

FOREST STRUCTURE AND FRUIT AVAILABILITY  
AS COMPLEMENTARY FACTORS INFLUENCING HABITAT  
USE BY A TROOP OF MONKEYS (*CERCOPITHECUS CEPHUS*)

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Among the parameters which may affect the ranging behaviour and troop movements of wild primates, food is one of the best documented for a number of species (for example Clutton-Brock 1977, Goodall 1977, Richard 1977, Waser 1977). Most studies conclude that habitat utilization is closely related to food supply. When food is scarce, both the ranging patterns and the diet composition are modified. Another parameter has been shown by Struhsaker (1975) to be important for the Red Colobus (*Colobus badius*) : interactions between groups play a role in the differential use of the troop home range. More recently, Freeland (1979) has suggested that food availability has little effect on habitat use and regulation of group size and has proposed an interpretation based on disease-related control "via regulation of group size and social and spatial isolation between groups".

In most studies, the habitat is described in very broad terms, such as "moist evergreen forest" or a "montane forest". Sometimes a more precise description is provided such as in Goodall's (1977) study of the Mountain Gorilla. In this study, eleven types of vegetation were described, based on plant species composition ; however, even in this case, ranging behaviour was not analysed in relation to forest structure.

Vertical use of the forest is most often analysed in terms of mean height classes, with no details on the foliage density nor on the nature of the locomotion supports (except in the studies devoted to positional behaviour). Yet, Oldeman (1974) described equatorial forests as heterogeneous and dynamic systems for which the classic concept of layers or strata cannot be strictly applied. Recording the types of locomotion supports used by the

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five species of nocturnal Prosimians found in north-east Gabon, Charles-Dominique (1971) showed that each species was bound to different microhabitats characterized both by the diameter and orientation of the supports used and by the foliage density, whereas the relative height above the ground level was less directly important. Charles-Dominique argued that the use of the various microhabitats was related to the abundance of the main food species eaten.

It is obvious that forest structure and food availability are closely linked. But one can predict that the physical structure of the habitat alone, — for example the overall foliage density, the height of the canopy, the kind and abundance of lianas, the presence of emergents and the undergrowth structure — can lead to differential habitat use. All these parameters, particularly as they affect the penetrability of the milieu and visibility, can be expected to play a role in determining the pattern of movements of the animals in relation to their morphological adaptations and their defense strategies against predators, as pointed out by Bourlière (1979).

Dubost's (1979) study on several species of rain forest ruminants has shown that the shoulder height of each species can be related to the density of the undergrowth. Knowledge of such relationships in arboreal animals would yield information on habitat partitioning and on the reasons for the patchy distribution of a number of animal populations ; it could also be of interest to conservationists. Such habitat separation has been recently reported for two species of *Callicebus* (Kinzey and Gentry, 1979).

In north-east Gabon, *Cercopithecus cephus* is known to be found both in primary and secondary forests, as well as in swamp forests, the physical structures of which are quite different (Gautier and Gautier-Hion, 1969). When available, second growth and riparian forests only represent part of the troop's home range ; moreover, a particular forest type never has a homogeneous structure. These facts suggested that the monkeys reacted differently to differences in plant species composition and/or structure of forests. In this paper, we have attempted to answer the following questions :

1/ Are the *C. cephus* monkeys randomly using all the available vegetation types in their home range or not ?

2/ If not, is the differential utilization of the microhabitats related to their differential fruit supply and/or their physical structure ?

3/ Are there seasonal or diurnal variations in microhabitat use ?

4/ Are these temporal variations related either to fruit supply or to the activity of the monkeys ?

## STUDY SITE AND METHOD

### I. — *Study site and monkey populations*

The study was carried out on a *C. cephus* troop living in a protected area near the Makokou field station (N-E Gabon : 0°34'N, 12°52'E ; 430 m above sea level). The troop's home range is located on a plateau edging the Ivindo river and having a relatively abrupt slope. The troop included fifteen animals at the time of the study. Unlike most of the *C. cephus* troops previously observed (Gautier and Gautier-Hion, 1969 ; Gautier-Hion and Gautier, 1974), it was a single species troop, occasionally merging (for less than 15 % of the time) with a neighbouring mixed troop that included *C. nictitans*, *C. pogonias* and *C. cephus*. These association periods have been excluded from the present analysis, except for home range size determination, in order to avoid bias in the estimations of forest use.

### II. — *Structural analysis of the forest*

Four forest types were recognized and mapped with the help of a fellow botanist, Guy Caballé. Three main criteria were used : the height of the canopy, the height of the emergents, and the density of the undergrowth measured by the distance of visibility at breast height.

The canopy of the first forest type (F1) is at 20-30 m, with emergents up to 40-50 m ; the visibility at breast height is more than 30 m. The second forest type (F2) is not so high (15-25 m), with a distance of visibility in the undergrowth ranging from 10 to 30 m. Old tree-fall sites are found in this habitat. Patches of F3 type occur mainly at the top of the plateau slope. Many decaying trees and recent tree-falls are found here, probably due to the soil structure and the frequent occurrence of storms. The distance of visibility is always under 10 m ; no definite structure is apparent and the canopy frequently reaches ground level. There are many lianas. The fourth type (F1') is the same as F1, but its undergrowth was cleared nine years before the present study, and many lianas were destroyed. Here the ground is covered with herbaceous plants, and visibility is very good from two meters up to the tree crowns (> 50 m).

### III. — *Study period*

A previous detailed analysis of variations in seasonal diet of *Cercopithecus* species (Gautier-Hion, 1980) showed that in terms of food availability there is a critical period during the main dry season, which coincides with significant shifts in the monkeys' diet and a decrease in diet overlap between species. During the dry season, the overall fruit intake and the number of fruit

species eaten decreases. By contrast, the long rainy period that follows is rich in fruit and fruiting species, and the monkeys feed heavily on them.

We expected that these dietary changes would be associated with changes in ranging behaviour. For this reason, observations were made in July and August (dry season, DS) and in September-October (rainy season, RS). Comparable numbers of observations were made during the two seasons, and observations were preceded by two months of preparation (especially for capturing live monkeys).

#### IV. — *Troop observations : habitat use and time-budget*

The study area was divided by a trail system into one hectare quadrats. Trails were marked every 20 m by plastic labels giving the direction and distance from the origin of the grid. Three types of observations were made :

1/ Radio-tracking was used to follow the troop : two adult females were captured using a gun for long-distance injection of narcotics and equipped with micro-transmitters. A dose of 30 mg of ketamin per kg of body weight was used ; the total weight of the radio-collar was less than 100 g. The position of the animals was checked every half-hour (by goniometry) using an AVM receptor and a Yagi antenna. When plotted on a map, these data allowed precise localization of the animals to be made, as well as the determination of patterns and speed of movements. The radio-tracking sessions usually lasted either from 06.00 to 12.00 h or from 12.00 to 18.30 h, thus including all the activity periods of the monkeys. Some all-day observations were also undertaken. A total of 352 h of tracking was done : 282 h for female 1 (615 position checks) and 258 h for female 2 (545 position checks). Throughout this study, alternate weeks were devoted to radio-tracking and time-budget measurements.

