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RUTAS DE DESPLAZAMIENTO Y USO DE ALIMENTO Y DORMIDEROS EN MONO ARAÑA (*Ateles geoffroyi*) EN CALAKMUL, CAMPECHE, MÉXICO

TESIS

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POR:
BIÓL. JULIÁN PARADA LÓPEZ

ASESORES:

DR. RAFAEL REYNA HURTADO
DRA. SILVIA HERNÁNDEZ BETANCOURT

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DECLARATORIA

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A mis padres, por brindarme la vida, su apoyo y la educación que ha hecho de mí la persona que soy ahora. Sin ustedes simplemente yo no sería.

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Resumen

El movimiento es un proceso vital que influye en diversos aspectos ecológicos, como la búsqueda de alimento, refugio y parejas para el apareamiento. En el caso de primates frugívoros, existen pocos estudios que aborden los movimientos con base en características del hábitat. El objetivo de esta investigación es analizar los movimientos de monos araña (*Ateles geoffroyi*) en relación a las fuentes de alimento en una localidad de Calakmul, México, así como caracterizar los árboles dormideros. Se establecieron transectos para el registro de vegetación arbórea y se calculó el Índice de Valor de Importancia (IVI) para cada especie. Asimismo, se registraron los árboles dormideros usados, se registró la vegetación circundante y se calculó el IVI de cada especie. Se siguieron individuos de mono araña por 4 meses en la época de lluvias, tomando puntos GPS cada 5 min para establecer las rutas de movimiento. Posteriormente se construyeron segmentos de ruta hacia el alimento y se calculó la proporción de linealidad de segmentos con y sin fuentes de alimento. La especie *Pouteria reticulata* tuvo el mayor IVI en el área muestreada. Cuatro especies fueron usadas como dormideros y éstas tuvieron un IVI relativamente alto comparado con los árboles adyacentes. Se encontró una alta linealidad ($\mu>0.7$) pero no se encontraron diferencias entre la linealidad de segmentos con y sin fuentes de alimento ($P=0.07$). Se encontró que los movimientos de los monos araña tuvieron persistencia en la dirección, demostrando que recorrieron su ámbito hogareño eficientemente, que puede ser resultado del uso de un mapa cognitivo o memoria espacial. Esta aproximación es útil para entender la influencia del ambiente en las habilidades espaciales de los primates y para determinar ubicaciones importantes en términos de conservación.

Palabras clave: Desplazamiento, linealidad, direccionalidad, alimento, mono araña, Nuevo Becal.

Summary

Movement is a spatiotemporal process by which animals travel to get food and other resources needed to maximize their fitness. In frugivorous primates movements have been closely related to search for food, but information about movements based on habitat and other resources are generally lacking. Here we analyze the movements of spider monkeys (*Ateles geoffroyi*) to food sources in the Calakmul region, Mexico, and characterize sleeping sites used by spider monkeys. We recorded the floristic composition based on transects and calculated the Importance Value Index (IVI) for each tree species. We recorded sleeping trees used and trees adjacent and calculated diameter at breast height (DBH) and IVI. We followed individuals of a community of spider monkeys for 4 months during the rainy season and took GPS locations every 5 min to quantify travel routes. We calculated linearity ratios of route segments that ended and did not end at food trees and compared both types of segments, and determined the directional persistence of spider monkey movements. *Pouteria reticulata* had the greater IVI in the area. Four species used as sleeping sites had higher DBH and relative high IVI, compared to adjacent trees. Linearity ratios was high ($\mu>0.7$) and the directional persistence reveals that spider monkeys traveled efficiently, which might be result of the use of a cognitive map. This approach is useful to understand environmental influences on primate spatial abilities and to determine important locations for conservation planning.

Keywords: Travel routes, linearity, directionality, food sources, spider monkeys, Nuevo Becal.

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1. INTRODUCCIÓN

El estudio de los movimientos de los animales se ha convertido en la actualidad en un nuevo paradigma en ecología conocido como Ecología del Movimiento, que es considerada una subdisciplina que integra las investigaciones enfocadas en entender las causas y consecuencias de los movimientos de los organismos (Nathan, 2008; Bowlin *et al*., 2010).

El movimiento es un proceso vital que afecta un amplio espectro de procesos ecológicos (Nathan, 2008) como la búsqueda de alimento, encontrar sitios de descanso o para el apareamiento, factores que contribuyen a la sobrevivencia de las especies y su distribución geográfica (Mueller y Fagan, 2008). Asimismo, en ambientes silvestres, el movimiento es un proceso espaciotemporal en el cual los animales se mueven en paisajes heterogéneos (Bonnell *et al*., 2013) buscando mosaicos de áreas que sean convenientes a sus necesidades específicas. En este sentido, los animales no pasan todo su tiempo en una sola área debido a que sus necesidades cambian en el tiempo, y por lo tanto, los sitios que inicialmente eran apropiados en términos de disponibilidad de recursos, progresivamente se vuelven menos apropiados al agotar los recursos durante su explotación (Barraquand y Benhamou, 2008). De esta manera, al considerar simultáneamente las diferentes necesidades que deben cubrirse, se asume que el grado de beneficio de un ambiente local está directamente relacionado a la intensidad del uso del espacio (Barraquand y Benhamou, 2008; Bonnell *et al*., 2013) y consecuentemente del uso de los recursos dentro del mismo, lo que a su vez se relaciona con los patrones de movimiento de los animales.

En especies que forman grupos sociales y que viven al interior de las selvas, como los primates, los movimientos son efectuados en estos ambientes cerrados donde han desarrollado estrategias de búsqueda de recursos que son irregulares en su disponibilidad (van Schaik *et al*., 1993; Chapman *et al*., 1999), por lo que representan un grupo de estudio ideal para conocer los factores que determinan cómo se mueven estos animales para satisfacer sus necesidades y sobrevivir en su hábitat natural.

Se ha establecido que los patrones de abundancia de alimento y su distribución son fundamentales para entender la variación en los movimientos dentro del orden de los primates (Valero, 2004). La abundancia de alimento es regulada ampliamente por características abióticas del ambiente, como la precipitación anual, cantidad de nutrientes del suelo, intensidad de exposición a radiación solar y variaciones anuales en la temperatura, que en conjunto, afectan los patrones fenológicos de las plantas. Así, la disponibilidad y distribución de las plantas pueden influenciar directamente su explotación por primates (Richards y de Roos, 2001), así como sus patrones de desplazamiento, ya que estos animales se alimentan mayormente de materia vegetal como frutos, hojas, semillas y raíces. Sin embargo, existen otros recursos que pueden tener un papel importante en la ecología de los primates, tales como los sitios para dormir o dormideros, cuya relevancia se ha asociado a la formación de letrinas y dispersión de semillas, proceso que ejerce un fuerte impacto en el hábitat (Russo y Chapman, 2011; González-Zamora *et al*., 2012; González-Zamora *et al*., 2014).

En términos generales, la información concerniente al análisis de rutas de desplazamiento en relación a fuentes de alimento y el uso de dormideros por primates en América se ha centrado en algunas especies (e.g., *Callicebus cupreus, Cebus apella, Saguinus imperator, S. mystax* y *S. fuscicollis*, Garber, 1988, 1989; Janson, 1998; Bicca-Marques, 2005, 2006; Garber y Porter, 2014), acentuándose la falta de información en especies como el mono araña centroamericano (*Ateles geoffroyi*), del cual se han realizado pocos estudios sobre el tema (e.g., Valero y Byrne, 2007), así como del uso de otros recursos potencialmente importantes como los dormideros (González-Zamora *et al*., 2012). Dicha información proveería un conocimiento más preciso de las áreas que ocupan, los patrones de movimiento, explotación del alimento y selección de dormideros, que ayudaría al entendimiento de su ecología y contribuiría a su conservación.

Por lo descrito anteriormente, en este estudio se analizan las rutas de desplazamiento y su relación con el uso de alimento así como el uso de dormideros por monos araña (*Ateles geoffroyi*) en un ejido del municipio de Calakmul, Campeche, México.

2. MARCO TEÓRICO

2.1. Aspectos biológicos de *Ateles geoffroyi*

2.1.1. Distribución y características anatómicas

Los monos araña (*A. geoffroyi*) son de los primates más grandes del Neotrópico, con individuos adultos que alcanzan un peso entre 7.5-8.2 kg (Ford y Davis, 1992). Se distribuyen desde Tamaulipas en México hasta la frontera entre Panamá y Colombia (Rylands *et al*., 2006). Presentan un pelaje de color café amarillento combinado con pelos negros y marcas oscuras en la cabeza, hombros y extremidades, aunque para *A. g. yucatanensis*, la cabeza suele ser café oscuro en cabeza y cuello, con las mejillas pálidas y el cuerpo café grisáceo (Kellogg y Goldman, 1944). Sus extremidades son largas y delgadas, con cuatro dedos funcionales, sin pulgar en las manos; tienen una cola prensil que les ayuda en su alimentación en el dosel de la selva, les permite balancearse y moverse con mayor fluidez y velocidad (Kellogg y Goldman, 1944; Schmitt *et al.*, 2005).

