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ORIGINAL ARTICLE

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Disappearance rate of chimpanzee scats: Implications for census work on *Pan troglodytes*

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Abstract

Scat (faeces) decay rate estimates are used to calculate animal species abundance and density. For African great apes, this has been measured only for *Gorilla*; chimpanzee scats are assumed to decay at a faster rate due to lower fibre content. We provide the first systematic measure of scat decay rate duration for *Pan troglodytes schweinfurthii*, in Kanyawara, Kibale National Park, Uganda. We used two methods: (1) multiple visits to obtain prospective decay rates (PDR) ($N = 96$ scats) and (2) a novel approach of time-lapse photography (TLP) ($N = 17$ scats). Most of the visited scats (67%) decayed in ≤24 hr, and median decay rate duration from photographic documentation was 18 hr. Using regression analyses, we tested 11 covariables to determine predictors for decay rate duration. Greater volume of scat and reduced levels of diurnal dung beetle activity were positively associated with longer decay rate duration. Given a high prevalence of dung beetle activity (88% of scats), particularly within 3 hr post-defaecation, we suggest the use of the alternative term, *disappearance rate* of scats. With a rapid disappearance rate, scat count surveys of unhabituated chimpanzees are challenging; further work is then needed for *Pan* spp. to determine spatial and temporal differences at intra- and inter-species level.

Résumé

On utilise des estimations de taux de décomposition des crottes pour calculer l'abondance et la densité des espèces animales. Pour les grands singes africains, cela n'a été mesuré que chez les *Gorilla* ; les crottes de chimpanzés sont supposées se décomposer plus rapidement parce qu'elles contiennent moins de fibres. Nous présentons la première mesure systématique du rythme de décomposition pour *Pan troglodytes schweinfurthii*, à Kanyawara, *Kibale National Park*, en Ouganda. Nous avons utilisé deux méthodes : (1) des visites multiples pour obtenir des taux de décomposition potentiels (PDR) (N. de crottes = 96) et (2) une nouvelle approche par photographies à intervalles réguliers (TLP) (N. de crottes = 17). La plupart (67%) des crottes observées se décomposaient en moins de 24 hr, et la durée du temps de décomposition moyen selon la documentation photographique était de 18 hr. En employant des analyses de régression, nous avons testé 11 covariables pour déterminer des indicateurs pour la durée de la décomposition. Un plus grand volume de crottes et une activité diurne plus faible des bousiers étaient positivement liés à une durée de décomposition plus longue. Étant donné une forte prévalence de l'activité des bousiers (88% des crottes), spécialement dans les trois heures qui suivent la défécation, nous suggérons un terme alternatif, le *taux de disparition* des crottes.

Avec un rythme de disparition rapide, les études consistant à compter les crottes de chimpanzés non habitués sont difficiles et il faut donc poursuivre les recherches sur *Pan* spp. pour déterminer les différences spatiales et temporelles au niveau intra- et interspécifique.

KEYWORDS
ape census, decay, dung beetle, faeces, *Pan troglodytes schweinfurthii*, scat

1 | INTRODUCTION

Human activity increasingly threatens the diversity of flora and fauna in Africa. Hunting and habitat encroachment in the form of landscape modification for farming and settlement have caused major declines in animal populations and continue to trigger human–wildlife conflicts (Fa & Brown, 2009; Hoffman & O'Riain, 2012; Madden, 2004; Maisels et al., 2013). For great apes, "*behavioural adjustments*" (Krief et al., 2014) have been observed in response to anthropogenic activity (Hockings & Humle, 2009; Hockings, Yamakoshi, Kabasawa, & Matsuzawa, 2010). Habituation (i.e. when subjects tolerate human observers at close proximity: Williamson & Feistner, 2011) of *Gorilla* and *Pan* has permitted invaluable insights into their behavioural ecology for scientific study (Goodall, 1986; Mitani, Watts, & Muller, 2002; Robbins, Sicotte, & Stewart, 2005; Van Krunkelsven, Dupain, Van Elsacker, & Verheyen, 1999) and has also allowed viewings to take place for the purposes of ecotourism. However, with the occurrence of zoonotic disease transfer, resulting in the deaths of many apes (Goldsmith, 2005; Köndgen et al., 2008; Walsh et al., 2003), some researchers have chosen not to habituate ape study subjects (Deblauwe & Janssens, 2008). Of those that remain unprotected, most are cautious and shy towards humans, and producing abundance and density estimates to reflect the remaining numbers of African apes is challenging (Devos et al., 2008). Recent approaches include genetic censusing, setting up of camera traps and aerial surveys (Boyer-Ontl & Pruetz, 2014; McCarthy et al., 2015; Van Andel et al., 2015), but indirect field evidence of ape presence is still vital for gathering data for local conservation initiatives (Jachmann, 1991). For great apes, this includes foot and knuckle prints, feeding remains, scats, sleeping sites or "nest sites," as well as discarded tools (both used and unused) for extractive foraging (Doran et al., 2002; Kühl, 2008; McGrew, Pruetz, & Fulton, 2005; Tutin, Parnell, White, & Fernandez, 1995).

