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Behaviour and Diet of *Colobus angolensis palliatus* Peters, 1868, in Relation to Seasonality in a Tanzanian Dry Coastal Forest

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Key Words

Colobus angolensis palliatus · Colobinae · Dry coastal forest · Tanzania · Dietary diversity · Seasonality · Behaviour

Abstract

Observational data from a 1-month study (November 1991) on a troop of Tanzanian black colobus, *Colobus angolensis palliatus* Peters, 1868, are presented. The troop inhabits an area of dry semi-evergreen forest in the eastern portion of the Gendagenda South Forest Reserve, Tanzania, which is subject to a bimodal seasonal climate. We show that during a period at the end of the dry season, the troop spent significantly more time feeding at the expense of resting, had a higher dietary diversity and ranged over a much greater area than during a period at the beginning of the wet season.

Introduction

There is a growing volume of knowledge on aspects of *Colobus* dietary and behavioural variation. Workers have concentrated on the red colobus, *C. badius rufomitratus* Peters, 1879 [1–3], and *C. badius tholloni* Milne-Edwards, 1886 [4], and on the black-and-white colobus, which includes four distinct species [5]. Three of these species have been studied in some detail; *C. guereza* Ruppell, 1835 [6–9], *C. satanas* Waterhouse, 1838 [10], and *C. polykomos* Zimmermann, 1780 [11–14]. The fourth species *C. angolensis* Sclater, 1860, has been the subject of a habitat use study in a Kenyan forest [15] and notes on feeding and behaviour have been recorded by Groves [16], mainly in the Usambara Mountains, north-eastern Tanzania. A more detailed study by Maisels et al. [4] investigated seed and leaf diets of *C. angolensis angolensis* in tropical rain forest on nutrient-poor soils of Salonga National Park,

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Zaire. However, this species still remains the least studied of the colobus monkeys, and dietary data are few.

Distinct changes in diet and behaviour have been observed due to seasonal change in *C. polykomos* [11, 13] and due to habitat quality in *C. badius, C. satanus* and *C. guereza* [10], as well as *C. badius tholloni* and *C. angolensis* [4]. The range of *Colobus* seasonal dietary and behavioural plasticity is of particular interest. Previous studies have tended to concentrate on *Colobus* troops inhabiting relatively moist forests, e.g. Zairean tropical rain forest [4], moist monsoonal forest in Sierra Leone [11], moist high forest in Uganda [8] and moist montane forest in Tanzania [16]. In the light of this we decided to carry out a short study of *C. angolensis palliatus* Peters, 1868, in Gendagenda South Forest Reserve, Tanzania, a dry coastal forest [17–20].

Gendagenda South Forest Reserve

Gendagenda South Forest Reserve (5° 27′ S, 38° 38′ E) is located in Handeni District, Tanzania, 250 km north-west of Dar es Salaam [18, 21]. The *C. angolensis* troop studied here inhabits dry, semi-evergreen forest situated on the lower eastern slopes of the more northern of the Gendagenda peaks (which rises to 500 m). The study area is dominated by *Scorodophloeus fisheri* with *Manilkara sulcata* and *Balanites maughamii* [18].

Gendagenda Forest Reserve experiences two major periods of rain, the short rains, occurring between November and December, and the long rains from March to May [18, 22]. Mean annual rainfalls of 1,000 mm at 100 m altitude and 1,202 mm at 288 m altitude have been recorded from the two closest rainfall stations [18]. The coastal climate is particularly hot and humid during the period between the rainy seasons, and biological activity appears to follow a corresponding unimodal seasonality, with most tree species producing new leaf growth at the onset of the short rains [P. Clarke, pers. commun.]. Our study is focussed on this period of seasonal interchange between the end of the dry season and beginning of the wet season.

Methods

The study area was mapped in detail, trees were marked and identified (table 1) either in the field or from specimens matched at the University of Dar es Salaam. Two observers collected data by observation using 10×40 field glasses. Trails used by the local villagers intersected the study area at regular intervals making access to all locations easy. The troop was followed from dawn to dusk (5.30 to 19.00 h on 6 days: November 5, 9, 13, 17, 21 and 27, 1991. The observations were split by the onset of the wet season indicated by the beginning of steady rain (November 20). There was a brief spell of rain between November 10 and 12, but it was followed by dry weather until November 20. This early period of rain seemed to encourage early shoot development in some of the more opportunistic, deciduous tree species [23]. This period was therefore considered as a transitional period between the dry and wet seasons, in terms of food supply. With this in mind, diet-related analyses were plotted for each sample date rather than per season. Other results that compare the two seasons use only data from those sample dates in the relevant season. The *C. angolensis* troop under study comprised 8 individuals (2 males, 5 females and 1 juvenile) and ranged in an area of 30.6 ha that was close to the forest margin. The troop's territory was surrounded by locally farmed small holdings and troop members were very tolerant of human presence. Notes were kept on the behaviour of every visible member of the troop during each minute of a particular sample day. This data collection is different from the method devised by Oates [7, 8], which uses 10-min samples every half-hour, and was devised to circumvent the problem of poor visibility through dense foliage. However, the vegetation in Gendagenda forest is not dense rain forest, so complete observations were possible. The categories used to

