UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE MEDICINA

BIOLOGÍA EXPERIMENTAL

PATRÓN DIARIO DE ACTIVIDADES, DIETA Y NIVELES DE ESTRÉS DEL MONO ARAÑA (*Ateles geoffroyi)* EN UN PAISAJE FRAGMENTADO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

ORDÓÑEZ GÓMEZ JOSÉ DOMINGO

TUTORA PRINCIPAL DE TESIS:
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MÉXICO, D.F. FEBRERO, 2016.

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UNAM POSGRADO
Ciencias Biológicas

COORDINACIÓN

Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que el Subcomité de Biología Experimental y Biomedicina del Posgrado en Ciencias Biológicas, en su sesión ordinaria del día 26 de octubre de 2015, aprobó el jurado para la presentación del examen para obtener el grado de **DOCTOR EN CIENCIAS** del alumno **ORDÓÑEZ GÓMEZ JOSÉ DOMINGO** con número de cuenta **300586983** con la tesis titulada **"PATRÓN DIARIO DE ACTIVIDADES, DIETA Y NIVELES DE ESTRÉS DEL MONO ARAÑA (*Ateles geoffroyi*) EN UN PAISAJE FRAGMENTADO"**, realizada bajo la dirección de la **DRA. ANA MARÍA SANTILLÁN DOHERTY:**

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

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, D.F., a 11 de enero de 2016

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

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RESUMEN

Los primates son particularmente sensibles a la pérdida y fragmentación del hábitat debido a que presentan locomoción arbórea, ámbitos hogareños grandes y una gran proporción de frutas y hojas en su dietas. Para generar información adecuada para su conservación, un número creciente de trabajos han estudiado los efectos de la pérdida y fragmentación del hábitat sobre el comportamiento y los niveles de estrés de primates. Sin embargo, la mayoría de estos trabajos no consideran los efectos de los atributos del paisaje (e.g., cobertura forestal, densidad de borde, distancia media entre fragmentos) sobre estas variables de respuesta, ni la escala espacial (i.e., tamaño del paisaje) en la que estos efectos son mayores (conocido como la "escala del efecto"). Como consecuencia, nuestro conocimiento sobre la respuesta de primates a la pérdida y fragmentación del hábitat es aún muy limitado; particularmente en especies que consumen una alta cantidad de frutos y que tienen grandes ámbitos hogareños, como el mono araña (*Ateles geoffroyi*). Esta especie es considerada una de las más sensibles a la pérdida y fragmentación del hábitat, pero hasta la fecha se desconocen los atributos del paisaje que tienen un mayor impacto sobre su comportamiento y niveles de estrés. En el presente estudio se evaluó, considerando la "escala del efecto", el impacto de distintos atributos del paisaje sobre el patrón diario de actividades, la dieta, y los niveles de estrés (i.e., niveles glucocorticoides fecales [GCf]) de seis grupos de monos araña (*Ateles geoffroyi*) que habitan en la selva la selva Lacandona, Chiapas. Además, se evaluó el efecto de su patrón diario de actividades, dieta, disturbios antropogénicos directos (i.e., caza y tala) y densidad de alimento (suma de las áreas basales de especies de árboles frutales utilizadas por el mono araña [SABEF]) sobre sus niveles de estrés. Los resultados muestran que aunque la fuerza de las relaciones entre los atributos del paisaje y las variables de respuesta varió entre escalas, el paisaje de 126 ha mostró las relaciones más fuertes, probablemente debido a la alta conectividad que presentaron estos paisajes. El porcentaje de cobertura forestal fue la métrica del paisaje más fuertemente relacionada con el patrón diario de actividades y la dieta del mono araña, siendo estas relaciones positivas con el tiempo de viaje y el consumo de madera, y negativas con el tiempo de descanso y el consumo de hojas. Estos hallazgos sugieren que la menor área de forrajeo con la que cuentan los monos araña en los paisajes con menor cobertura forestal, provoca que estos animales disminuyan su tiempo de viaje invertido en el patrullaje y en la búsqueda de alimento, y por tanto, que descansen más y aumenten el consumo de hojas (recursos más ampliamente distribuidos en el espacio que los frutos). Sin embargo, contrario a lo esperado, el tiempo invertido en el consumo de fruta no se relacionó positivamente con el porcentaje de cobertura forestal en el paisaje, probablemente como consecuencia de las altas SABEFs en los paisajes con menor cobertura forestal. Respecto a la respuesta de estrés del mono araña, los niveles de GCf se relacionaron positivamente con el tiempo de viaje y la ocurrencia de caza, y negativamente con el tiempo de descanso y el consumo de fruta. Estas relaciones verifican que un mayor esfuerzo físico, una reducción en el consumo de recursos ricos en energía (frutos), y la ocurrencia de disturbios antropogénicos directos, incrementan los niveles de estrés. Por su parte, la SABEF se relacionó negativamente con los niveles de GCf, lo cual verifica que la escasez de alimento incrementa los niveles de estrés. Sin embargo, contrario a expectativas teóricas, el porcentaje de cobertura forestal en el paisaje se relacionó positivamente con los niveles de

GCf. Este resultado puede ser debido a que los monos araña que habitaron en paisajes con menor cobertura forestal realizaron un menor esfuerzo físico (i.e., invirtieron menor tiempo en el viaje y mayor en el descanso), sin reducir su consumo de fruta. En conjunto, los resultados de la presente tesis indican que los monos araña que habitan en paisajes con baja cobertura forestal no siempre presentan mayores niveles de estrés que los que habitan en paisajes con mayor cobertura forestal, y remarcan la importancia de conservar fragmentos pequeños con alta densidad de fruta para la conservación de monos araña que habitan en paisajes fragmentados.

ABSTRACT

Primates are particularly vulnerable to habitat loss and fragmentation due to their large home range sizes, and the great proportion of fruits and leaves in their diet. With the aim of generating important information for their conservation, an increasing number of works have studied the effects of habitat loss and fragmentation on the behavior and stress levels of primates. However, most of these studies have not considered the effects of landscape spatial attributes (e.g., forest cover, edge density, mean isolation distance between patches) on primates, nor the landscape scale (i.e., landscape size) at which these effects are highest (so-called "scale of effect"). As consequence, the knowledge about primates' responses to habitat loss and fragmentation is still limited; particularly in species that consumed a high quantity of fruits and have large home range sizes, as the spider monkey (*Ateles geoffroyi*). This species is considered one of the most sensitive to habitat loss and fragmentation, but to date, the landscape attributes that have a greatest impact in their behavior and stress levels are unknown. In the present study it was evaluated, considering the scale of effect, the impact of different landscape spatial attributes on the daily activity pattern, diet and stress levels (i.e., fecal glucocorticoids [fGC]) of six groups of spider monkeys (*Ateles geoffroyi*) in the Lacandona rainforest, Chiapas. Also, it was evaluated the effects of their daily activity pattern, diet, direct anthropogenic disturbance (i.e., logging and hunting), and food density (i.e., sum of the basal areas of fruiting-tree species [SBAFS]) on their stress levels. The results show that although the strength of the relationships between the landscape spatial predictors and the response variables varied across spatial scales, the 126 ha landscape size presented the strongest relationships, probably as a consequence of the high connectivity that these landscapes presented. The percentage of forest cover was the main driver of the daily activity pattern and diet of spider monkeys. This landscape attribute showed positive relationships with time traveling and wood consumption, and negative relationships with time resting and leaves consumption. These results suggest that the lowest foraging area that have the spider monkeys in the landscapes with lowest forest cover, causes that these animals decrease their travelling time spent in foraging and patrolling their home ranges, and therefore, that they rest more and increase their time spent feeding on leaves (resources more widely distributed in space than fruits). However, contrary to the expected, the time spent feeding on fruit did not present a negative relationship with the percentage of forest cover in the landscape, probably as consequence of the high SBAFSs in the landscapes with lower forest cover. Regarding the spider monkey's stress response, the fGC levels showed positive relationships with time travelling and the occurrence of hunting, and negative relationships with time resting and the time spent feeding on fruit. These relationships support that an increase in physical effort, a reduction in the consumption of high energy food stuffs (fruits), and the occurrence of direct anthropogenic disturbances increase the stress levels. The SBAFS was negatively associated with fGC levels, which supports that food scarcity increases stress levels. However, contrary to theoretical expectations, the percentage of forest cover in the landscape was positively associated with fGC levels, which could be supported by the low physical effort that spider monkeys conducted in the landscapes with lower forest cover (i.e., they invested lower time in travelling and higher in resting), without reducing their time spent feeding on fruit. Overall the results of this thesis indicate that spider monkeys

that inhabit in landscapes with low forest cover not always present higher stress levels than spider monkeys that inhabit in landscapes with higher forest cover, and emphasize the importance of conserving small fragments with high density of fruit resources for the conservation of spider monkeys that inhabit fragmented landscapes.

INTRODUCCIÓN GENERAL

La pérdida y la fragmentación del hábitat

Con el incremento de las poblaciones humanas y la explotación desmedida de recursos naturales, más de tres cuartas partes de la biosfera terrestre han sido transformadas a paisajes fragmentados (Ellis, 2013; Hansen et al., 2013). Esta pérdida y fragmentación del hábitat (i.e., rompimiento del hábitat: Fahrig, 2003) ha modificado los tipos y proporciones de las coberturas que componen los paisajes (i.e., composición del paisaje), y el arreglo espacial de éstas (i.e., configuración del paisaje) (Dunning et al., 1992). Debido a que las modificaciones en la composición y configuración del paisaje (i.e., estructura del paisaje) pueden afectar la fisiología (Brearley et al., 2012) y el comportamiento (Wolff et al., 1997) de diversas especies de organismos, estos procesos son una fuerte amenaza para la biodiversidad (Addicott et al., 1987; McGarigal y Cushman, 2002).

El porcentaje de cobertura forestal en el paisaje (i.e., medida de cantidad de hábitat) es la métrica del paisaje más utilizada para evaluar los efectos de la composición del paisaje sobre las especies. En general, los efectos de esta métrica impactan de manera negativa a las especies, y sus efectos son fuertes y suelen mantenerse constantes a través de diferentes escalas espaciales (e.g., Kurki et al., 2000; Smith et al., 2011; Thornton et al., 2011a; Wettstein y Schmid, 1999). No obstante, una serie de estudios sugieren que en regiones con un porcentaje de cobertura forestal relativamente alto (*ca.* > 30%), especies con dietas generalistas y/o que se alimentan preferente por plantas sucesionales pueden verse favorecidas por la pérdida de cobertura forestal (e.g., Carrara et al., 2015; Klingbeil y Willig, 2009; Pedlar et al., 1997). Por ejemplo, en la selva Lacandona, México, que conserva aproximadamente el 40% de su cobertura forestal original, el porcentaje de cobertura forestal en el paisaje se relaciona negativamente con la diversidad de especies de aves especialistas, y positivamente con la diversidad de especies de aves generalistas (Carrara et al., 2015). De forma similar, en la selva de Iquitos, Perú, que conserva más del 40% de su cobertura forestal original, el porcentaje de cobertura forestal en el paisaje tiene un efecto negativo sobre la abundancia de murciélagos que consumen altas cantidades de flores y frutos de especies de árboles sucesionales (Klingbeil y Willig, 2009).

Dentro de los predictores más utilizados para evaluar los efectos de la configuración del paisaje sobre las especies, se encuentran, el número de fragmentos, la distancia entre fragmentos, y la densidad de borde forestal (i.e., largo del borde de todos los fragmentos que componen un paisaje, dividido entre el tamaño del paisaje) (e.g., Carrara et al., 2015; Garmendia et al., 2013). A diferencia de los efectos de la cobertura forestal, los efectos de la configuración del paisaje varían dependiendo del tamaño del paisaje analizado, siendo más fuertes en paisajes con baja cobertura forestal (< 20-30%: Fahrig, 2003; Jackson y Fahrig, 2012; Smith et al., 2011; Virgós et al., 2001). Por ejemplo, en el bosque templado de Ontario, Canadá, la densidad de fragmentos afecta de manera negativa la diversidad de especies de aves, y sus efectos se incrementan en los paisajes con menor cobertura forestal (Smith et al., 2011). En las mesetas del centro de España, en paisajes con < 20% de cobertura forestal, la distancia del fragmento de estudio a los fragmentos grandes (> 10,000 ha), se relaciona negativamente con la abundancia del tejón europeo (*Meles meles*) (Virgós, 2001).

Al igual que los efectos de la cobertura forestal en el paisaje, los efectos de la configuración del paisaje pueden ser positivos o negativos dependiendo de la características de las especies de estudio (e.g., tipo de dieta, habilidad para deslazarse entre fragmentos) (revisión de Fahrig, 2003), y de la cantidad de cobertura forestal en el paisaje (e.g., Garmendia et al., 2013; Thornton et al., 2011a). Por ejemplo, mientras que en la selva Lacandona la densidad de borde afecta positivamente el número de especies de mamíferos medianos y grandes (Garmendia et al., 2013), en la selva de Petén que conserva apenas el 26% de su cobertura forestal, la densidad de borde afecta negativamente la presencia del mismo grupo de especies (Thornton et al., 2011a). Esta diferencia puede explicarse si se considera que mientras que en regiones con una alta cobertura forestal, una alta densidad de borde podría incrementar la conectividad entre fragmentos (i.e., una mayor densidad de borde implica que los fragmentos presentan formas más irregulares), en regiones con baja cobertura forestal una alta densidad de borde podría aumentar la probabilidad de que las especies pasen mayor tiempo en ambientes de borde donde puede aumentar su exposición a la depredación y a la caza (e.g., pastizales, campos de cultivo) (Woodroffe y Ginsberg, 1998). En este sentido, en la selva de Petén, la proporción de fragmentos ocupados por mamíferos medianos y grandes se relaciona negativamente con su vulnerabilidad a la caza

(Thornton et al., 2011b).

En paisajes con mayor densidad de borde y fragmentos más pequeños se pueden alterar las condiciones abióticas y bióticas cerca de los bordes de los fragmentos: cambios en general conocidos como “efectos de borde” (Laurance et al., 2006). Entre estos cambios cabe destacar el aumento en la mortalidad de árboles grandes en los bordes de los fragmentos debido a e.g., el incremento en la velocidad del viento (Laurance et al., 1998) y desecación (Kapos, 1989). Puesto que el área basal de un árbol se relaciona positivamente con su producción de fruta (Stevenson et al., 1998), fragmentos pequeños y/o con formas irregulares, por lo general presentan una baja calidad de hábitat para especies frugívoras (e.g., Arroyo-Rodríguez y Mandujano, 2006). Los efectos de borde pueden variar en función de la cantidad de cobertura forestal en el paisaje (Hernández-Ruedas et al., 2014). Por ejemplo, mientras que en una región de la selva de los Tuxtlas, que mantiene aproximadamente el 11% de su cobertura forestal original, el tamaño de los fragmentos se relaciona positivamente con el área basal de los árboles (Arroyo-Rodríguez y Mandujano., 2006), en la selva Lacandona, no se presenta esta relación (Hernández-Ruedas et al., 2014). Se sugiere que los efectos de borde parecen ser menores en regiones con una cobertura forestal relativamente alta, debido a que la cobertura forestal en el paisaje probablemente atenúa las variaciones abióticas que se presentan en los bordes de los fragmentos que matan árboles grandes. Soportando esto, Mesquita et al. (1999) reportan que la mortalidad de árboles grandes es mayor cuando la matriz del hábitat se compone por pastos para ganado, que cuando se compone por árboles de rebrote.

Finalmente, una serie de estudios indican que la escala (i.e., tamaño del paisaje) en la que los atributos de la configuración y composición del paisaje (i.e., estructura del paisaje) presentan sus mayores efectos sobre las especies (escala del efecto: sensu Jackson y Fahrig, 2015) varía en función del grupo taxonómico al que pertenece la especie de estudio (Jackson y Fahrig, 2015), y de su uso del espacio (e.g., tamaño de su ámbito hogareño, distancia media de dispersión) (Jackson y Fahrig, 2012, 2015). Por ejemplo, en un trabajo de revisión, Jackson y Fahrig (2015) reportan que los tamaños de los paisajes en los que se presenta la escala del efecto son mayores para mamíferos que para anfibios, y los mismos autores reportan en un trabajo en el que utilizaron modelos de simulación, que las probabilidades de encontrar la escala del efecto son altas en tamaños de paisajes que midan de 4 a 9 veces la distancia media de dispersión de la especie de estudio (Jackson y Fahrig, 2012). Debido a que el uso del espacio está en función de la cantidad de hábitat que necesita cada especie para cubrir sus requerimientos energéticos (Harvey y Clutton-Brock, 1981), estos resultados son razonables. Estos trabajos son de relevancia, ya que dan un marco teórico para la selección de escalas en las que se deben de evaluar los efectos de la estructura del paisaje sobre las especies (Jackson y Fahrig, 2015). Esto es importante, debido a que si la selección de escalas se realiza sin un sustento biológico, se puede llegar a conclusiones erróneas debido al uso de escalas espaciales incorrectas (Jackson y Fahrig, 2015).

En resumen, se puede concluir que los efectos de la pérdida y la fragmentación del hábitat sobre las especies no son fáciles de predecir. Estos efectos varían en función de: (1) la cantidad de hábitat en la región (e.g., Fahrig, 2003); (2) las características de las especies de estudio (e.g., tipo de dieta) (e.g., Carrara et al., 2015); y (3) el tamaño del paisaje en el que se analizan estos efectos (e.g., Smith et al., 2011).

Efecto de la pérdida y fragmentación del hábitat sobre el patrón diario de actividades y la dieta de primates

Debido a que los primates se distribuyen en regiones que presentan altos índices de deforestación (Estrada et al., 2012), y diversas especies presentan características como locomoción arbórea, ámbitos hogareños grandes y gran proporción de frutas y hojas en sus dietas, estos taxa son muy sensibles a la pérdida y fragmentación del bosque (Boyle y Smith, 2010a; Chaves et al., 2012; Michalski y Peres, 2005). Se estima que cerca de la mitad de las especies de primates se encuentran en peligro de extinción (Mittermeier et al., 2012). Analizar las relaciones entre los atributos de la configuración y composición del paisaje con el patrón diario de actividades y la dieta de primates, es una herramienta útil para identificar qué atributos del paisaje pueden tener mayor repercusión sobre la supervivencia de primates que habitan en paisajes fragmentados.

La pérdida y la fragmentación del hábitat pueden afectar la disponibilidad de recursos alimenticios para los primates, como consecuencia de la pérdida de hábitat (Arroyo-Rodríguez y Mandujano, 2006; Dunn et al., 2009; Rivera y Calmé, 2006) y probablemente el efecto de borde que incrementa la mortalidad de árboles grandes (Laurance et al., 2000) que producen altas cantidades de alimento (Stevenson et al., 1998). Dentro de las estrategias conductuales utilizadas por los primates para encarar la escasez de alimento provocada por la pérdida y fragmentación del hábitat, se sabe que estos: (1) ajustan su patrón diario de actividades (e.g., Chaves et al., 2011a; Dunn et al., 2009, 2010); (2) aumentan el consumo de frutas inmaduras y hojas (Asensio et al., 2007; Chaves et al., 2011a; Onderdonk y Chapman, 2000); (3) diversifican sus dietas (Onderdonk y Chapman, 2000; Rivera y Calmé, 2006; Silver y Marsh, 2003); (4) intensifican el uso de las especies de árboles disponibles (Boyle et al., 2012) como aquellas que son resistentes a la quema (Chaves et al., 2012; González-Zamora et al., 2014); y (5) consumen recursos localizados fuera de los fragmentos (e.g., árboles aislados, cercas vivas, plantaciones de mango [*Mangifera indica*]) (Asensio et al., 2009; Estrada et al., 2012).

