

主論文の要旨：

「ガボン、プチロアングのチンパンジーに関する社会生態学的研究」

チンパンジー3亜種のうち、中央アフリカの熱帯季節林に生息するツェゴチンパンジーに関する詳細な社会生態学的研究は少ない。本研究はアフリカ、ガボンの海岸域に発達したプチロアング森林に生息するツェゴチンパンジーを対象に、チンパンジーの離合集散性および食性に影響する環境要因を明らかにしたものである。まず、環境特性を把握するために1年間にわたって気温と降水量、果実の分布、現存量を定量的に調査し、この地域に明瞭な乾期があり、乾期と雨期で果実の分布および現存量に大きな季節変化が存在すること、海岸域と内陸域とで果樹の分布様式および種構成に著しい差違があることを見いだした。また、この地域には他の類人猿の生息域では果実を補う食物となっている地上性草本類の密度が低いことを明らかにした。次に、これらの環境特性がチンパンジーの食性およびグルーピング・パターンに与える影響を分析した。チンパンジーのフンに含まれる未消化の食物の分析により、プチロアングのチンパンジーの食性は果実を主要食物とすること、チンパンジーの食性は顕著な季節変動を示すことを明らかにした。チンパンジーが利用する果実の多様性は森林内の果実食物の多様性に相関するとともに、森林内の果実の分布とも相関していた。チンパンジーは森林内の果実食物が比較的一様に分散しているときは多くの果実種を利用し、果樹の分布に片寄りが大きいときは利用する果実種数は少なくなっていた。また、チンパンジーのベッドグループ・サイズを分析し、プチロアングのチンパンジーの離合集散の季節変動を決定する要因を明らかにした。他の調査地ではチンパンジーは遊動域内の果実密度が高い時に集まる傾向がみられるが、遊動域内の果実密度の如何にかかわらず遊動域内の果実の分布にかたよりが大きいときに集まり、かたよりが小さいときは分散する傾向がみられた。これらの結果を他地域のチンパンジーの生態特徴と比較した結果、プチロアングのチンパンジーは地上性草本類の不足によって果実の分布状況に強く影響される傾向が強く、限られた場所に集中分布をする果実種に集まり大きな集団を作ることが示唆された。これはサバンナに生息するチンパンジーと共通な特性である。地上性草本類の少ないプチロアングのチンパンジーが大きな集団をつくることから、地上性草本類の欠如はチンパンジーの凝集性を必ずしも低下させず、特定の森林環境のもとではむしろ凝集性を増加させるという可能性が示唆された。

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Socio-Ecological Study on the Chimpanzees of Petit Loango, Gabon

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by
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Chapter 1. INTRODUCTION

Chimpanzees live in a variety of habitats such as tropical rain forest, seasonal forest, woodland and woody savanna (Nishida and Hiraiwa-Hasegawa 1987). Socio-ecological features such as grouping pattern, home range size, diet etc. differ between these habitats (Boesch 1996; McGrew 1983). This implies that they have a flexibility to respond to various habitats (McGrew 1992). Therefore, comparison of chimpanzee response to various environmental factors between habitats may reveal the essential socio-ecological characteristics that are common among chimpanzees of various habitat. Although there are several studies on the relations between chimpanzee socio-ecology and characteristics of their habitat, little information is available on Pan t. troglodytes subspecies and on those living in tropical seasonal forest of central Africa (Wrogemann 1992), while detailed studies have been conducted on the eastern (Mahale, Matsumoto-Oda et al. 1998; Nishida and Uehara 1983, Gombe, Wrangham 1977; Goodall, 1986, Kibale, Chapman et al. 1995; Wrangham et al. 1996) and western (Bossou; Sugiyama and Koman, 1992, Yamakoshi 1998, Tai; Boesch 1996; Doran 1997) subspecies.

In this study, I present data on socio-ecological features of Pan t. troglodytes subspecies in the seasonal rain forest, the Petit Loango forest. Data presented here is considered to fill the gap of studies. There are also unique characteristics of the Petit Loango forest; scarce terrestrial herbaceous vegetations (Furuichi et al. 1997; Yamagiwa et al. 1995). There are lots of arguments to date about the importance of THV on chimpanzees foraging strategy and grouping pattern. Data from the habitat which lacks THV may clarify its influence on chimpanzee grouping pattern.

First, the vegetation of the forest is described in detail in order to make clear the environmental characteristics of the Petit Loango forest (Chapter 3). Several characteristics of the coastal area of the Petit Loango forest other than scarce THV is presented. Second, the general features of the diet of chimpanzees is presented in the Chapter 4. The seasonal variation in the diet is analysed in relation to the fruit phenology. Lastly, the data on seasonal

changes of the bed group size of chimpanzees is presented in the Chapter 5. It is analyzed in relation to fruit phenology. Through this analysis, it is suggested that the distribution of fruit food patches is primarily responsible for the size of bed groups of the chimpanzees in Petit Loango. In the end of the Chapter 5 the relationships between mean bed group size of chimpanzees and their diet is analyzed, and then the foraging strategies of the chimpanzees in the Petit Loango is re-constructed with reference to the environmental characteristics of Petit Loango forest.

Chapter 2: STUDY AREA AND METHODS

2-1. Study site

The Petit Loango Reserve (2° 20' S, 9° 35' E) is located in the southwestern coast of Gabon, central Africa. It covers an area of 500 km², surrounded by three hunting domains. The reserve faces the Atlantic Ocean to the west and contacts with lagoons in the north and south. There is no boundaries such as large rivers or huge mountains that restrict the movement of the apes and the elephants from/to the outside of the Reserve. The geography is almost flat. The soil is “sandy-argillaceous” or “argillaceous-sandy” and contains much salts and lime (Richard and Léonard, 1993). Forest of the study area was a complex mosaic closed canopy forest, open canopy forest, inundated forest, coastal scrub, secondary forest, and savanna. Closed canopy forest is characterized by closed canopy and a relatively low density of shrubs and small trees. Within the closed canopy forest, large patches of sometimes as large as 1 km² of Sacoglottis gabonensis monodominant patch was distinct. Open canopy forest is characterized by the partly or completely open canopy, with relatively much shrubs and small trees. Inundated forest is characterized by the wet and marshy ground throughout the year. Coastal scrub is characterized by the abundant shrubs and small trees with few emergents. Small patches of savanna about 0.3 km² were frequent between 0.2-0.5 km from shoreline.

The research on the primates living in the Reserve began in 1994 (Yamagiwa et al. 1995). Yamagiwa and his colleagues surveyed the density of diurnal primates in the interior area of the Reserve. In 1995, Furuichi entered in the coastal area of the Reserve, and compared the densities of the apes between coastal and interior area (Furuichi et al. 1997). Both of these researches were conducted during a short period. This study is the first long-term survey of the apes which covered more than one year.

Field study was conducted for 17 months during 1997 and 1998. The main study area was established in the coastal area covered approximately 20 km² (Figure 1). Annual rainfall

in 1998 was 2333 mm. The year was divided into two seasons; the rainy season (January to March, October to December) and the dry season (April to September). There was two weeks of dry period (1st to 13th of february) distinct in the middle of rainy season. According to the climatic data on the nearest city, Gamba, annual rainfall of 1998 fall within the range of recent 10 years, although the beginning of the dry season was earlier. Mean monthly maximum and minimum temperature ranged from 30.5 C° to 25.4 C° and from 25.0 C° to 21.2 C°, respectively (Figure 2).

2-2. Data collection

Vegetation census

A total of four km of vegetation transect was installed (Figure 1) consecutive three km in the coastal area and one km in the inland area. Transects ran from west to east, almost vertically to the shoreline. Coastal transect started from shoreline. Western end of the inland transect was about 10 km from the coast. I identified and measured the diameter of all trees of more than 5 cm of DBH in a 10 meter strip, that is, ≤ 5 m of ether side of the transect line. I classified the counted trees into 3 categories according to their DBH; large tree (DBH ≥ 30 cm), middle tree (DBH ≥ 10 cm and < 30 cm), and small tree (DBH < 10 cm). I regard the large trees as "adult" (Williamson 1988) i.e. fruit producing, although the minimum DBH of the fruit production would be smaller for several species. Transect line is divided by either 0.5 km and 50 m, and each {0.5 km (transect line) x 10 m (strip width) was called "segments", and each area of {50 m (length of segment) x 10 m (strip width)} was called "unit" for the present analysis. Similarities in the species composition between every pair of units was compared by using Pianka's α index (Pianka 1973) which was calculated by the following formula:

$$\alpha_{a,b} = \frac{\sum_{i=1}^S (p_{ia} \times p_{ib})}{\sqrt{\sum_{i=1}^S (p_{ia})^2} \times \sqrt{\sum_{i=1}^S (p_{ib})^2}}$$

wherein α_{ab} indicates the similarity between the unit a and b, S indicates the total number of tree species counted in the census, p_{ia} and p_{ib} indicates the number of individual tree of species i in the unit a and b, respectively.

The density of terrestrial herbaceous plants were assayed on the same transect. Quadrats of 1 m x 1 m were established at the eastern end of each unit, and I counted and identified the number of stems of herbaceous plants within these quadrats.

Fruit phenology and availability of water sources

Monthly fluctuation in fruit patch density, diversity and distribution is monitored by fallen fruits census. A total of 40.1 km of transects were installed in the study area (Figure 1). I walked along these transects once a month, counting and identifying the number of individual trees (or lianes) which had fallen fruits within a 2 m width strip of the transect line. Fruit food patch density in a given month is defined as the density of chimpanzee food and possible food trees counted in the census. Possible foods are determined in reference to the diet of other Pan t. troglodytes study sites i.e. Lopé, (Tutin et al. 1994), Ndoki, (Moutsamboté et al. 1994) and Okorobikó (Sabater-Pí 1979); fruit species eaten by chimpanzees of at least one of those sites were regarded as possible chimpanzee foods. Species diversity of fruit and possible food is indicated by the number of chimpanzee food and possible food species counted in the census. Distribution of fruit food patches was measured by the coefficient of dispersion (CD, Sokal and Rohlf 1995). This is the ratio of the variance to the mean number of fruit food trees on a 1 km sections of transect as unit; the larger the CD is, the more clumped the distribution.

Availability of water sources has been suggested to be an important factor which

influences chimpanzee party size (Baldwin, et al. 1981; McGrew, et al. 1981; Tutin, et al. 1983). I assessed its monthly fluctuation by counting the number of streams which crossed the transect during the monthly fallen fruit census. Although this number is not consistent with the real number of streams because some stream cross the transects several times as they curve, it reflects the amount of drinkable water sources.

Food and possible food for chimpanzees

Since chimpanzees in the study area were not well habituated to human observers, it was difficult to get dietary data from direct observation. Therefore, I used the data of fecal analysis as main source of the information on the diet of chimpanzees, and supplemented them with those data by direct observations and feeding remains. Feces collected in the field were washed carefully by hand in 1-mm mesh sieves. Fruit contents were sampled and identified afterwards. Only the fresh dung was used for analysis because some of the contents might have been lost from old dungs by the time of collection.

I have collected 274 fresh fecal samples in the Reserve through our field study period. All these samples were used in analyzing the general tendencies of the diet of chimpanzees in Petit Loango. Out of these samples, 227 feces which were found in the main study area from January to December 1998 were used for the analysis of the seasonal changes in the diet. I have measured the chimpanzee relative dependence on fruit foods in a given month by mean volume percentage of fruit remains per sample. Diversity of fruit diet was measured by mean number of fruit food species per sample. These figures were not calculated for March, April and September due to the small number of fecal samples. Number of fecal samples for other months are indicated in Figure 7a.

Bed group size

I use the term "chimpanzee bed" to refer to so-called "chimpanzee nest," because the

construction is not used as home-base or for breeding (Baldwin, et al. 1981). Two beds of within 15 m were regarded as belonging to the same bed group unless they were of different ages. Age of beds were classified as follows; fresh---<1 week old, vegetation all green, old---vegetation dry and changing in color, rotting---bed beginning to disintegrate. Differences of age in date between fresh beds were discriminated if they were confirmed by the condition of fecal remains or feeding traces. Bed group size is the number of beds in a given bed group. It is thought to be the number of weaned individuals who stayed together for one night. Bed group size of the old or rotting bed groups, however, do not well reflect the the number of weaned individuals who stayed together for one night, as some beds might have been lost (Tutin and Fernandez 1983). Only the bed group size of fresh bed groups were therefore used in present analysis.

Gorillas (gorilla g. gorilla) are living sympatrically in Petit Loango Reserve and they also construct beds of similar forms to those of chimpanzees (Furuichi et al. 1997). It was very difficult to distinguish the bed constructors unless beds were accompanied by fresh dung because most of the gorilla beds were constructed in the trees, like the chimpanzee beds. Nevertheless, there are tendencies that gorillas construct larger beds than chimpanzees, whereas chimpanzee beds are higher than those of gorillas (Suzuki and Takenoshita in prep-a). Thus, for the beds unaccompanied by ape feces, I estimated the bed constructors of given bed groups by the size and height of beds. The outline of the method is developed by Furuichi et al. (1997), and I modified it as summarized in Figure 3. The bed groups of chimpanzees used in this study was 182. Seventy-seven groups were confirmed by the fecal evidences and 105 groups were estimated by this method. Mean bed group size was calculated for each month. Data on February was excluded from present analysis due to the small sample size. Only one bed group consisting of a single bed was found in February.

Chapter 3. VEGETATION

INTRODUCTION

A number of studies have been conducted to date on the ecology of chimpanzees (Pan troglodytes) and gorillas (Gorilla gorilla) living sympatrically (Kuroda et al. 1996; Nishihara 1995; Remis 1997; Sabater-Pí 1977; Sabater-Pí 1979; Tutin et al. 1991; Yamagiwa 1996). Those studies revealed that the dietary overlap in the plant food of the two ape species is great, especially for fruit food (Kuroda et al. 1996; Tutin and Fernandez 1993; Williamson 1988). Accordingly, it is expected that the chimpanzees and the gorillas would be competing for fruit food (Kuroda et al. 1996; Yamagiwa 1996). However, such competition does not seem to be strong. In any study sites, the range of chimpanzees and gorillas are overlapping, and encounters of the individuals of the two species are rarely antagonistic (Suzuki and Nishihara 1992; Yamagiwa 1996). In the Ndoki forest, co-feeding of figs in the same tree was observed (Suzuki and Nishihara 1992).

It is suggested that the competition between chimpanzees and gorillas is avoided by differentiating feeding habit each other (Kuroda et al. 1996; Tutin et al. 1991). Chimpanzees depends heavily on fruits all through the year. Gorillas, on the other hand, depend on fibrous foods such as leaves, piths, barks and roots more frequently than chimpanzees, especially in the less-fruiting season (Nishihara 1995; Remis 1997; Tutin et al. 1991; Williamson 1988; Yamagiwa 1996).

