Sleeping Site and Tree Selection by Bale Monkeys (*Chlorocebus djamdjamensis*) at Kokosa Forest Fragment in Southern Ethiopia

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Abstract

Although selecting advantageous sleeping sites is crucial for nonhuman primates, the extent to which different factors contribute to their selection remains largely unknown for many species. We investigated hypotheses relating to predator avoidance, food access, and thermoregulation to explain the sleeping behavior of Bale monkeys (*Chlorocebus djamdjamensis*) occupying a degraded fragmented forest, Kokosa, in the southern Ethiopian Highlands. We found that the study group reused 11 out of 20 sleeping sites used during the 42 study days over a 6-month period. Sleeping sites were usually close to the last feeding trees of the day (mean distance =15.2 m) and/or the first feeding trees of the next morning (mean distance = 13.5 m). This may reflect an attempt to maximize feeding efficiency and reduce travel costs. Compared to the mean trees in the study area, sleeping trees were significantly shorter. Bale monkeys selected sleeping places in trees with high foliage density above and below them, lending support to the hypothesis that they select sleeping places that can conceal them from predators and at the same time offer shelter from cold weather. The monkeys also frequently huddled at night. Our results suggest that predator avoidance, access to food resources, and thermoregulation all likely influence the selection of sleeping sites by Bale monkeys.

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Introduction

The selection of sleeping sites is an essential aspect of the behavioral ecology of primates and may be crucial for individual survival. Several hypotheses have been proposed to account for the selection of sleeping sites in primates, including predator avoidance (Anderson, 1998; Bernard *et al.*, 2011), proximity or access to food resources (Chapman, 1989; Teichroeb *et al.*, 2012), range or resource defense (Day & Elwood, 1999; Smith *et al.*, 2007), thermoregulation (Fan & Jiang, 2008; Terrien *et al.*, 2011), and parasite avoidance (Hausfater & Meade, 1982; Heymann, 1995) (Table I). However, predator avoidance seems to be the most widely accepted explanation (Anderson, 1998; Bernard *et al.*, 2011; Fei *et al.*, 2012). Because primates spend about half of their lives at sleeping sites, they are vulnerable to predators at these locations during prolonged periods of time while sleeping (Anderson, 1998). Hence, selecting sleeping sites that minimize or serve to avoid predation has been suggested to be the main factor determining sleeping site selection (Anderson, 1998; Phoonjampa *et al.*, 2010; Reichard, 1998).

The predation avoidance hypothesis proposes that primates select sleeping sites that minimize the risk of being detected by predators and at the same time favor primates' detection of predators to increase their chances of escaping (Anderson, 1998). Some primates are suggested to change their sleeping sites frequently to decrease the predictability of a predator finding them (e.g., François' langur [*Trachypithecus francoisi*: Qihai *et al.*, 2009]; wild saddleback tamarin [*Saguinus fuscicollis*: Smith *et al.*, 2007]).

Table I Hypotheses and predictions testing for factors influencing the selection of sleeping sites and trees by Bale monkeys at Kokosa forest fragment in southern Ethiopia, February– July 2014

Hypothesis	Prediction
Antipredation	P1) Favor sleeping sites and trees located in familiar/well-known areas, increasing their chance of successful escape in case of attack
	P2) Prefer a sleeping place in trees that has greater foliage density below (from the monkey to the ground) and above (from the monkey to the sky) to conceal them from terrestrial and aerial predators
	P3) Enter sleeping sites before sunset (before nocturnal predators become active) and exit sleeping sites after sunrise (when nocturnal predators become inactive)
	P4) Prefer tree characteristics (e.g., tall, large DBH, and large crown diameter) that help reduce access and detection by predators
	P5) Change sleeping sites frequently to reduce the chances of being detected by predators
Food access	P6) Select sleeping trees near to food sources, i.e., to the last feeding tree of the day and/or the first feeding tree of the next morning
	P7) Prefer sleeping sites in habitats with greater food resources than in other habitats with less food resources
	P8) Prefer sleeping sites in the core area containing potentially greater food sources than in the periphery within their home range
Thermoregulation	P9) Prefer to sleep in an area sheltered from wind (large trees, large crown diameter), that is located in vegetation types with denser foliage
	P10) Prefer to sleep in places with dense foliage
	P11) Prefer to sleep in social huddles rather than sleep alone

Other primary species prefer sleeping sites that provide better concealment with dense foliage or canopy cover to reduce the risk of detection by predators (Phoonjampa *et al.,* 2010; Wang *et al.,* 2011). The predator avoidance hypothesis also predicts that primates will favor sleeping sites and trees located in familiar or well-known areas, increasing their chance of successful escape in case of attack (Jose-Dominguez *et al.,* 2015). For example, some primates reuse a few favorite sleeping sites that are thought to reduce predation risk (e.g., tufted capuchin monkey [*Cebus apella*: Di Bitetti *et al.,* 2000]; white-headed langur [*Trachypithecus leucocephalus*: Li *et al.,* 2011]). The physical characteristics of potential sleeping trees (e.g., height, trunk diameter) influence the selection of sleeping sites (Anderson, 2000; Hernandez-Aguilar *et al.,* 2013; Hernandez-Aguilar & Reitan, 2020; Seiler *et al.,* 2013). Researchers suggest that to reduce the risk of predation, primates prefer large trees with little liana cover located on steep slopes or in areas with dense ground vegetation cover (Bernard *et al.,* 2011; Chu *et al.,* 2018; Hernandez-Aguilar *et al.,* 2013; Hernandez-Aguilar & Reitan, 2020).

