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Evaluation of faecal analysis as an indirect method for determination of chimpanzee dietary composition

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Abstract

The study used 2,635 chimpanzee (*Pan troglodytes schweinfurthii*) faecal samples and each sample was analysed while wet, and after drying. The two methods used in this analysis were proportional (5%) scores and volume measurement. Results from analyzing dry samples significantly increased the visibility of small and rare food remnant items in chimpanzee faeces. There was no significant difference in the duration in terms of person hours needed to analyse either wet and dry faecal samples, or in using proportional scores and actual volume measurements methods. The analyses of wet and dry faecal samples were positively correlated and so was the use of proportional scores and volume measurement methods. There was a significant difference in results obtained by analysis of wet and dry faecal samples. This difference was also registered between proportional scoring and volume measurement when analysing dry samples, except for seeds with diameter that is more than 5 mm ($t = 0.22$, $p = 0.83$). The difference was, however, significant between results obtained by the two methods while analysing wet samples for seeds of > 5 mm ($t = 3.67$; $P = <0.001$) and fibre ($t = -2.19$; $P = 0.032$) components. Therefore, the differences in the two methods especially in as far as fruit seed is concerned and the fact that chimpanzees are frugivorous implies that the two method should not be mixed or used concurrently in the same study but the proportional scoring method of wet samples provides quick insights and inter-site comparison while using faecal analysis to determine chimpanzee diet.

Key words: *Pan troglodytes Shweinfurthii*, proportional scoring, Uganda, volume measurement

Introduction

The diets of wild chimpanzees (*Pan troglodytes Shweinfurthii*)) have been studied using a variety of methods. These fall into two main categories, namely direct as recorded by direct observations, and indirect as those recorded from characteristic food remains, either left *in situ* or *ex-situ*. Faecal analysis (*ex-situ*) is, most times the most feasible method to study unhabituated or semi habituated primate populations that do not allow close approach of researchers to clearly see food items eaten and also to allow periodic dietary comparisons (Kuroda *et al*., 1996). For unhabituated populations, the otherwise unobtainable dietary information can be obtained from macroscopic inspection of fecal samples (faecal analysis). This method has made a significant contribution to understanding food intake in various primate species and in increasing knowledge of the diet of our closest living relatives, the common chimpanzee (*Pan troglodytes*) and the bonobo (*P. paniscus*) (Phillips and Mcgrew, 2013). Secondly, faecal analysis is the most feasible way of documenting diet composition in the dense African tropical forests, where systematic observation is difficult. Whereas direct observations are often assumed to provide the most comprehensive reflection of diet, wild primates in such habitats are logistically challenging to observe, hence it is most useful to combine both observation and faecal analysis for accurate monitoring of dietary trends (Matthews *et al*., 2020).

Faecal analysis as a technique has proven useful in constructing lists of fruit foods, as many seeds are swallowed whole, pass through the alimentary canal undigested and can be identified to species level (McGrew *et al*., 1979; Kano and Mulavwa, 1984; Williamson *et al*., 1990; Tutin and Fernandez, 1993). It is also important in documenting the frequency of insect eating (Uehara, 1984; Tutin and Fernandez, 1993). In theory, faecal material can be considered a proxy for diet intake integrated over a certain period of time (Matsuda *et al.*, 2018). For the physical macroscopic faecal content quantification, however, there is lack of standardisation of faecal analysis method because quantification has been done by analysing wet samples and /or dry faecal samples (Kuroda *et al*., 1996). Percent faecal constituents have been typically estimated by qualitative scores and not empirically measured. A more refined method developed by Malenky and Wrangham (1992) dealt with indigestible green leaf fragment component of faecal samples. Improved scope and accurate quantification of faecal remains is important for standardising of faecal analysis methodology. The objective of this study, therefore, was to compare volume measurement and proportional scoring of either wet or dry faecal samples as proxy faecal analytical methods for estimating chimpanzee diets, and whether these two methods present any differences in results within their domiciles.

Methods

Study site and faecal sample management

Freshly deposited chimpanzee faecal samples were collected from Kalinzu Forest Reserve, South Western Uganda, while following chimpanzee during habituation for two years. Kalinzu Forest Reserve lies in south-western Uganda (0017'S, 30007'E). It is 137 Km^2 and covers an exceptional altitudinal range, which combined with its topographical, climatic and geological diversity, and its location in western albertine rift valley close to the upper Pleistocene forest refugia, gives rise to a medium altitude moist evergreen tropical forest habitat with high biodiversity. Kalinzu forest is inhabited by approximately 230 chimpanzees at a density of 1.55 Km^{-2}; ranking third after Kibale at 2.32 Km^{-2} and Bugoma at 1.9 Km^{-2} (Plumptre *et al*., 2003).