The Petit Loango forest is one of the habitats where the chimpanzees (Pan t. troglodytes) and the gorillas (gorilla g. gorilla) are living sympatrically. The forest which developed in the coast is distinct from other study sites by the scarce terrestrial herbaceous vegetation (Furuichi et al. 1997; Yamagiwa et al. 1995), which is important fallback foods for both the chimpanzees and gorillas in other study sites (Malenkey et al. 1994). Therefore, lack of THV foods might cause strong competition for fruits between chimpanzees and gorillas, and then reduce the density of one or both of them. However, the densities of the

apes in the Petit Loango forest seem to be high (Furuichi et al. 1997; Suzuki and Takenoshita in prep-a).

In the Petit Loango forest, the influence of the forest elephants (Loxodonta africana) on the interspecies relationships of the apes should not be neglected. The elephants are living in high density in the Petit Loango Reserve (Suzuki et al. 1999). The ecology of the elephants would affect the interspecies relationship between chimpanzees and gorillas, as it is suggested that the ecological features of forest elephants is similar to that of chimpanzees and gorillas (White et al. 1994).

The purpose of this chapter is to investigate the characteristics of vegetation of the Petit Loango which should influence the density, ranging and grouping pattern of chimpanzees and gorillas, and interspecies relationships between them. Our interest is the possibility whether there are specific features in the vegetation of the Petit Loango forest that buffer the possibly strong interspecies competition for fruit foods among the chimpanzees, gorillas, and elephants caused by the lack of THV.

RESULTS

Tree density, species diversity, and food tree density

We counted total of 2992 trees (748 ind. / ha) of 125 species, and 75 woody lianes (18.7 ind. / ha) of 26 species in the transect. Forty seven percent of trees (1421 ind.) were small trees. Total basal area of the middle and large trees was 133.8 m² (33.45 m² / ha). Total basal area of lianes with ≥ 5 cm DBH was 0.58 m² (0.15 m² / ha).

Out of the top 10 tree species in terms of the number of trees along the transect, 8 species of fruits were eaten by chimpanzees, gorillas and the elephants (Table 1). Sixty-seven percent of the middle or large trees were possible fruit foods for the chimpanzees, 63 % for the gorillas, and 47 % for the elephants.

THV density

Herbaceous plants were extremely scarce in both coastal and inland area. No stems of Marantaceae, Zingiberaceae, Araceae, Commelinaceae, or Palmae was counted in the quadrat. We sometimes observed the stems of such herbaceous plants out of the transect, but they were quite rare.

Density and distribution of the fruit food species

The density of the fruit food trees appeared to be higher in areas within 2.0 km from the shoreline than in other areas for the chimpanzees, gorillas, and elephants. First, large food trees were more frequent in the segments between 1.0 and 2.0 km from the shoreline in terms of both the tree density and the basal area than in the other segments (Figure 4). The high density of Sacoglottis gabonensis, which is the important food for the apes and the elephants, was mainly responsible for the high fruit food tree density between one and two kilometers from the shoreline.

Next, although the fruit tree density and basal area in the segment within 0.5 km from the shoreline were not as high as those between 1.0 and 2.0 km from the shoreline, Eugenia sp. and Annona sp., which were consumed by the chimpanzees, gorillas and the elephants, were highly available in this segment. The former is a low tree species which produces fruits even when its DBH is less than 30 cm. The density of Eugenia with the DBH ≥ 10 in this segment was 102 individuals per ha, and its basal area was 3.10 m² per ha. The latter is a small woody vine which occurs in the coastal scrub. Fruits of those species were highly preferred by the chimpanzees when they were fruiting. In addition, clumps of large trees of Manilkara fougilloyara and M. cf. lacera occurred frequently along the shoreline, though only one tree was counted in our transect. This species was also preferred by the chimpanzees and gorillas, and consumed by the elephants.

Forest structure

Forest structure was different both between coastal and inland transect and within the coastal transect (Table 2). The segment of coastal transect within 0.5 km away from the shoreline contained more small trees but less large trees than the other segments. The segments within 0.5-2 km away from the coast contained more large trees but less small trees than in the other segments. Forest structure was similar between the segments within 2-3 km from the coast and segments of inland transect. Both segments contained more middle trees, but less large trees.

Species composition

The forest in the coastal area appeared to be less diverse than in the inland area in terms of the tree species. In the coastal transect, density of tree species was lower than in inland transect. The number of tree species in a given sample area in the coastal transect was smaller than that of inland transect (Figure 5).

Species composition also differed between the coastal and the inland transect and within the coastal transect by the distance from the coast. First, the species composition within 0.5 km from the shoreline was different from those of the other areas. Species-area curve for the coastal transect reached a small plateau at around 0.5 km from the coast (Figure 5). Matrix of α index also indicates the units within 0.5 km from the shoreline clustered (Figure 6a). Within the fruit food for the apes and elephants, Eugenia sp. were frequent. As mentioned above, Eugenia sp. was preferred by chimpanzees and gorillas, but not frequently consumed by the elephants.

Next, the units between 1.0 and 2.0 km from the coast were clustered by the similarity of tree species composition among them and difference from other units (Figure 6a). Within the ape and elephant fruit food species, Sacoglottis gabonensis, Irvingia gabonensis, Hexalobus crispiflorus were abundant in this area. Sacoglottis gabonensis and Irvingia

gabonensis were highly preferred by chimpanzees, gorillas, and elephants. Hexalobus crispiflorus was preferred by the gorillas and elephants, but not frequently consumed by the chimpanzees (Suzuki et al. 1999).

Species composition of the units between 2.0 and 3.0 km from the shoreline were similar to those of the inland transect (Figure 6a). Small and middle trees of Garcinia cf. smeathmannii were common within these units. Within the ape and elephant fruit food species, Strombosiopsis sp. was frequent in these area, but this species was not frequently consumed by them.

Distribution of large trees

Marked difference was found on the distribution of large tree species between the coastal and the inland area; the coastal area appeared to be a mosaic of the small monodominant patches of 0.2-0.5 km width, while the species were well mixed in the inland area. Matrix of α index exhibited several small clusters of four to ten consecutive units in the coastal transect, (Figure 6b). Only single or two species were responsible for the large similarities within such clusters. In contrast, such clusters was not observed in the inland transect; most of the units resembled mediately, i.e. values of α index being 0.5-0.6, with each other (Figure 6b). The dominant tree species which formed monodominant (or bi-dominant) patches along the transect were Dalbergia sp. (unit 1-8), Berlinia grandifolia (unit 11-13), Sacoglottis gabonensis (unit 22-25), mix of Irvingia gabonensis and Hexalobus crispiflorus (unit 17-21, 26-33), and Anthostema aubryanum (unit 51-54). We also observed monodominant patches of other species out of the transect; Vitex doniana and Uapaca guineensis along the large streams, Manilkara fouilloyara and M. cf. lacera along the shoreline, Staudtia gabonensis, and Khaya ivorensis in the closed canopy forest. Many of these species are important fruit foods for the apes and the elephants (Chapter 4, Suzuki et al. 1999).

According to the difference in the forest structure, species composition and distribution presented here, we refer the term "coastal forest" to the area <2 km from the coast, including "coastal marginal forest" to the zone <0.5 km from the coast, "transition forest" to the zone within 2-3 km from the coast, "inland forest" to more interior areas.

DISCUSSION

Tree density in the Petit Loango forest was similar to that of other seasonal tropical forest where the chimpanzees, gorillas and the elephants are living sympatrically, i.e., Lopé (Table 3). The density of chimpanzee and gorilla fruit food trees were also consistent with Lopé. Therefore, fruit food density in the Petit Loango forest appears to be comparable to those of other seasonal tropical forest study sites like Lopé.

In contrast, the density of herbaceous plants was quite low in comparison with other study sites. In the other habitats of Pan t. troglodytes and Gorilla g. gorilla, there are plenty of herbaceous plants e.g. 2.25 stems / m² in Ndoki and 7.66 stems / m² in Lopé (Malenky et al. 1994; Rogers and Williamson 1987). Therefore, the scarcity of the THV is the major difference between Petit Loango and other tropical seasonal forests habitats of the chimpanzees and gorillas. This difference might be caused from the difference in soil structure. The soil of the Petit Loango forest may be alkalic because it contains much lime (Richard and Léonard, 1993). As many herbaceous plants do not prefer alkalic soil, THV is scarce in Petit Loango.

The scarcity of THV might be the limiting factors to the density of chimpanzees, gorillas and elephants, especially to those of gorillas and elephants because these two species depend on herbaceous foods more than chimpanzees do. According to Furuichi's calculation, the density of chimpanzees (0.78 individuals per km²) was consistent with that in Lopé while the density of gorillas (0.21 individuals per km²) was lower than that in Lopé (Furuichi et al. 1997). As for the elephants, our data suggests that the density of elephants in the study area is consistent with that in Lopé (0.3-3 individuals per km², White 1994). When we take into

account that the density of fruit food of the elephants in Petit Loango was almost ten times as much as that in Lopé (Table 3), the density of the elephants is likely to be limited by the scarcity of THV in Petit Loango.

Tree density, forest structure and species composition changed from the coast to inland area. The coastal forest, within two kilometers from the shoreline, is different from the inland forest and characterized by; (1) abundant large trees with few small trees, (2) low species density, and (3) mosaic of monodominant patches of 0.2-0.5 km diameter. Data from vegetation survey in Petit Loango conducted by Furuich (unpubl data) exhibits the same tendency, although the end of coastal forest was one kilometer further to the interior area. The second and the third characteristics were consistent with the transition forest.

The density and distribution of fruit food trees for the chimpanzees, gorillas, and elephants were quite different between the coastal forest and the inland forest. First, the inland forest was high in the density of fruit food trees for the chimpanzees, gorillas and the elephants, in comparison with the inland forest. Thus the coastal forest appears to be more attractive in terms of fruit foods for both the apes and the elephants. However, it would be more attractive to the chimpanzees and gorillas than to the elephants because some fruit species specific to the coastal marginal forest such as Eugenia sp. and Annona sp. is highly preferred by the apes but not frequently eaten by the elephants. Second, many of the fruit tree species for the apes and the elephants formed small monodominant patches of 0.2-0.5 km in diameter in the coastal forest. Since fruiting season of the tree species which form such monodominant patches are mostly restricted to the short period (Suzuki and Takenoshita, in prep-b), fruit foods is likely to concentrate in the monodominant patches which are fruiting, while there are almost no foods are available out of such fruiting forest patches, as there are scarce alternative food resources such as THV. Therefore, distribution of fruit food in a given short period would be clumped, and each fruiting monodominant forest patches may function as single patches for the chimpanzees and gorillas, although food patch is often referred to be a single fruiting tree in other study sites (Chapman et al. 1995; White and Wrangham 1988).

As the patch size is large, scramble competition among the individuals of the same species would be small in the coastal forest, because many individuals can feed on the same patch (Janson 1988; Wrangham 1993). In contrast, inter- and intra-species contest competition would be strong in the coastal forest because the number of available patches are limited and the size of each patch is large. It indicates that the tree distribution specific to the coastal forest of Petit Loango rather enhances the interspecies competition between the gorillas and the elephants.

Such strong inter- and intra-species competition would affect the ranging and feeding patterns of the chimpanzees and gorillas. For example, foraging group size would be large in the coastal forest. It is confirmed at least for the chimpanzees (Chapter 5). Niche separation between the apes and the elephants such the differentiations in the diet, or the differentiations in the home range would be expected. It is shown that the dietary overlap in terms of fruit food between chimpanzees and gorillas is smaller in Petit Loango than in other study sites where the chimpanzees and gorillas are living sympatrically (Chapter 4).

Strong interspecies competition may induce the seasonal differentiation in the use of the coastal forest between the chimpanzees, gorillas and elephants. Suzuki et al. (1999) showed that during the months when the density of the elephants in the study area was high, either the density of chimpanzees or that of gorillas were low. This suggests that the apes avoided to use the coastal forest when the elephants were abundant.

Finally, I would like to speculate the formation of the coastal forest of Petit Loango. It might have been as follows: At first, the grassland has developed on the sand reef which developed along the coast (Richard and Léonard, 1993). Next, the elephants penetrated to those grassland. The elephants dispersed the seeds which they have consumed in the interior area. Therefore, forest which consisted mainly of the elephant food species has developed. The fact that the density of elephant food species is higher than that of Lopé support this idea. Finally, the chimpanzees, gorillas and other frugivorous primates have penetrated into that forest.

In the future those species that are dispersed by the apes and the monkeys will

increase. In addition, as a consequence of the seed dispersal by the apes, monkeys and the elephants, the mosaic of monodominant forest patches will turn into the mixed species forest like the inland forest.

If this is right, Petit Loango offer not only the example of the socio-ecology of chimpanzees and gorillas living in a unique environment, but also the example of their penetration to the new habitat. Further investigation is needed.

Chapter 4. DIET

INTRODUCTION

Chimpanzees are mainly frugivorous, although they have a wide range of diet breadths (Pan t. schweinfurthii, Goodall 1986; Nishida and Uehara 1983; Yamagiwa 1996, P. t. troglodytes, Kuroda et al. 1996; Sabater-Pí 1979; Tutin et al. 1991, P. t. verus, Sugiyama and Koman, 1992, Yamakoshi 1998). Their main food is ripe fruits. During the period of fruit scarcity they depend on fibrous foods such as the leaves, piths, or barks for alternative food resources. Particularly, piths of terrestrial herbaceous plants (THV) is important food resources which supplement the shortage of ripe fruits (Malenky et al. 1994; Wrangham et al. 1998; Wrangham 1993).

In Petit Loango, the density of the fruit foods for chimpanzees in this forest are similar to other seasonal forest where the chimpanzees are living (Chapter 3). As the Petit Loango forest is tropical seasonal forest, there are certain periods of fruit scarcity. The forest have developed along the coast and is characterized by the scarce THV densities (Furuichi et al. 1997; Yamagiwa et al. 1995; Chapter 3). How the chimpanzees supplement their nutritional intake in the periods of fruit scarcity is of interest.

