CHAPTER FIVE

Aspects of Diet, Foraging, and Seed Predation in Ugandan Forest Baboons

James D. Paterson

INTRODUCTION

The common "olive" savannah baboon, *Papio cynocephalus anubis*, is a widely spread and locally common monkey in Africa. Baboons have a large number of characteristics in common with humans, they are omnivorous and often have similar taste preferences, but differ in prefering fruits at an immature state as well as many items that present a pronounced bitter or astringent taste to human perception. They live in large communal social groups, are hierarchically organized, and are opportunistic, seizing any opportunity to obtain food, especially the concentrated nutrients in domesticated species. Thus they can play the role of classic "pest" or "weed" primates. In most of their social and behavioral characteristics, they parallel humans, and on previous occasions (Paterson, 1973, 1976) I have argued that baboons and humans are the survivors of a coevolutionary radiation involving a predator–prey relationship between hominids and cynopithecini. The parallels in diet and behavior can be seen as

James D. Paterson • Emeritus, Department of Anthropology, University of Calgary, Canada.

Primates of Western Uganda, edited by Nicholas E. Newton-Fisher, Hugh Notman, James D. Paterson, and Vernon Reynolds. Springer, New York, 2006.

a consequence of humans and baboons competing for the same resources—a scramble competition—in much the same environments, combined with a pattern of predation by humans on other primates. The result is that much of baboon social structure and behavior can be considered as a response to competition and especially to predation by humans. Even today, humans eat baboons in many areas, and actively compete with them for access to resources.

Baboons have typically been studied in short-grass savanna environments because of the acknowledged difficulties of observing and tracking them in high grass or forest areas (Washburn & DeVore, 1961; DeVore & Washburn, 1963; Paterson, 1976). This chapter represents a rare study of baboons in a forest/forest-edge habitat. Baboons are noted as having extremely broad ranges of dietary input, but the patterns for forest-resident populations may be the most divergent from the averages. Harding (1981) stated in a comparative study that focused on savanna- and thicket-dwelling populations, that baboons had the most diverse diets of any primate species, with all nine of the dietary compartments assessed being utilized by them. The plant species listed in their dietary range is further expanded in forest habitats. Okecha and Newton-Fisher (Chapter 4, this volume) record 51 plant species consumed by the Sonso troop in 1999–2000, with few of the species recorded in other studies. My earlier study on Busingiro Hill (Paterson, 1973, 1976) recorded 31 plant species in the baboon diet, in addition to a very high level of geophagy.

METHODOLOGY

Subjects

The Sonso baboon troop, resident in the clearing of the Budongo Sawmills Limited, is undoubtedly a recent immigrant population, as they were not present in the area during 1970–1971 (personal observations). It is likely that the troop moved into the sawmill clearing after the cessation of intensive sawing operations in 1978. They appear to have been resident at least from 1990, as Vernon Reynolds noted their presence during his visit to Sonso (V. Reynolds, personal communication). The logical origin for the troop is as an offshoot of forest-edge populations in the Nyabyeya or Nyakafunjo area, which voluntarily moved, or was forced by population pressures, down the Royal Mile to the Sonso clearing.

The troop, in September and October 1996, comprised 12 individuals, with a very unbalanced sex ratio. There were three adult males, two adult females, one 2-year-old juvenile female, five juvenile males (one aged 4–5 years, one 3+ years, two 2+ years, and one 1+ year), and an infant-2, holding membership in the group. The unusual sex ratio (3:1, males to females) is likely the result of historical events. Baboons are male dispersers, with most males leaving the natal group as young adults and moving into another troop. Bercovitch (1992, 1994, 1995) noted, in the Amboseli population, that aging males also migrate, moving into a new troop where they are less likely to be persecuted by younger males who have recently arrived at high ranks. By November 1996, composition of the Sonso troop had changed to just 10 members with the departure or disappearance of one adult male, the 3-year-old juvenile male, and the infant-2, counterbalanced by birth of an infant male on October 9. It is possible the first two individuals moved together to another group in the Nyakafunjo area and that the infant-2 was the baboon body noted in passing by our research assistant (however, we were unable to relocate it). Since the Sonso troop is essentially at the end of a linear transfer corridor, the resident adult males likely emigrated from the Nyabyeya or Nyakafunjo area and might return along that corridor. The second demographic factor is that until shortly before this study, the troop must have had a third adult female. In light of the presence of three juveniles at the 2 to 2+ age level, a third female had to have been present until at least March 1995. The situation at the time—with one female considerably older than the other and only one juvenile female—placed the long-term survival of the troop in jeopardy, yet the troop remained viable through 2004 (J. Wallis, personal communication). Without the production of more female offspring, the troop has the potential to die out, leaving an empty range open to be filled by a new migration from the Nyabyeya or Nyakafunjo areas.