Chimpanzees were followed from dawn to dusk during which fresh chimpanzee faecal samples were collected in a bid to determine the dietary components. The faeces that scattered on the ground or among branches were ignored due to the difficulty in picking a representative sample of such. At collection, the date, location, and time of collection, and the visible contents of the faecal sample by majority constituent were noted. After a day's collection, the faecal samples were preserved in plastic bags with 100% ethanol. From the entire collection, a total of 2,635 faecal samples were processed. These were collected over a period of 24 months. The number of faecal samples collected per day varied from 24 to 206 with an average of 101 faecal samples collected daily.

At the end of each month, the faecal samples were individually placed in a metal sieve with 1 mm x 1 mm mesh and washed in running water. Once the soluble solution had gone, faecal remnant sorting was carried out. This sorting included separating out the different food remains and determining the percentage occurrence of each category in each sample. In each faecal sample, the constituents were sorted and separated into fruit seed and pulp, fiber, pith, mammalian remains, insect remains, whole leaf, and soil/stone. Non-fruit foods were represented in faeces as undigested fragments. The fruit category was represented by seed remnants, which were used to identify species names, by relating the seed to the fruit and the plant species that bore the fruit in the forest and confirming the plant species name with the Makerere herbarium; except where more than one species in the same genus had indistinguishable seeds, as was the case for *Ficus* spp. Indistinguishable seeds in this genus were treated as a single fruit "species group". We evaluated faecal content by the proportional scores and then by volume of each food category when faecal samples were wet. The samples were then sun dried, re-divided into the same categories of seed, skin and pulp of fruit, leaf matter, pith, insect, and mammal and re-evaluated.

Time taken from the start of sorting to the completion of the measurement of the different faecal content categories without any interruption or stopping was recorded for each sample. Number of samples processed in a day (9.00 am. to 6.00 pm.) taking off only an hour for lunch were also recorded in each method and man hours required for each samples recorded. This was done by dividing the number of minutes by the number of samples processed to completion. Where interruptions occurred, such samples were not considered in data analysis for this parameter. The sorting of the faecal samples was done once every month during the last week of every month.

Faecal content analysis

Faecal content analysis involved determining the percentage of each faecal content category in each sample after processing, and the results therefrom generated by two methods as follows:

(i) Proportional scoring method

Proportional scores were done by estimating the percentage occurrence of each faecal constituent in a series of 5% additions. This means that the least faecal constituent was 5% and the most was 100%. Those that were below 5% were recorded as present, but not included in the analysis. In each faecal sample, dry and wet, the faecal constituents that remained visible and identifiable were sorted and separated into fruit seed and pulp, fiber, pith, mammalian remains, insect remains, whole leaf, and soil/stone. The fruit seed/pulp faecal remains were sorted according to plant species identified.

Seeds were used to identify species names, by relating seed to the plant that bore the fruit with such a seed in the forest; and the process was confirmed with the Makerere University herbarium, when not sure. The seeds category was divided into two categories of $\leq$ and $\geq$ 5 mm in diameter because large seeds were not easily measured with the cylinder using the volumetric method. Whole large ($\geq$ 5 mm in diameter) and small seeds ($\leq$5 mm diameter) abundance were estimated by percent occurrence per faecal sample. Non-fruit foods (i.e. fiber, pith, insect, mammalian remains and whole leaf) were represented in faeces as undigested fragments. Occurrence of insects and avian remains was by observation from the undigested chitinous body parts - heads, legs, and feathers (not to species level, but to those broad categories). Mammalian remains found in faecal samples included bones (small, intact or fragments), skin, teeth, hair, claws and ligaments. This identification was to help put the different food faecal remains into the different categories of seed (2 sizes), fibre, and animal remains and then score them either by proportional scores, or measure their volumes as described below.

(ii) The volume method

After using the proportional scoring method, the volume of faecal constituents of seed and fiber of each faecal sample was also measured using a measuring cylinder. The volume of seeds >5 mm in diameter was measured by the water displacement method. The volume of different individual seeds of the same species was determined and the average obtained to determine the volume of that particular seed species and multiplied by the number of seeds in the sample. Since Chimpanzees are mostly frugivorous, seed was predominant and varied, and this is why the seed category was divided into large and small to determine their estimation in diet by the two methods. Secondly, when poured into the measuring cylinder, big seeds would leave spaces in between themselves hence presenting difficulty to measure volume in this way. It was thus observed that evaluating combined large and small seeds by volume was not practical. With seed separated into the two sizes, the volume of the different faecal constituents in each sample was measured and the percentage occurrence of each constituent calculated.

