Assessing habitat availability and connectivity for the jaguar *Panthera onca,* in the Yucatan peninsula, Mexico

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Abstract

Current trends in biodiversity conservation are based on maintaining suitable habitat conditions not just within protected areas, but also on adjacent, sustainably managed lands. This is especially challenging for the conservation of large carnivores such as the jaguar that require connected habitats to minimize extinction risks and facilitate movement while minimizing conflicts with humans. This study provides spatially explicit habitat information for jaguar management and the implementation of corridors linking its populations in the Yucatan peninsula, Mexico, an area of international significance for the species. First, both comprehensive and sex-based habitat suitability models based on jaguar occurrence records and a combination of land use and land cover (LULC), distance to infrastructures (human settlements and roads), and climate (mean annual precipitation) were constructed using MaxEnt. Then, this information was used to derive a cost surface for mapping suitable corridors, linking four locations (nodes) where current jaguar observations were concentrated. The performance of all models was excellent, but slightly higher for either the female (AUC = 0.928±0.014), or the male (AUC = 0.942±0.042) models than for the comprehensive one (AUC = 0.889±0.047), despite its larger sample size. While LULC was a better predictor for the female model, all models showed that highly suitable areas were scarce in the region and were mostly associated with tropical evergreen forests. Suitable habitat patches were more fragmented for the male or comprehensive models than for the one for females only. Five potential corridors of varying quality have been identified between the population nodes, the best one being from Calakmul to Sian Ka'an along the eastern Caribbean coast, followed by Sian Ka'an to Ria Lagartos. The corridor connecting northern locations from Ria Lagartos to Ria Celestun had the poorest habitat conditions. The suitable habitat models and corridors support the potential value for conservation of productive lands under sustainable forest management since most potential suitable habitats for jaguars were found outside protected areas. These results can be useful to highlight areas of potential opportunities or conflicts for jaguar conservation in a human-dominated landscape and to target areas for further jaguar surveys.

Keywords: biodiversity conservation, landscape ecology, habitat modeling, corridor, connectivity, jaguar, Mexico.

Résumé

Les courants actuels en biologie de la conservation privilégient le maintien d'habitats essentiels autant dans les aires protégées que sur les terres adjacentes montrant une gestion durable des habitats. Ceci peut être particulièrement critique lorsque des terres doivent être aménagées afin de permettre la conservation de populations de grands carnivores tel que le jaguar, qui requiert une bonne connectivité d'habitats, permettant une minimisation des risques de conflit avec l'humain et favorisant le déplacement des populations de jaguars. Cette étude vise à produire des informations spatiales pour la gestion de populations de jaguars ainsi que l'implémentation de corridors reliant ces populations dans la péninsule du Yucatan, au Mexique, une aire d'importance internationale pour l'espèce. À l'aide de MaxEnt, on a d'abord créé un modèle général d'habitats potentiels ainsi qu'un modèle basé sur le genre (male ou femelle), en utilisant les donnés d'occurrences du jaguar et une combinaison de variables de couverture et utilisation du sol, de distance à des infrastructures (i.e., habitations et routes) et de climat (précipitation moyenne annuelle). Cette information a ensuite été utilisée afin de développer une analyse de coût de déplacement dans des corridors reliant quatre lieus (nœuds) où les observations actuelles de jaguar sont concentrées. Bien que tous les modèles aient une excellente performance, les modèles basés sur le genre (femelle AUC = 0.928±0.014, male AUC = 0.942±0.042) avaient une performance supérieure au modèle général (AUC = 0.889±0.047), et ce, malgré la plus petite taille de l'échantillon. La variable couverture et utilisation du sol était un meilleur facteur dans le modèle des femelles, mais tous les modèles ont prédit que peu d’habitats avaient un fort potentiel dans la région et que les quelques habitats potentiels étaient associés à des forêts tropicales sempervirentes. Les habitats potentiels (i.e., avec un bon potentiel ou un très bon potentiel) étaient moins nombreux, mais plus fragmentés et de plus petite taille dans le modèle des males ou le modèle général que dans le modèle de femelles. Cinq corridors potentiels de qualité variable ont été identifiés entre les nœuds de populations, le meilleur étant celui qui relie Calakmul à Sian Ka’an sur la côte Caribéenne est, suivi par celui reliant Sian Ka’an à Ria Lagartos. Le corridor reliant le site du nord de Ria Lagartos à Ria Celestun présentait le plus faible potentiel. Les modèles d’habitats potentiels et de corridors démontrent l’importance de conserver les terres productives par une gestion durable des forêts puisqu’elles regroupent des habitats favorables au jaguar, et ce, à l’extérieur d’aires protégées. Ces résultats permettent l’identification d’aires présentant un bon potentiel pour la conservation du jaguar dans un paysage dominé par l’humain ou de sélectionner des aires pour échantillonner des populations de jaguars.

Mots clés: Biologie de la conservation, écologie du paysage, modélisation d’habitat, corridor, connectivité, jaguar, Mexique.

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List of abbreviations

AUC Area under the curve

BR Biosphere Reserve

CENJAGUAR Mexican National Census of the Jaguar and its Prey

CONABIO Comisión Nacional para el Conocimiento y uso de la Biodiversidad (Mexican National Commission for Biodiversity Knowledge and Use)

CONANP Comisión Nacional de Áreas Naturales Protegidas (Mexican National Commission for Natural Protected Areas)

ENN Euclidean distance to the nearest neighbor

FAO Food and Agriculture Organization of the United Nations

GARP Genetic Algorithm Rule-Set Prediction

GIS Geographic Information System

INEGI Instituto Nacional de Estadística, Geografía e Informática (Mexican National Institute of Statistics, Geography and Informatics)

IUCN International Union for Conservation of Nature

JCU Jaguar Conservation Unit

LULC Land use and land cover

MaxEnt Maximum Entropy for species distribution modeling

ROC Receiver Operating Curve

SDM Species distribution models

SEMARNAT Secretaría de Medio Ambiente y Recursos Naturales (Mexican Secretariat of the Environment and Natural Resources)

UTM Universal Transverse Mercator

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Contributions of Authors

I was responsible for developing the idea for this project with the diligent support of my supervisory committee. I did the literature review, data compilation, statistical analysis, and wrote the thesis with its objectives, methodology section, results and discussion. Prof. De Blois and Dr. Cuauhtémoc Chávez provided significant contributions through feedback on different parts of my project, specifically on the methodology and results interpretation. Prof. de Blois edited the thesis. The data for this study was provided by my co-supervisor Dr. Gerardo Ceballos and Dr. Cuauhtémoc Chávez as part of their research and partnership on the National Census of the Jaguar and its Prey (CENJAGUAR).

I presented the results of my thesis at the 35th Société Québécois pour l'Étude du Biologie du Comportement (SQEBC) in 2010, the eighth world conference of the International Association for Landscape Ecology (IALE) in August 2011, and at the QCBS annual symposium in December of the same year.

This thesis is written based on the McGill thesis guidelines for manuscript style theses, and chapter 3 will be submitted for peer review.

Chapter 1

General Introduction

This study addresses the configuration of habitat for the jaguar *(Panthera onca)* and regional, structural connectivity, in the Yucatan peninsula in Mexico. Jaguars are of international importance for conservation and are classified as near-threatened species (Caso et al. 2008). Over the last century, the gradual decrease in jaguar populations has resulted in an international effort to delineate conservation units and corridors at the continental level (Sanderson et al. 2002; Rabinowitz & Zeller 2010). In Mexico, the national strategy first evaluated the status of jaguar populations and their prey (Chávez & Ceballos 2006); however, nationwide monitoring has given an emerging need to produce information that is appropriate to decision-making at the landscape level. The Yucatan peninsula has been identified as potentially the largest area of habitat in the northern part of the jaguar's global range. However, habitat restricted to protected areas might be insufficient to adequately conserve this species. In this context, I developed an approach to provide spatially explicit habitat information to help with the conservation, monitoring, and management of jaguars. In this thesis, I first review the literature (chapter 2), focusing on current challenges in biodiversity conservation, aspects of landscape connectivity, threats for large carnivores, and the conservation framework in Mexico, and end by describing the land uses in the Yucatan and their relationship with habitat maintenance. In chapter 3, I develop an approach using a combination of a Species Distribution Model (SDM) and

Geographic Information System (GIS) to assess the suitability of habitat for jaguars. I also present the results of my assessment of habitat configuration and its connectivity in the landscape. Finally, I conclude my main findings in chapter 4, describing how my approach can help practitioners and conservation biologists to better allocate resources for the management of jaguars in the landscape scale.

Hypotheses and Objectives

Following the assumption that in a human-dominated landscape, suitable habitat for jaguars will be mostly found outside protected areas, the overall objective of my research is to develop spatially explicit information for the conservation and management of jaguar habitat in the Yucatan peninsula, Mexico.

More specifically, I hypothesized that:

1. The combination of land uses, land cover, anthropogenic infrastructure and climate can predict the availability of suitable habitats for the jaguar, regardless of sex.

2. The configuration of habitat patches can be used to evaluate connectivity.

I focused on five specific objectives:

1. To model and map potentially suitable habitat patches for jaguars using species distribution models, based on a combination of land use and land cover, infrastructure, and climate.

2. To assess the value of using sex-based information in mapping suitable habitat and to compare the results of sex-based models (female or male records) with a comprehensive model using all jaguar records.

3. To quantify the spatial configuration of potential habitat patches.

4. To identify corridors linking population nodes trough the more suitable habitat patches.

5. To interpret maps in relation to the current network of protected areas and conservation units for jaguars.

By achieving these objectives, I hope to further our understanding of the landscape process and pattern that help maintain jaguar habitat within different land uses/land covers, to elaborate rules for network and connectivity that are informed by landscape context, and to propose a methodology to highlight areas of potential opportunities or conflicts for jaguar conservation in human-dominated landscapes.