Nest counts and their decay rate have been used to estimate species abundance and density in all great ape taxa (Hall et al., 1998; Stokes et al., 2010; Wich, Dellatore, Houghton, Ardi, & Koh, 2015); however, differentiating nest sites of sympatric apes has proved challenging (*cf* Sanz, Morgan, Strindberg, & Onononga, 2007). Furthermore, observer bias as to when a nest has decayed can further hinder estimates (Plumptre & Reynolds, 1997). Scat counts have been used to determine species abundance and densities of a variety of fauna (Barnes, 2001; Beauchamp, Wone, Bros, & Kutilek, 1998; Li, Buzzard, & Jiang, 2014; Plumptre & Harris, 1995; Vernes, 1999), including gorillas where it is seen as a potential alternative to using nest count data (Morgan, Sanz, Ononogna, & Strindberg, 2006; Takenoshita & Yamagiwa, 2008; Todd, Kuehl, Cipolletta, & Walsh, 2008). In addition, scats of chimpanzees have been differentiated from other sympatric primates, including gorillas, due to size, form, odour, consistency and associated traces (Basabose, 2002; Morgan et al., 2006; Poulsen, Clark, & Smith, 2001; Tutin, 1996). Methods include a faecal standing plot which involves recording the total number of scats encountered within the study area (Hedges, 2012). Another is locating fresh scats and monitoring them with one or more revisits until they have decayed (Plumptre & Harris, 1995), giving a "prospective decay rate" (Laing, Buckland, Burn, Lambie, & Amphlett, 2003). The most common method applied though has been faecal accumulation rate, also known as marked sign count (Hedges, 2012; Lange, 1969). This involves an observer monitoring a select site (e.g. latrine) or a certain area to assess scat accumulation by noting how many have been deposited since the last visit and how many have decayed (Hedges & Lawson, 2006). Finding and monitoring fresh scats prior to the actual accumulation survey allow the calculation of a mean "retrospective decay rate" (Laing et al., 2003). To convert scat counts into animal densities, defaecation rate and scat decay rates are normally required. Both have been estimated for some studies, or data from other sites have been used, although, given that spatial and temporal heterogeneity can occur (Kuehl, Todd, Boesch, & Walsh, 2007), local data are preferable to obtain more accurate findings. Defaecation rates have been calculated for all ape taxa, particularly to assess their ecological role as seed dispersers (Beaune et al., 2013; Galdikas, 1982; Gross-Camp, Masozera, & Kaplin, 2009; McConkey & Chivers, 2007; Voysey, McDonald, Rogers, Tutin, & Parnell, 1999; Wrangham, Chapman, & Chapman, 1994); however, previous studies on prospective scat decay rates have been done only for western gorillas (Kuehl et al., 2007).

Rainfall and diet influence decay rate of scats of African large mammals (Barnes & Dunn, 2002; Barnes et al., 1997; White, 1995). For gorillas, degree of canopy cover, age of scat and normalised difference vegetation index (NDVI, expressing vegetation structure and rainfall) are all predictors (Kuehl et al., 2007). Coprophagy may be another factor (Livingston, Gipson, Ballard, Sanchez, & Krausman, 2005), but for Kanwayara's ape community, it is little practiced (Phillips & McGrew, 2013). Factors influencing scat decay rate also vary temporally; for instance, seasonality in great ape diet is reflected in scat content (Rogers et al., 2004; Tutin & Fernandez, 1993; Wrangham et al., 1994; Yamagiwa & Basabose, 2006), in which more fibrous matter in scats positively correlated with greater intake of pith and leaves, which tends to occur in wetter periods (Sept-Nov, Apr-May) for the Kanyawara chimpanzees (Malenky & Wrangham, 1994; Phillips & McGrew, 2014). Cellulose and hemicellulose quantities can be greater in scats when there is an increase in intake by apes of fibrous foods, as they are less digestible (Milton & Demment, 1988). This may result in longer scat decay rates (Hedges, 2012). Scat decay rates for *Pan* are not available, but they are thought to decay at a quicker rate than gorilla scats, due to their lower fibre content (Morgan et al., 2006). If chimpanzee scats decay sooner (e.g. <48 hr, the shortest decay rate for gorilla scats, which can take days to weeks: Kuehl et al., 2007; Takenoshita & Yamagiwa, 2008), then estimating the density of remaining wild *Pan* populations may be restricted by using scat count methods.

We present the first systematic measurement for decay rate of scats for *Pan troglodytes schweinfurthii*, for the Kanyawara community in Kibale National Park, Uganda, in order to evaluate the utility of gathering such data for use in future abundance and density estimates for *Pan*, in particular, for unhabituated populations. Furthermore, we examine covariables that may influence and cause heterogeneity in decay rates (Kuehl et al., 2007).

2 | MATERIALS AND METHODS

Samples were collected from fully habituated individuals (*P. troglodytes schweinfurthii*) of the Kanyawara community; Phillips and McGrew (2013) give background information on this community for this study. The apes inhabit a mature, mid-altitude, semi-deciduous and evergreen ecotype comprising of primary, swamp and regenerating forest logged pre-1992 (O'Driscoll Worman & Chapman, 2004). Gaps in canopy cover persist from past logging activities and also from the natural falling of large trees and edaphic reasons (e.g. waterlogged areas preventing tree growth). Natural clearings have also been maintained by the activity of elephants (*Loxodonta africana*). Herbaceous vegetation is eaten by the Kanyawara apes in these open areas. At the time of the study, the Kanyawara community numbered ca. 50 individuals of which 21 were adults. The Kanyawara chimpanzees were categorized into the following age classes: infant 0-5 yr; juveniles >5–8 yr adolescents >8–15 yr; and adults >15 yr. We collected data over 162 days between June and December 2008, spanning the late part of a dry season, the wet season and the early part of a second dry season. Rainfall is a general proxy applied to differentiate seasonal differences at tropical sites for primates (Stampone, Hartter, Chapman, & Ryan, 2011). Mean maximum and minimum monthly temperatures in the combined dry periods and the wetter period were 27.9 ± *SE* 0.4°C and 14.1 ± *SE* 0.1°C; and 28.3 ± *SE* 0.5°C and 14.1 ± *SE* 0.1°C (C. Chapman, personal communication). Mean monthly rainfall during the dry seasons combined was 52.7 ± *SE* 6.6 mm and in the wet season was 212.1 ± *SE* 65.9 mm. 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 as set by the Department of Archaeology and Anthropology, University of Cambridge.

