Validation of the Calakmul–Laguna de Terminos corridor for jaguars *Panthera onca* in south-eastern Mexico

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Abstract The fragmentation of jaguar *Panthera onca* populations as a result of habitat loss is considered to be one of the main challenges for the conservation of the species. Corridors have been proposed as a means of maintaining connectivity and the long-term viability of jaguar populations. The corridor that connects the jaguar conservation units of Calakmul and Laguna de Terminos in Mexico has been considered to be a link for the movement of individuals between these units but its functionality had yet to be verified. During 2012–2014 we divided the corridor into four sections, where we used camera traps to verify the corridor's functionality. We obtained 106 photographs of jaguars, proving the presence of jaguars (including resident jaguars and females) in three of the corridor sections. We did not record any individuals in more than one section of the corridor. The presence of several resident jaguars and females throughout the corridor suggests that portions of the corridor should be incorporated into the Calakmul and Laguna de Terminos jaguar conservation units. Nevertheless, to confirm that the corridor is fully functional it is necessary to obtain evidence of movement of jaguars among the various sections of the corridor. Our results suggest that the area should be included in regional conservation strategies.

Keywords Campeche, Chenkan, conservation, jaguar conservation unit, Mesoamerican Biological Corridor, Mexico, *Panthera onca*

Introduction

The jaguar *Panthera onca*, similar to other large predators, is considered to be a key species because of its role in maintaining ecosystem structure (Ritchie et al., 2012), although this important biological function has not been sufficiently valued. The jaguar's range of distribution had declined by 54% by 2002 (Sanderson et al., 2002), and this declining trend has continued (Caso et al., 2008), mostly as a result of habitat destruction, and hunting in retaliation for predation on cattle and domestic animals. In Mexico it is estimated that only 16% of land area now has potential habitat for the species (Rodríguez-Soto et al., 2011). This potential habitat is mainly found in jaguar conservation units (areas with a stable prey community, known or believed to contain a resident population of at least 50 breeding individuals; Sanderson et al., 2002) located in the southern and eastern portions of the Yucatán Peninsula, in areas such as Calakmul (which includes the Maya Reserve in Guatemala and Río Negro in Belize) and Sian Káan (Rabinowitz & Zeller, 2010; Rodríguez-Soto et al., 2011). Smaller units have also been identified, with the potential to maintain jaguar populations in the long term, including in Yum-Balam and Petenes and on the west coast of Campeche (Fig. 1; Rabinowitz & Zeller, 2010).

The isolation of jaguar populations as a result of fragmentation and habitat loss is one of the most serious threats to the long-term survival of the species (Rabinowitz & Zeller, 2010). The accumulated effects of isolation (genetic drift, inbreeding, deleterious effects on sperm production and fertility, and low juvenile survival) have the potential to reduce fitness and increase the risk of extinction of these isolated populations (Frankham, 2005). Given this situation, corridors have been considered to be a valuable conservation tool to promote movement between patches of adequate habitat, and provide an opportunity for mitigating the negative effects of isolation (Hilty et al., 2006).

Biological corridors have been proposed as one of the most important strategies for the long-term conservation of the jaguar because of the fragmentation of jaguar populations (Rabinowitz & Zeller, 2010; Zeller et al., 2011; Rodríguez-Soto et al., 2013). To identify areas where biological corridors could potentially connect jaguar populations at the continental level, Rabinowitz & Zeller (2010) modelled the paths that jaguars could be using to move from one jaguar conservation unit to another. In the case of the Yucatán Peninsula in Mexico they identified a series of possible corridors connecting the main jaguar conservation unit populations in the area (Calakmul and Sian Káan) with the outermost jaguar conservation units of Petenes–Ria Celestun, Yum-Balam–Ria Lagartos, and Pantanos de Centla–Laguna de Terminos, as well as with each other (Fig. 1; Rabinowitz & Zeller, 2010).

