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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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ABSTRACT

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).

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