UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE ECOLOGÍA

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ECOLOGÍA ESPACIAL DEL JAGUAR (*PANTHERA ONCA*) Y SUS IMPLICACIONES PARA LA CONSERVACIÓN DEL PAISAJE DE LA SELVA LACANDONA, CHIAPAS, MÉXICO.

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

M.C. JESÚS ANTONIO DE LA TORRE DE LARA

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CIUDAD UNIVERSITARIA, CD. MX. . **ENERO, 2017.**

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MÉXICO, D.F. ENERO 2017.

UNAM POSGRADO
Ciencias Biológicas

COORDINACIÓN

Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted, que el Subcomité de Ecología y Manejo Integral de Ecosistemas, en su sesión ordinaria del día 29 de febrero de 2016,, aprobó el jurado para la presentación de su examen para obtener el grado de **DOCTOR EN CIENCIAS**, del Posgrado en Ciencias Biológicas, del alumno **DE LA TORRE DE LARA JESÚS ANTONIO** con número de cuenta **506021350,** con la tesis titulada: **" ECOLOGÍA ESPACIAL DEL JAGUAR (*Panthera onca)* Y SUS IMPLICACIONES PARA LA CONSERVACIÓN DEL PAISAJE DE LA SELVA LACANDONA, CHIAPAS, MÉXICO "**, bajo la dirección del **DR. RODRIGO ANTONÍO MEDELLÍN LEGORRETA:**

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a 03 de noviembre de 2016

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

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A todos los jóvenes de la Selva Lacandona, de quienes depende el futuro de esta selva.

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Resumen

Entender como utilizan el espacio, a distintas escalas, las especies que se encuentran en riesgo de extinción es esencial para desarrollar los planes de manejo y conservación adecuados para estas especies con la finalidad de asegurar su persistencia a largo plazo. El jaguar (*Panthera onca*) es el mayor felino que se encuentra en el Continente Americano. Sin embargo, en los últimos cien años esta especie ha perdido más de la mitad de su distribución histórica debido tanto a la cacería directa de los jaguares como la de sus presas, así como a la pérdida y fragmentación de su hábitat. Bajo este contexto, la presente tesis espera contribuir en la conservación del jaguar desde tres perspectivas y escalas diferentes. En el primer capítulo me enfoqué en hacer una síntesis de la información más actualizada acerca del estatus de conservación de esta especie a escala continental. Para esto recopilé toda la información actualizada acerca de la distribución geográfica del jaguar, identifiqué las diferentes sub-poblaciones de la especie en el continente, estimé un tamaño poblacional para estas sub-poblaciones, evalué cada una de estas sub-poblaciones bajo los criterios de la IUCN, e identifiqué las poblaciones más amenazadas. La mayor relevancia de este análisis es que, aunque potencialmente existe una sub-población muy grande jaguares en la región de la Amazonía, prácticamente todas las demás sub-poblaciones están amenazadas ya sea por su pequeño tamaño poblacional, poca disponibilidad de hábitat, aislamiento, alta densidad humana ó bajo nivel de protección. Este análisis ilustra que si no se toman las medidas pertinentes en un futuro próximo, la mayor parte de las sub-poblaciones de jaguar muy probablemente se extinguirán. En el segundo capítulo me enfoqué a describir y comparar la ecología espacial de los jaguares y de los pumas (*Puma concolor*) en la región de la Selva Lacandona. Utilizando la información recopilada en campo por medio de collares con GPS, en este capítulo describo la ecología espacial de jaguares y pumas en un bosque lluvioso tropical dominado por actividades humanas. Los resultados mostraron que los jaguares utilizan áreas muchísimo más extensas que los pumas. Además, los jaguares y pumas que presentaron traslape en sus áreas de actividad mostraron muy poco traslape en sus áreas núcleo y evitaron utilizar los mismo sitios al mismo tiempo. Los pumas mostraron mayor actividad en los periodos del día con más luz, en cambio lo jaguares fueron más activos en los periodos del día con menos luz y esta separación temporal probablemente facilita la coexistencia de estas dos especies. Este estudio

sugiere que la destrucción y fragmentación del hábitat probablemente tiene un efecto más severo en los jaguares que en los pumas y que los jaguares requieren de áreas más extensas de bosque bien conservado en comparación con los pumas. Para conservar a los jaguares a largo plazo en la región de la Selva Lacandona, grandes áreas con bosque en buen estado de conservación tienen que ser aseguradas. De acuerdo con los datos obtenidos es necesario conservar parches de selva de al menos 180 km^2 para que una hembra de jaguar pueda cumplir con sus requerimientos espaciales. Finalmente, ya que uno de los principales retos de la ciencia aplicada a la conservación es lidiar con la fragmentación de los hábitats de las poblaciones, en el tercer capítulo me enfoqué en aplicar el conocimiento de la ecología espacial de los jaguares para diseñar una estrategia de conectividad para mantener la integridad de la población de esta especie en la región de la Selva Maya. Utilizando datos de jaguares seguidos por medio de radio-telemetría de GPS e información obtenida por medio de percepción remota, se identificaron los sitios con una mayor probabilidad ocurrencia de la especie en el paisaje del sur de la Selva Maya. Este análisis de idoneidad de hábitat lo combiné con un modelo de probabilidad de movimiento para evaluar la conectividad de los parches de hábitat a lo largo de la distribución de la especie en este paisaje. Los sitos que tuvieron una mayor probabilidad de ser ocupados por los jaguares y los sitos más adecuados para funcionar como corredores son aquellos que conservan mayor cobertura forestal y aquellos que se encuentran más alejados de actividades humanas. Por medio de este análisis identifiqué los parches de hábitat y los corredores que son necesarios para establecer una estrategia de conectividad para la especie en la región, así como las prioridades de manejo y conservación para este paisaje. Bajo el esquema de desarrollo humano actual en la región, se espera que esta información aporte elementos críticos para crear una propuesta de desarrollo la cual sea compatible con la conservación del jaguar y los paisajes naturales del sur de la Selva Maya.

Abstract

Understanding how the endangered species use the space at different scales is essential to develop proper management and conservation plans to ensure their persistence in long-term. The jaguar (*Panthera onca*) is the largest felid in the American continent. However, this species has disappeared from more than half of its distribution range due to direct hunting, prey depletion and fragmentation and destruction of its habitat. Under this context, the present thesis contributes to jaguar conservation through three different perspectives and scales. In the first chapter, I updated the jaguar conservation status at continental scale. To this I gather all the available information of the current jaguar distribution range, I identified the different subpopulations of the species throughout its range, I estimated the subpopulation sizes, I evaluated these subpopulations under the IUCN criteria, and finally, I identified the most threatened jaguar populations. The major outcome of this analysis is that, although there is very large jaguar subpopulation in the Amazon region, virtually all other jaguar subpopulations are threatened, either by their low population size, limited habitat availability, high human density, isolation and low level of protection. This analysis illustrated that if suitable measures are not taken, most of jaguar populations would disappear in a near future. In the second chapter, I focused in describing and comparing the spatial ecology of jaguars and pumas (*Puma concolor*) at the Greater Lacandona Ecosystem region. Using satellite GPS collars, I compare the spatial ecology of jaguars and pumas in a tropical rainforest dominated by human activities in southern Mexico. I found that jaguars had home ranges that were 2 to 6 times larger than those of pumas. Jaguars and pumas with overlapping home ranges showed little overlap of core areas and avoided using the same sites at the same time, suggesting territoriality and avoidance. Further evidence comes from pumas exhibiting greater movement rates during the periods of the day with more light and jaguars during the darkest. This temporal separation probably facilitates their coexistence. My data suggest that habitat destruction and fragmentation has more severe effects on jaguars than on pumas, since jaguars require larger areas of conserved forest compared with pumas to meet their spatial requirements. Thus, to conserve jaguars in this region, large areas of primary forest should be preserved. According to our estimates, patches of at least 180 km² of primary forest are required to provide the annual spatial requirements of female jaguars. Finally, since one of the

most important and significant challenges in science applied to conservation is to deal with fragmentation of wildlife habitats, in the third chapter I aimed in applying the spatial ecology of jaguars to design a strategy of connectivity to maintain the viability of this species at the Mayan Forest landscape. Using the data obtained through GPS satellite radio collars and information obtained through remote sensing, I identified the sites with a high probability of jaguar occupancy, and I integrated this analysis of habitat suitability with a movement probability model to assess the connectivity across the species distribution at the region. The sites with a higher occupancy probability and the most suitable sites to act as corridors are those with a higher forest cover and the sites located a greater distances from human activities. With this analysis I identified the habitat patches and corridors needed to establish the conservation and management priorities for this fragmented landscape. Under the accelerated human development in this region, this strategy to maintain the connectivity will be crucial for decisions makers from Mexico and Guatemala to invest in programs of sustainable development compatible with jaguar conservation and the Mayan Forest landscape.

1. Introducción general

1.1 Evolución y biogeografía de la familia Felidae

Con 37 especies existentes, la familia Felidae, es el grupo más especializado dentro del Orden Carnívora ya que se alimentan casi exclusivamente de carne (Kruuk 1986; Sunquist & Sunquist 2009). Frecuentemente los félidos son llamados hipercarnívoros ya que prácticamente se alimentan únicamente de otros vertebrados (Meachen-Samuels & Van Valkenburgh 2009a; Slater & Van Valkenburgh 2009; Sicuro & Oliveira 2011). Todas las especies representantes de esta familia enfrentan las mismas tareas de acechar, capturar, someter y consumir a sus presas. Por esta razón y probablemente por su reciente evolución, la morfología de estas especies es marcadamente similar, aunque los pesos de estas especies varíen en dos rangos de magnitud (Kruuk 1986; Kitchener et al. 2010). Desde las especies más pequeñas como *Prionailurus rubiginosus* y *P. planiceps* que pesan aproximadamente 1.5 kg, hasta el león (*Panthera leo*) y el tigre (*P. tigri*s) donde los machos más grandes pueden llegar a pesar hasta 300 kg (Sunquist & Sunquist 2009; Kitchener et al. 2010; Sicuro & Oliveira 2011).

Los primeros felinos se originaron en el Oligoceno aproximadamente hace 28.5 millones años (Ma). Para algunos autores, el primer felino bien establecido fue *Proailurus*, el cual era del tamaño de un gato montés (e. g. *Lynx rufus)* y prácticamente tenía la misma forma de un felino moderno (Turner 1997; Hunt Jr. 1998; Werdelin et al. 2010). La diversificación filogenética de los felinos comienza a partir de un complejo de especies denominado *Pseudaelurus*, hace aproximadamente 16-17 Ma. Este complejo tuvo especies representadas en Europa, Arabia, Asia y Norteamérica e incluye a los ancestros de las especies que evolucionaron posteriormente (Rothwell 2003; Werdelin et al. 2010). A partir de *Pseudaelurus* se diversifican dos ramas en la evolución de los felinos. La primera dio origen a los dientes de sable (subfamilia Machairodontinae) hace 12 Ma en Eurasia (Turner 1997; Werdelin et al. 2010). Los miembros más recientes de los dientes de sable (*Smilodon*) se extinguieron al final de la última glaciación hace 10,000 años (Turner 1997; DeSantis et al. 2012). La otra rama, que evolucionó de manera paralela, fue la de los gatos con dientes cónicos (Subfamilia Felinae). Esta rama se originó aproximadamente hace 11 Ma y de aquí derivan todas las especies de felinos existentes actualmente (Turner 1997; Werdelin et al. 2010).

El estudio de Johnson et al. provee una base firme para entender las relaciones y la evolución de las 37 especies existentes y las agrupa en ocho linajes diferentes (Johnson et al. 2006). El linaje más ancestral, el cual denominaremos "Panthera", ramificó hace aproximadamente 10.8 Ma de los primeros felinos con dientes cónicos que existieron, e incluye a las cinco especies del género *Panthera* y a las dos especies de panteras nebulosas del género *Neofelis*. El siguiente linaje "Bay Cat" está compuesto por tres especies asiáticas (*Pardofelis mamorata*, *Catopuma badia*, *C. temminckii*) y divergió hace aproximadamente 9.4 Ma, seguido del linaje "Caracal" que se ramificó hace 8.5 Ma y que está compuesto por tres especies africanas (*Caracal caracal*, *Profelis aurata* y *Leptailurus serval*).

El siguiente linaje, que llamaremos "Ocelote", se originó hace 8 Ma e incluye a las siete especies de pequeños felinos del genero *Leopardus*. El quinto linaje "Lince" está compuesto por las cuatro especies del genero *Lynx*, el cual se separó hace 7.2 Ma, seguido del linaje "Puma" que incluye a las dos especies del genero *Puma* (*P. concolor* y *P. yagouaroundi*) y al guepardo (*Acinonyx jubatus*) el cual se separó hace 6.7 Ma. Los dos últimos linajes están compuestos por los felinos pequeños del viejo mundo, que divergieron hace 6.2 Ma. El primero, "Leopard Cat", lo forman las cuatro especies del genero *Prionailurus* y el gato de Pallas (*Otocolobus manul*) y el segundo “Felis” que lo componen las cinco especies del genero *Felis* (Johnson et al. 2006; O’Brien & Johnson 2007).

Utilizando relojes moleculares y la evidencia fósil se puede trazar una idea de cómo estas especies existentes colonizaron sus áreas de distribución actuales (Johnson et al. 2006). Aparentemente, el ancestro común de los felinos existentes surgió en Asia y las primeras divergencias del grupo ocurren con la aparición de linaje “Panthera” y subsecuentemente aparición del linaje “Bay Cat”. La primera migración ocurre cuando el progenitor del linaje “Caracal” llegó a África hace aproximadamente 5.6 a 8.5 Ma (Johnson et al. 2006; O’Brien & Johnson 2007). La segunda migración ocurre cuando el ancestro común de cinco de estos linajes (“Ocelote”, “Lince”, “Puma”, “Leopard Cat” y “Felis”) migró por estrecho de Bering hacia Norteamérica hace 8.0 a 8.5 Ma. Esta migración precede a la diferenciación de los linajes del “Ocelote”, “Puma” y “Lince” hace 6.7 a 8.0 Ma. Con la aparición del puente de Panamá hace 2.3 Ma ocurre la diversificación de varias especies, la cual es facilitada por el Gran Intercambio Biótico Americano (Webb 2006; Woodburne 2010), en este momento es cuando ocurre la tercera migración del linaje “Ocelote” a Sudamérica. Posteriormente, el ancestro de los linajes “Leopard Cat” y “Felis” migra de Norteamérica a Asia y Europa. Estas primeras cuatro migraciones se facilitaron gracias a que durante el Mioceno Tardío-Plioceno Temprano (6.4 Ma) y Plioceno Tardío-Pleistoceno Temprano (2.9 Ma), el mar descendió de 90 a 100 metros del nivel que tenemos en los tiempos modernos, permitiendo la formación de puentes entre los distintos continentes (Johnson et al. 2006; O’Brien & Johnson 2007).

Actualmente, cuatro de estos ocho linajes están presentes en las zonas geográficas donde originalmente se establecieron. Los linajes “Bay Cat” y “Leopard Cat” se encuentran limitados a Asia, el linaje “Caracal” a África (aunque *C. aurata* está presente también en la Península

Arábiga y en el suroeste de Asia) y el linaje "Ocelote", que se originó en Sudamérica, al Neotrópico (Johnson et al. 2006; O'Brien & Johnson 2007; Morales & Giannini 2010). Pero los demás linajes incluyen especies en otros continentes de donde se originaron. En el caso del guepardo, la explicación más plausible es que sus ancestros migraron de Norteamérica hacia Asia y Europa y posteriormente a África. El registro fósil indica que existieron formas similares en Europa, Asia, África y Norteamérica desde hace 3.5 Ma hasta hace 10,000 años (Van Valkenburgh et al. 1990; Turner 1997; Christiansen & Mazák 2009; Hemmer et al. 2011), pero después de las extinciones pleistocénicas todas estas especies desaparecieron, quedando solamente el guepardo distribuido en África y parte de Asia (Turner 1997). De igual manera los antecesores de los linces Euroasiático (*Lynx lynx*) e Ibérico (*L. pardinus*) pudieron haber migrado más recientemente por el estrecho de Bering hacia Eurasia hace 1.6 - 1.3 Ma (Johnson et al. 2006).

El ancestro común de las especies existentes del linaje "Panthera" apareció hace 6.4 Ma (O'Brien & Johnson 2007), y las especies de este linaje se extendieron por Asia, Europa, Norteamérica y Sudamérica. En el caso del león se tiene el registro fósil desde hace 3.5 Ma (Turner 1997). Especies hermanas estuvieron representadas en Europa y Asia (*Panthera spelea*) (Sala 1969; Tchernov & Tsoukala 1997; Yamaguchi et al. 2004; Sotnikova & Nikolskiy 2006; Sommer & Benecke 2006; Barnett et al. 2009; Stuart & Lister 2011) y América (*P. atrox*) (Yamaguchi et al. 2004; Montellano-Ballesteros & Carbot-Chanona 2009; Barnett et al. 2009; DeSantis et al. 2012), las cuales se extinguieron al final del Pleistoceno (Barnett et al. 2009), quedando solamente *P. leo* distribuido en África y parte de Asia. Los jaguares (*Panthera onca*) probablemente se originaron del jaguar europeo (*P. gombaszoegensis*), especie que estaba ampliamente distribuida por Europa y Asia durante el Pleistoceno (Hemmer et al. 2001; Lewis et al. 2010). Los registros más antiguos de esta especie datan de 1.6 Ma en Europa y los del jaguar en América de hace 850,000 mil años (Daggett & Henning 1974; Schultz et al. 1985; Turner 1997; Hemmer et al. 2001; Arroyo-Cabrales 2002). Estos intervalos de tiempo sugieren que los jaguares se originaron en Eurasia entre el Mioceno Tardío-Plioceno Temprano, con una población que se extendió posteriormente hacia Norteamérica y que consecutivamente paso hacia Sudamérica durante el Gran Intercambio Biótico Americano (Hemmer et al. 2001; Arroyo-Cabrales 2002). Los jaguares al igual que los pumas (*P. concolor*), después de colonizar Sudamérica se extinguieron de Norteamérica al final del Pleistoceno y posteriormente volvieron a recolonizar Norteamérica (Culver et al. 2000; Eizirik et al. 2001). Adicionalmente, durante el Pleistoceno se plantea que ocurrió la migración desde Eurasia de *Felis silvestris*, y de los ancestros que dieron origen a *F. margarita* y *F. nigripes* hacia África (Johnson et al. 2006; O'Brien & Johnson 2007).

1.2 Patrones de distribución y diversidad de los félidos existentes

La historia evolutiva de los felinos silvestres nos sirve para entender los patrones de distribución y diversidad de las especies existentes. Los felinos se distribuyen desde el nivel del mar hasta los 6000 m de altitud y están presentes en todos los continentes a excepción de la Antártida y Australia (Sunquist & Sunquist 2009). Actualmente, once especies se encuentran mayormente limitadas solamente a la parte tropical de Asia: *Neofelis diardi*, *Neofelis nebulosa*, *Panthera tigris*, *Catopuma badia*, *Catopuma temminckii*, *Pardofelis mamorata*, *Prionailurus bengalensis*, *Prionailurus planiceps*, *Prionailurus rubiginosus*, *Prionailurus viverrinus* y *Felis bieti*. Cuatro especies están limitadas solamente a Europa y a la parte más templada de Asia (Eurasia): *Otocolobus manul*, *Lynx lynx*, *Lynx pardinus* y *Panthera uncia*. En África, las especies limitadas solamente a este continente son: *Felis nigripes*, *Profelis aurata* y *Leptailurus serval*. Al Neotrópico (Centro y Sudamérica incluyendo las partes tropicales de México) son seis especies del genero *Leopardus* las que se encuentran limitadas a esta región: *L. colocolo*, *L. geoffroyi*, *L. guigna*, *L. jacobitus*, *L. tigrinus* y *L. wiedii*. El lince canadiense (*Lynx canadensis*) es la única especie que se encuentra limitada a la parte Neártica de Norteamérica.

Todas las demás especies incluyen poblaciones en más de dos regiones dentro de su área de distribución. El león se distribuye a lo largo del Sub Sahara en África y tienen una pequeña población en la India. El leopardo (*Panthera pardus*) tiene una distribución muy amplia, la cual abarca gran parte de África y Asia. El caracal (*C. caracal*) se encuentra en África y suroeste de Asia. El guepardo se distribuye en África en el Sub Sahara con una pequeña población en el sureste de Asia. El gato silvestre (*Felis silvestris*) es una de las especies más ampliamente distribuidas ya que se encuentra en Europa, una buena parte de Asia y en África. El gato de la jungla (*Felis chaus*) se encuentra en parte de Asia al norte de la Península Arábiga y una pequeña porción de Egipto. El gato de arena (*Felis margarita*) se distribuye al norte de África, la Península Arábiga y el Suroeste de Asia. En América, el jaguar, el ocelote (*L. pardalis*), el puma y el jaguarundi se distribuyen tanto en Norteamérica como en Sudamérica. El gato montés *(Lynx rufus*) se distribuyen en Norteamérica y el límite sur de su distribución se encuentra en la parte tropical de México.

La formación de los ensambles regionales de los félidos silvestres se ha explicado a partir de que las especies que fueron colonizando los distintos continentes ocuparon un espacio vacío con respecto a sus características morfológicas y morfométricas (morfoespacio). Especies que son morfológicamente muy similares ocupan un espacio diferente en sus área de distribución (alopatría), o si no es así, se segregan utilizando hábitats o patrones de actividad diferentes

(Morales & Giannini 2010, 2013). Por ejemplo, las especies que están representadas en el Neotrópico que tienen características morfométricas muy similares no se traslapan en sus áreas de distribución, pero en el caso del jaguarundi (*P. yagouaroundi*) morfológicamente es muy similar a las demás especies de pequeños felinos con las que convive (*L. wiedii*, *L. colocolo*, *L. tigrinus*), sin embargo, sus patrones de actividad difieren ya que éstos son diurnos y las otras especies que son nocturnas (Morales & Giannini 2010).

Los felinos los podemos encontrar en todos los tipos de hábitats, desde desiertos hasta los bosques tropicales (Sunquist & Sunquist 2009), aunque algunas especies están más asociadas a hábitats más boscosos y otras especies a hábitats más abiertos. Utilizando el área de distribución de cada especie (International Union for Conservation of Nature 2013) y los biomas terrestres (Olson et al. 2001), podemos calcular el porcentaje en cada uno de los biomas que abarca el área de distribución de cada una de las especies. Las especies que están más asociadas a hábitats abiertos (> del 80% de su distribución) son: *P. leo*, *C. caracal*, *A. jubatus*, *F. margarita*, *F. nigripes*, *P. uncia*, *O. manul* y *L. jacobita* (praderas, sabanas, matorrales y desiertos). Las especies que están asociadas a hábitats boscosos son: *P. tigris*, *N. nebulosa*, *N. diardi*, *P. marmorata, C. temminckii*, *P. planiceps*, *P. bengalensis*, *P. viverrinus*, *L. pardinus* y *L. guigna* (bosques tropicales, bosques secos y bosques templados). Las zonas con una mayor riqueza de especies de felinos en el mundo (hotspots) se encuentran en los bosques tropicales de Asia, el centro de la India y en la transición entre los Andes y el Amazonas en Perú y Bolivia (Figura. 1).

1.3 Estatus de conservación de la familia Felidae

Actualmente, muchas de las especies de felinos silvestres enfrentan problemas de conservación a causa de presiones antropogénicas (Woodroffe & Ginsberg 1998; Cardillo et al. 2004; Karanth &

Chellam 2009). La declinación de estas especies se debe a causas históricas como la cacería furtiva y la retaliativa, pérdida de hábitat y a su limitada capacidad de respuesta a las reducciones poblacionales debido a sus bajas tasas de crecimiento demográfico (Woodroffe & Ginsberg 1998; Treves & Karanth 2003; Cardillo et al. 2004; Inskip & Zimmermann 2009). Entre las características que los hacen vulnerables están su especialización en la alimentación y uso de hábitat, sus bajas densidades poblacionales y las grandes áreas requeridas para su supervivencia (Noss et al. 1996; Weber & Rabinowitz 1996; Woodroffe & Ginsberg 1998; Cardillo et al. 2004; Karanth & Chellam 2009).

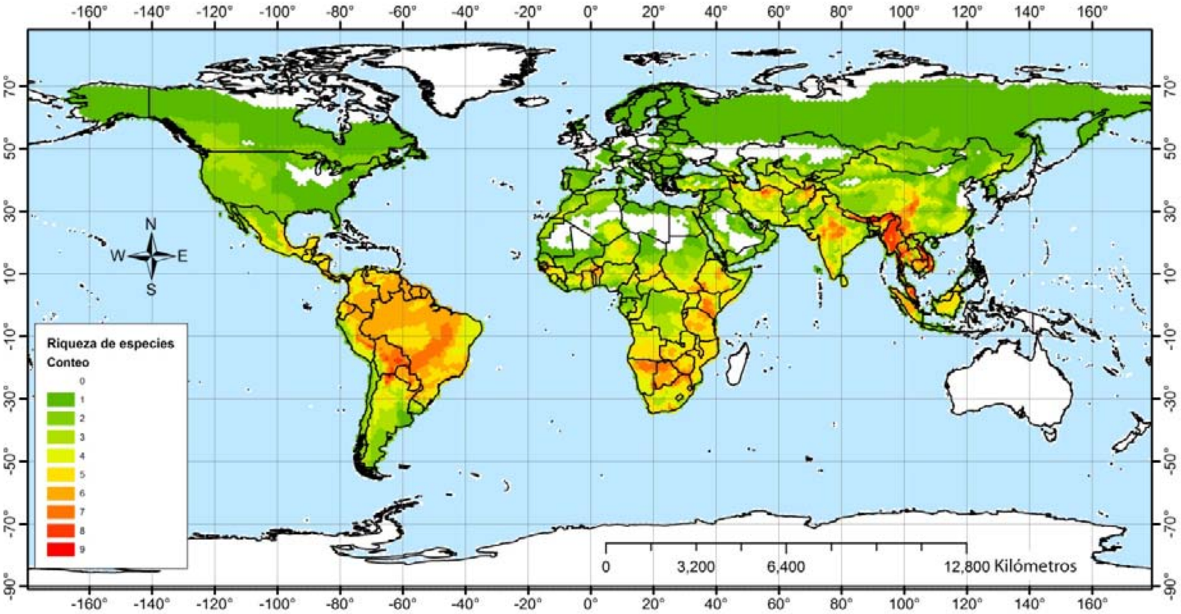

Figura 1. Sitios con mayor riqueza de especies de felinos en el mundo (hotspots) utilizando los mapas de distribución potencial de 36 especies (obtenido de International Union for Conservation of Nature, 2013) y una retícula de 1 grado cuadrado.

Como depredadores tope, las poblaciones de félidos requieren de áreas extensas de hábitat relativamente bien conservado y con cantidades suficientes de presas silvestres (Quigley & Crawshaw Jr. 1992; Ceballos et al. 2002; Sunquist & Sunquist 2009). El incremento de la población humana en el último siglo y a la destrucción de los hábitats naturales han ocasionado la declinación de estas especies en todo el mundo (Woodroffe & Ginsberg 1998; Woodroffe 2000; Ripple et al. 2014). Además, los grandes felinos han sido históricamente perseguidos por considerarse peligrosos para la gente y su ganado (Treves & Naughton-Treves 1999; Treves & Karanth 2003; Marchini & Macdonald 2012; Treves & Bruskotter 2014). También, varias especies de grandes y pequeños felinos han sido sujetas a sobreexplotación por el comercio internacional de pieles, huesos, así como la cacería deportiva (Nowell & Jackson 1996; Sunquist & Sunquist 2009; Packer et al. 2009; Macdonald et al. 2010a). Las poblaciones de los grandes felinos han declinado de manera significativa en el último siglo. Por ejemplo, los tigres y los leones actualmente se encuentran limitados a solamente el 6 y 17% respectivamente de su distribución histórica (Bauer et al. 2015; Goodrich et al. 2015), se estima que los jaguares han perdido más del 50% de su distribución geográfica en los últimos cien años (Sanderson et al. 2002), y que los pumas (*Puma concolor*) se han erradicado prácticamente de todo el Este de los Estados Unidos, a excepción de una pequeña población remanente en el estado de Florida (Nielsen et al. 2015).

La Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza (IUCN – por sus siglas en Inglés) es la autoridad internacional para categorizar el estado de conservación de las especies mundialmente (International Union for Conservation of Nature 2013). La Lista Roja de la IUCN utiliza tres categorías de especies amenazadas ("Críticamente en Peligro", "En Peligro" y "Vulnerable"), las cuales son asignadas con base a criterios cuantitativos que reflejan distintos grados de amenaza de extinción. Los criterios que utiliza la Lista Roja de la IUCN son el tamaño poblacional, el área de distribución, la tasa de disminución de la población ó rango geográfico y la probabilidad de extinción. La categoría de

“Casi Amenazada” se aplica a especies que no califican como amenazadas actualmente, pero podría estar cerca de calificar como tal si grado de amenaza no disminuye o si las acciones de conservación enfocadas a la especie cesan. Actualmente, 16 de las 36 especies de felinos existentes se encuentran dentro de las tres categorías de riesgo (o de amenaza) de la Lista Roja de la IUCN (Macdonald et al. 2010a), las cuales representan mayor riesgo de extinción (1 como “Críticamente en Peligro; 6.como “En Peligro”; y 9 como “Vulnerable”). Nueve de estas especies actualmente se encuentran como “Casi Amenazadas” y 11 como en “Preocupación Menor”. Según la Lista Roja de la UICN actualmente las poblaciones de 29 de estas especies continúan disminuyendo (Sunquist & Sunquist 2009; International Union for Conservation of Nature 2013).

1.4 Factores ecológicos que determinan el uso del espacio en los félidos silvestres

De manera similar a todas las especies de mamíferos, en los felinos silvestres la forma del cuerpo, estilo de vida, organización social y la manera en cómo utilizan el espacio refleja su historia evolutiva y las distintas estrategias que tienen para responder a diferentes circunstancias ecológicas (Eisenberg 1981; Sunquist & Sunquist 1989; Kitchener et al. 2010; Macdonald et al. 2010b). Todos los felinos silvestres son carnívoros altamente especializados para acechar, capturar y matar a su presas (Eisenberg 1986; Kruuk 1986). Por consecuencia, esta especialización está determinada por una serie de factores ecológicos que pueden ser medibles y nos permiten hacer inferencias para todas estas especies debido a la uniformidad en su biología, forma y función (Kruuk 1986; Sunquist & Sunquist 1989; Sicuro & Oliveira 2011). A continuación se describen los diferentes factores ecológicos que afectan las estrategias de forrajeo y el uso del espacio por parte de los félidos silvestres.

a) Relaciones alométricas

Básicamente el tamaño del depredador determina el tamaño de la presa que pueden depredar. La teoría del forrajeo óptimo sugiere que los felinos pequeños pueden subsistir de pequeñas presas abundantes, mientras que los felinos grandes requieren presas grandes ya que los costos de alimentarse de animales pequeños es demasiado alto como para satisfacer las demandas fisiológicas relacionadas con en el tamaño corporal (Macarthur & Pianka 1966; Gittleman 1985; Carbone et al. 1999a, 2007). Pero esto además conlleva a un mayor gasto energético para perseguir, someter y defender presas más grades (Gittleman 1985; Carbone et al. 2007).

Los felinos muestran distintas estrategias de cacería dependiendo de su tamaño corporal y el tamaño de sus presas (Carbone et al. 1999a, 2007), y los podemos dividir en tres grandes grupos con relación a su masa corporal y el tamaño de las presas que predominantemente depredan: a) especies que depredan sobre presas más pequeñas que ellos mismos (< 15 kg – especialistas en presas pequeñas); especies que depredan sobre presas de su propio peso o más grandes (>25 kg – especialistas en presas grandes); y c) especies que pueden depredar sobre presas de ambos tamaños dependiendo de qué presa es preferida y su disponibilidad (15–25 kg - generalistas) (Meachen-Samuels & Van Valkenburgh 2009a, 2009b).

Dependiendo del tamaño de las presas que predominantemente utilicen, los felinos silvestres muestran diferentes adaptaciones morfológicas. Las especies que se especializan en presas más grandes se distinguen por tener un cráneo más grande, colmillos más robustos, hocico más amplio, un ángulo de apertura mayor en la boca y extremidades anteriores más robustas; estas características les confieren una ventaja para dominar y matar presas más grandes (Christiansen 2007, 2008; Meachen-Samuels & Van Valkenburgh 2009a, 2009b; Slater & Van Valkenburgh 2009; Sicuro & Oliveira 2011). En cambio, las especies que se especializan en presas pequeñas tienen caninos más pequeños, un hocico más angosto, la mandíbula ligeramente más larga y una fuerza en la mordida relativamente mayor en proporción al peso que las especies más grandes (Meachen-Samuels & Van Valkenburgh 2009a, 2009b; Slater & Van Valkenburgh 2009), estas características les permiten capturar presas pequeñas pero que son más agiles. Las especies generalistas muestran características entre los otros dos grupos lo que indica que pueden estar adaptados para depredar presas de ambos tamaños (Christiansen 2007; Meachen-Samuels & Van Valkenburgh 2009a, 2009b).

No solo el tamaño del depredador determina el tamaño de las presas que pueden depredar, sino que también determina la cantidad de presas necesarias para mantenerse. Los felinos de mayor tamaño generalmente requieren áreas de actividad más grandes ya que sus necesidades metabólicas son mayores que las de los felinos más pequeños (Gittleman & Harvey 1982; Reiss 1988; Jetz et al. 2004; Macdonald et al. 2010b). Utilizando 52 estudios de ecología espacial de félidos solitarios (20 especies diferentes), donde se reporta el tamaño del área de actividad y el peso promedio en la población, podemos observar que existe una correlación positiva entre estas dos variables ($R^2 = 0.38, p < 0.001$; Figura 2), es decir, entre más grande es el tamaño corporal de la especie más grande serán sus áreas de actividad. Sin embargo, el tamaño del área de actividad en los felinos silvestres, como en todas las demás especies de mamíferos, no solamente se explica por el peso ya que existen otros factores ecológicos que subyacen las diferencias en el uso del espacio, las cuales se explicarán a continuación (Swihart et al. 1988; Kelt & Van Vuren 2001; Grigione et al. 2002; Jetz et al. 2004; Nilsen & Linnell 2006).

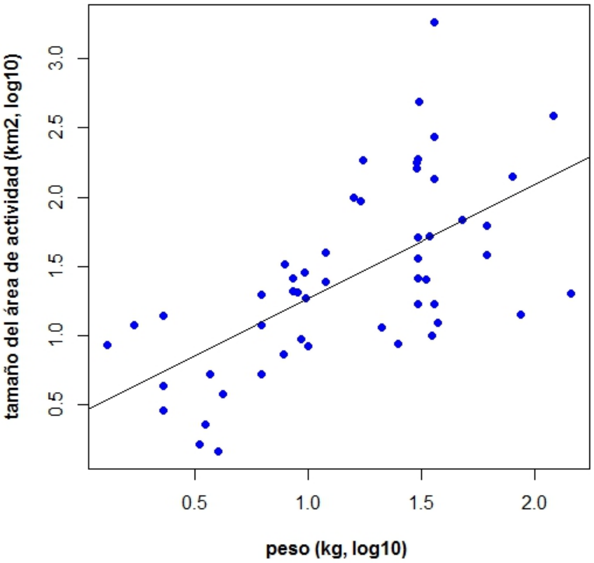

Figura 2. Relación entre el peso corporal y el tamaño de las áreas de actividad en los felinos silvestres utilizando datos de 52 estudios de ecología espacial de 20 especies diferentes ($R^2 = 0.38, p < 0.001$).

b) Relación depredador-presa

El uso del espacio en los felinos silvestres está directamente relacionado con el tiempo de búsqueda invertido para el forrajeo (Macarthur & Pianka 1966). Por consecuencia, el área de actividad está dada en función de los recursos disponibles en el ambiente (Sandell 1989; Sunquist & Sunquist 1989). La densidad de los carnívoros está directamente relacionada con la densidad de sus presas (Eisenberg 1986; Kruuk 1986; Carbone & Gittleman 2002; Karanth et al. 2004), es decir a mayor densidad de presas mayor será la densidad de los carnívoros. Una correlación entre la densidad y el tamaño del área de actividad nos podría indicar una dependencia de estas dos variables a la disponibilidad de presas (Sandell 1989). Utilizando los datos de 28 estudios de ecología espacial de felinos silvestres (de 10 especies diferentes), donde se reporta el área de actividad mínima de las hembras y también la densidad de la población (Figura. 3), podemos observar una fuerte correlación negativa entre estas dos variables ($R^2 = 0.72, p < 0.001$). Esto nos sugiere que los felinos silvestres pueden ajustan sus áreas de actividad dependiendo de la cantidad de alimento disponible en el ambiente.

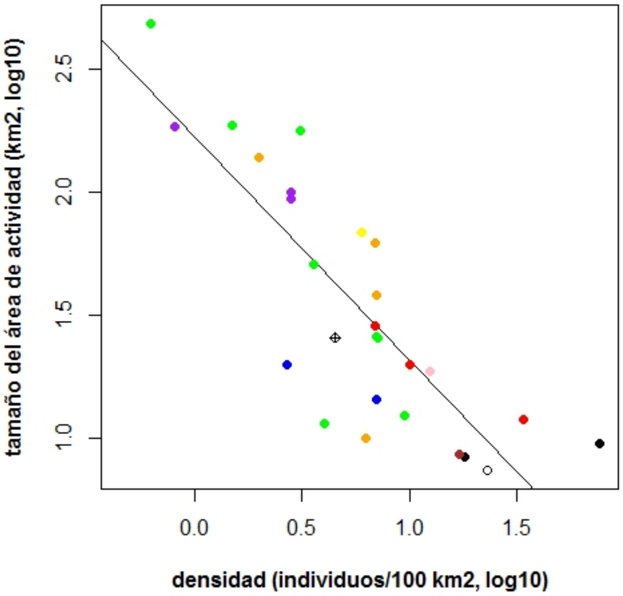

Figura 3. Relación entre la densidad y el tamaño del área de actividad en los felinos silvestres utilizando 28 estudios de ecología espacial de 10 especies ($R^2 = 0.72, p < 0.001$). Verde = *P. pardus*; naranja = *P. onca*; rojo = *L. rufus*; azul = *P. tigris*; negro = *L. pardinus*; rosa= *L. pardalis*; café = *F. nigripes*; morado = *L. lynx*; amarillo = *P. concolor*; blanco = *C. caracal*; cruz = *L. canadiensis*)

También es importante considerar que existe una gran variación intra-especifica entre los tamaños de las áreas de actividad en los félidos silvestres y parte de esta variación se ha explicado por la densidad de presas en los distintos sitios. Por ejemplo, el tamaño de las áreas de actividad aumenta considerablemente de zonas más templadas a zonas más áridas en los leopardos (Marker & Dickman 2005; Odden & Wegge 2005), lo mismo sucede con los linces euroasiáticos en zonas de mayor a menor productividad (Herfindal et al. 2005). En ambos estudios las variables ambientales medidas están correlacionadas con la abundancia de presas. También, si la disponibilidad de presas aumenta a lo largo del tiempo, el tamaño de las áreas de actividad pueden reducirse como se ha demostrado con el gato montés y con los leones (Benson et al. 2006; Loveridge et al. 2009). En cambio, si la disponibilidad de presas disminuye, los felinos pueden aumentar el tiempo activo de búsqueda de presas y como consecuencia el tamaño de sus áreas de actividad, como sucede con los linces euroasiáticos (Schmidt 2008).

La distribución de las presas tanto espacial como temporalmente también tiene consecuencias en el tiempo de búsqueda invertido para el forrajeo en los felinos silvestres y por lo tanto tiene implicaciones en la manera en como estas especies utilizan el espacio (Macarthur & Pianka 1966; Sunquist & Sunquist 1989). Características claves del paisaje y los hábitats influyen en la distribución de las presas y éstas pueden ser aprovechadas por los felinos silvestres, por ejemplo, los leones seleccionan sitios cercanos a los cuerpos de agua ya que en estos lugares es donde se concentran una mayor cantidad de presas (Valeix et al. 2009; de Boer et al. 2010). Si las especies presa tienen movimientos estacionales los felinos también pueden mostrar cambios en sus áreas de actividad, como es el caso en algunas poblaciones de pumas (Pierce et al. 1999; Grigione et al. 2002), y jaguares (Cavalcanti & Gese 2009). La distribución de las presas en el tiempo y en el espacio es un factor crítico para hembras que están criando cachorros, porque ellas se encuentran confinadas a un área cercana a la madriguera lo que restringe su radio de forrajeo (Sunquist & Sunquist 1989; Moen et al. 2008; Steyn & Funston 2009).

c) Cobertura para la cacería

Prácticamente todas las especies de felinos silvestres dependen de las condiciones físicas del ambiente, utilizando casi cualquier tipo de cobertura para acechar y acercarse lo más posible para poder capturar a su presa (Sunquist & Sunquist 1989). En varios estudios se ha ilustrado la importancia de estos sitios para el uso del espacio por parte de estas especies (Bothma et al. 1994; Fuston et al. 2001; Muntifering et al. 2006; Balme et al. 2007; Podgórski et al. 2008). Incluso, el éxito de la cacería depende en gran medida de la cobertura disponible para el acecho y el número de estos lugares puede ser limitado (Kruuk 1986; Fuston et al. 2001; Balme et al. 2007).

d) Interacción entre especies de felinos

Todos los felinos son muy similares en forma y función, por lo tanto las especies que coexisten pueden estar destinadas a la rivalidad (Sunquist & Sunquist 1989; Macdonald et al. 2010a). Sin embargo, se ha encontrado evidencia de desplazamiento de caracteres en comunidades de felinos, lo cual sugiere una repartición de recursos en los ensambles regionales (Kiltie 1984, 1988; Dayan et al. 1990; Morales & Giannini 2010, 2013). Estudios que se han realizado siguiendo dos o más de estas especies en un mismo sitio nos pueden dar una idea de los mecanismos que permiten su coexistencia. Con respecto al uso del espacio, cuando dos o más especies de felinos coexisten pueden utilizar hábitats diferentes o evitar los mismos sitios activamente (Scognamillo et al. 2003; Harmsen et al. 2009; Odden et al. 2010; Sollmann et al. 2012; Bhattarai & Kindlmann 2012), o mostrar una segregación temporal en el uso del espacio (Romero-Muñoz et al. 2010). En cuanto a la dieta, la separación ecológica se puede dar depredando sobre diferentes tipos de presas en términos de especie, tamaño, clase y edad (Karanth & Sunquist 1995, 2000; Nuñez et al. 2000; Scognamillo et al. 2003; Novack et al. 2005; Andheria et al. 2007; Foster et al. 2010b; Odden et al. 2010; Bhattarai & Kindlmann 2012), o mostrando una mayor actividad con relación a la actividad de sus principales presas (Karanth & Sunquist 2000; Ramesh et al. 2012).

e) Organización social

La manera en cómo están organizados socialmente los felinos es un reflejo de diversas circunstancias ecológicas y evolutivas (Leyhausen 1969; Macdonald 1983; Gittleman 1989;

Sandell 1989; Packer et al. 1990, 2005; Mosser & Packer 2009; Macdonald et al. 2010b). La mayoría de los felinos silvestres son solitarios con excepción de los leones y bajo algunas condiciones los guepardos, donde los machos ocasionalmente forman coaliciones (Caraco & Wolf 1975; Kruuk 1986; Marker et al. 2008; Sunquist & Sunquist 2009; Macdonald et al. 2010b). Los individuos en las especies solitarias tienen muy poco contacto con sus conspecíficos y estas interacciones se limitan la mayoría de las veces al apareamiento y en el caso de las hembras a la crianza de los cachorros (Sandell 1989). Sin embargo, el hecho de que estas especies no sean gregarias y cooperativas, no necesariamente implica que no sean sociales (Leyhausen 1969; Mizutani & Jewell 1998; Cavalcanti & Gese 2009). Las característica de las presas principales, la forma de cazar, la eficiencia del forrajeo y la disponibilidad del alimento son factores de selección que promueven la vida solitaria (Sandell 1989). La mayoría de felinos se alimentan de presas que son pequeñas e indivisibles (Carbone et al. 1999b, 2007; Meachen-Samuels & Van Valkenburgh 2009a, 2009b), o si se alimentan de presas grandes lo hacen sorprendiendo en hábitats con poca visibilidad (Kruuk 1986; Sunquist & Sunquist 1989; Balme et al. 2007). Con la presencia de conspecíficos en las inmediaciones inmediatas la eficiencia del forrajeo y la disponibilidad de presas disminuye para estas especies (Eisenberg 1986; Kruuk 1986; Sandell 1989).

La organización social en los felinos solitarios puede clasificarse en la manera en que los individuos se reparten el espacio y por el grado de traslape entre las áreas de actividad de hembras y machos. Las áreas de actividad de los machos generalmente son dos o tres veces más grandes que las de las hembras y suele traslaparse con las áreas de actividad de varias hembras (Sunquist & Sunquist 1989; Marker & Dickman 2005; Soisalo & Cavalcanti 2006; Cavalcanti & Gese 2009; Goodrich et al. 2010). Las áreas de actividad de machos y hembras pueden ser exclusivas o con traslape y a su vez éstas pueden variar entre especies o dentro de una misma especie. Esto indica que la manera en cómo los individuos se reparten el espacio es el resultado de las tácticas escogidas dependiendo de las diferentes condiciones que se presentan en el ambiente (Sandell 1989). Los territorios tenderán a ser compartidos cuando éstos son muy grandes, ya que al aumentar el tamaño de los territorios, los costos de excluir a los vecinos también aumentan (Eisenberg 1986; Jetz et al. 2004).

En el caso de las hembras, que se encargan de criar por sí solas a su progenie, el uso del espacio está dado por la suficiente disponibilidad de presas para mantenerse a ellas mismas y a sus cachorros (Sandell 1989). Las áreas de actividad serán exclusivas si el alimento está uniformemente distribuido en el espacio y en el tiempo (Sunquist 1981; Mizutani & Jewell 1998; Vashon et al. 2008; Goodrich et al. 2010; Hojnowski et al. 2012). Pero si las presas varían en el espacio y en el tiempo o si son impredecibles, las áreas de actividad tenderán a ser mayores para satisfacer las necesidades continuamente (Jenny 1996; Jetz et al. 2004; Marker & Dickman 2005; Grassman et al. 2005; Cavalcanti & Gese 2009). Áreas más grandes mantendrán más recursos pero otros individuos pueden utilizar estas mismas áreas. Por lo tanto, se facilita el sistema de traslape.

En cambio, el uso del espacio de los machos en los felinos solitarios está determinado por los recursos en las temporadas que no son las de apareamiento y por las hembras receptivas durante la temporada de apareamiento (Sandell 1989; Sliwa 2004; Ferguson et al. 2009). Los machos pueden mostrar áreas de actividad permanentes y exclusivas, tratando de monopolizar a las hembras (Sunquist 1981; Vashon et al. 2008; Ferguson et al. 2009; Goodrich et al. 2010). Esta estrategia se puede dar cuando las hembras están uniformemente distribuidas en el espacio, de esta manera el macho puede tener control del número de hembras con las que se puede aparear (Sandell 1989). La otra estrategia es mostrar áreas de actividad no permanentes y con un extenso traslape con otros machos, en este caso los machos vagan a lo largo de un territorio extenso y compiten por el acceso a las hembras (Schmidt et al. 2003; Herfindal et al. 2005; Burdett et al. 2007; Cavalcanti & Gese 2009; Manfredi et al. 2011). Este sistema social se daría en el caso de que las densidades fueran bajas y por consecuencia se mueve en busca de hembras dentro de un área muy grande en vez de permanecer y asegurarse de tener pocas hembras (Sandell 1989).

Entre las presiones selectivas que se han atribuido a la formación de grupos sociales en los felinos silvestres están el incrementar la eficiencia de forrajeo, mejorar la producción de la progenie, mayores defensas a la depredación, mejorar el éxito reproductivo y la defensa del territorio (Caraco & Wolf 1975; Lamprecht 1978; Bygott et al. 1979; Macdonald 1983; Packer & Pusey 1982, 1983; Van Orsdol 1984; Eisenberg 1986; Kruuk 1986; Cooper 1991; Packer & Ruttan 1988; Packer et al. 1990; Packer et al. 1992; Stander 1992a, 1992b; Pusey & Packer 1994; Heinsohn et al. 1996; Fuston et al. 2001; Packer et al. 2001;Durant et al. 2004; Trinkel & Kastberger 2005;Marker et al. 2008; Mosser & Packer 2009; Macdonald et al. 2010b). Sin embargo, estos factores están asociados a la sociabilidad en los felinos que forman grupos sociales y no tienen tanto peso en cómo usan el espacio en los felinos solitarios.

2. Enfoque de la tesis

La presente tesis se centra en el jaguar (*Panthera onca*), el mayor felino presente en el continente Americano. Históricamente, el jaguar habitaba desde sur de los Estados Unidos hasta el norte de Argentina (Seymour 1989). Sin embargo, esta especie ha sido extirpada de más de la mitad de su distribución histórica en los últimos 100 años (Sanderson et al. 2002; Caso et al. 2008). Las evaluaciones más recientes acerca del estatus de conservación de esta especie han concluido que los jaguares continúan declinando en la mayor parte donde aún se distribuyen (Swank & Teer 1989; Medellín et al. 2002, 2015; Sanderson et al. 2002; Caso et al. 2008; Rabinowitz & Zeller 2010). Sin embargo, el jaguar actualmente se encuentra categorizado solamente como "Casi Amenazado" dentro de la Lista Roja de la IUCN (Caso et al. 2008).

Las principales amenazas para la especie son tanto la cacería directa de los jaguares como la de sus presas, así como la destrucción y la fragmentación de su hábitat. La cacería directa de los jaguares está relacionada con la cacería de los ganaderos en represaría con el jaguar por depredar ganado domestico (Conforti & Azevedo 2003; Palmeira et al. 2008; Rosas-Rosas & Valdez 2010; Carvalho & Pezzuti 2010; Marchini & Macdonald 2012). También la cacería directa puede estar relacionada con otros factores como el miedo y la cacería deportiva e incidental (Conforti & Azevedo 2003; Carvalho & Pezzuti 2010; Marchini & Macdonald 2012). Los hábitats de los jaguares, en toda su área de distribución, están siendo transformados en tierras para agricultura, pastos para la ganadería y asentamientos humanos. Además, las carreteras, hidroeléctricas y otros tipos de infraestructura humana están fragmentando las poblaciones de esta especie (Swank & Teer 1989; Nowell & Jackson 1996; Sanderson et al. 2002; Caso et al. 2008; Haag et al. 2010).

La transformación de los ecosistemas naturales están ocasionado que se pierda el hábitat que está disponible para la especie y como consecuencia sus poblaciones se están aislando. Aunque los jaguares son capaces de moverse incluso largas distancias a través de hábitats fragmentados, generalmente evitan completamente paisajes modificados y asentamientos humanos (Conde et al. 2010; Haag et al. 2010; Cullen et al. 2013). También la fragmentación, en algunas áreas de la distribución de la especie, está limitando el flujo génico, causando una reducción en la diversidad genética y en el tamaño efectivo de las poblaciones (Haag et al. 2010).

Debido a que el jaguar es una especie solitaria, territorial y a sus grandes necesidades de espacio para cumplir con sus requerimientos energéticos, se requiere mantener grandes extensiones de hábitat en buen estado de conservación para salvaguardar una población mínima viable de esta especie (Quigley & Crawshaw Jr. 1992; Ceballos et al. 2002; Conde et al. 2010; Cullen et al. 2013). Al igual que otros grandes felinos, el tamaño de las áreas de actividad de los jaguares está determinado en función de la disponibilidad de presas y de la cobertura forestal (Schaller & Crawshaw 1980; Quigley & Crawshaw Jr. 1992; Ceballos et al. 2002; Conde et al. 2010; Cullen et al. 2013). En general, las hembras utilizan hábitats mejor conservados y evitan moverse por sitios perturbado por actividades antropogénicas (Colchero et al. 2009; Conde et al. 2010). Este patrón se ha explicado por perturbaciones como la cacería de subsistencia, ya que los jaguares compiten por las mismas presas con los humanos (Jorgeson & Redford 1993; Novack et al. 2005).

Bajo este contexto teórico, el presente trabajo espera contribuir en la conservación del jaguar desde tres perspectivas y escalas diferentes, las cuales están representadas en los tres capítulos que conforman la presente tesis. El primer capítulo está enfocado en hacer una síntesis de la información más actualizada acerca del estatus de conservación del jaguar a escala continental. Para esto se recopiló toda la información actualizada acerca de la distribución geográfica del jaguar a escala continental, se identificaron las diferentes sub-poblaciones de la especie en el continente, se estimó un tamaño poblacional para estas sub-poblaciones, se evaluó cada una de las sub-poblaciones bajo los criterios de la UICN y finalmente se identificaron las poblaciones más amenazadas. La mayor relevancia de este análisis es que aunque potencialmente existe una sub-población muy grande jaguares en la región de la Amazonía, prácticamente todas las demás sub-poblaciones están amenazadas ya sea por su pequeño tamaño poblacional, poca disponibilidad de hábitat, aislamiento, alta densidad humana ó bajo nivel de protección. Este análisis ilustra que si no se toman las medidas pertinentes en un futuro próximo, la mayor parte de las sub-poblaciones de jaguar muy probablemente se extinguirán. Este análisis también demuestra que las evaluaciones de cualquier especie dentro de los criterios de la Lista Roja de la IUCN no pueden estar basadas o significativamente sesgadas por el estado de conservación de una sola sub-población muy grande, sino que también es necesario incorporar el estado de conservación de cada una de las sub-poblaciones remanentes y ponderar de acuerdo al grado de amenazas que presenten cada una de éstas. En este primer capítulo las preguntas a contestar fueron las siguientes: 1) ¿Cuáles son las sub-poblaciones de jaguar más amenazadas a lo largo del continente Americano?; 2) ¿Cuáles son las sub-poblaciones de jaguar en donde se tienen que priorizar los esfuerzos de conservación en los próximos años?

En el segundo capítulo de esta tesis, se enfocó describir y comparar la ecología espacial de los jaguares y de los pumas en la región de la Selva Lacandona. El jaguar y el puma son los felinos más grandes del Neotrópico y son simpátricos a lo largo de toda el área de distribución del jaguar. En los últimos años se han realizado avances muy significativos en el entendimiento de la ecología e historia natural de los jaguares y pumas a todo lo largo de su área de distribución. Sin embargo, existe muy poca información acerca de los requerimientos espaciales, patrones de movimiento, o de cómo la perturbación del hábitat por actividades humanas afecta el uso del espacio de estas especies. Además, esta información es crucial para desarrollar los planes de manejo y conservación adecuados para jaguares y pumas en los bosques tropicales de Centroamérica. Utilizando la información recopilada en campo por medio de collares satelitales de GPS durante más de dos años, en este capítulo describo la ecología espacial de jaguares y pumas en un bosque lluvioso tropical dominado por actividades humanas. Este estudio es el primero en presentar datos de jaguares y pumas seguidos simultáneamente utilizando radio-telemetría de GPS y los datos presentados en este capítulo demuestran diferencias en el uso del espacio de estas dos especies que no habían sido documentadas previamente. En este segundo capítulo mi interés fue contestar las siguientes preguntas: 1) ¿Cuál es el tamaño de las áreas de actividad utilizadas por los jaguares y pumas en los bosques tropicales del sur de México?; 2) ¿Cómo los jaguares y pumas comparten el espacio cuando estas dos especies coexisten?

Ya que uno de los principales retos de la ciencia aplicada a la conservación es lidiar con la fragmentación de los hábitats de las poblaciones de fauna silvestre, el tercer capítulo de esta tesis tuvo como objetivo aplicar el conocimiento de la ecología espacial de los jaguares para diseñar una estrategia de conectividad para mantener la integridad de la población de la especie en la región de la Selva Maya. La población más grande jaguares en Mesoamérica está localizada en la Selva Maya, la cual se encuentra entre México y Guatemala, y representa una de las pocas poblaciones viables a largo plazo de la especie. Sin embargo, el paisaje de la Selva Maya está siendo transformado en tierras para la agricultura, la ganadería y asentamientos humanos. Además, de que las carreteras, desarrollos turísticos y otra infraestructura están fragmentando las grandes extensiones de selva que aún quedan en esta región. Utilizando datos de jaguares seguidos por medio de radio-telemetría de GPS durante un año y medio, e información obtenida por medio de percepción remota, se identificaron los sitios con una mayor probabilidad ocurrencia de la especie en la región. Este análisis de idoneidad de hábitat para el jaguar se integró con un modelo de probabilidad de movimiento para evaluar la conectividad de los parches de hábitat a lo largo de la distribución de la especie en el sur de la Selva Maya. Mi predicción fue que los sitos que tienen una mayor probabilidad de ser ocupados por los jaguares y los sitos más adecuados para funcionar como corredores son aquellos que conservan la cobertura forestal y aquellos que se encuentran más alejados de actividades humanas. Por medio de este análisis se identificaron los parches de hábitat y los corredores que son necesarios para establecer una estrategia de conectividad para la especie en la región, así como las prioridades de manejo y conservación para este paisaje. Bajo el esquema de desarrollo humano actual en la región, se espera que esta información aporte elementos críticos para crear una propuesta de desarrollo la cual sea compatible con la conservación del jaguar y los paisajes naturales del sur de la Selva Maya. En este último capítulo mi interés fue contestar las siguientes preguntas: 1) ¿Qué variables del paisaje de la Selva Maya están correlacionadas positiva y negativamente con el uso y el movimiento de los jaguares?; 2) ¿Cuáles son las áreas que se deben priorizar para conservar a largo plazo la población de jaguar del sur de la Selva Maya?

