

Primates create seedling growth hotspots through pattern of dung deposition

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RUNNING HEAD: Do primates create nutrient hotspots?

KEYWORDS

Fertilizer, nutrient, primate, red colobus, *Piliocolobus tephrosceles*, Kibale National Park, Uganda

Abstract

Primates play important roles in tropical forests through seed dispersal and herbivory. They comprise a large part of the biomass of forest communities and tend to have clumped patterns of defecations (i.e., at favored food trees or sleeping sites). Therefore, they may also play important roles in accelerating ecosystem nutrient cycling. Here we conduct a controlled growth experiment to quantify the effect of the addition of primate dung on the growth of both light demanding and shade tolerant seedlings over 1 year in Kibale National Park, Uganda. A mixed model analysis revealed that light demanding species were affected by the natural dung treatment and plants with small initial size had accelerated growth, whereas there was no effect on plant growth for shade tolerant species.. The long-term implications of increased dung deposition on the local tree community is unclear as shade tolerant species may only show an effect over the long-term and light demanding species may only be able to take advantage of the increased growth if subsequently exposed to high light conditions, such as a treefall gap.

1 | INTRODUCTION

It is well recognized that animals can play important roles in structuring plant communities (Power, 1997). There are several detailed studies that quantify these roles (e.g. for prairie dogs, *Cynomys* spp. (van Nimwegen et al., 2008), sea otters, *Enhydra lutris* (Estes and Palmisano, 1974), or beavers *Castor canadensis* (Naiman, 1988)). However, the role played by elephants (*Loxodonta africana*) is perhaps the best known (Laws, 1970, Dublin et al., 1990, Stuart et al., 1985), because they can shift forests to grasslands (Stuart et al., 1985) or prevent forests from recovering (Lawes and Chapman, 2006, Paul et al., 2004).

Primates also play important roles in determining tropical forest structure and regeneration by acting as seed dispersers (Andresen, 2000, Kaplin and Lambert, 2002, Effiom et al., 2013). Their importance is demonstrated by the fact that primates constitute between 25 and 40% of the frugivore biomass in these forests and they defecate or spit out a large number of viable seeds ((Chapman, 1995, Wrangham et al., 1994, Lambert and Garber, 1998); reviewed by (Chapman and Dunham, 2018)). For example, in a single day, the individuals in the redbtail monkey (*Cercopithecus ascanius*) population in Kibale could potentially remove 24,492 fruits/km² and disperse their fruits (Lambert, 1999). In addition, the extensive herbivory of some folivorous primates can influence the forest community structure by retarding tree growth and increasing mortality for specific tree species (Chapman et al., 2013b, Chapman et al., 2013a).

Given the biomass of folivorous and frugivorous primates and the amount of food they eat daily, primates produce large amounts of dung. This suggests that primates may also play an important role in nutrient cycling – a topic that has rarely been studied (Stevenson and Guzmán-Caro, 2010, Feeley, 2005, Pouvelle et al., 2008). In general, large animals are thought to play an important role in accelerating ecosystem biogeochemical cycling (Ripple et al., 2015). Nutrients that would have been locked in mature leaves, taking months or years to fall to the forest floor and decompose, are liberated for use through animal consumption, digestion, defecation, and urination. On the other hand, nutrients in fruits will not be liberated much faster than if they were not eaten. Both folivorous and frugivorous primates will however change the spatial distribution of nutrients. Many species of primates use one or a few sleeping sites at fixed locations (Chapman et al., 1989, Anderson, 1984, Neves et al., 2010) and at these sites large amounts of dung are deposited daily (Lieberman et al., 1979, Chapman, 1989). Furthermore, while travelling a group will typically follow arboreal pathways (Di Fiore and Suarez, 2007), which will therefore receive substantial amounts of dung.

Receiving input from dung is important because in tropical rainforests available nutrients are recycled quickly back into plant materials and soils are therefore usually poor in nutrients (Sugihara et al., 2015). Plant growth is therefore nutrient-limited, and the addition of Nitrogen (N), Phosphorus (P), and Potassium (K) can increase seedling growth (Santiago et al., 2012). As a result, sites receiving substantial amounts of dung may represent “hotspots” for seedling growth. Primates may often create such hotspots. For example, howler monkeys (*Alouatta palliata*), who have a mixed diet of fruits and leaves, produce dung that contained 1.8–2.1% N and 0.3–0.4% P (based on dry mass measurements) (Milton et al., 1980, Nagy and Milton, 1979). The N and P levels will be a function of the species and their diet, but in general, dung contains much greater concentrations of nutrients than leaf litter (~1% N and 0.04% P for tropical moist forests; Vitousek & Sanford 1986). Thus, primate dung is expected to be an important natural fertilizer.

