CHAPTER FOUR

The Diet of Olive Baboons (*Papio anubis*) in the Budongo Forest Reserve, Uganda

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INTRODUCTION

Baboons (genus *Papio*) are large-bodied, semi-terrestrial monkeys that occupy a diversity of habitats. Across populations, they show wide variation in dietary composition and in their foraging behavior (Whiten *et al.*, 1991). Early studies concluded that baboons were generalist feeders (De Vore & Hall, 1965; Rowell, 1966; Ransom, 1971; Harding, 1981), with Rowell (1966) saying of Ugandan baboons: "a list of plants eaten would probably be approximate to the botanical species for the area," but it is now clear that baboons selectively exploit their environment (Hamilton *et al.*, 1978; Norton *et al.*, 1987; Whiten *et al.*, 1991).

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Such selectivity would be predicted from a consideration of the wide variation in nutritional content and digestibility of potential food items, together with the need for foraging baboons to satisfy nutritional and energetic demands. The baboon foraging adaptation, in general terms, may be to selectively exploit a wide array of plant foods to satisfy energetic and nutritional needs when faced with a shifting mosaic of possibilities (Norton *et al.*, 1987).

The variation in diet between baboon populations has been used to investigate the influence of ecology on both diet and foraging behavior (Hill & Dunbar, 2002), but few such quantitative data have been published for forest-dwelling baboons (cf. Paterson, Chapter 5, this volume). These data are likely to be important, as savannah and forest habitats will present different ecological conditions and resources to foraging baboons. Tropical forests typically show less dramatic seasonality in comparison with savannah habitats, and so forest-living baboons should experience a wider and potentially more consistent resource base, which may influence both dietary composition and feeding time.

Furthermore, such data will be useful for interspecific comparisons. Forest-living baboons may be significant competitors with sympatric chimpanzees (*Pan troglodytes*) despite contrasts in foraging strategies. While baboons follow a selective–generalist strategy, chimpanzees typically show a reliance on ripe fruit (Wrangham, 1986). Baboons may have the advantage in scramble competition where the two species target fruit of the same plant species, as they are better able to digest unripe fruit (Wrangham *et al.* 1998; Lambert, 2005). There are few data available to test whether such competition occurs. Peters and O'Brien (1981) reported a dietary overlap between baboons and chimpanzees of only 18.3%, but a much greater degree of overlap (around 50%) was found recently in a study of sympatric baboons (*Papio cynocephalus*) and chimpanzees (*Pan t. schweinfurthii*) in the Mahale Mountains National Park, Tanzania (Matsumoto-Oda & Kasagual, 2000).

Here, as a preliminary step in investigating potential feeding competition and to broaden the knowledge of baboon foraging strategies, we describe the diet of forest-living olive baboons (*Papio anubis*) from the Sonso region of the Budongo Forest Reserve, where they live sympatrically with chimpanzees (*P. t. schweinfurthii*). The diet of these chimpanzees has been well studied (Newton-Fisher, 1999b; Tweheyo & Obua, 2001), but comparable data for baboons have not been collected.

METHODOLOGY

Study Site and Subjects

This study was conducted in the Budongo Forest Reserve, Uganda, in the region (compartment N3) of the largely defunct Sonso sawmill and the Budongo Forest Project (BFP) field station. Budongo forest is classified as moist, medium-altitude, and semi-deciduous (Eggeling, 1947; Langdale-Brown *et al.*, 1964; Howard *et al.*, 1991), and is one of the most botanically diverse forest reserves in Uganda (Synnott, 1985; Howard, 1991).

The olive baboons that were the subjects of this study were members of the Sonso Sawmill troop. This troop consisted of nine individuals at the beginning of the study, increasing to 10 with the birth of an infant, and represented an immigrant population. Baboons were not present in this area in the early 1970s, but were resident from the early 1990s (V. Reynolds, personal communication). It seems likely that baboons moved into the sawmill clearing after the cessation of the intensive sawing operations, and came from a population of olive baboons living beyond the edge of the forest (Paterson, Chapter 5, this volume). These baboons were partially habituated at the start of the study; they were commonly sighted within the site of the BFP field station, coming mainly to raid garbage.

