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Identifying Species in Chimpanzee (*Pan troglodytes*) Feces: A Methodological Lost Cause?

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Abstract Ascertaining the full range of dietary constituents of a primate population allows the identification of habitats with important food resources and can assist efforts to conserve primates. For unhabituated populations, we can acquire otherwise unobtainable dietary information from macroscopic inspection of fecal samples. This method has made a significant contribution to understanding food intake in various primate species. Increasing knowledge of the omnivorous diet of our closest living relatives, the common chimpanzee (*Pan troglodytes*) and the bonobo (*P. paniscus*), which range and forage in various habitats to meet daily nutrient requirements, provides more scope to assess human omnivory and its evolution from our last common ancestor. However, macroscopic inspection may lead to bias toward undigested and therefore identifiable food items, e.g., fruit seeds, vs. pulverized components, e.g., leaves, that are unidentifiable at this level. This study seeks to validate findings from macroscopic inspection by comparing species identified in fecal samples from select individuals vs. data from direct observations of their feeding. We collected data from 10 adult chimpanzees of the Kanyawara community in Kibale National Park. We identified 86% of species from which fruit had been eaten vs. only 21% from which leaves had been eaten in fecal samples analyzed. This study provides empirical support for previous assumptions and confirms the limitations of macroscopic inspection of feces for identifying the nonfrugivorous dietary elements to species level. However, valuable insights into seasonality of diet can be gleaned from macroscopic inspection. Also, if we combine data on species identified in feces with direct observation of food intake, we can establish *when* food items were eaten, which enables estimations of gut passage rates for wild populations. Finally, analyzing fecal samples collected from various group members can provide insight into the dietary repertoire at the individual level.

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Introduction

Macroscopic inspection of fecal samples has greatly expanded our knowledge of the range of dietary constituents in unhabituated primate populations, such as insectivory and seasonal consumption (red howlers [*Alouatta seniculus*]: Julliot and Sabatier 1993; Japanese macaques [*Macaca fuscata*]: Hanya *et al.* 2003; chimpanzees: McGrew 1983; Pruetz 2006; Schöning *et al*. 2007; sympatric gorillas [*Gorilla gorilla*] and chimpanzees: Deblauwe 2008; Head *et al*. 2011; Tutin and Fernandez 1993a; and bonobos: Surbeck *et al*. 2009). Using this indirect method illuminates aspects of diet, but the repertoire of food items recorded is incomplete, as food items may not be identifiable to species level and even to plant or animal part in fecal samples, having undergone both mastication and digestion to varying degrees. Even with systematic analyses (McGrew *et al.* 2009), important elements, such as fruit skins and seeds, tend to be more taxonomically identifiable than lesser ones. Greater difficulty arises in establishing the nonfrugivorous dietary component, such as ingestion of nonchitinous invertebrates, e.g. caterpillars, maggots (*cf.* Deblauwe 2008), or of foliage, e.g., leaves, stems, and pith of nonwoody plants (Basabose 2002). These items tend to be either fully digested, and invisible to the naked eye, or pulverized to the point that they are no longer recognizable.

The limits of macroscopic inspection are well known (Doran *et al.* 2002; McGrew 1983; McGrew *et al.* 1988; Moreno-Black 1978; Tutin and Fernandez 1993b). However, to date, no study has systematically compared all-day behavioral observation of feeding by an individual with the content of its subsequent fecal samples. We identified plant and animal species from macroscopic inspection of fecal samples, collected from 10 adult Eastern chimpanzees (*Pan troglodytes schweinfurthii*) of the Kanyawara community in Kibale National Park, Uganda. We sought to evaluate the effectiveness of this indirect method for elucidating consumed plant and animal species and predicted that the most nonrepresented or lost species in fecal samples would be nonfrugivorous food items. Thus, our hypothesis was: Frugivory is overestimated and folivory and faunivory underestimated in the primate diet when identifying foods to species level using macroscopic inspection.

The Kanyawara community eats ≥113 species of plant (Kibale Chimpanzee Project 2009). We compared findings from fecal analysis with species we saw individuals eat. We also investigated sex differences in the diet: If either sex fed on more plant species per focal sample, or ate a greater proportion of foods that were pulverized in feces, e.g. leaf and pith, this might influence the number of species identified during macroscopic inspection of scats.

Methods

Study Site

Kanyawara is in the western part of Kibale National Park (0°13′–0°41′N, 30°19′–30°32′E) in Uganda, at *ca*. 1500 m elevation (Wrangham *et al.* 1994). This mature, mid-altitude

semideciduous and evergreen ecotype has swamp, primary, and regenerating forest that was logged pre-1992 (O'Driscoll Worman and Chapman 2004). Dominant trees in unlogged areas are *Parinari excelsa*, *Celtis gomphophylla*, and *Markhamia lutea* (Sekercioglu 2002), whereas the woody shrub *Acanthus polystachyus* dominates previously logged areas (Osborne *et al.* 2001). There are distinct wet and dry seasons: May–August and December–February are drier than other months (Chapman *et al.* 2001). We collected data over 162 d between June and December 2008 (excluding August). Thus, data covered 2 of the 4 mo of one dry season (D_1), all of one wet season (W) (September–November), and 1 of 4 mo of a second dry season (D_2) (December). Total rainfall for 2008 was 1622 mm; during the study period, mean monthly rainfall during the dry seasons combined was 52.7 ± SE 6.6 mm and in the wet season was 212.1 ± SE 65.9 mm. Mean maximum and minimum monthly temperatures in the dry and wet seasons were 27.9 ± SE 0.4 °C (range: 18.3–38.0°C; $N = 78$ d) and 14.1 ± SE 0.1°C (range: 0.0–17.0°C); and 28.3 ± SE 0.5°C (range: 14.1–43.3°C; $N = 84$ d) and 14.1 ± SE 0.1°C (range: 11.9–17.5°C) (C. Chapman, *pers. comm.*).

