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ORIGINAL ARTICLE

Non-dietary analytical features of chimpanzee scats

Caroline A. Phillips[1,2] · Richard W. Wrangham[3] · William C. McGrew[2,4]

Abstract Non-dietary aspects of ape scats such as scat weight and diameter are correlated with age and sex of defaecator for gorillas and orangutans. Defaecation rates of primates, including apes, illuminate their role as primary seed dispersers. We assess if non-dietary features of scats for East African chimpanzees (*Pan troglodytes schweinfurthii*) reveal such insights for members of the Kanyawara community in Kibale National Park, Uganda. Our objective is to see if such data yield useful perspectives for future census work on unhabituated chimpanzees, that is, what can scats tell us about a wild study population, beyond diet? We followed ten adults from this community, as well as travelling parties, comparing observed vs. unobserved defaecations, and collected data on scat weight and dimensions, defaecation rate, scat encounter rate, and interval between defaecations. Few non-dietary features of chimpanzee scats significantly differentiated sex or age of the defaecator, but total scat length and height distinguished adults from juveniles/infants. Defaecation rates and distance travelled were similar for adult males and females, indicating the importance of both sexes as potential primary seed dispersers. Observed travelling parties vs. non-observed travelling parties yielded similar data, indicating the potential to assess party size from scat encounter rates over a set distance. We provide detailed measurements of scat dimensions for this ape taxon which previously have been lacking. This research builds upon prior work by recording more in-depth data for focal subjects and travelling parties on defaecation and scat encounter rates. The findings presented should assist in the interpretation of scat data when censusing unhabituated chimpanzees.

✉ Caroline A. Phillips
  Caroline.Phillips@wits.ac.za

1   Present Address: Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

2   Department of Archaeology and Anthropology, University of Cambridge, 13A Fitzwilliam Street, Cambridge CB2 1QH, UK

3   Department of Human Evolutionary Biology, Peabody Museum, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138, USA

4   School of Psychology and Neuroscience, University of St. Andrews, St. Andrews KY16 9JU, UK

Introduction

Understanding population densities and species distribution is vital to initiate action plans for conserving wild primates. Such endeavours are achieved by completing census work across sites (surveying and monitoring the current status of remaining populations). Researchers face logistical challenges during census efforts when study subjects are wary to human observers at close proximity (i.e., unhabituated, Williamson and Feistner 2011). For primates, reconnaissance surveys are a common census technique, although the use of camera traps and mirrors can help to gain insight into animal behaviour (Boyer-Ontl and Pruetz 2014; Anderson et al. 2016). Surveys traversing large areas within home ranges determine: (1) presence/absence of species in a region; (2) population density and distribution;

and (3) behavioural ecology of unhabituated animals. Workers also seek indirect evidence, such as food remains, sleeping sites, foot or handprints, or scats, and opportunistic sightings and vocalisations of study subjects (Doran et al. 2002; Hernandez-Aguilar 2009; Williamson and Feistner 2011; Kalan et al. 2016). However, most primates remain unhabituated, and given ongoing threats to wildlife through habitat encroachment, zoonotic disease transfer, and hunting by humans (Travis et al. 2008; Linder and Oates 2011; Bezanson et al. 2013; Chaves et al. 2012; Rimbach et al. 2013), this approach will likely continue to be needed.

The following is a brief review of survey-related techniques that have been applied across primate taxa, especially in studies of great apes. Indirect evidence such as sleeping sites (usually arboreal nests), trails, feeding sites and remains, artefacts (e.g., tools), knuckle-prints, footprints, hair and excreta have been used at many great ape study sites (McGrew et al. 1988; Tutin 1996; Rogers et al. 2004; Johnson et al. 2005; Koops 2011). Scats are commonly sought out to confirm ape presence, in particular, for sympatric gorillas (*Gorilla* spp.) and chimpanzees (*Pan* spp.) (Furuichi et al. 1997; Morgan et al. 2006; Sunderland-Groves et al. 2003). Analyses of scat content has also proved helpful in understanding dietary and non-dietary aspects of great ape behaviour. At the molecular level, genetic work on scats have increased our understanding of ape phylogenetics (Morin et al. 2001; Thalmann et al. 2007; Clifford et al. 2004; Chancellor et al. 2012), gene flow (Kanthaswamy and Smith 2002; Goosens et al. 2003) and paternity (Morin et al. 1994; Field et al. 1998; Constable et al. 2001; Inoue et al. 2013) as well as kinship, sex ratio, group size, and ranging (McGrew et al. 2004). Faecal glucocorticoid metabolites have detected stress responses in wild apes to social hierarchy and human encounters (Muehlenbein et al. 2012; Murray et al. 2013; Shutt et al. 2014) as well as reproductive cycles of females (Emery Thompson 2005). Stable isotope analysis of scats has provided insight into seasonality in great ape diet (Blumenthal et al. 2012; Phillips and O'Connell 2016) as well as infant weaning of apes (Bădescu et al. 2016). At the macroscopic level, scat consistency and presence of parasites have been used to indicate the health status and self-medication of study subjects (Wrangham 1995; Ashford et al. 2000; Krief et al. 2005) and inspection of scats has contributed greatly to understanding diet composition and seed dispersal across ape taxa (McGrew et al. 1988; Tutin and Fernandez 1993; Wrangham et al. 1994; Basabose 2002; Stanford and Nkurunungi 2003; Phillips and McGrew 2013, 2014). Thus, analysing scats may provide a wealth of data on great apes, but non-dietary features of scats have been little studied.