Data Collection

Data were collected between September 1999 and February 2000, for a total of 20 weeks, divided evenly between the wet and dry season. Scan and *ad libitum* sampling (Altmann, 1974) was conducted from dawn to dusk or until poor visibility set in. Altogether, 7722 feeding records were taken for both seasons, representing 2621 and 5301 feeding records for rainy and dry seasons, respectively. Lower sampling in the wet season was the result of data collection being interrupted by heavy rain and poorer levels of habituation of the study subjects.

RESULTS

The Sonso baboons spent 47% of the time that they spent feeding consuming fruits and seeds (34% on fruits, 13% on seeds), 17% of this time eating leaves, and 17% feeding on food items raided from garbage. The remaining 19% of

feeding time was spent on stems, bark seedlings, roots, and items obtained through agricultural crop raiding.

A total of 51 identified wild plant species were recorded as providing food items for baboons during the 6-month study period (Table 1). The cumulative number of species eaten approached an asymptote after about 12 weeks of study (Figure 1), suggesting that these 51 species represent the bulk of the diet of this baboon population. Observations were made in both the wettest and driest seasons, and so any large seasonal shifts in diet should be included in these data, although undoubtedly more species would be recorded with longer observation time and at other times of the year. Twenty-one species were regularly and consistently consumed, with each accounting for 0.5% or more of the time spent feeding (Table 2).

Diet by Food Item (Figure 2)

Leaves

The bulk of foliage was provided by *Broussonetia papyrifera* (paper mulberry), accounting for an average of 13% of total feeding records. Other species that contributed appreciably to the amount of recorded feeding on leaves were *Amaranthus* sp. (herb), *Desmodium intotuene* (creeper), and *Pannicum maximum* (grass).

Fruit

During the wet season, *Celtis durandii* constituted the highest proportion of fruit records (7%), while those of *Raphia farinifera* constituted the highest records (7%) during the dry season. *C. durandii* is one of the most common main canopy trees in the study area (Plumptre, 1996; Newton-Fisher, 1997). It produces large quantities of fruit from September through October and occasionally into December. *R. farinifera*, a palm tree, produces long strands of nuts. The mesocarp of a ripe fresh nut is scraped from the central nut and eaten by the baboons. The remaining nut is eaten only after it has become hydrated and begun to sprout (below). Other species that contribute appreciably to fruit diet are *Lantana camara*, *B. papyrifera*, *Physalis peruviana*, *Psidium guajava*, *Ficus sur*, *Ficus exasperata*, *Cleitopholis patens*, *Tetrapleura tetraptera*, and *Margaritaria discoideus. Lantana camara*, *B. papyrifera*, and *P. guajava* are

Table 1. Food items in the diet of the olive baboons from the Sonso sawmill troop, Budongo Forest, Uganda

Species	Leaves	Fruit	Seed	Stem	Bark	Root	Seedling
Acalypha sp.	✓						
Aframomum sp.	✓	✓	✓	✓		✓	
Albizia coriaria					✓		
Albizia zygia			✓		✓		
Amaranthus sp.	✓		✓				
Aneiloma euquietiale						✓	
Brachiaria brizantha			✓				
Broussonetia papyrifera	✓	✓					
Caloncoba schweinfurthii		✓					
Canna indica		✓		✓			
Celtis durandii		✓					
Citropsis sp.		✓					
Cleitopholis patens		✓					
Climbers (unknown)		✓				✓	
Coffea robusta		✓					
Coffea sp.		✓					
Commelina sp.	✓						
Cordia melinii		✓					
Croton macrostachys		✓					
Curcunis arculeatus		✓					
Datura sp.		✓					
Desmodium intotuene	✓					✓	
Eleusine jaegeri			✓				
Erythrophleum suaveolens		✓					
Euphorbia teke	✓						
Ficus exasperata		✓				✓	
Ficus polita		✓					
Ficus sansibarica		✓					
Ficus saussureana		✓					
Ficus sp.						✓	
Ficus sur		✓					
Ficus varifolia		✓				✓	
Iodes africana		✓					
Khaya anthotheca					✓		
Lantana camara		✓					
Leptapsis sp.	✓						
Marantochloa sp.	✓			✓		✓	
Margaritaria discoideus		✓					
Myrianthus holstii		✓					
Palisota mannii	✓	✓					
Pannicum maximum	✓						

(*Cont.*)

Table 1. *(Continued)*

Species	Leaves	Fruit	Seed	Stem	Bark	Root	Seedling
Physalis peruviana		✓					
Pollia condensate		✓					
Prunus africana		✓					
Psidium guajava		✓					
Raphia farinifera		✓	✓	✓			✓
Ricinodendron heudelotii			✓				
Sarcophrynium schweinfurthianium	✓				✓		
Teclea nobilis		✓					
Tetrapleura tetraptera		✓					
Unknown	✓	✓					

Data are from scan sampling and ad libitum observations. A ✓ indicates that the baboons were observed to feed on the item.

exotics. *F. sur* was the primary fig species consumed between September and November 1999, while *F. exasperata* became the main fig species between December 1999 and February 2000.

