



# 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.

### Permanent link

http://nrs.harvard.edu/urn-3:HUL.InstRepos:41687325

## Terms of Use

This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Open Access Policy Articles, as set forth at http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#OAP

# Share Your Story

The Harvard community has made this article openly available. Please share how this access benefits you. <u>Submit a story</u>.

**Accessibility** 

- Applying wet sieving fecal particle size measurement to 1 frugivores: a case study of the Eastern chimpanzee (Pan 2 troglodytes schweinfurthii) 3 4 5 Taylor E. Weary1\*, Richard W. Wrangham1, Marcus Clauss2 6 7 Department of Human Evolutionary Biology, Harvard University, Cambridge, 8 MA 02138 9 2Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland 10 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 22 23 \*Correspondence to: 24 Taylor Weary 25 Peabody Museum, 50B 11 Divinity Avenue 26 27 Cambridge, MA 02138 (310) 403-8715 28 29 taylorweary@alumni.harvard.edu 30 31 Grant sponsorship: Herchel Smith-Harvard Undergraduate Science Research
- 32 Fellowship

33	ABSIKAUI
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	<b>Results:</b> 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 $\pm$ 0.31 mm) than during two drupe-fruit seasons (1.68
50	$\pm 0.37$ 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.

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

In order to explore these effects we included the most comprehensive setof 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 ( $0^{\circ}$ 34' N, 30 $^{\circ}$ 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.

## [Table 2 here]

148	The three sample collection months corresponded approximately to three
149	fruit 'seasons' in each of which the chimpanzees' diet was dominated by a
150	different species of ripe fruit (Table 2). Figs (Ficus natalensis) were the most
151	frequently eaten fruit species in January (50% feeding time), and drupe fruits
152	were the main fruit types in the second and third seasons (77% feeding time on
153	Pseudospondias microcarpa, and 73% feeding time on Linociera johnsonii,
154	respectively). For Kanyawara chimpanzees, seasons when the diet is dominated
155	by figs are typically those when drupes are less available (Wrangham et al.,
156	1996), and they are associated with poorer energy harvesting (Thompson and
157	Wrangham, 2008). The fact that diets in the July and August seasons were both
158	dominated by drupes therefore suggests that the quality of food would be higher
159	than in January. Terrestrial herbaceous vegetation ('foliage'), representing the
160	stems, piths, and leaves of a number of species of terrestrial herbs and shrubs, is a
161	major class of fallback foods for the Kanyawara community and is typically eaten
162	in inverse proportion to the availability of preferred foods such as ripe fruits
163	(Wrangham et al., 1991; Wrangham et al., 1998).
164	No more than one fecal sample was taken per day from any individual.
165	Fecal samples were placed in water-tight plastic bags in the field immediately
166	after defecation to prevent loss of moisture, and were weighed at the end of the
167	day. About ten grams of each sample were stored in 50 mL plastic test tubes with
168	just enough laboratory grade ethanol (70% solution for January and 96% for July-

169 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.

- 201
- 202

#### Calculations

203 We used the dry-matter weights on each sieve to calculate fecal particle 204 size (FPS) according to a variety of scenarios. FPS was calculated by first 205 expressing the dry weight on each sieve as a proportion of the total dry mass 206 retained on all sieves. Note that if the FPS is calculated for the whole cascade 207 (FPS0.025-16), then the total dry mass is the sum of that retained on all these sieves, 208 whereas if the FPS is calculated from a subset of the cascade (e.g., FPS0.125-4), 209 then the total dry mass is only the sum of that retained on that subset of sieves 210 (i.e., ignoring the material on the other sieves), and the proportions for each sieve 211 change accordingly. The FPS was calculated according to the dMEAN procedure 212 of Fritz et al. (2012) as