Data Collection

The study was conducted with several observing techniques: focal animal sampling; regular scan sampling; and, unfortunately for statistic analyses, the most useful turned out to be a regularized form of *ad libitum* sampling. Data was collected through focal animal sampling (Altmann, 1974), using 30-min samples of individual animal behavior, and through the use of half-hourly-interval sampling (scans) of activity collected by the assigned research assistant. Ecologically relevant data was gathered in several ways:

1. Sample plots of forest structure. The plots were 10 by 25 m in size, and two plots were placed in proximity to each other, to make up a "sample quadrat" for use in calculating a version of Morisita's Index of similarity (Krebs, 1999; C. Chapman, personal communication). Within each plot, each tree of more than 4 m in crown height was numbered with an aluminum tag, identified, and the diameter at breast height (DBH), the crown height, and the phenological state were recorded. Each was also mapped as to position within the plot. Sixteen plots yielding eight sample quadrats were positioned around the Sonso clearing in areas either utilized or traversed by the baboon troop during the study period. Each sample plot was assessed for crown density using a Lemmon Crown Densiometer (Lemmon, 1956, 1957) to evaluate overstory at each end and at the middle of the plot.
2. Biological sampling proceeded throughout the course of the study period; collection of food species for identification where these were unknown to the research assistants resulted in more than 20 species being added to the herbarium.
3. Fecal sampling for several purposes was also carried out. Samples identified and associated with specific individuals were regularly collected. Each sample was divided and treated in different ways. A set of samples was preserved in 95% ethanol for DNA analysis by Dr C. J. Jolly. A sample was completely dried on a glass slide before being placed in a dry vial and a sample was washed through a medium-small stainless steel strainer, the residue sun-dried on photocopy paper and stored in a dry vial. The net weight of dried samples averaged 11% of the wet weight, indicating that approximately 89% of the feces was water. Washed samples were examined under a microscope, all recognizable seeds and other materials extracted and evaluated for damage. Assessments of fiber content, of bark fragments, and two submillimeter-sized seeds were recorded. All other material was counted, either as intact or damaged. While this technique—similar to that presented by Overdorff and Strait in 1996—cannot assess the role of seed disperser, it clearly reveals the role of seed predator since neither damaged nor destroyed seeds can be classified as eligible for germination.

The data on the Busingiro Hill population (four groups ranging in size from 28 to 70 individuals) was collected January 1970 through April 1971. The species diet list is included for comparison with the Sonso population. Data was collected using an *ad hoc–ad libitum* method.

RESULTS

The primary observer expended a total of 302 fieldwork hours, that is actual time either with or searching for the troop. Of this time, 202 h (67%) were spent in actual proximity when observations were being recorded. The general difficulty of observing conditions, as noted earlier, which resulted in a much lower number of focal sample hours being recorded (39.5 h of focal data = 19.5% of the contact hours), falls into this category. The remaining contact time is recorded in *ad libitum* notes. The half-hourly-interval scans made by the research assistants were not added into these totals. A further 300 h were expended in preparation and preservation of botanical and fecal sample materials, and in setting and evaluating sample plots.

Diet Diversity

Baboons are noted as having extremely broad ranges of dietary input. Whiten *et al.* (1991) noted: "foraging profiles described even at the level of very gross food types show remarkable variations across the habitats: . . . 3 to 74% (fruit), 1 to 53% (subterranean items), and 8 to 53% (leaves)." At Sonso, study subjects were repeatedly recorded as ingesting more than 10 different species of food materials during the course of a half-hour focal sample, and it was not unusual to observe several different species being consumed within a minute. Yet on other occasions, intensive feeding on a single foodstuff would persist for several hours.

Baboons, like humans, are omnivores but their tastes differ in some respects from those of humans. They are much more likely to eat fruits at a very unripe state—inedible to most humans—and consume a great quantity of leafy material and pith from grasses and trees, which humans find tasteless or unpleasantly astringent. Table 1 presents the lists of observed plant food species at Sonso and at Busingiro Hill. There is relatively little overlap between the two lists, with only two tree species and two grass species appearing in both. This is due to the ecological difference between the two sites. Sonso is a clearing, mostly artificial, within a selectively logged, mixed forest habitat, while Busingiro Hill is a mosaic of high-grass–tree savanna and *Maesopsis* colonizing forest. The variance in the

Table 1. Species observed to be consumed at two study sites within the Budongo forest reserve

Sonso (1996)	Busingiro (1970–1971)
Trees	Trees
Albizia coriaria	*Albizia grandibracteata*[a]
Broussonetia papyrifera	*Albizia zygia*
Calconcoba schweinfurthi	*Annona chrysophylla*
Celtis durandii	*Calconcoba schweinfurthi*
Cleistopholis patens	*Cassia mannii*
Croton macrostachys	*Combretum molle*
Ficus exasperata	*Cordia ovalis*
Ficus polita	*Erythrina abysinica*
Ficus sur	*Ficus capensis*
Ficus variifolia	*Ficus igens*
Khaya anthotheca	*Ficus vallis-choudae*
Lychnodiscus cerospermus	*Grewia mollis*
Margaritaria discoideus	*Jacaranda ovalifolia*
Psidium guajava	*Lannea kerstingii*
Raphia farinifera	*Maesopsis eminii*
Ricinodendron heudelotii	*Mangifera indica*
	Psidium guajava
	Spathodea campanulata
	Strychnos innocua
Herbs and Shrubs	Herbs and Shrubs
Aframomum sp	*Centrosema pubescens*
Aneiloma aequietiale	*Commelina erecta*
Canna indica	*Dioscorea dumeforum*
Desmodium intotueme	*Indigoflora emarginella*
Desmodium repandum	*Oxytenanthera abysinica*
Desmodium canum	*Securinega virosa*
Lantana camara	
Marantochloa leucantha	
Pollia condensata	
Grasses	Grasses
Eleusine jaegeri	*Hyparrhenia cymbarica*
Pannicum maximum	*Hyparrhenia folipendula*
Pennisetum purpureum	*Paspalum conjugatum*
	Pannicum maximum
	Pennisetum purpureum

[a] Known to contain bioactive compounds (Krief, 2004; Krief *et al.*, 2004).

two lists serves to highlight the catholic and opportunistic dietary patterns of baboons.