Both methods of proportional scoring and volume measurement were used to analyse the wet and dry faecal samples to evaluate differences in results obtained and the duration of application in determination of diet in chimpanzees. The following were evaluated:

(i) the differences in time taken to process wet compared to dry faecal samples using proportional scoring and volume measurement methods;
(ii) the differences in percent occurrence of faecal contents as per scores and volume in each sample;
(iii) the differences in visibility of rare and small faecal remnants (small seed, chitin) ; and
(iv) the differences in percentage occurrence of each seed species' sizes (<5 mm, >5mm).

Statistical analysis

Frequencies and presence of different fruit species and other food items in faecal samples and conversion of volumes faecal constituents to percentages were assessed using descriptive statistics. Proportional scores and volume of the different food categories were calculated per sample and means calculated for all the samples processed per month. To examine the relationship between wet and dry faecal samples' comparisons, Spearman's correlation coefficient was used. The student t-test was used to test the following:

(i) whether there was a significant difference between results obtained by using proportional scoring and volume measurement of wet and dry faecal samples; and
(ii) whether there was a significant difference between results obtained by proportional scoring and volume measurement of wet and dry faecal constituents in wet samples.

Results

Time taken to analyse faecal samples by the two methods

Volumetric method

Faecal analysis of wet samples using volume measurement method needed a much longer period than dry samples. A maximum of 15 samples was washed at a time to make sure samples would not dry before the analysis. Fifteen samples needed 8.5 person hours, each sample taking 34 minutes to complete sorting into the different categories and measuring them.

When analysing dry samples, sorting the different seeds and other faecal remains was faster than when sorting wet faecal samples. Thirty five samples were completed in 8.5 hours, each sample, requiring 21.4 minutes. The sorting took this long, especially where two or more seeds with less than 5 mm diameter occurred. This occurred when both seeds of *Musanga* and *Ficus* genera were present together in a given faecal sample which was mostly the case.

Proportional scoring method

In the proportional scoring method, each faecal sample was analysed to completion in 23.2 minutes when wet and 14.7 minutes when dry, including the four hours required for the drying process. The difference in duration between wet and dry sample analysis was significant for this method ($t = 5.296$, $P = 0.119$).

Comparing the two methods, proportional scoring method required less time for data processing than volume measurement. The timing measurement in this case was standardised to 3 faecal constituents of fruit seed, fiber, and one other faecal remain such as insect or mammalian body parts. This difference in duration between proportional scoring and volume measurement was, however, not significant both for wet samples ($t = 4.459$, $P = 0.140$) and dry samples ($t = 4.397$, $P = 0.142$) at 95% probability including the time of drying for the dry samples.

Comparison of results from analyzing wet and dry faecal samples

Visibility of occurrence of different faecal constituents

There was a difference in visibility of occurrence of small seeds in the wet and dry faecal samples. Visibility increased slightly with dry samples especially in samples where seeds less than 5 mm in diameter occurred in very small quantities (Fig. 1). In other fruit seeds, visibility was the same in both dry and wet samples. Ease of finding/ sorting/location of faecal remains in non-fruit seeds constituents was better for fiber, whose categorisation increased in amounts by 4.5%, pith by 2.6% and insect chitinous remains by only 2.6%. Mammalian remains were more visible in wet samples than in dry ones (Fig. 1). Ease of visible identification decreased in the mammalian remains constituent by 0.6% in the dry faecal samples. However, visible location and identification stayed the same in seeds beyond 5 mm in diameter. Generally, there

