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DEPARTAMENTO DE MEDICINA LEGAL, TOXICOLOGÍA Y ANTROPOLOGÍA FÍSICA

IMPACTO DEL EFECTO BORDE EN LA ECOLOGÍA, COMPORTAMIENTO Y COMPOSICIÓN DE TROPA EN PRIMATES SILVESTRES (*MACACA NEMESTRINA*) EN EL PARQUE NACIONAL KHAO YAI, TAILANDIA

TESIS
QUE PRESENTA
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PARA LA OBTENCIÓN DEL TÍTULO DE
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A mis padres,
hermanos & Cía

Al monito que viene
y a quien lo alimenta

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ขอขอบคุ

King สำหรับความเป็นเพื่อนที่ดีและความช่วยเหลือในทุกๆอย่างตลอดเวลาที่ผมทำงานอยู่ที่เขาใหญ่

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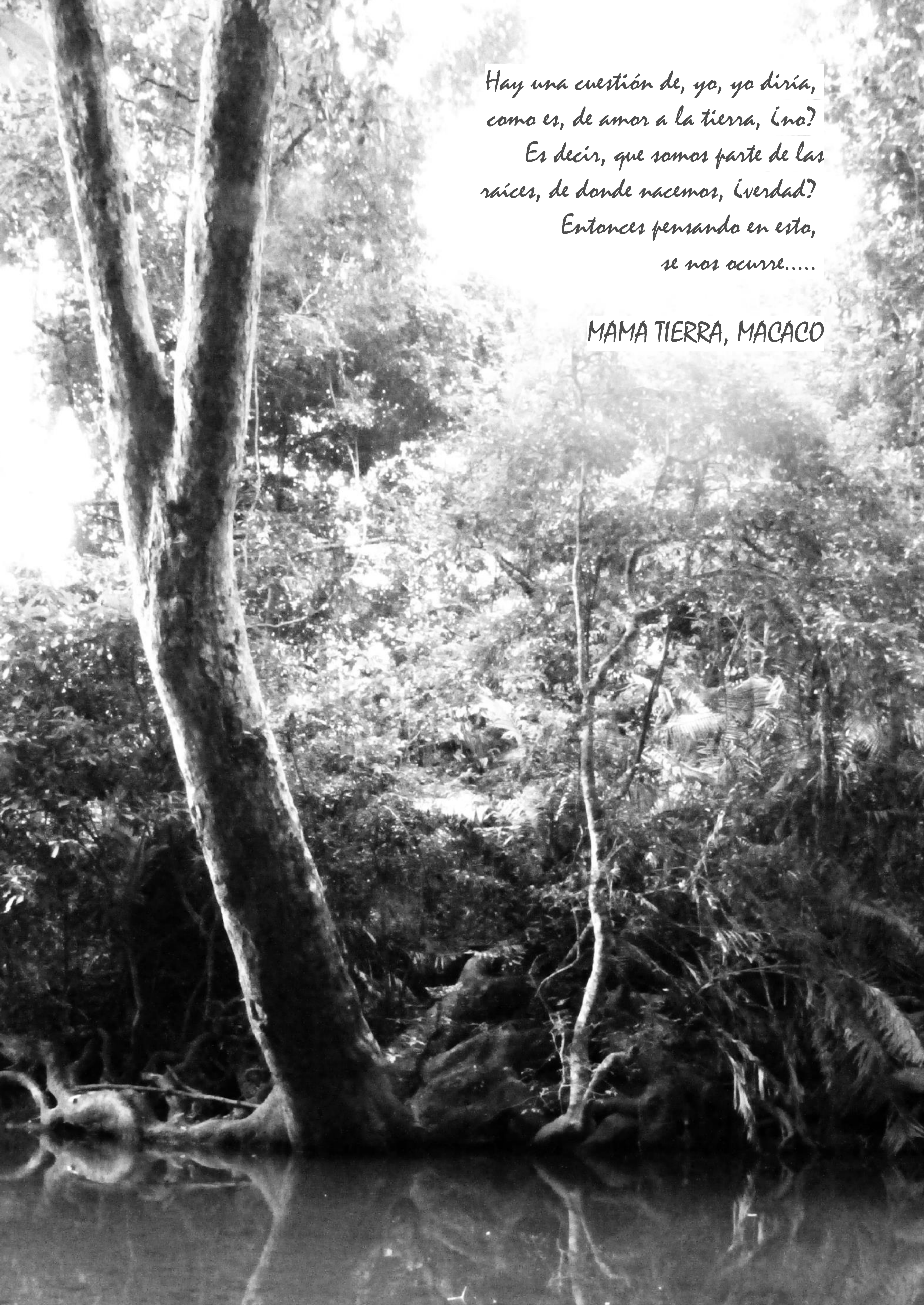


Hay una cuestión de, yo, yo diría, como es, de amor a la tierra, ¿no? Es decir, que somos parte de las raíces, de donde nacemos, ¿verdad? Entonces pensando en esto, se nos ocurre.....

MAMA TIERRA, MACACO

Resumen

Los patrones de movimiento son cruciales para entender la ecología, evolución y conservación de los primates, pero los estudios detallados son escasos para muchas especies. Por otro lado, las teorías sociecológicas sugieren que los recursos alimentarios y la presión a ser depredado son los factores más importantes para explicar el porqué y el cómo los animales sociales viven en grupo. Durante las últimas décadas se ha producido una gran pérdida de bosque en todo el planeta, lo que ha creado nuevos escenarios de contacto entre el ser humano y la fauna salvaje, donde la abundancia y distribución de recursos se han podido alterar.

En esta disertación se pretende dar un poco de luz al impacto antrópico en la ecología de la fauna salvaje y en concreto en la de una especie de primate no territorial, *Macaca leonina* (anteriormente, *Macaca nemestrina leonina*). Para ello hemos estudiado durante 16 meses variables de desplazamiento y factores ecológicos en la elección de áreas dormidero en una tropa con alimentación natural y seguidamente comparado con los datos existentes de una tropa semiabastecida.

El tamaño del ámbito hogareño, del área núcleo y la distancia recorrida diaria fueron mayores en la tropa no abastecida que en la tropa semiabastecida, la cual presenta una filopatria mayor, y en concreto a las zonas humanizadas. Además, encontramos indicios de territorialidad en la tropa semiabastecida, la cual muestra una agresividad mayor que la no abastecida durante los encuentros con congéneres en cualquier contexto; sin embargo, en la tropa no abastecida los encuentros agresivos estuvieron asociados principalmente a las áreas dormideros. La tropa no abastecida de macacos usó más áreas dormidero y con menos frecuencia que la tropa semiabasatecida. Las áreas dormidero de la tropa no abastecida estaban localizados en las zonas más usadas de su ámbito hogareño y fuera de las zonas donde son habituales los encuentros con congéneres; pero los dormideros más usados se localizan dentro de las zonas de encuentros. Por general, los macacos eligieron un área dormidero que estaba cerca de la última área de alimentación del día o de la primera del día siguiente y adaptaron la hora de entrada y salida en correspondencia con los cambios estacionales.

La falta de territorialidad, su poca filopatria y las diferencias estacionales en los patrones de movimiento hacen pensar que la abundancia de alimento modela el uso del hábitat. El patrón de uso de las áreas dormideros nos sugiere que la selección sigue principalmente una estrategia conjunta para evitar ser depredado y maximizar la eficiencia de forrajeo. Los altos grados de agresividad asociados a las áreas dormidero nos puede indicar la existencia de competición por este importante recurso.

Los resultados indican que la alteración humana de los recursos alimentarios modifican y modelan claramente los patrones de actividad y relaciones intergrupales en esta especie, así como su flexibilidad ecológica.

Palabras clave: Aprovisionamiento, ámbito hogareño, filopatria, socioecología, territorialidad.

Abstract

Movement patterns are fundamental to understand the ecology, evolution, and conservation of primates, but we are lacking detailed studies for most species. Socioecological theory states that food resources and predation

pressure are the most important factors explaining why and how animals live in social groups and also the way they travel and move. During the last decades a great loss, fragmentation and deterioration of natural habitats has occurred worldwide. Such a scenario has importantly affected wildlife, not only by reducing their distribution and mobility in a smaller landscape, but by negatively affecting the quantity, quality and distribution of food available. In addition, this reduction in habitat available has created new settings of contact between humans and wildlife.

With this dissertation we aim to shed light on the anthropogenic impact on wildlife, particularly on a Southeast Asian primate species, *Macaca leonina* (previously categorized as *Macaca nemestrina leonina*). To that aim, first, the ecological factors affecting movement patterns, intergroup encounters and sleeping sites were studied over 16 months in a free ranging macaque group that fed from natural food; and second, we compared these findings with those of a neighboring macaque group, highly dependent on human food provisioning (semiprovisioned group).

The home range, core area and daily path length, critical values to understand the movement ecology of macaques, were greater for the group feeding on natural food than for the semiprovisioned group. The latter troop also presented high fidelity to the areas of the home range occupied by humans. In addition, we found territorial traits in the semiprovisioned troop, which showed more aggression during intergroup encounters in any context than the other group. Aggressive encounters in the wild feeding group were mostly associated to sleeping sites.

The free ranging group used more sleeping sites, which were also less frequently revisited, than that of the semiprovisioned group. Further, sleeping sites of free ranging macaques were located in the most used areas of the home range and away from those areas frequently used in intergroup encounters. However, the most used sleeping trees were found in such intergroup encounter areas. Most nights, macaques chose sleeping sites next to the last feeding area the day before or to the closest feeding area the day after. They also adjusted the time entering and leaving the sleeping site to seasonal light changes.

The studied free ranging troop had a home range larger than that of other groups previously studied. Its low site fidelity, seasonal differences in space patterns, and lack of territoriality suggests that food availability regulates macaque movement patterns. Macaques' sleeping site reuse patterns and their proximity to feeding areas concord with a strategy that aims to avoid predation during sleep and maximizes foraging efficiency. Finally, the observed high degree of aggression at the most used sleeping site areas before going to sleep suggests that macaques could be competing for sleeping sites, and that these sites are valuable resources for the species.

Our findings indicate that the modification of food resources by humans structures movement patterns, increases intergroup aggression, and modifies sleeping site selection in this species. This study highlights the flexibility of the study species and the effect that can cause in the ecosystem it lives in.

Keywords: food provisioning, home range, site fidelity, socioecology, territoriality.

INTRODUCCIÓN

Los primates actuales pueden ayudar en el conocimiento acerca de nuestro pasado. Estudios detallados en la morfofisiología, ecología y etología de primates vivos nos proporcionan múltiples claves para el entendimiento de los posibles orígenes de nuestra conducta, de su evolución y variabilidad. A estas evidentes conexiones filéticas se debe el que la Primatología esté incluida en el Catalogo NI-UNESCO en el Área de Conocimiento de la Antropología Física y representada por las subdisciplinas de Comportamiento de los primates (Cod. 240211) y Somatología de los primates (Cod. 240212). Su enseñanza en las universidades españolas está a cargo fundamentalmente de antropólogos.

Hasta siglo XX los estudios en primates se centraban básicamente en taxonomía y evolución. En 1914 se crea en Tenerife la Casa Amarilla, primera estación primatológica del mundo. Allí el psicólogo Wolfgang Köhler empieza con los primeros estudios en cognición y comportamiento de chimpancés en cautividad. En 1931 Clarence Ray Carpenter estudió monos aulladores en Barro Colorado, Panamá, y en 1938 funda la colonia de macacos Rhesus provenientes de la India en Cayo Santiago, frente a Puerto Rico. Pero no es hasta la segunda parte del siglo XX, que comienzan los estudios modernos de campo sobre primates y hasta la década de los setenta se sientan las bases de la primatología actual, aportando conocimiento de las especies en su ámbito natural. En 1948 los primatólogos Kinji Imanishi, Junichro Itani y Shunzo Kawamura, de la Universidad de Kyoto, comenzaron un estudio longitudinal sistemático con las tropas de macacos japoneses. En la década de los cincuenta Sherwood Washburn incluye a los primates en el análisis de la evolución humana e investiga sobre la vida social de los babuinos, más tarde asesorará a Inven DeVore en el estudio sobre babuinos en Kenya. El alemán George Schaller, es conocido por ser el pionero en estudios de primates superiores africanos, centrándose concretamente en la ecología y comportamiento de gorilas de montaña; sus estudios serán continuados a posteriori por Dian Fossey. Seguidamente, en 1960 el paleoantropólogo Louis Leakey promovió los estudios que Jane Goodall comienza en África para estudiar comportamientos y hábitos en chimpancés y así ser usados como modelo para ancestros del humano. Poco más tarde, Louis Leakey también incentivó a Dian Fossey a desarrollar sus estudios en gorilas (1967) y a Biruté Galdikas-Brindamour en orangutanes (1971). A principios de los setenta, Altmann (1974) propone su conocido método observacional usando como modelo macacos Rhesus y que actualmente sigue en vigencia.

La gran pérdida de hábitats que sufre el planeta en las últimas décadas pone en peligro la subsistencia de muchas especies de animales y plantas; esto ha hecho que gran parte de los esfuerzos se hayan centrado en la conservación de los bosques que albergan estas comunidades. En los bosques tropicales habitan el 90% de las especies de primates actuales, por consiguiente gran parte de los estudios en esta área se han volcado en analizar como la pérdida de hábitat impacta en la ecología, y comportamiento de los primates. Gran parte de los monos del viejo mundo, los cercopitécidos, han demostrado tener una gran flexibilidad para adaptarse a esta pérdida de hábitat y han ocupado más o menos con éxito un nicho ecológico que hace de interfaz entre las áreas perturbadas por el ser humano y el bosque natural. Entre los cercopitécidos, el género *Macaca* es probablemente el que más éxito ha tenido ocupando estos hábitats y recientemente se incrementa el conocimiento sobre las poblaciones de primates que viven en contacto con el ser humanos al ser comparadas con aquellas que habitan en el interior del bosque. Además, también recientemente se ha introducido al ser humano como un componente más de los ecosistemas, haciendo imprescindible introducir al ser humano en los estudios ecológicos y de conservación. Es por ello, que en los últimos 20 años, una parte importante de los trabajos en primatología se centran en la "etnoprimatología", que estudia las conexiones culturales y ecológicas entre ser humano y primates no humanos. En el sureste asiático hay una larga historia de contacto e interacción entre humanos y primates no humanos, y entre humanos y macacos en particular. Aunque, en ciertas especies como el macaco japonés y el macaco de cola larga, hay gran cantidad de estudios sobre poblaciones que viven en contacto próximo con el hombre, en otras muchas es escaso su conocimiento. Esto hace imprescindible el estudio de como las poblaciones que viven en el bosque han modificado sus patrones de movimiento, ecología y comportamiento para sobrevivir, a lo que está orientado el trabajo de investigación que constituye esta tesis. Además, esta información es básica para poder realizar unos planes de manejo en las zonas donde este contacto es problemático y crear buenos planes de conservación de las especies de primates y de las zonas de bosque primigenio donde viven.

Centrado en estos propósitos generales y tras un primer contacto con la primatología durante una estancia académica de siete meses en la Estación Biológica de los Tuxtlas (Universidad Autónoma de México) durante 2007, el autor se involucró en 2008 en un proyecto conjunto entre la Universidad de Lieja (Bélgica) y la Universidad King Monkugt of Technology deThonburi (Tailandia), que pretende ampliar la escasa información de la distribución y ecología de la especie de macaco *Macaca leonina* (anteriormente llamado *M. nemestrina leonina*) en su hábitat natural en Tailandia. En ese momento, el proyecto se centraba en el estudio de una tropa semiabastecida en el Parque Nacional de Khao Yai, pero datos sobre tropas que habitan en el interior del bosque eran casi inexistentes. Por ese motivo surgió la posibilidad de realizar un proyecto de tesis doctoral para rellenar ese hueco de información. Tras un primer viaje en 2010 para una primera toma de contacto y pedir los permisos necesarios y un estudio piloto en el 2011, en 2012 se empezó la toma de datos en el campo durante 14 meses consecutivos.Dada la trascendencia que pueden tener los resultados obtenidos en esta investigación para la primatología y ecología en general, y la propia naturaleza de estos estudios que se prolongan en el tiempo, vimos oportuno realizar la tesis en formato de artículos y así hacer accesible cuanto antes los avances de nuestro estudio a la comunidad investigadora, a la vez que se obtiene un acreditado refrendo de la importancia y adecuación del mismo.

La presente tesis se compone de nueve capítulos, de los que tres los constituyen artículos científicos aceptados en revistas internacionales y aparecen en esta disertación como tres capítulos que pueden ser leídos de manera independiente. La bibliografía de los artículos está separada de la bibliografía usada en el resto de la disertación.

En el primer capítulo se describe el contexto del estudio, su importancia y objetivos.

En el segundo capítulo se describe los antecedentes en el estudio de la especie, su filogenia, su distribución actual y sus características generales.

En el tercer capítulo de método se describe de manera general la zona de estudio, calendario, animales de estudio y metodología empleada en la toma de datos, aunque para una descripción más detallada se debe consultar la metodología de los capítulos cinco, seis y siete.

En el cuarto capítulo se muestran resultados generales de los patrones de actividad y dieta de la tropa de estudio.

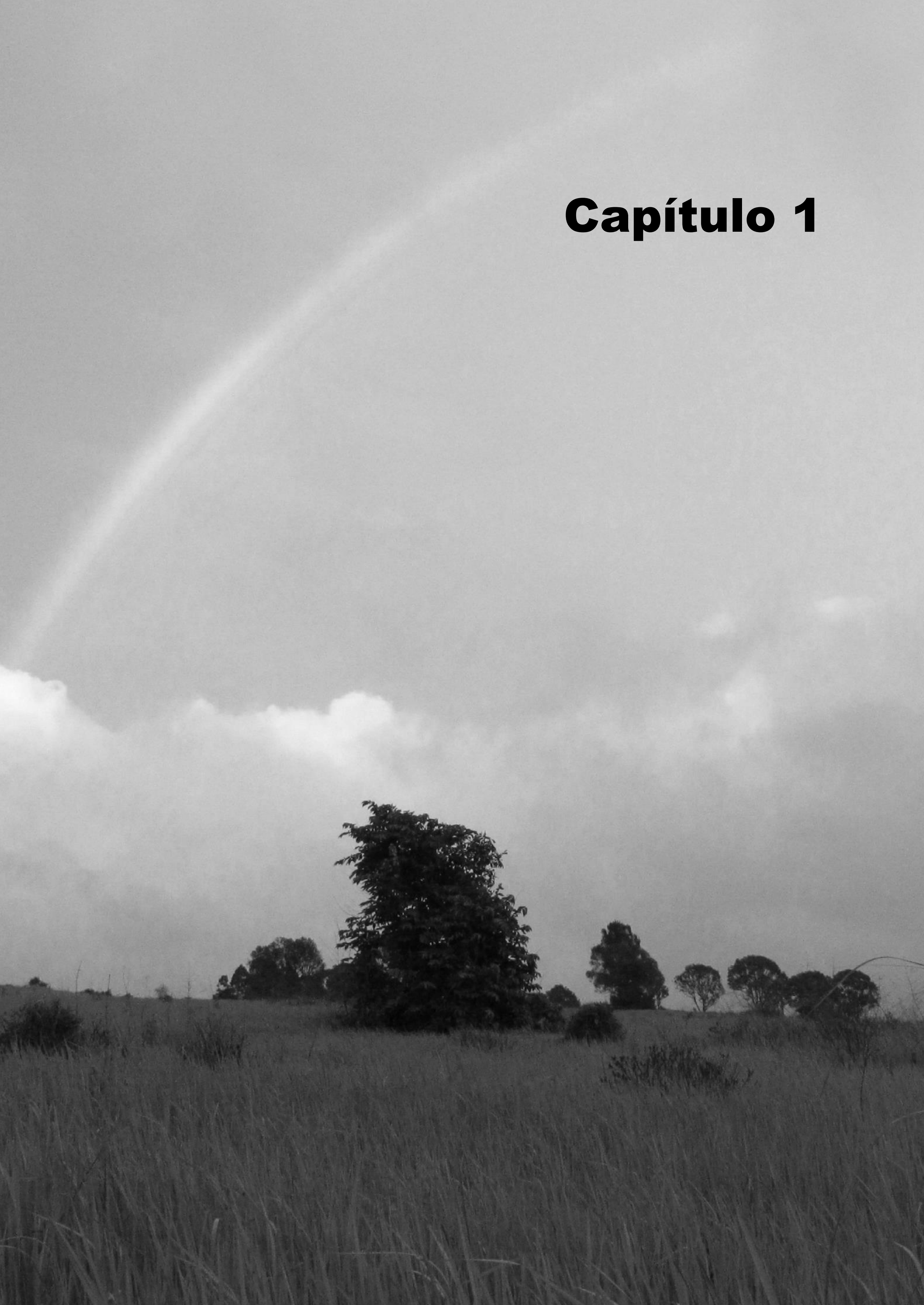
En el quinto capítulo presentamos el artículo publicado en la revista *American Journal of Primatology* 77: 841-853 (Factor de impacto: 2,435; Q1 en revistas de Zoología), con título "Ranging and site fidelity in northern pigtailed macaques (*Macaca leonina*) over different temporal scales". En este artículo se estudia los patrones de movimineto y filopatria durante 16 meses usando diferentes escalas de tiempo y creamos un nuevo estimador para en cálculo de ambito hogareño y área nucleo, así como un índice de filopatria. Además utilizamos otros estimadores comúnmente usados para hacer comparable nuestro estudio con otros anteriores y futuros.

En el sexto capítulo presentamos el artículo publicado en la revista *Biotropica* 47(6): 733-744 (Factor de impacto: 2,084; Q2 en revistas de Ecología), con título "Non-territorial macaques can range like territorial gibbons when partially provisioned with food". Aquí evaluamos si el aprovisionamineto de comidad de procedencia humana en animales no territoriales, puede dirigir los patrones movimiento e incluso el comportamiento de animales no territoriales a unos similares a los presentados por animales territoriales. Además, se calculó el grado de fideliad a áreas humanas respecto a la disponibildad de recursos naturales vs. comida de origen humano.

En el séptimo capítulo se presenta el artículo actualmente en prensa y publicado online en la revista *International Journal of Primatology* 36(5): 931-949 (Factor de impacto: 1,993; Q1 en revistas de Zoología), con título "Exploring the multiple functions of sleeping sites in northern pigtailed macaques (*Macaca leonina*)". Por último en este capítulo analizamos los factores ecológicos que condicionan la selección de áreas usadas como dormideros de la tropa de bosque y la comparamos con los resultados previamente obtenidos por Albert y colaboradores en 2011 para la tropa semiprovisonada.

A continuación le siguen la discusión, conclusiones y bibliografía general del trabajo.

Capítulo 1



CONTEXTO GENERAL, JUSTIFICACIÓN Y OBJETIVOS

La pérdida de hábitat es una gran amenaza para la biodiversidad y procesos ecológicos (Andrén 1994; Fahring 1999, 2013), sin embargo, la fragmentación del hábitat (división del paisaje en unidades más pequeñas) desencadena varios y diferentes efectos. Estos efectos pueden ser perjudiciales o incluso beneficiosos, según la especie y el grado de fragmentación (Laurance & Bierregaard 1997; Fahring 1999, 2013). Los mamíferos que habitan en bosques, como es el caso de los primates, se pueden ver considerablemente afectados por la fragmentación de hábitat (Chapman & Peres 2001; Arroyo-Rodríguez & Dias 2009) y producir extinciones locales, cambios en la densidad, en el tamaño de grupo (Estrada & Estrada-Coates-Estrada 1984,1996; Bicca-Marques 2003; Silver & Marsh 2003), alteración de sus patrones de estrategia de forrajeo y en el flujo génico entre poblaciones (Marsh 2003).

Las carreteras y otras infraestructuras humanas como alojamientos, áreas de recreo y restaurantes entre otros, fragmentan el paisaje y convierten áreas de interior de bosque en zonas de borde (Bennet 1991; Forman & Alexander 1998; Coffin 2007; Fahrig & Rytwinski 2009; Benitez-Lopez et al. 2010). Esta característica de la fragmentación de hábitat, el efecto borde, es entendido como "el área de transición entre bosque no modificado y el hábitat resultado del manejo humano" (Marsh 2003). En estas zonas de borde las condiciones abióticas (humedad, temperatura y velocidad del viento) y bióticas (densidad y riqueza de especies) se ven alteradas (Saunders et al. 1991). En las zonas de borde se incrementa la densidad de comedores de semillas, lo que puede reducir la regeneración de ciertas especies de plantas (Laurance 1997; Pizo 1997). Además el efecto borde provoca cambios en la vegetación (Laurance et al. 2000; Arroyo-Rodríguez & Mandujaro 2006) que puede afectar a la dieta de los primates por verse reducida la calidad y abundancia de alimento (Tuttin 1999; Arroyo-Rodríguez & Mandujaro 2006).

Otra de las consecuencias del efecto borde es el hecho de que puede poner en contacto con más frecuencia a los humanos y animales salvajes, y por lo tanto a humanos y el resto de primates. El estudio de primates (humanos y no-humanos) es un campo en continua expansión. Hasta hace poco, la mayoría de los estudios en primates no-humanos no tenían en cuenta la influencia del ser humano (Burton & Carrol 2005). Sin embargo, durante las últimas dos décadas, la etnoprimatología ha surgido como una nueva disciplina del área de estudio en primatología (Brotcorne 2015) y estudia las interconexiones culturales y ecológicas de humanos y primates no humanos (Riley 2006). Por tanto, la etnoprimatología es el enfoque multifacético y multidisciplinar (Sponsel et al. 2002), que parte desde la antropología biológica y antropología cultural para estudiar la interfaz (conexión física y funcional) entre primates no humanos y los humanos. Este campo de la primatología se ocupa de como los humanos entienden el hábitat en el que viven y como esto modela su comportamiento hacia los primates no humanos y naturaleza en general, y de qué forma esto influye en ellos (Riley et al. 2011). Esta visión holística donde primates humanos y no-humanos son coparticípes incluye: el conocimiento del comportamiento y biología de primates no-humanos por parte de las poblaciones indígenas y la presencia en sus mitos y folklore, la de primates no humanos en la dieta humana, el uso como mascotas, transmisión bidireccional de enfermedades, la competición por recursos, el impacto debido a la alteración y destrucción del hábitat y el impacto del ecoturismo entre otros (Wallis & Lee 1999; Fuentes & Wolfe 2002; Paterson & Wallis 2005; Jones-Engel et al. 2005; Fuentes 2006a,b; Riley 2007a,b, 2010; Riley et al. 2011)

Desde al menos los últimos 10.000 años las zonas de contacto entre humanos y el resto de primates se extienden principalmente entre los trópicos de Cáncer y Capricornio. En zonas donde se han dado largos periodos de permanencia simpatrida se puede producir fenómenos de co-ecología donde ambos taxones se influyen recíprocamente (Riley et al. 2011). Sin embargo, debido a la gran perturbación antrópica sufrida en los bosques tropicales y su consecuente fragmentación producida durante las últimas décadas, se han creado nuevas zonas de contacto donde humanos y primates no humanos están forzados a interactuar (Biquand et al. 1994; Woodroffe 2000; Hill et al. 2002; Lee & Priston 2005; Corlett & Primack 2011; Laurance et al. 2011).

La visión y el comportamiento del ser humano hacia los otros primates varían bastante entre los diferentes grupos humanos. Los primates han sido cazados tanto como fuente de alimento y medicina tradicional como por ser considerados plagas o peste, sujetos de investigaciones biomédicas, mascotas, e incluso cuando son considerados tótems o venerados como dioses (Fa 1984; Riley et al. 2011). En países del sur y sureste de Asia donde se practica el Hinduismo y/o Budismo las zonas de contacto entre humanos y otros primates están fuertemente asociadas a las ciudades y lugares sagrados como los templos (Aggimarangsee 1992; Wolfe 2002; Fuentes et al. 2005), donde se produce un alto nivel de protección y de alimentación a los animales. Esto se puede explicar por el hecho de que en Asia existen muchos relatos incluidos en su folklore y mitología donde los monos son partícipes, por ejemplo en los *Jataka* (Historias populares budista); se narra que Buda se reencarnó, entre otros animales, en un mono, por tanto por medio de esta protección y aprovisionamiento se obtienen méritos en su sistema de creencias (Riley et al. 2011). Del mismo modo en el *Ramayana* (Texto épico de la India antigua), los monos son considerados de los héroes más sobresalientes y Hanuman es el héroe mono más destacado y quien posee habilidades sobrenaturales (Wolfe 2002).

La socioecología sugiere una relación entre los factores ecológicos y los patrones de agrupamiento social, y consecuentemente su comportamiento social (Crook & Gartlan 1966; Wramgham 1980; van Shaik 1989; Sterck et al. 1997). Por ello, los animales pueden modificar su comportamiento bajo ciertas restricciones ambientales. Van Schaik (1989) argumenta que la distribución de recursos, la posibilidad de ser defendidos y la presión a ser depredado modelan los sistemas sociales y las relaciones intergrupo.

