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International Journal of Primatology
The Official Journal of the International
Primatological Society

ISSN 0164-0291

Int J Primatol
DOI 10.1007/s10764-015-9865-x



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

Juan Manuel José-Domínguez¹ ·
Norberto Asensio² · Carmen J. García García¹ ·
Marie-Claude Huynen³ · Tommaso Savini⁴

Received: 16 June 2015 / Accepted: 12 August 2015
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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

Norberto Asensio and Tommaso Savini contributed equally to this work.

✉ Norberto Asensio
norberello@gmail.com

¹ Laboratory of Anthropology, Department of Legal Medicine, Toxicology and Physical Anthropology, University of Granada, Granada 18012, Spain

² Faculty of Environment and Resource Studies, Mahidol University, Salaya, Nakhon Pathom 73170, Thailand

³ Primate Research Group, Behavioral Biology Unit, University of Liège, Liège 4020, Belgium

⁴ Conservation Ecology Program, King Mongkut's University of Technology Thonburi, Bangkok 10150, Thailand

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 geoffroyi*: 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*, *Euoticus pallidus*, *Sciurocheirus alleni*, *Otolemur crassicaudatus*: 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 km²; 101°22 E, 14°26 N). This forest covers *ca.* 10 km² 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

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

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 $1286 \pm \text{SD } 654$ 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–Smirnov 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,

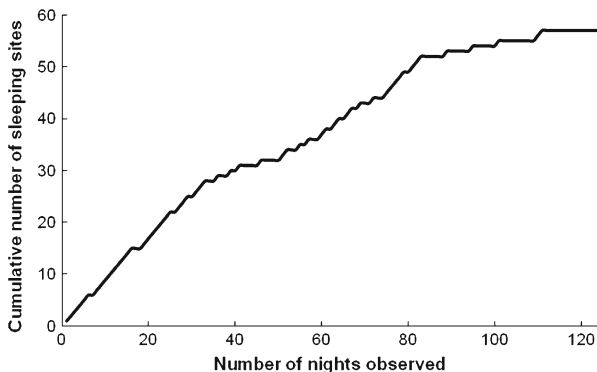


Fig. 1 Cumulative number of new sleeping sites vs. the number of nights observed in *Macaca leonina* in Khao Yai National Park from April to May 2011 and from May 2012 to June 2013.

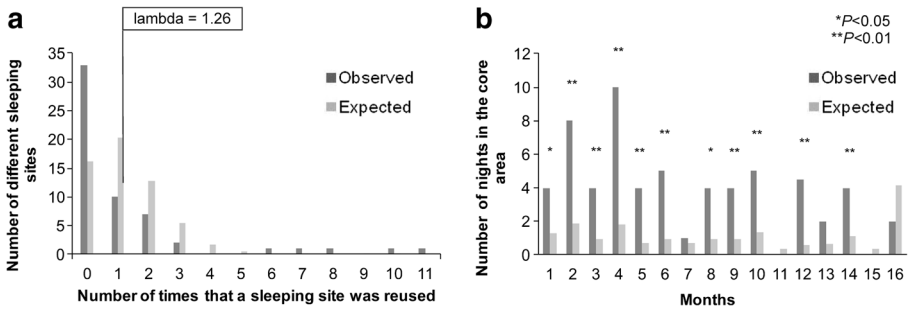


Fig. 2 Frequency of sleeping site use by the *Macaca leonina* group in Khao Yai National Park from April to May 2011 and from May 2012 to June 2013. **a** Observed and expected frequencies of sleeping site reuse. Expected frequencies are based on the Poisson distribution with a lambda (arithmetic mean 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

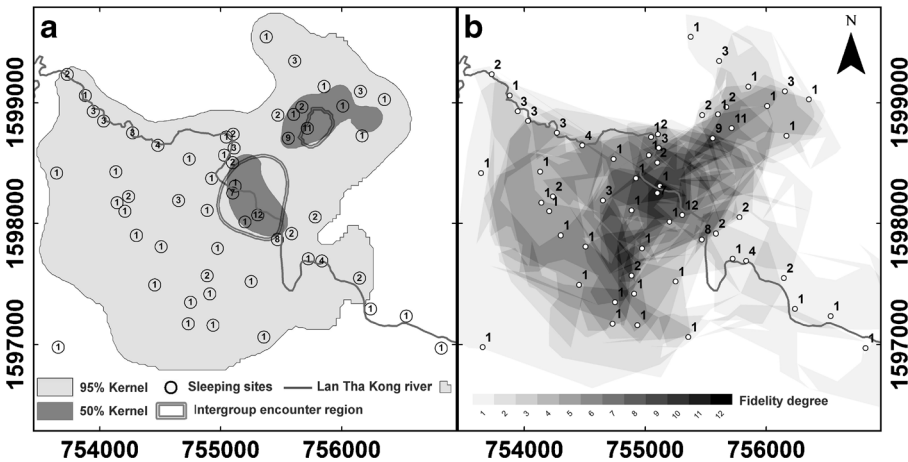


Fig. 3 Location and frequencies of sleeping sites of *Macaca leonina* in Khao Yai National Park in relation to (a) yearly home range (95 % kernel) and core area (50 % kernel) and (b) the number of months in which the macaques used an area (fidelity degree). Universal Transverse Mercator coordinates for 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.

