



Applying Wet Sieving Fecal Particle Size Measurement to Frugivores: A Case Study of the Eastern Chimpanzee (*Pan Troglodytes Schweinfurthii*)

Citation

Weary, Taylor E., Richard W. Wrangham, and Marcus Clauss. 2017. Applying Wet Sieving Fecal Particle Size Measurement to Frugivores: A Case Study of the Eastern Chimpanzee (*Pan Troglodytes Schweinfurthii*). *American Journal of Physical Anthropology* 163, no. 3: 510-518.

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1 **Applying wet sieving fecal particle size measurement to**
2 **frugivores: a case study of the Eastern chimpanzee (*Pan***
3 ***trogodytes schweinfurthii*)**
4
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11
12 Number of pages: 25
13
14 Number of figures: 2
15
16 Number of tables: 6
17
18 Abbreviated title: Chimpanzee diet and fecal particle size
19
20 Key words: nutritional ecology, digestive physiology, frugivory, fallback foods,
21 mastication
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31 Grant sponsorship: Herchel Smith-Harvard Undergraduate Science Research
32 Fellowship

ABSTRACT

33
34 **Objectives:** Fecal particle size (FPS) as quantified by wet sieving analysis is a
35 measure of chewing efficiency relevant for the understanding of physiological
36 adaptations and constraints in herbivores. FPS has not been investigated
37 systematically in frugivores, and important methodological problems remain. In
38 particular, food items that are not chewed may skew estimates of FPS. We
39 address such methodological issues and also assess the influence of diet type and
40 age on FPS in wild chimpanzees.

41 **Materials and Methods:** 130 fecal samples of 38 individual chimpanzees (aged
42 from 1.3 to ~55 years) from the Kanyawara community of Kibale National Park
43 (Uganda) were collected during three fruit seasons and analysed using
44 standardized wet sieves (pores from 16 mm to 0.025 mm). The effects of using
45 different sieve series and excluding large seeds were investigated. We also
46 assessed the relationship between FPS and sex, age and fruit season.

47 **Results:** The treatment of seeds during the sieving process had a large influence
48 on the results. FPS was not influenced by chimpanzee sex or age, but was smaller
49 during a fig season (0.88 ± 0.31 mm) than during two drupe-fruit seasons (1.68
50 ± 0.37 mm) (0.025-4 mm sieves, excluding seeds).

51 **Discussion:** The absence of an age effect on FPS suggests that dental senescence
52 might be less critical in chimpanzees, or in frugivores in general, than in
53 folivorous herbivores. To increase the value of FPS studies for understanding
54 frugivore and hominoid dietary evolution we propose modifications to prior
55 herbivore protocols.

56 Chewing efficiency is a critical variable influencing energy acquisition
57 from food in herbivores, because the size of a particle influences the speed at
58 which it can be digested or fermented (Dehority and Johnson, 1961; Bjorndal et
59 al., 1990). This effect is explained by smaller particles having a larger surface-to-
60 volume ratio, therefore offering enzymes or microbes a larger attack area for their
61 digestive action. Strictly speaking, chewing efficiency (or chewing effectiveness)
62 is the rate at which a defined amount of a defined food is reduced to a certain
63 mean particle size, and this rate is influenced by factors like oral anatomy, dental
64 design and wear stage, number, direction and intensity of chewing movements as
65 well as the force applied during chewing (Pérez-Barbería and Gordon, 1998).
66 Because this number of factors can only be observed under very controlled
67 experimental settings, a convenient proxy for chewing efficiency is the particle
68 size of the digesta, measured as fecal particle size (FPS). In terrestrial mammalian
69 herbivores, chewing is the main determinant of digesta particle size, with
70 comparatively little change due to gastrointestinal digestion (Poppi et al., 1980;
71 McLeod and Minson, 1988; Spalinger and Robbins, 1992). Therefore, fecal
72 particle size has been used repeatedly as a proxy for ingesta particle size
73 reduction, mainly in non-primate herbivores (Fritz et al., 2009; Steuer et al., 2010;
74 Clauss et al., 2015) and to some extent in primates (Dunbar and Bose, 1991;
75 Matsuda et al., 2014; Venkataraman et al., 2014). With the exception of a study
76 on geladas (*Theropithecus gelada*) (Venkataraman et al., 2014), however, the
77 cited investigations were mainly focused on comparisons among species, and
78 rarely investigated causes of variation within a species.

79 Here we consider the value of investigating fecal particle size for
80 assessing chewing efficiency in the Eastern chimpanzee (*Pan troglodytes*
81 *schweinfurthii*), a frugivorous primate. Our study population was the Kanyawara
82 community in Kibale National Park, Uganda. Ripe fruits dominate the Kanyawara
83 chimpanzee diet (yearly average of feeding time spent eating ripe fruits = 65-
84 75%, varying across months from ~ 35% to 95%). Ripe fruits are complemented
85 principally by pith and young leaves, which together average about 25% of
86 feeding time, ranging from ~ 20-45% (Wrangham et al., 1998; Potts et al., 2011).
87 The fact that FPS measurement is non-invasive makes it especially useful for
88 studying the chimpanzee, an endangered species for which most wild populations
89 remain unhabituated (Phillips & McGrew, 2014).