Chapter 2

Literature review

2.1 Challenges in biodiversity conservation

The effects of human domination over natural ecosystems, which drive land conversion and consequently cause habitat degradation, remain the main threat for tropical biodiversity (Heywood & Watson 1995; Vitousek et al. 1997; Jaakkola 1998; Sala et al. 2000; Foley et al. 2005). Despite the undeniable benefits for human livelihood obtained from land conversion, the resultant loss of biodiversity could in the end be costly to human wellbeing (Millennium Ecosystem Assessment 2005; Walpole et al. 2009). Globally, it is recognized that, although land changes are not solely the result of poverty or population growth, monitoring both the impacts of poverty alleviation on ecosystems and the effects of conservation strategies on the poor remains an important challenge (Lambin et al. 2001). In this context, there is a need to develop integrative conservation approaches that combine different levels of protection both relevant to biodiversity and human needs.

As global biodiversity continues to decline, conservation strategies that include protected areas along with sustainably managed forests and agriculture could help preserve valuable habitats and conserve biodiversity (Butchart et al. 2010; Pereira et al. 2010). The International Union for Conservation of Nature (IUCN) recognizes different levels of protection, from strict reserves to protected areas that permit the sustainable use of natural resources (IUCN et al. 2008). However, the expected gradient of conservation does not always match the level of protection given by the IUCN. For example, the human influence on strict nature reserves (category Ia) could be higher than expected in comparison to areas that allow habitat or species management (category IV) (Leroux et al. 2010). It is therefore important to set conservation objectives through the use of informed management strategies for conservation that take into account human activities and human modified habitats. Within the IUCN Red List, several tools have been used to estimate species geographic distribution, and to identify and rank potential threats (Cassini 2011). In modified landscapes, these strategies will depend on spatially explicit conservation models and assessments that combine human and ecological dynamics (Turner II et al. 2007). For example, species persistency in remnant patches of habitat has drawn the attention of several ecological studies focusing on plant communities (de Blois et al. 2001; Dalle et al. 2006), birds, or mammals (Daily et al. 2001; Daily et al. 2003).

2.2 Landscape connectivity

Protected habitats within nature reserves, or suitable land cover are often few and far apart in production landscapes. Furthermore, the effects of habitat fragmentation can be either positive or negative for biodiversity (Fahrig 2003), depending on different resources that can affect the quality of habitat between fragments (Jules & Shahani 2003). The creation of wildlife corridors connecting populations and habitat patches has become a key element for conservation planning in fragmented landscapes (Taylor et al. 1993; Hobbs 1997; Beier & Reed 1998). Different approaches mostly based on binary patterns of suitability have been developed in the last decades to study connectivity. Some approaches that have helped to delineate networks of connections are based on Graph Theory (Bunn et al. 2000; Minor & Urban 2008) or Minimum Planar Graphs (Fall et al. 2007). Further, there is a need to incorporate or to quantify the cost of (or resistance to) movement associated with processes at large spatial scale (Rouget et al. 2006).

In recent years, establishing wildlife corridors has become a widely used method to provide connectivity at a landscape level, and their implementation and monitoring is considered critical for conservation (Crooks & Sanjayan 2006). Corridors can be created using a cost surface to estimate the movement cost between suitable locations while taking into account habitat quality (Chetkiewicz et al. 2006). Similar to least cost paths, wildlife corridors capture key environmental gradients along with a connecting route (Rouget et al. 2006). Nevertheless a corridor is more than just a linear connection and its delineation requires finding adjacent grids cells with the same or similar cost value (Adriaensen et al. 2003). The design of habitat linkages should find a route or various routes that minimize the cumulative cost (or friction) of movement between locations (Adriaensen et al. 2003; Sawyer et al. 2011).

To better inform the creation of corridors or routes it is important to consider the available knowledge about the target species for the maintenance of ecological and evolutionary process, such as gene flow (Horskins et al. 2006). Empirical data and expert knowledge are important to provide spatially explicit assessments and to select variables relevant to species' movements, especially in modified landscapes (Lombard et al. 2010). Using of a focal species for linkage design, for example a large carnivore, could also help maintain connectivity also for other species without losing sight of the specifics needs of the target species (Beier et al. 2009). This approach also helps to avoid misrepresentation of the species use of habitat on a landscape (Sawyer et al. 2011). Finally, this approach could be complementary to global conservation assessments for carnivores based on potential suitable habitat models and connectivity analyses (Crooks et al. 2011; Rondinini et al. 2011b).

2.3 Threats for large carnivores

The long-term effect of human encroachment on carnivores and the direct conflicts with humans affecting habitat selection and the movement of species have been widely discussed (Weber & Rabinowitz 1996; Lindberg et al. 1998; Woodroffe 2000; Linnell et al. 2001; O'Brien et al. 2003; Treves & Karanth 2003). Nevertheless, management for these animals needs to evolve from actions supported by economic drivers – eradication, regulated harvest, and preservation – to promote a more socially inclusive perspective, modify the behavior of humans, livestock, or carnivores, and prevent direct conflict (Treves & Karanth 2003). Further, networks of habitats need to be mapped to identify threats and areas for conservation at the landscape level (Redford et al. 2003), especially for species with larger distribution ranges, which have an overall lower level of habitat connectivity compared with species with smaller distribution ranges (Crooks et al. 2011).

One of the most important wide-ranging carnivores in America, considered a keystone species (Mills et al. 1993), is the jaguar (*Panthera onca*), categorized on the IUCN Red list as near-threatened species. Over the last decades, many efforts have been deployed to describe the geographical distribution of jaguars and to expand the ecological knowledge of this species. Experts concluded that, due to habitat loss, hunting pressure, and direct conflicts with humans, current jaguar's range is approximately half its historical distribution (Sanderson et al. 2002). Consequently, many areas were defined as Jaguar Conservation Units (JCU), and complementary studies have focused on defining the connectivity among known jaguar populations across the continent (Rabinowitz & Zeller 2010). The jaguar is the only large and wide-ranging carnivore with no subspecies (Eizirik et al. 2001; Ruiz Garcia et al. 2006) thus maintaining the gene flow between populations is essential to avoid genetic drift (Haag et al. 2010).

Many studies have addressed issues of human-jaguar conflicts (Rabinowitz 1986; Chávez & Zarza 2009), while others seek to describe the current geographic distribution and population demography in different areas such as Brazil and Mexico (Ceballos et al. 2002; Silveira et al. 2010; Nunez Perez 2011; Sollmann et al. 2011). Specifically in the case of the latter, a national strategy named CENJAGUAR aims to monitor jaguar populations and their prey in order to assess the status of this species nationwide (Chávez & Ceballos 2006). However, national studies have shown the difficulties in defining areas for conservation at scales larger than those at which most management decisions are taken (Rodriguez-Soto et al. 2011). This emphasizes the need to better categorize specific areas for management at a scale relevant for practitioners, such as the Yucatan peninsula, believed to maintain some of the most important jaguar populations in the northern part of the range (Ceballos et al. 2002).

2.4 Conservation in Mexico

In Mexico, the main conservation instrument has been the creation of natural protected areas by the Mexican National Commission for Natural Protected Areas (CONANP). Generally, the Commission has prevented vegetation loss inside protected areas (Figueroa & Sánchez-Cordero 2008), but its complexity and a tendency to displace local residents have created conflicts over the use of natural resources (García-Frapolli et al. 2009). Although the Calakmul biosphere reserve (BR) is the largest terrestrial reserve in Mexico covering 7,231.85 km^2 (Folan et al. 1992), in the Yucatan the system of protected areas is more targeted to coastal and marine ecosystems. This is evidenced by the distribution of the main nature reserves and other protected areas as follows: center east on the Caribbean coast the Sian Ka'an BR and Uyamil Flora and Fauna protected area; to the northeastern tip of Yucatan is Ria Lagartos BR and Yum-Balam Flora and Fauna protected area; and finally to the northwest on the Gulf of Mexico the Ria Celestun BR and Los

Petenes BR (Smardon & Faust 2006). This also emphasizes the importance of conservation in areas outside protected areas.

Other conservation initiatives in the area include the Mesoamerican Biological Corridor that aims to protect biodiversity while promoting sustainable development within biological corridors going from the southern part of Mexico to Panama (Miller et al. 2001). Controversy, however, has also arisen concerning the commercialization interests of private industries with the development project *"Plan Puebla Panama"* for connecting the same region through roads and highways (Pisani & Label 2003), which could create more rapid land use changes driven by this development plan.

2.5 Land uses in the Yucatan

In the peninsular Yucatan, the main land uses are shifting agriculture, cattle ranching, and forest extractions (INEGI 2009) done mainly by smallholders organized in *ejidos* – groups of various ethnicities with collective land grant and communal property right over resources (Klooster 2003). At the large scale, legacies of development policies centralized on resource exploitation in the last 100 years have had important implications on land-use decisions in the long-term (Klepeis 2003). For example, a large proportion of cropland is being used intensively for monocultures and cash crops, especially in the northern part of the peninsula (Roy Chowdhury & Keys 2006; Roy Chowdhury 2010). The southern part has been impacted by a rise of cattle grazing, mainly due to the conversion of traditional activities by colonizers coming from other parts of Mexico (Klepeis 2003). Additionally, the economy has moved towards tourism development on the east coast affecting the forest cover (Klepeis & Turner II 2001; Abizaid & Coomes 2004). Nevertheless, at the fine scale, the traditional cultivation of maize in association with other crops (known as *milpa*) is still widely practiced (Klepeis & Turner II 2001). In this system, the consecutive use of forest fallows and extractive activities of timber fuel, fruits and fibers is a complementary activity for most small landowners (Abizaid & Coomes 2004; Dalle & de Blois 2006).

In spite of land use pressures, the Yucatan peninsula is found within the Mesoamerican biodiversity hotspot (Myers et al. 2000) because of its geographic location, biodiversity, and cover of tropical forest that makes it of high relevance for conservation. Depending on the spatial or temporal scale of observation, both rapid deforestation (rate of up to 0.76 per cent per year between 1976 and 2000) (Turner II et al. 2001; Manson 2006), and sustainable land use with limited forest loss in some *ejidos* have been reported (Dalle et al. 2011). As indicated in many studies, the loss of mature forest as a result of increasing deforestation is certainly of concern (Velazquez et al. 2003; Mas et al. 2004; FAO 2005). However, the deforestation rate can be lower in inhabited forests under management with higher economic benefits than in unoccupied protected areas (Bray et al. 2008).