Alternatively, the food access hypothesis suggests that primates select sleeping sites close to feeding trees to minimize traveling costs and increase feeding efficiency (Chapman, 1989; Phoonjampa *et al.,* 2010; Teichroeb *et al.,* 2012). For instance, they prefer to sleep in feeding trees, close to their last feeding tree of the day or the first feeding tree of the next morning (Day & Elwood, 1999; Smith *et al.,* 2007; Teichroeb *et al.,* 2012). The thermoregulation hypothesis suggests that primates prefer to sleep in places that provide shelter from extreme weather that allows them to conserve energy (Smith *et al.,* 2007; Stewart *et al.,* 2018). In addition, the selection of sleeping sites may be affected by habitat disturbance (Anderson, 2000; Gazagne *et al.,* 2020; Qihai *et al.,* 2009). For example, habitat alteration affects forest-dwelling primates in many ways, including reducing the availability and quality of tall and large trees suitable for sleeping, reducing canopy connectivity, decreasing the availability and quality of food resources, and increasing vulnerability to predators, hunting pressure, and exposure to parasite infections (Gazagne *et al.,* 2020; Gonzalez-Zamora *et al.,* 2012; Kiene *et al.,* 2021; Mekonnen *et al.,* 2017, 2020). The aforementioned hypotheses are not mutually exclusive (Franklin *et al.,* 2007; Li *et al.,* 2013) and it is important to consider the relative contribution of each to a species' behavior. For instance, animals may employ one sleeping site strategy when the perceived risk of predation is high and another one when it is low (Franklin *et al.,* 2007).

Today, large areas of intact forest are rare and many primate populations are forced to inhabit small forest fragments in human-dominated landscapes (Almeida-Rocha *et al.,* 2017; Estrada *et al.,* 2017). In fact, areas of large continuous forest suitable for large primate populations comprise only 20% of remaining tropical forest, which is disappearing at a rate of 7.2% each year (Potapov *et al.,* 2017). In forest fragments, anthropogenic disturbances decrease overall habitat quality and food availability (Arroyo-Rodríguez & Mandujano, 2006; Mekonnen *et al.,* 2017) and the availability of suitable sleeping trees (Gazagne *et al.,* 2020). In these fragmented landscapes, large predators are often eliminated (Strampelli *et al.,* 2018), which may affect sleeping site selection (Gazagne *et al.,* 2020; Gonzalez-Zamora *et al.,* 2012). As fragmented habitats have become so common, and because the extent to which different factors that contribute to their selection of sleeping sites have likely changed, it is important to study sleeping site selection in this context.

Reliable information on the sleeping site and tree selection patterns of a particular primate species is essential for understanding its ecological adaptations (Velazquez-

Vazquez *et al.,* 2015) and the strategies that influence the species survival (Anderson, 1998; Fei *et al.,* 2012). However, the relative contributions of different factors influencing sleeping site and tree selection remain largely unknown for most primates (Fei *et al.,* 2012). For example, the sleeping site and tree selection patterns of Bale monkeys (*Chlorocebus djamdjamensis*) have never been studied before. The Bale monkey is an arboreal, territorial, bamboo specialist endemic to the southern Ethiopian Highlands that is classified as Vulnerable by the IUCN (Gippoliti *et al.,* 2019; Mekonnen, Fashing, Sargis, *et al.,* 2018b). A single species of highland bamboo (*Arundinaria alpina*, Syn. *Yushania alpina*) accounts for up to 81% of its annual diet in continuous forest (Mekonnen *et al.,* 2010; Mekonnen, Fashing, Bekele, *et al.,* 2018a). However, habitat disturbance significantly reduces food availability and habitat quality, with bamboo accounting for 86% of stems ≥2 m tall in continuous forest and for only 2%–40% of stems in fragments (Mekonnen et al., 2017; Mekonnen, Fashing, Bekele, *et al.,* 2018a). The abundance of large trees is greater in continuous forest than in forest fragments. The mean tree height, canopy size, and diameter at breast height (DBH) of large trees are all greater in continuous forest than in forest fragments (Mekonnen *et al.,* 2017).

The main predators of Bale monkeys in forest fragments are domestic dogs and humans, while other potential predators include spotted hyenas (*Crocuta crocuta*), African wolves (*Canis lupaster*), and birds of prey (e.g., tawny eagles [*Aquila rapax*], martial eagles [*Polemaetus bellicosus*], augur buzzards [*Buteo augur*]) (Mekonnen *et al.,* 2020; Mekonnen, *unpubl. data*). According to local farmers, leopards were extirpated from most forest fragments occupied by Bale monkeys decades ago. Consequently, changes in food availability and habitat structure, along with associated changes in the monkeys' diet (Mekonnen, Fashing, Bekele, *et al.,* 2018a) and forest strata use (Mekonnen, Fashing, Sargis, *et al.,* 2018b), as well as changes in the density or presence of large predators, might be expected to influence sleeping site and tree selection patterns of Bale monkeys in fragments.