90 Two hypotheses guided our approach. First, we expected tooth wear, and
91 hence chewing efficiency, to be related to age. An age effect was previously
92 demonstrated in geladas (*Theropithecus gelada*), a graminivore specialized in
93 eating tough diets of grass or sedge leaves: in the dry season, old geladas
94 produced larger fecal particles than younger individuals (Venkataraman, et al.,
95 2014). This suggests that chewing efficiency was reduced in old gelada,
96 presumably due to molar wear. In contrast, Edward's sifakas (*Propithecus*
97 *edwardsi*) (King, et al., 2005) and mountain gorillas (*Gorilla beringei beringei*)
98 (Glowacka, et al., 2016) maintain their molar morphology related to shearing
99 function despite increased age-related occlusal wear. However whether FPS
100 increases in old individuals of these species is unknown. We hypothesized that
101 chimpanzee FPS would increase with age, particularly in past-prime individuals.

102 Second, again prompted by findings in geladas (Venkataraman, et al.,
103 2014), we tested the hypothesis that fecal particle size would rise during a season
104 of reduced availability of preferred ripe fruits, because we expected preferred diet
105 items to have structural properties that would be advantageous for digestion (i.e.,
106 properties that lead to smaller particles at similar chewing investment compared
107 to less-preferred diet items).

108 In contrast to most previous studies on fecal particle size in herbivorous
109 mammals, we anticipated methodological complications due to the inclusion of
110 large seeds from fruits in the feces of chimpanzees. Seeds of ripe fruits are often
111 swallowed unchewed (Wrangham et al., 1994). Therefore, they will be retrieved
112 in sieve analysis of feces and skew the resulting measurement of FPS upwards.
113 Additionally, chimpanzees sometimes egest large plant particles, including
114 complete leaves that function in self-medication by being swallowed unchewed
115 (Wrangham, 1995). Such material would similarly affect fecal particle size
116 measurements. Finally, previous studies have used a range of sieve pore-sizes
117 (Fritz et al., 2009; Matsuda et al., 2014). Whereas variation in the number of
118 sieves within a sieve column (i.e., the 'middle' sieves) has little effect on the
119 resulting fecal particle size measurement (Fritz et al., 2012), expanding the sieve
120 column at either end (i.e., adding sieves with smaller or larger pores) can strongly
121 influence the calculated mean particle size.

122 In order to explore these effects we included the most comprehensive set
123 of sieves, and the largest number of intra-specific samples, used in primate studies

124 so far, and compared fecal particle size measurements calculated based on
125 different sieve series and exclusion protocols.

126

127 **METHODS**

128 **Field site**

129 The Kanyawara community of wild chimpanzees (*Pan troglodytes*
130 *schweinfurthii*) has been studied continuously by the Kibale Chimpanzee Project
131 (KCP) since 1987. Their home range consists of about 37.8 km² of forest (Wilson
132 et al., 2001) in Kibale National Park (0° 34' N, 30° 21' E) in western Uganda.
133 The habitat is mainly evergreen forest transitional between lowland and montane
134 rainforest, interspersed with secondary forest, grassland, and swamp, at an
135 average elevation of ~1,500 meters above sea level (Chapman and Wrangham,
136 1993). Trained Ugandan field assistants conduct all-day behavioral observations
137 of the chimpanzees. During the study period, individuals were well habituated and
138 individual identification was reliable. The Kanyawara community has never been
139 provisioned. In 2015 it included ~ 55 individuals.

140 [Table 1 here]

141 Over a total of six weeks during the months of January, July and early
142 August 2015, we collected 130 fecal samples opportunistically from 38
143 chimpanzees aged 1.3 to ~55 years old. Age categories are shown in Table 1.
144 Ages of the chimpanzees were known to within less than a week for most
145 individuals younger than 25 years of age, and estimated to within five years for
146 those older than 25 years.

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[Table 2 here]

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The three sample collection months corresponded approximately to three fruit 'seasons' in each of which the chimpanzees' diet was dominated by a different species of ripe fruit (Table 2). Figs (*Ficus natalensis*) were the most frequently eaten fruit species in January (50% feeding time), and drupe fruits were the main fruit types in the second and third seasons (77% feeding time on *Pseudospondias microcarpa*, and 73% feeding time on *Linociera johnsonii*, respectively). For Kanyawara chimpanzees, seasons when the diet is dominated by figs are typically those when drupes are less available (Wrangham et al., 1996), and they are associated with poorer energy harvesting (Thompson and Wrangham, 2008). The fact that diets in the July and August seasons were both dominated by drupes therefore suggests that the quality of food would be higher than in January. Terrestrial herbaceous vegetation ('foliage'), representing the stems, piths, and leaves of a number of species of terrestrial herbs and shrubs, is a major class of fallback foods for the Kanyawara community and is typically eaten in inverse proportion to the availability of preferred foods such as ripe fruits (Wrangham et al., 1991; Wrangham et al., 1998).

No more than one fecal sample was taken per day from any individual. Fecal samples were placed in water-tight plastic bags in the field immediately after defecation to prevent loss of moisture, and were weighed at the end of the day. About ten grams of each sample were stored in 50 mL plastic test tubes with just enough laboratory grade ethanol (70% solution for January and 96% for July-August) to fully immerse it for preservation. An equivalent portion of each

170 sample was dried to constant weight in a food dehydrator at 71°C to determine
171 dry matter concentration. These data, however, proved unreliable in later
172 calculations, most likely due to heterogeneity between fecal subsamples (see
173 Discussion).