Seeds

Two main species contributed to the bulk of seed diet: *Ricinodendron heudelotii* and *R. farinifera*. *R. heudelotii* produces a fruit containing two hard-shelled

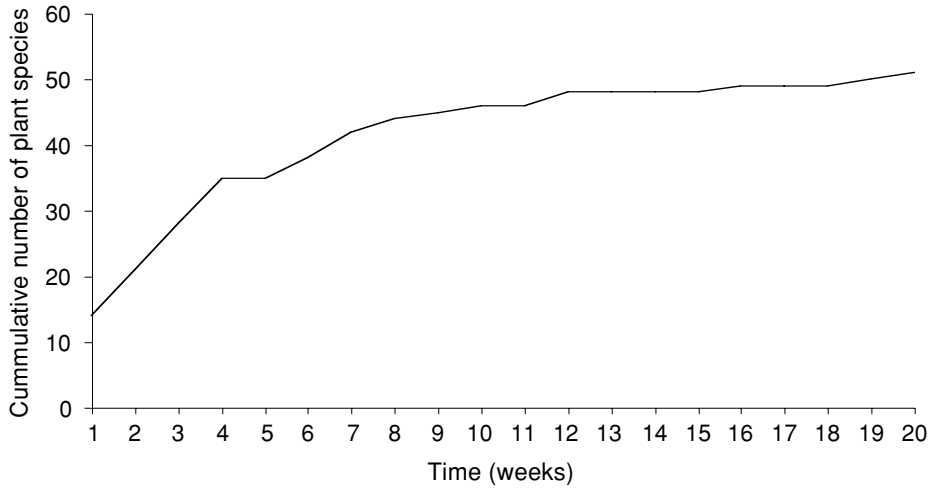

Figure 1. Cumulative number of species on which baboons were observed to feed, plotted by number of weeks of observation.

Table 2. Species accounting for 0.5% or more of time spent feeding

Species	Percentage
Broussonetia papyrifera	17.65
Raphia farinifera	12.49
Ricinodendron heudelotii	8.52
Celtis durandii	5.78
Lantana camara	4.17
Ficus exasperata	4.11
Physalis peruviana	3.42
Sarcophrynium schweinfurthianium	2.74
Psidium guajava	2.54
Amaranthus sp.	2.07
Ficus sur	1.92
Desmodium intotuene	1.73
Pannicum maximum	1.49
Pennisetum purpureum	1.39
Aframomum sp.	1.17
Khaya anthotheca	1.09
Cleitopholis patens	1.07
Eleusine jaegeri	0.96
Marantochloa sp.	0.75
Tetrapleura tetraptera	0.71
Palisota mannii	0.60

nuts. The baboons were not seen eating the flesh of this fruit, nor climbing up trees to obtain them; they made use of the fruit after it had fallen and rotted sufficiently and the nut had been disengaged. They usually cracked the hard nut with their molar teeth and ate the endosperm, spitting out the shell. *R. farinifera* seeds were only eaten when hydrated and sprouting, the baboons uprooting the seedling, consuming the meristem or pith, cracking the nut, and eating the remainder of the embryo. Other species that provided seeds to the diet were *Amaranthus* sp., *Albizia zygia*, *Eleussine jaegeri*, and *Brachiaria brizantha*. The last two of these are grasses, which are mainly available during the dry season (December 1999–February 2000).