Diversos estudios coinciden en que en fragmentos pequeños y con baja disponibilidad de recursos, los primates modifican su patrón diario de actividades y dieta para cubrir sus requerimientos energéticos y optimizar su gasto de energía (e.g., Boyle y Smith, 2010b; Boyle et al., 2012; Chaves et al., 2012; Dunn et al., 2009). Por ejemplo, en un estudio en el que compararon entre dos fragmentos de diferentes características el esfuerzo alimenticio (i.e., tiempo dedicado a la alimentación y al viaje entre el tiempo dedicado al descanso [Cavigelli, 1999]) realizado por monos aulladores (*Alouatta palliata*), los autores reportan que el esfuerzo alimenticio es mayor en el fragmento de menor tamaño y con menor disponibilidad de alimento, y que éste se relaciona negativamente con el consumo de fruta y positivamente con el consumo de hojas (Dunn et al., 2010). Debido a que en comparación con las frutas, las hojas son un recurso bajo en energía (Felton et al., 2009), estos resultados sugieren que ante una menor disponibilidad de recursos ricos en energía, los primates incrementan su esfuerzo alimenticio para cubrir sus requerimientos energéticos. En la misma línea, en fragmentos pequeños los monos saki barbudos (*Chiropotes satanas chiropotes*) parecen optimizar su gasto energético viajando menos y descansando más (Boyle y Smith, 2010b), como posible consecuencia del alto costo energético que implica el viaje (Chapman y Chapman, 2000).

Es importante mencionar que si bien la disponibilidad de recursos alimenticios para primates tiende a ser menor en fragmentos pequeños (e.g., Boyle et al., 2012; Dunn et al., 2009), la fragmentación del hábitat no es un proceso selectivo. La fragmentación puede resultar en fragmentos pequeños con alta cantidad de fruta, en los cuales primates altamente frugívoros podrían cubrir sus requerimientos energéticos sin realizar un gran esfuerzo físico. Soportando esto, una serie de estudios indican que diversas especies de primates pasan la mayor parte de su tiempo en áreas significativamente menores a la mitad de su ámbito hogareño, las cuales presentan alta disponibilidad de recursos alimenticios (i.e., áreas núcleo) (e.g., *Pan troglodytes schweinfurthii*: Emery Thompson et al., 2007; *Microcebus murinus*: Radespiel et al., 2003). Por otra parte, en paisajes conformados por fragmentos con una alta calidad de hábitat (i.e., alta disponibilidad de recursos alimenticios), y con matrices que contienen elementos utilizados por los primates para su alimentación (e.g., plantaciones de mango [*Mangifera indica*] y de cacao [*Theobroma cacao*]: Estrada et al., 2012; cercas vivas conformadas por especies de árboles comestibles: Asensio et al., 2009), los primates tienen acceso tanto a los recursos contenidos dentro de los fragmentos, como a los localizados en la matriz del hábitat (Asensio et al., 2009; Estrada et al., 2012). Por tanto, aunque de manera general los estudios indican que en fragmentos pequeños los primates desarrollan estrategias conductuales para encarar la escasez de alimento (Boyle et al., 2010b, 2012; Chaves et al., 2011a, 2012; Dunn et al., 2009, 2010), es importante considerar que en fragmentos pequeños con una alta calidad de hábitat y/o altamente conectados con otros fragmentos y/o ubicados en paisajes con matrices que contienen recursos alimenticios, las modificaciones del comportamiento también podrían indicar que los primates están realizando un menor esfuerzo alimenticio para cubrir sus requerimientos energéticos.

Desafortunadamente, el conocimiento sobre los efectos de la pérdida y fragmentación del hábitat sobre el patrón diario de actividades y la dieta de primates es aún muy limitado. Los trabajos realizados se han limitado a comparar las variables de respuesta entre sitios perturbados y conservados (Arroyo-Rodríguez et al., 2013). Para evaluar de manera objetiva los efectos de la pérdida y fragmentación del hábitat sobre el comportamiento de los primates (o cualquier especie), primero se tienen que caracterizar los efectos de estos procesos sobre la estructura del paisaje, para posteriormente evaluar mediante análisis multi-escalares los efectos de los atributos de los paisajes sobre el comportamiento de los primates. Esto permitirá establecer relaciones causales entre los atributos de la estructura del paisajes y el comportamiento de los primates (Arroyo-Rodríguez et al., 2013), así como la identificación de las escalas en las que estos atributos presentan sus mayores efectos ("escala del efecto" Jackson y Fahrig, 2015).

Predictores proximales y distales de la respuesta de estrés de primates que habitan paisajes fragmentados

Aunque el estudio del patrón diario de actividades y la dieta de primates en paisajes fragmentados permite identificar las distintas estrategias conductuales utilizadas por los primates para contrarrestar los efectos adversos de la pérdida y fragmentación del hábitat, la alteración del comportamiento no siempre es un buen indicador de la adecuación (Cavigelli, 1999). Sin embargo, mediante la medición de hormonas indicadoras de los niveles de estrés (e.g., glucocorticoides) en muestras como excretas, se pueden identificar los factores que podrían disminuir la adecuación de primates en paisajes fragmentados, sin utilizar métodos invasivos que alteran su comportamiento, y/o los ponen en peligro (e.g., efectos de anestesia sobre ritmo cardiaco) (Foerster y Monfort, 2010; Muller y Wrangham, 2004). El estrés es una respuesta adaptativa que se presenta cuando el sistema nervioso periférico aferente percibe uno o diversos factores que pueden alterar la homeostasis del organismo (i.e., estresores) (Abbott et al., 2003; Foerster y Monfort 2010; Sapolsky et al., 2000). Durante la primera fase de esta respuesta, el SNC activa la médula adrenal para secretar catecolaminas al torrente sanguíneo, y en cuestión de segundos, obtener energía del catabolismo de diversos metabolitos para aumentar el estado de alerta, concentración, y agudizar los sentidos (Sapolsky et al., 2000; Stratakis y Chorousos, 1995). Por su parte, en la segunda fase de esta respuesta, el eje hipotálamo-hipófisis-corteza adrenal (HHA) (previamente activado por el SNC) libera la hormona liberadora de corticotropina (CRH, por sus siglas en ingles) para estimular la hipófisis anterior y secretar la hormona adrenocorticotrópica (ACTH, por sus siglas en ingles) al torrente sanguíneo. Una vez en el torrente sanguíneo, la ACTH activa la corteza adrenal e induce la secreción de glucocorticoides como el cortisol y la corticosterona. Finalmente, los glucocorticoides son transportados por medio de la sangre al hígado para inducir gluconeogénesis, y movilizar reservas energéticas para encarar los efectos adversos producidos por los estresores (Sapolsky 1993; Stratakis y Chorousos, 1995). Aunque el estrés es una respuesta adaptativa, si el estresor se presenta durante un tiempo prolongado (e.g., escasez de alimento, enfermedad), la gluconeogénesis podría provocar el consumo de energía potencialmente utilizable para el mantenimiento y la reproducción del organismo (Sapolsky, 2002), y por tanto, una disminución en su adecuación (Busch y Hayward, 2009; Sanderson et al., 2015).

De manera general, los factores que repercuten sobre los niveles de estrés de los primates que habitan en paisajes fragmentados pueden clasificarse en predictores proximales y distales. Los predictores proximales son aquellos que tienen un efecto directo sobre los niveles de estrés, como el esfuerzo físico, el consumo frecuente de alimentos bajos en energía, o la temperatura ambiental (Cavigelli et al., 1999; Dunn et al., 2013). Por otra lado, los predictores distales son aquellos que afectan la duración e intensidad de los comportamientos que se asocian de manera directa con los niveles de estrés, i.e., que influyen sobre los predictores proximales (Fig. 1).

En general, los estudios coinciden en que primates que habitan fragmentos pequeños presentan niveles más elevados de glucocorticoides, como consecuencia de la baja disponibilidad de alimento (i.e., predictor distal) que suelen presentar estos sitios (e.g., *Piliocolobus tephrosceles*: Chapman et al., 2006; *Alouatta palliata*: Dunn et al., 2013). Esto ha sido sustentado por estudios que han relacionado niveles altos de glucocorticoides con una menor disponibilidad de alimento, y un mayor esfuerzo físico y alimenticio (e.g., *Lemur catta*: Cavigelli, 1999; *A. palliata*: Dunn et al., 2013; *Cercopithecus mitis*: Foerster et al, 2012) (Fig. 1). Por ejemplo, Dunn et al. (2013) reportan que el tiempo invertido en el viaje (i.e., predictor proximal) se relaciona positivamente con los niveles de glucocorticoides del mono aullador (*A. palliata*), y que este tiempo aumenta en periodos en los que la disponibilidad de fruta (i.e., predictor distal) es menor. Esto sugiere, que ante la escasez de fruta, los monos aulladores realizan un mayor esfuerzo físico para encontrar y consumir este ítem rico en energía (Dunn et al., 2013). En la misma línea, Foerster et al. (2012) reportan que los monos azules (*C. mitis*) incrementan sus niveles de glucocorticoides cuando aumentan su tiempo de alimentación, pero disminuyen su tiempo dedicado al consumo de sus ítems alimenticios preferidos (e.g., hojas jóvenes y frutas) (i.e., predictores proximales). Esto indica que ante la escasez de alimento, los monos azules realizan un mayor esfuerzo alimenticio (Foerster et al., 2012).

Desafortunadamente, debido a que la mayoría de los estudios que han evaluado los efectos de la pérdida y fragmentación del hábitat sobre los niveles de glucocorticoides de primates no han considerado el efecto de la configuración y composición del paisaje sobre sus niveles de estrés, nuestro conocimiento sobre los factores que incrementan los niveles de estrés de primates que habitan en paisajes fragmentados es aún muy limitado. La mayoría de los estudios se han limitado a comparar los niveles de glucocorticoides de primates entre sitios perturbados y conservados (e.g., Chapman et al., 2006; Dunn et al., 2013; Gómez-Espinosa et al., 2014; Jaimez et al., 2012; Martínez-Mota et al., 2007; Rangel-Negrín et al., 2009). Por tanto, para incrementar el conocimiento necesario para la realización de planes de manejo y conservación de primates que habitan en paisajes fragmentados, es importante realizar estudios multi-escalares que identifiquen cuáles atributos de la estructura del paisaje presentan mayor efecto sobre los niveles de estrés de primates, y las escalas del paisaje en las que estos efectos son mayores.

Otros factores que pueden incrementar los niveles de estrés de primates que habitan paisajes fragmentados son los disturbios antropogénicos directos. Los disturbios antropogénicos directos son actividades como la caza o la tala que pueden amenazar de manera directa la supervivencia de primates, o que incrementan su estado de alerta. Aunque los estudios que han evaluado los efectos de los disturbios antropogénicos directos sobre los niveles de estrés de primates son escasos, estos sugieren que sus efectos varían entre especies y sitios (Aguilar-Melo et al. 2013; Behie et al., 2010; Rimbach et al., 2013 [Fig. 1]). Por ejemplo, Rimbach et al. (2013) reportan que la ocurrencia de tala y caza incrementa los niveles de glucocorticoides del mono araña café (*Ateles hybridus*), pero no los del mono aullador rojo (*Alouatta seniculus*), lo cual se puede explicar, si se considera que el mono araña es una especie más sensible a la deforestación que el mono aullador (Boyle y Smith, 2010; Mittermeier et al., 2012). En la misma línea, a diferencia de Behie et al. (2010), Aguilar-Melo et al. (2013) reportan que la presencia de turistas no afecta los niveles de glucocorticoides del mono aullador (*A. palliata*), como posible consecuencia de que en su región de estudio los monos aulladores están habituados a la presencia humana.

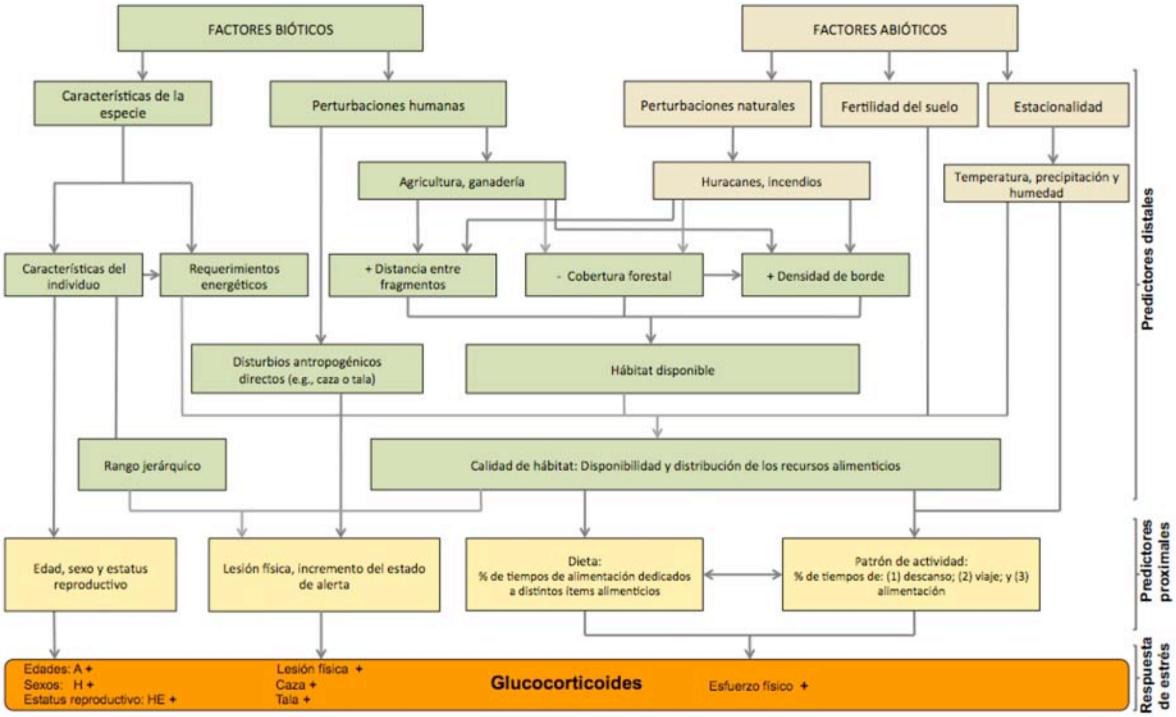

Fig. 1. Esquema que ejemplifica el efecto y la relación de los principales predictores proximales y distales de los niveles de glucocorticoides de primates que habitan paisajes fragmentados. Los cuadros de color verde representan las causas distales de origen biótico, y los cuadros de color hueso las causas distales de origen abiótico. + Aumento de los valores de la variable medida, **-** decremento de los valores de la variable medida. A = adulto, H = hembra, HE = hembra embarazada.

Finalmente, debido a que los glucocorticoides son moléculas que responden ante diversos factores independientes a la pérdida y fragmentación del hábitat, y a los disturbios antropogénicos directos (e.g., estado reproductivo: Cavigelli, 1999; nivel jerárquico: Foerster y Monfort, 2010; sexo: Meyer y Bowman, 1972 [Cuadro 1 y Fig. 1]), para identificar de manera adecuada los predictores proximales y distales de la respuesta de estrés de primates que habitan en paisajes fragmentados, es importante controlar el mayor número posible de estos factores en los análisis estadísticos (e.g., modelos lineales, modelos lineales mixtos). De lo contrario, los resultados obtenidos podrían mostrar un sesgo debido a un factor no analizado, que podría presentar un fuerte efecto sobre los niveles de glucocorticoides.

Cuadro 1. Principales factores distintos a los provocados por la pérdida y fragmentación del hábitat que influyen sobre los niveles de glucocorticoides de primates.

Factor	Efecto	Causa	Referencia
Edad	A > J	Riesgos ecológicos y sociales*	*Macaca mulatta*: Gust et al., 2000 *Pan troglodytes schweinfurthii*: Seraphin et al., 2008
Sexo	H > M	Riesgo de lesión durante encuentros agonísticos*	*Macaca mulatta*: Meyer y Bowman, 1972 *Alouatta palliata*: Aguilar-Cucurachi et al., 2010
Embarazo	HE > HNE	Incremento de la producción de la CRH en la placenta	*Lemur catta*: Cavigelli, 1999 *Papio cynocephalus*: Gesquiere et al., 2008
Jerarquía	B > A	Depende de la estabilidad social y de los costos metabólicos de ser dominante	*Cercopithecus mitis albogularis*: Foerster y Monfort, 2010
	A > B		*Lemur catta*: Cavigelli, 1999
Hora del día	M > T	Pico adrenal que se presenta antes de la fase activa	*Pan troglodytes*: Murray et al., 2013 *Callithrix jacchus*: Raminelli et al., 2001

*Hipótesis mencionadas en los trabajos que no se han comprobado.
A = adulto; J = juvenil; H = hembra; M = macho; HE = embarazada; HNE = hembra no embarazada; CRH = hormona liberadora de corticotropina; B = jerarquía baja; A = jerarquía alta; M = mañana; T = tarde.

Efectos de la pérdida y fragmentación del hábitat sobre el patrón diario de actividades, la dieta y la respuesta de estrés del mono araña (*Ateles geoffroyi*)

El mono araña (*Ateles geoffroyi*) es una especie que habita preferentemente el estrato superior del dosel de los bosques del Neotrópico. Su dieta se compone principalmente por frutas (67±16.3%) y hojas (21±12%) (González-Zamora et al., 2009), presenta ámbitos hogareños amplios pero muy variables (e.g., 30 – 304 ha; Chaves et al., 2011; Asensio et al., 2012), y una organización social de fisión-fusión que se caracteriza porque individuos del mismo grupo se separan y juntan en subgrupos de diferente composición, para reducir la competencia intragrupal y patrullar sus ámbitos hogareños (Aureli y Schaffner, 2008).

Debido a que el mono araña consume fruta de diversas especies de árboles, y defeca un alto porcentaje de semillas en sitos distantes a los árboles parentales (e.g., rango: 443-1250 m; Link y Di Fiore, 2006), es una especie importante para el mantenimiento de la diversidad vegetal de las selvas del Neotrópico (González-Zamora et al., 2014; Link y Di Fiore, 2006). Desafortunadamente, como consecuencia de su alta dependencia a la fruta y grandes ámbitos hogareños, el mono araña es altamente sensible a la pérdida y fragmentación del hábitat (Boyle y Smith, 2010a; Michlaski y Peres, 2005; Mittermeier et al., 2012). Actualmente la IUCN reporta al mono araña (género *Ateles*) como en peligro de extinción (Cuarón et al., 2013).

Al igual que otras especies de primates, los monos araña parecen ajustar su patrón diario de actividades y dieta para encarar los efectos provocados por la pérdida y fragmentación del hábitat sobre la disponibilidad de alimento (Chaves et al., 2011, 2012; González-Zamora et al., 2009, 2011). Por ejemplo, en revisiones que se han realizado sobre el patrón diario de actividades y la dieta de *A. geoffroyi* en toda su área de distribución (González-Zamora et al., 2009, 2011), los autores reportan que los monos araña que habitan en fragmentos invierten menor tiempo en el descanso y mayor en el consumo de hojas, que los monos araña que habitan en selvas continuas. Esto es consistente con lo reportado para otras especies de primates (e.g., *C. satanas*: Boyle y Smith, 2010b), y sugiere que ante la menor disponibilidad de alimento que suele presentarse en fragmentos, los monos araña realizan un mayor esfuerzo alimenticio para cubrir su requerimientos energéticos (González-Zamora et al., 2009). Sin embargo, debido a que los trabajos que han analizado los efectos de la pérdida y fragmentación del hábitat sobre el comportamiento del mono araña, únicamente han analizado la variación de su patrón diario de actividades y dieta entre dos condiciones (i.e., fragmentos y selva continua: Chaves et al., 2011, 2012; González-Zamora et al., 2009, 2011), se desconoce de qué manera la estructura del paisaje puede influir sobre el comportamiento de este primate en paisajes fragmentados.