There are many large frugivorous mammals in Petit Loango such as guenons (Cercopithecus pogonias, C. cephus and C. nictitans), mangabeys (Cercocebus albigena, C. torquatus), gorillas (Gorilla g. gorilla) and elephants (Loxodonta africana). They are potential competitors for the chimpanzees. Particularly, the competition between chimpanzees and gorillas would be strong, as their dietary overlap is large, especially in the fruit foods (Kuroda et al. 1996; Tutin and Fernandez 1993; Tutin et al. 1991; Yamagiwa 1996). However, it is suggested that the competition between chimpanzees and gorillas is avoided by differentiating feeding habits each other (Kuroda et al. 1996; Tutin et al. 1991). Chimpanzees depend heavily on fruits all through the year. Gorillas, on the other hand, depend on fibrous foods such as leaves, piths, barks and roots more frequently than

chimpanzees, especially in the less-fruiting season (Nishihara 1995; Remis 1997; Tutin et al. 1991; Williamson 1988; Yamagiwa 1996) .

However, as the THV is scarce in Petit Loango, the feeding competition on fruits between chimpanzees and gorillas would be stronger than the other habitats, especially during the periods of fruit scarcity. In addition, clumped distribution of food trees which is specific to the coastal area of the Petit Loango appears to enhance the competition between the apes (Chapter 3). In this chapter, I investigate the dietary responses of the chimpanzees to these environmental characteristics of Petit Loango. The points is that (1) under the scarcity of THV, what plays a role of “fallback food” for chimpanzees and that (2) whether the dietary overlap between chimpanzees and gorillas is high, as is expected by the scarce THV density and clumped distribution of food trees in Petit Loango (Chapter 3). First, I analyze the general tendencies of the diet of chimpanzees in Petit Loango. Next, I analyze seasonal change in the diet of chimpanzees in relation to the fruit phenology in their habitat.

RESULTS

General tendencies

Plant foods: Sixty-five items of 58 species (27 families) of plant foods were confirmed by fecal analysis, observations of feeding remains and direct observation (Table 4). Fruit dominates the diet of chimpanzees at Petit Loango in terms of the frequency and the amount of consumption. One or more species of fruit remains were found in all the analyzed feces. Mean percentage volume of fruit remains was 69.7 %, and the mean number of fruit species was 2.7 species per fecal sample. Although terrestrial herbs are scarce in the Reserve, remains of at least one species of fibrous plant food were found in 98.2 % of the analyzed feces. Mean percentage volume of fibrous remains was 29.2 %. The fibrous food remains mainly consisted of the leaves, which were probably taken from trees and woody vines. Seed consumption was confirmed for six species. Seed eating of Irvingia gabonensis

was confirmed by the direct observation; the chimpanzees removed the unripe pulp and ate only the unripe seeds. Seed eating of Ceiba pentandra was confirmed by the feeding remains. Cracked seed remains of Irvingia gabonensis, Eugenia sp., Diospyros spp, Landolphia spp. and Uapaca guineensis were found in the feces, and 19 % of the fecal samples contained cracked seeds of at least one species.

Non-plant foods: Other than plants, chimpanzees at Petit Loango consumed invertebrates, vertebrates, and honey. Remains of insects were found in 4.7 % of fecal samples in total. A species of weaver ants was found in 1.5 % of the samples, and an unidentified species of roach-like insects in 2.2 % of the samples. It should be noted that no termites remains was found in the fecal samples, although several species of termites were found in the main study area. Over one year period, chimpanzees at Petit Loango consumed vertebrate prey more frequently than insects. Remains of vertebrate prey such as teeth, skin, and hairs and bones were found in 10.2 % of the fecal samples. The prey animals were monkeys, snakes, and possibly ungulates. A field assistant who came from a village nearby the Reserve said he had seen a chimpanzee to eat a juvenile white-collared mangabey (Cercocebus torquatus) which had been caught in the trap set by a villager. Chimpanzees were observed to eat honey by using tool-sets on three occasions. In all cases, chimpanzees broke the nest of honey bees by using hard woody baton of about 80 cm long and 7 cm diameter and then inserted small sticks into the nest to extract honey (Takenoshita et al. in prep).

Seasonality of the diet

Plant foods: The fruit species eaten, parts eaten, the degree of dependence on fruits and the diversity of fruit species changed seasonally (Table 4). In the late rainy season (from January to February), they consumed larger amount and more species of fruits. Mean percentage volumes of fruit remains and the number of fruit species per fecal sample in this season tended to be higher than in the other months. They depended on two to four main

fruit species. In January, Ficus spp. and Irvingia gabonensis was the main fruit menu, and several other fruit species was consumed supplementarity. Seeds of Irvingia gabonensis were frequently consumed in this month. In February, Anthocleista vogelli, Grewia coriacea, Diospyros spp. and Erythroxylum manii were consumed as the main menu.

In the early dry season (May), the chimpanzees ate less fruits in terms of amount and diversity. Mean proportion of fruit remains per feces was less than 50 % only in this month (43.2 %). Fruit remains in feces mostly consisted of seeds and pulp of Ficus spp. Vitex doniana was also consumed constantly throughout the month.

In the middle to late dry season (June, July and August), the chimpanzees consumed mostly single fruit species; Vitex doniana in June, and Sacoglottis gabonensis in July and August. Those species were fruiting in more clumped distribution in the forest than other fruit food species in other seasons. Ficus spp., Pseudospondias longifolia, Staudtia gabonensis and unidentified species of Linaceae were consumed supplementarity.

In the early rainy season (October to December), main fruit foods appeared along the waters and the coastal forest. The chimpanzees did not depend on a particular species. They consumed mainly Ficus spp., Uapaca guineensis and Pycnanthus angolensis, and Irvingia gabonensis, Diospyros spp. supplementarity in October. In November, they consumed mainly Eugenia sp. and Annona sp. which occurred in the coastal scrub. Ficus spp. and Uvaria spp. were also consumed supplementary. Seeds of unripe fruits of Irvingia gabonensis were consumed frequently in this month. In December, Eugenia sp., Annona sp., Landolphia spp., Irvingia gabonensis, Ficus spp., Lanea welwitschii and Diospyros spp. composed the main fruit menu. Seeds of Eugenia sp. were consumed frequently in this month.

Non-plant food: Due to the small sample size, seasonality on the non-plant food consumption were difficult to detect. Insect remains were found in the fecal samples for two months in 1998. Remains of roach-like insects were found only in October 1997. Vertebrate remains were found in the fecal samples for seven months in 1998.

Association between the fruit diet and fruit phenology

The amounts of fruits in the diet of chimpanzees fluctuated seasonally, but the fluctuation was not related to the fluctuation of fruit phenology in the study area (Figure 7). Chimpanzees appeared to eat more fruits when the fruit food is more abundant, but monthly mean percentage volume of fruit remains per feces was not correlated with fruit patch density ($R^2 = 0.302$, $df = 8$, $p = 0.12$). Fruits seemed to be their main food throughout the year. The mean percentage volume of fruit remains per feces was smaller than 50 % only in the early dry season.

Fruit diversity in the chimpanzee diet was influenced by the distribution of fruit patches. The number of fruit species in the middle to late dry season when the fruit patch distribution was highly clumped ($CD > 5$, June, July and August) was significantly smaller than the other months (Mann-Whitney's U tests, $n_1 = 3$, $n_2 = 6$, $df = 10$, $p < 0.05$, Figure 7). The mean number of fruit species per fecal samples was not correlated with fruit species counted in the monthly fruits census ($R^2 = 0.284$, $df = 8$, $p = 0.13$).

Dietary overlap with sympatric gorillas

Fruit foods for the chimpanzees overlapped with those of gorillas and elephants. Of the 61 species of fruits for the chimpanzees, 49 % (30 species) was also consumed by the gorillas. However, these figures underestimated the real overlap because of the small number of fecal samples for the chimpanzees and gorillas. The number of fresh fecal samples were only 106 for the gorillas. Out of the seven fruit species which were found in more than 50 % of the chimpanzee feces collected in at least one month, six species were consumed by the gorillas.

DISCUSSION

General tendencies

Diet of the chimpanzees in the Petit Loango Reserve was similar to that of other study sites of chimpanzees. The chimpanzees in Petit Loango was mainly frugivorous, although they consume varieties of food categories such as fibrous foods, seeds, animals and honey.

It is likely that the leaves complement the scarcity of THV in Petit Loango. Fibrous remains in the feces of chimpanzees were mainly composed of leaves. It is also likely that seeds complement the scarcity of THV to some extent. Chimpanzees consumed several species of seeds in the early to middle rainy season. In the Lopé Reserve, chimpanzees depend on seeds of unripe fruits during the "bad year" of fruit production (Tutin et al. 1991).

Non-plant diet was different from other study sites to some extent. Insect consumption was less frequent than the chimpanzees in other habitat (Table 5). It is likely to be caused by the low density of termites, which is the major insect food for the chimpanzees of other study sites (Kuroda et al. 1996; McGrew 1983). However, the driver ants, which are also eaten by the chimpanzees in other study sites (McGrew 1983), were not found in any fecal samples although they were commonly seen in the main study area. It is possible that this is a local difference in the feeding habits (McGrew 1983; Nishida et al. 1983). Certain degree of vertebrate consumption like other populations was confirmed (McGrew 1983; Basabosé and Yamagiwa 1997).

Seasonality

The diversity of fruit diet was small when the distribution of fruit patches were highly clumped. This can be explained by the tree distribution specific to the coastal area of the Petit Loango. Food species of the chimpanzees form small monodominant forest patches of 0.2-0.5 km in diameter in the study area (Chapter 3). In such conditions, each fruiting

monodominant forest patch may function as a single patch for the chimpanzee, although the food patch for chimpanzees are often defined as a single fruiting tree in other study sites (Chapman et al. 1995; White and Wrangham 1988).

When those fruiting forest patches are large and separated from each other, i.e. when the fruit tree distribution is clumped, the chimpanzees would stay in one of these forest patch. They cannot feed on many fruit species as the food diversity is low within a given forest patch. By contrast, when the small fruiting forest patches of various species were available, the chimpanzees would travel through many forest patches of different fruit species. They consequently use many fruits.

This assumption is consistent with the seasonal change in grouping pattern of the chimpanzees. When the distribution of fruit patches was clumped, the chimpanzees formed large parties (Chapter 5). They appeared to stay together in a large monodominant forest patch, feeding on the dominant fruit species which is only abundant in such monodominant patch.

Dietary overlap with sympatric gorillas

Fruit foods for the chimpanzees in Petit Loango seemed to be overlapping with those of the gorillas. Most of the main chimpanzee fruit foods were also eaten by the gorillas. Forty-nine percent of the fruit food species which were confirmed to be consumed by the chimpanzees in Petit Loango were common with those for the gorillas. However, this figure seems lower than those of Ndoki (83 %, calculated from Moutsamboté et al. 1994) and Lopé (78%, calculated from Tutin et al. 1994). Although this difference is partly because of the small number of gorilla fecal samples in Petit Loango, it is possible that the niche differentiation in terms of fruit foods exists between chimpanzees and gorillas in Petit Loango, as interspecies competition between chimpanzees and gorillas are expected to be stronger than in other study sites due to the scarcity of THV and the clumped distribution of food trees (Chapter 3).

Chapter 5. SEASONAL VARIATION IN THE BED GROUP SIZE

INTRODUCTION

Chimpanzees have fission-fusion social structure (Goodall 1986; Nishida 1968). Individuals of a unit-group (or community) do not forage together, but usually they disperse into temporal subgroups (or parties). There is no stable membership in such parties. The size and composition of parties vary seasonally (Chapman et al. 1995; Nishida 1968; Tutin et al. 1983; Wrangham 1977).

Many factors have been confirmed to influence the fission-fusion nature of the chimpanzee. However, the association between those factors is still uncertain (Chapman et al. 1995). Some studies assert that foraging efficiency is the limiting factor of foraging group size in primates (Chapman et al. 1995; Janson and Goldsmith 1995; Wrangham et al. 1993). The individuals must travel further when they are in a large group in order to get enough foods for the energy and nutrient requirements of all group members. Following environmental factors appear to influence the party size of chimpanzees through affecting their foraging efficiency; (1) food density or food patch density, (2) food patch size, and (3) food patch distribution. When food density is high, amount of foods in a given area increases which then reduces traveling costs and thus allow chimpanzees to form large parties. This has been confirmed on the chimpanzees of Gombe (Wrangham 1977), Kibale (Chapman et al. 1995), and Tai (Doran 1997). Similarly, when the food patch density is high, inter-patch distances become shorter to increase foraging efficiency, then party size can be larger (Chapman et al. 1995). When the patch size is large, many individuals can feed from a given patch, and thus party size becomes larger. The difference in the party size of chimpanzees and bonobos (Pan paniscus) is partly explained by the difference of patch size in their habitats (White and Wrangham 1988). When the food patches are concentrated in a small area, distance between patches becomes shorter, which then reduces travelling costs and allows chimpanzees to form large parties (Chapman et al. 1995). However, there is not many

quantitative studies on the influence of food patch distribution on chimpanzee party size.

In addition to the foraging cost, predation pressure has also been suggested to affect the group size (Baldwin et al. 1981; Janson and Goldsmith 1995; McGrew et al. 1981; Tsukahara 1993; Tutin et al. 1983). Availability of water sources and shade can affect party size of chimpanzees in hot and dry habitats (Baldwin et al. 1981; McGrew et al. 1981; Tutin et al. 1983).

In this chapter, I present data on fission-fusion nature of the chimpanzees in Petit Loango. As mentioned in Chapter 3, there are very scarce THV in the study area. There are lots of arguments about the importance of THV on chimpanzees grouping pattern. Malenky and his colleagues (1994) assert that wherever THV exists regularly in time and space, it may offer alternative food resources in the period of fruit scarcity and buffer the influence of fruit patch distribution on the foraging pattern of chimpanzees. According to their hypothesis, chimpanzees groups can keep cohesive wherever THV is abundant, regardless of the fluctuation of density, size and distribution of the fruit patches. On the contrary, THV is not significant factor which affect party size of chimpanzees in the Kibale forest (Wrangham et al. 1996). Data from the habitat which lacks THV may clarify its influence on chimpanzee grouping pattern.

First, I present the data on seasonal changes of the bed group size of chimpanzees. It is analyzed in relation to environmental factors such as patch density, patch distribution, and availability of water sources. Through this analysis, I will suggest that the distribution of fruit food patches is primarily responsible for the size of bed groups of the chimpanzees in Petit Loango. Next, the relationships between mean bed group size of chimpanzees and their diet is analyzed. Then I will discuss the reasons why bed group size of Petit Loango chimpanzee depend more on fruit patch distribution than on other environmental factors with reference to the environmental characteristics of the Petit Loango forest.

