

Seed dispersal by forest chimpanzees in Uganda

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ABSTRACT. The role of chimpanzees (*Pan troglodytes*) as seed dispersers in the Kibale Forest Reserve of western Uganda was assessed by analysing 1849 dung samples from two chimpanzee communities and by conducting germination trials on dispersed and non-dispersed seeds. Of the chimpanzee dung samples, 98.5% contained seeds, and fig seeds were the most common. The number of large seeds (>2 mm) per dung sample was often high, even for species with a relatively large seed. For example, *Mimusops bagshawei* has a 15-mm diameter seed and had an average of 26.5 seeds per sample. In addition, many seed species were found in the dung repeatedly over several months. Germination trials demonstrated that the species of seed commonly collected from dung were viable. Comparisons of both the rate and success of germination of chimpanzee-dispersed seeds with seeds collected directly from the parent trees, showed that gut passage increased the speed and probability of germination. The number of large seeds dispersed by the chimpanzee population was estimated at 369 large seeds km⁻¹ day⁻¹. We suggest that in Kibale, chimpanzees may play a more significant role in primary seed dispersal than implied by their low numbers and biomass.

KEY WORDS: chimpanzees, conservation, forest regeneration, monkeys, primates, seed dispersal, Uganda.

INTRODUCTION

The role of mammalian frugivores as seed dispersers has recently received considerable attention (e.g. Chapman 1989, Estrada & Coates-Estrada 1984, Garber 1986, Gautier-Hion 1984, Howe 1980, Tutin *et al.* 1991). A number of researchers have suggested that for the maintenance and preservation of tropical forests, it is critical to maintain the frugivores that facilitate seed dispersal (Chapman *et al.* 1992, Galdikas 1982, Howe 1984, Pannell 1989). However, little is known about the relative importance of different species or classes of frugivores in seed dispersal and forest maintenance.

In the forests of Africa, some of the largest frugivores are the great apes (Goodall 1986, Rogers *et al.* 1990). Seeds dispersed by apes have been found to be viable (chimpanzees, *Pan troglodytes*, Takasaki 1983; bonobos, *Pan paniscus*,

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Idani 1986; gorillas, *Gorilla gorilla*, Tutin *et al.* 1991). Since they consume large fruit meals from many tree species, have large home ranges, and often use a variety of habitats, including various stages of regenerating forest, African apes may play an important role in the dissemination of seeds and in the regeneration of the tropical forests.

In this study we assess seed dispersal rates for chimpanzees in the Kibale Forest Reserve of western Uganda and consider their significance. We first document the relative abundance of the species of seed dispersed by chimpanzees and describe their viability. For the commonly eaten species, we compare the viability and rate of germination of seeds collected from chimpanzee dung with those of non-dispersed seeds collected from parent trees. Finally, we consider the potential importance of chimpanzees as primary seed dispersers relative to the other diurnal frugivorous primates in Kibale Forest. Until the fate of seeds dispersed by chimpanzees can be determined, the actual importance of these frugivores to the reproduction of the different tropical tree species cannot be fully assessed.

METHODS

Study site

Kibale Forest Reserve is located in western Uganda (0° 13' – 0° 41' N and 30° 19'–30° 32' E) near the base of the Ruwenzori Mountains. The forest is transitional between lowland rainforest and montane forest (Butynski 1990, Skorupa 1986, 1988, Struhsaker 1975). The canopy is typically between 20 m and 30 m in height, but some trees exceed 55 m. One of the study communities inhabits a region known as Kanyawara which consists of a series of moderately undulating valleys, and is at an elevation of approximately 1500 m. Throughout the study area trees such as *Diospyros abyssinica* (11.3% of 2111 enumerated trees >10 cm DBH), *Markhamia platycalyx* (10.8%), *Celtis durandii* (9.7%), *Uvariopsis congensis* (8.8%), and *Bosqueia phoberos* (8.0%) are common (based on 26 transects, each 200 m long by 10 m wide). In addition, there are sections of swamp, exotic softwoods, regenerating forest, and grasslands. The second community is located 12 km to the south in a similar area of undulating hills (Ngogo). The elevation of this area is approximately 150 m less than that of the Kanyawara community and slightly drier (5% less rain) and warmer (+0.5°C) (Butynski 1990). At Ngogo, *Uvariopsis congensis* (18.5% of 2622 enumerated trees from 24 transects) is the most common tree species, followed by *Diospyros abyssinica* (12.7%), *Chrysophyllum* spp. (11.8%), *Celtis durandii* (10.5%), *Funtumia latifolia* (6.7%), and *Tabernaemontana* spp. (*T. (Conopharyngia) holstii* and *T. (Gabunia) odoratissima*) (6.2%). Tree species nomenclature follows Hamilton (1991) and Berg & Hijman (1989).

