Use of sleeping trees by ursine colobus monkeys (Colobus vellerosus) demonstrates the importance of nearby food

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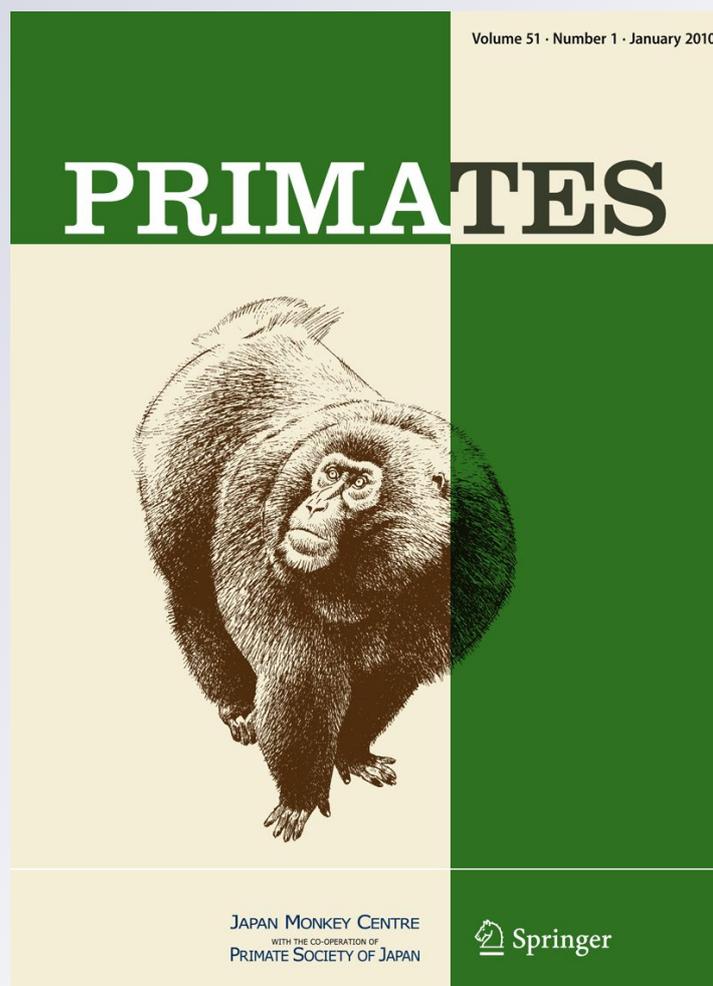
Julie A. Teichroeb · Teresa D. Holmes · Pascale Sicotte

Abstract Examination of the characteristics and locations of sleeping sites helps to document the social and ecological pressures acting on animals. We investigated sleeping tree choice for four groups of *Colobus vellerosus*, an arboreal folivore, on 298 nights at the Boabeng-Fiema Monkey Sanctuary, Ghana using five non-mutually exclusive hypotheses: predation avoidance, access to food, range and resource defense, thermoregulation, and a null hypothesis of random selection. *C. vellerosus* utilized 31 tree species as sleeping sites and the species used differed per group depending on their availability. Groups used multiple sleeping sites and minimized their travel costs by selecting trees near feeding areas. The percentage that a food species was fed upon annually was correlated with the use of that species as a sleeping tree. Ninety percent of the sleeping trees were in a phenophase with colobus food items. Entire groups slept in non-food trees on only one night. These data strongly support the access to food hypothesis. Range and resource defense was also important to sleeping site choice. Groups slept in exclusively used areas of their home range more often than expected, but when other groups were spotted on the edge of the core area, focal groups approached the intruders, behaved aggressively, and slept close to them, seemingly to prevent an incursion into their core range. However, by sleeping high in the canopy, in large, emergent trees with dense foliage, positioning themselves away from the main trunk on medium-sized branches, and by showing low rates of site reuse, *C. vellerosus* also appeared to be avoiding predation in their sleeping site choices. Groups left their sleep sites later after cooler nights but did not show behavioral thermoregulation, such as huddling. This study suggests that access to food, range and resource defense, and predation avoidance were more important considerations in sleeping site selection than thermoregulation for ursine colobus.