RESULTS

Bed group size

Chimpanzees formed large bed groups in the dry season than in the rainy season (Mann-Whitney's U test, $df = 11$, $U = 7$, $p < 0.05$), especially in June, July and August. Mean monthly bed group size showed clear fluctuation, ranging from 2.07 to 5.22 (Figure 8). This seasonal fluctuation is not likely the simple reflection of the density of chimpanzees at the study area in a given month which also fluctuated seasonally (Suzuki et al. 1999). Indeed, monthly mean bed group size was largest in August when extremely large number of bed groups were found compared to the other months (36 bed group). The number of bed groups found in other months was not diverged, however, while the mean bed group sizes varied between these months. No correlation was found between number of bed groups counted at a given month and mean monthly bed group size when August was excluded from analysis ($R^2 = 0.140$, $df = 9$, $p = 0.28$).

Patch density, patch distribution and availability of water sources

Chimpanzees seemed to form large bed groups when food patches were abundant. Monthly fruit food patch density was not correlated with the mean monthly bed group size ($R^2 = 0.145$, $df = 10$, $p = 0.248$, Figure 9a). Mean bed group size has only one peak during the middle to late dry season (Figure 8) while there were two peaks of fruit food patch density; late rainy season and middle to late dry season (Figure 7b).

On the other hand, chimpanzee seemed to form large bed groups in the month when the distribution of fruit patches was clumped. The value of CD was higher in the middle to late dry season when the mean bed group size was large (Figure 7c). Distribution of fruit food patches showed significant positive correlation with mean bed group size ($R^2 = 0.392$, $df = 10$, $p < 0.05$, Figure 9b). It should be noted, however, CD was positively correlated with fruit patch density ($R^2 = 0.444$, $df = 11$, $p < 0.05$).

Large bed groups were observed also when water source was scarce. Density of the

streams showed marginally negative correlation with mean bed group size ($R^2 = 0.437$, $df = 10$, $p < 0.05$, Figure 9c). Many streams remained in the first two month of the dry season when the mean bed group size were not so large as middle to late dry season when most of the streams were dried up (Figure 2). Distribution of fruit patches was clumped in the month when the water sources was scarce. The value of CD was highest in the middle to late dry season when most of the streams on the transects were dried up. However, correlation between CD and stream density was not significant ($R^2 = 0.220$, $df = 11$, $p = 0.12$).

Which factors are more important for the chimpanzee bed group size?

As above the fruit patch density, patch distribution and availability of water sources were not independent factors, I took multiple regression analysis. Then fifty seven percent of the variance of mean monthly bed group size was explained in a multiple regression of mean bed group size on the fruit patch density, patch distribution and availability of water sources, but only marginally ($R^2 = 0.567$, $p = 0.101$, mean bed group size = $-0.08 \times$ patch density + $0.225 \times$ CD - $0.384 \times$ stream density + 3.308). It should be noted that the regression coefficient of fruit patch density turned to negative. It means that the mean bed group size was not positively related to fruit patch density. In addition, almost the same degree of the variance of mean monthly bed group size can be explained significantly only by the combination of fruit patch distribution and availability of water sources ($R^2 = 0.565$, $p = 0.03$, mean bed group size = $0.191 \times$ CD - $0.405 \times$ stream density + 3.253). Therefore, it seems that the bed group size of the chimpanzees were affected not by the abundance of fruit patches but by the distribution of fruit patches and availability of water sources.

Associations between the bed group size and diet

The association between the bed group size of chimpanzees and their dependence on fruit foods and the diversity of fruit species in their diet are analyzed here. Chimpanzees did

not seem to form large bed groups when they depend heavily on the fruit foods. Mean volume percentage of fruit remains per fecal sample was not correlated with mean bed group size ($R^2 = 0.128$, $df = 7$, $p = 0.385$).

Chimpanzees appeared to feed on less fruit species during the month when they formed large bed groups. The number of fruit species per feces was fewer in the middle to late dry season when mean bed group size was large, although the correlation between these variables were not significant ($R^2 = 0.138$, $df = 7$, $p = 0.19$). The number of fruit species per feces showed marginally negative correlation with CD, opposite to the mean bed group size ($R^2 = 0.362$, $df = 9$, $p < 0.10$).

DISCUSSION

The variation in the chimpanzee bed group size of Petit Loango clearly suggest that the central subspecies have fission-fusion social structure like eastern (Goodall 1986; Nishida 1968; Wrangham et al. 1996) and western (Boesch 1996; Tutin et al. 1983) subspecies, although I could not confirm the outline of unit-group. It is also clear that the seasonal fluctuation in their grouping is common between three subspecies (Pan t. verus; Boesch 1996; Doran 1997; Tutin et al. 1983, P. t. schweinfurthii; Nishida 1968; Wrangham 1977; Chapman et al. 1995; Matsumoto-Oda et al. 1998, P. t. troglodytes; present study). However, some unique characteristics were found on the fission-fusion of the chimpanzees in Petit Loango.

First, mean bed group size of the Petit Loango chimpanzee was larger than those of other Pan t. troglodytes subspecies living in the seasonal rain forest (Table 6). It is likely that the vegetation unique to the coastal area of the Petit Loango forest causes this difference. The vegetation of coastal area of the Petit Loango is different from that of other seasonal forest chimpanzee habitats in two points; (1) scarce THV density, (2) clumped distribution of large fruit trees (Chapter 3), and (3) scarce water sources in the dry season. These characteristics are rather similar to savanna habitat such as Mt. Assirik, Senegal (Baldwin et

al. 1981; McGrew et al. 1981; Tutin et al. 1983). It is consistent with the fact that the mean bed group size of the chimpanzees in Petit Loango was as large as that of Mt. Assirik (Table 6).

It is likely that the bed group size is affected by the size of the unit group, as the diurnal party size is (Boesch, 1996). Unfortunately, the number and the size of the unit group which used the study area were not confirmed due to the difficulties in direct observation and individual discrimination. The number of the largest party observed was 21, which has been thought to represent 60-100 % of unit group in various habitats (Tutin et al. 1983). Applying these percentages, the size of the unit group in the study area was estimated to be 21-35 individuals. This is almost consistent with the estimated unit group size in Mt. Assirik, i.e. 28 individuals (Tutin et al. 1983). Therefore, even when the unit group size is concerned, the mean bed group size in Petit Loango might be consistent with that in Mt. Assirik.

Large bed groups of chimpanzees in the savanna habitat was explained by higher predation pressure and clumped distribution of food resources which is related to the limited water sources and limited water sources themselves (McGrew et al. 1981; Tutin et al. 1983; Baldwin et al. 1981). Predation pressure would not likely, however, to be responsible for the large bed group size of chimpanzees in Petit Loango. Predation pressure would not be high, as mentioned above. Therefore, clumped distribution of food resources which was caused by the lack of THV, clumped distribution of fruit trees and limited water sources is likely to be responsible for the large bed group size of the chimpanzees in Petit Loango.

Second, not the fruit patch density but the fruit food distribution was responsible for the seasonal fluctuation in bed group size of the chimpanzee in Petit Loango; the more clumped the patches were, the larger the party sizes. The chimpanzee of Petit Loango appeared to gather into large parties to share the large clumps of patches, whereas they dispersed when fruit patches were dispersed, even with overall high patch density. Fluctuation of fruit patch distribution is likely to be caused by that of water source availability. According to fecal data, the chimpanzees seemed to depend heavily on the fruits of Sacoglottis gabonensis and Vitex doniana in the middle-late dry season when they formed

larger bed groups. These fruit species were concentrated in the restricted area where the streams were remained even in those periods.

This is not the case with the other study sites, however. Food availability has been suggested to be major factor which influenced the party sizes of chimpanzees in both eastern and western subspecies (P. t. schweinfurthii; Chapman et al. 1995; Matsumoto-Oda et al. 1998; Wrangham 1977, P. t. verus; Doran 1997).

It is possible that the this difference is caused by the difference in the method to measure the grouping pattern of the chimpanzees; I measured the relative gathering of chimpanzees by counting bed group size while the diurnal party size from direct observation was used in other studies. It is shown that bed group size of the chimpanzee is smaller than diurnal party size (Fruth and Hohmann 1994; Fruth and Hohmann 1996).

However, it is not unusual to assume that the variation of bed group size reflects the variation of diurnal party size. Some studies suggest that the variations in bed group size of chimpanzees correspond to that of diurnal party size. Bed group size of the chimpanzees in Mt. Assirik was larger in the dry season than in the rainy season, and larger parties were observed in the dry season although the difference was not statistically significant (Baldwin et al. 1981; McGrew et al. 1981). Chimpanzees in the Lopé forest is shown to form larger bed groups around the fruiting trees than in other locations (Wrogemann 1992). This means that when the chimpanzees gathered to feed from a food patch, they are likely to stay together in the same bed group, suggesting that the bed group size of given night reflects the party size of consecutive day.

Therefore, I can say that the fruit patch distribution is more important factor which influences the fluctuation of party size of the chimpanzees. The importance of fruit patch distribution is likely to be derived from the unique vegetation of the study area. One point is scarce terrestrial herbaceous vegetation (Furuichi et al. 1997; Yamagiwa et al. 1995; Chapter 3). As the distribution of THV is less clumped than that of fruits (Malenky et al. 1994), the influence of fruit patch distribution is likely to be buffered where there are abundant THV foods. In Petit Loango, however, the clumped distribution of fruit patch cannot be mediated

by THV. Therefore, the grouping pattern of chimpanzees would be highly influenced by the distribution of fruit patches.

Another point is that the forest of the study area consists of mosaic of monodominant forest patches of 0.2-0.5 km width (Chapter 3). Most of the tree species which form such monodominant forest patch such as Sacoglottis gabonensis, Irvingia gabonensis, Hexalobus crispiflorus, Vitex doniana, Uapaca guineensis, etc. were important food for the chimpanzees in Petit Loango, had and clear fruiting periods. Therefore, fruit availability is high within the areas where the their dominant tree species is fruiting no matter how the food patch density in the wider area is, while almost no fruits are available in other areas where their dominant tree species is not fruiting. Distance between the fruit patches i.e. individual trees is likely to be small within the fruiting monodominant forest patch. In such conditions, each monodominant forest patch may function as single patch in the habitat in the coastal area of Petit Loango, although food patch for chimpanzees are often referred to as a single fruiting tree in other study sites (Chapman et al. 1995; White and Wrangham 1988). Consequently, the size of entire clump, which was referred to be as patch distribution in this paper, would limit the party size of the chimpanzee, density and size of single fruit tree being less important. Therefore, in the middle-late dry season, the chimpanzees in Petit Loango appeared to gather in a monodominant forest patch which was larger than the other season and share the abundant food of dominant tree species, whereas in the rainy season they appeared to dispersed into small parties when the fruit trees were dispersed even with overall high patch density. This is supported by the fluctuation of diversity in the fruit diet of the chimpanzees. If the chimpanzees had stayed in a large monodominant forest patch in when they gathered, the diversity of fruit diet would be low, as only a few fruit species are available other than fruits of the dominant tree species. It is confirmed that the number of fruit species per feces tended to be smaller when the mean bed group size was large.

The bed group size of chimpanzees was not correlated with their relative dependence on fruit food, unlike the western subspecies (P. t. verus) of the Tai forest (Doran 1997). Therefore, the seasonal variations in the group size of the chimpanzee in the Petit Loango

forest is not likely to be mere reflection of the food abundance. It reflects chimpanzees' effort to use the fruit food efficiently in response to the seasonal variation of fruiting status such as fruit patch density and distribution.

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Table 1. Top 10 species in the transect in terms of the number of trees and basal area (DBH ≥ 10 cm)

Species	Number of trees	BA	Fruits consumption ²⁾		
			Chimp	Gorilla	Elephant
<i>Garcinia cf. smeathmannii</i>	1	10	**	**	**
<i>Diospyros sp.</i> ¹⁾	2	8	*	*	*
<i>Hexalobus crispiflorus</i>	3	2	**	**	**
<i>Diospyros sp.</i> ¹⁾	4		*	*	*
<i>Antostema aubryanum</i>	5	4			
<i>Uvariastrum pierreanum</i>	6		*	*	**
<i>Dichostemma glaucescens</i>	7				
<i>Irvingia gabonensis</i>	8	5	**	**	**
<i>Eugenia sp.</i>	9		**	**	**
<i>Sacoglottis gabonensis</i>	9	1	**	**	**
<i>Diogoia zenkeri</i>		9			
<i>Berlinia grandiflora?</i>		3			
<i>Strombosiopsis sp.?</i>		6	**		**
<i>Klainedoxa gabonensis</i>		7	**	**	**

1) several species is likely to be mixed.

2) double asterisk indicates that feeding is confirmed in the Petit Loango. Single asterisk indicates possible food

Table 2. Densities of each tree class in each segment

Segment	Small tree	Middle tree	Large tree	Total
Coastal transect				
0-0.5 km from the shoreline	424 (49%)	358 (41%)	92 (11%)	874
0.5-1 km	314 (40%)	330 (42%)	134 (17%)	778
1-1.5 km	208 (31%)	342 (50%)	128 (19%)	678
1.5-2 km	320 (39%)	380 (46%)	124 (15%)	824
2-2.5 km	422 (47%)	392 (44%)	76 (9%)	890
2.5-3 km	322 (38%)	444 (53%)	74 (9%)	840
Inland transect				
Segment A	408 (47%)	352 (41%)	104 (12%)	864
Segment B	422 (49%)	344 (40%)	98 (11%)	864

Table 3. Comparison between Petit Loango and Lope

Study site	Tree density (inds./ha, DBH ≥10 cm)	BA (m ² /ha, DBH ≥10 cm)	Fruit food tree density (DBH ≥70 cm) ²⁾		
			Chimpanzee	Gorilla	Elephant
Lope ¹⁾					
Marantaceae forest	384.5	40.9	9.6	7.9	1.5
Closed canopy forest			8.1	4.4	1.9
Petit Loango					
Coastal transect	374	34.0	12.3	11.0	11.0
Inland transect	348	31.7	9.0	8.0	9.0
Total	355	33.5	11.5	10.3	10.5

1) Tree density and BA were quoted from Williamson (1988). Fruit food tree density for the chimpanzees and gorillas were quoted from Tutin et al. (1994). Fruit food species for the elephants were quoted from While (1993), and densities were calculated by Tutin et al. (1994).

2) Fruit food of Petit Loango includes possible foods which is added from the data on other study sites of central subspecies (see text).