Collection of dung samples

Chimpanzee dung samples were collected between September 1987 and September 1991. Dung, collected during behavioural observations of the chimpanzees and opportunistically, was placed in plastic bags and transported back to

the field camp. Each dung sample was weighed, and seeds longer than 2 mm were extracted. For large-seeded species (>2 mm), the exact number of seeds in the dung was determined. For smaller seeds their abundance was ranked as rare, few, common, and abundant, and these categories were subsequently calibrated to actual counts.

The species of seed was determined by comparison to a reference collection from identified fruits. Seeds that could not be identified were assigned a temporary identification code and were planted and grown for identification. Because of their small size and the large number of seeds per dung sample, no routine attempt was made to determine the species identity of *Ficus* species. Other small seeds were normally not identified to species (e.g. *Urera hypsiloides*).

Germination trials

In March 1990, we initiated a programme to determine the viability of the seeds passed by chimpanzees. This programme is still continuing, but here we report on the results obtained after 18 months of study. Representative seeds of known species or types were placed between cloth towelling in individually labelled petri dishes and watered daily. Seeds with obvious insect damage were excluded from these trials. The seeds were examined daily to assess whether they had germinated. The number of days required for germination for chimpanzee dispersed seeds was compared with that required for seeds collected directly from parent trees. Whenever possible, ripe fruits were collected from small limbs that had been broken off by chimpanzees during their feeding or, for the smaller trees, by climbing the tree and picking ripe fruits.

Tree abundance

The abundance of fruiting trees was determined by marking trees along a series of belt transects in each of the two study areas. Fifty belt plots were built along randomly selected trails from within the existing trail systems (26 at Kanyawara and 24 at Ngogo). The plots were 200 m by 10 m, producing a sampling area of 5.2 ha at Kanyawara and 4.8 ha at Ngogo. Each tree greater than 10 cm DBH (Diameter at Breast Height) within 5 m of each side of the transect was individually labelled, measured at breast height, and identified to species. A total of 4733 trees were marked. Every month the phenological status of all marked trees was determined by noting the presence of fruit and flowers, and assessing the types of leaves present (no leaves, leaf buds, young leaves, and mature leaves).

RESULTS

Seed dispersal rates

A total of 1849 chimpanzee dung samples was analysed ($N = 1128$ Kanyawara, $N = 721$ Ngogo). On average, dung samples weighed 81.1 g (mode = 50.0, median = 70.0, SD = 48.03, range 1–350 g, $N = 1824$). This underestimates the original weight because some samples were collected from chimpanzees

defecating from trees, which led to specimens being scattered. However, chimpanzees typically defecate while on the ground, often along the side of a fallen log. Thus, the majority of the dung samples were intact. The frequency distribution of dung weights suggests that the typical weight was 50 to 120 g.

Seeds occurred in 98.5% of the dung samples (98.8% at Kanyawara, 98.1% at Ngogo, $X^2 = 1.45$, $P > 0.10$). Overall, 77.3% of all dung samples contained seeds larger than *Ficus* and *Aframomum* seeds (approximately 2 mm), but Ngogo samples contained larger seeds more often (Kanyawara 73.6%, Ngogo 83.1%, $X^2 = 22.61$, $P < 0.005$). The number of seed species (or types) found in the chimpanzee's dung averaged 2.8 per sample (SD = 1.39, range 0–8, $N = 1849$), and there was no significant difference between Kanyawara (mean = 2.9 species/sample, SD = 1.43, range 0–8) and Ngogo (mean = 2.7 species/sample, SD = 1.31, range 0–7). The length of the seeds found in the dung ranged from less than 1 mm (e.g. figs) to approximately 27.4 mm for *Cordia millenii* (Appendix 1). No fruits of species with seeds longer than *C. millenii* were eaten by chimpanzees (based on >1000 h of behavioural observations).

The mean number of seeds per dung sample was high for common species (i.e. typically at least 10; Table 1). We found up to 189 seeds per dung for large trees (e.g. *Mimusops bagshawei*, Table 1).