174

175 **Laboratory analysis**

176 Fecal samples were analyzed at the Clinic for Zoo Animals, Exotic Pets
177 and Wildlife of the University of Zurich using a standardized wet sieving method
178 (Fritz et al., 2012). The sieve cascade (Retsch, Haan, Germany) contained 11
179 sieves with pore sizes (linear dimension of holes) of 0.025 mm, 0.040 mm, 0.063
180 mm, 0.125 mm, 0.25 mm, 0.5 mm, 1.0 mm, 2.0 mm, 4.0 mm, 8.0 mm, and 16.0
181 mm. In contrast to previous FPS studies, the two finest sieves were added to
182 further differentiate the very small particles. Fecal samples were left in beakers of
183 water overnight with magnetic stirrers to disintegrate the sample without changing
184 particle sizes. Subsequently the sample was poured onto the sieve cascade on a
185 sieving machine (Retsch AS 200 digit, Haan, Germany) set to a vibration
186 amplitude of approximately 2 mm, with a water throughput of 2 liters per minute,
187 and sieved for 10 minutes. The size of the largest particles on the largest sieve
188 was noted as the length of that particle (maximum particle length, or MPL). The
189 remains on each sieve were transferred onto pre-weighed petri dishes, dried at
190 103°C for at least 15 h, and weighed after cooling to room temperature in a
191 desiccator using an analysis balance with measuring accuracy of 1 mg (Kern AEJ
192 220-4M, Kern, Balingen, Germany). Larger seeds passed intact in the feces were

193 removed manually from the three largest sieves (16 mm, 8 mm, 4 mm), and their
194 amount weighed individually for each sieve and subtracted. Thus, the results
195 contained, for these three sieves, the dry matter weight of the complete fecal
196 sample, and of the fecal sample without seeds. The total weight of the removed
197 seeds (as a proportion of the total dry matter retained on all sieves) was used as a
198 proxy for the amount of large-seeded fruit contributing to the fecal sample. Fig
199 seeds were evident on smaller sieves, but were too numerous to be sorted out
200 reliably.

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Calculations

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We used the dry-matter weights on each sieve to calculate fecal particle size (FPS) according to a variety of scenarios. FPS was calculated by first expressing the dry weight on each sieve as a proportion of the total dry mass retained on all sieves. Note that if the FPS is calculated for the whole cascade (FPS_{0.025-16}), then the total dry mass is the sum of that retained on all these sieves, whereas if the FPS is calculated from a subset of the cascade (e.g., FPS_{0.125-4}), then the total dry mass is only the sum of that retained on that subset of sieves (i.e., ignoring the material on the other sieves), and the proportions for each sieve change accordingly. The FPS was calculated according to the dMEAN procedure of Fritz et al. (2012) as

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$$FPS = \sum_{i=1}^n p(i) * \frac{S(i+1) + S(i)}{2}$$

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where i is the number of sieves in the respective cascade (with 1 as the number of the smallest sieve), $p(i)$ the proportion of dry matter on sieve i , and $S(i)$ the pore

216 size of the sieve. For the largest sieve $S(i_{max})$, no 'higher' sieve $S(i_{max}+1)$ exists by
217 definition. In this case, the manually measured maximum particle length MPL is
218 used to calculate the size of particles on that sieve, and $S(i+1)$ corresponds to
219 MPL. Alternatively, particles on the largest sieve can simply be ascribed the size
220 of that sieve, without considering MPL. In this way, FPS was calculated for
221 various sieve cascades and scenarios with and without excluding large seeds. The
222 different FPS are indicated by subscripts of the range of the sieve cascade (e.g.
223 $FPS_{0.025-16}$), whether or not MPL was included (e.g. $FPS_{0.025-16MPL}$ vs. $FPS_{0.025-16}$),
224 and whether or not seeds were included (e.g. $FPS_{0.025-16MPL(s)}$ vs. $FPS_{0.025-16MPL}$).

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Statistical analysis

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Because most data were not distributed normally we used nonparametric tests. Differences in the proportion of large fruit seeds and fecal dry matter concentration between the seasons were compared by U-test, correcting for multiple comparison by Sidak adjustment. We used the complete dataset (all 130 samples) to test for differences between the 13 calculated FPS measurements; these differences were assessed by related-samples Wilcoxon signed rank test between all pairs of measurements, again with Sidak adjustment. Next, means for each individual were calculated per season, to compare measurements for the two sexes (individuals > 14 years of age; U-test) and test for a correlation with age (Spearman's ρ) and with the proportion of large seeds within each season. Subsequently, means for each individual were calculated for each fruit type (figs or drupes). Again, differences between sexes and correlations with age and

239 proportion of large seeds were evaluated, and the difference between the two fruit
240 types was assessed using the related-samples Wilcoxon signed rank test in those
241 14 individuals (males and females, aged six to 34 years) for which data were
242 available from periods of both fruit types. Finally, the data from these 14
243 individuals was used in a General Linear Model (GLM), using ranked data due to
244 a lack of normal distribution of the original data, with FPS as the dependent
245 variable, age as covariable and both sex and fruit type as cofactors. Statistical
246 analyses were performed using SPSS (IBM®, Version 22), with the significance
247 level generally set to 0.05.

248

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RESULTS

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Figure 1 shows a view of a typical fecal sample fractionated by sieve analysis. The 16 mm sieve often contained large fibrous strands of stems or even whole leaves as in Figure 1; large seeds (mainly from drupe fruits) were evident on sieves of 4, 8 and 16 mm.

