

Research Paper

The optimal foraging strategy used by Campbell's Monkeys, *Cercopithecus campbelli*, in the dry season in the Taï National Park (Côte d'Ivoire)

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Abstract

This study aimed to highlight the options selected by Campbell's monkey (*Cercopithecus campbelli*) to optimize foraging in the Taï National Park, Côte d'Ivoire. A group of *C. campbelli*, habituated to human's presence, was followed for two months in the dry season to test whether the three parameters (the distance traveled to reach the foraging sites, the time spent on these sites and the abundance of food resources on the sites) of Charnov's marginal value theorem (MVT) were correlated with each other. Group scan sampling and *ad libitum* sampling techniques were used to collect data on the activities of individuals and the departure times from foraging sites, respectively. The study showed that although mainly frugivorous, Campbell's monkeys increased significantly the consumption of a broad spectrum of invertebrates during the long dry season. Moreover, no correlation was observed between the three parameters taken two by two. The polyspecific association of *C. campbelli* with other primate species in particular *C. diana* and *C. petaurista*, seems to have very little impact on their optimization choices analyzed in light of Charnov's MVT. During the study period, usual food resources were scarce, and monkeys shifted their diet towards invertebrates, which maybe viewed as an optimization option during food scarcity periods.

Keywords: Food ecology, optimal foraging, Forest guenons, Taï National Park, West Africa

Introduction

In the wild, animals face a trade-off between the costs and benefits that their lives bring to them. In the case of feeding which is an important activity, animals must find a food resource rich enough to compensate for the energy lost during the day. To achieve that, they adopt different foraging strategies (research and consumption of food) to balance this trade-off¹⁻³. These include the Central Place Foraging theory of Orians and Pearson⁴ according to which birds would make repeated foraging trips from a central location which is their nest. They would have to make a choice about the type and quantity of prey based on the distance travelled⁵. There is also the Optimal Foraging Theory of Mac Arthur and Pianka⁶, which is a model of optimal prey selection. The factor that can influence the choice of a specialist or generalist diet of an individual is the relative abundance of the most profitable prey in his environment⁷; hence the choice is based on prey that can bring the maximum of nutrients and that requires little energetic losses to be captured. These strategies aim to optimize the time spent in foraging, the distance travelled, the quality and quantity of food sought for by spending

as little energy as possible⁸. Selected as being the most effective strategies for the survival of species in their living environment, these strategies require different behavioural and cognitive adaptations depending on the level of evolution of the species and its environment⁹⁻¹¹. In Primates, there are two major phenomena that have been discovered to optimize foraging. On the one hand, there is “Lévy’s walk”, used by the spider monkey, *Ateles geoffroyi*¹², which is a random move to optimize the search for widely dispersed and sometimes rare resources. On the other hand, animals use a cognitive map that is a mental representation of the physical environment of the individual, and their movements are not random¹³. For instance, chimpanzees (*Pan troglodytes*)¹⁴ and sooty mangabeys (*Cercocebus atys*)¹⁵ have this spatio-temporal memory that allows them to retain feeding sites and to go directly when looking for a food resource. Nevertheless, having a cognitive map is not enough to optimize its foraging. The individual must be able to assess the costs and benefits of going to a particular location and take into account climatic factors^{16,17}, the time spent at feeding sites, the presence of other competing species and/or predators¹⁸. Polyspecific association with other species can be beneficial because vigilance is shared and thus individuals can feed more often^{19,20} but it can also have a cost e.g. due to possible competition with the associated species²¹⁻²⁴. For the Marginal Value Theorem (MVT) of Charnov²⁵ which is a model of foraging strategy considering the use of habitats where food resources are aggregated into different types of patches, individuals have to travel between these patches to feed and the cost varies with the distance travelled to reach a patch. Here there is a compromise between the time spent at the patch, the distance travelled to reach it and the food abundance of the patch. Koné *et al.*⁷ studied foraging strategies for Lowe’s Monkeys (*Cercopithecus lowei*) in a forest relict in Abidjan (Côte d’Ivoire). They took into account the parameters set out by Charnov²⁵ and showed that the group was ready to travel a longer distance if the targeted site was richer in food than the others. Based on these evidences, we conducted this study that aims to find out optimization options for foraging Campbell’s Monkeys and determine whether their association with other primates has an impact on these selected optimization options.

