Food Density and Ranging Patterns of Gorillas and Chimpanzees in the Kahuzi-Biega National Park, Zaire

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ABSTRACT Diet and ranging patterns of gorillas (Gorilla gorilla graueri) and chimpanzees (Pan troglodytes schweinfurthii) were studied during the 1994 dry season in the montane forest of Kahuzi-Biega National Park. A transect census was also made to estimate the diversity and density of trees in primary forest, secondary forest and swamp. Although the diversity of trees in this area was lower than those estimated in lowland tropical forest, more than half of the total 50 tree species were used for foods either by gorillas or by chimpanzees during the study period. A semi-habituated group of gorillas and a unit group of chimpanzees extensively overlapped their diet and ranging areas, but gorillas tended to consume fibrous foods qualitatively and quantitatively and to range in wider area than did chimpanzees. Gorillas daily traveled in both primary and secondary forest to avoid reuse of the previous ranging areas, while chimpanzees persistently range in a small patch of primary forest. The diversity and density of food trees with bearing fruits were higher in primary forest than in secondary forest, and both apes preferred the fruit species which trees appeared at low densities in the transect. The low density of chimpanzees may be owed to the small size and fragmented distribution pattern of primary forest in this area. The differences in foraging patterns between gorillas and chimpanzees may reduce ecological competition between them.

Key Words: Density of food tree / Diet / Ranging / Gorilla / Chimpanzee

The composition of ape's diet reflects variations in the availability of foods in their habitats in relation to ape's specific foraging strategies. Gorillas exhibit frugivorous characteristics in various habitats of lowland tropical forests (Sabater Pi, 1977; Tutin & Fernandez, 1985; Nishihara, 1995), while they are regarded as folivores at higher altitudes and as intermediate at lower altitudes of montane forests (Casimir, 1975; Goodall, 1977; Fossey & Harcourt, 1977; Watts, 1984; Yamagiwa, et al., 1992a, 1994). Although chimpanzees tended to show frugivorous and omnivorous characteristics across habitats (Nishida & Uehara, 1983; Ghiglieri, 1984; Sugiyama & Koman, 1987), fruit constitutes a small part in the composition of their diet in higher montane forest (Yamagiwa et al., 1992a). These differences may possibly be caused by the tendency that fruit diversity is low at higher altitudes.

Trees seasonally produce large amounts of fruits than the other plant forms, such as vines, herbs or epiphytes, and form large food resources for gorillas and chimpanzees. The particular fruit species constitute their most preferred food items, and the seasonal availability of fruits influence on ranging patterns of gorillas and chimpanzees (Casimir, 1975; Baldwin et al., 1982; Ghiglieri, 1984; Goodall, 1986; Williamson et al., 1988; Yamagiwa & Mwanzu, 1994). The 'keystone food' (sensu Leighton & Leighton, 1983), such as terrestrial herbaceous vegetation, is also important for ape's surviving during the period of fruit scarcity (Wrangham, 1986; Rogers & Williamson, 1987; Malenkey & Stiles, 1991; Tutin et al., 1991).
In 1990, we conducted a census on a sympatric population of gorillas and chimpanzees in the montane forest (1,800-3,308 m above sea level) of Kahuzi-Biega National Park, Zaire. The estimated density of chimpanzees (0.13 individual/km²) was far lower than that of sympatric gorillas (0.43-0.47 individual/km²) and the lowest among chimpanzee's populations inhabiting forested habitats (Yamagiwa et al., 1992b, 1993a). The montane forest of Kahuzi may form the upper limit of chimpanzee's distribution and may not provide them suitable habitat. Differences in the availability of foods and in foraging strategies between gorillas and chimpanzees may produce the lower density of chimpanzees in the montane forest.

Since then, we have conducted a ecological survey on the same population to elucidate the differences in diet and ranging patterns between gorillas and chimpanzees. In order to compare the carrying capacity of montane forest with those of other types of habitats, it is necessary to collect data on abundance and availability of each ape's food. Therefore, we conducted a vegetation survey with using the line-transect methods (Yamagiwa et al., 1993b) to estimate the structure of forest and the densities of each tree species in their habitats. These methods were also used for the same purpose in various habitats of apes (Tutin et al., 1994; Yumoto et al., 1994; Idani et al., 1994; Moore, 1994).