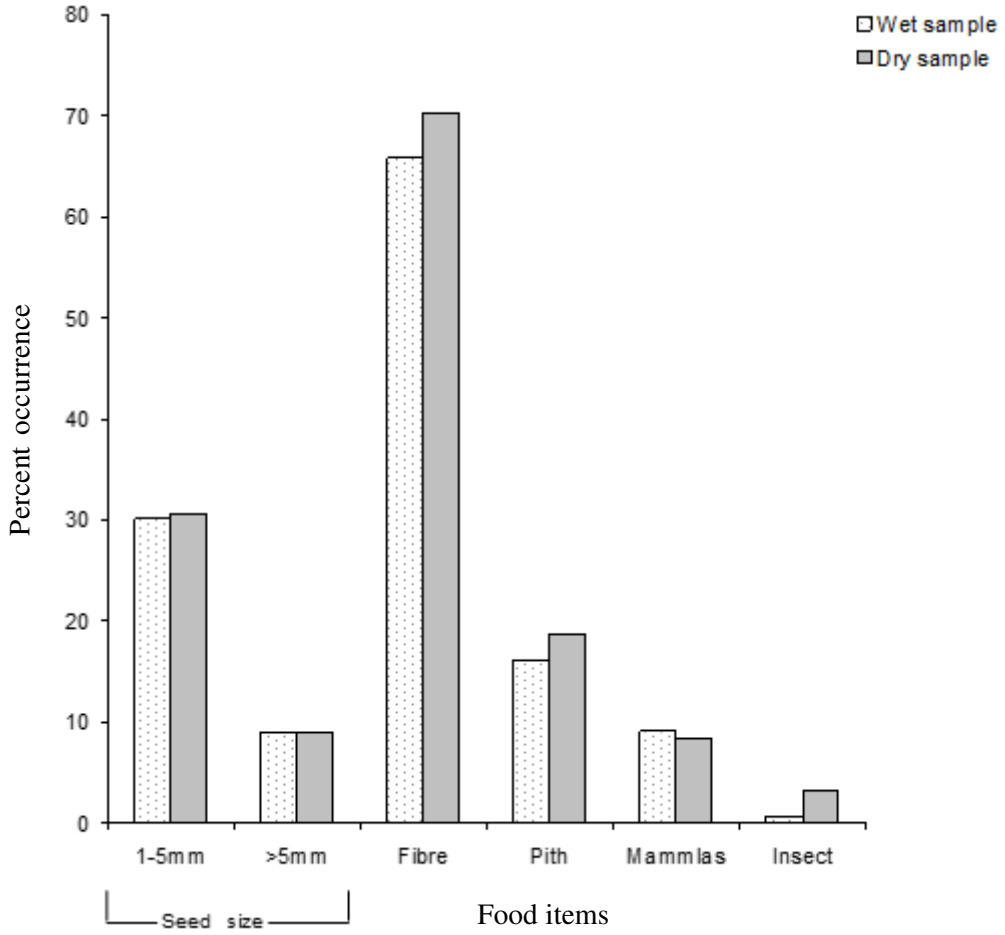

Figure 1. Food items in faecal samples of chimpanzee in Kalinzu Forest Reserve in Uganda.

was increase in visibility of occurrence of dry faecal sample remains but not for mammalian remains (Fig. 1).

Proportional scoring method

There was an increase in the mean percent scores obtained from processing the dry samples into different food categories, except for mammals. This increase was noted in seeds with less than 5 mm diameter, while all seeds with diameter more than 5 mm showed no change. There was also an increase in amounts of categories in other faecal constituents. Fiber and insect remains showed a remarkable percent increase of 4.3 and 3.9%, respectively (Fig. 2).

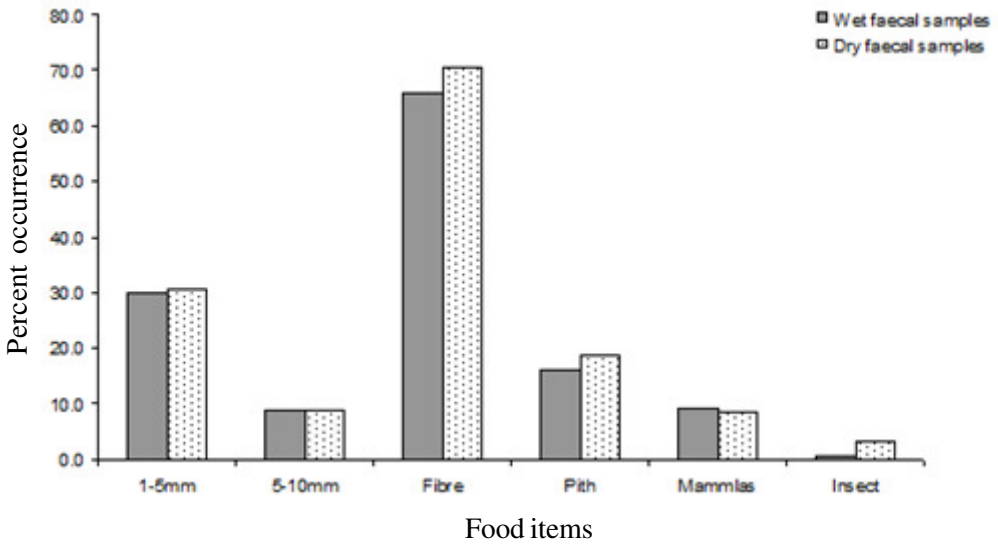

Figure 2. Occurrence of food items in wet and dry faecal samples of chimpanzees of Kalinzu Forest Reserve in Uganda.

