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Pre-dispersal Seed Handling Treatment by Five Sympatric Non-human Primates in Kibale National Park, Uganda

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Abstract
The aim of this study was to compare the seed dispersal potential of five non-human primates that exist sympatrically in Kibale National Park, Uganda. A total of 4,455 seeds of 18 different plant species were collected from 110 faecal samples. The results showed that the quantity of potentially dispersible seeds varied significantly among the five primate species. The Shannon index of diversity showed that olive baboon dispersed a relatively high level of seed diversity, compared to others primates (H=1.74). Chimpanzees dispersed the highest percentage of whole seeds while red-tailed monkeys' faecal samples had the greatest proportion of broken seeds. Dung beetles were found in 29% of the faecal samples with greatest proportion of them found in red-tailed monkey faeces (45%). *Ficus* sp. dominated in terms of the number of seeds dispersed (3,025) and accounted for 68% of all seeds collected from samples, 4.8% of which were visually identified as unviable for germination. Each primate species differed significantly from all other groups. *Pan troglodytes (*chimpanzee) dispersed a diversity of intact seeds and colobines (folivores) play a minimal role in seed dispersal. In addition, *Papio anubis (*olive baboon) may be an important factor driving the distribution of the invasive plant species, *Lantana camara*.
Keywords *Lantana camara*, non-human primates, *Papio anubis*, seed dispersal, sympatry.

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Introduction

Primates are recognized as important seed dispersers for tropical plants, although a variety of dispersal mechanisms are found within tropical forests [1]. In many of these habitats, primates vary in their abundance and diversity, but many of these species are predominant frugivores [2], ingesting, defecating and dropping large numbers of different seeds [3]. Different primate species may, however, play dissimilar roles as seed dispersers [2]. In a single location, Cercopithecus monkeys may act primarily as seed splitters, while chimpanzees are predominantly seed swallowers [4]. These handling treatments affect the placement and density at which seeds are dispersed. A single primate species' role in seed dispersal may also vary depending on seasonal fluctuations, the floral community assemblage, soil quality and the microclimate in which the primate lives [5]. Difficulty exists in assessing how effectively different seeds are dispersed by primate species primarily because seed dispersal effectiveness depends on a variety of processes, which are often categorized into dispersal "quality" and dispersal "quantity" [6].

Following from Stevenson [3], the quantity of seed dispersal refers to the total number of seeds removed from the host; which is the product of the number of visits made by the dispersers and the number of seeds removed from the tree.' The quality of seed dispersal depends principally on two components. Firstly the treatment that the seeds receive from the dispersers – hands, beaks or mouth and gut – which may affect germination potential after gut passage. Secondly, the density of the seeds in the deposition and characteristics of the deposition site which may affect seedling development, e.g., appropriate substrate and light availability. The quality of a particular seed disperser for a plant species depends on three criteria: (1) the number of seeds dispersed; (2) germination potential of the seed after handling or gut passage; and (3) the suitability of the microsite for germination where the seed is deposited [2]. Once deposited, the viability of germination and establishment depends on the abiotic environment and the likelihood of encountering post dispersal seed predators and secondary dispersers [7]. Primate species vary considerably in these aspects of seed dispersal and demonstrate a variety of movement patterns and fruit processing that ultimately influence the deposition of seeds [4].

In this study, we characterized the seed dispersal quantity and quality (seed treatment) patterns in Red colobus (*Procolobus rufomitratis*) – strict folivores; black and white colobus (*Colobus guereza*) – folivores subsisting on fruits; red-tailed monkey (*Cercopithecus ascanius*) – both folivore and frugivore; olive baboon (*Papio anubis*) – generalist omnivore and chimpanzee (*Pan troglodytes*) – a selective omnivore. This study attempted to investigate the success of the 5 different primate species in their roles as seed dispersers in the Kanyawara region, Kibale National Park, Uganda. This national park contains one of the highest primate densities of any tropical forest [8] and our investigation was based on their relative importance as dispersers of the diversity of floral species found in the park. We aimed to determine both the quantity and diversity of the seeds dispersed by these primates while also investigating the quality of those dispersed seeds. By combining these approaches, we provided insight into how they differ in their importance as dispersers in the Kanyawara region. Our hypothesis was that these five non-human primates that live in sympatry in Kibale disperse large numbers of seeds of high quality. We also hypothesized that due to their variation in ecology, they differed in their importance as seed dispersers for the floral community in Kibale.