Our objective was to conduct a controlled growth experiment to quantify the effect of the addition of primate dung on the growth of seedlings over one year in Kibale National Park,

Uganda. However, plant species have different resource allocations (Zanne and Chapman, 2005, Zanne et al., 2005) and recruitment strategies (Coley, 1983). For example, light-demanding species are better adapted to recruit in gaps and thus use new resources mainly for growth, while shade-tolerant seedlings tend to slowly build their way to the canopy over years or decades and invest more in their roots and defensive mechanism (e.g., plant toxins) so they are not disrupted by herbivory in their slow climb (Grubb, 1977, Richards, 1996, Wright, 2002). Furthermore, these different strategies might vary dependent on the size of the plant (e.g., a small plant might invest more resources into growth than a larger plant). Therefore, we tested for differences in the effect of primate dung addition between light demanding and shade tolerant species while controlling for initial size; we expected light-demanding species to have a greater increase in height and gain more new leaves compared to shade tolerant species.

2 | METHODS

2.1 | Study Design

The study was conducted between April 2016 and May 2017 in Kibale National Park (795 km²; 0° 13' - 0° 41' N and 30° 19' - 30° 32' E) in western Uganda near the foothills of the Rwenzori Mountains. Kibale is a mid-altitude (920 - 1590 m), moist-evergreen forest that receives a mean annual rainfall of 1676 mm in two rainy seasons ((based on data collected between 1990 and 2016 (measured at Kanyawara, Chapman and Lambert, 2000, Stampone et al., 2011)). The park is primarily forest (~60%) with areas of anthropogenic and natural grassland (~15%), and woodlands (~6%) (Chapman and Lambert, 2000).

In April 2016, ten experimental plots (4 x 4 m) were set up in an area of old-growth forests, with a control plot placed 15 m away (direction randomly determined). Each set of plots (i.e. sites) were separated by 40 m from the next and were at least 10 m away from any trail, tree fall gap, or other type of disturbance. If the random direction chosen for the control plot was within 10 m of a trail, tree fall gap, or any other type of disturbance, or if the slope or habitat type appeared different, a new random direction was selected. Approximately 200 red colobus defecations were collected from our long-term focal group and dispersed throughout each experimental plot.

Within each of the 4x4 m plots thirty apparently healthy seedlings between 30 and 100 cm in height (average 63.2 cm) were selected on an ad hoc basis and regardless of species. Seedling height was measured from ground level (clearing fallen leaves) to the tip of the main stem and the number of leaves were counted. To enable the same seedling to be found the next year, we secured a labelled tag on the forest floor next to it. In May 2017, the plots were revisited, the seedlings relocated, their height remeasured, and the number of leaves recounted. If the seedling had died, this was noted and no measurements were made.

2.2 | Data Analysis

For the analyses of changes in seedling height and leaf number under different treatment conditions, species were either considered as light demanding or shade tolerant species (as per (Zanne and Chapman, 2005, Zanne et al., 2005, Hamilton, 1991). In the final analysis, we did not consider plants that died between the two years nor plants for which the species type (light demanding vs. shade tolerant) was unknown. We also sorted out plants that lost height (more than 2 cm) between the two years, because this is more likely explained by damage to the plant and measurement errors rather than stagnant growth. Doing the same analysis while including all plants or choosing 5 cm as a threshold resulted in the same qualitative results. We were able to

include 466 plants in the final analysis. For each of the ten plots treated with monkey dung, we included between 17 and 29 plants (mean \pm sd = 24.3 ± 3.4) and between 13 and 27 (mean \pm sd = 22.3 ± 4.4) for each of the control plots. These 466 plants belonged to 30 species: 12 light demanding and 18 shade tolerant species. A total of 57 light demanding plants and 186 shade tolerant plants were included in the experimental plots, and 52 light demanding plants and 171 shade tolerant plants were included in the control plots.