The aim of this paper is to provide baseline information on densities of tree and shrub species in the montane forest of Kahuzi-Biega National Park. Densities of ape's foods are compared between different types of vegetation. The proportion of fruiting trees in the transect for each food species are listed, and differences in fruit consumption between gorillas and chimpanzees are described by fecal analysis qualitatively and quantitatively. Ranging patterns of gorillas and chimpanzees are discussed in relation to ape's diet and availability of their food.

METHODS

The Kahuzi-Biega National Park is located in the west of Lake Kivu and covers an area of 6,000 km² at an altitude of 600 to 3,308 m (Fig 1). The Park consists of the highland region (600 km²) and the lowland region, which are interconnected by a corridor of forest. Forty-four species of larger mammals (including ten primate species) are found in the highland region and fifty-six species (fourteen primate species) in the lowland region (Mankoto et al., 1994).

Both gorillas and chimpanzees are continuously distributed in the Park. The population censuses of 1987 and 1990 estimated the apes' densities to be 0.27-0.32 gorillas/km² and 0.27-0.33 chimpanzees/km² in the lowland region; and 0.43-0.47 gorillas/km² and 0.13 chimpanzees/km² in the highland region (Yamagiwa et al., 1989, 1992b, 1993a).

The highland region is made up of bamboo Arundinaria alpina forest (37%), primary montane forest (28%) in the western and northern parts of the Park, secondary montane forest (20%) in the eastern part, Cyperus latifolius swamp (7%) and other vegetation (8%), as described by Goodall (1977) and Murnyak (1981). Dominant tree species in each vegetation type are Podocarpus sp., Ficus spp. and Symphonia globulifera in primary forest; Hagenia abyssinica, Myrionanthus holstii and Vernonia spp. in secondary forest; Hypericum lanceolatum and Rapanea pulchra in Cyperus swamp (Casimir, 1975; Goodall, 1977).

Meteorological data are available from the Meteorological Station at Centre de Recherches en Sciences Naturelles (1,600 m above sea level), which is located c. 5 km from our study site. The mean annual rainfall from 1982 to 1994 was 1,604 mm/year with a clear dry season (June, July and August). The mean monthly temperatures was 19.7°C (maximum: 26.2°C, minimum: 13.1°C) and was constant for 13 years (range: 19.2-20.3°C).
Food density and ranging of apes

Figure 1. Map (below) indicates the location of Kahuzi-Biega National Park in eastern Zaire. Black area shows the montane forest of the Park (600 km²). Map (A) indicates vegetation of the montane forest and study site. Dotted area, Cyperus swamp; horizontal lined area, bamboo forests; white area within the park, primary or secondary montane forests. Map (B) indicates the areas in which fresh trails and beds of gorillas (hatched area) and chimpanzees (dotted area) were found during the bamboo season (September-November) in 1990.

The 1990 census revealed 25 gorilla groups and 9 solitary male gorillas, and 3 unit-groups of chimpanzees in the highland region at an altitude of 1,800 to 3,308 m (Yamagiwa et al., 1992b, 1993). Since 1991 we designated the main study area around Tshibati; this comprises 60 km² along the eastern border of the Park at an altitude of 2050-2350 m.