Los estudios que han analizado la respuesta de estrés del mono araña en paisajes fragmentados muestran resultados opuestos (Rangel-Negrín et al., 2009; Rimbach et al., 2013; Rimbach et al., 2014). Por ejemplo, mientras que Rangel-Negrín et al. (2009) reportan que los monos araña (*A. geoffroyi*) presentan niveles más elevados de glucocorticoides en fragmentos que en selva continua (i.e., áreas >30,000 ha), Rimbach et al. (2013) reportan que el tamaño del fragmento no es un buen predictor de los niveles de glucocorticoides del monos araña (*A. hybridus*). La falta de concordancia entre los resultados reportados en estos estudios, puede deberse a que la región de estudio de Rangel-Negrín et al. (2009) corresponde a un bosque tropical seco, mientras que la región de estudio de Rimbach et al. (2013) a un bosque tropical húmedo, lo que sugiere que la producción de fruta en los fragmentados estudiados por Rimbach et al. (2013) es mayor, y por tanto, que los monos araña en su región de estudio presentan un menor estrés de tipo alimenticio. Estos resultados remarcan la importancia de considerar en los análisis estadísticos predictores que sean indicadores de la cantidad de alimento, ya que si bien, un fragmento pequeño tiene menor cantidad de hábitat, estos pueden presentar una alta densidad de recursos alimenticios (e.g., árboles con áreas basales grandes: Hernández-Ruedas, 2014). Desafortunadamente, debido a que ningún estudio ha evaluado en diferentes sitios, el efecto de la disponibilidad de alimento y de los atributos de la estructura paisaje sobre los niveles de estrés del mono araña, el conocimiento necesario para la realización de planes eficaces de conservación de monos araña que habitan paisajes fragmentados es sumamente limitado.

En cuanto a los disturbios antropogénicos directos, Rimbach et al., (2013) reportan que en fragmentos donde hay actividades de caza y tala, el mono araña (*A. hybridus*) presenta niveles de glucocorticoides más elevados. Esto es lógico si se considera que el mono araña es una especie altamente sensible a la deforestación y a la caza, como consecuencia de sus altos requerimientos energéticos, gran tamaño corporal y hábitos diurnos (Boyle y Smith, 2010a; Mittermeier et al., 2012; Peres, 2000).

La selva Lacandona, uno de los últimos refugios del mono araña de manos negras (*Ateles geoffroyi*)

El área mexicana de la selva Lacandona es la región de selva alta perennifolia más extensa y con mayor biodiversidad de México (Medellín, 1994; Myers et al., 2000). El clima de esta región es cálido y húmedo, y presenta una temperatura y precipitación media anual de 24 °C y 2,875 mm, respectivamente. Desafortunadamente, como resultado de la deforestación provocada por las poblaciones humanas que se empezaron a asentar en esta región en los años 1970s (Aguilar y Mora, 1992), el área mexicana de la selva Lacandona ha perdido cerca del 50% de su cobertura forestal original (Couturier et al., 2012; De Jong et al., 2000). En específico, en base a su grado de pérdida y fragmentación de hábitat, el área mexicana de la selva Lacandona se puede clasificar en dos zonas: (1) la Reserva de la Biósfera de Montes Azules (RBMA), la cual abarca 331,200 ha de selva continua (Gómez-Pompa y Dirzo, 1995); y (2) la región de Marqués de Comillas (RMC), la cual está compuesta por 203,999 ha de fragmentos de bosque rodeados por matrices dominadas por campos de cultivo, pastizales para ganado y asentamientos humanos (ver Fig. 1 de CAPÍTULO I). Es importante mencionar que los fragmentos de selva localizados en la RMC presentan una estructura forestal similar a la que presenta la RBMA (Hernández-Ruedas et al., 2014). Esto, como posible consecuencia de la reciente deforestación (<40 años) que ha sufrido la RMC y la alta cobertura forestal (*ca.* 40%) que aún conserva.

Debido a que el área mexicana de la selva Lacandona es uno de los últimos refugios del mono araña de manos negras (*Ateles geoffroyi*), y en esta región los monos araña aún se encuentran en fragmentos de selva, una serie de estudios realizados en la selva Lacandona han analizado la variación del patrón diario de actividades (Chaves et al., 2011a), la dieta (Chaves et al., 2011b; 2012), y dispersión de semillas (Chaves et al., 2015; González-Zamora et al., 2014) del mono araña, entre fragmentos y selva continua. Respecto a su patrón diario de actividades, podemos destacar que contrariamente a la reportado para otras regiones de Mesoamérica (González –Zamora et al., 2011), los monos araña que habitan en selva continua invierten mayor tiempo en el viaje que los monos araña que habitan en fragmentos. Esto sugiere, que en esta región, los monos araña que habitan en fragmentos no realizan un mayor esfuerzo alimenticio respecto a los monos araña que habitan en selva continua (Chaves et al., 2012). Apoyando esto, en la selva Lacandona, los fragmentos en los que se ha estudiado al mono araña presentan altas densidades de recursos alimenticios, y estos animales no presentan diferencias en el consumo de fruta entre fragmentos y selva continua (Chaves et al., 2012). Un aspecto que hay que resaltar de la dieta del mono araña en la selva Lacandona, es el alto porcentaje de tiempo que esta especie invierte en el consumo de madera (15.7% de su tiempo total de alimentación: Chaves et al., 2012), el cual puede deberse al alto contenido de minerales como el sodio y el calcio que contienen en su madera las especies de árboles que utiliza esta especie para consumir este recurso (*Licania platypus, Ficus* spp.) (Chaves et al., 2011b). Debido a que el consumo de madera es mayor en hembras lactantes, la madera parece ser un recurso importante para el suplemento de minerales que requieren las hembras durante esta etapa (Chaves et al., 2011b).

Respecto a la dispersión de semillas, en la selva Lacandona los monos araña dispersan semillas de al menos 68 especies de árboles, y el recambio y el número promedio de especies es mayor en selva continua (RBMA) que en fragmentos (RMC) (González-Zamora et al., 2014, 2015). Debido a que en la selva Lacandona el mono araña es un importante dispersor de semillas, y la resiliencia de un ecosistema depende del mantenimiento de su biodiversidad, la implementación de cercas vivas en esta región podría favorecer una mayor dispersión de semillas por parte del mono araña, y por tanto, un aumento de la resiliencia de esta región.

Desafortunadamente, aunque se cuenta con información importante sobre el comportamiento y la dispersión de semillas del mono araña para la selva Lacandona, aún no se conoce de que manera los efectos de la pérdida y fragmentación del hábitat sobre la estructura de los paisajes, afectan el patrón diario de actividades, la dieta y los niveles de estrés del mono araña en esta región. Obtener esta información sería valioso para la realización de planes de manejo y conservación eficaces para el monos araña en la selva Lacandona, ya que permitiría identificar los atributos de la estructura del paisaje que presentan mayor efecto sobre su comportamiento y niveles de estrés, así como la escala del paisaje en la que estos efectos son mayores.

Objetivos

Los objetivos principales del presente trabajo fueron evaluar los efectos de la estructura espacial del paisaje sobre el patrón diario de actividades, la dieta y los niveles de estrés de seis grupos de monos araña (*Ateles geoffroyi*) que habitan en la selva Lacandona, Chiapas, y evaluar los efectos de su patrón diario de actividades, dieta y de disturbios antropogénicos directos sobre sus niveles de estrés.

En específico, con el objetivo de identificar qué atributos de la estructura del paisaje mejor predicen el patrón diario de actividades y la dieta del mono araña en paisajes fragmentados, en el CAPÍTULO I se evaluó la relación de distintos atributos del paisaje (porcentaje de cobertura forestal del paisaje, número de fragmentos, densidad de borde y promedio de la distancia entre todos los fragmentos del paisaje) con el patrón diario de actividades y la dieta del mono araña en diez escalas espaciales (i.e., tamaños del paisaje) diferentes. Esto último, con el objetivo de identificar la escala en la que los atributos del paisaje presentan las relaciones más fuertes con el patrón diario de actividades y dieta del mono araña (i.e., la escala del efecto).

Por otra parte, con el objetivo de identificar los factores que mejor predicen los niveles de estrés del mono araña en paisajes fragmentados, en el CAPÍTULO II se evaluó el efecto del patrón diario de actividades, dieta, disturbios antropogénicos directos (i.e., predictores proximales), cobertura forestal, grado de fragmentación y densidad de alimento (i.e., predictores distales) sobre los niveles de glucocorticoides fecales del mono araña. Además, con el objetivo de analizar de qué manera las características del hábitat repercuten sobre los predictores proximales de la respuesta de estrés del mono araña, analizamos las diferencias del patrón diario de actividades y la dieta de los monos araña entre los seis sitios de estudio.

CAPÍTULO I:

Which is the appropriate scale to assess the impact of landscape spatial configuration on the diet and behavior of spider monkeys?

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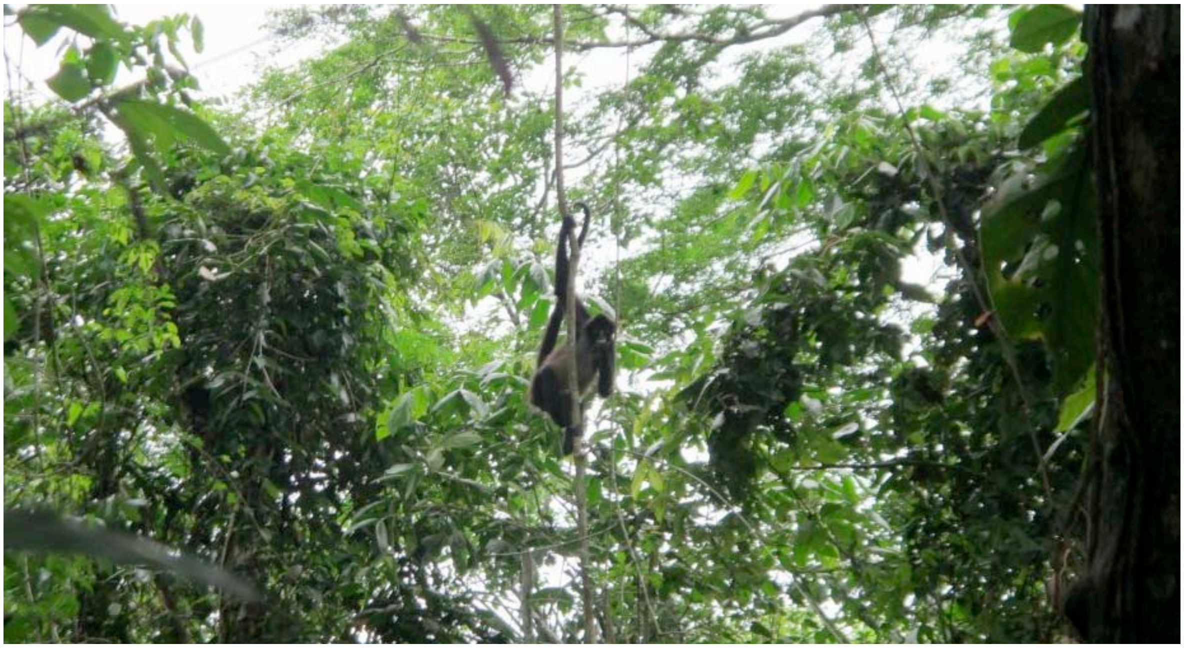

American Journal of Primatology 77:56–65 (2015)

RESEARCH ARTICLE

Which is the Appropriate Scale to Assess the Impact of Landscape Spatial Configuration on the Diet and Behavior of Spider Monkeys?

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Understanding the response of species to changes in landscape configuration is required to design adequate management and conservation strategies. Yet, the most appropriate spatial scale (i.e., landscape size) to assess the response of species to changes in landscape configuration (so-called "scale of effect") is largely unknown. In this paper, we assess the impact of landscape forest cover, forest fragmentation, edge density, and inter-patch isolation distance on the diet and behavior of six communities of spider monkeys (*Ateles geoffroyi*) in the fragmented Lacandona rainforest, Mexico. We evaluated the strength of the relationship between each landscape predictor and each response variable within ten different-sized landscapes (range = 50–665 ha) to identify the landscape size that best predicted changes in diet and behavior. The strength of most associations varied across spatial scales, with the 126-ha landscape showing the strongest relationships between landscape predictors and response variables in many cases. Yet forest cover represented the main driver of the diet and behavior of spider monkeys, being positively associated with time traveling and time feeding on wood, but negatively related to time resting and time feeding on leaves. Although weaker, the impact of edge density was opposite to forest cover for most response variables. Forest fragmentation and isolation distance showed the weakest associations with the diet and behavior of this species. Our findings thus indicate that different landscape attributes operate on different response variables at different spatial scales. Therefore, the scale of effects cannot be generalized to all response variables and to all predictors, and a multi-scale analysis will be required to accurately assess the impact of landscape configuration on species' responses. Am. J. Primatol. 77:56–65, 2015. © 2014 Wiley Periodicals, Inc.

Key words: landscape approach; landscape structure; landscape heterogeneity; scale dependency

INTRODUCTION

In a world increasingly dominated by human-modified landscapes, understanding the response of species to changes in landscape configuration is of key relevance for designing effective conservation strategies [Ellis, 2013]. This has been the focus of a large number of studies in fragmented landscapes [Ewers & Didham, 2006; Fahrig, 2003; Fischer & Lindenmayer, 2007; Tscharntke et al., 2012; Villard & Metzger, 2014], but it was not until very recently that we have become aware of the fact that the effect of landscape attributes on wild species is dependent on the spatial scale at which these attributes are measured [Arroyo-Rodríguez & Fahrig, 2014; Fahrig, 2013; Jackson & Fahrig, 2012]. As new studies show, the impact of landscape configuration on species are only evident within certain spatial scales (so-called "scale of effect") [Fahrig, 2013; Jackson & Fahrig, 2012], challenging our ability to identify the spatial extent (or landscape size) at which spatial patterns best predict the response of species and populations [Fahrig, 2013]. In fact, the scale of effect is unknown for most species and variables of interest, limiting thus our understanding of the impact that habitat spatial shifts have on

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biodiversity [Fahrig, 2013; Jackson & Fahrig, 2012], and particularly on primates [Arroyo-Rodríguez & Fahrig, 2014].

The scale of effect has been evaluated for a few vertebrate species in urban [Garden et al., 2010], semi-urban [Eigenbrod et al., 2008], and natural (i.e., outside urban areas) landscapes [Smith et al., 2011]. For example, Eigenbrod et al. [2008] show that automobile traffic density is negatively related to the abundance of anurans, with the strongest effects being apparent at landscapes with a radius of 500 m; yet, there is a large variation in the strength of such association among anuran species [Eigenbrod et al., 2008]. Smith et al. [2011] report that the total amount of habitat in the landscape is positively related to the number of forest bird species, and that such an association is consistent across more than two orders of magnitude in landscape size. However, in their study, the impact of fragmentation *per se* was scale dependent, with effects varying from positive to negative depending on landscape size [Smith et al., 2011]. Finally, Fahrig [1998] also reports that the impact of habitat loss and fragmentation on patch occupancy by mid- and large-sized mammals depends on landscape size, with forest-dwelling species (i.e., arboreal or semi-arboreal species) responding more strongly to fragmentation (i.e., density of forest patches) than to habitat loss.

Arboreal primates are expected to be strongly affected by changes in landscape configuration [reviewed by Arroyo-Rodríguez & Fahrig, 2014; Arroyo-Rodríguez & Mandujano, 2009] yet, to our knowledge, only two studies have assessed the impact of landscape configuration on primates at different spatial scales [Arroyo-Rodríguez et al., 2013; Thornton et al., 2011]. In particular, Thornton et al. [2011] find that the occurrence of spider monkeys (*Ateles geoffroyi*) is positively related to landscape forest cover and negatively related to fragmentation, and that these effects are particularly strong when measured within 500-ha landscapes. In contrast, they found that the distribution of black howler monkeys (*Alouatta pigra*) was not related to landscape configuration, but Arroyo-Rodríguez et al. [2013] report that the population structure of this primate species in forest patches is significantly related to landscape characteristics, and that the impact of each landscape metric is scale-dependent. In general, these two studies on primates support others conducted with other taxonomic groups [Eigenbrod et al., 2008; Garden et al., 2010; Smith et al., 2011]; namely, that the scale of effect is species dependent and that they may vary from one landscape metric to another. They also highlight the need for more studies if we are to attain a comprehensive understanding of the relative effects of landscape configuration on wild primates. These should not only be focused on the relationship between landscape metrics and primates' distribution and diversity, but also look into animal diet and behavior, as these variables are directly linked to animal's fitness in human-modified landscapes [Danchin et al., 2008].

Ateles geoffroyi is an arboreal and highly frugivorous primate species [Di Fiore et al., 2008, 2011; González-Zamora et al., 2009]. A few studies have evaluated their diet and behavior in forest patches [Chaves et al., 2011a,b, 2012; González-Zamora et al., 2011], but we still do not know which is the appropriate spatial scale to assess the impact that landscape configuration may have on the diet and behavior of this species. This information is especially relevant given that spider monkeys are considered to be strongly sensitive to the transformation of their natural habitats [Boyle & Smith, 2010a; Garber et al., 2006; Michalski & Peres, 2005]. In fact, this species is classified as "Endangered" in the IUCN red list, and it is estimated that populations have declined by as much as 50% over the course of the past 45 years [Cuarón et al., 2013].

Here, we evaluate for the first time the impact of landscape configuration (i.e., landscape forest cover, forest fragmentation, edge density, and mean inter-patch isolation distance) on the diet and daily activity pattern of *A. geoffroyi* in a fragmented rainforest under different landscape size scenarios. Each landscape attribute was calculated for ten different-sized landscapes (range 50–665 ha), and we then evaluated the strength of the relationship between each landscape predictor and the response variables within each landscape scale to identify the spatial scale (i.e., landscape size) that best predicted changes in the diet and behavior of spider monkeys in the region. As spider monkeys have home ranges that are usually smaller than 170 ha [e.g., Chaves et al., 2011a; Di Fiore & Campbell, 2007; Fedigan et al., 1988; Wallace, 2008], we predict that the scale of effect for most response variables and landscape attributes will be lower than 170 ha. This is because the diet and behavior of primates are expected to be more strongly affected by habitat characteristics within their home range (e.g., food availability) than by spatial attributes of the areas located outside their home ranges [Arroyo-Rodríguez et al., 2013; Asensio et al., 2012a,b; Ramos-Fernández et al., 2013]. Also, because this is a forest-dependent species, we predict that all response variables will be more strongly related to differences in landscape forest cover (a surrogate of habitat amount) than with fragmentation (i.e., number of forest patches in the landscape) or patch isolation [Fahrig, 2003, 2013], being this pattern consistent across several spatial scales [Fahrig, 1998; Smith et al., 2011].

METHODS

Study Area

We conducted the fieldwork for this study in the Lacandona rainforest, in southern Chiapas, Mexico

(Fig. 1). Climate in this region is warm and humid. The mean annual temperature ranges between 24 and 26°C, and the mean annual rainfall between 2,500 to 3,500 mm. Rainfall is relatively constant throughout the year but there is a pronounced dry season between February and April (Comisión Federal de Electricidad, Mexico City). Two areas can be distinguished within our study region based on their degree of human disturbance. On the one hand, the Montes Azules Biosphere Reserve (MABR) encompasses 331,200 ha of continuous old-growth forest. Outside this reserve, the Marqués de Comillas Region (MCR) encompasses 203,999 ha of fragmented forests embedded in a matrix dominated by agricultural lands, secondary forests, cattle pastures, and human settlements. Deforestation in MCR started in the 1970s, but it was particularly accelerated and extensive between 1984 and 1986 [Martínez, 2003]. Nowadays, approximately 40% of old-growth forest cover remains in MCR in the form of forest patches of different size and degree of transformation (Fig. 1).

Study Sites and Data Collection

Following Arroyo-Rodríguez and Fahrig [2014], we adopted a sample site-landscape approach. This means that response variables were evaluated in sample sites using standardized sampling efforts, and the landscape variables were measured within a specified radius from these sample sites [also see Fahrig, 2013]; in this case, the centroids of the activity areas of the study communities. Specifically, we studied six communities of spider monkeys (*A. geoffroyi*) located in six different sites: five communities inhabiting five different forest patches (L1 = 1,125 ha, L2 = 141 ha, L3 = 67 ha, L4 = 28 ha, and L5 = 460 ha) located in MCR and a community within MABR (CF = 331,200 ha; Fig. 1). The average Euclidian distance between two study sites (edge to edge) was 7.2 km (range = 0.4–18.9 km). We selected these communities because: (i) they inhabit sites with different landscape configuration; and (ii) spider monkeys are well habituated to human presence.

