

## 4 *Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo*

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### **Introduction**

Trends in feeding ecology that occur within and between populations over time have important implications for understanding the socioecology of a

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particular species. Chapman *et al.* (2002) showed that primate foraging behavior and diets can vary considerably over small spatial and temporal scales. Such behavioral flexibility raises questions about both stereotypic characterization of primates and traditional comparative studies that do not incorporate intraspecific variation. Although chimpanzees have been studied at several long-term sites, questions still remain about the degree and nature of intraspecific variation in chimpanzee foraging ecology. Some general patterns such as frugivory and dietary diversity are consistent across all populations and habitats. Other aspects of feeding ecology differ between sites or even the same site in different years (Wrangham, 1977; Nishida & Uehara, 1983; Nishida *et al.*, 1983; Newton-Fisher, 1999). Assembling reports from different populations over a large geographic distribution provides the most complete depiction of the feeding ecology of this species and may elucidate patterns that are not apparent when comparing only a few populations in a restricted area of their range. Chimpanzees and gorillas are sympatric in certain regions, and descriptions of their dietary composition and overlap within a shared habitat contribute to understanding the behavioral ecology of these species and facilitate attempts at characterizing their coexistence. We report our preliminary observations of chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) feeding behavior at a new study site in the Goulougo Triangle, Republic of Congo (ROC). We specifically examine the diet composition and diversity of these chimpanzees in comparison to other sites and provide preliminary descriptions of dietary overlap with sympatric gorillas studied during the same time period.

Chimpanzees reside in a range of habitats from savanna to dense forests, and consume a wide variety of food items from several plant and animal species. Dietary composition is closely related to habitat, but has also been shown to vary over short time periods and increase with the length of the study at a particular site (Wrangham, 1977; Nishida & Uehara, 1983; Nishida *et al.*, 1983). For example, Hunt & McGrew (2002) reported that 33 and 60 food items were consumed by chimpanzees residing in the arid climates of Semliki and Assirik, respectively. Wrangham (1977) reported that this many food species could be consumed during a single month in the woodland forests of Gombe. In a similar habitat at the nearby Mahale site, researchers reported that after 7 years of study the cumulative diet composition of chimpanzees was 205 foods, which increased to 328 after 16 years (Nishida, 1974; Nishida & Uehara, 1983). Despite these differences in diet composition, chimpanzees in all habitat types have been characterized as persistent frugivores.

Chimpanzees thrive on a diverse, fruit-based diet and spend more time consuming fruits than any other food item (Wrangham, 1977; Nishida & Uehara, 1983; Tutin *et al.*, 1991; Newton-Fisher, 1999). Time spent feeding

on fruits varies between populations, but comprises more than half of the feeding time at all sites (Table 4.1). Although it provides no indication of the importance of specific fruit species in the diet, the relative proportion of fruit species consumed of the total diet composition is also cited as an indication of frugivory. The overall mean proportion of fruit in the diet at 12 sites listed in Table 4.1 was 55%, with values ranging from 31%–88% at different sites. Although this range of values is large, the proportion of a particular food category in the chimpanzee diet can also vary to this extent over different time periods at the same site and may be attributable to fluctuating availability of preferred foods such as fruit. Hladik (1977) reported that fruit accounted for 68% of the food intake of chimpanzees in Gabon during a 1-year study period, but ranged from 40%–90% on a daily basis. Leaves normally constituted 28% of food intake, but increased to 50% during certain periods within Hladik's study (Hladik, 1977). Newton-Fisher (1999) reported from Budongo Forest that fruit was the most commonly consumed food item (65% of all observations), followed by leaves (20%) and flowers (8%), but that leaf consumption increased to 41% of feeding time during one month and flowers to 45% and 57% during two other months.

A combination of behavioral and ecological modifications allows chimpanzees to sustain this dietary pattern during periods of fruit scarcity (Wrangham, 1977). The flexibility of fission-fusion sociality enables chimpanzees to adjust their association patterns and ranging behavior to effectively forage during lean periods (Wrangham, 1977; Chapman *et al.*, 1995; Wrangham *et al.*, 1996; Sugiyama, 1999; Boesch & Boesch-Achermann, 2000; Fawcett, 2000; Anderson *et al.*, 2002). During such times, chimpanzees have also been shown to increase their dietary diversity, including consumption of less preferred fruits and foliage such as terrestrial herbaceous vegetation (THV) (Tutin *et al.*, 1991; Doran, 1997; Basabose, 2002). The amounts of leaves and THV consumed by different populations vary greatly. Wrangham reported that time spent eating leaves accounted for 21.2% of feeding time at Gombe, but only 2.6% of the monthly feeding time at Kibale in Uganda (Wrangham, 1977; Wrangham *et al.*, 1996). THV consumption for chimpanzees at Kibale ranged from 12.3%–19.9% of the monthly feeding time, but accounted for only 3.2% of the feeding time for chimpanzees at Budongo, Uganda (Wrangham *et al.*, 1996; Newton-Fisher, 1999). These reports clearly indicate the high degree of variation in chimpanzee feeding behavior.

The fruit consumption and dietary diversity of gorillas is also more variable across Africa than was previously thought from early studies of mountain gorilla feeding ecology (Doran & McNeilage, 1998). Gorillas are considered folivorous and possess anatomical specializations designed to efficiently digest large quantities of fiber such as THV and foods high in secondary

Table 4.1. Comparison of chimpanzee diet composition and time allocated to feeding on particular food categories

| Diet composition<br>Subspecies-study site | Methods | % Fruit | % Seeds | % Leaves | % Stems/pith | % Flowers | % Bark | % Other | Plant food<br>items | Plant<br>species |
|---|---------|---------|---------|----------|--------------|-----------|--------|---------|---------------------|------------------|
| <i>P. t. schweinfurthii</i>               |         |         |         |          |              |           |        |         |                     |                  |
| Gombe, Tanzania <sup>a</sup>              | D       | 43      | 7       | 27       | 8            | 10        | —      | 7       | 201                 | —                |
| Mahale, Tanzania <sup>b</sup>             | D       | 31      | 5       | 36       | 11           | 9         | 4      | 5       | 328                 | 198              |
| Budongo, Uganda <sup>c</sup>              | D       | —       | —       | —        | —            | —         | —      | —       | 118                 | 58               |
| Budongo, Uganda <sup>d</sup>              | D       | —       | —       | —        | —            | —         | —      | —       | 91                  | 49               |
| Semliki, Uganda <sup>e</sup>              | D       | 39      | 15      | 30       | 9            | 3         | 3      | —       | 33                  | —                |
| Bwindi, Uganda <sup>f</sup>               | F       | 50      | —       | —        | —            | —         | —      | —       | 60                  | 34               |
| Kahuzi, D. R. C. <sup>g</sup>             | F, T, D | 38      | —       | 31       | 19           | —         | 6      | 5       | 99                  | 75               |
| Kahuzi, D. R. C. <sup>h</sup>             | D, T, F | 40      | 3       | 30       | 17           | 5         | 2      | 4       | 156                 | 110              |
| <i>P. t. troglodytes</i>                  |         |         |         |          |              |           |        |         |                     |                  |
| Belinga, Gabon <sup>i</sup>               | F, T    | 85      | —       | 4        | 7            | —         | —      | 4       | 46                  | 43               |
| Lope, Gabon <sup>j</sup>                  | F, T    | 66      | 11      | 12       | 5            | 4         | 2      | 1       | 161                 | 132              |
| Goulougo, Rep. Congo <sup>k</sup>         | D, F, T | 56      | 7       | 16       | 8            | 8         | 3      | 2       | 158                 | 116              |
| Ndoki, Rep. Congo <sup>l</sup>            | D, F, T | 80      | 6       | —        | 14           | —         | —      | —       | 52                  | —                |
| Ndoki, Rep. Congo <sup>m</sup>            | D, F, T | 88      | —       | 3        | 5            | 2         | —      | 3       | 114                 | 108              |
| <i>P. t. verus</i>                        |         |         |         |          |              |           |        |         |                     |                  |
| Assirik, Senegal <sup>n</sup>             | F, T, D | 57      | 10      | 10       | 3            | 10        | 7      | 3       | 60                  | —                |
| Bossou, Guinea <sup>o</sup>               | D       | 52      | 7       | 18       | 13           | 5         | 3      | 2       | 246                 | —                |