Algunos primates y en especial especies de cercopitecinos muestran gran flexibilidad ecológica y tolerancia a perturbación antrópica. La creación de áreas protegidas y su manejo, puede perturbar las bases en la que los modelos sociecológicos, como son la abundancia y distribución de recursos (Fuentes 2006). El género *Macaca* está bien adaptado a ambientes antropogénicamente modificados y hay casos en los que la cultura humana beneficia a estas poblaciones. Este es el caso de *Macaca fascicularі* en Bali, donde la modificación del hábitat por parte del ser humano es beneficiosa para los macacos y a su vez el hombre obtiene provecho cultural y económico (Fuentes 2005). Sin embargo hay muchos casos en los que se pueden producir efectos negativos en una o ambas direcciones y en el ecosistema (Sapolky & Else 1987;

Engel et al. 2002; Wolfe et al. 2004; Kanurai 2004; Mallapur 2013; Brotcorne et al. 2015).

Por otro lado, los patrones de movimiento son cruciales para entender la ecología, evolución y conservación de los primates y animales en general. Por ello, es crucial un adecuado y preciso herramientas que nos ayuden a delimitar bien el de *ámbito hogareño*, entendido como el área usada en un periodo de tiempo dado excluyendo salidas ocasionales (Burt 1943; Jewell 1963), *área núcleo,* entendida como la región más usada del ámbito hogareño (Kaufmann 1962; Asensio et al 2012a) y la *filopatria,* entendida como las áreas visitadas recurrentemente del ámbito hogareño y área núcleo (Easley & Kinzey 1986, Switzer 1993; Asensio et al 2012b).

Parámetros tan importantes en ecología como son la preferencia de hábitat (Aebischer, Robertson & Kenward 1993), el solapamiento entre grupos vecinos o individuos (Fieberg & Kochanny 2005; Ringhton & Mills 2006; Olsen *et al.* 2011) o la estimación de la capacidad de carga de un hábitat (Downs, Gates & Murray 2008) requieren del ámbito hogareño, área núcleo o uso del espacio para su cálculo. Por tanto, los estudios centrados en patrones de movimiento deben usar las últimas herramientas analíticas para alcanzar la mayor precisión posible.

En conclusión, la visión holística que realiza la etnoprimatología nos puede ayudar a entender mejor la compleja relación existente y así facilitar la supervivencia de las poblaciones de primates no-humanos, muchos de los cuales están en peligro de extinción (Ripley et al. 2011).

Importancia de nuestro estudio

Este proyecto de tesis doctoral forma parte de un estudio mayor con título "Distribución, ecología y comportamiento de macaco de cola de cerdo (*Macaca nemestrina*) en Tailandia" dirigido por la Drª. Marie-Claude Huynen (Universidad de Lieja, Bélgica) y el Dr. Tommaso Savini (King Monkugt University of Technology of Thonburi de Tailandia). Dicho estudio pretende aportar datos a la escasa información existente sobre la distribución, ecología y conservación de esta especie en su hábitat natural. Para ello, el proyecto se centra principalmente en la comparación de los patrones de movimiento, actividad general y de dieta en tropas en que la presencia humana influye directa o indirectamente, y en otras tropas con un contacto nulo o mínimo con el ser humano.

Hasta la fecha de inicio de nuestro estudio (2011), solo un proyecto de Máster realizado por Alice Latinne y otro de Doctorado realizado por Aurelie Albert nos habían aportado datos continuos sobre la patrones de movimiento, composición de tropa y ecología de una tropa (llamada Headquarters: HQ) que habita en los alrededores del Centro de Visitantes y de las principales instalaciones turísticas del Parque Nacional de Khao Yai (PNKY), y que además incluye en su dieta una parte considerable de alimentos de origen humano. Tras este primer paso, el siguiente lógicamente, era la obtención de información de macacos cuya dieta no dependiera de los alimentos humanos y para los que su ámbito hogareño no se centrara en áreas modificadas por el hombre.

Como consecuencia, y para este trabajo de investigación esta disertación se propuso la comparación de dos tropas que viven en hábitat con distintos niveles de perturbación de origen antrópico dentro del PNKY, para así poder analizar el impacto de la presencia humana en el uso del espacio, comportamiento ecológico y organización social de estas tropas de macacos. Para ello nos propusimos estudiar una tropa no abastecida, que es vecina de la tropa semiabastecida HQ estudiada por Albert (Albert 2012; Albert et al. 2011, 2013a,b), pero para la que su ámbito hogareño no está ligado a las instalaciones humanas del parque.

El PNKY era apropiado para realizar investigación por varias razones: (1) PNKY es un área protegida principalmente formada por bosque húmedo estacional; (2) contiene una población relativamente grande y estable de *Macaca leonina*, compuesta por una mayoría de tropas que viven en el bosque y de algunas tropas que son parcialmente abastecidas y están ligadas a áreas humanas; (3) es el mismo lugar donde previamente se ha estudiado a la tropa semiabastecida, por lo que comparte el mismo tipo de bosque, haciendo posible una mejor comparación; (4) la existencia de infraestructura cerca del lugar de estudio aseguraba la logística necesaria para la realización de la investigación.

Objetivos

Objetivo general

Obtener los primeros datos en un estudio a largo plazo en una tropa no asociada a ambientes humanizados en *Macaca leonina* y evaluar el impacto (efecto borde) producido por los visitantes e infraestructura asociada, sobre los patrones de movimiento y socioecología en dos tropas con distinto régimen alimentario que habitan en el mismo bosque en el PNKY.

Objetivos específicos

- Calcular el tiempo dedicado a distintas actividades diarias y tipo de alimentación de los individuos adultos que componen la tropa.
- Crear un método para estimar el tamaño y localización del ámbito hogareño.
- Estimar los patrones de movimiento (ámbito hogareño, área núcleo, distancia recorrida diaria y filopatria al área usada) para distintas escalas temporales y comparación entre ambas tropas.
- Determinar el efecto de la comida humana en las relaciones intergrupales de las tropas de macacos.
- Evaluar el impacto del número visitantes del parque vs. abundancia de recursos naturales, en los patrones de movimiento y filopatria de la tropa semiabastecida.
- Determinar los factores que influyen en la elección de las áreas dormideros en la tropa de bosque no abastecida y compararlo con los encontrados en la tropa semiabastecida.

Capítulo 2

ESPECIE DE ESTUDIO

MACACA LEONINA Blyth, 1863

El macaco de cola de cerdo norteño (*Macaca leonina* Blyth, 1863) está catalogado como especie vulnerable en la Lista Roja de Especies Amenazadas de la IUCN (Boonratana et al. 2008) y es una de las especies de primates menos estudiada del Sudeste Asiático (Choudhury 2008). Aunque se han llevado a cabo varios estudios, la mayoría son notas científicas (Davies 1990; Gippoliti 2001; Khamcha & Sukumal 2009) o parte de estudios en multi-especies (MacKinnon & MacKinnon 1987; Whitington 1992; Kitamura et al. 2002; Suzuki et al. 2006). Su ecología, comportamiento y patrones de movimiento en estado salvaje es poco conocida y limitada a los estudios de Choudhury (2008, 2009, 2010) en bosque lluvioso de Assam en el noreste de la India y Feeroz (1994, 2012) en Bangladesh. Sin embargo, la mayoría de la información en detalle proviene de una tropa que habita alrededor del Centro de Visitantes del Parque Nacional de Khao Yai (Tailandia), la cual se alimenta parcialmente de comida humana (Albert 2012; Albert et al. 2011, 2013a,b). Durante un año Albert y colaboradores estudiaron la dieta, actividad, patrones de movimiento y su papel como dispersores se semillas de esta especie. Sus resultados reflejan la capacidad de adaptación de la especie a un cierto grado de alteración humana y una alta eficiencia en la dispersión de semillas, hecho que hasta la fecha no le era reconocida. *Macaca leonina* es filogenéticamente cercana a *M. nemestrina*. Previamente, ambas especies habían sido consideradas subspecies de *M. nemestrina* (*M. n. leonina y M. n. nemestrina*) hasta que recientemente atendiendo a características morfológicas y ecológicas fueron consideradas como dos especies (Gippoliti 2001).

Su sistema social es multi-macho/multi-hembra, que consiste en varios adultos machos, varias hembras adultas y su descendencia (Melnick & Pearl 1987). Además muestran un alto grado de dimorfismo sexual, las hembras pesan de 4.7 a 10.9 kg y los machos de 6.2 a 14.5 kg (Albert 2012). La *sex ratio* está a favor de las hembras en una proporción mayor de 4:1. Las hembras suelen quedarse en la tropa que han nacido y los machos migran a otra tropa al llegar a la madurez.

Aunque la especie es considerada principalmente semiterrestre (Choudhury 2008; Albert et al. 2011), Choudhury (2008) encuentra gran variabilidad en su grado de presencia en el suelo. Esto puede estar asociado a la calidad del bosque en el que habitan, pero las horas de contacto con las tropas estudiadas no fueron muy elevadas, por lo que una falta de habituación de las tropas puede incrementar el grado de presencia arbórea. No obstante, Feeroz (2012) la clasifica como altamente arborícola. Esta diferencia, posiblemente sea debida a que en esa zona de estudio en Bangladés la especie es simpátrida con otra especie de macaco (*M. mulatta*) que ocupa el sustrato terrestre y por lo tanto *M. leonina* se ve obligada a usar doseles más altos. Su dieta es omnívora y la fruta es su principal fuente de alimento (Choudhury 2008; Albert et al. 2013a,b; Feeroz 1994, 2012)

Taxonomía, filogenia y distribución geográfica

Clase Mamalia
  Orden Primates
    Suborden Antropoidea
      Infraorden Catarrinos
        Familia Cercopithecidae
          Subfamilia Cercopithecinae
            Género *Macaca*
              Macaca leonina

El Orden Primates es un grupo instituido por Linneo para incluir en éste a los humanos, animales llamados cuadrumanos, y a los murciélagos. Más tarde, los murciélagos serían separados del grupo en un orden propio, los Quirópteros. Los Primates incluyen a los mamíferos placentarios de extremidades libres y generalmente provistas de cinco dedos, uno de ellos oponible generalmente. Tiene uñas planas, dentadura bunodonta (frugívoro o insectívoro).

Hasta la fecha, el orden Primates está compuesto por 16 familias, 78 géneros, 484 especies y 687 taxones (Mittermeier et al. 2013, Munds et al. 2013, Choudhury 2013, Li *et al.* 2015). El noventa por ciento de las especies de primates viven en bosques tropicales (Richard 1985; Mittermeier 1998). La familia Cercopithecidae pertenece al infraorden catarrinos, también llamados Monos del Viejo Mundo. Los cercopitecinos se caracterizan por poseer abazones, estómago sencillo y un par de callosidades isquiáticas (Fooden 1975 1980; Fa 1989).

Macaca es el género representante de los Cercopitecos en Asia y el de más extensa distribución dentro de los primates no humanos. La evidencia fósil muestra que los macacos poblaron durante el Pleistoceno la mayoría de Eurasia y Norte de África. Más tarde desaparecieron entre Asia y Europa dejando un espacio de más de 9.000 Km. (Fa 1989). Actualmente hay 23 especies identificadas que se extienden en el Norte de África y Este de Asia (Delson 1980; Fooden 1980; Thierry et al. 2004; Li et al. 2015), estando presentes en más de 20 países asiáticos (Roos et al. 2014).

Hace unos 10 m.a. aparece un ancestro semiterrestre de papión, el cuál diverge de algún cercopitecino temprano que ocupaba el dosel alto de los árboles y que competía con los colobos arbóreos (Delson 1975a,b). Al final del Mioceno se producen unos movimientos tectónicos, secándose el Mediterráneo, permitiendo la diferenciación de los papiones en cuatro grupos: *Theropithecus, Papio, Cercocebus y Macaca*. El representante más antiguo conocido del género *Macaca* es *Macaca libyca*, de hace unos 6 m.a., encontrado al Norte de Egipto. Según Delson (1975a,b), de esta especie pudieron surgir el linaje Asiático y el Mediterráneo. Aunque los colobos dominaban la fauna europea, los macacos se fueron haciendo más comunes, hasta finalmente ser los únicos Cercopitecinos en Europa durante el Villafranquiense y el Pleistoceno y hasta el último periodo interglaciar (Fa 1989).

El género *Macaca* se separó en Europa y en el área circunmediterránea del grupo de los Papiones hace unos 6 m.a. (Fa 1984a). La distribución del género ha sido modelada por una larga y compleja escala de cambios en el clima, ecología y distribución geográfica desde final del Plioceno y durante el Pleistoceno. Durante el Villafranquiense los fósiles aparecen asociados a climas templados y bosques caducos, alternados con pastizal abierto (Fa 1989).

Posteriormente algunos macacos se dispersaron por Eurasia a través del próximo oriente, una línea entró por el sur de Europa a principios del Plioceno, dando lugar a subespecies temporales de *Macaca sylvanus*; y otra línea se extendió hacia el Este llegando hasta la India en el Plioceno (Fa 1989).

La sistemática y la filogenia del género *Macaca* han sido problemáticas por la falta de registro fósil, que aunque sea más o menos buena en el área circunmediterránea no es así en Asia, de forma que se han usado distintos criterios de clasificación y hasta la fecha aún está en debate (Fooden 1980; Fa 1989; Hoelzer & Melnick, 1996; Abegg & Thierry 2002; Thierry, 2007). Atendiendo a los citados autores, podemos decir que las 23 especies se agrupan en al menos tres linajes: linaje *silenus*-*sylvanus* al que pertece *M. leonina* (13 especies), linaje *sinica-arctoides* (6 especies) y linaje *fascicularis* (4 especies).

La actual distribución geográfica de *Macaca leonina* comprende el noreste de República de la India, sureste y este de Bangladés, República de la Unión de Myanmar, suroeste de la República Popular China, Reino de Tailandia, República Democrática Popular Lao, Republica socialista de Vietnam y Reino de Camboya (Fig. 1, IUCN 2015; Roos et al. 2014).

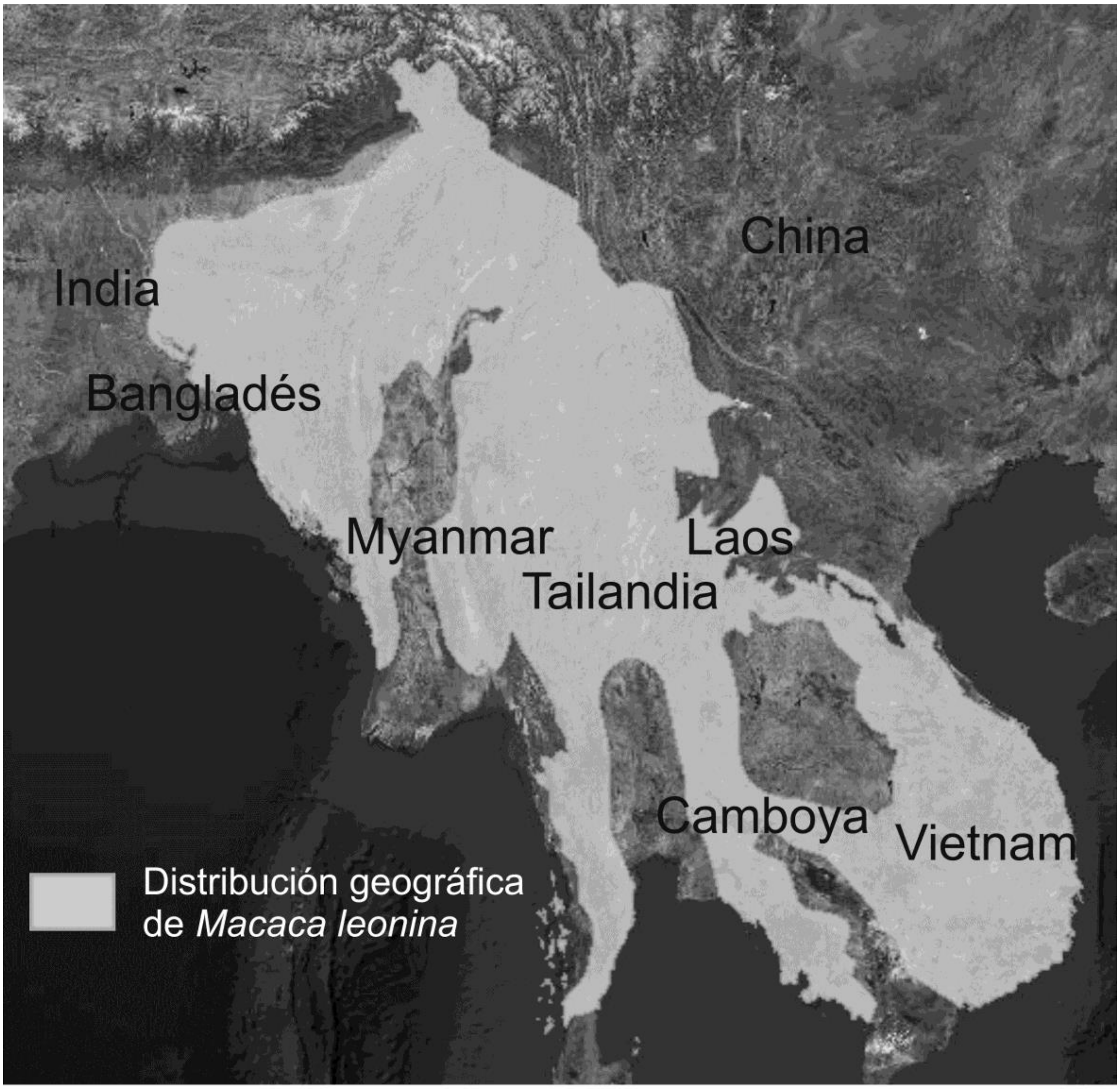


Fig. 1 Distribución geográfica de *Macaca leonina* (modificado de IUCN 2015)

Capítulo 3

MÉTODOS

Es esta sección, nos proponemos recapitular la metodología empleada en el trabajo. Empezados con una breve descripción del lugar y animales de estudio, y de los periodos del trabajo de campo. Posteriormente se describe el procedimiento en la toma de dato y su procesamiento. También hemos llevado a cabo la modificación de un reciente método creado para estimar los patrones de movimiento y propuesto un índice para poder cuantificar un método visual de filopatria. Se termina con el tratamiento estadístico de los datos. Para un conocimiento más detallado es aconsejable la consulta de los capítulos 5, 6, 7.

Características del área de trabajo

En el Reino de Tailandia se encuentran 18 especies de primates, de los cuales seis pertenecen al género *Macaca* (*M. leonina, M. nemestrina, M. assamensis, M. artoides, M. fascicularis y M. mulatta*; Roos et al. 2014).

El Parque Nacional de Khao Yai (150 km NE de Bangkok; 101º22’ E, 14° 26’N) es el parque nacional más antiguo de Tailandia, fue establecido en 1962 y cubre un área de 2.168 km^2 (Barttle 2009). Es en la actualidad el parque nacional que recibe más afluencia de visitantes al año (DNP 2014). Allí encontramos tres especies de primates que son simpátridas con *Macaca leonina*; una especie de lorísido de hábitos nocturnos (*Nictocebus coucang*) y dos de hylobátidos (*Hylobates lar* e *H. pileatus;* Srikosamatara & Hansel 2004).

El clima de Tailandia está regido por dos monzones anuales, lo que origina tres estaciones. La estación fría, de noviembre a febrero se produce cuando el aire frío y seco desciende desde China; la estación cálida, de marzo a mayo se produce cuando disminuye el monzón proveniente del noreste y aumenta la temperatura; y la estación de lluvias, de junio a octubre que se origina cuando el viento del suroeste trae las precipitaciones del Océano Índico (Barttle 2009).

La zona de estudio se encuentra en el boque de Mo Singto y cubre un área aproximada de 10 km^2 y está ocupada por bosque húmedo lluvioso estacional a una altitud de 700-890 m. La precipitación anual en la zona oscila entre 2.000-3.000 mm por año (Savini et al., 2008), la media de temperatura mensual entre 19°C a 24°C (Albert et al., 2011) y la humedad entre 65% a 77% (Savini et al., 2008). Además, en general, hay una marcada estacionalidad en la productividad de fruta, con un periodo de alta productividad de marzo a septiembre y un periodo de baja productividad de octubre a febrero (Bartlett, 2009).

Periodos de habituación y seguimiento

Se estudió una tropa de *Macaca leonina* llamada Chang (CH) que significa elefante en thai, durante 133 días (1.321 horas) divididos en dos periodos, uno que abarca desde abril y mayo de 2011 y otro desde mayo de 2012 a junio de 2013. *Durante abril-mayo de 2011 y mayo-junio de 2012* **(**53 días, 469 horas**)**, se recogieron datos de movimiento y zonas utilizadas como dormideros; además se habituó a los individuos de la tropa a ser seguidos por el observador, disminuyendo la distancia de observación progresivamente. Finalmente, durante los mismos meses también se realizó un estudio piloto para colectar datos de alimentación y comportamiento de la tropa. Este estudio nos ayudó en la práctica de la toma de datos, seguimiento de la tropa, identificación de especies consumidas por los macacos y al reconocimiento de actividades que en un principio eran confusas o no obvias para el observador. Finalmente este piloto permitió elegir y definir la metodología a seguir durante los siguientes doce meses de estudio.

Desde julio 2012 a junio 2013 **(**80 días, 852 horas**)**, durante cinco a siete días completos y consecutivos al mes, se continuó recogiendo datos de movimiento, áreas usadas como dormideros, así como datos en la alimentación y actividad general de los animales.

En 2011 la tropa fue seguida 18 días en abril y 13 días en mayo, con el fin de conocer bien su composición, reconocer las características individuales de sus componentes y familiarizarnos con el área se bosque usada por la tropa. Debido a la dificultad de encontrar y seguir a la tropa en sus casi 10 km^2 de su área de campeo, durante 2012 y 2013, se optó por seguir a la tropa por un mínimo de 5-8 días, para así asegurar una colecta mínima y sistemática al mes.

Animales de estudio

La composición de la tropa varió a lo largo del estudio. La composición fue anotada cada vez que hubo ocasión, completando en seis veces un conteo completo. La mayoría de los individuos adultos y parte de los juveniles pudieron ser reconocidos a lo largo del estudio, además, cada nacimiento o pérdida de infante u otro individuo fue registrado. De esta forma, se pudo hacer un seguimiento de la composición de grupo mensualmente. Durante 2011 la tropa estuvo compuesta por 49 individuos (4 machos adultos, 18 hembras adultas, 21 juveniles y 6 infantes) y durante el periodo comprendido entre 2012 y 2013 la composición varió de 60-67 individuos (3-4 machos adultos, 19-20, 2-3 subadultos, 20-29 juveniles y 7-14 infantes). La tropa principalmente ocupaba la un área al norte y noroeste del Centro de Visitantes y alojamientos turísticos del Parque, esta zona de perturbación antropogénica es principalmente usada por la tropa semiabastecida estudiada (Fig. 1, Capítulo 7) por Albert y colegas (2011, 2013a,b)

Toma de datos y tratamiento

Patrones de movimiento

Cada día de seguimiento los datos de patrones de movimiento se colectaron obteniendo la localización de la tropa y lugares usados como dormideros mediante el uso de un GPS (Sistema de Posicionamiento Global). Cada 30 minutos el observador tomó la posición de la tropa usando, siempre que fue posible, el centro geométrico de los componentes del grupo. La precisión de GPS fue de 9.4 ± SD 3.3 m (rango: 1-26 m) basados en 1.501 muestras. Se usó

Universal Transverse Mercator (UTM, zona 47 N) para proyectar las localizaciones.

Patrones de actividad

Para evaluar el tiempo empleado por la tropa para cada comportamiento o actividad, dividimos las actividades en las diferentes categorías generales: descanso, movimiento, alimentación, comportamiento social y otros (ver Etograma de actividades en Tabla 1). Los datos fueron recogidos usando 30-min *scan sampling* (muestreo de rastreo; Altmann 1974) para cada adulto observado. Este método de toma de datos, consiste en recoger la actividad instantánea de los individuos observables.

Actividad	**Descripción**
Descanso	Descanso, dormir u observar el entorno sin intención conocida.
Movimiento	Movimiento individual de desplazamiento corto de al menos tres segundos de duración o viaje colectivo del grupo.
Alimentación	Alimentación directa, manipulación o búsqueda activa de comida con objeto de introducirla en la boca.
Comportamiento Social	Comportamiento afiliativo, agonístico o neutro donde intervienen al menos dos individuos (e.g.: despioje, juego, pelea, comportamiento sexual y llamada, vocalización o gestualización dirigida a otros componentes del grupo).
Otros	Actividades como autoacicalamiento, masturbación, juego solitario y otros.

Tabla 1. Etograma de actividad

Para calcular la proporción de tiempo empleado en cada actividad, mensualmente usamos la media ponderada teniendo en cuanta el esfuerzo de muestreo (Harrison et al. 2009). Para ello, calculamos la proporción de eventos para cada actividad i por cada mes P_i usando la media diaria P_{ij} para una actividad en un día dado j ponderado por el esfuerzo de muestreo diario W_j (número de rastreo para ese día) como es expresado en la fórmula :

$$Pi = \frac{\sum(\mathrm{P}ij * \mathrm{W}j)}{\sum(\mathrm{W}j)}$$

Dieta

Para evaluar el tipo de alimentación mostrada por la tropa de estudio clasificamos los alimentos consumidos en:

- Fruta: cuando la parte ingerida es la pulpa de frutos carnoso.
- Semilla: cuando consumen la semilla de frutos carnosos o frutos de leguminosas y fagáceas.
- Invertebrados, pequeños vertebrados y hongos: cuando ingieren artrópodos, pequeños reptiles y huevos o pollos de aves.
- Otros: cuando consumen tallos, hojas, flores, sabia u otros.

Calculamos la composición de la dieta usando la formula anteriormente usada para el cálculo de los patrones de actividad. En este caso calculamos la proporción de eventos para cada tipo de alimento i por cada mes P_i usando la media diaria P_{ij} para un tipo de alimento en un día dado j ponderado por el esfuerzo de muestreo diario W_j (número de scans para ese día).

Periodos de alta y baja abundancia de fruta

Varios autores han demostrado que el número de tipos de fruta consumidas (especies) esta positivamente correlacionado con el número de especies en fructificación, lo que nos permite determinar los periodos de abundancia de fruta (Isbell 1983; Albert el al. 2013b). Durante 12 meses (Julio 2012 - Junio 2013) se calculó el número de especies frutales consumidas por los macacos cada mes para definir el periodo de alta y baja abundancia de fruta como los valores por encima y por debajo de la mediana respectivamente.

Cáculo del ámbito hogareño, área núcleo y distancia recorrida diaria

Se usó *Characteristic Hull Polygons* (*CHPs*), que es un reciente estimador para calcular el ámbito hogareño y área núcleo y ha demostrado mejor precisión que los tradicionalmente usados (Downs & Horner, 2009). Para ello, primero, se importaron todas las localizaciones a ArcGIS 9.3 para formar Triángulos de Delaunay mediante la unión de los puntos (Fig. 1a, Capítulo 5). Triángulos pequeños, representan aéreas de mucha actividad y viceversa. En base al perímetro del triangulo, dos criterios han sido utilizados con anterioridad para la delimitación de estas áreas. El primero fue usar un porcentaje fijo donde el 95% y 60% de los triángulos más pequeños definían el ámbito hogareño y área núcleo respectivamente (Downs & Horner, 2009); el segundo fue el clasificar como ámbito hogareño a todos los triángulos con perímetros más bajos que la suma de la media más dos veces la deviación estándar (perímetro < X + 2*SD) y aquellos menores a dos veces la desviación estándar por debajo de la media (perímetro < X - 2*SD) como el área núcleo (Downs et al.2012). Sin embargo, en vez de esta clasificación arbitraria, se delimitaron dichas áreas usando la herramienta estadística *hot spot analysis con rendering* en ArcGIS 9.3 (Fig. 1b, Capítulo 5). La herramienta selecciona los triángulos que están más agrupados y tienen perímetro menor, y provee un valor z (Fig.1c, Capítulo 5) con significación estadística. Aquellos triángulos con valor $z > 2$ son descartados, y todos aquellos delimitan el área del ámbito hogareño; de la misma forma, aquellos triángulos con valor $z < -2$ representan el área más usada y delimitan un área núcleo (Fig. 1d, Capítulo 5). Usando este método, se calcula los ámbitos hogareños y áreas núcleos totales, mensuales y diarios. Además, para comparar con otros estudios se calcularon los ámbitos hogareños y áreas núcleos usando otros estimadores (Capítulo 5 para más detalles).

Las distancias recorridas diarias se calcularon usando solo días en donde los macacos fueros seguidos el día completo. La distancia se calculó con la suma de los segmentos resultantes de conectar las localizaciones de grupo cada 30 min.