Most data for non-dietary analytical features concern either scat weight or defaecation rate (Williamson et al. 1990; Bradley et al. 2008; Takenoshita and Yamagiwa 2008; Todd et al. 2008). Weights of scats of mountain gorilla (*Gorilla b. beringei*), western lowland gorilla (*G. g. gorilla*) and Bornean orangutan (*Pongo pygmaeus*) correlate with defaecator age and sex, with adults defaecating heavier scats than juveniles and infants, and adult males producing heavier scats than females (Harcourt and Fossey 1981; Galdikas 1982; Tutin and Fernandez 1985). Differences in bolus size (diameter) exist among adult male and female mountain and lowland gorillas, as well as among adults, juveniles and infants (Schaller 1963; Tutin and Fernandez 1993; McNeilage et al. 2006; McFarland 2007; Todd et al. 2008). Faecal bolus diameter also has been used to contrast scats of sympatric eastern chimpanzees (*P. t. schweinfurthii*) and eastern lowland gorillas (*G. g. graueri*) (Yamagiwa et al. 1996).

Measuring defaecation rate when combined with dietary analyses of scats has illuminated seed dispersal roles for all ape taxa (McConkey and Chivers 2007 for gibbons (*Hylobates meulleri × agilis*); Wrangham et al. 1994, Gross-Camp et al. 2009 for chimpanzees; Tsuji et al. 2010, Beaune et al. 2013 for bonobos (*P. paniscus*); Rogers et al. 1998, Voysey et al. 1999 for gorillas; Galdikas 1982 for orangutans), and for other frugivorous primates: Estrada and Coates-Estrada (1991) for howler monkeys, *Alouatta palliata*; Chapman (1995) for sympatric primates in Africa, Asia and South America; Lucas and Corlett (1998) for long-tailed macaques, *Macaca fascicularis*; and Poulsen et al. (2001) for sympatric primates in Africa. Some tree species depend on primates as principal dispersers of their seeds, so knowledge of defaecation rate of study individuals, collected across seasons with seed content of scats and diurnal distance travelled, helps to reveal a primate's role in forest regeneration and conservation (Gross-Camp et al. 2009; Tsuji et al. 2010, Beaune et al. 2013).

Population densities also have been estimated through decay rate of great ape scats (Morgan et al. 2006; Morgan 2007), which may be a viable alternative to nest decay rates (Takenoshita and Yamagiwa 2008; Todd et al. 2008). Chimpanzee scats appear to decompose at a faster rate than gorilla scats, due to lower fibre content (Morgan et al. 2006). This raises the question as to whether they can also be used to estimate chimpanzee population densities (Takenoshita and Yamagiwa 2008). Measured decay rates of scats have not been published for any chimpanzee site, but data on decay and disappearance rates of scats for the Kanyawara community in Kibale National Park, Uganda, from June to December 2008, reveal a decomposition period of over 60 h for some scats in the dry season (Phillips et al. unpubl. data).