We used two procedures to monitor the decay rate of scats: 1) prospective decay rate (PDR), by making multiple revisits to each fresh scat (N = 96) to measure maximum scat height and to assess the decay process, in order to provide duration time estimates for decay rate of the chimpanzee scats; and 2) time-lapse photography (TLP) (N = 17 scats) in which a camera was programmed to take photographs of a selected scat at set time intervals. TLP photos provided absolute values rather than estimates for the decay process.

We assessed the effect on the decay rate of chimpanzee scats of canopy cover, rainfall, diet, proportion of fruit to fibre remains (using seasonal averages), scat volume, defaecation height, presence/absence of dung beetles (Scarabaeinae), diurnal dung beetle activity, scat temperature, and active ground surface temperature and humidity. Table 1 describes the methods used, with a rationale for measuring each covariable. We did not disturb or remove any faecal matter from the scats being monitored for decay rate.

During PDR sessions, we directly observed defaecations by 27 chimpanzees in total (14 adults, 6 adolescents, 4 juveniles and 3 infants), which allowed monitoring of scats across age classes. Follows occurred throughout their home-range, which over more than a decade has been found to average 16.4 km^2 per year (range 10.8–29.5 km^2) (Wilson, Kahlenberg, Wells, & Wrangham, 2012). For each session, we followed up to eight individuals of mixed age for ≤6 hr to observe defaecations, recording time of defaecation and defaecation height (including if arboreal or terrestrial). We then marked each defaecation site with a plastic peg and recorded the location using GPS (Garmin eTrex). On first encounter (<20 min post-defaecation), we photographed each scat (Nikon Coolpix 4500) as well as canopy cover (photo taken 0.5 m above each scat). We imported the canopy cover photos into Adobe Photoshop version 8.0© and used the histogram function to produce a percentage value for canopy cover (Kuehl et al., 2007). The presence of invertebrates, plus length, width and height of each stool (a distinct section of the total scat defaecated) per scat also were recorded (only five scats were scattered by hitting vegetation during descent in arboreal defaecations, Table S4). Whenever possible, we used these three parameters to calculate volume of scat defaecated. We revisited each scat up to eight times within the first 8 hr post-defaecation, either at approximate hourly intervals (48% scats), or every few hours (for scats where distance apart was too great for hourly visits). Each scat was observed for ~5 min per visit (to allow time for repeated visits to all scats being monitored). During observation, we documented: 1) presence of invertebrates (taxa listed in Table S1), in particular dung beetles. We collected dung beetle specimens (N = 21) that were found on monitored chimpanzee scats and checked taxonomic classification using the World Scarabaeidae Database (Schoolmeesters, 2017); 2) scat height,

TABLE 1 Covariables ($N = 11$) analysed to determine relationship with decay rate duration of chimpanzee scats in Kanyawara, Kibale National Park, Uganda

Covariables	Method	Rationale
Diet: fibre and fruit content per scat[a]	Percentage volume estimate from macroscopic inspection of scats collected from this community during study period (Phillips & McGrew, 2013, 2014).	We collected scats from members of this ape community during the time of this study and obtained dietary data from macroscopic inspection of these scats.
Rainfall level (mm)	Mean monthly level from daily rainfall recorded at Makerere Biological Field Station	Impact of rainfall may affect scat surface, and moisture levels may influence decay rate duration.
Defecation height (m)	Arboreal [estimated height]. Terrestrial [using 5-m tape measure]	Arboreal defecations can hit plant matter on descent which can scatter faecal matter and affect scat height at the start of the decay process if the impact inflicted as it hits the ground is greater *vs*. that from terrestrial defecations. Decay rate of arboreal defecations may therefore be faster if scat height is lowered from the "spreading out" of faecal matter on impact.
Canopy cover	Photo taken, percentage of black pixels in histogram of photo using Adobe Photoshop version 8.0©	Canopy cover influenced decay rate for gorilla scats (Kuehl et al., 2007) and may influence humidity levels which can affect decomposition by micro-organisms
Volume (cm^3)	Using sum of maximum height, width and length per stool [using 5-m tape measure]	By quantifying the amount of faecal matter, we could see if a greater volume of scat took longer to decay.
Presence/ absence Scarabaeinae		Although many invertebrates visit and utilise matter in primate scats, dung beetles can remove large quantities of faeces and so may have a significant effect on decay rate duration.
Scat temperature (°C)	Gemini Tinytag data logger inserted into scat	Scat temperature has not been tested as a predictor of mammal scat decay rate, but it may affect decomposition rate of faeces as it influences the activity rate of micro-organisms in the scat (Anderson & Coe, 1974).
Active surface temperature (°C)	Gemini Tinytag data logger within 10 cm from ground surface	Finally, as active surface ground temperature and humidity (<10 cm from ground level) may fluctuate during the decay process, measuring values taken at the same level of the scat defaecation site may provide insight into their influence on decomposition if they are found to be predictors.
Active surface humidity (%)	Gemini Tinytag data logger within 10 cm from ground surface	
Diurnal dung beetle activity (DDBA)	Total number (%) of photos with diurnal dung beetle activity [dung beetles visible, shifting of scat from underneath, soil piles within the scat] calculated from the total number of diurnal photos taken	See "presence/absence" above