We followed the six communities of spider monkeys from March to May 2013. This coincided with the dry season, and beginning of the rainy season and one of the annual peaks in fruit production in the region (May) [González-Zamora et al., 2014; Ochoa-Gaona & Domínguez-Vázquez, 2000]. We documented the diet and daily activity pattern of our study communities from 0700 to 1530 hours during 3 consecutive days, approximately once every 3 weeks. In order to avoid the potential effect of age class on monkey's behavior [Arroyo-Rodríguez et al., 2007], we sampled only adult individuals. Observations were carried out by two persons (J.D.O.G. and a local field assistant), with the

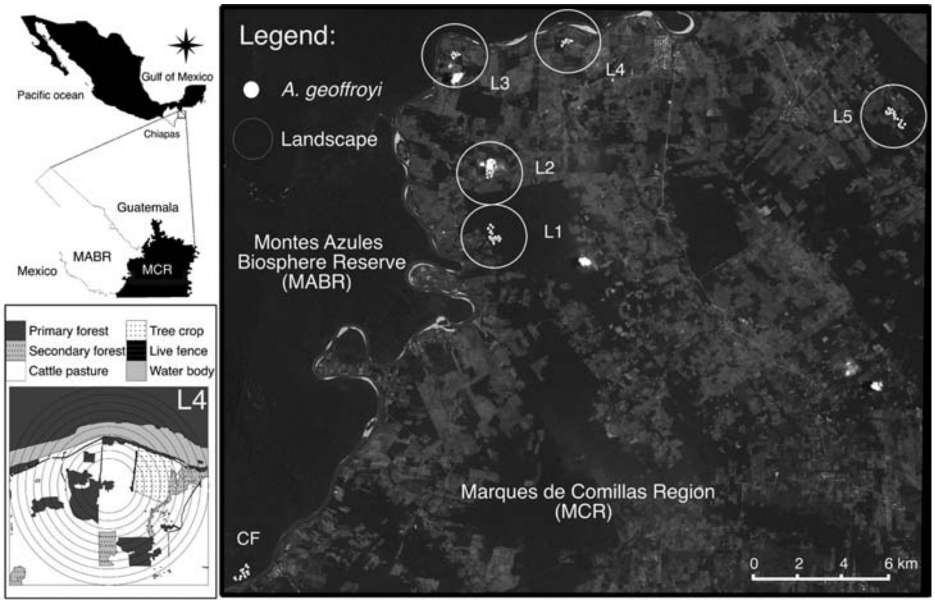

Fig. 1. Location of the study sites in the Lacandona rainforest, Mexico. Points represent the sites where the spider monkeys (*Ateles geoffroyi*) spent $\geq$30 min. These points were used to estimate the activity area of each group, and from the geographic center of each activity area we estimated the landscape structure in ten different-sized landscapes (see example in the left side of the panel). The circles within the main panel represent the largest buffer (radius = 1,455 m; area = 665 ha).

aid of high-resolution binoculars, following a focal animal sampling method [Altmann, 1974]. Focal animals were randomly changed at 3-min intervals or when animals moved out of sight, and in total we recorded 407 hr of focal observations (range per group = 66–69 hr).

During the focal observations we recorded four mutually exclusive behaviors: (i) resting (period of inactivity); (ii) feeding (mastication and/or ingestion of foodstuff); (iii) traveling (movement between tree crowns or within the crown of a tree that was not directly food related); and (iv) other activities. Yet, we focused the analyses on the three main activity budgets (i.e., resting, traveling, and feeding) because the rest of activities were rare and represented by a complex interplay of social activities. During feeding episodes, we also recorded the food items (fruits, leaves, wood, and other) consumed by the spider monkeys. We then calculated the percentage of total feeding time (TFT) consuming each item. We focused our analyses on fruits, leaves, and wood because they are the most important items in the diet of spider monkeys in the region [Chaves et al., 2012]. Arguably, our sampling effort is relatively small when compared with other studies on the behavior of *A. geoffroyi* [reviewed by González-Zamora et al., 2009, 2011], but the sampling effort was almost the same in all groups, thus avoiding biases related to differences among groups in sampling effort. Also, we believe it still is adequate for the objectives of this study because the values we obtained for the diet variables were within the range reported for the species [González-Zamora et al., 2011], and very similar to year-round average values reported for the species in our study region [Chaves et al., 2011a,b, 2012].

The research presented here was approved by the Secretary of Environment and Natural Resources (SEMARNAT) of Mexico (No. SGPA/DGVS/04045), and complied with the protocols approved by the appropriate Institutional Animal Care Committee: Comité de Ética en Investigación del Instituto Nacional de Psiquiatría Ramón de la Fuente. Further, the research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates and the legal requirements of Mexico.

Landscape Spatial Metrics

We used the method of minimum convex polygon to estimate the activity area of each community based on the locations that are more frequently used, that is those in which they spent $\geq$30 min, which were recorded with a GPS (Fig. 1). We selected this cut-off point to avoid overestimations in the activity area related to the inclusion of areas that are rarely used (e.g., those used during exploratory excursions) [see Asensio et al., 2012a]. We then identified the centroid of each activity area, and from this point we assessed the landscape configuration based on four parameters: (i) landscape forest cover (in percentage); (ii) degree of fragmentation (i.e., number of old-growth forest patches in the landscape); (iii) edge density (i.e., length of all old-growth forest borders within the landscape, divided by landscape size, expressed as m/ha); and (iv) mean isolation distance between all patches in the landscape (isolation distance, hereafter). We conducted all these analyses using a recent (May and April 2012) and high-resolution (2.5 × 2.5 m) SPOT satellite image (Fig. 1) and Quantum GIS 2.0.1 software.

Each of these landscape metrics was estimated within ten different-sized buffers (i.e., landscapes; Fig. 1). The smallest buffer had 50 ha, which is lower than the average home range size reported by Chaves et al. [2011a] for three communities of spider monkeys located in MABR. The largest landscape size was 665 ha, which was the maximum size before our six different landscapes started overlapping in space. Hence, because our landscapes did not overlap in space, we did not have problems of independence among samples (i.e., among landscapes) [see Eigenbrod et al., 2011]. We then located eight additional buffers with the same size between the largest and the smallest buffer, obtaining thus landscapes of 50 ha (radius = 399 m), 84 ha (516 m), 126 ha (634 m), 177 ha (751 m), 237 ha (868 m), 305 ha (986 m), 382 ha (1,103 m), 468 ha (1,220 m), 562 ha (1,338 m), and 665 ha (1,455 m).

Statistical Analyses

To identify the appropriate scale at which each landscape metric best predicted the diet and behavior of spider monkeys, we ran linear regressions between each landscape metric (predictors) and each response variable, and we used the coefficient of determination (R^2)—a estimator of the goodness of fit of each model—to assess the strength of each relationship. These analyses were done for each of the ten landscape sizes, and then, following Fahrig [2013], we plotted the R^2 values (as a dependent variable) against landscape size to identify the spatial extent at which the strongest associations between each response variable and each predictor were observable. We transformed percentages to proportions, and then, proportion data were arcsine-square-root transformed to meet normality assumptions. Edge density and mean inter-patch isolation distance were quadratic (x^2) transformed to ensure these factors were homogeneously distributed across the x-axis. We conducted all regressions with SPSS 20 (SPSS Inc., Chicago, Illinois, USA).

RESULTS

Overall, spider monkeys spent 19% of their time traveling (range per community: 13–25%), 48% resting (40–55%), 27% feeding (19–32%), and 6%

doing other activities (5–11%). With regard to their feeding, spider monkeys spent 57% of TFT consuming fruits (range: 41–77%), 20% of TFT consuming leaves (9–40%), 10% consuming wood (1–42%), and 13% consuming other items (5–24%).

Considering all landscape sizes, forest cover surrounding each site averaged 54.5% (range = 12.4–100%), and the mean values per site remained almost constant across spatial scales; although it tended to be lower in intermediate-sized landscapes (Fig. 2a). The number of forest patches in the landscape averaged 4 (range = 0–12 patches), and increased gradually with landscape size (Fig. 2b). Isolation distance averaged 23.6 m (range = 0–49.1 m), and it increased with landscape size (Fig. 2c). Finally, edge density averaged 59.5 m/ha (range = 0–157.1 m/ha), and it remained constant in the first six landscape sizes (50–305 ha), but then decreased with landscape size (Fig. 2d).

Impact of Landscape Configuration on Diet

Forest cover was the landscape attribute that best predicted changes in the diet of spider monkeys in the region (Fig. 3b and c). In particular, the time spent feeding on leaves increased in landscapes with lower forest cover ($R^2_{\text{mean}} = 0.71$, range = 0.61–0.80; Fig. 3b). The fit of this association increased with landscape size, reaching the maximum value in the 126-ha landscape, and then gradually decreased (Fig. 3b). The time feeding on wood was also positively related to forest cover ($R^2_{\text{mean}} = 0.62$, range = 0.47–0.70), and the fit of this association increased with landscape size; yet, only showed significant associations in ≥468-ha landscapes (Fig. 3c). Although it was not significant, the impact of edge density was also scale-dependent, with its highest influence on the time feeding on leaves (Fig. 3h) and wood (Fig. 3i) in the 126-ha landscape. Isolation distance was negatively related to time feeding on wood ($R^2_{\text{mean}} = 0.41$, range = 0.15–0.81), but the fit of this association was only significant in ≥468-ha landscapes (Fig. 3l). Finally, forest fragmentation showed the weakest associations with the diet of monkeys, and did not show a clear scale of effect.

Relationship Between Landscape Configuration and Behavior

Again, forest cover was the landscape metric that better predicted the behavior of spider monkeys (Fig. 4a and b), followed by edge density (Fig. 4g), and isolation distance (Fig. 4l). In particular, forest cover was positively and significantly related to time traveling ($R^2_{\text{mean}} = 0.79$, range = 0.73–0.83), which was consistent across all spatial scales (Fig. 4a). Forest cover was also significantly (but negatively) related to time resting ($R^2_{\text{mean}} = 0.70$, range = 0.58–0.77). The fit of this

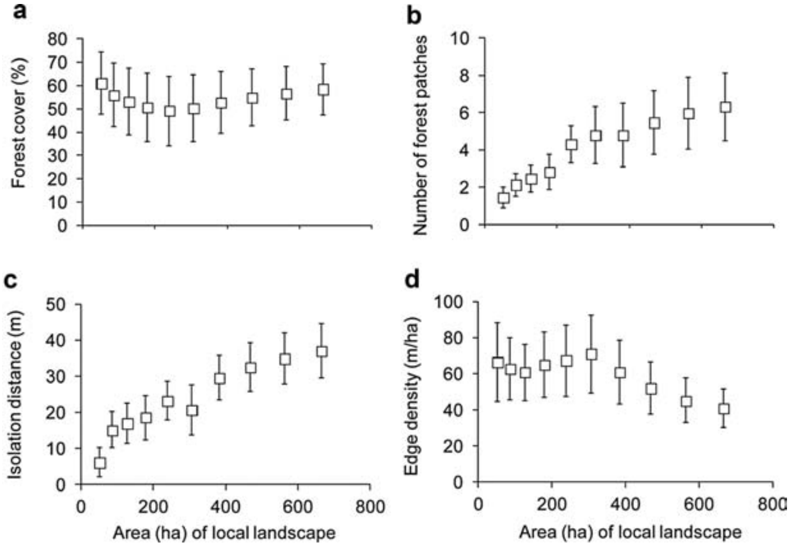

Fig. 2. Spatial configuration of landscapes surrounding the home range of six independent communities of spider monkeys (*Ateles geoffroyi*) inhabiting five forest fragments in the Marqués de Comillas Region, and a site within the continuous forest of the Montes Azules Biosphere Reserve, Lacandona rainforest, Mexico. We considered four spatial attributes (**a–d**) measured in ten different-sized buffers (landscapes) from the geographic center of each activity area. Mean (±SE) values per site are indicated for each landscape size. Isolation distance refers to the mean inter-patch isolation distance among all rainforest patches in the landscape.

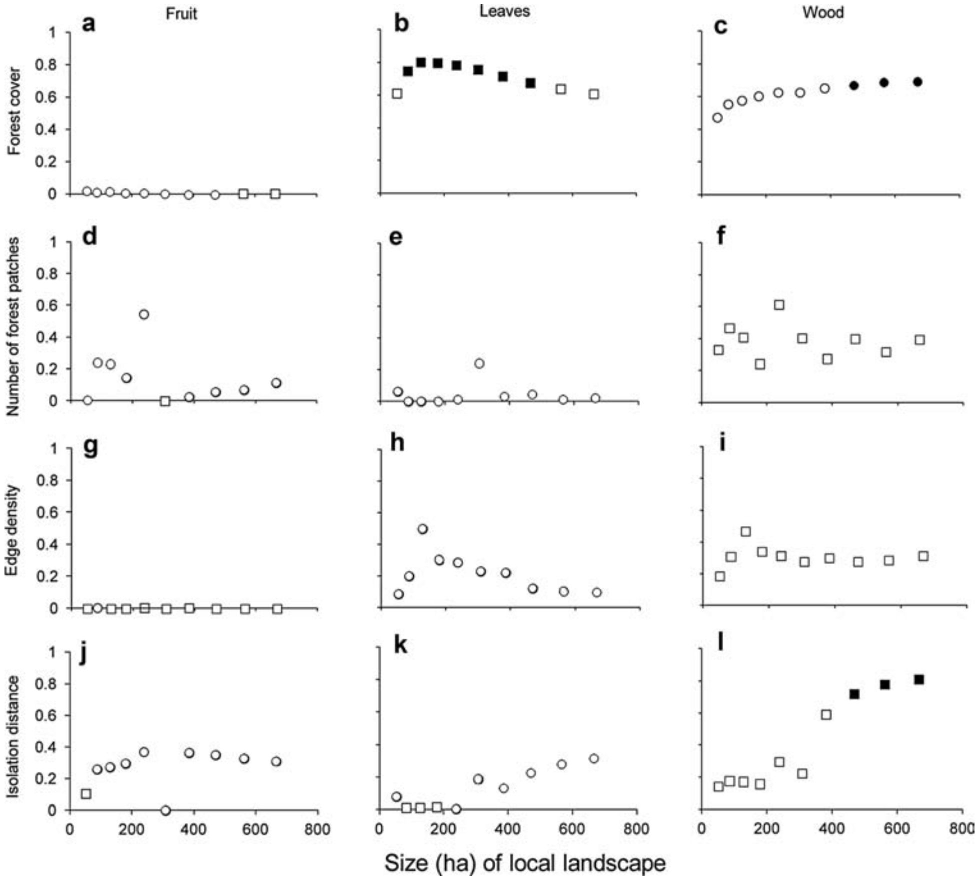

Fig. 3. Association between landscape size (x-axis) and the strength of the relationship (R^2, y-axis) between each landscape attribute (indicated in rows) and each characteristic of the diet of spider monkeys (i.e., percentage of time feeding on fruits, leaves, and wood) in the Lacandona rainforest, Mexico. Positive relationships between each landscape attribute and each behavior are indicated with circles, whereas negative relationships are indicated with squares. Black circles/squares indicate significant relationships ($P < 0.05$), and white circles/squares represent non-significant relationships ($P > 0.05$). The specific significance values are indicated in Table SI.

association increased with landscape size until 126-ha, and then gradually decreased (Fig. 4b). Edge density was significantly related (negatively) to time traveling ($R^2_{\text{mean}} = 0.76$, range = 0.53–0.91). Again we found a gradual increase in the fit of the association, up to 0.91 in the 126-ha landscapes, and then R^2 values decreased gradually with landscape size (Fig. 4g). Although it was not significant, this scale of effect (i.e., 126 ha) was also evident when assessing the association between edge density and time resting (Fig. 4h). Finally, isolation distance was strongly related (negatively) to time feeding ($R^2_{\text{mean}} = 0.39$, range = 0.00–0.77); this association gradually increased with landscape size, up to 0.77 in the 305-ha landscapes, and then gradually decreased (Fig. 4l).

DISCUSSION

This study shows that different attributes of the diet and behavior of spider monkeys were associated with different landscape spatial metrics, and that these associations varied across spatial scales (i.e., among landscapes of different sizes). Evidence indicates that the scale of effect is principally a function of species mobility [Jackson & Fahrig, 2012], and can also depend on the heterogeneity of the study landscape (i.e., on the variability in environmental gradients) [Brennan et al., 2002; Fahrig, 2013; Wiens, 1989]. In this sense, the Lacandona rainforest is highly heterogeneous in terms of landscape configuration and composition (Fig. 1), and hence, even relatively small changes in landscape size

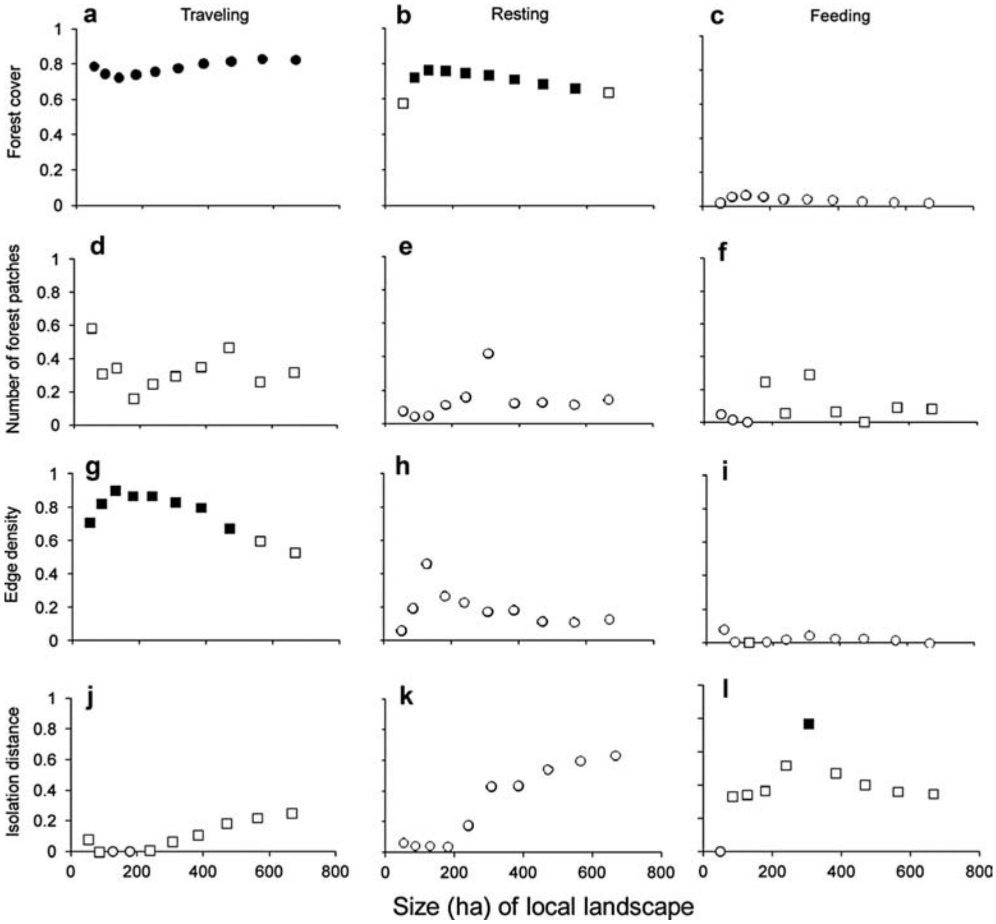

Fig. 4. Association between landscape size (x-axis) and the strength of the relationship (R^2, y-axis) between each landscape attribute (indicated in rows) and each activity pattern (i.e., percentage of time traveling, feeding, or resting) in the Lacandona rainforest, Mexico. Positive relationships between each landscape attribute and each behavior are indicated with circles, whereas negative relationships are indicated with squares. Black circles/squares indicate significant relationships ($P < 0.05$), and white circles/squares represent non-significant relationships ($P > 0.05$). The specific significance values are indicated in Table SI.

resulted in important changes in explanatory variables such as forest cover, edge density, and inter-patch isolation distance (Fig. 2). Such variations in environmental gradients are required to find significant associations between response variables and predictors [Cohen et al., 2003] as we did in this study. In particular, the strength of most associations was highest in the 126-ha landscape. This scale of effect was specifically evident when assessing the impact of landscape forest cover on time resting and time feeding on leaves, as well as when evaluating the impact of edge density on time traveling and resting and on time feeding on leaves and wood.