| Time spent feeding<br>Study site | Methods       | % Fruit | % Seeds | % Leaves | % Stems/pith | % Flowers |
|----------------------------------|---------------|---------|---------|----------|--------------|-----------|
| Budongo, Uganda <sup>c</sup>     | 15-min scans  | 65      | —       | 20       | 3            | 9         |
| Budongo, Uganda <sup>d</sup>     | 30-min focals | 64      | 8       | 27       | —            | —         |
| Gombe, Tanzania <sup>d</sup>     | 30-min scans  | 59      | —       | 21       | —            | —         |
| Kibale, Uganda <sup>e</sup>      | 15-min scans  | 79      | —       | 3        | 17           | —         |
| Goulougo, Rep Congo <sup>f</sup> | 20-min scans  | 57      | —       | 32       | 2            | 4         |

*Notes:*

D = Direct observation, F = Fecal analysis, T = Trail Signs;

<sup>a</sup> Wrangham, 1977;

<sup>b</sup> Nishida & Uehara, 1983;

<sup>c</sup> Newton-Fisher, 1999;

<sup>d</sup> Fawcett, 2000;

<sup>e</sup> Hunt & McGrew, 2002;

<sup>f</sup> Stanford & Nkurunungi, 2003;

<sup>g</sup> Yamagiwa *et al.*, 1996;

<sup>h</sup> Basabose, 2002;

<sup>i</sup> Tutin & Fernandez, 1985;

<sup>j</sup> Tutin & Fernandez, 1993;

<sup>k</sup> This study;

<sup>l</sup> Kuroda, 1992;

<sup>m</sup> Kuroda *et al.*, 1996;

<sup>n</sup> McGrew *et al.*, 1988;

<sup>o</sup> Sugiyama & Koman, 1992;

<sup>p</sup> Wrangham *et al.*, 1996.

compounds (Rogers *et al.*, 1990; Remis *et al.*, 2001). The degree of frugivory complementing their herbaceous diet has been shown to be positively correlated with tree species diversity at sites in east Africa. Tree species diversity is inversely related to altitude, and predictably, gorillas in the high altitude regions consumed fewer plant species than gorillas at low altitudes. (Stanford & Nkurungi, 2003; Ganas *et al.*, 2004). Researchers in the lowland forests of central Africa have reported that gorillas supplement their folivorous diet with many fruits (Williamson *et al.*, 1990; Tutin *et al.*, 1991; Remis, 1994; Fay, 1997; Tutin *et al.*, 1997; Doran *et al.*, 2002; Rogers *et al.*, 2004). The frugivorous tendencies of western lowland gorillas in areas where they are sympatric with chimpanzees have led researchers to suggest that resource competition may occur between these apes (Tutin & Fernandez, 1985; Tutin *et al.*, 1991; Yamagiwa *et al.*, 1996; Remis, 1997).

Chimpanzees and gorillas are sympatric throughout much of the Congo Basin and in some parts of eastern Africa. Several sites have reported a high degree of overlap in the diets of these sympatric apes (Table 4.2 summarizes these studies). Further examinations both of this dietary overlap and of specific foraging behaviors can lead to a better understanding of the ecological constraints and mechanisms governing the coexistence of these apes. Researchers at Kahuzi-Biega in the Democratic Republic of Congo (DRC) have suggested that dietary and ranging overlap of *P. t. schweinfurthii* and *Gorilla gorilla graueri* is high, but suggest that competition is avoided through mutual avoidance (Yamagiwa *et al.*, 1996). Studying *P. t. schweinfurthii* and *Gorilla gorilla beringei* at Bwindi Impenetrable Forest in Uganda, Stanford & Nkurungi (2003) have reported that gorillas show increased seasonal frugivory, which results in a high degree of dietary overlap with chimpanzees during particular months. However, it has been suggested that the degree of dietary overlap between these species may be most pronounced in the lowland forests of central Africa (Tutin & Fernandez, 1985, 1993; Tutin *et al.*, 1991; Nishihara, 1995; Kuroda *et al.*, 1996). Evidence of simultaneous exploitation of these shared resources was supported by several observations of co-feeding in the same tree canopy (J. M. Fay, pers. comm., 1998; Kuroda *et al.*, 1996; T. Nishihara, pers. comm., 1998). Although it is clear that dietary overlap occurs between these sympatric ape species, the ecological factors (such as forest productivity and seasonality) or demographic variables (such as ape abundance and group composition) that influence this phenomenon have been overshadowed by general methods and sampling bias. Cumulative food lists that do not provide an indication of the relative amount of food intake or temporal aspects of dietary convergence are often compared. Such comparisons are also based on the assumption that food lists compiled under

different circumstances are relatively representative of the diets of these species.

In this study, we provide the first descriptions of chimpanzee feeding ecology derived from prolonged direct observations of *P. t. troglodytes* residing in an undisturbed, dense lowland forest in the Congo Basin. Based on previous reports of dietary overlap between apes in the Ndoki region and the relatively high density of apes in the Goulougo Triangle study area (1.53–2.23 chimpanzees/km<sup>2</sup> and 2.34 gorillas/km<sup>2</sup>, respectively), we expected to see some degree of overlap between these sympatric apes (Morgan *et al.*, in press). We compare our results to previous studies to examine whether: (1) the diet composition or diversity of these chimpanzees is different from other sites; (2) the dietary overlap shown by chimpanzees and gorillas in the Goulougo Triangle resembles feeding overlap between sympatric apes at other sites; and (3) there is preliminary indication of niche differentiation by these apes as shown by divergent selectivity of the same species. In addition, preliminary data are provided on resource abundance in relation to foraging behavior. We assess whether our results support generalizations about chimpanzee feeding behavior, provide insights into the intraspecific behavioral flexibility of this species, and elucidate potential patterns in dietary overlap between these sympatric apes.

## Methods

### *Study site*

The Goulougo Triangle is located within the Nouabalé-Ndoki National Park (NNNP) (16°51'–16°56'N; 2°05'–3°03'E), Republic of Congo. The study area covers 30 000 ha of lowland forest and altitudes range between 330 and 600 m. Four habitat types occur in the Goulougo Triangle: monodominant *Gilbertiodendron* forest, *Gilbertiodendron* mixed species forest, mixed species forest, and swamp forest (based on Moutsambote *et al.*, 1994). The climate in the study area can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones (White, 1983). The main rainy season is typically from August through November, with a short rainy season in May. Average monthly temperatures and rainfall were recorded at Mbeli Bai base camp, ROC (17 km from the study area). The annual rainfall averaged 1728 ± 47 mm between 2000 and 2002 (E. Stokes, unpublished data). The average minimum and maximum temperatures during those years were 21.1 °C and 26.5 °C in 2000, 21.5 °C and 26.8 °C in 2001, and 21.9 °C and 26.5 °C in 2002, and showed little seasonal variation (E. Stokes, unpublished data).