2.1.2. Hábitos alimenticios

Los monos araña son principalmente de hábitos frugívoros y se consideran importantes dispersores de semillas (Chapman, 1995; Russo *et al*., 2005). En general para el género *Ateles*, se ha reportado que los frutos son el recurso alimenticio que conforma la mayor parte de la dieta, con un rango del 55 a más del 90% del tiempo total de alimentación (Di Fiore *et al*., 2008), por lo que se consideran especialistas en consumir frutos maduros, y éstos son parte fundamental de su dieta durante todo el año (Suarez, 2006). No obstante, pueden complementar su dieta mediante el consumo de otros recursos, como son hojas tiernas, flores, semillas, raíces aéreas, orugas, corteza de árboles desgastados y suelo de lamederos rico en minerales (Klein y Klein, 1977; McFarland Symington, 1987; Castellanos y Chanin, 1996; Link, 2003; Dew, 2005; Chaves *et al*., 2011a).

En el caso de *A. geoffroyi*, existen algunos estudios que reportan la dieta de esta especie en distintas ubicaciones geográficas. Por ejemplo, en Punta Rio Claro, Costa Rica, se registraron 26 especies consumidas por monos araña, entre las que destacaron por sus porcentajes en tiempo de alimentación frutos de las especies *Mortoniodendron anisophyllum* y *Elaeoluma glabrescens* (Riba-Hernández *et al*., 2003). En México, se cuenta con algunas investigaciones que determinan las especies arbóreas consumidas en diferentes localidades. En la región de los Chimalapas en el estado de Oaxaca, datos preliminares muestran que los monos araña utilizaron 23 especies como alimento, de las cuales en sólo 5 se registró únicamente consumo de hojas (Ortíz-Martínez y Ramos-Fernández, 2012). Sin embargo, en este estudio no se presenta información respecto a los porcentajes de tiempo de alimentación de cada especie. En contraste, en otro estudio realizado al norte de Oaxaca, los frutos representaron el 84% del tiempo de alimentación de los monos araña, mientras que las hojas contribuyeron con un 14% y el 2% restante correspondió a flores, tallos, corteza y bulbos. Las especies más consumidas en dicha investigación fueron, *Brosimum alicastrum*, *Sideroxylon capiri* y *Dialum guianense* y dos especies del género *Ficus* (Ortíz-Martínez *et al*., 2012).

En un estudio realizado en la selva Lacandona, los resultados mostraron que en sitios de hábitat continuo, las especies de árboles que contribuyeron al mayor porcentaje de tiempo total de alimentación fueron *Licania platypus*, *Spondias radlkoferi* y *Spondias mombin*, mientras que en fragmentos de selva las especies con mayor tiempo de consumo fueron *D. guianense, Ficus tecolutensis* y *S. radlkoferi* (Chaves *et al*., 2012). En la península de Yucatán, en un estudio sobre selectividad en alimento de una comunidad de monos araña en la reserva "Ya'ax'ché" en Quintana Roo, se encontró que el 59% del tiempo total de alimentación fue dedicado al consumo de frutos, mientras que las hojas representaron el 35%, el mesocarpio de las palmas representó el 5% y los tallos, flores, madera desgastada y savia el 1%. Las dos especies consideradas como las principales fuentes de frutos fueron *Mastichodendron foetidissimum* y *Manilkara zapota*, y la principal fuente de hojas fue *B. alicastrum* (Scherbaum y Estrada, 2013). Otro estudio realizado en Punta Laguna, Quintana Roo, determinó que respecto a la alimentación, tanto los frutos como las hojas de *B. alicastrum* representan en general una alta proporción en la dieta de dos grupos de mono araña (frutos: 29 y 22%, hojas: 8 y 10%, respectivamente), incluso los frutos de esta especie representan la mitad del consumo mensual de alimento (Ramos-Fernández y Ayala-Orozco, 2002). Otras especies de importancia en el sitio de estudio son *Ficus cotinifolia, Ficus ovalis, M. zapota, Sideroxylon capiri, Guazuma ulmifolia, Metopium brownei, Protium copal, Spondias mombin,* frutos y hojas de *Enterolobium* *cyclocarpum, Spondias lutea, Talisia olivaeformis, Dyospiros cuneata, Vitex gaumeri* y *Mosannona* spp. (Ramos-Fernández *et al*., 2003; Valero, 2004).

2.1.3. Ámbito hogareño

De acuerdo con diversos estudios, los monos araña tienen ámbitos hogareños que varían dependiendo del sitio donde se encuentren. En Costa Rica, se ha registrado un ámbito hogareño de 170 ha (Chapman, 1990), mientras que en la isla Barro Colorado, Panamá, se estimó un ámbito hogareño de 962 ha (Campbell, 2000). En México, las áreas de ámbito hogareño estimadas para *A. geoffroyi* han sido de 29.7-89.6 ha en hábitat continuo de la selva Lacandona (Chaves *et al*., 2011b), y en la Península de Yucatán se han reportado áreas de 95-166 y 152 ha en Punta Laguna, Quintana Roo (Ramos-Fernández y Ayala-Orozco, 2002; Valero, 2004). En Calakmul, Campeche, estudios preliminares muestran un ámbito hogareño de 184 ha en selva mediana subperennifolia (Hernández-Sarabia, 2013).

2.1.4. Reproducción

Se ha determinado que la duración de los ciclos ováricos y menstruales tanto en monos cautivos como en vida libre, tienen un periodo consistente de 20-24 días, periodo obtenido a partir de datos hormonales y exudados vaginales (Campbell *et al*., 2001). En hembras cautivas y en vida libre, los niveles de estrógeno y progesterona son similares durante la ovulación, aunque en libertad el ciclo tiende a durar 2-3 días más que en cautiverio (Campbell *et al*., 2001).

Las hembras de *Ateles* spp. presentan clítoris penduloso y es más largo que el pene de los machos en estado de flacidez (Wislocki, 1936). Su función principal es la comunicación del estado sexual mediante señales químicas de la orina y secreciones vaginales (Klein, 1971) que son detectadas por los machos a través del olfato. En éstos el pene es casi imperceptible ya que está retraído en el prepucio. En estado de erección, el pene es relativamente grande para su tamaño corporal y el extremo distal tiene forma similar al sombrero de un hongo (Campbell y Gibson, 2008). Los testículos son pequeños en relación al tamaño corporal y suelen estar descendidos desde el nacimiento (Wislocki, 1936).

2.1.5. Organización social

Los monos araña (*Ateles* spp.) son animales sociales que viven en comunidades que varían en número de individuos dependiendo del sitio donde se encuentren. Típicamente presentan un sistema social conocido como fisión-fusión, en el que la comunidad se divide temporalmente en subgrupos más pequeños que cambian en composición (sexo y clase de edad de los individuos) y tamaño durante el día (Chapman, 1990; Aureli *et al*., 2008), y se reúnen de nuevo en un sitio para dormir al finalizar sus actividades diarias. Se ha sugerido que este sistema social está asociado a beneficios relacionados a la disminución de la competencia intragrupal por recursos tróficos (Lehmann *et al*., 2007; Asensio *et al*., 2009), al igual que les confiere ventaja al formar pequeños subgrupos cuyo beneficio se traduce en la reducción del costo energético que suponen los desplazamientos largos hacia las fuentes de alimento (Chapman, 1990; Chapman *et al*., 1995) y permite a los individuos de la comunidad explotar de la forma más eficiente los recursos disponibles (Asensio *et al*., 2009).

2.1.6. Patrón general de actividades y comportamiento social

Las actividades realizadas por *A. geoffroyi* se han categorizado en cuatro tipos principales: alimentación, desplazamiento, descanso e interacciones sociales (González-Zamora *et al*., 2011). En términos generales, se ha observado que *A. geoffroyi* pasa la mayor parte de su tiempo descansando y alimentándose, con un rango aproximado de 30-40% del tiempo total de actividades dedicado a las actividades mencionadas (Chaves *et al*., 2011b; Ortiz-Martínez *et al*., 2012). Sin embargo, los registros de actividad varían dependiendo del tipo de hábitat (selva estacional o no estacional, selva continua o fragmentada) y de variables ambientales como la temperatura y precipitación (Chaves *et al*., 2011b; González-Zamora *et al*., 2011; Korstjens *et al*., 2006). Por ejemplo, en la selva Lacandona, México, se ha reportado que el tiempo dedicado a la alimentación difirió con base en el tipo de selva (48% en selva fragmentada vs. 40% en selva continua) y temporada de muestreo (50% en época lluviosa vs. 38% en época seca). Respecto al descanso, esta actividad difirió por periodo de muestreo, teniendo un mayor porcentaje de tiempo en la época seca (29% en época lluviosa vs. 38% en época seca) (Chaves *et al*., 2011b). Estos resultados son consistentes con lo reportado en diversos sitios de Mesoamérica (González-

Zamora *et al*., 2011), sugiriendo que en sitios donde la precipitación es mayor, existe una mayor producción de frutos y por lo tanto los monos araña pasan más tiempo alimentándose en dichos sitios. En contraste, hábitats con menor precipitación se asocian a una menor disponibilidad de alimento y alta temperatura, por lo que los monos araña dedican más tiempo al descanso, lo cual se ha sugerido como estrategia para reducir el gasto energético de actividades como el desplazamiento (Dunbar, 1992; Dunbar *et al*., 2009).