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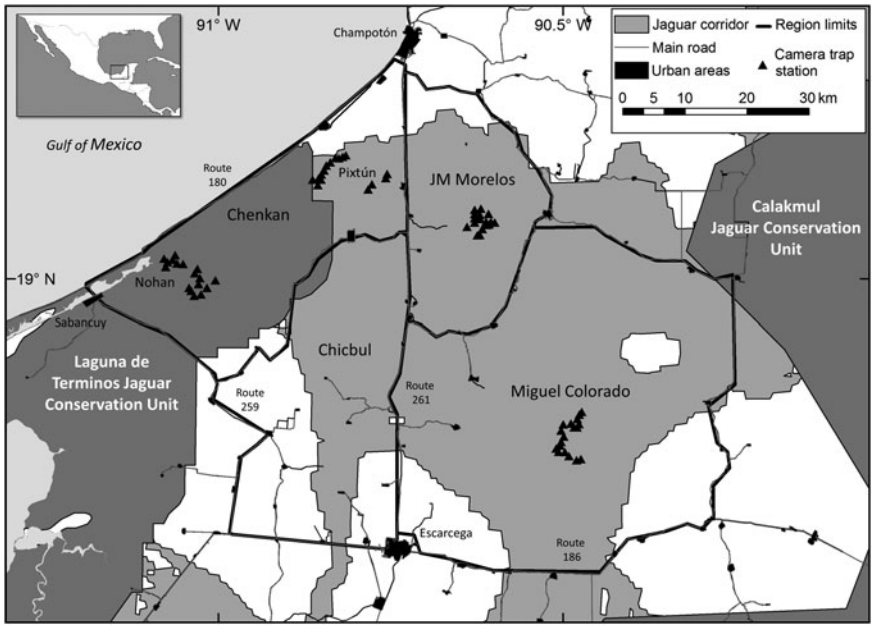

FIG. 1 Location of the Calakmul–Laguna de Terminos corridor between the Calakmul and Laguna de Terminos jaguar conservation units (Rabinowitz & Zeller, 2010), in south-eastern Mexico, with the locations where camera trapping surveys were conducted in the Chenkan (Nohan and Pixtún), JM Morelos, and Miguel Colorado regions during 2012–2014.

The presence of jaguars in the Pantanos de Centla–Laguna de Terminos jaguar conservation unit (which comprises the natural protected areas of the Pantanos de Centla Biosphere Reserve and the Laguna de Terminos Flora and Fauna Protection Area) has been verified (Hidalgo-Mihart et al., 2015); however, the population is at risk of becoming isolated from other populations in the southern and south-eastern regions of Mexico as a result of historical and current deforestation of the surrounding areas. During 1960–1980 there was widespread deforestation of tropical forests in the coastal plain of the State of Tabasco and western Campeche, in the area surrounding Laguna de Terminos and Pantanos de Centla (Tudela, 1989). By 2012 most of the land that was originally covered by tropical forests had been converted for agriculture and cattle production (Soto-Galera et al., 2010; Kolb & Galicia, 2012), and deforestation is ongoing.

Field assessments are essential to confirm the use of a corridor by the species for which it is intended (Hilty et al., 2006; Noss & Daly, 2006; Zeller et al., 2011). Given the possibility that the Pantanos de Centla–Laguna de Terminos jaguar conservation unit (and the natural protected areas it contains) could become isolated, field validation is essential to prove the presence of jaguars in the area that is proposed as the main corridor connecting this unit with the main jaguar population in Calakmul (Fig. 1). Additionally, Mexican environmental authorities have identified that the isolation of this population could potentially affect the conservation of the species in this jaguar conservation unit, and have stated that the determination of the functionality of the Calakmul–Laguna de Terminos corridor is a priority (Comisión Nacional de Áreas Naturales Protegidas, 2016). Hence, the objective of this work was to conduct on-site verification of the presence of jaguars in the corridor connecting the Laguna de Terminos and Calakmul jaguar conservation units.

Study area

The study was carried out in the state of Campeche in south-eastern Mexico, near the coast in the municipalities of Carmen and Champotón. The study area includes most of the area proposed by Rabinowitz & Zeller (2010) as the corridor joining the jaguar conservation units of Laguna de Terminos and Calakmul. The climate in the region is warm-humid, with mean temperature of 27°C and up to 2,000 mm of precipitation per year (Instituto Nacional de Estadística y Geografía, 2013). The altitude is 0–100 m: the area is mostly flat, with some small hills in its southern and eastern portions. Flat areas near the coast are subject to annual flooding during the wet season, which can last up to 8 months. The area is between two natural protected areas (Calakmul Biosphere Reserve and Laguna de Terminos Flora and Fauna Protection Area).