Here we investigated three hypotheses about the sleeping site selection of Bale monkeys (*Chlorocebus djamdjamensis*) (Table I). Following the antipredation hypothesis, we predicted that with the loss of large trees in their degraded habitat Bale monkeys would select the best sleeping trees from what they have available, such as tall trees with large DBH and dense canopy cover, that could function to avoid predation. Next, following the food access hypothesis, we predicted that Bale monkeys would select sleeping sites near to the last feeding trees and/or the first feeding trees of the next morning to minimize travel costs between sleeping and feeding trees, which would enhance feeding efficiency. Finally, following the thermoregulation hypothesis, we predicted that Bale monkeys would prefer to sleep in a huddle rather than alone and select large trees with a higher crown diameter and denser foliage to shelter themselves from cold weather.

Methods

Study Area

We conducted our study in the community-owned Kokosa forest fragment (6°44′–06°45′N and 38°48′–38°51′E; 162 ha; elevation 2660 m) in southern Ethiopia (Mekonnen *et al.,* 2017). Annual rainfall (July 2013–June 2014) was 1676 mm SE ±

20.6 and exhibited a bimodal pattern with a short dry season and a long wet season (Mekonnen, Fashing, Bekele, *et al.*, 2018a). Mean annual temperature at Kokosa was 16.7°C SE ± 0.4 while mean annual low and high temperatures were 9.9°C SE ± 0.7 and 23.5°C SE ± 0.7, respectively (Mekonnen, Fashing, Bekele, *et al.*, 2018a).

The fragment contains mixed-bamboo forest, tree-dominated forest, and shrubland set amidst a larger matrix of cultivated land, human settlements, and grazing areas. Cutting of bamboo by the local community is common in the fragment, and remaining stands are dwindling (Mekonnen *et al.*, 2012).

Study Species, Group, and Habitat Characteristics

The Kokosa fragment is home to two groups of Bale monkeys whose home ranges overlap slightly. One group is habituated, while the other is not; no data were collected on the unhabituated group. The study group consisted of 28 individuals, including 4 adult males, 8 adult females, 10 juveniles, and 6 infants (Mekonnen *et al.*, 2017). The home range and core areas were estimated using a fixed kernel density estimation (KDE) method employing a combination of Home Range Tools (HRT) version 2.0 and ArcGIS 10.3 (Mekonnen *et al.*, 2017). Home range was defined as a fixed KDE with 95% isopleths (contour lines) and core areas with 50% isopleths (Mekonnen *et al.*, 2017). The group's home range was 39.9 ha and its core area was 8.8 ha over a 12-mo study period. The home range contained five habitat types: mixed-bamboo forest (17.1%), tree-dominated forest (8.0%), shrubland (29.5%), grazing land (37.9%), and cultivated land (7.5%) (Mekonnen *et al.*, 2017) (Electronic Supplementary Material [ESM] Table SI). The area contained 35 species of plants >2 m tall, though bamboo (*Arundinaria alpina*) accounted for 39.6% of these stems (Mekonnen *et al.*, 2017). Trees >10 cm in DBH had a mean DBH of 23.68 ± SD 1.20 cm, a mean height of 11.11 ± SD 0.42 m, and a mean crown diameter of 3.93 ± SD 0.12 m (Mekonnen *et al.*, 2017). The mean DBH of bamboo stems was 2.14 ± SD 0.04 cm, and mean height of bamboo stems was 4.37 ± SD 0.08 m (Mekonnen et al., 2017)..

Behavioral Observation

AM and a well-trained research assistant, Mengistu Birhan, collected the sleeping site data from the habituated study group at Kokosa for 6 mo from February to July 2014 involving 42 days of observation with a mean of 7.0 ± SD 1.26 consecutive days per month. We defined a *sleeping site* as the circular plot of 20 m radius from the center of a sleeping tree or trees, where one sleeping site could be composed of one or more sleeping trees occupied simultaneously (Albert *et al.*, 2011; Brotcorne *et al.*, 2014). We defined a *sleeping tree* as an individual tree at a sleeping site in which one or more monkeys slept overnight (Albert *et al.*, 2011). We defined a *sleeping place* as the location where an individual monkey slept in a tree (Reichard, 1998). We recorded the global positioning system (GPS) locations using a handheld Garmin GPSMap 62s (Garmin Ltd., Olathe, KS, USA; ≤4 m error) and species of each sleeping site and tree, and noted all instances of reuse (Fan & Jiang, 2008; Hernandez-Aguilar, 2009; Phoonjampa *et al.*, 2010).

We recorded the time each individual entered and exited a sleeping tree. To test the food access hypothesis, we recorded the GPS locations of the last feeding tree of the

day and first feeding tree of the next morning to estimate the distance between sleeping sites and the last or first feeding trees (Albert *et al.,* 2011). After the monkeys entered a sleeping site, we recorded the sleeping place of an individual in the tree as tree trunk, bough (the major branch that occurs between the trunk and a branch of a tree), branches (≤10 cm in diameter), bamboo stem, bamboo branches, liana, or others. We also recorded their sleeping posture and behavior as sitting (sleeping alone), social huddling (close aggregation of two or more monkeys), and lying (Albert *et al.,* 2011; Fan & Jiang, 2008). Sunrise and sunset times were determined from GPSMap 62s.