3. Objetivos

3.1 Objetivo general

Evaluar el estado de conservación del jaguar (*Panthera onca*) a escala continental y con base al conocimiento de la ecología espacial de la especie proponer estrategias de conservación a una escala local y regional.

3.2 Objetivos específicos

- Utilizando la información más actualizada acerca de la distribución y estimaciones de densidad del jaguar a todo lo largo de su área de distribución, evaluar el estatus de conservación de la especie a escala continental, así como identificar las sub-poblaciones más amenazadas de la especie.
- Describir cómo utilizan el espacio los jaguares y pumas en el paisaje de la Selva Lacandona, Chiapas, México.
- Aplicar el conocimiento de la ecología espacial de los jaguares para diseñar una estrategia de conservación para mantener la conectividad del paisaje del sur de la Selva Maya.

4. Hipótesis

H1. Dado que las amenazas para cada una de las sub-poblaciones de jaguar que se encuentran en el continente americano son diferentes, la probabilidad de extinción para cada una de las sub-poblaciones de jaguar será diferente.

H2. Ya que las áreas de actividad en los grandes depredadores están determinadas por el tamaño corporal y sus requerimientos energéticos, las áreas de actividad y los movimientos de los jaguares serán mayores que los de los pumas.

H3. Dado que las especies de félidos simpátricos muestran una segregación temporal en el uso del espacio y evitan los mismos sitios activamente, los jaguares y pumas con traslape en sus áreas actividad mostrarán poco traslape al nivel del área núcleo y evitarán utilizar los mismos sitios en el mismo periodo.

H4. Las áreas con mayor probabilidad de uso y de movimiento para los jaguares en el paisaje del sur de la Selva Maya estarán ubicadas en los sitios mejor conservados (mayor cobertura forestal) y en áreas alejadas de actividades humanas.

5. Capítulo 1. Evaluación del estatus de conservación del jaguar a escala continental.

The jaguar's spots are darker than they appear: Assessing global conservation status of jaguars

(Con formato para *Oryx;* aceptado el 5 de septiembre del 2016)

The Jaguar's spots are darker than they appear: Assessing global conservation status of jaguars

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The Jaguar's spots are darker than they appear: Assessing global conservation status of jaguars

Abstract

The IUCN Red List is a widely used informative tool to guide conservation policy and practice. However, in most cases, the evaluation of species under IUCN Red List criteria only takes into account the global status of the species. The IUCN system allows assessors to undertake assessments at the level of subpopulation following the IUCN categories and criteria, but these are often not implemented, because it is difficult to identify subpopulations or because of the high effort involved. In this paper, using the jaguar (*Panthera onca*) as model, we illustrate that wide-ranging species that are assigned under a particular category of threat within the IUCN Red List criteria may display considerable heterogeneity within the extinction risk for the taxon. Using all the information available on the conservation status of the species, we evaluated the jaguar's current geographic range and its subpopulations. We identified the most endangered subpopulations using the extent of occurrence, area of occupancy, population size, and the level of threats of each subpopulation. The main outcome of this analysis was that although a large subpopulation persists in Amazonia, virtually all others are threatened or endangered by their small size, high human density, isolation, and deficient protection. Based on this approach, future conservation efforts can be prioritized for the most threatened subpopulations. Our results indicate that assessors of the IUCN Red List would consider the value of undertaking assessments at the subpopulation level for future assessments. It is urgent to include sub-global assessments for the jaguar under the IUCN Red List of Threatened Species.

Keywords: assessment, conservation, endangered, IUCN, jaguar, *Panthera onca*, subpopulations, threats.

Introduction

Assessment of extinction risk is one of the most informative tools available to guide conservation policy and practice (Mace et al., 2008). However, the specific facts and processes that lead to listing, assessing, or delisting species are rarely available other than the schematic listings within the International Union for Conservation of Nature (IUCN) Red List of Threatened Species or other national protocols. The IUCN Red List uses three categories of threatened species (Critically Endangered, Endangered, and Vulnerable), which are assigned on the basis of quantitative criteria to reflect varying degrees of threats of extinction. The category of Near Threatened is applied to taxa that do not qualify as threatened now, but may be close to qualifying as threatened; this category is also applied to taxa that do not meet criteria currently for a threatened category, but are likely to do so if ongoing conservation action abates or ceases (IUCN, 2012).

However, in most cases, the evaluations of species under IUCN Red List criteria are only undertaken at the global level of the species. The IUCN Red List system allows assessors to undertake assessments at the level of subpopulation following the proper categories and criteria (IUCN Standards and Petitions Subcommittee, 2016), but these are often not implemented, usually because it is difficult to identify subpopulations or because the effort involved is high. This is problematic, especially in species with a wide distribution range, because the allocation of any of the risk categories does not necessarily reflect the status of the species throughout its range (Wallace et al., 2010). Even so, there are many species that have lost most of their habitat within their geographic range, but they do not qualify within these risk categories because they still maintain a wide range or a single, large population. This is the case of the jaguar (*Panthera onca*), the largest felid on the American continent.

The jaguar ranged historically from southwestern United States to central Argentina (Seymour, 1989). However, since 1900 its range has decreased considerably, and it is found currently only from northern Mexico to northern Argentina, although it occasionally disperses to the extreme southwestern United States (Medellín et al., 2002, 2016; Sanderson et al., 2002). The species' historical range was approximately 19,000,000 km²; estimates of its current distribution include only 46% (9,000,000 km²) of the original range (Sanderson et al., 2002). Previous efforts to evaluate its conservation status at regional and continental scales have concluded that jaguars are declining throughout much of their range (Swank & Teer, 1989; Sanderson et al., 2002; Zeller, 2007; Medellín et al., 2016). However, jaguars are still listed on the IUCN Red List only as Near Threatened, the second lowest risk category, based on the inminent closeness of qualify for the Vulnerable category under A2cd or A3cd criteria. The main reason for not classifying jaguars in a higher extinction risk category such as Vulnerable or Endangered is due to its wide geographic range, and because it still maintains numerically one large subpopulation in the Amazon basin (Caso et al., 2008).

Because assessment of subpopulations can help to draw attention to conservation priorities that might otherwise be obscured, in this paper we undertake an assessment for a wide-ranging and lower risk species, the jaguar, and we present a methodology for identifying subpopulations within the species' range and then assessing each subpopulation against the IUCN Red List categories and criteria. We used available information on the jaguar's range and estimates of density to assess the conservation status of jaguars throughout its range.

Additionally, we developed a threats evaluation system to assess the level of threats for each subpopulation and to allocate the conservation priorities for each subpopulation. Our specific aims were: 1) to provide an estimate of the current geographic range for the species and its subpopulations; 2) to provide an estimate of total size and subpopulation sizes for jaguars; 3) to identify the most threatened subpopulations throughout the jaguar's range. With this analysis, we illustrate that wide-ranging species that are assigned under a particular category of threat within the IUCN Red List criteria may display considerable heterogeneity within the extinction risk for the taxon, and that assessments, especially for those species that have a wide distribution range, should be based on the level of threats for all the subpopulations throughout its entire range. We hope that this information encourages future assessors to consider the value of undertaking assessments at the subpopulation level.

Methods

Geographic range of jaguars

To determine the current range of jaguars, we compiled the most recent information on jaguar distribution, integrating it from all available sources. We included information from the Jaguar Conservation Units (JCU) (Sanderson et al., 2002; Zeller, 2007; Rabinowitz & Zeller, 2010), and the population maps that were published for the countries within the jaguar's range (Beisiegel et al., 2012; Moraes Jr., 2012; Cavalcanti et al., 2012; De Oliveira et al., 2012; De Paula et al., 2012; Carrillo-Percastegui & Maffei, 2016; Figueroa et al., 2016; García-Anleu et al., 2016; González-Maya et al., 2016; Hoogesteijn et al., 2016; Maffei et al., 2016; Mora et al., 2016; Moreno et al., 2016; Payán Garrido et al., 2016; Chávez et al., 2016; de Azevedo et al., 2016; de Thoisy, 2016; Díaz-Santos et al., 2016; Espinosa et al., 2016). We mapped polygons to define Jaguar Subpopulations (JSs) at the continental scale. Each polygon was delineated based on the information available for jaguar distribution in each country. Because the information was obtained from different sources, we recognized that criteria for defining JSs in each country were dissimilar. For instance, JSs in Mexico and Brazil were delineated with very detailed maps using expert knowledge. In other cases, we complemented the JCU information with maps of the jaguar's range that were published recently for each country. We unified all this information by generating detailed Geographic Information System (GIS) layers that represented the JSs on a map. Although most of this information has not been published in peer-reviewed journals, it represents the latest knowledge of the species' range that was based on the assessments of jaguars by experts who are working in the different countries.

To define the JSs, we applied the IUCN Red List concept of subpopulation (IUCN, 2012; IUCN Standards and Petitions Subcommittee, 2016): "*geographically or otherwise distinct groups in the (global) population between which there is little demographic or genetic exchange (typically one successful migrant individual or gamete per year or less); a subpopulation may or may not be restricted to a region*". Because the taxonomic and genetic research suggested little difference among jaguar subpopulations (Larson, 1997; Eizirik et al., 2001; Ruiz-Garcia et al., 2006), we defined the JSs as discrete units that followed these criteria: 1) we only considered polygons greater than 2000 km², with the aim of including in this analysis only regions where resident subpopulations of the species occurred. For this, we consider as criterion include only sites that potentially could contain a subpopulation of at least 5 resident jaguars considering the lower density estimate throughout the distribution range of the species (0.25 jaguars / 100 km² - Paviolo et al., 2008); 2) We identified geographical, natural, and anthropogenic barriers between the different JS polygons, such as: a) mountain ranges within the species' distribution range that potentially divide the JSs (the upper elevation limit of the species is 3000 m.a.s.l. - Caso et al., 2008); b) urbanized areas and large areas modified by human activities. We considered JSs as independent if the distance of habitat that was modified by human activities (areas intervened) between any one JS and the nearest one was greater than 50 km. For this, we used the GlobCover land-use classification (Arino et al., 2012). We reclassified the “Natural and Semi-natural Terrestrial Vegetation” layers as “natural vegetation” and the “Cultivated and Terrestrial and Management” layers as “intervened”, according to the GlobCover land-use classification (Arino et al., 2012). In this analysis, we assumed that the JSs included both the JCU and the corridors under the scheme proposed by Rabinowitz & Zeller (2010).

Using the JSs polygons, we delineated an approximation of the current jaguar range at the continental scale. We estimated the extent of jaguar occurrence (EOO) using the Minimum Convex Polygon that enclosed the range of each JS (IUCN Standards and Petitions Subcommittee, 2016; Joppa et al. 2016). Top level predators such as jaguars are particularly threatened in regions of high human population density by direct persecution and habitat loss (Woodroffe, 2000; Cardillo et al., 2004), and jaguar extinction can be predicted according to certain thresholds of human population density (Woodroffe, 2000). Given these two factors, we performed an estimation of the jaguars’ area of occupancy (AOO) in each JS using a grid of the human population density in the American Continent for the year 2000 at a resolution of 30 arc-seconds (~1 km) (Center for International Earth Science Information Network et al., 2011). We defined two scenarios of AOO, because threshold values of human population density that predict the extinction of jaguars range from 12 to 24 people per km^2 (mean 17 people per km^2– Woodroffe, 2000). Our lowest estimate was defined by obtaining in each JS the “natural vegetation” layers (Arino et al., 2012), and excluding the sites where human density was higher than 12 people per km². Our upper estimate was defined also by obtaining the "natural vegetation" layers, and excluding the areas where human density was higher than 24 people per km². Finally, we calculated our lower and upper estimates of AOO at the reference scale of 4 km² (2 km grid size) such is suggested in the IUCN Red List Guidelines (IUCN Standards and Petitions Subcommittee, 2016).

We contrasted our estimations of jaguar range and AOO with the historic distribution of the species to estimate range loss for jaguars. The historic distribution of jaguars was estimated from the historical distribution maps of Patterson et al. (2007). All geographic analyses were performed with ArcGIS 10.2 (ESRI, 2013)

Jaguar Subpopulations

For each JS, we estimated total area covered, and we listed the biomes and eco-regions found within the JS using the classification of Olson et al. (2001). We compiled all published jaguar density estimates that used camera traps, including papers published in indexed journals, book chapters, and technical reports. A total of 31 studies from Mexico to Argentina, published between 2004 and 2014, contained 78 density estimates. Because the majority of jaguar camera trap studies do not meet the requirements necessary to produce unbiased density estimates and probably overestimate the true jaguar densities (Tobler & Powell, 2013), we conservatively corrected the estimate for each study using the inferior interval of the density estimate (subtracting the standard error to the density estimate reported). Each study was classified according to the biome and eco-region using the coordinates reported in the sources (Table 1). In the case of the JSs with no available density estimates or no available estimates for one kind of biome, we used the most conservative density estimate reported for the nearest jaguar JS.

A “subpopulation” was defined as the estimated number of individuals in each JS, and we used the term “population” to refer to the sum of all subpopulations across the range (IUCN, 2012; IUCN Standards and Petitions Subcommittee, 2016). We estimated the subpopulation size for each JS by extrapolating the density estimates to our layers of AOO. For each JS, we performed two estimates of jaguar population size. The lower population size estimate was implemented using our lowest AOO scenario, and our upper population size estimate was implemented using our upper AOO scenario. For these estimates, we assumed that jaguar density declined linearly as the human population density increased (Woodroffe, 2000). This implies that jaguar densities across the JSs were estimated for each cell contained in the AOO maps using the linear regression formula: $y = xm + b$; where y was the estimated jaguar density value adjusted according the human population density, x was the value of human population density (Center for International Earth Science Information Network et al., 2011), m was the constant rate at which jaguar densities declined as the human population density increased, and b was the jaguar density defined for each biome in each JS (Table 1). We used the Raster Calculator Tool of ArcGIS 10.2 to estimate the jaguar density adjusted according the human population density for each grid cell in the AOO maps (ESRI, 2013). Finally, using the jaguar density values of each grid cell, we estimated the number of jaguars for the each biome or biomes that were contained in each JS.

Importantly, jaguar densities vary according to different habitat types, prey availability, degree of fragmentation, seasons, and human disturbance. Also, density estimates using the camera trapping technique could be skewed, depending on how the methodology was used by different researchers throughout the range of the species (Tobler & Powell, 2013). For these reasons, our estimates of subpopulation sizes should be taken with caution, because we are extrapolating from the available information to vast areas. However, our approach was robust because we extrapolated jaguar densities only for sites where the human population density was not greater than 12 people/km² (for our lower estimate) or 24 people/km² (for our upper estimate), and because our approach assumed that jaguar densities were not homogeneous across the biomes. That is, jaguar densities were adjusted according to the human population density across the JS.

Assessment under the IUCN threat categories

Based on the EOO, AOO, and the estimated population size, we assessed the conservation status of each JS using the criteria of the IUCN Red List (IUCN Standards and Petitions Subcommittee, 2016). We used this evaluation to illustrate the risk of extinction of each JS independent of the conservation status of the other JSs. To conduct the assessments, we evaluated each JS against the five IUCN Red List criteria: A) declining population; B) geographic range size; C) small population size; D) very restricted distribution; and, E) quantitative analysis of extinction risk (IUCN, 2012). With this evaluation, each JS was classified in one of the next five categories of the IUCN Red List: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN) and Critically Endangered (CR).

Because little information exists about the recent decline of jaguars within the JS, to apply Criterion A, we estimated the jaguars' AOO in the recent past. For this, we used the UMD Land Cover Classification, developed from a collection of satellite images acquired between 1981 and 1994 (Hansen et al., 1998; Hansen et al., 2000), and a grid of the human population density in the American Continent for the year 1990 at a resolution of 30 arc-seconds (Center for International Earth Science Information Network et al., 2011). In a similar way that we estimated the current AOO, we defined two scenarios for our recent past AOO estimation. Our lowest estimate was defined by obtaining in each JS the natural vegetation layers from the UMD Land Cover

Classification, and excluding the sites where human density was higher than 12 people per km² in the year 1990. Our upper estimate was defined also by obtaining the "natural vegetation" layers, and excluding the areas where human density was higher than 24 people per km² in the year 1990. We rescaled the recent past AOO maps at the reference scale of 4 km², and we suspected (*sensu* IUCN Standards and Petitions Subcommittee, 2016, page 18) the percentage of range reduction for each JS based on the recent past and current AOO estimated areas. We set generation time at seven years based on approximate age of maturity (3 years for females and 4 years for males) plus half the length of the reproductive lifespan (6 years) (Eizirik et al., 2002; Quigley & Crawshaw, 2002). Therefore, the declines either in the past or in the future were suspected for a maximum period of 21 years.

Criterion B was applied using our estimates of the EOO and AOO of jaguars in each JS. Criteria C and D were applied using the mean of our estimates of population size in each JS and using the patterns of jaguar occurrence within the JS according to our estimate of the AOO. Criteria C and D were applied using the number of "mature individuals" which is defined as the number of individuals known, estimated or inferred capable of reproduction (IUCN Standards and Petitions Subcommittee, 2016). Given that most jaguar density studies only report data on adult individuals, we assumed that our estimations of jaguar subpopulations size only include "mature individuals".

Criterion E was applied using a Population Viability Analysis using VORTEX version 10.0.8 (Lacy & Pollak, 2015). To assess the JSs under criterion D, we estimated the probability of extinction of each JS based on their estimated population size and for time intervals of 21 years (3 generations), 35 years (5 generations), and 100 years. Because most of the demographic parameters for jaguars are unknown, our generic model was based on the parameters used by

Eizirik et al. (2002) to model the viability of jaguar populations (Table 2). We did not include catastrophes in our model, and we used 500 iterations in each JS model.

Level of threats for Jaguar Subpopulations

To assess the level of threats for each JS, we developed a threats evaluation system, which was applied independently to each JS. This assessment system was based on five criteria: A) Extent of habitat, B) Degree of human disturbance, C) Viability of the populations, D) Isolation from the other JSs, and E) Level of protection. Extent of habitat was based on the percentage of natural habitats contained in each JS, and we estimated the extent of habitat calculating the remaining areas with "natural vegetation" in each JS (Arino et al., 2012). Because the hunting pressure of large carnivores and their prey species is likely be higher in areas of high human population density (Woodroffe, 2000; Dupain et al., 2012; Espinosa et al., 2014; Fa et al., 2015; Ziegler et al., 2016), the degree of human disturbance was measured using a human population density grid (Center for International Earth Science Information Network et al., 2011), and by calculating the mean human density in each JS. To estimate the viability of the populations, we used our estimates of population size for each JS, and we used the criteria defined by Eizirik et al. (2002). JSs with a population size less than 300 individuals were designated as non-viable, JSs with 300 to 650 individuals were designated as viable in the medium term (100 years with 99% of probability), and JSs with more than 650 individuals were designated as viable in the long term (200 years with 99% of probability) (Eizirik et al., 2002). Degree of isolation was defined using the minimum distances to the four nearest JSs, and distances were estimated using the Proximity Tools of ArcGIS 10.2 (ESRI, 2013). The level of protection of each JS was determined by the percentage of protected area within the species range in each JS; this percentage was estimated using the WDPA database of protected areas of the world (UNEP-WCMC & IUCN, 2015). We overlayed our estimation of the species range with the terrestrial protected areas of the American Continent, and we estimated the percentage protected in each JS. We included in this analysis the national protected areas recognized by national governments, areas designated under regional and international conventions, privately protected areas, and territories that were conserved by indigenous people and communities. All of these protected areas met the definitions of protected areas by IUCN and the Convention of Biological Diversity (UNEP-WCMC & IUCN, 2015).

We defined three levels of scores to evaluate the JSs according to the five criteria. The highest level of threat for each criterion was assigned the score of "4", the medium level of threat was assigned the score of "3", and the lowest level was assigned the score of "2". Therefore, each population could get a maximum score of "20" and a minimum score of "10" (Table 3). JSs with a high level of threat (H) were defined as those with a final score ≥ 17, which is equivalent to having more than three criteria with the highest threats score. JSs with a medium level of threats (M) were defined as those that obtained a final score ≥ 13 to ≤16, which is equivalent to having more than one criterion with the highest threats score. JSs with final scores ≤ 12, which is equivalent to having only one criterion with the maximum, were defined as those with a low level of threat (L).

Results

Current geographic range and level of protection

According to our estimates, the geographic range of jaguar covers approximately 8,420,000 km^2 (Table 4). Jaguars are still found in 18 countries across the continent, from northern Mexico to northern Argentina; they have disappeared from El Salvador and Uruguay, and are practically extinct in the US (Fig 1). Using the area covered by the JSs, we estimated that the jaguar's geographic range has contracted by 51% in the last century. However, using our estimation of the AOO, the picture is even more dire; the AOO covers approximately 7,400,000 km² and jaguar range may have decreased by 45% in the last century. About 38.4% of the geographic range of the species is protected. Brazil has the largest proportion of area protected; 66 % of the protected jaguar range is in Brazil, followed by Venezuela (8%), Peru (8%), Bolivia (5%), and Colombia (3%). We identified 34 JSs, which varied greatly in size from 2,241 to 6,691,521km². One subpopulation, the Amazonia JS, covers 79% of the total range of the species globally (Table 4). This means that jaguars have declined about 82% throughout their range outside of Amazonia.

Jaguar population size

We estimated a jaguar global population of around 64,000 individuals (Fig. 2 & Table 4). The largest subpopulation, the Amazonia JS, has ~57,000 jaguars; the remaining 33 JSs have a mean estimated population of 209 ± 293 jaguars. Today the Amazon JS represents about 89.2% of the total jaguar population, leaving only 10.8% in the rest of the range.

Assessment of the Jaguar Subpopulations under the IUCN threat categories

Based on our assessment of the JSs under IUCN criteria, jaguars are virtually threatened everywhere except in the Amazonia JS (Fig. 3 & Table 5). According to our assessment and using the precautionary principle, 25 JSs should be classified as Critically Endangered, and 8 JSs qualify as Endangered. Only the Amazonia JS maintain the status of Least Concern. Most JSs qualified for one of the threat categories under at least three criteria (C, D, and E).

Level of threats for Jaguar Subpopulations

According to our evaluation, most of the JSs included high levels of threats (Fig. 3 & Table 6). We identified 17 JSs with scores that exceeded the threshold for a high level of threat in agreement with our evaluation, and 14 JSs exceeded the threshold for a medium level of threat. Only the Amazonia, Araguaia, and Selva Maya JSs scored as having a low level of threat. Most of the JSs with highest levels of threats were in the southern portion of the species' range in Brazil and Argentina (n= 11). Additionally, three JSs in northern South America had high levels of threats, and these occurred in Santa Helena-Guayas in Ecuador, and in Paramillo San Lucas and Sierra Nevada de Santa Marta in Colombia. In Central America, the JSs with highest levels of threats were in Central Panama and the Honduras Caribbean JSs. In Mexico, the JS with highest levels of threats was the Sierra de Tamaulipas (Table 6).

Discussion

Our results support and provide greater robustness to prior assessments of range loss and population decline of jaguars at the continental scale (Sanderson et al., 2002; Zeller, 2007). Jaguars have been extirpated from more than half of their original range in the last 100 years, and the most recent assessments of the regional and continental conservation status of the species have concluded that the jaguar continues to decline in much of its current distribution (Swank & Teer, 1989; Medellín et al., 2002, 2016; Sanderson et al., 2002; Zeller, 2007; Caso et al., 2008). Our estimate of range loss for jaguars using the area covered by the JSs is similar to the approach of Sanderson et al. (2002) (~ 54% of range loss). However, we included areas to the current range of the species that previously had been classified as unknown areas of occurrence (Sanderson et al., 2002; Zeller, 2007), and for the first time we assessed the jaguar status across the species' historical range, approximately 16,300,000 km^2 (Patterson et al. 2007). This implies that our estimates of the loss of jaguar range and population decline are more accurate than previous approaches, because our analysis was based on the most recent information on jaguar distribution and on a more precise historic range of the species. Our estimate of the global AOO of jaguars yields a very grim scenario for the species than previous assessments had projected; according to our analyses, jaguars have already disappeared from ~55% of their historic range and the vast majority of its JSs are Endangered or Critically Endangered.

Our global estimate of the jaguar population extrapolate localized density estimates to extensive areas that ignore local conditions, such as fragmentation, prey availability, and different levels of threats for the species, and that may seem doubtful. However, our approach and estimate are realistic and conservative, because we are extrapolating jaguar densities only for sites where human population density did not exceed the thresholds at which jaguar extirpation were predicted (Woodroffe, 2000), and because we are assuming that jaguars densities decreased in relation to the increase in human population density. Furthermore, there are other estimates of local population sizes that suggest that our approach is reasonable (Tobler et al., 2013; Chávez et al., 2016; de Thoisy, 2016; Di Bitetti et al., 2016; Díaz-Santos et al., 2016; Espinosa et al., 2016; Figueroa et al., 2016; García-Anleu et al., 2016).

Amazonia, with its very large population size, represents the only remaining stronghold for the species, and several studies have highlighted the great importance of this region for jaguar conservation overall (Sanderson et al., 2002; Sollmann et al., 2008; De Oliveira et al., 2012; Tobler et al., 2013). Even then, this subpopulation is likely to be affected in the next decades by deforestation and other threats, because human transformation of the region is accelerating rapidly (Rosa et al., 2012, 2013; Coe et al., 2013; Morton et al., 2013). Ochoa-Quintero et al.

(2015) predicted that by 2030, only 22% of the landscapes in the Amazon will be able to sustain at least 75% of the focal species, including jaguars, due to habitat fragmentation.

Assessments of any species should not be based or affected significantly by the existence of a single large subpopulation; the “all the eggs in one basket” approach has proven dangerous in the past. Rather, conservation plans should integrate an assessment of the species’ entire range (Ceballos & Ehrlich, 2002; Wallace et al., 2010). Data for an area that is covered by only one subpopulation will likely result in a biased assessment, while all other subpopulations may become extinct. Because most of the JSs are seriously threatened, and sub-specific classification has been rejected, we propose that jaguar conservation assessments should include not only one global category, but should consider subpopulations/sub-global assessments. Data on only range size of this species has biased the assessment, and conservation resources have not been allocated specifically for endangered subpopulations, given the species somewhat positive global status overall. In addition, the causes of decline in most JSs have not stopped; on the contrary, they are accelerating, and further endangerment of the jaguar in most of its range is quite likely. The main threats for the species throughout its range are hunting, depletion of prey, and habitat loss and fragmentation (Sanderson et al., 2002; Caso et al., 2008; Haag et al., 2010).

Based on our evaluation of threats, it is important to prioritize the conservation actions focused on the species in the near future. Identification and implementation of corridors to maintain connectivity should be a priority in the JSs that have the highest degree of isolation and the lowest population sizes (Rabinowitz & Zeller, 2010). For example, JSs from the Atlantic Forest in Brazil and Argentina are threatened not only by their isolation and low population numbers, but they are threatened also by their low genetic diversity, lack of gene flow, and small effective population sizes (Haag et al., 2010). Another priority is to plan reserves throughout the range of the species to ensure the long-term connectivity and conservation of most JSs. In most of these, the area protected is less than 25%. Vast areas of high-quality habitat are required to ensure the viability of a population of jaguars over the long term (Quigley & Crawshaw Jr., 1992; Ceballos et al., 2002; Sanderson et al., 2002); only very few regions where the species currently ranges maintain protected areas that are large enough to ensure the protection of at least 300 jaguars to guarantee population viability over the next 100 years (Eizirik et al., 2002). Furthermore, many protected areas throughout the species' range have limited or no real protection. The jaguar is considered an umbrella, charismatic, and symbol or flag species in many conservation programs throughout Latin America (Medellín et al., 2002, 2016; Sanderson et al., 2002; Rabinowitz & Zeller, 2010), and ensuring areas large enough to maintain viable populations of jaguars is a unique opportunity to ensure the protection of biodiversity with which jaguars coexist (Thornton et al., 2015). Additionally, in JSs that are threatened by high human densities and by high risk of losing natural habitats, sustainable development policies should be implemented to ensure the conservation of jaguar habitats and the well-being of human communities that coexist with this felid.

Our analysis is the first to provide an estimate of population size for jaguars globally, and it also establishes the basis to determine geographic conservation priorities for this iconic umbrella species using the vulnerability of its individual populations. Greater detail is needed about the areas occupied by the species across its range. Additional density estimates for more biomes and ecoregions will also help improve the definition of JSs in the future. Also, more accurate estimates of the distances that jaguars can travel between fragmented landscapes will indicate where conservation efforts should be allocated. It is urgent to include the sub-global assessments for jaguars under the IUCN Red List of Threatened Species; our analysis and further research will result in a robust regional conservation strategy that could be designed and implemented by local conservation leaders across the species' range.