In 1991, we found four groups of gorillas and a single unit-group of chimpanzees in the study area. These groups had extensively overlapping ranging areas (Yamagiwa et al., 1994). Until 1994, a group of gorillas and the unit-group of chimpanzees have been semi-habituated and occasionally
Table 1. Density of trees in each vegetation type and part eaten by gorillas and chimpanzees in the 1994 dry season.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Density (individuals/ha)</th>
<th>Part eaten</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S</td>
<td>P</td>
</tr>
<tr>
<td><em>Macaranga kilimandscharica</em></td>
<td>81.1</td>
<td>6.6</td>
</tr>
<tr>
<td><em>Bridelia bridentifolia</em></td>
<td>21.8</td>
<td>7.4</td>
</tr>
<tr>
<td><em>Neoboutonia microcalyx</em></td>
<td>21.1</td>
<td>25.6</td>
</tr>
<tr>
<td><em>Agoria salicifolia</em></td>
<td>19.6</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Sapium ellipticum</em></td>
<td>12.6</td>
<td>21.9</td>
</tr>
<tr>
<td><em>Cnopharyngia durissima</em></td>
<td>11.4</td>
<td>12.8</td>
</tr>
<tr>
<td><em>Nuxia congesta</em></td>
<td>9.6</td>
<td>2.9</td>
</tr>
<tr>
<td><em>Millettia dura</em></td>
<td>8.5</td>
<td></td>
</tr>
<tr>
<td>Allophylus sp.</td>
<td>8.0</td>
<td>5.4</td>
</tr>
<tr>
<td>Dombeya goetzenii</td>
<td>7.0</td>
<td>5.4</td>
</tr>
<tr>
<td>Hagenia abyssinica</td>
<td>6.8</td>
<td></td>
</tr>
<tr>
<td><em>Maesa lanceolata</em></td>
<td>5.7</td>
<td></td>
</tr>
<tr>
<td><em>Galindera coffeoides</em></td>
<td>4.7</td>
<td>21.9</td>
</tr>
<tr>
<td><em>Xympocarpus monopora</em></td>
<td>4.1</td>
<td>3.7</td>
</tr>
<tr>
<td><em>Lindackeria huxhamensis</em></td>
<td>3.3</td>
<td>4.5</td>
</tr>
<tr>
<td>Aidia micrantha</td>
<td>2.8</td>
<td>3.7</td>
</tr>
<tr>
<td>Strombosiopsis tetrandra</td>
<td>2.7</td>
<td>2.5</td>
</tr>
<tr>
<td>Hypericum revolutum</td>
<td>2.4</td>
<td></td>
</tr>
<tr>
<td>Erythrina tomentosa</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td><em>Albizia gummierea</em></td>
<td>1.6</td>
<td>3.3</td>
</tr>
<tr>
<td>Vernonia ampla</td>
<td>1.3</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Psychotria palustris</em></td>
<td>1.1</td>
<td>3.3</td>
</tr>
<tr>
<td><em>Cassia spicata ruvurzoriiensis</em></td>
<td>1.1</td>
<td>4.1</td>
</tr>
<tr>
<td><em>Syzygium parvifolium</em></td>
<td>0.9</td>
<td>11.1</td>
</tr>
<tr>
<td><em>Ficus thomningii</em></td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Myriantus holstii</em></td>
<td>0.8</td>
<td>5.0</td>
</tr>
<tr>
<td><em>Trichysia sp.</em></td>
<td>0.8</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Ekebergia capensis</em></td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Eria arborea</em></td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td><em>Ficus oreedryadum</em></td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Manniophyton fulvum</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>Microdesmus pierlotiana</td>
<td>0.3</td>
<td>5.8</td>
</tr>
<tr>
<td>Acantius pubescens</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Bersana ugandensis</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td><em>Maesopsis eminii</em></td>
<td>0.2</td>
<td>7.0</td>
</tr>
<tr>
<td>Polycias fulva</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Rytginia sp.</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Senecio manni</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Xylopia sp.</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Entandrophragma excelsum</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Alchornea hirtella</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Anthoecista sp.</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td><em>Gambieya gorungosana</em></td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td>Morinda sp.</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>Musnularia acuminata</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td><em>Newtonia buchananii</em></td>
<td>5.0</td>
<td></td>
</tr>
<tr>
<td>Parinari exelsa</td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td><em>Symphonia globulifera</em></td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Unidentified sp. (Muzo)</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>Unidentified sp. (Lushesha)</td>
<td>0.8</td>
<td></td>
</tr>
</tbody>
</table>

Vegetation: S, secondary; P, primary; Sw, swamp
Food: F, fruit; L, leaf; P, pith; B, bark; Fl, flower; Gm, gum
G, gorilla; C, chimpanzee.
* One or more trees with bearing ripe fruits were observed in the transect.
tolerated the presence of human observers when we stayed at a distance of 20-50 m. We have continuously collected data on their ranging and diet by direct observations, feeding remains on their fresh trails and fecal analysis.