Forestry is such an important activity in the area that some *ejidos* have maintained communal forest reserves where farming and grazing are forbidden. This activity is centered in the selective extractions of hardwood including mahogany *(Swientenia macrophyla),* and Spanish cedar *(Cedrela odorata)* and of non-timber resource such as the *chicle* gum (Dalle & de Blois 2006; Manson 2006; Ellis & Porter Bolland 2008). Mexico's leadership with community-based forest management is recognized internationally as a sustainable model (Klooster 1999; Bray 2003; Scherr et al. 2004). Land tenure rights in Mexico may have favored this community arrangement compared to other places in Latin America where most of the forests belong to the government (in Mexico 80% of forests are under *de jure* common property arrangement) (Klooster 2003). Although forestry activities are a very important source of income that complements the livelihood of smallholders (Ellis & Porter Bolland 2008), in most developing countries, community-based forestry only contributes to a small share of the forest industry (Scherr et al. 2004). This can be explained partially by its strong reliance on international markets and sources of external funding or public subsidies (Scherr et al. 2004). This system could have an important role in helping to reach the Millennium Development Goals of global poverty reduction and the promotion of environmental sustainability (Millennium Ecosystem Assessment 2005). Consequently, it has become urgent to identify areas where both conservation and rural livelihood can meet (Harvey et al. 2008). Finally, conservation planning should be done at a scale manageable in coexistence with humans (Redford et al. 2003), not just to an ideal scheme to preserve global hotspots (Ceballos & Ehrlich 2006). Biodiversity conservation should be an essential consideration in all types productive activities (Wiens 2009).

Chapter 3

Assessing habitat availability and connectivity for the jaguar *Panthera onca*, in the Yucatan peninsula, Mexico [*]

Paola Gómez García, Cuauhtemoc Chávez, Gerardo Ceballos and Sylvie de Blois

Abstract

Current trends in biodiversity conservation are based on maintaining suitable habitat conditions not just within protected areas, but also on adjacent, sustainably managed lands. This is especially challenging for the conservation of large carnivores such as the jaguar that require connected habitats to minimize extinction risks and facilitate movement while minimizing conflicts with humans. This study provides spatially explicit habitat information for jaguar management and the implementation of corridors linking its populations in the Yucatan peninsula, Mexico, an area of international significance for the species. Using MaxEnt, we first constructed both comprehensive and sex-based habitat suitability models based on jaguar occurrence records and a combination of land use and land cover (LULC), distance to infrastructures (human settlements and roads), and climate (mean annual precipitation). Then, we used this information to derive a cost surface for mapping suitable corridors, linking four locations (nodes) where current jaguar observations were concentrated. The performance of all models was excellent, but slightly higher for either the female (AUC = 0.928±0.014), or

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the male (AUC = 0.942±0.042) models than for the comprehensive one (AUC = 0.889±0.047), despite its larger sample size. While LULC was a better predictor for the female model, all models showed that highly suitable areas were scarce in the region and were mostly associated with tropical evergreen forests. Suitable habitat patches were more fragmented for the male or comprehensive models than for the one for females only. Five potential corridors of varying quality have been identified between the population nodes, the best ones, characterized by greater amount of highly suitable areas and larger habitat patches, were located to the east along the Caribbean coast. Community forestry in that area may have led to the maintenance of a forest cover suitable to jaguars, whereas other land uses (e.g., cattle grazing, higher density of human populations) may create more tension between jaguars and humans. The corridor connecting northern locations is in an area of higher road density and higher number of human settlements resulting in the poorest habitat conditions. It is important to consider sustainable practices that can reconcile the need to sustain livelihood with our stewardship of the land and its biodiversity. The suitable habitat models and corridors support the potential conservation value of productive lands since most potential suitable habitats for jaguars were found outside protected areas. These results help highlight areas of potential opportunities or conflicts for jaguar conservation in a human-dominated landscape and are valuable in selecting target areas for further jaguar surveys.

3.1 Introduction

Maintaining habitat conditions within protected areas and in adjacent lands is important to biodiversity conservation (Daily 2001; Butchart et al. 2010; Pereira et al. 2010). The balance between conservation and land use is especially key for large carnivores that require connected habitats to minimize extinction risks and facilitate movement at the landscape, regional, or even continental scales (Crooks et al. 2011; Redford et al. 2011) especially where they enter into potential conflict with humans (Weber & Rabinowitz 1996; Woodroffe 2000; Treves & Karanth 2003). As infrastructure, including roads, and agricultural expansion restrict the movement of large carnivores (Kerley et al. 2002; Fahrig & Rytwinski 2009; Jhala et al. 2009), and unsustainable hunting pressure increases, the need to identify all remaining suitable habitat patches in areas of critical conservation value is higher than ever (Redford et al. 2003). This work will help identify target areas not only for further survey or monitoring, but also for reconciling production and conservation.

One carnivore of international conservation interest is the jaguar (*Panthera onca*) – the largest felid in the new world (Seymour 1989), considered as a near-threatened species by IUCN (Caso et al. 2008). By 2000, the jaguar's continental distribution range was estimated to one half of its original size, between southern United States and northern Argentina (Sanderson et al. 2002). Continental scale assessments have helped to identify areas for conservation for jaguars and lessons learned from conservation of other large felids such as the tiger in Asia have inspired broad scale strategies such as the determination of habitat conservation units across the distribution range (Weber & Rabinowitz 1996; Sanderson et al. 2002; Wibisono & Pusparini 2010).

Within continental conservation schemes, however, it is important to recognize regional dynamics to provide information at a scale relevant for the management of large carnivores. In Mexico, the Yucatan peninsula contributes to maintain suitable habitat for jaguars in the northern part of the continental range, but land changes are threatening these habitats and protected nature reserves might not be sufficient (Ceballos et al. 2002; Ceballos 2007; Figueroa & Sánchez-Cordero 2008; Chávez & Zarza 2009; Visconti et al. 2011). On the one hand, the protected area designation in Mexico, specifically in the Yucatan, has caused conflicts with local people over the use of natural resources, creating a complex scenario for conservation (García-Frapolli et al. 2009). On the other hand, some practices, such as community-based forestry or ecotourism, could help strengthen the conservation role of nature reserves because of their similarity in maintaining forest cover (Klooster 2000). For instance, a study in the forest *ejidos* – a communal property scheme in Mexico – of the South Sierra (Oaxaca) suggested that jaguar conservation could be a win-win situation by using the jaguar as an ecotourism attraction (Durán et al. 2010). The conservation value of protected areas in a fragmented landscape may need to be sustained through connections with productive lands serving as corridors (Ellis & Porter Bolland 2008). However, this would also require innovative ways to promote benefits for human population.

In this study, we aim to provide spatially explicit habitat information for the management of the jaguar and the implementation of connectivity paths linking jaguar populations in the Yucatan peninsula, Mexico. This is done by: 1) modeling and mapping suitable habitat patches using all reliable records of jaguar's occurrence in the study area; 2) assessing the value of using available sex-based information to map suitable habitats; 3) quantifying the spatial configuration of potential habitat patches; 4) identifying corridors linking population nodes through suitable habitat patches; 5) interpreting the resulting maps in relation to the current network of protected nature reserves and jaguar conservation units.

3.2 Methodology

3.2.1 Study area

The Yucatan peninsula, located in southeast Mexico, includes three states: Quintana Roo, Yucatan and Campeche. The study area is delimitated by the coordinates 21º 38′ to 17º 49′ N and 91º 00′ to 86º 43′ W, and covers 125,933 km^2 (Figure 3.1). The uniform topography with elevation of only 400 meters above sea level, results in a uniform climate with a mean annual temperature of 24º C. The mean total annual precipitation ranges from 400 to 1500 mm, with rainy days mostly concentrated between May and November. Most soils are limestone and there are few surface water bodies. The main vegetation type is tropical forest, from short deciduous forest or dry forest in the northern and central peninsula to tall evergreen in a gradient of humidity to the south and east coast (Leopold 1950;

White & Hood 2004). Dominant tree species include mahogany *(Swietenia macrophylla)*, Spanish cedar (*Cedrela odorata)*, gum tree or zapote *(Manilkara zapota),* and Mayan nut *(Brosimum alicastrum)* in the tall forest. In the short forest, guayacan *(Guaiacum sanctum),* gumo-limbo *(Bursera simaruba),* and ceiba *(Ceiba schotti)* are some of the more important tree species (Martinez & Galindo-Leal 2002; White & Hood 2004). Wetlands present along the coastal zones are characterized by four species of mangroves: red mangrove *(Rhizophora mangle),* buttonwood *(Conocarpus erectus)*, white mangrove *(Laguncularia racemosa)*, and black mangrove *(Avicennia germinans)*.

Within the area, the human population growth rate is above the national mean of 2.1%. According to the 2005 national population census done by the Mexican National Institute of Statistics, Geography and Informatics (INEGI), the population reached 3.7 million, with some contribution from immigration. The Yucatan peninsula is home to a significant proportion of indigenous Maya in Mexico (INEGI 2005). The main economic activities among smallholders in the peninsula include agriculture, cattle grazing, and forest extraction (INEGI 2009). Over time, changes in national policies and economic factors have resulted in changes in preferred activities through time (Klepeis 2003). Although traditional shifting cultivation, known locally as *milpa*, is still commonly practiced (Abizaid & Coomes 2004), agriculture has intensified or converted to monocultures of maize and to cash crops such as chili (Roy Chowdhury & Keys 2006). The southern part has been impacted by a rise of cattle grazing, mainly due to colonizers coming from other parts of Mexico (Klepeis 2003). In the eastern part, forestry for selective timber extractions and non-timber products is an important component of the livelihood of smallholders (Geoghegan et al. 2001). The economy, however, is moving towards tourism development in various areas especially along the Caribbean Coast (Klepeis & Turner II 2001; Abizaid & Coomes 2004). Extensive road building and expansion of highways have created pressure on the forest (Pisani & Label 2003). Furthermore, a system of protected areas has been targeted towards coastal and marine ecosystems, and less to protect the interior tropical forest (Smardon & Faust 2006).

