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Habitat Use by White-thighed Colobus in the Kikélé Sacred Forest: Activity Budget, Feeding Ecology and Selection of Sleeping Trees

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Abstract: Understanding habitat preference and use is an important aspect of primate ecology, and is essential for setting conservation strategies. This study examined the activity budget, feeding ecology and selection of sleeping trees of a population of white-thighed colobus (*Colobus vellerosus*). A group of 18 was followed during 72 days over a full annual cycle in the Kikélé Sacred Forest of the Bassila administrative region in central Benin (West Africa). Activity budget and diet were determined using scan sampling. The structure of the habitat and the physical characteristics of sleeping trees were determined using plot surveys. Resting, feeding, moving, social interactions and other activities accounted for 56.6%, 26.3%, 13.0%, 3.3%, and 0.7% of the activity budget, respectively. The group spent more time feeding and less time moving in the dry season compared to the rainy season. The diet was composed of 35 plant species belonging to 16 families, with items including leaves, fruits, seeds, buds, bark, flowers, gum, and inflorescences. Only three tree species were used as sleeping trees: *Celtis integrifolia*, *Cola cordifolia*, and *Holoptelea grandis*. Our findings suggest that the monkeys prefer tall (22.53 ± SD 3.76 m) and large-trunked (112.07 ± SD 14.23 cm) sleeping trees. The results of this study can be used for sound management of the white-thighed colobus in the study area and elsewhere.

Key Words: activity budget, feeding ecology, sleeping trees, *Colobus vellerosus*, conservation, West Africa

Introduction

Crucial components of an animal's habitat are the provision of food and resting sites that are safe from predators (Gautier-Hion *et al.* 1983). Activity budgets are reliable indicators of the coping strategies of primates in their environment, and are often related to the ways animals conserve energy (Milton 1998). Activity budgets are influenced by factors such as group size and habitat quality (Teichroeb *et al.* 2003; Wong *et al.* 2006). With their folivorous diet, colobines tend to reduce energy expenditure by spending long periods of time resting (Irwin 2008a, 2008b; Korstjens *et al.* 2010). As leaves are superabundant and widely dispersed, it is supposed that folivorous primates such as colobines do not experience intra-group scramble competition for food (for example, *Colobus guereza*: Fashing 2001; *Procolobus rufomitratus*: Snaith 2008; *Colobus vellerosus*: Saj and Sicotte 2007; Teichroeb and Sicotte 2009). This has also been found in Asian colobines (Yeager and Kirkpatrick 1998; Yeager and Kool 2000). For this reason colobine monkeys would be expected to form large groups, which is not always the case. This is the "folivore paradox" (Steenbeek and van Schaik 2001; Snaith 2008).

The colobine diet varies in species composition with the food resources available and the floristic composition of their habitats. Colobine monkeys also eat fruits and other plant parts besides leaves (for example, *Procolobus verus*: Oates 1988, Davies *et al.* 1999; *Colobus polykomos*: Dasilva 1994, Davies *et al.* 1999; *Procolobus badius*: Davies *et al.* 1999; *Colobus vellerosus*: Teichroeb *et al.* 2003).

Sleeping sites (nests of leaves, holes in trees, or the branches of trees) are night refuges for diurnal animals, and affect habitat use. The study of sleeping sites, therefore, may help to understand some aspects of their behavior. The choice of sleeping sites by animals is influenced by predation avoidance and access to food (Albert *et al.* 2011; Holmes *et al.* 2011; Teichroeb *et al.* 2012), thermoregulation (Fan and Jiang 2008), and social factors (Anderson 1998). The white-thighed colobus (*Colobus vellerosus*) is endemic to West Africa and is listed as Vulnerable on the IUCN Red List (Oates *et al.* 2008). Despite conservation efforts in Côte d'Ivoire, which covers a significant part of its range, the conservation status of *C. vellerosus* is deteriorating, and the species may now be Endangered (Gonedelé Bi *et al.* 2010). Most of the behavioral studies on *C. vellerosus* have been conducted in Ghana. According to Wong *et al.* (2006), its diet is dominated by leaves (79%), but also comprise fruits (10.7%), flowers and buds (6%), seedpods (4%) and sap (0.3%). Wong and Sicotte (2007) found that the activity budget of *C. vellerosus* comprises 22.0% feeding, 68.6% resting, 6.8% moving, and 2.6% social activities, and is influenced by group size and group composition as well as food availability (Teichroeb *et al.* 2003).