Vegetation in the study area is composed of a broad mosaic of plant associations, classified by Miranda & Hernández (1951) as medium sub-evergreen rainforest, lowland rainforest, natural savannah, fragmented forests, mangroves, and agricultural areas. Within these ecosystems slash-and-burn agriculture is practised to prepare the land for the cultivation of annual crops. There has been a considerable transformation of natural habitats into grasslands for cattle raising, characterized mainly by the presence of induced pastures (Soto-Galera et al., 2010). Land tenure in the area is dominated by a system of common lands

(ejido), with the exception of some privately owned properties located towards the coast.

Methods

Delimitation and characterization of the study area

To facilitate the detection of jaguars along the corridor we divided the study area into four regions (Chenkan, Chicbul, JM Morelos and Miguel Colorado), delimited by the presence of the main paved roads and their inclusion in a natural protected area or a jaguar conservation unit (Rabinowitz & Zeller, 2010; Table 1; Fig. 1).

We characterized the land use of each of the study regions from a mosaic of seven ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) satellite images (pixel size 15 × 15 m) from 2008–2009. We performed a supervised classification of the mosaic image from 350 verification points distributed throughout the study area where the land use was known. We classified the image based on the reflectance captured and stored by the ASTER sensor (visible and infrared) using the MaxLike algorithm in *ENVI 4.5* (Exelis Visual Information Solutions, Boulder, USA). Besides water, six land use categories were identified: three natural systems (natural savannah; preserved tropical forests, including tropical deciduous and sub-deciduous forests, as well as secondary forests in advanced successional stages; mangroves) and three human-dominated systems (secondary growth, identified as secondary forests in early successional stages; induced grasslands, identified as areas where the original vegetation has been eliminated and is currently covered by induced pastures or agricultural areas; urban areas). We added the area covered by each of the land use categories per region and divided by the total area of the region to obtain the percentage of each land use per region.

Jaguar detection along the corridor

To determine the presence of jaguars along the Calakmul–Laguna de Terminos corridor we performed camera trap surveys over 3 years (May–August 2012, July–December 2013, and July–October 2014) in the regions of Chenkan, JM Morelos and Miguel Colorado. We did not carry out a camera trap survey in the Chicbul region because the installation of camera traps was not authorized by the land owners.

We surveyed two sites in the Chenkan region (Nohan and Pixtún), one in JM Morelos and one in Miguel Colorado (Fig. 1). The decision to survey two sites in the Chenkan region was made because the Mexican environmental authorities showed particular interest in determining the presence of jaguar populations there (Comisión Nacional de Áreas Naturales Protegidas, 2016).

During the three study periods 20 camera traps (Cuddeback, Non Typical Inc., De Pere, USA; Moultrie, Moultrie Products, LLC., Birmingham, USA; Acorn, Ltl Acorn Outdoors, Green Bay, USA) were placed in single stations for at least 45 days at each of the four sites. Cameras were not set simultaneously in the four regions because of the prevailing flood regimes which complicate the temporal access to some of the study sites. The cameras were located at a minimum distance of 1 km apart. They were attached to trees close to trails where we found evidence of use by medium or large mammals. Cameras were set at a height of 50 cm above the ground, and programmed to operate 24 hours per day. Circa 5 m in front of each camera we placed a partially open sardine can to attract carnivores.

Once the cameras were removed, the photographs were stored and processed using *Camera Base* (Tobler, 2014). To calculate the sampling effort per site, we obtained the number of camera days that each individual camera functioned on the field by counting the number of days from when the camera was activated to the date of the last photograph taken. We considered a camera day to be a period of 24 hours during which the camera was operating. The total sampling effort for each study period and each study site was obtained by adding the number of camera days that each camera operated on each site.