[a]Fruit and fibre content are considered two separate covariables to assess effect of each on scat decay rate process.
Methods of data collection and rationale provided. Covariables only measured for scats monitored using time-lapse photography shaded in grey. Data collected June–December 2008.

measuring from the highest section of the scat; and 3) estimated (%) proportion of the scat remaining. Each scat was monitored ≤60 hr post-defaecation. We used a scat threshold height of <0.5 cm to reduce observer bias (Kuehl et al., 2007; Walsh & White, 2005) and to indicate when monitoring should cease based on preliminary observations of scats from these apes. As a few of the monitored scats ($N = 5$) were ≤0.5 cm in height at the start of the decay process, and as scat height sometimes increased with disturbance of extraneous matter, and faecal matter by dung beetle activity, we also applied a further measure. This was the proportion of the total scat remaining before monitoring ceased (Hedges, 2012) which was ~10% of the faecal matrix (matter excluding undigested and part-digested food components such as seeds). Using Wiles' (1980) classification for age of scat, at this stage of decay, the scat would be considered "barely recognisable," that is "*Decomposition and removal of fecal* [matrix] *so extensive that only with care and examination of indirect evidence can the remaining materials be identified as components of an [animal] dropping.*" Timings for scat decay rate were then categorized into four periods: ≤12 hr, >12–24 hr, >24–48 hr and >48 hr. We could not categorize data into equal periods due to safety issues (i.e. this would have involved nocturnal revisits). We provided estimates only for prospective decay rate if the process had finished between revisits, which became less frequent when the scat was over 24 hours old, due to longer travel times needed to visit each of the scats.

For TLP, we used a Canon Powershot S3I5 camera (secured in a modified Peli case and stand) set on time-lapse mode to record an image at 5-min intervals (Figure S1 and Video S1). The camera was set up within 15 min post-defaecation, and a photograph of the canopy cover was also taken at this time. We also inserted a Gemini Flexi-probe connected to a Gemini Tinytag Plus2 data logger into the centre of a stool of each scat <5 min post-defaecation to measure scat temperature which the data logger recorded at 10-min intervals. The same data logger also recorded active surface temperature, and a separate data logger recorded humidity at this level at 10-min intervals. The camera and data loggers were left to record data for ≤60 hr to provide adequate time for the decay process of the scats and to ensure that monitoring of the battery life in the camera was possible.

2.1 | Data analyses

We used Mann–Whitney *U* tests (Fowler & Cohen, 1990) to test seasonal differences (Chapman, White, & Wrangham, 1996) in maximum scat height (cm) within 20 min of defaecation, after one, two, four and within 24–30 hr post-defaecation, to see if this provided further support for rainfall as a predictor of scat decay rate duration. We used this same test to determine any seasonal differences in total decay rate duration, as well as scat temperature, active surface temperature and humidity. Normality of data was tested using the Anderson–Darling test.

Regression analyses were used to determine the relationship between covariables and scat decay rate duration (Table S2 and S3). Data were logged transformed and were homoscedastistic (Breusch-Pagan test). Normality of data was tested using the Shapiro–Wilk test. We assessed multicollinearity using variance inflation factors (VIF); values indicated strong multicollinearity for fruit and fibre proportions for our ordinary least squares regression model for the time-lapse photography data and so were removed. For our prospective decay rate data, six continuous covariables (rainfall, canopy cover, defaecation height, fruit proportion, fibre proportion and scat volume) and one categorical covariable (dung beetle presence/absence) along with our four decay-rate periods ranked (1–4) were included in our ordered logistical regression model (ologit in STATA: Williams, 2005). No variables were found to violate the parallel lines (proportional odds) assumption (Brant test). For decay rate durations obtained from time to lapse photography sessions, having an observation sample size of 14 and eight covariables (rainfall, canopy cover, defaecation height, scat temperature within 20 min; scat temperature within 1 hr; active ground temperature, active ground humidity and diurnal dung beetle activity (dung beetles visible, shifting of scat from underneath, soil piles within the scat) overfitting in our ordinary least square regression model was a concern (Babyak, 2004). Therefore, we ran an ordinary least squares regression of covariables that were significantly associated with decay rate duration. This was diurnal dung beetle activity (DDBA) only. Statistical analyses were performed on MINITAB® Release 14 and STATA/MP 14.2. The alpha value was set at 0.05 (two-tailed).