Keywords Sleep tree · Predation risk · Range defense · Thermoregulation · Foraging strategies

Introduction

For animals, selection of suitable sleeping sites impacts fitness in several ways because of the great amount of time spent in these sites and the defenseless state of sleep (Anderson 1984, 1998; Anderson and McGrew 1984; von Hippel 1998; Day and Elwood 1999; Di Bitetti et al. 2000). Studying the sleeping site ecology of primates can provide information about anti-predator strategies (Anderson 1998, 2000; Fan and Jiang 2008; Holmes et al. 2011), availability of preferred sleeping sites (Anderson 1984), resource exploitation (Anderson 1984; Fan and Jiang 2008), parasite avoidance strategies (Hausfater and Meade 1982; Anderson 1984; Di Bitetti et al. 2000), and the social aspects of sleeping (Anderson 1984; Anderson and McGrew 1984; Di Bitetti et al. 2000). The comparative sleeping site ecology of arboreal primates can also allow us to infer hominin sleep behavior, since early hominin species are believed to have retained arboreal adaptations for foraging and

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Table 1 Hypotheses and associated predictions investigated in sleeping site selection by ursine colobus at the Boabeng-Fiema Monkey Sanctuary, Ghana

Hypothesis	Predictions[a]	Predictions met?
Predation avoidance	*Select sleeping trees with:*	
	(1) Greater DBH than other trees in home range	(1) Yes
	(2) Greater height than other trees in home range	(2) Yes
	(3) Larger crown diameter than other trees in home range	(3) Yes
	Also:	
	(4) Avoid sleeping in the same trees on consecutive nights	(4) Mostly
	(5) Avoid sleeping in fruiting trees	(5) Mostly
	(6) Sleep on thin, emergent branches that twitch when disturbed	(6) Yes
Access to food	(1) Select sleep sites in close proximity to food sites used during the day	(1) Yes
	(2) Sleep in food species	(2) Yes
	(3) Forage in sleeping trees prior to or following sleep	(3) Yes
Range and resource defense	(1) Will sleep in periphery of home range if other groups are within 50 m	(1) Yes
	(2) Sleep most often in range of exclusive use	(2) Yes
Thermoregulation	(1) Sleep in larger huddles (>2) during periods of cooler temperatures	(1) No
	(2) Sleep at lower elevations during periods of cooler temperatures	(2) No
	(3) Sleep in trees or sites with less exposure to the elements (e.g., wind, temperature, rainfall)	(3) No
Null: random site choice	(1) Sleep in the area where they finish foraging at the end of the day	(1) No
	(2) Sleep tree species are used relative to their density in the home range	(2) No
	(3) Sleep in trees of average size	(3) No
	(4) Sleep in all areas of the home range relative to availability	(4) No

[a] Predation avoidance predictions: Anderson 1984; Anderson and McGrew 1984; Reichard 1998; von Hippel 1998; Anderson 2000; Di Bitetti et al. 2000; Smith et al. 2007; Fan and Jiang 2008; Holmes et al. 2011. Access to food predictions: Anderson 1984; Chapman 1989; Chapman et al. 1989; Heymann 1995; von Hippel 1998; Day and Elwood 1999; Smith et al. 2007; Fan and Jiang 2008. Range and resource defence predictions: Heymann 1995; von Hippel 1998; Day and Elwood 1999; Smith et al. 2007. Thermoregulation predictions: Cui et al. 2006; Li et al. 2010; Liu and Zhao 2004; Smith et al. 2007

possibly for sleeping in trees despite having developed derived bipedalism (Wrangham and Carmody 2010).

We investigated sleeping tree choice by ursine colobus monkeys (*Colobus vellerosus*) at the Boabeng-Fiema Sanctuary, Ghana, using five non-mutually exclusive hypotheses: predation avoidance, access to food, range and resource defense, thermoregulation, and a null hypothesis (Table 1). Sleeping primates have reduced awareness of their surroundings, making them more vulnerable to predation (Anderson 2000; Smith et al. 2007). Ursine colobus are diurnal and they sleep at night in relatively exposed trees. The predation avoidance hypothesis proposes that primates select sleeping sites that reduce primate detection by predators, enhance primates' detection of predators, and that are less accessible to predators (Anderson 1998; Reichard 1998; Smith et al. 2007; Holmes et al. 2011). The most common nocturnal predators are big cats, so diurnal primates often use sleeping sites that make them less accessible to felines hunting at night and allow the detection of these predators. For arboreal primates, this means sleeping in very tall trees, without many lianas, where there are plenty of sleeping positions away from the main trunk (Bert et al. 1967; Anderson and McGrew 1984), on smaller branches that may create noise and vibrations and dissuade an approaching predator (Gautier-Hion 1970; Anderson 1984, 2000). Indeed, leopards are a known predator for ursine colobus (Bodendorfer et al. 2006). The access to food hypothesis suggests that primates select sleeping sites in relation to their proximity to feeding sites, maximizing their access to these areas while minimizing their time and energy spent in travel (Anderson 1984; Chapman 1989; Day and Elwood 1999). Thus, primates may sleep within trees that are food species or forage near sleeping trees, before retiring in the evening and/or in the morning (Chapman 1989). The range and resource defense hypothesis proposes that primates select sleeping sites that allow the best defense of the home range from conspecifics, sleeping on the border of the home range or core area when other groups are nearby to prevent incursions into important areas of their range (Ramirez 1989). Groups may also sleep primarily in areas of their home range that are exclusively used to avoid boundary disputes with conspecific neighbors (Dawson 1979; Heymann 1995). The thermoregulation hypothesis proposes that sleep site choice and behavior while sleeping are dictated by the need to maintain a constant body temperature during the night