We identified 59 species of seed in the chimpanzee dung (Appendix 1). Of these species, 40 (68%) were from trees, 9 (15%) were herbs, 6 (10%) were shrubs, 2% were vines, and 2% were lianas. The 40 tree species represent 56% of the 72 tree species (>10 cm DBH) identified in our phenology transects.

Seeds of *Ficus* spp. were the most frequently occurring seeds in chimpanzee dung (89.9% Kanyawara, 83.5% Ngogo), followed by *Aframomum* spp. (Table 1, 42.9% Kanyawara, 22.5% Ngogo). These two genera contained 10 and 7 species respectively and fruited throughout the year.

The frequency of occurrence of seeds in dung typically showed marked seasonal and annual variability (Figure 1). For example, the frequency of occurrence of *Mimusops bagshawei* in dung peaked between February and May in 1988, but did not peak again until December 1989 and January 1990. Such variation reflected phenological data on fruit availability. Despite seasonal peaks, seeds of several of the common food species were found in the dung samples repeatedly over several months (Table 1, mean per year over 3 complete years of the species listed = 5.4, months range 0.2–12 months, SD = 3.47). Generally there was at least one fruiting fig tree available, which was reflected in the relatively continuous appearance of *Ficus* seeds in chimpanzee dung (Figure 1). Thus, for certain tree species, chimpanzees were responsible for the dispersal of large numbers of seeds over several months.

Overall, the type and number of seeds found in dung samples were similar between the two study sites. Differences were generally explicable by differences in the density and fruiting pattern of adult trees between the areas. For example, *Monodora myristica* was found in 20.0% of the dung samples at Ngogo, but was found in only 5.9% of the dung samples at Kanyawara: the density of adult

Table 1. Parameters related to the seeds most commonly found in the dung of the Kanyawara and Ngogo communities of chimpanzees of Kibale Forest Reserve, Uganda (N = 1128 Kanyawara, N = 721 Ngogo).

Species/site	% of dung containing seeds	No. of seeds ² per dung (maximum)	Mean no. of months available y ⁻¹	Density (trees ha ⁻¹)	Selectivity %/ density	Selectivity %/ density × month
<i>Uvariopsis congensis</i>						
Kanyawara	9.9	18.0 (88)	3.7	35.58	0.28	0.08
Ngogo	14.6	19.2 (105)	5.7	101.04	0.14	0.03
<i>Mimusops bagshawei</i>						
Kanyawara	32.1	26.5 (189)	4.7	1.73	18.55	3.95
Ngogo	17.8	16.0 (77)	3.0	3.13	5.69	1.90
<i>Ficus spp.</i>						
Kanyawara	89.9	modal rank = common	12.0	6.53	13.77	1.15
Ngogo	83.5	common	12.0	4.19	19.93	1.66
<i>Cordia abyssinica</i>						
Kanyawara	12.1	18.7 (152)	7.9	—	—	—
Ngogo	3.3	11.5 (35)	1.7	—	—	—
<i>Aframomum</i> (type 1)						
Kanyawara	42.9	modal rank = rare	11.7	—	—	—
Ngogo	22.5	rare	9.7	—	—	—
<i>Aframomum</i> (type 2)						
Kanyawara	5.7	modal rank = rare	7.7	—	—	—
Ngogo	0.4	rare	7.7	—	—	—
<i>Aframomum</i> (type 3)						
Kanyawara	10.7	modal rank = rare	10.7	—	—	—
Ngogo	10.4	rare	7.0	—	—	—
<i>Aframomum</i> (type 4)						
Kanyawara	29.7	modal rank = rare	2.3	—	—	—
Ngogo	1.7	rare	1.3	—	—	—
<i>Monodora myristica</i>						
Kanyawara	5.9	10.7 (63)	3.7	0.19	31.05	8.39
Ngogo	20.0	12.4 (43)	5.0	0.42	47.62	9.52
<i>Warburgia stuhlmanni</i>						
Kanyawara	0.0	0.0 (0)	0.0	0.00	—	—
Ngogo	21.4	14.0 (90)	6.3	0.21	101.91	16.18
<i>Pseudospondias microcarpa</i>						
Kanyawara	6.7	17.9 (68)	2.0	0.77	8.70	4.35
Ngogo	5.7	10.9 (45)	3.7	1.25	4.56	1.23
<i>Tabernaemontana spp.</i> ¹						
Kanyawara	7.3	18.1 (89)	3.0	3.85	1.90	0.63
Ngogo	8.2	16.8 (210)	3.0	33.96	0.24	0.08
<i>Chrysophyllum spp.</i>						
Kanyawara	0.3	4.3 (9)	0.7	1.73	0.17	0.24
Ngogo	7.2	11.3 (56)	2.0	64.58	0.11	0.06
<i>Phytolacca dodecandra</i>						
Kanyawara	3.5	46.8	4.0	—	—	—
Ngogo	2.8	27.9	3.0	—	—	—

¹*T. holstii* and *T. odoratissima* both occurred.²This figure is calculated using only samples that contained at least one seed of the indicated species.