Data Collection

Focal Individuals The Kanyawara community numbered *ca*. 50 individuals during the study. We encountered 43 individuals: 9 adult males, 12 adult females, 7 subadults, and 15 juveniles and infants. We followed 5 male and 5 female fully habituated chimpanzees individually from when they arose from their arboreal beds (nest) in the morning until they made another arboreal bed in the evening (a focal sample; Martin and Bateson 2007). Each focal sample ($N = 19$) lasted up to 3 consecutive days ($\bar{x} = 2.5 \pm \text{SE}\ \ 0.2$ days, range: 1–3 d), and we followed nine individuals twice for test–retest comparison. We conducted the research in compliance with the Department of Archaeology and Anthropology, University of Cambridge and International Primatological Society guidelines for research on animals. For 48 d, from 06:15 to 19:15 h, focal sampling time pooled for the 10 individuals totaled 502 h, of which 392 h were direct observation and 110 h (22%) were out of view. Median total focal sampling time in view for the 10 individuals from pooled data (expressed in hours: minutes) was 8:10 h d^{-1} (range: 5:15–12:05 h d^{-1}).

Feeding Data We directly observed feeding by the focal individual during each follow. We defined food intake as "item placed into mouth, remaining there (or parts thereof) and seen to be either chewed or swallowed." Food intake included food wadges, when an individual ingested and masticated but then spat out food item residues. We recorded food item eaten and categorized them as plant, nonplant, or unknown. We further subdivided plant food items into monocotyledon or dicotyledon (for flowering plants), species, and plant part; fruit (ripe or unripe and then whole, flesh, seed), blossom, leaf (bud, young, mature), pith, outer stem, wood (including bark, twig, and branch), and other (roots, fungi, etc.) (Ghiglieri 1984; Morgan and Sanz 2006; Tutin and Fernandez 1993a). Nonplant food items were invertebrates (whole, part, adult, nymph, larva, pupa), soil, honey (including honeycomb) (Morgan and Sanz 2006; Tutin and Fernandez 1993a), vertebrates (whole, part), and other.

Permanent staff of the Kibale Chimpanzee Project helped in plant species identification. All plant parts collected have been seen to be eaten by members of the Kanyawara chimpanzee community over the last 21 yr.

Fecal Samples From the 10 focal individuals, we collected fecal samples within 20 min of defecation and estimated the percentage of the deposited scat obtained. We defined complete collection as ≥95%, as we could not always collect all fecal matter. Incompleteness was due to scat consistency, i.e., feces too loose to collect using a spatula or a ziplock bag; rushed collection because of concern of losing a moving focal subject; or failure to locate all of the scat if dispersed over a large area, especially from arboreal defecations. Overall we collected 102 scats (72%) complete and 39 incomplete, all of which we analyzed for this study. We placed samples into prelabeled plastic storage bags, sealed, and weighed them (g) using a Kenex KX digital scale (400 g × 0.1 g capacity) back at camp.

Macroscopic Inspection After following an individual (for up to 3 consecutive days), we macroscopically inspected fecal samples in a gravel-based, medium-flowing stream, *ca.* 1.3 km from the Makerere University Biological Field Station. Before macroscopic inspection, we removed 4 subsamples from 103 scats for off-site analyses (phytolithic, stable isotopic, and genetic; Phillips 2011), and then analyzed the fecal matter that remained.

We added clear stream water to each bagged sample and then gently squeezed the water-filled bag from the outside to soften and break down fecal boli (McGrew *et al.* 2009). We then poured the contents into three stacked Endecott soil-test sieves of 20 cm diameter and 4.5 cm height, with mesh sizes 4 mm, 1 mm, and 0.5 mm. This tiered system sped up counting and identification and allowed findings to be compared with other macroscopic inspection studies that used sieves of 1 mm mesh size (Head *et al.* 2011; Tutin *et al.* 1991). We removed as much of the fecal matter as possible from bags by repeatedly rinsing them with water and then pouring the contents into the top of the three stacked sieves.

We removed soluble matter and matrix by repeatedly pouring stream water into the top sieve for sluicing. This exposed food items such as fruits, e.g. seeds, skins; nonfruit plant matter, e.g. fiber, bark, leaf and stem fragments; and other food remains (McGrew *et al.* 1988; Tutin and Fernandez 1992). Gentle use of an artist's soft-bristled brush assisted in the passage of matrix through sieve-meshes. Before analysis, we removed with needlepoint forceps all extraneous, noningested matter such as dead leaves, twigs, and dung beetles (McGrew *et al.* 2009). We then photographed for reference purposes each set of exposed food items, identified them, and whenever possible, counted food items individually.