TABLE 4. Species of Plant Foods Eaten by Chimpanzees at Petit Loango, Gabon

Family	Species	Life form	Part eaten				Evidence	Month in which the species was eaten													
			PL	SD	LF	FL		Jan	Feb	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
Anacardiaceae	<i>Fegimanra africana</i>	T	x				F											+			
	<i>Lanea welwitschii</i>	T	x				F, R	+												+	+
	<i>Pseudospondias longifolia</i>	T	x				F, R				++	+	+		+	+					
	<i>Trichoscypha cf. albiflora</i>	T	x				F													+	
	Anacardiaceae sp.	T	x				D, F, R							+		+	+				
Annonaceae	<i>Annona</i> sp.	S	x				F	+	+											++	+
	<i>Hexalobus crispiflorus</i>	T	x				F	+	+												+
	<i>Pachypodanthium manii</i>	T	x				F														+
	<i>Uvaria baumannii</i> *	L	x				F	+	+		+									+	+
	<i>Uvaria cf. versicolor</i> *	T	x				F														
	<i>Uvaria muricata</i> *	L	x				F														
Apocynaceae	<i>Landolphia</i> sp.1*	L	x	x			F	+													+
	<i>Landolphia</i> sp.2*	L	x				F														
	<i>Landolphia</i> sp.3*	L	x				F														
Bombacaceae	<i>Ceiba pentandra</i>	T		x		x	D, R													D	T
Burseraceae	<i>Canarium</i> sp.	T	x				F							+							

TABLE 4 Species of Plant Foods Eaten by Chimpanzees at Petit Loango, Gabon (Continued)

Family	Species	Life form	Part eaten				Evidence	Month in which the species was eaten											
			PL	SD	LF	FL		Jan	Feb	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Irvingiaceae	<i>Irvingia gabonensis</i>	T	x	x			D, F, R	+	+							+	+	+	
	<i>Klainedoxa gabonensis</i>	T	x				F					+				+			
Loganiaceae	<i>Anthocleista cf. vogelii</i>	T	x				F		++	+									
Mimosaceae	<i>Calpocalyx heitzii</i>	T		x			D, F	+											
Moraceae	<i>Ficus elasticoides?*</i>	T	x				F, R	++	+	++	++	+	++	+		+	+	+	
	<i>Ficus recurvata?*</i>	L	x				D, F												
	<i>Ficus sp.6*</i>	L	x				D			+									
	<i>Musanga cecropioides</i>	T	x				F					+							
	<i>Myrianthus arboreus</i>	T	x				F									+		+	
Myristicaceae	<i>Pycnanthus angolensis</i>	T	x				F, R							+	+	+			
	<i>Staudtia gabonensis</i>	T	x				F, R					+	+	+	+	+			
Myrtaceae	<i>Eugenia sp.</i>	T	x	x			F										++	+	
	<i>Syzygium sp.</i>	T	x				F									+			
Olacaceae	<i>Strombosia zenkeri</i>	T	x				F											+	
Rubiaceae	<i>Coffea sp.</i>	S	x				F						+	+					
	<i>Nauclea didderichii</i>	T	x				D, F						+	+			+		

TABLE 4. Species of Plant Foods Eaten by Chimpanzees at Petit Loango, Gabon (Continued)

Family	Species	Life form	Part eaten				Evidence	Month in which the species was eaten												
			PL	SD	LF	FL		Jan	Feb	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Rubiaceae	Rubiaceae sp.1	T	x				F								+					
	Rubiaceae sp.2	T	x				F											+	+	
Sapotaceae	Gambeya sp.	T	x				F												+	
	Manilkala fouilloyara	T	x				D, F, R		+											
	Manilkara cf. lacera	T	x				F												+	
Scytopetalaceae	Scytopetalum sp.1	T	x				F												+	
Tiliaceae	Grewia coriacea	T	x				F		+	+										
Verbenaceae	Vitex doniana	T	x				D, F					++	++	+	+	+	+			
Vitaceae	Cissus dinklagei	L	x				F		+										+	+
Palmae	Elaeis guineensis	T	x				F			+										

T: tree; S: shrub; L: liana; *: months are checked for the genus; PL: pulp; SD: seed; LF: leaf; FL: flower; D: direct observation; F: fecal specimen; R: remains of eating; +: present in at least one fecal sample of the month; ++: present in half or more of the total samples of the month.

Table 5. Comparison of the frequency of insect between study sites

Study site	Number of fecal samples	Number of samples which contained at least one type of insect remains	Percentage	v.s. Petit Loango ¹⁾	Source
Mahale (M group)	1053	510	48%	p < 0.001	Uehara (1986)
Mahale (K group)	507	248	49%	p < 0.001	
Belinga	25	6	24%	p < 0.001	Tutin and Fernandez (1985)
Lope	1854	574 or 575	34%	p < 0.001	Tutin and Fernandez (1993)
Ndoki	214	106 ²⁾	50%	p < 0.001	Suzuki (1995)
Petit Loango	274	13	5%	-	This study

1) chi-square test. 2) only the feces which contained the termite remains were counted

Table 6. Comparisons of bed group size between study sites.

Study site	N	Average	Range	SD	Source
Lope	213	2.46	1-26	3.18	Wrogemann (1992)
Okorobiko	66	3.12	1-12	2.48	Baldwin et al. (1981)
Mt. Assirik	83	5.43	1-18	4.58	Baldwin et al. (1981)
Petit Loango	100	5.01	1-21	4.98	This study

Mann-Whitney's U test; Lope v.s. Okorobiko---n.s., Lope v.s. Mt. Assirik--- $p < 0.001$, Lope v.s. Petit Loango-- $p < 0.001$, Okorobiko v.s. Mt. Assirik--- $p < 0.001$, Okorobiko v.s. Petit Loango--- $p < 0.05$, Mt. Assirik v.s. Petit Loango---n.s.

FIGURE LEGENDS

Figure 1: Study area

Figure 2: Monthly rainfall and density of streams during the study period.

Figure 3: Estimation of bed constructor by the builder points. For the bed groups whose constructors were not confirmed by fecal remains were compared with those of known constructors. Height of the highest and the lowest bed, and diameter of the largest and the smallest bed in a bed sites were chosen as parameters compared. Two positive builder points (BP) were given to the bed groups whose highest/smallest bed is higher/smaller than 99 % of chimpanzee bed groups, one positive BP for the bed groups whose highest/smallest bed was higher than 75 % of chimpanzee bed groups, two negative BP for bed groups whose highest/smallest bed was lower/smaller than 99 % of gorilla bed groups, one negative BP for bed groups whose highest/smallest bed was lower/smaller than 75 % of gorilla bed groups. The same rating of BP was made on the lowest/largest bed of the bed groups. The BP from 4 parameters were summed for each bed group. We assumed a bed site as chimpanzee's if the sum of the BP was positive, as gorillas if the sum of the BP was negative. The bed sites whose sum of BP was zero were left undetermined. For detail, see Furuichi et al (1996) and Suzuki and Takenoshita (in prep-a).

Figure 4. Densities and BA of the fruit food trees of each segments; a) density (inds. / ha), b) Basal area (BA).

Figure 5: Comparisons of the species diversity between the coastal and the inland transect by species area curve.

Figure 6: Matrix of α indices. Each unit of the coastal transect is numbered from one (nearest to the shoreline) to 60 (2.95-3.00 km from shoreline). Each unit of the inland transect was numbered from S1 to S20. The similarity between every two units was indicated. The darker, the larger the index, i.e. the more similar these units are. For example, the cell pointed by the arrow in Figure 6a indicates that the α index of unit 56 and unit 24 is less than 0.1. Cells on

the diagonal indicate the similarity of each unit itself and accordingly, one. If the tree species composition is uniform, α index is same between every pair of unit, then colors of all cells are supposed to be same. If the species composition gradually changes, α index decrease according to the distance between units, then the matrix are supposed to exhibit the gradatio pattern which is parallel to the diagonal. If several square of the dark cells appears in the matrix, it means that the species composition of the forest along the transect changes drastically in some places.

Figure 6a. All DBH classes.

Figure 6b. Large trees (DBH \geq 30 cm).

Figure 7. Monthly fluctuation of fruit diet of the chimpanzee and fruit phenology.

a) Mean volume % of fruit remains per feces and the number of fruit species per feces.

Figures on the columns indicates the number of fecal samples analysed for each month.

b) Fruit patch density and the number of fruiting species.

c) Fruit patch distribution (CD). The larger the CD is, the more the distirution is clumped.

Figure 8. Monthly fluctuations of mean bed group size of the chimpanzees.

Figure 9. Correlation between bed group size, fruiting status and diet

a) bed group size v.s. patch density

b) bed group size v.s. patch distribution (CD)

c) bed group size v.s. availability of water sources.

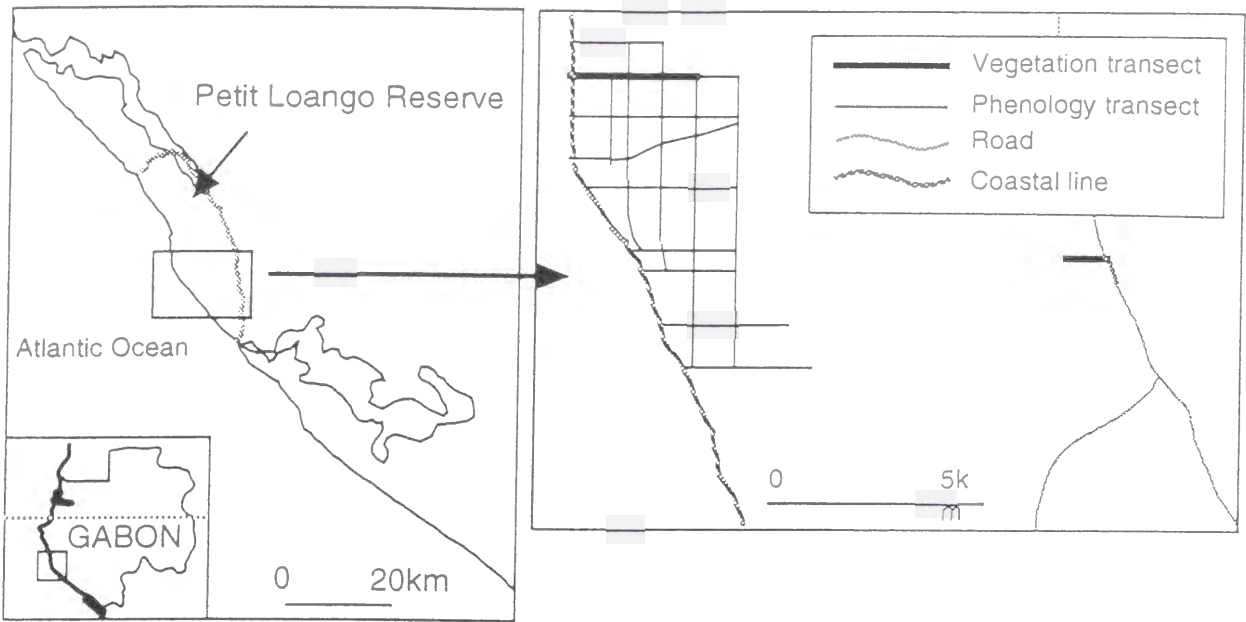


Fig. 2

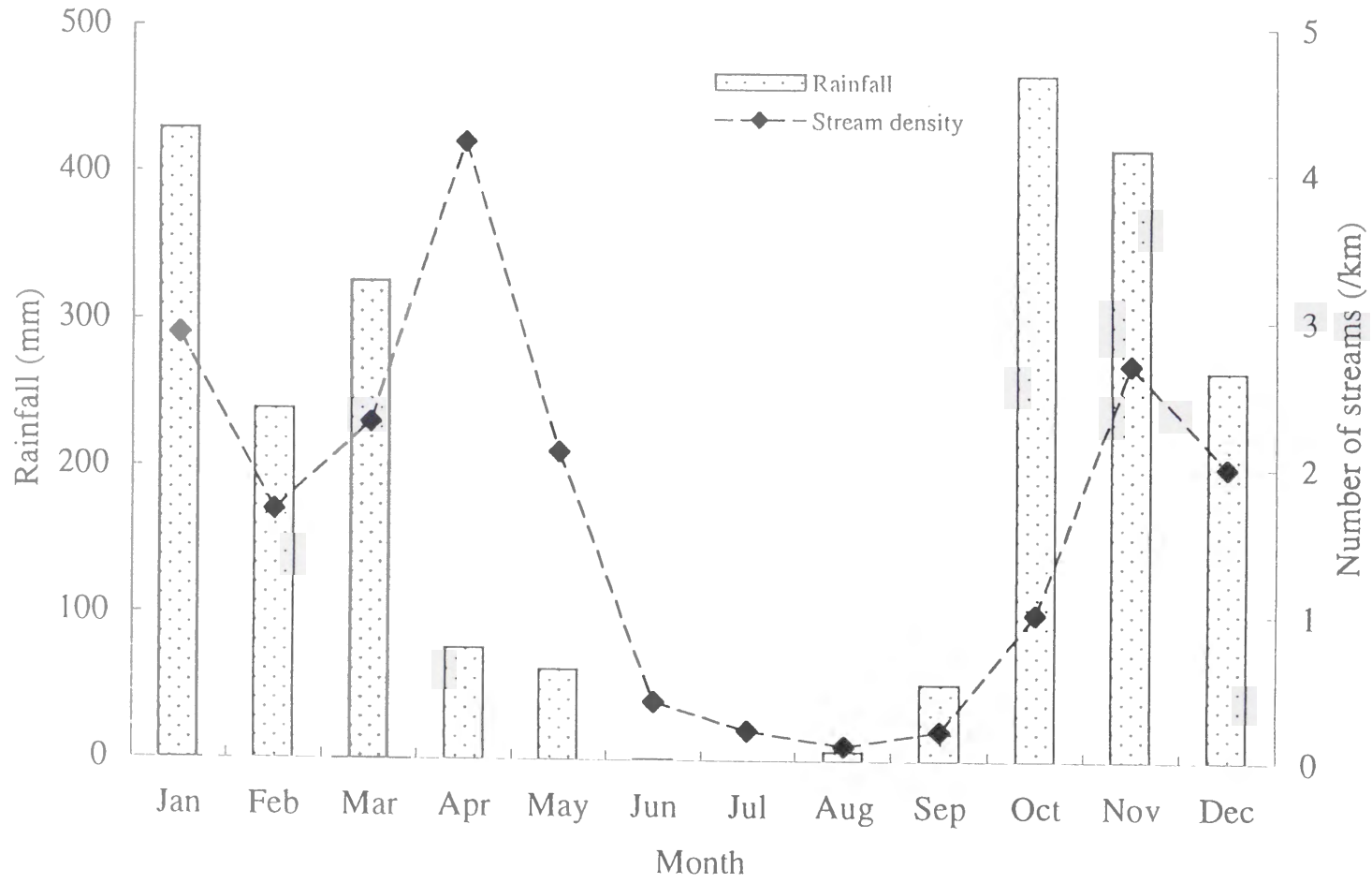
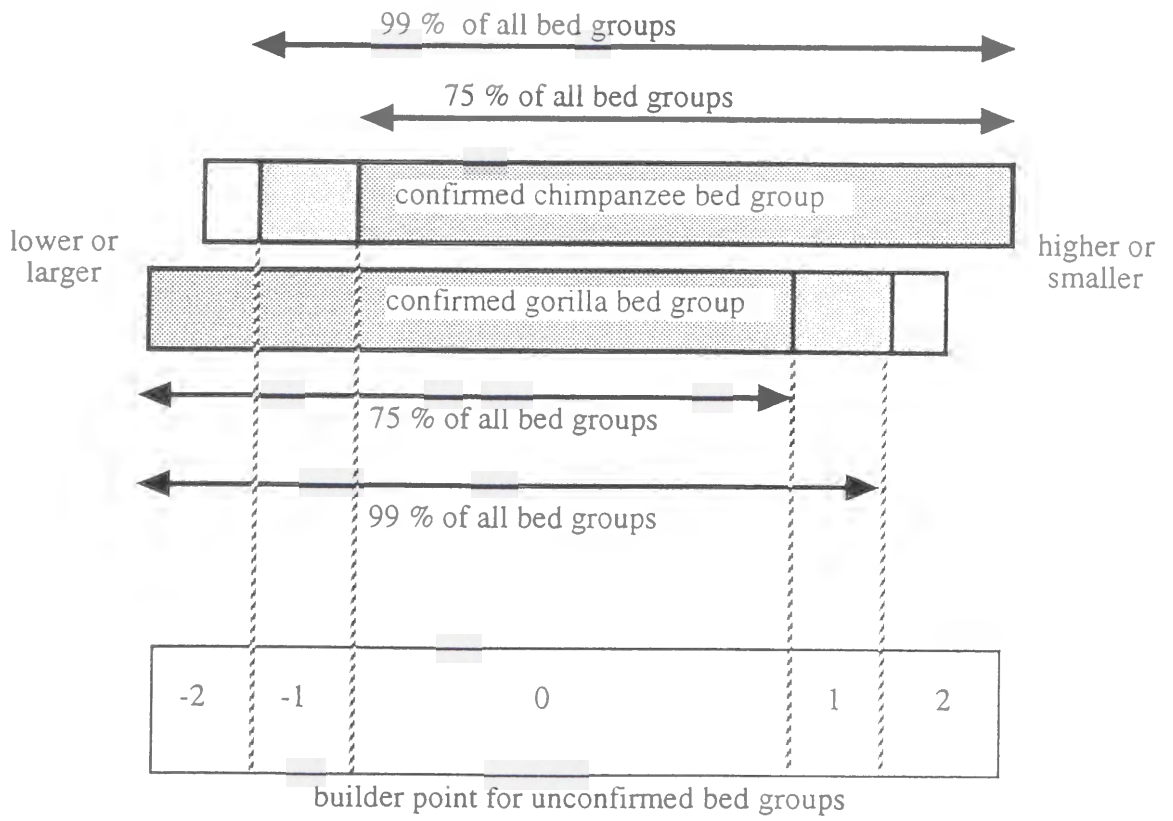