Table 4.2. Sites where sympatric chimpanzees and gorillas have been studied

| Site / Country                             | Altitude (m) | Vegetation classification  | Sympatric apes                                   | Ape density Indiv/km <sup>2</sup>            | Method (# chimp; # gorilla)                | Dietary diversity Parts (Spp.) | # Overlap species | % Dietary overlap |
|--|--------------|--|--|--|--|--------------------------------|-------------------|-------------------|
| <b>Belinga<sup>d</sup></b><br>Gabon        | 700-1000     | Primary forest, secondary forest   | <i>P. t. troglodytes</i><br><i>G. g. gorilla</i> | 0.49 <sup>f</sup><br>0.44 <sup>f</sup>       | F (25; 246)<br>T (35; 165)<br>D (14; 11)   | 46(43)<br>104(89)              | 46                | 100<br>60         |
| <b>Lope<sup>b</sup></b><br>Gabon           | 100-200      | Semi-evergreen tropical rainforest, colonizing forest, Marantaceae forest, mixed species, closed canopy forest, Sacoglottis forest, savanna and forest savanna | <i>P. t. troglodytes</i><br><i>G. g. gorilla</i> | 0.2-1.1 <sup>f</sup><br>0.3-1.0 <sup>f</sup> | F (1854; 3565)<br>D (857; ?)<br>T (277; ?) | 161 (132)<br>213 (-)           | 123               | 73<br>57          |
| <b>Okorobiko<sup>c</sup></b><br>Eq. Guinea | <750         | Dense and secondary forest, regenerating forest, Brachystegia, Landolphia, plantations   | <i>P. t. troglodytes</i><br><i>G. g. gorilla</i> | 0.3-1.5                                      | (43)                                       |                                |                   |                   |
| <b>Ndoki<sup>d</sup></b><br>Rep. Congo     | 300-600      | Monodominant <i>Gilbertiodendron</i> forest, semi-deciduous mixed species forest, swamp forest   | <i>P. t. troglodytes</i><br><i>G. g. gorilla</i> | 1.3<br>1.3                                   | F (42; 29)<br>D (7; 8)<br>T                | 52<br>79                       | 47                | 90<br>59          |
| <b>Ndoki<sup>f</sup></b><br>Rep. Congo     | 300-600      | Monodominant <i>Gilbertiodendron</i> forest, semi-deciduous mixed species forest, swamp forest   | <i>P. t. troglodytes</i><br><i>G. g. gorilla</i> | 2.7<br>1.9-2.6, 2.3-2.6                      | F (214; ?)<br>D<br>T                       | 114 (108)<br>182 (152)         | 64                | 59<br>42          |



|                              |           |   |                             |                             |              |           |    |
|------------------------------|-----------|---|-----------------------------|-----------------------------|--------------|-----------|----|
| <i>Goulougo</i> <sup>a</sup> | 330–600   | Monodominant  | <i>P. t. troglodytes</i>    | 1.5 (1.2, 1.9) <sup>k</sup> | D (650; 342) | 67        | 58 |
| Rep. Congo                   |           | <i>Gilbertiodendron</i> forest, semi-deciduous mixed species forest, swamp forest   | <i>G. g. gorilla</i>        | 2.3 (1.8, 3.0) <sup>k</sup> | F (497; 631) | 107 (80)  | 84 |
| <i>Kahuzi</i> <sup>b</sup>   | 1800–3300 | Bamboo forest, secondary montane forest, <i>Cyperus</i> swamp   | <i>P. t. schweinfurthii</i> | 0.1                         | F (394; 256) | 99 (75)   | 73 |
| Congo                        |           |   | <i>G. g. graueri</i>        | 0.4–0.5                     | D (47; 39)   | 129 (79)  | 70 |
| <i>Bwindi</i> <sup>c</sup>   | 2000–2300 | <i>Parinari</i> -dominated forest, <i>Chrysophyllum</i> -dominated upland forest, <i>Newtonia</i> -dominated forest, swamp, bamboo zone | <i>P. t. schweinfurthii</i> |                             | T (11, 12)   | 60 (>34)  | 94 |
| Uganda                       |           |   | <i>G. g. beringei</i>       |                             | D            | 133 (>96) | 33 |

Notes:

<sup>a</sup>Tutin & Fernandez, 1985;

<sup>b</sup>Tutin & Fernandez, 1993;

<sup>c</sup>Jones & Sabater Pi, 1971; Sabater Pi, 1979;

<sup>d</sup>Kuroda, 1992;

<sup>e</sup>Kuroda *et al.*, 1996;

<sup>f</sup>This study;

<sup>g</sup>Yamagiwa *et al.*, 1996;

<sup>h</sup>Stanford & Nkurunungi, 2003;

<sup>i</sup>Tutin & Fernandez, 1984;

<sup>j</sup>White, 1992;

<sup>k</sup>Morgan *et al.*, in press;

Methods: D = Direct observation, F = Fecal analysis, T = Trail signs. Dietary overlap is number of food items shared by apes divided by the total number of food items for each species.

### **Data collection**

#### *Direct observations*

During 47 months between February 1999 and October 2004, we made contact with chimpanzees and gorillas, respectively, on 650 and 342 occasions for a total observation time of ~1500 hours and 54 hours, respectively. Data for this study were collected while conducting reconnaissance surveys of the semi-habituated chimpanzees in the Goulougo Triangle. Lack of full habituation may have biased our observations toward chimpanzees feeding and socializing in the canopy. While searching for chimpanzees, we frequently encountered gorillas but did not attempt to maintain prolonged contact. During each observation we recorded all food items (fruit, leaf, flower, seed, pith, bark, meat, insect, honey, soil) and species consumed. Interspecific co-feeding events with chimpanzees occurred when another primate species fed simultaneously upon food items from the same individual source.

Time spent feeding was measured by instantaneous group scans that were conducted at 20-minute intervals during chimpanzee encounters (Altmann, 1974). Scan data were collected during two field seasons (June 2000–June 2001, September 2001–December 2002), totaling 414 hours of direct observation ( $n = 195$  contacts, average duration =  $127 \pm 116$  min). Data collected included general activity patterns of all individuals present and any food item consumed.

#### *Fecal analysis*

A total of 497 chimpanzee and 631 gorilla fecal samples were analyzed for food content between June 2000 and March 2004. The feces of the two ape species were distinguishable by form, consistency, and associated traces. The contents of all fecal samples were examined macroscopically following the methods of Tutin *et al.* (1991). Fresh (<12 hours old) and recent (<24 hours old) samples were transported back to camp to be sluiced in a 1-mm mesh sieve. Older samples were examined on the path. All seeds were identified to species level and counted. The abundance of small seeds was ranked on a five-point scale of abundance (absent, rare, few, common, abundant). As it is often difficult to identify the species of foliage in feces, the abundance of green leaf fragments and fiber categories were independently ranked on the same scale with respect to the total mass of the fecal sample. When possible, the species of foliage was identified. The species and abundance of social insect remains, meat, bone, and soil found in fecal samples were also recorded.

### *Feeding traces*

During 2001 and 2002, we recorded all feeding traces that were attributed with certainty to either chimpanzees or gorillas based on the presence of other verifying signs (presence, feces, odor, imprints, hair, etc.). These data were used to compile a more comprehensive food list for both chimpanzees and gorillas.

### *Tree diversity*

Hall, Harris, & Finkral (unpublished data) conducted a floristic inventory of two mixed species forest sites in the Goualougo Triangle study area. The inventory was designed to gain an unbiased understanding of tree species diversity within the semi-deciduous forests of the southeastern sector of the NNNP. They chose a 2.25-km<sup>2</sup> area within which a sampling grid was laid out on the ground. A total of sixteen 30-m × 30-m plots were laid out at 500-m intervals along four parallel 1.5-km transects. Within each plot, diameters were measured and species identified for all trees > 10 cm diameter at breast height (DBH).

### *Data analysis*

#### *Food list*

Food lists, including the species, life form of the species, and food item consumed, were compiled for chimpanzees and gorilla based on direct observations, fecal remains, and feeding traces. The life form of the plant was divided into five categories: tree, shrub, herb, liana, or other. The diet of chimpanzees and gorillas was broken into seven categories: fruit, seeds, leaves, stems/pith, flowers, bark, and other. In order to distinguish between fruit and seed categories we considered seed consumption to have taken place only if the apes actively sought to consume the seed component of a given fruit or pod. It was not necessary to consume the pulp of a fruit in order to feed on the associated seed(s). We report the five fruits and leaf species that were either most frequently directly observed being consumed or identified in fecal analysis.