Jaguars were identified individually on the basis of their pattern of spots (Karanth, 1995; Silver et al., 2004). As both sides of an individual were not photographed simultaneously, identification was based on a single side, to estimate the minimum number of individuals present in the area (Paviolo et al., 2008). A population is assumed to be resident if it includes several individuals that remain in their home ranges for extensive periods of time and there is evidence of reproduction or at least of potentially reproductive females (Karanth et al., 2006; Macdonald et al., 2010; Andresen et al., 2012). When possible, we determined the sex of the jaguars from the photographs. On the basis of individual identifications we determined whether individuals had been photographed in one or several of the study regions, and whether they had been photographed in one or more surveys. We established that a jaguar was a resident of a region if it was photographed there over more than 1 year.

Results

Land use and conservation status of the study regions

The four study regions were considered to be part of the corridor. Only the western portion of Chenkan is located within the jaguar conservation unit of Laguna de Terminos (Table 1), and none of the other areas studied are in natural protected areas. The land use differs between the four regions (Table 1), with the best preserved region being Miguel Colorado (80.43% of the land was classified as

TABLE 1 Details of the four study regions in the corridor between Laguna de Terminos and Calakmul jaguar conservation units in Campeche, Mexico (Fig. 1), with status, protection status, and land use.

Region	Status (according to Rabinowitz & Zeller, 2010)	Protection status	Size (km^2)	Land use (%)				
				Preserved tropical forest	Secondary-growth forest	Induced grasslands	Mangrove	Natural savannah
Chenkan	Laguna de Terminos jaguar conservation unit; corridor	Western portion included in Laguna de Terminos*	1,033	29.33	19.55	17.71	4.53	27.11
Chicbul	Corridor	Not protected	1,037	31.84	38.47	26.8		
JM Morelos	Corridor	Not protected	669	56.66	34.67	8.32		
Miguel Colorado	Corridor	Not protected	2,229	80.43	15.43	3.63		

*Laguna de Terminos Flora and Fauna Protection Area (Federal natural protected area)

preserved tropical forest), followed by Chenkan (60.97% preserved tropical forest, mangroves or natural savannah), JM Morelos (56.66% preserved tropical forest) and Chicbul (34.67% preserved tropical forest).

Camera-trap survey

It was impossible to sustain the same sampling effort for all sites and study periods (Table 2) because a number of cameras were vandalized and there were a number of technical failures. The minimum number of active camera traps per site in one season was 14, and the minimum number of operating days was 45. The site with the greatest camera trapping effort during the 3 years was Miguel Colorado (2,673 camera days), followed by JM Morelos (2,470), Pixtún (2,396) and Nohan (2,157; Table 2).

We obtained a total of 106 photographs of jaguars (42 in 2012, 32 in 2013 and 32 in 2014; Table 2). The site with the highest number of jaguar photographs during the 3 years was Miguel Colorado (66), followed by JM Morelos (27), Pixtún (11) and Nohan (2; Table 2). The minimum number of individuals identified during the three sampling periods was eight in Miguel Colorado, six in JM Morelos, five in Pixtún, and two in Nohan (Table 2). None of the identified jaguars was photographed at more than one site.

Females were identified in Miguel Colorado, Pixtún and JM Morelos (Table 2) but evidence of reproduction was found only in Pixtún, where a lactating female was photographed. In Nohan we were unable to determine the sex of the two jaguars photographed. In Miguel Colorado, Pixtún and JM Morelos we recorded resident jaguars (i.e. the same individual was photographed in 2 or more years). We recorded four resident jaguars in Miguel Colorado (one male during 3 years, two females during 2 years, and two of undetermined sex during 2 years), two in JM Morelos (both of undetermined sex), and two in Pixtún (one female and one of undetermined sex). We did not identify the presence of resident jaguars in Nohan.