Chimpanzee scats can be distinguished from those of other sympatric primate species with relative ease due to size, form, odour, consistency, and associated traces (Tutin 1996; Poulsen et al. 2001; Basabose 2002; Morgan et al. 2006). However, no descriptive information and little non-dietary systematic measurements (i.e., scat dimensions and weight) are available. The lack of such data applies across fauna in general, and the logistical difficulties of observing study animals likely explains this paucity. For species that are mostly arboreal, locating and measuring of scats that have been scattered by understory vegetation on descent is taxing, but solutions are being found to locate primate scats, such as training dogs to do so (Orkin et al. 2016). Also, determining scat dimensions (i.e., diameter, length, width and height) and volume is difficult when scat consistency is less than solid. Nevertheless, non-dietary information provides insights into age, sex, health, and population density of apes.

We present findings from measuring non-dietary analytical features of scats from the habituated Kanyawara chimpanzee community in Kibale National Park, Uganda to see if it can contribute to future census work on unhabituated chimpanzees (e.g., to find out how accurately scats inform about age and sex of individuals).

Methods

Study site and study population

Habitat and seasonality at the study site, as well as background information on the Kanyawara chimpanzee community, are described in Phillips and McGrew (2013). The Kanyawara chimpanzees were categorised into the following age classes: infant 0–5 years; juveniles 5–8 years; adolescents 8–15 years; and adults 15 years and older. The Uganda Wildlife Authority and Uganda National Council for Science and Technology permitted data collection on the Kanyawara chimpanzee community and research adhered to ethical guidelines set by the Department of Archaeology and Anthropology, University of Cambridge.

Data collection

Most data presented come from scat samples collected <20 min post-defaecation from following ten fully habituated adult chimpanzees (five males and five females) for up to three consecutive days each (focal sample: Martin and Bateson 2007). We obtained two focal samples for nine of the ten focal subjects for test and retest purposes. To be certain of defaecator identity, we collected scat samples from unobserved defaecations only when the focal subject was travelling alone. For unobserved defaecations, an independent scat was defined as faecal matter (>50% of total scat) within a circular area of ∼20 cm diameter. Faecal matter found outside this area was excluded from sample collection. We determined this criterion through preliminary calculations of total distance between each stool (a section of scat defaecated) per scat ($N = 75$) which gave a median value of 19 cm (range 0–4.2 m, Table S1, Supplementary Information). Median distance between each stool per scat was 10 cm (range 0–4.2 m); Kuehl et al. (2007) found the same for western lowland gorillas. For 58% ($N = 109$) of stools, minimum distance was zero as they were touching.

Defaecation rates for members of the Kanyawara community are given by: (1) number of scats produced per individual per day by the observed focal subjects; (2) total number of scats observed to be defaecated by all members of a party per follow; and (3) total number of scats not seen to be deposited that were encountered along a transect (25 m wide) through an area recently (<20 min) traversed by members of the community. This approximates to an unobserved chimpanzee party (Todd et al. 2008). Following both party types and encountering scats in which the defaecation was seen vs. unseen allowed the validation of scats to provide information on party-size, age and sex of defaecator. To consider the role of each sex as primary seed dispersers, we analysed content of scats collected from the ten focal subjects at macroscopic level. We used percentage volume estimates of food remains in scats [i.e., its percentage (100%) of the total volume of food-item content per sieve] to determine composition of frugivory, folivory and faunivory in the diet (Basabose 2002; Phillips and McGrew 2014) and seed content (using percentage estimate of total volume of fig and non-fig seeds, Table S2, Supplementary Information) for both males and females in this community (Wrangham et al. 1994).

We recorded for observed defaecations: (1) defaecation time; (2) defaecator sex and age class (adult, adolescent, juvenile and infant); (3) location (to the nearest trail or transect and by using GPS); (4) defaecation height (m) which was the distance between the platform used to defaecate and where the scat landed (measured with a 5 m tape measure, but estimated for arboreal defaecations); (5) defaecation platform to see if a sex preference existed in the nature of the platform used for terrestrial defaecations, that is, whether they perched—further specifying if on a root, log, broken branch, rock, soil mound—or were walking, or had stopped to defaecate either standing or crouching, and for arboreal defaecations, whether the chimpanzee was nested or not; (6) number of stools per scat and distance between them (cm) using 5 m tape measure; and (7) scat dimension (i.e., length, width and height of stools (cm)), using self-made callipers, consisting of a metal 20 cm ruler with a detachable, washable plastic

strip fitted around the ruler, allowing it to be slid up or down. For any arboreal defaecations scattered upon descent, the area coverage (m^2) was measured (when possible) using the 5 m measuring tape.