Monodora myristica was higher at Ngogo (0.42 trees ha⁻¹) than at Kanyawara (0.19 trees ha⁻¹) (Table 1). *Warburgia stuhlmanni* was found in 21.4% of the dung samples in Ngogo, but was absent from dung at Kanyawara. Correspondingly, this tree was absent in the transect survey conducted in the Kanyawara forest and is thought not to occur in the area.

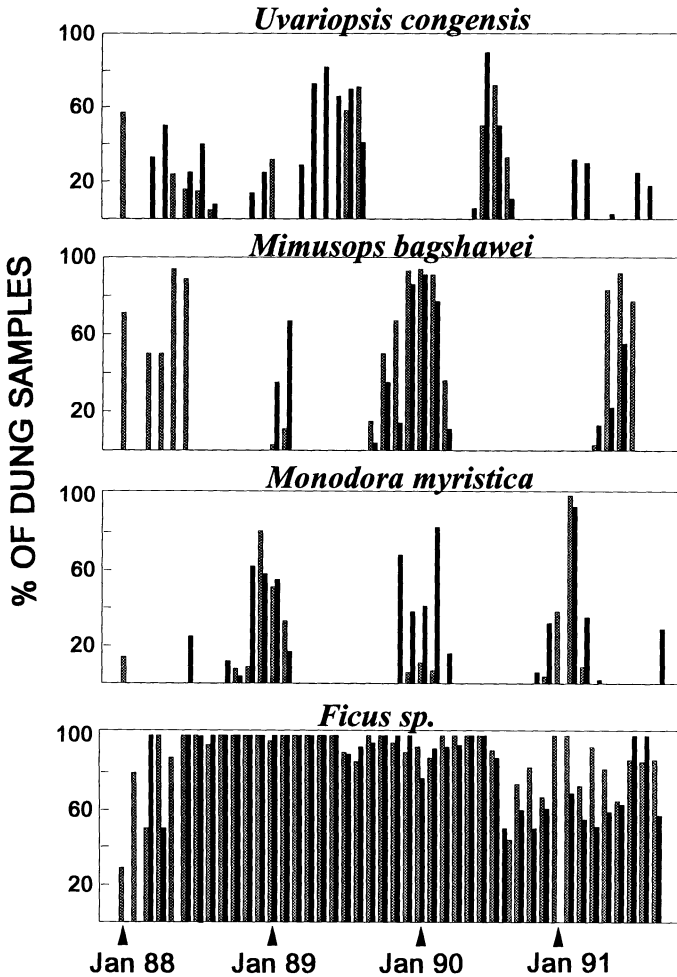


Figure 1. The percentage of chimpanzee dung samples found each month in the Kibale Forest Reserve, Uganda that contain specific species of seeds. The solid bars represent samples collected from the Ngogo study site, and the shaded bar represent those from the Kanyawara study community.

Effect of gut passage on germination

Some portion of all of the seed species that were commonly found in chimpanzee dung were viable (Table 2). The percentage of the chimpanzee-dispersed seeds that germinated under our field laboratory conditions averaged 30%, ranging from 10.7% for *Monodora myristica* to 87.5% for *Mimusops bagshawei*. The time between planting of the chimpanzee-dispersed seeds and the first sign of germination averaged 189 days (range for individual seeds: 96 to 312 days). The germination success reported here is likely to be much higher than that observed under natural conditions where many seeds in chimpanzee dung are killed by seed predators, and many newly established seedlings are killed by herbivore activity (C. A. Chapman and L. J. Chapman unpublished data).

Table 2. The germination success for seeds that have passed through chimpanzees and seeds from the same species that have not been dispersed. The mean and range in the number of days required for germination are also presented.