Habitat types, plant communities and seasonal variation in resource availability influence diet composition. In Benin, *C. vellerosus* is restricted to the Guineo-congolese zone and Guineo-sudanian zone (Djègo-Djossou and Sinsin 2009). The species is legally protected in forest reserves (Djègo-Djossou, 2013) whereas in the Kikélé Sacred Forest its protection is based on traditional beliefs (Djègo-Djossou *et al.* 2012). The studies mentioned above were conducted in typical Guinea-Congo semi-deciduous forests, and here we report for the first time on the activity budget, food resources and dietary composition, as well as the physical characteristics of the trees selected as sleeping sites, of *C. vellerosus* in a dry forest in the Kikélé Sacred Forest.

Methods

Study site

The Kikélé Sacred Forest (13 ha) is in the Bassila administrative region near the village of Kikélé in central Benin, West Africa (Fig. 1). This forest is occupied by a single, multi-male/multi-female group of *Colobus vellerosus* of 18 individuals that has been protected by traditional beliefs for decades (Djègo-Djossou *et al.* 2012). The Sacred Forest is extended by a gallery forest that surrounds the entire village and is fragmented by agricultural clearings and access roads.

The climate of Kikélé is of the Sudanian dry type, characterized by a dry season from mid-October to mid-April, alternating with a rainy season from mid-April to mid-October. Although the climate is dry, yearly rainfall (1300 mm) is higher compared to other regions in Benin (950–1200 mm). The vegetation of this Sacred Forest contains tall trees that are typical of semi-deciduous forests. There are several vegetation types: dense forest, woodland, and savanna. The most common species in this region are similar to those of the Boabeng-Fiema Monkey Sanctuary, Ghana. They include *Cola gigantea* (Sterculiaceae), *Celtis zenkeri* and *C. toka* (Ulmaceae), *Antiaris toxicaria* (Moraceae), *Holoptelea grandis* (Ulmaceae), *Erythrophleum suaveolens* (Leguminosae - Caesalpinioideae), and *Khaya grandifoliola* (Meliaceae) (Adomou 2005). Besides *C. vellerosus*, the mammal fauna of the Kikélé Sacred Forest comprises a few individuals of *Cercopithecus mona* and various rodents, including the rare Beecroft's flying squirrel *Anomalurus beecrofti*.

Data collection: Activity budget and food resources

Data were collected using instantaneous scan sampling (Altmann 1974) during an annual cycle from February 2010 to January 2011. In optimal conditions, the scans were made every 30 minutes from 6:30 am to 6:30−7:00 pm when the monkeys would retire to a sleeping tree. Observations were made twice a month during three consecutive days with an interval of at least seven days between each observation period. During each scan, data were registered for five minutes on the first five adult or sub-adult monkeys seen clearly (Arroyo-Rodriguez *et al.* 2007). A total of 1,772 scans were made over 886 hours of observations. Activities recorded were grouped into five categories: social interactions, resting, moving, feeding and other (auto-grooming, vocalization, scratching, urination). When feeding, the plant species and parts eaten were recorded.