The members of the Sonso troop also ate gums, bark, insects, and about once per month one of the adult males took a domestic chicken. The male we named "Studly" was the main predator on three observed occasions. (The first observed incident occurred within half an hour of our arrival at Budongo Forest

Project [BFP]!). They also obtain an indeterminate amount of human domestic foods, foraging for the young leaves of bean plants, sweet potato roots, cassava stems and tubers, Uganda yam (taro) roots, as well as discarded food waste such as matoke, bananas, rice, millet, posho, etc. The amount of feeding time devoted to, and calories derived from, human foodstuffs, garbage, and garden raiding at Sonso during this study was equivocal. By far the majority of their food and caloric intake was derived from native and exotic vegetation. The two most important species during the September–October period for the troop were the exotics *Broussonetia papyrifera* and *Lantana camara*. These provided more than 90% of the observed ingested material in some weeks. Inspection of fecal samples collected during September–October showed that they contained substantial quantities of seeds, especially those of *Ficus sur*, *Psidium guajava*, *L. camara*, and *B. papyrifera*. During the latter half of October, and in November, both behavioral observation and examination of fecal samples indicate a slow shift toward more fibrous foodstuffs, with several varieties of low growing creepers, especially *Desmodium intotueme*, *Desmodium repandum*, *Desmodium canum*, leaves of *Broussonetia*, piths of grasses of the *Eleussine* and *Pennisetum* genera, *Aframomum* spp, *Canna indica* (an exotic Asiatic lily), as well as the fruits of *Celtis durandii*, *Raphia farinifera*, and *Cleistopholis patens* becoming important components of their diet. In addition, some novel observations of gummivory combined with bark ingestion, pure bark feeding, and seed predation are reported below.

Seed Predation

This study has identified four species of trees that are subjected to seed predation by the baboons. *Ricinodendron heudelotii*, *C. patens*, *C. durandii*, and *R. farinifera* all suffer complete destruction of their embryos through the actions of the baboons. In light of the identification of these species being preyed on during this 3-month study, it may be expected that other species suffer seed predation at other seasons of the year. Each of the identified species is exploited in a distinctive fashion.

R. heudelotii produces a 3- by 1.5-cm cherry-like fruit with a green skin, with yellow-green flesh smelling of peaches, containing two hard-shelled nuts each about 1 cm in diameter. The baboons were not seen to eat the flesh of this fruit, or to climb into the trees to obtain them; they were seen only to make use of the fruit after it had fallen and rotted sufficiently that the flesh could be disengaged from the nut. They then crack the nut between their molar teeth, and use their tongue and incisors to extract the nutmeat, spitting out the remains of the nutshell. The nut is extremely hard, and the initial cracking produces a sound that is audible for 20–30 m.

C. patens produces a very similar fruit. It is almost exactly the same in design—a double-pitted cherry—but turns black on ripening and falling to the ground. The flesh is green, with a minimal odor like green feed (chopped unripe barley) or shredded cabbage. The nut case is distinctively rough textured and, judging from the sounds produced by feeding baboons, it is less hard than the *Ricinodendron* nut. Baboons again feed primarily on the ground from dropped fruit; only on one occasion were two juveniles observed to eat the unripe fruit still attached to the parent tree. Both the flesh and the nut are consumed; normally the flesh of a ripe fruit is ingested and then the endocarp is cracked to extract the nutmeat. Rotted fruits, those from which the flesh has separated, are not consumed.

C. durandii is a very common secondary forest species and the fruits are much favored by all primates as food. The flesh of this 5–6-mm-diameter fruit is yellow and bland, and the kernel is dark brown and rugose. Baboons consume them both from the trees and as pickups from the ground. In mastication, they crush the whole fruit and the shell fragments can be found in the feces. None of the *C. durandii* seeds were passed intact.

R. farinifera, unlike the previous species, is a palm. It produces long masts of fruits, and the baboons process these twice. The fresh, ripening fruit, about 5 cm in length and 4 in diameter, is selected from the fruit mast. Baboons use their incisors to pick off the outer scales, which are discarded, and the paste-like mesocarp is scraped from the central nut. This nut is too hard for any primate to crack and is immediately discarded. This mesocarp is only 2–3 mm in thickness and similar in texture to a fig paste. It appears to be sufficiently nutrient-rich to be worth the effort for an adult baboon to climb up to the fruit mast and feed. The second use of the *Raphia* nut occurs weeks or months later, once it has hydrated and begun to sprout. Baboons then pull up the seedling and consume the meristem or pith, and access the remainder of the embryo.

Seeds of exotic (introduced) species were also consumed and destroyed by the baboons. *C. indica* is an exotic lily once planted at the Sawmill manager's residence, and has spread extensively around the edges of the clearing. The ripening seedpods are opened and the bean-like seed consumed; residues of these seeds were never found in the fecal samples. *L. camara*, a berry-producing, spreading shrub 3–4 m high was strongly favored during September and October, although rarely did any of the grape-like seeds pass intact through the baboon digestion. *Lantana* seeds did however contribute a major proportion of the crushed shell material found in the fecal samples. Native tree species *Croton macrostachys*, *Margaritaria discoideus*, and on occasion, *Calconcoba schweinfurthi* were similarly fed upon without intact seed being identified in the samples.