From 24th to 29th August 1994, we made a vegetation survey by the line-transect methods (Yamagiwa et al., 1993b) to estimate the density of tree species in different types of vegetation within the study area. A belt transect of 5,000 m in length and 20 m in width was plotted to pass in most types of vegetation in which gorillas and chimpanzees ranged in the 1994 dry season (from June to September). Bamboo forest was not included in the transect, because both apes rarely visited it during this season. Every tree and shrub above 10 cm in diameter at breast height (DBH) and its phenology (bearing unripe fruit, ripe fruit, or flower) was recorded within the transect.

The semi-habituated groups of gorillas and chimpanzees were followed daily and their travel routes were recorded on a 1/25,000 map. The location of their night bed site was also recorded on the map with its type of vegetation, topography and altitude.

The composition of diet for gorillas and chimpanzees was estimated from direct observations, feeding remains on their fresh (up to two days old) trails and fecal analysis. Fresh (up to 1 day old) feces were collected mainly in ape's bed sites, washed in 1-mm mesh sieves, dried in sun-light and stored in plastic bags. The contents of each sample were divided into seeds, fruit skins, fiber, leaves, fragments of insects, and other matter. Volume percentage of each content was recorded by 5% interval. Plant specimens were identified at the National Botanical Garden in Belgium.

In the present paper, we used data on the composition of ape's diet during the 1994 major dry season (from 16 June to 15 September) and data on their ranging and fecal samples for 1 month (from 16 August to 15 September 1994) just before and after the transect census.

RESULTS

Density of food diet of apes
The belt transect passed for 3,170 m in secondary forest, 1,212 m in primary forest, and 618 m in a Cyperus swamp. We found the total 2033 trees (1571 in secondary forest, 451 in primary forest and 11 in Cyperus swamp) above 10 cm in DBH consisting of 48 species from 28 families and 2 unidentified species within the transect (Table 1). Euphorbiaceae and Rubiaceae were represented by the largest number of species (7 species for each) and were found at relatively high densities. Six families were represented by 2 or 3 species, and the other 20 families were represented by a single species.

In secondary forest, the top ten species constituted 81% of the total number of 40 tree species. Macaranga kilimandscharica represented the most frequent (33%) species. In primary forest, the top ten species constituted 67% of the total number of 40 tree species. Neoboutonia microcalyx represented the most frequent (14%) species. Twenty seven species were found in both secondary and primary forests. Among these common species, 5 species were found at higher densities in secondary forest, 6 species in primary forest, and 16 species evenly in both types of forest. The total tree density in secondary forest (247.8/ha) was higher than those of primary forest (186.1/ha) and Cyperus swamp (8.9/ha).

During the 1994 dry season, gorillas and chimpanzees were found to use 32 and 38 tree/shrub species for food, respectively. Gorillas tended to eat less kinds of fruit but to eat more parts of single tree species than did chimpanzees (Table 2). Among these, 20 food tree species for gorillas and 26 species for chimpanzees were found in the transect. The top 20 species included 10 food species for gorillas and 11 food species for chimpanzees in secondary forest, and 8 for gorillas and 13 for
chimpanzees in primary forest. Five out of six species found in *Cyperus* swamp were used for food by either of apes.

More than half (26) of tree species were observed to bear fruits. The top 20 species included 13 fructifying species in secondary forest and 16 fructifying species in primary forest. Among these fruits, 1 species was eaten only by gorillas, 7 species were eaten only by chimpanzees, and 10 species were eaten by both apes. The density of total food trees with bearing fruits was different between secondary and primary forests. The density in secondary forest was lower for gorillas and higher for chimpanzees than those in primary forest (10.9/ha vs 23.1/ha for gorillas; 53.2/ha vs 26.8/ha for chimpanzees). The difference in density of food trees for chimpanzees mainly owed to the density of *Macaranga kilimandscharica*, which appeared at the highest density in secondary forest. Excluding the density of this species, the density of fructifying food trees for chimpanzees in secondary forest (17.5/ha) was lower than that in primary forest (25.2/ha).