#### *Interspecific dietary overlap*

Interspecific dietary overlap was calculated as the number of food species shared by gorillas and chimpanzees divided by the total number of food species consumed by each ape (Tutin & Fernandez, 1984, 1993). We also calculated interspecific dietary overlap in food items consumed.

### *Feeding analysis of fecal samples*

The total number of fruit species was tallied for each fecal sample. These data were used to calculate the average number of fruit species consumed each month. Monthly averages of green leaf and fiber were also calculated. A foliage score for each fecal sample was calculated by summing the abundance of green leaf and fiber scores.

We analyzed an average of  $13.43 \pm 8.28$  chimpanzee and  $19.12 \pm 12.34$  gorilla fecal samples per month during the study period. We adopted the method of Doran *et al.* (2002) to determine if sample size had an effect on the amount of fruit and fiber in the fecal samples per month. We did not find a significant relationship between sample size and: mean number of fruit species per fecal sample ( $r_s$  chimp = 0.05,  $n = 37$ ,  $p = 0.77$ ;  $r_s$  gorilla =  $-0.21$ ,  $n = 34$ ,  $p = 0.24$ ), or foliage score ( $r_s$  chimp =  $-0.30$ ,  $n = 37$ ,  $p = 0.86$ ;  $r_s$  gorilla = 0.21,  $n = 34$ ,  $p = 0.25$ ). Only the months with more than five samples for each species were included in the comparison of chimpanzee and gorilla feeding patterns (Figures 4.1a,b).

## **Results**

### *Chimpanzee diet*

Chimpanzees consumed 158 vegetative food items of 116 species, which represented 41 families. The life form of these chimpanzee food items included 83 tree species, 11 strangler species, 10 lianas, 10 species of herbaceous vegetation, and 2 shrubs. Of all the feeding observations recorded for chimpanzee parties, 92% were of feeding on plant items. The food list composition and proportion of time spent consuming fruits, leaves, flowers, seeds, and bark/pith are shown in Table 4.1. The vegetative component of the chimpanzee diet consisted primarily of fruits, which accounted for 56% of feeding events and 57% of time spent feeding (Table 4.1). Leaves were the second-most prevalent food item in species representation (16%) and accounted for 32% of time spent feeding. Chimpanzees spent 4% of their feeding time consuming flowers and buds. The top five most frequently consumed fruit and leaf species are shown in Table 4.3.

An additional 18 non-plant food items were also identified, including meat, social insects, honey, soil, and water. In contrast to other sites with frequent monkey predation, chimpanzees in the Goualougo Triangle have thus far only been observed feeding on duikers (*Cephalophus monticola*, *Cephalophus callipygus*, *Cephalophus dorsalis*). Social insect predation included ants (*Dorylus* spp., *Oecophylla longinodo*), termites (*Macrotermes* spp.), and bees

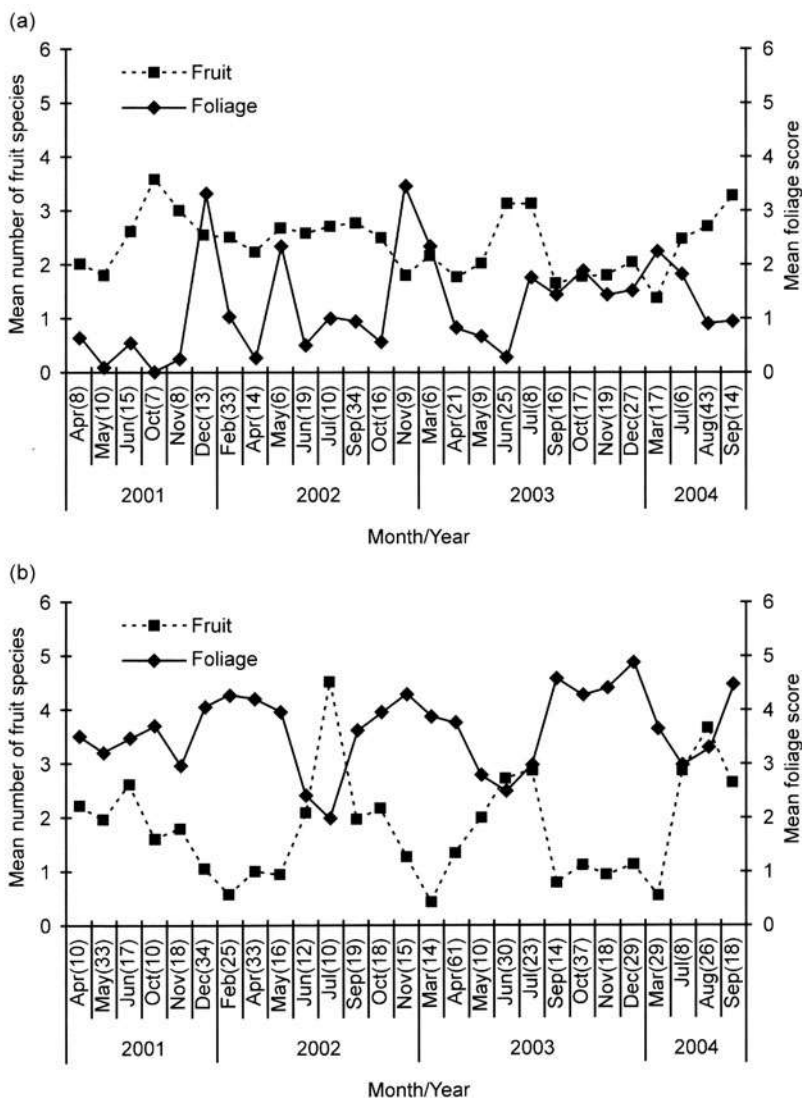


Figure 4.1. (a) Mean number of fruit species and foliage consumed by chimpanzees; abundance scores are per fecal sample per month. (b) Mean number of fruit species and foliage consumed by gorillas; abundance scores are per fecal sample per month.

(*Apis* sp., *Trigona* sp.). Chimpanzees frequently used tools to extract termites and ants from their nests (Sanz *et al.*, 2004). Tool use was also observed in honey gathering at the nests of at least three different bee species. Soil from termite mounds was also consumed. Similar to other long-term study sites, we

Table 4.3. Top five fruit and leaf species consumed by chimpanzees in Goulougo as shown by percent of feeding observations, group scans, and fecal analysis