Table 1. Mean time spent browsing particular tree species, expressed as a percentage of the total time spend feeding during a season

Family	Species	Kizigua	Dry season feeding, %	Wet season feeding, %
Bombacaceae	*Adansonia digitata* L.	Mbuyu	25.3	81.0
Balanitaceae	*Balanites maughamii* Sprague	Mkonga	24.2	1.4
Combretaceae	*Combretum schumanii* Engl.	Mperamwitu	0.4	–
Combretaceae	*Terminalia* sp. aff. *kilimandscharica*	Mkurungo	2.9	0.4
Ebenaceae	*Diospyros zombensis* (Burtt) White	Mpweke	1.6	–
Salvadoraceae	*Dobera loranthifola* Harms.	Misiga	5.9	–
Sapindaceae	*Lecaniodiscus fraxifolius* Bak.	Mbwewe	2.3	–
Sapotaceae	*Pachystela brevipes* Engl.	Mchocho	0.9	–
Fabaceae	*Pterocarpus tinctorius* Welw.	Mninga maji	–	1.7
Fabaceae	*Scorodophloeus fisheri* Taub.	Mhande	1.7	–
Fabaceae	*Tamarindus indica* L.	Mkwaju	31.3	7.0
	unidentified sp. 1	Champanda	2.4	2.0
	unidentified sp. 2	unidentified	1.1	6.5

Results are presented for the period at the end of the dry and beginning of the wet season.

classify behaviour are similar to those defined by Oates [7, 8]: sleeping, resting (inactive), feeding, moving, watching (vigilance behaviour), grooming (social and personal) and aggressive behaviour.

Dietary diversity was calculated according to Oates's [7] measure of dietary diversity (H′);

$$H' = -e^{s \cdot \pi} \ln \pi,$$

where s is the number of species consumed, π is the relative abundance in the diet of each species. The greater H′, the greater the dietary diversity in a period.

Results

Results in figure 1 show that the total time allocated to sleeping, watching and moving were comparable between seasons. Differences in the time spent engaged in grooming and aggressive behaviour were notable but not statistically significant.

Feeding and Resting

The troop mainly fed from 6.00 to 9.00 h during the period at the end of the dry season; smaller but substantial peaks also occurred at 13.00 and again at 17.00 h. Observations from the beginning of the wet season showed an early morning feeding peak at 6.00 h and a midday peak at 13.00 h without an early evening feeding peak.

Compared to the period at the end of the dry season, the troop spent nearly 50% more time resting during the period at the beginning of the wet season, and this was mainly due to increased resting in the morning. Resting increased at 18.00 h in both seasons, but this coincided with the approach of dusk when the troop was settling down to sleep. Significantly more time was spent resting during the period at the start of the wet season than the period at the end of the dry season when compared with

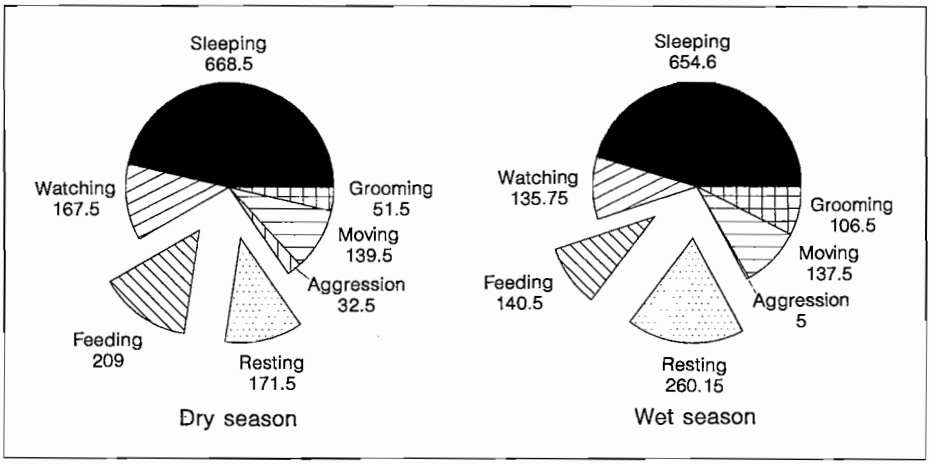

Fig. 1. Mean total time, in minutes, spent on a particular activity by troop members during 24 h. Results are presented as separate pie charts for the periods at the end of the dry and beginning of the wet season.

time allocated to feeding, which conversely showed that more time was spent feeding at the end of the dry season than at the beginning of the wet season ($\chi^2=43.88$; $p<0.01$; d.f. = 1).