Materials and methods

Study site

This study was coordinated from the Makerere University Biological Field Station (MUBFS) in the Kibale National Park, Uganda (0° 13'-0° 41' N and 30° 19'-30° 32' E) located in the east of the Rwenzori Mountains. The park is considered to resemble most closely a moist Montane forest [9], but judged to occur in the transition between lowland and Montane forest [10]. The altitude of the reserve varies between 1,100m and 1,590m [9] and the highest point reached in this study was 1,571m. The Kanyawara region, where this study took place, is composed of rolling hills interspersed with steep valleys.

Faecal sample collection

Faeces from five primate species were collected between the 16th and 28th July 2012 from 0700 to 1730 hours, with the majority collected between 0700 and 1300 hours. Faecal samples were placed into plastic bags and labelled by sample number, primate species and the date on which the faeces were collected. These bags were then transported back to the MUBFS lab for analysis.

Opportunistic collection was combined with prior knowledge of primate group home ranges and behavioral observations of group locations during pseudorandom walks on trails around the Kanyawara region of the Kibale National Park. We alternated between different species groups during each collection day. Sleeping sites of certain groups, most frequently Chimpanzee troops/individuals, were located and coordinates stored using a GPS map 70CSX Garmin™, which allowed early morning collection of samples around these areas.

Faecal sample characterization

Once found, faecal sample deposition sites were given a GPS coordinate (36N UTM format). If multiple faecal samples were found within the error radius provided by the GPS logger (e.g. ± 6m), these were given the same coordinates. The time of discovery of each sample was also recorded. Relative soil compactness between sites was assessed by dropping a machete from shoulder height and the depth of soil penetration recorded in centimeters. Foliage density directly above the faecal sample location was recorded as the mean of 3 observers' estimation of percentage canopy cover. "Visitors" at faecal samples were visually recorded and placed into ant, dung beetle and fly categories, and categories of combinations of the afore-mentioned.

Faeces were weighed (Mattler™ BD202 scale) to the nearest 0.1gm, Seeds >2mm were extracted, counted individually and identified. Where species were not known seeds were placed into morpho-specific categories (Sp. 1, 2…. n). Following previously methodology [11], seeds <2mm were sorted into categories of absent, rare, common, very common and abundant. These groups were calibrated into figures of 0, 25, 50, 75 and 100, respectively. Conditions of seeds were categorized into "broken" or "whole" dependent on the potential viability of seeds to germinate, e.g., the outer casing of seed removed during digestion was considered "broken".

Statistical analysis

Standard numerical analysis was performed using Minitab™ Statistical Software v13.32. Frequency histograms were generated through Microsoft™ Excel, 2003 while comparisons of diversity were carried out using PAST© v2.15 [12]. In diversity analysis, 20 data sets for each primate species were randomly sampled and used to represent each species group to compare seed diversity between species.

Results

Seed quantity

In total 4,455 seeds from 18 different plant species were collected from 110 faecal samples. Chimpanzees (57%), Olive baboons (27%) and red-tailed monkeys (13%) were the major contributors to the number of seeds dispersed. Although black and white and red colobus accounted for 41% of all faeces, only small amounts (3%) of seeds were from either species. Using the Shannon index of diversity, the olive baboon dispersed a relatively high level of seed diversity, compared to the red-tailed monkey (H=1.74 and H=0.22, respectively) (Table 1). The olive baboons also had a higher distribution of seeds in the faecal samples (M=1.70) with the lowest level of dominance in the samples used in this analysis (D=0.21). All seeds (107) of the invasive plant species, *Lantana camara*, were only collected from olive baboon faeces, but 21% of them deemed unviable.

The quantity of potentially dispersible seeds varied among the five primate species (Kruskal Wallis, H=83.35, df =4, $p<0.05$). Fig. 1 indicates differences in median values of seed numbers for all between-group evaluations, except between groups 3 and 5 (red-tail monkey and baboon) and groups 1 and 2 (black and white colobus and red colobus). However, pairwise comparison between groups 3 and 5 showed a difference in seed quantity (Mann-Whitney U, W=546.5, p=0.0174) as well as between groups 1 and 2 (Mann-Whitney U, W=532.0, p=0.0228). Accordingly, each species differed from all other groups. Dung beetles were found in 29% of the faecal samples with greatest proportion of them found in red-tailed monkey faeces (45%).