Several species of plants demonstrated variable patterns of survival and predation in the seeds recovered from fecal samples. *B. papyrifera*, the paper mulberry—a translocated exotic—benefited most from the baboon feeding, with high numbers of the 1-mm seed surviving and relatively few being damaged (Figure 1A). An unidentified discoidal 1-mm seed (Figure 1B) was found consistently in samples throughout the study period but the relative proportions of intact and damaged seed reversed between September–October and November–December. *F. sur* was the major fig species consumed, but small amounts of fruit were ingested from *Ficus polita* during November (Figure 1C). Roughly 50% of fig seeds were damaged, and there was a clear "seasonal" effect of the mid-September fruiting of *F. sur* and the November crop of *F. polita*. Baboons were never seen to feed in the *Ficus mucuso* trees beloved of the chimpanzees during November. Indeed, on occasion they were seen to move through a large *F. mucuso* tree, avoiding both the masses of fruit and the 30+ chimpanzees feeding there.

Another exotic—*P. guajava*, the guava (Figure 1D)—was present both in observed feeding and in fecal samples. Guavas were taken at an extremely green state, mastication noise indicating both the hard fruit and the immature seed being crushed. The seeds are large and relatively hard, yet somewhat below 50% survive oral treatment and gut passage. A native ground plant common on the forest floor is *Pollia condensata*, which is used by local people as a "natural bead," and which they consider to be poisonous. Since intact *Pollia* seeds (Figure 1E) were generally more prevalent than damaged ones, the plant may derive some small benefit in seed dispersal from its association with baboons. The final component of Figure 1(F) shows the counts of identifiable insect exoskeleton parts, and minerals—crystals and stony fragments—that were regularly encountered in the samples. The former are deliberately consumed, as observations of bark removal and scale bug consumption were recorded on several occasions. In addition, consumption of arthropods was associated with *Khaya* bark ingestion. The crystal and mineral items were most likely accidental inclusions in soils and

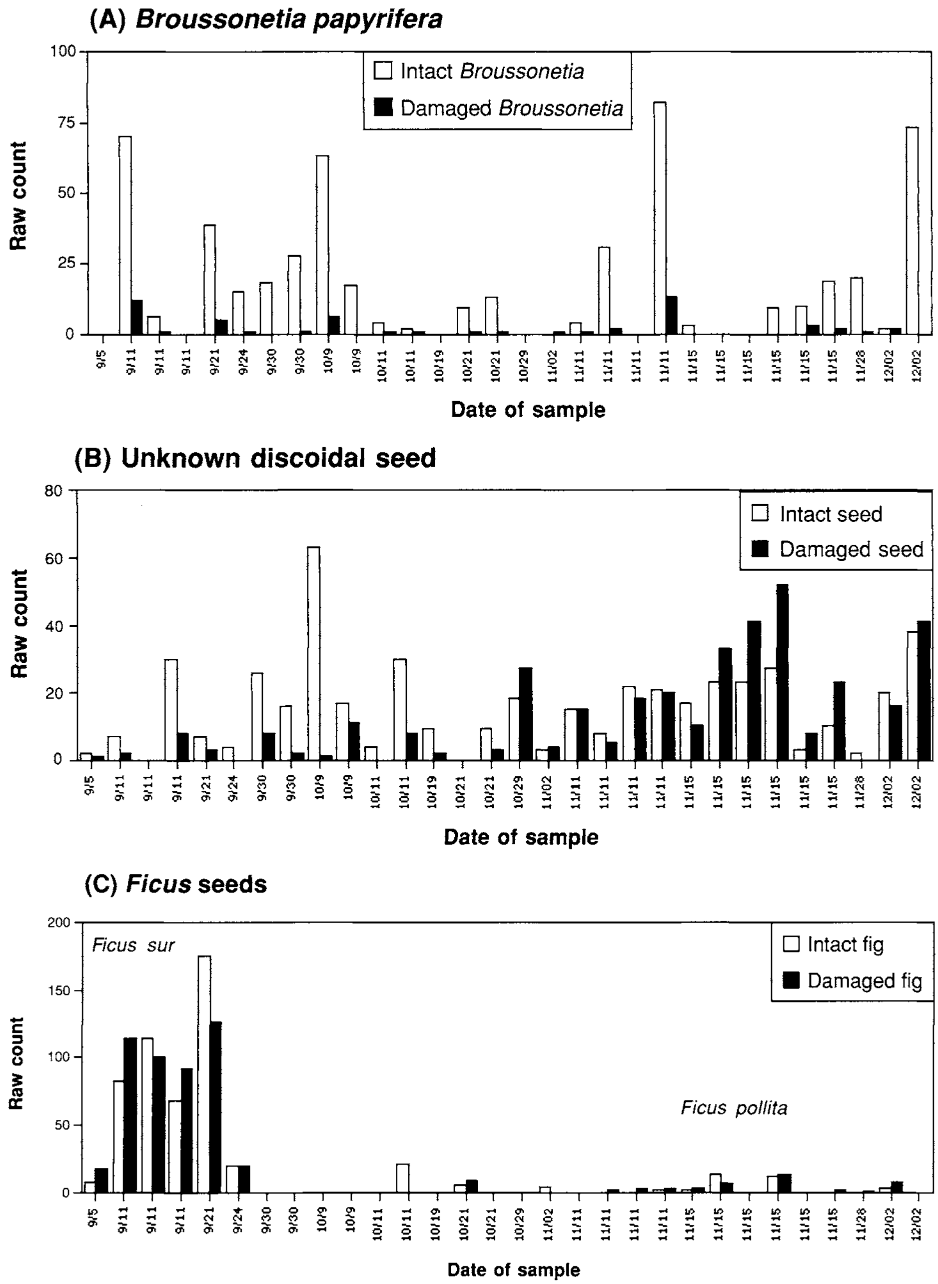
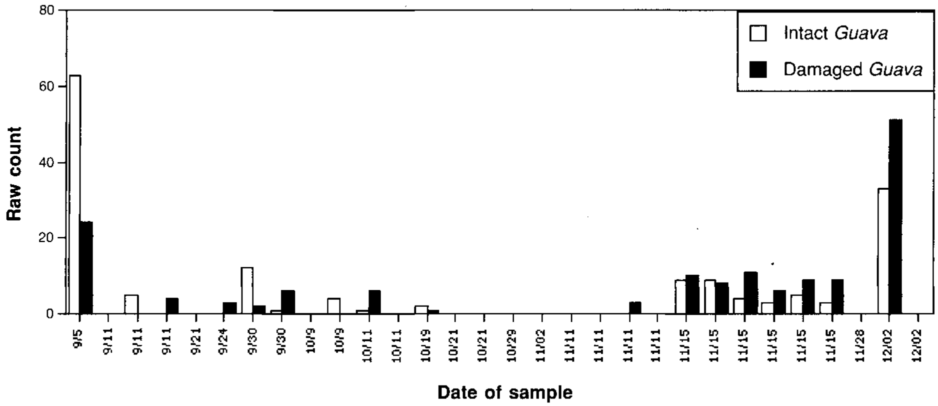
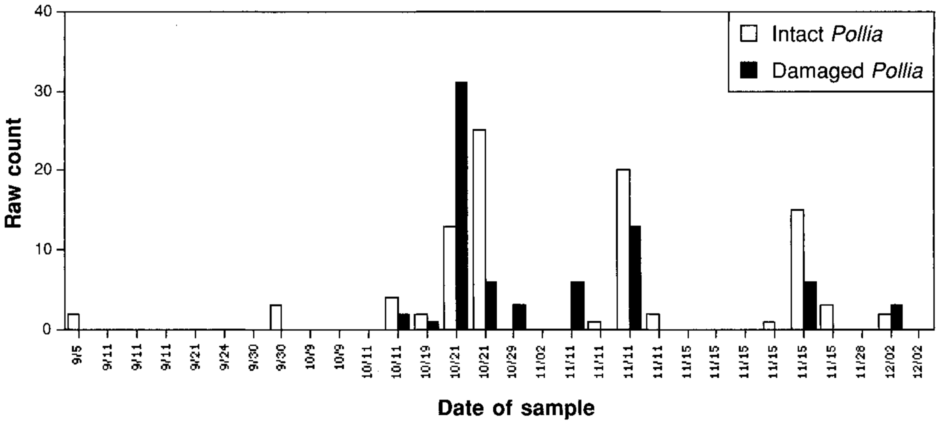