Moving

Movements occurred during isolated periods rather than continuously during the day. The main periods of movement were at 9.00 and 14.00 h in the period at the end of the dry season and 14.00 and 16.00 h in the period at the beginning of the wet season.

The total ranging area of the *C. angolensis* troop in Gendagenda Forest Reserve decreased dramatically from 30.6 ha (with 20% of time spent resting and 66.6% of time spent feeding in a core area of 0.1 ha) at the end of the dry season to 10.43 ha (with 79.5% of time spent resting and 91.6% of time spent feeding in the core area) during the beginning of the wet season.

Composition of Diet

The results in table 1 show that foliage and fruit of *Combretum schumanii* Engl., *Diospyros zombensis* White, *Dobera loranthifolia* (Warb.) Harms., *Lecaniodiscus fraxifolius* Bak., *Pachystela brevipes* (Baker) Engl. and *S. fisheri* Taub. are only ingested during the dry season. In contrast, *Pterocarpus tinctorius* Welw. is only browsed during the wet season. These plant species may be considered as indicative of their respective seasons.

During the wet season, the main food is *Adansonia digitata,* which makes up 81% of the wet season feeding time, whereas during the dry season, *Tamarindus indica* L. (31.3%), *A. digitata* L. (25.3%) and *B. maughamii* Sprague (24.2%) all make significant contributions to the troop's diet (fig. 2). Consequently the troop's dietary diversity

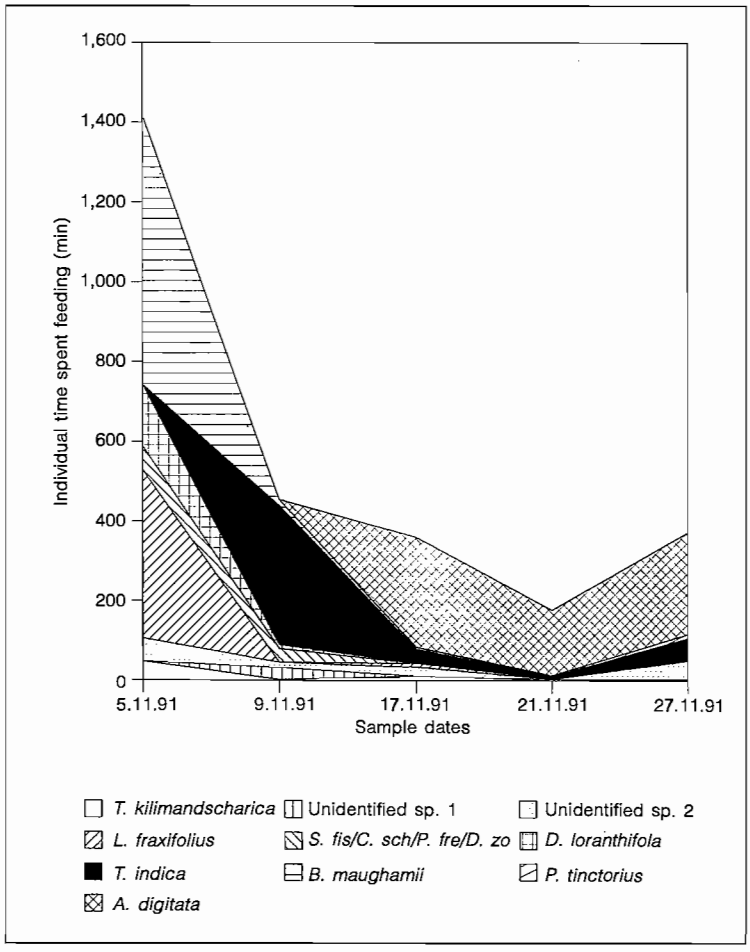

Fig. 2. A plot of the total individual time, in minutes (cumulative for each troop member), spent feeding on a particular tree species on a particular date.

(H′) at the end of the dry season was 1.70, whereas at the beginning of the wet season it was only 0.59, clearly showing a decrease in dietary diversity over time. There was also a steady decrease in the total individual time spent feeding over time (fig. 2).