213 
$$FPS = \bigotimes_{i=1}^{n} p(i) * \frac{S(i+1) + S(i)}{2}$$

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

210	size of the sieve. For the largest sieve $S(lmax)$ , no 'higher' sieve $S(lmax+1)$ 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	FPS0.025-16), whether or not MPL was included (e.g. FPS0.025-16MPL vs. FPS0.025-16),
224	and whether or not seeds were included (e.g. FPS0.025-16MPL(s) vs. FPS0.025-16MPL).
225	
226	Statistical analysis
227	Because most data were not distributed normally we used nonparametric
227 228	Because most data were not distributed normally we used nonparametric tests. Differences in the proportion of large fruit seeds and fecal dry matter
227 228 229	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
<ul><li>227</li><li>228</li><li>229</li><li>230</li></ul>	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
<ul> <li>227</li> <li>228</li> <li>229</li> <li>230</li> <li>231</li> </ul>	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;
<ul> <li>227</li> <li>228</li> <li>229</li> <li>230</li> <li>231</li> <li>232</li> </ul>	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
<ul> <li>227</li> <li>228</li> <li>229</li> <li>230</li> <li>231</li> <li>232</li> <li>233</li> </ul>	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
<ul> <li>227</li> <li>228</li> <li>229</li> <li>230</li> <li>231</li> <li>232</li> <li>233</li> <li>234</li> </ul>	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
<ul> <li>227</li> <li>228</li> <li>229</li> <li>230</li> <li>231</li> <li>232</li> <li>233</li> <li>234</li> <li>235</li> </ul>	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
<ul> <li>227</li> <li>228</li> <li>229</li> <li>230</li> <li>231</li> <li>232</li> <li>233</li> <li>234</li> <li>235</li> <li>236</li> </ul>	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 $\rho$ ) and with the proportion of large seeds within each season.
<ul> <li>227</li> <li>228</li> <li>229</li> <li>230</li> <li>231</li> <li>232</li> <li>233</li> <li>234</li> <li>235</li> <li>236</li> <li>237</li> </ul>	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 $\rho$ ) and with the proportion of large seeds within each season.

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	
249	RESULTS
250	Figure 1 shows a view of a typical fecal sample fractionated by sieve
251	analysis. The 16 mm sieve often contained large fibrous strands of stems or even
252	whole leaves as in Figure 1; large seeds (mainly from drupe fruits) were evident
253	on sieves of 4, 8 and 16 mm.
254	[Figure 1 here]
255	The proportion of such seeds as well as the fecal dry matter concentration
256	was significantly higher during the two drupe fruit seasons than during the fig
257	season (Table 2). Across all fecal samples, there was a highly significant positive
258	correlation between the proportion of large seeds and the fecal dry matter
259	concentration (r = 0.58, $P < 0.001$ ). The calculated proportion of particles
260	escaping the finest sieve averaged below 0.2, but showed high variation and
261	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	
289	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 liked 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 specific308 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

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

*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 $4.15 \pm 3.33$ mm. In contrast, Matsuda
416	et al. (2014) reported a mean FPS of $1.90 \pm 0.96$ mm for <i>P. t. schweinfurthii</i> 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 FPS0.063-16
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

study in general. However, when using the FPS<sub>0.063-8</sub> of the fig period  $(1.99 \pm 1.29 \text{ mm})$  of the present study (and thus excluding large unchewed particles), the data are very similar. These results emphasize the importance for comparative studies not only of defining the diet items consumed by different populations, but also of 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

-07	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; Cuozzo 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.
478	
479	ACKNOWLEDGEMENTS
479 480	ACKNOWLEDGEMENTS Research was funded through the Herchel Smith-Harvard Undergraduate
479 480 481	ACKNOWLEDGEMENTS Research was funded through the Herchel Smith-Harvard Undergraduate Science Research Program. The Uganda Wildlife Authority, the Uganda National
<ul><li>479</li><li>480</li><li>481</li><li>482</li></ul>	ACKNOWLEDGEMENTS 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
<ul> <li>479</li> <li>480</li> <li>481</li> <li>482</li> <li>483</li> </ul>	ACKNOWLEDGEMENTS 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
<ul> <li>479</li> <li>480</li> <li>481</li> <li>482</li> <li>483</li> <li>484</li> </ul>	ACKNOWLEDGEMENTS 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
<ul> <li>479</li> <li>480</li> <li>481</li> <li>482</li> <li>483</li> <li>484</li> <li>485</li> </ul>	ACKNOWLEDGEMENTS 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
<ul> <li>479</li> <li>480</li> <li>481</li> <li>482</li> <li>483</li> <li>484</li> <li>485</li> <li>486</li> </ul>	ACKNOWLEDGEMENTS 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 Otal and staff members of the Kibale Chimpanzee Project, where long-term support was funded by the Leakey Foundation, NSF grants 1355014 and 0849380, and
<ul> <li>479</li> <li>480</li> <li>481</li> <li>482</li> <li>483</li> <li>484</li> <li>485</li> <li>486</li> <li>487</li> </ul>	ACKNOWLEDGEMENTS 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 Otal 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-