Figure 1. (A)–(F) Seed survival and destruction over 15 weeks. x-axis is date of sample collection; y-axis is raw frequency of seeds in 1-cm^3 sample.

(D) *Psidium guajava*



(E) *Pollia condensata*



(F) Frequencies of insect parts and mineral fragments

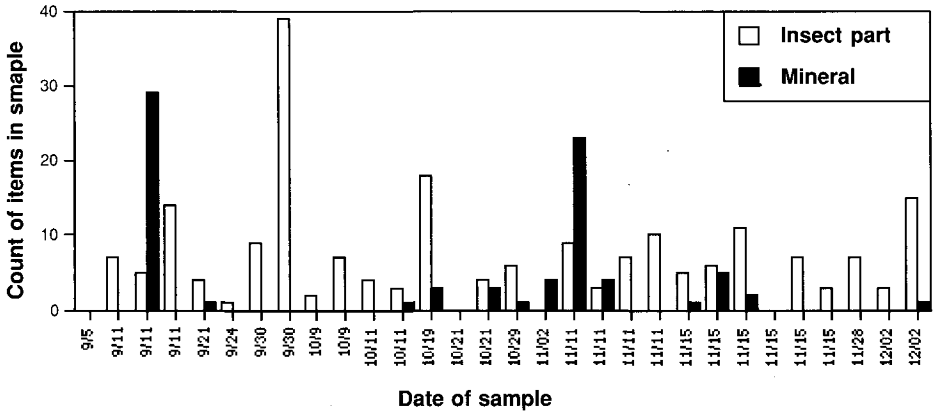


Figure 1. *(Continued)*

on plant materials rather than geophagy. No geophagy was observed at Sonso, unlike at Busingiro, where the brick used in the Busingiro House buildings and soils from collapsed termite mounds were regularly consumed by all members of the main study troop. X-ray diffraction analysis (courtesy of Mr. D. Harvey, Department of Geology and Geophysics) of a sample of the brick revealed that the major components were dehydrated clays "Gibbsite" -($Al(OH_3)$) and "Goethite" -($Fe_2O_3H_2O$), which dissociate in an acid solution to produce an alkaline slurry with some effects like the commercial "Kaopectate" (cf. Tweheyo *et al.*, Chapter 8, this volume).