Discussion

Field verification of jaguar corridors is a priority for establishing effective conservation strategies because it helps to determine whether corridors are functional and to identify the key connecting sites between jaguar conservation units (Zeller et al., 2011; Petracca et al., 2014). We confirmed the presence of jaguars in all the surveyed sites along the Calakmul–Laguna de Terminos corridor, with evidence of resident jaguars and females in Miguel Colorado, JM Morelos and Pixtún. Hence, it is likely that these three sites fulfil the conditions for supporting resident and reproductive populations (Karanth et al., 2006; Macdonald et al., 2010; Andresen et al., 2012). The only site where these conditions were not met was Nohan, where only two photographs of jaguars (two individuals) were obtained, indicating there is not a resident population in the area. However, as we were unable to identify the sex of the jaguars in these photographs it was not possible to rule out the presence of females. We believe it is likely that the Nohan site functions as a transit area for jaguars.

The only region of the corridor where we were unable to conduct camera trap surveys was Chicbul. The region appears to be dominated by secondary forests and induced grasslands, and these ecosystems are scarcely used by jaguars in western Campeche (Hidalgo-Mihart et al., 2015), making this part of the corridor less suitable for jaguars. This has been confirmed by recent mammal surveys in the region, which failed to record the presence of jaguars (Rangel-Negrín et al., 2014). When we were attempting to gain authorization to perform camera trapping in Chicbul we conducted several informal interviews with local authorities and inhabitants. Local inhabitants informed us that

Table 2 Data from camera trap surveys conducted at four sites in the Calakmul–Laguna de Terminos corridor in Campeche, Mexico (Fig. 1) during 2012–2014, with number of photographs of jaguars *Panthera onca*, number of camera days, and number of individual jaguars identified.

Nohan			Pixtún			JM Morelos			Miguel Colorado		
No. of photographs	Camera days	Total no. of individuals	No. of photographs	Camera days	Total no. of individuals	No. of photographs	Camera days	Total no. of individuals	No. of photographs	Camera days	Total no. of individuals
2012											
1	892	1 (unidentified sex)	2	1,046	1 (unidentified sex)	5	687	1 (male)	34	934	5 (1 male, 1 female, 3 unidentified sex)
2013											
1	625	1 (unidentified sex)	5	779	1 (unidentified sex)	6	872	2 (1 male, 1 unidentified sex)	20	842	4 (1 male, 1 female, 2 unidentified sex)
2014											
0	640	0	4	571	4 (1 female, 3 unidentified sex)	16	911	6 (2 male, 1 female, 3 unidentified sex)	12	888	3 (1 male, 2 unidentified sex)
Total (all years)											
2	2,157	2 (unidentified sex)	11	2,396	5 (1 female, 4 unidentified sex)	27	2,470	6 (3 male, 1 female, 3 unidentified sex)	66	2,664	8 (1 male, 3 female, 4 unidentified sex)

jaguars had not been recorded in the region for over 20 years. Although this information was not acquired systematically, this method has been considered to be a relatively reliable approach in determining the species' distribution (e.g. Brown & López González, 2001; Zeller et al., 2011; but see Caruso et al., 2016, regarding possible biases in interviews with local people). Nevertheless, the presence of jaguars passing through Chicbul should not be ruled out, as in other parts of south-eastern Mexico jaguars have been killed in areas dominated by agricultural and livestock activities and that are located at a considerable distance from forest covered areas (Hidalgo-Mihart et al., 2015). However, the reduced probability of jaguar presence in the Chicbul area implies that it should not be considered a priority for conservation and management within the corridor. Conservation efforts should instead be focused in the area between Miguel Colorado and Nohan, passing through JM Morelos and Pixtún.

With at least eight individuals, the resident jaguar population of Miguel Colorado was the biggest population found in this study. The population resides in an area of the corridor where the largest tract of remnant forest remains. Miguel Colorado is adjacent to the Gran Calakmul region (Galindo-Leal, 1999), which is home to the main jaguar population in Mexico (Ceballos et al., 2005). Given its high connectivity, the integrity of its natural ecosystems and the size of its jaguar population, we believe the Miguel Colorado area should form part of the Calakmul jaguar conservation unit. It is likely that Miguel Colorado is the western limit of the range of the Calakmul population, and it could be the main source of jaguars that pass through the Calakmul–Laguna de Terminos corridor. The Miguel Colorado area is not protected, nor is it included in the Mexican Priority Terrestrial Regions (Arriaga et al., 2009). In the southern Campeche region adjacent to Miguel Colorado deforestation and habitat loss are occurring at a rapid rate, mainly in non-protected areas (Ramírez-Delgado et al., 2014). Although no specific data are available for Miguel Colorado, it is likely that a similar situation exists there. In the future the integrity of the Miguel Colorado area should be preserved through efforts to protect both the habitat and the jaguars living there.