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[Figure 1 here]

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The proportion of such seeds as well as the fecal dry matter concentration was significantly higher during the two drupe fruit seasons than during the fig season (Table 2). Across all fecal samples, there was a highly significant positive correlation between the proportion of large seeds and the fecal dry matter concentration ($r = 0.58$, $P < 0.001$). The calculated proportion of particles escaping the finest sieve averaged below 0.2, but showed high variation and included negative values, indicating that the dry matter concentration measured in

262 the subsample for dry matter determination was most likely not representative of
263 the subsample used for sieve analysis; the proportion of escaped dry matter was
264 also significantly correlated with the fecal dry matter concentration ($r = 0.44$, $P <$
265 0.001).

266 [Table 3 here]

267 As expected, FPS calculated while excluding large seeds was invariably
268 smaller than those that included the weight of the seeds, and FPS calculated
269 including the MPL for the largest sieve were larger than those that did not use
270 MPL (Table 3). With the exception of two pair wise-comparisons, differences
271 between all 13 FPS calculated were significant. Excluding seeds and ignoring
272 MPL led to reductions in standard deviations (Table 3).

273 [Table 4 here]

274 Within seasons, there were no differences in FPS between the sexes, and
275 there were no significant correlations with age or with the proportion of large
276 fruits in the fecal sample (Table 4). Rather, there was substantial variation across
277 all age-classes and for all fruit types (Fig. 2).

278 [Figure 2 here]

279 [Table 5 here]

280 For those 14 individuals for which FPS measurements existed for both the
281 fig and the drupe fruit period (see above, “Statistical Analysis”), the FPS for the
282 fig period was always smaller. Most differences were statistically significant
283 (Table 5).

284 [Table 6 here]

285 In the GLM using ranked data, FPS varied significantly among fruit
286 periods, but was not significantly associated with age and did not differ
287 significantly between the sexes (Table 6).

288

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DISCUSSION

290 Chewing efficiency as measured by digesta or fecal particle size is a
291 crucial component of herbivore digestive physiology; for example, ungulate
292 herbivores can be ranked according to their chewing efficiency, their chewing
293 efficiency is linked to other physiological measurements such as digesta retention
294 times or digestibility, and scenarios of increasing chewing efficiency during
295 mammalian ungulate evolution have been invoked (Clauss et al. 2009, Fritz et al.
296 2009, Clauss et al. 2015). By contrast, chewing efficiency in frugivores has not
297 been studied in detail. The present study investigated individual and seasonal
298 variation in fecal particle sizes in wild chimpanzees. Apart from typical
299 methodological aspects of sieve analysis of feces, such as the choice of the sieve
300 sizes used in the sieve cascade, additional considerations apply when dealing with
301 frugivorous or omnivorous species (such as chimpanzees) as compared to
302 herbivorous ungulates. With an improved and standardized methodology for
303 frugivores, the study of FPS can provide informative comparisons of digestive
304 strategies and nutritional ecology beyond ungulate herbivores. For instance,
305 comparisons between humans and apes will be particularly instructive, given that
306 humans are adapted to external processing of their foods (Wrangham and

307 Conklin-Brittain, 2003). We here discuss methodology first, and then our specific
308 results.

309

310 **Methodological aspects**

311 Previous work has shown the importance of using similar sieve cascades,
312 and especially of using the same maximum and minimum sieve sizes, in
313 comparative studies (Fritz et al., 2012); in particular, it is important that the
314 smallest and the largest sieve size is similar. Our calculations using different cut-
315 off sieve sizes at the lower end (Table 3) underline this fact. Additionally, a
316 standardized method is required for dealing with those parts of the fecal matter
317 that do not represent chewed material. In material that contains relevant
318 proportions of sand from the ingestion of soil, for example, the amount of dry
319 matter retained on a sieve must be corrected for its ash content (Schwarm et al.,
320 2013). For frugivorous primates, the problem of including both large (cherry-
321 kernel size) and small (fig-seed size) seeds in sieve analyses of fecal material was
322 mentioned briefly by Matsuda et al. (2014), but it was not investigated how their
323 inclusion or exclusion affects sieve results. Evidently, the inclusion of large seeds
324 in the material retained on sieves used for the calculation of FPS will lead to
325 larger values (Table 3) that do not appropriately reflect the chewing efficiency of
326 the species, because chewing this material is mostly avoided. Manually removing
327 seeds from the material retained on a sieve, and weighing them individually, as in
328 the present study, allows for an assessment of this effect.

329 However, manual removal of seeds at an earlier instance might yield even

330 more reliable results. An important limitation of the present study was the large
331 variation in the calculated amount of particulate matter passing through the finest
332 sieve. If physical collection of this material is logistically not feasible under the
333 respective laboratory conditions, as in the present study, then this fraction is
334 calculated as the difference between the assumed total dry matter in the
335 subsample submitted to sieve analysis and the sum of the dry matter actually
336 retained on the sieves. The assumed dry matter is derived from drying another
337 subsample of the same defecation, typically performed directly in the field. In the
338 present study, both subsamples—the one submitted to drying, and the one
339 submitted to sieve analysis—often contained large seeds. Large seeds contain less
340 water than other fecal matter, and the dry matter content of fecal samples hence
341 increased with an increasing proportion of large seeds contained in them. If the
342 proportion of large seeds in both subsamples of a defecation is not identical—a
343 likely possibility, given their large size and the comparatively small amount of
344 total material defecated—then these discrepancies may easily lead to an over- or
345 under-estimation of the actual non-seed dry matter contained in the subsample
346 submitted to sieve analysis. This source of error could only be avoided if either
347 the particles escaping the smallest sieve were also caught and quantified (e.g. via
348 the use of filter paper or centrifugation of the eluent), or by removing (and
349 quantifying) large seeds prior to dry matter analysis.