As focal subjects were sometimes unobservable, some defaecations must have been missed (Phillips and McGrew 2013). Other unobserved defaecations included some of those from their arboreal beds (i.e., nocturnal defaecations or before the start of a focal sample: Todd et al. 2008). To compensate for missed diurnal defaecations, we calculated defaecation rate per hour for the ten adult chimpanzees based on dividing the total number of defaecations observed (OD) by the total time each individual was in view per daily focal sample (T_{IV}). We then used the 13-h diurnal period (DP) to prorate defaecations for the ten adult chimpanzees between un-nesting and nesting. This calculation for diurnal defaecation rate (DDR) throughout DP assumes defaecation rate was steady (Todd et al. 2008):

$$\text{Diurnal defaecation rate (DDR)} = \frac{\text{OD}}{T_{IV}}(\text{DP}).$$

To determine defaecation rate by an observed party (total party size included chimpanzees of all ages), we followed 15 mixed-sex parties for ≤ 4 h (range 00:46–03:58 h). Mean party size at the start of each follow was $12.5 \pm$ SE 13.9 individuals, but fission and fusion occurred during each follow. We followed each party (≥ 10 m behind) recording all observed defaecations in order to calculate: (1) total scats encountered; (2) interval time per scat encounter; and (3) defaecation rate per hour. Finally, we recorded scats that were encountered (i.e., unobserved defaecations of a travelling party) whilst we traversed a ≤ 3 km transect (range 0.2–2.9 km) which followed the direction travelled by 16 mixed-sex parties (followed for ≤ 05:36 h; mean party size at beginning of follow: $10.8 \pm$ SE 1.41). We again recorded: (1) total scats encountered; and (2) interval time per scat encounter based on total scats encountered, to compare with follows of observed parties, to see how similar the data were for observable vs. unobservable defaecations for a party of chimpanzees.

To determine scat weight (g), we first wet-weighed bagged samples of collected scats on a Kenex KX digital scale (400 g $\times$ 0.1 g capacity). We then deducted the average weight of ten pre-weighed sample bags from the total weight of each bagged sample to calculate scat weight. To allow for any partial assemblages of scats, we adjusted their wet-weights based on the estimated proportion (%) of scat that had been collected, to approximate a 'complete' scat.

Data analyses

Samples sizes were small for statistical analyses, therefore, we used mean and median total repeated values for each

individual rather than values for each focal sampling day to minimise pseudo-replication of data. Statistical analyses were done on MINITAB® Release 14 and SPSS version 21.0. The alpha value was set at 0.05 and normality of data was tested using the Anderson–Darling test.

For repeated measures from the ten focal subjects, we used Mann–Whitney U tests (two-tailed) to compare sexes for observed defaecation rates per day and distance travelled per day. We applied Wilcoxon signed-rank tests (two-tailed) to investigate seasonal changes in daily defaecation rates, using pooled values for focal subjects that were available in both wet and dry periods. We also tested for sex differences in defaecation interval time, defaecation rate per km and across a diurnal period (DP) using Student's t tests (two-tailed). DP was based on the earliest and latest time observed for a chimpanzee to leave an overnight, arboreal bed (un-nest) and later to construct a new bed (nest). We also used this test for sex differences in scat seed content, and to compare percentage volume estimates of food remains in scats collected from both males and females. Paired t tests (two-tailed) were used to compare diurnal variation for defaecation rates by sex across DP.

We applied Mann–Whitney U tests (two-tailed) to compare total scats encountered and interval between scat encounters for both observed and unobserved parties. We correlated total scats encountered vs. party-size and total time that parties were followed with Spearman Rank Correlation tests (homoscedasticity was confirmed by testing variance using ANOVA).

To assess sex differences in scat weight and scat dimensions, again Mann–Whitney U tests were done, and to compare scat weights across DP, which was divided into a 'morning/early afternoon' phase (06:15–12:29 h, 'DPam') and an 'afternoon/evening' phase (13:00–19:15 h, 'DPpm') Friedman tests (two-tailed) were used. Student's t tests (two-tailed) were applied to determine age-class differences in scat dimensions.

Results

Defaecation rate

During focal observations, we saw a total of 324 defaecations by the ten adults, as well as defaecations by seven adolescents, three juveniles and three infants ($n_{adults} = 292$; $n_{adolescents} = 21$; $n_{juveniles} = 6$; and $n_{infants} = 5$). Median defaecation rate for the focal subjects was 6.4 day^{-1} per individual (range 2.9–7.5 day^{-1}). Defaecation rate did not differ by sex (♀ 6.7 day^{-1}; vs. ♂ 5.8 day^{-1}; Mann–Whitney: $W = 34.5$, $p = 0.17$, $n =$ five females, five males). For adolescents, infants and juveniles, median defaecation rate was only one per day, presumably

because of the challenge of observing their defaecations during focal adult follows. Thus, we give below non-dietary findings only for adult scats, except for scat dimensions for which all age-classes are included.