(Chivers 1974; Anderson 1984; Aquino and Encarnación 1986). Therefore, individuals may huddle together at night and choose sleeping sites that are at a lower elevation or protected from rain and wind (e.g., Liu and Zhao 2004; Cui et al. 2006). For the null hypothesis, sleeping site selection was predicted to be random with respect to tree species, tree size, and area of the home range. We focused on these five hypotheses because their predictions do not overlap with each other (Table 1) and these explanations for sleep site choice potentially have great fitness consequences. However, other non-mutually exclusive hypotheses for sleeping site choice are addressed in the discussion.

Methods

Study site and study species

This research was conducted at the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana (7°43′N and 1°42′W), a dry semi-deciduous forest fragment, 192 ha in size, consisting of a mosaic of primary forest, regenerating farmland (secondary forest), and woodland (Fargey 1991). BFMS is surrounded by farmland but connects to several smaller forest fragments via a narrow, riparian forest. Nineteen bisexual groups of ursine colobus monkeys (*Colobus vellerosus*) (Kankam et al. 2010) and a growing population of Campbell's mona monkeys (*Cercopithecus campbelli lowei*) are protected at BFMS by a hunting ban (Saj et al. 2005). These two diurnal primate species do not appear to compete for sleeping sites, as they can often be found sleeping in the same trees (JAT, TDH, personal observation). However, interspecies competition for sleeping sites (i.e., Tenaza and Tilson 1985; Day and Elwood 1999) has rarely been investigated and is worthy of closer investigation.

    C. vellerosus at BFMS have been studied under the direction of PS since 2000. They are mainly folivorous (annual diet 74% leaves) (Saj et al. 2005). Groups range in size (9–38 individuals, mean = 15, N = 15, Wong and Sicotte 2006) and are multi-male/multi-female, uni-male/multi-female, or all-male bands (AMB's) (Saj et al. 2005). There is no mating or birth season (Teichroeb and Sicotte 2008b). Between-group encounters (BGEs) are usually aggressive, with adult males as the main participants. Group males, solitary males, and males in AMBs also attack and interact with bisexual groups during male incursions (Sicotte and MacIntosh 2004; Teichroeb et al. 2011). Targeted aggression towards infants occurs during BGEs, male incursions, and when new males immigrate (Sicotte and MacIntosh 2004; Saj and Sicotte 2005). Male infanticide in this population accounts for 38.5% of the infant mortality (Teichroeb and Sicotte 2008a). Putative

sires may aid females in infant defense if they are present in the group (Saj and Sicotte 2005; Teichroeb and Sicotte 2008a, b).

Study groups and data collection

Sleeping trees were recorded for four groups of *C. vellerosus* (RT, B2, DA, and WW) on 298 nights over 13 months (July–November 2004, January–August 2005). The study groups varied in size (mean group size, RT: 13; B2: 15; DA: 24.5; WW: 30.5) and occupied overlapping home ranges. We were in contact with the groups for 2406 hours during 202 follow days and each study group was followed for two two-day periods per month from dawn to dusk (6:00 a.m.–6:00 p.m.) by JAT and a research assistant. We were able to record sleeping trees for the groups on 298 nights because all of the trees occupied by the groups at dusk (6:00 p.m.) and in the early morning (6:00 a.m.) were recorded as sleeping sites. Groups were confirmed to be in the same trees in the morning as in the evening each time they were checked (N = 199). Thus, sleeping trees were generally recorded for three nights consecutively, twice a month for each group.

    Behavioral observations were taken throughout full-day follows using 10-min focal samples (Altmann 1974) that were alternated among adult and subadult individuals. At least 1 h was left between focal samples on the same individual. Focal-animal samples totaled 433.3 h (RT: 106.5 h; B2: 102 h; DA: 99.8 h; WW: 125 h).

    The home ranges of the study groups were determined from 4950 location scans performed every 30 min throughout full-day follows (RT: 1181 scans; B2: 1166; DA: 1213; WW: 1390). During these scans, the location of the group was recorded relative to a map of the field site, which had been divided into 50 × 50 m quadrats. Home ranges were defined as all quadrats entered by a group during the 13 months of observation. The locations of BGEs and the presence of other groups in the study groups' home ranges were recorded during follows. In this way, the degree of home range overlap was determined, and defined as the proportion of quadrats in the home ranges where other groups had been observed. Quadrats in the home range where no other groups had been observed during the 13-month study were considered to be used exclusively by that group.