2.3 | Structure of Statistical Models

We used mixed models to analyze whether the treatment of plants with monkey dung affected their growth in height and changes in the number of leaves dependent on the type of plant. As dependent variables, we used either height or number of leaves in 2017 (*Measurement₂₀₁₇*) and as independent variables the *Treatment* (control or dunged), and the *Type* of the plant (light demanding or shade tolerant). Furthermore, we included either height or number of leaves in 2016 (*Measurement₂₀₁₆*) to control for differences between plants in initial size. Because our question was whether treatment affected plant growth dependent on species type, and whether this effect is dependent on the initial size/number of leaves of the plant, we tested for the effect of the three-way interaction *Treatment:Type:Measurement₂₀₁₆*. Thus, the structure of the model (without random effects) was:

$$\begin{aligned} \textit{Measurement}_{2017} \quad \sim \quad & \textit{Treatment} + \textit{Type} + \textit{Measurement}_{2016} + \\ & \textit{Treatment:Type:Measurement}_{2016} + \\ & \textit{Treatment:Type} + \textit{Treatment:Measurement}_{2016} + \\ & \textit{Group:Measurement}_{2016} \end{aligned}$$

We included all two-way interactions that were part of the three-way interaction because all terms that are part of higher terms must be included into such a model. With regard to the random effect structure, we included the random intercepts for *Species* and *Site* and the random slopes *Measurement₂₀₁₆|Species* and *Measurement₂₀₁₆|Site* because plants of different species and plants in different areas may show variation in growth due to their species and unknown environmental factors (e.g., differences in micro-climate or soil composition).

2.4 | Fitting the Models

We calculated a Gaussian linear mixed models using the *lmer* function of the *lme4* package v1.1-15 (Bates et al., 2014) in the R programming language v3.4.3. (RCoreTeam, 2018). Despite the fact that the number of leaves represents a count variable, we did not use a Poisson regression because the number of leaves in the previous year was included as an independent variable. Therefore, using a Poisson model with a log-link function would have assumed that the relationships for leaves between the two years is $\log(\textit{Leaves}_{2017}) \sim \beta * \textit{Leaves}_{2016}$ with β the coefficient estimated by the linear model (all other terms were excluded to simplify the formula). It appeared to us that such a relationship would be less reasonable than a linear relationship for the number of leaves between the two years. We used Maximum Likelihood (ML) rather than Restricted Maximum Likelihood (REML) to fit the model (Bolker et al., 2009). *Height₂₀₁₇* and *Leaves₂₀₁₇* were cube-root transformed before running the model to improve the normality of the model residuals. To maintain the proportional relationship between *Height₂₀₁₇* and *Height₂₀₁₆* and *Leaves₂₀₁₇* and *Leaves₂₀₁₆* respectively we also cube-root transformed these two independent variables. Furthermore, we standardized *Height₂₀₁₆* and *Leaves₂₀₁₆* after the cube-root transformation by calculating z-scores (i.e., transformed this variable to a mean of 0 and standard

deviation of 1) to improve model convergence. We checked the assumption of normally distributed and homogeneous residuals by visually inspecting histograms and a qqplots of residuals, and plots of residuals plotted against fitted values. Furthermore, we visually inspected the distribution of residuals of random effects for a normal distribution. To ensure that no influential cases affected the stability of the models, we excluded subjects one at a time from the data and compared the coefficients of the resulting models (using a function kindly provided by Roger Mundry). To detect potential problems with collinearity, we ran a standard linear model (excluding the random effects) and calculated the Variance Inflation Factor (VIF) using the VIF function of the R-package *car* v2.1-6 (Fox and Weisberg, 2011). All VIFs were below 1.03, indicating no issues with collinearity.

To establish the significance of the full models, we compared the full with the null models (which only comprised the control variable *Measurement*₂₀₁₆ and all random effects) by calculating likelihood ratio tests using the R-function *anova* (with the argument “test = ‘Chisq’”) (Forstmeier and Schielzeth, 2011, Dobson, 2002) For the effects of individual terms, P-values were based on likelihood ratio tests comparing the full model with a model excluding the respective term by using the *drop1* function.

3 | RESULTS

Treatment significantly affected growth in height, but the effect was dependent on the plant type and its initial height in 2016: growth of light demanding species was affected by the dung treatment whereas there was no effect on plant growth for shade tolerant species (Table 1). This effect on the growth of light demanding species was dependent on initial size of the plants and only smaller plants benefited from the dung treatment, (Figure 1). These effects were confirmed when dividing the data into two sets, one that only included light demanding species, and one that only included shade tolerant species. We ran the same model as above, but excluded all terms comprising plant type as predictor variable (because each of the two datasets only included plants of one type). For light demanding species, the full model was significantly better than the null model ($\chi^2 = 14.154$, $df = 2$, $P < 0.001$), and the interaction *Treatment:Height*₂₀₁₆ showed a significant effect on *Height*₂₀₁₇ ($\chi^2 = 6.371$, $df = 1$, $P < 0.05$; Table 2). The model predicted that a plant with an initial height of 30 cm would grow to about 31 cm without the addition of dung and to 37.6 cm with the addition of dung. Plants with an initial height of 80 cm were predicted to grow to ~89 cm on average in the second year regardless of the addition of dung, and larger plants treated with dung seemed to have a slight disadvantage: for plants with an initial size of 100 cm, the model predicted a growth to 109 cm when treated with dung and to 113 cm without the addition of dung. Thus, for the widest range in height of tested plants (30 – 80 cm) the addition of dung increased the growth between the two years, whereas for some larger plants (80 – 100 cm) the dung appeared to slow down the growth. For the shade tolerant species, the full model was not better than the null model ($\chi^2 = 2.0711$, $df = 2$, $P = 0.355$).