The results obtained by analysis of wet faecal samples using proportional scoring method was positively correlated to results obtained by analysis of dry samples (Table 1), but the correlation was more positive in fruit seed than fiber. Analysis of faecal matter remnants of insect chitin and mammalian fragments were, however, not considered in this comparison. There was significant difference between results yielded by the analysis of wet and dried samples using proportional scoring. This difference was especially registered in results from analysing seed with diameter less than 5 mm, but no significant difference occurred in results yielded by analysis of fruit seed with diameter of more than 5 mm. However, when the two fruit seed size categories were combined as one, there was a significant difference in results. The significant difference also occurred in results from fiber analysis. Therefore, there was an overall significant difference in results obtained by the analysis of wet and dry faecal samples using the proportional scoring method.

Table 1. Wet chimpanzee faecal sample analysis compared to dry sample analysis results using proportional scoring and volume measurement

Food item	N	Correlation	Mean	SD	SE	t	P-value
Proportional scoring of wet samples versus dry samples							
Seeds<5 mm diameter	187	0.839	5.48	19.08	1.4	3.928	<0.000
Seeds>5 mm diameter	71	0.965	0.39	5.1	0.61	0.651	0.517
All seed	258	0.859	4.08	16.61	1.03	3.947	<0.000
Fibre	88	0.67	-8.18	23.72	2.53	-3.24	0.002
Volume measurement of wet samples versus dry samples							
Seeds<5 mm diameter	205	0.809	9.011	22.45	1.57	5.747	<0.000
Seeds>5 mm diameter	77	0.881	-5.25	10.79	1.23	-4.27	<0.000
All seed	258	0.859	5.117	20.93	1.25	4.106	<0.000
Fibre	93	0.652	-16.51	25.81	2.68	-6.17	<0.000

Volume measurement method

The volume of seed faecal constituents that was less than 5 mm was higher in the dry samples than those obtained by processing wet samples (Fig. 3). Seeds with diameters more than 5 mm registered no difference in volume after processing the dry and wet faecal samples. Fiber content volume value was higher by 6.3% in the dry faecal samples than in the wet ones (Fig. 3). Pith, mammalian and insect faecal constituents were not included in this comparison because of the difficulty in the measurement of their volumes.

The results from analyses of the two categories of samples (wet and dry) were positively correlated in all faecal constituents. Results also showed a significant difference between results obtained by analysing wet and dry faecal sample constituents by the volume measurement method both for all fruit seed of all sizes ($t = 4.106$; $p < 0.001$) and fiber (Table 1).

Proportional Scoring versus Volume Measurement methods

There was a general percentage difference in results obtained by using Proportional Scores and Volume measurement in wet faecal samples (Fig. 4.). Volume measurement results were lower in percent occurrence of seed than those of proportional scoring. The wet samples presented a big decrease (6.8%) from proportional scored results for seeds more than 5 mm diameter. A decrease of 3.6% was observed in seeds with less than 5 mm diameter in the wet samples using both