Índice de capacidad de defender un territorio (Defendability index)

Se calculó este índice (M) siguendo Lowen & Dunbar (1994):

$$M = N(\frac{sv}{d^2})$$

donde N es el número de grupos independientes de forrajeo, s la distancia de detección de intrusos, v la media de distancia diaria recorrida, y d es el diámetro de un círculo hipotético que con un área igual a la del ámbito hogareño. Animales territoriales deben tener $M \geq 0.08$, lo que significa que por su movilidad, potencialmente pueden patrullar los bordes de su ámbito hogareño, mientras los animales no territoriales normalmente tienen un $M < 0.08$, lo que significa que la relación del tamaño del ámbito hogareño y sus viajes diarios no le permiten patrullar sus bordes.

Filopatria de ámbito hogareño y área núcleo

Varios estudios han examinado la filopatria usando el solapamiento de pares de áreas en periodos sucesivos (Young et al. 2006, 2008; Janmaat et al. 2009; Asensio et al. 2012b). Recientemente Ramos-Fernandez y colaboradores (2013) propusieron un estimador de filopatria a lo largo de todos los periodos deseados (no solo de dos en dos). Este método crea un mapa de interceptación superponiendo todos los ámbitos hogareños o área núcleo mensuales, y genera una figura con un gradiente de uso (Fig. 2, Capítulo 5). Lo cual ofrece un claro avance a la limitación por pares del método anteriormente usado y proporciona una evaluación visual rápida de las regiones del ámbito hogareño y área núcleo más utilizadas. Pero el método carece de una vía para cuantificar ese grado de uso. Por ello, se propone un índice para cuantificar dicho grado. El grado de filopatria fue estimada cuantificando el número de meses que una misma determina área fue usada, para ello se siguió el método de Ramos-Fernández y colaboradores. (2013). Basándose en este método se calculó el índice de fidelidad mensual (*f*) para ambos, ámbito hogareño o área núcleo usado la formula siguiente:

$$f = \frac{\sum_i^j p_i o_i}{nA}$$

donde j es el número de solapamientos de áreas en un mes dado, *p* es el número de veces que cada área fue solapada durante todos los meses, *o* es tamaño del área solapada, *n* el número de meses estudiados, y *A* es el tamaño mensual del correspondiente ámbito hogareño o área núcleo. Los valores del índice varían de 0 a 1,; valores cercanos a 1 indican una filopatria muy alta. Para calcular la filopatria a escala de tiempo menor se usaron los ámbitos hogareños diarios para cada mes.

Masa grupo

Siguiendo a Grant y colaboradores (1992), se calculó la masa grupo (kg) por unidad de área (ha) para cada grupo estudiado. Se tomó en cuenta el peso medio para adultos machos y hembras de macacos y gibones (Macacos: Fooden 1975, Malaivijotnond et al. 2012; Gibones: Jungers et al.1984). El peso de los inmaduros se consideró como la mitad de un adulto (Clutton-Brock & Harvey 1977) y los infantes fueron excluidos.

Efecto del turismo en la filopatria a áreas humanas

Se definió el área humana creando un polígono que usa las localizaciones de los edificios humanos y aplicando el estimador *minimum convex polygon*. El índice de filopatria al área humana (*f'*), se calculó usando la formula anteriormente vista, donde *o* es el tamaño de área solapada dentro del polígono creado.

Interacciones intergrupales

Los datos de encuentros entre tropas de macacos se tomaron *ad libitum* (Altmann 1974). Se tomó la posición de todos los encuentros y se calculó la frecuencia de los encuentros (encuentros/hora) y se clasificaron como *encuentros no agonísticos o de baja intensidad de agresión*, aquellos encuentros en donde se produjo comportamiento afiliativo, evitación o pequeñas carreras a individuos de la otra tropa y *encuentros altamente agonísticos*, aquellos en los que hubo persecuciones, ataques bidireccionales y peleas colectivas en la que el macho alfa tomó parte en ataques. Se definió el *área de encuentros intergrupal*, como el área donde se localizaron el 50% de los encuentro, esta área se estimó usando Kernel (Worton 1989). Consideramos un encuentro cuando hubo contacto visual entre tropas.

Áreas dormidero

Consideramos área dormidero como el área en la cual se localizan los árboles dormideros en el ámbito hogareño de los macacos. La localización fue tomada usando el centro geométrico de todos los árboles dormidero que compone un área dormidero. Además se anotó la hora de entrada y salida de las áreas dormidero y se contó el número de veces que cada uno fue usado a lo largo del estudio. Por último se tomó la localización de la última y primera zona de alimentación para cada día de seguimiento que fue posible.

Análisis de datos

Se usaron test estadísticos a una significación de $\alpha = 0.05$, los datos fueron procesados en SPSS v.15.0 (SPSS Inc. USA). Para comparar los valores mensuales del ámbito hogareño, área núcleo, viajes diarios e índices de filopatria entre los periodos de abundancia de fruta o entre grupos de estudio. Para aquellos datos que seguían una distribución normal el test t- Student y para aquellos que no la seguían aún tras ser transformados se usó el test de Mann-Whitney.

Se usaron modelos lineales generalizados (GLM) para analizar el efecto del abastecimiento de comida en la filopatria al área humana. Como variable dependiente, se utilizó la filopatria mensual de ámbito hogareño y área núcleo al área humana. Como variables independientes fueron usadas el número mensual total de visitantes en el parque (como una aproximación a la abundancia de comida de procedencia humana; DNP 2014) y el índice de abundancia de fruta durante el periodo de estudio de la tropa semiabastecida (*Food Abundance Index,* FAI; Albert et al. 2013b). Se combinaron todos los factores independientes y sus interacciones como posibles modelos. Dados el bajo tamaño de muestra (N=12) se usó el menor para AICc para seleccionar el mejor modelo. Los parámetros del test GML y sus errores estándares se estimaron con ecuaciones generalizadas ponderadas.

Para ver si el reuso de las área dormidero fue por azar, se generaron las frecuencias esperadas de distribución usando parámetros Poisson lambda (Sokal and Rohlf 1995) y se compararon con las observadas mediante el test Pruebas de Bondad de Ajuste de Kolomogorov-Smirnoff (Day & Elwood 1999).

Se investigó si los macacos seleccionaron áreas dormidero en las áreas más familiares, se combinó la localización de cada área dormidero en el mapa de filopatria (Fig. 2, Capítulo 5 y Fig. 3, Capítulo 7) y el número de noches que cada área dormidero fue usada. Para testar si la elección de la zona fue por azar también colocamos 200 puntos al azar en el mapa de filopatria y comparamos para ver la *preferencia* usando la formula:

$$preferencia = log_{10}\left(\frac{u_i/\sum u_{i,j}}{f_i/\sum f_{i,j})}\right)$$

donde u fue el número de noches que los macacos estuvieron en un área usada en i meses (grado de filopatria), y f es el tamaño de dicha área. Cuando el valor de *preferencia* fue cercano a 0 no hubo relación entre el área elegida para dormir y la filopatria del área *preferencia* > 0 indica preferencia a dormir en esa zona, y *preferencia* < 0 indica que evita dormir en esa zona.

Se investigó la localización del área dormidero en el ámbito hogareño y el área núcleo. Se calculó la probabilidad binomial de que los dormideros se encontraran en el área núcleo (mensual y total) usando el tamaño relativo del ámbito hogareño y área núcleo. Para comparar la localización de las áreas dormideros en relación con el área de encuentro intergrupal, se usó probabilidad binomial usando: a) valores esperados derivados de las frecuencias observadas en que los encuentros ocurrieran fuera o dentro del área núcleo, y b) valores esperados derivados de las frecuencias observadas del numero de noches pasadas dentro o fuera del área de encuentro intergrupal. Por definición, cada área es usada el 50% del tiempo, siendo la probabilidad 0,5 para cada área (Brotcorne et al. 2014).

Siguendo a Albert y colaboradoes (2011), para cada noche se midió la distancia entre la última zona de alimentación y/o primera zona al día siguiente a: a) área dormidero (distancia observada), b) el área dormidero más cercana (estrategia de múltiples áreas de forrajeo, *Multiple Place Foraging Strategy*), c) el área dormidero de uso frecuente más cercano (estrategia de múltiples áreas de forrajeo modificada), y la distancia media a todos las áreas de forrajeo (estrategia de área de forrajeo central, *Central Place Foraging Strategy*). Se usó el test de rangos Wilcoxon para comparar entre cada estrategia.

Finalmente se usó correlación de Spearman para estudiar la relación entre la hora del ocaso y crepúsculo y la entrada y salida de los dormideros.

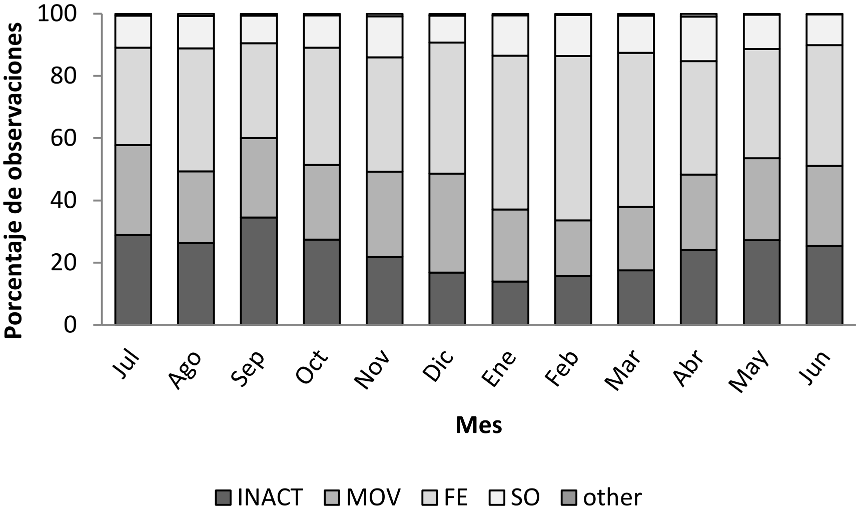
Capítulo 4

Patrones de actividad y dieta en la tropa de estudio

Analizamos los patrones de actividad y dieta durante doce meses desde julio de 2012 a junio de 2013.

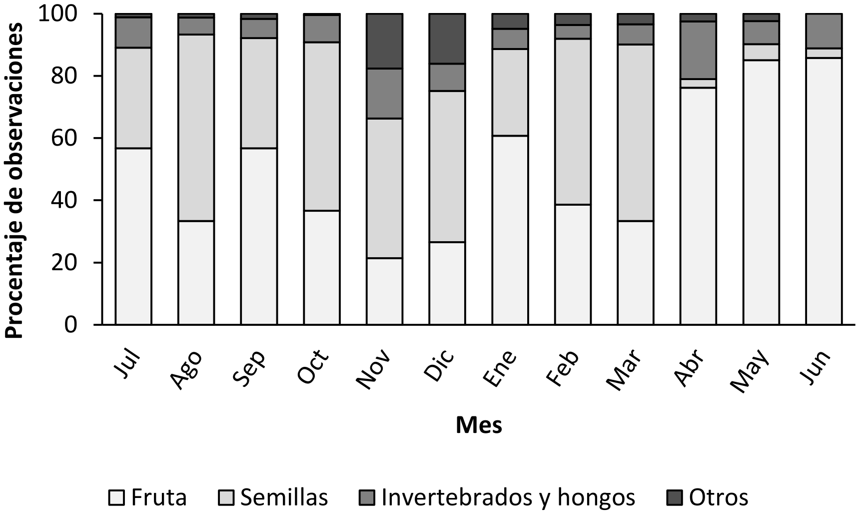
Patrones de actividad

Para un total de 11.373 observaciones, los macacos de media (± DS) emplearon el 40,0 ± 7,2 % del tiempo en alimentación, el 24,8 ± 3,7% en movimiento, el 23,3 ± 6,2 % en descanso, el 11,2 ± 1,8 % en actividades sociales y el 0,6 ± 6,2 % en otras actividades. La desviación estándar sugiere a que no hay gran diferencias a lo largo de año, pero si observamos los valores mensuales (Fig. 2), encontramos una ligera disminución de actividad dedicada al descanso y un aumento de tiempo dedicado a alimentación durante la estación fría que es coincidente con los meses de menos productividad.

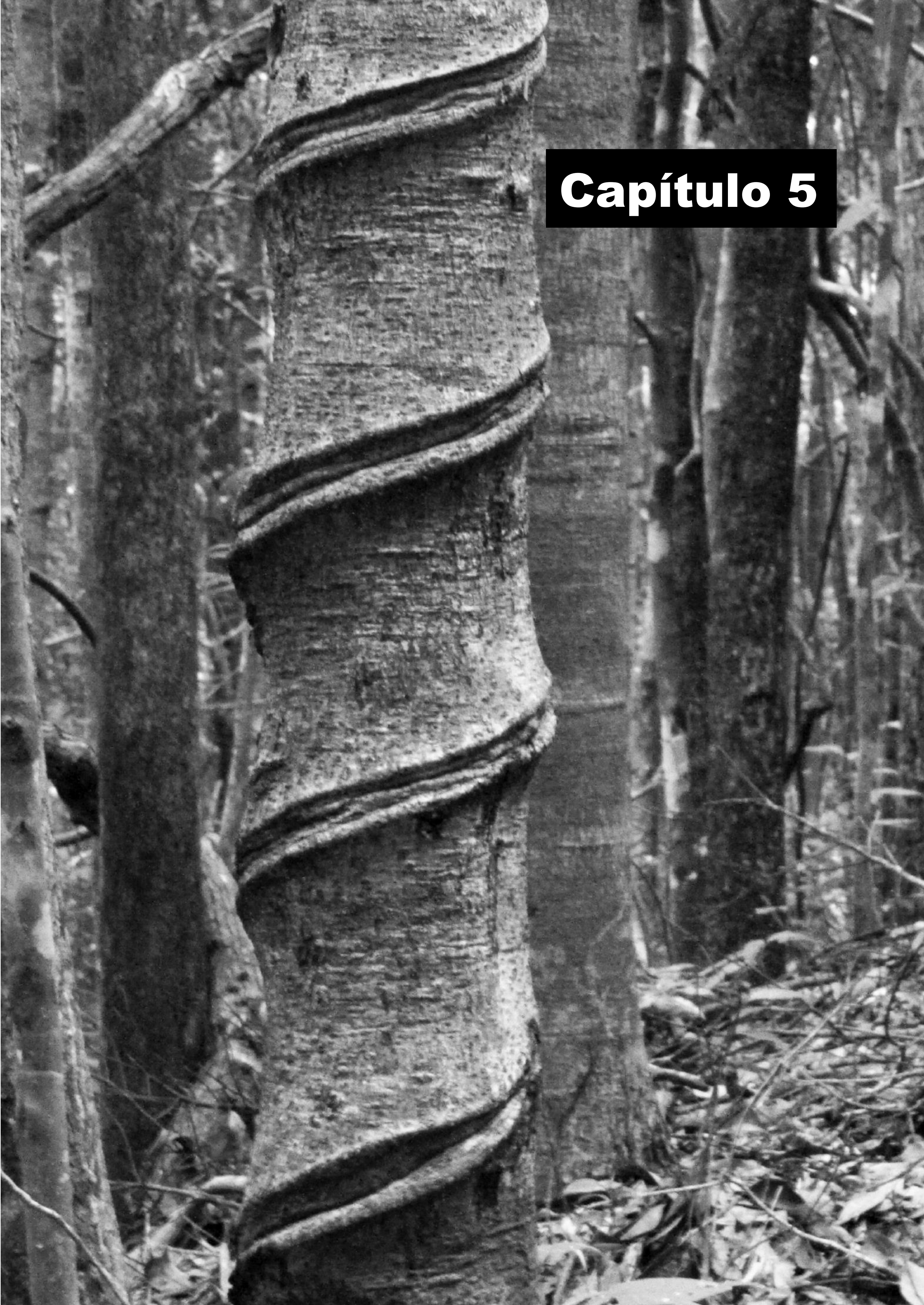


Alimentación

Para un total de 2.725 observaciones, los macacos de media emplearon el 50,9 ± 22,6 % el consumo de pulpa de frutos carnosos, el 35,3 ± 21,5 % en semillas, el 9,1 ± 4,3% en pequeños animales y hongos movimiento y el 4,6 ±5.9% en otras fuentes de alimento. Contrariamente con los patrones de actividad, el tipo de alimentación presenta unas medias anuales con altos valores de desviación estándar, sugiriendo un cambio de tipo de alimentación a lo largo de año. Atendiendo a los valores mes a mes (Fig. 3) vemos que los macacos consumen casi exclusivamente fruta carnosa en tres los meses de alta productividad de fruta y disminuye en la época de baja productividad. Por su parte en consumo de semillas es bastante alto en la mayoría del año pero bastante variable y casi nulo en los tres meses de gran consumo de fruta. El consumo del resto de alimentos esta en baja proporción a lo largo del año, pero hay un notable incremento en los meses de noviembre y enero.



Capítulo 5



Ranging and site fidelity in northern pigtailed macaques (*Macaca leonina*) over different temporal scales

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RESEARCH ARTICLE

Ranging and Site Fidelity in Northern Pigtailed Macaques (*Macaca leonina*) Over Different Temporal Scales

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Space-use patterns are crucial to understanding the ecology, evolution, and conservation of primates, but detailed ranging data are scarce for many species, especially those in Southeast Asia. Researchers studying sitefidelity to either home ranges or core areas have focused mainly on territorial species, whereas less information is available for non-territorial species. We analyzed the ranging patterns and sitefidelity of one wild troop of northern pigtailed macaques over 16 months at different temporal scales. We used characteristic hull polygons in combination with spatial statistics to estimate home ranges and core areas. The total home range and core areas were 449 ha and 190 ha, respectively. Average daily path length was 2,246 m. The macaques showed a high defendability index according to the expected ranging of a non-territorial species in which movement does not theoretically permit the defense of a large territory. Overall, the study troop ranged more extensively than conspecific groups and closely related species studied elsewhere. These differences may reflect variable troop size, degree of terrestriality and habitat characteristics, but could also reflect methodological differences. The location, size and shape of home ranges and core areas, and extent of daily path lengths changed on a monthly basis resulting in low sitefidelity between months. The macaques also showed clear shifts in the location of daily home ranges with low sitefidelity scores between consecutive days. Daily home range and daily path length were related to seasonality, with greater values during the fruit-abundant period. Low site fidelity associated with lack of territoriality is consistent with macaques structuring their movement based on available food sources. However, ranging patterns and sitefidelity can also be explained by macaques feeding on the move, a foraging strategy that hinders frequent and long visits to the same location. Am. J. Primatol. 77:841 853, 2015. © 2015 Wiley Periodicals, Inc.

Key words: home range; delaunay triangulation; hotspot analysis;fidelity index; food abundance

INTRODUCTION

Empirical data on space-use patterns are crucial to understand the ecology, evolution and conservation of animal species [Nathan 2008]. However, we lack detailed information on the ranging patterns for many threatened primate species, especially those from Southeast Asia. Researchers commonly employ ranging variables such as home range (HR), core area (CA) and daily path length (DPL) to understand the way animals use their habitat and the resources therein. Such estimates are fundamental for studies of habitat preferences [Aebischer et al., 1993], spatial overlap between neighboring groups or individuals [Fieberg & Kochanny, 2005; Olsen et al., 2011; Righton & Mills, 2006], or estimations of the carrying capacity in a patch of habitat [Downs et al., 2008].

The HR is broadly defined as the area used by individual animals or groups, over a given period, excluding occasional sallies [Burt, 1943; Jewell, 1966]. The CA is the most used portion of the HR [Kaufmann, 1962], and some authors consider it as the minimum area needed for an individual or group to survive and reproduce [Powel, 2000; Samuel et al., 1985] as it includes the most critical resources [da

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Silva Júnior et al., 2009; Thompson et al., 2009]. However, some studies have shown that critical resources may also occur outside core area boundaries [Asensio et al., 2012a; Buchanan et al., 1998; Osborn, 2004; Stoner & Timm, 2004]. DPL is another important measure of space use, defined as the distance traveled in a single day between morning and evening roosting sites. DPL seems to reflect short-term resource distribution as daily movement is largely a direct response to the current location of food [Garland, 1983].

Researchers can also study ranging patterns by analyzing recurrent visits to and use of particular regions of the landscape over time, i.e., sitefidelity. Several studies have measured site fidelity across multiple taxa [Asensio et al., 2012b; Burdett et al., 2007; Cords, 1987; Easley & Kinzey, 1986; Hellickson et al., 2008; Janmaat et al., 2009; Kitchen et al., 2000; Switzer, 1993]. Some authors consider that strong sitefidelity reflects spatial stability in the location of resources for an animal over time whereas weak fidelity is the result of temporal shifts in the spatial distribution of resources [Doncaster & Macdonald, 1991; Kie et al., 2010; Rivrud et al., 2010]. Most studies of site fidelity have focused on territorial species in which individuals range in areas actively defended against conspecifics [e.g., Hellickson et al., 2008; Switzer, 1993; Wauters et al., 1995; Webb & Shine, 1997]. Territoriality is a form of competition transferred to the defense of an area containing the resources on the condition of resources being stable and located within a defensible range [Browns & Orians, 1970]. In addition, defense of a territory usually implies regular patrols [Davies & Houston, 1984]. Therefore, a territorial animal should have stronger sitefidelity than a non-territorial animal for which fluctuations in the spatial distribution of resources should be the single predominant factor affecting ranging patterns [Burt, 1943; Borger et al., 2008].

Diet, foraging strategies and food availability are key variables to understand ranging patterns [Boonratana, 2000; Clutton-Brock & Harvey, 1977; Di Fiore, 2003; Hanya et al., 2006; Isbell, 1983; Olupot et al., 1997], and animals should modulate movement to minimize the costs (e.g., energy, predation risk or competition) and maximize the benefits derived from their movements [Ricklefs, 1990; Zhao, 1999]. In addition, animals may use spatial memory to decrease predation risk and maximize energetic efficiency in travel and food seeking [Janson & Byrne, 2007; Janson & Chapman, 1999]. Interpreting ranging and site fidelity depends critically on the temporal scale, as different scales capture distinct patterns of resource distribution [Asensio et al., 2014]. For example, Spencer et al. [1990] found in cotton rats (*Sigmodon hispidus*) that body mass correlated with the size of the weekly home range area, but not with the size of the daily home range area. Fidelity over large temporal scales (e.g., across years) should be greater in comparison to smaller scales because animals have many opportunities to revisit familiar areas in the long term [Janmaat et al., 2009]. The use of different temporal scales provides valuable information about the spatial requirements of a species during particular periods [Asensio et al., 2009; Chapman, 1988; Kie et al., 2010; Rivrud et al., 2010]. Moreover, in comparative studies, we should account for the particulars of different methods of estimating ranging and sitefidelity (e.g., kernels, minimum convex polygon), as these can produce highly variable estimates because they are differentially sensitive to subtle changes in range use characteristics [Downs et al., 2012].

The northern pigtailed macaque (*Macaca leonina*) is an omnivorous primate that lives in multimale/multi-female troops [Melnick & Pearl, 1987]. The species is considered non-territorial as it does not engage in agonistic encounters with conspecific groups at HR boundaries, it does not patrol HR borders, and its HR overlap with neighboring troops is extensive (25 48%) [Choudhury, 2008]. Some studies describe pigtailed macaques as semiterrestrial [Albert et al., 2011], but others consider them mainly terrestrial [Boonratana et al., 2008] or mainly arboreal [Choudhury, 2008; Feeroz, 2012]. Moreover, the species shows great flexibility in exploiting different habitat types and canopy levels with variability in its ranging, feeding, and habitat preferences in response to different habitat conditions [Albert et al., 2013a,b; Choudhury, 2008; Feeroz, 2012]. Although those macaques are omnivorous, fruit is the most important food item for this species. The diet included 36% fruit in semiprovisioned troops [Albert et al., 2013a] and 76 87% in wild feeding troops [Choudhury, 2008; Feeroz, 2012]. The HR of pigtailed macaques measured over long periods (a year or more) is 44 347 ha [Choudhhury, 2008; Albert et al., 2013a,b], while monthly HR and CA are 7 83 ha and 0.5 14 ha, respectively [Albert et al., 2013b]. The pigtailed macaque often shows an opportunistic foraging strategy in which all individuals simultaneously travel and eat between food patches [Agetsuma, 1995; Caldecott, 1986; Caldecott et al., 1996].

Although several studies of wild northern pigtailed macaques have taken place at the northwestern edge of the species range [Choudhury, 2008; Feeroz, 2012], detailed descriptions of ranging patterns are available only for a semiprovisioned troop in Khao Yai National Park, central Thailand [Albert et al., 2013b]. In this study we monitored a non-provisioned troop of northern pigtailed macaques also inhabiting the seasonally wet evergreen forest of Khao Yai National Park over a 16-month period. We estimated range sizes and site fidelity using both short (across five to seven consecutive days within each month) and long (across 16 months) temporal scales, to provide a comprehensive picture of ranging patterns. We first estimated home ranges and core areas using a recently developed analytical method based on characteristic hull polygons [Downs & Horner, 2009] and compared the results with traditional estimation techniques (minimum convex polygon, kernels and grid cells) to facilitate comparison with published studies. Moreover, we investigated how general fruit abundance and frugivory might affect seasonal variation in HRs, CAs, and DPLs. Second, as information on this species is limited, we calculated the defendability index of Lowen & Dunbar [1994] to determine if the ratio of the DPL to HR area is consistent with that expected for an animal that does not actively defend a territory. Third, we investigated the site fidelity over both short and long temporal scales to better understand the range requirements of a wild feeding troop. As in other non-territorial animals, we predicted that our troop would show lower site fidelity on shorter time scales because animals would avoid revisiting areas recently exploited, returning to them only after longer periods allowing for food regeneration. Fourth, even if macaques did not usually revisit exploited areas in the short-term, we expected that short-term site fidelity would decrease during the low-fruit season because macaques would spend little time in any particular area as suggested by Terborgh [1983] for capuchin monkeys (*Cebus* sp.).

METHODS

Study Site

We collected data in the Mo Singto forest, Khao Yai National Park, Thailand (2,168 km^2; 101°22 E, 14° 26N), which covers approximately 10 km^2 of mainly seasonally wet evergreen forest at an altitude of 700 890 m [Savini et al., 2008]. The climate is monsoonal with a wet season (May October), a cold dry season (November February) and a hot dry season (March April). Annual precipitation ranges from 2,000 to 3,000 mm [Bartlett, 2009], mean monthly temperature ranges from 19°C to 24°C [Albert et al., 2011] and mean humidity from 65% to 77% [Savini et al., 2008]. In general there is marked seasonality in fruit abundance with a high abundance period (high-fruit) in March September and a low-abundance period (low-fruit) in October February [Bartlett, 2009].

Study Group

We studied the wild and completely unprovisioned CH troop during 1,321 hr in two periods: 312 hr during April May 2011, when the troop comprised 49 individuals (4 males, 19 females, 26 immatures) and 1009 hr during May 2012 June 2013, when the troop comprised 60 67 individuals (3 4 males, 19 20 females, and 37 44 immatures). We could distinguish all macaques by individual characteristics such as face, coloration patterns and scars. Analysis on adult diet over a 12-month period (July 2012 June 2013) included fruits and seeds (86%), invertebrates and small vertebrates (10%) and other plant matter (5%) [José-Domńguez, unpublished data]. The study troops HR was adjacent and partly overlapping with that of a semi-provisioned troop studied previously [Albert et al., 2013b].

Our research conforms to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human primates. Permission to conduct research was granted by the Department of National Parks, Wildlife, and Plant Conservation and adhered to the legal requirements of Thailand. This research is part of the requirements to fulfill the doctorate degree of JMJD.

Data Collection

We collected ranging data of CH troop over 16 months (April May 2011 and May 2012 June 2013]. The troop was well habituated to researchers who could approach to a distance of 1 3 m. Whenever possible we followed the troop for a minimum of five consecutive full days (from sleeping site to sleeping site) per month: our sample included 31 observation days (23 complete) in April May 2011 and 102 days (81 complete) in May 2012 June 2013. We used a sample of 5 to 7 consecutive days in each month to calculate monthly ranges, hereaftermonthly HRs andmonthly CAs.

We recorded troop locations using track-log data at 30 min intervals with a handheld global positioning system [GPS, GPSmap 62s, Olathe, KS] at roughly the center of the troop. The GPS accuracy was 9.4±SD 3.3 m (range: 1 26 m) based on 1501 30-min interval readings. We used the universal transverse Mercator (UTM) format (zone 47N) projection.

Low and High-Fruit Abundance Seasons

Several authors have demonstrated that the number of fruit species consumed by animals is positively correlated with the number of species fruiting, which allows classifying fruit abundance seasons [e.g., Albert el al., 2013b; Isbell, 1983]. Therefore, over 12 months (July 2012 June 2013) we recorded the number of fruit species consumed by macaques to define high-fruit and low-fruit seasons as the months with scores above and below the median, respectively.