Data collection: Habitat characteristics

Vegetation structure was determined in two forest patches—Patch 1 in the Kikélé Sacred Forest and Patch 2 a connected gallery forest—through plot surveys following Braun-Blanquet (1932). Patch 2 was visited by the monkeys only occasionally. A total of 16 plots were set up at random in

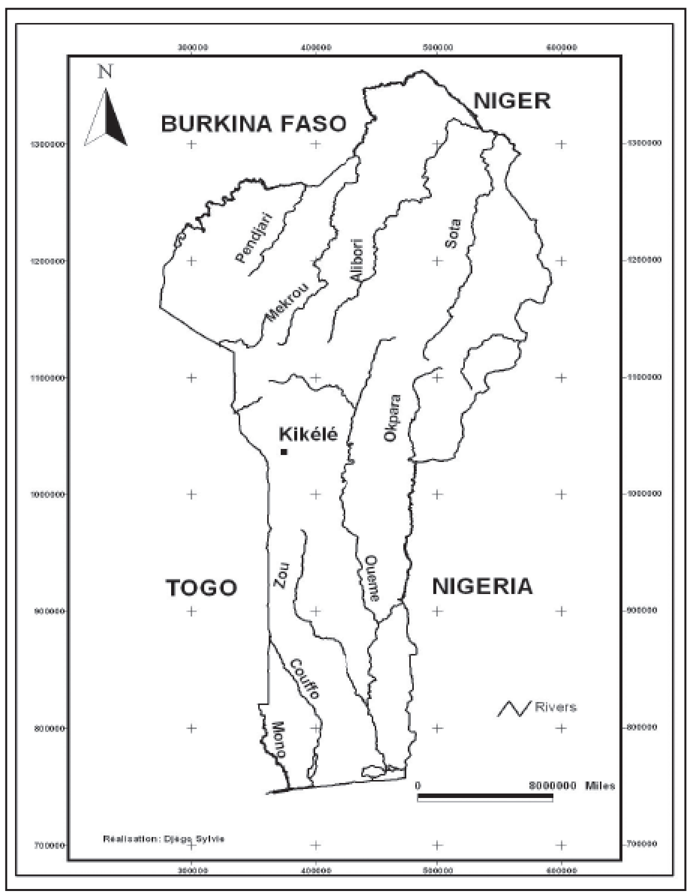

Figure 1. Map of the study site showing the location of the Kikélé Sacred Forest, Benin.

four locations over the home range of the *C. vellerosus* group: 10 square plots of 30 × 30 m in Patch 1 (six in the dense forest, two in the woodland, and two in the savanna); and six rectangular plots of 25 × 20 m in Patch 2 (gallery forest). Plants with a diameter at breast height (DBH) of 10 cm or more were identified in each plot (Chapman *et al.* 1992). The height and the location of each sleeping tree were also recorded.

Data analysis: Activity budget, diet and foods resources

The time spent on each activity was estimated indirectly by calculating the percentage between the number of records of the activity and the total number of records. Data were computed using Statistica 10.0 and the significance level was set for analyses $\alpha = 0.05$. The three-day observation period is the unit of analysis (N = 24). An analysis of variance was performed to compare the times spent in each activity in the dry season and the wet season. The proportions of the items consumed were estimated indirectly by calculating the percentage of feeding records for each item against the total number of feeding records records.

Data analysis: habitat structure and computation of ecological indexes

Three indices were computed to assess the habitats occupied by the colobus monkeys. The Shannon-Wiener Index of Diversity was used to estimate plant species diversity. Sorensen's Coefficient (S) was calculated to compare similarity between the two forest patches: S = 2C/A+B, where C is the number of species shared in both patches; A and B the number of species specific to each patch. If $S \leq 0.5$ the communities compared are dissimilar; if $S > 0.5$, the communities compared are similar. The Evenness Index of Pielou was used to examine how evenly the species recorded are represented in each habitat.

We also calculated the patch attendance rate through the ratio between the number of days where the colobus used Patch 1 and/or Patch 2, and the total number of observation days. We calculated the average diameter and height of sleeping trees and all the trees in each plot.