350 Additionally, we observed that the tough skins of drupe fruits such as
351 *Pseudospondias microcarpa* and *Linociera johnsonii* were expelled almost
352 entirely intact, and therefore should be treated as indigestible fruit material in the

353 same way as seeds (as done in FPS calculations that excluded material on 16 and
354 8 mm sieves). Similarly, some long, folded strands of foliage or stems, as well as
355 unchewed whole leaves and hair from mammals consumed in occasional
356 predation events, should be excluded from FPS calculations. Similar exclusions of
357 long, tangled matter have been recommended previously in a macroscopic study
358 of chimpanzee feces, albeit for a different particle weighing technique (Phillips
359 and McGrew, 2014).

360 Another methodological issue concerns a possible change in digesta
361 particle size during digestion. Although it has been shown that digestion has only
362 a small effect on particle size in ungulate herbivores (Poppi et al., 1980; McLeod
363 and Minson, 1988; Spalinger and Robbins, 1992), reduction in digesta particle
364 size along the digestive tract has been demonstrated for animals feeding on less
365 rigid plant material, such as dugongs (*Dugong dugon*) feeding on sea grass
366 (Lanyon and Sanson, 2006), or captive collared peccaries (*Pecari tajacu*) and a
367 captive sloth (*Choloepus didactylus*) fed diets consisting mainly of domesticated
368 fruits and/or vegetables (Schwarm et al., 2013). To what extent the wild fruits
369 ingested by free-ranging chimpanzees are subjected to particle size reduction
370 during digestion (as opposed to during ingestive mastication) is currently
371 unknown. Likewise, studies also remain to be performed on the degree to which
372 smaller seeds, such as fig seeds, are actually swallowed whole, or are deformed or
373 reduced in size by mastication.

374

375 **Chimpanzee fecal particle size: effect of diet**

376 Within each of the studied seasons there was no significant correlation
377 between the proportion of seeds in the fecal sample and its FPS. However, there
378 was a distinct and surprising difference among the fruit periods: FPS was larger
379 when drupe fruits rather than figs were the main diet item. The opposite
380 relationship was expected, since in Kanyawara drupes are generally preferred
381 foods, whereas figs tend to be fallback foods (Wrangham et al., 1996; Marshall
382 and Wrangham, 2007). In line with these expectations, the pulp of *F. natalensis*
383 fruits has been found to contain less metabolizable energy (134-236
384 kilocalories/gram of organic matter) than the pulp of *P. microcarpa* (164-254
385 kcal/g OM) or *L. johnsonii* (207-284 kcal/g OM) (Conklin-Brittain et al., 2006).
386 Consumption of drupes (including *Pseudospondias microcarpa*) has also been
387 shown to correlate with reproductive timing for adult females in Kanyawara
388 (Emery Thompson and Wrangham, 2008), again indicating their high energetic
389 value. Drupes are therefore expected to be a higher-quality food. In theory the low
390 FPS during the fig season could be explicable by chimpanzees ‘wadging’ a
391 significant proportion of their fig meals, i.e. if they chewed the fruits and sucked
392 the solubles but did not swallow the solids, leaving them as a ‘wadge’ that
393 combined seeds and other low-value parts (skins, fibrous strands, and large
394 particles of pulp). ‘Wadging’ could allow larger food particles to be over-
395 represented in the unswallowed portions of the chewed food, leaving swallowed
396 portions to have disproportionately low FPS. However, the Kanyawara
397 chimpanzees do not ‘wadge’ figs of *F. natalensis*. Thus while wadging could

398 contribute to the reduction of FPS for some foods, it did not do so for *F.*
399 *natalensis* fruits.

400 Alternatively, the presence of larger seeds in drupes (that are not spat out but
401 swallowed whole) may negatively affect chewing efficiency, forcing chimpanzees
402 to exert fewer and/or more restrained masticatory movements, in contrast to the
403 small seeds in figs that can be masticated without difficulty. Additionally, during
404 the fig season, THV was a larger proportion of the Kanyawara diet than during
405 the drupe season. Fibrous vegetation, while a lower quality food option, does not
406 contain these large seeds that may hinder chewing efficiency.

407 The reasons for lower FPS during the fig season are thus uncertain. Whatever
408 the reason, however, the finding of low FPS during the fig season supports the
409 hypothesis that in contrast to typical herbivores, particle size may be less critical
410 for frugivores, because the less-preferred diet items apparently do not exhibit
411 structural properties that render them less prone to particle size reduction.

412

413 **Comparison to other FPS studies in chimpanzees**

414 The FPS measured in this study was substantially higher than in two
415 previous studies. $FPS_{0.063-16}$ Kanyawara was 4.15 ± 3.33 mm. In contrast, Matsuda
416 et al. (2014) reported a mean FPS of 1.90 ± 0.96 mm for *P. t. schweinfurthii* in the
417 Kalinzu Forest, Uganda, and recalculation of values for captive chimpanzees
418 (probably mostly *P. t. verus*) given in Fritz et al. (2009) yields a mean $FPS_{0.063-16}$
419 value of 2.02 mm. The comparison indicates a larger proportion of large (and
420 hence potentially less well chewed) material in the chimpanzees of the present

421 study in general. However, when using the $FPS_{0.063-8}$ of the fig period (1.99 ± 1.29
422 mm) of the present study (and thus excluding large unchewed particles), the data
423 are very similar. These results emphasize the importance for comparative studies
424 not only of defining the diet items consumed by different populations, but also of
425 defining how to handle material that was evidently not subjected to mastication.