We calculated two totals for identified plant and animal species: The first was the total number of plant and animal species identified 1) from macroscopic inspection of all fecal samples ($N = 141$); and 2) by direct observation of food intake by the 10 focal individuals, over the total feeding time of 115 h, across 48 focal sampling days ($N = 19$ focal samples). The second total was plant and animal species identified during macroscopic inspection of 81 of the 141 fecal samples that had been defecated *ca*. 24 h or more after the first observed feeding bout for each focal individual (normally collected from the morning of the second day, through to completion of the focal sample, which was

either on the same day or at the end of a third day). The fecal sample set used to calculate the second total is referred as "≥24 h" in the text that follows. This interval allowed for digestion and passage of food items eaten on the first day of each focal sampling period. Gut passage rate was calculated at 31–48 h for captive chimpanzees (Lambert 2002; Milton and Demment 1988). We applied a more conservative start time of 24 h, as passage rate of food items is unknown for wild chimpanzees, and their diet is more varied, so that some of the foods consumed at Kibale may have had a faster passage rate. As we recorded multiple feeding bouts on a single plant species, on the same day, we provide the range of times in which 18 plant species were seen to be eaten before fecal sample collection and were recognizable in feces, in order to estimate their passage rates.

To validate macroscopic fecal findings for the second total, we included only plant and animal species that were seen to be eaten by the focal individuals on the first or the second days of a focal sample (depending on the length of the focal sample, i.e., either 2 or 3 d in total). Thus, we analyzed data from total feeding time of 68 h (59% of total feeding time), over 29 of 48 focal sampling days. For both totals, we pooled data from fecal sample analysis and observed feeding for each focal sample to assess diversity of species consumed by each adult chimpanzee.

Per focal sample, we calculated the ratio of fruit to leaf species 1) seen to be eaten over the 29 days; and 2) in fecal samples collected *ca*. 24 h after the first observed feeding bout, to see how observed folivory was represented in fecal samples.

Statistical Analysis

We tested normality of data using the Anderson–Darling test. We tested sex differences for total plant species eaten per day and for pith and leaf consumption from terrestrial species per focal sample using a Mann–Whitney test (two-tailed). We also used this test to determine if the number of plant species identified in fecal samples that were not seen to be eaten was greater in the first 24 h of the focal sample period. We used Spearman's rank correlation test (two-tailed; $\alpha = 0.05$) to test the relationship between the total number of plant species identified per fecal sample and the fecal mass (g) analyzed. We also applied this test to see if a relationship existed between total time a focal individual was out of view during a focal sample, and how many plant species that had not been seen to be eaten were found in concurrent fecal samples. We performed statistical analyses in MINITAB Release 14 and SPSS version 21.0.

Results

Plant Foods

Feeding Data Over 48 focal sample days, the 10 focal individuals ate parts from 47 plant species, of which we identified 42 to species, 4 to genus level, and one was unidentified (a fern), representing 29 families. We summarize these taxa, along with parts ingested ($N = 84$, including various fruit parts but not unripe fruit parts, if fruit

had already been counted as eaten ripe), plant life form (such as tree, climber, etc.), and habitat (McGrew *et al*. 1988) in Table I. Males ate a median of 8.8 plant species d^{-1} ($N = 5$, range: 1–13), and females at a median of 6.9 d^{-1} ($N = 5$, range: 3–11). This sex difference, which is based on small sample sizes, was nonsignificant (Mann–Whitney test: $W = 112.5$, $P = 0.59$). The median total plant species eaten per focal sample was 13 for both males and females, in which 53% (range: 22–82%) for males and 50% (range: 22–75%) for females were species eaten as leaves or pith. The chimpanzees ate fruit parts from 29 species (Table I). As well as trees, strangler figs, and climbers, this included 10 terrestrial plant species, which we further divided into shrubs and terrestrial herbaceous vegetation (THV; Malenky *et al*. 1994). They ate whole fruits from 18 species but only fruit seeds or fleshly pulp from the rest (Table I). They consumed fruit parts from 9 of the 14 *Ficus* spp. known to be eaten by the Kanyawara community, and also ate leaves from *F. exasperta* and *F. asperifolia.* Other species from which they ate both fruit and leaves were *Pseudospondias microcarpa*, *Aframomum* spp., *Marantachloa leucantha*, *Maesa lanceolata*, and *Tabernaemontana pachysiphon*. The focal individuals also ate leaves from another 12 species: 4 trees, 1 climber, and 7 terrestrial plants; and pith (or the stem) from 53% of 15 THV species (Table I). They ate blossoms from *Lepistemon owariensis*, *Piper capense*, and *Urtica massaica*, and wood from fallen, dead trunks of *Neoboutonia macrocalyx*.

We observed only eight wadging bouts during the 48 d, in which the focal individuals wadged parts of five species: fruit of *Mimusops bagshawei*, fruit of *Psycotria mahonii*, pith of *Marantachloa leucantha*, *Pseudospondias microcarpa*, and leaves of *Trichilia splendida*.

During the first or second day of all focal samples ($N = 29$ days) males ate a median of 11.5 plant species (range: 6–17), and females 11 (range: 7–14) (Mann–Whitney test: $W = 101$, $P = 0.62$, $N = 10$ for males, $N = 7$ for females). The chimpanzees ate only 39 ($N = 72$ plant parts) of the 47 plant species eaten over all the 29 d they were followed (the other 8 species eaten on the last day of all 3-d follows are underlined in Table I). These 39 represent 26 families. The 10 focal individuals ate most of the fruit species ($N = 24$) on the first and second days. Eleven THV species were eaten over the 29-d period. Chimpanzees did not eat the piths of two species (*Zea mays* and *Musa acuminata*) crop-raided by an adult female, the leaves of an unknown fern, and the seeds of *Brillantaisia* spp. Species for which they ate leaf and pith comprised 53% of total species for both sexes, a proportion similar to that calculated for the 48-d period.