Materials and Methods

Field of study

The study was conducted in the TNP located in western Côte d’Ivoire in West Africa. The TNP covers 536,017ha and is located between latitudes 5°08’ and 6°24’ North and longitudes 6°47’ and 7°25’ West. Data were collected in the Taï Monkey Project (TMP) research area, which is spread over 150 ha east of the station of the *Centre de Recherche en Ecologie*. The natural park, very rich in biodiversity, preserves a dense primary rainforest, belonging to the great Guinean-Congolese floristic region. This park has been classified as a Biosphere Reserve since 1977 and has been listed as a UNESCO World Heritage Site since 1982. The TNP has four seasons: the long dry season (December to March), the long rainy season (April to July), the short dry season (August to September) and the short rainy season (October to November). It is home to a diverse fauna and among the diurnal primates we encounter Chimpanzee, *Pan troglodytes*, Western Red Colobus, *Piliocolobus badius*, Olive Colobus, *Procolobus verus*, King Colobus, *Colobus polykomos*, Sooty Mangabey, *Cercocebus atys*, Diana Monkey, *Cercopithecus diana*, Lesser Spot-nosed Monkey, *Cercopithecus petaurista*, Putty-nosed Monkey, *Cercopithecus nictitans* and Campbell’s Monkey, *Cercopithecus campbelli*²⁶. *C. campbelli* is present in the rainforests of West Africa, between Gambia and western Côte d’Ivoire²⁷. Its diet is composed of ripe fruits (46%), young leaves (8%), flowers (1%) and invertebrates (33%)^{9,18}. Individuals of this primate species live in harem with a dominant male and several adult females. These monkeys move from tree to tree in the low and medium strata of the canopy^{9,20,28}. This study focused on a group of *C. campbelli* habituated to human presence by the TMP since the 1990s. This group is composed of 19 individuals including one dominant male, 8 adult females, 5 subadults, 3 juveniles and 2 newborns.

Behavioural Data Collection

The monitoring of the behaviour of individuals was carried out during the long dry season, from February 6 to April 1, 2016 with a total of 31 days of follow-up, i.e. 326 hours of observation. We started data collection between 7h and 8h30 and followed the group until 17h40. We used two sampling methods described by Altmann²⁹ to record the activities and movements of entire group. First, we used the group scan sampling like Buzzard^{9,18,23} and Koné *et al.*⁷, respectively for the study of the feeding behaviour of *C. campbelli* and *C. lowei*. This sampling was carried out on average 21 times per day with an interval of 30 minutes between each scan so as to collect independent data. Each scan lasted a maximum of 10 minutes, according to the field obstacles during observation. That allowed to gather data about a maximum of individuals^{7,9,18,20}. During each scan, we recorded for each

individual, age class, sex, activity and other primate species present. In total we performed 558 valid scans including 4,042 behavioural observations. We considered five categories of activities: foraging, locomotion, resting, vigilance and social interactions (Table 1). When individuals were foraging, we noted the consumed food item (young leaves, buds, flowers, unripe fruits or ripe fruits, invertebrates). Primates that can be found in association with the group of *C. campbelli* studied are *C. diana*, *C. pataurista*, *Ptilocolobus badius*, *Procolobus verus*, *Colobus polykomos*, and *Cercocebus atys*. The groups met were mostly habituated to human presence.

The second method used is the *Ad libitum* sampling, which was used to record all other relevant behaviour whenever they occur such as the arrival and departure times on a site to determine the time spent at this site. At each stop site, we marked the central tree according to the positioning of individuals with a ribbon that we numbered. Then we recorded the geographical position of the stop site thanks to a Global Positioning System (GPS).

Table 1: Behavioural repertoire used to observe *C. campbelli*

Behaviour	Description
Foraging (F)	Individuals seeking food, selecting items, eating or preparing an item or chewing a food present in its cheek pouches or drinking water
Social interactions (S)	Any interactions with another individual. Mating, conflict, games, grooming, juvenile care
Locomotion (L)	Individual moves while walking, running or jumping and breaks for less than 3 seconds
Resting (R)	Individual sitting or lying with eyes closed or open, but without movement
Vigilance (V)	Individual sitting, on all fours or standing looking at the horizon and changing the direction of his head several times. This position is accompanied or not by cries of alarm
Undefined (U)	Behaviours that have not been defined in the study or can not be distinguished for lack of visibility

Floristic and phenological characterization of the different stop sites

At each marked stop site, we made a 15x15m plot with the numbered central tree in the middle of the plot. In each plot, we inventoried all plant species (shrub, tree or liana) with a Diameter at Breast Height (DBH, measured at 1.30 m above the ground) equal or greater than 5 cm. We decided to take 5 cm in diameter as the threshold and not 10 cm as generally recommended during phenological surveys³⁰⁻³² because our pilot observations in the field revealed that *C. campbelli* also used and fed plant species with smaller DBH. In addition, Buzzard⁹ found that *C. campbelli* more often uses fruit trees with a diameter of less than 10 cm. The phenological state of each individual was noted in order to subsequently determine the food abundance of each site. We considered five phenological classes to determine the amount of young leaves, buds, flowers, unripe fruits and ripe fruits compared to the entire plant cover of the individual studied: 0%,] 0; 25%],] 25 ; 50%],] 50 ; 75%],] 75 ; 100%]. These food items are normally eaten by *C. campbelli*^{9,18,23}. This phenological data collection was carried out during the same study period (February-March) for a total of six non-consecutive days with an average of six sites per day. In total we characterized 36 sites, for a total surface of 8,100 m² of vegetation.