    The tree species composition of each group's range was determined by a large-tree survey and a quadrat survey. The large-tree survey consisted of measuring [diameter at breast height (DBH), crown diameter, and height] and mapping every tree ≥40 cm DBH in the home range of each group. During the quadrat survey, every tree ≥10 cm DBH was measured (DBH) and counted in randomly placed quadrats (50 × 50 m) that made up at least 10% of

the home range of each group. The fruiting/flowering/leafing cycles of 207 trees were monitored using phenology surveys. Samples of up to five randomly selected individuals of each food tree species were examined biweekly for the percentage of crown cover made up of young and mature leaves, flower buds and flowers, ripe and unripe fruits, and seed pods of different maturities (scale: 0, 0%; 1, 1–25%; 2, 26–50%; 3, 51–75%; 4, 76–100%; with each category summing to 4 when the plant parts were present, Sun et al. 1996). Rainfall (mm) and minimum and maximum temperatures were also recorded every day at a station located <1 km from the study groups' home ranges.

Data analyses

We defined a "sleeping site" as an area of the home range that is used for sleeping by a group of colobus. In our sample, a sleeping site consisted of one or several sleeping trees (range 1–8) in which the group spent a night. To avoid skewing the analyses of the tree species and size of sleeping trees, those trees that were used for sleeping more than once were only given a single entry in the data set. In addition, for each tree species, a mean measure of DBH, height, and crown diameter was calculated when comparing the size of sleep trees versus non-sleep trees. Pearson correlations were used to examine whether the time that groups left their sleep site was dependent on nighttime temperature or rainfall the previous day. Pearson correlations were also used to determine whether the percentage that each tree species was used for sleeping correlated with its density in the large tree survey, the quadrat survey, or the percent that it was fed upon in the overall diet. For these correlations, a Bonferroni correction was applied, lowering the alpha level to 0.017. For all other tests, the alpha level was set at 0.05. Analyses were done with SPSS 19.0 and GraphPad Software.

Results

Sleep patterns and site fidelity

Individuals in groups generally slept together in the same tree or in neighboring trees, with a mean of 2.5 trees used per night (range 1–8). Full groups were observed in a single sleeping tree on 21.5% of nights ($N = 64/298$). Individuals spread out in the crowns of sleeping trees, along medium-sized branches ($\sim$range of diameters 5–20 cm), and the only huddling observed was by mothers with their infants or juveniles. The smaller groups used fewer trees to sleep in than larger groups (mean number of trees used per night for groups in ascending order of size is RT: 1.8; B2: 2.2; DA: 2.5; WW: 3.4).
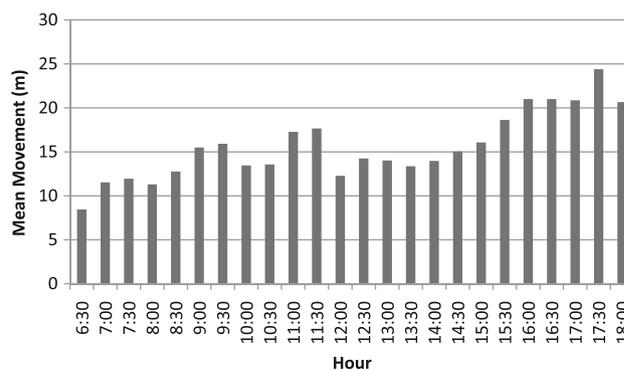

Fig. 1 Mean distance covered every 30 min for the four study groups during full day follows

It took the groups a mean of 72.9 min after sunrise to move from their sleeping trees in the morning, and they entered their sleeping trees a mean of 36.1 min before sunset. Groups left their sleeping trees later in the morning after cooler nights (Pearson: $N = 152$, $r = -0.193$, $P = 0.017$), but heavy rainfall the night before had no effect ($N = 152$, $r = 0.036$, $P = 0.66$). Groups usually traveled away from their sleeping trees in the late morning and slept the following night a mean of 88.3 m away (range 0–242 m, $N = 181$ full-day follows). The longest mean daily movements were typically seen between 1700 and 1730 as groups made their way to their sleeping sites (Fig. 1). During our follows (three consecutive days of recording sleep trees), groups reused sleeping trees consecutively on only 8.6% of nights (RT: 6.85%; B2: 6.67%; DA: 6.94%; WW: 13.92%).

Sleeping tree characteristics

The four study groups used 193 trees from 31 species as sleeping sites. Large, emergent trees were favored. The mean DBH of sleeping trees was 107.1 cm (SD ± 59.24), while the mean DBH of all trees in the groups' ranges measured in the quadrat survey was 35.25 cm (±39.64) and the mean DBH of all large trees (≥40 cm DBH) in the ranges was 77.77 cm (±35.51). The smallest tree that was ever used as a sleeping tree had a DBH of 42.5 cm, so for the following analyses only data from the large tree survey were used in comparisons. The mean height of the sleeping trees was 41.41 m (±12.28), whereas the mean height of all large trees in the ranges was 30.62 m (±13.98). The mean crown diameter of sleeping trees (18.58 m ± 8.47) was similar to that for all large trees in the ranges (18.2 m ± 7.32).