3.2.2 Jaguar data

We compiled jaguar occurrence records from diverse sources such as bibliographic records and field surveys. Bibliographic records were taken from freely available databases such as CONABIO (Mexican National Commission for Biodiversity Knowledge and Use), and WILCHIS online (López-Wilchis 2003). Published records of jaguar presence included points from direct capture and telemetry data from GPS collars (Ceballos et al. 2002; Chávez & Zarza 2009). Photographic records from camera-traps were gathered from diverse organizations working on the Mexican national census of the jaguar CENJAGUAR (Chávez & Ceballos 2006). Only one record of a footprint was included as it was assumed to be reliable (Pereira Lara 2006). A complete list of sources can be found in Appendix I.

3.2.3 Landscape data

We selected the environmental and anthropogenic variables relevant to habitat selection based on the current knowledge about the species' ecology. We used a reclassified version of the Mexican national forest inventory (SEMARNAP et al. 2000) to map LULC relevant to jaguar habitat. In this classification, the evergreen tropical forest represents the greater portion of the study area (36.9%) and includes the tall and medium perennial and sub-perennial forest. It is followed by the sub-deciduous tropical forest (17.9%). The sub-evergreen tropical forest and the deciduous tropical forest covered a smaller percentage (7.3% and 6.5% respectively). As for the land uses, pasturelands including cultivated and induced grasslands cover 13%. Human settlements and agriculture were combined into the same land use type along with other covers that represented less than 2% of the landscape (e.g., water bodies, palm forest) and all together represented 13.5% of the study area. The resulting eight LULC are described in Appendix II.

The soil layer was obtained from CONABIO (1995), and we used soil units in correspondence with the world soil resources map from the Food and Agriculture Organization of the United Nations (FAO et al. 2003). Although high-resolution climatic data is now available via online datasets, for our model we only required the mean annual total precipitation from 1950 to 2000 from the WorldClim dataset (resolution of 30 arc-seconds or approximately 1 km^2) (Hijmans et al. 2005). In preliminary tests, temperature had, as expected, a weak contribution to the model, which could be explained by its low mean annual variability (Kampichler et al.

2010). Elevation and slope have been widely used to determine potential habitat for other felines in the *Panthera* genus (Gavashelishvili & Lukarevskiy 2008; Khorozyan et al. 2010), but the incorporation of a Digital Elevation Model (DEM), given the uniform topography in the area was not necessary (Chávez & Zarza 2009). As well, hydrographic information was not used due to the lack of permanent surface water in this region.

We obtained the information about human settlements and roads from the Mexican National Institute of Statistics, Geography and Informatics (INEGI). We selected only paved roads of 2 to 4 lanes because smaller roads are thought not to represent a barrier for jaguar movement (C. Chávez personal communication). As for human settlements, previous studies in the area have demonstrated that settlements smaller than 200 inhabitants do not have a negative effect on species' occurrence (Chávez & Zarza 2009; Kampichler et al. 2010) (Table 3.1).

3.2.4 Mapping and data analysis

All spatial information was mapped using the coordinate system Universal Transverse Mercator (UTM) zone 16 north. All layers were rasterized to 1km^2 grid cells which became the sampling units. The dominant LULC within a cell was noted. For each grid cell, we calculated the Euclidean distance to the nearest neighbor (ENN) grid cell with human settlements or roads using the distance function in ArcGis 9.3 (Environmental Systems Research Institute).

We used a set of filters and rules in an iterative process to select jaguar records for analysis. First, we selected only presence records with geographic information and retained those from 1990 or greater. For records lacking a collection date (e.g., records obtained from institutional databases), we only selected those located on a land cover equivalent to recently selected points to take into account recent land use changes. Then we used three criteria to select multiple subsamples of the records: individuality (i.e., retain only one sample per unique individual), unique geographic location, and independence (i.e., records were considered independent if they were located at least 1 km from each other). This distance corresponds to our grid size and it is comparable to the one used for the global habitat models for mammals by Rondinini et al. (2011b). Finally, the subsample retained for spatial analysis was the one with the largest number of records after the rules and filters had been applied which allowed us to give the same weight to each record. We used the same process to sample male and female records. Filtering was done within the open-source database management system PostgreSQL (PostgreSQL Global Development Group 2006) and re-sampling was implemented in R statistics package (R Development Core Team 2004).

3.2.5 Potential habitat model

We used the species distribution model (SDM) algorithm of Maximum Entropy (Phillips et al. 2006) to predict the potential habitat for the jaguar. MaxEnt is commonly used to derive a prediction from incomplete biological data (Phillips et al. 2006; Warren & Seifert 2011). It has demonstrated strong predictive capacity compared to other presence-only distribution models (e.g., the Genetic Algorithm Rule-Set Prediction, GARP) (Phillips et al. 2006; Peterson et al. 2007; Phillips 2008; Rodriguez-Soto et al. 2011), and has better performance for small sample sizes at large spatial scales (Elith et al. 2006). To evaluate the model's accuracy, MaxEnt computes the Area Under the Receiver Operating Characteristics (ROC) curve, known as AUC, by comparing sensitivity (correctly predicted presences or the absence of commission error) versus 1-specificity (incorrectly predicted presences or the absence of omission error). Additionally, we conducted a jackknife analysis to assess the contribution of each explanatory variable independently: the contribution was normalized by MaxEnt into a percentage value (Phillips et al. 2006; Elith et al. 2011).

We constructed three sets of models: a comprehensive model using all presence records, a model with only records of females, and a model with records of males. Modeling separately the distribution for males and females can contribute to our understanding of the implications of predicting habitat preferences based on sex, providing the available records are appropriate (Boydston & López González 2005; Conde et al. 2010). The data set was partitioned randomly so that 70% was used for calibration and 30% for validation of the models. For each model, we performed 10,000 iterations, and used the settings recommended in MaxEnt given the sample types and sizes (Phillips et al. 2006; Elith et al. 2011). In addition to the AUC, we also did a visual inspection of the model output by comparing predicted probabilities of presence in cells with their observed values. This helped identify threshold values for habitat suitability class.

3.2.6 Suitability class

We defined a cell as unsuitable if the predicted probability of presence for that cell was below the lowest predicted probability value assigned to an observed presence (Phillips et al. 2006). However, our aim was also to define a range of potential habitat suitability instead of the commonly used binary suitable-unsuitable division, thus we ranked suitable areas into three classes, from low to high. After testing different threshold rules, we decided to use fixed values to classify suitability despite the limitations (Liu et al. 2005) because it allowed comparision between models.

1. Unsuitable – cells holding values below the lowest predicted probability for an observed presence (Pearson 2007).
2. Low – up to 0.3 probability of presence; this would correspond to poor quality habitat.
3. Moderate – values ranging from 0.301 to 0.5; this would correspond to secondary habitat where the species could be found but not necessarily persist in the absence of primary habitat (Rondinini et al. 2011b).
4. High – above 0.5. Primary habitat for the species.

3.2.7 Configuration of potential habitats

Since we used the finest available resolution for the environmental data (1 km^2), we aggregated cell of the same class to remove small patches that would have led to an over estimation of patchiness in our landscape. We clustered like-values neighboring cells (Crooks & Sanjayan 2006) using aggregation rules (e.g., eight neighbors, cluster) in the image processing software ERDAS (Imaging 2005) which resulted in a grid with minimum patches of 4 km^2. Home range size estimations vary in the literature, but most reports minimum home range size larger than our aggregated cell size (Astete et al. 2008; Kelly & Silver 2009). We computed class and patch metrics to quantify the spatial configuration of potential habitat using the software Fragstats 3.3 (McGarigal et al. 2002). Class and patch metrics calculated for each model were: number of patches by class, the average and maximum patch size by class, the total area for a class, the percentage of the landscape occupied by each suitability class, and the average ENN of the same class (Table 3.2).

3.2.8 Connectivity analysis

After suitable habitat patches were identified, we measured structural connectivity at the regional scale (Taylor et al. 1993). For the connectivity analysis, we identified and mapped nodes that were defined as distinct spatial clusters of jaguar observations corresponding to areas of jaguar surveys. These were the nodes or populations between which we wanted to evaluate structural connectivity. The four nodes were given the names of the nearest BR that is Calakmul (CA), Sian Ka'an (SK), Ria Lagartos (RL), and Ria Celestun (RC) (Figure 3.1). As habitat size contributes to habitat quality, we also identified core areas defined as patches $\geq$ 100 km^2 which were composed of habitat of high suitability or contiguous habitat of high and moderate suitability. These core areas were considered as preferential paths for jaguar movement in corridor analysis linking nodes. Core area of 100 km^2 is a conservative estimate as it is larger than most estimations of home-range size for jaguar (de Azevedo & Murray 2007; Astete et al. 2008; Kelly & Silver 2009; Chávez 2010; Silveira et al. 2010; Sollmann et al. 2011).

The comprehensive habitat model (see results section) provided data on habitat suitability and patch size for the connectivity analysis to derive a cost surface for connectivity between the nodes. Our approach is analogous to the connectivity analysis for carnivores by Crooks et al. (2011) and differs from the jaguar continental scale analysis of Rabinowitz and Zeller (2010) as we used the SDM map as a substitute for expert-derived cost surface.

We employed CorridorDesign, a free online spatial analysis tool for wildlife corridor planning, to define the most permeable surface of the landscape that connected two nodes, minimizing distances and taking into account habitat suitability (Majka et al. 2007). We created five corridors that could potentially connect all nodes and then compared them quantitatively in terms of percentage of suitable habitat and the average distance between the core areas, also taking into account the amount of unsuitable habitat.

Finally, we compared the spatial correspondence of our corridors with the sub-regional JCUs originally derived from a combination of GIS and expert opinion

(Sanderson et al. 2002; Zeller 2007). We also examined the spatial distribution of protected areas in relation to our corridors.