Species	% germination success (sample size)		Mean number of days to germinate	
	From dung	Not from dung	From dung	Not from dung
<i>Chrysophyllum</i> spp.	33.2 (208)	0 (100)	177 (96–253)	—
<i>Tabernaemontana</i> spp.	19.5 (128)	11 (100)	156 (106–283)	266 (250–283)
<i>Monodora myristica</i>	10.7 (131)	0 (100)	150 (122–270)	—
<i>Mimusops bagshawei</i>	87.5 (140)	0 (100)	170 (120–311)	—
<i>Pseudospondias microcarpa</i>	29.9 (194)	0 (100)	245 (113–298)	—
<i>Aframomum</i> spp.	42.9 (84)	0 (100)	156 (122–191)	—
<i>Cordia millenii</i>	12.5 (16)	0 (30)	181 (110–253)	—
<i>Uvariopsis congensis</i>	15.5 (233)	0 (100)	232 (179–312)	—
<i>Ficus</i> spp. ¹	—	—	151 (111–197)	189 (121–282)
<i>Cordia abyssinica</i>	18.2 (22)	0 (50)	273 (220–274)	—

¹We were unable to identify the species of *Ficus* seeds that were found in the chimpanzee dung, and for the germination trials the exact number of seeds planted was not determined.

We contrasted the probability and rate of germination between seeds dispersed by chimpanzees and those collected directly from parent trees for 10 species commonly found in chimpanzee dung. Chimpanzee-dispersed seeds of all 10 species had a higher probability of germinating (median 19.5%) than non-dispersed seeds (median 0%). Only *Tabernaemontana* spp. (8.5%) and *Ficus* spp. showed any germination from seeds that were not dispersed (Table 2). Further, mean latency from planting to germination was greater for seeds collected from the tree, than for chimpanzee-dispersed seeds (*Tabernaemontana* spp.: 110-day increase; *Ficus* spp.: 38-day increase).

This evidence suggests that passage through a chimpanzee's gut improves percentage germination and shortens the time to germination. Although seeds collected from trees may have been damaged, we were careful to reject seeds with visible damage. When the trials were completed all ungerminated seeds were opened, and appeared to be dead, confirming that the trials were run for an adequate duration to test germination potential.

Chimpanzee versus monkey seed dispersal

To compare chimpanzee seed dispersal with dispersal by other primates, we calculated the number of seeds per dung for the three most abundant frugivorous monkeys at the Kanyawara study site (*Cercopithecus mitis*, *C. ascanius*, *Cercocebus albigena*). In 83 monkey dung samples (*Cercopithecus mitis* N = 20, *C. ascanius* N = 16, *Cercocebus albigena* N = 47), we found a mean of 0.37 large seeds per dung, about 2% of the number of seeds in an average chimpanzee dung. The common frugivorous monkeys occur at higher total population density (180 km⁻²) than chimpanzees (2.5 km⁻²) (Table 3). To take account of this difference, we estimated total defecation rates by populations of chimpanzees and

Table 3. The densities, diet, and day range for the diurnal primate species found in Kibale Forest, Uganda. With the exception of *Pan troglodytes*, the information presented on densities is from Waser 1987, and diet and range use data are from Cords (1987), Melnick & Pearl (1987), Oates (1977), Waser (1977), and Struhsaker & Leland (1987). *Papio anubis*, *Perodicticus potto*, *Galago inustus*, and *G. demidovii* also occur in the area.

Species	Population density (individuals km ⁻²)	Biomass density (kg km ⁻²)	% of fruit in diet	Day range (m)
Frugivores				
<i>Pan troglodytes</i>	2.5	85 ¹	82%	?
<i>Cercocebus albigena</i>	9.0	60	58	1270
<i>Cercopithecus mitis</i>	41.0	127	21–43%	1298
<i>Cercopithecus l'hoesti</i> ²	5.0	13	?	?
<i>Cercopithecus ascanius</i>	130.0	328	43.7%	1447
Folivores ³				
<i>Colobus guereza</i>	58.0	317	13.6% ⁴	535
<i>Colobus badius</i>	300.0	1760	~28	557

¹Calculated based on the proportion of adults to immatures in the Kanyawara community (adult weight is based on estimates derived from a regression of bone measurements from Kibale animals to body weight at Gombe National Park, Tanzania male = 50 kg, female = 40.5 kg; immatures were assumed to weigh half as much as an adult).

²Since the diet of *C. l'hoesti* is poorly known this species is not used in the calculations in Table 4.

³Data on folivores are included here for completeness, but are not used in our calculations because these species rarely eat ripe fruits of large-seeded species, and may never pass seeds undigested in their dung.