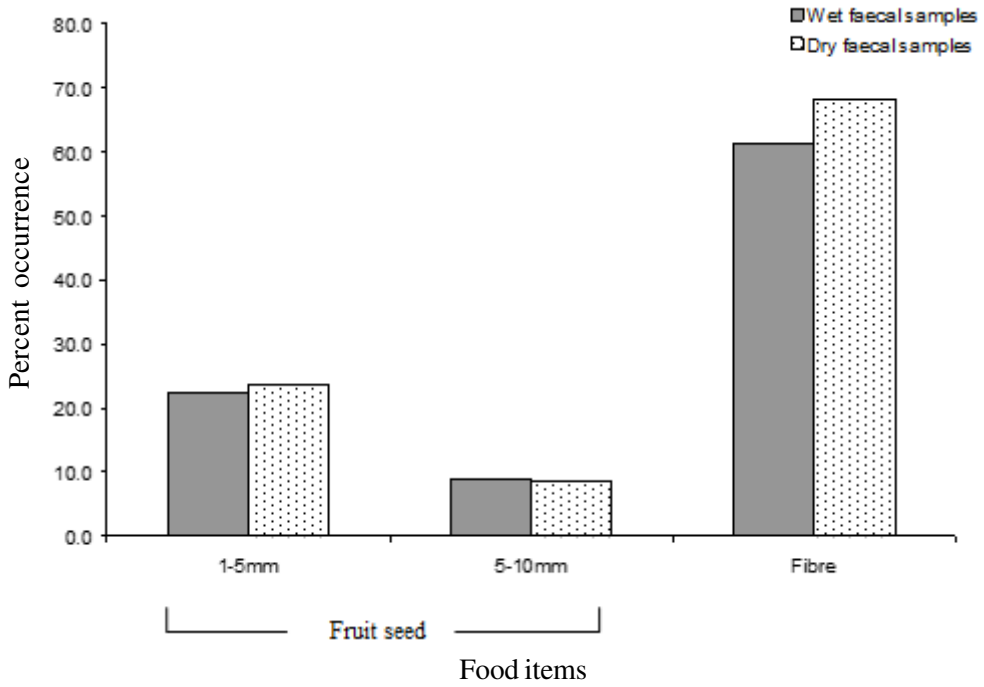

Figure 3. Volume of different fruit seed sizes and fiber in wet and dry faecal samples of chimpanzees of Kalinzu Forest Reserve in Uganda.

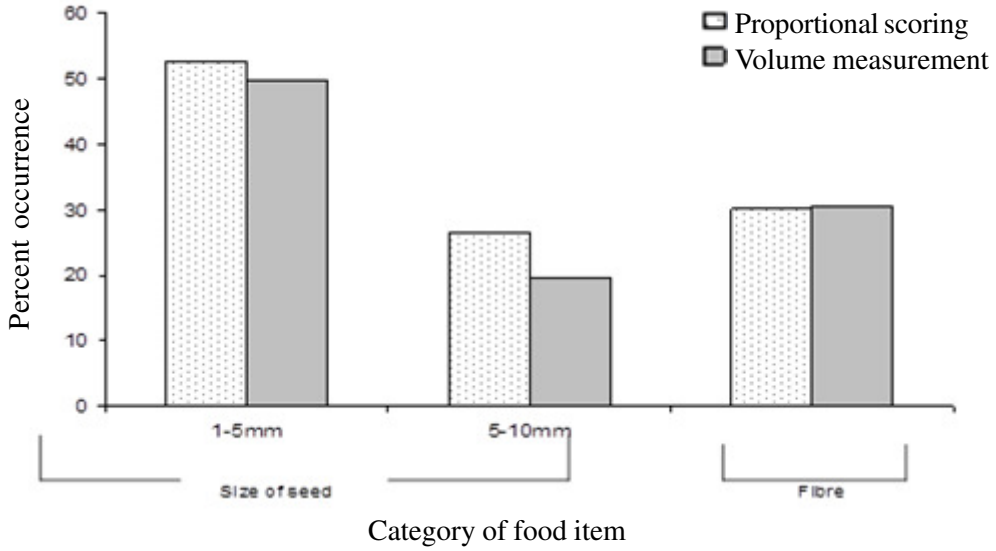

Figure 4. Occurrence of seed and fiber in analysing wet faecal samples using proportional scoring and volume measurement.

methods; while the fiber category showed a 0.5% percentage increase in wet samples between the two methods (Fig. 4).

In the dry sample analysis, a decrease was also observed in the seed category results obtained by analyzing faecal samples using the volume measurement method. Fiber presented an increase of 9.6% in dry samples over wet samples. A 2% decrease from proportional scored results to measured results was recorded in seeds with more than 5 mm diameter and a decrease of 4.5% was observed in seeds with less than 5 mm diameter (Fig. 5).

In analysing dry faecal samples, the results obtained by the two methods were significantly different in the faecal constituent of all seed and fiber (Table 2). When all seed sizes were combined, the difference in results between the two methods remained significant (Table 2). In wet sample analysis, the two methods produced significantly different results in the fiber and all seed categories, but not in seed category of ≥ 5 mm (Table 2). Where significant difference occured, it was mainly brought about by seeds of smaller diameter and fiber.