2/ Time-budget estimation covered 370 h. During each half-day period, the activity of the first visible animal, its height above the ground and the forest type used (this latter measure was only plotted during 100 hours) were recorded at five minute intervals. Five classes of activity were recognized : *locomotion* (walking, climbing or jumping) ; *feeding* (the animal was handling a fruit or a leaf, chewing, pulling something from its cheek pouches, or displaying distended cheek pouches ; these activities essentially correspond to fruit-feeding, since leaf consumption is very low except for the case of the adult male, Gautier-Hion, 1980) ; *foraging* (the animal was either resting or walking slowly, very attentive to its nearby environment, searching under leaves or bark, or obviously preying on insects and eating them) ; *resting* (the animal was sitting on a support) ; *social behaviour* (grooming, playing, etc.).

3/ During both the radio-tracking and time-budget observations, the position of the whole troop was recorded every half-hour (a total of 1238 data points). The following method was used for analysing the data : when the troop was found in one quadrat, one point was scored ; when scattered across two quadrats, 1/2 point was noted for each quadrat ; in three, 1/3 point, etc. The troop was never observed to be scattered over more than four quadrats.

Once tabulated the total data provided a measure of the relative use of each quadrat ; this approximated to a measure of the time spent in it. By measuring the relative area of each forest type in each quadrat, the time spent by the troop in each forest type was calculated using the formula :

$$U_{Fi} = \Sigma U_q \times Fi_q$$

where  $U_{Fi}$  = % use of type  $Fi$  forest ;  $U_q$  = % use of quadrat  $q$  ;  $Fi_q$  = % of quadrat  $q$  covered by type  $Fi$ .

This measure reduces, in principle, the differences to be found between habitats, since it assumes non-preferential use of a forest type within a given quadrat. But it gives an average value for the total troop, all the members of which cannot be seen at the same time. The results thus obtained are validated by the more precise data obtained when considering the exact location of a given monkey during time-budget observations (cf. Fig. 2).

#### V. — *Estimate of fruit availability*

The mean contribution of fruit to the diet (in % dry weight) varies from 70 % during the dry season to 84 % during the rainy season (Gautier-Hion, 1980). For the same period, animal matter intake varies from 7 to 13.5 %, with leaves making up the remainder. Although insect availability may be an important factor determining habitat use, it was not taken into account during this study, essentially because of the difficulty of estimating this parameter. The potential influence of insect supply on habitat use is examined in the discussion of results at the end of the present paper.

The amount of fruit available was estimated weekly by visiting six quadrats chosen among those used the week before by the troop (according to the radio-tracking position checks). Two quadrats were selected among the least used, two among the most used and two others were in an intermediate position. This sample was chosen to test the hypothesis that time spent in one quadrat is related to fruit availability in the same quadrat. A total number of 57 quadrats was thus analysed within the home range of the troop, and 39 additional quadrats in the home range of the neighbouring mixed troop.

All the trees and liana species bearing ripe fruit known to

be eaten by monkeys (Gautier-Hion, 1980) and/or seen eaten the days before the phenological analysis was carried out, were recorded (N = 17 species). The presence of flowers, unripe and/or ripe fruit was noted ; the location of the fruiting trees in each quadrat was plotted on a map. No attempt was made to estimate the overall fruit production.

The number of fruiting trees (X) found in the quadrats analysed (27 in the DS ; 30 in the RS) was used to estimate the confidence limits of the total number of fruiting trees (N) available on the home range (46 ha in DS ; 43 ha in RS) for the same period, by applying a binomial law.

$X \sim B(N, p)$  where  $p = a/A$  ;  $a$  = number of quadrats analysed and  $A$  = number of quadrats in the home range. The confidence limits of N are given by :  $X - Np \leq \varepsilon \sqrt{Np(1 - p)}$ .

## VI. — Estimate of the «fruit-feeding value»

The fruit-feeding value of a given area of the home range has been estimated for a given period from : 1/ the number of the fruiting species in it ; 2/ the number of trees with ripe fruits ; 3/ a «selection ratio» for the different species which takes into account both the relative abundance in the study area of the plant species considered, and the relative number of times the fruiting trees were seen to be visited by monkeys for feeding. For each species, the selection ratio was calculated using the following equation :

$S_i = C_i/N_i \times 100$ , where  $S_i$  = mean selection ratio of a fruiting tree of species  $i$  for the period considered ;  $C_i$  = relative consumption given by the number of feeding-visits effected by monkeys to species  $i$  trees divided by the total number of visits ;  $N_i$  = relative frequency given by the number of species  $i$  fruiting trees divided by the total number of fruiting trees.

Therefore, the selection ratio of a given area  $a$  is :

$$S_a = \sum_{i=1}^n S_i \times N_{ai} \times \frac{1}{a}, \text{ where } N_{ai} = \text{number of trees of species } i \text{ in the area } a.$$

species  $i$  in the area  $a$ .

## RESULTS

### I. — HABITAT STRUCTURE AND HABITAT USE

#### A. — Home range size and vegetation structure

During the study period, the *C. cephus* troop visited 52 quadrats (Fig. 1A). The whole area was not evenly used, as the seven most visited quadrats accounted for 50 % of the visiting

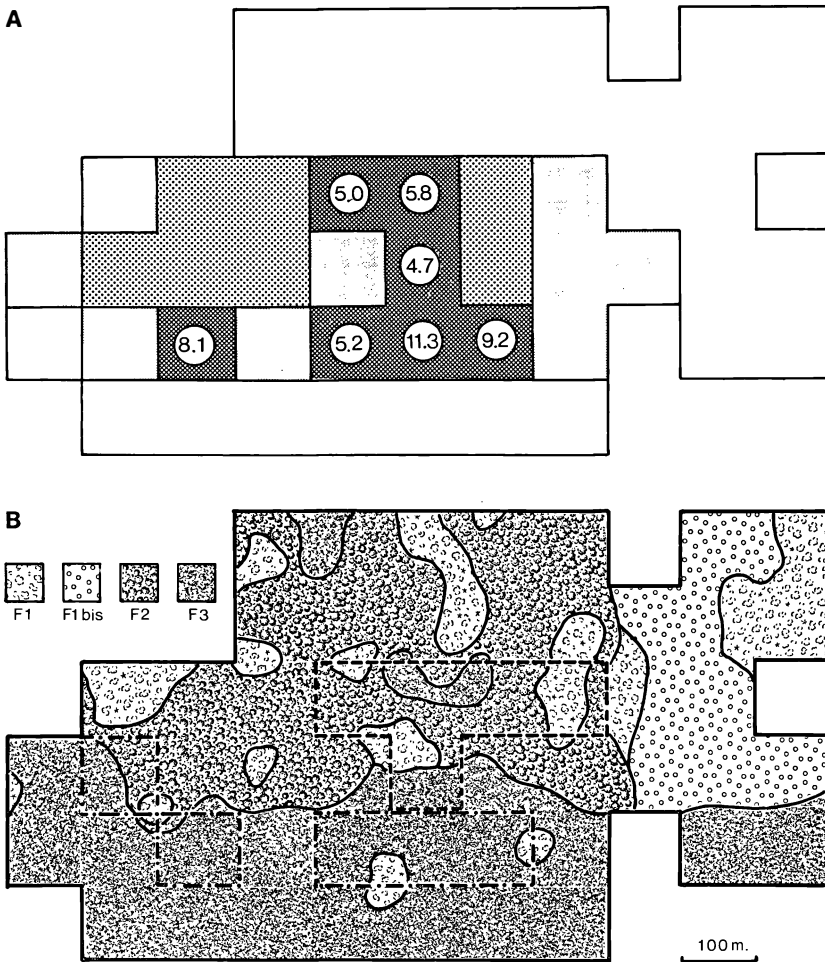


Figure 1. — A : Total home range of the troop. 50 % of the day time is spent in the seven darkest quadrats (numbers indicate their percentage use) ; 75 % in these latter quadrats and the 7 medium colored ones ; 90 % in the 23 colored quadrats. B : patchy forest structure of the home range (see text) ; - - - - - delimits the area in which 50 % of the sleeping sites were found ; - . - . - delimits the area in which 50 % of the total day resting period occurs.

time ; 14 quadrats for 75 % and 23 for 90 %. The central area was most often visited, whereas the marginal areas (29 ha) accounted for only 10 % of the time. The troop home range included a vegetation mosaic, made of 15.5 % of F1 forest, 13,2 % of F1', 32.1 % of F2 and 39.1 % of F3, distributed as shown in figure 1 B.