| Top fruit species                  | Chimpanzee              |                 |                  | Gorilla                 |                 |  |
|------------------------------------|-------------------------|-----------------|------------------|-------------------------|-----------------|--|
|                                    | Feeding obsv. (n = 550) | Feces (n = 497) | Scans (n = 1390) | Feeding obsv. (n = 179) | Feces (n = 631) |  |
| <i>Ficus</i> spp.                  | <b>17.3</b>             | <b>49.5</b>     | <b>43.4</b>      | 3.4                     | 4.8             |  |
| <i>Greenwayodendron suaveolens</i> | <b>6.7</b>              | <b>21.9</b>     | 0.7              | <b>11.7</b>             | <b>9.5</b>      |  |
| <i>Irvingia grandifolia</i>        | <b>5.6</b>              | 0.2             | 0.4              | —                       | —               |  |
| <i>Duboscia</i> sp.                | <b>3.8</b>              | <b>17.1</b>     | 3.4              | <b>19.6</b>             | <b>40.9</b>     |  |
| <i>Landolphia</i> sp.              | <b>3.8</b>              | 4.0             | 1.1              | 0.6                     | 0.2             |  |
| <i>Mammea africana</i>             | 3.3                     | 2.2             | <b>7.5</b>       | 1.7                     | —               |  |
| <i>Antiaris toxicaria</i>          | 2.7                     | 6.2             | <b>6.7</b>       | —                       | —               |  |
| <i>Celtis adolfi-friderici</i>     | 2.5                     | <b>7.8</b>      | <b>6.0</b>       | —                       | 1.7             |  |
| <i>Manilkara mabokeensis</i>       | 2.0                     | —               | <b>5.2</b>       | —                       | —               |  |
| <i>Tetrapleura tetraptera</i>      | —                       | 7.2             | —                | 1.7                     | <b>13.3</b>     |  |
| <i>Chrysophyllum lacourtiana</i>   | 1.6                     | <b>19.3</b>     | —                | <b>8.9</b>              | <b>8.9</b>      |  |
| <i>Grewia</i> sp.                  | 1.1                     | 3.8             | 1.5              | <b>7.3</b>              | <b>8.1</b>      |  |
| <i>Klainedoxa gabonensis</i>       | 2.7                     | 1.0             | 1.5              | <b>6.1</b>              | 3.0             |  |
| Total of top five                  | 37.2                    | —               | 68.8             | 53.6                    | —               |  |
| Chimpanzee                         |                         |                 |                  |                         |                 |  |
| Top leaf species                   | Feeding obsv. (n = 143) |                 |                  | Scans (n = 1390)        |                 |  |
| <i>Celtis mildbraedii</i>          | <b>62.9</b>             |                 | <b>87.8</b>      |                         |                 |  |
| <i>Celtis adolfi-friderici</i>     | <b>4.9</b>              |                 | <b>1.3</b>       |                         |                 |  |
| <i>Triplochiton scleroxylon</i>    | <b>4.2</b>              |                 | <b>5.1</b>       |                         |                 |  |
| <i>Liane</i> sp.                   | <b>3.5</b>              |                 | <b>3.2</b>       |                         |                 |  |
| <i>Daltonia africana</i>           | <b>2.1</b>              |                 | —                |                         |                 |  |
| <i>Milicia excelsa</i>             | 0.7                     |                 | <b>1.3</b>       |                         |                 |  |
| Total of top five                  | 77.6                    |                 | 98.7             |                         |                 |  |

Items in **bold** font are top five species for each column.

observed chimpanzees using leaf sponges to gather water from tree basins. Leaves used by local human populations for medicinal purposes were recovered intact in chimpanzee feces throughout this study.

The frugivorous tendency of chimpanzees and folivorous tendency of gorillas was evident in the results of fecal analyses. A greater proportion of chimpanzee fecal samples contained at least one fruit item (fecal samples with fruit: chimpanzee = 98.8%; gorilla = 79.9%). The average number of fruit species per fecal sample was higher for chimpanzees than gorillas (mean number of fruit species per fecal sample: chimpanzees =  $2.33 \pm 1.22$ ,  $n = 497$ , range = 0, 7; gorillas =  $1.63 \pm 1.42$ ,  $n = 631$ , range = 0, 8). A paired comparison of the monthly averages of these values showed a significant difference between chimpanzees and gorilla fruit consumption ( $t = 3.51$ ,  $df = 26$ ,  $p < 0.01$ ). In contrast, gorillas consumed more foliage than chimpanzees. Foliage was present in a greater proportion of gorilla (94.1%) versus chimpanzee (46.1%) fecal samples and in greater amounts per sample (abundance score of fecal samples: gorilla =  $3.74 \pm 1.54$ ,  $n = 631$ , mode = 4, range = 0, 8; chimpanzee =  $1.07 \pm 1.57$ ,  $n = 497$ , mode = 0, range = 0, 8). The monthly averages of foliage scores also showed a significant difference between chimpanzees and gorilla ( $t = -13.35$ ,  $df = 26$ ,  $p < 0.01$ ).

In mixed forest, the 25 most common tree species and their exploitation by apes are listed in Table 4.4. Four important chimpanzee fruit species (*Greenwayodendron suaveolens*, *Celtis adolfi-friderici*, *Manilkara mabo-keensis*, *Duboscia* sp.) and three leaf species (*Celtis mildbraedii*, *Celtis adolfi-friderici*, *Triplochiton scleroxyn*) were represented in this list of trees. This list does not include a single representative of the *Ficus* genus, which was identified by all measures as an important food for chimpanzees (Table 4.3). Of the species listed above that were both important in chimpanzee diet and prevalent in the study area, four were also consumed by gorillas.

#### *Dietary overlap between chimpanzees and gorillas*

Of the total number of plant species eaten by apes, 52% of food species overlapped in the chimpanzee and gorilla diets ( $n = 67$  shared species). Our data indicated that 84% of gorilla food species were consumed by chimpanzees and 58% of chimpanzee food species were consumed by gorillas. A lower degree of overlap was found in specific food items (30.1% of chimpanzee food items shared with gorillas, 54.7% of gorilla food items shared with chimpanzees), a finding which is most likely affected by skewed sampling effort toward chimpanzees. The highest degree of dietary overlap

Table 4.4. Most common tree species in mixed species forest to the Goulougo Triangle, ranked by stem density

| Rank | Genus  | Stems/ha     | M/ha        | C/G* |
|------|--|--------------|-------------|------|
| 1    | <i>Diospyros bipindensis</i>                 | 29.17        | 0.41        |      |
| 2    | <i>Diospyros canaliculata</i>                | 18.75        | 0.36        |      |
| 3    | <b><i>Celtis mildbraedii</i></b>             | <b>13.89</b> | <b>1.25</b> | C/G  |
| 4    | <b><i>Greenwayodendron suaveolens</i></b>    | <b>13.89</b> | <b>0.68</b> | C/G  |
| 5    | <i>Strombosia pustulata</i>                  | 12.50        | 0.96        | C    |
| 6    | <i>Pancovia</i> sp.                          | 11.81        | 0.30        | C/G  |
| 7    | <i>Strombosia nigropunctata</i>              | 10.42        | 0.54        |      |
| 8    | <i>Entandrophragma cylindricum</i>           | 8.33         | 2.21        |      |
| 9    | <i>Nesogordonia papaverifera</i>             | 8.33         | 1.31        |      |
| 10   | <i>Anonidium mannii</i>                      | 8.33         | 0.55        | C/G  |
| 11   | <i>Petersianthus macrocarpus</i>             | 7.64         | 1.91        | C/G  |
| 12   | <i>Sterculia oblonga</i>                     | 7.64         | 1.46        |      |
| 13   | <b><i>Celtis adolfi-friderici</i></b>        | <b>7.64</b>  | <b>0.50</b> | C/G  |
| 14   | <i>Camptostylus mannii</i>                   | 7.64         | 0.14        |      |
| 15   | <i>Strombosiopsis tetandra</i>               | 6.94         | 0.41        |      |
| 16   | <i>Guarea</i> vel sp. aff. <i>Thompsonii</i> | 6.25         | 0.26        |      |
| 17   | <i>Cola lateritia</i>                        | 5.56         | 0.52        | C    |
| 18   | <i>Strombosia grandifolia</i>                | 4.86         | 0.69        |      |
| 19   | <i>Trichilia</i> sp.                         | 4.86         | 0.06        |      |
| 20   | <i>Terminalia superba</i>                    | 4.17         | 1.62        |      |
| 21   | <i>Cleistanthus mildbraedii</i>              | 4.17         | 0.62        |      |
| 22   | <i>Diospyros crassiflora</i>                 | 4.17         | 0.36        | C/G  |
| 23   | <i>Barteria</i> sp.                          | 4.17         | 0.09        |      |
| 24   | <i>Angylocalyx pynaertii</i>                 | 3.47         | 0.18        | C/G  |
| 25   | <i>Xylopia chrysophylla</i>                  | 3.47         | 0.16        |      |

## Notes:

\*Consumed by chimpanzees (C), gorillas (G), or both (C/G).