Stems

These accounted for 7% of feeding records, of which *Sarcophrynium schweinfurthianium* (herb species found in swamps along River Sonso) contributed 2.7%. Of the tree species, only the stem of *R. farinifera* trees that had been

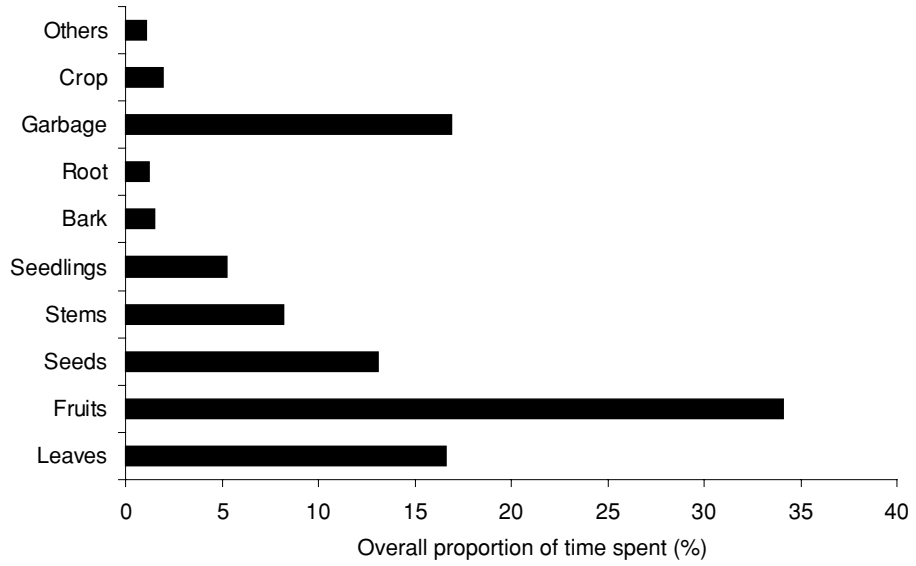

Figure 2. Breakdown of baboon diet by proportion of time spent feeding on each food item.

felled by local people to tap alcohol was consumed. The fermented stems were also consumed by other primates and bush pigs. Other species from which the baboons ate the stems were *Pennisetum purpureum*, *Afromomum*, and *Marantochloa*.

Bark

The bark of trees was occasionally eaten, in some cases to obtain gums. Bark alone accounted for only 1.6% of the total food. Overall, the bark of *Khaya anthotheca* was the most eaten (1.1%), followed by *F. exasperata* (0.44%). Other species that contributed bark to the diet were *Ficus varifolia* and *Albizia zygia*.

Roots

These accounted for an average of 1.2% of total food. Herb species formed the highest proportion of these items, including species such as *D. intotuene*, *Aframomum*, *Marantochloa*, and *Aneiloma aquietiale*. Many climbers were also uprooted and the root bark chewed. It was, however, difficult to identify climber species, and these were recorded as unidentified climber species. Of the tree species, the baboons were only recorded feeding on roots of *Ficus* seedlings.

Seedlings

Overall, seedlings accounted for about 5% of the food. Seedlings of *R. farinifera* contributed the whole of this proportion. The baboons uprooted the seedling, stripped off the outer part, and consumed the pith.

Garbage Raiding

Items raided from garbage accounted for approximately 17% of the overall food. It was difficult to make a concise list of the various items raided from garbage, although it included most of what people in the camp ate and/or any edible item dumped in the garbage pits, ranging from processed food items such as bread, margarine, and biscuits to locally grown food items such as cassava, potatoes, and fruit. Baboons spent as much time feeding on garbage as they did on the most consumed plant species: *B. papyrifera*. It was also noted that the intensity of garbage raiding increased appreciably during the dry season, possibly due to the decline in seasonal availability of plant items (see Figure 3).

Crop Raiding

This accounted for a very small proportion of the overall feeding recorded (about 2%). Among the primate species, baboons have been reported to be the most notorious crop raiders (Naughton-Treves, 1998). This small proportion can be attributed to the fact that crops were only grown in small gardens belonging to the houses of Budongo Sawmills Limited labor line, which were easily guarded and were not otherwise available to this baboon population.

Other

Baboons were also observed to feed on other items. These included insects (particularly termites and grasshoppers), birds (and their eggs), and mushrooms. On one occasion, a baboon named "Magezi" fed on chicks of domestic fowls. Mushrooms were encountered seasonally, and were their favorite when encountered.

Season Changes in Diet

Baboons feed for longer on fruit and stems in the wet season that in the dry season (fruits: $U = 22$, $p < 0.05$; stems: $U = 19$, $p < 0.05$), but there were no significant seasonal differences in feeding time for leaves, seeds, bark, roots, or seedlings. Diet in the dry season appeared to be broader than in the wet season (Figure 3).