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Table 1. Densities in jaguars per 100 km² that were used to extrapolate the population size for each jaguar population in each biome: Moist Broadleaf Forest (MBF); Dry Broadleaf Forest (DBF); Grasslands, Savannas, Scrublands (GSS); Flooded Grasslands and Savannas (FGS); Montane Grassland and Scrublands (MGS); Tropical Coniferous Forest (TCF); Deserts (D); Mangroves (M).

No.	Jaguar Subpopulation	MBF	DBF	GSS	FGS	MGS	TCF	D	M	References
1	Mexican Pacific	1.8	1.5				0.65	0.65	0.65	Núñez-Pérez (2011); de la Torre & Medellín (2011); Gutiérrez-González et al. (2012)
2	Sierra de Tamaulipas	0.75					0.75	0.65		Gutiérrez-González et al., (2012); Chávez et al. (2016)
3	Gulf of Mexico	1.8	1.5						0.65	de la Torre & Medellín (2011); Chávez et al. (2016)
4	Selva Maya	1.8	1.5				0.65		0.65	Núñez-Pérez (2011); de la Torre & Medellín (2011); Chávez et al. (2016)
5	Maya Mountains	5.75					4	0.65	0.65	Silver et al. (2004)
6	Honduras Caribbean	1.55					1		1	Mora et al. (2016)
7	Honduran Mosquitia	1.55	1				1		1	Mora et al. (2016)

8	Indio-Maíz Tortuguero	1.5					1		1	Díaz-Santos et al. (2016)
9	Talamanca	1.34								González-Maya et al. (2016)
10	Osa Peninsula	4							0.65	Salom-Pérez et al. (2007)
11	Central Panama	2							0.65	Moreno et al. (2016)
12	Biogeographic Choco	1.5	1.5			0.65			0.65	Moreno et al. (2016)
13	Paramillo-San Lucas	1.5	1.5							
14	Sierra Nevada de Santa Marta	1.5	1			0.65		0.65	0.65	
15	Serrania de Perija-Catatumbo	1.5	1.5			0.65		0.65		
16	Santa Helena-Guayas	1.5	1.5			0.65		0.65		
17	Amazonia	1*	1*	1*	1*	0.65		0.65	0.65	Maffei et al. (2004); Soisalo & Cavalcanti (2005); De Oliveira et al. (2012); Tobler et al. (2013)
18	Maranhão-Babaçu	0.67								Moraes Jr. (2012)
19	Nascentes Parnaíba	0.67	0.67	0.67						
20	Boquerião da Onça		0.5	0.5				0.5		De Paula et al. (2012)
21	Serra da Capivara							0.2		De Paula et al. (2012)
22	Chapada Diamantina		0.3	0.3				0.3		De Paula et al. (2012)

23	Araguaia	0.67		0.67			Moraes Jr. (2012)
24	Goiás and Tocantins	0.67		0.67			Moraes Jr. (2012)
25	Sertão Veredas Peruaçu	0.67	0.67	0.67	0.67		De Oliveira et al. (2012)
26	Mato Grosso	1	1	1			De Oliveira et al. (2012)
27	Chapada dos Guimarães		0.69	0.69			Moraes Jr. (2012)
28	Emas			0.69			Sollmann et al. (2011)
29	Espinhaço de Minas	0.69		0.69			Moraes Jr. (2012)
30	Sooretama	0.33				0.33	Paviolo et al. (2008)
31	Mantiqueira-Rio Doce	0.33					Paviolo et al. (2008)
32	Pontal do Paranapanema	0.33		0.33			Paviolo et al. (2008)
33	Serra do Mar	0.33		0.33		0.33	Paviolo et al. (2008)
34	Iguaçu	0.33		0.33			Paviolo et al. (2008)

* In the Amazonia JS, we used the most conservative density estimates of 1 jaguar/100 km² (De Oliveira et al., 2012) for most of biomes because the most of this vast area have never been surveyed for jaguars and the extrapolation for this area probably come with enormous uncertainty. However, density estimates for the Amazonia JS in the MBF biome range from 1 to 4.4 jaguars/100km² (De Oliveira et al., 2012; Tobler et al., 2013), in the DBF biome range from 2.27 to 5.37 jaguars/100km² (Maffei et al., 2004), and in the FGS biome the density estimate is 6.6 jaguars/100km² (Soisalo & Cavalcanti, 2006).

Table 2. Demographic parameters used in our base model of VORTEX to evaluate the JS under criterion E of the IUCN Red List.

Parameters	**Values the base model**
Inbreeding depression	3.4 lethal equivalents per individual, and 1.57 recessive lethal alleles
Extinction definition	No animals of one or both sexes.
Reproduction system	Polygynous
First age of reproduction	3 years for females and 4 years for males
Maximum breeding age	10 years
Sex ratio at birth	0.5
Adult males in the breeding pool	90 %
% of adult females breeding	Reproduction is density-dependent according with the next formula: ((50*[1-((N/K)^2)])+(30*[(N/K)^2]))*(N/(0.50+N))
Number of offspring per female per brood	1 to 4 litters; 5% of the females produce litter of size 1, 40% produce litter of size 2, 30% produce litter of size 3 and 25% produce litter of size 4.
Mortality of females	34% (ages 0-1), 17% (ages 1-2), 19% (ages 2-3), and 20% (adults).
Mortality of males	34% (ages 0-1), 17% (ages 1-2), 35% (ages 2-3), 30% (ages 3-4) and 30% (adults).

Table 3. The five criteria used to evaluate the level of threats in each JS. We defined three thresholds for the five criteria according to the level of threats. In the JSs with higher levels of threats, we assigned the value of 4, to the medium levels the value of 3, and to the lowest level of threats the value of 2. JSs that had higher total scores were the most endangered populations according to our classification.

Criterions	**Units**	**Maximum (4)**	**Medium (3)**	**Low (2)**
A. Habitat availability	% of natural habitats within the JS	< 50	< 75 to ≥ 50	≥ 75
B. Degree of human perturbation	Mean of human density within the JS	≥ 500	≥ 100 to < 500	< 100
C. Viability of the population	Population size	< 300	≥ 300 to ≤ 650	< 650
D. Isolation	Minimum distances to the mean of nearest 4 JSs in km	> 200	>100 to ≤ 199	≥50 to ≤ 100
E. Protection	% of area protected within the JS	< 25	≥ 25 to ≤ 50	> 50

Table 4. The extent of occurrence (EOO), our lower and upper scenarios of the estimated areas of occupancy (AOO) in each Jaguar Subpopulation, and the lower and upper estimates of Jaguar Subpopulation size (mature individuals).

No.	**Jaguar Subpopulation**	**Area covered by the JS in km²**	**EOO in each JS in km² (Minimum Convex Polygon)**	**Lowest estimation of AOO in each JS in km²**	**Upper estimation of AOO in each JS in km²**	**Lower estimate of mature individuals (Critical Human Density = 12 persons/km²**	**Upper estimate of mature individuals (Critical Human Density = 24 persons/km²)**
1	Mexican Pacific	195,848	1,274,871	117,964	151,000	852	1,179
2	Sierra de Tamaulipas	54,447	94,043	36,860	43,048	149	218
3	Gulf of Mexico	9,059	13,804	3,436	7,016	26	52
4	Selva Maya	88,923	182,895	80,016	83,308	764	1,079
5	Maya Mountains	17,856	28,246	7,248	9,556	217	332
6	Honduras Caribbean	6,333	9,999	1,532	2,284	9	16
7	Honduran Mosquitia	26,502	39,294	19,124	23,764	188	231
8	Indio-Maíz Tortuguero	26,766	43,303	13,132	18,332	101	152

9	Talamanca	15,141	17,887	7,712	11,484	25	69
10	Osa Peninsula	2,241	3,305	0	1,788	0	21
11	Central Panama	5,129	7,809	2,532	2,932	26	35
12	Biogeographic Choco	159,175	278,753	89,164	105,244	697	1,035
13	Paramillo-San Lucas	38,186	38,342	19,728	32,732	70	214
14	Sierra Nevada de Santa Marta	8,662	8,765	0	3,832	0	25
15	Serrania de Perija-Catatumbo	43,367	52,370	21,552	29,340	106	198
16	Santa Helena-Guayas	10,592	10,866	1,324	4,240	5	13
17	Amazonia	6,691,521	9,874,482	6,244,810	6,289,556	56,223	58,183
18	Maranhão-Babaçu	22,414	22,522	7,140	19,652	10	45
19	Nascentes Parnaíba	148,027	162,275	118,360	118,360	491	491
20	Boquerião da Onça	12,327	15,239	10,564	10,600	10	13
21	Serra da Capivara	81,466	103,542	52,704	57,080	132	169
22	Chapada Diamantina	25,110	30,076	14,496	16,188	21	24
23	Araguaia	122,212	143,080	103,832	103,832	531	566
24	Goiás and Tocantins	124,726	141,670	88,976	90,444	315	349
25	Sertão Veredas Peruaçu	138,305	162,923	72,528	76,396	202	239

26	Mato Grosso	112,103	146,001	91,696	91,696	762	782
27	Chapada dos Guimarães	44,246	48,245	24,512	24,536	72	80
28	Emas	15,169	15,182	9,212	9,212	30	31
29	Espinhaço de Minas	29,599	32,261	17,684	21,592	59	81
30	Sooretama	4,974	5,006	232	1,796	0	1
31	Mantiqueira-Rio Doce	5,249	5,285	1,204	1,804	2	3
32	Pontal do Paranapanema	34,888	44,925	13,636	16,444	12	16
33	Serra do Mar	56,400	116,227	16,012	26,968	23	45
34	Iguaçu	46,011	56,705	15,100	24,080	26	43

Table 5. The IUCN classification of each Jaguar Subpopulation based on the evaluation of each Jaguar Subpopulation against the IUCN Red List criteria. Some of the Jaguar Subpopulations qualified to different categories of risk according with the uncertainty of our estimations of AOO and Jaguar Subpopulation size. The final column shows the category of each Jaguar Subpopulation assigned under the most precautionary principle.

No.	**Jaguar Subopulation**	**A. Population size reduction**	**B. Geographic range**	**C. Small population size and decline**	**D. Very small or restricted population**	**E. Quantitative Analysis**	**IUCN Red List category assigned under the most precautionary principle**
1	Mexican Pacific			EN C2a(i)	VU D1		EN
2	Sierra de Tamaulipas			CR C2a(ii)	EN D	VU E	CR
3	Gulf of Mexico	VU A2a+4c	VU B1ab(i)	CR C2a(ii)	CR D	EN E; CR E	CR
4	Selva Maya			EN C2a(ii)	VU D1	VU E	EN
5	Maya Mountains	VU A4c		CR C2a(ii); EN C2a(ii)	EN D1;VU D1	VU E	EN
6	Honduras Caribbean	VU A2a+4c	VU B1ab(i)+2ab(ii)	CR C2a(i)	CR D	CR E	CR
7	Honduran Mosquitia	VU A4c		CR C2a(ii)	EN D	VU E	CR

8	Indio-Maíz Tortuguero			CR C2a(ii)	EN D	VU E	CR
9	Talamanca		VU B1ab(i)	CR C2a(ii)	CR D; EN D1	EN E; CR E	CR
10	Osa Peninsula	VU A4c	EN B1ab(i); VU B2ab(ii)	CR C2a(ii)	CR D	CR E	CR
11	Central Panama		VU B1ab(i)	CR C2a(ii)	CR D	EN E; CR E	CR
12	Biogeographic Choco			EN C2a(ii)	VU D1	VU E	EN
13	Paramillo-San Lucas			CR C2a(ii)	EN D	VU E; EN E	CR
14	Sierra Nevada de Santa Marta		VU B1ab(i)	CR C2a(ii)	CR D	CR E	CR
15	Serrania de Perija-Catatumbo	VU A4c		CR C2a(ii)	EN D	VU E	CR
16	Santa Helena-Guayas	VU A4c	VU B1ab(i)	CR C2a(i)	CR D	CR E	CR
17	Amazonia						LC
18	Maranhão-Babaçu	VU A4c		CR C2a(ii)	CR D	EN E; CR E	CR
19	Nascentes Parnaíba			EN C2a(ii)	VU D1	VU E	EN
20	Boquerião da Onça		VU B1ab(i)	CR C2a(ii)	CR D	CR E	CR
21	Serra da Capivara	VU A4c		CR C2a(i)	EN D	VU E	CR
22	Chapada Diamantina			CR C2a(i)	CR D	CR E	CR
23	Araguaia			EN C2a(ii)	VU D1	VU E	EN
24	Goiás and Tocantins	VU A4c		EN C2a(i)	VU D1	VU E	EN
25	Sertão Veredas Peruaçu	VU A2a+4c		CR C2a(i)	EN D	VU E	CR

26	Mato Grosso			EN C2a(i)	VU D1	VU E	EN
27	Chapada dos Guimarães	VU A2a+4c		CR C2a(i)	EN D	EN E	CR
28	Emas	VU A4c	VU B1ab(i)	CR C2a(i)	CR D	EN E	CR
29	Espinhaço de Minas			CR C2a(i)	EN D	EN E	CR
30	Sooretama	VU A2a+4c	VU B1ab(i)+2ab(ii)	CR C2a(i)	CR D	CR E	CR
31	Mantiqueira-Rio Doce	VU A4c	VU B1ab(i)+2ab(ii)	CR C2a(i)	CR D	CR E	CR
32	Pontal do Paranapanema	VU A4c		CR C2a(i)	CR D	CR E	CR
33	Serra do Mar			CR C2a(i)	CR D	EN E; CR E	CR
34	Iguaçu	VU A4c		CR C2a(i)	CR D	EN E; CR E	CR

Table 6. The 34 Jaguar Subpopulations with values of the five criteria that were used to evaluate the level of threats of each Subpopulation.

No.	**Jaguar Population**	**Percentage of natural cover**	**Human population density**	**Mean jaguar numbers (viability)**	**Mean distance to the four nearest JSs (km)**	**Percentage protected**	**Total score**	**Classification of threats level**
1	Mexican Pacific	86.08	488.3	1,016	161.00	8.87	14	M
2	Sierra de Tamaulipas	93.75	1033.1	184	858.00	16.73	18	H
3	Gulf of Mexico	79.25	263.6	39	301.00	66.47	15	M
4	Selva Maya	95.32	216.8	922	131.00	50.67	12	L
5	Maya Mountains	90.10	884.5	275	183.83	49.74	16	M
6	Honduras Caribbean	45.78	1096.1	13	240.00	29.59	19	H
7	Honduran Mosquitia	85.90	116.6	210	284.00	87.46	15	M
8	Indio-Maíz Tortuguero	74.69	408.5	127	160.00	63.79	14	M
9	Talamanca	81.24	572.0	47	99.00	48.16	15	M
10	Osa Peninsula	69.94	307.7	11	206.00	63.53	16	M

11	Central Panama	73.03	1687.5	31	186.00	57.96	16	M
12	Biogeographic Choco	74.17	928.4	866	86.00	11.62	15	M
13	Paramillo-San Lucas	72.06	521.0	142	138.00	9.16	18	H
14	Sierra Nevada de Santa Marta	75.61	1451.2	13	228.00	38.87	17	H
15	Serrania de Perija-Catatumbo	65.51	1151.8	152	100.00	25.28	16	M
16	Santa Helena-Guayas	51.66	4544.6	9	534.00	2.10	19	H
17	Amazonia	93.02	83.6	57,203	51.00	42.75	11	L
18	Maranhão-Babaçu	70.72	392.0	28	366.00	20.95	18	H
19	Nascentes Parnaíba	61.13	53.1	491	59.00	19.58	14	M
20	Boquerião da Onça	68.81	155.6	12	63.00	5.88	18	M
21	Serra da Capivara	60.66	106.8	151	294.00	20.30	16	M
22	Chapada Diamantina	54.70	195.3	23	141.00	17.05	17	H
23	Araguaia	76.93	27.8	549	69.00	35.33	12	L
24	Goiás and Tocantins	55.54	132.5	332	89.00	10.01	15	M
25	Sertão Veredas Peruaçu	35.87	151.0	221	101.63	12.96	18	H
26	Mato Grosso	78.57	29.6	772	329.00	13.94	14	M
27	Chapada dos Guimarães	42.51	380.7	76	166.00	10.90	18	H

28	Emas	42.39	58.9	31	235.00	10.79	18	H
29	Espinhaço de Minas	58.70	209.1	70	225.00	7.49	18	H
30	Sooretama	44.41	744.9	1	297.53	15.10	20	H
31	Mantiqueira-Rio Doce	51.64	2024.6	3	225.11	7.90	19	H
32	Pontal do Paranapanema	25.26	220.5	14	298.00	29.24	18	H
33	Serra do Mar	77.36	5757.6	34	307.24	44.02	17	H
34	Iguaçu	59.12	771.1	35	338.00	14.37	19	H

Fig. 1. a) Jaguar Subpopulations identified; b) 1. Mexican Pacific, 2. Sierra de Tamaulipas, 3. Gulf of Mexico, 4. Selva Maya; c) 5. Maya Mountains, 6. Honduras Caribbean, 7. Honduran Mosquitia, 8. Indio Maíz-Tortuguero, 9. Talamanca, 10. Osa Peninsula, 11. Central Panama; d) 12. Biogeographic Choco, 13. Paramillo-San Lucas, 14. Sierra Nevada de Santa Marta, 15. Serrania de Perija-Catatumbo, 16. Santa Elena Guayas; e) Amazonia; f) 18. Maranhão-Babaçu, 19. Nascentes Parnaíba, 20. Boquerião da Onça, 21. Serra da Capivara; 22. Chapada Diamantina; 23. Araguaia, 24. Goiás and Tocantins; 25. Sertão Veredas Peruaçu, 26. Mato Grosso; 27. Chapada dos Guimarães; 28; Emas; 29. Espinhaço de Minas, 30. Sooretama; 31. Mantiqueira-Rio Doce, 32. Pontal do Paranapanema, 33. Serra do Mar, 34. Iguaçu.

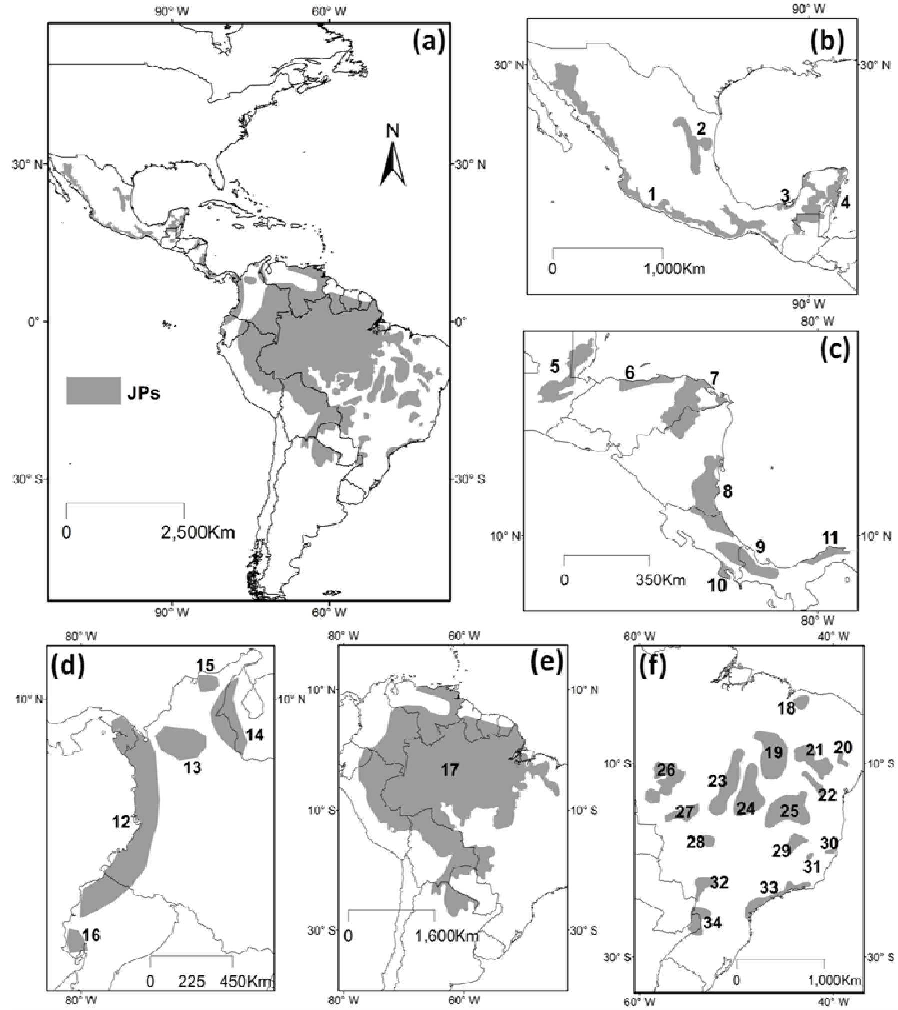


Fig. 2. Color gradient shows jaguar densities across the range of the species according to our lower (a, b, c, & d) and upper (e, f, g, & h) estimates of JS sizes. Extrapolation of the density estimates was only implemented in sites where the human population density was not greater than 12 people/km² (for our lower estimate) or 24 people/km² (for our upper estimate). Additionally, jaguar densities were adjusted according to the human population density across the JS.

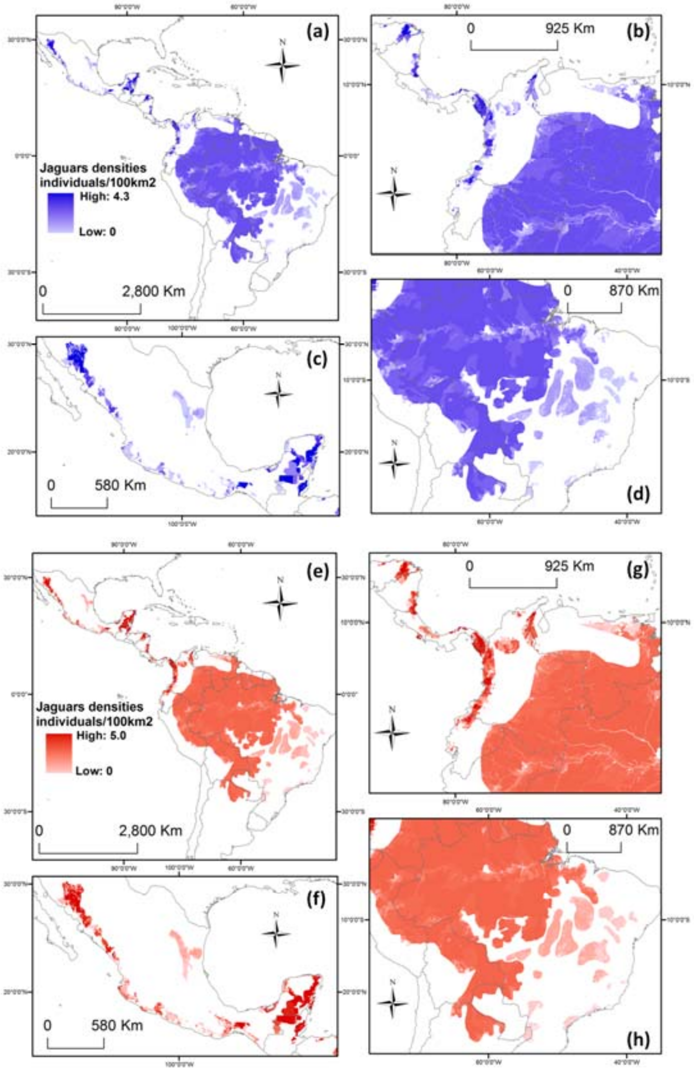
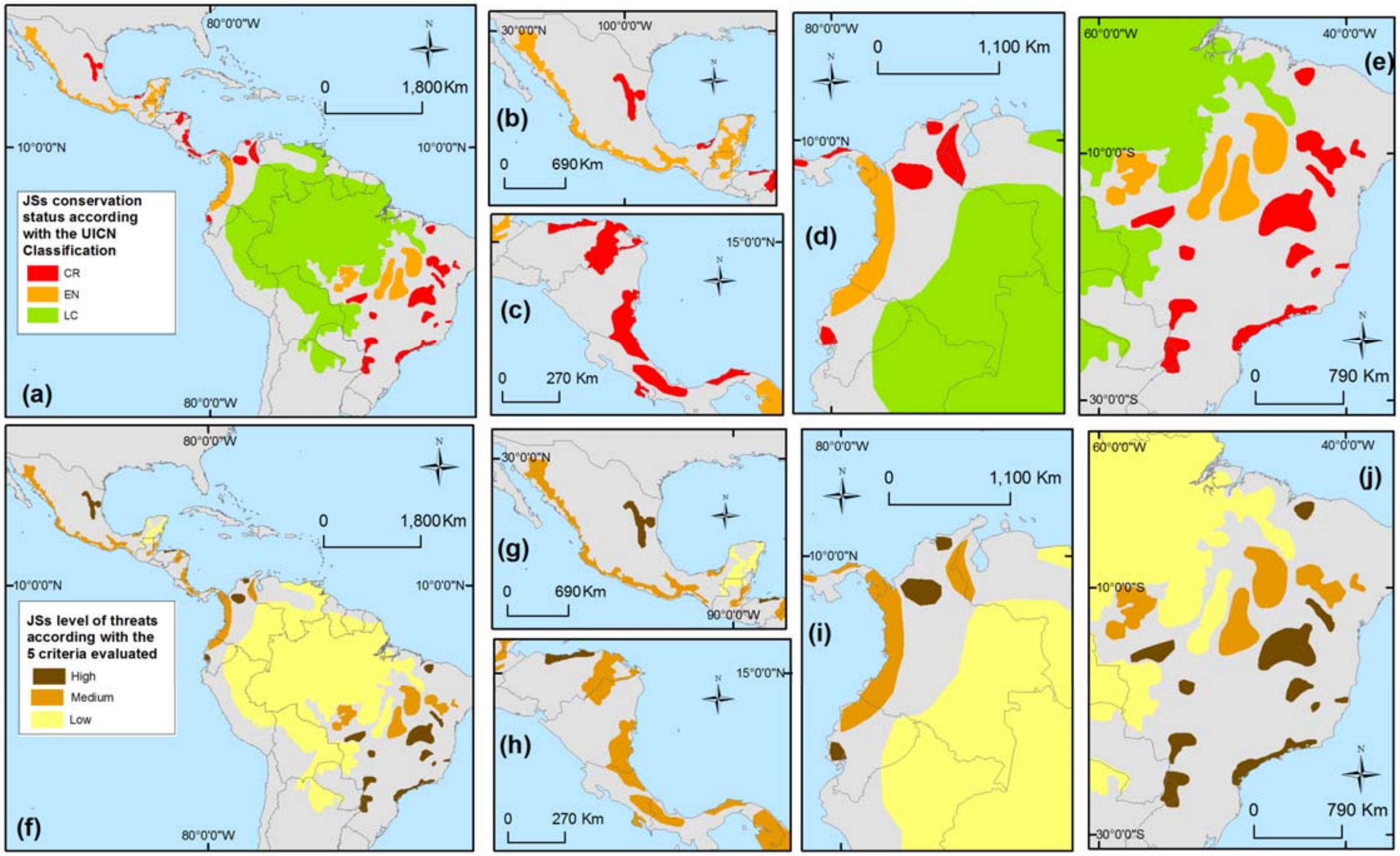


Fig. 3. Conservation status of Jaguar Subpopulations according to the IUCN Red List criteria in: a) the entire species range, b) Mexico, c) Central America, d) northern South America, and e) southern Amazonia; and level of vulnerability of Jaguar Subpopulations according to the levels of threat in f) the entire species range, g) Mexico, h) Central America, i) northern South America, and j) northern Amazonia.



6. Capitulo 2. Ecología espacial de jaguares (*Panthera onca*) y pumas (*Puma concolor*) en el paisaje de la Selva Lacandona.

Spatial requirements of jaguars and pumas in Southern Mexico.

(Con formato para *Mammalian Biology*)

Spatial requirements of jaguars and pumas in Southern Mexico.