Fig.3



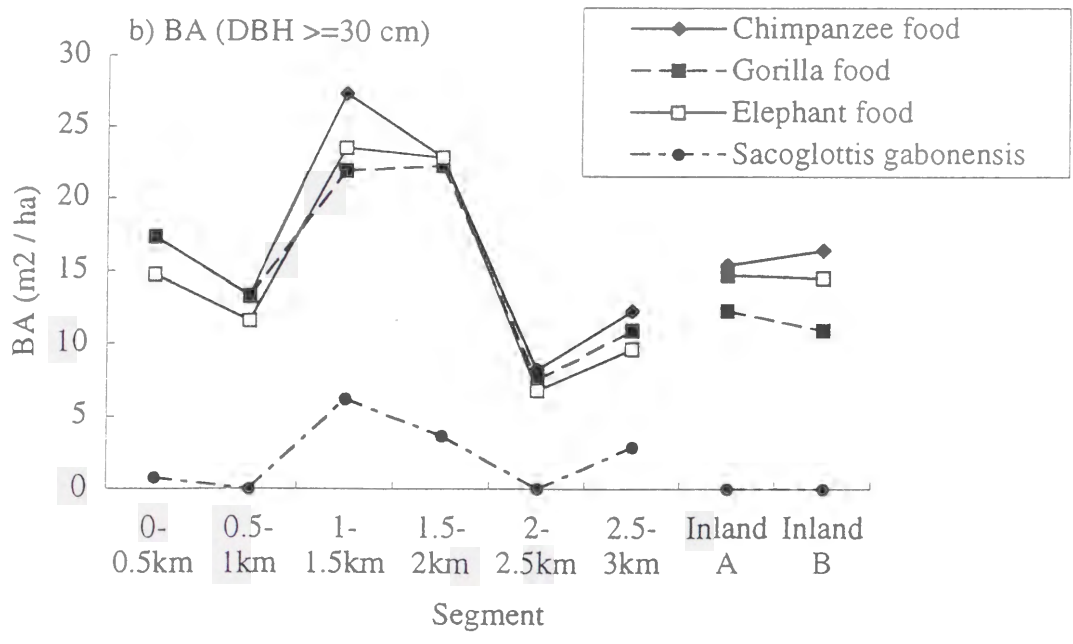
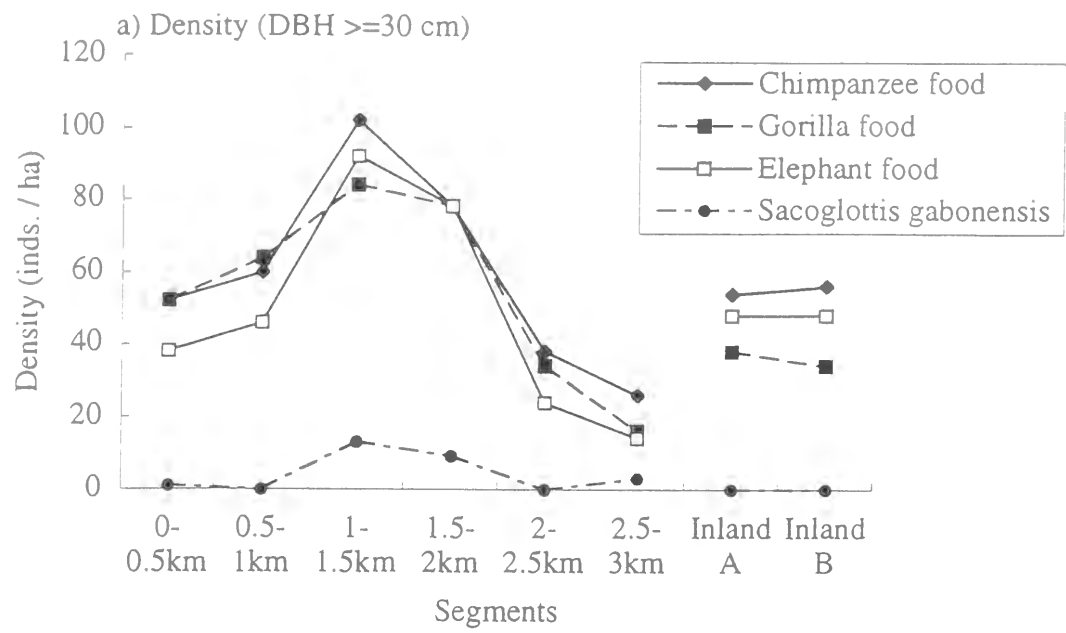
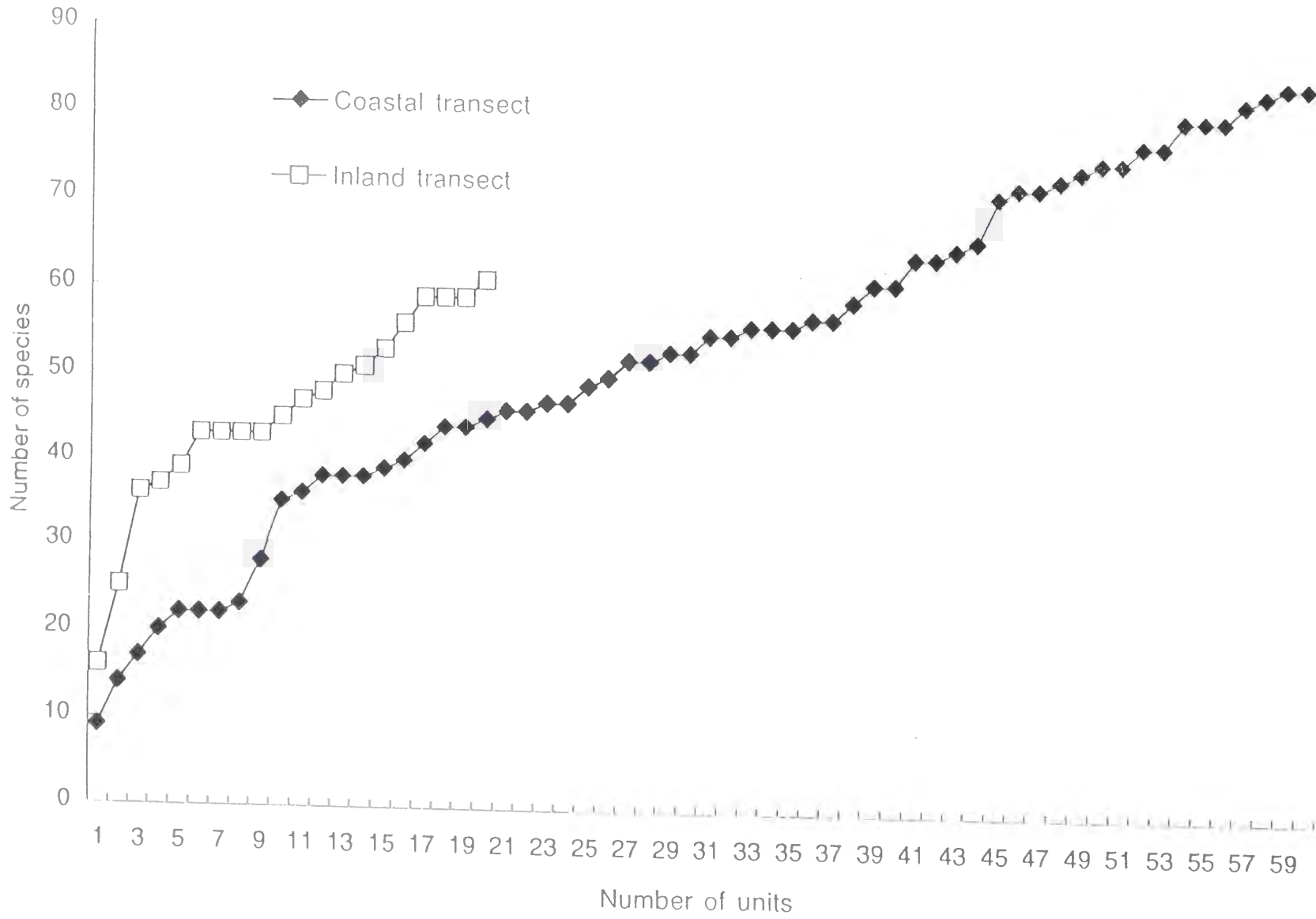