Results

Activity budgets

The time the *C. vellerosus* group spent resting was more than twice the time it spent feeding (56.6% vs. 26.3%), and more than four times the time allocated to moving (56.6% vs. 13.0%) (Fig. 2). Social interactions and other activities accounted for only 3.3% and 0.7% of the activity budget, respectively.

Activity budgets varied seasonally and monthly (Fig. 3). Seasonal fluctuations in feeding (df = 23, F = 5.02, p = 0.03) and moving (df = 23, F = 12.6, p = 0.01) were statistically significant, while those for resting, social interactions and other activities showed no difference (df = 23, F<4.28 and p >0.05 in each case). Regardless of the month, the time spent on resting was always more than 50% of the total activities.

Daily activity pattern

The monkeys were very active in the early morning; activities were dominated by moving and feeding. Activities could be broadly categorized into three periods: (i) in the morning, between 7:00 am and 10:00 am; (ii) in the afternoon, between 12:00 am and 2:00 pm, activities were dominated by resting and social interactions (grooming, physical contacts, playing, and scratching); whereas (iii) in the afternoon and early evening, between 3:30 pm and 5:30 pm, feeding, moving and social were the predominant activities. The large majority of social interactions were affiliative (94% were grooming and playing).

Habitat characteristics

Sixty species of 28 families were recorded in Patches 1 and 2. Most of the trees were of the families Moraceae (18% of the species) and Leguminosae (13%). Although the number

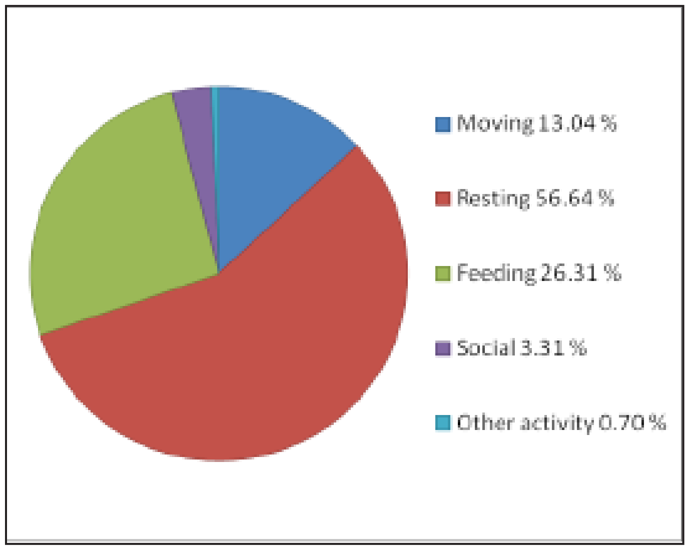

Figure 2. Activity budget of *Colobus vellerosus* in the Kikélé Sacred Forest, Benin.

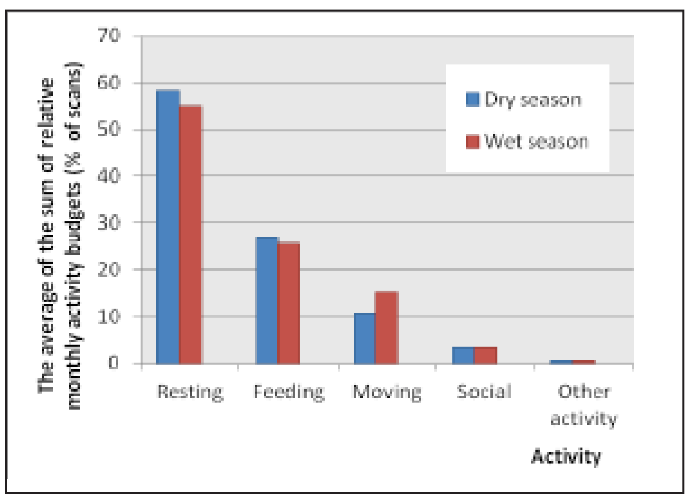

Figure 3. Seasonal variations in the activity budget of *Colobus vellerosus* in the Kikélé Sacred Forest, Benin.