426

427 **Chimpanzee fecal particle size: no relationship with sex or age**

428 Chimpanzees are moderately sexually dimorphic, with males averaging 33%
429 higher body mass than females (Plavcan and van Schaik, 1992). However, there
430 was no influence of sex on FPS. This finding corresponds to results from several
431 other mammalian herbivores (sheep, equids, rhinoceroses, and elephants) where
432 no intra-specific differences in FPS with body mass were evident (Pérez-Barbería
433 et al., 2008; Clauss et al., 2015).

434 Similarly, but contrary to data from geladas (Venkataraman et al., 2014),
435 FPS in chimpanzees showed no relationship to age. This result suggests that
436 chimpanzee diets tend to have fewer mechanical demands on masticatory function
437 than gelada diets. Folivores such as geladas consume foods that are both tough
438 and hard, which necessitates more average daily chewing cycles and larger
439 average bite forces compared to frugivorous primates (Taylor, 2002). To cope
440 with this, geladas have a highly specialized hypsodont dentition with shearing
441 crests that are formed from repeated use, similar to a mechanism described for
442 Edward's sifakas (King et al., 2005) and mountain gorillas (Glowacka, et al.,
443 2016), but that wear down substantially in old age. This wear pattern is apparently

444 responsible for prime adults having greater chewing, and thus digestive,
445 efficiency than infants and past-prime adults (Venkataraman et al., 2014).
446 Irrespective of measures of particle size, associations between tooth wear and
447 senescence have been demonstrated in primate species (e.g., King et al., 2005 for
448 *Propithecus edwardsi*).

449 Our data indicate that chimpanzees, on the other hand, have consistent
450 chewing efficiency throughout life. The youngest chimpanzees that we sampled
451 were 16 to 45 months old. Those ages compare to 0-6 years as the period during
452 which suckling occurs (Machanda et al., 2015). The oldest-aged samples came
453 from 42- to 55-year-old individuals, sufficiently old for their teeth to be visibly
454 worn (R. Wrangham, pers. obs.). Unfortunately, although wear in chimpanzee
455 teeth has been demonstrated (Klukkert et al., 2012), a study that systematically
456 links wear to age is still lacking. The fact that no age-related trends in FPS were
457 detectable indicates that chewing efficiency remained stable both during the
458 weaning process and even when molars become worn with age. This observation
459 indicates that for a mainly frugivorous diet, particle size reduction may be less
460 critical than for a folivorous diet—because there is no discernable optimization in
461 FPS across the lifespan as evident by an age- or wear-induced loss of chewing
462 efficiency. It also suggests that fruit pulp is less resistant to mastication, and
463 requires less wear-susceptible adaptations, than leaves or grasses. The former
464 hypothesis could be tested using *in vitro* digestion assays with natural foods in
465 different stages of particle size reduction (cf. Bjorndal et al., 1990). The latter
466 hypothesis has been confirmed repeatedly in physical analyses of primate

467 feedstuffs (Lucas et al., 2012), and leads to the hypothesis that frugivores are less
468 constrained, in their longevity, by dental functionality than folivores. Some
469 support for this proposal could come from other observations. Ring-tailed lemurs
470 (*Lemur catta*) are frugivores that can survive in the wild even with substantial
471 tooth loss (Sauther et al., 2002; Cuzzo and Sauther, 2004). Similarly, edentulous
472 chimpanzees have been recorded surviving in the wild for years (Miles and
473 Grigson, 1990). The absence of an effect of age on FPS could thus be
474 representative for other primates, including hominins, where tooth wear, tooth
475 loss, and/or reduced chewing efficiency may represent less of a longevity
476 constraint than in those mammalian species that rely on their teeth for the killing
477 of live prey or the grinding of tough plant diets.

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ACKNOWLEDGEMENTS

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Research was funded through the Herchel Smith-Harvard Undergraduate
Science Research Program. The Uganda Wildlife Authority, the Uganda National
Council of Science and Technology, and the Makerere University Biological
Field Station kindly provided permission and logistical help. For field assistance
we thank Martin Muller, Melissa Emery Thompson, Zarin Machanda, Emily Otali
and staff members of the Kibale Chimpanzee Project, where long-term support
was funded by the Leakey Foundation, NSF grants 1355014 and 0849380, and
NIH National Institute on Aging award R01AG049395. Research was non-
invasive and adhered to the legal requirements of Uganda. We thank David Watts

489 and two anonymous reviewers for their helpful comments. The authors declare no
490 conflicts of interest.