Overall, the tree species most frequently used for sleeping was a mahogany species (Meliaceae), *Khaya grandifoliola* (23.9%, 36 trees). *K. grandifoliola* is a hardwood species with a large spreading crown and dense foliage (Hawthorne 1990). However, study groups differed

Table 2 Top five tree species used as sleeping sites by four groups

Group	Sleep species rank	Species	% used, of all sleep trees	Stem density (#/ha)[a]	% of diet	Ranking in diet[b]
RT	1	*Antiaris toxicaria*	43.4	1.48	22.5	1
	2	*Khaya grandifoliola*	11.6	1.93	4.9	6
	3	*Milicia excelsa*	10.1	0.89	2.5	12
	4	*Albizia coriaria*	8.5	1.04	6.2	3
	4	*Angeissus leiocarpus*	8.5	2.37	0.07	36
B2	1	*Khaya grandifoliola*	69.9	2.98	14.0	2
	2	*Antiaris toxicaria*	9.2	0.47	14.1	1
	3	*Ceiba pentandra*	6.7	0.63	6.9	4
	4	*Milicia excelsa*	4.9	0.39	2.2	14
	5	3-way tie[c]	1.8	–	–	–
DA	1	*Aubrevillea kerstingii*	43.7	1.52	37.4	1
	2	*Milicia excelsa*	12.1	0.51	5.8	4
	3	*Khaya grandifoliola*	10.5	0.44	1.9	11
	4	*Ceiba pentandra*	5.3	0.25	8.3	3
	5	*Canarium schweinfurthii*	4.2	0.19	0	Non-food species
WW	1	*Aubrevillea kerstingii*	28.8	1.36	18.6	1
	2	*Pterygota macrocarpa*	13.3	0.43	5.8	5
	3	*Triplochiton scleroxylon*	12.6	0.79	6.4	4
	4	*Khaya grandifoliola*	11.5	0.93	4.8	7
	4	*Antiaris toxicaria*	11.5	0.57	2.4	13

[a] Density of that particular species for all trees in the range ≥40 cm DBH, calculated from the large tree survey

[b] Ranking in the diet of that particular group

[c] Three-way tie between *Albizia coriaria, Angeissus leiocarpus,* and *Bombax buonopozense*

in their top tree species chosen for sleeping. The RT group slept most often in *Antiaris toxicaria* trees (Moraceae, 43.3% of nights in 6 individual trees), B2 slept most often in *K. grandifoliola* trees (Meliaceae, 69.9% of nights in 22 individual trees), while DA and WW favored *Aubrevillea kerstingii* trees (Mimosaceae, DA: 43.7% of nights in 13 individual trees; WW: 28.8% of nights in 10 individual trees). All of these species have relatively hard wood, large crowns, and dense foliage (Kryn and Fobe 1959; Hawthorne 1990). The choice of top sleeping species depended, in part, on the density of the tree species in each group's home range (Table 2). For instance, DA and WW's top species used, *A. kerstingii*, was never used by RT or B2; this species was not present in RT's range and had an extremely low density in B2's range (0.08/ha). However, overall use of each species as sleeping sites did not correlate with the density of that species in the large tree survey (Pearson: $N = 30$, $r = 0.16$, $P = 0.39$) or in the quadrat survey ($N = 30$, $r = -0.06$, $P = 0.74$).

Proximity of sleeping trees to food

Three of four groups slept most frequently in the tree species that they also ate from most frequently during the 13-month study (Table 2). The overall use of each tree species as sleeping sites correlated with the percentage that it was fed upon in the overall diet (Pearson: $N = 30$,

$r = 0.83$, $P < 0.0001$). Indeed, 90.6% (681/752) of trees were slept in when they were in a colobus food phenophase, and on only one of 298 nights (0.03%) did the entire group sleep in trees that did not contain food. Of the sleeping tree species, 80.6% (25/31) were food species fed upon at least once during the study. This was similar to the percentage of large food trees available in the home range according to the large tree survey (78.3%).

Feeding bouts recorded in focal samples showed that when groups entered their sleeping trees in the evening, they fed in at least 20.5% of these trees, and before they moved in the morning, they fed in at least 29.4% of the trees. In addition, on 91.7% of nights, the monkeys fed in the 50×50 m quadrat containing the sleeping tree or in an adjoining quadrat in the morning or the evening. Some trees (19.5%, 141/723) were in a fruiting phenophase when they were chosen as sleeping sites.