of food plants was similar in the two patches, the monkey troop used the forest of Patch 1 every day and entered the gallery forest of Patch 2 on only 57% of the days. Sorensen's Index (0.33) showed a significant difference between the patches. The Evenness Index of Pielou had similar value for both patches (0.97) indicating an even distribution of recorded species (Table 1). The Shannon-Wiener Index of Diversity was also high in both patches, with its value being slightly higher in Patch 2 (H = 5.19) than in Patch 1 (H = 4.87) (Table 1).

Food plants and items consumed

The colobus monkeys ate 60 items; 59 plant parts (leaves 53.1%, fruits 33.3%, seeds 2.5%, stems 1.3%, bark 1.4%, buds 3.1%, flowers 2.45%, and petioles 2.8%) and one prey (ants). The plant parts came from 35 species belonging to 16 families (Table 2). The best represented families in the diet were the Leguminosae (29% of species) and Moraceae (23%). Leaves and fruits contributed more than 90% of the diet (Fig. 4).

Characteristics of sleeping trees

Over 72 nights, *C. vellerosus* used 13 trees of three species as sleeping sites in Patch 1. The species were *Celtis integrifolia*, *Cola cordifolia*, and *Holoptelea grandis*. The troop's favorite species was *C. integrifolia*; six trees (DBH = 90–125 cm) were used on 86% of the 72 nights. Five *H. grandis* (DBH = 100–135 cm) were used on 10%, and two *C. cordifolia* trees (DBH =110–120 cm) were used on 4%. The frequency of use of different trees in each species varied. Two *Celtis integrifolia* trees were used more than the other four individuals. The average diameter at breast height (DBH) and mean height of the 13 sleeping trees were 112.07 ± SD 14.23 cm and 22.53 ± SD 13.76 m, respectively, while the averages for all trees measured were 53.72 ± SD 38.26 cm for mean DBH, and 17.23 ± SD 9.81 m for mean height. Of note is that a sleeping tree could be used for several consecutive nights. One sleeping tree was used for two consecutive nights on twelve occasions, three consecutive nights on two occasions, and once for four consecutive nights.

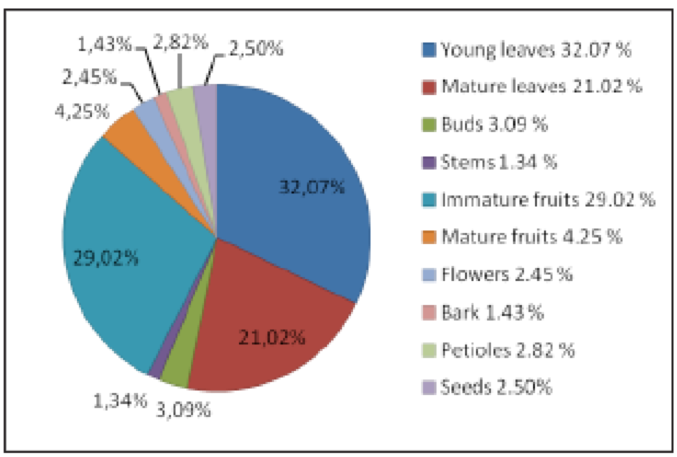

Figure 4. Annual diet of *Colobus vellerosus* in the Kikélé Sacred Forest, Benin.