Seed Quality

Chimpanzees dispersed the highest percentage of whole seeds (99%) while red-tailed monkeys' faecal samples having the greatest proportion of broken seeds (23%). The greatest number of broken seeds found in any species group was the olive baboon (144) (Fig. 2). *Ficus* sp. dominated in terms of the number of seeds dispersed (3,025) and accounted for 68% of all seeds collected from samples, 4.8% of which were visually identifiable as unviable for germination. The second largest plant species contributor, in terms of the total seeds collected was *Uvariopsis congensis* (845) which accounted for 20% of the seeds, importantly <1% of *Uvariopsis congensis* seeds were "broken". Chimpanzees contributed the greatest number of fig seeds (1791) with 99% of those remaining intact after digestion.

All of the olive baboon faecal samples were found in open sites with a canopy cover <5% (Table 2) with lowest average soil compactness value, indicating the faeces was located on the most compact soil of the groups (mean=2.4±1.7). Black and white colobus and chimpanzee faecal samples were collected under the densest cover.

The locations of faecal samples (Fig. 3) that were found in Kibale National Park indicated that chimpanzee faeces (black circles) were the most widely distributed across the park. Olive baboons were restricted to a single group around the MUBFS (shaded area of approximate coordinates 02570, 62300). Chimpanzee samples were also found in less frequently in large groups or clumps, than any other group, which accounts, in part, for their wider distribution.

Discussion

Primate species exhibit a variety of seed handling behaviors and the seeds themselves being an important food source for some species are not dispersed but destroyed [5]. Here we discuss our evidence that seed swallowers, namely *Pan troglodytes (*chimpanzee), disperse a diversity of intact seeds and colobines (folivores) play a minimal role in seed dispersal. In addition, *Papio anubis (*olive baboon) may be an important factor driving the distribution of the invasive plant species, *Lantana camara*.

The five primate species studied are potential dispersers of large numbers of seeds, with chimpanzees dispersing the highest number of seeds per sample. We suggest that this is a result of their previously cited attraction to clumped food resources [13]; in this case, the main food sources during the study period were from *Ficus* sp. The fact that the quantity of seeds was disproportionately represented by *Ficus* sp. is an indirect reflection of the low level of rainfall that Kibale National Park (KPN) undergoes during the month of July [9, 14]. Figs are important and common food source for many tropical primates [10]. Their relative importance is heightened during periods of low fruit abundance [10] which often coincides with periods of low rainfall. The particularly high intake rate of figs by chimpanzees recorded in this study is again in line with the previous literature [10].

Table 1 Number of seeds, level of seed dominance, seed diversity and seed distribution in five primate species.

Diversity index	Black and white colobus	Red colobus	Red-tailed monkey	Olive baboon	Chimpanzee
Taxa_S	2	2	6	13	8
No. of seeds	50	13	546	1149	2102
Dominance_*D*	0.51	0.86	0.92	0.21	0.53
Shannon_*H*	0.69	0.27	0.22	1.74	0.85
Margalef_*M*	0.26	0.39	0.79	1.70	0.92

N=20 for each specie

Dispersal of large numbers of seeds is, however, not a prerequisite for high seedling recruitment rate due to susceptibility of faecal material to degradation, specifically fungal pathogens, and the post-dispersal effects of dung beetles [15]. Also of interest, is the large quantity of *Uvariopsis congensis* seeds found in both baboon, and especially, chimpanzee faeces. This may be another indirect effect of low rainfall during the study, although chimpanzees in the Budongo Forest, Western Uganda, are known to preferentially choose *Uvariopsis congensis* trees as nesting sites [16]. If chimpanzees in Kibale choose similar nesting sites, seed representation in the faecal samples collected may be due to proximity to *Uvaryosis congensis* fruits.

Table 2 Mean canopy cover (%) and mean soil compaction (cm) of the locations where the faecal samples were collected. Lower values of soil compactness indicate more compact soil.