From 16 August to 15 September 1994, around the transect census period (from 24 to 29 August), we collected 377 gorilla's fecal samples and 221 chimpanzee's fecal samples during 24 and 20 days,

### Table 2. Number of species per plant form per plant part eaten by gorillas and chimpanzees in the study area during the 1994 dry season.

<table>
<thead>
<tr>
<th>Plant form</th>
<th>Fruit/seed</th>
<th>Leaf</th>
<th>Pith/stem</th>
<th>Bark</th>
<th>Root</th>
<th>Other</th>
<th>Total*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree</td>
<td>G</td>
<td>C</td>
<td>G</td>
<td>C</td>
<td>G</td>
<td>C</td>
<td>15</td>
</tr>
<tr>
<td>Vine</td>
<td>3</td>
<td>8</td>
<td>7</td>
<td>2</td>
<td>9</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>Herb</td>
<td>2</td>
<td>3</td>
<td>11</td>
<td>7</td>
<td>5</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>Shrub</td>
<td>10</td>
<td>18</td>
<td>8</td>
<td>7</td>
<td>1</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>Other</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>7</td>
<td>6</td>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>Total</td>
<td>20</td>
<td>37</td>
<td>51</td>
<td>31</td>
<td>22</td>
<td>19</td>
<td>79</td>
</tr>
</tbody>
</table>

*Total shows number of species per plant form (sp.) and number of species × parts (Parts).

Other: Plant form, epiphyte, fern and grass; Parts eaten, flower, frond, gum, petiole.

### Table 3. Percentage of trees with bearing fruits in the total number of each food tree species and rate of its fruit consumption by apes.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Rank of density</th>
<th>% of trees with fruit</th>
<th>Fecal samples including seeds % in total</th>
<th>No.of days observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myrianthus holstii</td>
<td>25</td>
<td>25</td>
<td>93.9</td>
<td>18</td>
</tr>
<tr>
<td>Bridelia bridelifolia</td>
<td>2</td>
<td>6</td>
<td>20.5</td>
<td>3</td>
</tr>
<tr>
<td>Ficus thonningii</td>
<td>25</td>
<td>27</td>
<td>28.6</td>
<td>18</td>
</tr>
<tr>
<td>Ficus oreadryadum</td>
<td>28</td>
<td>100.0</td>
<td>10.9</td>
<td>17</td>
</tr>
<tr>
<td>Syzygium parvifolium</td>
<td>24</td>
<td>4</td>
<td>54.5</td>
<td>2</td>
</tr>
<tr>
<td>Trichysia sp.</td>
<td>25</td>
<td>23</td>
<td>53.3</td>
<td>2</td>
</tr>
<tr>
<td>Gambeya gorungosana</td>
<td>21</td>
<td>2</td>
<td>25.0</td>
<td>4</td>
</tr>
<tr>
<td>Ekerbergia capensis</td>
<td>28</td>
<td>29</td>
<td>66.7</td>
<td>5</td>
</tr>
<tr>
<td>Newtonia buchanani</td>
<td>12</td>
<td>1</td>
<td>41.7</td>
<td>16</td>
</tr>
<tr>
<td>Maesa lacelata</td>
<td>12</td>
<td>1</td>
<td>61.1</td>
<td>3</td>
</tr>
<tr>
<td>Milletia dura</td>
<td>8</td>
<td>2</td>
<td>22.2</td>
<td>4</td>
</tr>
<tr>
<td>Galinia coffeoides</td>
<td>13</td>
<td>2</td>
<td>55.4</td>
<td>5</td>
</tr>
<tr>
<td>Maesopsis eminii</td>
<td>7</td>
<td>1</td>
<td>11.8</td>
<td>2</td>
</tr>
</tbody>
</table>

Rank: the species at highest density was scored 1 in each S (secondary forest) and P (primary forest). G, gorilla; C, chimpanzee.