3 | RESULTS

For 96 scats monitored with multiple revisits, our prospective decay rate for 67% of scats was ≤24 hr. Of the 10 scats that took longer than 48 hr to decay, seven occurred during dry periods of the study, with three taking over 60 hr to decay. The shortest time for a scat to reduce in height to <0.5 cm with <10% matrix remaining was 40 min, which also occurred in the dry period of July (Figure 1). Figure 2 shows both mean and median scat height across the decay process in wet and dry periods. Scat height was lower after 24 hr in the wetter period (Mann–Whitney *U* test: $W = 2{,}075.5$, $p < .05$, $N_{wet} = 45$, $N_{dry} = 38$ scats, median scat height for both <0.5 cm; Figure 1). From our ordered logistic regression model for the prospective decay rate data, only volume was significantly associated with scat decay rate duration; smaller volume would take a shorter time to decay ($p = .024$; Table S2).

Of the 17 scats monitored using TLP, median scat decay rate was 18 hr (range 6–56 hr, $N = 14$, as data were incomplete for three scats due to weather conditions affecting the camera). No seasonal difference was found for scat decay rate (Mann–Whitney *U* test: $W = 87$, $p = .137$, $N_{dry} = 6$, $N_{wet} = 8$). Mean faecal temperature at the start of the decay process was 28 ± *SE* 1.0°C which reduced to 20 ± *SE* 0.4°C after an hr. Median active surface temperature and humidity around the scat post defaecation were 19°C and 89%

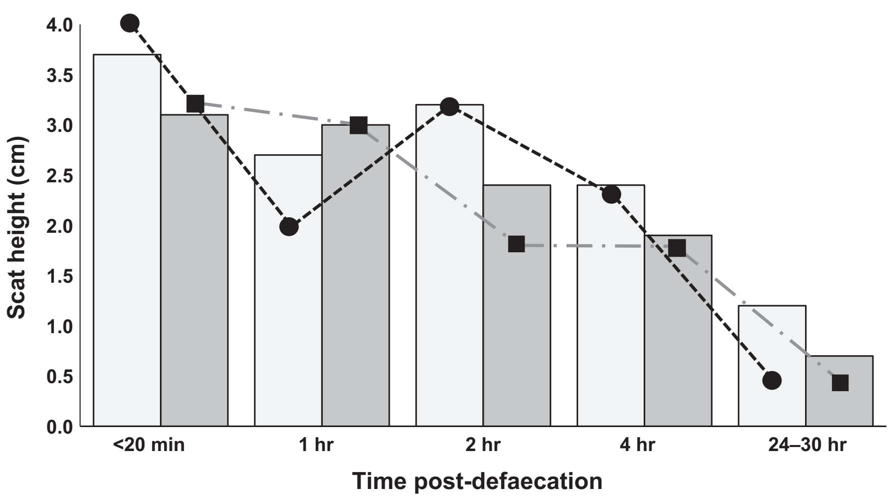

FIGURE 1 Mean maximum height of chimpanzee scats (bars) at set time intervals of decay process in both dry (light grey) and wet (dark grey) periods. Median maximum scat height for each time interval in the dry (circle, dashed line) and wet (squares, dotted-dashed line) periods. Data collected in Kanyawara, Kibale National Park, Uganda, in June–December 2008