## B. — *Horizontal use of space*

Differences between the percent use of each forest type and the percentage expected from its surface area have been compared (Tab. I). For the whole study period, F2 and F3 were significantly more frequently visited while F1 and F1' were significantly avoided. F3 was the preferred forest type.

TABLE I

*Percentage area and use of each forest type based on radio-tracking observations.*

Differences have been tested ( $\chi^2$ ) for the percentage use of each forest type against the percentage expected from its surface area  
(\*\*\* =  $p < 0.001$ ; \*\* =  $p < 0.01$ ; \* =  $p < 0.05$ ; NS =  $p > 0.05$ ).

Forest type	% of area	% of total daily use	% of use ; fruit feeding period	% use rest period	% of use sleeping sites
F1	15.5	12.45 **	12.46 NS	12.11 *	17.17 NS
F1'	13.1	2.34 ***	3.82 ***	0.32 ***	10.18 NS
F2	32.1	35.47 *	43.58 ***	26.35 **	53.40 ***
F3	39.1	49.74 ***	40.15 NS	61.22 ***	19.25 ***
N =		1238	380	462	69

*Daily variations.* — The relative use of each forest type during the day has been calculated hourly both for the whole troop (radio-tracking observations ; Fig. 2 A) and for individuals (time-budget observations ; Fig. 2 B). Results were comparable and showed large daily variations in the forest type used. Variations were more marked for the second type of observations in which the precise locations of the animals were checked. At dawn, F1 and F2 were most often used ; as the day progressed, F3 was more and more visited with a peak in the middle of the day. A reverse trend was observed during the afternoon.

*Activity distribution in time and space.* — Diurnal variations in habitat use have been compared to the daily distribution of recorded activities (Fig. 2 C). Locomotion and fruit-feeding were maximal in the morning and in the afternoon ; rest occurred in the middle of the day. Foraging for insects took place evenly throughout the whole day, except in the early morning and late afternoon, when the light was poor. Social activities were seldom observed (for a detailed analysis, see Quris *et al.*, 1981).

Two main periods could be distinguished during the day, on the basis of the dominant activity taking place at that time ; the first, the « fruit-feeding period », lasted from 06.30 to 08.00 h



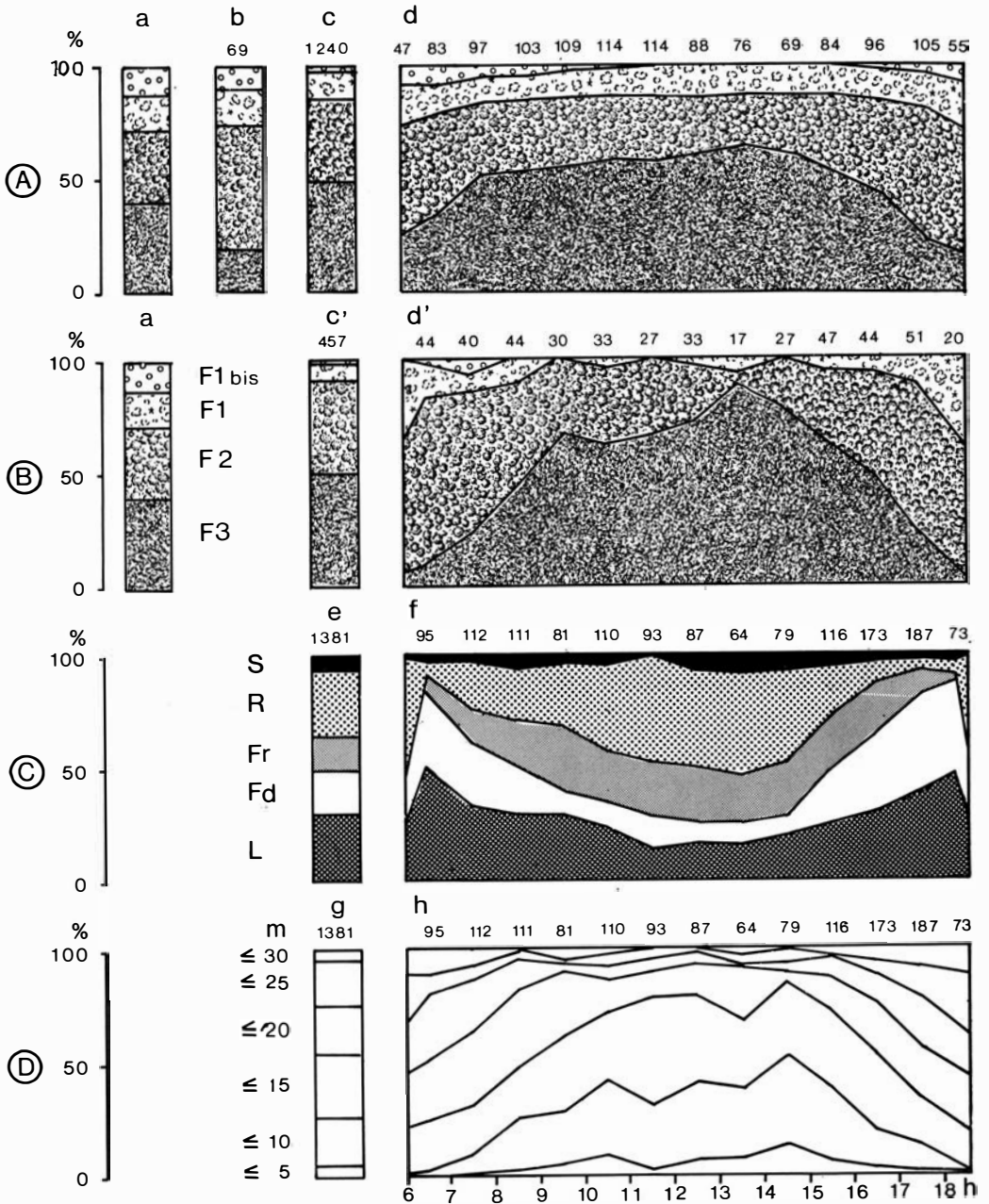


Figure 2. — A : Percentage use of each forest type by the entire troop (from radio-tracking observation) ; B : percentage use of each forest type by individuals recorded during time-budget measurements. a : percentage area of forest types ; from top to bottom, F1, F2, F3 ; b : percentage use of forest types during the night ; c, c' : during the day ; d, d' : diurnal variations of the percentage use of forest types. C : Time-budget of the troop ; e : percentage time spent in each activity during the day (S : social activities ; R : resting ; Fr : foraging ; Fd : feeding ; L : locomotion) ; f : diurnal distribution of activity. D : Cumulative percentage of the use of the height classes ; g : mean height classes used during the day ; h : diurnal variations. N : is given above each graph.

and from 15.30 to 18.00 h and corresponded to a maximum of searching for and feeding on fruit; the second, called «resting period», lasted from 10.00 to 15.00 h and corresponded to a maximum of inactivity. The relative use of the different vegetation types has been calculated for these two periods (Tab. I). During the fruit-feeding period, F2 was significantly more often visited than other forest types and F1' was significantly avoided; F1 and F3 were apparently visited in proportion to their surface areas. During the rest period, F3 was significantly more visited than the other forest types and F1' was again avoided.