Primate species	foliage cover (%)	Soil compactness (cm)
Black and white colobus	57.6 ±12.6	4.3 ±2.4
Red colobus	49.0 ±17.4	4.4 ±2.3
Red-tailed monkey	34.8 ±15.1	4.3 ±2.6
Chimpanzee	50.9 ±26.7	3.5 ±1.9
Olive baboon	2.4 ±4.7	2.4 ±1.7

The values after ± are standard deviations.

Red-tailed monkeys are also attracted to clumped food resources [13], but they represented a lower number of seeds per faecal sample compared to the chimpanzees, due to their "scatter-dispersal behavior" of spitting seeds up to 100m from the mother plant [5]. Olive baboons dispersed the highest diversity of seeds, reflecting their generalist feeding behavior. They also distributed the number of seeds dispersed evenly among the faecal samples. Colobines (red colobus and black & white colobus) dispersed low numbers of seeds per faeces, with the lowest number of plant species across the 20 randomly selected samples, which we propose is due to their behavioral adaptations to folivory, constrained by their anatomical morphology.

Despite dispersal of three times as many taxa, the high dominance of *Ficus* sp. in red-tailed samples accounts for the lower Shannon index value. When using the Margalef index, which emphasizes less on dominance and more on variation in taxa, the red-tailed monkey showed greater diversity than black and white colobus monkeys (Table 1). We have included the Margalef indices because we believe that it more accurately represents the diversity of seeds found in red-tailed monkeys in this study.

Chimpanzees were able to disperse the largest percentage of large seeds (>2mm especially *Uvariopsis congensis*) and all of the seeds were intact post-digestion. Lambert [17] found that 80% of large seeds remained intact post digestion by chimpanzees. We suggest that the difference between our own results and Lambert's is because our study took place in a period of low fruit abundance, with chimpanzees during our study predominantly relying on *Uvariopsis congensis* which seem relatively impervious to degradation. Our study also highlights the particular effectiveness of chimpanzees as small seed dispersers, not only in the total number of fig seeds dispersed (1791), but also the exceptional efficiency in which fig seeds remain viable post-digestion (98.9%). Underlying this high viability is their seed swallowing behavior, and the adaptations of *Uvariopsis congensis* to produce seeds that will remain intact throughout the chimpanzee digestive tract.

No large seeds (>2mm) were found in red-tailed monkey samples, which is an expected outcome as many cercopithecines tend to spit seeds >4mm wide due to the potential to cause blockages in the cercopithecine digestive system [17]. Red-tailed monkeys also provided the greatest proportion of seeds unviable for germination (23%). We tentatively suggest that this behavior may have an impact on plant fitness due to mother-seedling competition, but we feel that further discussion is outside the scope of this study. We suggest that if red-tailed monkeys prove inefficient dispersers of large seeds, studies should be carried out to investigate whether plants have adapted mechanisms to reduce seed predation/inefficient dispersal by red-tailed monkeys.