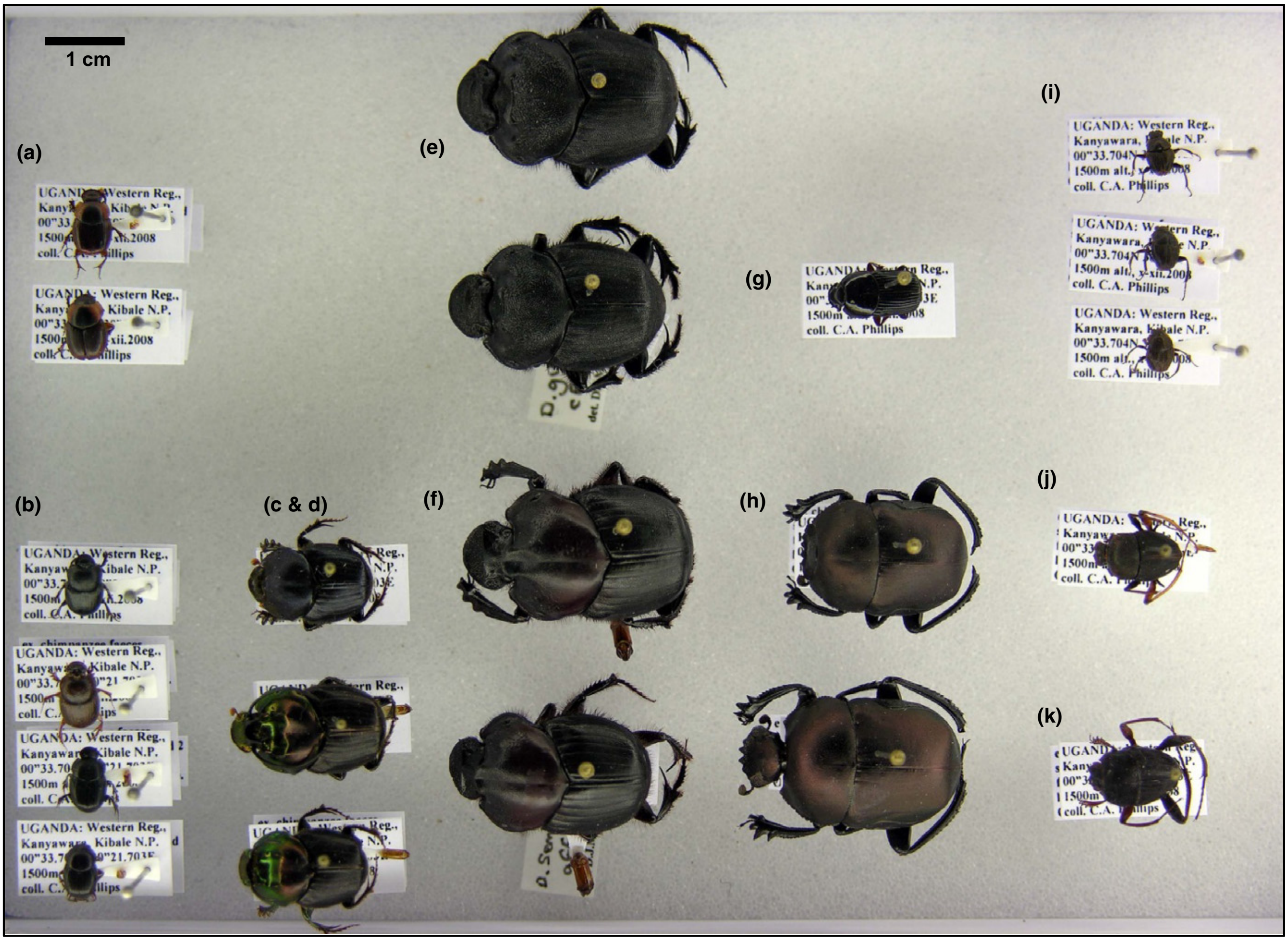

FIGURE 2 Dung beetles collected from chimpanzee scats monitored for decay rate in Kanyawara, Kibale National Park, Uganda, between June and December 2008. Identified by D Mann as follows: (a) *Onthophagus* sp. 2; (b) *Onthophagus* sp. 1; (c) *Proagoderus* sp. 1; (d) *Proagoderus* sp. 2; (e) *Diastellopalpus* aff. *gilleti* [D'Orbigny]; (f) *Diastellopalpus* aff. *semirubidus* [D'Orbigny]; (g) *Oniticellus pseudoplanatus* [Balthasar]; (h) *Garreta* aff. *crenulatus* [Kolbe]; (i) *Sisyphus* sp. 1; (j) *Sisyphus* sp. 2; (k) *Neosisyphus* sp. 1 [Colour figure can be viewed at wileyonlinelibrary.com]

(range 16.3–24.7°C; 74.1–100%). No seasonal difference was found for either temperature ($W = 72$, $p = .41$, $N_{dry} = 7$, $N_{wet} = 10$) or humidity ($W = 50$, $p = .22$).

Diurnal dung beetle activity was statistically associated with decay rate duration in both ordinary least squares regression models (model with seven covariables: $F_{(8,5)} = 2.39$, $p = .048$, $R^2 = .79$; Table S3; model with just DDBA: $F_{(1,12)} = 7.79$, $p = .016$, $R^2 = .39$: Figure 3, Table S3). Higher dung beetle activity statistically predicted shorter decay rate duration.

Dung beetles were found on 88% of scats monitored for PDR. Eleven taxa of dung beetle from six genera were identified by DM from the 21 beetles collected (Figure 2). All have been recorded in primate scats (Chao, Simon-Freeman, & Grether, 2013) and in both primary and disturbed forested regions in Kibale National Park (Nummelin & Hanski, 1989). These were further categorized into the following guilds: rollers ($N = 4$, roll balls of faecal matter and transport to nest to create brood chamber), tunnellers ($N = 6$, drag faecal matter under the scat into nest) or endocoprids ($N = 1$, makes a brood chamber within the scat). When compared to data on dung beetle presence on scats during PDR sessions, six of the 11 taxa (from four genera) identified were recorded on scats visited in both the wet and dry seasons (Table 2), with *Diastellopalpus gilleti* occurring most frequently (42% of scats); 82% of these scats from the wetter period ($N = 23$ of 28 scats). This dung beetle was recorded for Uganda only recently (Chao et al., 2013). Of the six taxa identified during visits to scats, all but *Oniticellus pseudoplanatus* were recorded within the first 3 hr on 45 scats; this beetle was also found on scats in the wet season only (Table 2, Figure 4). Earliest observed dung beetle activity was within a minute post-defaecation.

4 | DISCUSSION

Median decay time for scats using both TLP and for 67% of scats using PDR at Kanyawara was ≤24 hr. For gorilla studies at sites in Gabon, Democratic Republic of Congo, and Central African Republic decay rate duration was 2–21 days (Kuehl et al., 2007; Takenoshita & Yamagiwa, 2008). We did not attempt retrospective decay rate; instead, we sought to obtain a timescale for the decay process of