⁴Includes immature fruits.

monkeys (Table 4). Table 4 suggests that although chimpanzees constitute only 1.4% of primate frugivore populations at Kanyawara by numbers (2.5/180 individuals km⁻²) and 14.2 of the primate frugivore biomass (85/600 kg km⁻²), they defecate 45.3% of the seeds defecated by the frugivorous primates. In other

Table 4. Estimated large seed defecation rates of frugivorous primates at the Kanyawara study site in Kibale Forest, Uganda.

	Chimpanzees	Arboreal frugivorous monkeys
Population density (no. km ⁻²)	2.5 ¹	180 ²
No. seeds per defecation	22	0.37
No. defecations day ⁻¹	6.7	6.7 ³
Total seeds defecated km ⁻² day ⁻¹ (by population)	369	446
Total seeds defecated km ⁻² day ⁻¹ (by individual)	147	2.48

¹Chapman & Wrangham 1993.

²Waser 1987 – sum of densities for *Cercopithecus mitis*, *C. ascanius*, and *Cercocebus albigena*.

³Estimated from observations of chimpanzee defecation in Gombe National Park (Wrangham unpublished data). During 196.2 hours of focal observations on adult males in 17 days, the subject was scored as defecating once every 3.1 hours. Under certain conditions, defecation was difficult to observe, e.g. in large groups or thick vegetation. In an attempt to compensate for periods of low observation probability, we scored mean inter-defecation interval. The mean interval was 1.8 ± 1.8 h (N = 47), suggesting that in 12 hours chimpanzees would defecate 6.7 times. Monkey defecations rates are unknown: the table shows the effect if they are as high as those of chimpanzees.

areas of the Kibale Forest, such as Ngogo, baboons are frequently observed and may contribute significantly to the dispersal of seeds.

DISCUSSION

The significance of an animal population as a seed-dispersing agent depends on both the number of seeds dispersed (influenced by population density and number of fruits eaten per day) and the dispersed seeds' fate (influenced by the effect of gut passage on seed survival, the microhabitat of seed deposition, etc.). In addition, the relative importance of a particular seed-dispersing population depends on the seed dispersal capacity of other frugivores. In our study of the chimpanzees of Kibale, we have demonstrated that they disperse a mean of 2.8 species of seed each time they defecate, and that the number of seeds passed per defecation is high. In addition, for many plant species they reliably disperse seeds over a number of months.

For the 10 fruiting tree species that we tested, our data show that dispersal by chimpanzees improved the rate of germination and reduced latency to germinate. Idani (1986) tested the germination potential of 17 species of seed that had been passed by bonobos (*Pan paniscus*). He found 77% germination success and presented evidence that the rate of germination was enhanced for 50% of the germinating species. Takasaki (1983) demonstrated that three species of seed were viable after passage through chimpanzee guts. Studies of baboons (Lieberman *et al.* 1979) and howler monkeys (Estrada & Coates-Estrada 1984) have indicated increased probabilities of germination following passage through these animals, although a study of seeds passed by three bird species, two bat species, and one species of monkey demonstrated that ingestion by these animals did not consistently affect germination (Lieberman & Lieberman 1986). However, if dispersal is important for spatial distribution of a parent tree's offspring, the important element to document is not the exact probability of germination, but simply the fact that some passed seeds are viable.

To date we have no quantitative information on the effect of defecation site on germination and seedling establishment. However, based on the quantification of seed mortality (>5000 seeds) and seedling growth (>500 seedlings) for a number of tree species, it is our impression that the microsites in which chimpanzees defecate are often suitable for both germination and seedling establishment.

Despite large differences in population density between chimpanzees (2.5 km⁻²) and arboreal frugivorous monkeys (180 km⁻²) in Kibale Forest, our preliminary estimates indicate that chimpanzees play a more significant role in primary seed dispersal than their low numbers and biomass might imply. We have not, as yet, considered the seed dispersal performed by the monkeys or chimpanzees when they feed in a fruiting tree, fill their mouths or cheek pouches, and then travel away from the tree, spitting seeds out as they travel

(Corlett & Lucas 1990, Rowell & Mitchell 1991). For some species of fruiting trees, this type of dispersal may play a significant role in its propagation.