Location of sleeping trees in the home range

By definition, the four groups spent 50% of their time during the day in the core areas of their home ranges. Forty-nine percent of the sleep trees (101/205) were located in core areas. Groups used the trees within the core area more often than expected, however—sleeping in this part of the home range on 69.8% of nights (208/298). For all study groups, the majority of the home range overlapped

with that of other groups (RT: 88%; B2: 67%; DA: 78%; WW: 96%) and relatively few quadrats were exclusively used (RT: 4/26 quadrats, 12% of the home range; B2: 10/53, 33%; DA: 10/68, 22%; WW: 3/60, 4%). Thirty percent (62/205) of sleep trees were located in areas of exclusive use, and groups spent more nights in these quadrats than expected based on availability (Fig. 2). Overall, 44% (131/298) of nights were spent in areas of exclusive use.

When there were no other groups within 50 m, groups slept in their core area on 69.2% (189/273) of the nights, but when another group was nearby, they slept in their core area on only 25.7% (19/74) of the nights. Despite the fact that much of the core area overlapped with other groups and was not exclusively used (RT: 60%; B2: 42.9%; DA: 50%; WW: 62.5%), when other groups were spotted on the edge of the core area near dusk, focal groups would often
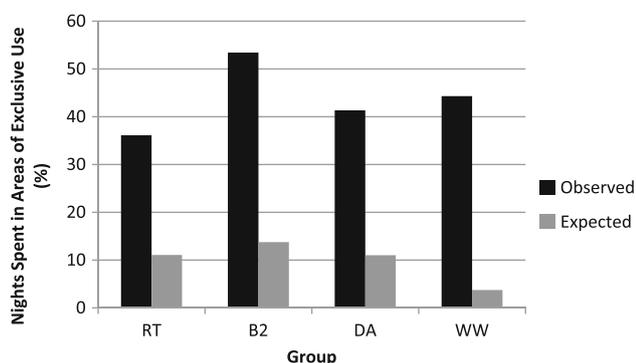
approach the intruders, display and/or direct chases towards them, and sleep within 50 m ($N = 12$).

Characteristics of trees chosen most often as sleep sites

The top 12 individual trees that were used for sleeping most often by the four groups had some features in common. Though the tree species varied, all of these trees were large, all were food trees, 91.7% (11/12) were in the core area of the home range, and 66.7% (8/12) were in an area of exclusive use for that group (Table 3).

Discussion

Our data most strongly support the access to food hypothesis for the choice of sleeping sites by *C. vellerosus* at BFMS (Table 1). The range and resource defense hypothesis was also strongly supported, while the predation avoidance hypothesis received moderate support. No support was found for the thermoregulation or the null hypotheses (Table 1). This population of *C. vellerosus* minimized their travel costs by selecting sleeping trees near feeding areas or by sleeping directly in feeding trees on most nights (Chapman 1989). This strategy often allowed the monkeys to stay in their sleeping trees until late morning and feed before having to move, which suggests an energy-saving strategy (e.g., *C. polykomos*, Dasilva 1992).

C. vellerosus used multiple places as sleep sites but did not exactly fit the definition of multiple central place foragers provided by Chapman et al. (1989). While *C. vellerosus* slept in different locations on the majority of nights and fed in the quadrat of the sleeping tree or the adjoining

Fig. 2 Observed and expected percentage of nights spent in areas of the home range that were exclusively used. Expected usage was calculated as an equal number of nights spent in each quadrat of the home range for each group

Table 3 Characteristics of the top twelve individual trees used for sleeping by *C. vellerosus*

Tree ID	Species	Times used	# Groups	Group(s)	Food?	Rank in diet[a]	In core area?	In exclusively used area?	DBH (cm)	Height (m)	Crown diameter (m)
28WW1	*Triplochiton scleroxylon*	20	1	WW	Y	4	Y	Y	130	50	29
28WW2	*Triplochiton scleroxylon*	20	1	WW	Y	4	Y	Y	87.3	35	11.5
186KY1	*Antiaris toxicaria*	16	1	RT	Y	1	N	N	77	–	13
48DN1	*Aubrevillea kerstingii*	15 (WW-13, DA-2)	2	WW, DA	Y	1	Y-WW, N-DA	N	126	60	23.6
190MH1	*Khaya grandifoliola*	14	1	B2	Y	2	Y	Y	152	60	23.6
177MH1	*Khaya grandifoliola*	14	1	B2	Y	2	Y	Y	144.7	49.6	36
28DN1	*Aubrevillea kerstingii*	14	1	WW	Y	1	Y	Y	162.5	60	33
9KYR1	*Pterygota macrocarpa*	14	1	WW	Y	5	Y	Y	96	40	15
148KY1	*Antiaris toxicaria*	13	1	RT	Y	1	Y	N	90	33.6	16.8
152MH1	*Khaya grandifoliola*	13	1	B2	Y	2	Y	Y	–	60	–
68MH1	*Khaya grandifoliola*	13	1	DA	Y	12	Y	N	209	55.6	40.7
9DN1	*Aubrevillea kerstingii*	13	1	WW	Y	1	Y	Y	82.7	40	12.8