In contrast to height, we did not detect an effect of dung treatment on the change in the number of leaves; the model including the three-way interaction *Treatment:Type:Height*₂₀₁₆ was not significantly better than the null model only comprising *Height*₂₀₁₆ as fixed effect and all random effects ($\chi^2 = 8.3021$, $df = 6$, $P = 0.2168$). Therefore, we did not further test for the significance of single terms (Forstmeier and Schielzeth, 2011).

4 | DISCUSSION

In this study, we asked: “Do primates create ‘hotspots’ for seedling growth through their defecations”? Our experiment discovered that small light demanding species in Kibale benefitted from the augmentation of red colobus dung to the area where they were growing, whereas there was no effect on plant growth for shade tolerant species. Our expectation was that both light demanding and shade tolerant growth forms would benefit from the addition of nutrients in the primate dung. Why the shade tolerant species did not show an altered growth rate is puzzling. It is possible that the increased N and P provided by the dung was not needed by the plants (i.e., they were not nutrient limited). This seems unlikely for two reasons: first, the soils in the Kibale area are loxic ferralsols which are from geologically old parent materials and low in nutrients and fertility (Rode et al., 2003, Rode et al., 2006, Majaliwa et al., 2010); second, the fact that small light-demanding species show a positive growth effect indicates that growth is nutrient limited, at least under some circumstances.

It is possible that if we had extended the temporal scale of the research, an effect would have been found. Studies of N and P enrichment to soils have found an effect of plant growth in some systems, but the effect was not evident within one growing season (Hatch et al., 2000). The growth process of many shade tolerant species is often very slow while they build their way to the canopy (Grubb, 1996). For example, *Chrysophyllum* sp. seedlings and saplings grow extremely slowly in the shaded understory; their mean height only doubling every 27 years (Connell and Green, 2000) – thus, a 20 cm seedling could take almost 70 years to reach a meter in height if it survived that long in the understory and did not have the growth advantage of a light gap. The growth rate of saplings (12 species, 331 individuals) that had an initial average height of 1.41 m in 1991 (range 14 cm to 5 m) were analyzed in Kibale. When they were first measured, they were judged as being in the shade. After 21 years, their average growth rate was 7.8 cm per year (C. Chapman unpublished data). This suggests that if monitoring was continued over several years, maybe even decades, a growth effect of nutrient enrichment from dung might be found. It would also be valuable to see if the addition of dung is beneficial to shade-tolerant species when the seed is germinating and the seedling is establishing.

Light demanding species typically do not persist in the understory for long. Rather, their strategy is to disperse widely and aim to be deposited in a light gap, such as a tree fall, where they can grow rapidly (Coley and Barone, 1996). The fact that the light demanding species were able to grow rapidly matches this fast life-history strategy and likely the plants did not invest heavily in plant secondary compounds to deter herbivory or the storage of energy reserves (Zanne and Chapman, 2005, Grubb, 1996). However, the long-term fate of these seedlings is unknown because they would likely have to be exposed to high light conditions, such as a treefall gap, before they could reach the canopy (Denslow et al., 1990). Without such an event, the chances of the seedling persisting are low and it may simply be killed by herbivores (Loiselle and Farji-Brener, 2002).

In contrast to light demanding species with small initial sizes (30 – 80 cm), the model predicted that the growth of light demanding species with a larger initial size (80 – 100 cm) were actually hampered by the addition of dung. These results, however, should be considered with care. The linear nature of our models made it necessary that the lines for the growth rate of dung treated vs. control plants would have to intersect at one point, and a model with another (more complex) structure might have predicted that growth rate actually converge for plants larger than

80 cm. Furthermore, this effect was only seen for a small part of the range for which we had fewer data points (see Fig. 1). Thus, to investigate if larger plants treated with dung really had a disadvantage would require to measure plants over a larger range of initial height and implement a model that allows the growth lines to converge.