From 16 August to 15 September, 337 gorilla's fecal samples and 221 chimpanzees fecal samples were collected during 24 and 20 days, respectively.
respectively. The median of the number of samples collected per day was 17 (range: 1-24) for gorillas and 11 (range: 1-27) for chimpanzees. Table 3 shows the percentage of fecal samples including fruit seed for each species in the total number of samples and the number of days in which fruit seed was observed in fecal samples. The percentage of fruiting trees in the total number of trees for each species and its rank of density in the transect were also presented.

Among tree species found in the transect, gorillas and chimpanzees consumed 8 common fruit species during this period. Fruit of Myrianthus holstii was consumed by both apes almost every day. Fruit of Bridelia bridelifolia was more preferred by gorillas, and fruit of Ficus spp. was more preferred by chimpanzees. Five fruit species were only consumed by chimpanzees.

Both gorillas and chimpanzees did not consume frequently the fruit species found at higher densities in the transect or in fully fruiting during this period. Except for Bridelia bridelifolia and Syzygium parvifolium, the fruit species consumed by gorillas were not listed within the top 20 ranks. Seeds or fruit skins of Macaranga kilimandscharica, which appeared at the highest density in secondary forest, were not found in fecal samples of both gorillas and chimpanzees during this period. The fruit species consumed frequently (more than 10% of fecal samples and more than 10 days) by chimpanzees were not listed within the top 10 ranks. These observations suggest that both apes tended to eat such preferred fruit species which were available at low densities during the census period. 

Bridelia bridelifolia was found at higher density and Maesa lanceolata was only found in secondary forest, while Myrianthus holstii was found at higher density and Newtonia buchananii was only found in primary forest during the census. The results of fecal analysis (Table 3) suggest that day range of gorillas and chimpanzees should include both secondary and primary forest to search their preferred fruits.

From fecal analysis and feeding remains on their fresh trails, it was estimated that 29 vine, 20 herb and 22 other (epiphite, fern and grass) species were used for food by gorillas, and 18 vine, 15 herb and 17 other species by chimpanzees (Table 2). Gorillas tended to eat more leaf and bark species from these plants than chimpanzees. The mean volume percentage of fiber and foliage in fecal samples was also higher for gorillas (67.0%, N=377, range: 5-100%) than for chimpanzees (8.2%, N=221, range: 0-70%). Most of vines, herbs, epiphytes, ferns and grasses, which were used for foods by both apes, were usually found in secondary forest. Cyperus latifolius was occasionally eaten by gorillas in large amounts, while it was rarely eaten by chimpanzees. These results suggest that gorillas needed to range more frequently in secondary forest and swamp than chimpanzees during this season.

**Ranging patterns of gorillas and chimpanzees**

The study group of gorillas consisted of 23 individuals including 1 fully adult male, 1 young male, 8 adult female, 10 independent immatures and 3 dependent infants. They usually formed a cohesive group during feeding, resting and traveling period. On the other hand, chimpanzees of the study group usually formed small parties and occasionally moved alone. The group contained c. 20 individuals including 4 adult males and 5 adult females based on individual identifications, the mean party size was 6.2 (N=11, range: 2-10), calculated from direct observations from 16 August to 15 September 1994.

We could follow the fresh trails of gorillas easily and recorded their complete daily route on the map. On the other hand, trails of chimpanzees were difficult to find on the ground and we recorded only a part of their day range, because of small party size and their arboreal habits.

Figure 2 shows the travel routes and the location of night bed sites of gorillas and chimpanzees recorded from 16 August to 15 September 1994. Gorillas used wider range than chimpanzees, and did
not use the same area continuously. Chimpanzees consistently used the small area for traveling and building their beds. Gorillas tended to travel and build night beds in secondary forest rather than in primary forest (location of bed sites: 13 vs 4 times, respectively). Chimpanzees used both secondary and primary forests for night bed sites (10 vs 7), but tended to use the particular primary forest.