Discussion

Activity budget

Colobus vellerosus of the Kikélé Sacred Forest showed an activity pattern similar to that of most colobines, with time spent on resting much greater than that spent on feeding. Table 3 shows the activity budgets of several species of black-and-white colobus monkeys and that of *C. vellerosus* in the Kikélé Sacred Forest recorded in this study. With the exception of *Colobus guereza* in Ituri, Democratic Republic of Congo, and *C. angolensis ruwenzorii* in Nyungwe, Rwanda, with 44% and 32% of the time spent on resting, respectively, all studies show that black-and-white colobus monkeys spend more than 50% of the time resting. Long resting time among colobines has been explained in a number of ways. Some authors have linked it to the need to ferment leaves for their digestion or to the quality of the habitat (Marsh 1981; Oates 1988; Korsjtens *et al.* 2010). It has also been considered a strategy of behavioral thermoregulation for *Colobus polykomos*, as it may limit energy losses (Dasilva 1992, 1994).

Differences in group activity budgets may be explained by differences in group size as social activities are more frequent in larger troops (Teichroeb *et al.* 2003), as well as by other factors such as predation risk, the social structure of troops, seasonality, and the availability and distribution of food resources (Kinnaird and O'Brien 2000). The time that *C. vellerosus* spent resting in Kikélé Sacred Forest was lower than that recorded for the same species in Ghana. This could be explained by the small size of the Kikélé group and the relatively poor quality of the habitat (Wong and Sicotte 2007). Our results contrast with the theory that indicates that time

Table 1. Habitat characteristics in the Kikélé Sacred Forest, Benin.

Designation	Habitat	Area (ha)	Floristic diversity	Potential food plants (% of spp.)	Shannon Wiener Index	Pielou Evenness Index
Patch 1 (Sacred Forest)	Dense forest	6.38	40	51%	4.87	0.97
	Woodland	2.10	16	44%	3,52	0,72
	Savanna	3.56	26	27%	3,11	0,55
Patch 2	Gallery forest	6.25	32	50%	5.19	0.97

spent resting increases when it is hotter (Chaves *et al.* 2011). We found no difference in time spent resting by colobus in dry and rainy seasons. This is probably a consequence of the degraded habitat; Kikélé Sacred Forest is a small fragmented forest.

Feeding

Fifty eight percent of the plant species occurring in the study area contribute to the diet of *Colobus vellerosus*. Our findings are congruent with previous works that suggest that the Leguminosae provides the main food sources for colobus monkeys (Davies *et al.* 1988). Consumption of *Erythrophleum suaveolens* leaves by *C. vellerosus* was also confirmed despite their toxicity (see Kay and Davies 1994).

Feeding generally ranks after resting in the activity budget of colobines, unlike other primates where feeding is the primary activity (for example, *Cercopithecus ascanius*: Cords 1987; *Lagothrix lagothricha*: Defler 1996). The diet of the *C. vellerosus* group was dominated by leaves, as has been reported elsewhere for this species. However, when compared to other sites, leaves are much less dominant (i.e., 53% vs. 74% in Ghana, Saj *et al.* 2005; Tan 2006; Wong *et al.* 2006). Foods such as fruits, seeds and ants also seem to be important components. This could result either from a locally higher diversity of food resources or a shortage in the preferred food (i.e., leaves); leading to exploration and inclusion of alternative foods in the diet.

Sleeping sites and their characteristics

The monkeys of the Kikélé Sacred Forest chose the Patch 1 forest for their sleeping sites and never slept in Patch 2, the gallery forest. This may be an anti-predation strategy because gallery forest used to be exploited by people from the surrounding villages (i.e., Manigri, Bassila), and colobus monkeys were hunted there over many years. Although there is currently no hunting in the Kikélé Sacred Forest, this finding

Table 2. Food plants consumed by Colobus vellerosus in the Kikélé Sacred Forest, Benin.