The location of all observed sleeping sites was recorded (Fig. 2 Ab). The monkeys preferred to rest in the F2 forest during the night and avoided F3; F1 and F1' were apparently used in proportion to their surface areas in the study site (Tab. I).

More precise results were obtained by analysing the locations where each daily activity was performed during the time budget analysis. F1 and F1' were used significantly more often for fruit-feeding than for other activities; F3 was preferred and F1, F1' and F2 were avoided by resting animals. No differences between forest types were found for insect foraging (Tabl. II).

### C. — Vertical use of space

*C. cephus* monkeys displayed an overall preference for the heights ranging from 5 to 20 m (about 70 % of the sightings, N = 1381, Fig. 2 Dg). The cumulative percentage use of the tree height classes during day-time, showed (Fig. 2 Dh) that monkeys tended to occupy the upper forest levels before 08.00 h and after 17.00 h when the light was poor. As the day progressed, a tendency to stay at lower levels was observed, particularly between 10.00 h and 15.00 h, after which time the monkeys tended again to enter the highest forest layers.

TABLE II

*Distribution of diurnal activities according to forest types where they are performed, based on time-budget observations.*

All activities are compared to the expected percentage according to areas of each forest type; each activity to all the other activities.  
Levels of significance indicated as in table I.

Forest type	% of area	All activities	Loco-motion	F-feeding	Foraging	Resting
F1, F1'	28.8	8.5 ***	9.2 NS	18.7 ***	3.9 NS	3.6 *
F2	32.1	44.0 ***	53.2 *	48.6 NS	49.0 NS	29.2 ***
F3	39.1	47.5 ***	37.6 *	32.7 ***	47.1 NS	67.2 ***
N =		457	109	107	104	137

Such a daily pattern of vertical distribution can be related to the structure of the different forest types. As monkeys increased their use of the lowest F3 forest, they were observed at lower levels (below 15 m in 70 % of the sightings, against only 35 % in F2 ;  $\chi^2_1 = 83.2$ ,  $p < 0.001$ ). This trend was also linked with the vertical distribution of activities. For a given forest type, differences between the heights at which various activities were performed have been tested. Both in the highest F2 forest and the lowest F3, fruit-feeding was performed at a higher level than all other activities (respectively 19.5 m,  $n = 80$ , and 13.5 m  $n = 55$ , versus 16.9 m,  $n = 176$  and 11.3 m,  $n = 244$  ;  $\chi^2_2 = 13.47$ ,  $p < 0.01$  and  $\chi^2_3 = 15.22$ ,  $p < 0.01$ ).

In F3, rest occurred at lower heights than all other activities (10.9 m ;  $n = 128$ , versus 12.3 m,  $n = 171$  ;  $\chi^2_2 = 7.01$ ,  $p < 0.05$ ). Such a difference was not found in F2 forest. Not surprisingly, feeding on fruit occurred where fruit were numerous, that is to say mainly in the tree crowns. When entering into the lowest forest, the monkeys tended to enter lower layers more for resting than for other activities.

#### D. — *Seasonal variations*

No significant difference in the use of F1 and F1' was found between dry and rainy seasons, for either period of the day (Tab. III) The same was true for F2 and F3 during the rest

TABLE III

*Seasonal differences in the percentage use of each forest type.*  
DS = dry season ; RS = rainy season. Levels of significance indicated as in table I.

Forest type	Total daily use		Fruit-feeding period			Resting period			
	DS	RS	DS	RS	DS	RS			
F1	12.8	NS	12.2	12.6	NS	12.2	13.5	NS	10.7
F1'	3.1	NS	1.5	4.1	NS	3.5	0.5	NS	0.1
F2	38.5	*	32.4	52.0	**	35.2	27.0	NS	25.8
F3	45.6	**	53.9	31.3	***	49.1	59.0	NS	63.4
N =	731		507	228		152	258		204

period. On the other hand, during the fruit-feeding period, F3 was used more and F2 less in rainy season than in dry season. Consequently, whatever the season, rest was strongly correlated with F3 vegetation, whereas feeding on fruit could have taken place preferentially in one or other forest type.