But, why is this landscape size important for spider monkeys? The scale of effect is not only a function of species mobility and landscape heterogeneity but also of the specific patterns or processes that are being assessed, as patterns and processes are scale dependent [Wiens, 1989]. In this sense, primates make repetitive use of relatively stable areas (i.e., home ranges) across seasons, and the availability of resources within such areas are key drivers of the diet and activity of spider monkeys [e.g., Asensio et al., 2012a,b; Chaves et al., 2011a; Ramos-Fernández et al., 2013]. Accordingly, we predicted that landscape attributes should show the strongest impact on spider monkey's behavior when considering a landscape size close to the size of their home range. The home range size of spider monkeys can be highly variable among study sites [reviewed in Di Fiore & Campbell, 2007; Wallace, 2008], but in human-modified landscapes they rarely exceed 170 ha [Chaves et al., 2012; Di Fiore & Campbell, 2007; Ramos-Fernández et al., 2013; Wallace, 2008], which would explain why in our study the effect of landscape attributes increased until the value of 126 ha, and decreased after this.

Naturally, the home range size in human-modified landscapes depends on landscape connectivity, and our results indicate that landscape connectivity was particularly high in <126-ha landscapes. For example, these landscapes showed a very large amount of remaining forest cover (averaging >50%), low degree of fragmentation (two to three forest fragments), low inter-patch isolation distance (ca. 20 m), and relatively high edge density (>60 m/ha) (Fig. 2). Overall, these landscape attributes can allow the monkeys make a better use of resources located within different parts of the landscape. Accordingly, it is reasonable to think that spider monkeys are responding to the 126-ha landscape because: (i) this landscape size showed a reasonably high spatial heterogeneity; (ii) the study response variables are expected to be principally associated with local habitat characteristics; and (iii) this landscape size showed a high connectivity, allowing the monkeys to make use of resources from different landscape elements.

It is particularly relevant that by conducting a multi-scale analysis we have higher confidence on the impact that landscape spatial changes may have on the diet and activity pattern of spider monkeys [Arroyo-Rodríguez & Fahrig, 2014; Brennan et al., 2002; Fahrig, 2013]. In this sense, we found that, as predicted, forest cover represented the main driver of the diet and behavior of spider monkeys, which was consistent across spatial scales [Fahrig, 1998; Smith et al., 2011]. This finding is consistent with different empirical and theoretical studies that demonstrate that habitat loss (i.e., the loss of forest cover or the reduction in forest patch size) can negatively impact the diet and behavior of primates [Arroyo-Rodríguez & Dias, 2010; Boyle & Smith, 2010b; Chaves et al., 2011a; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Dunn et al., 2010], as well as other attributes of populations and communities [reviewed by Fahrig, 2003, 2013]. Leaf consumption was strongly and negatively associated with forest cover, a finding also reported by other studies of spider monkeys in the region [Chaves et al., 2011a, 2012]. This relationship results from the preference of spider monkeys for fruit over leaves [Chaves et al., 2012; Di Fiore et al., 2008, 2011; González-Zamora et al., 2009; present study], and the reduced availability of fruit in small tracts of forest due to the patchy distribution of this foodstuff. Also, when feeding on fruit, spider monkeys have to travel longer distances, and accordingly, we found that forest cover was not only associated to higher consumption of fruit but also more time traveling, and consequently lower time resting.

Wood represents an important foodstuff for spider monkeys in the region [Chaves et al., 2012; present study], as it represents one of the principal sources of sodium and calcium for spider monkeys [Chaves et al., 2011b]. Similar to fruit, wood is patchily distributed in the forest as only a handful of tree species serve as source of this foodstuff for spider monkeys [e.g., *Licania platypus* and *Ficus* spp.; Chaves et al., 2011b]. Correspondingly, we found that forest cover was positively associated to the consumption wood in spider monkeys, a relationship that was consistent across several spatial scales. We think that this finding was related to the fact that in our study forest cover was almost constant across different landscape sizes (Fig. 2a). However, there is a limit to how far the spider monkeys can range in their search for wood, which will also be determined by the degree of landscape connectivity. This can explain why there was a negative association between isolation distance and wood consumption when considering larger landscapes (i.e., $\geq$468 ha; Fig. 3l).

The diet and behavior of spider monkeys were negatively associated with edge density, and this correlation was strongest within the 126-ha landscapes. We believe that this association is driven by the effect of forest cover over the behavior of spider monkeys given that: (i) forest cover is strong and negatively related with edge density and the fit of this correlation was strongest in the 126-ha landscape ($R^2 = 0.87$); and (ii) landscape forest cover showed a much stronger impact that edge density on the behavior of spider monkeys.

As reported for other animal species [Betts et al., 2006; Smith et al., 2011; and others reviewed in Fahrig, 2003], our results indicate that forest fragmentation has a lower impact on primates than habitat availability. In this sense, it has been proposed that forest fragmentation exerts its highest impact on animals at landscapes with less than 30% of forest cover [Fahrig, 1998], but in our study area the average landscape forest cover was 55%. With high habitat availability around the study patches, we can expect that the remaining patches are relatively large and highly connected with other neighboring patches [Fahrig, 2003], increasing thus the availability of space and resources. In fact, the increase in the number of forest patches with landscape size (Fig. 2b) did not result in a higher impact of fragmentation on the response variables (Figs. 3 and 4), thus supporting the idea that under such landscape context, fragmentation does not impact significantly the diet and behavior of this primate species.

In summary, as a general guideline for primatologists interested in evaluating the impact of landscape configuration on the diet and behavior of spider monkeys, we suggest that it is best to characterize the landscape within a radius of approximately 634 m from the center of the study sites (i.e., landscape area of approximately 126 ha). Yet it is evident that the scale of effects cannot be generalized to all response variables or to all predictors, and hence, when possible, a multi-scale analysis is suggested to accurately assess the impact of landscape configuration on species responses [Fahrig, 2013]. Also, as we did not cover the annual variation in plant phenology, and our sampling schedule (i.e., 0700–1530 hours) did not include all periods of primates' activity (e.g., early morning and mid-late afternoon), additional multi-scale analyses are needed (particularly those including larger sample sizes) to assess the scale of effect in other regions and with other response variables. Doing this will help determine if the patterns found in this study can be applicable to other sites and regions, and accordingly improve our understanding on the response of primates to landscape modifications. This will be of key relevance to design and implement effective management and conservation plans.

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SUPPORTING INFORMATION

Additional Supporting Information (Table SI) may be found in the online version of this article at the publisher's web-site.

Supplementary information

Table SI. Coefficients of determination (R^2) and significance values (in parentheses) of the association between each landscape attribute and each characteristic of the diet (i.e., percentage of time feeding on fruits, leaves, and wood) and activity pattern (i.e., percentage of time traveling, feeding, or resting) of spider monkeys (*Ateles geoffroyi*) in the Lacandona rainforest, Mexico.

Landscape attribute/response variable	Size (ha) of local landscape									
	50	84	126	177	237	305	382	468	562	665
Forest cover vs.										
Time feeding on fruits	0.021	0.015	0.016	0.011	0.008	0.006	0.001	0.000	0.000	0.000
	(0.786)	(0.814)	(0.811)	(0.842)	(0.868)	(0.889)	(0.947)	(0.988)	(0.969)	(0.959)
Time feeding on leaves	0.610	0.747	0.802	0.795	0.781	0.757	0.717	0.678	0.638	0.611
	(0.066)	(0.026)	(0.016)	(0.017)	(0.019)	(0.024)	(0.034)	(0.044)	(0.057)	(0.066)
Time feeding on Wood	0.473	0.555	0.577	0.605	0.627	0.628	0.655	0.676	0.693	0.697
	(0.131)	(0.089)	(0.080)	(0.068)	(0.060)	(0.060)	(0.051)	(0.045)	(0.040)	(0.039)
Number of forest patches vs.										
Time feeding on fruits	0.007	0.243	0.234	0.153	0.546	0.000	0.027	0.060	0.074	0.119
	(0.876)	(0.320)	(0.331)	(0.443)	(0.093)	(0.996)	(0.757)	(0.641)	(0.603)	(0.503)
Time feeding on leaves	0.069	0.005	0.002	0.004	0.019	0.245	0.035	0.049	0.018	0.029
	(0.614)	(0.889)	(0.934)	(0.900)	(0.792)	(0.319)	(0.723)	(0.674)	(0.802)	(0.747)
Time feeding on Wood	0.334	0.472	0.412	0.247	0.614	0.408	0.279	0.403	0.318	0.398
	(0.230)	(0.131)	(0.169)	(0.316)	(0.065)	(0.172)	(0.281)	(0.175)	(0.244)	(0.179)
Edge density vs.										
Time feeding on fruits	0.000	0.001	0.002	0.002	0.002	0.004	0.005	0.001	0.001	0.000
	(0.994)	(0.958)	(0.941)	(0.940)	(0.942)	(0.906)	(0.897)	(0.952)	(0.951)	(0.985)
Time feeding on leaves	0.085	0.203	0.504	0.309	0.285	0.236	0.226	0.122	0.104	0.099
	(0.576)	(0.370)	(0.114)	(0.252)	(0.275)	(0.328)	(0.340)	(0.498)	(0.532)	(0.543)
Time feeding on Wood	0.186	0.313	0.470	0.348	0.312	0.283	0.303	0.279	0.289	0.316
	(0.393)	(0.248)	(0.133)	(0.218)	(0.249)	(0.278)	(0.258)	(0.281)	(0.272)	(0.245)

Isolation distance vs.										
Time feeding on fruits	0.105	0.261	0.278	0.298	0.371	0.001	0.367	0.354	0.332	0.311
	(0.531)	(0.300)	(0.282)	(0.262)	(0.200)	(0.957)	(0.202)	(0.213)	(0.231)	(0.250)
Time feeding on leaves	0.084	0.011	0.013	0.016	0.008	0.195	0.141	0.229	0.284	0.319
	(0.577)	(0.845)	(0.830)	(0.808)	(0.866)	(0.381)	(0.464)	(0.337)	(0.276)	(0.243)
Time feeding on Wood	0.147	0.182	0.174	0.159	0.299	0.226	0.593	0.719	0.780	0.810
	(0.454)	(0.399)	(0.410)	(0.433)	(0.262)	(0.341)	(0.073)	(0.033)	(0.020)	(0.015)
Forest cover vs.										
Time traveling	0.795	0.753	0.728	0.745	0.762	0.782	0.808	0.820	0.833	0.830
	(0.017)	(0.025)	(0.031)	(0.027)	(0.023)	(0.019)	(0.015)	(0.013)	(0.011)	(0.011)
Time resting	0.577	0.724	0.769	0.766	0.754	0.737	0.717	0.692	0.663	0.639
	(0.080)	(0.032)	(0.022)	(0.022)	(0.025)	(0.029)	(0.034)	(0.040)	(0.049)	(0.056)
Time feeding	0.027	0.064	0.071	0.062	0.051	0.048	0.043	0.037	0.030	0.025
	(0.754)	(0.628)	(0.610)	(0.635)	(0.667)	(0.676)	(0.693)	(0.714)	(0.744)	(0.766)
Number of forest patches vs.										
Time traveling	0.590	0.312	0.349	0.166	0.253	0.300	0.355	0.472	0.267	0.324
	(0.074)	(0.250)	(0.217)	(0.423)	(0.309)	(0.261)	(0.212)	(0.131)	(0.294)	(0.238)
Time resting	0.082	0.049	0.051	0.117	0.162	0.427	0.128	0.133	0.119	0.151
	(0.581)	(0.674)	(0.666)	(0.507)	(0.428)	(0.159)	(0.486)	(0.477)	(0.503)	(0.447)
Time feeding	0.051	0.018	0.000	0.251	0.059	0.296	0.067	0.008	0.095	0.088
	(0.667)	(0.803)	(0.976)	(0.312)	(0.642)	(0.264)	(0.622)	(0.866)	(0.552)	(0.569)
Edge density vs.										
Time traveling	0.715	0.827	0.907	0.872	0.873	0.835	0.803	0.677	0.601	0.530
	(0.034)	(0.012)	(0.003)	(0.006)	(0.006)	(0.011)	(0.016)	(0.044)	(0.070)	(0.101)

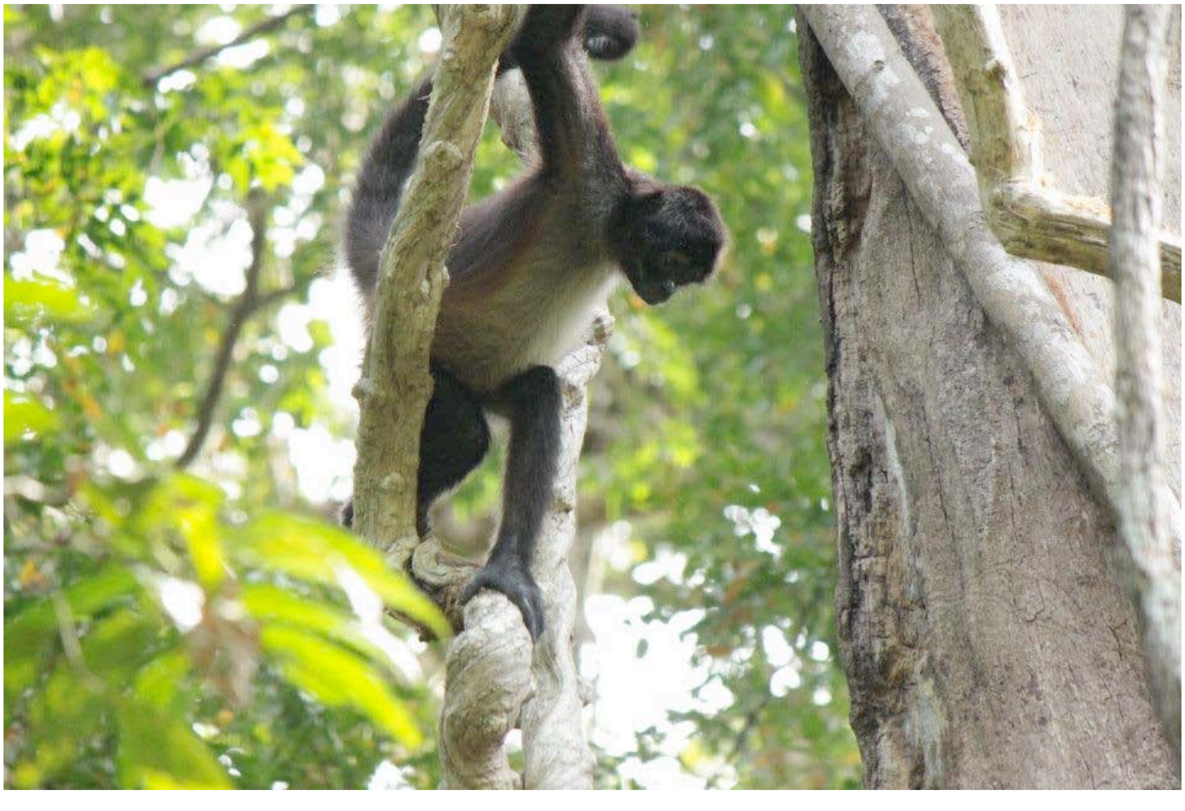
Time resting	0.065	0.202	0.469	0.273	0.236	0.183	0.191	0.120	0.114	0.134
	(0.625)	(0.372)	(0.133)	(0.287)	(0.328)	(0.398)	(0.386)	(0.502)	(0.513)	(0.476)
Time feeding	0.084	0.010	0.001	0.010	0.024	0.047	0.029	0.029	0.018	0.001
	(0.578)	(0.853)	(0.945)	(0.854)	(0.771)	(0.679)	(0.747)	(0.748)	(0.799)	(0.954)
Isolation distance vs.										
Time traveling	0.079	0.000	0.001	0.001	0.009	0.067	0.111	0.188	0.224	0.255
	(0.589)	(0.998)	(0.962)	(0.947)	(0.857)	(0.620)	(0.519)	(0.390)	(0.344)	(0.307)
Time resting	0.068	0.047	0.044	0.041	0.179	0.438	0.442	0.548	0.600	0.635
	(0.618)	(0.679)	(0.691)	(0.700)	(0.403)	(0.152)	(0.150)	(0.092)	(0.070)	(0.058)
Time feeding	0.002	0.336	0.343	0.368	0.523	0.766	0.477	0.407	0.362	0.348
	(0.935)	(0.228)	(0.222)	(0.201)	(0.104)	(0.022)	(0.129)	(0.173)	(0.206)	(0.218)

CAPÍTULO II:

Proximate and distal predictors of the spider monkey's stress response in fragmented landscapes

José D. Ordóñez-Gómez, Jurgi Cristóbal-Azkarate, Víctor Arroyo-Rodríguez, Ana M. Santillán-Doherty, Ricardo A. Valdez, Marta C. Romano

En: PLoS ONE (aceptado bajo correcciones menores)



Short Title: Stress Levels of Spider Monkeys in Fragmented Landscapes

Proximal and Distal Predictors of the Spider Monkey's Stress Levels in Fragmented Landscapes

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Abstract

The rapid loss, fragmentation and degradation of tropical forests threaten the survival of many animal species. However, the way in which these phenomena affect animal health has been poorly explored, thus limiting the design of appropriate conservation strategies. To address this, here we identified using general linear mixed models the effect of proximal (diet, activity pattern, hunting and logging) and distal (sum of the basal areas of fruiting-tree species [SBAFS], landscape forest cover and degree of forest fragmentation) variables over fecal glucocorticoid metabolite (fGC) levels – hormones associated with animal health and fitness – of six groups of spider monkeys (*Ateles geoffroyi*) inhabiting six landscapes with different spatial structure in Mexico. Proximal variables showed a stronger predictive power over fGC than distal. In this sense, increases in travel time, the occurrence of hunting, and reductions in rest time and fruit consumption, resulted in higher fGC levels. Regarding distal variables, increases in SBAFS were negatively related to fGC levels, thus suggesting that food scarcity increase stress levels. Nevertheless, contrary to theoretical expectations, spider monkeys living in smaller tracts of forest spent less time travelling, but the same time feeding on fruit as those in more forested areas. The lower net energy return associated to this combination of factors would explain why contrary to theoretical expectations, increased forest cover was associated with increased levels of fGCs in this groups. Our study shows that, at least in the short term, spider monkeys in fragmented landscapes do not always present higher levels of stress compared to those inhabiting continuous forest, and the importance of preserving fruit sources and controlling hunting for reducing the levels of stress hormones in free ranging spider monkeys.

Introduction

Land-use change has converted more than three quarters of the terrestrial biosphere into human-modified landscapes [1,2]. Because biodiversity is often threatened in these emerging landscapes, an increasing number of studies have been directed to better understand the response of species to such landscape changes and inform conservation plans (reviewed in [3–5]). The majority of these efforts have been focused on assessing the impact of forest patch and landscape spatial attributes on animal behavior [6,7], and on other attributes of animal and plant populations [8,9] and assemblages [10–12]. However, the complexity of the effects set off by habitat loss and fragmentation over the living conditions of animals hampers our ability to pinpoint which are the proximal factors (e.g., daily activity patterns, diet, intra and intergroup conflicts) that lead to the negative effects of these broad phenomena over species' demography, and how these are in turn associated with distal effects, such as landscape metrics. This is further complicated by the slow life histories of many animal taxa such as primates, and by the fact that the response of species to changes in habitat spatial metrics (e.g., forest loss and fragmentation) depends on the spatial scale (i.e., landscape size) at which these metrics are measured (i.e., the so-called "scale of effect"; sensu Jackson and Fahrig [13]).