Characteristics of Sleeping Sites and Trees

At each sleeping site, we recorded the GPS location at its center, and dominant habitat type within a circular plot of 20 m radius from its center. We recorded habitat types as mixed-bamboo forest, tree-dominated forest, shrubland, cultivated land, or grazing land (Mekonnen *et al.,* 2017) (ESM Table SI). We recorded the GPS location, species, and physical characteristics of each sleeping tree (Albert *et al.,* 2011; Fan & Jiang, 2008; Phoonjampa *et al.,* 2010; Seiler *et al.,* 2013) once the monkeys vacated it in the morning (Table II). When this was not possible, the sleeping trees were marked, and we returned on subsequent days. We measured tree height using the direct reading

Table II Characteristics of sleeping trees and places and descriptions used in this study at Kokosa forest fragment in southern Ethiopia, February–July 2014

Characteristics	Description (unit)
Diameter at breast height (DBH)	Measured using a measuring tape (cm)
Tree height (height)	The height of the sleeping tree or bamboo measured using a Range finder (m)
Crown diameter	The mean diameter of two horizontal measurements taken from the edge of the largest branches of a sleeping tree crown both east–west and north–south (m)
Height of the sleeping place of a monkey in a tree	Measured using a rangefinder (m)
Coverage of lianas on the sleeping tree	Recorded on a scale of 0–4; 0 = no liana coverage, 1 = <25% coverage, 2 = 26%–50% coverage, 3 = 51%–75% coverage, and 4 = >75% coverage
Relative height of each sleeping tree compared with that of surrounding trees	Recorded as emergent (when the tree canopy was higher than its neighboring trees), equal (if the tree canopy was of the same height as the neighboring trees, or lower (if the tree canopy was lower than the neighboring trees)
Foliage density from the sleeping place of a monkey to the sky	Recorded on a scale of 0–4; 0 = clear visibility with no leaf coverage, 1 = high visibility (1%–25% leaf coverage), 2 = medium visibility (26%–50% leaf coverage), 3 = low visibility (51%–75% leaf coverage), and 4 = no visibility (76%–100% leaf coverage)
Foliage density from the sleeping place of a monkey to the ground	Same as above.

feature on a Nikon Forestry 550 Laser Rangefinder. We used a measuring tape or Nikon Forestry 550 Laser Rangefinder to measure horizontal distances.

Data Analysis

We tested data for homogeneity of variances and normality using the Levene and Shapiro-Wilk tests, respectively. When data were normally distributed, we used parametric tests, and when they were not, we used nonparametric tests. When necessary, we log-transformed tree height, DBH, and crown diameter data to fit the assumptions of normality.

We used the vegetation data collected in the home range of Bale monkeys from previous behavioral ecology studies (Mekonnen *et al.,* 2017). To assess habitat-wide species composition, tree height (m), DBH (cm), and crown diameter (m), we used data from 185 large trees (≥10 cm DBH) sampled in twenty-seven 50 m × 10 m vegetation plots placed along three randomly established transects. We also used previous data on the stem density (≥2 m tall), DBH (cm), height (m), and crown diameter (m) of bamboo sampled from 14 randomly selected vegetation plots (Mekonnen *et al.,* 2017).

To test whether Bale monkeys chose larger trees for sleeping than the size of mean trees available in their range, we compared the mean height, DBH, and crown diameter of tree species used for sleeping with those of the corresponding available tree species using Student's *t*-test. To assess whether Bale monkeys prefer specific tree species for sleeping, we used the standardized resource selection index following a use-availability design, which is one of the most effective methods for measuring the preference of resources (Krebs, 1999; Manly *et al.,* 2002). We calculated sleeping tree species selection ratios by dividing the frequency of observed use (percentage of tree species used by Bale monkeys for sleeping) by the frequency of expected use (percentage availability/density of the same tree species in the home range of the group) (Krebs, 1999; Manly *et al.,* 2002). A selection ratio near 1 indicates no selectivity for that tree species, <1 indicates the tree species is avoided, and >1 indicates the tree species is selected (Krebs, 1999). We used a χ^2 test to compare nominal variables.

We estimated the distance from the last feeding tree of the day to the sleeping tree, and the distance from the sleeping tree to the first feeding tree of the next morning. We used the home range (95% KDE), core area (50% KDE), and habitat type shapefiles for the group over a 12-mo study period (Mekonnen *et al.,* 2017) to compare the distribution of sleeping sites within the core area vs. outside the core area (hereafter the periphery) and also within each habitat type. We calculated the density of sleeping sites per hectare by dividing the number of sleeping sites by the home range size. Further, to determine whether or not Bale monkeys preferred to sleep in the core area, we calculated sleeping site use ratios by dividing the frequency of observed use of sleeping nights (observed number of sleeping nights in core area vs. periphery) by the frequency of expected use of sleeping nights (expected number of sleeping nights in core area vs. periphery) (Krebs, 1999; Manly *et al.,* 2002). We calculated the expected number of sleeping night/site use values in the core area and in the periphery of their home range by multiplying the total number of sleeping nights/sites with the corresponding percentage representations of the core area (22.1% of the KDE home range) and periphery (77.9% of the home range) of their home range. Similarly, we calculated habitat selection ratios of each habitat by dividing the frequency of observed use

(number of sleeping sites used in each habitat type) by the frequency of expected use of sleeping sites with respect to % of home range area accounted for by each habitat type (Krebs, 1999; Manly *et al.,* 2002). A selection ratio near to 1 indicates no selectivity for an area, <1 indicates an area is avoided, and >1 indicates an area is selected (Krebs, 1999). We used chi-square goodness-of-fit tests (χ^2) to compare the observed vs. the expected frequencies of sleeping sites used in the core area vs. periphery of the home range. We also used a χ^2 test to examine the Bale monkeys' relative tendencies to sleep in huddles vs. alone. We conducted all statistical tests using R version 4.0.2 (R Development Core Team, 2020) with significance level set at $P \leq 0.05$.