Fig. 5



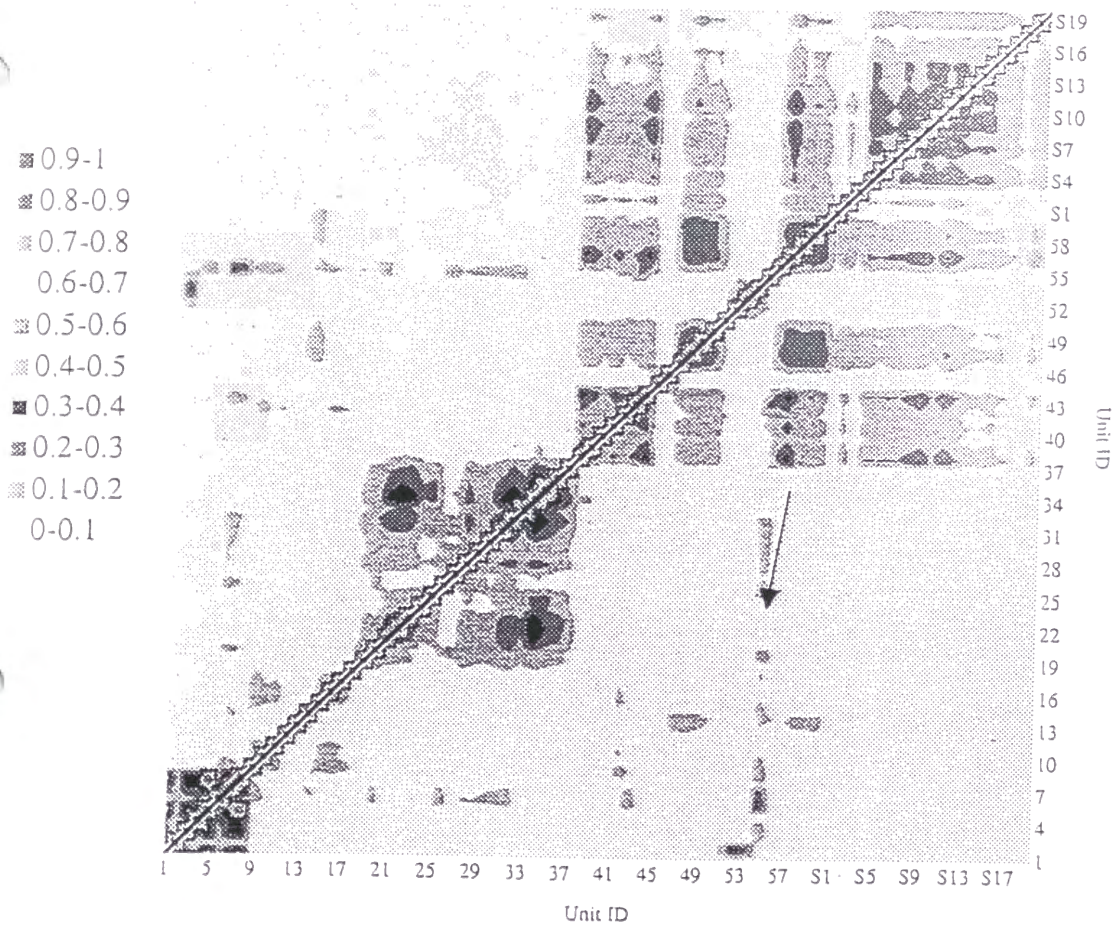


Fig. 6.4

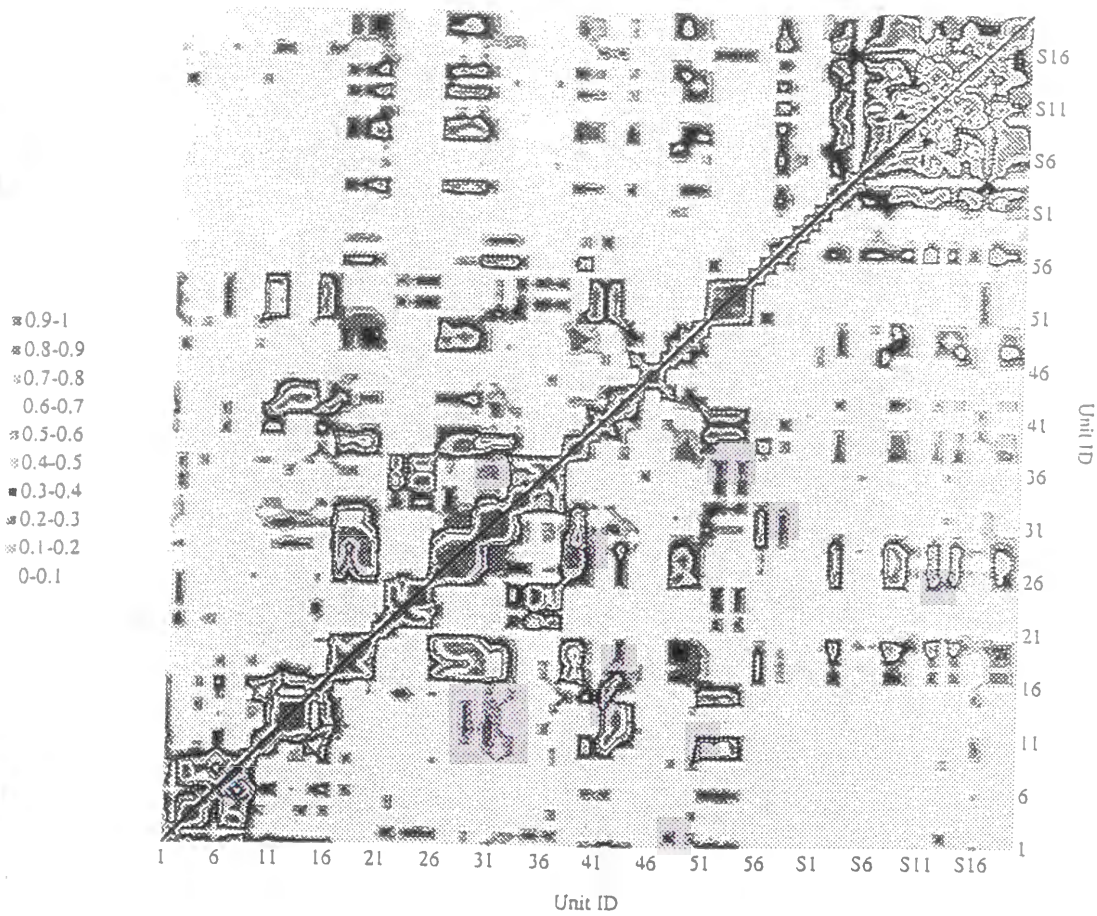


Fig. 7

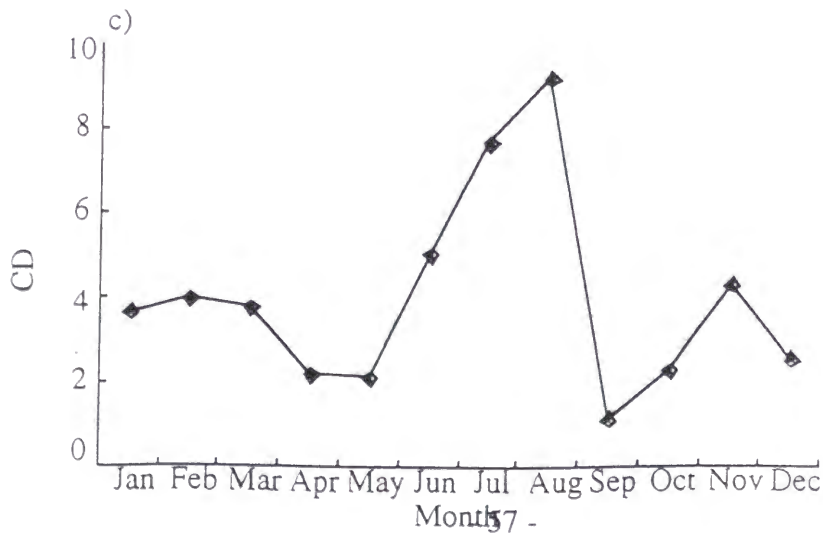
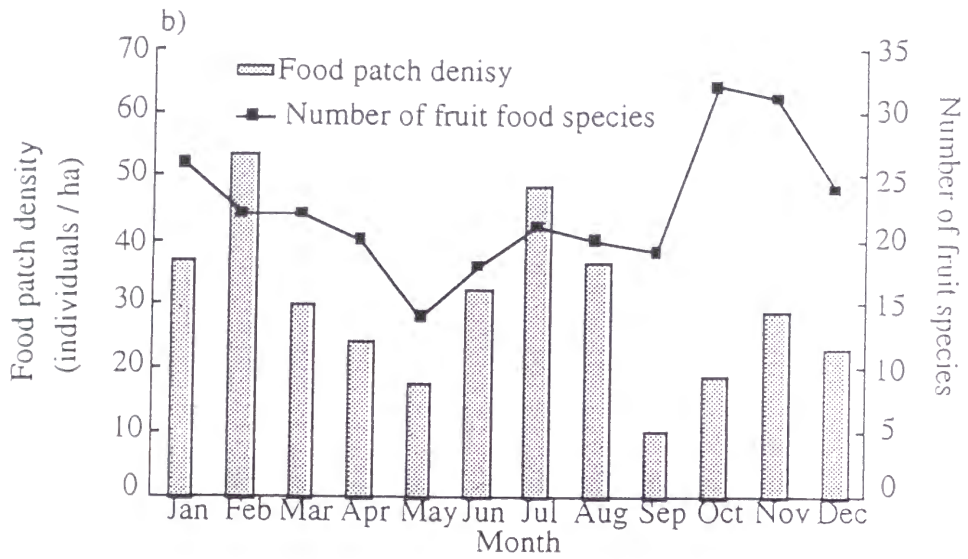
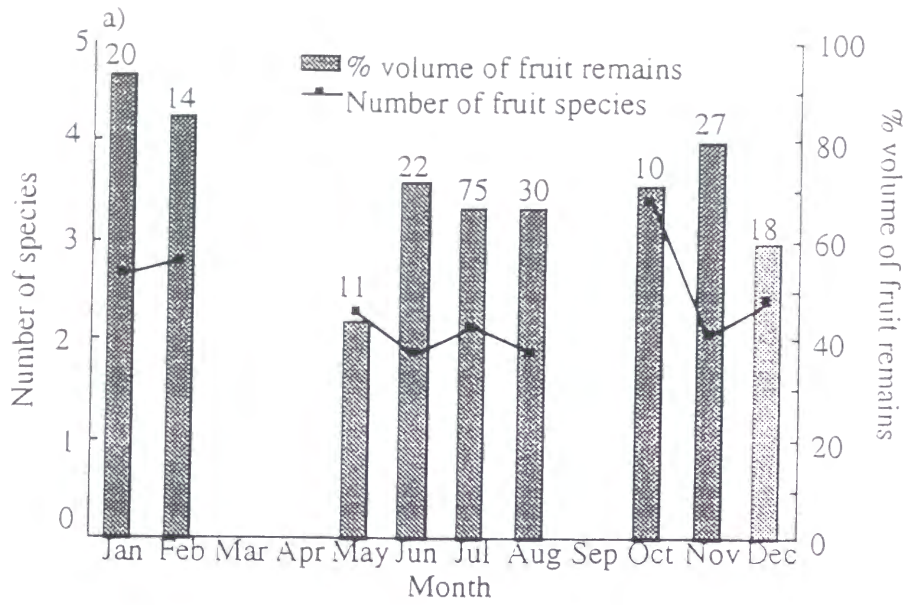


Fig. 8

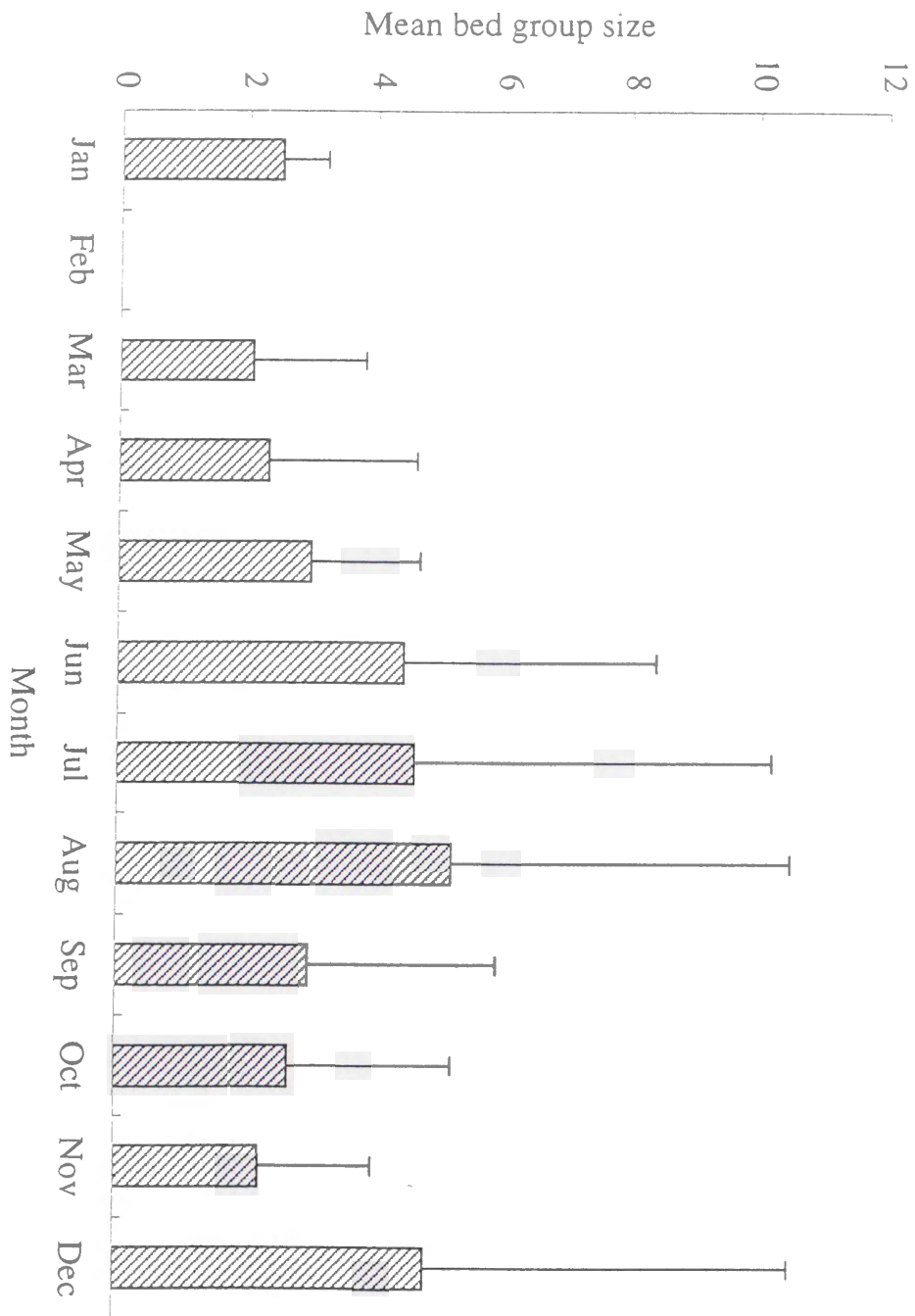
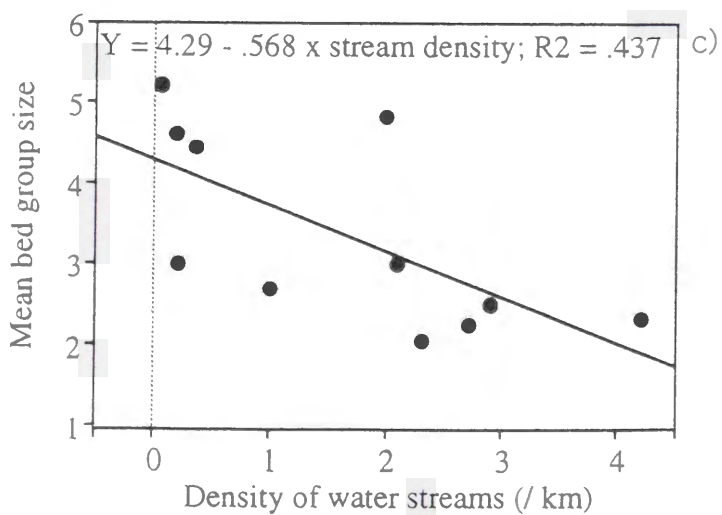
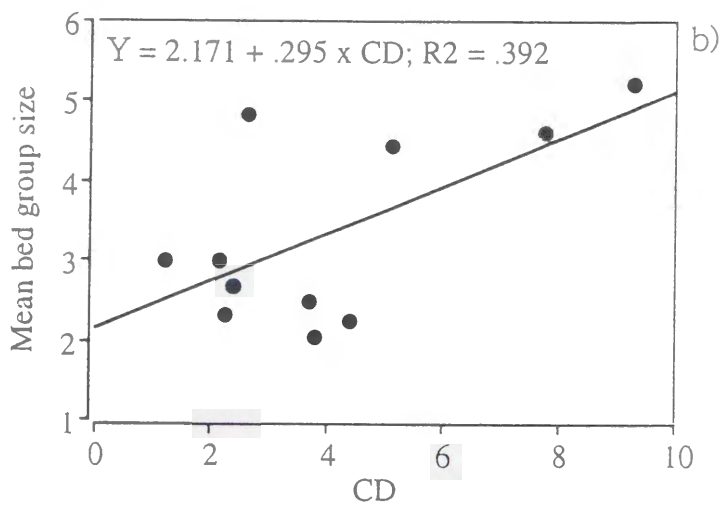
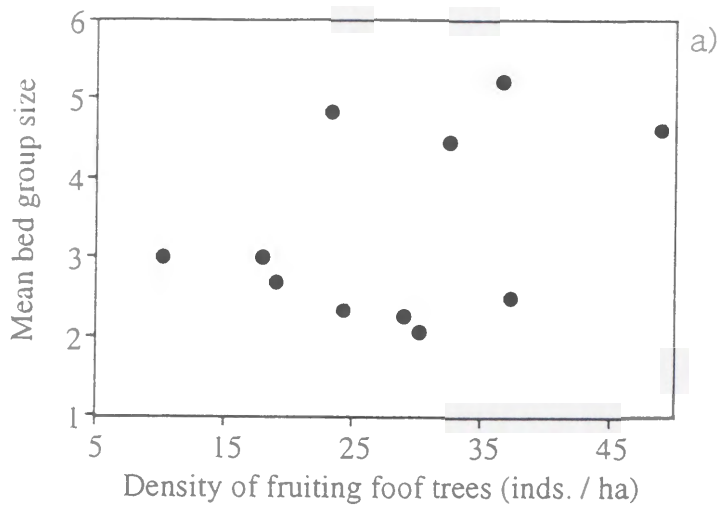


Fig. 9



Appendix 1. Plant list of the study area.