[a] Rank in the diet of that particular group

quadrat in the evening and/or the morning, true multiple central place foragers should re-use a sleeping site over several nights to deplete the food in that area before moving on to another site (Sigg and Stolba 1981; McLaughlin and Montgomerie 1989; Chapman et al. 1989). *C. vellerosus* did not appear to deplete the food around a sleeping site before moving on, a strategy that may not be useful for primates in small ranges (*C. vellerosus* mean range size 12.3 ha) who are able to return to the vicinity of the sleeping site fairly regularly. Multi-male, forest-dwelling primate groups usually use multiple sleeping sites in various areas of their home range and do not return to one central place for sleep (Anderson 1984; Holmes et al. 2011), sometimes acting as true multiple central place foragers (Chapman et al. 1989). This could be due, in part, to the general high availability of suitable sleeping trees in forest environments (Anderson 2000), which allows these primates to sleep nearer several food sources. In contrast, central place foragers (Orians and Pearson 1979; Andersson 1978, 1981; Schoener 1979) spend each night in a fixed, central place (e.g., a nest, burrow, cliff, or cave, Chapman et al. 1989). Primates are not generally central place foragers if multiple sleeping site are available, but if suitable sites are limited, group size may increase at sleeping sites or population size may be constrained (reviewed in: Anderson 2000).

It has been suggested that primates may not sleep in food trees that are fruiting because these trees may also attract predatory animals that use fruit as an indication that prey species are nearby (Sugardjito 1983). However, a majority of the trees in the tropics are foliated most of the time, so the presence of leaves does not necessarily indicate the presence of prey to predators. Hence, for folivores, sleeping in food trees may not carry the same kind of threat that it does for frugivores or granivores. This may explain why *C. vellerosus* often slept directly in food trees (a result also reported for *C. guereza*, von Hippel 1998).

Groups in this population of *C. vellerosus* seemed to prefer to sleep away from other groups when they could, sleeping in non-overlapping areas of their home range more often than expected, a preference also found for *Saguinus oedipus* (Savage 1990), *S. mystax, S. fuscicollis* (Smith et al. 2007), *Cebus apella* (Zhang 1995), and *Colobus guereza* (von Hippel 1998). This strategy has been suggested to give groups exclusive access to feeding areas, reduce the chance of an encounter with other groups near the sleeping site, and provide shorter travel distances to greater areas of the home range in the morning (Smith et al. 2007). For another black-and-white colobus species (*C. guereza*), von Hippel (1998) suggested that avoidance of other groups at sleeping sites was a strategy to gain exclusive access to the feeding areas around the sleeping site in the morning. For *C. vellerosus*, our measure of the avoidance of other groups was examining areas that were exclusively used versus areas that overlapped with other groups. Thus, we did not interpret avoidance of other groups as a strategy to acquire food, since groups would have had exclusive access to these areas regardless of where they slept. Rather, sleeping away from other groups may be more about security. Male *C. vellerosus* from bisexual groups perform incursions towards other groups that are usually aggressive and sometimes include attacks against females and infants (Sicotte and MacIntosh 2004; Teichroeb et al. 2011). Sleeping away from these males in parts of the home range that are exclusively used may allow both males and females with infants to sleep with greater safety because it allows for protection of infants (e.g., Reichard 1998).

Our results also show the importance of range and resource defense as a consideration in sleep tree choice (Heymann 1995; Day and Elwood 1999). *C. vellerosus* were more likely to sleep outside their core area if they slept within 50 m of another group. Indeed, they were seen to move towards groups they detected on the borders of their range, direct displays and aggression at them, and sleep close to them. This appeared to prevent the encountered group from moving further into the range, and thus likely functioned to defend resources (Dawson 1979) or potentially other group mates (e.g., infants, females). Therefore, though groups prefer to avoid one another when sleeping, in the presence of another group they respond by challenging and displaying their intention to defend their range and/or group members.

Predation avoidance is the most prevalent explanation for sleep site selection in the primate literature (e.g., *Papio* spp., Hamilton 1982; *Hylobates lar*, Reichard 1998; *Cebus apella nigritus*, Di Bitetti et al. 2000; *Saguinus mystax, S. fuscicollis,* Smith et al. 2007; *Nomascus concolor jingdongensis*, Fan and Jiang 2008; *Nasalis larvatus*, Matsuda et al. 2010; *H. pileatus*, Phoonjampa et al. 2011). Although food was an important consideration of sleeping tree choice for *C. vellerosus*, our study also provides support for the predation avoidance hypothesis, as evidenced by the fact that small feeding trees were never slept in. Sleeping trees were always large emergents that were among the largest in the home range. By sleeping high in the canopy, away from the main trunk (Bert et al. 1967; Anderson and McGrew 1984), in trees with dense foliage (Anderson 1984; von Hippel 1998), and by showing low rates of site reuse (Heymann 1995), *C. vellerosus* appear to be concealing themselves from predators. Sleeping on medium-sized branches may also facilitate the detection of predators that may climb onto the branch, because leaves create noise and thinner branches vibrate with movement (Gautier-Hion 1970; Anderson 1984). Thinner branches may also be unable to support the weight of larger predators (Anderson 2000), thus dissuading them from climbing onto these