Our results show that some tropical seedlings appear to benefit from the nutrients that would result from monkey dung being deposited in their vicinity. This can have important consequences for plant communities in Kibale, an area with many different primate species, relatively large population densities of many of these species (Table 3), and, consequently, relatively large amounts of dung potentially defecated by primates. Because primate abundance and ecology has been extensively studied (Chapman et al., 2005, Chapman et al., 2018b), we were able to obtain data from the literature on the weight of an average defecation for each common diurnal primate species and the number of times they defecate daily in addition to primate density. From this, we estimated that primates in Kibale are defecating 63.7 kg of dung over an area of one square kilometer every day (Table 3). Thus, it appears that common diurnal primates are depositing a substantial amount of dung each day and, since their ranging tends to focus on important feeding and sleeping sites (Anderson, 1984, Di Fiore and Suarez, 2007), they are creating nutrient hotspots in the forest. However, it is unclear what the long-term impacts of these hotspots will be on the local tree community as shade tolerant species did not show an increased growth while small light demanding species did; it is not clear if they can be successful without exposure to high light conditions, such as a treefall gap. Differences in life expectancy under a closed forest canopy are likely to be critical to the relative value of nutrient additions to both light demanding and shade tolerant species (Denslow et al., 1990). Since shade tolerant species often have slow growth rates this requires long-term monitoring as is often the case in ecological studies.

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Table 1: Results of a linear mixed model with cube-root transformed $Height_{2017}$ as the dependent variable. The full model comprising all variables was significantly better than the null model only comprising $Height_{2016}$ and all random effects ($X^2 = 23.863$, $df = 6$, $P < 0.001$). *Treatment* and *Type* were both binary variables with two categories each (*Treatment*: Control and Dung; *Type*: Light and Shade). $Height_{2016}$ was a numerical variable which was cube-root transformed and then standardized by calculating z-scores before running the model. The original mean \pm SD of the cube-root transformed $Height_{2016}$ was 3.93 ± 0.417 . Significant results are shown in boldface. *Because the three way-interaction including all variables is significant, the P-value of this term has only limited interpretability and is therefore not shown here.

Term	Estimate (SE)	χ^2	P
(Intercept)	4.053 (0.028)	-	-
Treatment(Dung)	0.067 (0.031)		_*
Type(Shade)	0.08 (0.029)		_*
Height ₂₀₁₆	0.459 (0.023)		_*
Treatment(Dung):Type(Shade)	-0.093 (0.036)		_*
Treatment(Dung):Height ₂₀₁₆	-0.072 (0.031)		_*
Group(Understory):Height ₂₀₁₆	-0.087 (0.025)		_*
Treatment(Dung):Type(Shade):Height₂₀₁₆	0.076 (0.035)	4.563	<0.05

Table 2: Results of linear model with cube-root transformed $Height_{2017}$ as the dependent variable for light demanding species only. For details, see caption of Table 1.

Term	Estimate (SE)	χ^2	P
(Intercept)	4.049 (0.027)	-	-
Treatment(Dung)	0.067 (0.03)		_*
Height ₂₀₁₆	0.47 (0.02)		_*
Treatment(Dung): Height₂₀₁₆	-0.076 (0.029)	6.371	<0.05

Table 3: An estimation of the amount of dung produced by the diurnal primates of Kibale National Park, Uganda

Species	Group/km ²	Group size	Ind/km ²	Dung weight (kg)	# /day	Dung(kg)/day
<i>Colobus badius</i>	3.4	8	27.2	0.016	6.0	2.61
<i>Piliocolobus tephrosceles</i>	7	47	329	0.015	6.0	29.61
<i>Cercopithecus ascanius</i>	7	19	133	0.009	12.8	15.32
<i>Cercopithecus mitis</i>	1.8	11	19.8	0.011	10.4	2.27
<i>Lophocebus albigena</i>	3.4	17	57.8	0.025	6.0	8.67
<i>Papio anubis</i>	0.3	33	9.9	0.07	6.0	4.16
<i>Pan troglodytes</i>			1.5	0.109	6.6	1.08
					Total	63.72

Group density from Chapman et al. (2018a), group size from Gogarten et al. (2015), chimpanzee density from Emery-Thompson et al. (2007). Dung weight and defecation rate from Lambert (2002), Wrangham et al. (1994), and Chapman unpublished (for the colobines)

Figure 1: Effect of dung treatment on plant growth on a) light demanding species (n = 109 plants) and b) shade tolerant species (n = 357 plants). The solid (control) and dashed (dung treatment) lines show the $Height_{2017}$ predicted by the linear mixed model. The dotted lines depict the bootstrapped 95% confidence intervals (n = 1000 bootstraps). The model was calculated with cube-root transformed $Height_{2017}$ and $Height_{2016}$ values and $Height_{2016}$ was further scaled to a mean of 0 and SD of 1 before running the model. However, to improve the interpretability of the plot both measurements were back-transformed to its original scale .