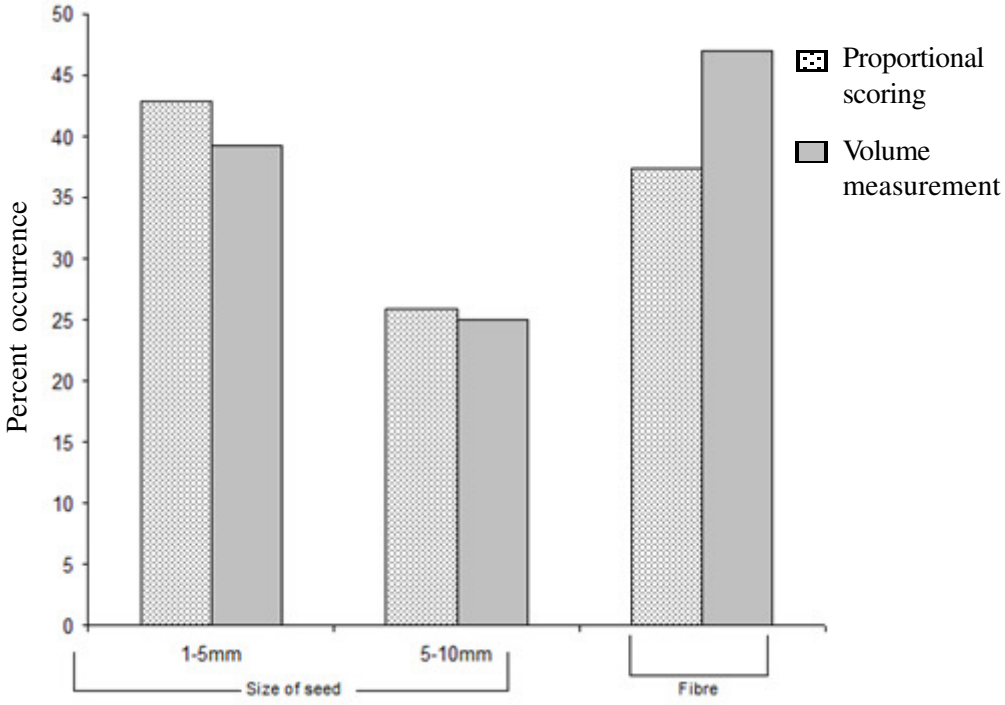

Figure 5. Occurrence of seed and fibre in analyzing dry chimpanzee faecal samples from Kalinzu Forest Reserve using Proportional Scoring and Volume Measurement.

Table 2. Proportional scoring versus volume measured results in dry and wet faecal samples

Food item	N	Correlation	Mean	SD	SE	t	P-value
Proportional scoring versus volume measured results in dry faecal samples							
Seeds<5 mm diameter	203	0.912	3.565	12.94	0.91	3.926	0
Seeds>5 mm diameter	72	0.791	0.344	13.58	1.6	0.215	0.83
All seed	275	0.897	2.722	13.16	0.79	3.43	0.001
Fibre	92	0.861	-10.11	13.94	1.45	-6.96	0
Proportional scoring versus volume measured results in wet faecal samples							
Seeds<5 mm diameter	191	0.941	-1.347	12.67	0.92	-1.47	0.144
Seeds>5 mm diameter	72	0.723	5.713	13.21	1.56	3.669	0
All seed	263	0.928	0.586	13.18	0.81	0.721	0.472
Fibre	90	0.98	-1.548	6.723	0.71	-2.19	0.032

Discussion

The proportional scoring method produced higher fiber component values in the dry samples than in wet samples. Fiber, while wet, is held together by water molecules and appears little in amount when wet than when dry (Matthews *et al.*, 2020). In comparison, results from volume measurement method yielded a higher volume in all fruits' seeds less than 5 mm in diameter and the fiber component. Again, the increase in dry sample volume was as a result of disentanglement of food items from each other, the disentanglement superseded the increment brought about by volume of water for the wet samples. However, the fiber component in both dry and wet faecal samples needs to be compared with the direct consumption of leaf for final conclusion on accuracy of result. The drawback in dry sample analysis may be the additional time involved in drying that increases the mean duration for analyzing one sample hence ending up with no significant difference between the time needed to analyse a single sample using the two methods ($P = 0.147$). The difference was also not recorded for the wet samples because it took a lot of time sorting the entangled wet items since whether it is by scoring or measurement, the categories had to be first sorted.

Studies on wild apes' diet have been done using faecal analysis. Some studies have relied on wet faecal sample analysis (Tashiro *et al*., 1999; Hashimoto *et al*., 2000) while others relied on dry sample analysis (Williamson *et al*., 1990; Wrangham *et al*., 1996; Tweheyo and Obua, 2001). In one study, an attempt was made to measure weight of faecal contents and only measured green leaf fragments (Wrangham *et al*.,

1992). In all the other studies, estimation of faecal contents was by scoring method, referred to in this study as proportional scoring method.

The analysis of wet and dry faecal samples was compared using the results obtained by the analysis using the Proportional Scores and Volume Measurement methods. Based on processing of the wet and dry samples using proportional scores, results of 3 out of the 4 processed faecal content categories were significantly different. However, based on processing of the wet and dry samples using the volumetric method, results of all faecal categories were significantly different. This implies that processing of wet samples will always provide significantly different results from those obtained by processing dry samples no matter the method. In comparison of the use of proportional scoring and volumetric method, results of 2 out of the 4 analysed faecal content categories had significantly different results after processing wet samples but after processing dry sample results of 3 out 4 faecal content categories were statistically significant. This implies that while processing dry samples, the two methods will always present more significantly different results than dealing with wet samples. There is a 50% chance of producing significantly different results when processing wet samples. Therefore, mixing of methods is less risky when processing wet faecal samples than dry samples. This indicates that, proportional scoring can be used in processing faecal samples when wet especially for frugivorous chimpanzees where seed and fibre are the main remnants as analysed in this study. Most fruit leaves recognisable remains, particularly seed (Tashiro *et al*., 1991).