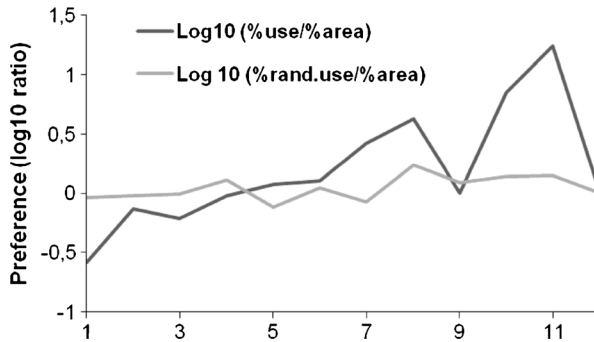


Fig. 4 Log ratios of the proportion used/area available for sleeping site locations vs. the number of months in which the macaques (*Macaca leonina*) used an area (fidelity degree) with observed and random sleeping site selection in Khao Yai National Park. Positive values indicate that a site is used 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 $227 \pm \text{SD } 203$ 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 $127 \pm \text{SD } 115.9$ 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: $t=-3.34$, $P=0.001$, $\text{df}=79$). 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 1 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, <i>N</i> =1596	—
Percentage of consecutive nights in the same sleeping site	7 %, <i>N</i> =101	22 %, <i>N</i> =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, <i>N</i> =96	147±SD 168 m, <i>N</i> =74
Observed distance from the sleeping site to the first feeding area	127±SD 116 m, <i>N</i> =80	150±SD 113 m, <i>N</i> =63
Mean distance from the last feeding area to the nearest sleeping site (MCPF 1 ^b)	116±SD 77 m, <i>N</i> =96	84 m ^c
Mean distance from the first feeding area to the nearest sleeping site (MCPF 1)	84±SD 61 m, <i>N</i> =80	—
Mean distance from the last feeding area to the nearest preferred sleeping site (MCPF 2 ^c)	484±SD 427 m, <i>N</i> =96	138 m ^c
Mean distance from first feeding area to the nearest preferred sleeping site (MCPF 2)	388±SD 377 m, <i>N</i> =80	—
Mean distance to all sleeping sites to last feeding area (CPF ^d)	1179±SD 225 m, <i>N</i> =96	202 m ^c
Mean distance to all sleeping sites to first feeding area (CPF)	1144±SD 199 m, <i>N</i> =80	—
Percentage of nights macaques chose the nearest sleeping site to the last feeding areas	50 %, <i>N</i> =96	—
Percentage of nights macaques chose the nearest sleeping site to the first feeding areas	68 %, <i>N</i> =80	—
Percentage of nights macaques chose the nearest sleeping site to the last/first feeding areas	77 %, <i>N</i> =92	42 %, —
The mean time entering the sleeping site	17 h 57±SD 26 min, <i>N</i> =120	18 h 16±SD 16 min, <i>N</i> =84
The mean time leaving the sleeping site	06 h 30±SD 22 min, <i>N</i> =97	06 h 05±SD 18 min, <i>N</i> =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

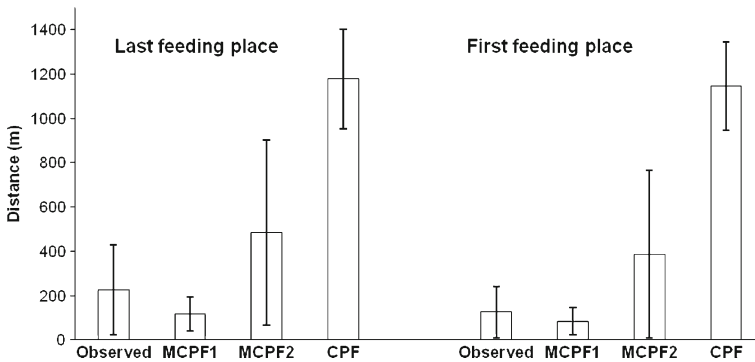


Fig. 5 Mean (\pm SD) distances between the last and first feeding site of the day and the observed sleeping site, the nearest sleeping site (multicentral place foraging [MCPF1]), the nearest heavily used sleeping site (MCPF2), and the mean distance to all sleeping sites (central place foraging CPF) of 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 \pm SD 26 min ($N=120$, range=16:55–18:40 h) and that of leaving it 06:30 h \pm SD 22 min ($N=97$, range=05:50–07:46 h). Therefore, macaques spent a mean of 12 h 32 min \pm 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 \pm SD 15 min ($N=120$) before sunset and left it 24 \pm 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 ouakaryi*: 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 \pm 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 intraspecific 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.

Acknowledgments Our express our gratitude to the Department of National Parks, Wildlife, and Plant Conservation of Thailand and the Superintendents of Khao Yai National Park and the National Research Council of Thailand for granting research permissions. We wish to thank L. Powel and D. Ngoprasert for statistical advice and N. Tantipisanuh for her help with some of the GIS analyses. Finally, we are very grateful to P. Garber, J. M. Setchell, I. Matsuda, and the four anonymous reviewers for their helpful comments and constructive criticism. This research was partially funded by PTT Exploration and Production (Thailand) and the Conservation Ecology Program, KMUTT (Thailand).

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