Macroscopic Inspection We collected a mean of 8.3 ± SE 0.6 fecal samples per focal sample, and identified 5.4 ± SE 0.5 (range: 3–11) plant species per fecal sample. The number of plant species identified per sample and the mass (g) of the fecal sample analyzed did not correlate significantly (Spearman rank correlation test: $r_s = 0.10$, $P = 0.23$, $N = 140$), so we treated the incomplete and complete scats as one data set. We identified 60% of the 47 plants in all fecal samples ($N = 141$): 27 to species and 1 to genus (Table I), representing 19 families. All were eaten by focal individuals over the 48-d focal sampling period. Of these, we identified 86% (11 trees, 2 strangler figs, 5 shrubs, 2 climbers, and 4 THV species) from fruit parts. We identified some easily from fruit that had been defecated whole (Table II). All 141 samples contained fruit

Table I Plant and non-plant foods seen to be eaten by 10 adult chimpanzees [✚]; identified during macroscopic inspection of 141 faecal samples [●] at Kanyawara, Kibale National Park, Uganda, from June-December 2008

Plant food items Life form Species	Family	Hab	Plant part Fruit Seed	Pulp	Skin	Whole	Blos	Leaf Y	M	Pith	Stem	Wood
Terrestrial herbaceous vegetation												
Acalypha ornata Hochst. ex A.Rich.	Euphorbiaceae	OR						✚				
Acanthus polystachius Delile	Acanthaceae	OR								✚		
Aframomum spp.	Zingiberaceae	OR	✚ ●	✚				✚		✚		
Aneilema aequinoctiale (P.Beauv.) Loudon	Commelinaceae	OR						✚ ●				
Brillantaisia spp.	Acanthaceae	OR	✚									
Hoslundia opposita Vahl	Lamiaceae	OR	✚ ●	✚ ●	✚ ●	✚ ●						
Fern	Unknown	BO						✚				
Lepistemon owariensis (P. Beauv.) Hallier f.	Convolvulaceae	OR					✚	✚ ●	✚ ●	✚	✚ ●	
Maesa lanceolata Forssk.	Maesaceae	OR	✚ ●	✚	✚ ●	✚		✚		✚		
Marantochloa leucantha (K.Schum.) Milne-Redh.	Marantaceae	OR	●			✚		✚		✚		
Musa acuminata Colla	Musaceae	FM								✚		
Piper capense L.f.	Piperaceae	BO					✚			✚		
Triumfetta tomentosa Bojer ex Bouton	Malvaceae	BO						✚				
Urtica massaica Mildbr.	Urticaceae	OR					✚ ●					
Zea mays L.	Poaceae	FM								✚		
Tree												
Celtis africana Burm.f.	Ulmaceae	MF						✚				
Celtis gomphophylla Baker	Ulmaceae	BO	●			✚						
Celtis zenkeri Engl.	Ulmaceae	OR						✚				
Cordia africana Lam.	Boraginaceae	MF	✚ ●	✚ ●	✚ ●	✚						
Ficus exasperata Vahl	Moraceae	MF	✚	✚				✚ ●				
Ficus natalensis Hochst.	Moraceae	MF	●	●	●	✚						
Ficus vallis-choudae Delile	Moraceae	OR	●	●	●	✚*						
Ficus sur Forssk.	Moraceae	MF	✚* ●	✚* ●	●							
Mimusops bagshawei S.Moore	Sapotaceae	MF	●	●	●	✚* ●					●	
Monodora myristica (Gaertn.) Dunal	Annonaceae	MF	✚ ●	✚								
Myrianthus arboreus P.Beauv.	Moraceae	MF	✚ ●	✚								
Neoboutonia macrocalyx Pax	Euphorbiaceae	MF										✚
Pseudospondias microcarpa Engl.	Anacardiaceae	MF	✚ ●	✚	✚	✚		✚				
Psycotria mahonii C.H. Wright	Rubiaceae	MF	●	●	●	✚ ●						
Pterygota spp.	Sterculiaceae	OR						✚				
Secamone africana (Oliv.) Bullock	Apocynaceae	MF	✚* ●	✚* ●								
Trichilia splendida A.Chev.	Meliaceae	MF						✚				
Uvariopsis congensis Robyns and Ghesq.	Annonaceae	MF	✚ ●	✚ ●	✚ ●	✚ ●						
Strangler fig												
Ficus cyathistipula Warb.	Moraceae	MF	✚ ●	✚ ●	●							
Ficus ottoniifolia lucanda (Ficalho) C.C. Berg	Moraceae	MF				✚						
Ficus sansibarica macrosperma Mildbr. and Burret C.C. Berg	Moraceae	MF	✚ ●	✚		●						
Ficus conraui Warb.	Moraceae	MF	✚	✚								
Shrub												
Chaetacme aristata Planch.	Ulmaceae	BO						✚				
Dovyalis macrocarpa	Flacourtiaceae	OR	✚ ●	✚	✚	✚						
Ficus asperifolia Miq.	Moraceae	BO	●	●		✚* ●		✚ ●	✚ ●			
Pancovia turbinata Radlk.	Sapindaceae	OR						✚				
Tabernaemontana pachysiphon Stapfr.	Menispermaceae	OR	●			✚ ●		✚				
Tarenna pavettoides (Harv.) Sim	Rubiaceae	OR	●			✚						
Toddalia asiatica L. (Lam).	Rutaceae	MF	●			✚						
Climber												
Jasminium spp.	Oleaceae	MF						✚	✚			
Phytolacca dodecandra L'Hér.	Phytolacceae	OR	●	●	●	✚ ●					●	
Urera hypsiloides	Urticaceae	MF	✚									
Nonplant food items			Hair	Bone	Organ	Tissue	Larva	Chitin	Frag	Comments		
Piliocolobus tephrosceles	Cercopithecidae	—	●	●	✚	✚				Ate internal organs		
Apis mellifera	Apidae	—					✚			Eaten with honey		
Fig wasps – unidentified	Agaonidae	—						●		Exoskeleton chitin		
Ants – unidentified	Unknown	—						●		Not seen to be eaten		
Honey and comb	—	—							✚ ●	—		
Soil	—	—							✚ ●	From exposed roots		
Plant remains in feces	—	—							✚	*P. microcarpa* seeds		