489	and two anonymous reviewers for their helpful comments. The authors declare no							
490	conflicts of interest.							
491	LITERATURE CITED							
492 493	Bjorndal KA, Bolten AB, and Moore JE. 1990. Digestive fermentation in herbivores: effect of food particle size. Physiol Zool 63:710-721.							
494 495 496	Chapman CA, and Wrangham RW. 1993. Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. Am J Primatol 31:263-273.							
497 498 499	Clauss M, Nunn C, Fritz J, Hummel J. 2009. Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. Comp Biochem Physiol A 154:376-382.							
500 501 502	Clauss M, Steuer P, Erlinghagen-Lückerath K, Kaandorp J, Fritz J, Südekum K- H, and Hummel J. 2015. Faecal particle size: digestive physiology meets herbivore diversity. Comp Biochem Physiol A 179:182-191.							
503 504 505 506 507	Conklin-Brittain NL, Knott CD, and Wrangham RW. 2006. Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In: Hohmann G, Robbins M, and Boesch C, editors. Feeding ecology of primates. Cambridge: Cambridge University Press. p 443-469.							
508 509 510	Cuozzo FP, and Sauther ML. 2004. Tooth loss, survival, and resource use in wild ring-tailed lemurs ( <i>Lemur catta</i> ): implications for inferring conspecific care in fossil hominids. J Hum Evol 46:623-631.							
511 512 513	Dehority BA, and Johnson RR. 1961. Effect of particle size upon the in vitro cellulose digestibility of forages by rumen bacteria. J Dairy Sci 44:2242-2249.							
514 515	Dunbar RIM, and Bose U. 1991. Adaptation to grass-eating in gelada baboons. Primates 32:1-7.							
516 517 518	Fritz J, Hummel J, Kienzle E, Arnold C, Nunn C, and Clauss M. 2009. Comparative chewing efficiency in mammalian herbivores. Oikos 118:1623-1632.							
519 520 521	Fritz J, Streich WJ, Schwarm A, and Clauss M. 2012. Condensing results of wet sieving analyses into a single data: a comparison of methods for particle size description. J Anim Physiol Anim Nutr 96:783-797.							
522 523	Glowacka H, McFarlin SC, Catlett KK, Mudakikwa A, Bromage TG, Cranfield MR, Stoinski TS, and Schwartz GT. 2016. Age-related changes in molar							