Ethical Note

Permission to conduct this research was granted by the Ethiopian Wildlife Conservation Authority. This project also adhered to the legal requirements of Ethiopia and complied with the American Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates. The authors declare that they have no conflict of interest.

Data Availability The data sets summarized and analyzed for this study are available from the corresponding author on reasonable request.

Results

Characteristics of Sleeping Trees

Individuals slept in 264 trees and 34 bamboo stems; thus, the group used a mean of 7.1 ± SD 2.4 trees per night (range 3–17). Of these, 194 (65.1%) trees were used only once, while the remaining 104 (34.9%) trees were used two to four times. Fourteen different tree species and bamboo (*Arundinaria alpina*) were used for sleeping. *Maesa lanceolata* and *Cupressus lusitanica* were the first and second most frequently used sleeping plant species, accounting for 82 (27.5%) and 65 (21.8%) of sleeping plants, respectively. Bamboo, the Bale monkey's top dietary species, was the third most frequently used sleeping plant species accounting for 34 (11.4%) of the total.

Bale monkeys preferred some tree species over others for sleeping; that is, they disproportionately selected for some species relative to their availability in the home range. The top five species chosen in decreasing order of selectivity were *Cupressus lusitanica*, *Allophyllus abyssinicus*, *Maytenus obscura*, *Schefflera volkensii*, and *Ilex mitis* (Table III). Notably, bamboo was chosen as a sleeping substrate much less than expected relative to its availability. Sleeping trees did not have significantly larger DBH and crown diameter than the mean trees available. In fact, sleeping trees were shorter than other available trees (Table IV; ESM Fig. S1).

Sleeping Place Characteristics of Bale Monkeys

Bale monkeys slept at a mean height of 7.1 ± SD 1.95 m (range: 4–14 m; $N = 298$ records), while the mean height of sleeping trees was 9.6 ± SD 2.92 m. Bale monkeys

Table III Use, availability, and preference of sleeping trees (ST, N = 298) used by Bale monkeys (*Chlorocebus djamdjamensis*) compared to other available trees in the home range of our study group at Kokosa forest fragment, southern Ethiopia, February–July 2014

Species	Growth form	No. (%) of ST used	% of ST used	Height of sleeping place (m)	No. of trees available /ha[a]	% of available trees/ha[a]	Selection ratio (SR)	Selection status	SR rank
Maesa lanceolata	Tree	82	27.5	6.9 ± 1.5	153.12	4.52	6.08	Selected	8
Cupressus lusitanica	Tree	65	21.8	6.7 ± 1.3	14.29	0.42	51.90	Selected	1
Arundinaria alpina	Bamboo	34	11.4	7.0 ± 2.3	1341.43	39.59	0.29	Avoided	15
Galiniera saxifrage	Tree	29	9.7	6.6 ± 1.6	66.93	1.98	4.90	Selected	9
Maytenus obscura	Tree	25	8.4	6.1 ± 1.3	11.53	0.34	24.71	Selected	3
Canthium oligocarpum	Tree	19	6.4	6.9 ± 0.9	50.26	1.48	4.32	Selected	10
Ilex mitis	Tree	16	5.4	11.1 ± 2.9	21.80	0.64	8.44	Selected	5
Schefflera volkensii	Tree	15	5.0	8.6 ± 2.1	8.04	0.24	20.83	Selected	4
Allophyllus abyssinicus	Tree	7	2.3	7.7 ± 1.2	2.17	0.06	38.33	Selected	2
Bersama abyssinica	Tree	1	0.3	7.0	60.74	0.11	2.73	Selected	12
Croton macrostachyus	Tree	1	0.3	8.5	2.86	0.08	3.75	Selected	11
Erythrina brucei	Tree	1	0.3	9.6	1.43	0.04	7.50	Selected	6
Juniperus procera	Tree	1	0.3	7.0	1.48	0.04	7.50	Selected	6
Nuxia congesta	Tree	1	0.3	8.0	11.53	0.34	0.88	Avoided	14
Schefflera abyssinica	Tree	1	0.3	5.0	5.03	0.15	2.00	Selected	13

[a] Data extracted from Mekonnen et al. (2017)

Table IV Differences between sleeping trees and other available trees, showing mean ± standard deviation and statistical tests in the home range of our study group at Kokosa forest fragment, southern Ethiopia, February–July 2014

Variable	Sleeping trees ($N = 264$)	Available trees in the home range ($N = 185$)[a]	Test value	df	P value
DBH (cm)	25.50 ± 19.74	23.68±1.20	$t = -1.06$	df = 434.67	0.288
Height (m)	9.8 ± 2.91	11.1±0.42	t = 2.86	df = 251.66	**0.004**[b]
Diameter of the crown (m)	4.12 ± 1.41	3.93±0.12 m	t = -1.32	df = 366.45,	0.188

[a] Data extracted from Mekonnen *et al.* (2017).