Data analysis

To compare the frequency of activities and items consumed, we used the Pearson's Chi-squared test with a risk of error $\alpha = 0.05$. Then, to determine if the group takes into account the three parameters of the MVT of Charnov, we calculated the distances between the sites using GPS/UTM coordinates and the time spent at a site. To determine food abundance of each site, we first calculated the production rate of the different items [young leaves (YI), flowers (FI) or fruits (Fr)] for a given plant species. The production of buds was grouped with that of flowers and the production of ripe fruits with that of unripe fruits. The production rate is calculated as follow³³:

$$T_{\text{spX}} = \frac{\left(\frac{1}{100}\right) \times [(0 \times N_{0\%}) + (25 \times N_{]0;25\%}) + (50 \times N_{]25;50\%}) + (75 \times N_{]50;75\%}) + (100 \times N_{]75;100\%})]}{N_{\text{spX}}}$$

With T_{spx} : Production rate of the studied item of species x ; $N_{x\%}$: Number of individuals of the species having $X\%$ of item studied; N_{spx} : Total number of individuals of the species x .

Then, we calculated the productivity index of species x :

$$P_{spx} = DBH_{meanspx} \times T_{spx} \times D_{spx}$$

With $DBH_{meanspx}$: Mean diameter at breast height of species x ; D_{spx} : Density of the species x and T_{spx} : Production rate of the studied item of species x .

Finally, we summed up the productivity indices of all the species present on a site:

$$PI_x = \sum_{i=1}^N P_{spi}$$

With x : type of production studied (Tot, Yl, Fl or Fr) and spi = plant species present on the site i , $i = 1, \dots, N$.

We calculated this index under several conditions, either by taking the total production of the individual (PI_{tot}), i.e. by considering the production of young leaves, fruits and flowers of the individual; or by taking into account only the production of young leaves (PI_{Yl}), flowers (PI_{Fl}) or fruits (PI_{Fr}). Then a map was made with QGIS 2. 16. 3. to represent the sites according to their PI_{tot} and the time spent by primates. GPS coordinates used were under the WGS84 / UTM Zone 29 projection system. As our data do not follow a normal distribution, we used nonparametric tests. We realized the Spearman Correlation test between the three parameters with a risk of error $\alpha = 0.05$. Finally, we realized a Mann-Whitney test on the three parameters based on the association of primate species on the sites. To test the effect of polyspecific association on the foraging strategies of *C. campbelli*, we chose to compare two conditions according to diets and interspecific competition risks. On the one hand (condition 1), *C. campbelli* is alone or in presence of *P. verus* and/or *P. badius* which are mainly folivorous primates and generally do not compete with *C. campbelli*³⁴. On the other hand (condition 2), *C. campbelli* is in association with *C. diana* and/or *C. petaurista*, which may be in interspecific competition for access to food because their diets overlap^{18,35}. *Colobus polykomos*, which by its diet should be put in condition 1, and *Cercocebus atys* were put in condition 2 because they were observed only in presence of *C. diana* and/or *C. petaurista* during scans. This allowed us to see if the other primates and *C. diana* in particular, which is the species whose diet overlaps the most with *C. campbelli* and which has been described as the “core species” of polyspecific groups in the TNP^{18,20}, could influence or not, by their presence, the foraging behaviour of *C. campbelli*. All statistical analysis and graphics were done with the R Software (version 3.3.2).

Results and Discussion

Activity budget and feeding behaviour of *C. campbelli*

Results indicate that in the study period, locomotion was the most frequent activity (46%; $N = 4,042$) followed by foraging (28%). The least observed behaviours were resting (5%) and social interactions (7%) (Figure 1).

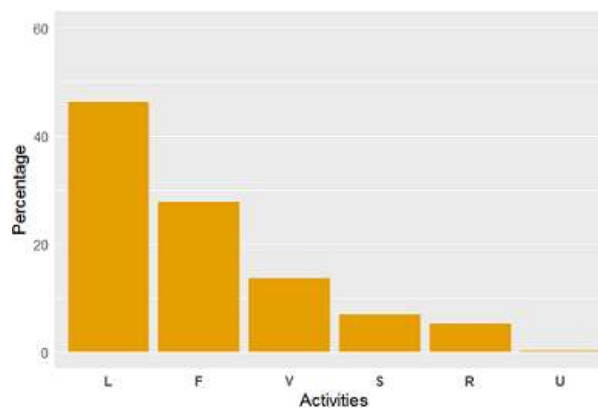


Figure 1: Activity budget of *C. campbelli* group studied ($N = 4,042$) (L: Locomotion; F: Foraging; V: Vigilance; S: Social interactions; R: Resting; U: Undefined)