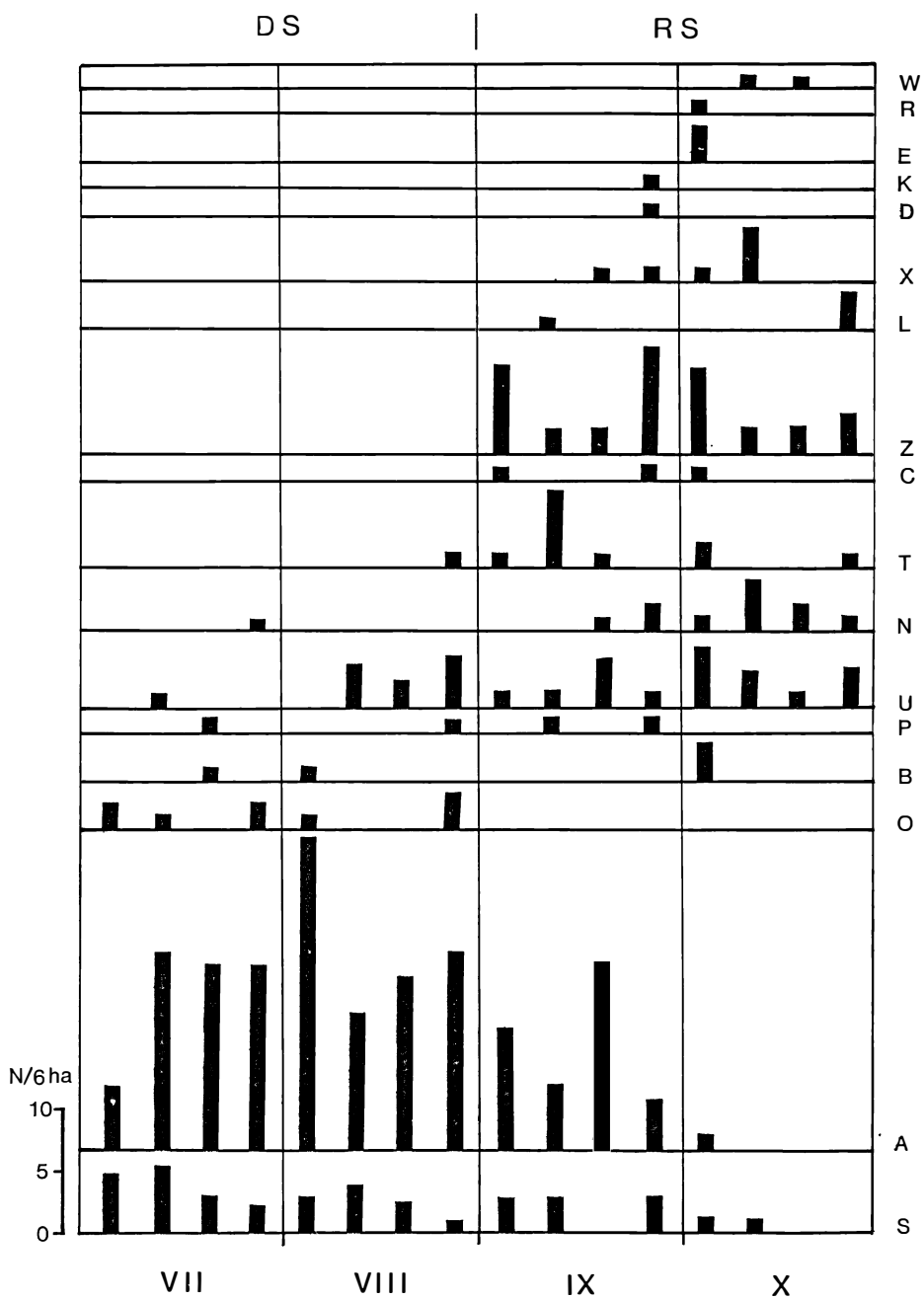


Figure 3. — Variation of the number of trees with ripe fruit for the 17 plant species analysed on 96 ha (6 ha/week). Letters refer to the latin names in table V.



rainy period. Figure 4 shows the distribution of the plant-species bearing ripe fruit on the 57 quadrats analysed on the troops' home range, during the dry and the rainy seasons (27 and 30 quadrats respectively).

The total number of fruiting trees of these species has been estimated for the total home range; it is quite comparable between the two seasons (Tab. IV). Differences occur in the total number of species by hectare; the most striking difference between the two seasons lies in the diversity of fruiting species, with twice as many species fruiting during the rains as in the dry season.

TABLE IV

*Seasonal fruit availability in the troop's home range.*

( ) : 95 % confidence limits ;  $\pm$  = standard deviation (see methods).

Seasons	Total n° fruiting trees	Mean n° fruiting trees/ha	Total n° fruiting species	Mean n° fruiting species/ha
DS	183 (157-213)	3.52 $\pm$ 2.33	7	1.70 $\pm$ 0.84
RS	186 (165-269)	3.57 $\pm$ 3.09	14	2.27 $\pm$ 1.53

B. — *Fruit species eaten and their selection ratio*

Twenty-one species were found to be eaten during the dry and rainy seasons combined, 10 in the dry season and 16 in the rainy season (Tab. V). Among the fruit eaten, 53 % came from trees and 47 % from lianas. Whole fruits were taken in 10 % of the cases, pulp in 52 %, seeds in 5 %, arils in 33 %.

A few common fruit species (here called "major species") made up the staple diet of the monkeys during the dry season. *Polyalthia suaveolens* accounted for 45 % of the trees visited for feeding and *Coelocaryon preussi* for 26 % (making up a total of 71 %). Other fruiting species were only occasionally visited. This correlated well with the relative abundance of these species in the habitat, since *P. suaveolens* had a relative frequency of 63 % (2.09 fruiting trees per ha), *C. preussi* of 25 % (0.68 trees per ha), while others were very rare (Tab. V). *P. suaveolens* is a medium sized tree producing a large number of fruit looking like black olives. *C. preussi* has a similar height but a larger crown; only the laciliate arils covering the kernels are eaten.

Four species accounted for 75 % of the trees visited during the rainy season: the lianas *Cissus dinklagei* (31 %) and *Salacia elegans* (18 %) and the trees *Pancovia pedicellaris* (14 %) and *P. suaveolens* (12 %). *Cissus* is a common fruiting species in the study area (relative frequency: 23.5 %) which produces a great

TABLE V

*List of plant species with ripe fruit available to monkeys during the dry and the rainy seasons, with their relative level of consumption (Ci), their relative frequency (Ni) in the study quadrats and their selection ratio (Si; see methods).*

27 quadrats have been studied during the dry season, and 30 during the rainy season. § = species found with ripe fruit in the home range but not in the control quadrats. T1, T2, T3 = small, medium, tall trees; L = lianas; F = entire fruit; P = pulp; S = entire seed; A = aril.

Fruit species	Qua- lity	Part eaten	Dry season			Rainy season		
			Ci	Ni	Si	Ci	Ni	Si
ANNONACEAE								
A <i>Polyalthia suaveolens</i>	T2	P	44.8	63.2	70.9	11.7	25.2	46.4
B <i>Xylopia hypolampra</i>	T3	A	1.7	1.1	154.5	—	—	—
C <i>Xylopia quintasii</i>	T2	A	—	—	—	3.9	2.8	139.3
D <i>Xylopia staudtii</i>	T2	A	—	—	—	0	0.9	0
E <i>Xylopia sp.</i>	T2	A	—	—	—	0	2.8	0
APOCYNACEAE								
F <i>Landolphia sp.</i>	L	P	—	—	—	3.9	§	—
G Unidentified	L	P	—	—	—	1.3	§	—
COMBRETACEAE								
H <i>Combretum racemosum</i>	L	S	—	—	—	2.6	?	—
CONNARACEAE								
<i>Byrsocarpus dinklagei</i>	L	A	1.7	§	—	—	—	—
J <i>Castanola paradoxa</i>	L	A	—	—	—	1.3	§	—
DICHAPETALACEAE								
K <i>Dichapetalum sp.</i>	L	P	—	—	—	1.3	0.9	144.4
EUPHORBIACEAE								
L <i>Uapaca sp.</i>	T2	P	—	—	—	1.3	0.9	144.4
FLACOURTIACEAE								
M <i>Caloncoba sp.</i>	T1	P	3.5	§	—	—	—	—
HIPPOCRATEACEAE								
N <i>Salacia elegans</i>	L	P	3.5	1.1	318.2	18.2	7.5	242.7
INVINGIACEAE								
O <i>Klainedoxa gabonensis</i>	T3	P	6.9	4.2	164.3	—	—	—
MELIACEAE								
P <i>Trichillia priureana</i>	T2	A	1.7	1.1	154.5	—	—	—
MORACEAE								
Q <i>Musanga cecropioides</i>	T2	F	—	—	—	1.3	§	—
R <i>Ficus sp.</i>	L	F	—	—	—	0	0.9	0
MYRISTICACEAE								
S <i>Celocaryon preussi</i>	T2	A	25.9	25.3	102.4	1.3	7.5	17.3
T <i>Pycnanthus angolensis</i>	T2	A	5.2	§	—	2.6	5.6	46.43
U <i>Staudtia stipitata</i>	T2	A	0	4.2	0	0	14.0	0
RUBIACEAE								
V <i>Cuivera sp.</i>	T2	P	—	—	—	2.6	?	—
W <i>Nauclea diderichii</i>	T2	P	—	—	—	1.3	0.9	144.4
SAPINDACEAE								
X <i>Pancovia pedicellaris</i>	T1	P	—	—	—	13.8	6.5	212.3
VITACEAE								
Y <i>Cissus dinklagei</i>	L	F	5.2	§	—	31.2	23.4	133.3
N =			58	95		68	107	

deal of fruit. *P. suaveolens* shows a high frequency of fruiting trees in September, a proportion which falls off sharply in October. The two remaining fruiting species are less abundant : *P. pedicellaris*, a small tree with a relatively low fruit production amounted to 6.5 % of the fruiting tree population and *S. elegans* to 7.5 %. The relative scarcity of the latter tree species suggests that their fruits are very attractive to *C. cephus* and are actively searched for.