However, the daily route of gorillas shows that they tended to visit small primary forest patches daily. Among 18 days in which we recorded their complete day range, they visited primary forest at least once in 17 days. It is likely that their daily travel was made to uncover the areas recently used and to visit both secondary and primary forests.

**DISCUSSION**

The present study shows that the diversity of tree species in montane forest is lower than that of lowland forest. Tutin et al. (1994) recorded 129 tree species above 10 cm in DBH in 2 transects (each 5,000 m in length and 5 m in width) plotted in Marantaceae Forest and 146 tree species in a transect plotted in Closed Canopy Forest of Lopé Reserve, central Gabon. Yumoto et al. (1944) recorded 6,922 trees above 10 cm in DBH from c. 150 species in a transect (8,000 m × 10 m) in the Itebero region of Kahuzi-Biega National Park, eastern Zaire. These two areas are covered with lowland tropical forests and are inhabited by gorillas and chimpanzees. Comparing these records with the results of this study (2033 trees from 50 species in a transect of 5,000 m × 20 m), lowland forests produce more trees than montane forest in terms of density and diversity.

Fruit production of trees constitute the major food resources for frugivorous primates, and its abundance and seasonal availability may have great influences on density of these primates (Clutton-Brock, 1977; Oates, 1987). The low density (0.13/km²) of chimpanzees in montane forest of Kahuzi
may be a result of low production and diversity in tree fruits at higher altitudes. White (1994) estimated the highest density (1.1 individual/km²) of chimpanzees in Closed Canopy Forest, in which the highest diversity of tree species was found in Lopé Reserve. We estimated higher density (0.27-0.33 individual/km²) of chimpanzees in the Itebero region, in which abundance and diversity of trees were higher than those of Kahuzi region (Yamagiwa et al., 1992b; Yumoto et al., 1994).

Tutin and Fernandez (1984) reported that chimpanzees occurred at highest densities in primary forest in Gabon. Our transect census found 40 tree species in both secondary and primary forests. However, the transect line passed 2.6 times longer in secondary forest than in primary forest. This possibly means that diversity of tree species is higher in primary forest. Although the total density of trees was slightly higher in secondary forest, the density of chimpanzee's food trees with bearing fruits was higher in primary forest, when excluding Macaranga kilimandscharica, which was found at the highest density in secondary forest and was rarely eaten by chimpanzees. It seems likely that primary forest may keep higher density of fruiting trees than secondary forest by its high diversity of tree species. Thus, the size and distribution of primary forest may be one of the most important factors influencing the density of chimpanzees.

By contrast, density of gorillas is not varied with density or diversity of trees. Densities of gorillas (0.3-1.2 individual/km²) estimated in various habitats of montane forest fall into a range (0.1-2.61 individual/km²) of those estimated in lowland tropical forests (Jone & Sabater Pi, 1971; Tutin et al., 1992; Fay & Agagnana, 1992; Murnyak, 1981; Aveling & Aveling, 1987; Yamagiwa et al., 1989, 1993a; Nishihara, 1994). This similarity probably owes to their folivorous characteristics and wide range in various types of vegetation. Gorillas inhabiting montane forest feed regularly on fibrous foods and their range is not limited to the forested area (Schaller, 1963; Fossey & Harcourt, 1977; Casimir, 1975). Gorillas inhabiting lowland forests tend to eat many kinds of fruits, but they also consume large amounts of fibers and foliage, in particular, during the period of fruit scarcity (Rogers et al., 1988; Yamagiwa et al., 1994; Nishihara, 1995). Yamagiwa and Mwanza (1994) reported that gorillas changed their food choice and day range according to the availability of fruits in lowland forests of the Itebero region, Zaire. Such flexible foraging strategy may enable gorillas to survive at similar densities in various habitats in tropical forests.