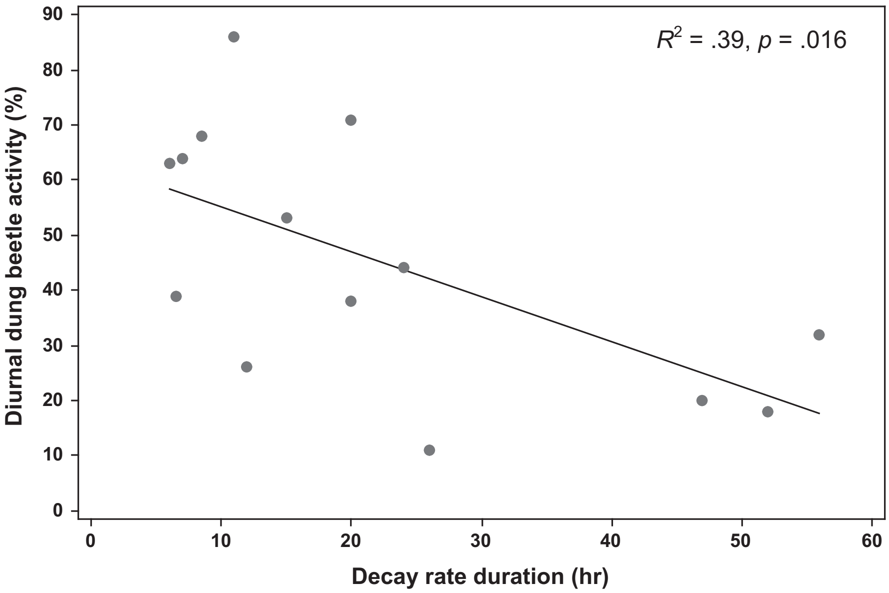

FIGURE 3 Scatterplot with regression line of diurnal dung beetle activity and total decay rate duration of chimpanzee scats (N = 14) in Kanyawara, Kibale National Park. Kanyawara. Data collection June–December 2008

chimpanzee scats across seasons for the Kanyawara chimpanzees. This study was more a "first step" to evaluate the likelihood of there being any "*standing stock*" (Hedges, 2012) to complete a scat count survey, to then be able to calculate retrospective decay rates used for population density estimates. With such a short decay rate of ≤24 hr for most of the scats at Kanyawara, to conduct scat counts using retrospective decay rate during our study would have required the monitoring of fresh scats and the survey to be done on the same day. For censusing of unhabituated chimpanzee populations, workers would need to locate scats at nest or feeding sites early in the morning. It would require much travelling by researchers in a concentrated, short period. Both spatial and temporal heterogeneity in scat decay rate was observed at gorilla study sites (Kuehl et al., 2007). It is possible that differences in rainfall level or degree of dung beetle activity across chimpanzee study sites are not drastic, but intra-site differences in elevation, canopy cover and food resource availability are noted within both Kibale National Park and other regions of Uganda (Stanford and Nkurunungi, 2003 for Ruhija community at Bwindi Impenetrable National Park; Potts, Watts & Wrangham, 2011 for Ngogo community in Kibale) which could all have some influence on scat decay rates. To ascertain the typicality of Kanyawara as a site to represent scat decay rates for *P. troglodytes*, scat decay rate duration needs to be obtained from other chimpanzee sites, in order to establish any spatiotemporal contrast, and also at bonobo sites to align and compare findings between sole extant congeneric species. Research at more arid and open chimpanzee study sites such as Ugalla in Tanzania, or Fongoli in Senegal, might yield different chimpanzee scat decay rates to that found in more closed, evergreen habitat such as Kanyawara. Generally, having less rainfall and potentially, greater solar exposure in a more open habitat, the scats may disappear at a slower rate due to hardening the outer crust. Such sites may provide a greater opportunity to explore the use of scat count surveys to estimate chimpanzee densities should such conditions be found to affect the decay process.

TABLE 2 Dung beetle taxa identified on scats

Dung beetle taxa	Guild	Wet	Dry	≤3	≥5 < 24	>24	>48
Diastellopalpus gilleti	Tunneller	23	5	22	11	4	0
Diastellopalpus semirubidus	Tunneller	11	1	7	1	1	0
Garreta crenulatus	Roller	3	6	3	0	0	0
Onthophagus sp.	Tunneller	9	4	5	0	3	0
Neosysiphus sp.	Roller	2	4	2	3	2	0
Proagoderus sp.	Tunneller	10	2	7	10	0	0
Oniticellus pseudoplanatus	Endocoprid	6	0	0	1	1	0

Taxon, guild and total number of scats in both wet (N = 44 scats) and dry (N = 23 scats) periods that dung beetles were present. Total number of scats (N = 69) that taxa were present at set times between <3 and >48 hr. Data collected in Kanyawara, Kibale National Park, Uganda, from June to December 2008.

Maximum height and proportion of scat remaining were easily measured when monitoring decay of chimpanzee scats at this site; however, scat height did increase during the decay process within hours of defaecation in drier periods (Figure 1). This increase may therefore be viewed as an "*undecay*" event (Hedges, 2012), but generally, scat height decreased as the scat aged, indicating (as with gorilla scats: Kuehl et al., 2007) this to be a useful variable to measure for chimpanzee scat decay rate. Increase in scat height resulted from dung beetle activity that disturbed both faecal matter and surrounding extraneous matter, especially by species in the genus of *Diastellopalpus*, a large beetle that was most often present on scats monitored. This beetle was observed to bury considerable amounts of material from scats monitored into nests within 3 hr of defaecation. For the shortest decay rate duration of 40 min in a dry period, dung beetle activity was observed within 5 min post-defaecation.