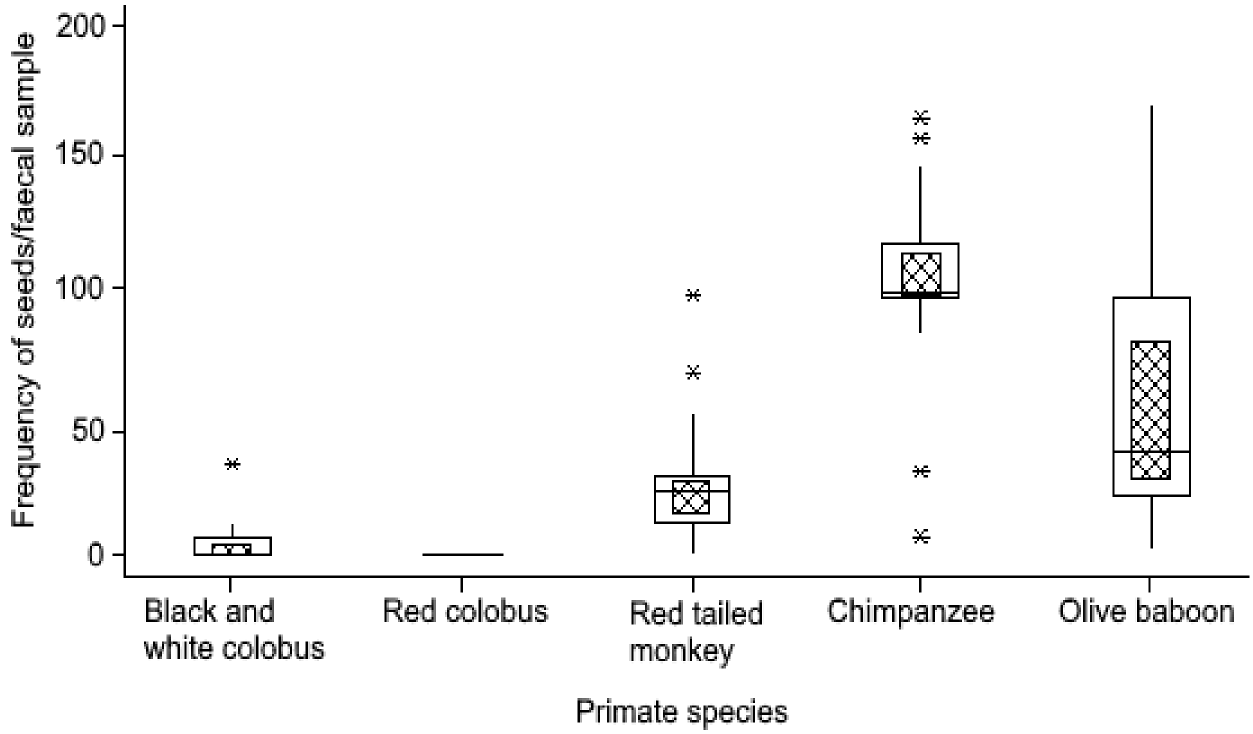

Fig. 1 Boxplot indicating total number of seeds extracted from black and white colobus, red colobus, red-tailed monkey, chimpanzee and olive baboon. Hatched areas within the quartile ranges for each species represents the 95% confidence intervals around the median.*indicates outliers.