When the selection ratios are compared (Tab. V), it becomes obvious that : 1/ some rare species (e.g. *Trichillia*, *Salacia*, *Pan-*

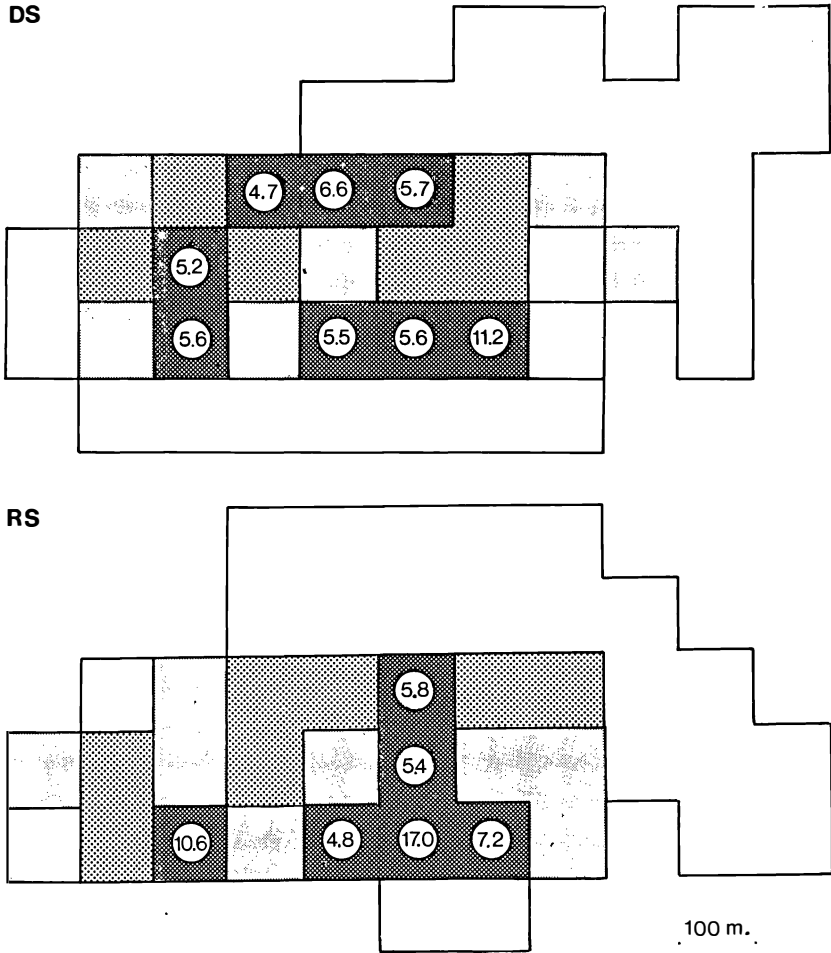


Figure 5. — Troop home range in dry (DS) and rainy (RS) seasons. Symbols as in fig. 1.



*covia*) appear to be very attractive to the monkeys ; and 2/ a given species may be heavily consumed when only a small number of other species are fruiting at that time, but far less so when other kinds of fruit become available. This is particularly the case for *C. preussi*.

### C. — Seasonal ranging patterns

During the dry season, 46 ha were visited by the *C. cephus* troop, eight of them accounting for 50 % of the time (Fig. 5A). During the rainy season, the home range covered 43 ha and the troop spent half of its time in 6 ha (Fig. 5B). Among these six

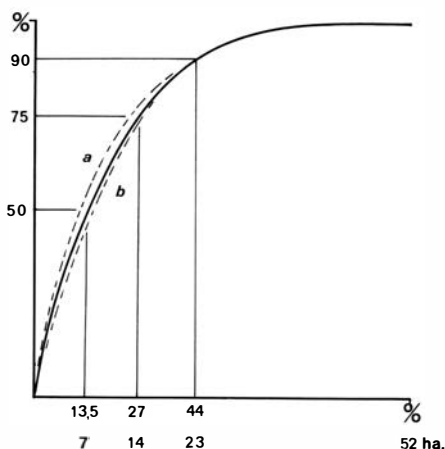


Figure 6. — Overall ranging patterns of the troop for the total period (solid line), for the dry season (b) and the rainy season (a). Percentage use of the home range (vertical axis) is given related to its area (in % and hectares ; horizontal axis).

hectares, five were the same as those preferred during the dry season. On the whole, six new hectares were added to the dry season home range during the following rains, while the use of nine others was discontinued. Both the newly visited hectares and those which were abandoned were visited only occasionally by the troop. On the other hand, the core area of the range remained very similar throughout the study period.

The overall ranging patterns for the total study period and for both seasons are shown in Figure 6. No significant difference can be found when the patterns of seasonal habitat use of the 52 hectares of the home range are compared (Kolmogorov-Smirnov,  $D_{max} = 0.086$ ,  $p > 0.05$ ). Whatever the season, about 50 % of the time was spent by the troop in less than 15 % of its home range, and 90 % in less than half of it.

D. — *Daily movements and areas visited*

Mean daily distances travelled by the two radio-equipped females during the rainy season were very similar (1 318 m vs 1 306 m); in the dry season, differences were not significant (1 303 m vs 1 206 m :  $\epsilon = 1.14$  ;  $p > 0.25$ ). A notable exception occurred in July, when female 1 left the troop for a short visit to a *Coelocaryon* fruiting tree 150 m away from the other monkeys. Finally no significant difference can be discerned for the movements of a given animal between the two seasons (for example female 2 : 1 206 m vs 1 306 m ;  $\epsilon = 1.09$  ;  $p > 0.27$ ).

On average, eleven hectares were visited daily, namely nine during the total "fruit-feeding period" and two new ones during the "rest period". Five hectares were visited during the morning feeding period and five during the afternoon ; four of them being different from those already visited in the morning. No seasonal variation in this pattern was noticed (Tab. VI).

TABLE VI

*Surface area visited daily by the troop.*

Figures based on radio-tracking observations and expressed in number of quadrats  $\pm$  standard deviation.

N° quadrats visited	All the day	During fruit-feeding period		
		Total	Morning	Evening
Dry season	10.9 $\pm$ 2.6	8.9 $\pm$ 3.0	5.0 $\pm$ 1.9	5.1 $\pm$ 1.5
N =	8	9	18	22
Rainy season	11.0 $\pm$ 1.8	9.0 $\pm$ 0.8	5.0 $\pm$ 2.5	5.4 $\pm$ 1.5
N =	4	4	16	19
Both seasons	10.9 $\pm$ 2.3	8.9 $\pm$ 2.5	5.0 $\pm$ 2.2	5.2 $\pm$ 1.5
N =	12	13	34	41

Theoretical calculations were made of the number of hectares which ought to be visited to encounter an increasing number of species in fruit, according to their abundance and distribution in the study area (Fig. 7). These calculations show that visiting eleven hectares during the dry season gives a good probability (nearly 100 %) of encountering at least the three most numerous fruiting species, and a more than 60 % chance of finding more than four. To encounter the seven available species, the troop would have to increase its searching area considerably. In the rainy season, visits to eleven hectares allow monkeys to encounter at least eight of the fourteen species available, and give them a 70 % chance of finding more than ten. To enlarge this

number, monkeys would again have to increase greatly the surface area visited every day. Therefore, whatever the season, an area of eleven hectares seems a well-adjusted compromise, allowing the monkeys to encounter the majority of the most common species without expending too much energy on travel.