During feeding, the most consumed items were invertebrates to 81% (N = 1,121). However, the invertebrates consumed could not be identified in the field. In comparison, other items have been little consumed (Figure 2). In total, 19 plant species were consumed by individuals (Table 2). Among ripe fruits consumed (N=157), fruits of *Dialium aubrevillei* were the most frequently consumed (80%) followed by those of *Sacoglottis gabonensis* (11%). Only two plant species were selected for their flowers (N=23): *Pentaclethra macrophylla* (70%) and *Pentadesma butyracea* (30%).

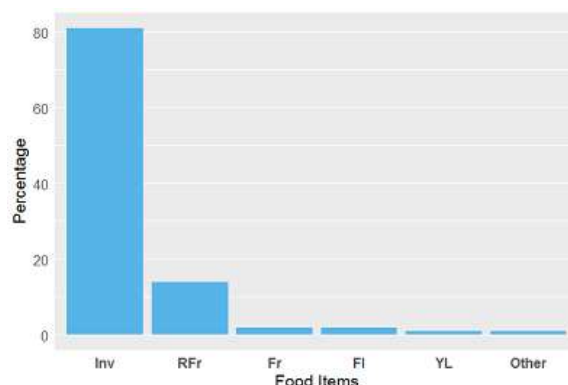


Figure 2: Food items consumed by individuals (N = 1,121)
(Inv: Invertebrates; RFr: Ripe fruits; Fr: Unripe fruits; FI: Flowers; YL: Young leaves; Other: undefined items)

Table 2: List of food items consumed by *C. campbelli*

Food Items	Percentage (%)	Food Items	Percentage (%)
Unripe Fruits	2	Ripe Fruits	14
<i>Diospyros mannii</i>	6	<i>Dialium aubrevillei</i>	80
<i>Diospyros soubreana</i>	24	<i>Diospyros mannii</i>	1
<i>Napoleona leonensis</i>	6	<i>Diospyros soubreana</i>	3
<i>Magnistipula butayei</i>	6	<i>Parinari sp.</i>	3
<i>Sacoglottis gabonensis</i>	24	<i>Sacoglottis gabonensis</i>	11
<i>Xylopi aethiopica</i>	18	<i>Xylopi aethiopica</i>	1
Not identified	18	Not identified	1
Young Leaves	1	Flowers	2
<i>Oldfieldia africana</i>	33	<i>Pentaclethra macrophylla</i>	70
<i>Dialium aubrevillei</i>	17	<i>Pentadesma butyracea</i>	30
<i>Diospyros canaliculata</i>	17	Others	1
Liana	17	Stem (<i>Cercestis afzelii</i> - liana)	8
Not identified	17	Gum (<i>Strephonema pseudocola</i>)	17
Invertebrates	81	Water	75

In term of characterization of stop sites and movements of the studied group, a total of 42 stops at 30 different sites were recorded and the DBHs of 768 plants were measured. On sites, there were between 16 to 38 individuals maximum recorded with DBH \geq 5 cm. The average DBH of individuals is 13.64 with a standard deviation of 14.79. This indicates that there is a strong deviation from the average with a majority of young individuals with DBH \leq 10 cm and some older individuals with an average diameter of 58 cm. In terms of plant species, we inventoried 102 plant species comprising 37 different families (Table 3). The average species richness of each plot is 13.93 ± 2.69 .

Table 3: List of plant species most often encountered at stop sites

Plant species	Family	Total	Percentage
<i>Diospyros mannii</i> Hiern	Ebenaceae	105	13.67
<i>Diospyros soubreana</i> F.White	Ebenaceae	90	11.72
<i>Calpocalyx brevibracteatus</i> Harms	Fabaceae	50	6.51
<i>Memecylon lateriflorum</i> (G. Don) Bremek.	Melastomataceae	30	3.91
<i>Heritiera utilis</i> (Sprague) Sprague	Malvaceae	24	3.13
<i>Soyauxia floribunda</i> Hutch.	Peridiscaceae	24	3.13
<i>Scytopetalum tieghemii</i> (A. Chev.) Hutch. & Dalziel	Lecythidaceae	23	2.99
<i>Polyalthia oliveri</i> Engl.	Annonaceae	22	2.86
<i>Coula edulis</i> Baill.	Coulaceae	21	2.73
<i>Diospyros canaliculata</i> De Wild.	Ebenaceae	21	2.73
<i>Spondianthus preussii</i> Engl.	Phyllanthaceae	19	2.47
<i>Uapaca esculenta</i> A. Chev. ex Aubrév. & Leandri	Phyllanthaceae	18	2.34
<i>Xylopia parviflora</i> (A. Rich.) Benth.	Annonaceae	18	2.34
<i>Strephonema pseudocola</i> A. Chev.	Combretaceae	17	2.21
<i>Napoleonaea leonensis</i> Hutch. & Dalziel	Lecythidaceae	16	2.08
<i>Trichoscypha arborea</i> (A. Chev.) A. Chev.	Anacardiaceae	14	1.82
<i>Xylopia quintasii</i> Engl. & Diels	Annonaceae	14	1.82
<i>Diospyros sanza-minika</i> A. Chev.	Ebenaceae	13	1.69