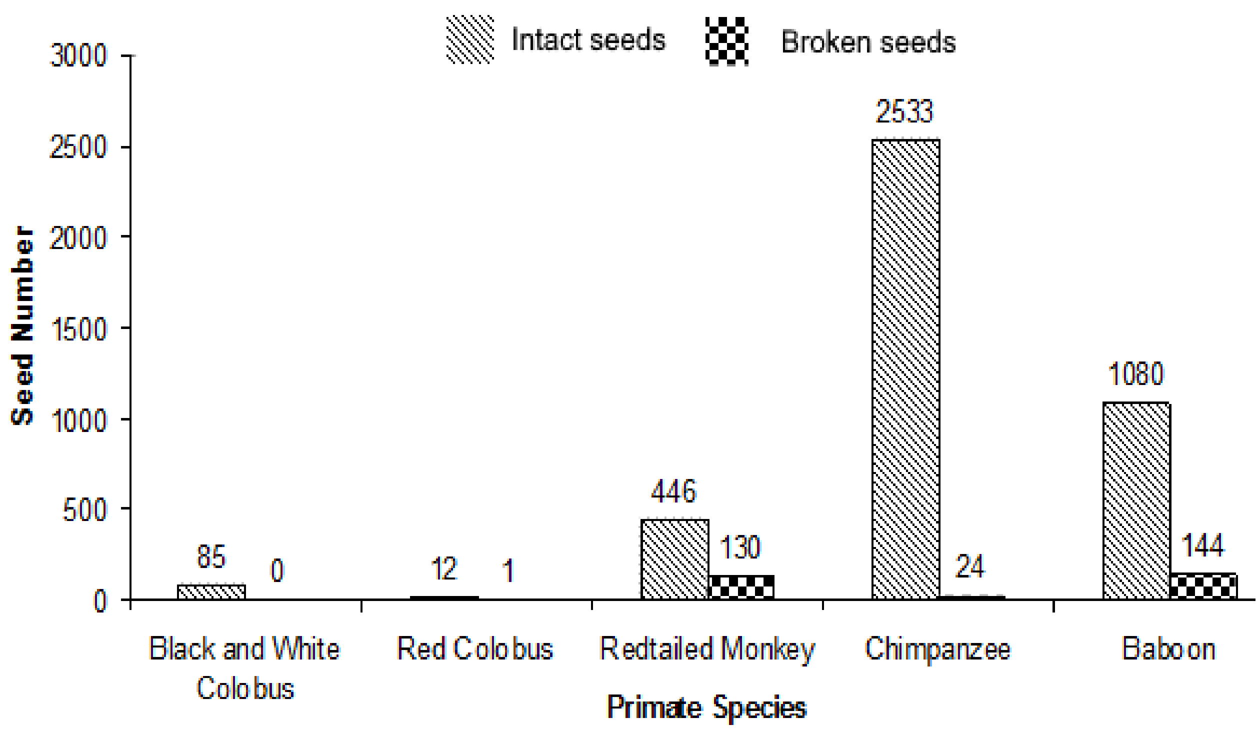

Fig. 2 The frequency of seeds found in faecal samples of 5 non-human primate species in Kibale National Park, Uganda. Numbers above each bar are specific values for each column.