Estimating Home Range, Core Area and Daily Path Length

We used characteristic hull polygons (CHPs), a relatively recent non-probabilistic method of HR estimation [Downs & Horner, 2009], to calculate HRs and CAs. We first imported all recorded locations into ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA) to form Delaunay triangles of various shapes and sizes based on their density and spatial distribution (Fig. 1a). The rationale behind CHPs is that small triangles represent areas of high ranging activity while large triangles represent unused or less frequently visited areas. Therefore, small triangles best represent the HR and the CA whereas large triangles are out of the ranging delineation (Fig. 1b). Based on the triangle perimeter length, two criteria usually define the HR and the CA: (1) a fixed percentage where 95% and 60% of the smallest triangles define the HR and CA, respectively [Downs & Horner, 2009] or (2) all triangles with perimeters of less than two standard deviations above the mean for the HR and those with perimeters of less than the mean form the CA [Downs et al., 2012]. However, to perform a less arbitrary selection of which triangles form the HR and the CA, we applied a spatial statistical tool, hot spot analysis with rendering, in ArcGIS 9.3. This tool assesses whether long or short triangle perimeters are statistically clustered in space. Specifically, this analysis provides a *z* score with a *p* value for each triangle representing its clustering intensity (Fig. 1c). Therefore, for statistically significant positive *z*-scores, the larger the score is, the more intense the clustering of high values (hot spots of large perimeter triangles) is. Conversely, for statistically significant negative z-scores, the smaller the score is, the more intense the clustering of low values (cold spots of small perimeter triangles) is. Accordingly, we eliminated long perimeter triangles that were statistically clustered (*z*-scores >2) and the remaining triangles formed the HR (*z*-scores<2). We used the short perimeter triangles inside the home range, classified as significantly clustered, to define

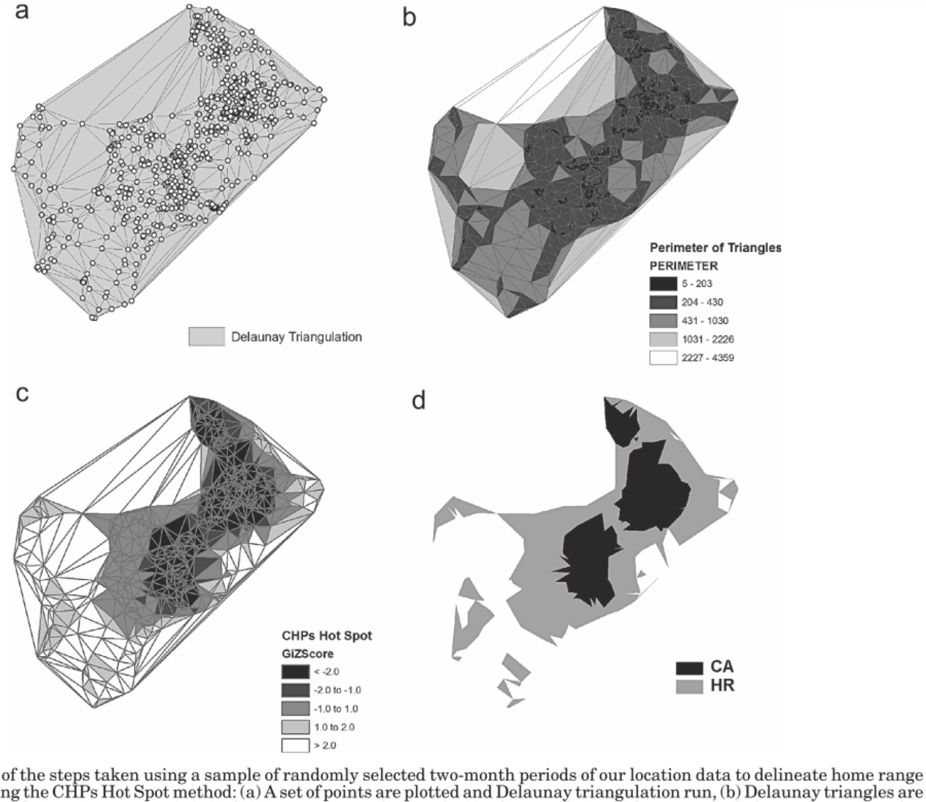

Fig. 1. Example of the steps taken using a sample of randomly selected two-month periods of our location data to delineate home range and core area using the CHPs Hot Spot method: (a) A set of points are plotted and Delaunay triangulation run, (b) Delaunay triangles are classified based on their perimeter size (m), (c) CHPs are generated using the Hot Spot analysis, (d) home range (light grey) correspond to triangles with Z-values≤ 2 and core area (dark grey) to values<-2.

the CA (z-scores<-2; Fig. 1d). Using this CHPs Hot Spot method, we calculated both the total (16 months) and monthly HRs and CAs of the troop. We also defined daily HRs using this method. Because there were not usually enough triangle samples in single days, we did not calculate daily CAs.

To allow comparison with previous studies on pigtailed macaques we also calculated the total and monthly range sizes of the troop using (1) fixed kernel volume contours with a smoothing parameter selected by least-squares cross-validation [Worton, 1989]: 95% HR and 50% CA, (2) minimum convex polygons [MCP: Mohr, 1947] enclosing 100% and 95% (HR), and 50% (CA) of group locations, and (3) a grid of 1-ha square cells for which we counted the number of cells containing the 100% and 95% of group locations (HR), and the 50% of locations (CA).

We estimated the total HR and CA using both complete and incomplete day records; the locations recorded during incomplete days are important to have a complete delineation of a HR in the long-term [Blundell et al., 2001; de Solla et al., 1999]. DPL was the sum of the total 30 min travel segments resulting from consecutive GPS locations during a complete day.

We calculated the defendability index as the fractional monitoring rate (M) following Lowen & Dunbar [1994]:

$$M \quad N\frac{\sum sv}{d^2}\Bigg)$$

where N is the mean number of independently foraging parties, s is the detection distance (the distance at which intruders can be detected), v is the mean of DPL and d is the diameter of a hypothetical circle with an area equal to the total HR. Territorial animals should have $M \geq 0.08$, suggesting that the mobility of the animals allows them to reach HR boundaries at least once daily. By contrast, non-territorial animals usually have $M < 0.08$, suggesting reduced mobility in relation to the size of the HR and boundary length, which does not permit to defend a territory.

Home Range and Core Area Fidelity

Several studies have examined the overlapping areas between pairs of successive periods (e.g., months, years) to investigate site fidelity [e.g., Asensio et al., 2012b; Janmaat et al., 2009; Young et al., 2006; Young et al., 2008]. Ramos-Fernandez et al. [2013] proposed an estimate of site fidelity based on the recurrent use of particular areas across all (not just successive) periods. We employed the latter method to estimate long- and short-term fidelity of HRs and CAs. First, we delineated an interception map overlaying all monthly HRs or CAs, and then we generated a figure showing a gradient of use of all overlapping regions. This figure depicts the number of periods in which an area was used (Fig. 2). We estimated site fidelity of the study troop by counting the number of days (short-term) or months (long-term) in which different regions of either HR or CA overlapped. This method provides a quick visual assessment of the regions of the HR or CA that are reused over time and allows a determination of fidelity by examining the relationship of area size and its repeated use.

Because Ramos-Fernandez et al. [2013] method consists mostly of a visual assessment tool, we created an index to quantify its estimation of site fidelity. This index is based on the region size and the number of times that it is reused over time steps (i.e., months or days in our study). Using the 16 monthly HRs or CAs (long-term fidelity), we calculated the site fidelity index (f) for either HR or CA as follows:

$$f \quad \frac{{}^{\;\;j}_{i\;2}\; p_i o_i}{nA}$$

where j is the number of overlapping areas in a given month, p is the number of times that each area overlapped over all months, o is the overlap area size, n is the number of study months, and A is the total area used as HR or CA. We calculated short-term site fidelity similarly, considering the overlay of the 5 7 consecutive daily HRs for each study month. The index values range from 0 to 1 reflecting no and complete site fidelity respectively.

Data Analysis

We used SPSS v.15.0 (SPSS Inc., Chicago, IL) for statistical analyses. We performed Mann-Whitney U-tests to conduct between-season comparisons of the number of fruit species eaten, daily and monthly ranging patterns (HR, CA, DPL and short-term site fidelity).

RESULTS

Low and High-Fruit Abundance Seasons

The median of fruit species consumed across the 12 months was 11.5±IQR 8 species. The high-fruit season corresponded to March August (N 6) and the low-fruit season to September-February (N 6). The number of fruit species eaten by macaques was greater during the high-fruit season (median: 15.5±IQR 4.75 species, N 6) than that during the low-fruit season (median: 8.5±IQR 4.0 ha, U 2, 2-tailed P 0.009).

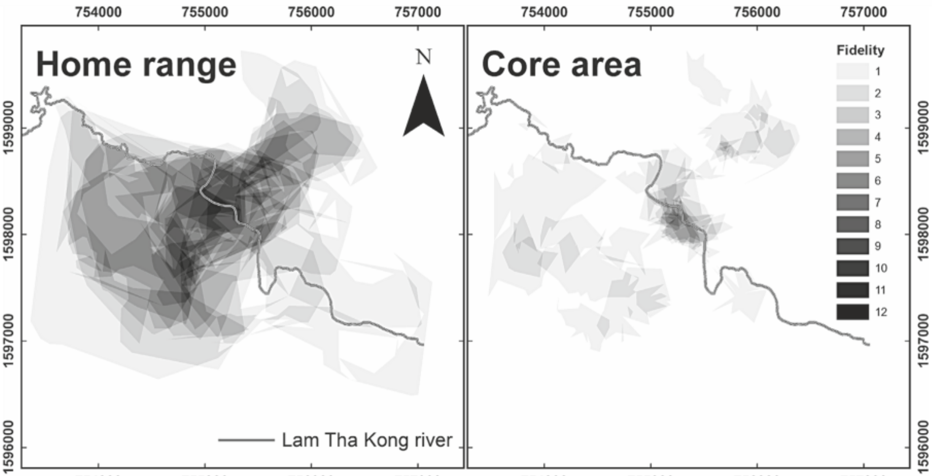

Fig. 2. Long-termfidelity map based on the union of the 16 monthly home ranges and core areas during the study. Panels show site fidelity to home range and to core area. The different shades of grey (1 12) represent the repeated use of different areas. Lighter shades represent areas with none or little overlap, whereas darker shades represent areas with high or maximum overlap. Universal Transverse Mercator (UTM) coordinates for latitude and longitude are given in meters in the horizontal and vertical axes of the frame.

Home Range, Core Area and Daily Path Length

We recorded a total of 2,744 locations during 133 days (104 complete days) of troop follows with a monthly average of 172±SD 66.4 locations,*N* 16. The total HR and CA based on all location samples over 16 months were 449 ha and 190 ha respectively (Fig. 3). The study troop showed wide variation in monthly ranging patterns with HRs and CAs that varied markedly in size and shape. Monthly HR values varied widely over the 16 months (mean: 142.3±SD 89.3, range: 44 354 ha) as did monthly CAs (21.6±SD 19, range: 7 77 ha; Fig. 4). The average daily HR was 23.4±SD 15.0 ha (range: 2 70 ha,*N* 104).

Different range estimators produced discrepant estimates of range sizes measured over periods of one month or the entire study period. In general CHP hot spot produced the smallest ranges and MCP the largest ones (Table I, Fig. 3).

The average DPL using 104 complete days was 2,246±SD 619 m (range: 1,246 3,891 m). We obtained similar results, but with a larger SD, when we computed the average of 16 monthly means (DPL 2,212±SD 480 m, range: 1,520 3,112 m).

There were not significant seasonal differences in monthly HRs (for high-fruit, median: 127.5±IQR 75.1 ha, *N* 6; for low-fruit, median: 60.8.7±IQR 86.8 ha,*N* 6;*U* 8.0, 2-tailed*P* 0.132), monthly CAs (for high-fruit, median: 15.1±IQR 9.6 ha,*N* 6; for low-fruit, median: 11.4±IQR 5.0 ha, *N* 6; U 11.0, 2-tailed *P* 0.310). However, daily HRs (for high-fruit, median: 26.8±IQR 12.2 ha,*N* 6; for low-fruit, median: 12.6±IQR 8.3 ha,*N* 6; U 2.0, 2-tailed *P* 0.009) and monthly DPL were significantly longer during the high-fruit season than during the low-fruit season (for high-fruit, median: 2,487±SD 663 m, *N* 6; for low-fruit, median: 1,765±SD 314 m, *N* 6; *U* 1.0, 2-tailed *P* 0.004). For each DPL we calculated the day length using the sunrise and sunset time computed by the GPS for the study site location. Because mean day length was longer during the high-fruit season (12.1 hr) than the low-fruit season (11.5 hr), we also investigated DPL corrected for (i.e., divided by) day length. Even with this correction, however, the macaques moved farther during the high-fruit than during the low-fruit season (for high-fruit, mean: 194±49 m/hr, *N* 36; for low-fruit, mean: 152±30 m/hr, *N* 33; *Z* – 2.545, 2-tailed*P* 0.000).

The *M* index, based on the total HR (449 ha) during the 16 months, one foraging party and an estimated detection distance between troop of 50 m, was 0.019, resembling that of other non-territorial species [Lowen & Dunbar, 1994].

Site Fidelity to Home Range and Core Area

The study troop showed an unstable use of space across months, with macaques using most area in just one or two months and not using any

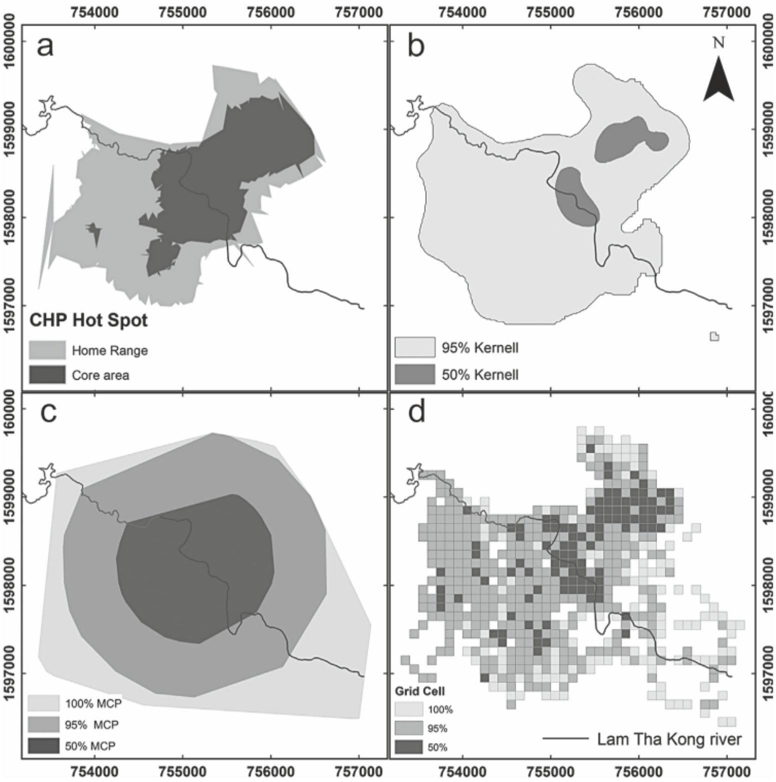

Fig. 3. Study troop range based on the total observation time (16 months) using different methods: (a) CHPs Hot Spot, (b) Kernel 95 and 50%, MCP 100%, 95% and 50%, and Grid Cell 100, 95, and 50%. Universal Transverse Mercator (UTM) coordinates for latitude and longitude are given in meters in the horizontal and vertical axes of the frame.

part of the HR or CA in all 16 study months (Fig. 2 and 5). For example, macaques used 35% and 71% of the area covered by the union of all monthly HRs and CAs, respectively, for only one month. Only 8% of the region enclosed by all monthly CAs overlapped in three or more months, whereas this proportion was 50% when we considered the HR (Fig. 5). The overlap intensity of monthly CAs decreased more steeply than that for the HR, indicating lower site fidelity to the CA than to the HR. The maximum fidelity (7 to 9 overlapping months) for CA occurred in a very small region of <1.5 ha (0.5%). Similarly, the maximum fidelity to the HR area (12 overlapping months) occurred in a very small region of less than 1 ha. The total site fidelity index across the 16 months was 0.18 for HR and 0.05 for CA. The average daily HR fidelity index over the 16 months was lower (0.08 ±SD 0.037, range 0.01 0.13) than that based on a monthly time scale. Macaques daily fidelity did not differ between the high-fruit (median: 0.10± IQR 0.04, N 6) and the low-fruit season (median: 0.07±IQR 0.09, N 6; U 11.5, 2-tailed P 0.589).

DISCUSSION

Comparison of Ranging Patterns With Other Related Macaque Species

Our findings show that the time window and range estimator chosen can greatly affect the shape and size of a HR or a CA. This supports the notion of different time scales capturing different phenomena [Kie et al., 2010; Rivrud et al., 2010]. A 16-month HR or CA may not include areas that are important for macaques over shorter temporal scales (days or weeks). For instance, individual trees may provide fruit for only a few weeks or even a few days at the study site [Asensio et al., 2011], therefore areas with critical resources classified as daily or monthly core areas may be excluded in macaques longer term areas (e.g., yearly CA). This discrepancy challenges

Fig. 4. Monthly home ranges (HR) and core areas (CA) of the study troop during the 16-month study period based on CHPs Hot Spot and monthly averages of daily path length (DPL).

the possibility of finding a CA that comprises the minimum area needed to survive and reproduce [Buchanan et al., 1998; Asensio et al., 2012b]. In addition, comparisons with other studies must carefully take into account the length of the study and methods used.

Overall, our study troop showed larger HRs, CAs and longer DPLs than other troops of northern pigtailed macaques, even if these studies employed estimators that tend to inflate the size of HRs and CAs such as kernels, MCP and grid cells [Downs et al., 2012]. For example, Choudhury [2008,2010] studied seven troops over 290 hr in total (16 33 members, 72% frugivory, 133 hr of observations on two troops) in northeast India and reported HR sizes (using 1.25-ha cells) of 83 347 ha, and a DPL of 690 2,240 m. These smaller HRs might be the consequence of the reported absence of terrestriality in many of these troops [Choudhury, 2010] in contrast to the semiterrestriality of our study troop [terrestrial (height$\leq$1m) 55.5% of adults time; José-Domńguez, unpublished data]. Arboreal animals

TABLE I. Total and Monthly Home Range and Core Area Sizes (ha) Calculated by Different Ranging Estimators

	CHP Hot Spot		Kernel		MCP			Grid Cell		
	HR	CA	95%	50%	100%	95%	50%	100%	95%	50%
Total	448.9	190.5	575.3	46.6	961.7	682.5	228.7	586	452	108
Apr-11	307.9	76.8	720.7	90.2	598.0	556.8	200.2	122	113	34
May-11	354.5	17.3	673.9	152.1	484.4	474.2	212.6	120	112	36
May-12	213.2	54.8	343.5	53.1	268.5	254.5	92.1	94	88	32
Jun-12	139.4	33.2	260.0	42.6	200.6	187.9	103.8	100	90	22
Jul-12	167.4	17.3	309.8	30.7	252.4	235.9	106.6	109	101	31
Aug-12	90.6	8.3	149.0	17.0	126.4	124.2	60.1	84	75	18
Sep-12	49.0	17.9	89.8	10.1	109.7	82.7	14.3	59	53	12
Oct-12	45.8	9.7	87.2	13.5	109.7	77.6	21.7	52	46	10
Nov-12	120.8	10.7	216.2	32.9	83.6	131.1	77.7	65	59	19
Dec-12	166.2	12.1	285.0	54.0	143.7	240.0	68.4	78	71	20
Jan-13	72.7	12.6	87.6	4.4	107.9	89.4	22.0	71	64	17
Feb-13	44.0	6.6	75.4	6.3	61.9	57.7	26.0	56	48	11
Mar-13	102.8	15.6	173.8	15.3	218.5	198.7	62.5	70	62	10
Apr-13	163.9	10.8	258.7	41.2	220.3	197.8	81.4	100	92	28
May-13	152.3	27.1	259.3	12.8	223.3	189.8	104.4	97	89	26
Jun-13	86.7	14.7	115.1	8.0	132.9	113.6	31.8	68	62	13
MEAN	142.3	21.6	256.6	36.5	208.9	200.7	80.3	84.1	76.6	21.2
SD	89.3	19.0	193.0	38.6	145.4	138.5	58.4	22.5	21.8	9.0

Characteristic hull polygons with hot spot analyses (CHP Hot Spot);fixed-kernel (LCSV smoothing factor); minimum convex polygon (MCP). Grid cells size 1 ha.

may have smaller HRs and DPLs than those that are exclusively terrestrial given the extra energy required to move in three dimensions [Carbone et al., 2005; Rodman, 1979]. In addition, fully terrestrial macaque troops inhabited the best quality forests [i.e., forest with good canopy cover, Choudhury, 2008], which may indicate that fruit was abundant enough that macaques did not need to forage on the ground. Absence of terrestriality in these troops could, however, also be the result of niche partitioning with other macaque species (Feeroz, 2012).

Smaller HR, CA (estimated using Kernels) and DPL in the semi-provisioned troop of northern pigtailed macaques neighboring our study troop are likely the result of food supplementation [Albert et al., 2013b]. This troop (30 39 members, 12-months study) had a considerable proportion of its diet obtained from human resources (28% of feeding time). Moreover, the smaller troop size might have led to fewer travel constraints than for our larger study troop, which would require extra effort to coordinate the simultaneous travel of many individuals [Janson & Goldsmith, 1995; Olupot et al., 1994, but see Chapman & Chapman, 2000; Dias & Strier, 2003]. Finally, sleeping sites of the semi-provisioned troop, mainly attached to a small human settlement [Albert et al., 2011], might also have affected the more limited ranging. Several studies show that when animals rely on anthropogenic food sources located at fixed places, HR, CA, DPL, and time traveling decrease [e.g., Altman & Muruthi, 1988; Boutin, 1990; Kreiter & Wise, 2001; Monadjem & Perrin, 1998; Saj et al., 1999; Wheatley et al., 1996]. However, when food resources are dispersed in more than one location, ranging variables may increase [e.g. Marriott, 1988; Sha & Hanya, 2013; Unwin & Smith, 2010].

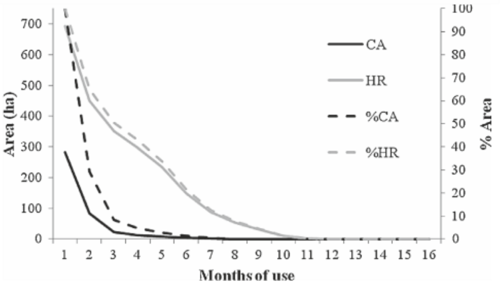

Fig. 5. The size and percentage of home range and core area as a function of overlap intensity indicating the number of months a specific area is used over the study period (ranging from 1 to 16 months).

The phylogenetically closest species to the northern pigtailed macaque is the southern pigtailed macaque (*M. nemestrina*), whereas the Siberut macaque (*M. siberu*) is the most similar species in terms of lifestyle and ecology [Richter et al., 2013]. Overall, both species show smaller ranges than our study troop of northern pigtailed macaques

[Caldecott, 1986 Richter et al., 2013]. Caldecott [1986] reported macaque troops (30 55 individuals, 9% terrestriality, 74% of frugivory) with HRs of 62 to 70 ha, based on grid cell analysis. Richter et al. [2013] found that a Siberut macaque troop of 29 individuals (25% of terrestriality and 76% of frugivory) had a HR and CA (MCP) several times smaller than those of our study troop. These differences may be a consequence of the highly productive habitats of the Sundaic forest where the troops of *M. nemestrina and M. siberu*live [Corlett & Primak, 2011] and thus macaques could meet their energy requirements by using a small but high-quality range [e.g., Li & Rogers, 2005; McLoughlinet al., 2000; Potts et al., 2011].

Site Fidelity of Northern Pigtailed Macaques

The study troop had a consistently low long-term site fidelity both for HR and CA, with no area used in all 16 months of the study. The most re-used areas for both CA and HR were mainly foraging regions surrounding the most frequently used sleeping sites. The macaques sometimes spent 1 2 hr foraging in these areas before entering sleeping sites (José-Domńguez unpublished data). This result concurs with the notion of the species not being territorial as confirmed by the*M*index of the study troop. By contrast, the territorial white-handed gibbon (*Hylobates lar*) at the same study site, with relatively small HRs [14 49 ha; Savini et al., 2008], had high site fidelity values based on monthly HRs [Brockelman et al., 2014]. Low site fidelity associated with an apparent lack of territoriality is consistent with the idea that northern pigtailed macaques movement patterns reflect the spatio-temporal fluctuations of resources. In contrast, the semi-provisioned troop of northern pigtailed macaques in KhaoYai frequently visited the same patches of fruit over several consecutive days [Albert et al., 2013b], which produced a small range (HR, CA, and DPL) and high site fidelity [José-Domńguez et al., unpublished data].

Given the large number of individuals and absence of anthropogenic food for our study troop, the low short-term site fidelity may suggest that their food sources are rapidly depleted, so that it is more advantageous to move to another patch [Stephens & Krebs, 1986]. This scenario may force macaques to move constantly in search of new food resources [e.g., Wrangham et al., 1993]. Like some other cercopithecines living in large groups (Japanese macaques, mandrills and drills), pigtailed macaque troops can spread across all habitat layers and different individuals can simultaneously forage and feed on a wide variety of food items while travelling [Agetsuma, 1995; Caldecott, 1986; Caldecott et al., 1996; Choudhury, 2008]. In addition, troops with many individuals likely have a longer searching range in which they can potentially advertise food resources to other members by means of social cues or calls. For instance, we often observed macaques smelling each other s mouths, a behavior that allows them to gain information about what others have been eating [e.g.,*Macaca tonkeana* , Riley, 2005]. Moreover, this foraging strategy implies long DPLs and large HRs [Caldecott et al., 1996] to gather the necessary resource requirements of a large troop, which in turns creates low site fidelity.

Seasonal Variation of Ranging Patterns

Monthly HRs and CAs were not larger during the high-fruit abundant season compared to the low-fruit season. Nonetheless, daily HR and DPL were longer during the high-fruit season, which supports the view that short-term general food abundance influences daily range. This difference could also be the result of longer day lengths during the high-fruit season, which logically could inflate DPL values [Gerber et al., 2012]. However, the distance travelled in the high-fruit season was significantly longer even when controlled for the day length difference between seasons. This suggests that food availability may be the main driving factor explaining seasonal differences in DPL.

Contrary to our fourth prediction, macaques do not appear to revisit recently exploited foraging areas more often in the high-fruit season than in the low-fruit season. This lack of differences between seasons may reflect nutritionally important dietary components others than fruit. For example, our study troop mostly obtained protein from small animals (invertebrates, lizards, and passerine eggs). Although these items constituted only the 10% of the diet, foraging on these resources requires considerable time and ranging effort in specific areas [Crompton & Andau, 1986; Terborgh, 1983]. Moreover, this activity is sporadic and cryptic to the observer; therefore it may be underrepresented in our results. It is also possible, however, that stochasticity and the small sample size (*N* 12 months) produced bias in our results.

Animals can respond to periods of food scarcity in two ways: increasing their range to seek additional resources (energy-maximizing strategy) [Hanya et al., 2006; Li & Rogers, 2005] or decreasing it to save energy (energy-minimizing strategy) [Fan et al., 2008; Strier, 1992]. Based of an observation on the semi-provisioned troop, Albert et al., [2013b] predicted that wild pigtailed macaques would use an energy-maximizing strategy similar to other semi-terrestrial cecopithecine species [e.g., vervet monkeys: Barrett, 2005]. However, our study troop decreased its daily HR and DPL during the low-fruit season. Therefore, this troop rather approaches an energy-minimizing strategy as seen in other primate taxa, including chimpanzees [Wrangham, 1977], gibbons [Fan et al., 2008; Raemaekers, 1980], howlers monkeys [Milton, 1980] and Japanese macaques [Hanya et al., 2006].

New Methods for Estimating Site Fidelity and Range Size

We used a novel sitefidelity index that adds to the graphical method of Ramos-Fernandez et al. [2013], as it quantifiesfidelity, allowing comparison between species or groups and also between different periods. The sitefidelity index may also be useful to investigate habitat use, allowing one to associate different habitat types with the degree to which particular areas are re-used.

Finally, we believe that our method CHPs Hot Spot offers some advantages in identifying HRs and CAs without the potentialflaws that other methods such as MCP or kernels may intrinsically contain. MCPs often include large areas never truly used by animals and do not provide information about space use within the polygon [Powell, 2000]. Kernels accuracy is highly dependent on the shape, number and homogeneity of the locations, as well as the selection of a smoothing factor; any of which may bias HR estimation [Downs & Horner, 2009; Downs et al., 2008, 2012; Girard et al., 2002; Hemson et al., 2005; Mitchell & Powell, 2008; Row & Blouin-Demers, 2006], moreover its only assumption (locations must be independent and identically distributed in space) is often violated due to the nature of animal ranging (Downs et al., 2012).