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Abstract

Understanding how large felids use space is essential for the design of conservation plans that are required for their survival. Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest felids in the Neotropics, and they are sympatric throughout the entire range of the jaguar. However, there is very little information about the spatial requirements of these two species in the tropical rainforests of Central America. Using satellite GPS collars, we compared the spatial ecology of jaguars and pumas in a tropical rainforest in southern Mexico. We found that jaguars had home ranges that were 2 - 6 times larger than those of pumas. The mean annual home range for female jaguars was 181.4 ± 4.0 km² and 431.6 ± 152.6 km² for males. Annual home range for the only female puma tracked was 34.3 km², and 72.0 ± 85.2 km² for males. Jaguars and pumas with overlapping home ranges showed little overlap of core areas and avoided using the same sites at the same time, which suggested territoriality and avoidance. Further evidence of avoidance was derived from our observation that pumas exhibited greater movement during the lightest periods of the day and jaguars moved most during the darkest. This temporal separation probably facilitates coexistence. Our data suggest that habitat destruction and fragmentation has more severe effects on jaguars than on pumas. According to our estimates, patches of at least 180 km² of primary forest are required to meet the annual spatial requirements of female jaguars. Thus, to conserve jaguars in this region, large tracts of primary forest should be preserved. Importantly, this population of jaguars depends on the adequate preservation of connectivity between natural reserves of Mexico and Guatemala.

Keywords: GPS radio-telemetry; Greater Lacandona Ecosystem; home ranges; *Panthera onca*; *Puma concolor*.

Introduction

Understanding the details of how large felids use space is essential to develop and implement effective conservation plans for these species. Large felids require large home-ranges for their survival and, thus, they are often observed at low population densities (Carbone and Gittleman, 2002; Woodroffe and Ginsberg, 1998). Diverse factors determine the patterns of space use of solitary large felids. Variables that dictate home range in these animals include body size (Carbone et al., 2007, 2005; Gittleman and Harvey, 1982; Gittleman, 1985; Jetz et al., 2004), prey availability (Herfindal et al., 2005; Marker and Dickman, 2005; Odden and Wegge, 2005; Schmidt, 2008), and sociality (Azevedo and Murray, 2007; Cavalcanti and Gese, 2009; Goodrich et al., 2010; Logan and Sweanor, 2001; Seidensticker et al., 1973). Additionally, interactions between species, in particular other large carnivores, can influence space use patterns. Co-occurring species of large carnivores may use different habitat types, actively avoid using the inhabited sites, or segregate their space use temporally (Bhattarai and Kindlmann, 2012; Harmsen et al., 2009; Odden et al., 2010; Scognamillo et al., 2003; Sollmann et al., 2012).

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest felids in the Neotropics, and are sympatric throughout the entire range of the jaguar. As with most large species of Carnivora, jaguar and puma populations are declining due to habitat destruction and hunting (Ripple et al., 2014; Treves and Bruskotter, 2014; Woodroffe and Ginsberg, 1998). The present distribution of jaguars ranges from northern Mexico to northern Argentina, with some individuals occasionally reaching the southern portions of the United States (Arizona and New Mexico) (Sanderson et al., 2002; Sunquist and Sunquist, 2009). Given this large range it is perhaps not surprising that jaguars occupy diverse habitat types, which include tropical rainforests, mangroves, wet grasslands, arid scrublands, and pine oak forests (Sanderson et al., 2002).

In comparison, pumas (mountain lions) are found in an even wider range of habitat types and they have a larger distribution that ranges at present from Patagonia to Northern British Columbia (Sunquist and Sunquist, 2009). Pumas are smaller in areas where they live in sympatry with jaguars, and their body size is larger in areas outside the jaguar's distribution (Iriarte et al., 1990). Although jaguars are larger than pumas, there is overlap in their size and the size of prey they can hunt effectively and, thus, they are potentially competing species. Several studies have examined interactions between these species in areas of sympatry. It appears that coexistence between jaguars and pumas is facilitated by differential habitat use, active avoidance, temporal segregation of space, or by differential prey use (Aranda and Sánchez-Cordero, 1996; Emmons, 1987; Foster et al., 2010; Harmsen et al., 2009; Novack et al., 2005; Nuñez et al., 2000; Romero-Muñoz et al., 2010; Scognamillo et al., 2003; Sollmann et al., 2012).

Recently, there have been significant advances in understanding jaguar and puma ecology in tropical ecosystems (Aranda and Sánchez-Cordero, 1996; Cavalcanti and Gese, 2009; Chávez, 2009; Colchero et al., 2011; Conde et al., 2010; Emmons, 1987; Foster et al., 2010; Franklin et al., 1999; Harmsen et al., 2009; Novack et al., 2005; Nuñez, 2006; Núñez et al., 2002; Rabinowitz and Nottingham Jr., 1986; Romero-Muñoz et al., 2010; Scognamillo et al., 2003; Sollmann et al., 2012). However, information about spatial requirements, movement behaviors, and the impact of habitat destruction is still lacking. Thus, current conservation and management plans for these species in Neotropical ecosystems suffer from insufficient information.

The aim of this study is to describe and compare the spatial ecology of jaguars and pumas in a tropical rainforest with regionally heavy human activities in southern Mexico. Using GPS telemetry, we documented home range size, movement patterns, and interactions between jaguars and pumas. This is the first study that present data of jaguars and pumas tracked simultaneously using GPS radio-telemetry, and the results presented in this study illustrate differences in the space use between jaguars and pumas that have not been documented previously. We were interested in answering two questions: (1) what is the home range size used by jaguars and pumas in the tropical rainforests of southern Mexico? (2) How do jaguars and pumas share space when they coexist? Because home range size in large predators is determined by body size and energetic requirements (Gittleman and Harvey, 1982; Gittleman, 1985), we predicted that home range areas and movement rates will be greater in jaguars than in pumas. Given that coexisting felids show temporal segregation in their space use and avoid the same sites actively (Bhattarai and Kindlmann, 2012; Harmsen et al., 2009; Odden et al., 2010; Scognamillo et al., 2003; Sollmann et al., 2012), we predicted that jaguars and pumas with overlapping home ranges would show little overlap at core home-range areas and they would avoid using sites at the same time.

Materials and Methods

Study site

We investigated home ranges and movements by jaguars and pumas in the Greater Lacandona Ecosystem (GLE) in southeastern Mexico. This region contains the largest remaining portion of tropical rainforest in Mexico. Found in the most bio-diverse region of Mexico, the GLE is a valuable natural resource and part of what is called the 'Mayan Forest', given its important cultural associations (de la Torre and Medellín, 2011; Medellín, 1994). Despite importance for conservation of numerous species, the GLE continues to be subjected to anthropogenic destruction. Of its original 1,500,000 ha of rainforest, 2/3 has been lost due to human impact in the past 40 years (Jong et al., 2000; Mendoza and Dirzo, 1999).

Within the GLE are seven Natural Protected Areas (NPAs). These cover the largest forested areas of this region: Montes Azules (3,312 km²), Lacantún (619 km²), Bonampak (48 km²), Yaxchilán (26 km²), Chan-kin (122 km²), Naha (38 km²), and Metzabok (33 km²) (Fig. 1).

Our study area was in the north of GLE and covered approximately 2,500 km², including Yaxchilán (Usumacinta river as the border with Guatemala on the north), Bonampak, Lacantún, and Montes Azules NPAs (Fig. 1). The study area also encompassed the Sierra la Cojolita, a tract of natural habitat in the north of GLE that is protected by local communities. Three indigenous communities inhabit the Mexican part of our study area: Lacanja Chansayab (˜1000 people), Nueva Palestina (˜20,000), and Frontera Corozal (˜15,000). The main economic activities in this region include ranching, farming, and ecological and archeological tourism. The climate is hot (mean of 25 °C) and the mean rainfall per year is 2,800 mm, with the greatest concentration in June-September, and the lowest in March-April (reviewed O'Brien (1998)).

Data collection

We captured jaguars and pumas using foot snares (Frank et al., 2003). At the site of each snare trap we also placed a VHF radio transmitter to monitor if traps were triggered (Halstead et al., 1995). Traps were checked every 4 hours throughout the night and, depending on weather conditions, several times during the day. All capture and handling protocols followed the American Society of Mammalogists' IACUC guidelines (Sikes et al., 2011).

Upon capture, we immobilized animals using medetomidine (0.06 mg/kg) combined with ketamine (3.5 mg/kg) using a dart fired from a CO_2 pistol or rifle. While immobilized, we examined individual body condition and determined sex. We estimated age based on coat color, tooth wear (Stander, 1997), and gum-line recession (Laundré et al., 2000). Body mass and linear measurements were recorded. Weight was recorded using a portable scale.

We used satellite global positioning system (GPS) collars Telonics® GEN IV, model TGW-4580. We programmed GPS collars to acquire a location every 4.8 hours (4 locations/day), and to send data through the ARGOS system every 4 days. All collars included a programmable release mechanism (model CR-2a, Telonics®), and we scheduled the drop-off mechanism to release 12-14 months after capture. The GPS collars were recovered when possible using the locations that were obtained after their release through the ARGOS system and by searching for the VHF pulse using a receiver.

Data analysis

For comparisons with other studies, we estimated annual home range size using 95% minimum convex polygon estimations (Mohr, 1947). However, to provide a more precise description of the annual home ranges of jaguars and pumas, we also used the 50% and 95% of fixed kernel estimators (Worton, 1989). We defined the core area within a home range as the area enclosed by the 50% isopleth. To prevent under-smoothing in kernel estimates, we utilized the rule-based *ad hoc* method of Kie (2013). We used the package "adehabitat HR" (Calenge, 2013) for R 3.1.1 (2007, The R Foundation for Statistical Computing) to estimate minimum convex polygons and kernel home ranges.

We evaluated spatial and dynamic interactions among jaguars and pumas. We calculated three indices of distribution overlap using the fixed kernel estimator to quantify overlap of shared space used for simultaneously tracked individuals: the volume of intersection (VI - Seidel, 1992), Bhattcharyya's affinity (BA – Bhattacharyya, 1943), and the utilization distribution overlap index (UDOI - Fieberg and Kochanny, 2005). The VI index gives the minimum joint space use between two utilization distributions. The BA is a product based on two utilization distributions. The BA measures the affinity between two individuals, and it assumes that individuals use space independently of one another. The UDOI is a product-based index of degree of joint space use similar to Hulbert's (1978) index of niche overlap. UDOI assumes that animals use space independently of one another. Index values in VI, BA, and UDOI ranges from 0 (for two home ranges with no overlap), and 1 (for two home range with the same utilization distribution), but the UDOI index can be > 1 if the two utilization distributions are distributed non-uniformly and have a high degree of overlap. Therefore, UDOI index values <1 indicated less overlap relative to uniform space use, whereas values >1 indicated higher than normal overlap relative to uniform space use (Fieberg and Kochanny 2005). The VI and BA statistics are most appropriate for quantifying the degree of similarity of two utilization distribution estimates, and the UDOI index is most appropriate for quantifying shared space use. We used the function “kerneloverlap” in the “adehabitat HR” package for R 3.1.1 to estimate the BA, VI, and UDOI indices.

To evaluate whether jaguars and pumas with overlapping home ranges avoid simultaneous use of the same space, we used the Proximity Analysis (Prox) of Bertrand et al. (1996). Prox determines the proportion of simultaneous fixes (ST), which are proximal fixes based on a given distance threshold (dc). The Prox index is calculated as: Prox = ST/dc. We defined the distance threshold between two simultaneous fixes as 2.5 km and 24 hours as a temporal threshold between simultaneous fixes. We chose these wide thresholds to provide distance and time intervals that were sufficiently large to determine conservatively that tracked cats were not using the same space simultaneously. We only included in this analysis the simultaneous fixes between the tracked animals that were successful during the same time slot as defined previously. We used the package “wildlifeDI” (Long et al., 2014) for R 3.1.1 to perform the Prox.

To determine rate of movement of both species, we used only the sequential locations that we obtained every 4.8 hours. For all sequential locations, we calculated the distance traveled from the *initial location* to *final location* between the time intervals of 4.8 hours, and then we calculated the distance travelled in km/hr. The mean distance travelled per hour (km/hr) was used as a response variable in comparisons among individuals and between species during different seasons and day periods using a linear mixed model. Species, sex, season, and day periods were treated as fixed effects, and individual as a random effect. We defined “dry season” from

November to April and “rainy season” from May to October. To define day periods, we used the time thresholds between the day (sunrise to the sunset - 0500 h -1659 h) and the night (sunset to the sunrise - 1700 h – 0459 h). Because samples that we obtained from the sequential locations spanned both day and night, in our model we assigned each sequential location based on the percentage of day and night that was included in the elapsed time between sequential locations to obtain a better representation of day periods. We defined three categories of day periods: “light” (≥ 66.6% of day), “dark” (≥ 66.6% of night) and “light and dark” (< 66.6 and > 33.3 % of day or night). We used the lme4 library (Bates et al., 2014) for R 3.1.1 to perform the linear mixed effect models.

Results

We successfully deployed satellite global positioning system collars on four jaguars and three pumas (Table 1). A total of 2,523 3D GPS fixes were obtained from the collared animals (1,134 from jaguars and 1,389 from pumas). The 3D GPS fixes are locations calculated from four or more GPS satellites that provide a location estimate for the GPS/ARGOS system with a typical accuracy of 2 - 10 m. Mean horizontal error was 5.01 ± 4.61 m for jaguar localizations and 5.88 ± 6.13 m for pumas. The fix success of the GPS collars was very low for most of the individuals probably due to the closed forest canopy (Table 3). We only recovered three of the collars deployed (JH15, JM04 and PH18). We could not recover three collars (JH05, PM19, PM20), because after the release mechanisms were activated, we did not obtain fixes through the ARGOS satellite system to search for these collars. We also never found the VHF in the field. Additionally, we lost the signal of jaguar male JM11 after five months of tracking through the ARGOS satellite system. Thus, data presented for animals JH05, JM11, PM19, and PM20 corresponded only to data obtained through the ARGOS satellite system. Animals JH05, PM19, and PM20 were tracked for an entire year, and jaguar JM11 was tracked for five months (Fig. 2 and Table 3).

The home range sizes of the individuals that were tracked plotted against the number of months of tracking indicated that our sampling effort to describe the annual home range size of jaguars and pumas in our study area was adequate (Fig. 2). Home range size varied (t_4 = 2.66; $P < 0.05$) between jaguars and pumas; jaguars inhabited larger home ranges compared to pumas (Fig. 3; Table 1). The mean annual home range for female jaguars that was estimated using the 95% fixed kernel was 181.4 ± 4.0 km^2 and for male jaguars it was 431.6 ± 152.6 km^2 (Table 1). Annual home range using the 95 % fixed kernel for the only female puma tracked was 34.3 km^2, and the mean annual home range of male pumas was 72.0 ± 85.2 km^2 (Table 1). There was no correlation between the home range size and the number of fixes obtained per individual (r_6 =0.033, P = 0.94).

Jaguars shared part of their home ranges with conspecifics at 95% fixed kernels. Home range overlap between the individuals (with data for the sexes pooled) ranged from 0.09 to 0.41 as indicated by all three indices of overlap (Table 2). However, very little of this overlap was observed in core areas (0 to 0.02 - Table 2). For pumas (sexes pooled), home range overlap between individuals ranged from 0.07 to 0.53 as determined by the three indices of overlap, and overlap of core areas ranged from 0 to 0.19 (Table 2). Analysis of proximity indicated that jaguars with overlapping home ranges avoided occupying the same sites at the same time. Mean percentage of simultaneous fixes between jaguars below the threshold was almost zero (0.003 ± 0.005). On the other hand, pumas showed nearest distances in simultaneous fixes between conspecifics (Table 2).

Jaguars and pumas shared the space at the home range level, because home range overlap of jaguars and pumas that were tracked simultaneously ranged from 0.02 to 0.63 (Table 2).

However, little overlap was observed in core areas (ranged from 0 to 0.05 - Table 2). Mean percentage of simultaneous fixes below the distance threshold between the female jaguar JF15 and three pumas was very low (0.04 ± 0.02).

A total of 1,114 sequential locations were obtained from the seven tracked animals (435 from jaguars and 679 from pumas). We did not detect differences between the mean rate travelled by jaguars and pumas, or between sexes and seasons. However, movement rates varied among different day periods between species ($X^2 = 25.29, P < 0 .0001$). Jaguar movements were greater during the "light & night" (0.161 km/hr ± 0.027) and "night" periods (0.160 km/hr ± 0.019) than during the "light" period (0.140 km/hr ± 0.019), and puma movements were greater during the "light period" (0.173 km/hr ± 0.025) than during the "night" (0.121 km/hr ± 0.024) and "light & night" (0.116 km/hr ± 0.039) periods.

Discussion

We found significant differences in space use between the two largest neotropical felids, jaguars and pumas. Average home range size of jaguars was 2 -6 times larger than that of pumas in GLE. However, we did not find differences in the mean rate travelled by these species. Although jaguars used wider home ranges than pumas, movement rates within their home range were similar in both species. Larger home range sizes of jaguars are likely due to the larger body mass of this species. At our study site, male jaguars are 1.68 times heavier than male pumas and female jaguars are 1.60 times heavier than female pumas. Allometric relationships between body mass and home range size have been well-documented (Harestad and Bunnell, 1979; Lindstedt et al., 1986; McNab, 1963). Such patterns are due in part to the metabolic requirements of larger species. Higher metabolic demands may result in increased spatial requirements or time expenditures for the search and pursuit of correspondingly larger prey (Carbone et al., 2007, 2005; Gittleman and Harvey, 1982; Gittleman, 1985). Further evidence comes from other studies that have documented that jaguars often take larger prey relative to pumas, and that pumas hunt a wider spectrum of prey than jaguars (Emmons, 1987; Novack et al., 2005; Nuñez et al., 2000; Rabinowitz and Nottingham Jr., 1986; Scognamillo et al., 2003).

Jaguars and pumas with home range overlap demonstrated a low degree of spatial overlap in the core area, which suggested that they had areas of exclusivity within their home range (Azevedo and Murray, 2007). Furthermore, our results showed that even though jaguars and pumas had overlapping home ranges, they tended to avoid the same sites temporally (Harmsen et al., 2009; Scognamillo et al., 2003). We interpret these results as evidence of spatial and temporal avoidance between jaguars and pumas. Spatial segregation that is observed in solitary felids implies territoriality, because core areas are usually associated with regions of high resource concentration (Azevedo and Murray, 2007; Nuñez, 2006; Plowman et al., 1998; Samuel et al., 1985). Spatial territoriality affects the interactions of jaguars and pumas, and it could facilitate the coexistence of these sympatric species through resource partitioning (Azevedo and Murray, 2007; Harmsen et al., 2009; Noss et al., 2012; Scognamillo et al., 2003). Scent marking using scat, scrapes, or urine may provide spatial and temporal information and, thereby, reduce the probability of confrontation, and these signs may help to maintain exclusive territories and the sharing of space simultaneously (Harmsen et al., 2009; Nuñez, 2006). A caveat to these results is that other individuals that were not tracked in our study could have occupied the area simultaneously unbeknownst to us.

We documented a temporal separation of activity between jaguars and pumas in GLE. Jaguars were more active during periods that included the nighttime and pumas were more active during the daytime. These differences in their activity patterns also could allow the coexistence of these sympatric felids in tropical forests by the avoidance behavior between them (Romero-

Muñoz et al., 2010). Temporal separation between coexisting felids also could be facilitated by differences in the activity patterns of their main prey (Emmons, 1987; Karanth and Sunquist, 2000; Ramesh et al., 2012; Sunquist and Sunquist, 1989).

Our results differed from other studies that have tracked both species simultaneously. Nuñez (2006) and Scognamillo et al. (2003) reported similar home range areas for jaguars and pumas in dry tropical forest of Mexico and in Los Llanos, Venezuela. In the tropical rainforest of Calakmul, Mexico, pumas used larger areas than jaguars (Chávez, 2006). Jaguar home ranges in other studies ranged from 10 - 125 km² in females and from 25 - 625 km² in males (Azevedo and Murray, 2007; Cavalcanti and Gese, 2009; Ceballos et al., 2002; Chávez, 2009; Crawshaw Jr. and Quigley, 1991; Nuñez, 2006; Rabinowitz and Nottingham Jr., 1986; Schaller and Crawshaw, 1980). However, other studies that estimated jaguar home ranges using GPS tracking yielded similar results to our own (Chávez, 2009). In the case of pumas, home range estimates are limited in neotropical ecosystems, but estimates in other studies ranged from 35 - 161 km² in females and 62 - 763 km² in males. Our puma home range estimates were similar to those from the dry tropical forest in the Mexican Pacific, the Venezuelan Llanos, and temperate areas in South America, but our estimates were smaller than those that were estimated for temperate and arid areas of North America (Chávez, 2006; Dickson and Beier, 2002; Franklin et al., 1999; Logan and Sweanor, 2001; Nuñez, 2006; Scognamillo et al., 2003; Spreadbury et al., 1996). Home ranges of both species vary throughout their geographic range, and this variability is likely a reflection of plasticity in the movement of these species in response to resource availability. In these species, home range sizes were inversely related to abundance and availability of prey (Crawshaw Jr. and Quigley, 1991; Logan and Sweanor, 2001; Rabinowitz and Nottingham Jr., 1986).

Home ranges of male jaguars were 2.3 times larger than those of female jaguars, and home ranges of male pumas were 2.0 times larger than those of female pumas. Both species are solitary except for periods of mating and breeding. Usually, females have smaller home ranges than males, and the home ranges of males include and overlap with the home ranges of several females (Cavalcanti and Gese, 2009; Logan and Sweanor, 2001; Rabinowitz and Nottingham Jr., 1986; Schaller and Crawshaw, 1980; Seidensticker et al., 1973). Home ranges of females must contain sufficient prey to meet the energetic requirements that raising cubs demands (Eisenberg, 1986; Logan and Sweanor, 2001; Sandell, 1989). Another factor that determines space use in solitary female felids is the availability of safe refuges for offspring (Nuñez, 2006; Steyn and Funston, 2009). On the other hand, home ranges of males must be large enough to cover the home ranges of several females to improve their fitness, and to avoid other males that would kill their cubs (Cavalcanti and Gese, 2009; Eisenberg, 1986; Ferguson et al., 2009; Goodrich et al., 2010).

Our data show that jaguars required larger areas compared with pumas to meet their spatial requirements in southern Mexico. This has important implications for the conservation plans for these species at the landscape scale, because habitat destruction and fragmentation would have more severe effects on jaguars than on pumas. Although jaguars and pumas do not use sites exclusively that are covered completely with forest, they preferred primary forest in contrast to modified environments that were associated with human activities (Colchero et al., 2011; Conde et al., 2010; Cullen et al., 2013; Dickson et al., 2005; Foster et al., 2010). According to our estimates, we would need to conserve primary forest patches of at least 180 km^2 to meet the annual spatial requirements of a female jaguar in the south of Mexico. The GLE landscape is a mosaic of primary forest that is surrounded by a mixture of human-modified habitats (crops, pastures, paved roads, and towns). To ensure the long term conservation of jaguars in this important region, large extensions of primary forest should be guaranteed and deforestation should be controlled completely.

Additionally, two jaguars and one puma tracked in this study repeatedly crossed the Usumacinta River into Guatemala. These observations suggest that jaguars and pumas of the GLE in Mexico and Sierra del Lacandon National Park in Guatemala belong to the same population. The jaguar population of GLE has been identified as a crucial source population that is required to secure the future of this species in the Mayan Forest, and adequate preservation of this population depends on maintaining the connectivity between the Natural Protected Areas of GLE in Mexico with those located in the Guatemalan Mayan Forest (de la Torre and Medellín, 2011). The Sierra La Cojolita is a large tract of forest that is outside protected areas of the GLE, and it is absolutely critical for maintaining the connectivity in this landscape. We believe firmly that the Sierra La Cojolita should be incorporated into the regional strategy to conserve jaguars. We suggest that productive activities in this area should be compatible with conservation of natural habitats, enacting payments for ecosystem services to halt deforestation, and developing a management plan in conjunction with the local communities. Only in this way can we guarantee the connectivity of the Mayan Forest landscape and the long-term conservation of this bi-national population of jaguars.

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Table1. Estimated annual home range size of jaguars and pumas in the northern Greater Lacandona Ecosystem, Chiapas, Mexico.

Animal ID	**Species**	**Sex**	**Minimum Convex Polygon (95%) km²**	**Fixed Kernel (95%) km²**	**Fixed Kernel (50%) km²**	**Total number of locations**	**Fix success (%)**	**Period tracked**
JF05	*P. onca*	♀	133.3	184.2	40.2	88	4.8	January 2012-January 2013
JF15	*P. onca*	♀	156.2	178.6	40.4	393	21.6	August 2012 – August 2013
JM04	*P. onca*	♂	280.1	322.3	71.1	576	31.6	January 2012 – January 2013
JM11	*P. onca*	♂	296.2	540.9	142.6	72	4.0	August 2012 – January 2013
PF18	*P. concolor*	♀	20.9	34.3	8.2	852	46.8	March 2013 –March 2014
PM19	*P. concolor*	♂	7.6	11.7	3.7	270	14.8	March 2013 –March 2014
PM20	*P. concolor*	♂	82.2	132.3	35.0	267	14.7	March 2013 –March 2014

Table 2. Percentage of overlap at 95 % and 50 % of the fixed kernel using the UDOI, VI, and BA indexes, and results of the Proximity Analysis (Prox) for jaguars and pumas with adjacent or overlapping home ranges.

Types of interactions		**Individuals pairs**	**95% UDOI**	**50% UDOI**	**95% VI**	**50% VI**	**95% BA**	**50% BA**	**Prox**
Jaguars adjacent	males	JM04 - JM11	0.00	0.00	0.00	0.00	0.00	0.00	-
	females	JF05 -JF15	0.00	0.00	0.01	0.00	0.02	0.00	-
Jaguars overlapping	female-male	JF05 - JM04	0.09	0.00	0.18	0.02	0.28	0.02	0.01 (52)
		JF05 -JM11	0.05	0.00	0.12	0.00	0.22	0.00	0.00 (6)
		JF15 -JM11	0.20	0.00	0.23	0.00	0.41	0.00	0.00 (31)
Pumas overlapping	males	PM19 -PM20	0.07	0.00	0.08	0.00	0.24	0.00	0.16 (59)
	female-male	PF18 -PM20	0.35	0.04	0.31	0.08	0.53	0.19	0.24 (135)
Jaguars – Pumas overlapping	female jaguar- female puma	JF15 - PF18	0.08	0.00	0.08	0.00	0.25	0.00	0.03 (83)
	female jaguar- male puma	JF15 -PM19	0.02	0.00	0.02	0.00	0.12	0.00	0.04 (21)
		JF15 -PM20	0.50	0.00	0.40	0.04	0.63	0.05	0.07 (14)

Fig. 1. Location of the study area in the Greater Lacandona Ecosystem (GLE), Chiapas, Mexico, and the 95% Minimum Convex Polygons of the jaguars and pumas that were tracked in this study.

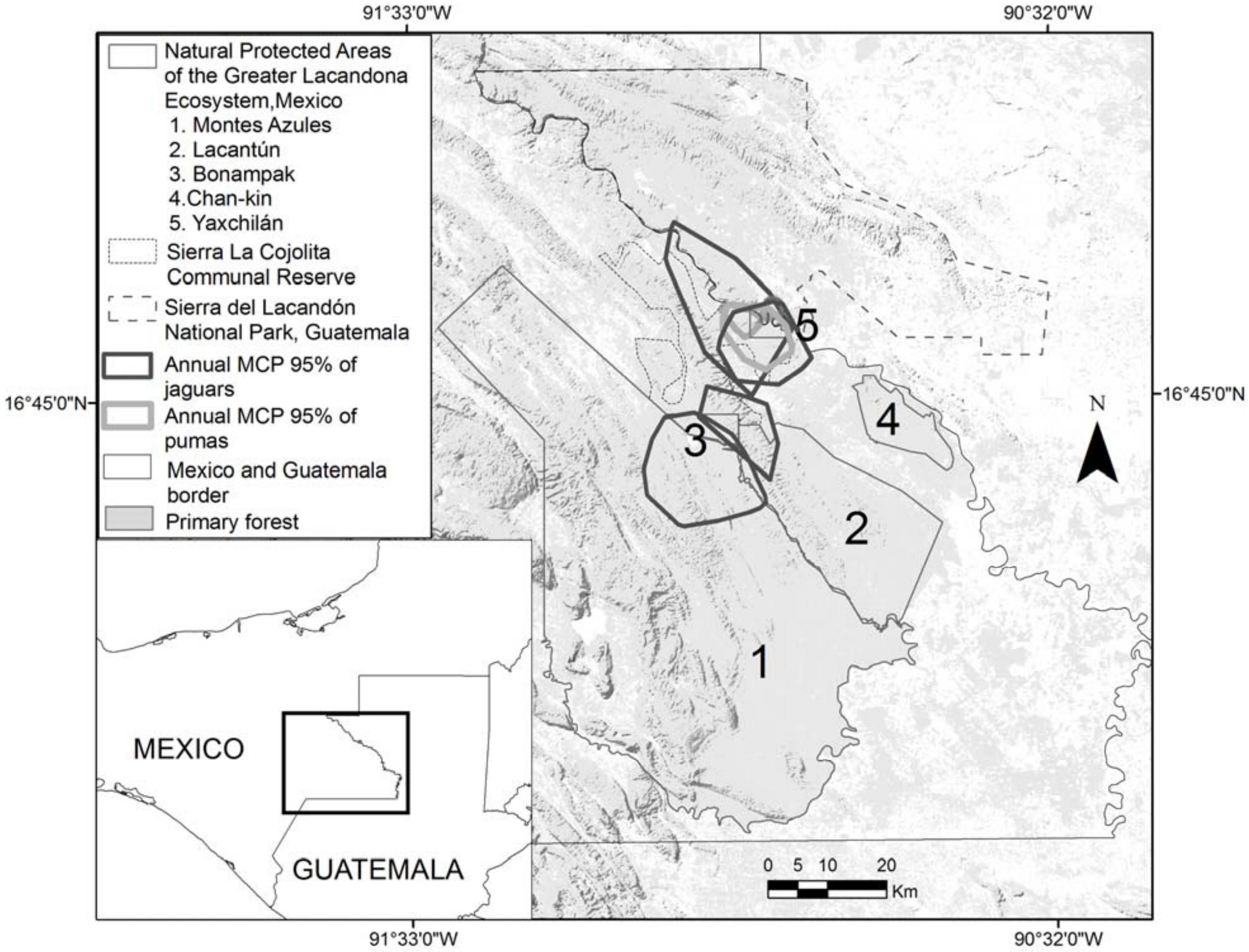


Fig. 2. The 95% Minimum Convex Polygon home ranges of jaguars (a) and pumas (b) that were tracked in the Greater Lacandona Ecosystem (GLE) and obtained by cumulative sequential samples plotted versus the number or months tracked. The graphs show that home range sizes stabilized before the 12 months of tracking for most individuals. This indicated the adequacy of our sampling effort to describe the annual home range sizes of jaguars and pumas in our study area.