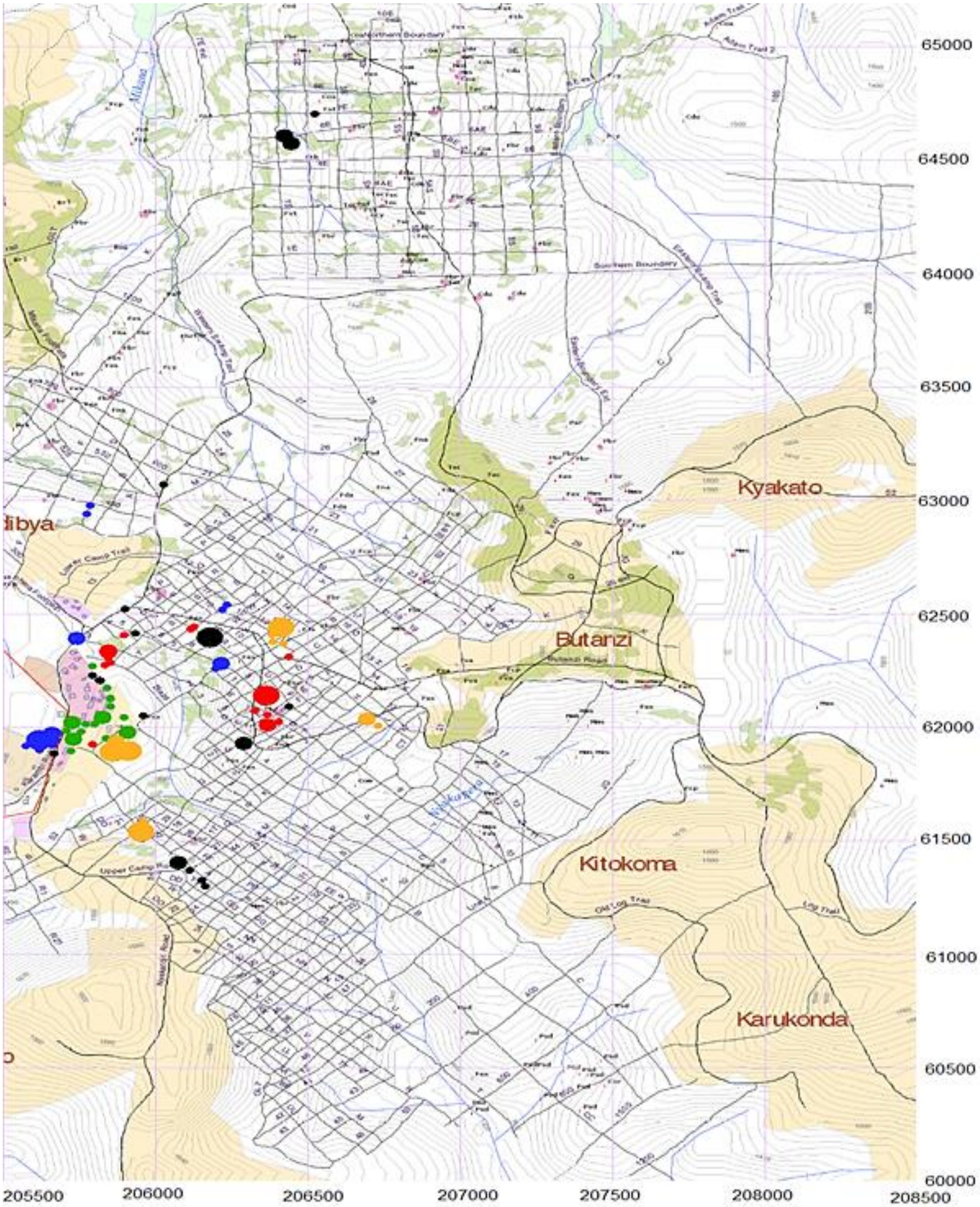

Fig. 3 A map of the Kanyawara region of Kibale National Park, Uganda (0° 13' - 0° 41' N and 30° 19' - 30° 32' E). Faecal sample distributions are shown with colored circles. The size of the circle is proportional to the number of samples found at that location. Red = Red tailed monkey. Black = Chimpanzee. Orange = Red colobus. Blue = Black and white colobus. Green = Olive baboon. Gridline values are the last 6 digits of UTM format GPS coordinates.

Most of the olive baboon seeds (81%) were dispersed whole, confirming the findings of Gautier-Hion et al. [18] that *Papio anubis* is a seed swallower. For olive baboons, however, our study found that they drop their faeces in areas with low canopy cover which is a key abiotic factor governing plant dispersion and seed recruitment [6]. The seeds were also dispersed in areas with low soil compactness values (Table 2), or areas of hard soil types, again reducing the chances of seeds successfully germinating. All of the faecal samples from olive baboons were collected from the forest edge, where forest regeneration is slow. Combining the low quality location of faeces deposition with the limited distribution into these edge zones highlights the inefficient role of olive baboon's seed dispersal in Kibale National Park, despite the high number and high quality of seeds post-digestion.

The interesting finding of this study is that baboons play a role in dispersing the invasive plant species *Lantana camara*. All of the *Lantana camara* seeds collected in this study were derived from baboon faeces, suggesting that the other primate species studied play little role in their dispersal. The baboon-*Lantana camara* dispersal interaction was also of particular interest because of the low efficiency in seed viability. *Lantana camara* were dispersed with 23% of seeds deemed unviable, while all other seeds were dispersed at a rate of 8.8% of seeds considered unviable. Our results indicate that the olive baboon is, usually, a particularly efficient disperser of seeds; in terms of maintaining a seed's viability to germinate. We suggest that this variation in *Lantana* dispersal efficiency is due to *Lantana camara* seeds not being adapted to survival in the baboon's digestive tract, due to the recent introduction of the plant in Uganda. We have observed that in the Kanyawara region of Kibale, *Lantana camara* is restricted to human-influenced clearings, roads/trails and forest edge zones, as are the olive baboons in this study (Fig. 3). We suggest that the overlapping distribution of the olive baboon and *Lantana camara* in Kibale may account, in part, for the successful spread of *Lantana camara*. However, a larger sample size of baboon faeces along with faecal samples from a greater variety of baboon groups and sites may shed further light on this primate-plant interaction.

Conclusions

Out of the five primate species studied for seed dispersal, olive baboons and chimpanzees disperse the highest diversity of seeds. Olive baboons, however, do not play a key role in forest regeneration due to dispersal of their seeds along the forest edge where they are more susceptible to seed predation and poor environmental conditions. They may have also contributed to the distribution of the highly invasive *Lantana camara* around the Kanyawara area of Kibale National Park. Colobines, being largely folivores, play a minor role in seed dispersal and forest regeneration. Red-tailed monkeys dispersed the highest proportion of broken seeds, yet still disperse a large quantity of seeds. Our study indicates a complex primate-plant interaction for red-tailed monkeys and we suggest further work to provide insight into this relationship. Red-tailed monkey faeces also showed the greatest association with dung beetles. These are important secondary seed dispersers and could enhance high seed recruitment per sample due to protection of seeds from predators. *Ficus* species had the highest percentage of seeds dispersed by all the primate species, followed by *Uvariopsis congensis*. Their presence in the primate groups may have been as a result of high availability during the study period compounded by low fruit abundance during the driest month of the year in Kibale National Park.

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