Two rare unidentified seeds and several species of grasses are represented in Figure 2. These two unidentified seeds were occasional findings in samples

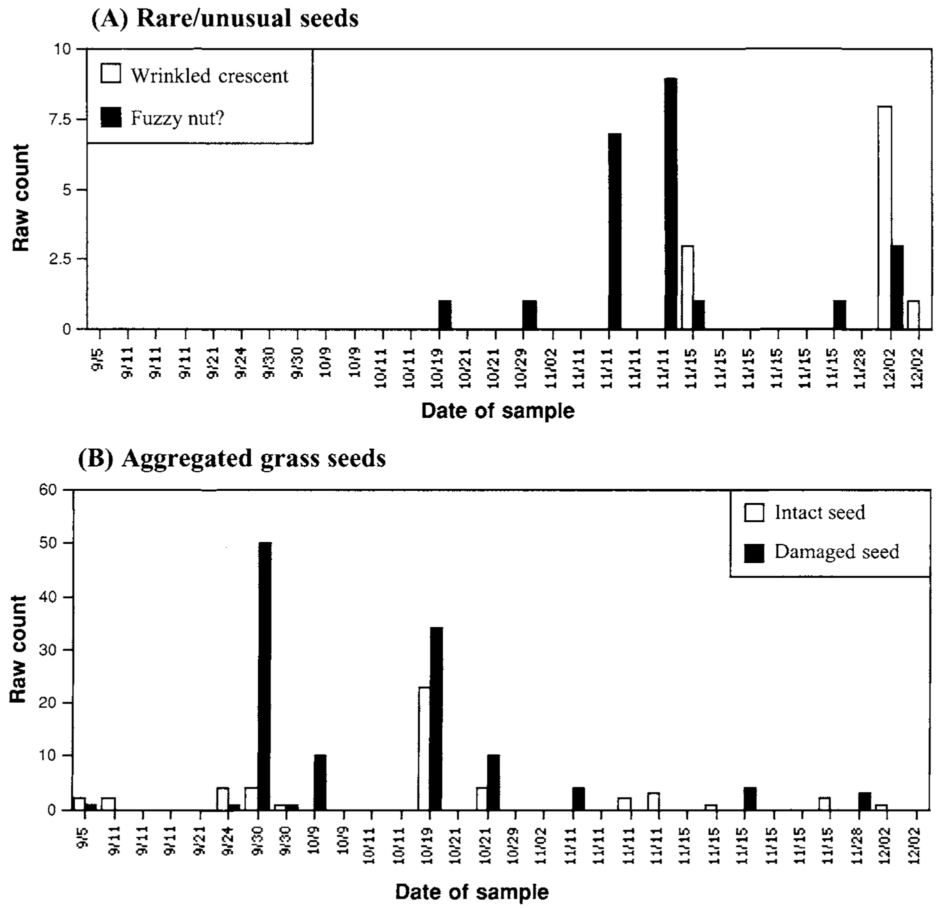


Figure 2. (A) Rare or unusual seeds noted in fecal samples. (B) Grass seeds of Eleusine, Pennisetum and Pannicum genera, intact seeds and remnants of damaged seed. *x*-axis is date of sample collection; *y*-axis is raw frequency of seeds in 1-cm^3 sample.

predominantly from November and early December. Grass seeds were frequently observed to be consumed during the study, with elevated intake during late September to late October, when *Pannicum maximum*, "Guinea grass," and *Brachiaria brizantha*, a minor component, were in seed. Relatively few grass seeds made it through the digestive path, and no intact seeds of *Pannicum* were encountered in the samples.

Pith, Root, and Bark Eating

The Sonso baboons were observed to feed on the structural components of a number of forest and grassland plants, specifically the internal, soft, and less fibrous material sometimes called "pith," the root structures either whole or in part of both trees and understory plants, and either the outer or inner bark of particular tree species. Table 2 presents a listing of the plants that are treated in this fashion by the Sonso baboons.

Pennisetum purpureum, known as Napier grass or elephant grass; *Marantochloa leucantha*, a common ground-level succulent; *R. farinifera*, the swamp-resident small nut palm; and *B. papyrifera*, the paper mulberry (an imported species), are the most frequently affected plants. As regards the other major grass species, *Pannicum maximum*, no pith consumption was observed. *Khaya* bark consumption is treated separately below, and cambium consumption is irregular in both time and space. Many *Ficus exasperata* and *Ficus variifolia* trees within the forest, but not all, show some evidence of bark gnawing along the buttresses of moderate-sized specimens. Some of this is known to be done by

Table 2. Pith, root, and bark ingested by Sonso baboons, and consequences for the plant involved