We found no seasonal difference in defaecation rates (Wilcoxon test: $T = 7.5$, $p = 0.31$, $n =$ median defaecation rates per day from seven adults; median$_{wet} = 6.0$ day^{-1}, median$_{dry} = 6.0$ day^{-1}). Mean interval between observed adult defaecations was 01:59 h ($\male = 01:41$, range 00:02–04:11, $n =$ five individuals; $\female = 02:18$, range 00:02–10:35, $n =$ five individuals). We found no sex difference (Student's t test: $T = -1.31$, $p = 0.25$, $n =$ five females, five males). No sex differences in defaecation rates across DP occurred either ($\female$ 11.5 day^{-1}; $\male$ 8.5 day^{-1}; T $= -2.42, = 39$, $p = 0.05$, $n =$ five males, five females). Across DP, the defaecation rate for females was higher in the afternoon/evening phase (DPam: $2.6 \pm$ SE 0.4 vs. DPpm: $4.0 \pm$ SE 0.7; paired t test: $T = -3.3$, $p < 0.05$, $n = 4$); for males, no difference existed between the two phases ($T = -1.07$, $p = 0.36$, $n = 4$).

Per day, travel distance averaged $2.3 \pm$ SE 0.3 km for females (range 0.5–4.9 km) and $2.5 \pm$ SE 0.1 km for males (range 1.3–4.4 km) with no sex difference ($W = 23$, $p = 0.40$, $n =$ five males, five females). No sex difference occurred for defaecation rate per km ($\female = 3.5$ km^{-1} vs. $\male = 2.5$ km^{-1}; $T = 1.49$, $p = 0.18$, $n =$ five females, five males).

Mean percentage of food remains in scats ($n = 112$) analysed at macroscopic level showed no sex differences in frugivory, folivory, or faunivory (Table S2 and S3, Supplementary Information), or in scat seed content (Student's t test: non-fig seeds $T = -0.13$, $p = 0.90$, $n =$ five males and five females: fig-seeds $T = -0.79$, $p = 0.46$, Table S3, Supplementary Information).

For observed defaecations of a known party size, the mean number of total scats was $5.8 \pm$ SE 0.9 per party (mean party size $12.5 \pm$ SE 13.9 individuals, range 2–15), median interval per scat encounter was 12 min, and defaecation rate per hr was $3.3 \pm$ SE 0.5. For scats encountered for the unobserved party, mean total was $7.1 \pm$ SE 1.7 scats per party (mean party size at beginning of follow: $10.8 \pm$ SE 1.41, range 0–26), median interval per scat encounter was 8 min. We found no difference between party types (i.e., observed defaecations vs. unobserved defaecations) for total number of scats encountered or interval per scat encounter (Mann–Whitney: total number scats: $W = 240.5$, $p = 1.00$, $n = 15$ and 16 parties followed; interval duration $W = 270$, $p = 0.24$). We found no correlation between total scats encountered and party size (Spearman: $r_s = 0.21$, $p = 0.45$), or for total time a party was followed ($r_s = 0.27$, $p = 0.34$).

Scat weight

Median scat weight for the ten followed adults was 120 g (range 14–288 g, $n = 198$). Not all scats could be collected due to: scat consistency (i.e., scats too loose to collect using a spatula or a plastic bag); risk of losing a focal subject who kept moving away during sample collection; and failure to locate all of the scat if displaced over a large area, especially from arboreal defaecations. Therefore, using our calculated 'complete' scat weights, scat weight did not differ between females (95 g) and males (143 g) (Mann–Whitney: $W = 21$, $p = 0.21$; $\female$ range 14–288 g, $N = 105$ scats from 5 individuals; $\male$ range 19–289 g, $n = 93$ scats from five individuals). No difference in median scat weight existed between the two phases of DP for either sex (DPam: $\female = 111$ g; $\male = 146$ g; DPpm: $\female = 107$ g; $\male = 145$ g; Friedman: $\female$ $S = 1.8$, $p = 0.18$, $n = 5$; $\male$ $S = 0.2$, $p = 0.66$, $n = 5$).

