could also be implemented in habitat patches and corridors in the Tabasco sub-region in Mexico. In Guatemala, there is a similar scheme known as Payment for Forest Conservation, which could also be implemented in the Ixcan and San Roman sub-regions.

Although most of the corridors that we identified in this analysis still hold great surfaces of primary forest, the total percentage of area covered with primary forest within all corridors is only 52.3%. Additionally, only three corridors retained primary forest on >75% of their surface, and most corridors retained primary forest ($n = 40$) on 25–75% of their surface (mean of $51.4 \pm 18.6$). This implies that management actions for most corridors should include the conservation of primary forest and the restoration of original vegetation in cleared areas. According to our analysis, to maintain all the corridors with ≥75% of primary forest it would be necessary to restore a surface of at least 594 km$^2$, which would be expensive initially, but decisive for the future of the species in the region.

It is essential to work with local ranchers to reduce the risk of predation of jaguars on domestic cattle and to ensure that local ranchers receive compensation for livestock losses by jaguar attacks (Peña-Mondragón et al., 2016). All corridors that crossed paved roads in the Southern Mayan Forest should include mitigation measures to avoid wildlife collisions. Mitigation measures to reduce collisions should include the construction of wildlife crossings, and installation of road signs and speed bumps. Additionally, we advocate a moratorium on the extension and construction of new paved roads in this region, because this construction compromises the movement of jaguars and other wildlife among the different habitat patches.

Finally, the jaguar is considered a flagship species in Latin America, and many conservation programs use the jaguar as an umbrella species (Medellín et al., 2016, 2002; Rabinowitz and Zeller, 2010; Sanderson et al., 2002; Thornton et al., 2015). The use of umbrella species is an attractive conservation tool, because it maximizes the benefits of conservation by an optimal investment of resources and research efforts (Branton and Richardson, 2011; Fleishman et al., 2001; Thornton et al., 2015). Given that jaguars require extensive areas of primary forest to maintain breeding populations, and that jaguars avoid fully modified areas, this setting provides a robust framework to use this species as an umbrella to develop conservation plans at the Mayan Forest landscape scale. The information provided in this study provides critical elements for generating a robust conservation plan for this entire region, because conservation measures that will be implemented to protect jaguars should ensure the persistence of most biological diversity of this ecosystem, which is already recognized as the most biodiversity-rich land area of Mexico (Medellín, 1994).

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