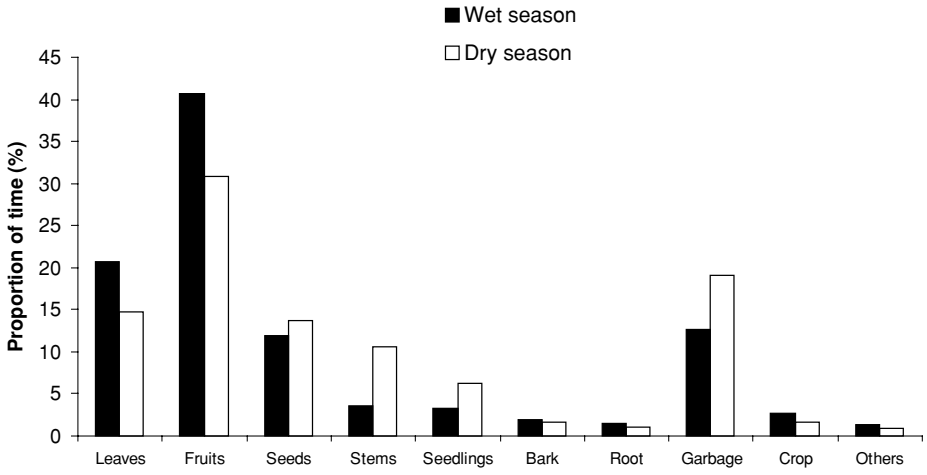

Figure 3. Comparison of baboon diets between wet and dry seasons.

DISCUSSION

The olive baboons of Sonso consumed a variety of food items and broadly appeared to follow a generalist feeding strategy: their diet included, among others, leaves, fruits, stems, seedlings, roots, bark, and animal items. Fruit appeared to be eaten in preference to leaves, stems, and seeds, whenever available, and the high proportion of fruit in the diet appears typical of most *Papio anubis* populations (Table 3).

The baboons fed on the seeds of only a few plant species, mainly *R. heudelotii* and *R. farinifera*. Seeds constitute a class of food item that imposes time and energy costs on would-be consumers. In contrast to fruit, seeds have been selected to avoid destruction during ingestion and gut passage: they may have hard rinds, sticky resins, irritant hairs, or poisonous secondary chemicals. Even if an animal can open such seeds it may not be worth the necessary time and

Table 3. Dietary profiles of olive baboon populations based on proportion of time spent feeding on different categories of food

Population	Fruit (%)	Leaves (%)	Roots (%)	Other (%)
Bole, Ethiopia	41	41	1	17
Budongo, Uganda	47	17	1	35
Chololo, Kenya	23	27	15	35
Gilgil, Kenya	10	53	27	10
Gombe, Tanzania	49	14	7	30
Masai Mara, Kenya	46	44	8	2
Shai Hills, Ghana	59	8	17	16

Sources: Data taken from Hill and Dunbar (2002:Table 1), where original sources are indicated, except for Budongo, for which data are from this study.

energy (Raemaekers *et al.*, 1980), particularly if easier food sources are available, which may be the case for the Sonso baboons.

These baboons showed considerable selectivity in the food items they consumed. This was true even for fruit and leaves, items that the baboons fed on the most. The animals were observed to concentrate on leaves and fruits of *B. papyrifera*; fruits of *C. durandii*, *Ficus* spp., and *R. farinifera*; and seeds of *R. heudelotii*. Many of the species on which the baboons fed were patchy in their distribution (Newton-Fisher, 1997; Newton-Fisher *et al.*, 2000). *B. papyrifera*, for example, was locally abundant but concentrated in areas bordering the old sawmill clearing, while *R. farinifera* is not particularly abundant and is confined to areas of swamp forest. *F. sur* and *R. heudelotii* also appear to be unevenly distributed in the Sonso region. Targeting patchily distributed species implies considerable selectivity of plant food items by the baboons.

The generalist aspect of the baboon foraging strategy is evident when compared with the feeding behavior of the sympatric chimpanzee population (Newton-Fisher, 1999b). The diet for both baboons and chimpanzees contained a similar number of plant species, which were targeted for at least 0.5% of the time spent feeding (19 species for baboons, 17 species for chimpanzees). But while these species accounted for 93% of chimpanzee feeding time, they represented only 75% of baboon feeding time. Furthermore, the baboons did not focus their efforts as noticeably as did the chimpanzees on the most commonly consumed plant species (Figure 4).