Scat dimensions

Table 1 gives mean total scat length (calculated by adding up lengths of all stools per scat), stool length per scat, and stool width and height, for each age class. For defaecations from different platforms, Table 2 gives scat dimensions for adult males and females. Median scat length did not differ between the sexes ($\female = 11.6$ cm, range 4.1–23 cm, $n = 50$ scats from five individuals; $\male = 13.7$ cm, range 5–24.1 cm, $n = 47$ scats from five individuals; Mann–Whitney: $W = 20$, $p = 0.14$, $n = 5$). We found no sex difference for stool length per scat ($\female = 6.2$ cm vs. $\male = 8.2$ cm; $W = 35$, $p = 0.14$, $n = 5$), nor for scat width and height ($W = 29.5$, $p = 0.75$, $n = 5$ for width; $W = 26$, $p = 0.83$ for height, $n =$ ten individuals; scat width $\female = 4.8$ cm, range 1.2–11 cm, $n = 50$; $\male = 5.2$ cm, range 2.5–12.7 cm, $n = 47$; scat height $\female = 3.1$ cm, range 0.7–12.7 cm, $n = 50$; $\male = 3.4$ cm, range 0.8–8.6 cm, $n = 50$). Between age classes, total scat length differed between adults vs. juveniles/infants, and adolescents vs. juveniles/infants ($p < 0.05$: Table 1). Scat height was greater for adults vs. juveniles/infants, and stool length was longer for adolescents vs. juveniles/infants ($p < 0.05$: Table 1).

Both adult males and females defaecated on average two stools per scat ($\female$ $\bar{x} = 2$ per scat; $N = 316$ stools; $\male$ $\bar{x} = 2.1 \pm$ SE 0.3 per scat; $n = 262$ stools; range 1–4 stools for both sexes) with a median total stool distance of 18 cm per scat (range 0–2 m). This supports the finding followed from our preliminary scat calculations of removing faeces only an area of ~ 20 cm diameter. For arboreal defaecations, most could not be found or collected, as they hit vegetation on descent and scattered. Of samples that could be measured, defaecation area for

Table 1 Mean (±SE) and range (cm) of scat dimensions: total scat length; stool length, width and height per scat for adults, adolescents, juveniles and infants of the Kanyawara chimpanzee community, Kibale National Park, Uganda

Age class (No. of subjects)	Total scat length	Stool length	Stool width	Stool height
Adults (N = 10)	13.7 ± 0.9	7.8 ± 0.4	5.2 ± 0.2	3.2 ± 0.2
	10.1–18.0	5.5–9.5	4.4–6.2	2.0–3.9
Adolescents (N = 7)	12.7 ± 1.1	7.1 ± 0.7	4.7 ± 0.60	1.9 ± 0.47
	8.0–16.0	4.4–9.1	3.1–7.5	0.4–3.6
Juveniles (N = 3)	8.8 ± 1.2	6.6 ± 2.3	5.3 ± 1.1	1.6 ± 0.8
	6.6–10.9	3.3–10.9	3.9–7.5	0.5–3.1
Infants (N = 3)	5.3 ± 1.2	5.3 ± 1.2	3.8 ± 0.2	1.4 ± 0.6
	3.0–6.6	3.0–6.6	3.0–5.0	0.4–2.6
Dimensions compared by age-classes (Student's t test)				
Adults vs. adolescents	$p = 0.48$	$p = 0.44$	$p = 0.50$	$p = 0.94$
	$T = 0.73$	$T = 0.81$	$T = 0.71$	$T = -0.07$
Adults vs. juveniles/infants	$p < 0.05$	$p = 0.19$	$p = 0.44$	$p < 0.05$
	$T = 4.74$	$T = 1.47$	$T = 0.83$	$T = 2.58$
Adolescents vs. juveniles/infants	$p < 0.05$	$p < 0.05$	$p = 0.89$	$p = 0.57$
	$T = -3.62$	$T = 3.43$	$T = 0.14$	$T = -0.59$

Table 2 Mean percentage (±SE) of defaecations for each platform, from pooled mean totals for five adult female and five adult male chimpanzees of the Kanyawara community, Kibale National Park, Uganda. Mean defaecation height (m) by sex listed for defaecation platforms