Items in **bold** font are important foods consumed by chimpanzees. Rank indicates species position in relation to all other species with regards to density. Area is the percent each species contributes to the total basal area per hectare.

occurred in fruit items, followed by leaves and stems. Dietary overlap did not occur with meat species or social insects. Chimpanzees and gorillas employ different foraging strategies to feed on social insects. Chimpanzees used a complex tool set to extract two different species of *Macrotermes* from epigeal and subterranean nests, whereas gorillas gathered *Cubitermes* by breaking the nest with their hands (Sanz *et al.*, 2004). Gorillas have not yet been observed eating ants or honey, but ant traces have been recovered in their feces.

There was overlap in the five fruit species most frequently consumed by chimpanzees and gorillas (Table 4.3). All measures (direct observation of



feeding events, fecal analysis, group scans) indicated that *Ficus* was the most frequent food item for chimpanzees. They were observed consuming 13 species of this genus, whereas only 4.8% of gorilla feces contained *Ficus* seeds and direct observations of gorillas revealed only three species. *Duboscia* was the most common fruit item consumed by gorillas during direct observations and recovered in feces. This was also identified as an important food item for chimpanzees. *G. suaveolens* was the second most common item for chimpanzees (21.9% of feces) and third for gorillas (9.5% of feces). Overlap also occurred in the consumption of *Chrysophyllum lacourtiana*. Although our observation time was biased toward chimpanzees, all but one of the top foods for gorillas identified in the study were listed as important foods by Doran *et al.* (2002), who studied feeding in habituated western lowland gorillas.

Over the duration of the study, chimpanzees and gorillas showed different patterns in fruit and foliage consumption (Figure 4.1). Chimpanzees consistently consumed a greater variety of fruit species (as measured by the average number of fruit species per fecal sample) than gorillas, but this was not related to their foliage consumption each month. Gorillas consumed more foliage than chimpanzees in all months surveyed. Foliage scores consisted of both green leaf fragments and fiber. The level of consumption and relative contribution of these components clearly differed between chimpanzees and gorillas (Figures 2a, b). There was not a significant difference in the average monthly green leaf scores between chimpanzees and gorillas ( $U = 51.5$ ,  $n = 24$ ,  $p = 0.25$ ), but average monthly fiber scores were different ( $U = 0.0$ ,  $n = 24$ ,  $p < 0.01$ ). Our results indicated a trend rather than a negative correlation between the monthly fruit and foliage intake of chimpanzees ( $r_s = -0.36$ ,  $n = 29$ ,  $p = 0.06$ ). In contrast, there was an inverse relationship between the average number of fruit species and foliage scores for gorillas over the same time period ( $r_s = -0.62$ ,  $n = 29$ ,  $p < 0.01$ ).

Chimpanzees and gorillas were observed co-feeding on eight occasions in six different species of fruit tree. This included co-feeding in the same tree crown ( $n = 4$ ) and co-feeding in the same tree but separated by vertical distance, with a solitary silverback gorilla feeding on fallen fruits on the ground while chimpanzees foraged in the canopy of the same tree ( $n = 4$ ). There were six additional occasions when gorillas approached a tree where chimpanzees were feeding, but fled after detecting human presence. Co-feeding parties could be lengthy, lasting an average of 46 minutes ( $sd = 41$ , range = 18–150 minutes;  $n = 8$ ) and ranging in size from 3–22 individuals. Average chimpanzee and gorilla party size during co-feeding events was  $7.0 \pm 6.2$  ( $n = 8$ , range = 2–18) and  $2.8 \pm 1.8$  ( $n = 6$ , range = 1–6),<sup>1</sup> respectively. Most of these intersections occurred in two species of *Ficus*

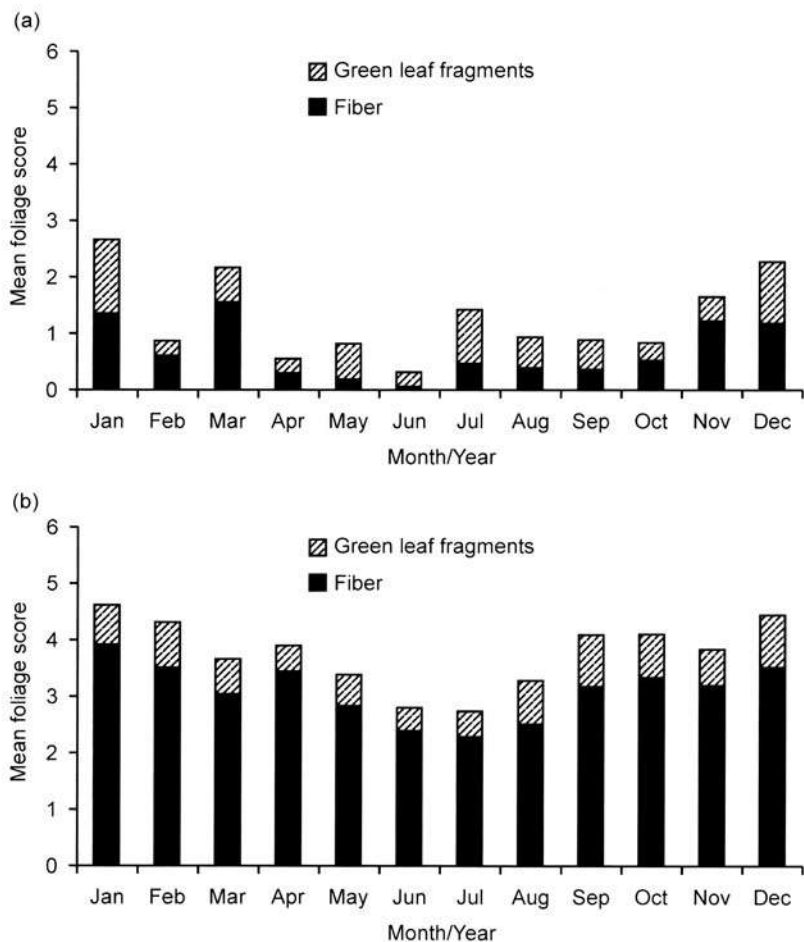


Figure 4.2. (a) Average abundance of foliage consumed each month by chimpanzees. (b) Average abundance of foliage consumed each month by gorillas.

trees (*Ficus calyptrate* and *Ficus recurvata*), but co-feeding was also observed at *C. lacourtiana*, *Mammea africana*, and *Treulia africana*.

## Discussion

The chimpanzees of the Goulougo Triangle are frugivores who regularly supplement their diet with vegetative plant parts, meat, and social insects.

They have a diverse diet that currently encompasses more than 176 food items and continues to expand. As documented at other sites with sympatric chimpanzees and gorillas, we observed a high degree of dietary overlap and occasional interspecific encounters at food sources (Tutin & Fernandez, 1985, 1993; Kuroda, 1992). Food list overlap showed that chimpanzees and gorillas consume many of the same plant foods, but fecal analysis indicated that their patterns of fruit and foliage consumption differed over the same time period. Divergences in dietary selectivity were indicated by differences in fruit consumption and exploitation of common tree species in the study area.

Chimpanzees in the Goulougo Triangle were persistent and selective in their fruit consumption throughout the year. We found that this central subspecies community of chimpanzee allocated more than half of their feeding time to fruits, a finding similar to that found for other subspecies residing in east and west Africa (Hladik, 1977; Wrangham, 1977; Wrangham *et al.*, 1991; Wrangham *et al.*, 1996; Newton-Fisher, 1999; Fawcett, 2000). We observed that 56% of the food list comprised fruits, which was within the range of other sites. However, given that chimpanzee diets vary considerably over different temporal and spatial scales and that the chimpanzees were not completely habituated during the course of this investigation, continued research will be required to determine if our findings are representative of the feeding ecology of the chimpanzees in this population.