Species, family and parts eaten listed. Plant foods classed as four plant life-forms. Fruit parts also eaten unripe (*). Leaves as young (Y) or mature (M); blossom (Blos); dead wood (Wood). Habitat (Hab): naturally occurring or previously logged regenerating forest (OR); mid-altitude forest, both primary and swamp (MF); both open areas and mid-altitude forest (BO); and farmland (FM). Parts of nonplant foods include fragments (Frag) of soil, seeds in feces and honey and comb. Food items seen to be eaten on third day of focal sample underlined. Plant species eaten on two or more days of focal sample shaded in gray

seeds (mean total seed count per sample = 758 ± SE 89, range: 1–4915 per sample, $N = 102$). We identified 11 species by seeds alone (see Table I). The median number of fruit species per fecal sample was 2 (range: 2–6).

We identified only four species of leaves (21% of total species, Table I) in only 10 fecal samples with a mean of only 1 species per fecal sample across 8 focal samples.

Table II Nonplant foods eaten by eight adult chimpanzees (four males, four females) at Kanyawara, Kibale National Park, Uganda, June–December 2008

Food item	Chimpanzee	Sex	No. of direct observations	Total feeding time (min)
Red colobus monkey	TU	M	1	26
(*Piliocolobus tephrosceles*)	PG	M	1	27[a]
Honey	PG	M	1	2
Honey and bee larvae (*Apis mellifera*)	ST	M	1	19[a]
Soil fragments	ST	M	1	2
	TU	M	3	<1[a]
	YG	M	3	2[a]
	PG	M	1	<1[a]
	OU	F	1	<1[a]
	TG	F	1	<1
	LR	F	1	<1
	WL	F	2	<1[a]

Number of observed bouts and total feeding time (min)

[a] Observed on first or second day of focal sample only

Aneilema aequinoctilae and *Ficus asperifolia* were recognizable from whole, folded leaves in samples and *Ficus exasperata* from large fragments. We saw three males and an adult female fold and swallow leaves of these species, without chewing, and suspect that they were ingested for self-medication, based on previous studies of this community (Huffman and Wrangham 1994; Wrangham 1995). We identified a further four *Ficus* spp. by their fruit parts, e.g., seeds of *F. sansibarica* were larger than those of other *Ficus* spp. and brown in color. *Ficus* spp. were present in 72% of fecal samples. The second and third most frequently identified species by fruit parts were *Mimusops bagshawei* (66% of fecal samples) and *Aframomum* spp. (44%).

We collected 5.1 ± SE 0.5 fecal samples 24 h or more after the first observation of feeding per focal sample ($N = 81$total for ≥24 h fecal sample set). We identified 4.1 ± SE 0.4 (range: 2–7) plant species per fecal sample over 17 focal samples from macroscopic inspection data (fecal samples were not available *ca*. 24 h after first-observed food bout for two). This frequency for the ≥24 h sample set was only 20% less than that found for all 141 fecal samples analyzed. The median number of fruit species per fecal sample was 2 (range: 2–5). Again, we found no correlation between the number of plant species identified per sample and the mass (g) of feces analyzed (Spearman rank correlation test: $r_s = 0.03$, $P = 0.76$, $N = 79$). We recovered 62% of the 39 plant species in the ≥24 h fecal samples during macroscopic inspection: We identified 19 from fruit parts, but did not find *Hoslundia opposite*, *Marantachloa leucantha*, and *Ficus sur*, *F. cyanthistipula*, and *F. natalensis*. Only leaves of *Aneilema aequinoctilae* and *Ficus asperifolia* were recognizable, and in only three samples. We found *Ficus* spp. in 67% of samples, with fruits of *Mimusops bagshawei* and *Aframomum* spp. again being the most frequently encountered nonfig species in 56% and 25% of samples.

The proportion of fruit to leaf species eaten by the 10 focal individuals varied across the focal samples ($\bar{x} = 53 : 42$; Fig. 1); however, we did not detect leaf consumption in any fecal sample for seven focal individuals ($N = 14$ focal samples). The three samples with identifiable leaf species occurred in the wetter period, with a ratio of 97:3 (%) fruit to leaf species.

Nonplant Foods

Feeding Data Eight of the 10 focal individuals ate nonplant food items over the 48 d. These were 1) internal organs and the carcass of an infant red colobus monkey (*Piliocolobus tephrosceles*); 2) honey plus honeycomb from a raided arboreal hive; 3) honey bee larvae (*Apis mellifera*), determined from collection of discarded honeycomb post-feeding; and 4) soil fragments extracted from exposed tree roots for 71% bouts of geophagy. Both males and females practiced geophagy ($N = 13$ bouts, range: 5–120 s duration), but only males ate the other three food items (Table II). An adult male practiced coprophagy for 2 min, extracting and reingesting *Pseudospondia microcarpa* seeds from feces he had defecated <1 min before. We saw most geophagy events on the first or second day of a focal sample, and two focal individuals ate meat or honey during this period; another two did so on the last day of the 3-d focal sample (Table II).