524 525 526	topography and shearing crest length in a wild population of mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol 160(1): 3-15.
527 528 529	King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, and Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. PNAS 102(46): 16579-16583.
530 531	Klukkert ZS, Teaford MF, and Ungar PS. 2012. A dental topographic analysis of chimpanzees. Am J Phys Anthropol 148: 276-284.
532 533	Lanyon JM, and Sanson GD. 2006. Mechanical disruption of seagrass in the digestive tract of the dugong. J Zool (Lond) 270:277-289.
534 535 536	Lucas PW, Copes L, Constantino PJ, Vogel ER, Chalk J, Talebi M, Landis M, and Wagner M. 2012. Measuring the toughness of primate foods and its ecological value. Int J Primatol 33:598-610.
537 538 539	Machanda Z, Brazeau NF, Bernard AB, Donovan RM, Papakyrikos AM, Wrangham R, and Smith TM. 2015. Dental eruption in East African wild chimpanzees. J Hum Evol 82:137-144.
540 541	Marshall AJ, and Wrangham RW. 2007. Evolutionary consequences of fallback foods. Int J Primatol 28:1219-1235.
542 543 544 545	Matsuda I, Tuuga A, Hashimoto C, Bernard H, Yamagiwa J, Fritz J, Tsubokawa K, Yayota M, Murai T, Iwata Y et al. 2014. Faecal particle size in free- ranging primates supports 'rumination' strategy in the proboscis monkey ( <i>Nasalis larvatus</i> ). Oecologia 174:1127-1137.
546 547	McLeod MN, and Minson DJ. 1988. Large particle breakdown by cattle eating ryegrass and alfalfa. J Anim Sci 66:992-999.
548 549	Miles AEW, and Grigson C. 1990. <i>Colyer's</i> Variations and diseases of the teeth of animals. Cambridge: Cambridge University Press.
550 551	Pérez-Barbería FJ, and Gordon IJ. 1998. Factors affecting food comminution during chewing in ruminants: a review. Biol J Linn Soc 63: 233-256.
552 553 554 555	Pérez-Barbería FJ, Pérez-Fernàndez E, Robertson E, and Alvarez-Enríquez B. 2008. Does the Jarman-Bell principle at intra-specific level explain sexual segregation in polygonous ungulates? Sex differences in forage digestibility in Soay sheep. Oecologia 157:21-30.
556 557	Phillips CA, and McGrew WC. 2014. Macroscopic inspection of ape feces: What's in a quantification method? Am J Primatol 76: 539-550.

558 559	Plavcan JM, and van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. Am J Phys Anthropol 87:461-477.
560 561 562	Poppi DP, Norton BW, Minson DJ, and Hendricksen RE. 1980. The validity of the critical size theory for particles leaving the rumen. J Agric Sci 94:275-280.
563 564 565	Potts K, Watts DP, and Wrangham RW. 2011. Comparative feeding ecology of two chimpanzee communities in Kibale National Park, Uganda. Int J Primatol 34:669-690.
566 567 568	Sauther ML, Sussman RW, and Cuozzo F. 2002. Dental and general health in a population of wild ring - tailed lemurs: A life history approach. Am J Phys Anthropol 117:122-132.
569 570 571 572	Schwarm A, Ortmann S, Fritz J, Rietschel W, Flach EJ, and Clauss M. 2013. No distinct stratification of ingesta particles and no distinct moisture gradient in the forestomach of nonruminants: the wallaby, peccary, hippopotamus, and sloth. Mamm Biol 78:412-421.
573 574	Spalinger DE, and Robbins CT. 1992. The dynamics of particle flow in the rumen of mule deer and elk. Physiol Zool 65:379-402.
575 576 577 578 579	Steuer P, Clauss M, Südekum K-H, Hatt J-M, Silinski S, Klomburg S, Zimmermann W, Fickel J, Streich WJ, and Hummel J. 2010. Comparative investigations on digestion in grazing ( <i>Ceratotherium simum</i> ) and browsing ( <i>Diceros bicornis</i> ) rhinoceroses. Comp Biochem Physiol A 156:380-388.
580 581	Taylor A. 2002. Masticatory form and function in the African apes. Am J Phys Anthropol 117:133-156.
582 583 584	Thompson ME, and Wrangham RW. 2008. Diet and reproductive function in wild female chimpanzees ( <i>Pan troglodytes schweinfurthii</i> ). Am J Phys Anthropol 135:171-181.
585 586 587 588	Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, and Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas ( <i>Theropithecus gelada</i> ). Am J Phys Anthropol 155:17-32.
589 590 591	Wilson ML, Hauser MD, and Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Animal Behaviour 61:1203-1216.
592 593	Wrangham RW. 1995. Relationship of chimpanzee leaf-swallowing to a tapeworm infection. Am J Primatol 37:297-303.