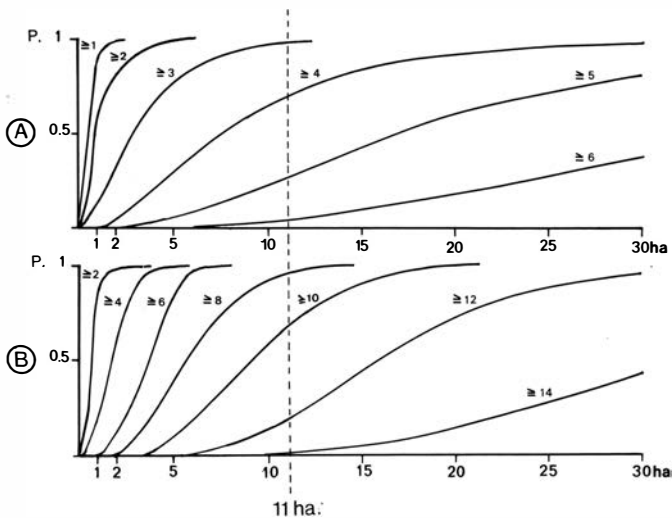


Figure 7. — Theoretical curves giving the probability to encounter a given number of fruiting species according to the area visited. The vertical dashed line indicates the mean actual area visited daily by the troop.

#### F. — *Fruit-feeding value and selection of forest types*

To test the hypothesis that differential use of various forest types during the fruit-feeding period is related to their differential fruit supply, the relative fruit-feeding value (see section on method) of the various forest types was compared to that of the total home range for the two seasons (Tab. VII).

The relatively little use made of F1 and F1' was not related to their fruit-feeding value which appears high, particularly in the dry season. Furthermore, whatever the seasonal variations of this value, no obvious difference occurred in their use by the *C. cephus* troop. This was obvious for F1', which remained the least used habitat, even in the dry season when it was apparently the richest in fruit. While no striking seasonal difference in feeding value could be found for F2 (an estimate of confidence limits at 0.95 shows that the number of fruiting trees does not differ significantly), its use decreased during the rainy season. At the same time, the percentage use of F3 increased, while its fruit-feeding value also increased with, notably, a significant increase of the number of fruiting trees (95 % confidence limits).

TABLE VII

*Seasonal variations of the relative fruit-feeding value and relative use of the four forest types.*

Forest type	Relative abundance Fruiting trees/ha		Relative abundance Fruiting species/ha		Selection ratio		Relative use	
	DS	RS	DS	RS	DS	RS	DS	RS
F1	1.67	1.37	1.23	1.22	1.47	1.28	0.82	0.79
F1'	1.99	0.52	1.54	0.84	2.09	0.76	0.31	0.26
F2	1.00	0.91	1.14	0.88	1.07	1.01	1.62	1.10
F3	0.40	1.10	0.61	1.06	0.39	0.96	0.80	1.25

However, this high value did not differ from that of F2. Thus when its richness in fruit became comparable to that for F2, the densest F3 forest was favoured, whereas the use of the most open F1 and F1' forests remained low whatever their fruit supply might be.

G. — *Fruit supply and feeding strategy during the fruit-feeding period*

As previously shown, habitat selection by *C. cephus* cannot be explained primarily in terms of fruit supply, though this parameter may act as a limiting factor during periods of low fruit availability (as was apparently the case for the use of F3 during the dry season). However, within each forest type, more subtle parameters could be expected to play a role in influencing the use of the food resource. This can be shown by analysing in detail the strategy of fruit searching during a given short period of time, taking into consideration the amount of fruit available at the same time. We have done so twice during our study period : in the middle of the dry season, and later during the rains.

Only the daily fruit-feeding period was considered. During the dry season, a positive correlation existed between the time spent in a given area of the home range and the number of simultaneously fruiting trees found there (Tab. VIII). This correlation was mainly due to the most common fruiting species (more than 70 % of the visits) and was still found when only *Polyalthia* was considered ( $r = 0.828$ ,  $p < 0.01$ ). On the contrary, no positive correlation was found with the number of fruiting species. Thus in dry season, the monkeys' feeding strategy was to rely on the most abundant fruiting species. The small number of other species in fruit and their very low densities both meant

that the animals could not diversify their diet without paying an excessive energy cost.

During the rainy season, no positive correlation was found between time spent in one part of the home range and the total number of either fruiting trees or fruiting species (Tab. VIII). However, these correlations did exist if we consider only the four species constituting the staple diet (more than 75 % of visits, Tab. V). The first seven most frequently visited quadrats included sixteen trees of these species, as against eight in the seven least visited ; the single most favoured quadrat also included five different fruiting species, among which three were selectively searched for. Thus during the rainy season, the increased number of fruiting species allowed the monkeys to select some highly attractive species, even if their densities were low : four species, among which two were scarce, significantly influenced the ranging patterns during the period of fruit-feeding.

TABLE VIII

*Correlations between habitat use during the fruit-feeding period and food parameters.*

(Spearman rank correlation ; number of quadrats analysed = 14 in dry season ; 14 in rainy season). Levels of significance indicated as in table I.

Food parameters	Dry season	Rainy season
N° fruiting trees/ha (all species)	0.704 **	0.306 NS
N° fruiting trees/ha (major species)	0.720 **	0.589 *
N° fruiting species/ha (all species)	0.362 NS	0.284 NS
N° fruiting species/ha (major species)	0.360 NS	0.628 *

## DISCUSSION

The available vegetation types within the home range of a *C. cephus* troop were used unevenly. The most preferred forest type was the lowest and densest one ; the most strongly avoided was the highest with the more open understorey. These preferences varied greatly according to activity and time of day ; they differed less clearly according to season. Three categories of factors may influence such choices : predation, competition and food availability. They will be discussed in turn.

1/ Whatever the season, the forest with the more open understorey was favoured by monkeys for night-resting. Though sleeping sites were sometimes located near fruiting trees, which monkeys rapidly visited at dawn and dusk, such a choice could not be explained by food availability. There was no obvious shortage

of sleeping sites and the observed tendency of neighbouring troops of different species to join together for the night can probably be ascribed to increased protection from predators. It must be remembered that during the night, all potential predators in north-eastern Gabon are scansorial (leopards and pythons). An open understory reduces the number of locomotion supports which could help them to reach the canopy where the monkeys are sleeping. Predators are also easier to locate when detected in an open environment.

The best evidence for this interpretation is given by the quasi-experimental situation provided by the F1' forest type ; here clearing has resulted in the monkeys abandoning the site during the day (17.5 % of relative use vs 82.5 % for F1 with natural undergrowth), while the site continued to be used for resting during the night.

2/ Whatever the season, the densest F3 forest was favoured during the day resting period, and more than 67 % of the monkeys recorded at rest have been located in this habitat category. Rest is clearly incompatible with active searching for food ; furthermore, this lack of activity leads to a decrease in watchfulness and requires as secure a place as possible. F3 forest — with its poor penetrability and low field of visibility due to the tangle of lianas, high foliage density and the absence of any strong support for locomotion — is probably the best suited for this purpose, all the more so as resting monkeys have been found to occupy the lowest levels.