Macroscopic Inspection We found four nonplant food items across all fecal samples analyzed ($N = 141$): 1) hair and bone fragments of a red colobus monkey; 2) honeycomb; 3) soil fragments; and 4) ant and fig wasp exoskeletons. We found no bee larvae in any samples. We found hair and bone fragments of red colobus monkeys in only three fecal samples from two adult males (Table II). Honeycomb occurred in only two samples and soil fragments in 23 samples (16%). We found arthropod exoskeletal parts of ant heads, or fig wasp abdomen and heads, in 19 samples (13%; ants $N = 4$, fig wasps $N = 15$) but saw neither eaten directly.

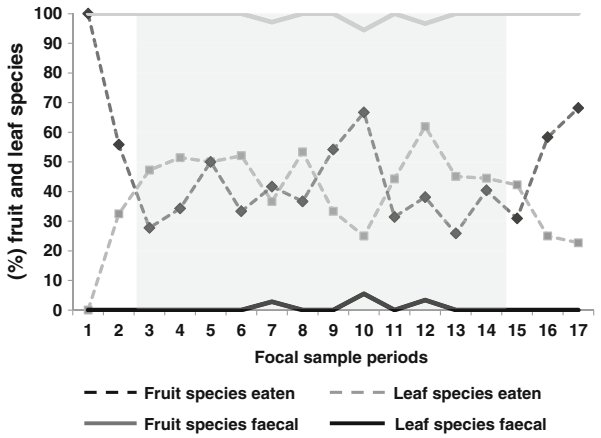

Fig. 1 Leaf and fruit species eaten (%) by 10 adult chimpanzees at Kanyawara, Kibale National Park, Uganda, over 17 focal sample periods (June–December 2008) vs. proportion of leaf and fruit species identified in their fecal samples ($N = 81$). Shaded area denotes focal sample periods during wet season, between two drier periods.

The three samples with hair and bone fragments are included in the ≥24 h fecal sample set. We identified these parts in one fecal sample 16 h after one adult male (PG) had eaten red colobus intestines (with *Aframomum* spp. leaves). We saw no intake of other body parts. A second male (TU) ate parts of a red colobus carcass on the third day of the focal sample. We found both hair and bone fragments in two fecal samples collected 26.5 and 48.5 h before this meat-eating event. TU had hunted red colobus successfully *ca*. 24 and 48 h before analysis of these samples (P. Bertolani, *pers. comm*.), but we did not record body parts consumed by the male.

For chitinous exoskeleton, 14 of the 19 samples were included in the ≥24 h fecal sample set. For samples with fig wasps ($N = 10$), four of the six focal individuals had eaten *Ficus* spp. 15.5–53 h before sample collection. We found soil fragments in 16 fecal samples. Eight of the 10 focal individuals are listed in Table II for geophagy; for three (TG, YG, LR) we did not see them eat soil fragments before sample collection. Others had practiced geophagy, but we did not encounter soil fragments in their fecal samples. Two males, TU and ST, had ingested soil fragments 13–51 h before, and a female (WL) <0.5 h before. For the male and female not listed in Table II, we found soil fragments in their fecal samples, but we saw no geophagy during their respective focal samples. The two samples with honeycomb were also included in the ≥24 h fecal sample set: we saw one male (ST) raid an arboreal bee hive 53 h before fecal collection, but did not see the other male (TU) eat apian body parts during the 31.5 h before fecal collection.

Gut Passage Rates

Although only a small proportion of fecal samples had nonplant foods, their passage rate was easier to calculate owing to their rarity of occurrence. For arboreal nonfig fruit, consumption was 7–57 h before; for two *Ficus* spp. ≤25 to ≤39 h before; and for two THV fruits 12–46.5 h before fecal sample collection (Table III). *Ficus exasperta* leaves had ranges of 19–22 h, and ≤25 h. Finally we estimated a gut passage rate between 18.5 and 32 h for *Urtica massaica*. Estimating the passage rates of parts of these species was difficult; the focal individuals ate some repeatedly in the same hour, throughout the same day, or on consecutive days of the focal sample. They ate parts of 24 plant species repeatedly across 2.3 ± SE 0.1 d per focal sample ($N = 17$ focal samples). For *Aframomum* spp., *Ficus asperifolia*, *Mimusops bagshawei*, *Celtis africana*, and *Lepistemon owariensis* they ate fruit or leaves on two or more days of ≤76% of focal samples. These 24 species are shaded in gray in Table I.

During macroscopic inspection, we encountered species in fecal samples that 1) we did not see the focal individual eat; or 2) the focal individuals did not eat before collection of the sample in which the food item was found, but did eat afterwards during the focal sample. We found these Unobserved, yet Consumed, Identifiable Plant Species (UCIPS) in 75% of fecal samples collected within 24 h of first observing an individual feeding, and in 32% of fecal samples collected *ca*. 24 h afterwards. The median total number of UCIPS in fecal samples collected within the first 24 h was three, which was statistically higher than UCIPS in samples collected after 24 h ($N = 1$) (Mann–Whitney test: $W = 373$, $P < 0.01$, $N = 17$ focal samples). Some of these species were eaten during the focal sample, indicating repeated daily food intake. We did not see the chimpanzees eat all of the plant species identified in their fecal samples during 10 of 19 focal samples

Table III Estimated passage rates of food-items: Observed feeding *versus* macroscopic inspection data for 10 adult chimpanzees at Kanyawara, Kibale National Park, Uganda, June–December 2008