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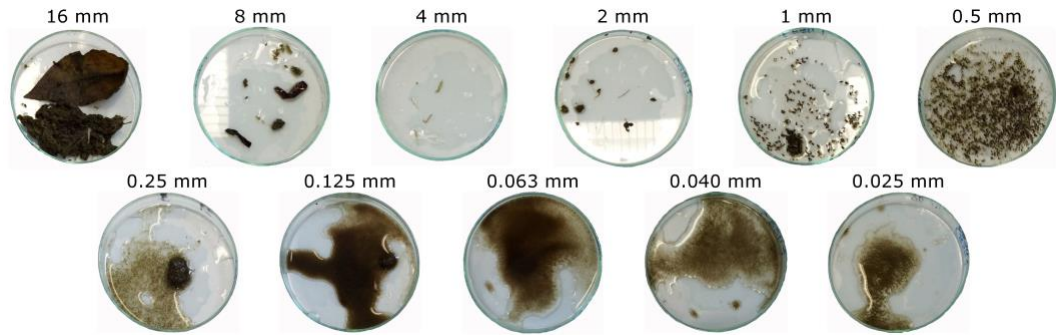
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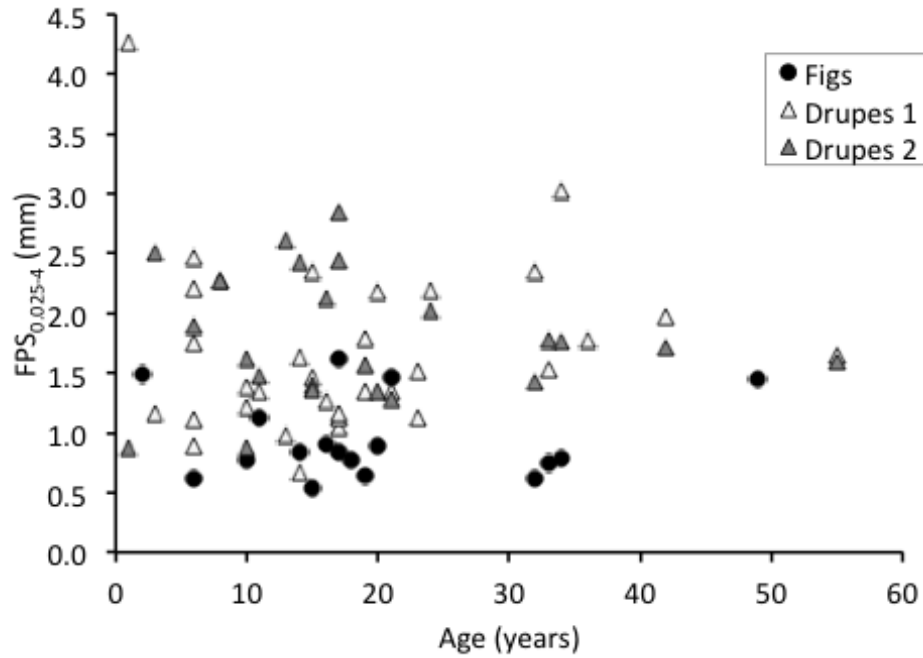
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FIGURES AND TABLES



611
612 **Figure 1** Wet sieved material from a single chimpanzee fecal sample. Sample
613 collected from AT, an adult male, during the fig period when he was 15.2 years
614 old. Large, undigested particles are apparent in the largest sieves.
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617 **Figure 2** Mean fecal particle size for each individual (n=38) compared with age.
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619 **Table 1** Demographic composition of the chimpanzee (*Pan troglodytes*
620 *schweinfurthii*) sample population (numbers of individuals in each sex-age class).

	Infant (0-4 years)	Juvenile (5-9 years)	Adolescent (10-14 years)	Prime Adult (15-41 years)	Old Adult (42+ years)	Total
Female	4	3	2	12	1	22
Male	1	3	4	6	2	16
Total	5	6	6	18	3	38

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Table 2 Chimpanzee (*Pan troglodytes schweinfurthii*) fecal samples by season and dietary composition.

Dates	Fecal samples/ individuals (n)	Fruit species eaten most frequently	Number of food scans (% of scans with preferred fruit)	Proportion of large seeds mean ± SD (minimum-maximum)	Dry matter concentration (% wet weight)
January 6-11	17/17	<i>Ficus natalensis</i>	330 (50)	0.02 ± 0.05 ^a (0-0.19)	26.0 ± 2.3 ^a (21.3-29.3)
July 5-19	67/33	<i>Pseudospondias microcarpa</i>	439 (77)	0.42 ± 0.46 ^b (0-0.96)	35.4 ± 11.8 ^b (17.2-63.3)
July 20-August 3	46/23	<i>Linociera johnsonii</i>	278 (73)	0.53 ± 0.14 ^b (0.27-0.75)	31.7 ± 8.7 ^b (16.3-53.9)

625 Food scans are the times recorded in KCP's archive of 15-minute interval
626 behavior scans in which the chimpanzees were observed feeding. For the
627 proportion of large seeds and fecal dry matter concentration, different superscripts
628 indicate significant differences between the seasons.

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631 **Table 3** Mean ± SD (minimum-maximum) fecal particle size (FPS) in 130 fecal
632 samples of 38 individual chimpanzees (*Pan troglodytes schweinfurthii*) measured
633 using different cascades of sieves (indicated by the sieve size of the smallest and
634 largest sieve), with large seeds (s) or without them, and with or without using the
635 maximum particle length (MPL) when including the largest sieve.

Method	FPS (mm)	Proportion of particles passing the finest sieve
0.025-16 MPL (s)	9.03 ± 6.59 (0.70-42.36) ^a	0.17 ± 0.23 (-0.78-0.72)
0.025-16 MPL	5.17 ± 6.58 (0.67-42.36) ^b	
0.025-16 (s)	7.54 ± 3.55 (0.70-15.60) ^c	0.21 ± 0.21 (-0.53-0.74)
0.025-16	3.95 ± 3.30 (0.67-14.76) ^d	
0.025-8 (s)	6.45 ± 3.17 (0.70-11.71) ^e	0.28 ± 0.21 (-0.49-0.76)
0.025-8	3.10 ± 2.39 (0.61-10.49) ^f	
0.025-4 (s)	1.75 ± 0.89 (0.50-5.74) ^g	0.28 ± 0.21 (-0.49-0.76)
0.025-4	1.62 ± 0.84 (0.50-5.74) ^h	
0.063-16 MPL (s)	9.28 ± 6.65 (0.90-42.89) ⁱ	0.28 ± 0.21 (-0.49-0.76)
0.063-16 MPL	5.41 ± 6.71 (0.84-42.89) ^j	
0.063-16	4.15 ± 3.33 (0.84-14.80) ^k	0.28 ± 0.21 (-0.49-0.76)
0.063-8	3.29 ± 2.41 (0.74-10.54) ^{bd}	
0.125-4	2.24 ± 0.91 (0.59-5.78) ^l	0.28 ± 0.21 (-0.49-0.76)