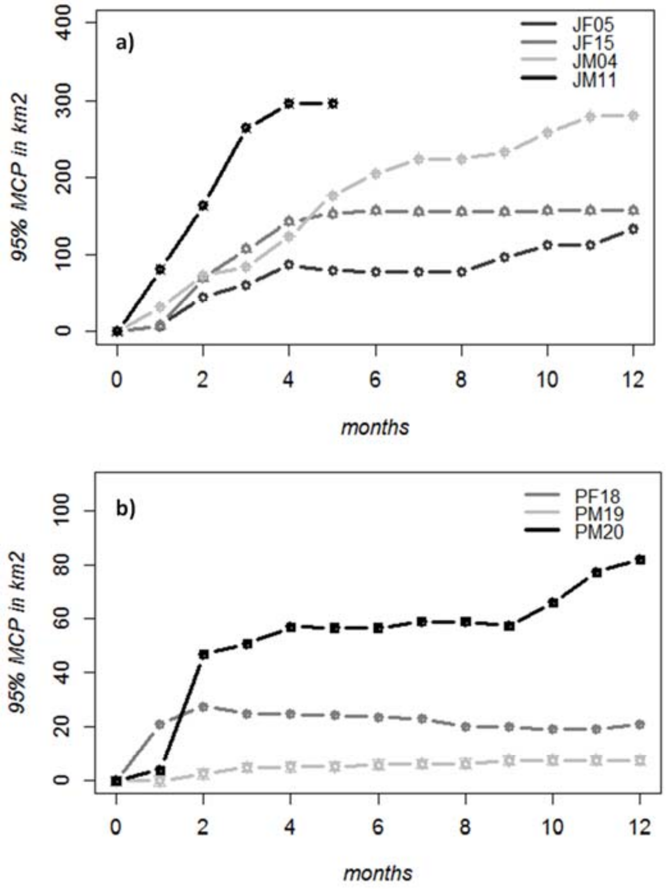
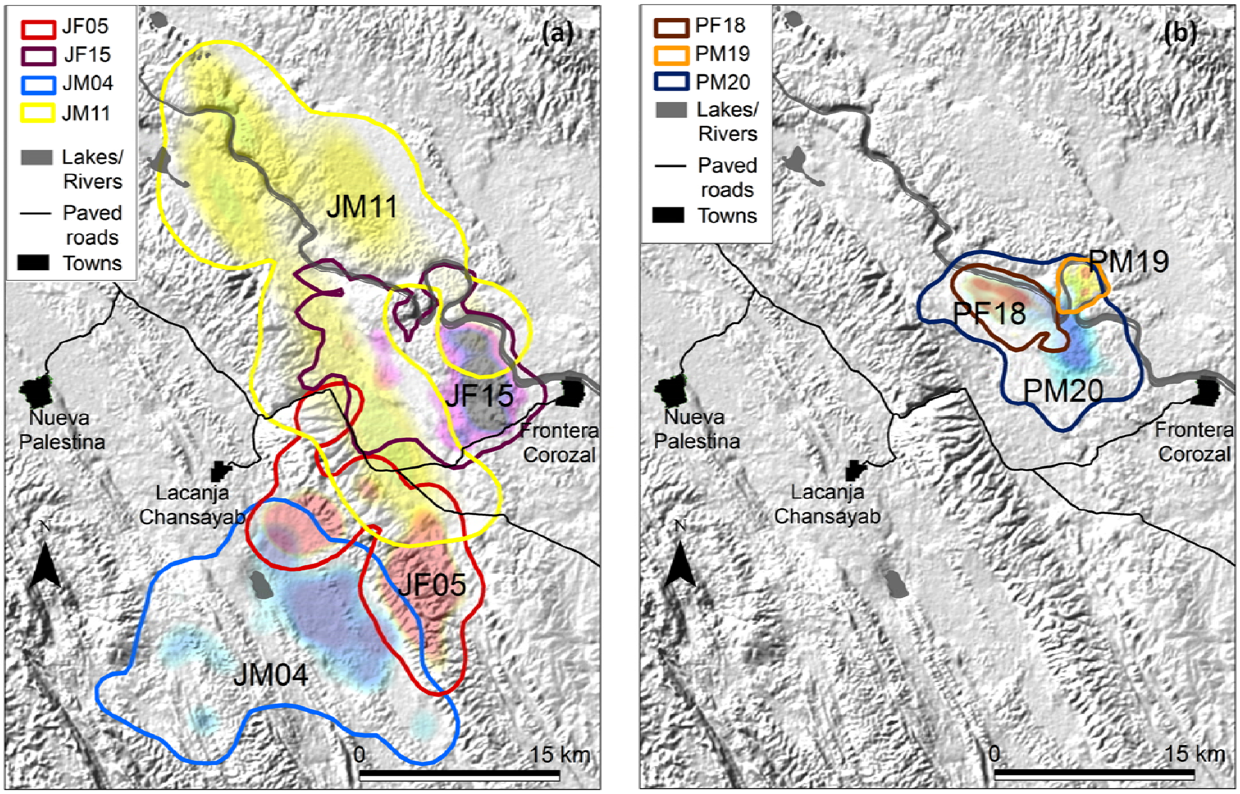


Fig. 3. (a) Annual home ranges of jaguars as estimated using the 95 % of fixed kernel in the Greater Lacandona Ecosystem (GLE). (b) Annual home ranges of pumas using 95 % fixed kernels. The color gradient reflects areas of high (greater color intensity) and low (less color intensity) use according to the observed distribution of big cat utilization.



7. Capitulo 3. Hábitat y corredores para los jaguares en el sur de la Selva Maya: Prioridades de conservación para un paisaje fragmentado.

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

(Con formato para *Biological Conservation*)

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 in the 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.

Keywords: connectivity, circuit theory, corridors, Guatemala, *Panthera onca*, Mexico, Greater Lacandona Ecosystem, Resource Selection Functions, Selva Maya, Step Selection Function.

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; 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 Jr., 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, but 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; Medellin, 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; Medellin, 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 km² (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 and IUCN, 2015): Bonampak (48 km²) and Yaxchilán (26 km²); our study area also includes six protected areas with sustainable use of natural resources (IUCN categories V-VI): Montes Azules (3 312 km²), Lacantún (619 km²), Chan-kin (122 km²), Naha (38 km²), Metzabok (33 km²), and Cañon del Usumacinta (461 km²). The Guatemalan section includes a large portion of the Mayan Biosphere Reserve, and includes seven strictly protected areas: Laguna del Tigre National Park (2 899 km²), Rio Escondido Biotopo (451 km²), Sierra del Lacandón National Park (2 028 km²), San Román Biological Reserve (608 km²), El Rosario National Park (110 km²), Dos Pilas Cultural Monument (31 km²), and Laguna Lechuá National Park (143 km²). Additionally, it includes two protected areas with sustainable use of natural resources: the Wildlife Refuges Petexbatún (404 km²) and El Pucté (167 km²).

Our study area encompassed the Selva Maya Jaguar Conservation Unit (No. 155) defined by Sanderson et al. (2002), and the Montes Azules/Sierra del Lacandon (No. 7) and Selva Maya (No. 8) Jaguar Conservation Units defined by Zeller (2007). The dominant vegetation type of this area is tropical rainforest, but flooded forest, flooded savannas, and wetlands are present as well (de la Torre and Medellín, 2011; García-Anleu et al., 2016; Mendoza and Dirzo, 1999). The main economic activities in this region include ranching, farming, and ecological and archeological tourism. Thus, the landscape outside the protected areas is composed of a matrix of primary forest surrounded by secondary forest, agricultural fields, and managed grasslands for livestock.

2.2 Research design and data collection

2.2.1 Data telemetry

We captured five jaguars using foot snares (see Frank et al., 2003). All capture and handling protocols followed the American Society of Mammalogists' IACUC guidelines (Sikes et al., 2011). Our fieldwork was based in Yaxchilán on the border with Guatemala, and in Bonampak (Fig. 1). We conducted three trapping seasons, one in Bonampak (November 2011 to January 2012), and two in Yaxchilán (July to September 2012 and February to April 2013). In Bonampak, we covered an area of approximately 60 km² with foot snares and in Yaxchilán we covered an area of 25 km². We used 8 -15 foot snares during each trapping day. Captured jaguars were fitted with a satellite GPS collar (Telonics®, GEN IV, model TGW-4580). This model included a component for sending information through the ARGOS satellite system. We programmed the global positioning system collars to acquire a location every 4.8 hours (4 locations/day), and to send data packets through the ARGOS system every four days. All collars included a programmable release mechanism (model CR-2a, Telonics®), and we scheduled the release of the collars 12 -14 months after jaguars were captured. The collars were recovered, when possible, using the locations obtained after their release through the ARGOS system and searching the VHF pulses using a receiver. For all analyses, we used only the 3D GPS fixes that we obtained from collared animals that were calculated from four or more GPS satellites that provided a location estimate with a typical accuracy of 2 - 10 m. Mean horizontal error was 5.01 ± 4.61 m for all the 3D jaguar localizations that we obtained.

2.2.2 Landscape variables

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

Given that habitat use and movement by jaguars would be limited by the amount of surrounding forest, as it is by other large predator species (Beier, 1995; Dickson et al., 2005), we estimated forest cover in a neighborhood of 240 m (FCov-240) and 510 m (FCov-510) around each pixel using the Focal Statistic tool of ArcGIS 10.2 (ESRI, 2013). This allowed us to obtain an output raster where the value for each output cell was a mean function of the values of all the input cells that were in a specified neighborhood around that location. For creating the maps FCov-240 and FCov-510, the original FCov-30 pixel values were used with the focal mean in the 8 x 8 and 17 x 17 windows, respectively, around each sample location.

Because, jaguars are known to use riparian habitats to move through landscapes and use sites with permanent water more frequently (Emmons, 1987; Núñez et al., 2002; Rabinowitz and Nottingham Jr., 1986; Schaller and Crawshaw, 1980), we constructed a raster with the minimum distance to all the main water runoffs (DistW) of our study area using a layer of the hydrological drainage system of the entire study area (Tapia and Nuñez, 2008). Jaguar habitat use and movements are affected by different terrain conditions. For instance, jaguar mobility would be facilitated in areas of high topographic complexity, especially if the flat areas of suitable habitat have been cleared (Dickson et al., 2005; Morato et al., 2014). However, jaguars are frequently associated with lowland areas, and jaguar occupancy and movements would be hampered by the mountain ranges at higher altitudes (Rabinowitz and Zeller, 2010; Sunquist and Sunquist, 2009; Zeller et al., 2011). For these reasons, we considered three terrain variables. Using a 30 m digital elevation model, we obtained elevation ranges (ELEV). We created a layer called a topographic position index (TPI) to characterize the slope's position in the terrain and landform (TPI). We estimated the Shannon Index in a neighborhood of eight pixels to evaluate differences in heterogeneity for ruggedness (SHANN). This index incorporated richness and evenness into a single measure, and to calculate it we used three landform classes that we expressed as canyons, slopes, and ridges. In general, higher values reflected more diversity and better balance among unique landform values. Thus, a high index value was achieved by maximizing the number of landforms within the neighborhood and by balancing representation of those landforms (Riley et al., 1999).

Because human activity affects habitat use by jaguars negatively due to disturbance and persecution (Colchero et al., 2011; Conde et al., 2010; Espinosa et al., 2014), we also generated raster layers with minimum distances to towns (DistT) and paved roads (DistR), which we obtained from INEGI (Instituto Nacional de Estadistica e Informatica) for Mexico and IGN-SEGLAPAN (Instituto Geográfico-Secretaria de Planificación y Programación de la Presidencia) for Guatemala. Given that the average size of the cleared areas transformed to create grassland for livestock is 1 km² in our study area (equivalent to 100 ha), we additionally constructed a raster layer with the minimum distance to the nearest deforested patches <1 km² (DistD) to evaluate the distances that jaguars use from the boundaries that separated the forest from open modified areas. For all these explanatory variables, we generated raster layers of 30 m of resolution (Table 1).

2.3 Analytical methods

2.3.1 Resource Selection Probability Functions (RSPF)

To define jaguar habitat, we calculated RSPFs using the use vs. availability design (Boyce, 2006; Boyce et al., 2002; Lele and Keim, 2006; Manly et al., 2002). RSPFs quantified landscape characteristics used by jaguars relative to those landscape characteristics that were available across the study area (second order of habitat selection - Johnson, 1980). RSPFs were estimated using design II of Manly et al. (2002), and they were constructed through conditional logistic regressions using the logit link (Lele and Keim, 2006). We defined resource units from telemetry data as those used by tracked individuals, and available resource units were identified from random points that we obtained from the minimum convex polygon that enclosed all GPS locations obtained that were buffered by 5 km (Conde et al., 2010). We used the Hawths tools extension for ArcGis 9.3 to generate random points. We tested several used:availability ratios (1:2, 1:4, 1:6, 1:8, 1:10, 1:20, 1:40, and 1:50) to ensure that logistic regression approximated the point process model and that the coefficients converged (Benson, 2013; Northrup et al., 2013). We tested all explanatory variables for multicollinearity using the Pearson's correlation matrix (Dormann et al., 2013). We used the package R 3.1.1 to implement the correlation analysis (R Core Team, 2016). We did not include variables in the same candidate model that were correlated at > 0.5. We tested 46 RSPFs with different combinations of explanatory variables (Table A.1), and we tested these models using the log and the logit links to ensure that the exponential model did not outperform the logistic model (Lele, 2009; Lele et al., 2013; Watson et al., 2014). Finally, we tested the number of bootstrap samples needed to ensure stable results, from 99 to 5,000 bootstrap samples. For the best RSPF models, we considered independent variables with confidence intervals that did not include 0 to be informative predictors of resource selection. We used the package "ResourceSelection" (Lele et al., 2014) from R 3.1.1 (R Core Team, 2016) to estimate RSPFs. Then, we used the Akaike Information Criterion (AIC) to identify the best RSPF models based on model parsimony (Burnham and Anderson, 2002). We considered models comparable if ΔAIC was < 2.0, and we compared the AIC weights (*wi*) to determine the most appropriate models that described jaguar habitat.

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

2.3.2 Patches occupied by jaguars

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

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

2.3.3 ***Estimating movement models***

To understand how the landscape structure affects jaguar movements, we used step selection functions combined with conditional logistic regression (Fortin et al., 2005; Thurfjell et al., 2014; Ziółkowska et al., 2016). For each observed step we calculated its length (*d*) and turning angle (α) using the package "adehabitatLT" (Calenge, 2013) from R 3.1.1 (R Core Team, 2016). Steps were divided into "active" and "passive", based on step length (Ziółkowska et al., 2016), with all steps ≥ 500 m constituting active steps.

Each observed step was paired with 100 control steps that shared the same starting point, but differed either in length, direction, or both. The length and turning angles of control steps of a given individual jaguar were sampled from those observed of the other individuals to avoid problems of circularity (Fortin et al., 2005). We used the command "movement.ssfsamples" of the "Geospatial Modelling Environment" package (Beyer, 2012) to generate the control steps. For each observed and control steps we calculated the exact values of the predictors covariables at the endpoint of steps (Thurfjell et al., 2014; Ziółkowska et al., 2016).

We constructed our movement model with the package "ResourceSelection" (Lele et al., 2014) from R 3.1.1 (R Core Team, 2016) using the log link, which is applicable for step selection functions (Thurfjell et al., 2014). The step selection functions were fit using the observed steps matched to their respective control steps (Lele and Keim, 2006; Northrup et al., 2013). We tested 54 step selection function models with different combinations of explanatory variables. Then, we used the Akaike Information Criterion (AIC) to identify the best step selection function models (Burnham and Anderson, 2002). We considered models comparable if ΔAIC was < 2.0, and we compared the AIC weights (*wi*) to determine the most appropriate models that described jaguar movements. We then mapped the jaguar movement surface by spatially applying our best step selection function across the study area using the Raster Calculator Tool (ESRI, 2013).

2.3.4 ***Mapping connectivity among patches***

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

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

2.3.5 Categorization of habitat patches and corridors

We used the following variables to categorize habitat patches: 1) patch size, 2) protection status, and 3) isolation. We classified habitat patches according to their size as patches that could maintain a viable population, as breeding patches, and as stepping-stone patches (Beier et al., 2008). We calculated the smallest continuous area to maintain a viable population of 50 individuals (Morato et al., 2014; Rodríguez-Soto et al., 2011). If we assume a mean density of three jaguars for each 100 km^2 in GLE (de la Torre and Medellín, 2011), the minimum continuous area to maintain 50 individuals would be 1,666 km^2. We assumed that breeding patches were areas sufficiently large enough to support a breeding event, and the minimum size of breeding patches was determined by the mean annual home range area of female jaguars in the study area. The mean home range size for female jaguars that were tracked for one year at GLE estimated using the 95 % fixed kernel was 181.4 ± 4.0 km^2 (de la Torre et al., n.d.). Habitat patches smaller than 180 km^2, which cannot hold resident female jaguars but which are important for jaguar movements throughout the landscape, were classified as stepping-stone patches. The level of protection of each habitat patch was determined by the percentage of protected area within each habitat patch; this percentage was estimated using the WDPA database of protected areas of the world including the strictly protected areas and the sustainable use protected areas according to the IUCN categories of protected areas (UNEP-WCMC and IUCN, 2015). Additionally, we estimated the area protected by Payments for Ecosystem Services (PES) in each habitat patch. The PES is a conservation scheme used by the Mexican Government that provides economic compensation to local communities for conserving their land with natural forest. Habitat patches were classified according to their percentage of protection as *protected* (>75%), *partially protected* (> 25% to < 75%), and *unprotected* (< 25 %). Additionally, we estimated the total minimum distance from each habitat patch to each of the nearest five habitat patches to evaluate their isolation, and we classified them as *low isolation* (3.9 km), *medium isolation* (>3.9 km to < 10 km), or *high isolation* (> 10 km). These thresholds distance values were defined according with the maximum Euclidian distances travelled by jaguars between the time lapse intervals of 4.8 hours (3 960 m) and 24 hours (10 095 m).

We used the following variables to categorize corridors: 1) total area of jaguar habitat that was connected by a corridor; 2) protection status; 3) percentage of primary forest within each corridor's boundary; and 4) number of paved roads crossed by corridors. Corridors that connected areas >1,666 km^2 were classified as connecting viable populations, corridors that connected a total area between > 180 km^2 and < 1,666 km^2 were classified as connecting breeding patch, and corridors that connected a total area < 180 km^2 were classified as connecting stepping stone patches. We estimated the percentage of area of each corridor that was included within the protected areas in Mexico and Guatemala, and in PES. Corridors with > 75% of their total area protected were designated as *protected*, corridors with 25 -75% of their total area protected were designated as *medium protected*, and corridors with < 25% of their total area protected were designated as *unprotected*. We classified the priority management actions for each corridor according to the total percentage of primary forest included within the corridor's boundary. Corridors that retained > 75% of primary forest were designated as *conservation*, corridors that retained > 25 and < 75 % of primary forest were designated as *conservation and habitat restoration*, and corridors that retained < 25% primary forest were designated as *restoration*. Because large felids avoid areas near paved roads (Colchero et al., 2011; Conde et al., 2010; Dickson and Beier, 2006; White et al., 2015), and individuals may be killed in vehicle collisions (Gubbi et al., 2014; Kerley et al., 2002; Schwab and Zandbergen, 2011), we counted the number of putative corridors that crossed segments of paved roads in the Southern Mayan Forest landscape to evaluate where the paved roads potentially interrupted connectivity.

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

3. Results

3.1 Jaguar habitat

A total of 1 288 GPS fixes that were obtained from five jaguars (2 ♂ and 3 ♀) was used to develop the habitat model for jaguars in the Southern Mayan Forest. Sensitivity analysis indicated that our results stabilized prior to the 1:50 use:availability ratio with 5000 bootstrapped samples. Examination of the likelihoods and AIC values for our 46 models indicated that our best model included the percentage of forest cover (FCov-30 m), the nearest distance to deforested patches that were >1 km² (DistD), and that the TPI and elevation (ELEV) were the variables associated most strongly with resource selection by jaguars (Table 2). This model had a ΔAIC value of 15.63 from the second best ranked model (*wi* = 1), all the variables were informative, and the 95% CI did not overlap 0 (Table 3; Appendix A).

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

Area under the ROC curve was 0.79 (± 0.68, 0.89) for true positives and 0.47 (± 0.36, 0.57) for false positives, which indicated a reasonable discrimination at a probability threshold of occurrence of 0.65 (± 0.54, 0.72). Suitable habitat for jaguars in the southern Mayan Forest region encompassed 11 650 km² (the upper 0.65 probability of resource selection). However, we only identified 27 polygons greater than 5 km² where jaguar presence had been recorded recently (Table 4, Fig. 2). These polygons encompassed an area of 9 983 km^2 and were situated in seven different sub-regions (Table 4).

3.2 Jaguar corridors

We analyzed a total of 452 movement steps, of which 43.5 % were classified as active. Our analysis revealed that the best step selection functions included the forest cover in a neighborhood of 240 m (FCov-240), and that the TPI and elevation (ELEV) were the variables associated most strongly with movement probability by jaguars (Table 5). All the variables were informative, and the 95% CI did not overlap 0 (Table 5). However, this model only had a ΔAIC value of 0.54 for the second best ranked model (*wi* = 0.35) (Appendix C). The second ranked model included the variables forest cover in a neighborhood of 240 m (FCov-240), the nearest distance to deforested patches that were >1 km² (DistD), TPI, and elevation (ELEV), but the variable nearest distance to deforested patches was not informative because the 95% CI overlapped 0 (*wi* = 0.35). The third best ranked model was very similar to our best model (*wi* = 0.24), and included the forest cover in a neighborhood of 510 m (FCov-510), TPI, and elevation (ELEV). For these reasons, we used the first ranked model to construct the resistance surface for the connectivity analysis.

We identified 50 potential corridors using Circuit Theory analysis to design a connectivity strategy for jaguar populations in the Southern Mayan Forest (Fig. 3; Table 6; Appendix D). These corridors would allow for connectivity between the 27 habitats patches identified previously.

3.3 Categorization of habitat patches and corridors

We identified only two habitat patches with viable populations, which were the Montes Azules Biosphere Reserve in GLE, Chiapas, Mexico (2 389 km^2) and the Mayan Biosphere Reserve in Guatemala (5 159 km^2). We identified three breeding patches with areas that ranged from 281 - 801 km^2, and 22 stepping-stone patches with areas that ranged from 7 -128 km^2 (Fig. 4). The total percentage of area that was protected within habitat patches was 77 %. Viable population patches were almost completely in protected areas in Mexico and Guatemala, and these habitat patches combined encompassed 65% of the total area protected among all the habitat patches (Table 4). The only breeding patch that was protected was Sierra del Lacandon in Guatemala. Most of the stepping-stones patches were unprotected, with the exception of three habitat patches that were protected and four patches that were partially in protected areas and under PES conservation schemes in the Marques de Colmillas sub-region (Table 4).

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

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

4. Discussion

4.1 Jaguar habitat use and movements

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

These results supported our predictions that jaguar habitat use is positively associated with the best preserved sites in our study area. Although jaguars do not use primary forest exclusively, they preferred areas with a high percentage of forest cover in contrast to modified environments that were associated with human activities. Large areas with primary forest provide prey availability, forest cover for stalking prey, and refuge for rearing cubs (Ceballos et al., 2002; Conde et al., 2010; Crawshaw Jr. and Quigley, 1991; Cullen et al., 2013; Foster et al., 2010; Rabinowitz and Nottingham Jr., 1986). Furthermore, our results indicated an edge effect in habitat use by jaguars. Jaguars avoided using areas that were located at nearby sites of cleared areas, because the probability of use increased as the distance from deforested parches that were > 1 km² increased. All deforested patches < 1 km² in our study area were associated with human activities, and these included cropland, open pastures for livestock, secondary forest, and sites near roads and towns. Theses human activities affected the spatial distribution of jaguars by modifying the surrounding natural landscape, which reduced the abundance of potential prey species and disrupted jaguar hunting in nearby sites (Carroll and Miquelle, 2006; Colchero et al., 2011; Conde et al., 2010; Escamilla et al., 2000; Espinosa et al., 2014; Foster et al., 2010; Linkie et al., 2006; Takahata et al., 2014; Woodroffe, 2000). Human activities not only had an impact at the local scale, but also at the landscape scale, which could limit the range of jaguars in the Southern Mayan Forest (Naves et al., 2003; Woodroffe, 2000).

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

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

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

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

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

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

Most of the stepping-stone habitat patches that we identified were unprotected completely. The maintenance of these stepping-stone patches is vital and should be integral to achieving the linkage of the jaguar population in the Southern Mayan Forest. Although relatively small patches of habitat might not normally support resident jaguars, these areas are important, because individuals can rest and feed in them, and their existence facilitates the dispersion of jaguars to larger habitat parches (Rabinowitz and Zeller, 2010; Schadt et al., 2002; Söndgerath and Schröder, 2002). Actually, we have recorded several individuals with camera traps in the last five years, including two females with cubs, using the smaller stepping-stone patches (7 km^2) in the Marques de Comillas sub-region (unpublished data of the first author). However, reducing the threats to jaguars within the stepping-stone patches is crucial to ensure their functionality and integrity. Most of these habitat patches are surrounded by livestock pastures, and jaguars are poached frequently in these areas by ranchers in retaliation for depredation of domestic cattle (Peña-Mondragón et al., 2016). If jaguar poaching is not eradicated, the stepping-stone patches will continue to act as ecological traps for jaguars (Balme et al., 2010; Delibes et al., 2001).

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

4.3 Conservation and management implications

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

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

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

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

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

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

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

Type	**Variable name**	**Abbreviation**	**Description**	**Resolution (m)**	**Units**	**Data range**
Forest cover	Forest Cover 30 m	FCov-30	Percentage of forest coverage in each pixel of 30m	30	%	0 - 0.999
	Forest Cover 240 m	FCov-240	Percentage of forest coverage 240 meters around the pixel	30	%	0 - 0.999
	Forest Cover 510 m	FCov-510	Percentage of forest coverage 510 meters around the pixel	30	%	0 - 0.999
Water Runoffs	Distance to water courses	DistW	The minimum distance to the nearest water runoff	30	km	0 - 9.3
Terrain	Topographic Position Index	TPI	Classification of landscape according the slope position	30	-	-116.4 – 163.7
	Elevation	ELEV	Elevation	30	m.a.s.l.	0 – 3,320
	Shannon	SHANN	Differences of ranges of elevation values within a radius of 8 pixels	30	-	0 – 5.17
Human	Distance to towns	DistT	The minimum distance to the nearest town	30	km	0 – 23.3
	Distance to paved roads	DistR	The minimum distance to the nearest paved roads	30	km	0 – 43.3
	Distance to deforestation edge	DistD	The nearest distance to the deforested patch >1 km²	30	km	0 – 29.3

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

Variable	**Units**	**Maximum (3)**	**Medium (2)**	**Low (1)**
1) Total area of jaguar habitat that was linked	km²	>1,666	180 to < 1,666	< 180
2) Protection status	% protected within each corridor	< 25	25 to75	> 75
3) Primary forest within each corridor's boundary	Percentage of primary forest in each corridor	> 75	25 to75	< 25
4) Paved roads that interrupt the connectivity.	Number of paved roads crossed by each corridor	> 2	1	0

Table 3. Estimated coefficients (β), standard errors (SE), 95% confidence intervals (95% CI), z values (z), and P values (P) for the best Resource Selection Probability Function for habitat use of jaguars in the Southern Mayan Forest. We estimated the coefficients and the standard errors for percentage of forest cover (FCov-30), minimum distance to deforested patches > 100 ha (Dist-D), the Topographic Position Index (TPI), and the Elevation (ELEV) by bootstrapping (B = 5,000).