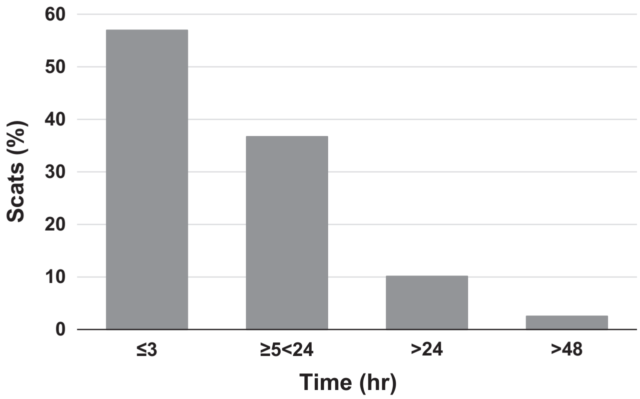

FIGURE 4 Percentage of scats (total N = 69) per time interval (between <3 hr and >48 hr) where dung beetles were present. Data collected in Kanyawara, Kibale National Park, Uganda, June–December 2008

From our ordered logistical regression model using prospective decay rate estimates, only volume was a predictor for decay rate duration, having a positive association, so the smaller the scat volume, the quicker it decayed, which is unsurprising. Further testing of the influence of diurnal dung beetle activity using photographic evidence shows the value of the alternative method of time-lapse photography. More importantly, a lower proportion of fibre remains in chimpanzee scats may not be the primary predictive covariable for scat decay rate duration as hypothesized (Morgan et al., 2006). Instead, a stronger relationship between the removal of faecal matter by dung beetles and a scat decay rate of <24 hr emerged for chimpanzee scats in this tropical forest ecotype (i.e. higher dung beetle presence and activity results in a shorter scat decay rate duration). Removal of faecal matter for human and jaguar scats by dung beetles revealed a disappearance rate of <24 hr in tropical, forested habitats in the Brazilian Amazon (Norris & Michalski, 2010). Dung beetle activity is mentioned as a factor of the decay process of scats for other African large mammals (Hedges, 2012; Todd et al., 2008), but data on how this may have influenced decay rate duration are unavailable. Our study provides a systematic measure of diurnal dung beetle activity in great ape scats. "Disappearance rate" has been used as an alternative term to "decay rate," and for chimpanzee scats, the former in this locale may be a more apt descriptor. Of the 11 dung beetle taxa identified, five arrived within 3 hr of defaecation, four of which were repeatedly recorded on scats within 24 hr. In previous studies of Scarabaeinae, rollers were observed to arrive <3 hr and tunnellers >5 hr for scats monitored in this region. Chao et al. (2013) suggested that rollers removed faecal matter before the arrival of large tunnellers as the latter are able to hoard larger quantities of faecal matter in a short timeframe. Our findings show large tunnellers (and not just rollers) arriving on chimpanzee scats in the early stages of decay of <3 hr, not just rollers across both wet and dry periods. Such a timeframe is congruent with our disappearance rate of ≤24 hr. Another factor is the dispersal of seeds by dung beetles (Shepherd & Chapman, 1998). Although our proportional measure of scat decay rate was based on remaining faecal matrix, the removal of seeds by dung beetles could have further influenced disappearance rates for scats of this ape community.

TLP used in this study succeeded in obtaining scat decay rates and insight into diurnal dung beetle activity, although with one camera, only 17 attempts were achieved during the 6-month study. Using multiple cameras would increase the sample size of scats monitored. Further limitations included the lack of nocturnal viewing of the decay process which could not be monitored with the camera used (rectifiable if a passive infra-red setting was available), plus data from three films could not be analysed fully, as the lens was affected by moisture during heavy rainfall. There also was concern over security of equipment left for monitoring and data collection; however, TLP produced absolute values for decay rates and required less travelling time by workers during census work, once each camera was set up.

Unlike for elephant scats, rainfall levels did not predict chimpanzee scat decay rate at this site. Most scats (79%) were defaecated under canopy coverage of >70% which may have reduced impact of rainfall on the scats monitored. Decay rates of scats monitored for large mammals have shown great variation across months and between habitats (Plumptre & Harris, 1995). Problems can arise in calculating decay rates for each season as long-lived scats can survive from one season into the next and decay at a different rate to scats deposited in the subsequent season (Plumptre, 2000). We found no seasonal differences in scat decay rate, but a longer-term study at this site might show temporal and spatial trends in the predictive covariables analysed (Hedges, 2012; Kuehl et al., 2007) and might resolve why scat height measured at 24–30 hr in the wetter season was lower compared to that in the drier periods. Future studies of ape scat decay rate could include exclusion experiments, such as "containing" the scat in a way to prevent dung beetle activity and measuring decay rate duration in comparison with other scats across the site and seasons exposed to dung beetle activity (Norris & Michalski, 2010). Furthermore, if removal of faecal matter by dung beetles is a primary predictor for chimpanzee scat decay rate, a study on nocturnal behaviour of dung beetles in Kibale National Park would further clarify our findings and ascertain more information on their diel activity, which is currently understudied (Chao et al., 2013).

5 | CONCLUSION

We provide the first systematic measure of scat disappearance rate for *Pan troglodytes schweinfurthii* at Kanyawara, Kibale National Park, typically ≤24 hr, but over 60 hr during drier periods. With such a short timeframe for the completion of scat counts, it may be more productive to continue to do nest count surveys for *Pan*; however, further study is needed of both *Pan* species to determine intra- and inter-species and site differences both spatially and temporally. We also provide data from the novel use of time-lapse photography to measure ape scat decay covariables, including diurnal dung beetle activity, scat temperature, and temperature and humidity values around scats at the active surface ground level. Both volume and removal of scat material by dung beetles were two predictors of scat decay rate duration, but with such a high prevalence of dung beetle activity, we suggest that the alternative term of disappearance rate of chimpanzee scats is more appropriate.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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