Table 4 below, shows the different values of the three parameters of Charnov's MVT at the various foraging sites: time spent at a foraging site, distance travelled to reach the foraging site and food abundance at the site. The average distance travelled by our group between two sites is 170.91 ± 111.29 m. The average time spent at a site is 63.24 ± 59.57 min.

Table 4: The different stop sites with distance travelled to reach them, time spent at site and their food abundance (PI)

Stops	Distance (m)	Time (min)	Sites	PI _{tot}	PI _{Fr}	PI _{YI}	PI _{FI}
1	105.36	18	A	0.05	0	0.05	0
2	300.34	44	B	0	0	0	0
3	154.03	320	C	0	0	0	0
4	91.81	60	D	0.12	0	0.12	0
5	64.40	189	E	0.49	0	0	0.49
6	302.04	122	F	0.06	0.06	0	0
7	203.21	58	G	0.20	0	0.14	0.06
8	323.64	31	H	0	0	0	0
9	71.69	71	I	0	0	0	0
10	286.72	62	J	0	0	0	0
11	97.08	34	K	0	0	0	0
12	238.08	92	L	0	0	0	0
13	141.89	108	E	0.49	0	0	0.49
14	212.66	49	M	0.04	0	0.04	0
15	235.14	20	N	0	0	0	0
16	100.30	32	O	0.12	0	0.09	0.03
17	155.33	17	P	0.04	0	0.04	0
18	80.32	82	K	0	0	0	0
19	99.37	15	K	0	0	0	0
20	99.37	32	Q	0	0	0	0

Stops	Distance (m)	Time (min)	Sites	PI _{tot}	PI _{Fr}	PI _{Yl}	PI _{Fl}
21	38.47	50	R	0.02	0	0.02	0
22	38.47	63	Q	0	0	0	0
23	169.96	18	S	0.03	0	0.03	0
24	264.76	16	T	0.60	0	0.02	0.58
25	68.62	15	U	0	0	0	0
26	235.59	36	V	0.16	0	0.10	0.06
27	95.08	33	T	0.60	0	0.02	0.58
28	265.75	27	B	0	0	0	0
29	117.15	37	W	0.03	0	0.03	0
30	171.77	53	X	0.07	0.01	0.07	0
31	342.02	21	O	0.12	0	0.09	0.03
32	148.56	24	Y	0.18	0	0	0.18
33	48.80	132	E	0.49	0	0	0.49
34	101.32	162	Z	0.09	0	0.04	0.05
35	78.55	26	G	0.20	0	0.14	0.06
36	93.43	23	C	0	0	0	0
37	557.41	153	V	0.16	0	0.10	0.06
38	84.81	40	AB	0.03	0	0.03	0
39	66.22	14	AB	0.03	0	0.03	0
40	222.46	95	AC	0	0	0	0
41	208.06	71	AD	0.08	0	0	0.08
42	398.18	91	AE	0.06	0	0.06	0

Stops in orange are those where *C. campbelli* were alone or in presence of *P. verus* and/or *P. badius*. For the other stops, they were with *C. diana* and the other primates. PI_{Tot}: Total Productivity Index, PI_{Fr}: Fruits Productivity Index, PI_{Yl}: Young leaves Productivity Index, PI_{Fl}: Flowers Productivity Index.

As for food abundance per site, in 11 sites, there was no production of consumed items at all; no production of flowers in 22 sites, only two sites produced fruits and 15 sites did not produce any young leave. We found that during the study period few sites harboured food items (young leaves, flowers and fruits) that are usually consumed by *C. campbelli* (Figure 3). Only two sites have a PI_{tot} greater than 0.20.

Previous studies emphasized that Campbell's monkey are generally frugivorous^{9,23} but phenological data showed that fruits and flowers were scarce during the study period leading the study monkeys to modify its diet with a predominance of invertebrates. During the long dry season of 2001, invertebrates accounted for 20-35% of the diet of *C. campbelli*⁹, while our study reveals that they account for 81% of their diet. Nevertheless, fruit production between the two years seems different. In Buzzard's study in 2001, there was a high production of fruits, which was not the case during our data collection. If we consider invertebrate consumption in 2001 during a season with less fruit (May to August), we find that *C. campbelli* consume about 50% of invertebrates. Our results confirm those of Buzzard and further show that invertebrates can take a larger proportion in the diet of *C. campbelli*. Knowing that the group moves a lot to find food, individuals have to compensate their energy expenditure by eating items with high nutritional value. Invertebrates can fulfil this role of compensation because they are rich in proteins. In addition, they are generally easily accessible and present in large quantities in the environment^{36,37}.