Defaecation platform	Defaecation (%)	Defaecation height, m	Scat dimensions (cm)			
			N	L	W	W
Tree						
♂	28.2	9.6 ± 5.50	5	9.9 ± 4.2	5.7 ± 2.3	1.2 ± 0.6
♀	59.6	8.9 ± 2.90	20	11.6 ± 4.0	5.3 ± 1.5	2.5 ± 1.0
Bed (day and night)						
♂	12.9	8.7 ± 3.00	–	–	–	–
♀	1.9	8.0 ± 7.50	–	–	–	–
Perch log						
♂	33.2	0.3 ± 0.1	14	14.3 ± 4.5	4.8 ± 1.3	4.2 ± 1.7
♀	19.3	0.3 ± 0.1	16	5.3 ± 3.8	4.5 ± 1.5	3.8 ± .2.0
Perch broken branch						
♂	10.0	0.2	–	–	–	–
♀	11.1	0.5	–	–	–	–
Perch root						
♂	35.7	0.1 ± 0.01	8	13.6 ± 2.9	4.9 ± 1.3	4.9 ± 1.6
♀	4.1	0.1	–	–	–	–
Perch other (e.g., rock)						
♂	12.2	0.7 ± 2.70	–	–	–	–
♀	5.2	5.1	–	–	–	–
Walk or stand						
♂	25.9	0.5 ± 0.10	6	9.9 ± 4.2	4.9 ± 1.2	2.9 ± 0.6
♀	17.8	0.4 ± 0.02	7	7.5 ± 6.5	4.2 ± 0.9	2.9 ± 1.4
Crouch						
♂	37.0	0.1 ± 0.02	11	14.5 ± 4.5	5.9 ± 1.0	3.6 ± 1.0
♀	11.6	0.1 ± 0.05	3	9.1 ± 7.3	4.9 ± 4.3	4.1 ± 3.0

Total scat length (L), mean stool width (W) and height (H) from pooled mean total for all ten chimpanzees. Number of defaecations measured ($N = 90$)

females was $\bar{x} = 1.1$ m^2 (1.03×1.03 m, $n = 10$ scats) and for males $\bar{x} = 0.4$ m^2 (0.63×0.63 m, $n = 8$ scats). Defaecation heights ranged from 4.5 to 12 m. Sex difference could not be tested statistically (only ≤3 individuals per sex available).

Defaecation platform

Of 286 adult defaecations seen, most (55%) were terrestrial: 30% entailed perching on: a fallen log (18%) root (8%), broken branch (2%), soil mound, rock or vine (2%). The remaining defaecations occurred when an individual walked or stood quadrupedally (12%), crouched, or was already lying down (13%). Females defaecated more often from trees ($\bar{x} = 60\%$ per female, $n = 5$ adults) than terrestrially, and males more often on the ground, in particular on perches ($\bar{x} = 33\%$ on log; $\bar{x} = 36\%$ on root per male, $n = 5$ adults) or crouched ($\bar{x} = 37\%$).

Discussion

Unlike other great apes, there seem to be few non-dietary analytical features that distinguish scat differences between the sexes in adult chimpanzees. Scat weights were similar for males and females in this study, but they differ between male and female Bornean orangutans and western gorillas (Galdikas 1982; Tutin and Fernandez 1985). A more pronounced contrast in body mass between male and female *Gorilla* (♀ = 71.0 kg vs. ♂ = 175.2 kg) and *Pongo* (♀ = 35.6 kg vs. ♂ = 78.5 kg) compared to *Pan* (♀ = 33.7 kg vs. ♂ = 59.7 kg) may explain sex differences in scat weight and scat dimension (Smith and Jungers 1997; Remis 2000). For diet composition (i.e., frugivory, folivory and faunivory intake) differences were also found between sexes for both gorillas and orangutans (Remis 2000 for western gorillas, Doran-Sheehy et al. 2009; Galdikas 1988 for Bornean orangutans), which could further explain the contrasting scat weights. Using percentage volume estimates of food remains in scats to determine diet composition, as applied in some of the above-cited studies, we found no difference in diet between the focal male and female chimpanzees, or in total number of plant foods eaten per day (Phillips 2012), total time spent feeding, total number of feeding bouts per day, or total bouts during morning vs. afternoon/evening feeding times (Phillips and McGrew 2014) that could influence scat content and weight.