There is also a resident jaguar population in JM Morelos. However, a large portion of this area is covered by secondary vegetation in various stages of recovery and by lands destined for agricultural and livestock activities. Similar to other non-protected areas in Campeche (Ramírez-Delgado et al., 2014), it is threatened by the expansion of agricultural and livestock activities. Potential negative interactions between jaguars and cattle has been reported for the region (Chávez-Tovar & Zarza-Villanueva, 2009), and during the study period at least two jaguars were killed for attacking livestock (Pérez-Hernández, 2014; A. Jesús de la Cruz, pers. comm.). Efforts must be intensified to reduce

deforestation in this region and mitigate these negative interactions.

Pixtún, in the Chenkan region, also has a resident jaguar population. Deforestation has occurred mainly in the tropical forests, whereas other types of habitats, such as mangroves and natural savannahs, have not been extensively affected, primarily because of their natural characteristics, which include flooded periods. The main problem in the area is the deforestation associated with plantations of the African oil palm *Elaeis guineensis*, a crop that increased from 3,145 ha in 2009 to 20,295 ha in 2014 in the state of Campeche (Gobierno del Estado de Campeche, 2015). Likewise, there has been a considerable development of high-impact tourism in the coastal region, which is expected to undergo significant growth in the coming years (Gobierno del Estado de Campeche, 2012), with an anticipated negative impact on the region's natural ecosystems.

The only study area in which there is unlikely to be a resident jaguar population is Nohan, in the Chenkan region. This assumption is supported by the fact that only two records, of different individuals, were obtained during the study. However, Nohan and its wetlands (mostly mangroves and savannahs) probably serve as transit sites for jaguars travelling to and from the Laguna de Terminos jaguar conservation unit, and therefore it is important to preserve the integrity of these ecosystems. The region surrounding Nohan is partially protected by the Laguna de Terminos protected area; however, habitat loss is considerable there (c. 2,000 ha of mangrove and tropical forest were lost during 2005–2010; Reyes-Gómez & Vázquez-Lule, 2009), and therefore conervation efforts should be increased in this area. Likewise, actions aimed at mitigating the negative interactions between jaguars and cattle should also be intensified; during the study period at least three jaguars were reported to have been killed as a result of this (Pérez-Hernández, 2014).

Corridor functionality

Although jaguars were detected at several locations within the corridor (including those that meet the conditions for the existence of a resident population), the same individual must be recorded at several sites to demonstrate the functionality of the Calakmul–Laguna de Terminos corridor. It is possible that this could be achieved by an increased camera trapping effort, including in intermediate sites; however, it is also possible that there are landscape elements in the corridor that are limiting jaguar mobility. The movement of jaguars through the corridor could be hindered by the presence of highways, as well as by increased human activity over wide areas. Among the most important barriers is the Federal Highway 261: Escarcega-Champotón. With c. 3,200–4,000 vehicles per day (Secretaría de Comunicaciones y Transportes, 2015), travelling at a mean speed of 110 km per hour, this highway could be significantly affecting the corridor's functionality. Deforestation, a decline in prey species as a result of the expansion of agricultural and cattle-raising activities, tourism and subsistence hunting may also be affecting the mobility of jaguars throughout the corridor.

Specific preservation actions need to be implemented in several sections of the corridor. Perhaps the most meaningful action would be the inclusion of the Calakmul–Laguna de Terminos corridor as part of the Mesoamerican Biological Corridor (an international conservation strategy that invests resources in private and communal lands in regions connecting natural protected areas), which aims to support sustainable development projects that maintain natural processes, such as connectivity (Álvarez-Icaza, 2013). To capitalize on the recent interest of the Mexican environmental authorities in the jaguar and other threatened species present in the Chenkan area (Comisión Nacional de Áreas Naturales Protegidas, 2016), new data are needed to justify their inclusion in conservation schemes.

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