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

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

ID	**Sub-region**	**Name**	**Area (km²)**	**Patch size**	**Protected by natural reserves (%)**	**Protected by PES (%)**	**Protection**	**Mean distance to 5 nearest habitat patches (km)**	**Isolation**	**Reference**
MF-01	Mayan Forest	Mayan Forest	5159.03	B	82.8	0.00	PR	20.94 ± 16.89	H	a,b
SL-01	Sierra del Lacandón	Sierra del Lacandón	801.52	B	95.9	0.00	PR	5.21 ± 3.32	M	a,b
TA-01	Tabasco	Benito Juarez	100.77	S	9.2	0.25	UN	12.48 ± 9.03	H	c
TA-02	Tabasco	Niños Heroes	71.50	S	0.9	0.00	UN	16.48 ± 10.44	H	c
TA-03	Tabasco	Corregidora	39.19	S	0.6	0.00	UN	18.09 ± 13.14	H	c
TA-04	Tabasco	Francisco I. Madero	102.29	S	0.0	0.00	UN	19.62 ± 14.61	H	c
GLE-01	Lacandona	Montes Azules	2389.72	V	93.9	1.64	PR	3.17 ± 1.89	L	e,f
GLE-02	Lacandona	Yachilán-Cojolita	299.25	B	7.2	7.47	UN	8.95 ± 10.19	M	e,f
GLE-03	Lacandona	Chankin	281.01	B	40.8	0.00	PP	3.14 ± 3.52	L	d
MC-01	Lacandona	Benito Juarez	30.55	S	0.0	8.94	UN	8.85 ± 2.27	M	d,g
MC-02	Lacandona	Emiliano Zapata	21.95	S	0.0	11.50	UN	12.02 ± 6.14	H	d,g
MC-03	Lacandona	Quetzalcoaltl	10.55	S	0.0	0.03	UN	15.08 ± 9.40	H	d,g
MC-04	Lacandona	Arroyo Delicias	76.40	S	0.0	11.86	UN	9.93 ± 5.47	M	d,g
MC-05	Lacandona	Galacia	19.39	S	0.0	93.98	PR	12.06 ± 7.50	H	d,g
MC-06	Lacandona	Chajul	12.08	S	0.0	66.88	PP	10.25 ± 8.06	H	d,g
SR-01	San Roman	El Chorro	15.97	S	0.0	0.00	UN	9.17 ± 5.11	M	a, b
SR-02	San Roman	El Manantial	7.37	S	0.0	0.00	UN	7.92 ± 3.66	M	a, b
SR-03	San Roman	Gancho de Fierro	10.59	S	0.0	0.00	UN	6.54 ± 4.21	M	d
SR-04	San Roman	El Pucte 1	15.67	S	79.5	0.00	PR	6.06 ± 4.32	M	a, b
SR-05	San Roman	El Pucte 2	128.30	S	54.0	0.00	PP	9.27 ± 6.74	M	a, b

SR-06	San Roman	Petexbatín 1	101.26	S	22.4	0.00	UN	5.43 ± 2.92	M	a, b
SR-07	San Roman	Petexbatún 2	8.79	S	65.5	0.00	PP	16.87 ± 9.62	H	a, b
SR-08	San Roman	San Roman	37.77	S	64.4	0.00	PP	12.85 ± 4.02	H	h,i
LL-01	Ixcán	Cuarto Pueblo 1	15.15	S	0.0	0.00	UN	11.99 ± 7.90	H	h,i
LL-02	Ixcán	Cuarto Pueblo 2	12.54	S	0.0	0.00	UN	10.71 ± 4.14	H	h,i
LL-03	Ixcán	Santa Maria Tzeja	115.36	S	0.0	0.00	UN	17.54 ± 5.66	H	h,i
LL-04	Ixcán	Laguna Lechúa	102.38	S	96.1	0.00	PR	21.34 ± 4.30	H	h,i

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

Table 5. Estimated coefficients (β), standard errors (SE), 95% confidence intervals (95% CI), z values (z), and P values (P) for the best Step Selection Functions for movements of jaguars in the Southern Mayan Forest. We estimated the coefficients and the standard errors for percentage of forest cover in a neighborhood of 240 m (FCov-30, the Topographic Position Index (TPI), and the Elevation (ELEV) by bootstrapping (B = 5,000).

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

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

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

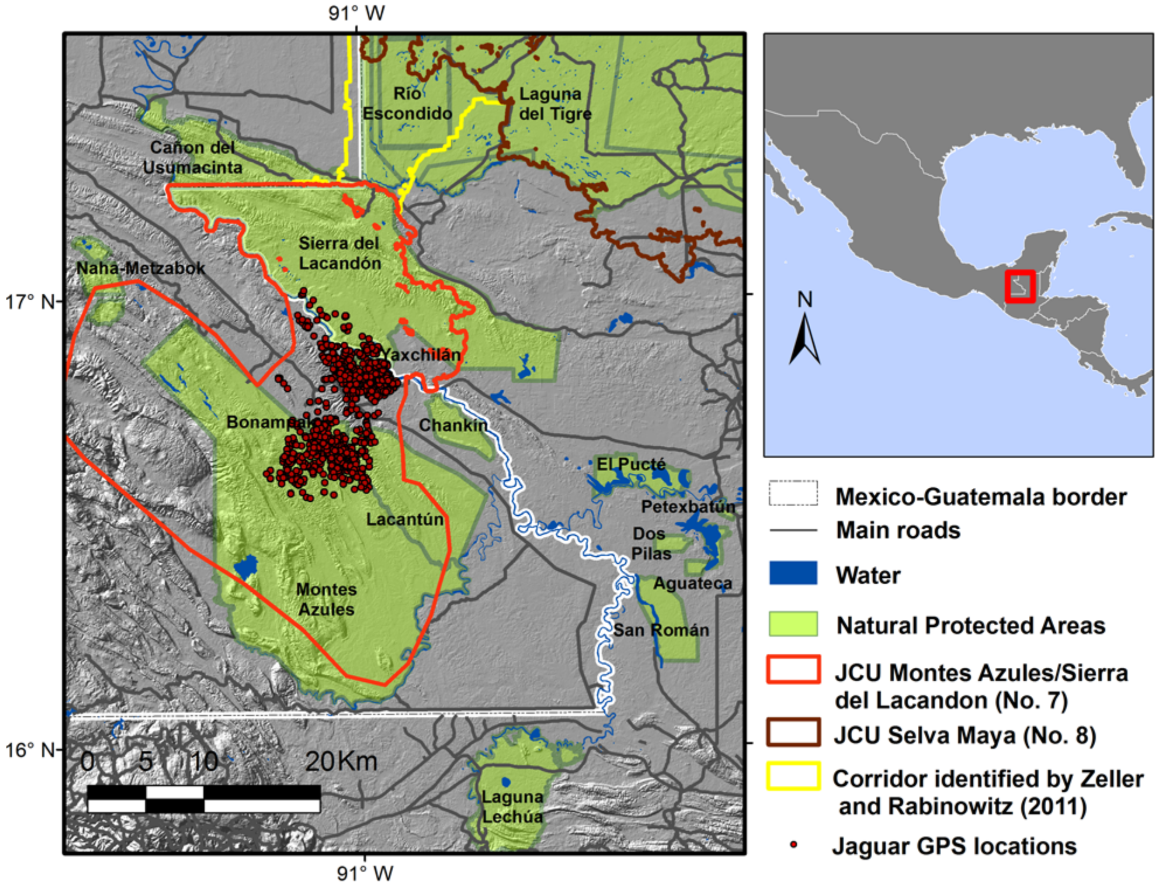


Fig. 1. Location of our study area in the Southern Mayan Forest in southern Mexico and northwestern Guatemala. The red points represent the locations of the jaguars tracked in this study.

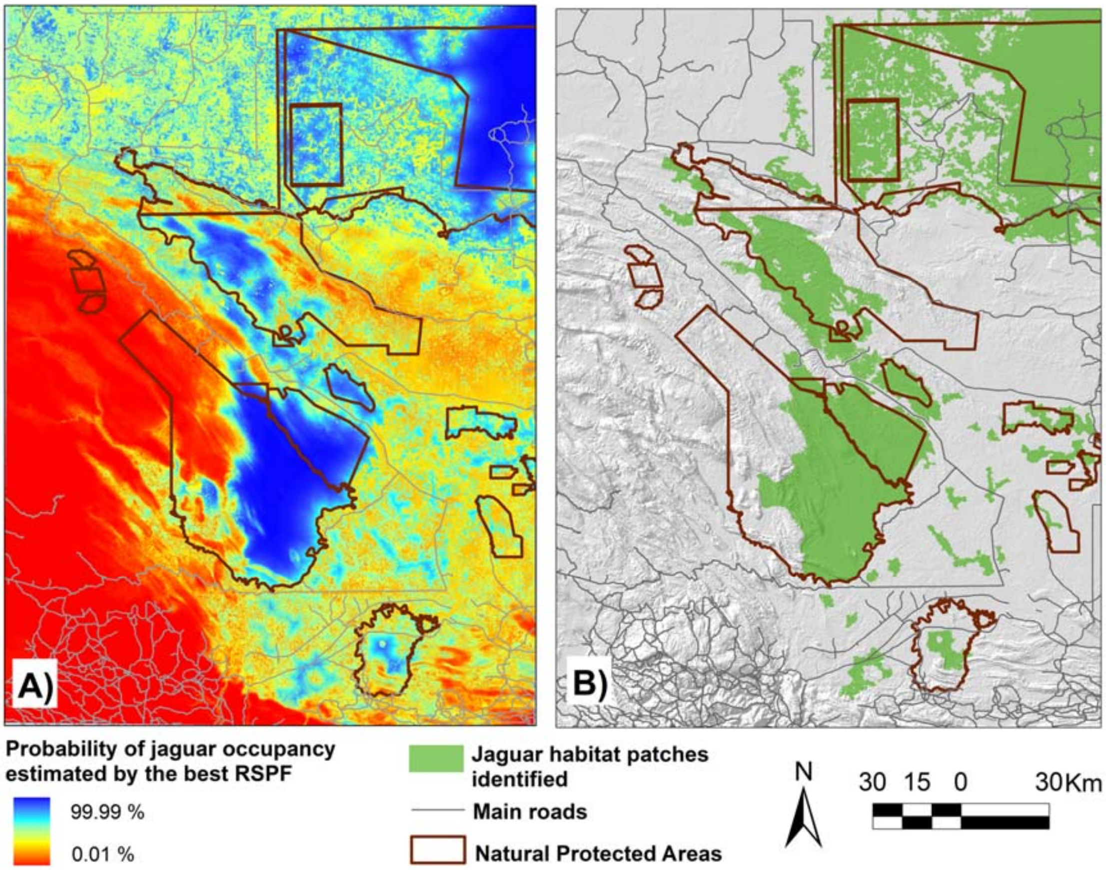


Fig. 2. Probability of jaguar occupancy in the Southern Mayan Forest landscape and habitat patches (upper 0.65 of jaguar occupancy probability) identified with occurrence that was documented in the last 10 years.

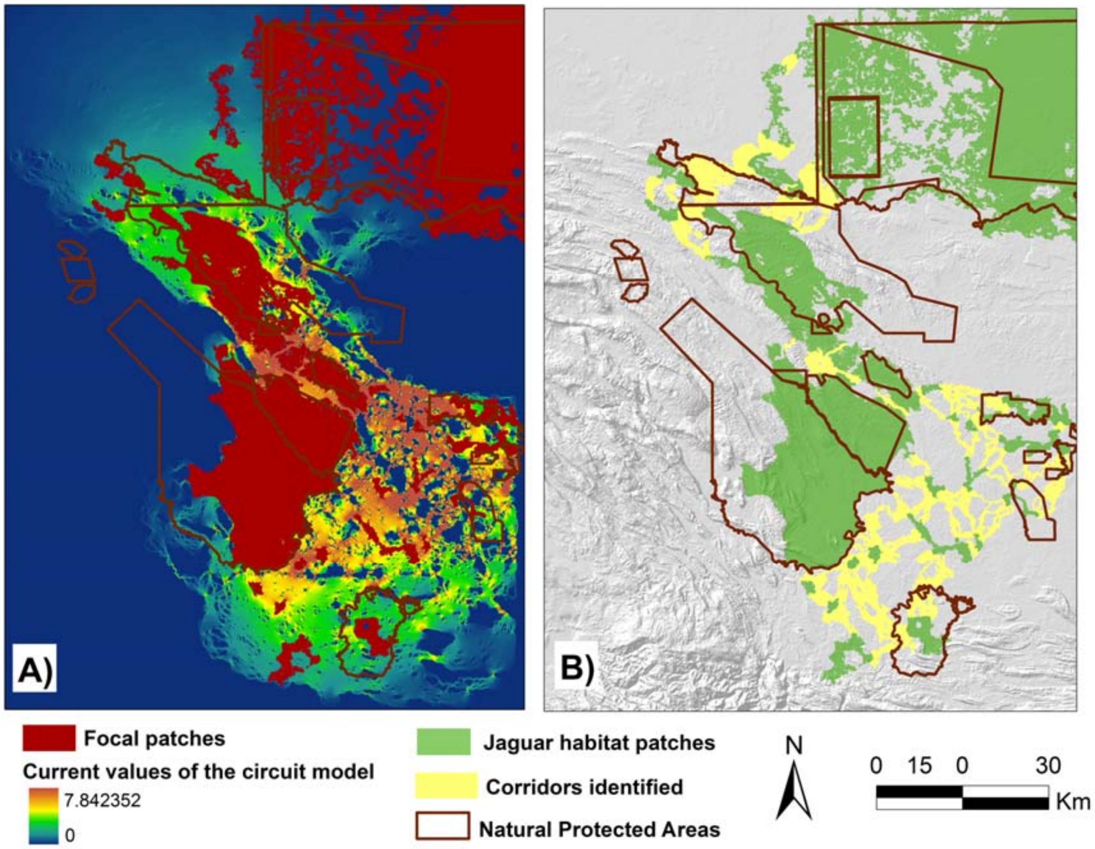


Fig. 3. Current map output from Circuit Theory analysis and corridors identified to link all the jaguar habitat patches.

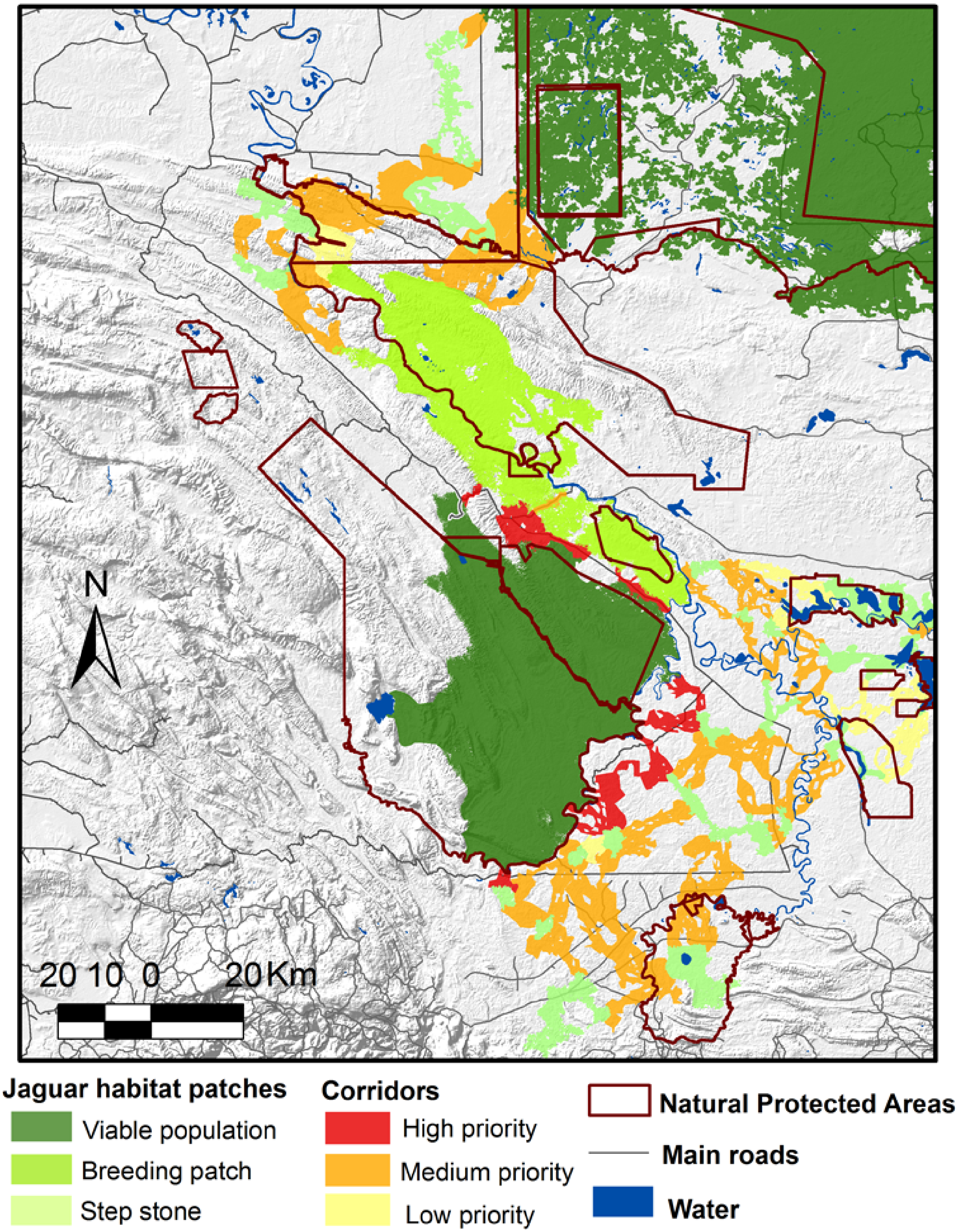


Fig. 4. Habitat patches and corridors for jaguars in the Southern Mayan Forest.

Supplementary information.

Appendix A.

Table A.1. Resource Selection Probability Functions models tested to define jaguar habitat in the Southern Mayan Forest.

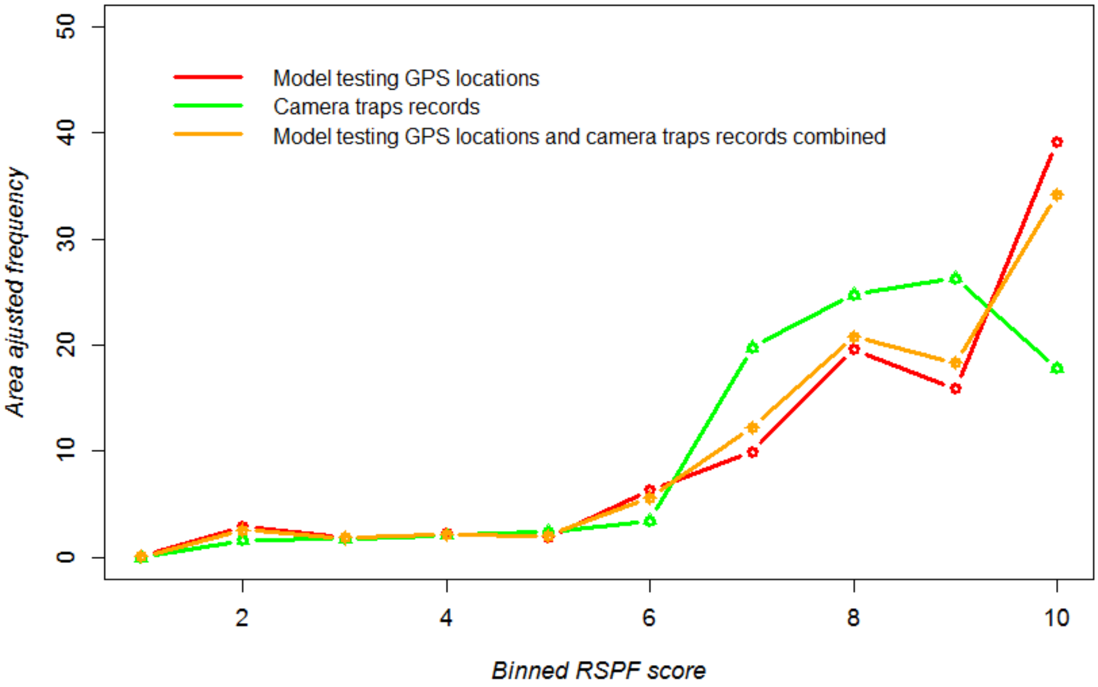
ID	model	df	LogLik	AICc	ΔAIC	Weight	Rank
17	FCov-30 + DistD + TPI + ELEV	5	-11390.07	22790.20	0	1	1
24	FCov-240 + DistD + DistW + ELEV	5	-11397.88	22805.80	15.63	0	2
19	FCov-30 + DistD + DistW + ELEV	5	-11402.64	22815.30	25.14	0	3
15	FCov-30 + DistD + DistT + ELEV	5	-11402.65	22815.40	25.17	0	4
21	FCov-240 + DistD + ELEV	4	-11404.62	22817.30	27.08	0	5
16	FCov-30 + DistD + ELEV	4	-11408.71	22825.50	35.27	0	6
22	FCov-240 + DistD + TPI + ELEV	5	-11408.07	22826.20	36.00	0	7
8	FCov-30 + DistR + DistD +SHANN	5	-11411.8	22833.70	43.46	0	8
26	FCov-510 + DistT + DistW + ELEV	5	-11432.57	22875.20	85.00	0	9
20	FCov-240 + DistD + DistT + ELEV	5	-11436.21	22882.50	92.29	0	10
25	FCov-510 + DistT + ELEV	4	-11467.4	22942.80	152.65	0	11
27	FCov-510 + DistW + ELEV	4	-11468.78	22945.60	155.40	0	12
18	FCov-30 + DistT + ELEV	4	-11475.08	22958.20	168.02	0	13
29	FCov-30 + DistW + DistD + SHANN	5	-11481.42	22972.90	182.70	0	14
30	FCov-510 + DistD + SHANN + TPI	5	-11481.42	22972.90	182.70	0	15
23	FCov-240 + DistT + ELEV	4	-11488.61	22985.30	195.07	0	16
31	FCov-30 + DistD + TPI + SHANN	5	-11488.45	22987.00	196.77	0	17
32	FCov-510 + DistD + SHANN	4	-11492.43	22992.90	202.71	0	18
37	FCov-30 + DistR + TPI + SHANN	5	-11508.18	23026.40	236.22	0	19
34	FCov-510 + DistT + TPI + SHANN	5	-11509.03	23028.10	237.92	0	20
35	FCov-510 + TPI + SHANN	4	-11510.38	23028.80	238.60	0	21
33	DistD + DistT + TPI + SHANN	5	-11513.69	23037.40	247.25	0	22
41	FCov-30 + DistT + TPI + SHANN	5	-11539.18	23088.40	298.23	0	23
43	FCov-30 + DistW + TPI + SHANN	5	-11543.64	23097.30	307.14	0	24
44	FCov-510 + DistD + TPI	5	-11543.64	23097.30	307.14	0	25
42	FCov-30 + TPI + SHANN	4	-11545.22	23098.50	308.30	0	26
9	FCov-240 + DistD + DistW + TPI	5	-11547.85	23105.70	315.56	0	27
12	FCov-510 + DistR + TPI	4	-11551.14	23110.30	320.14	0	28
3	FCov-30 + DistD + DistW + TPI	5	-11552.14	23114.30	324.14	0	29
39	FCov-30 + DistW + DistD + TPI	5	-11552.14	23114.30	324.14	0	30
10	FCov-240 + DistR + TPI	4	-11554.99	23118.00	327.84	0	31
5	FCov-30 + DistR + TPI	4	-11559.27	23126.60	336.39	0	32
40	FCov-30 + DistW + DistD	4	-11562.39	23132.80	342.64	0	33
14	FCov-510 + DistW + TPI	4	-11575.7	23159.40	369.24	0	34
13	FCov-510 + DistT + DistW + TPI	5	-11574.94	23159.90	369.75	0	35
7	FCov-240 + DistD + DistT + TPI	5	-11581.24	23172.50	382.35	0	36

1	FCov-30 + DistD + DistT + TPI	5	-11583.51	23177.10	386.88	0	37
45	FCov-30 + DistD + DistT	4	-11594.24	23196.50	406.33	0	38
6	FCov-240 + DistD + TPI	4	-11598.97	23206.00	415.80	0	39
2	FCov-30 + DistD + TPI	4	-11600.91	23209.90	419.68	0	40
46	FCov-510 + DistD	3	-11612.17	23230.40	440.17	0	41
38	FCov-240 + DistR + DistW + SHANN	3	-11630.57	23267.20	476.97	0	42
11	FCov-510 + DistT + TPI	4	-11630.6	23269.20	479.04	0	43
36	FCov-510 + DistW + TPI + SHANN	3	-11637.86	23281.70	491.55	0	44
8	FCov-240 + DistT + TPI	4	-11641.24	23290.50	500.33	0	45
4	FCov-30 + DistT + TPI	4	-11642.57	23293.20	502.99	0	46
0	Null model	2	-11698.68	23401.40	611.16	0	47

Supplementary information

Appendix B.

Figure B.1. Area-adjusted frequency categories of RSPF scores based on validation data set and independent camera trap records.



Supplementary information

Appendix C.

Table C.1. Step Selection Function models tested to define jaguar habitat in the Southern Mayan Forest.

ID	model	df	LogLik	AICc	ΔAIC	Weight	Rank
53	FCov-240 + TPI + ELEV	3	-893.414	1793.00	0	0.355	1
22	FCov-240 + DistD + TPI + ELEV	4	-892.642	1793.50	0.54	0.271	2
54	FCov-510 + TPI + ELEV	3	-893.771	1793.70	0.71	0.248	3
34	FCov-510 + DistT+ TPI+SHANN	4	-894.667	1797.50	4.59	0.036	4
20	FCov-240 + DistD + DistT + ELEV	4	-895.108	1798.40	5.47	0.023	5
35	FCov-510 + TPI + SHANN	3	-896.844	1799.80	6.86	0.011	6
23	FCov-240 + DistT + ELEV	3	-896.919	1800.00	7.01	0.011	7
25	FCov-510 + DistT + ELEV	3	-897.367	1800.90	7.91	0.007	8
21	FCov-240 + DistD + ELEV	3	-897.409	1800.90	7.99	0.007	9
17	FCov-30 + DistD + TPI + ELEV	4	-896.446	1801.10	8.15	0.006	10
52	FCov-30 + TPI + ELEV	3	-897.839	1801.80	8.85	0.004	11
7	FCov-240 + DistD + DistT+TPI	4	-897.161	1802.50	9.58	0.003	12
26	FCov-510 + DistT+ DistW+ELEV	4	-897.197	1802.60	9.65	0.003	13
24	FCov-510 + DistT+ELEV	4	-897.409	1803.00	10.07	0.002	14
27	FCov-510 + DistW+ELEV	3	-898.54	1803.20	10.25	0.002	15
37	FCov-30 + DistR + TPI + SHANN	4	-897.995	1804.20	11.25	0.001	16
41	FCov-30 + DistT + TPI + SHANN	4	-898.115	1804.40	11.49	0.001	17
8	FCov-240 + DistT + TPI	3	-899.202	1804.50	11.58	0.001	18
32	FCov-510 + DistD + SHANN	3	-899.294	1804.70	11.76	0.001	19
11	FCov-510 + DistR+ TPI	3	-899.63	1805.40	12.43	0.001	20
15	FCov-30 + DistD + DistT+ ELEV	4	-898.593	1805.40	12.44	0.001	21
42	FCov-30 + TPI + SHANN	3	-899.748	1805.60	12.67	0.001	22
44	FCov-240 + TPI + SHANN	3	-899.748	1805.60	12.67	0.001	23
31	FCov-30 + DistD + TPI + SHANN	4	-898.94	1806.10	13.14	0	24
1	FCov-30 + DistT + DistD + TPI	4	-899.219	1806.60	13.69	0	25
13	FCov-510 + DistT + DistW + TPI	4	-899.258	1806.70	13.77	0	26
10	FCov-240 + DistR + TPI	3	-900.486	1807.10	14.14	0	27
16	FCov-30 + DistD + ELEV	3	-900.828	1807.80	14.83	0	28
9	FCov-240 + DistD + DistW + TPI	4	-899.851	1807.90	14.96	0	29
38	FCov-240 + TPI	2	-901.945	1808.00	15	0	30
12	FCov-510 + DistD + SHANN	3	-900.941	1808.00	15.05	0	31
18	FCov-30 + DistT + ELEV	3	-901.188	1808.50	15.55	0	32
14	FCov-510 + DistW + TPI	3	-901.322	1808.80	15.82	0	33
36	FCov-510 + TPI	2	-902.407	1808.90	15.92	0	34

6	FCov-240 + DistD + TPI	3	-901.409	1808.90	15.99	0	35
28	FCov-30 + DistD + DistR + SHANN	4	-900.673	1809.60	16.6	0	36
45	FCov-30 + DistT + DistD	3	-901.717	1809.60	16.61	0	37
19	FCov-30 + DistD + DistW + ELEV	4	-900.828	1809.90	16.91	0	38
4	FCov-30 + DistT + TPI	3	-901.899	1809.90	16.97	0	39
49	FCov-30 + DistT + DistW + ELEV	4	-900.964	1810.10	17.19	0	40
5	FCov-30 + DistR + TPI	3	-902.208	1810.50	17.59	0	41
51	FCov-30 + DistT + DistD + DistW	4	-901.222	1810.70	17.7	0	42
29	FCov-30 + DistW + DistD + SHANN	4	-901.449	1811.10	18.15	0	43
30	FCov-240 + DistW + DistD + SHANN	4	-901.449	1811.10	18.15	0	44
50	FCov-30 + DistT + DistW + ELEV	4	-901.733	1811.70	18.72	0	45
33	DistD + DistT + TPI + SHANN	4	-901.739	1811.70	18.73	0	46
3	FCov-30 + DistD + DistW + TPI	4	-901.911	1812.00	19.08	0	47
39	FCov-30 + DistW + DistD + TPI	4	-901.911	1812.00	19.08	0	48
43	FCov-30 + TPI	2	-904.066	1812.20	19.24	0	49
2	FCov-30 + DistD + TPI	3	-903.125	1812.40	19.42	0	50
47	FCov-30 + DistT	2	-904.337	1812.70	19.78	0	51
46	FCov-510 + DistD	2	-904.338	1812.70	19.79	0	52
48	FCov-30 + DistT + DistW	3	-904.19	1814.50	21.55	0	53
40	FCov-30 + DistW+ DistD	3	-904.41	1814.90	21.99	0	54
0	Null model	1	-910.457	1822.90	29.98	0	55

Supplementary information

Appendix D.