Plant species and authority	Part eaten	Eaten before fecal sample collection (h)	Available cross-validation checks (N)
Arboreal fruit-bearing			
Celtis gomphophylla Baker	Frt (whole)	≤ 27.5	2
Cordia africana Lam.	Frt (whole)	19–47	12
Mimusops bagshawei S. Moore	Frt (whole)	21–23	56
Monodora myristica (Gaertn.) Dunal	Frt (seed, pulp)	23–55	4
Pseudospondias microcarpa Engl.	Frt (whole)	21–53	14
Psycotria mahonii C.H. Wright	Frt (whole)	≤ 23	1
Ficus spp.			
Ficus sansibarica macrosperma Mildbr. and Burret C.C. Berg	Frt (seed, pulp)	≤ 39	1
Ficus exasperata Vahl	Lvs	≤ 25	1
Ficus vallis-choudae Delile	Frt (whole)	≤ 22	1
Shrub or climber			
Dovyalis microcarpa Bamps	Frt (whole)	≤ 20	1
Phytolacca dodecandra L'Hér	Frt (whole)	17.5–26.5	11
Teranna pavettoides	Frt (whole)	23–31	2
Terrestrial herbaceous vegetation			
Aframomum spp.	Frt (seed, pulp)	12–46.5	10
Hoslundia opposita Vahl	Frt (whole)	20–24	3
Lepistemon owariensis (P.Beauv.) Hallier f.	Lvs	19–22	3
Maesa lanceolata Forssk.	Frt (whole)	22–30	4
Toddalia asiatica (L.) Lam	Frt (whole)	21–27	2
Urtica massaica Mildbr	Bl	18.5–32	2

(range: 1–7 UCIPS). We found almost all of these UCIPS in fecal samples collected within the first 24 h of the focal sample period, although 29% occurred in fecal samples ≤50 h later. The exceptions were seeds of *Secamone africana* and *Toddalia asiatica*, which we found in samples defecated 50 h and 26 h later (each by a different individual). We found no significant correlation between the percentage of time subjects were out of view and the number of UCIPS identified in fecal samples over the whole of each focal sample (Spearman rank correlation test: $r_s = -0.15$, $P = 0.56$, $N = 17$) or for samples defecated >24 h after the first feeding bout seen ($r_s = 0.45$, $P = 0.07$, $N = 17$).

Discussion

Plant and animal items we identified during macroscopic inspection of fecal samples did not differ from the observed feeding data collected over the same period in terms of which species we recorded: We observed chimpanzees eating all the species we identified in feces over the 48-d focal sample period. However, these items differed as

to when they appeared in the data set. The higher proportion of UCIPS found in fecal samples on the first day likely reflected the gut passage rate of food items eaten before the onset of the focal sample. The proportion of UCIPS identified, and the number of fecal samples in which they occurred, decreased *ca*. 24 h after first observing any feeding by the 10 focal individuals. Our findings 1) suggest that certain food items we saw them eat had been digested and were present in these later samples; and 2) provide an estimate as to when foods may begin to appear in samples for a wild primate population. Alternatively, UCIPS in these fecal samples may be food items consumed when the chimpanzees were out of view. The lack of a significant correlation between the total number of UCIPS and the total time that subjects were unobservable may be due to 1) small sample size ($N = 19$ focal samples); 2) individual feeding patterns, e.g., food availability to subordinates may differ from that to higher-ranking individuals, leading to variation in which species are found in feces; and 3) the species the chimpanzees ate when they were out of view.

We derived gut passage rates for 18 food items, most of which were fruits. Our data were limited, both for cross-validation checks (observed consumption vs. remains identified in fecal samples) and by having only two species of leaves with which to compare estimated passage rates of eight arboreal and seven terrestrial fruits. The chimpanzees often ate the same nonfig fruit species throughout the day, resulting in the recording of repeated bouts per day. The data were further confounded, as these nonfig fruit species were then identified in consecutive fecal samples collected for each focal individual. Gut-passage rate also varied for a single food type in a single feeding bout. Digestibility, retention time, and the amount eaten of various food types are also factors to consider when estimating gut passage rates of food items eaten by primates (Lambert 2002; Milton and Demment 1988). The high variability of estimates of gut-passage rates from our data prevented precise comparisons of the digestibility of fruits and leaves. Further work is needed to establish gut passage rates for nonfruit species for wild primate populations.

As predicted, identifiable fruit parts dominated our findings from fecal analyses, supporting the hypothesis that frugivory is overestimated from the identification of species from macroscopic inspection. Researchers have depended on the identification of seeds in macroscopic analyses to determine frugivory, seasonality of diet, and seed dispersal by primates (Gross-Camp *et al*. 2009; Poulsen *et al*. 2001). We found fruit seeds in all fecal samples analyzed in our study, similar to the findings of Wrangham *et al*. (1994) for this community at 98.8%; and for other chimpanzee communities at 98.4% for Bwindi Impenetrable National Park, Uganda (Stanford and Nkurunungi 2003); 98.2% for Lopé Reserve, Gabon (Tutin and Fernandez 1993b); and 98.8% for *Ficus* spp., Goualougo Triangle, Republic of Congo (Morgan and Sanz 2006). We found *Mimusops bagshawei* and *Aframomum* spp. most often in fecal samples, and these plant species were eaten over 2 or more consecutive days in ≤76% of focal samples. Wrangham *et al*. (1994) found *Ficus* spp. and *Aframomum* spp. seeds in 90% and 43% of samples ($N = 1128$) compared to 70% and 44% samples ($N = 141$) in our study. Both genera have species that fruit throughout the year (Wrangham *et al*. 1994). Wrangham *et al*. (1991) found *Mimusops bagshawei* in 22% of samples, and occurrence in fecal samples peaked periodically across 4 yr (1987–1991). The high frequency in our study may reflect one of these peaks, as members of this community, including focal individuals, often ate the fruit of this species in September–November 2008.