During the day, the animals face only two potential sources of danger, Man and the Crowned-Hawk Eagle (*Stephanoetus coronatus*), since scansorial felids and snakes are mainly nocturnal. Man is not a predator in the study site, but our own experience has shown that monkeys are much more difficult to detect in F3 forest than in other forest categories. Moreover, we have found that monkeys, when chased, tended to hide motionless in dense foliage instead of fleeing.

The Crowned-Hawk Eagle is a common bird in the study area and the monkeys react violently to sightings of the bird. Its predation pressure upon monkey populations is difficult to estimate ; it might however be far from negligible, as we observed three attacks (one of which was successful) during a period of 720 observation hours.

3/ Most fruit-feeding took place in early morning and late afternoon. Sixty seven per cent of the animals seen feeding on fruit were located in the highest and more open F1, F1' and F2 forests, with nearly 49 % in the latter type, while 33 % were recorded in F3. On the whole, fruit production was highest in F1 and F1' and lowest in F3 ; F2 was in an intermediate position. The fact that monkeys prefer F2 to F1 and F1' may be due

either to the fact that its understorey is more dense, thus affording a better protection against predators, and or to the fact that it abounds in other food items, especially insects. Indeed, 96 % of the foraging for insects occurred in F2 and F3 forest types (Tab. II), while no significant difference was found between them. Moreover, the F2 forest was no longer preferred for fruit-feeding during the rains, when fruits were as numerous in F3 as in F2.

All these results strongly suggest that the optimal habitat for *C. cephus* monkeys is one with a dense understorey providing them with safe resting places where predation pressure is minimal. It is only when food becomes too scarce and not diversified enough to meet their nutritional requirements that monkeys are forced to enter more open environments. However, these more open forests are exploited only in the morning or late afternoon when the understorey is dark enough to prevent predators which hunt by sight (eagle) to easily detect their prey. This suggests that to feed in a rich but potentially dangerous environment is less advantageous to the species than to search for food in a poorer habitat where less time has to be devoted to look out for predators or where the risk of predation is less important.

4/ Whatever the forest type and the season, fruit availability influenced habitat use only during the diurnal peaks of fruit-feeding. Two patterns were observed. When fruit-feeding species were scarce (dry season), the *C. cephus*'s strategy was to select parts of the home range containing the highest density of fruiting trees, focusing on the two most abundant species at the expense of diet diversity ; when the diversity of the species fruiting increased (rainy season), monkeys selected the areas which contained several highly attractive fruits. The potentially most critical factor during the dry season could thus be the low species diversity of fruiting trees. In such circumstances, the monkeys have a small number of fruit categories at their disposal, and run the risk of having an imbalanced diet.

5/ The potential role of insect availability could not be inferred from the present study. Since foraging for prey was kept at a constant level throughout the day (except at dawn and at dusk) and took place in F2 and F3 forests in accordance with their relative percentage use, it is likely that these two forest types were equally suitable for insect-collecting. But the same kind of prey is not necessarily found in each vegetation type and possible differences in insect availability may lead to further differences in habitat use, the more so as the prey spectrum of *C. cephus* is large (Gautier-Hion, 1980).

6/ Although it appeared that the F3 forest plays in the first place a protective role against diurnal predation of *C. cephus*, one may also wonder whether it also acted as a shelter against excess heat and solar radiations. During the dry season, the sky

is always overcast in the Makokou area, while sunshine is much more frequent during the rainy season. However, during the hottest part of the day, F3 forest is used in a similar way and to a similar extent in the dry season as it is the rains (Tab. III).

7/ The habitat preferences of the neighbouring polyspecific troop where a *C. cephus* troop was associated with *C. nictitans* and *C. pogonias*, have been analysed using the same methods as for the monospecific *C. cephus* troop, and during the same time period. Our unpublished results show that its home range included less than 20 % of F3 forest and that this forest type was not significantly selected, even for day-resting. However, when separated from *C. nictitans* and *C. pogonias*, the *C. cephus* members of this large mixed band tended to enter more frequently into the densest F3 forest than their associates. Consequently the preference of *C. cephus* for visiting the densest forest type, a characteristic not shown by *C. nictitans* and *C. pogonias*, contributes to some extent to an habitat partitioning with syntopic *Cercopithecus* species.

## RESUME

Ce travail analyse l'influence relative de la structure de la forêt et de la disponibilité en fruits sur les modes d'utilisation de l'habitat par une troupe de *Cercopithecus cephus*. Il montre que :

1/ La structure de la végétation est le facteur déterminant de l'utilisation de l'habitat pendant la période journalière de moindre activité et durant la nuit. Pour l'établissement de leur site de sommeil, les singes choisissent une forêt haute au sous-bois clair, tandis qu'une forêt basse et un couvert dense sont significativement recherchés pour le repos journalier.

2/ Que la disponibilité en fruits influence l'utilisation de l'habitat pendant les deux courtes périodes matinale et vespérale pendant lesquelles la collecte et l'ingestion de fruits par les animaux sont maximales. Quand la diversité des espèces fructifiant est faible, l'utilisation du domaine vital est déterminée par la distribution des deux espèces végétales les plus abondantes (saison sèche). Au contraire, quand cette diversité augmente (saison humide), les singes visitent les parties de leur domaine qui comprennent plusieurs espèces appétentes, même si leur densité spécifique est faible.

3/ En dépit de variations saisonnières de la disponibilité en fruits, les mouvements journaliers et la surface prospectée chaque jour par la troupe ne varient pas sensiblement d'une saison à l'autre. Ceci peut s'expliquer par le fait que cette surface correspond au compromis optimal d'un point de vue énergétique. On montre en effet que, quelle que soit la saison, les animaux



devraient considérablement augmenter la surface visitée pour accroître sensiblement leurs rencontres avec de nouvelles espèces végétales (en raison de leur faible densité). Il en résulte qu'en saison sèche, pendant laquelle un nombre réduit d'espèces fructifient, le facteur limitant pourrait être la faible diversité spécifique conduisant les animaux à un régime mal équilibré.

4/ La disponibilité en fruits n'a d'influence sur l'utilisation de l'habitat que si la structure de celui-ci convient aux animaux. On montre, en effet, que l'utilisation de la forêt haute au sous-bois clair, n'est pas accrue quand sa richesse en fruits augmente, tandis que, lorsque la forêt la plus dense devient aussi riche que les autres, elle est significativement la plus utilisée quelles que soit l'heure de la journée et l'activité en cours.

5/ La recherche et la capture des proies s'effectue tout au long de la journée (sauf aux heures de moindre luminosité) et dans la forêt claire comme dans la forêt dense ; elles ne semblent donc pas être déterminantes dans le choix de l'habitat.

6/ La sélection par *C. cephus* d'habitats de structure différente selon la période du cycle nyctéméral est interprétée en termes de stratégie anti-prédation. Pendant la nuit, les singes font face à la prédation qu'exercent des prédateurs non volants et venant du sol (pythons, panthères), en choisissant une forêt haute au sous-bois dégagé, qui comporte peu de supports permettant aux prédateurs d'atteindre la couronne des arbres où dorment leurs proies. Au contraire, pendant le jour, les singes choisissent les niveaux peu élevés d'une forêt au sous-bois encombré qui les dissimulent le mieux au prédateur diurne essentiel qu'est l'Aigle des singes (*Staeophanoetus coronatus*).

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