En cuanto a las interacciones sociales, se ha reportado que las hembras de mono araña exhiben débiles jerarquías de dominancia y bajas tasas de agresión y coaliciones entre ellas (Fedigan y Baxter, 1984; Chapman, 1990). No obstante, a pesar de la baja frecuencia de intercambios agresivos entre hembras (McFarland Symington, 1990), las hembras adultas residentes tienden a ser agresivas hacia hembras subadultas durante la alimentación, particularmente hacia hembras de reciente ingreso a la comunidad (Asensio *et al*., 2008). En el caso de los machos, generalmente interactúan unos con otros y con frecuencia intercambian conducta afiliativa (e.g. abrazos, acicalamiento) (McFarland Symington, 1990; Ramos-Fermández *et al*., 2009), por lo que son infrecuentes los contactos agresivos entre ellos. Cuando se trata de subgrupos compuestos por machos y hembras, los machos presentan una mayor tasa de agresión hacia las hembras que hacia otros machos, lo cual parece estar asociado con el nivel de parentesco de los individuos (Slater *et al*., 2009) y al estado reproductivo de las hembras, ya que los machos tienden a atacar a hembras receptivas (Slater *et al*., 2007).

2.1.8. Estado de conservación

A. geoffroyi es una especie en peligro de extinción cuya principal amenaza es la pérdida de su hábitat, aunque también está involucrada en el comercio ilegal de mascotas y en algunas regiones es sujeta a cacería (Cuarón *et al*., 2008). Se encuentra en la lista roja de Unión Internacional para la Conservación de la Naturaleza (UICN) y en la norma oficial mexicana NOM-059-SEMARNAT-2010 (SEMARNAT, 2010). Cuenta con aproximadamente 10 subespecies reconocidas, de las cuales *A. g. fronatus* y *A. g. geoffroyi* se encuentran en la categoría de menor riesgo (“least concern”) de acuerdo a la UICN, mientras que el resto de las subespecies se presentan en otras categorías de mayor riesgo (e.g vulnerable, amenazada, peligro de extinción). En el caso de las subespecies presentes en México, *A. g. vellerosus*, cuyas poblaciones se localizan en los estados de Oaxaca, Veracruz y Chiapas, se encuentra en peligro crítico de extinción, en tanto que la subespecie *A. g. yucatanensis* se localiza en la Península de Yucatán y se encuentra como vulnerable (Cuarón *et al*., 2008), ambas subespecies también están enlistadas en el apéndice II de la Convención sobre el Comercio Internacional de Especies Amenazadas de Flora y Fauna Silvestres (CITES).

2.2. Estudios de movimientos en primates en relación a la selección de recursos tróficos

Existen algunos modelos de movimiento que se han utilizado para describir y analizar los patrones de movimiento en diversas especies animales y que han sido relacionados principalmente al consumo de alimento. Un ejemplo es el patrón denominado Caminata de Lévy, que se ha sugerido como un modelo óptimo de forrajeo cuando el alimento se encuentra distribuido de forma agregada (Shlesinger y Klafter, 1986; Viswanathan *et al*., 1999), dando a los animales una habilidad de búsqueda a diferentes escalas espaciales (Viswanathan *et al*., 2008). La Caminata de Lévy se caracteriza por una alta frecuencia de pasos cortos conectados por desplazamientos largos ocasionales, es decir, la distribución de frecuencias es de ley de potencia (powe-law tail), donde la mayor parte de las frecuencias se concentra del lado izquierdo y hacia la derecha se encuentran los valores más altos (distribución de cola larga, Fig. 1) y se representa con la siguiente fórmula: $P(x) = x^{-\mu}$, donde $P(x)$ es la probabilidad de distribución de densidad de la longitud de pasos y µ es el exponente de Lévy, que toma valores entre 1 y 3. Sin embargo, algunos estudios que han aplicado este modelo sugieren que la Caminata de Lévy es óptima cuando µ = 2 ya que incrementa la tasa de encuentro con fuentes de alimento (Viswanathan *et al*., 1999; Bartumeus *et al*., 2005). Este patrón de movimiento se ha encontrado en algunas especies, como el albatros (*Diomedea exulans*, Viswanathan *et al*., 1996, 1999), el chacal (*Canis adustus*, Atkinson *et al*., 2002), el reno (*Rangifer tarandus*, Marell *et al*., 2002), la foca gris (*Halichoerus grypus*, Austin *et al*., 2004) y mono araña (*A. geoffroyi*, Ramos-Fernández *et al*., 2004). En este último estudio, se investigó una comunidad de monos araña en la Península de Yucatán con el fin de analizar sus patrones de movimiento desde una perspectiva del uso de espacio. Los resultados mostraron que los movimientos de los monos araña se ajustaron al patrón de Caminata de Lévy, determinando que las distancias de los movimientos tienen una distribución de ley de potencia, atribuyendo estas observaciones a la distribución espacial del alimento y a las señales olfativas y visuales de los frutos maduros. Sin embargo, Ramos-Fernández *et al.* (2004) señalaron que los resultados obtenidos también pueden ser producto de la memoria espacial, ya que si los monos tienen algún conocimiento de la ubicación del alimento, es posible asociarlo al patrón de Caminata de Lévy como la estrategia más adecuada para la explotación eficiente de los recursos alimenticios.

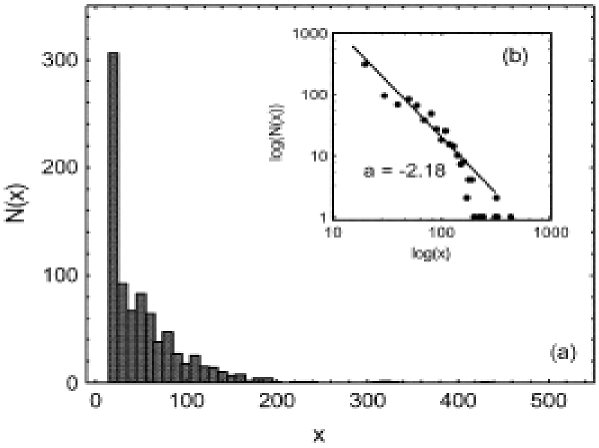

Figura 1. Ejemplo de gráfica de la distribución de ley de potencia del patrón de Caminata de Lévy. N(x) es equivalente a P(x) en el texto (probabilidad de distribución de densidad), la x representa las distancias de los pasos. Tomada de Ramos-Fernández *et al.* (2004)

Por otro lado, se han elaborado modelos de simulación para comparar los movimientos de forrajeo de monos araña en ambientes “artificiales” que contienen parches de alimento distribuidos al azar y con una estructura espacial variada. Los resultados de las simulaciones sugieren que la Caminata de Lévy aparece como una estrategia que incrementa la probabilidad de ingerir alimento en ambientes heterogéneos donde la ubicación de éste es parcialmente conocida (Boyer *et al*., 2006). Otros modelos de simulación también se han utilizado para medir la variación espaciotemporal en el uso de ciertos sitios dentro de un mismo hábitat a través de datos de movimientos de monos (e.g. colobos rojos, *Procolobus rufomitratus*, mono aullador negro, *Alouatta pigra*, mono araña, *A. geoffroyi*), encontrando que los monos araña presentan una alta agregación, es decir, que los grupos de monos araña se reúnen con frecuencia en los mismos sitios visitados principalmente durante la temporada seca (Bonell *et al*., 2013) en relación a fuentes de alimento y sitios de descanso.

Otras investigaciones han evaluado la influencia de factores ambientales en las rutas de movimiento y uso del espacio por primates. Por ejemplo, en un estudio realizado con macacos (*Macaca mulatta*, Beisner e Isbell, 2009), se encontró que la densidad y distribución de alimento influenció fuertemente las rutas de movimiento de los monos, mostrando que cuando los recursos alimenticios se hallaban de forma impredecible en el ambiente, los macacos se movían de forma más irregular (mayor frecuencia en cambios de dirección y puntos de detención), lo que indica poca eficiencia en sus movimientos hacia un objetivo. En este contexto, otros estudios sobre movimientos en relación a encuentros con fuentes de alimento, han evaluado la habilidad de algunas especies de monos para ser más eficientes en su búsqueda de recursos a través de "mapas mentales" o uso de la memoria espacial (e.g. mono araña, *A. g. yucatanensis*: Valero y Byrne, 2007; sakis de cara blanca, *Pithecia pithecia*: Cunningham y Janson, 2007, Anzelc, 2009; gibones, *Hylobates lar*: Asensio *et al*., 2011). Los resultados de estos estudios sugieren de manera general que los primates estudiados incrementan la eficiencia de búsqueda de alimento y forrajeo mediante la disminución de las distancias recorridas hacia los frutos, así como el nivel de linealidad (o direccionalidad) y velocidad de sus recorridos hacia ellos cuando están fuera de su vista, lo que indica que sus desplazamientos son dirigidos y posiblemente utilizan la memoria espacial.