The study of glucocorticoids (e.g., cortisol, corticosterone) can help us to assess the effects of habitat perturbation on wildlife's energetic physiology and fitness. These hormones are secreted by the adrenal glands in response to stressful challenges to the organism's homeostasis, their principal effect being the mobilization of energy reserves to overcome the stressor and the inhibition of non-vital functions [14–16]. This response is therefore adaptive, but higher levels of glucocorticoids (GC) are nonetheless indicators that organisms have to cope with a certain challenge using resources that could be allocated for maintenance and reproduction [17]. Accordingly, chronically elevated levels of GCs have been associated with pregnancy loss, lower birth weight and immunosuppression [18,19], and therefore, these hormones have been proposed as biomarkers of population health [20].

Due to their large size, diurnal habits and adaptability to human presence, it is relatively easy to follow arboreal primates and register their diet and behavior. This makes them a good model for identifying the proximal causes of stress in wildlife, and determining how these are in turn associated with broader phenomena, such as reduced resource availability and changes in landscape structure (e.g., forest cover and degree of forest fragmentation). Overall, studies show that primates living in smaller forest fragments have higher levels of GCs than those living in larger tracts of forest (e.g., *Piliocolobus tephrosceles*: [21]; *Alouatta pigra*: [22]; *Eulemur collaris*: [23]). Dunn et al. [24] related the higher levels of GCs in feces of a group of howler monkeys (*Alouatta palliata*) living in a small forest fragment to a lower availability of fruit, which in turn forced them to travel more and consume larger quantities of energy-poor leaves. Studies of *Pan troglodytes schweinfurthii* [25] and *Cercopithecus mitis* [26,27] have also related higher GC levels with food shortage and higher metabolic demands. In addition to this, other proximal factors such as human presence [28,29] and direct anthropogenic disturbances (e.g., logging, hunting) [30] may also impact GC levels in primates. Nevertheless, to date, no environmental physiology study has yet assessed the effect of landscape spatial metrics on stress levels of primates, despite evidence showing that landscape attributes like forest cover and forest fragmentation are important predictors of their occurrence [11], behavior [7] and population characteristics [31] in fragmented tropical landscapes.

Here, we used for the first time a patch-landscape approach (sensu Arroyo-Rodríguez & Fahrig [32]) to identify the main predictors of stress levels in spider monkeys (*Ateles geoffroyi*) living in human-modified landscapes. In particular, we analyzed what set of proximal (activity pattern, diet and direct anthropogenic disturbances) and distal (sum of the basal areas of fruiting-tree species [SBAFS] and landscape structure) variables better predicted the levels of fecal GCs (fGCs) in six groups of spider monkeys inhabiting landscapes with different degree of human perturbation in the Lacandona rainforest, Mexico. Given the highly energetic demands of spider monkeys [33,34] and the patchy distribution of fruit in space, we predict that fruit consumption (i.e., proximal predictor), forest cover and density of fruit sources (i.e., distal predictors) will present a negative effect on fGC levels. Also, because logging and hunting (i.e., direct anthropogenic disturbances) have a direct effect on the survival of arboreal animals, we predict that these activities will present a strong positive effect on fGC levels. This is a timely study for the conservation of *A. geoffroyi*, given that this large-bodied and highly frugivorous Neotropical primate [35] is considered one of the most sensitive species to habitat transformation [36–38]. In fact, *A. geoffroyi* is classified as “Endangered” in the IUCN red list, and it is estimated the populations have declined by as much as 50% over the course of the past 45 years [39].

Materials and Methods

Ethics Statements

This research was undertaken in accordance with the ethical and legal requirements of the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) of Mexico, and was authorized by permit number SGPA/DGVS/04045/13. It also complied with the protocols approved by the Ethical Committee of the Instituto Nacional de Psiquiatría Ramón de la Fuente Muñiz (approval no. 3330B) of Mexico, and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. The owners of the forest fragments granted us the permission to conduct this study in their land.

Study area

We conducted the fieldwork for this study in the Lacandona rainforest, in southern Chiapas, Mexico. This region presents two well-defined seasons: a dry season from January to May, and a rainy season from June to December. The average annual rainfall is 2881 mm, with the highest concentration of rainfall occurring between June and September (range: 423–511 mm/mo) and the lowest between February and April (range: 46–61 mm/mo). During the dry season the average monthly temperature is 26.3 °C (range: 22–28 °C) while during the rainy season it is 23.5 °C (range: 20–25 °C) (Comisión Federal de Electricidad, Mexico). Although there are no long-term published records on changes in fruit availability for our study region, a recent study of the seed rain produced by the spider monkey in latrines located beneath 60 sleeping sites in the region [40,41], suggests that in the Lacandona region the production of fleshy fruit (main food item for *A. geoffroyi* [33,34]) is higher during the rainy season than during the dry season, which has been associated with the fact that spider monkeys tend to consume smaller quantities of fruit during this period [42].

In terms of habitat configuration, our study region presents two well-distinguished areas: (i) the Montes Azules Biosphere Reserve (MA), which encompasses 331,200 ha of continuous forest; and (ii) the Marqués de Comillas Region (MCR), which is comprised of 203,999 ha of fragmented forest embedded in a matrix dominated by agricultural lands, cattle pasture, and human settlements. Deforestation in MCR started in the 1970s, but it was particularly accelerated and extensive between 1984 and 1996 [43], and as a result the MCR has lost approximately 60% of its original forest cover.

Studied spider monkey groups

We collected fecal samples and analyzed the behavior of spider monkeys (*Ateles geoffroyi*) belonging to six different groups living in separate sites (F1, F2, F3, F4, F5 and MA) characterized by landscapes of different structure. Group MA lived in the Montes Azules Biosphere Reserve (16°07’N, 90°56’W), while the other five groups inhabited different forest fragments within the Marqués de Comillas region (F1: 16°15’N, 90°50’W; F2: 16°18’N, 90°40’W; F3: 16°17’N, 90°50’W; F4: 16°20’N, 90°51’W; F5: 16°20’N, 90°48’W). Group MA was composed of 26 individuals (11 females, 4 males, 6 juveniles and 5 infants), Group F1 of 30 individuals (13 females, 5 males, 4 juveniles and 8 infants), Group F2 of 30 individuals (13 females, 4 males, 6 juveniles and 7 infants), Group F3 of 27 individuals (12 females, 6 males, 3 juveniles and 6 infants), Group F4 of 22 individuals (8 females, 5 males, 3 juveniles and 6 infants) and finally Group F5 of 23 individuals (6 females, 9 males, 5 juveniles and 3 infants).

Collection of proximal variables

Before the start of the data collection, and with the aim of habituating the study groups, identifying the group members and locating their most frequent travel routes, we followed each of the six study groups for *ca.* four hours every two weeks during two different periods (February-August 2012 and January-February 2013), for a total of 421 h (range: 65–72 h per group). We determined that the study groups were habituated to our presence, when they stopped threatening (e.g., shaking branches and vocalizing against us) and/or paying attention to us (e.g., gazing). We also identified as a sign of habituation the fact that females would sometimes allow their infants to get very close to us (*ca.* 3-6 m).

We conducted our study during the dry season of 2013 (March to May), because studies with spider and howler monkeys suggest that the effects of forest loss and fragmentation over the behavior [24,42] and stress levels [24] of primates are more marked during periods of seasonal reductions in the availability of fleshy fruit. We studied the daily activity pattern and diet, and collected fecal samples from each study group once every three weeks (i.e., sampling round) for three consecutive days from 0700 to 1530 h. To avoid the potential effect of age on monkey's behavior and hormone levels we sampled only adult individuals. Observations were carried out by two people (JDOG and a local field assistant), following a focal animal sampling method [44]. We switched focal animals randomly at 3-min intervals or whenever animals moved out of sight. Spider monkeys have high fission-fusion dynamics, therefore, to avoid biases due to sampling subgroups with adults of only one sex, during each fission event we selected a subgroup composed of adults of both sexes. The average number (±SD) of fission and fusion events per day was 1.278 (±0.712) and 0.759 (±0.671), respectively. We did not observe differences in the number of fission and fusion events per site (one-way ANOVA: $F_{5,48} = 1.546$, $P = 0.193$ for fission events; $F_{5,48} = 0.712$, $P = 0.617$ for fusion events). In total, we recorded 407 hours of focal observations (range per group = 66–69 hr) (see further details in [7]).

We recorded the diet and activity pattern considering six mutually exclusive behavioral categories: (i) time resting (period of inactivity); (ii) time traveling (movement between tree crowns or within the crown of a tree that was not directly food related); (iii) time spent feeding on fruit; (iv) time spent feeding on leaves; (v) time spent feeding on wood; and (vi) other activities (e.g., intra and inter group aggression, grooming, aggression towards the observer). We did not consider the effect of ‘other activities’ for analysis because their occurrence can potentially be associated to social dynamics within the groups such as changes in dominance hierarchy or reproductive competition, rather than to habitat effects. They were also very infrequent. During each observation day we also recorded the occurrence of direct anthropogenic disturbances, such as logging and/or hunting in the vicinity of the study groups. We classified as: (i) ‘logging days’, days in which we heard tree saws or tree axes; (ii) ‘hunting days’, days in which we detected gun shots and hunting dogs; and (iii) ‘no-disturbance days’, days in which we did not detect any signs logging or hunting activities.

Distal factors: landscape structure and food availability

The method that we followed to assess landscape spatial metrics has been described elsewhere [7]. Briefly, we used the method of minimum convex polygon to estimate the centroid of the activity area of each group based on the locations which spider monkeys spent ≥30 min. Then, from this point we calculated the percentage of forest cover and the number of forest fragments within ten different-sized buffers (i.e., landscapes) to test the relative impact of forest loss and fragmentation on spider monkeys' stress levels [32,45]. The scale of effect is related to spatial habitat use [13]. Accordingly, for the smallest buffer, we chose 50 ha as this is just below the 56 ha of the average spider monkey home range size reported for MA [42]. For the largest buffer, we chose 665 ha, which was the largest buffer that we could project without our six different landscapes started overlapping in space, loosing independence among samples. Using these two extreme values as reference, we then established eight additional buffers of incremental area (Table 1). After this, we ran linear regressions between each metric and the mean fGC levels of each site in order to identify the scale at which the strongest associations were presented (i.e., "scale of effect" [46]) (Table 1). We conducted all these analyses using a recent (April and May 2012) and high-resolution (2.5 × 2.5 m) SPOT satellite image and Quantum GIS 2.0.1 software.

To assess food availability within each site, we used the sum of the basal area of fruiting-tree species of which fruit is consumed by spider monkeys (SBAFS), as the basal area of a tree is a good proxy of the amount of fruit it can produce [47,48], and several studies report significant associations between this vegetation attribute and primate presence in forest fragments (e.g., *Cercocebus galeritus*: [49]; *A. palliata*: [50]). To calculate this, we randomly located 20 transects of 50 × 2 m within the activity area of each group, and we measured the diameter at breast height (dbh) of trees species with a dbh ≥ 10 cm. We then identified the tree species used by the spider monkey within these plots to calculate the SBAFS for each study group (Table S1). The species used by the spider monkey for fruit consumption were identified combining the data from: (i) the present study, (ii) a year-round study conducted in the study region [34], and (iii) a meta-analysis study of the food species reported for *A. geoffroyi* in Mesoamerica [33].

Fecal sample collection and fecal GC assay

While in the field, we opportunistically collected fecal samples throughout the day and immediately upon defecation (< 10 min), and we stored them in a cooler with frozen gel packs. We only collected samples if free of urine and other impurities, and from adult individuals. For each sample we registered location, date and time of collection, the sex of the individual the sample belonged to, and when female, whether she was lactating or non-lactating (pregnant and cycling females). Due to the large group sizes and fission-fusion dynamics of spider monkeys [51], we could not assign the identity of the individual who defecated to all samples. However, to reduce problems of data independence, during each observation day we collected only one sample per individual of the sampling subgroup. Back at the field station, every afternoon, we stored the samples at –20 ºC until their extraction (≤ 6 mo) in the Physiology Department of Centro de Investigación y de Estudios Avanzados, in Mexico City.

The protocols that we used to extract [52,53] and quantify [54] GC in feces have been previously used and validated to detect the activation of the HPA axis in response to stressful stimuli in spider monkeys (*Ateles geoffroyi*). Following the method described by Brown et al. [55] and modified by Brousset et al. [56], we dried out the samples at 65 ºC in a scientific oven (Precision Scientific 25EM) and pulverized and passed them through a sieve. Following this, we vortexed 0.40±0.01 g of each dried sample for 1 min in 5 mL of

80% ethanol and then placed them in a water bath at 80 ºC for 20 min. After the 20 min incubation period, we centrifuged the samples for 20 min at 460 × g and decanted the supernatant into a second tube. We then dried out the supernatants in a water bath at 36 ºC, added 0.3 mL ethanol and incubated the samples for 30 min at room temperature. Finally we centrifuged the samples for 20 min at 460 × g, and decanted the supernatants which were kept at –24 ºC until radioimmunoassay (RIA). This extraction method has shown to recover 56% of the cortisol metabolites content in spider monkey feces [52,53].

We quantified GC concentrations in the samples with a solid phase ^{125}I RIA method using cortisol CORT-CT2 CIS kits (Bio Internacional® B.P. 32-F91192 GIF-SUR-YVETTE CEDEX/France). The calibration range for assay was 0-2000 nmol l^{-1}. We incubated the samples for 2 hr at 37 ºC and measured radioactivity using a Packard Cobra II® (Packard Cobra II, A Canberra Co. Meriden, CT) scintillation counter for gamma radiation. The kit presents a low cross- reactivity with corticosterone (2.5%) and cortisone (2.2%). We assessed all the extracts in duplicate in a total of seven assays. Intra- and inter-assay coefficients of variation were 7.8% and 8.3%, respectively. We performed parallelism by comparing the slope of a serial dilution curve of pooled spider monkey fecal extracts to the slope of the standard curve, difference not being significant (t = 0.356, P = 0.726, N = 10). The slope of standards spiked with diluted fecal extract exhibited high accuracy (B = 0.969, R^2 = 0.992 N = 10, P = 0.000), indicating that the assay reliably measures fGCs across its range of concentration without interference from other fecal products.

Statistical analyses

Spider monkeys present a very short food passage time (mean = 4.4 h, range: 2.75–7.75 h [57]), which results in that cortisol levels have been observed to peak in feces as little as 7–8 h after a stressful stimulus [52]. Accordingly, here we assessed the effect of proximal predictors on fGC levels, by matching each individual's fecal sample with: (i) the percentage of time the group to which that spider monkey belonged spent travelling, resting and consuming food items (fruit, leaves and wood); and (ii) the occurrence of logging or hunting in the vicinity the day in which the sample was collected. To assess the effect of distal predictors on fGC levels, we matched the fGC value of the fecal samples with the landscape spatial metrics (i.e., forest cover and number of forest fragments) and the SBAFS corresponding to the sites in which we collected the samples. Finally, we log transformed our response variable (fGC levels) to achieve normal distribution.

We used the lmer function of the lme4 package [58] for R 3.2.2 to run linear mixed models (LMMs) to assess the effect of proximal and distal predictors on fGC levels. We used the r.squaredGLMM function of the MuMln package [59] to calculate the coefficient of determination (R^2) for each model. To reduce correlation and collinearity among predictors, we discarded variables that presented a Pearson correlation index > 0.7 and a variance inflation factor (VIF) > 4 (which indicate multicollinearity [60,61]). For calculating VIF, we used the function vif of the car package [62]. Because landscape spatial metrics and food availability (i.e., distal predictors) have been shown to be collinear with the daily activity pattern and diet (i.e., proximal predictors) of the spider monkey in our study region [34,42], we separately analyzed the impact of proximal and distal predictors on fGCs. Given that we only collected one sample per individual per sampling day of the study subgroup, we controlled for pseudoreplication effects by specifying observation day (nested within sampling rounds) and samples (nested within sites) as random factors. To reduce the variability of fGC levels due to factors not related to our independent variables, we used time of sample collection (AM or PM), sex, and lactating or non-lactating as control variables in all the models. We conducted multiple comparisons among the direct anthropogenic disturbances with the function ghlt of the package multcomp [63] for R 3.2.2 with *P* values adjusted using the Tukey method.

To select the most parsimonious models that best predicted the effect of predictor variables on fGC levels, we used the Akaike's information criterion (AIC). We ranked the models from the best (with lowest AIC) to the worst (with highest AIC), and considered the set of models with a difference in AIC (ΔAIC) < 2 from the top model as having equivalently strong empirical support and similar plausibility [61]. In order to check the assumptions of homogeneous and normally distributed residuals, we visually inspected Q-Q plots of residuals plotted against fitted values of each model.

Finally, we used the lmer function [58] to run a set of LMMs to analyze the effects of site on daily variation of activity pattern and diet of spider monkeys. We transformed percentages of the daily time spent in each time budget component (e.g., time travelling, time feeding on fruit) to proportions, and then, proportion data were arcsine-square-root transformed to meet normality assumptions. In each model we categorized site as fixed factor, and sampling round as random factor to account for the non-independence of repeated measures, and we applied a Bonferroni correction for multiple comparisons. We conducted *post hoc* pairwise comparisons between the study sites with the function lsmeans of the package lsmeans [64] with *P* values adjusted using the Tukey method. We carried out all analyses in R 3.2.2 [65].

Results

We recorded the occurrence of hunting in site F2 and logging in site F3 (Table 2) during the second and third sampling rounds. We observed the strongest relationships between landscape spatial metrics and fGC levels at 50-ha landscapes (forest cover: $r = 0.59$; number of fragments: $r = -0.56$; Table 1). Both, forest cover and number of fragments showed clear patterns and gradual changes between landscape sizes. It is important to mention that although sites F4 and F5 showed the lowest values of forest cover, these sites presented high SBAFS (Tables 2 and S1).

The best-supported models that assessed the effects of proximal predictors on fGC levels included: time traveling, time resting, direct anthropogenic disturbances, time feeding on fruit and time feeding on wood (Table S2). Increases in travel time resulted in significantly higher levels of fGC levels while the effect of rest time was the opposite (Table 3). The occurrence of hunting was associated with significantly higher fGC levels than no-disturbance (Table 3 and Fig 1). Fruit consumption tended to decrease fGC levels, although this effect did not reach significance ($P = 0.07$). Regarding distal predictors, the best-supported model included forest cover and SBAFS (Table S2), but the variance explained by such fixed factors was notably lower than that explained by proximal predictors (Table 3). Increased forest cover was associated with significantly increased levels of fGCs, while higher SBAFSs resulted in lower levels of stress hormones (Table 3).

Fig 1. Mean (±SE) log fecal glucocorticoid (fGC) levels of direct anthropogenic disturbances presented at six groups (MA, F1, F2, F3, F4, F5) of spider monkeys (*Ateles geoffroyi*) living in the fragmented Lacandona rainforest, Mexico. Letters indicate significant differences ($P < 0.05$) among direct anthropogenic disturbances.

We found significant effects of site in three of the five activity budgets we have studied (Table 4). Spider monkeys spent more time traveling in MA than in F4 and F5, and in F1 than in F5 (Fig 2a). In the case of wood consumption, spider monkeys spent more time feeding on wood in MA than in all other sites (Fig 2e), and in the case of leaves consumption spider monkeys spent more time feeding on leaves in F4 than in MA (Fig 2d). For time resting and feeding on fruit we found no significant effects (Table 4).

Fig 2. Relationships between means (±SE) of log-transformed fecal glucocorticoid (fGC) levels (squares) and means (±SE) of the arcsine-square-root (ASR) transformed of the proportion of the percentage of the daily time budgets (rhombus) of six groups of spider monkeys (*Ateles geoffroyi*) living in the fragmented Lacandona rainforest, Mexico. TT = time traveling; TR = time resting; TFF = time feeding on fruit; TFL = time feeding on leaves; TFW = time feeding on wood. Letters indicate significant differences ($P < 0.05$) among sites, and black lines in squares indicate the occurrence of direct anthropogenic disturbances within the sites.