Scientific name	Common name (Nagot)	Family	Food item[1]
Afzelia africana	Akpaka	Leguminosae - Caesalpinioideae	UFr
Albizia zygia	Itikpalala	Leguminosae-Mimosoideae	L, UFr, B, Ba
Anarcadium occidentale	Amê gnibo	Anacardiaceae	Fl
Anogeissus leiocarpa	Koloo	Combretaceae	ML
Azadirachta indica	Lili	Meliaceae	YL, ML, Re, St
Cassia sp.	Agbélékokpayan	Leguminosae - Caesalpinioideae	YL
Caesalpinia pulcherrima		Leguminosae - Caesalpinioideae	UFr, F
Ceiba pentandra	Araba	Malvaceae-Bombacoideae	YL
Celtis integrifolia	Afoufè	Ulmaceae	YL, MF, UFr
Cola cordifolia	Kpoé	Sterculiaceae	UFr, Lai,P,B
Cynometra vogelii		Leguminosae-Caesalpinioideae	MF, UFr, S
Daniellia oliveri	Iya	Leguminosae-Caesalpinioideae	UFr
Diospyros mespiliformis	Don'ko	Ebeneceae	Fr
Erythrophleum suaveolens	Ayinyin	Leguminosae - Caesalpinioideae	Fr, UFr
Ficus capensis	Adan Abo	Moraceae	UFr, YL
Ficus congensis	Kpolidi	Moraceae	UFr, YL
Ficus exasperata	Oupi	Moraceae	UFr, YL
Ficus ingens		Moraceae	UFr, YL
Ficus platiphylla		Moraceae	UFr, YL
Ficus polita		Moraceae	UFr
Ficus sycomorus		Moraceae	UFr
Ficus thonningii	Okpoto	Moraceae	YL
Holoptelea grandis	Kpakokpako	Ulmaceae	YL, UFr, B
Khaya senegalensis	Agao	Meliaceae	YL, UFr
Lonchocarpus cyanensens	Elou	Leguminosae - Papilionoideae	Fr
Luffa aethiopica		Curcubitaceae	UFr, L
Mimusops multinervis		Sapotaceae	Fr
Sarcocephalus latifolius	Ewé oïkikoro	Rubiaceae	L
Newbouldia leavis		Bignoniaceae	L
Parinari curratelifolia	Imèdou	Chrysobalanaceae	L
Parkia biglobosa	Igba	Leguminosae - Mimosoideae	Fl
Parquetima nigrescens		Asclepiadaceae	L
Pterocarpus erinaceus	Akpékpé	Leguminosae - Papilionoideae	YL
Strophantus sarmentosus		Apocynaceae	UFr, S, L
Tapinanthus voltensis	Afoman	Loranthaceae	UFr, L

[1]Legend: YL= young leaves; ML= matures leaves; L= leaves; UFr = Unripe fruit; R= resin; Fl= flowers; B= buds; S=seeds; Ba= bark; St= Stem; P= petiole.

Table 3. Comparison of the activity budget of the white-thighed colobus, Colobus vellerosus, at Kikélé with those of other Colobus species.

Species	Group size	Rest	Feed	Move %	Social %	Source
Colobus vellerosus						
Fragments surrounding Boabeng-Fiema	31–33	60	24	12	4	Teichroeb *et al.* (2003)
	15–16	58	23	17	2	
	7–8	59	24	15	2	
Fragments surrounding Boabeng-Fiema	8, 16, 17	68	22	7	3	Wong and Sicotte (2007)
Kikélé, Benin	13–18	56.64	26.31	13.04	3.13	This study
Colobus polykomos						
Tiwaï, Sierra Leone	9–11	55	31	12	2	Dasilva (1992)
Parc National de Taï, Ivory Coast	14	58	25	16	1	Bitty (unpubl. data)
	11–12	54	21	25	0	
	16	70	11	15	4	
Colobus guereza						
Kibalé, Uganda	9	57	20	5	11	Oates (1977)
Ituri, RDC	8–10	44	26	24	5	Bocian (1997)
Kakamega, Kenya	10–13	63	28	2	6	Fashing (2001)
Colobus angolensis ruwenzorii						
Ituri (RDC)	19–20	52	19	22	5	Bocian (1997)
Nyungwe, Rwanda	>300	32	42	20	5	Fashing *et al.* (2007)
Colobus angolensis palliatus						
Mbuyu Tundu, Kenya	5–6	64	22	3	4	Wijtten *et al*. (2012)
Colobus satanas						
Douala-Edea,Cameroun	13–17	54	23	4	13	McKey and Waterman (1982)