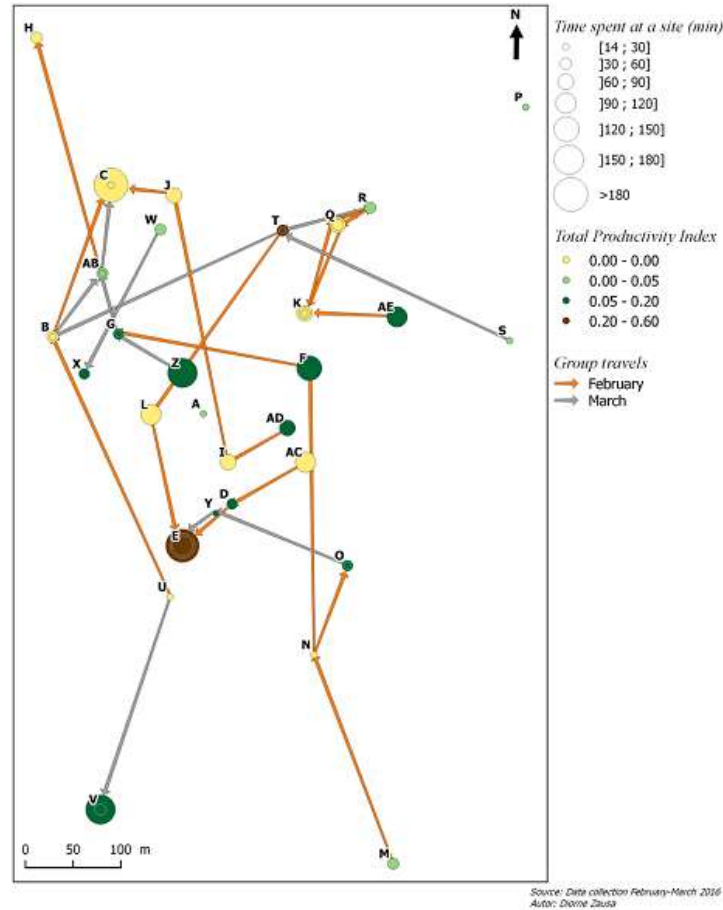


Figure 3: Mapping of stop sites chosen by our group of *C. campbelli*

Legend: Characterization of stop sites according to their food abundance (PI_{tot}) and the time spent at a site (in minutes) by the group. The movements of the group between certain sites are differentiated according to the month.

There were noticeable differences in time spent at different foraging sites. The monkey group happened to spend a long time in a site with a null PI (site C) and conversely, a short time in a site with a relatively high PI (site T). As for travel, the study group did not use the same itineraries from one foraging site to another one. There is no correlation between the three parameters taken two by two. With regard to distance travelled and time spent at a site, the values of r and p are as follows: $r = 0.0502$; $p = 0.752$. The group may travel a long distance to a foraging site (350 m) and stay there only a short time (about 25 min); conversely the group may travel a short distance to a foraging site (50 m) and spend a long time there (130 min) (Figure 4).

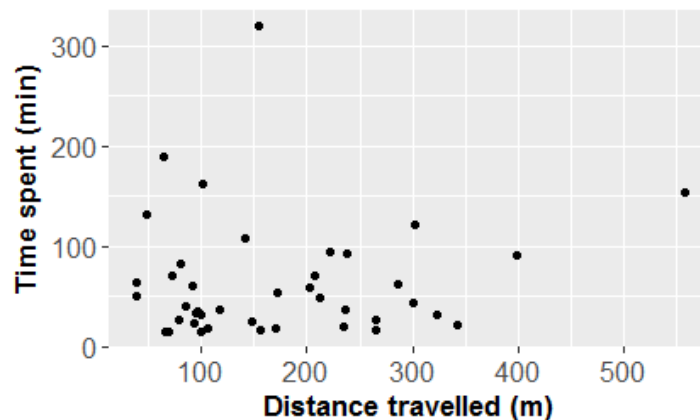


Figure 4: Time spent (min) at a site according to distance travelled (m) by our group to reach it

Considering the distance travelled and food abundance, regardless of the production that is taken into consideration the values are as follows PI_{tot} : $r = 0.0047$; $p = 0.976$ | PI_{Fr} : $r = 0.1962$; $p = 0.213$ | PI_{YL} : $r = 0.1173$; $p = 0.459$ | PI_{Fl} : $r = -0.0164$; $p = 0.918$ (Figure 5 A-D). Considering time spent at a foraging site and food abundance, the values are as follows PI_{tot} : $r = 0.1253$; $p = 0.429$ | PI_{Fr} : $r = 0.1778$; $p = 0.260$ | PI_{YL} : $r = -0.1464$; $p = 0.355$ | PI_{Fl} : $r = 0.1542$; $p = 0.329$ (Figure 5 E-H).