[b] Bold stands for significance difference

slept more frequently in trees of low or medium height, rather than in emergent trees ($\chi^2 = 42.53$, df = 2, $P < 0.001$). Further, the monkeys frequently chose sleeping places with moderate to high foliage density or cover (26%–75%) relative to the section of the tree below ($\chi^2 = 59.1$, df = 4, $P < 0.001$) and above ($\chi^2 = 102.56$, df = 4, $P < 0.001$) the sleeping place of the individual (Table V).

Sleeping Time and Behavior at Sleeping Sites

The mean sunset and sunrise times were 18:36 h (range: 18:32–18:45 h) and 6:19 h (range: 6:07–6:39 hr, $N = 42$ days), respectively. The mean time Bale monkeys entered sleeping trees was at 18:23 h (range: 17:00–19:13 h, $N = 275$ individual records), 13 min before sunset (range: −38 to 94 min, $N = 275$). The monkeys exited sleeping

Table V Position of Bale monkeys in a tree and sleeping tree characteristics at Kokosa forest fragment, southern Ethiopia, February–July 2014 and statistical differences with their expected use by chance

Features	Sleeping tree use	% of sleeping tree use	Chi-square test	df	P values
Relative height of sleeping tree					
Emergent	68	22.9	42.53	2	<0.001
Equal	108	36.4			
Lower	121	40.7			
Foliage density from the sleeping place in the tree to the ground					
Zero	2	0.6	59.10	4	<0.001
One	38	12.2			
Two	103	33.1			
Three	132	42.4			
Four	36	11.6			
Foliage density from the sleeping place in the tree to the sky					
Zero	5	1.6	102.56	4	<0.001
One	22	7.1			
Two	139	44.7			
Three	139	44.7			
Four	6	1.9			

trees at a mean of 6:41 h (range: 5:56–7:58 h, $N = 365$), 22 min after sunrise (range: −38 to 101 min, $N = 275$). Bale monkeys spent a mean of 12 h and 10 min each day in sleeping trees (range 11:31–13:20 h, $N = 269$). Bale monkeys were typically almost silent when they moved to sleeping sites and trees. Adult males were usually the last individuals to enter and exit sleeping sites.

The group slept in their last feeding tree of the day 26% (11/42) of nights and fed in their sleeping trees the next morning 41% (16/42) of nights. The mean distance between the last feeding tree and the sleeping tree was 20.6 ± SD 14.72 m, and the mean distance between the sleeping tree and the first feeding tree of the next morning was 21.8 ± SD 18.54 m. When the monkeys changed to a new sleeping site, they usually moved to the new site a few hours before sunset, even crossing open fields by running and galloping. Once they arrived at a new sleeping site, they usually fed on the nearby trees until entering the final sleeping trees. Members of the group slept more frequently in social huddles than alone (huddling = 69.3% vs. sitting 30.7%; $N = 257$ records; $\chi^2 = 14.84$, df = 1, $P < 0.001$).

Characteristics and Spatial Distribution of the Sleeping Sites

The group reused 11 out of the 20 sleeping sites (on two to six nights each), accounting for 79% (33/42) of all nights. Of these, one sleeping site was used six times (14%) and two sleeping sites were used five (12%) times each. The remaining nine (21%) sleeping sites were used only once. The group used the same sleeping site on two consecutive nights on four occasions.

We estimated the sleeping site (SS) density to be 1.05 sleeping sites/ha. Sleeping sites occurred in the core area at a significantly greater rate than expected by chance (core area SS use = 29 sites (69%) vs. periphery SS use = 13 sites (31%), N = 42 sleeping sites; $\chi^2 = 53.79$, df = 1, $P < 0.001$, Fig. 1; Table VI). The group used mixed-bamboo forest, tree-dominated forest, and shrubland habitats for sleeping more than expected by chance (ESM Fig. S2, $\chi^2 = 42.98$, df = 4, $P < 0.001$; Table VI).