may support the hypothesis of predator avoidance in the selection of sleeping sites, as indicated in studies of other primates (for example, *Saguinus mystax* and *S. fuscicollis*: Heymann 1995; *Macaca leonina*: Albert *et al.* 2011) and for *C. vellerosus* by Teichroeb *et al.* (2012). Although there is no predation, in Patch 1 the colobus monkeys chose sleeping trees to rest. Predator avoidance behaviors could also be associated with hunting in the vicinity of the study area, as mentioned above. However, other factors such as reducing time and energy needed for foraging could also determine sleeping tree selection (Anderson 1998).

The physical characteristics of the sleeping sites also support the idea that *C. vellerosus* at Kikélé selects sleeping sites to avoid predators. The sleeping trees were generally the largest and tallest trees, undoubtedly reducing the chances of predators climbing them. Some large and tall trees, however, were not used as sleeping sites. This was the case for a *Ficus* sp., *Albizia zygia*, and *Blighia sapida* (Sapindaceae); the first two being food species for the colobus monkeys. Selection of sleeping trees is probably also linked to other physical characteristics of the trees. *Celtis integrifolia* was the species the monkeys slept in most. Compared to the other trees, *Celtis integrifolia* has very rigid stems and its branches are well spread, which allows for a better distribution of colobus monkeys through the crown and, it could well be more comfortable. However, the monkeys seemed to prefer certain individual trees of the same species despite their similar physical characteristics. This may be a question of habit, or may be linked to their position, which may, for example, allow for better views of their surroundings (Bovy 2010; Maslarov 2012).

Use of the same sleeping tree on consecutive nights may be due to the lack of predators. In high-risk environments, primates often avoid consecutive use of the same sleeping sites so as to reduce detection by predators (Li *et al.* 2006; Phoonjampa *et al.* 2010). The selection of sleeping trees appears to be a compromise between several factors—species, diameter and height, and location—and the preference of *C. vellerosus* for *C. integrifolia* in Kikélé may also be explained by the fact that it is also used for feeding and resting during the day, with monkeys spending up to eight hours a day on its branches.

Conservation

The white-thighed colobus formerly occurred over a relatively wide swath of West Africa, east of Côte d'Ivoire from between the Sassandra and Bandama rivers to western Nigeria. It occurs in a number of protected areas, but hunting (primarily) and habitat loss are now major threats. It is declining fast in Côte d'Ivoire, rare in Benin and Togo, possibly extinct in Nigeria, and heavily hunted in Ghana (Gonedelé Bi *et al.* 2010; Oates 2011). Ginn and Nekaris (2014) indicated that it may have been extirpated already from southern Burkina Faso. Its survival will be strongly dependent on small sanctuaries and forest reserves, such as those in Benin. The permanence of the single troop in the Kikélé Sacred Forest and the other small populations in forest patches and forest reserves will depend on careful management, which will demand a good understanding of their population dynamics and ecological needs with regard to food resources and sleeping sites. Our study suggests that *C. vellerosus* shows an activity pattern similar to most colobines elsewhere. However, its diet seemed to be more balanced between leaves and other items such as fruits, seeds, ants, buds, bark, flowers, gum, and inflorescences. The choice of sleeping trees indicates persistence of predation avoidance behaviors despite the absence of predators. As Oates (2011) pointed out, hunting for its meat and fur is the main threat, exacerbated by logging and forest destruction since the 1970s. As such, translocation, forest restoration and active meta-population management are predictably the necessary future steps for its conservation.

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