The data also suggest limited overlap in the diets of the two species. *F. sur*, the top-ranked dietary item for chimpanzees (23% of feeding time), accounted for only 1.9% of baboon feeding time while *R. farinifera* (fruit, seed, stems

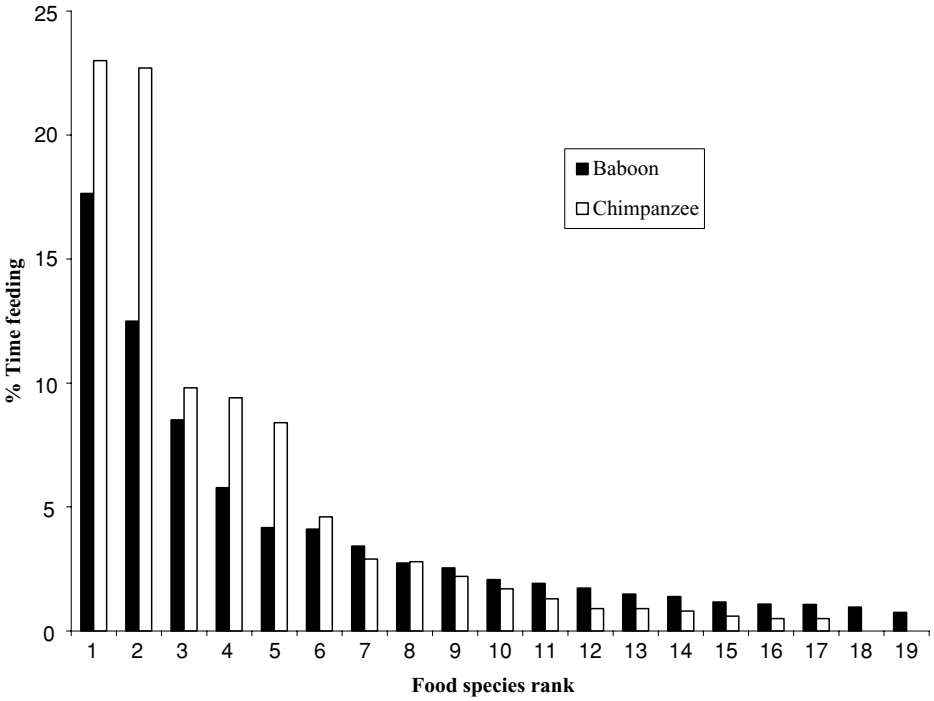

Figure 4. Comparison of top-ranked (by % feeding time) food species for sympatric baboon and chimpanzee populations. All species that accounted for 0.5% or more of feeding time are included.

and seedlings) for 12.5% of their feeding time, but chimpanzees fed on this species for only 0.6% of their feeding time (eating only the rotten wood). Only six of the species that were targeted by baboons for at least 0.5% of the time spent feeding were similarly targeted by chimpanzees. Both species spent considerable time feeding on the fruit and leaves of *B. papyrifera* (baboons: 17.7%; chimpanzees: 22.7%), as well as the fruit of *C. durandii* (baboons: 5.8%; chimpanzees: 8.4%) and that of *F. exasperata*, although baboons also targeted the roots of this species (baboons: 4.1%; chimpanzees: 2.2% of total feeding time targeting this species). These comparisons suggest that feeding competition between baboons and chimpanzees is unlikely to be important. Any scramble competition is most likely to occur with either *B. papyrifera* or *C. durandii*, but the first of these is a locally abundant, highly productive exotic and the second is common throughout the region (24% of the Sonso region is *Celtis*-dominated mixed forest; Newton-Fisher, 1997). Baboons spent little time feeding on the fruit of the fig species *F. sur* (1.9%) and *F. mucuso* (0%), which are important

staple foods for the sympatric chimpanzees (Newton-Fisher, 1999b); this suggests that their ability to consume and digest unripe fruit does not lead to significant scramble competition between these two populations.

Further studies of baboon diet and foraging behavior are required. The determination of distribution and abundance of plant food resources were beyond the scope of this study but remain an important next step to better address the nature of the baboon foraging strategy. In addition, a study of the dietary quality of preferred food items is essential to investigate why the baboons select or concentrate on a few plant items in the face of a diversity of plant food resources.