For some seeds, monkeys act as seed predators, breaking and chewing the seeds (e.g. *Cercocebus albigena* eating *Diospyros abyssinica*, Waser 1977). Furthermore, evidence suggests that the monkeys in Kibale eat less fruit than chimpanzees (Table 3). All long-term studies of chimpanzees have described them as highly frugivorous, spending at least 50% of their feeding time eating fruit (Wrangham *et al.* 1991). Further, a review of food items eaten by chimpanzees and bonobos across Africa found that fruits from 464 species of plant have been observed to be eaten, with a mean of 56.0 (SD = 28.4) species per site (range 23–97; R. W. Wrangham and G. Isabirye-Basuta unpublished data).

The importance of chimpanzees as primary dispersers is amplified by their large home ranges compared with monkeys (Baldwin *et al.* 1982, Goodall 1986), and long day ranges (Baldwin *et al.* 1982, Nishida & Hirawa-Hasegawa 1987, Wrangham 1977) which can include a number of different habitat types. In some areas, such as Kibale Forest, their ranges include various stages of regenerating forest and grassland (Chapman & Wrangham 1993). Thus, seed dispersal by chimpanzees may provide more long range dispersal, introduction to new habitats, and contribute more to outbreeding than dispersal by monkeys.

Evidence from other studies similarly suggests that large bodied frugivores play a more significant role in seed dispersal than their density would suggest. At Tanjung Puting, Kalimantan, 94% of orang utan (*Pongo pygmaeus*) dung samples contained seeds and there was a mean of 2.5 seed types per sample (Galdikas 1982). The maximum number of seeds per dung sample was 2028, and the median number of seeds was 111. Galdikas (1978) estimated orang utan density at 2 individuals km⁻² in the Tanjung Puting study area. Orang utan seed rain therefore falls at a rate of $2 \times 111 \times N$ km⁻², where N is the number of defecations per day. If N = 6, orang utans disperse seeds at rates four times higher than Kibale Forest chimpanzees. In other areas, population densities of orang utans range from 1 to 5 individuals km⁻² (Rodman & Mitani 1987).

Large frugivores can sometimes play especially significant roles in the dispersal of the seeds from particular species. For example, Tutin *et al.* (1991) documented that lowland gorillas (*Gorilla gorilla*) are the only important dispersers for *Cola lizae* (Sterculiaceae) in Gabon and suggested that the large size of the seeds (35 mm in length) contributes to their dependence on gorillas for dispersal. A similar case was presented by Chapman *et al.* (1992) for elephants and the large seeds (88 mm in length) of *Balanites wilsoniana*. We have no evidence that any seeds in Kibale are dispersed solely by chimpanzees, and note that many seeds defecated by chimpanzees are so small that they could be eaten by any frugivore (Appendix 1).

To confirm the suggestion that large frugivores, such as chimpanzees or orang utans, play a more significant role than their numbers suggest, the fate of the dispersed seeds must be quantified. It is possible that the seeds dispersed by these large animals are placed in locations unsuitable for germination, or that

seed predators are attracted to the large dung piles and kill the majority of the seeds. From the plant's perspective, the important issue is what frugivores, out of the total caste feeding on the fruit, result in the greatest contribution to subsequent generations. However, the data presented here suggest that the role of large bodied frugivores in forest regeneration may be of greater importance than would be inferred from their density. These findings demonstrate the potential importance of great apes in the maintenance and regeneration of tropical forest, and indicate the importance of understanding the processes structuring tropical forests when making informed conservation plans.

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APPENDIX I

Listing of all identified seeds found in the dung of the chimpanzees of the Kibale Forest Reserve. The size of the seed is presented when available. This represents a measurement of the longest axis of the seed (N = approx. 30 seeds). If measurements have not been made, the seeds have been classed as small (S) (<5mm), medium (M) (5–20 mm) and large (L) (>20 mm). For germination, a 'Yes' means that seeds of that species were tested for viability as outlined in the methods and did germinate; a '?' means that very few seeds were available for trials; although none were shown to be viable, data are inconclusive. *Ficus* spp. seeds were not identified in the dung, but observations confirm that the chimpanzees eat the listed species, and fig seeds were common in the dung samples. Life Form, T = Tree, H = Herb, V = Vine, L = Liana, S = Shrub. Nomenclature follows Hamilton (1991) and Berg & Hijman (1989).