Por otro lado, se han sugerido otros mecanismos o estrategias para localizar eficientemente los recursos, como los desplazamientos basados en rutas (route-based travel), en los cuales los primates representan mentalmente diversos puntos en el ambiente que se interconectan y se mueven a través de ellos mediante rutas aprendidas (Poucet, 1993; Milton, 2000), lo que les permite recorrer su hábitat con eficiencia, y a diferencia de la memoria espacial, no requiere almacenar información respecto a las características del ambiente ni actualizar su posición de manera constante mientras se desplazan (Di Fiore y Suarez, 2007).

2.3. Uso de dormideros por primates

Se ha establecido que los dormideros son un recurso que puede tener un fuerte impacto en la dinámica de las comunidades vegetales (Russo *et al*., 2005; Russo y Chapman, 2011) dada su asociación a la formación de letrinas por frugívoros. Entre las consecuencias ecológicas de las letrinas, puede mencionarse el patrón de deposición agregada de semillas de diversas especies, que generalmente se encuentran en conjunto con una gran cantidad de excremento y nutrientes (Feeley, 2005; Pouvelle *et al*., 2009). De esta manera, dicho patrón de dispersión de semillas puede influenciar el reclutamiento, la distribución espacial y el potencial regenerativo de las poblaciones de plantas (Russo *et al*., 2006). A pesar de su potencial importancia, no está claro cuáles son los aspectos que determinan la selección de dormideros por primates.

Se han propuesto algunos factores como posibles explicaciones de la selección de dormideros por primates, entre los que destacan: la protección o seguridad contra depredadores, comodidad e higiene ofrecidos por los árboles dormideros, dinámica social, termorregulación, disponibilidad, cercanía a fuentes alimenticias y agua y defensa territorial (Anderson, 1998, 2000; Day y Elwood, 1999; Di Bitteti *et al*., 2000; Franklin *et al*., 2007; Holmes *et al*., 2011; Fei *et al*., 2012).

Las especies arbóreas utilizadas como dormideros varían ampliamente entre las especies de primates y las áreas geográficas donde se ubican. Los resultados de varios estudios muestran que los árboles usados como dormideros presentan características similares para muchas especies de primates, entre las que pueden mencionarse (1) las elevadas alturas, que generalmente oscilan en un rango de 20-30 m, aunque algunos árboles superan esta altura; (2) promedio del diámetro a la altura del pecho (DAP) entre los 50-80 cm, con ciertos dormideros de mayor medida, y (3) diámetro de la corona de 13-19 m (Von Hippel, 1998; Day y Elwood, 1999; Di Bitteti *et al*., 2000; Pozo, 2005; Smith *et al*., 2007; Holmes *et al*., 2011; Teichroeb *et al*., 2012).

Un estudio realizado en Costa Rica mostró que *A. geoffroyi* utilizó algunos árboles como dormideros y de manera repetida. Las características de éstos fueron comunes dentro de su ámbito hogareño, se reportó que el número de dormideros utilizados se relaciona a las necesidades alimenticias de los monos araña (Chapman, 1989a, b).

En otro estudio realizado en México, se investigó la distribución espacial y densidad de árboles utilizados como sitios para dormir y formación de letrinas por monos araña, encontrando que la distribución de los dormideros fue variable y agregada (González-Zamora *et al*., 2012). Dicha variación se atribuyó a la distribución de fuentes de alimento y a la estrategia de forrajeo de los monos araña. Los árboles que representaron los dormideros, fueron las especies mayormente consumidas y los más abundantes en el hábitat.

Con los antecedentes descritos anteriormente, parece ser que la selección de árboles usados para dormir está asociada a la distribución y la distancia hacia las fuentes de alimento. Sin embargo, en el caso de *A. geoffroyi* no se ha estudiado con amplitud esta relación ni las características de los dormideros (DAP, diámetro de la corona, altura) utilizados (*A.g. yucatanensis*), así como su importancia ecológica.

3. HIPÓTESIS

- Los monos araña presentarán una alta linealidad y direccionalidad en sus rutas de desplazamiento hacia las fuentes de alimento, sugiriendo el posible uso de un mapa cognitivo o memoria espacial.
- Los árboles usados como dormideros presentarán mayor diámetro a la altura del pecho (DAP) en comparación con los árboles circundantes.

4. OBJETIVO GENERAL

Analizar las rutas de desplazamiento en relación al uso de alimento así como el uso y caracterización de dormideros por una tropa de monos araña (*Ateles geoffroyi*) durante la época lluviosa en el ejido Nuevo Becal del municipio de Calakmul, Campeche, México.

5. OBJETIVOS ESPECÍFICOS

- Describir las fuentes de alimento de los monos araña durante la época de lluvias en el ejido Nuevo Becal, Campeche.
- Comparar la linealidad de los desplazamientos entre segmentos de ruta con y sin presencia de fuentes de alimento.
- Determinar la persistencia en la direccionalidad de los movimientos de los monos araña.
- Caracterizar los sitios utilizados como dormideros por un grupo de monos araña en el ejido Nuevo Becal en la época de lluvias.

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7. ARTÍCULO CIENTÍFICO

Travel strategies, feeding behavior, and sleeping tree use of spider monkeys (*Ateles geoffroyi*) of Calakmul, Mexico

Julián Parada-López[1*], Rafael A. Reyna-Hurtado[2], Silvia F. Hernández-Betancourt[1,] and Colin A. Chapman[3].

[1]Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán. Km. 15.5 carretera Mérida-Xmatkuil, C.P 97100. Mérida, Yucatán, México.

[2]El Colegio de la Frontera Sur (ECOSUR), Unidad Campeche. Libramiento carretero km. 1.5. Av. Rancho Polígono 2-A, Parque Industrial de Lerma, 24500. Campeche, México.

[3]McGill School of Environment and Department of Anthropology, McGill University, Montreal, Quebec, Canada H3A 2T7 and Wildlife Conservation Society, Bronx Zoo, Bronx, NY.

*Corresponding author: jplbiol@gmail.com

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Abstract

Movement is a spatiotemporal process by which animals travel to get food and other resources needed to survive. In frugivorous primates movements have been closely related to search for food, but information about movements based on habitat and other resources are generally lacking. Here we analyze the movements of spider monkeys (*Ateles geoffroyi*) to food sources in the Calakmul region, Mexico, and characterize sleeping sites used. We recorded the floristic composition based on transects and calculated the Importance Value Index (IVI) for each tree species. We recorded sleeping trees used and trees adjacent and calculated diameter at breast height (DBH) and IVI. We followed individuals of a community of spider monkeys for 4 months during the rainy season and took GPS locations every 5 min to quantify travel routes. We calculated linearity ratios of route segments that ended and did not end at food trees and compared both types of segments, and determined the directional persistence of spider monkey movements. Four species used as sleeping sites had higher DBH and relative high IVI, compared to adjacent trees. Linearity ratios was high ($\mu > 0.7$) and the directional persistence reveals that spider monkeys traveled efficiently, which might be result of the use of a cognitive map. This approach is useful to understand environmental influences on primate spatial abilities and to determine important locations for conservation planning.

Keywords: Travel routes, linearity, directional persistence, spider monkeys, Nuevo Becal

Introduction

Movement is a vital process that influences several ecological processes (Nathan *et al*. 2008), such as searching for food, sleeping sites, and mates; factors contributing to individual fitness, species survival, and geographic distribution (Mueller and Fagan 2008). Movement is also a spatiotemporal process by which animals travel in heterogeneous landscapes (Bonnell *et al*. 2013) searching for areas that are profitable in regard to their specific needs. In this sense, animals do not spend all the time in a single area because their needs changes with time and sites transform over time (e.g., food patches are depleted) (Barraquand and Benhamou 2008). Thus, it is typically assumed that the degree of benefit of a local environment is directly related to the intensity in the use of that space (Barraquand and Benhamou 2008; Bonnell *et al*. 2013) and consequently of resource use, which in turn determine travel routes among environments.