Discussion

Our study shows that fGC levels of spider monkeys are affected by both proximal and distal variables. Consistent with our predictions, our results suggest that fruit consumption and a lower time spent on energetically costly activities (less traveling and more resting) result in lower levels of fGCs (for examples with similar results see [24,26,66]), and that direct anthropogenic disturbances activate the stress response in spider monkeys [30]. Regarding distal predictors, we verified that fGC levels are negatively related to SBAFS, thus suggesting that food scarcity within the sites increases stress levels [28,66,67]. However, contrary to our prediction, our results show a positive relationship between forest cover and fGC levels, suggesting that spider monkeys inhabiting landscapes with low forest cover do not necessarily always experience higher levels of stress. Below, we elaborate on the potential mechanisms that can explain these findings, as well as on the ecological and conservation implications of these.

In general, fGC levels were more strongly related to proximal than to distal predictors, reflecting that changes in habitat characteristics do not act directly over wildlife's physiology, but rather through their effects on their behavior. The positive effect of travel and the negative effects of rest and fruit consumption on fGC levels support that physical effort [24,26,66], and reductions in the consumption of high-energy food items (e.g., fruit) [24–27] result in higher levels of fGCs. These results are well supported given the high-energy demands of spider monkeys associated to their large body size and their high dependency on fruit [33–35], and reflect the energy-mobilizing role of GCs [14–16].

Consistent with other studies of *Ateles hybridus* [30] and *Canis lupus* [68], we also found that the occurrence of hunting in the vicinity of the groups is a source of stress for spider monkeys. Due to their size and diurnal habits, large primates are very vulnerable to hunting [69]. In Mexico, and particularly in the states of Campeche and Chiapas (where we conducted this study), spider monkeys are taken to black markets to be sold as pets [70]. Therefore, the observed reaction to hunting could indicate that spider monkeys are being poached in our study area. In agreement with this idea, we have observed spider monkeys confined as pets in several houses in the region, and we have received personal communications from local people that agree that this species is poached in the region for pet trade.

Overall, the observed effects of proximal predictors on stress levels would suggest that spider monkeys in fragmented landscapes are more stressed than in continuous forests as the literature indicates that: (i) spider monkeys in forest fragments spend less time resting than in continuous forests (see a review of spider monkey's activity pattern through their geographic range: [71]); and (ii) fruit availability, and their consumption by primates, tends to be lower in forest fragments than in large forest tracts (e.g., [72,73]).

Verifying that fruit availability is a key habitat component for primate stress levels [28,67] we found that fGC levels were negatively associated with SBAFS, which highlights the importance of preserving fruit sources for primate conservation [49,73]. However, contrary to what we could expect, in our study region, spider monkeys living in smaller tracts of habitat spent less time traveling (year round study: [42]; F4 and F5: Fig 2a). Moreover, these groups have high SBAFSs within their activity areas (F4 and F5: Table 2), and accordingly, fruit consumption did not differ among the study groups regardless of the size of the forest they inhabited (Fig 2c). The lower net energy return associated with higher traveling times but similar consumption of energy-rich fruit presented in spider monkeys living in the landscapes with highest forest cover would explain why contrary to what has been observed in other studies with primates [22,24,29,52], in our study, forest cover was positively associated with fGC levels.

The reason behind why in our study spider monkeys living in larger tracts of forest spent more time traveling compared to those living in smaller forest fragments requires further study. A possible explanation for this is that these groups have more neighboring groups (MA and F1: Table 2), which might force them to spend more time patrolling their home range. Along the same lines, Rimbach et al. [74] report that fGC levels in spider monkeys (*A. hybridus*) may increase as a consequence of competition for fruit monopolization, and this competition could be higher in larger tracts of forest with more neighboring groups. As for the lack of differences in fruit consumption among the study groups, this is probably related to the fact that deforestation in the region is relatively recent (< 40 years ago), the remaining forest cover is relatively high (approximately 40%), and the matrix that surrounds the forest fragments is highly heterogeneous; factors that together can contribute to reduce tree species mortality [75]. This is supported by Hernández-Ruedas et al. [75], who also found that in our study region, small forest fragments still harbor similar values of tree basal area and tree species density than the continuous forest.

Concluding remarks

Our study highlights the complex relationship between habitat transformation processes and primate stress levels, and the usefulness of assessing proximal and distal predictors of stress for obtaining a comprehensive understanding about the effects of habitat disturbance on animal physiology [20]. Unexpectedly, we found that spider monkeys living in smaller forest tracts had lower levels of fGCs, which we ultimately attributed to the lack of neighboring groups, and relatively high levels of resources probably associated to the recent and moderate degree of deforestation in the region [75]. However, our data suggests that the proximal driver of the relatively lower stress levels of these groups was a higher net energy return due to reduced activity but similar consumption of energy-rich fruit. Finally, we want to emphasize that these results should not be taken as a sign that spider monkeys in forest fragments are not threatened by extinction, as recent studies in the region demonstrate that the future of biodiversity in this region is uncertain (terrestrial mammals: [76]; primates: [31]; plants: [75]; birds: [12]; dung beetles: [77]) as there is increasing regional support for the production of oil palm (*Elaeis guineensis*) plantations [78], and forest loss is advancing at alarming rates (2.1% of annual loss; [79]). Thus, further studies are required to monitor the health of the remaining populations (e.g., through fGC analyses) to obtain a better understanding about the viability of spider monkeys in this biodiversity hotspot.

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Author Contributions

Conceived and designed the experiments: JDOG JCA VAR AMSD MCR. Performed the experiments: JDOG RAV. Analyzed the data: JDOG JCA VAR. Contributed reagents/materials/analysis tools: JDOG AMSD MCR. Contributed to the writing of the manuscript: JDOG JCA VAR MCR.

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Supporting Information

Table S1. Basal areas (m^2) of tree species used by the spider monkey (*Ateles geoffroyi*) for fruit consumption from six different sites located in the Lacandona rainforest, Mexico. For each site, basal areas were estimated within twenty 50 x 2-m plots (0.2 ha).
(DOC)

Table S2. Linear mixed models (LMMs) with a ΔAIC < 2 examining the effect of proximal and distal predictors of log-transformed fecal glucocorticoid levels of six groups of spider monkeys (*Ateles geoffroyi*) inhabiting the Lacandona rainforest, Mexico. Samples (nested within groups) and observation days (nested within sampling rounds) were specified as random factors in all models. Marginal R^2 (M R^2) represents the variance explained by fixed factors, and conditional R^2 (C R^2) represents the variance explained by both fixed and random factors. TT = Time traveling, TR = Time resting, DAD = Direct anthropogenic disturbances, TFF = Time feeding on fruit, TFW = Time Feeding on Wood, TFL= Time feeding on leaves, SBAFS = Sum of the basal areas of fruiting-tree species used by the spider monkey for fruit consumption.
(DOC)

Table 1. Pearson correlation coefficients between each landscape metric and the mean of log-transformed fecal glucocorticoid (fGC) values of six spider monkey (*Ateles geoffroyi*) groups in the Lacandona rainforest, Mexico.

Landscape metric/response variable	Size (ha) of local landscape*									
	50	84	126	177	237	305	382	468	562	665
Forest cover vs log (fGC levels)	**0.592**	0.527	0.510	0.518	0.529	0.540	0.547	0.547	0.551	0.549
Number of fragments vs log (fGC levels)	**-0.558**	-0.247	-0.240	0.096	-0.037	-0.005	-0.176	-0.304	-0.050	-0.095

*We indicate the highest coefficient values for each predictor in boldface.

Table 2. Variables used in linear mixed models to assess the effect of proximal and distal predictors of fecal glucocorticoid levels on six groups of spider monkeys (*Ateles geoffroyi*) living in the Montes Azules Biosphere Reserve (MA) and five sites (F1-F5) in the Lacandona rainforest, Mexico.

	MA	**F1**	**F2**	**F3**	**F4**	**F5**
Characteristics of the study sites						
Distal predictors						
Forest cover (%) in a 50-ha local landscape	100	98.2	62.0	51.5	34.1	21.9
Number of fragments in a 50-ha local landscape	0	1	1	2	1	4
SBAFS (m^2) in 0.2 ha of sampling area per site[a]	7.6	7.1	4.2	4.7	5.9	6.3
Number of spider monkey groups[b]	> 5	3	2	2	1	1
Site size (ha)	330,000	1,125	460	141	67	28
Characteristics of the study groups						
Proximal predictors (*N* = 54, 9 samples per group)						
Mean percentage of time traveling (±SD)	25.4 (±5.5)	20.0 (±3.1)	19.8 (±4.6)	19.5 (±4.1)	14.6 (±3.4)	12.9 (±3.9)
Mean percentage of time resting (±SD)	39.9 (±6.4)	44.6 (±12.1)	50.2 (±9.4)	51.4 (±7.6)	54.7 (±4.7)	47.9 (±9.9)
Mean percentage of time feeding on fruit (±SD)	12.7 (±6.6)	24.2 (±15.3)	12.1 (±4.8)	11.8 (±3.9)	14.1 (±8.5)	17.9 (±14.9)
Mean percentage of time feeding on leaves (±SD)	2.7 (±1.6)	3.6 (±2.5)	3.4 (±4.2)	6.6 (±7.1)	10.5 (±4.7)	6.2 (±5.3)
Mean percentage of time feeding on wood (±SD)	12.7 (±6.8)	1.4 (±2.8)	1.0 (±1.5)	0.5 (±0.8)	0.32 (±0.65)	0.7 (±1.2)
Presence of direct anthropogenic disturbances[c]	No-disturbance	No-disturbance	Hunting	Logging	No-disturbance	No-disturbance
Characteristics of the response variable (*N* = 252)						
Mean (±SD) values of fGC levels (nggn^{-1})	255 ± 40	216 ± 19	339 ± 43	294 ± 46	134 ± 18	113 ± 12
Feces collected[d] (N)	44	45	35	44	44	40

[a] Sum of basal areas of fruiting-tree species used by the spider monkey for fruit consumption.

[b] Number of groups living in the studied fragments and in MA (Montes Azules Biosphere Reserve).

[c] Distribution of collected samples across direct anthropogenic disturbances: No-disturbance = 188; Logging = 33; Hunting = 31.

[d] Distribution of collected samples across sexual status categories and collection time categories: Sexual status: Males = 82; Lactating female = 117; Non-lactating female = 53; Collection time: AM = 144; PM = 108.

Table 3. Results of the best-supported linear mixed models examining the effect of proximal and distal predictors on log-transformed fecal glucocorticoid levels of six groups of spider monkeys (*Ateles geoffroyi*) in the Lacandona rainforest, Mexico.

Predictor variables / Models	**Estimate**	**SE/d.f. ***	***t*/χ^2****	***P* *****	**VIF**	**AIC**	**M R^2**	**C R^2**
Proximal predictors								
TT+TR+TFF+TFW+DAD						139.82	0.321	0.404
Intercept	2.779	0.317	8.773	**0.000**				
Time travelling	0.020	0.006	3.633	**0.001**	1.704			
Time resting	-0.013	0.004	-3.023	**0.004**	1.855			
Time feeing on fruit	-0.007	0.004	-1.842	0.070	1.785			
Time feeding on wood	-0.009	0.005	-1.771	0.081	1.323			
Direct anthropogenic disturbances		2	9.508	**0.001**				
Sexual status		2	0.268	0.875				
Collection time		1	1.759	0.185				
Distal predictors								
Forest Cover+SBAFS						165.7	0.113	0.381
Intercept	2.338	0.170	13.208	**0.000**				
Forest cover	0.005	0.001	3.648	**0.001**	1.384			
SBAFS	-0.072	0.032	-2.267	**0.028**	1.384			
Collection time		1	1.742	0.187				
Sexual status		2	0.143	0.931				

In all models, samples (nested within groups) and observation days (nested within sampling rounds) were specified as random factors. The variance inflation factor (VIF) is indicated for continuous variables. Marginal R^2 (M R^2) represents the variance explained by fixed factors, and conditional R^2 (C R^2) represents the variance explained by both fixed and random factors. TT = Time traveling, TR = Time resting, TFF = Time feeding on fruit, TFW = Time feeding on wood, DAD = Direct anthropogenic disturbances, SBAFS = Sum of basal areas of fruiting-tree species used by the spider monkey for fruit consumption. Variables that significantly affected fGC levels in boldface.

*For continuous variables we reported the standard error, and for categorical variables the degrees of freedom (d.f.).

*For continuous variables we reported the *t* value, and for categorical variables the χ^2 value.

**For continuous variables we reported the *P* of the *t* value, and for categorical variables the *P* of the χ^2 value.

Table 4. Results of linear mixed models examining the differences of the daily activity pattern and diet among six groups of spider monkeys (*Ateles geoffroyi*) that inhabited different sites located in the Lacandona rainforest, Mexico.

Behavior	**Site**		
	χ^2	**d.f.**	***P***
Time traveling	36.946	5	0.000*
Time resting	6.239	5	0.284
Time feeding on fruit	3.291	5	0.654
Time feeding on leaves	20.444	5	0.001*
Time feeding on wood	69.583	5	0.000*

*P < 0.01 i.e., significant value obtained after applying the Bonferroni correction for multiple tests.

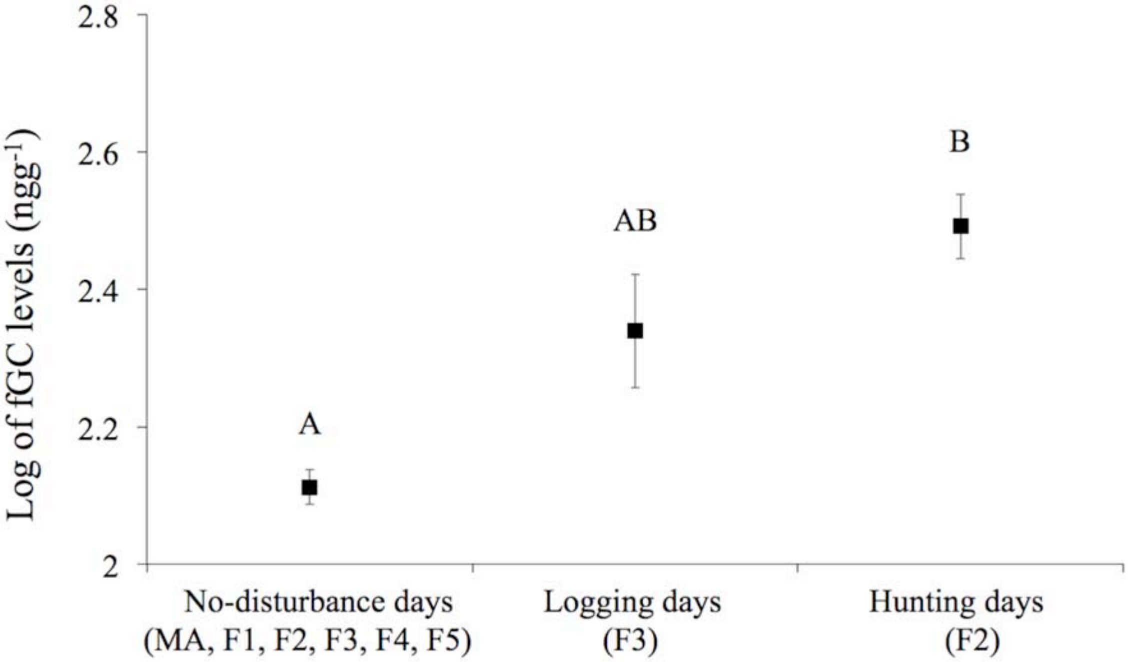

Fig 1. Mean (±SE) log fecal glucocorticoid (fGC) levels of direct anthropogenic disturbances presented at six groups (MA, F1, F2, F3, F4, F5) of spider monkeys (*Ateles geoffroyi*) living in the fragmented Lacandona rainforest, Mexico. Letters indicate significant differences ($P < 0.05$) among direct anthropogenic disturbances.

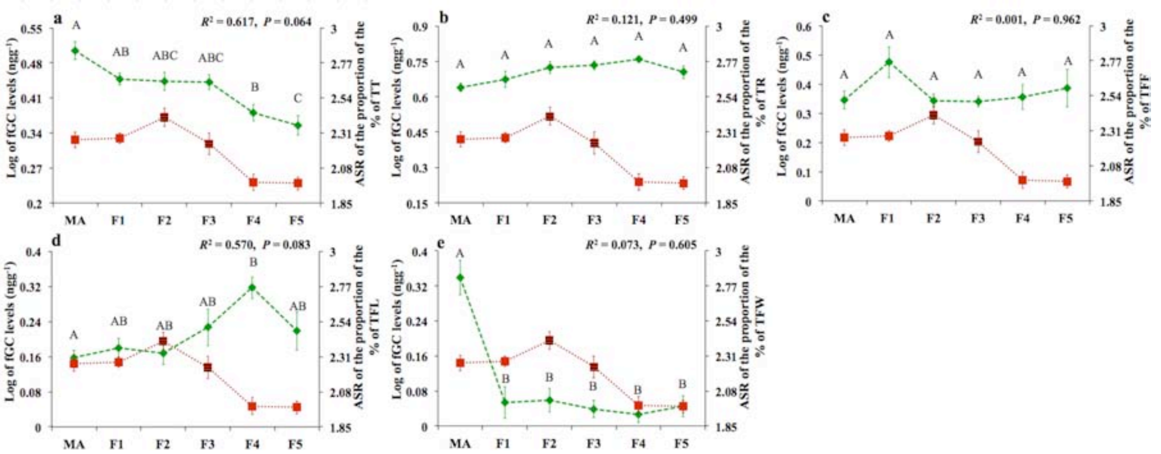

Fig 2. Relationships between means (±SE) of log-transformed fecal glucocorticoid (fGC) levels (squares) and means (±SE) of the arcsine-square-root (ASR) transformed of the proportion of the percentage of the daily time budgets (rhombus) of six groups of spider monkeys (*Ateles geoffroyi*) living in the fragmented Lacandona rainforest, Mexico. TT = time traveling; TR = time resting; TFF = time feeding on fruit; TFL = time feeding on leaves; TFW = time feeding on wood. Letters indicate significant differences ($P < 0.05$) among sites, and black lines in squares indicate the occurrence of direct anthropogenic disturbances within the sites.

Table S1. Basal areas (m^2) of tree species used by the spider monkey (*Ateles geoffroyi*) for fruit consumption from six different sites located in the Lacandona rainforest, Mexico. For each site, basal areas were estimated within twenty 50 x 2-m plots (0.2 ha).