Processing faecal samples immediately after washing them saves time needed for drying. However, the processor would still have to dry the samples in case of need of identification of un-identifiable content remains. Wet samples processing has an advantage of a possibility of daily analysis if the researcher does not want to preserve the faecal samples and avoid any negative implications of keeping the faecal samples in alcohol for long periods.

The difference in visibility of occurrence of food items, especially fruit seeds less than 5 mm in diameter and insect remains indicate a preference for analysing dry to wet faecal samples. Time component for waiting for faecal samples to dry notwithstanding, dry faecal sample analysis provides more visibility and better sorting of the small contents eaten by chimpanzees. These small items easily get entangled in small fruit seed, pith and fiber in wet samples. When samples were dried, each food item easily separated from another and became easily seen. Although the difference in visibility was only significant for rare seeds less than 5 mm in diameter, as a result of the registered difference, one would rather analyze dry samples not to miss the infrequent, small and fragile food remains in chimpanzee diet. There is, however, a disadvantage

of fiber exaggeration when processing dry faecal samples, because it tends to swell up and seem much higher in content (Goné and Wittig, 2019; Matthews *et al.*, 2020).

There was a significant difference in results obtained by proportional scoring and volume measurement of faecal constituents in analysing wet faecal samples, except for seeds with diameter of more than 5 mm. Similarly, a significant difference was observed between the two methods when analysing dry faecal samples' analysis, except for seeds with diameter that is more than 5 mm. Since results of fruit seed and fibre showed significant differences, it implies that fruit seed and fibre would play a big role in the determinant of which of the two methods to use. As indicated above, faecal contents would either be scored in wet samples for quick analysis or volumetrically measured or scored in dry samples for better accuracy. This is more so because chimpanzees are mainly frugivorous, eating manly fruit that ends up as seed and fibre in faecal contents. In Kanyawara (Kibale), for instance, fruit constituted 79% of chimpanzee diet (Wrangham *et al*., 1996), in Budongo it constituted 64.5% (Newton – Fisher, 1999); while in Gombe, it was 63% (Wrangham, 1997).

Since we are dealing with chimpanzees that are majorly frugivorous, the bias towards fruit food is likely in a food list constructed uniquely from faecal analysis. In no case was there found chewed fruit seed. Therefore, all fruit seeds pass through the chimpanzee digestive system, thus decreasing the bias further. Even when some fruit seed is missed in faecal analysis, it may not mean that the bias exists, suggesting that the missed fruit foods are likely to be eaten infrequently or in very small amounts. Such fruits may rarely be important in sustaining chimpanzees' diet. Therefore, for studies in frugivory, proportional scores or volume measurement produces similar results. Any of the two methods can be employed to come up with the same result. However, when analysing the wet samples, the two methods would present significantly different results, especially for fruit (seed) and leaf/pith (fibre). The amount of time the researcher has for the study, not withstanding, it is hence advisable to use the volume measurement method for more accuracy.

Conclusion

Much can be learned from faecal analysis in both wet and dry samples using the two methods especially for frugivorous large bodied primates. In the wet samples we recognise the possibility of missing the small animal matter fragments; while in the dry samples, there might occur an exaggeration of fibre contents but even in direct observation of feeding habits, some small and/or quickly taken-in food items may be missed due to dense vegetation particularly when chimpanzees are foraging at ground level. There is also no doubt that faecal analysis is an invaluable tool in studying the diet of apes in the tropical forests of Africa where visibility is limited, particularly at

ground level, and where fruit figures prominently in their diets. The scores derived from wet faecal analysis although not as accurate as analyzing the dry samples may be essential in quick seasonal, inter- annual and inter-specific differences in the ratio of fruit to vegetative foods in the diet to be quantified.

Accuracy and detailed chimpanzee diet determination from faecal analysis improves with volume measurement of dry faecal samples; especially for frugivorous species and this therefore, asserts an already valuable tool but more perfect in its use, and goes a long way in helping the users of the method. It is hence not advisable to mix the methods by for example analyzing the wet and later the dry samples nor to score and later measure volumes; but where possible the faecal analysis can be combined with direct observation to improve accuracy.

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