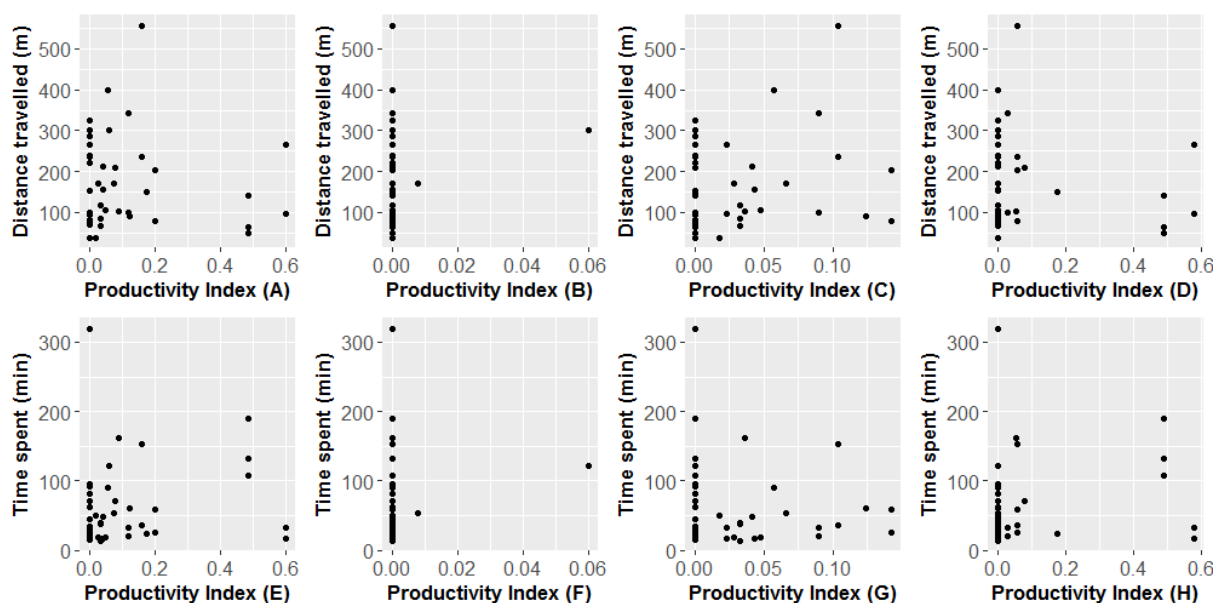


Figure 5: The relation between distance travelled (m) to reach a stop site and its food abundance index (PI) with total production (A), fruits production (B), young leaves production (C) or flowers production (D). The relation between time spent (min) at a site and its food abundance index (PI) with total production (E), fruits production (F), young leaves production (G) or flowers production (H).

Based on the study that was conducted on the Lowe's Monkeys in a relict forest in Abidjan⁷, we had predicted that in the TNP Campbell's Monkeys would display the same foraging strategies and therefore there would be a correlation between distance travelled by the group and food abundance of sites. However, no correlation was found between the three parameters tested in our study. This lack of correlation can be explained by several factors. First, the lack of plant items as food resources during the study period led the monkeys to consume up to 81% of invertebrates. Thus we assume that they were not looking for sites rich in plant material as required by their basic feeding ecology⁹ but rather rich in animal matter. The lack of correlation between the time spent at a foraging site and distance travelled can be explained by the fact that the group was moving in curve or zigzag. Yet, the hypothesis that *C. campbelli* adjusted the time spent at a foraging site with the distance travelled to reach a site could only work if the group was moving more or less linearly. Our methodology, based on that used by Buzzard^{9,18} and Koné *et al.*⁷ consisted in calculating the distance between two stops but not to follow the changes of direction during movements of the group. The observed frequent changes of direction by *C. campbelli* suggests the use of another foraging strategy, the "Lévy's walk". This strategy implies performing a large number of small movements in the environment. This optimizes the search for infrequent food items in a heterogeneous environment¹². This strategy was no doubt used by *C. campbelli* to cope with the scarcity of plant items. In addition, the use of their cheek-pouch allows them to reduce the time they spend on a site and thus to cope with interspecific competition and to reduce the risk of predation²². Another benefit of travelling frequently is the increase of the chance of detecting invertebrates disturbed by the movements in branches.