Discussion

In line with the predation avoidance hypothesis, during our study Bale monkeys often reused a few sleeping sites, a strategy that would increase their familiarity with the area and may enhance their chance of escape from predators. Although they selected sleeping trees that were lower than those available in the habitat, these trees had dense foliage, which may help conceal them from predators. These two strategies together, reusing several well-known sites and exhibiting a preference for leafy trees, may offer better protection against predation than using many sleeping sites, especially in a fragmented habitat with presumably low availability of suitable sleeping trees. Bale monkeys selected sleeping sites near the food sources they last used in the evening and first used the next morning. The monkeys also frequently spent the night in trees in which they had just fed. These results are consistent with the food access hypothesis, which holds that sleeping near to feeding trees facilitates feeding (Chapman, 1989; Teichroeb *et al.,* 2012). Further, Bale monkeys frequently huddled
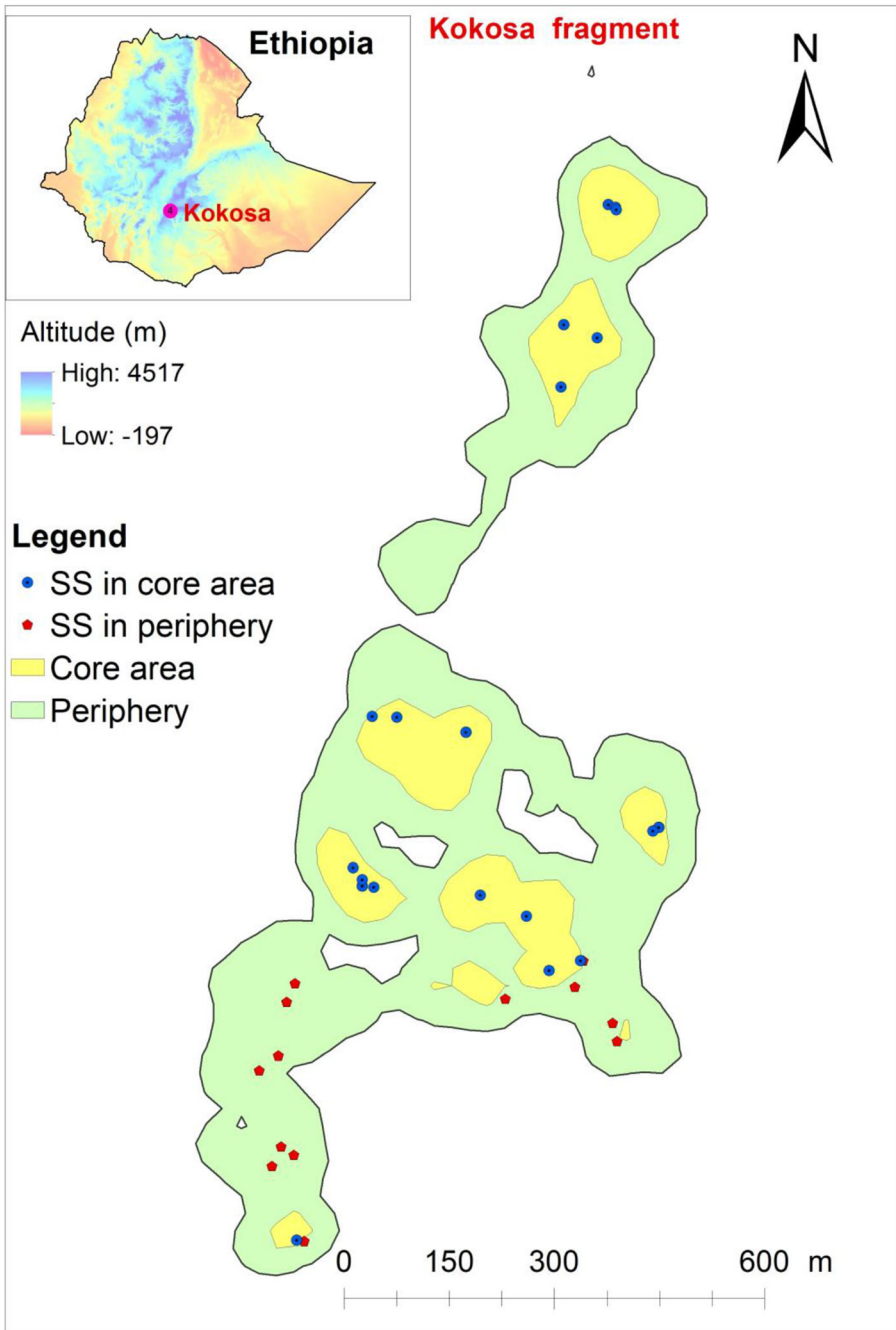
Fig. 1 Spatial distribution of sleeping sites (SS) in the core area and periphery in the 95% KDE home range of the Bale monkey group at Kokosa forest fragment in southern Ethiopia, February–July 2014.

together when they slept rather than sitting alone, suggesting that thermoregulation may also play a role in their selection of sleeping sites.

Table VI The periphery, core area, total area of available habitat types (ha) and their percentage representations within the 95% KDE home ranges of our group, observed use (observed number of sleeping site [SS] records), expected use (expected number of SS), and the calculated selection ratio of each habitat at Kokosa forest fragment, southern Ethiopia, February–July 2014

Periphery/core area	Area (ha)[a]	Area (%)[a]	Observed SS use	Expected SS use	Selection ratio	Selection status
Periphery	31.1	77.9	13	32.7	0.40	Avoided
Core area	8.8	22.1	29	9.3	3.12	Selected
Habitat types						
Mixed-bamboo forest	6.82	17.08	18	7.17	2.51	Selected
Tree-dominated forest	3.18	7.96	8	3.34	2.40	Selected
Shrubland	11.80	29.54	16	12.41	1.29	Selected
Cultivated land	2.99	7.49	0	3.15	0.00	Avoided
Grazing land	15.15	37.93	0	15.93	0.00	Avoided

[a] Data from Mekonnen *et al.* (2017)

Bale monkeys entered sleeping trees shortly before sunset (mean = 13 min) and exited shortly after sunrise (mean = 22 min), suggesting that safety from predators is a prime concern. Bale monkeys also often reused sleeping sites. This strategy increases their familiarity with the area, which may enhance their chance of escaping attacks by spotted hyenas and other nocturnal predators before the monkeys reach the safety of the sleeping tree (Albert *et al.,* 2011; Di Bitetti *et al.,* 2000). The reuse of familiar sleeping sites, and use of sleeping places with dense foliage above and below, are consistent with Bale monkey sleeping choice reflecting an antipredator strategy (Albert *et al.,* 2011; Fei *et al.,* 2012).