branches. *C. vellerosus* also tended to urinate and defecate in relative synchrony before leaving their sleeping tree in the morning, which Anderson (2000) also suggested functions as a predator avoidance mechanism. It is our impression that trees without lianas were chosen as sleeping sites. This would also decrease the accessibility of the sleeping tree to predators (Tenaza and Tilson 1985). Unfortunately, we did not measure liana coverage of sleeping trees when the study was conducted. This data needs to be collected before the predation avoidance hypothesis can be fully tested.

The large predators that may have once been at BFMS, such as leopards, have been extirpated (Saj et al. 2005). The remaining diurnal predators are several species of snakes, large raptors, and very occasionally, humans (Teichroeb and Sicotte 2012), while the remaining nocturnal predators are some small carnivores such as servals and civets (JAT, E. Wikberg, personal observation). The threat provided by these smaller, occasional predators is probably enough selective pressure to lead to the continued selection of sleeping sites that are safe from predation. However, it is possible that stronger support for the food hypothesis was found in this study because the threat of predation has been relaxed at this site—a similar effect to that seen in *Callithrix jacchus* in disturbed habitats (Mendes Pontes and Soares 2005). Selection for sleeping sites that provide access to food, in a relaxed predation environment, is a behavior that has been suggested to have the potential to be socially transmitted within a few generations (Anderson 2000). Nonetheless, primates have probably retained the fear and evasive reflex that has been selected for during millions of years of evolution with large carnivorous predators, even in the absence of true threat (Cosmides and Tooby 2000).

The thermoregulation hypothesis did not receive support in this study and thus is unlikely to have influenced which trees were chosen as sleep sites by *Colobus vellerosus*. The BFMS study site is flat, experiences tropical conditions (mean low temp. during the study 18.7°C, range 11–22, $N = 415$ nights), and the branches of tall, emergent trees seem relatively equally exposed to the elements (Smith et al. 2007). However, like *C. polykomos* (Dasliva 1993), *C. vellerosus* slept sitting up, hunched over, with their limbs tucked in, perhaps to conserve heat (but this species spends most of its time during the day in a sitting position as well, Schubert 2011). The study groups also took longer to leave their sleeping sites after cooler nights, as has been noted for *S. mystax* and *S. fuscicollis* (Smith et al. 2007), which may indicate that some sunbathing was necessary for the group to get active (Dasilva 1992, 1993). Despite this, *C. vellerosus* did not huddle together when sleeping (except for mothers and their infants) (Teichroeb et al. 2003), unlike in 82% of the sleeping arrangements observed in another

colobine, the higher-latitude *Rhinopithecus bieti*, which sleeps in clusters ranging from two to eight individuals (Li et al. 2010). Thus, thermoregulation was probably not a serious concern in sleeping site use by *C. vellerosus*.

Despite showing low rates of sleeping site re-use, the average distance between sleeping sites on successive nights for *C. vellerosus* was not very long (88.3 m). We interpret this as being the outcome of a mix of strategies. Groups had small home ranges (RT: 6.75 ha; B2: 12.75 ha; DA: 15.75 ha; WW: 14 ha) with even smaller areas of exclusive use (RT: 1 ha; B2: 2.5 ha; DA: 2.5 ha; WW: 0.75 ha) near the centre of their range. The preference for sleeping in areas of exclusive use meant that groups often ended up using sleeping trees that were only a quadrat or two away from their site on the previous night. However, these sites were still most often different from the previous night, providing fresh feeding areas and perhaps evasion of predators.

The results of this study suggests that access to food, predation avoidance, and range and resource defense were all important considerations of sleeping site selection, though we found the strongest support for the food hypothesis. We did not test some other hypotheses for sleeping site choice, such as the comfort hypothesis (Anderson 1984), the security hypothesis (Di Bitetti et al. 2000), and the parasite avoidance hypothesis (Hausfater and Meade 1982), but these may also influence the sleeping site ecology of *C. vellerosus*. For instance, this primate species preferred hardwood tree species as sleeping sites, which has been suggested to be due to the resulting increased security against branches breaking during the night (Di Bitetti et al. 2000), and frequently changing sleeping site location has been linked to parasite avoidance (Anderson 1984; Hausfater and Meade 1982). The sleeping site ecology of any animal will be influenced by adaptation to a host of factors that influence survival and reproductive success, which makes all hypotheses for sleeping site choice non-mutually exclusive and potentially important depending on species ecology.

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