Movement patterns in animals are commonly analyzed through theoretical models used to describe the observed travel behavior, such as Lévy walks (Bartumeus *et al*. 2005; Ramos-Fernández *et al*. 2004; Viswanathan *et al*. 1999; Viswanathan *et al*. 2008), Brownian motion (Bergman *et al*. 2000; Bovet and Benhamou 1988; Giuggioli *et al*. 2011; Marell *et al*. 2002), and fractal analysis (Nams 2005; Webb *et al*. 2009). The Lévy walk has been suggested to be optimal when resources are scarce and patchily distributed (Ramos-Fernández *et al*. 2004). In contrast, Brownian motion has been suggested to be optimal when resources are uniformly distributed (Humphries *et al.* 2010; Wittemyer *et al*. 2008). In fractal analysis, the main measure considered for analysis of travel paths is the tortuosity, which could indicate the intensity of use of a certain area within the animals' home range (Etzenhouser *et al*. 1998; Nams and Burgeois 2004).

Another approach of animals travel route analysis is the examination of mechanisms that lead the animals to their food sources. Several studies addressed this question and analyzed the movement efficiency of wild primates in terms of the degree of linearity of travel routes, angular progression of movements to measure directional persistence, level of backtracking and revisiting patterns of sites that primates had previously fed in (*Cercocebus atys* and *Lophocebus albigena* - Jaanmat *et al*. 2006, 2012, *Pithecia pithecia* - Cunningham and Janson 2007, Anzelc 2009, *Ateles geoffroyi* - Valero and Byrne 2007). These studies have found a high linearity and directionality in the movements of primates to their preferred foods when these are located beyond their visual field, suggesting that primates may use spatial memory as a mechanism to relocate food resources and to travel efficiently through their home range. Spatial memory is thought to allow animals to reduce uncertainty regarding their position with respect to locations and implies that an animal can code, store, recall, and decode spatial information (Fagan *et al*. 2013).

In the case of frugivorous primates, relevant information about their environment is the spatiotemporal patterns of food availability, which is of primarily interest when making decisions about foraging and ranging (Di Fiore and Suarez 2007). Thus, abundance and distribution patterns of fruits are crucial to understand their movement (Valero, 2004). Gathering information about the composition of vegetation in an area is useful because it provides details of the potential food sources available to primates.

In addition, data on other resources used by primates, like sleeping trees, are generally lacking. Sleeping trees are thought to be relevant since they may offer protection from predators, comfort and hygiene, promotes social bonding, and are selected when located near food sources (Anderson 1998, 2000; Chapman 1989; Day and Elwood 1999; Di Bitteti *et al*. 2000; Fei *et al*. 2012; Franklin *et al*. 2007; Holmes *et al*. 2011). Therefore, it appears that sleeping trees have biological relevance because of their influence in home range use and fitness (Di Bitteti *et al*. 2000; Hamilton 1982).

In this study we first provide general information about vegetation to characterize floristic composition of the forest. Then we characterized *A. geoffroyi's* sleeping sites, and examined their travel strategies in relation to feeding sites near the village of Nuevo Becal, Campeche, Mexico, a community forest that is located near Calakmul Biosphere Reserve in the Mexican Maya forest. We expected that 1) sleeping trees would have greater DBH than adjacent trees; 2) food trees strongly influence the travel routes of spider monkeys, and 3) travel routes shows high linearity and directional persistence patterns to feeding trees (i.e. more forwardness in the movements).

Methods

Study species and study area

The spider monkey is a threatened species in most of its distribution range. In Mexico, it is listed in the protection law of wildlife species (SEMARNAT 2010) and in the red list of the IUCN (IUCN 2015). It is threatened mainly due to habitat degradation driven by selective logging. This species are fruit-eating specialists, and a small number of plant species comprises ≥ 70-80% of the total feeding time (González-Zamora *et al*. 2009; Chaves *et al*. 2012). This suggests that spider monkeys are strongly selective in their food choices and highlights its vulnerability to disturbances that decrease the availability of their preferred foods.

Data collection was made in the community forest (25, 000 ha) near the village of Nuevo Becal, in the municipality of Calakmul in the state of Campeche, Mexico, which is located in the coordinates 18°40’0.7.7” N, 89°12’34.3” O, adjacent to the Calakmul Biosphere Reserve. Vegetation in the area is mainly semi-evergreen tropical forest with a mean height ~15-25 m, but there are also smaller areas of low flooded forest. The site is located 14 km northeast of the village. This locality has one of the largest forested area in Calakmul (520 km^2), and common activities outside the community forest are subsistence hunting (mainly of collared peccaries, *Pecari tajacu*, white-tailed deer, *Odocoileus virginianus*), sport hunting (Weber *et al*. 2006), and timber and non-timber products extraction such as palm leaves, honey, and gum, and selective logging inside and outside the community forest. Spider monkeys are not hunted in the area. The climate in the municipality is warm subhumid with summer rains, mean annual temperature of 24.6 °C and mean annual precipitation of 1200-1500 mm at the center and 1500-2000 mm at the south (García-Gil *et al*. 2002).

Floristic composition and vegetation structure

To provide a description of what resources are available to the population, five transects were established in areas where spider monkeys had initially been seen to travel. This method is economical in time and effort and is appropriate for rapid assessment of habitat (Gentry 1982). The diameter at breast height (DBH) was measured for each tree when DBH ≥ 10 cm. Two transects were 500 x 6 m and three were 1000 x 6 m, comprising a total sampling area of 2.4 ha. Tree species were identified with the help of the field assistant and using the guides of the flora of Yucatan Peninsula (Arellano-Rodríguez *et al*. 2003; Cabrera-Cano and Sánchez-Vázquez 2000), based on the description of the species, uses, common and Mayan names, and pictures of the plants.

An Importance Value Index (IVI) was calculated to describe the relative ecological importance of each species in a plant community, and is estimated by the sum of: relative dominance, which is the total basal area of one species/total basal area of all species x 100; relative density=number of individuals of one species per sampled area/number of individuals of all species per sampled area x 100; relative frequency=occurrence of one species in the sampling units/occurrence of all species in the sampling units (Curtis, 1959). Thus, to calculate IVI, we placed transects of 100 x 6 m over the same line and direction, separated by 100 m each. Thirteen transects were placed in north-south orientation, and eight were east-west, for a total of 21 transects.

Sleeping tree use

To locate sleeping trees, searches were made across the study area for two days per field session (a field session consisted in nine days of field work) looking for accumulation of feces on the ground. Spider monkey feces typically have an elliptical shape, brown yellowish color and several seeds are found in the fecal mass. Sleeping sites are easily identified by the accumulation of large amounts of dung. Once located, sleeping trees were marked with flagging tape and their DBH and location recorded. Also, the tree species within a radius of 20 m of a sleeping tree and their DBH were recorded to characterize the area. In addition, we calculated the IVI of sleeping tree species and species surrounding to compare them, considering each sampled area surrounding sleeping trees as a sampling unit.

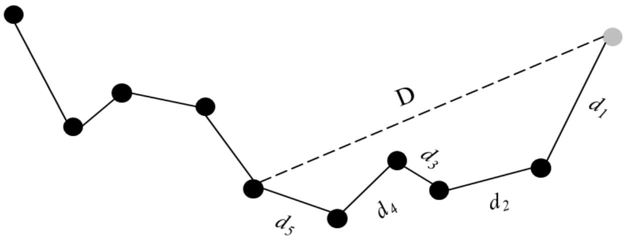
Collection of behavioral and spatial data

Prior to data collection, a 7-days habituation period was conducted to reduce the monkeys stress to human observers. Only seven days were used for habituation because the spider monkeys of the community forest are partially habituated to human presence since local people enters in the area. Given the limited time and economical resources available for field work, observations were made between August and November 2014 (rainy season), following focal animals for a mean of seven days per field session, excepting November which had only four days due to extremely bad weather.

A randomly selected individual from the first subgroup contacted in the morning was followed for as long as possible. Given the dense vegetation, lack of trails, poor visibility in the canopy, heavy rains and rapid movements of spider monkeys, it was impossible to follow individuals for long periods. Daily observations were made only starting in the mornings and mean following time was three hrs per day, ranging from 1-7 hrs, for a total of 23 hrs of observation. Geographic location was recorded every five minutes with a GPS (GARMIN GPS map 62s) to quantify travel routes. Only adults and subadults were followed, excluding the infants and juveniles since they followed their mother and do not provide additional information about ranging behavior (Gibson 2008; McFarland Symington 1988; Valero and Byrne 2007). Activities (feeding, resting, moving, and social interactions) were recorded at 15 min intervals in 5-min sessions using focal animal sampling. When spider monkeys fed, the tree species consumed, plant part, duration (in minutes) of feeding and GPS location were recorded.

The GPS recordings (in UTM coordinates) were entered in QGIS v. 2.4 (Quantum GIS Development Team 2014) to visualize and analyze the travel routes. The routes were created using a vector layer containing the GPS locations and points were joined with the *Points to path* tool (Hiatt 2013). Subsequently, we calculated the length of each step (distance between two GPS points). In addition, we estimated the home range area using the grid-cell count method, a non-statistical method which consists in superimposing a grid with cells of the same size over the GPS locations. Then, we summed the area of the cells, considering those that presented at least one GPS point (Kenward 2000). The cell size was determined by the mean step length of the focal individuals (65 m) (White and Garrot 1990), with the resulting cell size of 65 x 65 m. Since the grid-cell count is non-statistical, it is not very accurate and other methods are needed for a better estimation of home range, but those methods requires specialized procedures and their use would constitute a research paper itself, which is beyond the aim of the present study.