3.3 Results

3.3.1 Mapping and data analysis

We uncovered 206 jaguar records, 161 of which had geographic location (31 female records, 81 males, and 49 without sex information). Most points were recorded with camera traps (50.31%). Filtering and resampling led to 84 unique observations (22 females, 26 males, and 36 without sex information). Most observed records were associated with the land covers designated as evergreen tropical forest (72.78%), the sub-evergreen tropical forest (10.76%) and sub-deciduous tropical forest (9.46%), while fewer were within the deciduous tropical forest (1.90%). Note that available records in wetlands represented 4.43% and the only jaguar recorded in a mangrove association was a female (0.63%).

3.3.2 Potential habitat model

The performance of all models was excellent based on AUC, with a slightly higher value for either the female or the male models than for the comprehensive one, despite its larger sample size. The average training AUC for the comprehensive model was 0.889 (±0.047), female model AUC was 0.928 (±0.014), and male model AUC 0.942 (±0.042) (Figures 3.2, 3.3, and 3.4).

From the jackknife analysis of the contribution of predictors in MaxEnt, LULC was consistently a good predicting variable accounting for 21.8% of the variance for the comprehensive model, 61.9% for the females and 38% for the males. The tropical evergreen forest was the land cover with higher contribution for all models. The probability of finding female jaguar was generally ≥ 0.5 for tropical evergreen, wetlands, and mangroves. The probability of finding male jaguars was high for tropical evergreen and moderate for wetlands and pasturelands. The comprehensive model resulted in mean probability ≥ 0.5 for four LULC including tropical evergreen, sub-evergreen, wetlands and mangroves. When combining LULC with soils and precipitation the contribution increased to 61.2%, 86.2%, and 66.5% for the comprehensive model, the female and the male respectively. Although probability of presence increased with distances to anthropogenic features for all models, the effect of the proximity to human settlements and to roads was more important for the comprehensive model and for the males (38.8%, and 33.5% respectively) than for the females (13.8%).

3.3.3 Configuration of potential habitats

All models showed that highly suitable areas were scarce but their amount was comparable among models, covering 7%, 11%, and 5% of the landscape for the comprehensive, female, and male model respectively. However, there was considerable variation among the models in terms of suitable vs. unsuitable patches, the comprehensive model predicting 73.6% of the landscape as suitable (all suitable classes included), whereas the female model predicted only 35.4%, and the male model 34.1%. The difference is mostly due to low suitability patches in the comprehensive model that became unsuitable in the sex-based model. Despite the variation in the amount of unsuitable area predicted between the three models, the percentage and distribution of suitable areas of all models had similar spatial configuration, aligned from southwest to northeast.

In terms of suitability, habitats were less fragmented for the female model than for the others. The average patch size for the highly suitable areas was comparable in the three models (118.6, 118.8, and 95 km^2 for the comprehensive model, the female and the male respectively) but the size of the largest patch varied from 2,460 km^2 in the comprehensive model, to 6,360 km^2 for the female model, and 841 km^2 for the male model. That resulted in fewer but larger patches for the females than for the male or comprehensive model (Table 3.2). As described in the methodology this accounts for core habitats, so if habitat of lower suitability is added patches could be larger.

3.3.4 Habitat corridors

The connectivity analysis was done only for the comprehensive model as it integrates information about the two sexes, and the four nodes were determined regardless of sex. The best corridors (characterized by greater amount of highly suitable areas and larger habitat patches) were the one from Calakmul to Sian Ka’an (CA – SK) with 50% of core habitat (average patch size 350±235.33 km^2), followed by Sian Ka’an to Ria Lagartos (SK – RL) with 42% of core habitat (average area 388.40±480.62 km^2). These two corridors had also the shortest distance between core habitats (3.37±1.79 km and 7.39±4.66 km respectively). The corridor connecting northern locations from Ria Lagartos to Ria Celestun (RL – RC) had the poorest habitat conditions with only 2% suitability and smaller patches (14±9.16 km^2) and also the longest distance between core habitats (146.19±184.22 km^2). The two corridors crossing the center of the peninsula, connecting Calakmul to Ria Celestun (CA – RC), and Sian Ka'an to Ria Celestun (SK – RC), and had an intermediate amount of suitable versus unsuitable areas (23.8%, 10.4% respectively) (Figure 3.5, 3.6, and Table 3.3).

We considered each of five sub-regional JCUs for comparison with our corridors. They were: Calakmul, Ticul – Bala'an K'aax, Sian Ka'an, Petenes – Palmar, Dzilam – Yum Balam. There was between 36% and 90% overlap between the area included in a particular JCU and our proposed corridors (70±21%). The Sian Ka'an JCU and the SK – RL corridor had the greatest overlap, and the Ticul – Bala'an K'aax JCU and the SK – RC corridor had the least. We found that only 23.5% of the available core habitats were located within protected areas, as opposed to our corridors which include 91.8% of core habitats. Of the total area of our corridors regardless of habitat suitability, 17% falls in areas already under protection in the entire system of protected areas.

4. Discussion

We developed a regional approach to highlight the most suitable habitat for jaguars based on ecological modeling and GIS, which allowed us to determine potential corridors. We found that the distribution of highly suitable habitat is aligned from southwest to northeast of the Yucatan peninsula, mostly outside protected areas. The models were generally able to capture the combined effect of environmental and anthropogenic features (e.g., LULC, the proximity to roads and density of human settlements). We have high confidence in the areas predicted as highly suitable habitat, but caution should be taken for the areas designated as unsuitable and of low suitability value. Although we used a sufficient set of observations, the distribution of the available records is clumped in what we designated as "nodes" and despite the variation among observations, a good percentage of our jaguar records are associated with the evergreen tropical forest. This could have resulted in lower predicted probability of presence for areas that should be considered as "unknown" status, e.g., fewer records in the deciduous tropical forest. For example, short forest areas in and around Calakmul are seasonally inundated, the access is harder for larger animals and humans, a condition that could benefit preys that find shelter for part of the year there since the surrounded area has high hunting pressure (Reyna-Hurtado & Tanner 2005). The short forest is thought to be used seasonally by the female jaguars when it is no longer inundated given its prey abundance (Conde et al. 2010). If a larger number of preys is available along with lower hunting pressure by humans, those areas could become highly important for jaguars and not just as secondary habitat. We recommend more research in areas where jaguars are thought to be present regardless of the protection status. Even agriculture and cattle land are been used more by male than female jaguars (Conde et al. 2010).

Information from the sex-based models must be interpreted with care since sample size was low, especially for females. Sex-based models can provide important information especially for felids with strong differences in habitat preferences for example the female vs. male lions (Jhala et al. 2009). The sex-based samples resulted in models that discriminated better between suitable and unsuitable habitats than for the comprehensive model, and LULC was a better predictor for females than for males. Highly suitable patches were also much larger for the female. Behavior in terms of habitat selection is known to vary between sexes for the jaguar, with the females being considered generally less mobile than the males (Colchero et al. 2011). We propose to further investigate the potential suitable habitat for jaguars by sex at a regional scale as information becomes available to improve our knowledge of habitat selection.

We used two areas of comparable number of records and land cover (Ria Lagartos and Sian Ka'an record nodes), but with different availability of suitable habitat patches to illustrate some aspects of our findings. LULC was the most important predictor, but the other variables also contributed to habitat classification. The node near Ria Lagartos BR occurs in an area of higher road density and number of human settlements, whereas habitats found close to Sian Ka'an BR have higher suitability despite human presence. Land use changes resulted in less suitable habitat conditions, demonstrated by the increasing predation on cattle reported in the area and greater pressure of human-carnivore conflicts especially in the proximities of human settlements (Chávez & Zarza 2009). On the contrary, habitats from the southwest to the northeast have been maintained by community arrangements for forest management.

Portraying habitat and connectivity conditions has been a useful tool in the conservation and management of large and wide-ranging felids such as the tiger (Imam 2009; Xiaofeng et al. 2011), the lion (Jhala et al. 2009), and the leopard (Gavashelishvili & Lukarevskiy 2008). Evidence from DNA analysis reveals that the jaguar is the only large, wide-ranging carnivore with no subspecies (Eizirik et al. 2001; Ruiz Garcia et al. 2006), suggesting that populations are still functionally connected. Our study suggests that, in the Yucatan, this functional connectivity largely depends on the maintenance of suitable corridors outside protected areas, whereas core jaguar populations have been monitored mostly within or in the proximity of protected areas. There is evidence that the structural corridors that we identified are indeed being used by jaguars. For instance, recent scats samples indicating the presence of jaguars have been collected within the CA-SK and SK-RL corridors (Palomera and Chávez in prep.). However, the reduction of suitable areas resulting in habitat fragmentation could affect the movement patterns and gene flow causing genetic drift in isolated populations, as demonstrated in the remnant jaguar population of the Atlantic Forest region (Haag et al. 2010). Isolation can also result in higher vulnerability to land use changes creating habitat fragmentation and increasing hunting pressure with potential negative consequences on the food chain from the disappearance of top predator (Estes et al. 2011). For instance, cheetahs could have suffered from higher vulnerability to disease outbreaks caused by inbreeding depressions (O'Brien et al. 1985), although recent evidence seems to contradict that (Castro-Prieto et al. 2011). In our case, jaguar populations near Ria Celestun BR could have been more vulnerable if they became trapped in an area that offers limited connectivity through highly suitable habitats for safe movement. The jaguar records from this area are older than most observations we have and would need to be validated with current observations. Monitoring functional connectivity among the populations identified in the Yucatan would be important and the structural corridors that we identified provide a spatial framework for doing so. Our approach is comparable to the global strategy to evaluate habitat connectivity and fragmentation for carnivores based on suitable habitat models (Crooks et al. 2011; Rondinini et al. 2011b), except that we aim to understand regional dynamics. For any SDM exercise it is important to select the set of variables that will capture the habitat requirement of the species. For example, a study of jaguar distribution in Brazil showed that where prey was abundant the social organization and interspecific competition could be best represented by spatial models (de Azevedo & Murray 2007). In our case, data about prey distribution or poaching pressures on jaguars is not available. Thus, we cannot expect that our models will fully capture all biotic and abiotic interactions. Nevertheless, our results can be useful to highlight areas of potential opportunities or conflicts for jaguar conservation in a human-dominated landscape and to target areas for further jaguar surveys. It would be very important though to validate the habitat classification from our models based on a random field sampling of patches for all habitat suitability categories. Doing so could help us understand the value of different land covers as more jaguar data becomes available. Our methodology can also be replicated in other landscapes to assess habitat availability and its connectivity while understanding the process and patterns that maintain habitat conditions for the species under study.