Type of plant	Species	Part	Consequences for plant
Asiatic lilly	*Canna indica*	Pith	Destruction of stem
Grass	*Eleusine jaegeri*	Pith	Destruction of stem
Grass	*Pennisetum purpureum*	Pith	Destruction of stem
Herb	*Aframomum* sp	Pith	Destruction
Herb	*Aneiloma aequietiale*	Root nodes	Destruction
Herb	*Marantochloa leucantha*	Pith of petiole	Destruction of leaf
Tree	*Broussonetia papyrifera*	Leaf stems	Pruning
Tree	*Ficus exasperata*	Cambium	Unknown
Tree	*Ficus variifolia*	Cambium	Unknown
Tree	*Khaya anthotheca*	Outer bark	Unknown
Tree	*Albizia coriaria*	Root pith	Destruction of seedling
Tree	*Lychnodiscus cerospermus*	Root bark	Destruction of seedling
Tree	*Raphia farinifera*	Pith	Destruction of seedling

the chimpanzees, who seem to favor the slight vinegar tang of *F. variifolia*, but on five occasions baboons were observed actively gnawing on fig buttresses—four *F. exasperata* and one *F. variifolia*. By a very substantial amount, the two common plants *P. purpureum*, and *B. papyrifera* are the most affected by pith feeding, some being consumed every observation day. For 5 days in late November, pithing of *Pennisetum* became an intensive activity, with at least an hour each day being devoted to it by the whole troop. The remainder of the species in Table 2 are rare observational occurrences, and *Raphia* was discussed earlier. Perhaps the most interesting is *Albizia coriaria* (one of the adult females uprooted a 1-m-tall seedling and nibbled the outer bark off of the entire root) which is used by the West Nile district human population as an effective fish poison. However, bioactivity of this species of *Albizia* is unknown.

While pith consumption was observed during a study centered around Busingiro Hill (approximately 9 km west of the Sonso site, in 1970–1971) it was seen only on grasses—*P. purpureum* and *Paspalum conjugatum*. No bark consumption was observed at that time. The ecological circumstances of the Sonso population are very different from that of the Busingiro Hill populations with respect to vegetation, animal, and avian communities, as well as temperatures and precipitation. Both locations have numerous "exotic" or imported species present, but they are different sets (see Table 1). At Sonso, the exotic *Broussonetia papyrifera* has become a major pest species on any disturbed soil and, owing to its pattern of rapid growth, vegetative colonizing as well as massive fruiting on a twice-a-year pattern, is becoming the dominant species around the clearing. Primates of all five resident species pay great attention to it as almost all parts are edible. Leaves, petioles, flowers, and fruits have been observed in the diets of all five species.

Khaya anthotheca and *Khaya grandifoliola* (often these two species are not discriminable under field conditions) are commercially important mahogany trees in Uganda and present an unsolved puzzle, which served as the focal point for a study in 1997. It has been recognized by the researchers at the BFP that all five of the resident primate species at least occasionally consume *Khaya* bark, and some blue monkeys consume very large amounts (Fairgrieve, 1995). But in light of the condensed tannin component of its makeup, 14–17 mg/g as reported in Plumptre *et al.* (1994), the question must be 'Why?' Condensed tannins are most frequently viewed as toxins rather than attractors, but recent work on the benefits of various tannins as cancer preventives in humans may change this perspective. One of the common characteristics of *Khaya* trees is the presence of delaminated areas on the midtrunk and lower main branches. These have been labeled as "scabs" in previous reports. Close observation of the activities of a 2-year-old female baboon, particularly because she is an intensive investigator of *Khaya* bark, indicates that scabs, when encountered, are pried open and the underside eaten, and the cavity is also nibbled on. Strings of resin from these scabs, whether clear, white, or tan, are avidly consumed. To humans, the resin is almost tasteless, but remnant bark smells somewhat like malt vinegar and is somewhat bitter to the tongue, yet a fresh slash through the bark yields a watermelon-like odor. The cambium is always avoided as it produces an instant anesthesia effect. Direct observation of openings in the outer bark produced by baboons record a rapid recovery, with the area being closed over with new outer bark in 12–14 days. Examination of a number of lower trunk scabs found them to be inhabited by nymphs of wood-boring beetles, solitary brown ants, wasp larvae, and scale bugs.

Biochemical analyses of the bark using thin layer chromatography (TLC) were undertaken during 1997–2001. In addition to finding condensed tannins of the anthocyanidin cluster, my students and I found limonoids, at least one other terpenoid compound and two coumarins—scoparone and scopoletin—in the bark. Extended TLC plates have suggested the presence of as many as eight major compounds, some having as many as four variants, differing only slightly in molecular weight. The published identifications of *Khaya* bark chemicals are predominantly from West African species of *Khaya* and populations of *K. grandifoliola*, and hence may differ from the Uganda specimens. Table 3 shows the identified compounds and their bioactive effects. Note that in spite of direct TLC comparisons with control samples of the three identified sterols, none of these were detected in the Sonso bark collection.

However, the actual energy content of the bark may also contribute to the reasons for its consumption. Bomb calorimetry was conducted on four samples of gum and eight bark samples. The mean energy content of the *Khaya* gum was 2922 cal/g and the bark was 3720 cal/g, but the largest part of the bark energy is unavailable to primate digestion as it is derived from cellulose and hemicelluloses. The sugar content found by Reynolds *et al.* (1994) accounts for 578 cal/g of dry bark, or 15.5% of the average yield.

At this point a tentative hypothesis might be that the tree's bark is prone to invasion by insects, that the insect invasion causes the bark to delaminate—forming the scab, the tree tries to compensate or "drown" the insects with an overproduction of resin, which in turn attracts the attention of the primates,

Table 3. Phytochemicals found in *Khaya* bark

Compound	Subgroups	Effects	Reference
Terpenoids	Limonoid[a] (methyl angolensate)	Molluscicide	Odyek *et al.*, 1990 Harborne, 1991 Adesina *et al.*, 1971
Sterols	Campesterol Stigmasterol β-sitosterol	Antipyretic Anti-inflammatory	Adesina, 1983
Phenols	Flavonoids Isoflavones Anthocyanidins[a]	Antioxidants	Markham, 1982 Harborne, 1991
Coumarins	Scoparone[a] Scopoletin[a] Umbelliferone Aesculetin	Anticonvulsants	Gupta *et al.*, 1980 Adesina, 1983

[a] Compounds confirmed in this study.

who consume both insects and resin—thus providing the tree with a pest control service. In addition, one can speculate that the primates receive a medicinal dosage of bioactive compounds and some energy from the sugars in the bark and gum.