Previous work on this community and the neighbouring Ngogo community revealed lower scat weights (range 50–120 g), although this difference was explained by incomplete sample collection from arboreal defaecations (Wrangham et al. 1994). For other chimpanzee communities, scat weights were also lower; 65.7 g in the Dja Reserve, Cameroon (Poulsen et al. 2001), and 100 g in Nyungwe National Park, Rwanda (Gross-Camp et al. 2009). Our use of an estimation for 'complete' scat weight probably explains our heavier sample weights.

Scat dimensions did not differ between Kanyawara males and females. However, for census work, measuring total scat length or scat height may assist in differentiating ages of defaecators, particularly between adults and juveniles/infants. Our dimensions, provided across the age groups, may also help to recognise chimpanzee scats when compared with sympatric primates. Few published data on wild chimpanzee scat measurements are available. Yamagiwa et al. (1996) at Kahuzi-Biega National Park, Zaire, found scat diameters to be for infants <3 cm, juveniles 3–5 cm, adolescent and adults >4 cm. These resemble our width and height values for these age classes (Table 1). As previously mentioned, bolus diameter is used for gorillas to establish sex or age of defaecator, with silverbacks producing largest scats (Yamagiwa et al. 1996; Todd et al. 2008), but as scats measured in this study were not tubular, diameter was not a useful measure. Lambert (2002) gave mean scat length of 10 cm and width of 3.8 cm for scats from two captive adult chimpanzees, which is smaller than that for Kanyawara adults (~12–14 cm scat length vs. ~5 cm for scat width). This size difference could be due to many factors, such as differences in diet, diurnal activity rates, climate, or environmental surroundings.

Primates' role as primary seed dispersers for some tree species is usually determined from defaecation rate and content of scats. Estimated defaecation rate for the Kanyawara chimpanzees over a 12-h period was 6.7 day^{-1} per individual, based on recording a defaecation interval length of 01:48 h (Wrangham et al. 1994). Our estimate over the same period was higher, at 9.4 day^{-1} per individual (range 4.2–12.8 day^{-1}), but our interval length was similar at 01:59 h. Similar rates were found for adult bonobos at Lui Kotale, Democratic Republic of Congo at 7.6 day^{-1} and 01:35 h (Beaune et al. 2013). Lack of sex difference between our observed male and female defaecation rates (except that females defecate more in the latter part of the day), or their defaecation interval time (as in the bonobo study above), indicates that both sexes are equally 'effective' seed dispersers (Beaune et al. 2013). The focal adults in this study traversed similar distances per day and had similar percentage volume contents of seeds in their scats. Using a larger sample size, Pontzer and Wrangham (2006) found males traversed a greater distance than females for this community (♂ 2.4 km day^{-1} vs. ♀ ~1.9 km day^{-1}). Therefore, some bias between sexes within Kanyawara, such as core areas utilised by adult females and males, and the locations of these core areas (Kahlenberg et al. 2008; Bertolani 2013) may influence

seed dispersal. Although defaecation platform data agree with previous observations that most defaecations occurred terrestrially (Wrangham et al. 1994), females produced more arboreal defaecations than males. This may reflect the well-known female inclination across great apes to greater arboreality (Doran 1996); females followed in this study spent more time feeding in trees and males more at ground level (Phillips and O'Connell 2016).

Given no statistical differences between observed and unobserved parties for the total number of scats encountered or the interval between scat encounters, finding scats left by travelling parties of unhabituated chimpanzees could be a useful proxy for party-size. We found total scats encountered were ∼7 for a travelling party of 10–12 individuals, up to a 3 km distance. However, with no correlation between party-size and time followed for total scats encountered, the inference of providing a proxy for party size remains unproven.

Information on non-dietary features from chimpanzee scats is attainable and provides insights into defaecator age, based on total scat length and height measurements, along with a general estimate of party size over a set distance using defaecation encounter rates. However, compared to scats from gorillas and orangutans, such data do not reveal the sex of defaecator. Our findings are constrained by small sample sizes for most age-classes, and other factors such as the softer consistency of chimpanzee scats than gorilla scats may affect scat shape on defaecation for both sexes. *Pan* are less sexually dimorphic in body-size than *Gorilla gorilla* (Remis 2000), which may simply explain the similarity in non-dietary scat features between adult male and female chimpanzees.

This study provides the first in-depth overview of non-dietary analytical features of scats of *P. t. schweinfurthii,* and, therefore, may assist in the collection and interpretation of scat samples during census work on unhabituated chimpanzees. For example, we suggest that future studies use a maximum area of 20 cm diameter (located around the largest part of each scat) to differentiate between scats of individual chimpanzees.

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