Our suitable habitat models and corridors support the potential value for conservation of productive lands since most suitable habitats for jaguars have been found outside protected areas in this study. However this is also where we are likely to have more conflict caused by the interaction between carnivores and humans, these are considered as one of the main threats for jaguar conservation (Sanderson et al. 2002). There are studies that have addressed that issue in depth (Rabinowitz 1986; Rabinowitz 2005; Chávez & Zarza 2009) and the aim of the present study was to assess the distribution and availability of the suitable jaguar habitat not of the conflict areas. Nevertheless our results can inform monitoring and management efforts in areas outside protected reserves and our maps could be overlaid with conflict maps to identify areas for intervention and mitigation.

The combination of land uses that favor community organization and institutional incentives to consolidate community-managed forest enterprises have lead to better habitat conservation, while slowing the deforestation rate (Klooster 1999; Bray 2003, 2006; Bray et al. 2008; Ellis & Porter Bolland 2008; Durán et al.

2010). There are examples where management and legislation can revert the negative impacts of human encroachment to allow carnivore persistence at high human densities, as has been the case in parts of North America and Europe (Linnell et al. 2001). The implementation of management practices to maintain connectivity among core habitat for the jaguar could make in the long term the Yucatan a model landscape for conservation actions compatible with production activities. We hope that the spatially explicit information provided in this study will help practitioners and conservation biologists work towards a better coexistence of jaguars and humans.

Table 3. 1 Predictors used for the potential habitat model for jaguars.

Name	*Scale*	*Source*
Land use and land cover (LULC)	1: 250 000	National forest inventory SEMARNAP
Soil types	1: 1 000 000	CONABIO
Mean annual precipitation	30 arc-seconds $\approx$1 km^2 grid	WorldClim dataset www.worldclim.org
Distance from paved roads	1:1 000 000	INEGI
Distance from human settlements above 200 inhabitants	1: 1 000 000	INEGI

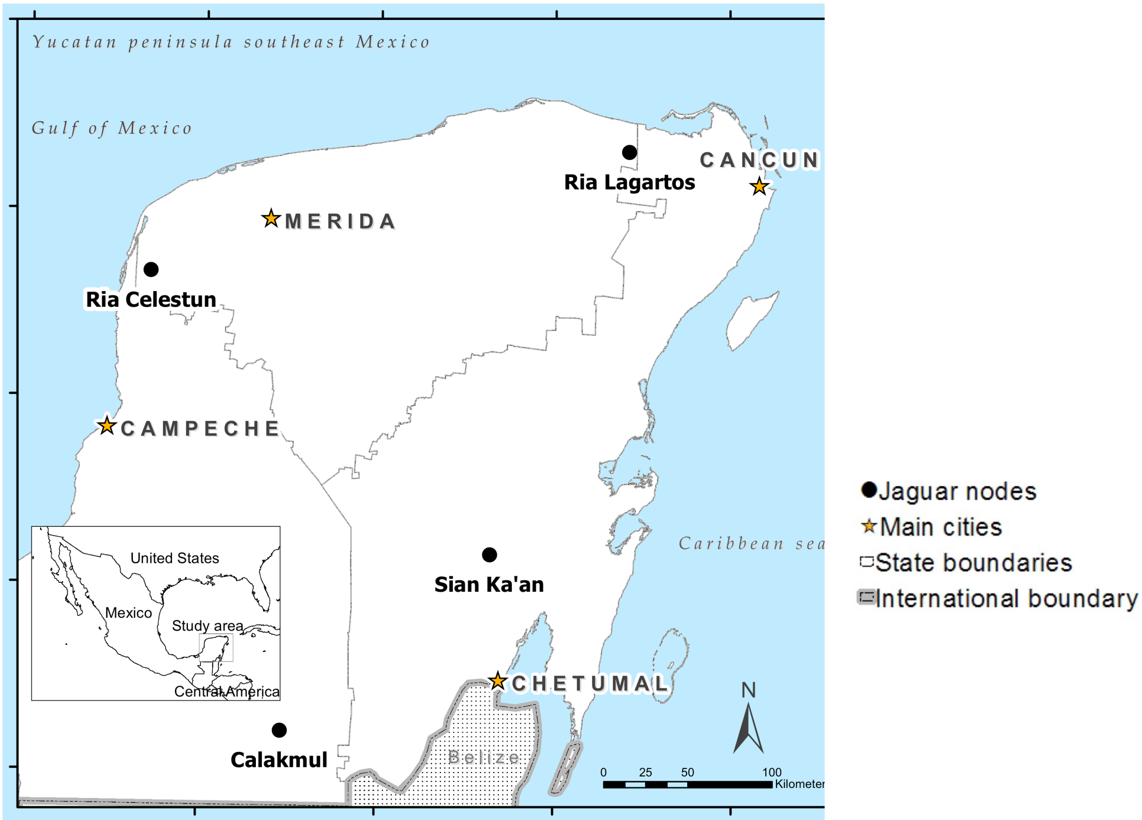
Table 3. 2 Class metrics from Fragstats analysis for each habitat suitability class and for each model.

Name of potential habitat model	*Habitat suitability class*	*Number of patches*	*Average patch size (km^2)*	*Largest patch per class (km^2)*	*Total area (km^2)*	*Average distance to the ENN (km)*	*Percentage of landscape (%)*
Comprehensive	Unsuitable	158	210.4	14,375	33,238	6.0	26.4
	Low	92	761.6	64,229	70,069	4.0	55.7
	Moderate	227	59.1	1,562	13,417	5.4	10.7
	High	76	118.6	2,460	9,017	7.0	7.2
Female model	Unsuitable	250	324.8	70,024	81,203	4.6	64.6
	Low	150	12.6	153	1,894	8.7	1.5
	Moderate	188	147.8	6,605	27,788	4.7	22.1
	High	124	118.8	6,360	14,727	6.2	11.7
Male model	Unsuitable	149	556.1	71,710	82,865	3.8	65.9
	Low	240	103.6	9,011	24,855	4.8	19.8
	Moderate	173	68.2	1,856	11,805	6.0	9.4
	High	65	95.0	841	6,174	9.6	4.9

Table 3. 3 Spatial characteristics of potential corridors in terms of available core habitats.

	Core habitat patches		
Name of habitat corridors	*Number of patches*	*Average patch size (km^2)*	*Average distance (km)*
Calakmul - Sian Ka'an (CA – SK)	5	358.00±235.33	3.37±1.79
Sian Ka'an - Ria Lagartos (SK – RL)	5	388.40±480.62	7.39±4.66
Calakmul - Ria Celestun (CA – RC)	12	62.33±67.62	38.57±99.20
Sian Ka'an - Ria Celestun (SK – RC)	5	71.60±74.17	54.59±51.54
Ria Lagartos – Celestun (RL – RC)	3	14.00±9.16	146.19±184.22

Figure 3. 1 Study area in the Yucatan peninsula showing the distribution of jaguar occurrences. The four nodes for corridor analysis are identified.



Yucatan peninsula southeast Mexico
Gulf of Mexico
Ria Lagartos
CANCUN
MERIDA
Ria Celestun
CAMPECHE
United States
Mexico
Study area
Central America
Caribbean sea
Sian Ka'an
CHETUMAL
Calakmul
Belize
N
0 25 50 100
Kilometer
Jaguar nodes
Main cities
State boundaries
International boundary

Figure 3. 2 Comprehensive potential habitat model for jaguars in the Yucatan peninsula using the full set of occurrences regardless of sex information (AUC = 0.889±0.047).