Leaf, flower, and stem material is also recognized as an important component of the Sonso baboon diet, and is represented by approximately 10–15% of the washed fecal sample in the form of "fibrous wool" in every sample. This study was unable to identify the species of leaf fibers in these samples, and the focus in observation was upon seed ingestion. Table 4 lists the minor (small amounts ingested) species, their families and the plant parts consumed for those plants observed to be ingested, but for which no identification in the fecal samples could be made.

Forest Structure

The forest structure around the Sonso clearing as assessed in the sample plots measured in 1996 is heterogeneous. The Morisita Index of Similarity for the plots range from 0.16 to 0.99, with most index values around 0.5. The primary interpretation of the Morisita values is that the forest is diverse in species

Table 4. Leaf, fruit, and flower material observed to be consumed but unidentifiable in fecal samples

Species name	Family	Plant part consumed
Achyranthes aspera	Amaranthaceae	Flower spike
Aframomum sp.	Zingiberaceae	Root-bulb
Alternanthera nodiflora	Amaranthaceae	Leaf, flower
Alternanthera pungens	Amaranthaceae	Leaf, flower
Aneilema beniniense	Commelinaceae	Whole plant
Aneilema sp.	Commelinaceae	Flower
Bidens pilosa	Asteraceae	Young leaf, flower
Broussonetia papyrifera	Moraceae	Fruit, flower, bark, leaf-petiole, leaf
Casaeria engleri	Flacourtiaceae	Leaf
Cucumella engleri	Cucurbitaceae	Leaf, fruit
Cyathua cylindrica	Amaranthaceae	Leaf, flower
Datura sauvelens	Solanaceae	Young leaf
Desmodium repandum	Fabaceae	Young leaf
Desmodium canum	Fabaceae	Young leaf
Diplocyclos palmatus	Curcubitaceae	Fruit, flower (creeper)
Greenwayodendron sauveiolens	Annonaceae	Leaf
Gynura scandens	Asteraceae	Young leaf
Mallotus oppositifolius	Euphorbiaceae	Leaf
Melanthera scandeus	Asteraceae	Leaf (creeper)
Olyra latifolia	Poaceae	Leaf (grass)
Ouratea hiernii	Ochnaceae	Leaf
Physalis peruviana	Solanaceae	Leaf, fruit (creeper)
Piper umbellatum	Piperaceae	Flower, fruit
Rubus pinnatus	Rosaceae	Fruit
Solanum anguivi	Solanaceae	Fruit
Solanum welsitschii	Solanaceae	Fruit
Sorghum arundinaceum	Poaceae	Leaf, seed

composition, and that there is a moderate degree of patchiness or local concentrations for most species. The crown density measurements cluster between 90 and 96%, with only a few canopy cover measurements at the edge of clearings falling to the 60% level. The diversity and heterogeneity of the forest is consistent with its history of having been logged in the 1940s and 1960s. As in other studies, the diversity and productivity of logged forests is higher than that of unlogged forest (Chapman et al, 2000; Johns & Skorupa, 1987; Sheppard, 2000).

CONCLUSION

Baboon diets have been discussed extensively over the last half-century, but most of the focus has been on the variations and extent seen in savanna-dwelling populations. Forest-living populations have essentially been ignored owing to the great difficulties inherent in observation on the forest floor, combined with research foci on behavioral rather than ecological issues. In this study of the Sonso baboons, the range of food materials included in the species diet is expanded substantially, and a number of unusual processing sequences are noted in addition to the variations on plant parts utilized. The Sonso baboons incorporate a rather high proportion of barks, piths, and gums into their diet and, as noted in the results, appear to ingest a number of phytochemical compounds that might be bioactive. Whether or not these bioactive compounds should be categorized as "regular diet components," "diet supplements," or as "medicinal compounds" is indeterminable at present. More research is required.

Baboons in forest conditions dramatically expand the range and variety of food materials, thus confirming their opportunistic omnivore categorization. At the same time, the differences in their preferences for unripe fruits and a broad range of nutmeats, piths, barks, and grasses points up the evolutionary disruptive selection that has forced their diet to diverge from but remain in substantial overlap with that of humans.

ACKNOWLEDGMENTS

My thanks to the Uganda National Council for Research and Technology for research permits, and the President's Office for permission to work in Uganda; Andy Plumptre for initially inviting me to study the Sonso baboons and for providing his maps and tree species listing; Vernon Reynolds as principal investigator for information about the project and sharing his enthusiasm; Jeremy Lindsell for toleration and good humor in his takeover of an unusual administrative job; Sandy Paterson, Titia Achobo, Andama Kennedy, and Jacan Godfrey for their field assistance in observation; and Tinka John for aid in tree identification in the sample plots. The staff and technicians of the Makerere University Herbarium are also thanked for their expertise in identification of a number of obscure plants. All of the BFP staff are thanked for making our stays at Sonso comfortable. Also thanks to the University of Calgary Research Grants Committee for partial funding of this project.