CONCLUSIONS

Ranging patterns of wild northern pigtailed macaques were highly variable and differed with the temporal scale used. Certain macaque ranging patterns, such as larger daily HR and longer DPL during the high-fruit season, partially reflect spatio-temporal changes of food abundance and an energy-minimizing strategy. However, we need to measure food availability directly to confirm these patterns. The macaques strategy of feeding on the move also explains some of their ranging patterns such as low site fidelity. Although the troop showed low site fidelity over all temporal scales considered, further studies should test whether it changes over even longer scales (e.g., several years) [e.g., Janmaat et at., 2009].

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Una vez que hemos rellenado la ausencia de información sobre tropas no abastecidas, vamos a ver en el siguiente capítulo cómo afecta la abundancia de comida de origen humano en los patrones de movimiento, filopatria y naturaleza de las relaciones intergrupales.

Capítulo 6

Non-territorial macaques can range like territorial gibbons when partially provisioned with food

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Non-territorial Macaques Can Range Like Territorial Gibbons When Partially Provisioned With Food

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ABSTRACT

Human food supplementation can affect components of animal socioecology by altering the abundance and distribution of available food. We studied the effect of food supplementation by comparing the ranging patterns and intergroup interactions of two groups of northern pigtailed macaques (*Macaca leonina*), a non-territorial primate species. One group was partially reliant on food provisioning, whereas the other group foraged wild food. We also compared the macaques movement with that of a group of white-handed gibbons (*Hylobates lar*), a territorial species inhabiting the same site. Home range, core area, and daily path lengths were significantly smaller for the semi-provisioned group than for the wild-feeding group. In contrast to wild-feeding macaques, supplemented macaques showed higher fidelity to home range, core area, and particularly to the region where human food was most accessible and abundant. The relationship of daily path length and home range indicated a low defendability index for wild-feeding macaques; the higher index for the semi-provisioned group was consistent with the territorial pattern found in gibbons. Semi-provisioned macaques showed further traits of territoriality with aggression during intergroup encounters. These findings indicate that human modification of food availability can significantly affect movement patterns and intergroup competition in macaques. The observed ranging dynamics related to food provisioning may decrease the efficiency of macaques as seed dispersers and increase predation on their home range, and thus have important consequences for plant regeneration and animal diversity.

Abstract in Thai is available with online material.

Key words: core area; home range; Khao Yai National Park; *Macaca leonina*; northern pigtailed macaque; site fidelity; socioecological models; white-handed gibbons.

SOUTHEAST ASIA HAS BEEN ONE OF THE MAJOR ZONES OF SYMPATRY BETWEEN HUMAN AND NONHUMAN PRIMATES for at least the last 10,000 yr (Fuentes 2006), and this long interaction has created a form of co-ecology where both taxa affect one another significantly (Fuentes 2006, Riley *et al.* 2011). The particularly strong anthropogenic disturbance and consequent fragmentation of tropical landscapes during recent decades have generated many new areas where animals and humans are compelled to interact (Biquand *et al.* 1994, Woodroffe 2000, Hill *et al.* 2002, Lee & Priston 2005, Corlett & Primack 2011, Laurance *et al.* 2011). With this proximity, animals may lose their fear of humans while discovering the ease of feeding from garbage, leftovers, or crops (Sprague 2002, Lee & Priston 2005, Albert *et al.* 2011, 2013a,b). This is aggravated by deliberate feeding of animals by people in lodges, temples (Brennan *et al.* 1985, Else 1991, Fa & Lind 1996, Richter *et al.* 2009, Knapp *et al.* 2013), and even protected areas (Orams 2002, Sangjun *et al.* 2006, Albert *et al.* 2011, 2013a,b).

This human animal coexistence provides an opportunity to explore animal socioecology models that link resource defensibility and predation pressures with social systems and intra- and intergroup interactions (Crook & Gartlan 1966, Wrangham 1980, Janson & van Schaik 1988, van Schaik 1989, Sterck *et al.* 1997). Living in groups has benefits, such as enhancing the likelihood of avoiding predators, but also increases the level of resource competition (van Schaik 1989, Janson & Goldsmith 1995, Chapman & Chapman 2000). Two basic competition regimes, contest and scramble, can be described based on the distribution of resources. Contest competition emerges when a resource can be economically defended, and thus, hierarchical relations and aggression are expected; scramble completion emerges when a resource is not

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economically defendable or is equally accessible among contestants, and thus, individuals are expected to show weak or non-existent hierarchies and low levels of aggression. The competitive regime affects the spatial organization of groups. For example, defense of a territory indicates between-group contest competition, whereas the spatial patterns of scramble competition are thought to be related to population density (van Schaik 1989, Sterck *et al.* 1997). Scramble competitors would increase travel distances under high population densities or dispersed and scarce resources to satisfy their energetic requirements (Wrangham *et al.* 1993, Chapman *et al.* 1995, Janson & Goldsmith 1995). Anthropogenic effects can influence key factors, for example, the abundance and spatial distribution of food resources, thereby providing scenarios that allow us to test socioecological models.

Food enhancement can affect animal socioecology (Kanurai 2004, Sapolsky & Share 2004, Silva & Talamoni 2004, Fuentes 2006, Riley *et al.* 2011). Food provisioning may alter movement ecology (*sensu* Nathan 2008) and consequently the spatial and social decisions of animals (Southwick *et al.* 1965, Kawanaka 1973, Lindburg 1977). Movement alterations may be observed as changes of ranging patterns such as the home range, for example, the area used over a given period of time excluding occasional sallies (Burt 1943, Jewell 1966); the core area, that is, the most used regions inside home ranges (Kaufmann 1962, Asensio *et al.* 2012a); or the daily path length (Carbone *et al.* 2005). When animals rely on human food, a concentrated hyper-caloric source of energy, they do not travel in search of wild food as much as non-provisioned animals do (Fa 1986). In general, both home range and daily path length greatly decrease when animals are food-provisioned (Altmann & Muruthi 1988, Boutin 1990, Monadjem & Perrin 1998, Kreiter & Wise 2001, Silva & Talamoni 2004). Because the supplied food is usually concentrated in specific spots, greater levels of contest competition may arise given the forced proximity between individuals and the economical defendability of the resource (Brennan *et al.* 1985). Food provisioning may affect another key aspect of movement ecology, the recurrent visit and use of particular regions of the home range or site fidelity, which generally varies according to the spatial distribution of resources over time (Easley & Kinzey 1986, Switzer 1993, Asensio *et al.* 2012b).

We can expect that food provisioning would also affect movement ecology, as the distribution and availability of resources are major influences on ranging patterns and territoriality. Non-territorial animals shift their ranging areas over time in response to variation in the spatial distribution of food (Burt 1943, Borger *et al.* 2008), while territorial species concentrate in exclusive, non-overlapping regions that have key resources such as mates, nest sites, or food (Wrangham *et al.* 2007, Wartmann *et al.* 2014). Therefore, territories are usually centered within the home range and not at the overlapping zones adjacent to its borders (Mitani & Rodman 1979). Under a regime of food provisioning, we might expect species to shift these patterns in response to a changed distribution of resources. Moreover, the existence of strong site fidelity is thought to reflect predictability of defendable resources as they can be monopolized by displaying aggression or hierarchy (Mitani & Rodman 1979, Doncaster & MacDonald 1991, Kie *et al.* 2010, Rivrud *et al.* 2010).

Like other cercopithecines, macaques (*Macaca* spp.) show great ecological and socioecological flexibility, adjusting their diet, group size, feeding strategies, and movement patterns to resource availability and habitat structure (Albert *et al.* 2014). Consequently, they are better able to tolerate human environments than many other species (Richard *et al.* 1989, Albert *et al.* 2014). The genus contains several of the last large seed dispersers remaining in the disturbed habitats of South-East Asia (Corlett 1998, Lucas & Corlett 1998, Kitamura *et al.* 2002, Albert *et al.* 2013c). The northern pigtailed macaque (*Macaca leonina*) is a non-territorial and semi-terrestrial primate that lives in multi-male/multi-female groups (Melnick & Pearl 1987, Choudhury 2008, Albert *et al.* 2011). Although the species is omnivorous, fruit often constitutes most of its diet (Choudhury 2008, Feeroz 2012, Albert *et al.* 2013a). The species has home range sizes varying from 83 ha for troops living in well-preserved forests to 347 ha for groups living in degraded forests (Choudhury 2008, Albert *et al.* 2013b).

At Khao Yai National Park (Thailand), some wild northern pigtailed macaques inhabit the park headquarters, the main tourist areas, and areas next to bungalows (Albert *et al.* 2011). Since the early 90s, these macaques have frequently fed from garbage bins, sometimes stolen food from careless humans, and occasionally broken into houses in search of food (W.Y. Brockelman pers. comm.). Despite the interdiction of feeding wildlife in the park, some people deliberately provide food to macaques (Albert *et al.* 2011, 2013a,b). Macaques at the site live in sympatry with two species of gibbons (*Hylobates lar* and *H. pileatus*). Gibbons are arboreal ripe-fruit specialists, and although they feed on a broad number of species, 3 7 species usually constitute the base of their monthly diet (Savini *et al.* 2008, McConkey 2009, Asensio *et al.* 2014). They often live in small pair-bonded groups comprising one breeding pair and one to four offspring, within a relatively small and stable home range (*ca* 25 40 ha: Bartlett 2009, Suwanvecho & Brockelman 2012). They are territorial and defend non-overlapping areas of their home range from neighboring groups (Brockelman *et al.* 2014).

We aimed to examine the effect of food provisioning on the movement ecology and intergroup interactions of northern pigtailed macaques by comparing two free-ranging groups in Khao Yai National Park, one large wild-feeding group (WF) and a smaller semi-provisioned group (SP) that forages on human food. We also compared their movement patterns with those of a group of white-handed gibbons living at the same site. We hypothesize that partial food provisioning modifies the movement patterns of macaques, making them range similar to a territorial species (gibbons), and altering the nature of their intergroup interactions. First, we predict that SP will have smaller home ranges and core areas and shorter daily path length than WF. Second, SP and gibbons will have core areas in fixed areas at the center of the home range, the area where supplemented food is found for SP groups and in boundary areas for the gibbon group. However, WF will have a core area fragmented in several nucleuses throughout the home range, shifting over time in response to the naturally changing location of food. Third, site fidelity will be greater for SP and gibbons compared to WF. Particularly, SP will have an especially strong fidelity to areas where human food is accessible, where resource defense is theoretically feasible. Fourth, SP and the gibbon group will have a higher defendability index (Lowen & Dunbar 1994) than WF in accordance with the movement of a territorial animal. Fifth, site fidelity to human areas of SP will be more related to the number of visitors to the park (used as a proxy of human food influx) than to the general fruit abundance in the forest. Finally, SP will have more agonistic intergroup encounters than WF.

METHODS

STUDY SITE. We conducted the study at Khao Yai National Park, Thailand (14°26′ N, 101°22′ E), which covers 2168 km^2 ~130 km NE of Bangkok. This park is the most visited protected site in Thailand, averaging up to 800,000 visitors per year with the main influx between November and February (DNP 2014). The study area was in the Mo Singto forest area, covering approximately 10 km^2 and including the park headquarters and some tourist zones. The study area consists mainly of seasonally wet evergreen forest between 700 and 890 m asl (Savini *et al.* 2008). It has a monsoonal climate with a wet season (June to October), a cold dry season (November to February), and a hot dry season (March to May). The annual average rainfall is 2504 mm, ranging from 69 mm during the dry season to 353 mm during the wet season; the mean monthly temperature ranges from 19°C in December and January to 24°C in March and April (Albert *et al.* 2011), and mean humidity ranges from 64.6 to 77.1% (Savini *et al.* 2008). Due to the consistent rainfall patterns, Khao Yai has a marked and regular seasonality in food abundance with a high-abundance period from March to September and a low-abundance period from October to February (Savini*et al.*2008, Bartlett 2009, Albert*et al.*2013b).

PRIMATE GROUPS. We studied two northern pigtailed macaque groups (WF and SP) and one group of white-handed gibbons habituated to researchers (Savini *et al.* 2009, Albert *et al.* 2011). WF comprised 60 67 individuals: 3 4 males, 19 20 females, and 37 44 immatures (2 3 subadults, 20 29 juveniles, and 7 14 infants); and behavioral data were collected during 12 consecutive months (852 h). The troop mainly ranged at the north and northwest of the park headquarters and the visitor center. They did not search actively for food on the road or forage from garbage bins, and on only three occasions was the dominant male observed receiving food on the road from visitors in cars. SP included 30 39 individuals: 1 3 males, 12 13 females, and 17 26 immatures followed for 12 mo (1029 h) by Albert *et al.* (2013a). SP ranged in the surroundings of the park headquarters and had a diet partly based on food provided by humans food, and the yearly percentage of total feeding time devoted to acquiring provisioned food was 28.1 percent ±23.2 SD (max=68.7% in January, min=1.5% in June, *N*=12; Albert *et al.* 2013b). Each primate group was followed for a total of 12 mo. The gibbon group consisted of 1 adult male, 1 adult female, and 2 immatures. WF was observed from July 2012 to June 2013; SP from April to July 2009, December 2009 to March 2010, and August to November 2010 (Albert *et al.* 2013a,b,c); and the gibbon group from January to December 2002.

ANIMAL LOCATIONS, HOME RANGE, CORE AREA, AND DAILY PATH LENGTH. We followed all three groups forfive to eight full days (sleeping site to sleeping site) a month. We recorded the geographical position of the macaque groups every 30 min using a handheld global positioning system (GPS). We plotted the position of gibbons every 30 min on a detailed map of research trails across their home range. The trails were ground-truthed and imported into ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA), which allowed extracting gibbon positions in relatively accurate UTM coordinates. We estimated yearly and monthly home ranges and core areas of macaques and gibbons groups using characteristic hull polygons (CHPs). CHPs are calculated using the Delaunay triangulation in which a triangulated irregular network is built from each point to other points without intersecting lines, so that all resulting triangles do not overlap (Duckham *et al.* 2008, Downs & Horner 2009). The rationale behind the CHPs method is that short-perimeter triangles represent areas of high ranging activity and long-perimeter triangles represent areas of low or null activity. To determine which triangles formed the home range and the core area, we applied a spatial statistical tool, theHot Spot Analysis with Rendering in ArcGIS 9.3. This tool assesses whether short- or long-perimeter triangles are statistically clustered or dispersed in space. We discarded the longest triangles that were statistically clustered, and the remaining triangles formed the home range. The shortest triangles that were statistically clustered defined the core area. We quantified the percentage of core area within the home range. Daily path length was calculated by summing the distances of consecutive 30-min track points across full days.

GROUP MASS. Following Grant *et al.* (1992), we calculated the group mass (kg) per unit area (ha) for each group. We took into account the known weight averages of adult males and females of both species (macaques: Fooden 1975, Malaivijotnond *et al.* 2012; gibbons: Jungers & Stern 1984). The mass of an immature individual was considered as half the weight of an adult (Clutton-Brock & Harvey 1977), and infants were excluded. For each group, we calculated the yearly mass values for the home range and core area.

HOME RANGE AND CORE AREA FIDELITY. The degree of site fidelity to home ranges and core areas was estimated by quantifying the number of months in which different home range or core area regions overlapped following the method of Ramos-Fernandez *et al.* (2013). This method creates an interception map overlaying all monthly home ranges and core areas and then generates a figure with a gradient of the use of all overlapping regions. Based on this method, we estimated a monthly fidelity index (f) to either a home range or a core area using the formula

$$f = \frac{\sum_i^j p_i o_i}{nA}$$

where j is the number of overlapping areas in a given month, p is the number of times that each area overlapped over all months, o is the overlap area size, n is the number of study months, and A is the corresponding monthly home range or core area size. Fidelity index values range from 0 to 1 with values close to 1 indicating high site fidelity.

Defendability index. We calculated the defendability index as the fractional monitoring rate (M) following Lowen and Dunbar (1994):

$$M=N\left(\frac{sv}{d^2}\right)$$

where N is the mean number of independently foraging parties, s is the detection distance (the distance at which intruders can be detected), v is the mean of daily path length, and d is the diameter of a hypothetical circle with an area equal to the yearly home range. Territorial animals should have $M \geq 0.08$, suggesting that the mobility of the animals allows them to reach home range boundaries at least once daily. By contrast, non-territorial animals usually have $M<0.08$, suggesting reduced mobility in relation to the size of the home range and boundary length, which does not permit the defense of a territory.

Tourist effect on fidelity to human areas. We defined the human area by applying a minimum convex polygon to the locations of buildings (houses, cafeteria, visitor center), and we estimated a fidelity index within the human area (f) using the above formula where o is the overlap area size inside the human area.

Macaque intra- and intergroup interactions. We recorded *ad libitum* (Altmann 1974) the occurrence of intergroup encounters (encounters/hour) and classified them as agonistic (screams, chases, or attacks between groups) or not agonistic (affiliative or avoidance behavior). Intergroup encounters were defined as occurring when two groups came into visual contact.

Data analysis. We compared the ranging patterns between WF and SP using the following monthly variables: home range size, core area size, and daily path length. In addition, we compared fidelity to home range and core area between gibbons and macaque groups. For comparisons with normally distributed data, we applied a Students t-test. When data were non-normally distributed, we applied the inverse transformation. If data did not follow a normal distribution even after transformation, we used a Mann Whitney U-test.

We ran a generalized linear model (GLM) to test the effect of supplemented food on the SP fidelity to human areas. As dependent variable, we used the home range and core area fidelity to human areas on a monthly basis separately. Explanatory variables of the GLM were the monthly total number of visitors (used as a proxy for the availability of human food) to the park (DNP 2014) and the fruit abundance index (FAI; Albert *et al.* 2013b) during the period when SP was followed. We tested all combinations of explanatory factors and their interactions as possible models. The smallest second-order information criterion (AICc) was used to select the best model in agreement with the small sample size (N=12). The parameters of the GLM tests and their standard errors were estimated with the weighted generalized estimating equations.

RESULTS

Home range, core area, and daily path length. We analyzed 1784 location points for WF (80 d), 2125 for SP (90 d), and 1431 for gibbons (79 d), with a monthly average of 148.7±26.1 (SD), 177.08±23.72 (SD), and 119.25±26.38 (SD) location points per day, respectively. The lower number of locations for gibbons resulted from their shorter daily activity period.

The yearly home range and core area sizes were 306.8 and 115.5 ha, respectively, for WF, 56.3 and 40.1 ha for SP, and 11.6 and 3.5 ha for the gibbon group (Fig. 1, Table 1). The core area of both macaque groups was roughly at the center of their home range. The gibbons core area was at the north of their home range with an unused region at the center, creating a donut-like home range.

Home ranges and core areas of macaques varied widely in size and shape over the study period (Fig. 2). Monthly home ranges and core areas were significantly larger for WF than for SP (t_{12} =4.543, P<0.001; core area: z_{12} =−2.243, P<0.05; Table 1). Both macaque groups and the gibbons exhibited core areas formed by several nuclei over 12 mo (Fig. 2). The yearly proportion of core area within the home range was remarkably large for SP (71.3%) compared to WF (37.6%) and the gibbons (30.3%).

We calculated the daily path length using a sample of 69 full days for WF, 86 for SP, and 63 for gibbons (Table 1). Daily path lengths were significantly longer in WF than in SP ($z_{69,86}$ =5.492, P<0.001).

Group mass. When considering the yearly home range, the group mass of WF (0.7 kg/ha) was close to four times less than the group mass of SP (2.6 kg/ha), and two times less than the group mass of gibbon group (1.6 kg/ha). When considering the yearly core area, the group mass of WF (1.85 kg/ha) was much smaller than that of SP (3.59 kg/ha) and gibbons (5.28 kg/ha).

Home range and core area fidelity. The three study groups showed more fidelity to a home range than to core area (Figs 3 and 4 and Table 1). However, WF had significantly lower site fidelity than SP to both home range (t_{12} =−5.972, P<0.001)

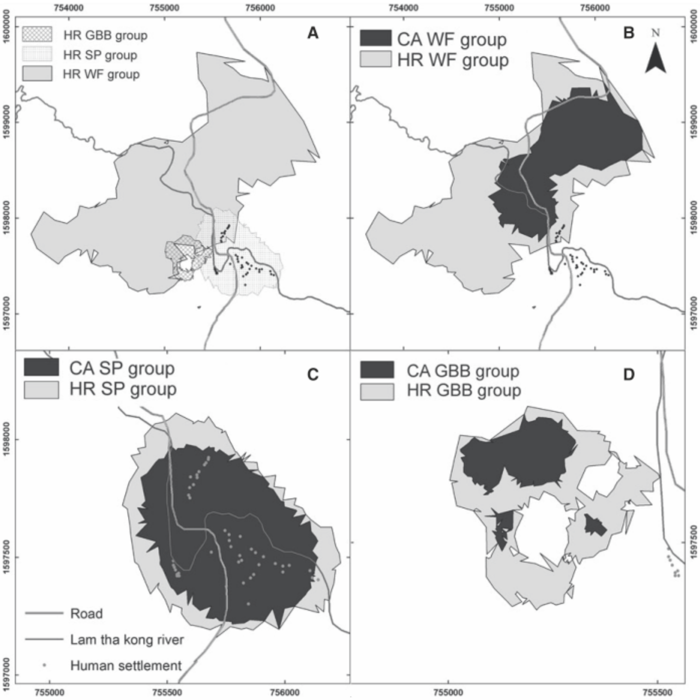

FIGURE 1. Study site and group locations at Mo Singto forest in the Khao Yai National Park (Thailand). (A) Location of the three groups home ranges and human settlements in the study site; home range and core area size for (B) wild-feeding macaque group (WF), (C) semi-provisioned macaque group (SP), and (D) gibbon group (GBB). Universal Transverse Mercator (UTM) coordinates for latitude and longitude are given in meters in the horizontal and vertical axes of the frame.

and core area (t_{12} =−7.723,P<0.001). WF macaques also had smallerfidelity values than gibbons to home range (t_{12} =−8.102, P<0.001) and core area (t_{12} =−5.63,P<0.001). While SP had greaterfidelity to core area than gibbons (t_{12} =3,P<0.01),fidelity to home range did not follow this pattern (t_{12} =0.407, P>0.05).

No part of the WFs home range or core area was used in every month. Therefore, these macaques did not have complete fidelity to any region of their home range or core area (Figs 3 and 4). However, both SP macaques and gibbons had areas used for up to 12 mo and for up to 10 mo in the home range and core area, respectively (Fig. 4). WF home range and core area area-fidelity curves (Figs 3 and 4) decreased steeply in the beginning, indicating that most area was used in a matter of few months. After the steep decrease, the curves became smoother, showing that the maximum site fidelity occurred in a very small region.The home range-fidelity curve of SP also indicated large areas used only during one and two months However, the curve decreased gently and constantly (as in gibbons fidelity curve), which reflected high fidelity to home range. SP and gibbon core area fidelity curves depicted a similar pattern, with greater levels of fidelity than those of WF. Finally, SP macaques displayed more site fidelity to core area than did gibbons because the SP macaques revisited large areas more frequently.

DEFENDABILITY INDEX. The defendability index (M) of WF was 0.027, a value corresponding to a non-territorial pattern; SP showed an$M$value of 0.111, indicating territoriality; and gibbons presented a defendability index of 0.341, reflecting a highly territorial pattern.

TOURIST EFFECT ON FIDELITY TO HUMAN AREAS. Greater sitefidelity to home range and core area for SP was found within the human polygon (Fig. 5). The best GLM model explaining home rangefidelity to a human area included only the number of visitors (Table 2), which had a positive significant effect on fidelity to home range ($F_{1,12}$ =14.2, P=0.003, Fig. 6). Similarly, only the number of visitors best explained fidelity when considering the core area with significant effect ($F_{1,12}$ =4.6,P=0.003).

TABLE 1. *Total and monthly average values of ranging patterns for the three study groups: wild-feeding macaques (WF), semi-provisioned macaques (SP), and gibbons (GBB).*

	WF	SP	GBB
Yearly HR (ha)	306.8	56.3	11.6
Yearly CA (ha)	115.5	40.1	3.5
Monthly HR (ha±SD)	105.1±48 **	37.8±17.7 **	8.2±2.9
Monthly CA (ha±SD)	13.6±5.5 *	8.9±4.3 *	1.3±0.4
DPL (m)	2.123±611 **	1.588±412 **	1.088±348
Yearly CA in HR (%)	37.6	71.3	30.3
Group mass in HR (kg/ha)	0.7	2.6	1.6
Group mass in CA (kg/ha)	1.8	3.6	5.3
Defendability index (*M*)	0.027	0.111	0.341
Fidelity index to HR (±SD)	0.32±0.07	0.61±0.15	0.63±0.11
Fidelity index to CA (±SD)	0.11±0.07	0.42±0.12	0.29±0.08

HR, home range; CA, core area; *M*, defendability index; DPL, daily path length.

Significant differences in HR, CA, and DPL between WF and SP: $^{*}P<0.05$ and $^{**}P<0.001$.

Averages are given as mean (±SD).

Macaque intra- and intergroup interactions. SP showed a smaller frequency of intergroup encounters (0.008/h) than WF (0.041/h). However, SP macaques were aggressive in all encounters (N=9), whereas WF macaques were aggressive in only 9 of 35 encounters.

DISCUSSION

Our findings show that partial food provisioning modifies the socioecology of macaques, altering their movement patterns and competitive regime regarding intergroup interactions. Home range, core area, and daily path length were smaller for macaques living under a human food supplement context. The presence of food in fixed spots meant that food-supplemented macaques did not need to travel in search of wild food. Food provisioning (using the number of park visitors as proxy for the abundance of human food) explained the sitefidelity of SP better than did natural fruit abundance (measured using fruit abundance index, or FAI). Predictable supplementation of food in a relatively small area (±20 ha) made the resources economically defensible, increasing macaque density (group mass per ha) and intensifying sitefidelity at the same level as gibbons. However, while the highest site fidelity regions for gibbons occurred within the home range boundaries, SP macaques were especially loyal to human areas. Therefore, their site fidelity varied according to the monthly tourist influx to the park. This intense and disproportional use of a great part of the home range by SP macaques created a large core area compared to that of WF.

SP showed a defendability index that corresponds to that of a territorial species, whereas the index of WF corresponds to the pattern expected for the non-territorial macaque. Furthermore, SP macaques had more aggressive encounters toward other conspecific groups than did WF. Both between-group contest and scramble competition depend on the abundance of food resources and the population density (Janson & van Schaik

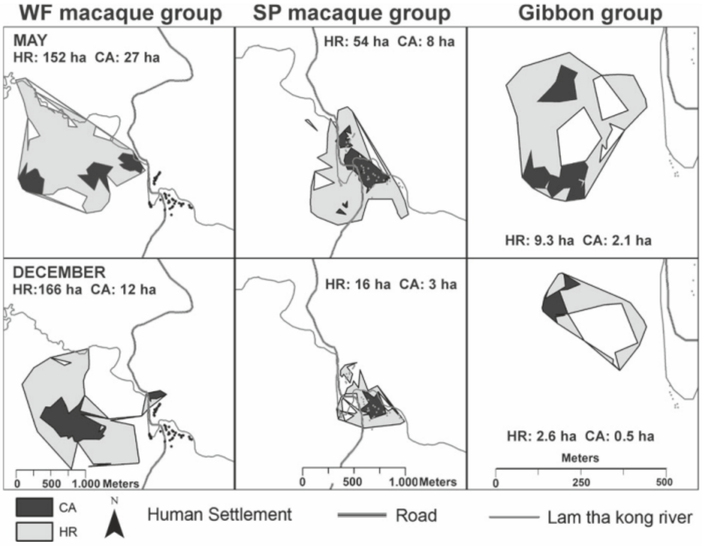

FIGURE 2. Size and locations of monthly home ranges and core areas for the wild-feeding macaque group (WF), semi-provisioned macaque group (SP), and gibbon group.