Table D.1. Pairwise cumulative resistances values between the habitat patches according with the Circuit Theory analysis. In the table are only shown the resistances values between habitat patches that not exceed the distance threshold of 15 km between them (Euclidian distance). This threshold value was established on the basis of the maximum distance traveled by the jaguars tracked within their home range (Euclidian distance) in a time lapse interval of 72 hours (15 710 m).

	MF-01	SL-01	TA-01	TA-02	TA-03	TA-04	GLE-02	GLE-03	MC-02	MC-03	MC-04	MC-05	MC-06	SR-01	SR-02	SR-03	SR-04	SR-05	SR-06	SR-07	SR-08	LL-01	LL-02	LL-03	LL-04
MF-01	0	**51.0**	**25.4**			**15.8**																			
SL-01		0	**36.2**	**45.0**	**46.7**																				
TA-01			0	**58.9**		**23.0**																			
TA-02				0	**41.9**																				
TA-03					0		**79.3**																		
TA-04						0																			
GLE-01							**36.4**	**5.3**	**69.4**		**54.5**	**42.8**	**25.6**									**31.7**			
GLE-02							0	**10.0**																	
GLE-03								0						**27.4**	**127.1**										
MC-01									**118.1**	**157.7**					**154.1**	**107.6**			**104.4**		**125.1**				
MC-02									0		**59.1**														

MC-03	0	**27.1**										**148.1**				
MC-04		0	**76.9**									**135.7**				**97.5**
MC-05			0	**46.4**												**121.9**
MC-06				0									**75.8**	**78.2**		
SR-01					0	**122.7**		**144.4**	**183.5**							
SR-02						0	**123.3**									
SR-03							0	**43.4**		**99.7**						
SR-04								0	**41.2**							
SR-05									0	**26.2**						
SR-06										0	**96.9**	**104.9**				
SR-07											0	**156.3**				
LL-01													0	**48.4**		
LL-02														0	**53.84**	
LL-03															0	**66.67**
LL-04																0

Supplementary information

Appendix E.

Table E.1. Values of variables considered for categorization of corridors.

No	ID	Habitat patched linked	Area covered (km2)	Total area of jaguar habitat that was connected by the corridor	% protected by nature reserves	% protected by PSA	Total % protected	% of primary forest within each corridor's boundary	Number of paved roads crossed by corridors	Classification priority
1	CORR-01	MF-01 to TAB-04	24.79	5261.31	0.00	0.00	0.00	17.42	1	MP
2	CORR-02	TA-01 to TA-04	64.47	203.06	0.00	0.00	0.00	21.20	1	MP
3	CORR-03	MF-01 to TAB-01	50.55	5259.80	8.30	0.00	8.30	18.85	0	MP
4	CORR-04	MF-01 to SL-01	160.93	5960.55	86.93	0.00	86.93	53.29	2	MP
5	CORR-05	TA-01 to TA-02	221.72	172.27	58.04	0.00	58.04	48.60	3	MP
6	CORR-06	SL-01 to TA-02	71.02	873.02	93.12	0.00	93.12	71.99	0	LP
7	CORR-07	TA02 to TA-03	48.51	139.96	1.38	0.00	1.38	68.52	0	MP
8	CORR-08	SL-01 to TA-01	46.98	902.29	66.89	0.10	66.99	95.29	0	MP
9	CORR-09	SL-01 to TA-03	67.33	840.71	87.02	0.00	87.02	81.60	1	MP
10	CORR-10	TA-03 to GLE02	86.32	338.44	1.45	3.49	4.94	53.92	1	MP
11	CORR-11	GLE-01 to GLE02	81.82	2688.97	2.85	11.33	14.18	74.20	3	HP
12	CORR-12	GLE-02 to GLE-03	9.62	580.26	0.00	0.00	0.00	62.71	1	MP
13	CORR-13	GLE-01 to GLE-03	34.87	2670.73	0.00	0.00	0.00	68.09	2	HP
14	CORR-14	SR-01 to SR-05	48.37	144.27	44.59	0.00	44.59	21.90	0	LP
15	CORR-15	GLE-03 to SR-02	19.72	288.38	0.00	0.00	0.00	30.13	0	MP
16	CORR-16	GLE-03 to SR-01	7.39	291.59	0.00	0.00	0.00	35.60	0	MP

17	CORR-17	SR-01 to SR-02	37.29	23.34	0.00	0.00	0.00	46.66	0	MP
18	CORR-18	SR-01 to SR-04	24.32	31.64	0.00	0.00	0.00	29.77	0	MP
19	CORR-19	SR-02 to SR-03	5.54	17.96	0.00	0.00	0.00	27.43	0	MP
20	CORR-20	SR-04 to SR-05	15.03	143.97	99.39	0.00	99.39	39.25	0	LP
21	CORR-21	SR-03 to SR-04	14.13	26.26	5.22	0.00	5.22	21.30	0	LP
22	CORR-22	SR-05 to SR-06	9.21	229.55	0.00	0.00	0.00	43.34	1	MP
23	CORR-23	SR-06 to SR-07	20.88	110.05	34.69	0.00	34.69	43.64	0	LP
24	CORR-24	SR-07 to SR-08	69.24	46.56	24.37	0.00	24.37	19.48	0	LP
25	CORR-25	SR-06 to SR-08	61.95	139.02	24.88	0.00	24.88	21.82	0	LP
26	CORR-26	SR-03 to SR-06	20.63	111.84	0.00	0.00	0.00	31.80	0	MP
27	CORR-27	MC-01 to SR-06	41.22	131.80	0.00	0.00	0.00	38.21	0	MP
28	CORR-28	MC-01 to SR-03	11.63	41.14	0.00	0.00	0.00	49.87	0	MP
29	CORR-29	MC-04 to SR-08	12.89	114.17	0.00	0.09	0.09	33.37	0	MP
30	CORR-30	MC-01 to SR-02	28.51	37.92	0.00	0.96	0.96	28.09	0	MP
31	CORR-31	MC-03 to SR-08	64.16	48.32	0.00	0.00	0.00	36.33	0	MP
32	CORR-32	MC-01 to MC-03	61.01	41.10	0.00	8.60	8.60	54.50	2	MP
33	CORR-33	MC-01 to SR-08	12.93	68.32	0.00	0.00	0.00	43.00	1	MP
34	CORR-34	MC-01 to MC-02	50.33	52.49	0.00	0.00	0.00	41.20	0	MP
35	CORR-35	GLE-01 to MC-02	62.94	2411.67	0.01	18.98	18.98	50.21	4	HP
36	CORR-36	MC-02 to MC-04	50.88	98.35	0.00	15.29	15.29	57.31	0	MP
37	CORR-37	MC-03 to MC-04	12.69	86.95	0.00	26.65	26.65	69.17	1	MP
38	CORR-38	GLE-01 to MC-06	10.36	2401.80	2.45	36.74	39.19	56.38	1	MP
39	CORR-39	GLE-01 to MC-04	37.45	2466.12	0.39	21.85	22.24	56.23	1	HP
40	CORR-40	GLE-01 to MC-05	85.08	2409.11	0.13	36.56	36.69	69.29	3	HP
41	CORR-41	MC-04 to MC-05	67.33	95.79	0.00	10.42	10.42	60.97	0	MP
42	CORR-42	LL-04 to MC-04	168.15	178.79	39.66	1.08	40.74	50.79	3	MP
43	CORR-43	MC-05 to MC-06	17.89	31.47	0.00	47.66	47.66	64.28	0	LP
44	CORR-44	LL-01 to MC-06	34.66	27.23	0.00	12.94	12.94	59.69	2	MP

45	CORR-45	LL-02 to MC-06	40.04	24.62	0.00	11.38	11.38	55.25	2	MP
46	CORR-46	LL-02 to LL-03	56.60	127.90	0.00	0.00	0.00	94.75	1	MP
47	CORR-47	LL-03 to LL-04	54.09	217.75	33.37	0.00	33.37	69.25	2	MP
48	CORR-48	LL-01 to LL-02	34.20	27.69	0.00	0.00	0.00	74.44	0	MP
49	CORR-49	GLE-01 to LL-01	14.06	2404.87	0.67	8.29	8.96	59.23	1	HP
50	CORR-50	LL-04 to MC-05	214.50	121.77	9.62	6.63	16.25	57.74	8	MP

8. Discusión general

En el caso del jaguar, el número de estudios enfocados en planificar y priorizar las acciones de conservación a escala continental han aumentado en los últimos años (Sanderson et al. 2002; Taber et al. 2002; Rabinowitz & Zeller 2010; Medellín et al. 2015). Aunque aún se mantienen poblaciones de jaguar muy numerosas en una gran parte de Sudamérica, principalmente en la región de la Amazonía, la mayor parte de la distribución de la especie afuera de esta región se ha perdido en los últimos cien años (Sanderson et al. 2002). Es necesario reconocer que la mayoría de las sub-poblaciones de jaguar actualmente presentan varias amenazas y que su riesgo de extinción es eminente (ver capítulo 2 de esta tesis). Por ejemplo, muy pocas de las sub-poblaciones identificadas afuera de la Amazonía son viables a largo plazo, en muchas de las áreas donde están presentes estas sub-poblaciones de jaguar la densidad humana es muy alta, además de que varias de estas sub-poblaciones se encuentran aisladas y el nivel de protección formal que tienen es muy bajo. La extinción de sub-poblaciones es el preludio a la extinción de cualquier especie y la extinción de las sub-poblaciones tiene como consecuencias la pérdida de los bienes y servicios que prestan estas sub-poblaciones a las ecosistemas (Ceballos & Ehrlich 2002).

Con base en el conocimiento de las sub-poblaciones más amenazadas a escala continental es importante priorizar las acciones de conservación enfocadas en la especie en un futuro próximo. Por ejemplo, la identificación e implementación de los corredores biológicos para mantener la conectividad entre las sub-poblaciones de jaguar deberá de ser una prioridad en aquellas sub-poblaciones en las cuales la probabilidad de extinción sea mayor por aislamiento y por bajo tamaño poblacional (Rabinowitz & Zeller 2010). En el caso de algunas sub-poblaciones que se encuentran en el Bosque Atlántico en Brasil y

Argentina están en riesgo de extinción no solamente por su aislamiento y bajo tamaño poblacional, sino también por su baja diversidad genética, flujo génico y tamaño efectivo poblacional (Haag et al. 2010). Muy probablemente esta situación es muy similar en otras sub-poblaciones de la especie que presentan el mismo grado de amenazas por aislamiento y bajo tamaño poblacional.

También es prioritario aumentar la superficie de hábitat protegido para la especie en gran parte de su área de distribución. En la mayoría de las sub-poblaciones identificadas, el porcentaje de protección del área ocupada por la especie es muy bajo. Los jaguares requieren de áreas muy extensas en buen estado de conservación para mantener una población viable a largo plazo (Quigley & Crawshaw Jr. 1992; Ceballos et al. 2002; Sanderson et al. 2002; de la Torre & Medellín 2011), y en muy pocas regiones en donde se distribuye la especie existe la superficie protegida para al menos asegurar la protección de una población mayor a los 300 jaguares, que según el criterio Eizirik et al. (2002), es el tamaño mínimo para asegurar la persistencia de la población en los próximos 100 años. Es necesario que en un futuro próximo se planifiquen reservas en todo lo largo del área de distribución de la especie con la finalidad asegurar la viabilidad de las sub-poblaciones remanentes. Con base en los requerimientos ecológicos que tienen los jaguares (Quigley & Crawshaw Jr. 1992; Ceballos et al. 2002; Conde et al. 2010; Cullen et al. 2013), asegurando las extensiones de hábitats necesarios para mantener una población viable de esta especie también es una oportunidad única para asegurar gran parte de la biodiversidad con la cual los jaguares coexisten en los diferentes paisajes donde la especie se distribuye, ya que el jaguar es una especie sombrilla, carismática y símbolo o bandera de muchos programas de conservación en toda América Latina (Medellín et al. 2002, 2015; Sanderson et al. 2002; Rabinowitz & Zeller 2010). Adicionalmente, en las sub-poblaciones donde la densidad humana es más alta y donde el riesgo de perder los hábitats naturales es mayor se deberán de implementarse políticas de desarrollo sustentable que aseguren la conservación del hábitat del jaguar y el bienestar de los pobladores humanos que coexisten con esta especie.

Aunque el jaguar aún no ha sido considerado dentro de las categorías de “Amenazado” dentro de la lista roja de la IUCN, los criterios utilizados para incluir a las especies que están amenazadas dentro de las categorías de la Lista Roja de la UICN no necesariamente reflejan que estado de conservación guardan la mayoría de las sub-poblaciones de la especie (Wallace et al. 2010). Al igual que el jaguar, otras muchas especies con distribuciones extensas podrían encontrarse en la misma situación, esto es que aunque aún se mantenga una o algunas poblaciones numerosas, si la mayor parte del rango geográfico de la especie se ha perdido, o si la mayoría de las poblaciones presentan una probabilidad alta de extinguirse a corto plazo, la especie deberían de considerarse dentro de las categorías de “Amenazadas”. Este enfoque abre la puerta para evaluar en el futuro las poblaciones de otras especies de manera similar a como se hizo en el análisis del primer capítulo de esta tesis, con la finalidad de mejorar los esquemas de evaluación de las especies dentro de los criterios de la Lista Roja de la UICN.

El conocimiento de los requerimientos espaciales de las especies que se encuentran amenazadas es fundamental para desarrollar los programas de conservación adecuados para asegurar la persistencia de estas especies a largo plazo. Anteriormente se habían realizado varios estudios enfocados en entender cómo los jaguares y pumas utilizan el espacio en diferentes paisajes (Rabinowitz & Nottingham Jr. 1986; Franklin et al. 1999; Logan & Sweanor 2001; Scognamillo et al. 2003; Chávez 2006; Nuñez 2006; Cavalcanti & Gese 2009; Conde et al. 2010; Colchero et al. 2011; Cullen et al. 2013). Sin embargo, hasta el momento no se había evaluado (dando seguimiento simultaneo mediante radio-telemetría de GPS, a individuos de ambas especies) el tamaño de las áreas de actividad y cómo los jaguares y pumas se reparten el espacio cuando coexisten. Al menos en los bosques tropicales de Centroamérica los jaguares utilizan áreas de actividad mucho más extensas que los pumas. Aunque ambas especies utilizan con mayor frecuencia áreas en buen estado de conservación (áreas con mayor porcentaje de cobertura forestal), la transformación de los bosques aparentemente tienen un impacto más significativo en los jaguares que en los pumas. También los análisis realizados para el segundo capítulo de estas tesis demuestran que es necesario conservar áreas de bosque de al menos 18,000 ha en la región de la Selva Lacandona para cumplir con los requerimientos espaciales de una hembra de jaguar durante año. Esta estimación ilustra la extensión de las áreas con selva que son necesarias para conservar una población de jaguares con hembras reproductivas.

Jaguares y pumas son simpátricos a lo largo de toda la distribución geográfica del jaguar y los jaguares son más grandes que los pumas en todas las áreas donde estas dos especies coexisten (Iriarte et al. 1990). Sin embargo, existe cierto traslape en los tamaños por lo cual ambas especies pueden tener un nicho similar y competir por los mismos recursos. Estudios anteriores han demostrado que la segregación entre los jaguares y pumas se puede dar a partir de depredar sobre diferentes presas (Emmons 1987; Nuñez et al. 2000; Scognamillo et al. 2003; Novack et al. 2005; Foster et al. 2010b), presentar patrones de actividad a diferentes horas del día (Scognamillo et al. 2003; Harmsen et al. 2009, 2011; Romero-Muñoz et al. 2010), y evitar los mismos sitios activamente (Harmsen et al. 2009; Foster et al. 2010a). Bajo el seguimiento simultaneo de jaguares y pumas mediante radio-telemetría de GPS se mostró que aunque individuos de ambas especies pueden presentar extensos traslapes en sus áreas de actividad, presentan muy poco traslape en las áreas que son más intensamente utilizadas. También se mostró que tanto jaguares y pumas que presentan traslape en sus áreas de actividad evitan utilizar los mismos sitios al mismo tiempo. Esta información nos sugiere que probablemente existe una repartición del espacio cuando ambas especies coexisten, lo cual puede ser otro mecanismo que facilite su coexistencia.

Aunque previamente se han realizado varias propuestas para mantener la conectividad de las poblaciones de jaguar a distintas escalas (Rabinowitz & Zeller 2010; Zeller et al. 2011; Morato et al. 2014), anteriormente no se había incorporado información acerca de la ecología espacial del jaguar para realizar una modelación de corredores. Entender como los diferentes atributos del paisaje, ya sea naturales o aquellos que son influenciados por las actividades humanas, afectan el uso del espacio por parte de las especies que están en riesgo nos permite trazar mejores estrategias de conservación con base en lo requerimientos ecológicos y en el comportamiento de estas especies. En el caso de la región sur de la Selva Maya los jaguares utilizaron como hábitat principal el bosque primario ya que la probabilidad de uso aumentó conforme aumentó el porcentaje de cobertura forestal. Aunque los jaguares no utilizan exclusivamente el bosque primario, este tipo de cobertura lo prefieren en comparación a los ambientes modificados por actividades humanas y este patrón ha sido observado en otros estudios con jaguares y otros grandes carnívoros (Dickson & Beier 2002; Thatcher et al. 2006; Conde et al. 2010; Foster et al. 2010a; Cullen et al. 2013; Zeilhofer et al. 2014; Ehlers et al. 2014). Además, la probabilidad de uso por parte de los jaguares aumentó conforme aumentó la distancia a los parches deforestados mayores a 100 ha. Esto nos indica que los jaguares utilizan preferentemente sitos alejados de áreas deforestadas para actividades humanas, ya que la mayoría de estos sitios incluyen cultivos, pastizales para la ganadería, bosques secundarios y sitios cercanos a poblados y carreteras. Otros estudios realizados con jaguares y otras especies de grandes carnívoros han encontrado resultados similares, en donde los paisajes modificados por las actividades antropogénicas crean un efecto de borde sobre las poblaciones de grandes carnívoros (Woodroffe 2000; Naves et al. 2003; Linkie et al. 2006; Carroll & Miquelle 2006; Conde et al. 2010; Takahata et al. 2014). Otras variables que fueron importantes para explicar la probabilidad de uso de los jaguares en el sur de la Selva Maya fueron el índice de posición topográfico y la elevación. En este caso, estas variables nos indican que los jaguares en esta región están más asociados a sitios de pendiente moderada y media, pero que evitaron los sitios más altos de las serranías ya que la probabilidad de uso disminuye conforme aumenta la elevación.

Por otro lado, la probabilidad de movimiento de los jaguares está facilitada por sitios que mantienen cobertura forestal a 240 m hacia los alrededores. Esto tiene implicaciones importantes para el diseño de corredores para los jaguares ya que nos sugiere que el ancho mínimo al cual los corredores pudieran ser funcionales para esta especie es de 240 m. Este resultado es similar a otros estudios enfocados en otras especies de grandes felinos, los cuales sugieren que el ancho mínimo de los corredores debería de ser de ≥ 400 m para ser funcionales para la dispersión (Beier, 1995, 1993). La probabilidad de movimiento de los jaguares también está asociada con valores positivos de índice de posición topográfico, lo que indica que los movimientos de los jaguares están facilitados por sitios con pendientes moderadas (Dickson et al., 2005), esto en especial cuando las áreas planas han sido completamente deforestadas (Morato et al., 2014). Sin embargo, la probabilidad de movimiento de los jaguares disminuye conforme la elevación aumenta, lo que indica que los jaguares evitan las partes más altas de las serranias. Esto sugiere que los movimientos de los jaguares podrian dificultarse por las serranias de mayores altitutes (Rabinowitz & Zeller, 2010; Zeller et al., 2011).

Con base en los parches de hábitat y los corredores identificados para los jaguares en el sur de la Selva Maya se pretende desarrollar una estrategia de conectividad utilizando al jaguar como especie focal. Básicamente, a esta escala solamente se identificaron dos parches de hábitat con poblaciones que podrían ser viables a mediano plazo, las cuales podrían contener una población mayor a 50 individuos. La mayor parte de estos parches de hábitat para la especie afortunadamente están protegidos dentro del sistema de Áreas Naturales Protegidas de México y Guatemala. Sin embargo, extensiones muy importantes de hábitat disponible para el jaguar en la porción que le corresponde a México actualmente no están formalmente protegidas. Estas áreas corresponden a lo que hoy es la Reserva Comunal Sierra La Cojolita y a las áreas forestadas alrededor del Área de Protección de Flora y Fauna Chan-kin, en la región de la Selva Lacandona. Una de las prioridades para mantener la integridad de la población de jaguares al sur de la Selva Maya debe ser alcanzar la completa protección de estas extensiones de selva que son fundamentales para mantener la conectividad e integridad de todo este paisaje.

Es importante resaltar que gran parte de los parches de hábitat y de los corredores identificados para los jaguares se mantienen gracias al esquema de conservación de Pagos por Servicios Ambientales, el cual es implementado por el Gobierno Federal Mexicano a través de la Comisión Nacional Forestal (CONAFOR). Las comunidades que reciben este esquema de compensación por conservar sus tierras con selva son las que potencialmente mantienen el hábitat y los corredores potenciales para los jaguares en la región de la Selva Lacandona, Chiapas, México. El hecho de que las comunidades locales reciban un pago conservar sus tierras con bosque es un incentivo para conservar estas áreas y para que las comunidades busquen alternativas de desarrollo que sean compatibles con la conservación del jaguar y su hábitat. Se debe de explorar la ampliación e implementación de este programa a otras regiones con la finalidad de mantener con bosque las áreas que se encuentren afuera de las Áreas Naturales Protegidas que son importantes como hábitat y corredores para los jaguares.

Finalmente, se espera que la información generada en el tercer capítulo de esta tesis sirva como una guía para las agencias de conservación y los tomadores de decisiones que trabajan en la región de la Selva Maya para desarrollar una planeación en la región la cual sea compatible con la conservación del jaguar y su hábitat. Solamente aterrizando esta propuesta de conectividad en programas de desarrollo sustentable enfocados en las comunidades locales se podrá asegurar la permanencia y la viabilidad de esta población de jaguares, la cual representa la población más grande de la especie en Mesoamérica.

9. Conclusión general

Aunque aún se mantienen una sub-población de jaguar muy numerosa en la región de la Amazonía, la mayor parte de la distribución de la especie afuera de esta región se ha perdido en los últimos cien años. La mayoría de las sub-poblaciones de jaguar actualmente presentan varias amenazas y su riesgo de extinción es eminente. Es necesario priorizar las acciones de conservación de la especie a escala continental en un futuro próximo, con base en el conocimiento de las sub-poblaciones y sus amenazas. Esto implica la identificación e implementación de los corredores biológicos para sub-poblaciones más aisladas y con tamaños poblacionales más bajos, aumentar la superficie de hábitat protegido para la mayoría de las sub-poblaciones de la especie, así como implementar políticas de desarrollo sustentable que aseguren la conservación del hábitat del jaguar y el bienestar de la población humana en las regiones donde el hábitat para la especie esté en mayor riesgo de perderse.

Los criterios para incluir al jaguar y otras especies dentro de la Lista Roja de la IUCN no solamente deben de estar basados en la evaluación del estado de conservación de la población global, sino que también deben de incluir el estatus de conservación de las sub-poblaciones remanentes de la especie y ponderar de acuerdo al grado de amenazas que presentan dichas sub-poblaciones.

Al menos para la región de Centroamérica la transformación de los bosques parece tener un impacto más significativo para los jaguares que para los pumas, ya que los jaguares requieren de áreas conservadas mucho más extensas para cumplir con sus requerimientos ecológicos. En la región de la Selva Lacandona al menos es necesario conservar áreas con bosque mayores a 18,000 ha para que cumplir con los requerimientos espaciales anuales de una hembra de jaguar. Por lo cual, las acciones de conservación enfocadas para conservar la población de esta especie en la región de la Selva Lacandona deben de ser de gran envergadura, ya que se requieren conservar extensiones gigantescas de bosque para seguir manteniendo una población reproductiva. Dentro de estas acciones la conservación y consolidación de las Áreas Naturales Protegidas existentes en la región es de total relevancia, así como mantener las áreas aún forestadas que se encuentran afuera de Áreas Naturales Protegidas, ya que son imprescindibles para mantener la conectividad.

Dentro de las variables que mejor explican el uso de hábitat por parte de los jaguares en el paisaje en el sur de la Selva Maya están el porcentaje de cobertura forestal y la distancia a los parches deforestados mayores a 100 ha. Esto nos indica que los jaguares prefieren los sitios con bosque primario, alejados de los cultivos, pastizales para ganadería y los sitios cercanos a poblados y carreteras. Otras variables que también explican el uso del espacio de los jaguares en esta región son el índice de posición topográfica y la elevación. Esto nos indica que los jaguares están más asociados a sitios con pendientes de moderadas a medias, pero que evitaron los sitios más altos de las serranías ya que la probabilidad de uso disminuye conforme aumenta la elevación. En cambio, la probabilidad de movimiento de los jaguares está facilitada por sitios que mantienen cobertura forestal a 240 m hacia los alrededores y por sitios con pendientes moderadas, esto en especial cuando las áreas planas han sido completamente deforestadas. Sin embargo, la probabilidad de movimiento de los jaguares disminuye conforme la elevación aumenta, lo que sugiere que los movimientos de los jaguares podrian dificultarse por las serranias de mayores altitutes.

Con base en los parches de hábitat disponibles y los corredores identificados para los jaguares en el sur de la Selva Maya se pretende desarrollar una estrategia de conectividad utilizando al jaguar como especie focal y sombrilla. Solamente aterrizando esta propuesta de conectividad para el paisaje del sur de la Selva Maya en programas de desarrollo sustentable enfocados en las comunidades locales se podrá asegurar la permanencia y la viabilidad de esta población de jaguares, la cual representa la población más grande de la especie en Mesoamérica. Es importante resaltar que gran parte de los parches de hábitat y de los corredores identificados para los jaguares se mantienen gracias al esquema de conservación de Pagos por Servicios Ambientales. Una de las prioridades para conservar a la especie en la región es buscar la ampliación y la implementación de este tipo de programas en otros sitios que sean importantes como hábitat ó corredores. Adicionalmente para mantener la integridad de la población de jaguares al sur de la Selva Maya, y de todo este paisaje, se debe alcanzar la completa protección de las grandes extensiones de selva que aún no están formalmente protegidas.

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