For analysis of movements in relation to food sources, route segments (defined as portions of the partial route of a given day) were determined by selecting the locations of feeding trees as ending points, from which we counted five steps backwards to indicate the starting point, making sure that the segments did not overlap and spider monkeys traveled directly to the food source. Subsequently, we calculated the route segment length, given by the sum of distances between GPS points constituting the segments; direct distance between starting and ending points of the route segments; linearity ratio, calculated by dividing the direct distance and route segment length (Anzelc 2009; Cunningham and Janson 2007; Valero and Byrne 2007) (Fig. 1). We chose five steps because location records were taken every 5 min, so the route segments involves trajectories of 30 min and the distance traveled during this time reduces the probability of visual detection of the food source (estimated visual field range in spider monkeys is 30-80 m, Valero and Byrne 2007). In addition, we randomly selected GPS locations where the animal did not arrive at a food trees and repeated this process to calculate linearity ratio to compare movement to feeding and non-feeding sites.



$$\mathrm{LR} = \frac{\mathrm{D}}{\Sigma\, d}$$

Fig. 1 Graphical representation of a hypothetical partial route and route segment. Gray point indicates a feeding tree, D represents the direct distance between starting and ending points, *d* indicates distance of each step. LR means linearity ratio.

Also, we represented the spider monkeys feeding patches using the heat map tool in QGIS, which estimates the density of spider monkeys location records based in kernel density estimation. Then, we superimposed the location of food trees, and this matched with the areas of major density, so we delineated polygons of these areas and were considered the feeding patches. In addition, we contrasted the route overlap considering the number of intersections within feeding patches to the number of intersections outside these patches.

Data analysis

For testing linearity, a Wilcoxon rank sum test was performed to compare the linearity ratios between route segments that ended in food trees and those that did not end at food trees, expecting that the formers would have greater linearity ratio (one-tailed test).

To determine the degree of directional persistence or backtracking of focal individuals, we used circular statistics (Batschelet 1981). To do this, first we calculated the turning angles of the steps by subtracting the bearing of step a to the bearing of step b, and bearing of step b to c, and take the absolute value, so if bearing of a= 37°, bearing of b=82°, and bearing of c=60°, the clockwise rotation needed to align successive steps are: when $a<b$, $|37-82|=45°$, when $b>c$, $|(82-60)-360|= 338°$ (Valero and Byrne 2007). The Rayleigh Z test was applied to overall data set of turning angles and those of the route segments to test if the distribution was uniform around the circle, which means that spider monkeys are traveling in a random fashion. If this distribution was not uniform, the V test was used to determine the clustering around a specified value. In this case we expected clustering around 0/360°, which indicates more directional movements than backtracking.

We analyzed the spatial distribution of feeding trees (i.e., random, uniform, and clumped) within the home range by creating a grid of 1 ha cell size. We plotted the UTM coordinates of feeding trees and counted the points within each cell. Then we used the Morisita index of dispersion (I_d) to assess the spatial arrangement (Morisita 1962) by the following formula:

$$I_d = n\left(\frac{\sum x_i^2 - \sum x_i}{(\sum x_i)^2 - \sum x_i}\right)$$

Where n is the number of samples (cells) and x_i is the number of trees in the i cell. I_d=1 indicate random distribution of feeding trees, >1 means a clumped distribution, and <1 for uniform distribution. We tested the hypothesis of clumped distribution with the Chi-squared statistic.

A one-way Kruskal-Wallis analysis of variance was used to explore for differences in mean step lengths between months. A Chi-squared goodness-of-fit test was performed to determine if there was difference in the degree of route overlap between feeding patch areas and non-feeding patch areas. Oriana 4 (Kovach 2012) and R v 3.0.1 (R Core Development

Team 2013) were used for statistical analysis. All statistical tests were considered significant when $P \leq 0.05$.

Results

Floristic composition and vegetation structure

We recorded 1457 trees from transects, belonging to 70 species, 53 genus and 25 families. The Sapotaceae had the majority of records (N=453) and Fabaceae had the greatest species richness (N=11), followed by Moraceae (N=5), Sapotaceae (N=5), and Sapindaceae (N=4).

Pouteria reticulata was the most abundant species (N=273, 18%), followed by *Brosimum alicastrum* (N=129, 8%), *Coccoloba acapulcensis* (N=101, 6.9%), *Manilkara zapota* (N=98, 6.7%), and *Bursera simaruba* (N=95, 6.5%). The first, second, and fifth transects are characterized by semi-perennial medium forest, where *P. reticulata* was associated mainly with *B. alicastrum*, *C. acapulcensis*, *Pouteria campechiana*, and *B. simaruba*. The third and fourth transects are characterized by semi-perennial medium forest in combination with low flooded forest (with greatest proportion in the fourth transect), the latter is a forest type characterized by the presence of *Haematoxylum campechianum*, which is associated with *M. zapota*, *Bucida buceras, Metopium brownei*, and *Erythroxylon confusum*.

The species *P. reticulata* had the highest IVI and was influenced mainly by its relative density, which was substantially greater than other tree species. In contrast, *B. alicastrum* had lower relative density, but higher relative dominance than *P. reticulata,* although the latter value strongly influenced its IVI (Table 1), which is related to DBH, which averages 28 cm in *B. alicastrum,* contrasting with average DBH of 16 cm of *P. reticulata.*

Table 1. Importance Value Indices of common tree species and species most consumed by spider monkeys (*) in the community forest of Nuevo Becal.

Species	Basal area (m^2)	Relative Dominance	Relative Density	Relative Frequency	IVI
Pouteria reticulata	6.25	10.95	18.73	5.98	35.67
*Brosimum alicastrum**	9.86	17.28	8.85	4.65	30.78

Bursera simaruba	5.6	9.81	6.52	5.31	21.64
*Manilkara zapota**	5.22	9.15	6.72	4.31	20.19
Coccoloba acapulcensis	2.05	3.60	6.93	6.31	16.84
Pouteria campechiana	3.22	5.65	4.46	4.65	14.76
Haematoxylum campechianum	2.64	4.62	4.25	1.99	10.87
Protium copal	1.22	2.15	2.47	2.99	7.61
Unidentified species	0.01	0.92	2.47	3.65	7.04
Swietenia macrophylla	1.67	2.92	1.50	2.32	6.76
Metopium brownei	1.02	1.79	2.53	1.99	6.33
*Licaria peckii**	1.04	1.83	1.37	1.99	5.19
*Pimenta dioica**	0.46	0.82	0.75	0.99	2.56

Sleeping tree use

Eight spider monkey sleeping trees were identified from 4 species; *Lysiloma latisiliquum, Swietenia macrophylla, B. buceras* and *Lonchocarpus castilloi*. In contrast, we recorded 372 trees around the eight sleeping trees, which the most abundant species were *B. simaruba* with 70 records (18%), *P. reticulata* with 51 (13%), and *M. brownei* with 32 (8.6%; Table 2). The mean height and DBH of the sleeping trees was 20.1± SD 2.09 m and 65.57 ± SD 31.16 cm (CI 95%=34.41-96.73), respectively, the latter is greater than mean DBH of adjacent trees (21.62 ± SD 9.47, CI 95%=12.15-31.09), and DBH of transect trees (20 ± SD 9.82, CI 95%=10.18-29.82).

Table 2. Summary of characteristics of sleeping tree species used by spider monkeys in Nuevo Becal in the rainy season. Species are presented according to the order that were found.

Species	Mean height	Mean DBH	Mean No. of adjacent species	Most abundant adjacent species
L. latisiliquum	20.6	86.89	19.6	*B. simaruba, P. reticulata, B. schlechtendalii, P. piscipula*
S. macrophylla	22	35.96	19	*B. simaruba, B. alicastrum, P. reticulata*
B. buceras	19	79.41	17.5	*P. reticulata, M. brownei*
L. castilloi	17	32.78	17	*M. brownei, Sabal yapa*

Quantifying the IVI of the sleeping trees and adjacent trees demonstrated that *B. simaruba,* and *P. reticulata* had the highest IVI, values influenced by their high relative density. Three species used as sleeping trees had relatively high IVI, which were influenced mainly by their relative dominance values (Table 3).