THV, such as Marantaceae and Zingiberaceae, is one of the important foods to support high density of gorillas in lowland forests (Wrangham, 1986; Rogers & Williamson, 1987). White (1994) reported the highest density (1.0 individual/km²) of gorillas in Marantaceae Forest among 4 types of forest in Lopé Reserve, Gabon. Nishihara (1994) also reported the far higher density (2.29-2.61 individual/km²) of gorillas in Ndoki Forest, Congo, where Marantaceae and Zingiberaceae are densely distributed and large amounts of aquatic herbs are usually available in swamps.

Gorillas were found at higher densities in secondary forest than in primary forest (Jones & Sabater Pi, 1971; Tutin and Fernandez, 1984). The results of the present study also shows that gorillas ranged widely in secondary forest rather than primary forest. Although the density of gorilla's food trees with bearing fruits was higher in primary forest, they fed regularly on other food items, such as leaf, pith or bark, which were more easily available in secondary forest.

However, most of the tree fruit species consumed frequently by both gorillas and chimpanzees occurred at low densities in the transect. This means that both apes need to travel long distance for searching such preferred fruits. Gorillas tended to use wide range including various types of vegetation, while chimpanzees continuously used a particular primary forest. These differences may be related to their foraging strategies. Gorillas usually travel, feed and rest together with forming a cohesive group. When they feed on fruits at low densities, they need to travel long distances. Ranging
patterns of the study group of gorillas shows that they daily travel to visit small patches of primary forest and to avoid reuse of previous range. Vedder (1984) reported that gorillas tended to travel to avoid overuse of their range in the Virunga region. Yamagiwa (1988) also reported that gorillas increased day range with increasing the size of group.

By contrast, chimpanzees travel and feed individually with occasionally forming small parties. These foraging patterns may enable them to reuse the particular food resources. Although their preferred fruits are available at low densities, they persistently range in a small patches of primary forest with searching the particular fruit species. Small fragmented primary forests may be responsible for the low density of chimpanzee population at the high altitudes of Kahuzi-Biega National Park, and the differences in foraging strategies between gorillas and chimpanzees may reduce ecological (exploitation) competition between them. However, data presented here are far from complete. In order to discuss on the carrying capacity of montane forest and sympatry of apes, seasonal and annual variations in fruit production and ecology of apes should be studied in detail in the future.

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ザイール共和国カフジ・ピエガ国立公園におけるゴリラとチンパンジーの遊動様式と食物樹の分布密度

ザイール国東部のカフジ・ピエガ国立公園は山地から低地へかけて連続的な植生が保存されており、ここに同所的に生息するゴリラとチンパンジーの生態学的調査が1987年以降続けられている。これまでに山地でも低地でも両種の類人猿がよく似た食性を示すにもかかわらず、山地ではチンパンジーの密度が非常に低いことが判明している。そこで1994年の乾季（6〜9月）に入りづけられた両種類人猿の集団を追跡して日々の遊動ルートを、直接観察、食痕、糞分析により食物メニューや調査した。また、8月のライン・トレコンセプト法によって樹木の構成と密度を調査し、20 m × 5,000 mのトランセクトに出現した胸高直径10 cm以上の木本種と果実や花の種子を記録した。一次林、二次林、湿地を含む植生帯に28科50種の樹木を記録したが、このうち20種のゴリラの食物樹と26種のチンパンジーの食物樹が含まれていた。二次林より一次林の方が食物樹種の多様性や密度が高く、食べられる果実をついている樹種の合計密度も高かった。両種の類人猿とも密度の低い樹種の果実を好む傾向があり、これらの果樹が一次林と二次林に分かれて出現するため、彼らは毎日複数の植生帯を訪問しなければならないことが明らかになった。ゴリラはよくまとまった集団で、同じ場所を重複利用しないように、しかも毎日一次林を通るように広く遊動する。チンパンジーは小さなパーティで特定の一次林を重複利用し、ゴリラより狭い範囲を遊動する。おそらく、一次林が小さなパッチ状に広い二次林に散らばっているカフジの山地林の植生が、チンパンジーの低密度の主因となっており、両種類人猿の採食様式の違いが両種類の採食競合を減らし同所的な共存を支えていると考えられる。