Family	Tree species	CF	F1	F2	F3	F4	F5	Sum
Moraceae	*Brosimum alicastrum*	0.476	0.945	0.297	0.935	0.876	0.237	3.766
	Brosimum costaricanum	0.014	0.016	0	0	0	0	0.03
	Brosimum lactescens	0.051	0.062	0	0	0	0	0.113
	Castilla elastica	0	0.149	0.494	0.241	0.109	0	0.993
	Ficus sp. 1	0	0	0	0	0.016	0	0.016
	Ficus sp. 2	0	0	0	0	0.027	0	0.027
	Ficus cotinifolia	0	0	0	0.047	0	0	0.047
	Ficus insipida	0	0	0	0	1.745	0	1.745
	Ficus tecolutensis	0.534	1.82	0	0	1.328	0.029	3.711
	Maclura tinctoria	0	0	0	0	0	0.139	0.139
	Pseudolmedia oxyphyllaria	0.034	0	0	0	0	0	0.034
	Trophis mexicana	0	0	0	0	0	0.589	0.589
	Trophis racemosa	0	0	0	0.063	0	0.401	0.464
Sum		1.109	2.992	0.791	1.286	4.101	1.395	11.674
Fabaceae	*Acacia cornigera*	0	0.015	0	0.044	0	0.204	0.263
	Acacia usumacintensis	0	0	0	0	0	0.166	0.166
	Cojoba arborea	0.996	0	0.262	0	0	0	1.258
	Dialium guianense	1.194	1.743	0.126	1.265	0.088	0.514	4.93
	Inga punctata	0.273	0	0	0	0	0	0.273
	Inga vera	0	0	0	0	0.082	0.215	0.297
	Lonchocarpus cruentus	0	0.013	0	0	0	0	0.013
	Lonchocarpus guatemalensis	0	0	0.014	0.278	0	0.134	0.426
	Pithecellobium arboreum	0	0.254	0	0	0.012	0	0.266
	Pterocarpus rohrii	0.166	0.012	0	0	0	0	0.178
Sum		2.629	2.037	0.402	1.587	0.182	1.233	8.07
Malvaceae	*Guazuma ulmifolia*	0	0	0	0	0	0.142	0.142
	Quararibea funebris	0.464	0	0.019	0	0	0	0.483
	Quararibea yunckeri	0	0	0.008	0	0	0	0.008
	Theobroma cacao	0.025	0	0	0	0.215	0.84	1.08
Sum		0.489	0	0.027	0	0.215	0.982	1.713
Anacardiaceae	*Mangifera indica*	0	0	0	0	0	0.506	0.506
	Spondias mombin	0	0	0.271	0	0	0.071	0.342
	Spondias radlkoferi	0.289	0.027	0.291	0.041	0.053	0.378	1.079

Sum		0.289	0.027	0.562	0.041	0.053	0.955	1.927
Sapotaceae	*Pouteria durlandii*	0.164	0.015	0	0.158	0.011	0	0.348
	Pouteria campechiana	0	0.047	0.013	0.042	0	0	0.102
	Pouteria sapota	0	0	0	0	0	0.619	0.619
Sum		0.164	0.062	0.013	0.2	0.011	0.619	1.069
Chrysobalanaceae	*Hirtella americana*	0	0	0.018	0	0	0	0.018
	Licania platypus	1.423	0.765	0	0	0.779	0.545	3.512
Sum		1.423	0.765	0.018	0	0.779	0.545	3.53
Arecaceae	*Attalea butyracea*	0	0	0.076	0.193	0.128	0.127	0.524
	Sabal mexicana	0	0.252	0.596	0.411	0	0.051	1.31
Sum		0	0.252	0.672	0.604	0.128	0.178	1.834
Meliaceae	*Guarea excelsa*	0	0	0	0.138	0.128	0	0.266
	Guarea glabra	0.352	0.117	0	0.214	0.094	0	0.777
Sum		0.352	0.117	0	0.352	0.222	0	1.043
Burseraceae	*Bursera simaruba*	0.198	0	0.53	0.123	0	0	0.851
	Protium copal	0.022	0.043	0	0.008	0.01	0	0.083
Sum		0.22	0.043	0.53	0.131	0.01	0	0.934
Rubiaceae	*Faramea occidentalis*	0.008	0.012	0.025	0	0	0	0.045
	Psychotria chiapensis	0.011	0	0	0	0	0	0.011
Sum		0.019	0.012	0.025	0	0	0	0.056
Ulmaceae	*Ampelocera hottlei*	0.684	0.028	0.451	0.118	0.011	0	1.292
Sum		0.684	0.028	0.451	0.118	0.011	0	1.292
Icacinaceae	*Calatola laevigata*	0	0.349	0.117	0.136	0	0.274	0.876
Sum		0	0.349	0.117	0.136	0	0.274	0.876
Lauraceae	*Nectandra ambigens*	0	0.202	0.095	0.019	0.076	0	0.392
Sum		0	0.202	0.095	0.019	0.076	0	0.392
Clusiaceae	*Garcinia intermedia*	0	0.169	0	0.188	0.01	0	0.367
Sum		0	0.169	0	0.188	0.01	0	0.367
Boraginaceae	*Cordia bicolor*	0	0.008	0.149	0	0	0.092	0.249
Sum		0	0.008	0.149	0	0	0.092	0.249
Magnoliaceae	*Talauma mexicana*	0.236	0	0	0	0	0	0.236
Sum		0.236	0	0	0	0	0	0.236
Polygonaceae	*Coccoloba barbadensis*	0	0	0.228	0	0	0	0.228
Sum		0	0	0.228	0	0	0	0.228
Combretaceae	*Terminalia amazonia*	0	0	0.059	0	0	0	0.059
Sum		0	0	0.059	0	0	0	0.059

Annonaceae	*Cymbopetalum mayanum*	0.018	0	0.012	0	0	0	0.03
Sum		0.018	0	0.012	0	0	0	0.03
Sapindaceae	*Cupania glabra*	0	0	0	0	0.018	0	0.018
Sum		0	0	0	0	0.018	0	0.018
Urticaceae	*Cecropia obtusifolia*	0	0	0	0	0.01	0	0.01
Sum		0	0	0	0	0.01	0	0.01
Euphorbiaceae	*Sapium nitidum*	0	0	0	0	0.001	0	0.001
Sum		0	0	0	0	0.001	0	0.001
Total sum		7.632	7.063	4.151	4.662	5.827	6.273	35.608

Table S2. Linear mixed models (LMMs) with a ΔAIC < 2 examining the effect of proximal and distal predictors of log-transformed fecal glucocorticoid levels of six groups of spider monkeys (*Ateles geoffroyi*) inhabiting the Lacandona rainforest, Mexico.

Model	AIC	ΔAIC	M R^2	C R^2
Proximal predictors				
TT+TR+DAD+TFF+TFW	139.82	0	0.321	0.404
TT+RT+DAD	140.23	0.41	0.299	0.397
TT+TR+DAD+TFF+TFW+TFL	140.63	0.81	0.325	0.409
TT+TR+DAD+TFL	140.88	1.06	0.308	0.403
Distal predictors				
Forest cover+SBAFS	165.7	0	0.113	0.381

Samples (nested within groups) and observation days (nested within sampling rounds) were specified as random factors in all models. Marginal R^2 (M R^2) represents the variance explained by fixed factors, and conditional R^2 (C R^2) represents the variance explained by both fixed and random factors. TT = Time traveling, TR = Time resting, DAD = Direct anthropogenic disturbances, TFF = Time feeding on fruit, TFW = Time feeding on wood, TFL = Time feeding on leaves, SBAFS = Sum of the basal areas of fruiting-tree species used by the spider monkey for fruit consumptio

DISCUSIÓN GENERAL Y CONCLUSIONES

Como resultado de la acelerada deforestación que se está presentando en los trópicos, durante las últimas dos décadas se ha incrementado el número de trabajos dirigidos al estudio de los efectos de la pérdida y fragmentación del hábitat sobre el patrón diario de actividades, la dieta y los niveles de estrés de primates. En general, estos estudios muestran que en fragmentos pequeños los primates presentan una flexibilidad conductual (e.g., Boyle y Smith, 2010b; Chaves et al., 2011, 2012; Dunn et al., 2009) y fisiológica (e.g., Chapman et al., 2006; Martínez-Mota et al., 2007; Rangel-Negrín et al., 2009) que les permite encarar la escasez de alimento. Sin embargo, debido a que la mayoría de estos estudios se han limitado a comparar el patrón diario de actividades, la dieta y los niveles de estrés de primates entre dos condiciones (e.g., fragmentos vs selva continua), los análisis han sido estrictamente cualitativos (Arroyo-Rodríguez et al., 2013). Esto ha impedido que se puedan establecer relaciones causales entre los atributos espaciales del paisaje (e.g., composición y configuración espacial del hábitat) y las variables de respuesta, y por tanto, que no se cuente con información precisa para la realización de planes de conservación para primates que habitan en paisajes fragmentados.

En la presente tesis, se evaluaron las relaciones de diversos atributos de la estructura espacial del paisaje con el patrón diario de actividades, la dieta y los niveles de estrés de seis grupos de monos araña que habitan en la selva Lacandona. Además, se evaluó el efecto de su patrón diario de actividades, dieta, disturbios antropogénicos directos (i.e., predictores proximales), y densidad de alimento (i.e., predictor distal), sobre sus niveles de estrés. Así, la presente tesis genera información valiosa para la realización de planes de manejo y conservación de monos araña que habitan en el área fragmentada de la selva Lacandona.

En el CAPÍTULO I de la tesis, los resultados muestran que la cobertura forestal es la métrica del paisaje que presenta relaciones más fuertes con el patrón diario de actividades y la dieta del mono araña, y que la escala del paisaje en la que se presentan las relaciones más altas (i.e., escala del efecto) es la de 126-ha (Fig. 3 y 4: CAPÍTULO I). La relación positiva entre la cobertura forestal y el tiempo de viaje es consistente con los resultados reportados previamente para esta región, los cuales muestran que los monos araña invierten mayor tiempo en el viaje en selva continua que en fragmentos (Chaves et al., 2011a). Esto sugiere que la mayor disponibilidad de hábitat provoca que los monos araña inviertan mayor tiempo en el viaje, como posible consecuencia de contar una mayor área para el forrajeo y el patrullaje. Por su parte, la relación positiva entre la cobertura forestal y el consumo de madera, puede explicarse si se considera que al igual que la fruta, la madera que consumen los monos araña se distribuye de manera parcheada en el espacio, debido a que solo un puñado de especies son utilizadas por el mono araña para el consumo de este recurso (*Licania platypus, Ficus* spp.) (Chaves et al., 2011b). Las relaciones negativas de la cobertura forestal con el tiempo invertido en el descanso y el consumo de hojas, sugieren que una menor área para el forrajeo ocasiona que los monos araña consuman una mayor cantidad de recursos que presentan una distribución homogénea en el espacio, y dan soporte a modelos socioecológicos de primates que proponen que un incremento en el consumo de hojas, resulta en un aumento en el tiempo de descanso (Korstjens et al., 2010).

Contrario a expectativas teóricas, no encontramos relaciones altas ni significativas entra la cobertura forestal y el tiempo dedicado al consumo de fruta. Aunque este resultado no fue esperado, puede explicarse si se considera que las áreas de actividad de los monos araña que habitaron en los paisajes con menor cobertura forestal, presentaron una densidad de fruta similar a la que presentaron las áreas de actividad de los monos araña que habitaron en los paisajes con mayor cobertura forestal (Table 2: CAPÍTULO II). El hecho de que los monos araña puedan cubrir sus altos requerimientos energéticos en paisajes con baja cobertura forestal, pero alta densidad de fruta, puede sustentarse con trabajos que reportan que los monos araña pasan la mayor parte de su tiempo en áreas de 2 a 6 veces menores al área total de su ámbito hogareño (Asensio et al., 2012; Ramos-Fernández et al., 2013). De manera particular, las altas densidades de fruta (i.e., altas SABEFs) que presentaron los paisajes de estudio con menor cobertura forestal (Table S1: CAPÍTULO II), concuerdan con la falta de relación que se presenta en esta región entre el tamaño del fragmento y el área basal de los árboles (i.e., indicador de la producción de fruta de un árbol: Stevenson et al., 1998), y refuerza la idea de que en regiones con una cobertura forestal relativamente alta los efectos de borde que matan árboles grandes parecen ser menores (Hernández-Ruedas et al., 2014).

Las fuertes relaciones que se presentaron en el paisaje de 126-ha entre la cobertura forestal y el patrón de actividades y la dieta del mono araña, confirman la importancia de hacer análisis multi-escalares para identificar las escalas espaciales en las que las métricas del paisaje mejor predicen el comportamiento de primates en paisajes fragmentados. En la presente tesis, estas relaciones pueden explicarse si se considera que en paisajes fragmentados, los monos araña rara vez presentan ámbitos hogareños >170 ha (Chaves et al., 2012; Di Fiore y Campbell, 2007; Ramos-Fernández et al., 2013; Wallace, 2008), y la conectividad de los paisajes <126 ha es alta: Estos paisajes mostraron una cobertura forestal alta (en promedio >50%) y una distancia de aislamiento entre fragmentos baja (*ca.* 20 m) (Fig. 2: CAPÍTULO I). Estos resultados indican que el tamaño del fragmento no siempre es un buen indicador de la cantidad de hábitat con la que disponen los monos araña en paisajes fragmentados, y sugieren que los monos araña que habitan en fragmentos grandes pero localizados en paisajes con baja cobertura forestal, podrían presentar una menor cantidad de hábitat respecto a la que presentan los monos araña que habitan en fragmentos pequeños pero localizados en paisajes altamente conectados.

El análisis de predictores proximales (i.e., patrón diario de actividades, dieta y disturbios antropogénicos directos) y distales (i.e., cobertura forestal, grado de fragmentación y densidad de alimento) de los niveles de los glucocorticoides fecales (GCf) permitió obtener una aproximación a la interacción entre características del hábitat y comportamientos que pueden que influir sobre los niveles de estrés del mono araña. Los predictores proximales presentaron relaciones más fuertes que los predictores distales, lo cual sugiere que los cambios en las características del hábitat no actúan directamente sobre los niveles de estrés del mono araña, sino a través de sus efectos sobre el comportamiento. El efecto positivo del tiempo de viaje, y el negativo del tiempo de descanso y el consumo de fruta sobre los niveles de GCf soportan que un mayor esfuerzo físico (Cavigelli, 1999; Foerster and Monfort, 2010; Dunn et al., 2013), y una reducción en el consumo de ítems ricos en energía (Dunn et al., 2013) incrementan los niveles de estrés de primates. Considerando que el mono araña es una especie con altos requerimientos energéticos, como resultado de su gran tamaño corporal y alta dependencia a la fruta (Di Fiore y Campbell, 2007), estos resultados están bien sustentados, y reflejan el rol de los glucocorticoides en la movilización de energía. Consistente con otros estudios (*Ateles hybridus*: Rimbach et al., 2013; *Canis lupus*: Bryan et al., 2015), la ocurrencia de caza se relacionó positivamente con el incremento de los niveles de GCf del mono araña. Considerando que los primates de tamaños corporales grandes son altamente sensibles a ser cazados (Peres, 2000), y en México los monos araña son tomados para ser vendidos como mascota principalmente de los estados de Campeche y Chiapas (Duarte-Quiroga y Estrada, 2003), estos resultados sugieren que el mono araña está siendo cazado en la selva Lacandona.

En relación a los predictores distales de la respuesta de estrés del mono araña, la relación negativa entre la SABEF y los niveles de GCf, verifica que la escasez de alimento incrementa los niveles de estrés (Behie et al., 2010; Cavigelli, 1999; Gesquiere et al., 2008). Sin embargo, contrario a lo esperado, la cobertura forestal presentó un efecto positivo sobre los niveles de GCf del mono araña. Aunque este resultado fue inesperado, puede sustentarse si se considera qué: (1) en los paisajes con mayor cobertura forestal los monos araña invirtieron mayor tiempo en el viaje (Fig 2: CAPÍTULO II); (2) los grupos de estudio que habitan en los paisajes con mayor cobertura forestal tienen más grupos vecinos con los cuales podrían competir por el alimento (Table 1: CAPÍTULO II), y Rimbach et al. (2014) sugieren que los niveles de GCf del mono araña (*A. hybridus*) se pueden incrementar como consecuencia de la competencia por monopolizar fruta; y (3) dentro del área de actividad de los grupos que habitan en los sitios con menor cobertura forestal, las SABEFs fueron altas (F4 and F5: Table S1: CAPÍTULO II), razón por la que probablemente los monos araña no presentaron diferencias en el consumo de fruta entre los paisajes con mayor y menor cobertura forestal. Sin embargo, si consideramos que de manera general, en Mesoamérica el mono araña descansa menos en fragmentos (revisión de González-Zamora et al., 2011), y la disponibilidad de fruta (Arroyo-Rodríguez y Mandujano, 2006) y su consumo por primates tiende a ser menor en fragmentos pequeños que en fragmentos grandes o selva continua (Dunn et al., 2009), los predictores proximales de la respuesta de estrés sugieren que en otras regiones es más probable que los monos araña que habitan en paisajes con menor cobertura forestal presenten mayores niveles de estrés.

En cuanto a la escala del efecto, si bien el coeficiente de asociación entre la cobertura forestal y los niveles de GCf fue alto, y constante a través de todos los tamaños de los paisajes (rango: 0.510–0.592: Table S2: CAPÍTULO II), éste fue menor a los que presentó la cobertura forestal con los tiempos dedicados al descanso, al viaje y al consumo de hojas (Table S2: CAPÍTULO II vs Table S1: CAPÍTULO I). Esto nuevamente refuerza que los cambios en las características del hábitat no actúan directamente sobre los niveles de estrés del mono araña, sino a través de los efectos sobre su comportamiento (i.e., predictores proximales).

Conclusiones generales

En resumen, los principales hallazgos de la presente tesis indican qué:

(1) Los atributos espaciales del paisaje son buenos predictores del patrón diario de actividades, la dieta y los niveles de estrés del mono araña, y por tanto, que es importante considerar sus efectos y las escalas en las que estos son mayores, para la realización de planes de conservación de monos araña que habitan en paisajes fragmentados.

(2) La conjetura de que una menor cantidad de hábitat es igual a una menor disponibilidad de alimento no siempre es acertada: fragmentos pequeños pueden presentar mayor densidad de alimento que fragmentos más grandes, y menos grupos de monos araña (F2, F3 vs F4, F5: Table 1: CAPÍTULO II). Por tanto, para hacer una buena interpretación de la variación de las respuestas de primates que habitan en paisajes con distinta estructura, es importante considerar en los análisis estadísticos atributos de la vegetación que se relacionen de manera directa con la disponibilidad de alimento, y de ser posible, el número de monos araña que habitan en cada sitio de estudio.

(3) Es incorrecto dar por hecho que primates que habitan en sitios con menor cobertura forestal presentan mayores niveles de estrés. La alta densidad de alimento y el menor número de grupos que pueden presentar estos sitios, puede ocasionar qué los monos araña

intensifiquen el uso de los recursos disponibles para no disminuir su consumo de fruta, e inviertan menor energía en el forrajeo y patrullaje.

Finalmente, si bien los resultados de la presente tesis sugieren que mediante el ajuste de su comportamiento, los monos araña que habitan en la selva Lacandona son capaces de subsistir adecuadamente en paisajes fragmentados con alta densidad de alimento, su persistencia en estos sitios es incierta. El incremento del apoyo por parte del gobierno para la producción de plantaciones de palma de aceite (*Elaeis guineensis*) (SAGARPA, 2013), y el alarmante avance en el cambio de uso de suelo que está presentando la región de Marqués de Comillas (2.1% anualmente; Couturier et al., 2012), están reduciendo las limitadas áreas de actividad que presentan los monos araña en paisajes con baja cobertura forestal. Esto puede ocasionar la pérdida de árboles clave que usan los monos araña para cubrir sus requerimientos energéticos (i.e., árboles con áreas basales grandes y que fructifican más de una vez al año [e.g., *Ficus* spp]), y por tanto, un incremento en sus niveles de estrés. Por otra parte, a mediano plazo, un aumento en el número de monos araña en paisajes con baja cobertura forestal, podría ocasionar que se supere la capacidad de carga de estos paisajes. Mientras que a largo plazo, la endogamia podría provocar la aparición de enfermedades congénitas, y una disminución en la diversidad genética (Hagell et al., 2013). Debido a esto, es importante realizar estudios longevos en los que se monitoreen los niveles de estrés de los monos araña que habitan en paisajes con baja cobertura forestal que están siendo transformados, ya que la ocurrencia de un disturbio dentro de sus reducidas áreas para el forrajeo podría tener fuertes consecuencias sobre su supervivencia. Aunado a esto, para incrementar la resiliencia de los monos araña que habitan en paisajes con baja cobertura forestal, es sumamente importante incrementar la conectividad entre fragmentos mediante la creación de corredores. Esto permitiría a los monos araña incrementar su área de actividad, y por tanto, disminuir su dependencia a ciertos árboles que producen altas cantidades de fruta. Por otra parte, para evitar el incremento de los efectos de borde que matan árboles que producen altas cantidades de fruta, es sumamente importante mantener la cobertura forestal que presenta esta región.

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