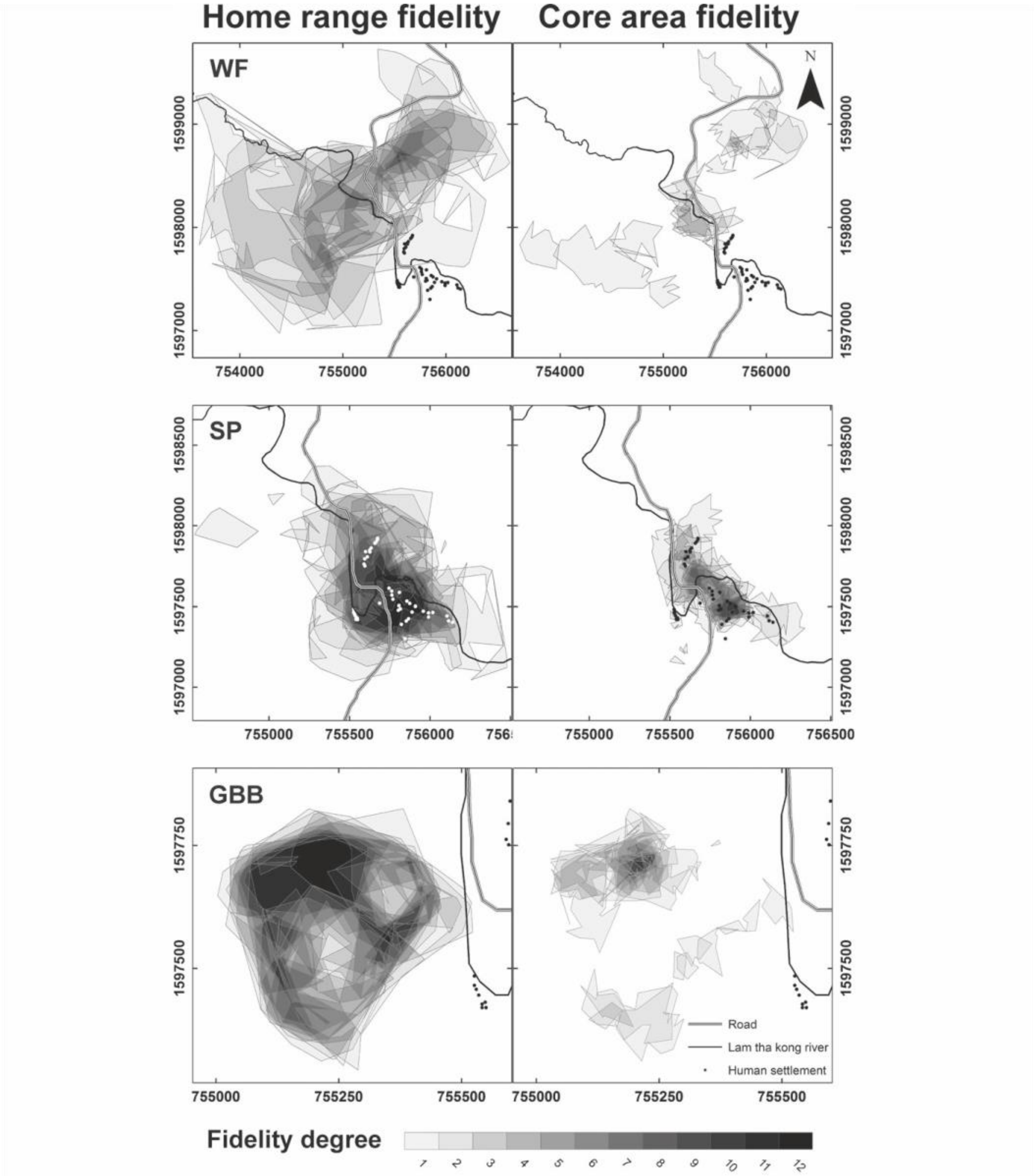

FIGURE 3. Site fidelity to home range and core area by wild-feeding macaque group (WF), semi-provisioned macaque group (SP), and gibbon group (GBB). The fidelity degree (gray gradient) shows the numbers of months an area was used. Universal Transverse Mercator (UTM) coordinates for latitude and longitude are given in meters in the horizontal and vertical axes of the frame.

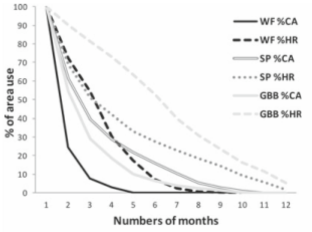

FIGURE 4. Percent of area used over the months (from 1 to 12 mo) by the wild-feeding macaque group (WF), semi-provisioned macaque group (SP), and gibbon (GBB) group. Horizontal axis represents numbers of months that the determinate area was used (fidelity degree), and vertical axis is the total percent of the area used in a determinate number of months. Solid and dotted lines represent home range (HR) and core area (CA), respectively, of the three groups.

1988), but scramble competitors are not expected to fight over resources (van Schaik 1989, Sterck*et al.*1997). Group encounters of non-territorial animals usually involve passive avoidance and/or tolerance (southern pigtailed macaques: Caldecott 1986; northern pigtailed macaques: Choudhury 2008; mangabey: Waser 1976; red howlers: Sekulic 1982; brown capuchins: Terborgh 1983). Aggressive encounters in non-territorial species can occur due to occasional clumping of key resources (rhesus macaques: Southwick *et al.* 1965 and Lindburg 1977; Japanese macaques: Kawanaka 1973). However, if key food resources occur in an economically defensible pattern over long periods, as is the case for SP macaques, territorial behavior may occur (Oates 1987). Therefore, assuming that territoriality is a form of contest competition transferred to the defense of an area containing the resources on the condition of resources being stable and located within a defensible range (Brown & Orians 1970), our results indicate that changes in food distribution can substantially alter the naturally non-territorial macaques patterns, ranging, and even behavior as a territorial species. These patterns also support our understanding of socioecological models as variation of one of its key elements, that is, resource distribution and availability, can cause significant changes in ranging and social behavior.

Some primates, especially cercopithecines, show a high ecologicalflexibility and tolerance of human disturbance. Because of their behavioral and ecological plasticity (*i.e.*, diet, range, group size), most cercopithecine species (79%) can live in disturbed habitats and use the human food found in anthropogenic areas (Chapman *et al.* 2002, Brotcorne *et al.* 2011, Albert *et al.* 2014). Moreover, a morphological feature, the cheek pouch, lets them store food under stress or competition, providing an additional advantage in a human environment (Lambert & Whitham 2001, Warren 2008, Warren *et al.* 2011). In our study, pigtailed macaques had theflexibility to modify their ranging patterns to better exploit an altered scenario of predictable human food concentrated in particular locations. As opposed to WF relying on wild food, SP restricted their movement to a small home range and a core area centered on regular human food spots as found in other taxa living in human environments (Fa 1986, Altmann & Muruthi 1988, Boutin 1990, Monadjem & Perrin 1998, Kreiter & Wise 2001). However, when human food is dispersed over a greater area, both home range and core area could increase (Sha & Hayna 2013).

CONSERVATION IMPLICATIONS. The establishment of protected areas and their management creates a matrix of interconnected areas of interaction between humans and wildlife, affecting the elements upon which socioecological models are based (e.g., food abundance and distribution) (Fuentes 2006). The genus*Macaca*is particularly well adapted to human-modified habitats; however,

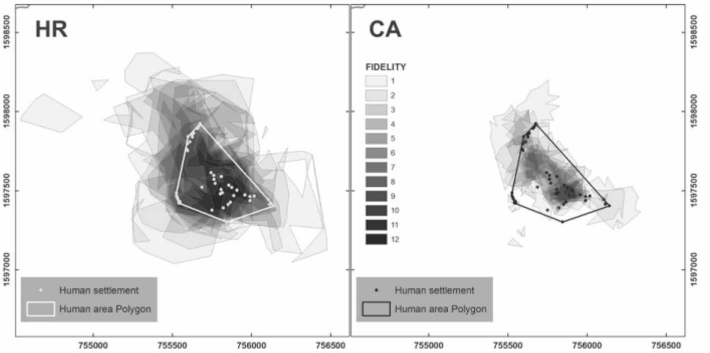

FIGURE 5. Semi-provisioned group (SP)**s**itefidelity to home range (HR) and core area (CA) in relation to the human settlement polygon along the study period. Fidelity degree (gray gradient) shows the numbers of months that an area was used. Universal Transverse Mercator (UTM) coordinates for latitudeand longitude are given in meters in the horizontal and vertical axes of the frame.

TABLE 2. *GLMs used to explain fidelity to human areas in relation to home range (HR) and core area (CA) with their corresponding AICc and Delta AICc values.*

Model HR	AICc	Delta AIC	Model CA	AICc	Delta AIC
#Visitors	−3.9	0	#Visitors	−12.88	0
#Visitors, FAI	−2.17	−1.73	#Visitors*FAI	−8.67	−4.21
FAI	0.61	−4.51	FAI	−5.88	−7
#Visitors*FAI	2.59	−6.49	#Visitors, FAI	−2.4	−10.48

FAI, fruit abundance index.

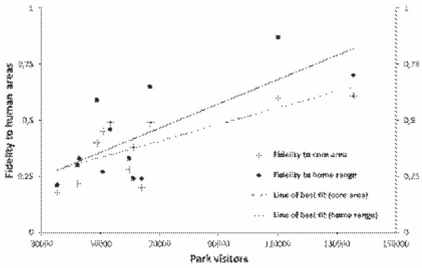

FIGURE 6. Relationship between the number of visitors and the home range (HR) and core area (CA) fidelity to human areas for the semi-provisioned group (SP). Dots and crosses represent the monthly home range and core area fidelity, respectively, related to the monthly number of visitors at the park. The bestfitting lines are presented for illustrative purposes.

negative effects on their population and ecosystem may arise. Animals relying on human food, like the SP macaques in this study, come in close contact with humans, which can have demographic consequences for the animals and may affect human well-being. Pathogens can be transmitted bidirectionally between human and nonhuman primates (Engel *et al.* 2002, Wolfe *et al.* 2004, Rouquet *et al.* 2005). For example, Sapolsky and Else (1987) reported high baboon mortality when a bovine tuberculosis outbreak was transmitted to a group that frequently fed on garbage. Additionally, animals are often killed by motor vehicles in places where they spend long periods along the road feeding from human food (Kanurai 2004, Mallapur 2013, Sha & Hayna 2013), as occurs in Khao Yai National Park (J.M. Josê-Dom ˆguez pers. obs.).

Macaques are one of the last large seed dispersers remaining in the disturbed habitats of South-East Asia (Corlett 1998, Lucas & Corlett 1998, Albert*et al.*2013c). As fruit is an important part of their diet, groups of northern pigtailed macaques include many individuals that cover large ranges and travel long distances (Choudhury 2008). This pattern results in a great number of seeds being dispersed over large areas. However, with partial food provisioning, macaque home ranges become smaller and daily path length shorter, decreasing the positive effect of macaques on the forest ecosystem of Khao Yai National Park. A food-provisioned group would disperse few seeds over short distances and some seeds would likely be transported into places where their establishment is not possible (e.g., roads and roofs) or even disperse invasive species present in human areas (e.g., *Syzyginum cumini, Solanum melongena*) like the SP group does (Albert *et al.* 2013a). Moreover, as macaques are efficient passerine nest predators (Pierce & Pobprasert 2013), a high macaque density within a small area may affect local passerine recruitment. This means that food supplementation has consequences far beyond the common negative effects on animal health such as obesity or poisoning. Food provisioning can ultimately affect the geographical patterning and regeneration of the plant and animal diversity. Managers of protected areas must consider this possibility when implementing policies on garbage management and rules against feeding wildlife.

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Tras ver como el aprovisionamiento de comida humana modifica los patrones de movimiento, su comportamiento y relaciones intergrupales, a continuación vamos a estudiar su influencia en una de las decisiones más importantes para un animal, la selección de su lugar de descanso durante la noche.

Durante el sueño el tono muscular disminuye y la capacidad de estar alerta también, luego es muy importante elegir un lugar que sea lo bastante seguro y a su vez permita descansar convenientemente.

En el siguiente capítulo vamos a estudiar los factores que influyen en la selección del área dormidero y como se ve afectada por la presencia de comida humana.

Capítulo 7

Exploring the multiple functions of sleeping sites in northern pigtailed macaques (*Macaca leonina*)

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Exploring the Multiple Functions of Sleeping Sites in Northern Pigtailed Macaques (*Macaca leonina*)

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Abstract Sleeping site selection in nonhuman primates may respond to various ecological factors, including predation avoidance, range defense, and foraging efficiency. We studied the sleeping sites used by a group of northern pigtailed macaques on 124 nights to test these hypotheses. The macaques used 57 different sleeping sites, of which 33 were used only once. They rarely used the same site on consecutive nights. These selection patterns are consistent with an antipredatory function, but may also be related to an antipathogenic strategy. Sleeping sites were located principally in the most heavily used areas of the home range and were generally away from areas of intergroup encounters. However, some of the most heavily used sleeping sites were in the area where intergroup encounters occurred, and intergroup encounters at sleeping sites always showed high levels of agonism, indicating possible intergroup competition over sleeping sites. On 77 % of nights, the study group selected the sleeping site nearest to either the last feeding area that day or to the first feeding area used the next morning, suggesting a foraging efficiency strategy. The mean distances from the sleeping site to the last and first feeding area were 227 m and 127 m, respectively, suggesting a multiple central place foraging strategy. The macaques entered sleeping sites a mean of 27 min before sunset and left 24 min after sunrise, and these times varied in line with

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the seasonal variation, maximizing daily activities. Overall, predator avoidance and food efficiency were the main factors influencing the selection of sleeping sites. Our observations differ from those found in a semiprovisioned group inhabiting the same study site, which used fewer sleeping sites and reused them much more often. This difference highlights the impact anthropogenic activities may have on sleeping site selection and the flexibility of sleeping patterns in a single species. Such flexibility may have helped the tree-to-ground evolutionary transition of sleep habits in primates.

Keywords Food provisioning · Human disturbance · Predation avoidance · Site fidelity · Sleep

Introduction

Primates generally spend more than half of their lives at sleeping sites (Fan and Jiang 2008; Phoonjampa *et al.* 2010; Smith *et al.* 2007; Teichroeb *et al.* 2012) so they must select sleeping sites carefully (Albert *et al.* 2011; Di Bitetti *et al.* 2000; Teichroeb *et al.* 2012). Several evolutionary and ecological considerations explain the selection of sleeping locations in primates, particularly those that maximize the chance of survival during sleep and thereby increase inclusive fitness (Anderson 1998). Predator avoidance (*Macaca radiata*: Ramakrishnan and Coss 2001; *Hylobates lar*: Reichard 1998; *Saguinus fuscicollis* and *S. mystax*: Smith *et al.* 2007), range defense (*S. midas midas*: Day and Elwood 1999) and access to food (*Ateles geofroyi*: Chapman *et al.* 1989; *Colobus vellerosus*: Teichroeb *et al.* 2012) are among the most important factors affecting sleeping site selection. However, other factors such as parasite avoidance and hygiene (*Papio cynocephalus*: Hausfater and Maede 1982; *P. anubis* and *P. hamadryas*: Nagel 1973), comfort (*Cebus capucinus*: Holmes *et al.* 2011; *Pongo pygmaeus*: Cheyne *et al.* 2013) and thermoregulation (*Hylobates agile*: Gittins 1982; *Nomascus concolor jindongensis*: Fan and Jiang 2008; *Cercopithecus aethiops*: Tollman 1982) may also be influential. In addition, topography and climate might be relevant in the selection of sleeping sites (Liu and Zhao 2004; Matsuda *et al.* 2008a, b). In summary, a combination of nonmutually exclusive factors may determine where a group of primates chooses to sleep, but predation avoidance, range defense, and access to resources are probably the most important.

The predator avoidance hypothesis proposes that sleeping sites should have physical characteristics that reduce the likelihood of detection by or vulnerability to capture by predators (Anderson 1998, 2000). Thus, arboreal and semiterrestrial primate species select primarily elevated places for sleep, usually trees, but also steep cliff ledges (some populations of *Papio*, *Macaca*, and *Presbytis*: Anderson 2000), and sometimes areas next to rivers (*Macaca leonina*: Albert *et al.* 2011; *Nasalis larvatus*: Matsuda *et al.* 2008a, b, 2011; *M. fascicularis*: van Schaik *et al.* 1996). Some callitrichids and strepsirrhines sleep in holes in tree trunks (*Callithrix jacchus*: Mendes Pontes and Lira Soares 2005; *Galago moholi*, *Euoticius pallidus*, *Sciurocheirus alleni*, *Otolemur crassicaudatos*: Bearder *et al.* 2003). In contrast to monkeys, great apes often increase safety from predators by building elevated nest platforms (*Pan troglodytes*: Hernandez-Aguilar 2009; *P. panicus*: Fruth and Hohmann 1993; *Gorilla*: Remis 1993, Sabater Pi 1985; *Pongo*: Ancrenaz *et al.* 2004, Cheyne *et al.* 2013), although gorillas (*G. gorilla*) may also build nests on the ground (Remis 1993). Primate behavior before entering a sleeping site often involves moving quickly and silently, possibly to conceal their presence from predators (*M. leonina*: Albert *et al*. 2011; *P. troglodytes*: Nissen 1931; *Hylobates lar*: Reichard 1998). The number of sleeping sites and their reuse patterns may also affect the likelihood of detection by predators, with unpredictable site usage decreasing predation risk (*Semnopithecus entellus*: Blaffer-Hrdy 1977). In addition, animals may prefer to sleep in well-known areas where they are familiar with escape routes (*Ateles geoffroyi*: Chapman 1989; *Saguinus midas*: Day and Elwood 1999; *Cebus paella*: Di Bitetti *et al*. 2000).

The range defense hypothesis states that sleeping sites are located in boundary areas to facilitate detection of neighboring conspecifics (*Saguinus midas*: Day and Elwood 1999; Teichroeb *et al*. 2012). However, some authors suggest that several primate species prefer to sleep in areas of exclusive use to avoid intergroup disputes (*S. oedipus*: Dawson 1979; *Cebus paella*: Di Bitetti *et al*. 2000; *S. mystax* and *S. fuscicollis*: Heymann 1995, Smith *et al*. 2007; *Hylobates pileatus*: Phoonjampa et al. 2010; *Colobus guereza*: Von Hippel 1998). This is consistent with the alternative risk hypothesis, which proposes that sleeping sites located in exclusive areas (*Macaca leonina*: Albert *et al*. 2011; *M. nemestrina*: Caldecott 1986; *H. pileatus*: Phoonjampa et al. 2010) decrease the risk of intergroup aggression and injuries (Wrangham *et al*. 2007).

The food hypothesis states that forest-living primates select sleeping sites to enhance foraging efficiency (Anderson 2000; *Pan troglodytes*, *P. panicus*: Basabose and Yamagiwa 2002, Fruth and Hohmann 1993; *Colobus vellerosus*: Teichroeb *et al*. 2012; *C. guereza*: Von Hippel 1998; *S. midas*: Day and Elwood 1999; *Hylobates agilis*: Gittins 1982; *H. lar*: Reichard 1998), by minimizing travel costs and maximizing access to food (Ricklefs 1990). Two major strategies have been proposed in this context: 1) the central foraging place strategy, in which animals return to sleep to a fixed area or same sleeping site (or set of sites) located in the center of current high food distribution (Orians and Pearson 1979) and 2) the multiple central place foraging strategy, in which animals use multiple and scattered sleeping sites, usually located close to the last feeding site exploited that day (McLaughlin and Montgomerie 1989). In this scenario animals should reuse certain sleep sites until all the food in the area is depleted before moving to a new area (Chapman *et al*. 1989). Central foraging place strategy is an appropriate strategy when resources are abundant because the energy employed in travel can easily be recovered, whereas multiple central place foraging strategy is theoretically better when resources are scarce because the travel cost to any given place is difficult to recover under these circumstances (Chapman *et al*. 1989).

Seasonal changes in photoperiod, that is, daylight hours between sunrise and sunset, may affect the time of entering and exiting sleeping sites (Reichard 1998). If primates leave their sleeping site as soon as the sun comes up and enter it only just before the sun goes down, they can maximize their daily activities (*Macaca leonina*: Albert *et al*. 2011; *Cacajao melanocephalus*: Barnett *et al*. 2012; *Saguinus mystax* and *S. fuscicollis*: Smith *et al*. 2007).

The pigtailed macaque (*Macaca leonina*), a nonterritorial, semiterrestrial species living in multimale, multifemale groups (Albert *et al*. 2011; Melnick and Pearl 1987), shows variable ranging, feeding, and habitat preferences in response to habitat conditions (Albert *et al*. 2013; Choudhury 2008; Feeroz 2012). Albert *et al.* (2011) studied sleeping site selection in a group of *M. leonina* inhabiting a tourist area in Khao Yai National Park, Thailand. The group used a total of 16 sleeping sites, located mainly within its core area, and the findings partially supported a multiple central place foraging strategy. Food provisioning affected the group's movement patterns, and they showed shorter daily path length, smaller home range and core area sizes, and greater site fidelity to human areas than macaques relying on wild food at the same site (José-Domínguez *et al*. 2015a, b).

In this study, we use a null model of random sleeping site selection to test hypotheses regarding sleeping site selection by a nonprovisioned troop of *Macaca leonina* over a 16-months period. First, the predator avoidance hypothesis states that sleeping site follows an unpredictable use of multiple locations to reduce the likelihood to be detected by predators. However, reuse of sleeping sites may also facilitate predator avoidance if located in familiar areas. Thus, we predicted that macaques would use multiple sleeping sites, they would rarely use them over consecutive nights, and that the ones used repeatedly would be located in well-known areas: core areas and/or areas of high site fidelity. Core areas and areas of high site fidelity refer to the most used regions (Kaufmann 1962) and the most recurrently visited areas (Easley and Kinzey 1986; Switzer 1993) of the home range, respectively. Second, based on the risk hypothesis (Wrangham *et al.* 2007), we predicted that macaques would avoid sleeping sites where intergroup encounters were frequent. Third, because *M. leonina* generally exploit a wide range of food resources distributed across large home ranges (Albert *et al*. 2013; Caldecott 1986; Choudhury 2008; José-Domínguez *et al*. 2015a, b; Richter *et al*. 2013), we predicted that they would predominantly use the closest sleeping sites to the last or first feeding area. We also predicted that macaques' sleeping site selection would best fit a multiple central place foraging strategy as it minimizes travel costs within a large home range. Fourth, we predicted that, like other diurnal primates, macaques would adjust to variations in the photoperiod by altering the arrival and departure times at sleeping trees to maximize their activities during daytime.

Methods

Study Site

We conducted this study in the Mo Singto forest in Khao Yai National Park, Thailand (2168 km^2; 101°22 E, 14°26 N). This forest covers *ca*. 10 km^2 of mainly seasonally wet evergreen forest at an altitude range of 700–890 m (Savini *et al*. 2008). The climate is monsoonal, with a cold season (November–February), in which the northeast monsoon brings cold and dry air; a hot season (March–May), in which the temperature rise when the northeasterly winds decrease; and a wet season (June–October), in which the southwest monsoon brings moisture in from the Indian Ocean). The annual precipitation ranges from 2000 to 3000 mm (Bartlett 2009); the mean monthly temperature ranges from 19 to 24 °C (Albert *et al.* 2011) with a mean humidity from 65 to 77 % (Savini *et al*. 2008).

As there are no longer tigers (*Panthera tigris*) and no reports of leopards (*Panthera pardus*) in the study site (Lynan *et al*. 2013), clouded leopards (*Neofelis nebulosa*) and pythons (*Python reticulatus* and *P. molurus*) are the most likely major threats to macaques. The clouded leopard, a mainly nocturnal and arboreal felid (Lynan *et al.* 2013), has been seen near macaque sleeping sites around dawn (Davies 1990). Pythons, which are both terrestrial and arboreal, search for prey actively at night and passively (stay and wait) during the day (Uhde and Sommer 2002); they have preyed on macaques in the study site (Khamcha and Sukumal 2009; Uhde and Sommer 2002). Other potential predators of macaques, particularly of infants and juveniles, include the Asian golden cat (*Catopuma temminckii*), the leopard cat (*Prionailurus benglensis*), the marbled cat (*Pardofelis marmorata*: Borries *et al.* 2014; Grassman 2000; Palombit 1992), the crested serpent eagle (*Spilornis cheela*), changeable hawk eagle (*Spizaetus cirrhatus*), the spot-bellied eagle owl (*Bubo nipalensis*), the brown fish owl (*Ketupa zeylonensis*), and the brown wood owl (*Strix leptogrammica*).

Study Group

We followed a wild *Macaca leonina* group (CH group) for two periods, totaling 16 months: April–May 2011, when the group comprised 49 individuals (4 adult males, 19 adult females, 26 immatures); and May 2012–June 2013, when the group comprised 60–67 individuals (3–4 adult males, 19–20 adult females, and 37–44 immatures). Over the 16 months, the group had a total home range of 575 ha (kernel 95 %, least-square cross validation smoothing factor) with a total core area of 47 ha (50 % kernel). Monthly home ranges varied from 75 to 721 ha and monthly core areas from 5 to 152 ha (José-Domínguez *et al.* 2015a, b).

Data Collection

We followed the macaques on 133 days. Whenever possible, we observed the group from sleeping site to sleeping site ($N=104$) for a minimum of five consecutive full days each month. We collected data on sleeping sites for 28 days during the first observation period and for 96 days during the second observation period.

We defined a *sleeping site* as the area in which the sleeping trees were located in the home range. We placed the location of the sleeping site at roughly the center of the observed sleeping trees using a GPS (GPSmap 62 s, Olathe, USA; ≤10 m error) based on the macaques' location in the evening and the next morning. We recorded the time at which macaques entered and exited the sleeping site. Because the macaques occasionally used more than one sleeping site on the same night, we also counted the number of times that they used in each sleeping site. We used the term *reused sleeping site* to refer to sites used more than once during the study and *heavily used sleeping site* for those reused six times or more.

We recorded the location and nature of encounters between our study group and other conspecific groups ad libitum (Altmann 1974). We defined *low agonistic encounters* as those involving avoidance, short rush toward the opposite group member, or submission, and *high agonistic encounters* as those involving chases, bidirectional and direct attacks, and collective fights in which the alpha male always took part. To define the *intergroup encounter region* we estimated the region containing the 50 % likelihood of encounter occurrence using the kernel method with least square cross-validation (Worton 1989).

Finally, we recorded the location of the last and first feeding place in the evening and in the morning, respectively.

Data Analysis

We performed statistical tests ($\alpha=0.05$) with SPSS v.15.0 (SPSS Inc., USA). To test whether sleeping site reuse was random, we generated an expected frequency distribution using Poisson lambda parameters (Sokal and Rohlf 1995) and compared them using a Kolomogorov–Smirnoff test for goodness of fit (Day and Elwood 1999) with the observed reuse distribution frequency.

To investigate whether macaques selected sleep sites in familiar areas we combined the sleeping site locations with site fidelity, defined as the number of times particular regions within the home range were repeatedly used. We did this by marking the 16 monthly home ranges on a single map and ranking regions by the number of months in which they were visited (fidelity, José-Domínguez *et al.* 2015a, b; Ramos-Fernandez *et al.* 2013). We also calculated the size of each region. To test whether the sleeping site selection differed from random (based on the area size) we plotted 200 random points in the fidelity map and calculated preference using the formula

$$\text{preference} = \log_{10}\left(\frac{u_i/\sum u_{i,j}}{\left(f_i/\sum f_{i,j}\right)}\right)$$

where u is the number of nights macaques spent in an area used in i months, and f is the size of that area. When the value of preference was close to 0 there was no relationship between sleeping site choice and use of that area; preference>0 indicated preference for an area, whereas preference<0 indicated avoidance of an area.

To investigate how sleeping site location corresponded to the macaques' range, we calculated the binomial probability of sleeping sites being in the total and monthly core areas according to their size relative to the home range and core area, respectively. To compare sleeping site selection to intergroup encounters we used a binomial test using 1) expected values derived from the observed frequency of encounters inside or outside the total core area and 2) expected values derived from the observed frequency of nights inside or outside the intergroup encounter region. By definition each area accounted for 50 % of the time, making the probability of being in each area 0.5 (Brotcorne *et al.* 2014).

Following Albert *et al.* (2011), for each night we measured the distance between the last and/or first *important feeding site*, defined as the area where >70 % of individuals were feeding simultaneously to 1) the sleeping site, i.e., observed distance; 2) the closest sleeping site, which is consistent with a multiple central place foraging strategy; 3) the closest heavily used sleeping site, which is related to a modified multiple central place foraging strategy; and 4) the mean distance to the rest of the sleeping sites macaques used during the study, which refers to a central place foraging strategy. We ran a Wilcoxon signed rank test to compare the distance for each strategy with the observed distance. To compare the distance to sleeping sites between the last and first feeding site we used a paired t-test.

Finally, we conducted Spearman correlations to test the relationship between the times of sunset and sunrise and the times of entry and exit from the sleeping site, respectively. We obtained the sunset and sunrise times for the study site from the GPS unit.

Ethical Note

Our research conforms to the Code of Best Practices for Field Primatology for the Ethical Treatment of Non-Human Primates (International Primatological Society). The Department of National Parks, Wildlife, and Plant Conservation of Thailand granted permission to conduct this research. This study is part of the requirements to fulfill the doctorate degree of J. M. José-Domínguez.

Results

We observed macaques entering sleeping sites 124 times, and recorded them the next morning on 105 occasions. Our study group used a total of 57 different sleeping sites. The cumulative number of sleeping sites seemed to reach an asymptote (Fig. 1). The mean distance between sleeping sites was 1286±SD 654 m (*N*=1596, range: 60–3830 m). The macaques split into two subgroups and slept in two different sleeping sites separated by 100 m on four nights and separated by 500 m on one night, meaning that the macaques used the observed sleeping sites 129 times during 124 nights.