Researchers in central and east Africa have suggested that leaves are an important resource for chimpanzees (Hladik, 1977; Nishida *et al.*, 1983; Tutin *et al.*, 1991; Fawcett, 2000). We found that the time spent feeding on leaves by chimpanzees in this study was higher than observed in other populations. The chimpanzees regularly fed upon several leaf species from different life forms such as trees and lianas as well as leaves in different stages of maturity. Specifically, our observations confirm suggestions that *C. mildbraedii* leaves may be a key resource for apes in northern Congo (Nishihara, 1995; Kuroda *et al.*, 1996). Direct observations showed that chimpanzees and gorillas in the Goulougo Triangle consumed *C. mildbraedii* leaves throughout the year, with significant increases when new leaves were available (Morgan, unpublished data). The apparent preference of chimpanzees for *C. mildbraedii*, based on direct observations and its abundance in the study area (13.9 stems/ha) make this a good candidate for being a staple food item in the diet of these apes. Important foods and their abundance in the environment have been suggested as playing a key role in ape social behavior (Wrangham, 1986). Investigating the importance of *Celtis m.* leaves in the diet of the Goulougo chimpanzees and the relationship of overall foliage intake to ape

social behavior in this region will be an important avenue of future research.

In a synthesis of the diet of western lowland gorillas from six sites, Rogers *et al.* (2004) showed this species to have a diverse feeding repertoire while remaining a selective fruit pursuer. Fruit consumption of western gorillas in the Goualougo and other sites in the region is less consistent than for chimpanzees, which could be the result of a selective fruit-eating strategy based on particular fruit species (Williamson *et al.*, 1990; Tutin *et al.*, 1991; Kuroda *et al.*, 1996; Fay, 1997; Remis, 1997; Remis *et al.*, 2001; Doran *et al.*, 2002; Rogers *et al.*, 2004). Foraging intersections and dietary overlap with chimpanzees occurred most often in the consumption of fruit. The overlap in fruits was followed by shared leaf and stem food items. Researchers have consistently reported a divergence in non-food plant items, such as insects and mammals. However, the degree of habituation and the sampling effort of observing gorillas were much less than for chimpanzees in this study, and this may have affected our overlap results. A higher degree of overlap is reported from all sites where the food list for one ape species is more complete than for the other species (Table 4.2). The gorilla food lists have been more complete at several of these sites (Belinga, Lopé, Ndoki, Bwindi), resulting in high or complete overlap for chimpanzees. Goualougo and (recently) Kahuzi (Basabose, 2002) are the only sites where chimpanzees are studied primarily by direct observation rather than indirect evidence (feces, trails signs). If an earlier estimate of diet composition is used to calculate overlap at Kahuzi, then it is 73% with gorillas, but if the more recent estimate of 110 food species is used, then overlap decreases to 54% (Yamagiwa *et al.*, 1996; Basabose, 2002). The proportion of dietary overlap in food lists is obviously influenced by skewed sampling effort, so interpretations of the degree of dietary overlap from short-term studies of unhabituated groups should be interpreted with caution. For comparisons of interspecific feeding ecology, it is more informative to depict feeding patterns between species at specific time intervals.

In the Goualougo Triangle, chimpanzee and gorilla diets clearly diverged in their patterns and degrees of foliage consumption during the same sampling period. Gorilla foliage scores were correlated with fruit consumption. This was in contrast to chimpanzees, who maintained relatively low foliage scores and stable fruit consumption over the same period. Chimpanzees consumed relatively low but equally attributable amounts of green leaf and fiber as indicated in their monthly foliage scores. In contrast, the stems and leaves of terrestrial herbaceous vegetation from the *Marantaceae* and *Zingiberaceae* families largely comprised the high levels of year-round foliage consumed

by gorillas, which is similar to other findings in central Africa (Tutin & Fernandez, 1985, 1993; Williamson *et al.*, 1990; Remis, 1994; Nishihara, 1995; White *et al.*, 1995; Kuroda *et al.*, 1996; Fay, 1997; Doran *et al.*, 2002; Rogers *et al.*, 2004). Although stem densities have been shown to vary across sites, gorillas consistently consume large amounts of terrestrial herbaceous vegetation, a reflection of their specialized digestive physiology (Doran *et al.*, 2002; Rogers *et al.*, 2004).

It is well documented that figs are a key resource for many chimpanzee populations, but members of the *Ficus* genus have not been particularly prevalent in reports of gorilla feeding ecology (Conklin & Wrangham, 1994; Wrangham *et al.*, 1996; Newton-Fisher, 1999; Basabose & Yamagiwa, 2002; Stanford & Nkurungi, 2003; but see Ganas *et al.*, 2004). The representation of *Ficus* spp. as locations for co-feeding events with gorillas, despite the relatively low stem density of this tree species (<1 stem/ha) suggests that this is also an important resource for apes in the Goulougo Triangle. Although gorillas in the Goulougo Triangle overlapped with chimpanzees in their fig consumption, their exploitation of this genus was less frequent and more selective. The fig species eaten by gorillas tend to be characterized by relatively large syconium that may provide more efficient nutritional intake for the foraging effort compared with smaller figs. Conklin & Wrangham (1994) found that there was significant variation in the nutritional content of different *Ficus* species. This is an indication of dietary selectivity that could be an important aspect of the niche differentiation between these sympatric apes.

In this chapter we also report on prolonged observations of co-feeding and found that these interspecific encounters may be linked to particular food resources. Associations between chimpanzees and gorillas occurred when both species were mutually attracted to a specific fruiting tree. There was no evidence that these species were otherwise attracted to each other. Chimpanzees in the Goulougo Triangle are amenable to co-feeding with gorillas at large fruiting tree species for relatively long periods. We did not observe any of the indications of mutual avoidance or competitive behavior between chimpanzees and gorillas that have been reported from other sites (Tutin & Oslisly, 1995; Basabose & Yamagiwa, 2002; Stanford & Nkurungi, 2003). Chimpanzees were also observed co-feeding with *Lophocebus albigena* and *Cercopithecus nictitans*. Their responses to mangabeys and guenons were more variable and included neutral co-feeding, displacement, threat, and active eviction from tree crowns. There were no indications of chimpanzee hunting behavior or apparent hesitation by monkeys to feed in proximity to chimpanzees. More detailed data will be necessary to determine the mechanisms

governing interactions between chimpanzees and other members of the primate community.

Researchers in central Africa have just begun to document the behavior and ecology of apes residing in this region. A better understanding of the flexibility in chimpanzee diets and their relationships with sympatric gorillas will enable us to proceed with more valid comparisons among species. Although several primate taxa in central Africa have been studied independently, little research has focused on the complex relationships within primate communities. Such research will only be possible if we ensure the immediate protection and long-term preservation of the remaining intact tropical forest ecosystems within the forests of the Congo Basin.

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### References

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–65.
- Anderson, D.P., Nordheim, E.V., Boesch, C., & Moermond, T.C. (2002). Factors influencing fission-fusion grouping in chimpanzees in the Tai National Park, Côte d'Ivoire. In *Behavioural Diversity in Chimpanzees and Bonobos*, ed. C. Boesch, G. Hohmann, & L.F. Marchant, pp. 90–101. Cambridge: Cambridge University Press.
- Basabose, A.K. (2002). Diet composition of chimpanzees inhabiting the montane forests of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology*, **58**, 1–21.