Table 3. Importance Value Index of the sleeping tree species and the most abundant adjacent species. Bold numbers are values of sleeping tree species

Species	Relative Dominance	Relative Density	Relative Frequency	IVI
Bursera simaruba	18.94	18.86	4.76	42.57
Pouteria reticulata	5.23	13.74	5.44	24.42
Swietenia macrophylla	9.68	5.66	4.76	**20.11**
Metopium brownei	5.51	8.62	5.44	19.57
Pouteria campechiana	4.28	5.39	5.44	15.12
Lysiloma latilisiquum	10.82	1.34	2.72	**14.89**
Brosimum alicastrum	3.78	4.58	4.08	12.44
Manilkara zapota	5.96	2.42	3.4	11.79
Bucida buceras	6.22	1.34	2.72	**10.29**
Bursera schlechtendalii	3.7	3.5	2.72	9.93
Piscidia piscipula	2.72	3.23	2.04	7.99
Pimenta dioica	1.79	2.69	3.4	7.89
Vitex gaumeri	1.92	2.15	3.4	7.48
Pseudobombax ellipticum	2.71	1.61	2.72	7.05
Protium copal	1.21	2.42	3.4	7.03
Lonchocarpus castilloi	1.47	1.61	2.72	**5.81**

Feeding behavior

Spider monkeys fed on 18 species, two of which could only be identified to genus level and five could not be identified. Feeding contributed with 28% of the focal sampling time. *B. alicastrum, M. zapota, Pimenta dioica*, and *Licaria peckii* were the four most commonly fed on trees, accounting for the 74% of the feeding time, so we considered these as the top food tree species in the rainy season (Table 4).

Table 4. Percentages of feeding time of each species consumed by spider monkeys per sampling month. Unidentified species were grouped in a single row.

Species	Months				Total %
	Aug	Sep	Oct	Nov	
Blepharidium mexicanum		9	2	5	3
Brosimum alicastrum		14	62	31	36
Coccoloba acapulcensis	7				1
Desmoncus quasilarius	1				0.2
Ficus spp.	3	7		26	5
Licaria peckii	26	18			9
Malpighia spp.	10	14			5
Manilkara zapota			32	11	16
Mosannona depressa			1	17	3

Pimenta dioica	24	38			13
Pouteria reticulata	9				2
Sabal yapa	1				0.3
Unidentified species	17		3	10	6
Vitex gaumeri	2				0.5

Nine food tree species occurred on transects, of which *B. alicastrum* and *M. zapota* had the greatest IVI, while *P. dioica* and *L. peckii* had smaller IVI values compared with other species in the transects (Table 1). Considering the focal animal sampling (N=116) and incidental observations (N=31), 147 feeding events were recorded. *B. alicastrum* and *M. zapota* were eaten most frequently mainly in October, followed by *P. dioica* and *L. peckii*, which had the majority of their feeding records in September and August, respectively. Also, these species had the greater number of focal samples with feeding time > 4 min. Of the total feeding time, only 1.5% the monkeys ate leaves, and 0.2% ate branches. Fruits constituted 98.3% of their feeding time.

Spider monkeys travel strategies

Mean linearity ratio of route segments that ended in food trees was 0.8 ± SD 0.17 (N=37), of which 75% with linearity ratios >0.7. Mean linearity ratio of the segments that did not end at a food trees was 0.72 ± SD 0.16 (N=10), and these linearity ratios were not statistically different, although this result was marginal (Wilcoxon sum rank test: W=240, one-tailed test, P=0.07). There was no significant difference in mean step length between months (one-way Kruskal-Wallis test: χ^2=5.3061, df=3, P=0.15). The fact that only 10 route segments did not end at food trees, suggests that food trees strongly influence travel routes. To confirm this assumption, we applied a buffer of 50 m to all GPS locations that were not food sources and superimposed the locations of the food trees recorded, and found that these areas enclosed 96% of the food trees, reinforcing the influence of these resources on spider monkey travel paths.

For the overall turning angle data and for the route segments turning angle data, we tested the null hypothesis that the turning angles would be uniformly distributed around the circle. In both cases we found that the distribution was significantly non-uniform, rather was concentrated in a specified value. Also we tested if the distribution of the turning angles would be concentrated around 0/360° and this proved to be the case (Fig. 2, Table 5).

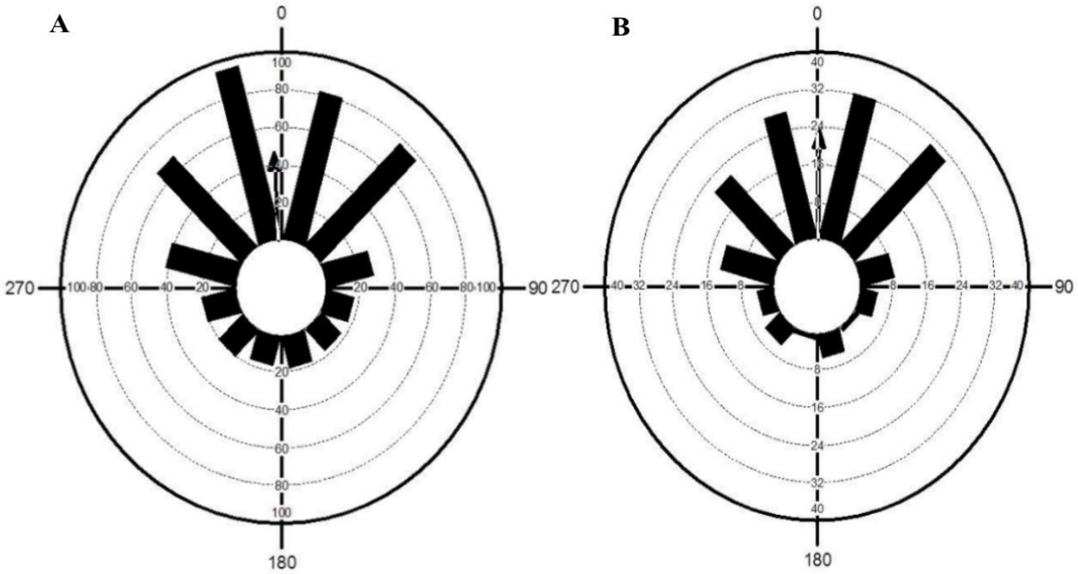


Fig. 2 Circular histograms showing the distribution and frequency (size of bars) of turning angles of the overall data set (a) and angles of route segments that ends in food trees (b). Arrows indicate mean vector.

Table 5. Circular analysis of turning angles of spider monkey movements in the rainy season in Nuevo Becal, Mexico. Z values indicate results of Rayleigh's test and u values are results of V test. Mean (µ), standard deviation (SD) and confidence intervals (CI) are in degrees.

Type of data set	N	µ (SD)	95% CI of µ	Mean vector length (r)	Z	P value	u	P value
All steps	492	356.37 (70.73)	349.14-3.5	0.467	107.17	<0.0001	14.61	<0.0001
Route segment steps	152	0.87 (59.37)	350.97-10.77	0.585	51.94	<0.0001	10.19	<0.0001

The home range of spider monkeys in the rainy season was composed of 205 cells, representing 86.61 ha. In contrast, we identified 6 feeding patches with areas of 6.19, 0.43, 0.17, 1.81, 3.84, and 0.62 ha, which comprised an area of 13.06 ha (15% of the home range). The degree of route overlap between feeding patch areas (N=193 intersections) and non-feeding patch areas (N=113 intersections) was significantly different (χ^2=20.91, df=1, P<0.001), indicating that feeding patches are more intensively used (Fig. 3). The distribution of feeding trees was significantly clumped (I_d=1.30, χ^2=2073.39, df=101, P<0.001), which is consistent with the difference in visits to food trees in feeding patches (N=67) against visits to food sources outside the patches (N=36) (χ^2=9.33, df=1, P=0.002).