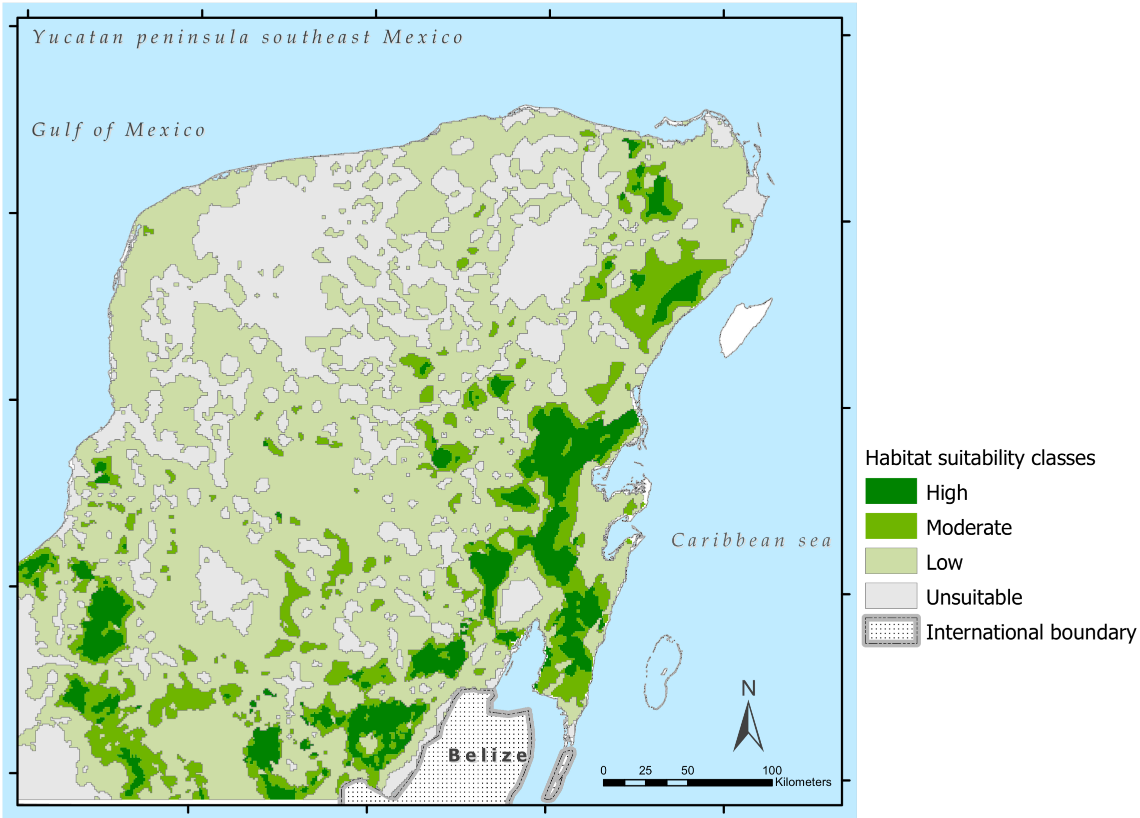
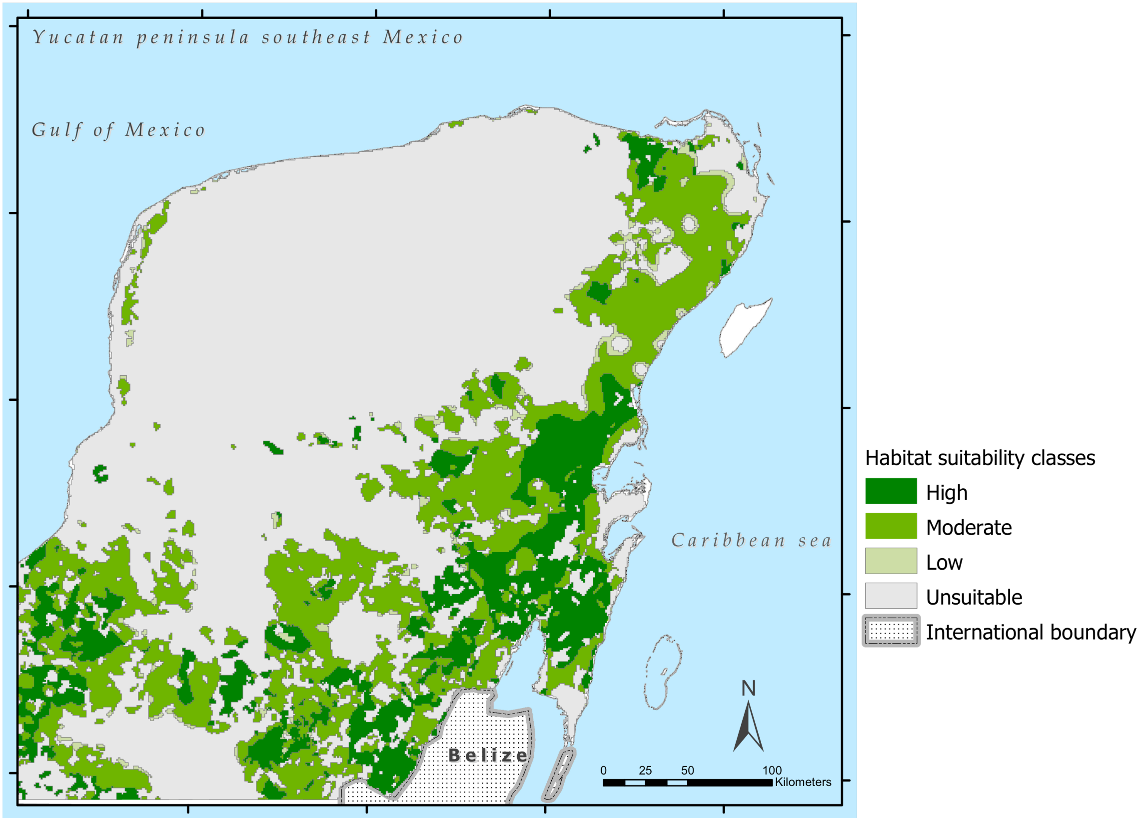

Yucatan peninsula southeast Mexico
Gulf of Mexico
Caribbean sea
Belize
Habitat suitability classes
High
Moderate
Low
Unsuitable
International boundary
N
0
25
50
100
Kilometers

Figure 3. 3 Female-based potential habitat model for jaguars in the Yucatan peninsula (AUC = 0.928±0.014).



Yucatan peninsula southeast Mexico
Gulf of Mexico
Caribbean sea
Belize
N
0
25
50
100
Kilometers
Habitat suitability classes
High
Moderate
Low
Unsuitable
International boundary

Figure 3. 4 Male-based potential habitat model for jaguars in the Yucatan peninsula (AUC = 0.942±0.042).

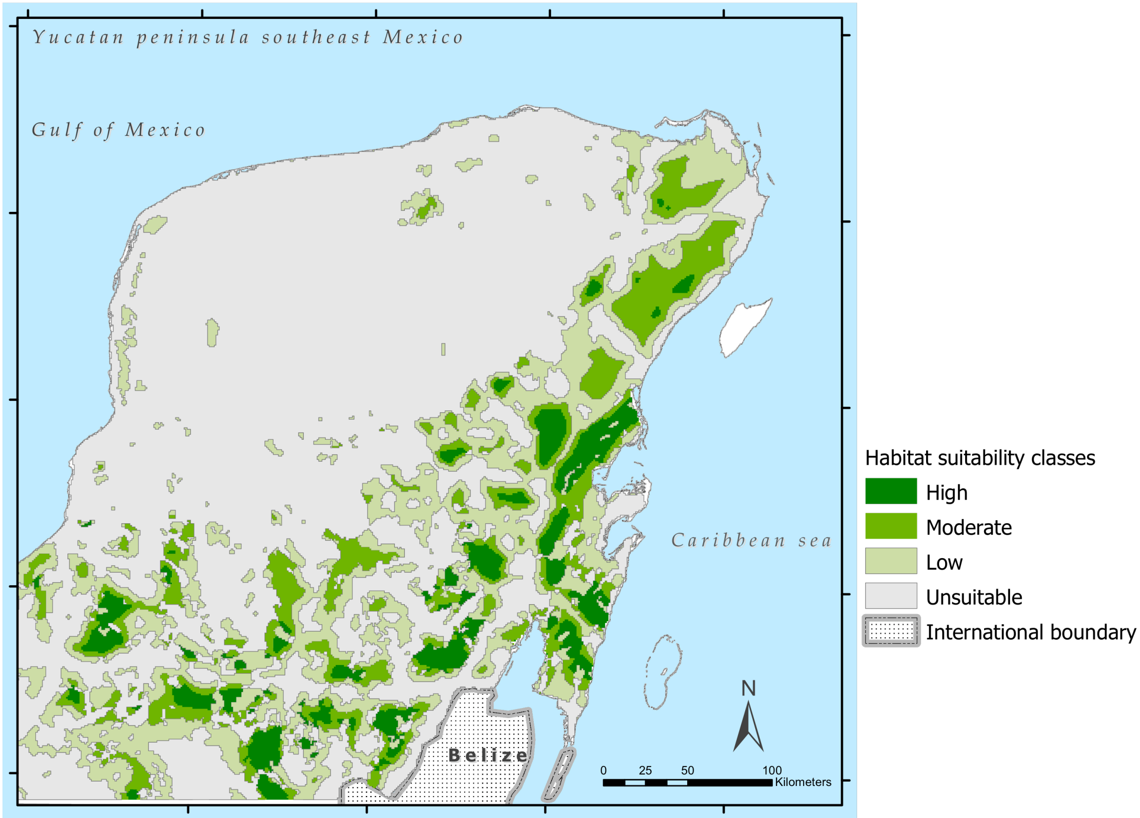
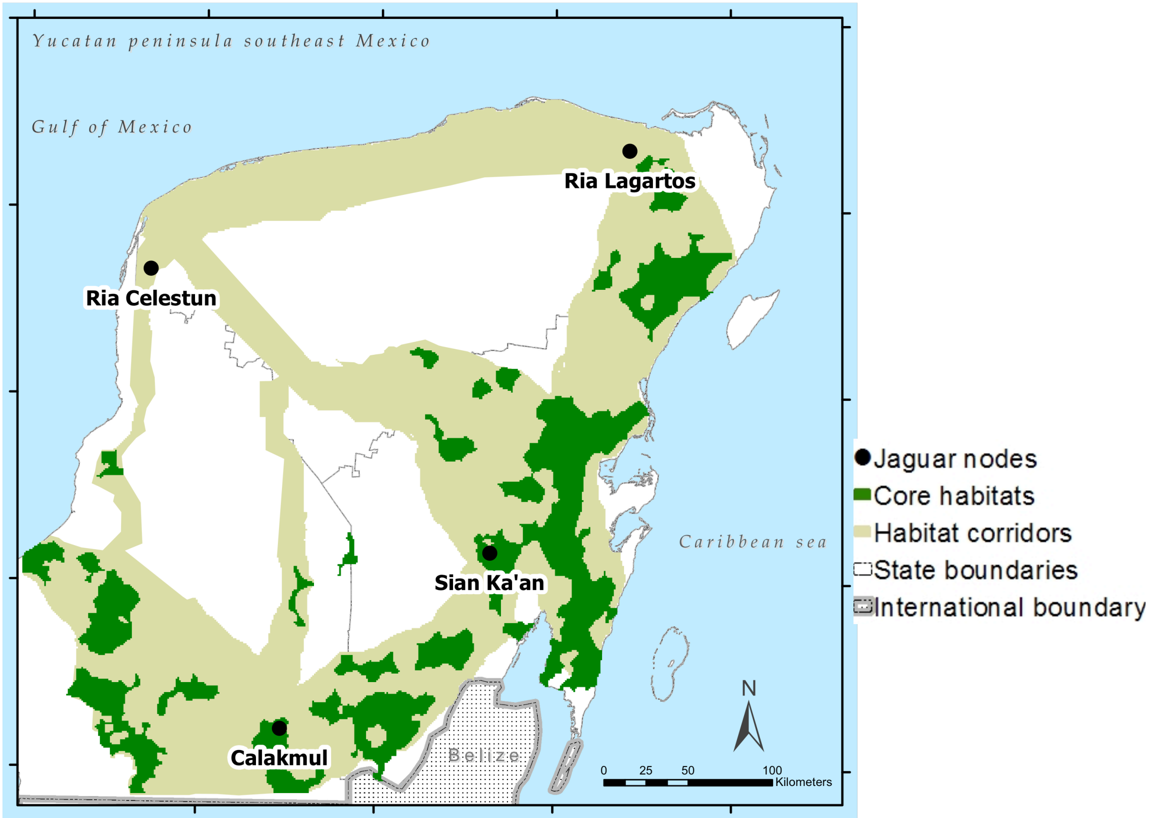
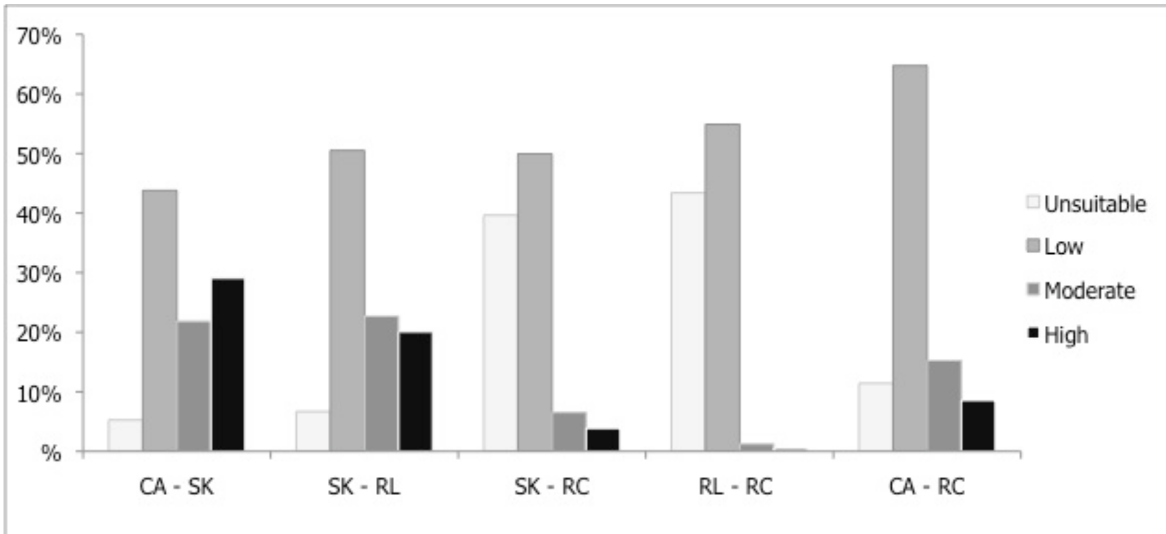