594	Wrangham RW, Chapman CA, and Chapman LJ. 1994. Seed dispersal by forest
595	chimpanzees in Uganda. Journal of Tropical Ecology 10:355-368.
596	Wrangham RW, Chapman CA, Clark-Arcadi AP, and Isabirye-Basuta G. 1996.
597	Socioecology of Kanyawara chimpanzees: Implications for understanding
598	the costs of great ape groups. In: McGrew WC, Marchant LF, and Nishida
599	T, editors. Great ape societies. Cambridge: Cambridge University Press.
600	Wrangham RW, Conklin NL, Chapman CA, and Hunt KD. 1991. The
601	significance of fibrous foods for Kibale Forest chimpanzees. Phil Trans R
602	Soc B 334:171-178.
603	Wrangham RW, Conklin-Brittain NL, and Hunt KD. 1998. Dietary response of
604	chimpanzees and cercopithecines to seasonal variation in fruit abundance.
605	I. Antifeedants. Int J Primatol 19:949-970.
606	
607	Wrangham RW, and Conklin-Brittain NL. 2003. Cooking as a biological trait.
608	Comp Biochem Phys A 136(1): 35-46.



Figure 1 Wet sieved material from a single chimpanzee fecal sample. Sample

- collected from AT, an adult male, during the fig period when he was 15.2 years
- old. Large, undigested particles are apparent in the largest sieves.





Figure 2 Mean fecal particle size for each individual (n=38) compared with age. 

619 <b>Table</b>	1 Demographic	composition	of the chin	npanzee ( <i>Pan</i>	troglodytes
------------------	---------------	-------------	-------------	----------------------	-------------

			1		1		0	~	
620	schweinfurthii)	sample	population	(numbers of	of indiv	iduals in	each s	sex-age c	:1

20	<i>schweinfurthii</i> ) 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		

623 **Table 2** Chimpanzee (*Pan troglodytes schweinfurthii*) fecal samples by season

F .	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	Ficus natalensis	330 (50)	$0.02 \pm 0.05_{a}$ (0-0.19)	$26.0 \pm 2.3_{a}$ (21.3-29.3)			
	July 5-19	67/33	Pseudospondi as microcarpa	439 (77)	$0.42 \pm 0.46_{\rm b}$ (0-0.96)	$35.4 \pm 11.8$ b (17.2-63.3)			
	July 20-August 3	46/23	Linociera johnsonii	278 (73)	$0.53 \pm 0.14$ b (0.27-0.75)	$31.7 \pm 8.7_{b}$ (16.3-53.9)			

624 and dietary composition.

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.

- 629
- 630

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	$0.17 \pm 0.23$ (-0.78-0.72)
0.025-16 MPL	5.17 ±6.58 (0.67-42.36) ь	
0.025-16 (s)	7.54 ±3.55 (0.70-15.60) c	
0.025-16	$3.95 \pm 3.30 \ (0.67 \text{-} 14.76)$ d	
0.025-8 (s)	6.45 ±3.17 (0.70-11.71) e	
0.025-8	$3.10 \pm 2.39 (0.61 - 10.49)$ f	
0.025-4 (s)	1.75 ±0.89 (0.50-5.74) g	
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	$0.21 \pm 0.21$ (-0.53-0.74)
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	
0.063-8	$3.29 \pm 2.41 (0.74 - 10.54)$ bd	
0.125-4	2.24 ±0.91 (0.59-5.78) 1	$0.28 \pm 0.21 \; (\text{-}0.49 \text{-} 0.76)$

636 Different superscripts indicate significant differences between FPS measures.

637

638

640

641 **Table 4** Results of statistical analyses (*P* values) testing for differences between

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	1.

FPS Method	Sex			Age			<b>Proportion seeds</b>		
Season	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

645

646

647 **Table 5** Mean SD (minimum-maximum) fecal particle size (FPS, in mm) in 14

648 chimpanzees (Pan troglodytes schweinfurthii) measured using different cascades

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	P
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

**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	Ag	Age		X	Fruit type		
	$F_{1,24}$	Р	$F_{1,24}$	Р	$F_{1,24}$	Р	
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	