Some species may have been absent from fecal samples because they were made into wadges and spat out after desired components had been expressed. We still found fruits that the chimpanzees had wadged in fecal samples analyzed during macroscopic inspection. We did not identify pith and leaf parts wadged, but this is more likely due to effects of mastication and digestion than to food-wadging *per se*.

Most (79%) leaf species eaten by the 10 focal individuals across the 48-d focal sampling period were undetected by macroscopic inspection. We found many leaf and pith fragments in fecal samples but could identify leaf species in only <10% of total samples analysed. The Kanyawara community feed on more pith species than the neighboring Ngogo community (Potts *et al*. 2011; Watts *et al.* 2012) and we saw pith consumption on 35 d. However, we did not identify pith species in any of the fecal samples. Similar results were obtained for *Gorilla gorilla gorilla* at Lope Reserve, Gabon, in which ≤97% of leaf and pith species eaten were unidentifiable in fecal samples (Rogers *et al*. 1990; Williamson *et al*. 1990). This long-acknowledged limitation of macroscopic inspection (Tutin and Fernandez 1993b) has led researchers to enlist other measures of the nonfrugivorous component of diet for primates. Some rely on feeding evidence encountered along trails (Doran *et al*. 2002; Rogers *et al*. 1990) or analyses of fecal samples at microscopic and molecular levels (Phillips 2011). At the individual level, our findings highlight that the "loss" of leaf species can be even greater (≥97%) despite a similarity across sites in the number of leaf vs. fruit species eaten per day. Proportions estimated at the individual level offer a more accurate representation for loss of leaf species in feces than those estimated at the group level, i.e. using pooled data from the 10 focal individuals.

Of the nonplant species eaten, we identified all but the soft-bodied bee larvae in fecal samples. This "disappearance" of a nonchitinous invertebrate from the observed dietary repertoire, during analysis of fecal samples, resembles that of other chimpanzee insectivory studies (Basabose 2002; Deblauwe and Janssens 2008; McGrew 1983), all of which inferred that insectivory by apes, most of which were unhabituated, was underestimated. However, the Kanyawara community shows infrequent insectivory, as seen in our results and other studies (Wrangham *et al.* 1991, 1996) when compared with other chimpanzee communities (Bogart and Pruetz 2011; Schöning *et al.* 2007; Tutin and Fernandez 1992). Chitinous exoskeletons found in ≤14% of fecal samples probably resulted from indirect insectivory by ingestion of THV plant parts and figs. Of the soil fragments found in 16% of samples, we validated geophagy by macroscopic inspection for only two males (8% of samples), but we collected most samples on the first day. Also, if the estimated gut passage rate for soil fragments of ≤51 h is correct, this lengthy interval would explain why soil fragments did not show up after observed geophagy. Some samples may have been contaminated by extraneous soil fragments when collected, but this is unlikely, as fragments were present in consecutive collected fecal samples of seven of 10 chimpanzees ($\bar{x} = 3.3$ per focal individual).

Conclusions

Many consumed food items were "lost" using the commonly applied method of macroscopic inspection. Our data corroborate previous speculations about the limitations of this indirect method (Tutin and Fernandez 1993b), in particular, its accuracy in reflecting the folivorous and faunivorous aspect of chimpanzee diet (McGrew *et al.*

1988; Ortmann *et al*. 2006). Studies of faunivory for two chimpanzee communities using fecal analysis have highlighted the challenge of validating direct observation with macroscopic inspection findings (Surbeck *et al*. 2009; Tutin and Fernandez 1993b). Although animal bones, hair, teeth and skin can be detected in primate feces, hunting is normally seasonal, and therefore short studies may underestimate the rate of faunivory detected in feces (chimpanzees: McGrew 1983; bonobos: Hohmann and Fruth 2008). Further, low rates of hunting may prevent cross-validation of this dietary aspect, as we found for this ape community. Their low prevalence of insectivory also prevented the exact rate of underestimation of insect feeding to be validated. However, indirect insect consumption, albeit a small proportion of their diet, was detected by using macroscopic inspection but not from direct observation.

Small sample sizes may affect the total number of species identified in feces (Hohmann and Fruth 2008; Tutin and Fernandez 1993b); however, sample size did not appear to strongly influence results in our study. The median total number of fruit species per sample, as well as the total plant species identified, was similar in the two fecal sample sets. The total plant species identified was *ca*. 20% less in the ≥24 h samples, but we also found fewer leaf species in this smaller fecal sample set. Repetitive exploitation may explain the similar findings. Over the additional 19 d of direct observation (the second or third day of 17 focal samples) <10 further plant species were eaten. Further, most UCIPS found in fecal samples within the first 24 h were then seen to be eaten during the focal sample.

Despite the limitations outlined, findings from macroscopic inspection of fecal samples can expand the range of known dietary constituents in primate populations (various species: Moreno-Black 1978; red howlers: Julliot and Sabatier 1993). Although we did not expand the list of plant species included in the dietary repertoire of the community across the 48-d focal sample period, we did at the individual level with the identification of UCIPS. Macroscopic analysis allows gut passage rates of food items to be estimated, when supplemented by direct observation of feeding, but our estimates for most species presented remain highly variable. A longer-term study involving the observation of individuals and the concurrent collection of fecal samples may determine more precise gut passage rates for more species and reduce confidence intervals in passage rate estimates, especially for plant species that are eaten over multiple days.

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