Family	Name	Life form	Density (trees / ha)	BA (m ² / ha)	Food consumption by the apes and the elephants ²¹
FERN					
Pteridophytes					
	Nephrolepis sp.	H			
ANGIOSPERMAE					
DICOTYLEDONEAE					
Acanthaceae					
	Thomandersia hensii	T			
Anacardiaceae					
	Antrocaryon sp.	T			G
	Fegimanra africana	T	1.25	0.744	G,C,E
	Lannea welwitschii	T			C
	Pseudospondias longifolia	T			G,C,E
	Sorindeia sp.	T	0.25	0.001	G*,C*
	Trichoscypha accumiata	T			G,C*
	Trichoscypha cf. albiflora	T			G,C
	?Trichoscypha scandens	L	0.25	0.002	
	ANACARDIACEAE sp.	T			G,C
	ANACARDIACEAE sp.2	T	0.25	0.001	
Annonaceae					
	Annona sp.	S			C,E
	Annona sp.2	T			
	Hexalobus crispiflorus	T	59.25	2.488	G,C,E
	Meiocarpidium lepidotum	T	0.25	0.012	
	?Monanthotaxis sp.	L			
	Pachypodanthium manii	T			G,C,E
	?Piptostigma sp.	T			
	Uvaria baumannii	L			G*,C,E*
	Uvaria cf. versicolor	T			G*,C*,E*
	Uvaria muricata	L			G*,C*,E*
	Uvaria sp. 1	L	0.75	0.004	G*,C*,E*
	? Uvaria sp.	T	0.25	0.002	G*,C*,E*
	Uvariastrum pierreanum	T	47	0.709	G*,C*,E
	?Xylopia acctiflora	T	0.25	0.001	
	Xylopia aethiopica	T			G*,C
	Xylopia quintasii	T	22.25	0.354	G*,C
	?Xylopia sp.	T	1.75	0.098	

Family	Name	Life form	Density (trees / ha)	BA (m2 / ha)	Food consumption by the apes and the elephants ²¹
	<i>Xylopia staudii</i>	T	2.5	0.008	
Apocynaceae					
	<i>Landolphia</i> sp.	L	0.25	0.001	G,C,E
	<i>Landolphia</i> sp.2	L			G,C
	<i>Landolphia</i> sp.3	L			C
	<i>Picralima</i> cf. <i>nitida</i>	T			
	<i>Rauvolfia vomitoria</i>	T	1.25	0.011	
	<i>Tabernaemontana</i> classa	T	4.25	0.038	C*
Bombacaceae					
	? <i>Adansonia digitata</i>	T			
	<i>Ceiba pentandra</i>	T	0.25	0.229	C
Burseraceae					
	<i>Canarium</i> sp.	T			C
Caesalpiniaceae					
	<i>Anthonotha macrophylla</i>	T			
	<i>Barteria nigritana</i>	T	2.75	0.029	
	<i>Berlinia</i> cf. <i>bracteosa</i>	T			
	<i>Berlinia grandifolia</i>	T	13.75	1.930	
	<i>Berlinia</i> sp.1	T	1.25	0.051	
	<i>Berlinia</i> sp.2	T	1.25	0.462	
	CAESALPINIACEAE sp.	T			
	?CAESALPINIACEAE sp	T	0.25	0.008	
	?CAESALPINIACEAE sp	T	0.25	0.144	
	CAESALPINIACEAE sp.1	T	1	0.138	
	CAESALPINIACEAE sp.2	T	2	0.008	
	CAESALPINIACEAE sp.3	T	0.25	0.006	
	<i>Cassia mannii</i>	T			
	? <i>Crudia</i> sp.	T			
	<i>Cynometra</i> sp.	T			
	<i>Dialium</i> sp.	T			C*
	? <i>Dialium</i> sp.1	T	6	0.161	C*
	? <i>Dialium</i> sp.2	T	3	0.449	C*
	<i>Erythrophleum ivorense</i>	T			
	<i>Grossweileroendron</i> balsa	T			
	? <i>Guibourtia demeusei</i>	T			
	? <i>Mezoneuron</i> sp.	LI			
	<i>Microberlinia</i> sp.	T			

Family	Name	Life form	Density (trees / ha)	BA (m ² / ha)	Food consumption by the apes and the elephants ²⁾
	?Oxystigma buchholzii	T			
	Pellegriniodendron?	T			
	Pentaclethra macrophylla	T			
	Piptadeniastrum africanum	T			
	Pterocarpus soyauxii	T			
	Sindola kleineana	T	1	0.291	
	Tetraberlinia sp.	T			
Clusiaceae					
	Allanblackia sp.	T			C
	Garcinia cf. smeathmannii	T	118.5	1.262	G,C,E
	Mammea africana	T			G*,C*,E
	Pentadesma butyracea	T			G*
	Symphonia globulifera	T	0.25	0.050	C*
Combretaceae					
	Combretum sp.				
Connaraceae					
	CONNARACEAE sp.1	?			
	CONNARACEAE sp.2	?			
	CONNARACEAE spp.	?			
Ebenaceae					
	Diospyros boala	T			G*,C*,E*
	Diospyros cf. piscatoria	T			G*,C*,E*
	Diospyros dendo	T			G*,C*,E*
	Diospyros ferrea	T			G*,C*,E*
	Diospyros zenkeri	T			G*,C*,E*
	Diospyros spp. Total ¹⁾	T	148.5	1.971	G*,C*,E*
Erythroxylaceae					
	Erythroxylum manii	T	4.5	0.566	C,E
Euphorbiaceae					
	Alchornea cordifolia	L			
	Anthostema aubryanum	T	32.75	1.925	
	Dichostemma glaucescens	T	46.75	0.515	
	?Euphorbia sp.	T	0.25	0.001	
	Macaranga sp.	T	8.25	0.183	
	Mapleunea membranacea	T	4.25	0.108	
	Margaritaria discoidea	T			
	Mildbraedia paniculata	S			

Family	Name	Life form	Density (trees / ha)	BA (m ² / ha)	Food consumption by the apes and the elephants ²⁾
	Ricinodendron heudelotti	T			
	Sapium ellipticum	T			C
	?Sapium sp.	T	0.25	0.001	
	Spondianthus preussii	T			
	Uapaka guineensis	T	1.25	0.884	G,C,E
	EUPHORBIACEAE sp.	T	2.75	0.159	
Flacourtiaceae					
	Caloncoba glauca	T	3.5	0.459	G*
	Casearia barteri	T	0.25	0.001	
	Scottelia coriacea	T			C
Hippocrataceae					
	Salacia spp.	S			G,C,E
Humiriaceae					
	Sacoglottis gabonensis	T	15	3.632	G,C,E
Irvingiaceae					
	Irvingia gabonensis	T	16.5	1.765	G,C,E
	Irvingia grandifolia	T	0.25	0.273	G*,C*,E
	Irvingia robur	T			G*,C*
	Klainedoxa gabonensis	T	4	1.264	G,C,E
Lecythidaceae					
	Petersianthus macrocarpus	T			
Linaceae					
	Hugonia sp.1	L	0.25	0.001	
	Hugonia sp.2	L	0.25	0.001	
	LINACEAE sp.	T			C
Loganiaceae					
	Anthocleista cf. vogelii	T	2.5	0.130	C
Loganiaceae					
	Strychnos sp.1	T			E
	Strychnos sp.2	LI			E
Luxemburgiaceae					
	?Testuela sp.	T	1.25	0.135	
Meliaceae					
	Entandrophragma cylindric	T			
	Entandrophragma utile	T			
	Khaya ivorensis	T			
Menispermaceae					

Family	Name	Life form	Density (trees / ha)	BA (m ² / ha)	Food consumption by the apes and the elephants ²⁾
	Triclisia sp.	T			
Mimosaceae					
	Calpocalyx heitzii	T			C
	Calpocalyx sp.	T			
	Calpocalyx sp.2	T	1	0.240	
	Cylicodiscus gabunensis	T			
	Tetrapleura tetraptera	T			G,C*,E
Moraceae					
	Chlorophora excelsa	T			
	?Ficus elasticoides	T	0.25	0.002	G*,C*,E*
	Ficus recurvata?	L			G*,C*,E*
	Ficus sp.1	?			G*,C*,E*
	Ficus sp.2	?			G*,C*,E*
	Ficus sp.3	?			G*,C*,E*
	Ficus sp.4	?			G*,C*,E*
	Ficus sp.5	?			G*,C*,E*
	Ficus sp.6	?			G*,C*,E*
	Ficus sp.7	?			G*,C*,E*
	Ficus spp. total ¹⁾	T/L	0.75	0.756	G*,C*,E*
	Musanga cecropioides	T			G,C,E
	Myrianthus arboreus	T			G*,C,E
	Treculia africana	T			G*
Myristicaceae					
	Pycnanthus angolensis	T	0.5	0.135	G*,C,E
	Staudtia gabonensis	T	0.75	0.385	C,E
Myrtaceae					
	Eugenia sp.	T	33	0.479	G,C,E
	Syzygium sp.	T	0.75	0.190	G,C
	Syzygium sp.2	T			
Ochnaceae					
	OCHNACEAE sp.1	T	0.25	0.001	
	OCHNACEAE sp.2	T	6.25	0.219	
Olacaceae					
	Coula edulis	T	5.25	0.403	
	Diogoia zenkeri	T	12	1.075	
	Heisteria parvifolia	T			G*,C*
	Ongokea gore	T			

Family	Name	Life form	Density (trees / ha)	BA (m2 / ha)	Food consumption by the apes and the elephants ^{b)}
	<i>Strombosia zenkeri</i>	T			C
	<i>Strombosiopsis</i> sp.	T	11.5	1.506	E
Pandaceae					
	<i>Panda oleosa</i>	T	0.25	0.026	C*,E
Papilionaceae					
	? <i>Baphia</i> sp.	T	0.25	0.008	
	<i>Dalbergia ecastaphyllum</i>	T	3.5	0.269	
	<i>Milletia</i> sp.1	T	0.75	0.003	
	? <i>Milletia</i>	T	0.5	0.002	
	PAPILIONACEAE sp.	L	0.25	0.001	
Passifloraceae					
	<i>Barteria</i> sp.	T	0.25	0.001	
	<i>Barteria</i> sp.2	T			
Rhamnaceae					
	<i>Maesopsis eminii</i>	T			
Rhizophoraceae					
	<i>Anisophyllea</i> sp.1	T			
	<i>Anisophyllea</i> sp.2	T			
	<i>Poga oleosa</i>	T			G,C*,E
Rubiaceae					
	<i>Coffea</i> sp.	S			C,E
	<i>Massularia acuminata</i>	T	6.5	0.026	
	<i>Mitragyna ciliata</i>	T	5.5	0.196	
	<i>Mussaenda</i> sp.	L			
	<i>Nauclea didderichii</i>	T			G,C,E
	<i>Nauclea</i> sp.	T			G*C*,E*
	<i>Rothmannia whitfieldii</i>	T	6.75	0.030	
	RUBIACEAE sp.1	T	1.25	0.009	C
	RUBIACEAE sp.2	T	14.25	0.606	G,C
	RUBIACEAE sp.3	T	1.25	0.021	G
	RUBIACEAE sp.4	T	1.25	0.018	
	RUBIACEAE sp.5	T	0.75	0.006	
Sapindaceae					
	<i>Blighia welwitschii</i>	T			
	<i>Chytranthus</i> sp.	T			
	<i>Eriocoelum macrocarpum</i>	T	3.5	0.268	
	SAPINDACEAE sp.	T	0.25	0.004	

Family Name	Life form	Density (trees / ha)	BA (m ² / ha)	Food consumption by the apes and the elephants ²¹
Sapotaceae				
Gambeya sp.	T			G*,C,E
Manilkala fouilloyara	T	0.25	0.015	G*,C,E
Manilkara cf. lacera	T			G,C,E
Tieghemella africana	T			C*,E
Scytopetalaceae				
Scytopetalum sp.1	T			G,C
Scytopetalum sp.2	T			G.C*
Sterculiaceae				
?Cola nitida	T			G*,C*
Cola sp.1	T	0.75	0.078	
Cola sp.2	T	0.75	0.003	
Cola sp.3	T	0.5	0.002	
Sterculiaceae sp.1	T			
Sterculiaceae sp.2	T			
Sterculiaceae sp.3	T			
Sterculiaceae sp.4	T			
Tiliaceae				
Duboscia macrocarpa	T	0.25	0.044	G,C*,E
Grewia coriacea	T	0.5	0.061	G,C,E
Ulmaceae				
?Celtis Tessmannii	T			G,C
Celtis sp.1	T			
Verbenaceae				
Vitex doniana	T	2	0.685	G,C,E
Vitaceae				
Cissus dinklagei	LI			G,C
MONOCOTYLEDONEAE				
Araceae				
Amorphophallus sp.	H			
Anchomanes difformis	H			
Nepthytis sp.	H			
Commelinaceae				
Palisota sp.	H			
Cyperaceae				
Cyperaceae spp.	H			
Gramineae				

Family	Name	Life form	Density (trees / ha)	BA (m2 / ha)	Food consumption by the apes and the elephants ²⁾
	GRAMINAE sp.1	H			
	GRAMINAE sp.2	H			
Liliaceae					
	Chlorophytum sp.	H			
Marantaceae					
	?Haumania sp.	H			
	?Marantochloa	H			
Palmae					
	Elaeis guineensis	T			C,E
	?Eremospata wenlandiana	H			
Zingiberaceae					
	Aframomum spp.	H			G*,C*

Unidentified species in the vegetation transect

49

3.33

1) For Diospyros spp. and Ficus spp., only sum of the density and BA of the genus were shown because most of the individual trees could not be identified specifically.

2) Asterisk indicates the possible foods estimated by other study sites (see text).