Our results showed that Bale monkeys selected some sleeping tree species over others and sometimes used bamboo to sleep in (Table III). Primates select sleeping tree species with architectural characteristics that provide enough support and comfort for individuals and offer greater protection from their potential predators (Brividoro *et al.,* 2019; Samson & Hunt, 2014; Velazquez-Vazquez *et al.,* 2015). We had not anticipated bamboo to be a candidate species for sleeping by Bale monkeys because it belongs to the grass (Poaceae) family and typically has a small DBH that does not provide much support, particularly for larger individuals. Nevertheless, the monkeys sometimes used bamboo to sleep in. To ensure the long-term survival of Bale monkeys, we suggest that the tree species that they selected as sleeping trees could be used as candidate species for forest restoration, along with bamboo and other important plant food species (Mekonnen, Fashing, Bekele, *et al.,* 2018a).

Hyenas and birds of prey are still present at our study site and the Bale monkeys' selection of appropriate sleeping trees and places may reflect a tradeoff strategy to avoid both types of predators. That is, the monkeys may be selecting sleeping trees tall enough to avoid terrestrial predators but lower than available trees in the habitat and not emergent to avoid birds of prey. In addition, selecting sleeping places in a tree with dense foliage above and below may help to conceal them both, from hyenas below and

from the predatory birds above. Within fragments (with the loss of predators such as large felids), there is potentially a lower predation pressure (Gazagne *et al.,* 2020; Yorzinski & Ziegler, 2007). However, adaptation to low predation pressure may require time (several generations) before it is evident. This may be why individuals inhabiting degraded habitats still select sleeping trees with characteristics that may serve an antipredator function (Gazagne *et al.,* 2020). Primates inhabiting such forest fragments could still choose sleeping trees that could fulfill some specific predation avoidance criteria (Table V). These sleeping trees offer appropriate protection against potential predators (such as dogs, humans, and hyenas) still present in the fragment (Albert *et al.,* 2011; Gazagne *et al.,* 2020).

The accessibility of food influences sleeping site selection in primates living in degraded and fragmented forests due to the lower availability and patchiness of food resources (e.g., northern pigtailed macaques [*Macaca leonina*: Gazagne *et al.,* 2020], long-tailed macaques [*Macaca fascicularis*: Brotcorne *et al.,* 2014], and François' langurs [*Trachypithecus francoisi*: Wang *et al.,* 2011]). Indeed, Bale monkeys avoid use of cultivated land for sleeping primarily because of intense negative human–Bale monkey interaction in response to their crop feeding behavior (Mekonnen *et al.,* 2020). Bale monkeys depend on bamboo and are most likely to select sleeping sites near to or inside mixed-bamboo patches to minimize travel costs, supporting the food access hypothesis (Mekonnen *et al.,* 2017). Bale monkeys preferred to sleep in their core area, which had greater availability of potential food tree species and bamboo than the periphery of their home range (Mekonnen et al., 2017; Mekonnen, Fashing, Bekele, *et al.,* 2018a). In addition to having more resources within than outside core areas, Bale monkeys could be selecting core areas to sleep to avoid anthropogenic disturbances, which frequently are higher on the edges of forest fragments than within core areas (Bersacola *et al.,* 2021; Willems & Hill, 2009). Similar trends have been found in other primate species inhabiting forest fragments (e.g., diademed sifakas [*Propithecus diadema*: Irwin, 2008], long-tailed macaques [*Macaca Fascicularis*: Brotcorne *et al.,* 2014], and spider monkeys [*Ateles geoffroyi*: Velazquez-Vazquez *et al.,* 2015]).

The Bale monkeys' selection of sleeping places with dense foliage above and below may also offer some buffer against the cold nights that are characteristic of the Ethiopian Highlands (Hillman, 1986). Social huddling at sleeping trees may be an additional strategy used by Bale monkeys to cope with cold weather, supporting the thermoregulation hypothesis. Black crested gibbons (*Nomascus concolor*), Skywalker hoolock gibbons (*Hoolock tianxing*), and Japanese macaques (*Macaca fuscata*) often huddle when it is cold (Fan & Jiang, 2008; Fei *et al.,* 2019) and that huddling reduces energy loss and increases body temperature (Hanya *et al.,* 2007). In fact, a study of southern bamboo lemurs (*Hapalemur meridionalis*) inhabiting a degraded fragment with a few remaining large trees in Madagascar showed that social huddling is more important than sleeping or resting place selection within trees to cope with environmental variables such as rainfall, wind, and cold air (Eppley *et al.,* 2017).

In conclusion, our results are consistent with all three hypotheses since Bale monkey sleeping site and tree selection were associated with the location of food resources as well as with strategies to avoid predation and to enhance thermoregulation. We found that sleeping sites and trees were strategically located near food sources, which may reduce energy expenditure and increase access to food. Bale monkeys often reused several sleeping sites, a strategy that increases their familiarity with the area and that

may increase their chance of escape in case of predator attacks. They also selected sleeping trees tall enough and with enough dense foliage to help conceal them from predators. Further, Bale monkeys more frequently huddled together than sat alone, suggesting that thermoregulation plays a key role in keeping their body temperature warm to conserve energy in response to the cold weather characteristic of the southern montane forests of Ethiopia.

Author Contributions AM, PJF, NCS, and RAHA conceived and designed the study. AM conducted the fieldwork and analyzed the data. AM, PJF, VVV, CAC, NCS, and RAHA wrote the manuscript.

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