Yucatan peninsula southeast Mexico
Gulf of Mexico
Caribbean sea
Belize
N
0 25 50 100
Kilometers
Habitat suitability classes
High
Moderate
Low
Unsuitable
International boundary

Figure 3. 5 Potential corridors for jaguars between nodes. The corridors were named according to the nearest biosphere reserve were nodes were found.



Yucatan peninsula southeast Mexico
Gulf of Mexico
Ria Lagartos
Ria Celestun
Sian Ka'an
Calakmul
Belize
Caribbean sea
N
0
25
50
100
Kilometers
Jaguar nodes
Core habitats
Habitat corridors
State boundaries
International boundary

Figure 3. 6 Percentage of suitable habitat by corridor. Darker bars indicate higher habitat quality. CA = Calakmul; SK = Sian Ka'an; RL = Ria Lagartos; RC = Ria Celestun.


70%
60%
50%
40%
30%
20%
10%
%
CA - SK
SK - RL
SK - RC
RL - RC
CA - RC
Unsuitable
Low
Moderate
High

Chapter 4

Discussion and conclusion

In chapter 3, I showed through spatial analysis and modeling that highly suitable jaguar habitat has become scarce in the Yucatan peninsula and is mostly concentrated along the east coast. There is still the potential for structural connectivity among core populations, but this connectivity has been much reduced in the north and western part of the peninsula. Suitable habitat models derived from sexed records are informative but may still be limited by the lack of relevant records. The remaining suitable patches are largely concentrated towards the east, along the Caribbean coast, which could have implications for conservation and development plans. Whereas community forestry may have led to the maintenance of a forest cover suitable to jaguars, other development activities along the coast, like mass tourism, may not be compatible with jaguar conservation. Additionally, habitat in other areas less impacted by tourism might become compatible as well, as we promote low impact cattle grazing practices to reduce human-jaguar conflicts. Even though we observed higher suitability on evergreen tropical forest, we should also remember that jaguars occur in various types of forest along with many other species, thus it is important not to divert resources away from those equally important ecosystems. It would be important to consider sustainable practices that can reconcile the need to sustain livelihood with our stewardship of the land and of its biodiversity.

The approach developed in this study is cost-effective, reduces subjectivity by means of computer-based analyses, and it is a novel contribution to the development of corridors. The models offer a very useful first approximation of the distribution of suitable habitats for planning future field surveys, conservation and management initiatives. We used a robust modeling technique (MaxEnt) to predict the potential distribution for presence-only data (Phillips et al. 2006; Peterson et al. 2007; Phillips 2008). We selected best available records compensating for spatial autocorrelation by filters and randomization to minimize commission and omission errors. The resultant information could be used to designate areas where to allocate resources for research, field surveys and monitoring, or to promote land uses or development compatible with jaguar conservation.

Although the model showed that the more suitable habitat is overlapping the evergreen tropical forest, we should not neglect the importance of other ecosystems where there is not enough jaguar data. Moreover, the presence of core habitats outside the protected areas indicate the need to make conservation sustainable, and make the producers and farmers (*ejidatarios*) our allies in conservation by promoting productive practices that are both economically profitable and sustainable in the long run. We should not, however, deviate resources away from areas that are already protected. We learned that suitable habitat for jaguars is not dependent on a type of land cover, and jaguars are indeed using human dominated lands, but whether they are in conflict or in coexistence with humans is a different story. There are biological and ecological interactions (including with humans) that cannot be captured by models; however, as more information becomes available we should incorporate it to make more robust predictions about the spatial configuration of suitable habitat.

Finally, we hope that this study will contribute to regional, national, and international efforts for jaguar conservation (Sanderson et al. 2002; Chávez & Ceballos 2006; Zeller 2007; Rabinowitz & Zeller 2010; Rodriguez-Soto et al. 2011) and to global strategies to understand habitat of terrestrial mammals (Rondinini et al. 2011a).

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Appendix I Description of jaguar records used for the potential habitat models

Source	*Number of records per state*			*Database type*	*Period*	*Record type*	*Total number of records*
CONABIO www.conabio.com.mx	3	14	4	Institutional	1901-1990	Biological collection	21
WILCHIS investigacion.izt.uam.mx/mamiferos	12	6	1	Online database	1969, 1970 or not available	Biological collection	19
Thesis (Pereira Lara 2006)	8	0	0	Published work	1991-2010	Indirect observations (footprint)	8
UNAM (Chávez & Zarza 2009)	6	8	22	Published work	1990-2008	Direct and indirect observations	36
UNAM (Ceballos et al. 2002; Chávez 2010)	0	20	20	Published work	1998 - 2008	Telemetry capture	40
CENJAGUAR (Unpublished data)	2	0	80	Institutional	2007 - 2010	Camera-trap	82
TOTAL	31	48	127				206

Appendix II Categories of LULC reclassified for the model from the Mexican national forest inventory classes

ID	*Category*	*Vegetation community*	*Name in the Mexican classification*	*Main species*	*% cover*
1	Tropical evergreen forest	Tall and medium forest communities including secondary succession	Selva alta y mediana perennifolia y subperennifolia y con vegetación secundaria arbustiva y herbácea	Mahogany (*Swietenia macrophylla*), Spanish cedar (*Cedrela odorata*), gum tree or zapote (*Manilkara zapota*), and Mayan nut (*Brosimum alicastrum*)	36.9
2	Tropical sub-deciduous forest	Medium height and broad-leaved including secondary succession	Selva mediana caducifolia y subcaducifolia y con vegetación secundaria arbustiva y herbácea	Guayacán (*Guaiacum sanctum*) Xu'ul de montaña (*Lochocarpus yucatanensis*)	17.9
3	Tropical sub-evergreen forest	Short communities characterized by semi-perennial vegetation including secondary succession	Selva baja subperennifolia y con vegetación arbustiva y herbácea	Gumo-limbo (*Bursera simaruba*), and Ceiba (*Ceiba schotti*) Association *Cameraria-Haematoxylon-Metopium*	7.3
4	Tropical deciduous forest	Short deciduous forest including secondary succession	Selva baja caducifolia y subcaducifolia y con vegetación secundaria arbustiva y herbácea	Ja'abin (*Piscida piscipula*) Yaytil (*Gymnanthes lucida*)	6.5
5	Wetland	Vegetation	Popal-tular	Popal (*Thalia*	2.5

		associated with water bodies		*geniculata L.*)	
6	Mangrove	Coastal vegetation including inundated areas	Manglar	Red mangrove (*Rhizophora mangle*) Buttonwood (*Conocarpus erectus*) White mangrove (*Laguncularia racemosa*) Black mangrove (*Avicennia germinans*)	2.4
7	Pastureland	Cultivated or managed grasslands, or abandoned agricultural lands	Pastizal inducido Pastizal cultivado	Grasses or graminoids	13
8	Other land uses (Urban and built-up and agriculture lands)	Human settlements Temporal agriculture with annual crops Temporal agriculture with perennial crops Irrigation agriculture Rain-fed agriculture Dry scrub and secondary vegetation Savanna Palm forest Salt and gypsum	Asentamiento humano Agricultura de temporal con cultivos anuales Agricultura de temporal con cultivos permanentes y semipermanentes Agricultura de riego (incluye riego eventual) Agricultura de humedad Selva baja espinosa y con vegetación secundaria arbustiva y herbácea Sabana Palmar	*Cyperus spp*. Palma de coyol (*Acrocomia mexicana*) Corozal (*Obyginia cohum*)	13.5

	vegetation Coastal dunes Water body No apparent vegetation	Vegetación halófila y gipsófila Vegetación de dunas costeras Cuerpo de agua Áreas sin vegetación aparente