Discussion

This publication is the result of a short study observing specific behavioural and dietary changes of a troop of *C. angolensis palliatus* to the seasonal changes in Gendagenda forest, a dry coastal forest in eastern Tanzania. The study was conducted mainly during the interchange period between the dry and wet seasons, the most interesting

time of year in terms of vegetation change. The results are preliminary, but give behavioural and dietary information on a previously unstudied *C. angolensis palliatus* population. Due to the problems of small sample size, general behavioural or seasonal extrapolation is not possible; however, similar seasonal changes in behaviour and diet have been found by other workers and the discussion highlights these other studies.

Much is known of the colobus's feeding-associated resting periods [8, 9, 19, 24, 25] and specialized foregut anatomy [26, 27]. This form of volatile fatty acid fermentation is probably an adaption to reduce leaf toxin levels prior to absorption [11, 28–30], and some behavioural changes have been explained by the need to reduce food toxin levels [10, 11, 13].

The change in season in this study coincided with a significant ($\chi^2 = 43.88$; $p<0.01$; d.f. = 1) shift in time spent feeding and resting, with the troop spending more time feeding and less time resting at the end of the dry season than during the period at the start of the wet season, when troop members spent less time feeding and more time resting. Marsh [31] noted a difference between the duration of feeding in two *Colobus* troops, one in the Tana River Primate Reserve, Kenya, and the other in the lower-quality Kibale forest, Uganda (30% time feeding at Tana, 45.3% at Kibale). He postulated that the difference was probably due to the quality of vegetation in the two forests. A basal level of resting was found in other studies to be necessary to allow efficient digestion and detoxification of the large volumes of plant matter ingested [8, 9, 11]. Struhsaker [2] found that *C. badius* rested only 34.8% of the daily time, whereas Oates [7] found that *C. guereza* rested 57.4% of the time. In our study, the basal level of resting was 22.2% of daily time during the period at the end of the dry season.

The ranging area decreased from 30.6 to 10.43 ha with the onset of the wet season. Increased ranging in monkey troops has been associated with poor diet or periods of poor food supply because good-quality food items are more difficult to find and further apart [13]. McKey [10] noted a significant decrease in range area when the movements of a *C. guereza* troop on a rich soil site were compared to those of a *C. satanas* troop on poor soils. We believe that the number of *C. angolensis* in Gendagenda may be restricted by the seasonal nature of the forest, which limits the carrying capacity of the species during the dry season when a larger range area is required.

Troop dietary diversity decreased from 1.70 at the end of the dry season to 0.59 at the start of the wet season. Similar shifts in dietary diversity have been noted in other studies, due to season and habitat quality. At Kibale forest, Uganda, Oates [7] recorded an overall yearly dietary diversity for a *C. guereza* troop of 2.08; in this period the diversity ranged from 1.21 in November to 2.14 in January. Similarly the index for *C. badius* at Kanyawara (Kibale) for 17 months, from November 1970 to March 1972, varied from 3.05 to 1.97 [3]. McKey [10] found that habitat quality played an important role in determining dietary diversity, and the dietary diversity of *C. satanas* living on a very nutrient-poor site was much higher than that of a troop of *C. guereza* living in a better-quality habitat.

Usually the presence or absence of one species is partially responsible for the change in dietary diversity, and in the Gendagenda troop, the appearance of edible portions of *A. digitata* is closely linked with a distinct decrease in wet season dietary diversity. The brief period of rain (10th to 12th November) will probably have promoted fresh growth of *A. digitata,* which is known to produce new growth soon after only a small amount of rain [23]. Oates [7] found that one species in particular, *Celtis durandii,* seemed to dictate the diversity of the *C. guereza* diet. In August 1971,

scarcity of *C. durandii,* measured by phenological studies, was linked with a high dietary diversity (1.98). Interestingly *C. durandii* also suffered heavy insect damage, confirming its high-quality food status. Maisels et al. [4] found that the diet of *C. angolensis angolensis* comprised a relatively high proportion of Leguminosae, 33.5%. The main leaf constituents of the diet were those of *Piptadeniastrum africanum, Albizzia antunesiana* and *Dialium* spp. However, high monthly dietary heterogeneity was observed; for example, the flowers of a single leguminous species, *Angylocalyx pynaertii,* made up nearly 40% of the March observations and the high pulp values during April to July were the result of ingestion of a single species, *Ongokea gore.*

Conclusions

A statistically significant difference was found in the time spent feeding and resting between the period at the end of the dry season and the period at the beginning of the wet season. We also found a major contraction in range area and dietary diversity with the onset of the wet season. Similar findings have been reported for other *Colobus* species, and our results suggest that the *C. angolensis palliatus* troop at Gendagenda may display similar behavioural adaptions under seasonal conditions.

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