Predator Avoidance Hypothesis

The arithmetic mean, i.e., λ, number of times a sleeping site was reused, was 1.26 (*N*=57; range: 0–11; Fig. 2a). The observed reuse frequency was significantly different from chance (Kolmogorov–Smirnoff test: *D*=0.282; *P*<0.05, Fig. 2a). The four most used sleeping sites represented 31 % of the total reuses, but none of these reached 10 %. On the 101 occasions in which we knew the sleeping site for the previous night,

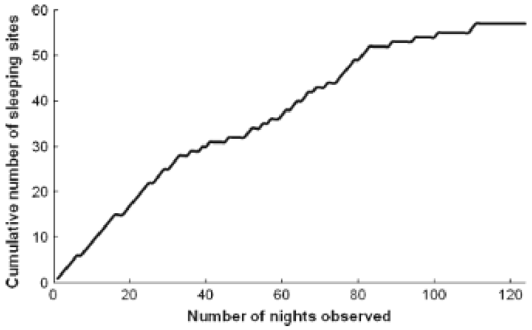

Fig. 1 Cumulative number of new sleeping sites vs. the number of nights observed in *Macaca leonina* in Khao Yai National Park from April to May 2011 and from May 2012 to June 2013.

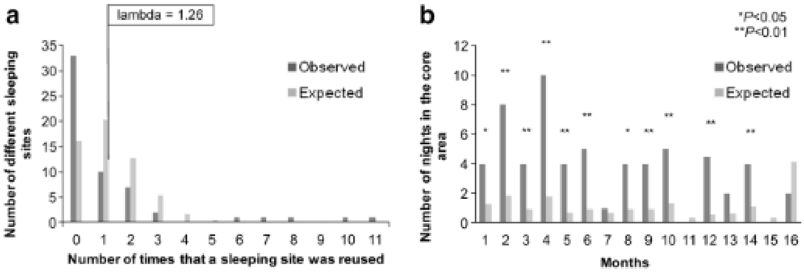

Fig. 2 Frequency of sleeping site use by the *Macaca leonina* group in Khao Yai National Park from April to May 2011 and from May 2012 to June 2013. **a** Observed and expected frequencies of sleeping site reuse. Expected frequencies are based on the Poisson distribution with a lambda (arithmetic mean of re-use) $X=1.26$. **b** Observed and expected number of times macaques were observed sleeping in the core area. Expected values are based on the binomial probabilities of the relative size of the monthly home ranges and core areas.

macaques used the same sleeping sites seven times; 50 % of these reuses concerned the two most used sites. The macaques did not use any sleeping site consecutively for more than two nights.

The distribution of sleeping sites within the home range was not random. Instead, macaques avoided sleeping in areas used in 1–3 months (preference<0), showed no preference for areas used in 4–5 months (preference=0), but had a clear preference for areas used for 6–12 months (preference>0; Figs. 3b and 4a). Twenty of the sleeping sites (used on 61 nights) were located along a river bank.

Range Defense and Risk Hypothesis

Across the 16 months of the study the macaques used sleeping sites all over their home range, but they slept significantly more in the core area than outside the core area

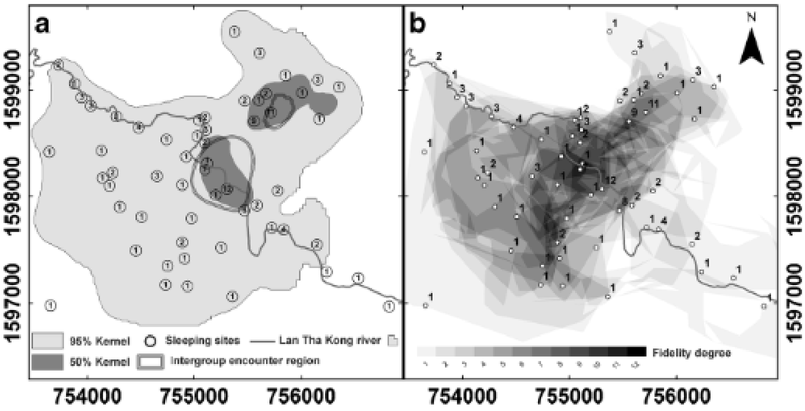

Fig. 3 Location and frequencies of sleeping sites of *Macaca leonina* in Khao Yai National Park in relation to (**a**) yearly home range (95 % kernel) and core area (50 % kernel) and (**b**) the number of months in which the macaques used an area (fidelity degree). Universal Transverse Mercator coordinates for latitude and longitude are given in meters in the horizontal and vertical axes. Data are for April to May 2011 and May 2012 to June 2013.

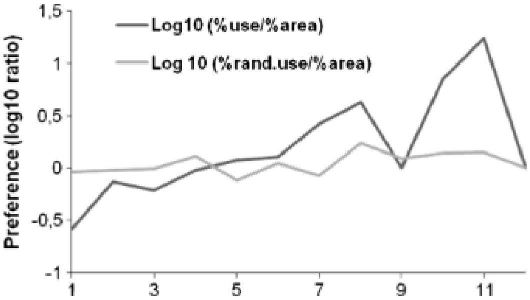

Fig. 4 Log ratios of the proportion used/area available for sleeping site locations vs. the number of months in which the macaques (*Macaca leonina*) used an area (fidelity degree) with observed and random sleeping site selection in Khao Yai National Park. Positive values indicate that a site is used in greater proportion than predicted by its availability. Data are for April to May 2011 and May 2012 to June 2013.

(binomial two-tailed test: number of sleeping sites in core area: $N_{\text{core}}=13$; $N_{\text{out-core}}=44$; $P<0.003$; number of nights spent in core area: $N_{\text{core}}=57$; $N_{\text{out-core}}=72$; $P<0.001$). The macaques used sleeping sites located outside the 95 % kernel of their home range on four occasions (Fig. 3a). The number of nights macaques slept in the corresponding monthly core area was higher than expected in 11 of the 16 months (Fig. 2b).

The group had 64 intergroup encounters during the study (0.06/h), of which 10 (16 %) were highly agonistic. Four of these encounters occurred at the sleeping site and included more intense aggression with chases, bidirectional attacks, and collective fights than encounters occurring elsewhere, which were related to other factors such as competition over a food resource. Intergroup encounters occurred more often outside the core area than inside it (binomial two-tailed test; $N_{\text{within}}=20$; $N_{\text{outside}}=44$; $P<0.003$). Although the study group rarely slept in the intergroup encounter region (binomial two-tailed test; $N_{\text{within}}=42$; $N_{\text{outside}}=87$; $P<0.0001$), the three most used sleeping sites were in this region (Fig. 3a).

Food Hypothesis

The macaques used the nearest sleeping site to the last feeding area 48 times (50 % of records) with a mean distance of 227±SD 203 m ($N=96$, range: 0–930 m). They used the sleeping site closest to the first feeding area the next day 55 times (68.8 % of records), with a mean distance of 127±SD 115.9 m ($N=80$, range: 0–675 m). The last feeding area was further from the sleeping site than the first feeding area (paired t-test: $t=-3.34$, $P=0.001$, df=79). On 71 times (77 %, $N=92$), the macaques used a sleeping site that was the closest to either the last feeding area on that day or to the first feeding area on the next morning. The mean distances from the observed sleeping site to both feeding areas were greater than those to the nearest sleeping site (Wilcoxon signed ranks test, last feeding area: $Z=-5.97$, $P<0.001$, $N=96$; first feeding area: $Z=-4.37$, $P<0.001$, $N=80$; Table I, Fig. 5). However, these distances were significantly shorter than that to the nearest heavily used sleeping site (last feeding area: $Z=-5.88$, $N=96$, $P<0.001$; first feeding area: $Z=-5.85$, $P<0.001$, $N=80$), and that to the mean distance to all sleeping sites (last feeding: $Z=-7.77$, $P<0.001$, $N=96$, first feeding: $Z=-8.51$, $P<0.001$, $N=80$).

Table I Sleeping site selection by *Macaca leonina* in Khao Yai National Park during April–May 2011 and May 2012–June 2013

	Study group	Semiprovisioned group[a]
Group size	49–67 ha	30–39 ha
Monthly home range (95 % kernel; range)	75–712 ha	6–73 ha
Number of observed nights (range)	124	154
Number of sleeping sites	57	16
Mean distance between sleeping sites	1286±SD 654 m, *N*=1596	—
Percentage of consecutive nights in the same sleeping site	7 %, *N*=101	22 %, *N*=101
Percentage of nights spent in the four most used sleeping sites	31 %	71 %
Reused sleeping sites (range)	0–11	0–36
Number of sleeping sites used only once	33	2
Number of months macaques slept inside the corresponding monthly core area more often than expected	11 of 16	8 of 12
Observed distance from the last feeding area to the sleeping site	227±SD 203 m, *N*=96	147±SD 168 m, *N*=74
Observed distance from the sleeping site to the first feeding area	127±SD 116 m, *N*=80	150±SD 113 m, *N*=63
Mean distance from the last feeding area to the nearest sleeping site (MCPF 1[b])	116±SD 77 m, *N*=96	84 m[e]
Mean distance from the first feeding area to the nearest sleeping site (MCPF 1)	84±SD 61 m, *N*=80	
Mean distance from the last feeding area to the nearest preferred sleeping site (MCPF 2[c])	484±SD 427 m, *N*=96	138 m[e]
Mean distance from first feeding area to the nearest preferred sleeping site (MCPF 2)	388±SD 377 m, *N*=80	—
Mean distance to all sleeping sites to last feeding area (CPF[d])	1179±SD 225 m, *N*=96	202 m[e]
Mean distance to all sleeping sites to first feeding area (CPF)	1144±SD 199 m, *N*=80	—
Percentage of nights macaques chose the nearest sleeping site to the last feeding areas	50 %, *N*=96	—
Percentage of nights macaques chose the nearest sleeping site to the first feeding areas	68 %, *N*=80	—
Percentage of nights macaques chose the nearest sleeping site to the last/first feeding areas	77 %, *N*=92	42 %, —
The mean time entering the sleeping site	17 h 57±SD 26 min, *N*=120	18 h 16±SD 16 min, *N*=84
The mean time leaving the sleeping site	06 h 30±SD 22 min, *N*=97	06 h 05±SD 18 min, *N*=43

[a] Data on the semiprovisioned group were extracted from Albert *et al.* (2011)

[b] MCPF 1: multicentral place foraging strategy in which the sleeping site nearest to the feeding area was selected

[c] MCPF 2: multicentral place foraging strategy in which the preferred sleeping site nearest to the feeding area was selected

[d] CPF: central place foraging

[e] Distance is given for both last and first feeding area; (—) information not available

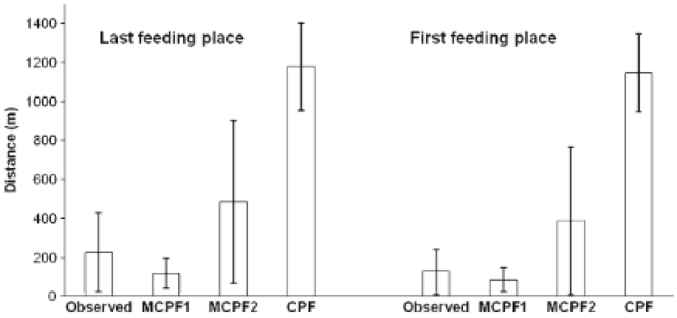

Fig. 5 Mean (±SD) distances between the last and first feeding site of the day and the observed sleeping site, the nearest sleeping site (multicentral place foraging [MCPF1]), the nearest heavily used sleeping site (MCPF2), and the mean distance to all sleeping sites (central place foraging CPF) of macaques (*Macaca leonina*) in Khao Yai National Park. Data are for April to May 2011 and May 2012 to June 2013.

Seasonal Variation in Times of Sunset and Sunrise

The mean time of entering the sleeping site was 17:57 h±SD 26 min (N=120, range=16:55–18:40 h) and that of leaving it 06:30 h±SD 22 min (N=97, range=05:50–07:46 h). Therefore, macaques spent a mean of 12 h 32 min±SD 42 min (N=96, range=11 h 27 min–14 h 00 min) in their sleeping sites. The entry and exit times from the sleeping site correlated significantly with the sunset and sunrise time, respectively (Spearman correlation: sunset: r_s=0.75, N=120, P<0.001; sunrise: r_s=0.64, N=97, P<0.001). The group entered the sleeping site a mean of 27±SD 15 min (N=120) before sunset and left it 24±SD 15 min (N=97) after sunrise.

Discussion

Predator Avoidance

The sleeping site selection patterns of our study group of *Macaca leonina* strongly support the predator avoidance strategy (Anderson 1998). As in other primates, the group used numerous sleeping sites, shifted them frequently, and only occasionally reused them on consecutive days (*Ateles geoffroyi*: Chapman 1989; *Nomascus nasatus*: Fei *et al*. 2012; *Hylobates pileatus*: Phoonjampa *et al*. 2010; *Colobus guereza*: Von Hippel 1998; *Cebus apella*: Zhang 1995). Reichard (1998) suggested that such usage patterns reduce odor that might be cues for predators. Irregular reuse of sleeping sites may also enhance parasite avoidance and improve hygiene (Hausfater and Maede 1982; Nagel 1973; Reichard 1998). Most reused sleeping sites, and those used on two consecutive nights, were located in the core area and in high site fidelity areas, where the group members might have a better knowledge of potential escape routes and predator presence (Di Bitetti *et al*. 2000; Dow and Fredga 1983). In further support of this possibility, the macaques spent almost half of all observed nights close to a river bank where the most heavily used sleeping sites were located. It is possible that sleeping next to the river gave extra predator protection to macaques, as suggested in other studies (Albert *et al.* 2011; Brotcorne *et al.* 2014; Fittinghoff and Lindburg 1980; Matsuda *et al.* 2008a, b, 2011; van Schaik *et al.* 1996). With one side of the sleeping site facing the river, macaques reduced the area to monitor, as most ground predators could not access the sleeping trees from the river, given its width (about 10–25 m), depth (*ca.* 1–2 m), and the lack of tree branches bridging the river. In addition, sleeping next to rivers may reduce the energy lost during the night because temperatures are warmer there than inland areas (van Schaik *et al.* 1996). Therefore, riverine refuging might play a double role in sleeping site selection.

Some presleep behavior patterns may minimize the risk of detection by predators. Several primate species show vigilance, cryptic behavior, and move quickly and in silence to the sleeping site (*Pan troglodytes*: Nissen 1931; *Eythrocebus patas*: Hall 1967; *Saguinus oedipus*: Dawson 1979; *Hylobates lar*: Reichard 1998; *S. midas midas*: Day and Elwood 1999; *S. mixtax* and *S. fuscicollis*: Smith *et al.* 2007; *H. pileatus*: Phoonjampa *et al.* 2010; *Cacajao melanocephalus ouakary*: Barnett *et al.* 2012; *Nomascus nasutus*: Fei *et al.* 2012). However, although the study group sometimes behaved cryptically and was vigilant when entering the sleeping area, fights, chases and screams occurred often (*pers. obs.* Juan Manuel José-Domínguez), as also observed in *Macaca fascicularis* (Brotcorne *et al.* 2014). Presleep behavior may be less important for large primate groups (Heymann 1995) than for small ones, because in large groups individuals have more chances to detect predators (van Schaik *et al.* 1983).

During daily activities, the macaques advertised the presence of predators to other group members by mobbing the predator, screaming and shaking branches, as reported by Albert *et al.* (2011). One morning, a pair of clouded leopards caused the macaques to delay their exit from the sleeping site and the alpha male alarm called for at least 30 min (*pers. obs.* Juan Manuel José-Domínguez). In addition, on one of six occasions when macaques encountered pythons during the day, a python caught an adult female for several minutes. Although the predation attempt was not successful, it demonstrates that this species may be a significant predator of macaques (Matsuda *et al.* 2008b; Morino 2010) at the site. However, the presence of a python on the ground at the sleeping site did not make the macaques spend the night elsewhere. The study macaques were usually vigilant for avian threats, some juveniles performed alarm calls and fled when they spotted an eagle (pers. obs. Juan Manuel José-Domínguez), and eagle predation on macaques has been previously reported (Fam and Nijman 2011). Nevertheless, the presence of a changeable hawk eagle (*Nisaetus cirrhatus*) near the sleeping site one morning did not elicit any notable response.

Interactions with Conspecific Groups

Most intergroup encounters occurred outside the core area. However, the intergroup encounter region greatly overlapped with the main nucleus of the core area next to the river (Fig. 3a). In fact, four of the five heavily used sleeping sites were in the intersection of the intergroup encounter region and the core area. This overlap might result from the home range being more than 10 times larger than the core area. This explains the clusters of encounter locations in the core area compared to the home range. Nevertheless, the study group slept outside the intergroup encounter region more than expected from random site choice, possibly to avoid direct competition with conspecifics and the associated danger of injury, as suggested by the risk hypothesis (Wrangham *et al.* 2007).

The use of a large number of sleeping sites by our group suggests a high availability of suitable sleeping sites in the landscape and thus little need for competition over such sites. Nevertheless, the intergroup aggression we observed may indicate that competition over sleeping sites exists. Unlike intergroup encounters in other circumstances that generally triggered only few agonistic interactions, those at sleeping sites were always highly agonistic. This suggests that the availability of suitable sleeping sites in terms of predation avoidance, foraging efficiency, or any other possible role, may be restricted. This shortage may explain why the group split into two different sleeping sites on the same night on occasion, as also reported by Albert *et al.* (2011). However, another explanation for the intergroup agonistic interactions at sleeping sites is the possibility of extra group copulations in such a context of proximity, which could create tension and consequent aggression between males.

Sleeping Site Selection and Foraging Places

The study group frequently slept close to food resources, which is consistent with the food hypothesis. As found in other studies supporting the food hypothesis (Albert *et al.* 2011; Chapman *et al.* 1989; Smith *et al.* 2007), the mean distance of the sleeping site from the last or first feeding area was significantly greater than to the nearest sleeping site. However, the observed distance fitted best a multiple central place foraging strategy (McLaughlin and Montgomerie 1989), as our group spent 77 % of nights in the sleeping site nearest to the last or first feeding areas. Variation in the distance to the nearest sleeping site may be due to the relatively large home range of the study group (575 ha) and the large number of sleeping sites dispersed all over it, which increased the likelihood of any sleeping site being close to another one. Moreover, these differences also could be due to macaques often foraging in a widely dispersed group (Agetsuma 1995; Caldecott 1986; Choudhury 2008). For instance, it was not always possible to observe all individuals simultaneously when the group spread in a large area, which may have caused some bias in data collection toward the behavior of only visible macaques. This possible bias may lead to underestimates of the importance of some feeding locations (the last and first one particularly) and increase the estimated distance to the sleeping site.

Our study group does not frequently revisit foraging areas exploited in previous days (José-Domínguez et al. 2015a, b). Therefore, macaques may have sometimes slept far away from the last feeding area because they were exploiting other parts of the home range the following day or they prefer to sleep in high fidelity areas. However, the group never reused a sleeping site for more than two consecutive nights, suggesting that they either depleted foraging sites in 1 day and are multiple central place foragers (Chapman *et al.* 1989) or that they do not fully follow such a strategy due to other factors, such as predation pressure.

Albert et al. (2011) concluded that the best explanatory for sleeping site selection in a semiprovisioned group of *Macaca leonina* was a multiple central place foraging strategy in which the nearest sleeping site was heavily used. The four most heavily used sleeping sites were clustered in pairs in a small area adjacent to human settlements, and the distance between them ranged 50–250 m. However, we suggest that their findings best fit a central place foraging strategy. Their study group has access to abundant food concentrated in a small human area. Under such conditions, moving around a small area with high-energy food available becomes very profitable, and thus using sleeping sites mainly located within this small area is an advantageous foraging strategy.

Photoperiod Influence

We found a high correlation between the sunset and sunrise time and the corresponding entry and exit times to and from the sleeping site. The macaques spent a mean of 12 h 32 min at their sleeping sites, which is considerably shorter than reported for other sympatric primates in the area (14 h 00 min–17 h 00 min in *Hylobates lar*: Reichard 1998; 11 h 45 min–17 h 06 min in *H. pileatus*: Phoonjampa *et al*. 2010) and other primates elsewhere (15 h 46 min–16 h 12 min in *Sanguinus fuscicollis* and *S. mystax*: Smith *et al*. 2007; 11 h 48 min–16 h 48 min in *Nomascus nasutus*: Fei et al. 2012). This difference may result from the foraging strategy or predator avoidance strategy used by different species, for example, arriving at the sleeping site before predators become active (Anderson 2000; Fan and Jiang 2008). Species living in large groups may detect predators more efficiently than those in small groups (van Schaik *et al*. 1983), meaning that a large group of *Macaca leonina* can stay active for longer than gibbons at the study site. Our study group entered the sleeping site a few minutes before sunset and left it a few minutes after sunrise, which fits a strategy to maximize feeding time during daylight hours, as found in other primate species (*Cacajao melanocephalus ouakary*: Barnett *et al*. 2012; *Macaca fascicularis*: Brotcorne *et al*. 2014; *C. calvus ucayalii*: Swanson-Ward and Chism 2003). The semiprovisioned group studied by Albert *et al*. (2011) spent a mean of 37 min less at the sleeping site (11 h 55 min±SD 43 min) than our group did. The sleeping sites of their group were near open areas and close to human infrastructure and artificial light, which allowed the macaques to remain active longer and probably enhanced their ability to detect predators compared to our group, which slept in more forested areas with larger canopies.

Sleeping Site Selection in Human-Modified Habitats

The sleeping site number, distribution, and reuse patterns of our study group contrast greatly with patterns found in macaques living in areas with high levels of human disturbance (*Macaca leonina*: Albert et al. 2013; *M. fascicularis*: Brotcorne *et al*. 2014). Some generalist primates seem attracted to the edge of human-modified habitats and forest where natural and human food are available (Albert *et al*. 2013; Brotcorne *et al*. 2014; Gumert *et al*. 2011; Saj et al. 1999; Sapolsky and Share 2004; Sha and Hanya 2013). These flexible primates apparently prefer to sleep near human settlements (*M. leonina*: Albert *et al*. 2011; *Papio cynocephalus*: Muruthi *et al*. 1991; *M. radiata*: Ramakrishnan and Coss 2001). The advantages of this site selection are 1) highly caloric and easily accessible anthropogenic food, which can provide nutritional benefits, especially in periods of natural food scarcity (*M. fascicularis*: Brotcorne *et al*. 2014; cf. Engel *et al*. 2002; Sapolsky and Else 1987); 2) better visibility and thus improved detection of approaching terrestrial predators (Brotcorne *et al*. 2014); and 3) lower predation pressure (Isabell and Young 1993; Ramakrishnan and Coss 2001; cf. Khamcha and Sukumal 2009). However, this preference for living at the edge of the forest near human-modified habitats may result in fewer available sleeping sites and sites that are of lower quality, given the presence of roads and buildings. For example, the sleeping trees of long-tailed macaques living next to a park headquarters in Bali had trunks with smaller diameter at breast height compared to those in the forest (Brotcorne *et al.* 2014). In terms of future habitat quality, high reuse of sleeping sites may also increase seed deposition by macaques in a small area (González-Zamora et al. 2012), which can reduce the per capita seed-to-seedling survival (Russo and Augspurger 2004) and produce a saturation of some biotic mortality agents, e.g., rodents, insects, for seeds (Bravo 2012; Chauvet *et al.* 2004; Howe 1989; Janzen 1971).

Conclusions

Sleeping site selection in *Macaca leonina* appears to be a trade-off between two main, nonmutually exclusive pressures: seeking safety from predators and maximizing food efficiency. The relatively large number of sleeping sites, infrequent reuse of sites and the tendency of macaques to sleep in well-known areas support the predator avoidance hypothesis, whereas the proximity of sleeping sites to the first or last feeding area is consistent with the food hypothesis (Anderson 1998). The sleeping site reuse patterns also support an antipathogenic response. Specific studies of pathogens are needed to confirm whether this is the case in *M. leonina* (Albert *et al.* 2011). The large number of sleeping sites used only once supports both the predator avoidance and the food hypotheses. Although sleeping site selection by macaques does not fully fit with any of the strategies proposed, it partially conformed to a multiple central place foraging strategy, which is theoretically the best strategy for groups ranging in large home ranges where resources are highly spread out (Chapman *et al.* 1989). The occurrence of conspecific intergroup aggression at sleeping sites supports a restricted availability of suitable sleeping sites, which could be a contestable resource, supporting suggestions that suitable sleeping sites are rare (Ramakrishnan and Coss 2001; Tenaza and Tilson 1985). The clear contrast in patterns of sleeping site use between the study group and a semiprovisioned group highlights the flexibility of *M. leonina* to different ecological circumstances. Although there may be some clear patterns in sleeping site patterns for a given species, e.g., sleeping on tall trees vs. building a nest on the ground, the ecological constraints and conditions particular to a given environment, e.g., habitat degradation, availability of anthropogenic food, may lead to intraspecies differences.

The observed flexibility in sleeping patterns in this semiterrestrial species may help understand primate sleep evolution. Through evolutionary time primates have developed a great variety of adaptations, primarily in arboreal niches, aimed to increase survival during sleep periods when animals are most vulnerable to predation (Anderson 2000). Only recently have some monkey populations (*Macaca fuscata*: Takahashi 1997; *Papio hamadryas*: Kummer *et al.* 1981) living under low predation pressure, and great apes, including humans, developed the more complex and variable requirements of sleeping in a terrestrial niche (Coolidge and Wynn 2009). This crucial tree-to-ground sleep transition may have been aided by the flexibility that arboreal primate sleepers previously had to adjust to different environmental pressures. Further studies should test whether other species also present flexible use of sleeping sites to better understand the evolution of primate sleep.

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Capítulo 8

Discusión

Los resultados nos sugieren que el abastecimiento parcial con comida humana alteran los patrones de movimiento, modifican la socioecología y el régimen competitivo entre grupos y así como los patrones de selección de áreas dormidero. Además muestran que la escala de tiempo usada en los análisis de los patrones de movimiento afectan considerablemente a la delineación del ámbito hogareño y área núcleo, lo que está en concordancia con el hecho que diferentes escalas de tiempo capturan distintos fenómenos (Kie et al. 2010; Rivrud et al. 2010). Ámbitos hogareños o áreas núcleos estimadas a partir de escalas de tiempo grandes (12 meses o más) pueden no incluir áreas que son importantes para periodos más cortos (días o semanas), ya que hay recursos que pueden ser utilizados para unos pocos días y estar localizados en áreas que son excluidas en las escalas grandes (ejemplo: ámbito hogareño anual), pero son cruciales para la supervivencia de los animales. Esto contradice la definición de área núcleo de algunos autores, los cuales consideran el área núcleo como el área mínima necesaria para sobrevivir y reproducirse (Buchanan et al. 1998; Asensio et al. 2012b); por lo tanto, la comparación con otros estudios deben tener en cuenta la escala usada en los análisis y el método empleado.

Comparación de los patrones de movimiento con estudios anteriores en tropas de macacos no abastecidos

En general la tropa estudiada muestra un ámbito hogareño (449 ha), área núcleo (190 ha) y distancia diaria recorrida (2.246 m) mayor que las encontradas en estudios anteriores, incluso cuando estos estudios calcularon tales áreas usando métodos que suelen sobreestimar el tamaño. Por ejemplo, durante 133 horas de estudio sobre dos tropas de *Macaca leonina* (16-33 individuos, 72% de la dieta se basaba en fruta) en el Noreste de la India, Choudhury (2008, 2010) encontró ámbitos hogareños que variaban de 83-347 ha y una distancia recorrida diaria de 690-2.240 m. Estos menores tamaños en los ámbitos hogareños puede deberse a que la mayoría de las tropas carecían de hábitos terrestres (Choudhury 2010), mientras que en nuestra tropa de estudio este valor alcanza el 55%. Debido a que los hábitos arbóreos requieren más gasto energético que los terrestres (Rodman 1979; Carbone et al. 2005), los animales arbóreos suelen moverse en áreas más pequeñas y recorrer diariamente distancias más cortas. La ausencia de hábitos terrestres puede ser debida también a una mayor abundancia de comida en los doseles altos del bosque, haciendo no necesario la búsqueda de comida en el substrato, o por la partición del nicho ecológico debido a la presencia de otras especies de macacos en la zona (Feeroz 2012).

La especie filogenética más cercana a *Macaca leonina* es *M. nemestrina*, ambas fueron consideradas dos subspecies hasta hace poco, no obstante, *M. siberu* es considerada la más similar en estilo de vida y ecología (Richter et al. 2013). Estudios en ambas especies muestran también ámbitos hogareños, áreas núcleo y distancias diarias recorridas menores a nuestra tropa de estudio (Caldecott 1986; Richter et al. 2013). Las tropas de *M. nemestrina* estudiadas por Caldecott (1986; 30-55 individuos, 9% de tiempo en el suelo, 74% de fruta en dieta) presentan un ámbito hogareño de 62-70 ha. Igualmente la tropa *M. siberu* estudiada por Richter y colaboradores (2013; 29 individuos, 25% de tiempo en suelo y 76% de fruta en dieta) también mostró un ámbito hogareño y área núcleo varias veces menor. Esto puede responder a la alta productividad de los hábitats en las regiones de estos estudios (Malasia e Indonesia; Corlett & Primak 2011), de manera que los macacos pueden abastecer sus requerimientos alimentarios usando un área menor pero más productiva (McLoughlin et al. 2000; Li & Rogers 2005; Potts et al. 2011).