Family/Species	Life Form	Length (mm)	Seeds /fruit	Germination
<i>Lannea welwitschii</i>	T	10.0	1	?
<i>Pseudospondias microcarpa</i>	T	13.2	1	Yes
Annonaceae				
<i>Monodora myristica</i>	T	20		Yes
<i>Uvariopsis congensis</i>	T	18.3	6	Yes
Apocynaceae				
<i>Tabernaemontana holstii</i> ¹	T	M		Yes
<i>Tabernaemontana odoratissima</i> ¹	T	M		Yes
Boraginaceae				
<i>Cordia millenii</i>	T	27.4	1	Yes
<i>Cordia abyssinica</i>	T	8	1	Yes
Canellaceae				
<i>Warburgia ugandensis</i>	T	7		Yes
Euphorbiaceae				
<i>Drypetes battiscombei</i>	T	9		
<i>Securinega virosa</i>	S	S		
Flacourtiaceae				
<i>Oncoba routledgei</i>	T	L		?
<i>Dasylepis eggelingi</i>	T	7.4	7	
<i>Dovyalis macrocalyx</i>	S	M	1	
Marantaceae				
<i>Marantochloa leucantha</i>	H	7		
Mimosaceae				
<i>Acacia hockii</i>	T			
Moraceae				
<i>Myrianthus arboreus</i>	T	20.1		
<i>Antiaris toxicaria</i>	T	10		
<i>Ficus sansibarica</i>	T	1.5	902	Yes ²
<i>Ficus sur</i>	T	S	1576	Yes ²
<i>Ficus trichopoda</i>	T	S		Yes ²
<i>Ficus cyathistipula</i>	T	2		Yes ²
<i>Ficus saussureana</i>	T	1		Yes ²
<i>Ficus exasperata</i>	T	1		Yes ²
<i>Ficus mucoso</i>	T	2		Yes ²
<i>Ficus natalensis</i>	T	S	234	Yes ²
<i>Ficus ottoniiifolia</i>	T	S	75	Yes ²
<i>Ficus thoningii</i>	T	S	806	Yes ²
<i>Ficus asperifolia</i>	S	S		Yes ²

APPENDIX I. Continued.

Family/Species	Life Form	Length (mm)	Seeds /fruit	Germination
Musaceae				
<i>Ensete ventricosum</i>	T	14		
Loganiaceae				
<i>Strychnos mitis</i>	T	M		Yes
Oleaceae				
<i>Linociera johnsonii</i>	T	M	1	
Palmae				
<i>Phoenix reclinata</i>	T	M		Yes
Passifloraceae				
<i>Passiflora subpeltata</i> ³	V	5		Yes
Phytolaccaceae				
<i>Phytolacca dodecandra</i>	S	S		
Rosaceae				
<i>Rubus apetalus</i>	V	S		
Rubiaceae				
<i>Vangueria apiculata</i>	T	14.2	3.2	
<i>Rothmania urcelliformis</i>	T	M		
Rutaceae				
<i>Teclea nobilis</i>	T	S		
<i>Toddalia asiatica</i>	L	S		
Sapotaceae				
<i>Chrysophyllum albidum</i>	T	L		Yes
<i>Mimusops bagshawei</i>	T	15.0		Yes
<i>Aningeria altissima</i>	T			
<i>Aphania senegalensis</i>	T			
Simaroubaceae				
<i>Harrisonia occidentalis</i>	S	3.8	5	
Solanaceae				
<i>Solanum mukiibi</i> ³	H	S		
Sterculiaceae				
<i>Cola giganteata</i>	T	L		
Thymelaeaceae				
<i>Peddiea fischeri</i>	S			
Ulmaceae				
<i>Celtis africana</i>	T	5	1	
<i>Celtis durandii</i>	T	5	1	
<i>Chaetacme aristata</i>	T	S	1	
Urticaceae				
<i>Urera hypsiloides</i>	L	S	1	
Zingiberaceae				
<i>Aframomum angustifolia</i>	H	S		Yes ²
<i>Aframomum mala</i>	H	S		Yes ²
<i>Aframomum mildbraedii</i>	H	S		Yes ²
<i>Aframomum usambarense</i>	H	S		Yes ²
<i>Aframomum verrucosum</i>	H	S		Yes ²
<i>Aframomum zambesiacum</i>	H	S		Yes ²
<i>Renealmia congolana</i>	H	S		

¹*T. holstii* and *T. odoratissima* are both eaten. Their seeds were not distinguished in the dung.²*Ficus* and *Aframomum* seeds have been repeatedly germinated from chimpanzee dung over the last three years, thus it seems likely that all species germinate, but we have not distinguished species from seeds.³From agricultural sources.