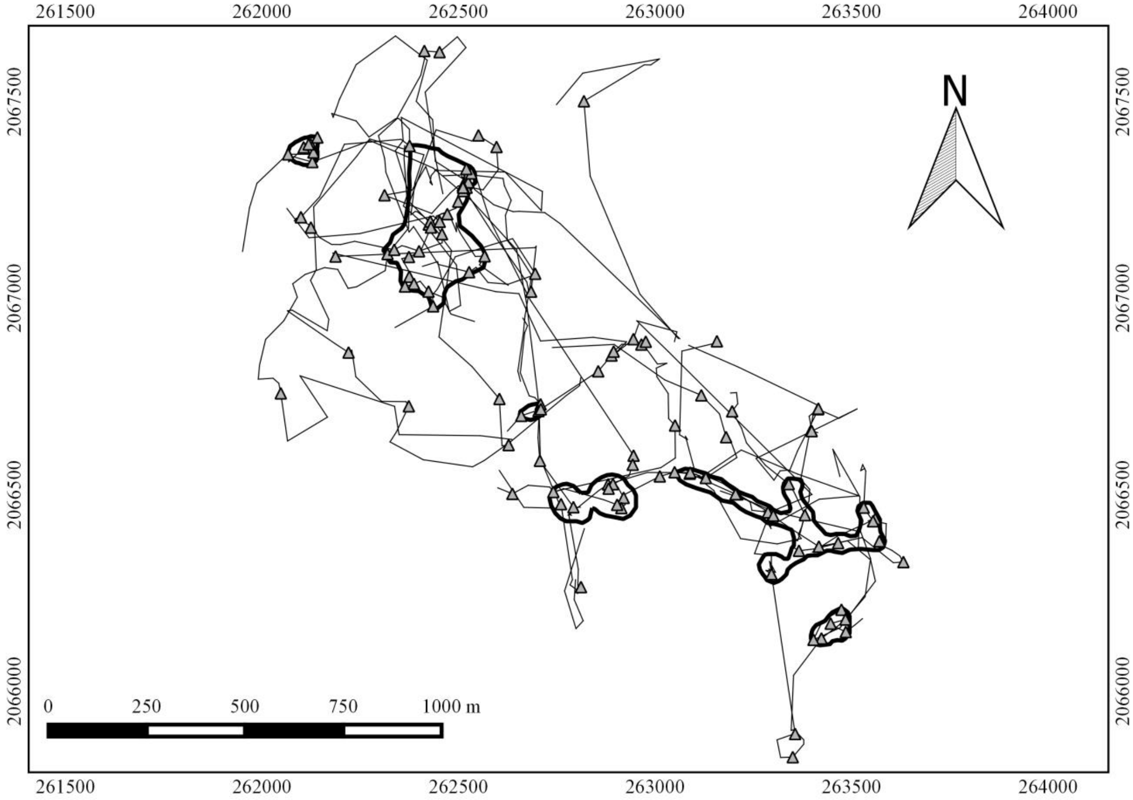


Fig. 3 Spider monkey travel routes in the rainy season in Nuevo Becal, Mexico. Triangles are the feeding trees. Thicker black lines are the different feeding patches, where the majority of route intersections enclosed in the largest.

Discussion

The density of trees recorded in transects is comparable with records of other forests in Mexico with spider monkeys. For example, in a study of this species in the Selva Lacandona, Chiapas, researchers used transects to determine vegetation composition

(Chaves *et al*. 2012), and recorded 1774 trees belonging to 96 species, 78 genera and 34 families in 30-90 ha considering forest fragments and continuous forest sites. In this study, we recorded a similar number of trees, species and family richness in a similar area (>86 ha). This highlights the great vegetation density of trees with DBH > 10 cm in our study site and its importance as a potential habitat to likely sustain a large viable population of spider monkeys, since the number and size of trees are related with primate abundance (Anzures-Dadda and Manson 2007; Worman and Chapman 2006).

Spider monkeys used a few tree species for sleeping that are among the largest in the area sampled, as evidenced by the clear difference in DBH of sleeping trees in relation to other trees recorded (mean DBH of transect and adjacent trees was 20 and 21 cm, respectively vs. 65 cm of sleeping trees), which is similar to the findings of other study of spider monkeys (Chapman 1989), and studies of other Neotropical primate species (golden-handed tamarin *Saguinus midas,* Day and Elwood 1999; tufted capuchins *Cebus apella,* Di Bitteti *et al.* 2000). In addition, sleeping trees used by spider monkeys in our study site had similar characteristics, which were straight trunks, large crowns and abundant lateral branches (personal observation) as were found in Lacandona rainforest (González-Zamora *et al.* 2012). This may reflect the importance of sleeping tree structure, since this type of trees can provide comfort (i.e., shelter from the elements, avoiding biting insects), reduce access for predators (i.e., height), and facilitate early detection of predators before an attack can be produced (Anderson 1984, 1998; Smith *et al*. 2007).

Of the total trees recorded, we only found ten trees with DBH equal to or greater than DBH of sleeping trees (65-72 cm), suggesting a low availability of large trees in the area sampled. This apparent lack of large trees with the characteristics mentioned above may affect negatively the survival of spider monkeys, because in physiological terms, brachiation is a costly mode of locomotion (Parson and Taylor 1977) and the monkeys need suitable places to rest in order to recover the energy expended during the day searching for food, participating in social interactions, or mating. In addition, high trees with large girth are associated with decreasing accessibility to terrestrial predators (Holmes *et al.* 2011), so the low availability of large trees may pose a risk of predation for spider monkeys. Also, the low availability of potential sleeping trees may produce competition for sleeping sites among individuals, which could result in aggressive encounters and have negative effects in spider monkey social organization. The relatively high IVIs of the sleeping tree species reflected the influence of the DBH, and may indicate this parameter as important to distinguish potential sleeping trees in Nuevo Becal, although further studies focused in evaluating the density of large trees, sleeping tree architecture and spatiotemporal variation in their use are needed to determine if DBH is a good predictor of sleeping tree selection.

In regard to food consumption, fruits of *B. alicastrum* were the item most consumed by spider monkeys at our study site, and had the greatest percentage of feeding time. This is similar to other results in other site of Yucatan Peninsula, where the fruit of this species where the most eaten and also had the greatest percentage of feeding time (Punta Laguna: Ramos-Fernández y Ayala-Orozco 2002; Valero 2004). In feeding terms, if we assume the importance of a species as a function of the time spider monkeys devoted to feed on that species, the high IVI of *B. alicastrum* and *M. zapota* is consistent with their highest percentage of feeding time. In fact, *B. alicastrum* is one of the most important food sources for spider monkeys and other species in Mesoamerica (i.e., *Pecari tajacu* and *Tayassu pecari*, Pérez-Cortez and Reyna-Hurtado 2008), since this species is widely distributed and has regular annual fruit production (González-Zamora *et al.* 2009), as well as *M. zapota*, which can produce fruits throughout the year (Mizrahi *et al.* 2001). On the other hand, *P. dioica* and *L. peckii*, which also largely contributed to feeding time showed low IVI values. This could reflect their low availability in our study site, but their fruits were ripe and abundant when spider monkeys ate them and contributed to a large proportion of feeding time on months (August and September, see table 4) when they were consumed, suggesting that spider monkeys may prefer fruits of these species over others in those months. Since food species had a significant clumped distribution in the home range, and given that the area is used for selective logging by local people, it is crucial to consider the distribution of these species as significant feeding locations that should remain unaltered to allow the monkeys a constant resource access, thus contributing to their long-term permanence in the area.

We found that spider monkeys traveled to their food sources very efficiently by means of high linearity (72% of overall route segments with linearity ratios >0.7) and directional persistence, as evidenced by the clustered distribution of turning angles around 0/360°, discarding the visual detection effect because route segments lengths were longer than the visual field estimation. Contrary to expected, there was no difference in linearity ratios between segments that ended in food trees and those that did not. The latter route segments were characterized by the presence of resting trees along the route, which may indicate the importance of resting times, or that these resting sites were just stop-over locations to the next feeding site. The high linearity to feeding trees reported in this study is similar to other results for spider monkeys in Yucatan Peninsula (Punta Laguna, Valero and Byrne 2007), but the difference in this study is that directional persistence were found in the rainy season, in contrast with the study of Valero and Byrne (2007) in which spider monkeys showed less directed movements to food sources in the same season. This difference may be due to a difference in fruit availability in the rainy season between sites. The greatest availability of food sources in the rainy season promotes more uniform distribution of those resources, so the distance between them are reduced and thus increases the probability of visual detection. Under this scenario, we would expect more random movements rather than goal-directed ones. In this sense, our results are similar to what is expected for the dry season, since the clumped or patchier distribution of food sources, which are common in this season, are related to more directed travel, as has been shown for other primate species (i.e., tamarin monkeys, *Saguinus mystax* and *Saguinus fuscicollis*, Garber 1988, 1989; chacma baboons, *Papio ursinus*, Noser and Byrne 2007).

The high linearity and directionality found in spider monkeys' movements to out-of-sight resources could be evidence of the use of a coordinate-based mental map or spatial memory, since spider monkeys most of the times computed the most efficient routes (direct travel) to reach their targets, which has also been suggested for chimpanzees (*Pan troglodytes*, Normand and Boesch 2009), white-faced sakis (*Pithecia pithecia*, Cunningham and Janson 2007), sooty mangabeys and grey-cheeked mangabeys (*Cercocebus atys* and *Lophocebus albigena*, Janmaat *et al.* 2006). Frugivorous primates are challenged to be efficient in their searches for resources because fruits are patchily distributed in space and time in tropical forests, so the ability to remember the location of food sources increase their search efficiency, which in turn would decrease foraging costs related to time and energy expended in foraging (Milton 1981). From an evolutionary perspective, spatial memory provides advantages in terms of improved choice of critical locations (Fagan *et al.*

2013), such as food patches, which have an effect in the energy intake that is necessary for crucial activities, such as social interactions and mating, which influence primate fitness.

The spider monkeys in Nuevo Becal are efficient to navigate their home range searching for food, increasing their energy intake and chance of survival. The study of forest-living primate movement patterns in terms of spatial and foraging cognition could allow researchers to get insights of how the environment influences their ability to cope with spatial and temporal variation of resources, as well as their evolutionary implications. Also, this approach is useful to localize important tree species used for food or sleeping without an extensive habitat assessment, which could be considered as “hot spots” of fundamental interest to primates and to develop appropriate conservation plans, being particularly important in unexplored, non-protected areas where primates inhabit.

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