Polyspecific associations and foraging strategies

In 97% of scans, the study group was associated with one to six species of primates. *C. campbelli* is most often found in association with four primate species (37%) or three (33%) ($X = 1.1337$; $df = 1$; $p = 0.287$, Figure 6).

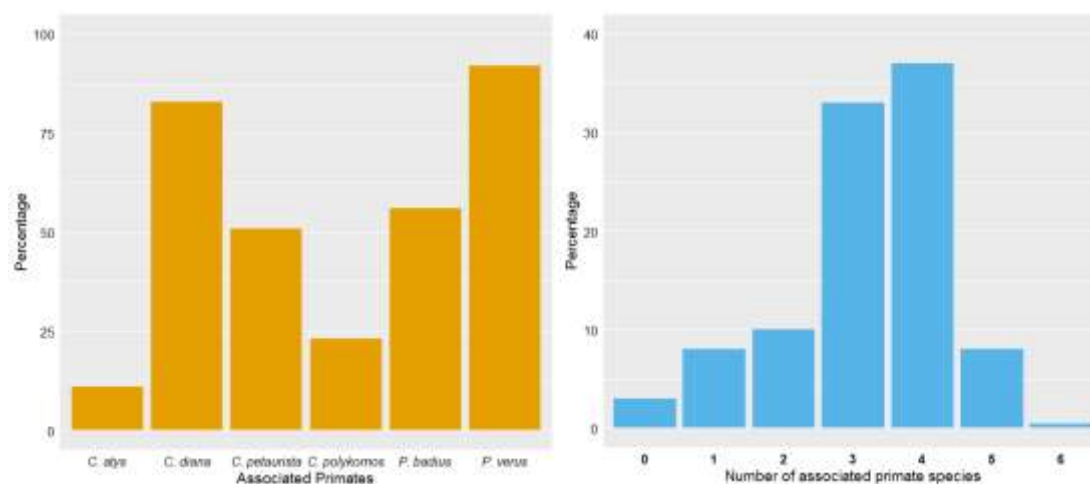


Figure 6: Percentage of associated primate species (left) and number of associated primate species (right) with our study group according to group scan sampling (N = 558).

The most common association triad found in association with *C. campbelli* (N=184) is “*C. diana* / *P. badius* / *P. verus*” (74%). The species that is most often found with *C. campbelli*, regardless of the number of associated primates, is *P. verus* (92% of scans), followed by *C. diana* (83%) (Figure 6, $X = 3.0962$; $df = 1$; $p = 0.079$). On the other side, when *C. campbelli* was in association with only one species of primate (N=47), it was 87% with *P. verus* and never with *C. diana*. Correlation tests show that there is no correlation between the three parameters of Charnov when the group is alone or in presence of *P. verus* and/or *P. badius* (Condition1). However, the group visits sites with young leaves more frequently ($W = 236.5$; $p = 0.021$, Mann-Whitney). In condition 2, in the presence of *C. diana* and other primates, the three parameters of Charnov are not correlated but the group tends to spend more time at a specific foraging site ($W = 90$; $p = 0.011$, Mann-Whitney).

Our observations follow results provided in previous studies showing that *C. campbelli* are very often associated with other primate species, particularly with *P. verus*, *C. diana*, *P. badius* and *C. petaurista*. *P. verus* and *P. badius* are predominantly folivorous. Leaves account for 77% and 75% of their diet, respectively^{34,38}. Thus they do not come into direct competition for food with *C. campbelli* when they are in association. To the contrary, the diet of *C. campbelli* overlaps with those of *C. diana* and *C. petaurista*^{18,22,23}. They are frugivorous and *C. diana* can also consume large numbers of invertebrates when fruits are scarce^{18,39}. The efficacy of vigilance behaviour in *C. diana*⁴⁰ and their ability to communicate with *C. campbelli* to announce the presence of a predator^{41,42} is a benefit that may explain why *C. campbelli* tend to spend a longer time at a site when in association with *C. diana*.

Conclusion

The study revealed that wild *C. campbelli* consume mostly invertebrates during the long dry season (February to March). This is the first foraging strategy that was highlighted in this study. Whether *C. campbelli* are alone or in association with other primates, the distance travelled to reach a site, the time spent at that site, and food abundance appear to be three parameters independent of each other. In summary, this wild guenon group oriented their strategy for foraging optimization towards another food source used less in other seasons of the year in this tropical forest.

Hence an inventory of invertebrates and their abundance at each foraging site would be required so as to test the links between the three parameters of the Charnov's MVT. This study opens further questions to take in consideration mainly by considering invertebrates as valuable food resources for *C. campbelli* during the periods of scarcity of fruits. In addition, it would be interesting to extend this study on the other three seasons of the year to identify seasonal variations in foraging behaviour.

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