636 Different superscripts indicate significant differences between FPS measures.

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641 **Table 4** Results of statistical analyses (*P* values) testing for differences between
 642 the sexes (in adult animals) or for correlations with age and the proportion of
 643 large seeds in feces of chimpanzees (*Pan troglodytes schweinfurthii*) in the three
 644 different seasons of this study.

FPS Method Season	Sex			Age			Proportion seeds		
	1	2	3	1	2	3	1	2	3
0.025-16 MPL (s)	0.485	0.773	0.456	0.804	0.726	0.105	0.524	0.554	0.468
0.025-16 MPL	0.699	0.100	0.383	0.677	0.443	0.019	0.524	0.815	0.523
0.025-16 (s)	0.394	1.000	0.902	0.765	0.981	0.175	0.524	0.529	0.750
0.025-16	0.485	0.167	1.000	0.619	0.494	0.078	0.524	0.798	0.713
0.025-8 (s)	0.589	0.384	0.259	0.844	0.676	0.676	0.713	0.240	0.587
0.025-8	0.699	0.482	0.073	0.694	0.660	0.514	0.713	0.544	0.376
0.025-4 (s)	0.818	0.650	0.383	0.959	0.451	0.790	0.399	0.027	0.932
0.025-4	0.818	0.592	0.383	0.959	0.343	0.790	0.399	0.189	0.932
0.063-16 MPL (s)	0.485	0.711	0.383	0.687	0.702	0.108	0.524	0.566	0.425
0.063-16 MPL	0.699	0.100	0.383	0.567	0.479	0.019	0.524	0.798	0.523
0.063-16	0.485	0.167	1.000	0.498	0.527	0.062	0.428	0.759	0.805
0.063-8	0.699	0.482	0.073	0.632	0.713	0.423	0.713	0.552	0.425
0.125-4	0.818	0.536	0.710	0.844	0.426	0.923	0.399	0.194	0.932

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647 **Table 5** Mean SD (minimum-maximum) fecal particle size (FPS, in mm) in 14
 648 chimpanzees (*Pan troglodytes schweinfurthii*) measured using different cascades
 649 of sieves (indicated by the sieve size of the smallest and largest sieve), with large
 650 seeds (s) or without them, and with or without using the maximum particle length
 651 (MPL) when including the largest sieve, measured both during the fig and the
 652 drupe fruit period, and the *P* values from pair-wise comparisons.

FPS	Fig period	Drupe period	<i>P</i>
0.025-16 MPL (s)	4.53 ±7.50 (0.99-30.04)	11.57 ±3.43 (6.88-19.52)	0.016
0.025-16 MPL	4.43 ±7.53 (0.99-30.04)	6.58 ±3.40 (2.45-13.32)	0.056
0.025-16 (s)	2.96 ±2.44 (0.92-10.00)	9.29 ±1.83 (6.79-12.51)	0.001
0.025-16	2.86 ±2.47 (0.92-10.00)	4.75 ±2.23 (2.45-8.81)	0.064
0.025-8 (s)	1.98 ±1.26 (0.80-4.34)	7.52 ±1.58 (5.10-10.63)	0.001
0.025-8	1.89 ±1.24 (0.80-4.34)	3.35 ±1.60 (1.50-7.02)	0.084
0.025-4 (s)	0.92 ±0.42 (0.54-2.12)	1.80 ±0.38 (1.17-2.46)	0.005
0.025-4	0.88 ±0.31 (0.54-1.61)	1.68 ±0.37 (1.17-2.46)	0.002
0.063-16 MPL (s)	4.71 ±7.73 (1.06-31.01)	11.80 ±3.44 (7.07-19.80)	0.016
0.063-16 MPL	4.62 ±7.76 (1.06-31.01)	6.83 ±3.42 (2.61-13.54)	0.056
0.063-16	3.00 ±2.55 (0.98-10.32)	4.95 ±2.23 (2.61-8.94)	0.064
0.063-8	1.99 ±1.29 (0.85-4.56)	3.54 ±1.61 (1.64-7.19)	0.084
0.125-4	1.07 ±0.32 (0.69-1.77)	2.38 ±0.41 (2.01-3.60)	0.001

653

654 **Table 6** Results of General Linear Models (using ranked data) with fecal particle
655 size (FPS) as the dependent variable, age as a covariable, and sex and fruit period
656 (figs vs. drupes) as cofactors for 14 chimpanzees (*Pan troglodytes schweinfurthii*)
657 sampled during both fruit periods.

FPS	Age		Sex		Fruit type	
	$F_{1,24}$	P	$F_{1,24}$	P	$F_{1,24}$	P
0.025-8	0.822	0.373	0.000	0.995	8.457	0.008
0.025-4	0.311	0.582	1.709	0.204	40.258	<0.001
0.063-8	0.797	0.381	0.010	0.922	8.866	0.007
0.125-4	0.078	0.782	1.077	0.310	76.118	<0.001

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