Efecto del abastecimiento de comida en los patrones de movimiento y filopatria en *Macaca leonina*

Tamaño de área usada

La tropa semiabastecida muestra un patrón de movimiento menor que la no aprovisionada y el tamaño de tropa es considerablemente menor, además, una proporción importante de su dieta es obtenida de recursos humanos (30-39 individuos, el 28% alimento humano en dieta). Un menor tamaño de grupo puede requerir un área más reducida para alcanzar sus necesidades nutricionales y un menor esfuerzo para coordinar el viaje simultaneo de una tropa mayor (Olupot et al. 1994; Janson & Goldsmith 1995, pero ver Chapman & Chapman 2000; Dias & Strier 2003). Sin embargo, varios estudios han demostrado que la presencia de comida humana en lugares fijos (cubos de basura, casas, carreteras) hace que los macacos semiabastecidos no necesiten viajar lejos en busca de comida natural, teniendo un ámbito hogareño y área núcleo más pequeños y recorriendo diariamente distancias más cortas (Altman & Muruthi 1988; Boutin 1990; Wheatley et al.1996; Monadjem & Perrin 1998; Saj et al.1999; Kreiter &

Wise 2001). Por el contrario, si los recursos están dispersos en varias áreas estos parámetros pueden incrementarse (Marriott 1988; Unwin & Smith 2010; Sha & Hanya 2013).

Filopatria

Independientemente de la escala temporal, los macacos no abastecidos muestran una filopatria baja para el ámbito hogareño y área núcleo. Las área con mayor índice de filopatria son aquellas cercanas a las áreas dormidero más usadas, lo que probablemente es debido a que los macacos suelen alimentarse en áreas cercanas en las horas previas a dormir. Al no ser territoriales no tienen la necesidad de patrullar los bordes de su ámbito hogareño, la baja filopatria asociada a la carente necesidad de patrullar nos hace pensar que sus movimientos reflejan la fluctuación espacio-temporal de los recursos. El alto número de individuos por tropa y el hecho de que no suelen visitar áreas que han sido explotadas en días anteriores, nos sugiere que los parches de comida son rápidamente agotados y es más ventajoso buscar otro nuevo (Stephens & Krebs 1986), por lo tanto, están forzados a estar constantemente en busca de nuevos parches de alimentos (Wrangham et al. 1993). Como otros cercopitecinos que viven en grupos numerosos, las tropas de *Macaca leonina* suelen dispersarse en pequeñas unidades en sus desplazamientos, usando distintos niveles de bosque para alimentarse simultáneamente de una amplia gama de recursos (Caldecott 1986; Agetsuma 1995; Caldecott et al. 1996; Choudhury 2008) y así evitar la competición alimentaria dentro del grupo. Además, mientras están en movimiento, mantienen el contacto con llamadas vocales y pueden informar a otros individuos de la localización de recursos importantes de alimentos (Obs. Pers.). Otra manera observada de obtener información de otros individuos es olfatear la boca (*Macaca tonkeana*, Riley, 2005).

Por el contrario la tropa semiabastecida presenta unos valores de filopatria mucho más altos y frecuentemente usa los mismos parches de alimento durante días consecutivos (Albert et al. 2013b), esto puede ser explicado por el menor número de individuos y a que obtienen un suplemento alimentario de la comida humana, tardando más en agotar los parches. Esta filopatria está ligada principalmente a áreas donde se encuentran localizadas las infraestructuras humanas y por tanto el aprovisionamiento de comida no natural. Esta alta filopatria se explica mejor por la abundancia de comida humana disponible (usando como indicador el número mensual de visitantes al parque) que por la abundancia de comida natural (índice de abundancia de alimento, *Food abundace Index*, FAI).

La predictibilidad de encontrar comida humana en un área pequeña (20 ha) hace los recursos defendibles, aumenta la densidad de macacos y la filopatria al mismo grado que una especie territorial como los gibones. Sin embargo, si los mayores índices de filopatria en gibones ocurren en las zonas cercanas a los bordes de su territorio, en la tropa semiabastecida ocurre en las zonas humanas, situada en el centro de su ámbito hogareño. Este uso intensivo de gran parte de su ámbito hogareño crea un área núcleo desproporcionalmente grande.

Estacionalidad de los patrones de movimiento

Los tamaños mensuales del ámbito hogareño y área núcleo no fueron diferentes entre los periodos de abundancia y escasez de fruta. Sin embargo, a escala diaria, el ámbito hogareño y la distancia diaria recorrida fueron mayores durante el periodo de abundancia de fruta, lo que apoya la idea de que la abundancia general de recursos influye en los patrones diarios de movimiento. Estas diferencias podrían ser también consecuencia de que en el periodo de mayor abundancia de fruta los días son más largos y, lógicamente, la distancia recorrida podría incrementarse (Gerber et al. 2012), pero la distancia recorrida fue mayor incluso controlando esa diferencia en la duración de los días. Esto sugiere que la abundancia de fruta debe ser el factor principal que controla la distancia recorrida diariamente.

Se podría esperar que en días sucesivos, a mayor abundancia de fruta los macacos revisitaran el mismo parche de alimento más a menudo que durante la época de escasez (*Cebus sp.*; Terborgh 1983); sin embargo, esto no se produjo. La ausencia de esta diferencia podría deberse a que existen otros componentes nutricionales importantes además de la fruta, como por ejemplo el aporte proteico de pequeños animales (invertebrados, pequeños reptiles, huevos y pollos de paseriformes). Aunque esto solo constituya el 10% de la dieta, son un recurso que requiere un considerable tiempo y un esfuerzo de búsqueda en áreas específicas (Terborgh 1983; Crompton & Andau 1986). Además, esta actividad es esporádica y críptica, por lo que puede ser subestimada en nuestros resultados. Finalmente es también posible que fenómenos estocásticos y el pequeño tamaño de muestra produzcan errores en nuestros resultados.

Los animales pueden responder a los periodos de escasez de comida de dos maneras: incrementando el rango de movilidad para obtener recursos adicionales (estrategia de maximización energética; Li & Rogers 2005; Hanya et al. 2006) o disminuyendo su rango de movilidad para ahorrar energía (estrategia de minimización energética; Strier 1992; Fan et al. 2008). Albert y colaboradores (2013b) predicen que, debido a ser semiterrestres, tropas no abastecidas de *Macaca leonina* usarían una estrategia de maximización energética como otros Cercopitécidos (*Chlorocebus pygerythrus*: Barrett 2005), sin embargo la tropa estudiada parece seguir una estrategia de minimización energética, también observada en otros primates como *Pan troglodites* (Wrangham 1977), *Nomascus concolor* e *Hylobates sp.* (Raemaekers 1980; Fan et al. 2008), *Alouatta palliata* (Milton 1980) y *Macaca fuscata* (Hanya et al. 2006).

Territorialidad

Además de la similitud anteriormente vista en los patrones de filopatria entre la tropa semiabastecida y gibones, la tropa no aprovisionada presenta un índice de capacidad de defender su territorio como es esperado en animales no territoriales, por el contrario, la tropa semiabastecida presenta un índice correspondiente a animales territoriales. Este índice de territorialidad no mide si un animal es territorial o no, sino si se mueve como es esperado para una especie territorial. El índice usa los patrones de movimiento (tamaño de ámbito hogareño y distancia diaria recorrida) para comprobar la capacidad que tienen los animales de patrullar sus fronteras. Por otro lado, la tropa semiabastecida mostró más agresividad hacia tropas vecinas que la tropa no aprovisionada. En animales no territoriales los encuentros entre grupos usualmente implican evitación y/o tolerancia (*Cercocebus albigena*: Waser 1976; *Alouatta seniculus*: Sekulic 1982; *Cebus apella*: Terborgh 1983; *Macaca nemestrina*: Caldecott 1986; *M. leonina*: Choudhury 2008). Encuentros agresivos en especies no territoriales pueden ocurrir en un contexto ocasional de acumulación de recursos importantes (*M. mulatta*: Southwick et al. 1965 and Lindburg 1977; *M. fuscata*: Kawanaka 1973), pero si estos recursos importantes ocurren durante un tiempo prolongado y de manera económicamente defendible, como en el caso de la tropa semiabastecida, la territorialidad puede emerger (Oates 1987). En resumen, considerando que la territorialidad es una forma de competición en la que los recursos son defendibles y para ello se defiende el área donde se encuentran (Brown & Orians 1970), nuestros resultados indican que cambios en la distribución de alimentos pueden substancialmente alterar los patrones naturales de animales no territoriales, como son los patrones de movimiento y comportamiento, a aquellos patrones presentes en especies territoriales.

Factores que afectan en la selección de las áreas dormideros en la tropa no abastecida de *Macaca leonina*

Depredación

Los patrones en la selección de la tropa estudiada son altamente coincidentes con la función de evitar ser depredado (Anderson 1998). Como en otros primates, la tropa usó numerosas áreas dormidero y alternó su uso frecuentemente y solo ocasionalmente su reuso fue en días consecutivos (*Ateles geoffroyi:* Chapman 1989*; Cebus apella*: Zhang 1995; *Colobus guereza*: Von Hippel 1998; *Hylobates pileatus*: Phoonjampa et al. 2010; *Nomascus nasatus*: Fei et al. 2012). Este patrón de selección reduce el olor que pueda dar pista de su presencia a depredadores (Reichard 1998). El reuso irregular de las áreas dormidero también ayuda a evitar el contagio de parásitos y mantener la higiene (Hausfater & Maede 1982; Nagel 1973; Reichard 1998). Las áreas dormidero más usadas y aquellas que ocasionalmente fueron usadas en dos noches consecutivas, se encontraban localizadas en las áreas mejor conocidas por la tropa (área núcleo y áreas de mayor filopatria), lo que podría ayudar a conocer mejor las posibles rutas de escape y advertir la presencia de depredadores (Dow

& Fredga 1983; Di Bitetti et al. 2000). Un mayor apoyo a la estrategia antidepredadora es el hecho que casi la mitad de las noches pasadas al lado del curso del río fueron en las áreas dormidero más usadas. Es posible que dormir en árboles adosados al curso del río proporcione una protección extra ante el ataque de depredadores (Fittinghoff & Lindburg 1980; van Schaik et al. 1996; Matsuda et al. 2008ab, 2011; Albert et al. 2011; Brotcorne et al. 2014). Si una cara del área dormidero pega al río se reduce el área que debe ser vigilada, ya que la mayoría de depredadores terrestres no pueden acceder al dormidero desde un río de 10-25 m de ancho y 1-2 m de profundidad, lo que tampoco facilita la conexión de ramas entre árboles de caras opuestas del río. Además, dormir en ramas cerca o sobre el río reduce la pérdida de energía durante la noche, ya que las temperaturas allí son más cálidas que en zonas lejos de ambientes ribereños (van Schaik et al. 1996), por ello los refugios ribereños pueden proporcionar una doble función.

El comportamiento previo de entrada al dormidero también puede minimizar ser detectados por los depredadores, por ello varios primates muestran un comportamiento de vigilancia con movimientos rápidos y silenciosos cuando se dirigen al área dormidero (*Pan troglodytes*: Nissen 1931*; Eythrocebus patas*: Hall 1967; Saguinus oedipus: Dawson 1979; *Hylobates lar*: Reichard 1998; *S. midas midas*: Day and Elwood 1999; *S. mixtax and S. fuscicollis*: Smith et al. 2007; *H. pileatus*: Phoonjampa et al. 2010; *Cacajao melanocephalus ouakary*: Barnett et al. 2012; *Nomascus nasutus*: Fei et al. 2012). Este comportamiento a veces fue observado en nuestra tropa, por el contrario peleas y gritos entre miembros del grupo fueron frecuentes (Obs. Pers.), hecho también observado en *Macaca fascicularis* (Brotcorne et al. 2014). Este comportamiento críptico puede ser menos importante en primates que viven en grupos grandes (Heymann 1995) que en grupos pequeños, debido a que viviendo en grupos grandes hay más probabilidad de detectar depredadores (van Schaik et al. 1983). Como Albert y colaboradores (2011), en nuestro estudio observamos que los macacos suelen alertar la presencia de depredadores (pitones, leopardo moteados y rapaces) a otros miembros de la tropa gritando y moviendo ramas.

Interacción con otros grupos de Macaca leonina

La mayoría de los encuentros con otros grupos fueron localizados fuera del área núcleo. Sin embargo, existe un gran solapamiento entre el área de encuentros y las áreas núcleo próximas al río (Fig. 3a, Capítulo 7). De hecho, cuatro de las cinco áreas dormideros usadas con más frecuencia se encuentran en esta área de solapamiento. Esta aparente contradicción puede deberse a que en el ámbito hogareño es 10 veces mayor que en el área núcleo y puede explicar el acúmulo de localizaciones de encuentro en el área núcleo en comparación con el ámbito hogareño. Sin embargo, en general, la tropa durmió fuera del área núcleo más de lo esperado por azar, posiblemente para evitar la posibilidad de heridas durante estos encuentros (Wrangham et al. 2007).

El uso de un gran número de áreas dormidero nos indicaría la existencia de un elevado número de estas áreas en el bosque y consiguientemente poca competición por ellas. Sin embargo, la agresividad observada en estas áreas durante los encuentros previos a la noche, nos sugiere competencia por este recurso y ello una baja disponibilidad de áreas dormidero adecuadas en términos de protección antidepredadora, eficiencia alimentaria y otra posible característica. Esto puede explicar el hecho que algunas veces las tropas se separan en dos áreas dormideros para pasar la noche, aunque también la agresividad en los encuentros podría ser para evitar cópulas extragrupales.

Cercanía a áreas de alimentación

La tropa frecuentemente durmió cerca de la primera o última zona de alimentación, lo que apoya la hipótesis alimentaria. Sin embargo, como en otros estudios que también apoyan dicha hipótesis (Chapman et al. 1989; Albert et al. 2011; Smith et al. 2007), la distancia media observada desde el área dormidero a la última o primera zona de alimentación fue mayor que a la del área dormidero más cercana. No obstante el 77% de las noches eligieron el área dormidero más cercana, haciendo que la elección observada se ajuste mejor a una estrategia de múltiples áreas de alimentación (Multiple Central Place Foraging, McLaughlin & Montgomerie 1989) que a otras estrategias propuestas. El gran tamaño del ámbito hogareño de la tropa, el alto número de áreas dormidero dispersas en él y la alta desviación estándar de las distancias observadas, incrementa la probabilidad de que otra área dormidero esté más cerca que la elegida, haciendo que las distancias medias no sean consistentes estadísticamente con la interpretación dada. Además estas diferencias pueden explicarse también por la estrategia de forrajeo usada por los macacos (Caldecott 1986; Agetsuma 1995; Choudhury 2008) y que discutimos anteriormente. Esta manera de forrajeo, donde los individuos del grupo se dispersan en una área extensa para alimentase, hace que no siempre fuera posible observar a todos los individuos del grupo y, por ello, perder la localización de áreas de alimentación (particularmente la última o primera) y de esta manera estimar erróneamente la distancia al área dormidero.

Como vimos, la tropa no suele revisitar áreas de alimentación que han sido explotadas en días previos, esto puede hacer que los macacos decidan dormir lejos de su última zona de alimentación para explotar otra zona del bosque al día siguiente o porque prefieren dormir en un área dormidero conocida. La estrategia de múltiples áreas de alimentación presupone el uso de la misma área dormidero hasta que los parches de alimentación han sido agotados (Chapman et al. 1989), pero nuestra tropa nunca usó la misma área dormidero consecutivamente más de dos días, por lo que deducimos que la tropa agota los parches de alimentación en un solo día o que no sigue estrictamente dicha estrategia debido a otros factores, como por ejemplo evitar depredadores.

Albert y colaboradores (2011) también concluyen que la tropa semiabastecida sigue una estrategia de múltiples áreas de alimentación. En este estudio la tropa usó 16 áreas dormidero, de las cuales cuatro fueron usadas el 71% de las noches. Estas cuatro áreas dormidero se encuentran agrupadas por parejas y localizadas en una pequeña área adyacente a las instalaciones humanas, distanciadas entre ellas 50-250 m. Contrariamente a lo que los autores concluyen, y atendiendo al área usada por la tropa no abastecida, sugerimos que la tropa semiabastecida se ajusta mejor a una estrategia de área central de forrajeo (Central Place Foraging Strategy, Orians & Pearson 1979). Debido a que el movimiento de esta tropa se centra principalmente es un área humana donde tiene acceso a abundante comida, moverse en derredor de un área con alimento altamente energético es muy rentable, por lo que usar principalmente las áreas dormideros localizados en un área pequeña es una estrategia ventajosa.

Influencia del fotoperiodo

Encontramos una alta correlación entre la hora de amanecer-anochecer y la salida-entrada de individuos en el área dormidero. De media la tropa estaba 12 h 32 min en sus áreas dormidero, lo que es considerablemente poco si se compara con otras especies de primates simpátridas en el área de estudio (14 h 00 min-17 h 00 min en *Hylobates lar*: Reichard 1998; 11 h 45 min-17 h 06 min en *H. pileatus*: Phoonjampa et al. 2010) y otros primates en otros lugares (15 h 46 min-16 h 12 min en *Sanguinus fuscicollis* and *S. mystax*: Smith et al. 2007; 11 h 48 min-16 h 48 min en *Nomascus nasutus*: Fei et al. 2012). Las diferencias pueden corresponder a las distintas estrategias de alimentación o antidepredadora usadas por las distintas especies, como por ejemplo llegar al dormidero antes que los depredadores nocturnos estén activos (Anderson 2000; Fan & Jiang 2008). Además, especies que viven en grupos numerosos pueden detectar más eficientemente depredadores que los grupos poco numerosos (van Schaik et al. 1983), lo que significa que los macacos pueden estar activos por más tiempo que los gibones en el mismo hábitat. La tropa entra en el área dormidero unos minutos antes de anochecer y salen minutos después de amanecer, lo que se ajusta a una estrategia para maximizar el tiempo de alimentación, como en otras especies de primates (*Cacajao calvus ucayalii*: Swanson-Ward and Chism 2003; *C. melanocephalus ouakary*: Barnett et al. 2012; *Macaca fascicularis*: Brotcorne et al. 2014).

Albert y colaboradores (2011) encontraron que la tropa semiabastecida pasaba 37 min menos tiempo en su área dormidero (11 h 55 min ± SD 43 min) que la no abastecida. Las áreas dormidero de la tropa de Albert y colaboradores se localizan en áreas abiertas, cercanas a instalaciones humanas y a luz artificial, lo que permite a los macacos permanecer activos más tiempo y probablemente facilitar la detección de depredadores en comparación con la tropas que duermen en áreas boscosas.

Selección de áreas dormidero en hábitats modificados por el hombre

El número de áreas dormidero usadas, su distribución y patrones de reuso de la tropa no abastecida, contrasta significativamente con los patrones encontrados en primates que viven en áreas de perturbación humana (*Macaca leonina*: Albert et al. 2013; *M. fascicularis*: Brotcorne et al. 2014). Algunos primates generalistas parecen estar atraídos por las áreas bordes (entre hábitats modificados por el ser humano y hábitat de bosque), donde la comida humana y natural está disponible (Saj et al. 1999; Sapolsky & Share 2004; Gumert et al. 2011; Sha & Hanya 2013; Albert et al. 2013; Brotcorne et al. 2014) y aparentemente prefieren dormir cerca de estas áreas (*Papio cynocephalus*: Muruthi et al. 1991; *M. radiata*: Ramakrishnan & Coss 2001; *M. leonina*: Albert et al. 2011). Las ventajas de esta selección son (1) comida humana hipercalórica y fácilmente accesible, que puede proporcionar beneficios nutricionales, especialmente en la época de escasez de alimento (*M. fascicularis*: Brotcorne et al. 2014; pero ver, Sapolsky & Else 1987; Engel et al. 2002); (2) mejor visibilidad, lo que mejora la detección del acercamiento de depredadores terrestres (Brotcorne et al. 2014); y (3) baja presión depredadora (Ramakrishnan & Coss 2001; Isabell & Young 1993; pero ver, Khamcha & Sukumal 2009). No obstante, esta preferencia a vivir en el borde del bosque cerca del hábitat modificado por el hombre, puede resultar en una menor disponibilidad de áreas dormidero y de peor calidad debido a la presencia de carreteras y edificios. Los macacos tienden a usar como árboles dormideros aquellos que tienen un diámetro de tronco mayor (Albert et al. 211). Brotcorne y colaboradores (2014) encontraron en el ámbito hogareño de una tropa semiabastecida de *M. fascicularis,* que los árboles que rodean a las instalaciones humanas poseen menor diámetro que aquellos dentro del bosque. En términos de calidad de hábitat futura, un reuso intensivo de áreas dormideros puede incrementar la deposición de semillas en un área pequeña (González-Zamora et al. 2012), y reducir la supervivencia de las semillas y plántulas (Russo & Augspurger 2004) al atraer agentes bióticos que son mortales para ellos, como roedores e insectos (Janzen 1971; Howe 1989; Chauvet et al. 2004; Bravo 2012).

Implicaciones en la conservación

El establecimiento de áreas naturales protegidas y su manejo crea una interfaz de áreas interconectadas donde se producen la interacción entre humanos, fauna y flora salvaje. Esto afecta a los elementos en los que los modelos sociecológicos están basados (e.g. distribución y abundancia de alimento; Fuentes 2006). El género *Macaca* está particularmente bien adaptado a los ambientes modificados por el hombre, sin embargo, efectos negativos pueden aflorar en sus poblaciones y en el ecosistema. Los animales dependientes de comida humana, como la tropa de macacos semiabastecida del estudio, están en contacto con el ser humano, lo que puede acarrear consecuencias demográficas para los animales y para el bienestar humano. Los patógenos pueden ser transmitidos bidireccionalmente entre primates humanos y no humanos (Engel et al. 2002; Wolfe et al. 2004; Rouquet et al. 2005). Un ejemplo se dio en una población de babuinos, donde se produjo una gran mortalidad por la tuberculosis bovina trasmitida a aquellos animales que solían comer restos de comida de la basura (Sapolsky & Else 1987). Animales que pasan largos periodos en los márgenes de las carreteras esperando el aprovisionamiento de comida a menudo son atropellados (Per. Obs.; Kanurai 2004; Mallapur 2013; Sha & Hayna 2013).

Los macacos son uno de los últimos grandes dispersores de semillas que permanecen en los hábitats modificados del sudeste de Asia (Corlett 1998; Lucas & Corlett 1998; Albert et al. 2013c). Como la fruta es parte importante de la dieta de *Macaca leonina*, las tropas están compuestas por numerosos individuos que recorren grandes distancias diariamente cubriendo grandes áreas. Esto resulta en que gran cantidad de semillas son dispersadas sobre extensas áreas y distintos tipos de hábitats. Sin embargo tropas semiabastecidas reducen sus ámbitos hogareños, recorren menos distancias diariamente y usan pocas áreas dormidero, reduciendo así el efecto positivo de los macacos en su ecosistema. Además tropas semiabastecidas dispersan semillas a distancias más cortas y a lugares donde la germinación o supervivencia de la plántula no es viable (e.g. carretera, tejados) o incluso pueden dispersar especies no autóctonas e invasivas que están presentes en la zona de borde (e.g. *Syzyginum cumini, Solanum melongena*). *Macaca leonina* es conocida por ser uno de los principales depredadores de huevos y pollos de paseriforme (Pierce & Pobprasert 2013), la alta densidad de macacos en un área pequeña puede afectar al éxito reproductor de estas aves. En resumen, el abastecimiento directo o indirecto de comida humana tiene otras repercusiones más allá, como la obesidad animal y envenenamiento, y finalmente puede afectar también a los patrones geográficos, de regeneración y diversidad de animales y plantas. El manejo de áreas protegidas debe considerar estás posibilidades para el tratamiento de las basuras producidas y para el establecimiento de reglas que eviten el aprovisionamiento de fauna salvaje.

Nuevo método del cálculo del índice de filopatria y estimación de ámbito hogareño

Usamos un índice para calcular la filopatria, que es un complemento al método gráfico de Ramos-Fernández y colaboradores (2013), el índice cuantifica la filopatria y permite la comparación entre especies, grupos o diferentes periodos. Este índice de filopatria puede ser usado para investigar el uso del hábitat (o áreas dormidero en nuestro caso), ya que permite asociar distintos tipos de hábitat a un grado de uso de un área en particular.

Finalmente el método "*Characteristic Hull Polygons with Hot Spot*", creado y usado como parte de esta tesis, ofrece algunas ventajas en la identificación de los ámbitos hogareños y áreas núcleo, sin los potenciales inconvenientes intrínsecos de otros métodos comúnmente usados (*Maximun Convex Polygons* y *Kernels*). *Maximun Convex Polygons*, usualmente incluye grandes áreas donde los animales nunca han estado y no ofrece información del uso del espacio (Powell, 2000). Por otra parte, la precisión del método Kernel depende de la forma, la homogeneidad de la distribución de las localizaciones y de un factor de suavizado de la forma (*smoothing factor*) (Girard et al. 2002; Hemson et al. 2005; Row & Blouin-Demers 2006; Mitchell & Powell 2008; Downs & Horner 2009; Downs et al. 2008, 2012), además su única asunción dice que las localizaciones deben ser independientes y estar idénticamente distribuidas en el espacio, hecho que a menudo es violado por la propia naturaleza del movimiento animal.

Capítulo 9

Conclusiones

Los resultados sostienen que la abundancia de comida rige los patrones de movimiento de *Macaca leonina* en su hábitat natural. Un aprovisionamiento parcial de comida de origen humano, en lugares fijos y de manera predecible en el tiempo, no solo modifica los patrones de movimiento sino que modula la socioecología de grupo, las interacciones con los grupos vecinos de congéneres y los patrones de elección de un recurso tan importante como son las áreas dormidero.

Las conclusiones extraídas se pueden concretar en:

(1) El método propuesto en la tesis "*Characteristic Hull Polygons with Hot Spot*", incluye un análisis geoestadístico que perfecciona el "*Characteristic Hull Polygons"* (Down et al. 2009), proporcionándole significanción estadística en la delineación de los ámbitos hogareños y áreas núcleo, sin los potenciales inconvenientes intrínsecos de otros métodos comúnmente usados.

(2) El índice desarrollado en este trabajo para calcular la filopatria, complementa notablemente al método gráfico de Ramos-Fernández y

colaboradores (2013), el cuál carecía de una cuantificación que permitiera comparaciones estadísticas del uso del espacio.

(3) La tropa no aprovisionada posee ámbitos hogareños mayores y viajan diariamente más que la semiabastecida. Estos patrones de movimiento y su alimentación, principalmente frugívora, hacen de la especie un importante dispersor de semillas en su ecosistema.

(4) La tropa no abastecida reduce el ámbito hogareño y la distancia viajada cada día durante los periodos de escasez de alimento, mostrando una estrategia de minimización energética.

(5) Los patrones de movimiento y la filopatria de ambas tropas están regidas por la distribución de los recursos alimentarios. Recursos dispersos y no predecibles, como los naturales, provocan baja filopatria; contrariamente, recursos de aparición temporal predecible y localizados, como los alimentos de origen humano, producen una alta filopatria tal como ocurre en especies territoriales como los gibones.

(6) La existencia de recursos de alto valor energético que se encuentran localizados en un área pequeña y pueden ser defendidos, alteran el régimen competitivo entre grupos y hacen aflorar rasgos de territorialidad en la tropa parcialmente abastecida.

(7) El patrón seguido en el uso de las áreas dormidero de *Macaca leonina* parece ser un balance entre una estrategia antidepredadora y maximizar su eficiencia en la búsqueda de alimento; sin embargo

también podría ser una respuesta con la que evitar el contagio de patógenos.

(8) El alto grado de agresión observado entre tropas cuando se producen encuentros en las áreas dormideros al anochecer, sugiere que las áreas dormideros adecuadas son poco abundantes y son por tanto un recurso apreciado.

(9) *Macaca leonina* ajusta su periodo de actividad a la variación estacional en la duración del día, lo que le permite optimizar su estrategia de forrajeo.

(10) El abastecimiento de comida altera los patrones de utilización de las aéreas dormidero, haciendo que la tropa semiabastecida use pocas áreas dormidero y las reutilice con más frecuencia.

(11) El aprovisionamiento de tropas de *Macaca leonina* en PNKY, produce muertes por atropello de animales cerca de la carretera, se crean conflictos macaco-humano donde los macacos roban comida y producen destrozos en infraestructuras. Por este motivo las autoridades del parque están capturando y exterminando algunos individuos de tropas próximas a lugares humanos.

(12) El abastecimiento de comida limita la función de *Macaca leonina* como dispersores de semillas e incrementa la depredación en ciertas especies de aves.

(13) Se constata que el abastecimiento directo o indirecto de comida humana tiene gran variedad de repercusiones, por lo que el manejo de áreas protegidas debe considerar estas posibilidades para el tratamiento de las basuras producidas y para el establecimiento de reglas y educación que eviten el aprovisionamiento directo o indirecto de fauna.

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