- Basabose, A.K. & Yamagiwa, J. (2002). Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric gorillas. *International Journal of Primatology*, **23**, 263–82.
- Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford: Oxford University Press.
- Chapman, C.A., Chapman, L.J., & Gillespie, T.R. (2002). Scale issues in the study of primate foraging: red colobus of Kibale National Park. *American Journal of Physical Anthropology*, **117**, 349–63.
- Chapman, C.A., Chapman, L.J., & Wrangham, R.W. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**, 59–70.
- Conklin, N.L. & Wrangham, R.L. (1994). The value of figs to a hind-gut fermenting frugivore: a nutritional analysis. *Biochemical Systematics and Ecology*, **22**, 137–51.
- Doran, D. (1997). Influence of seasonality on activity patterns, feeding behaviour, ranging and grouping patterns in Tai chimpanzees. *International Journal of Primatology*, **19**, 183–206.
- Doran, D. & McNeilage, A. (1998). Gorilla ecology and behavior. *Evolutionary Anthropology*, **6**, 120–31.
- Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P., & Shah, N. (2002). Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling. *American Journal of Primatology*, **58**, 91–116.
- Fawcett, K. (2000). *Female Relationships and Food Availability in a Forest Community of Chimpanzees*. Unpublished Ph.D. thesis, University of Edinburgh.
- Fay, J.M. (1997). *The Ecology, Social Organization, Populations, Habitat and History of the Western Lowland Gorilla (Gorilla gorilla gorilla Savage and Wyman 1847)*. Unpublished Ph.D. thesis, Washington University.
- Ganas, J., Robbins, M.M., Nkurunungi, J.B., Kaplin, B.A., & McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, **25**, 1043–72.
- Hladik, C.M. (1977). Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on diet. In *Primate Ecology*, ed. T.H. Clutton-Brock, pp. 481–501. London: Academic Press.
- Hunt, K.D. & McGrew, W.C. (2002). Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In *Behavioural Diversity in Chimpanzees and Bonobos*, ed. C. Boesch, G. Hohmann, & L.F. Marchant, pp. 35–51. Cambridge: Cambridge University Press.
- Jones, C. & Sabater Pi, J. (1971). Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. *Bibliotheca Primatologica*, **13**, 1–96.
- Kuroda, S. (1992). Ecological interspecies relationships between gorillas and chimpanzees in the Ndoki-Nouabalé reserve, northern Congo. In *Topics in Primatology, Volume 2: Behavior, Ecology, and Conservation*, ed. N. Itoigawa, Y. Sugiyama, G.P. Sackett & R.K.R. Thompson, pp. 385–94. Tokyo: University of Tokyo Press.

- Kuroda, S., Nishihara, T., Suzuki, S. & Oko, R.A. (1996). Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In *Great Ape Societies*, ed. W.C. McGrew, L.F. Marchant & T. Nishida, pp. 71–81. Cambridge: Cambridge University Press.
- McGrew, W.C., Baldwin, P.J., & Tutin, C.E.G. (1988). Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal. I. Composition. *American Journal of Primatology*, **16**, 213–26.
- Morgan, D., Sanz, C., Onononga, J.R., & Strindberg, S. (in press). Ape abundance and habitat use in the Goulougo Triangle, Republic of Congo. *International Journal of Primatology*.
- Moutsambote, J.-M., Yumoto, T., Mitani, M., Nishihara, T., Suzuki, S., & Kuroda, S. (1994). Vegetation and plant list of species identified in the Nouabale-Ndoki Forest, Congo. *Tropics*, **3**, 277–94.
- Newton-Fisher, N.E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology*, **37**, 344–54.
- Nishida, T. (1974). The ecology of wild chimpanzees. In *Human Ecology*, ed. R. Ohtsuka, J. Tanaka, & T. Nishida, pp. 15–60. Tokyo: Kyoritsu-Shuppan.
- Nishida, T. & Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. *African Study Monographs*, **3**, 109–30.
- Nishida, T., Wrangham, R.W., Goodall, J., & Uehara, S. (1983). Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *Journal of Human Evolution*, **12**, 467–80.
- Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabalé-Ndoki National Park, northern Congo. *Primates*, **36**, 151–68.
- Remis, M.J. (1994). *Feeding Ecology and Positional Behavior of Lowland Gorillas in the Central African Republic*. Unpublished Ph.D. thesis, Yale University.
- (1997). Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology*, **43**, 87–109.
- Remis, M.J., Dierenfeld, E.S., Mowry, C.B., & Carroll, R.W. (2001). Nutritional aspects of western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Houkou, Central African Republic. *International Journal of Primatology*, **22**, 807–36.
- Rogers, M.E., Abernathy, K., Bermejo, M. *et al.* (2004). Western gorilla diet: a synthesis from six sites. *American Journal of Primatology*, **64**, 173–92.
- Rogers, M.E., Maisels, F., Williamson, E.A., Fernandez, M., & Tutin, C. E. G. (1990). Gorilla diet in the Lope Reserve, Gabon: a nutritional analysis. *Oecologia*, **84**, 326–39.
- Sabater Pi, J. (1979). Feeding behavior and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains of Rio Muni (West Africa). *Zeitschrift für Tierpsychologie*, **50**, 265–81.
- Sanz, C., Morgan, D., & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist*, **164**, 567–81.
- Stanford, C.B. & Nkurunungi, J.B. (2003). Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: diet. *International Journal of Primatology*, **24**, 901–18.



- Sugiyama, J. (1999). Socioecological factors influencing population structure of gorillas and chimpanzees. *Primates*, **40**, 87–104.
- Sugiyama, Y. & Koman, J. (1992). The flora of Bossou: its utilization by chimpanzees and humans. *African Study Monographs*, **13**, 127–69.
- Tutin, C.E.G. & Fernandez, M. (1984). Nationwide census of gorilla and chimpanzee populations in Gabon. *American Journal of Primatology*, **6**, 313–36.
- (1985). Foods consumed by sympatric populations of *Gorilla gorilla* and *Pan troglodytes* in Gabon: some preliminary data. *International Journal of Primatology*, **6**, 27–43.
- (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lope Reserve, Gabon. *American Journal of Primatology*, **30**, 195–211.
- Tutin, C.E.G. & Oslisly, R. (1995). *Homo*, *Pan*, and *Gorilla*: coexistence over 60,000 years at Lope in central Gabon. *Journal of Human Evolution*, **28**, 597–602.
- Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A., & McGrew, W.C. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of the Royal Society of London*, **334**, 178–86.
- Tutin, C.E.G., Ham, R.M., White, L.J.T., & Harrison, M.J.S. (1997). The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity and effects on biomass. *American Journal of Primatology*, **42**, 1–24.
- White, F. (1983). *The Vegetation of Africa*. Paris: UNESCO.
- White, L. (1992). *The Effects of Mechanized Selective Logging on the Flora and Mammalian Fauna of the Lope Reserve, Gabon*. Edinburgh: University of Edinburgh.
- White, L.J.T., Rogers, M.E., Tutin, C.E.G., Williamson, E.A., & Fernandez, M. (1995). Herbaceous vegetation in different forest types in the Lope Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology*, **33**, 124–41.
- Williamson, E.A., Tutin, C.E.G., Rogers, M.E., & Fernandez, M. (1990). Composition of the diet of lowland gorillas at Lope in Gabon. *American Journal of Primatology*, **21**, 265–77.
- Wrangham, R.W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In *Primate Ecology*, ed. T. H. Clutton-Brock, pp. 503–38. London: Academic Press.
- (1986). Ecology and social relationships in two species of chimpanzee. In *Ecology and Social Evolution: Birds and Mammals*, ed. D.I. Rubenstein & R.W. Wrangham, pp. 352–78. Princeton: Princeton University Press.
- Wrangham, R.W., Chapman, C.A., Clark-Arcadi, A.P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In *Great Ape Societies*, ed. W.C. McGrew, L.F. Marchant, & T. Nishida, pp. 45–57. Cambridge: Cambridge University Press.
- Wrangham, R.W., Conklin, N.L., Chapman, C.A., & Hunt, K.D. (1991). The significance of fibrous foods for Kibale chimpanzees. *Philosophical Transactions of the Royal Society of London*, **334**, 171–8.

Yamagiwa, J., Maruhashi, T., Yumoto, T., & Mwanza, N. (1996). Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In *Great Ape Societies*, ed. W.C. McGrew, L.F. Marchant, & T. Nishida, pp. 82–98. Cambridge: Cambridge University Press.

### **Notes**

1. The sample size for gorillas at co-feeding events is smaller because on two occasions it was not possible to accurately count all gorilla group members present.