Seed Dispersal by the Tantalus Monkey, *Chlorocebus tantalus*: Implications for Forest Restoration and Expansion within an Afromontane Landscape in Nigeria

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Abstract: Although the frugivorous tantalus monkey (*Chlorocebus tantalus* Ogilby 1841) is widespread throughout much of Central and West Africa, its ecology remains largely unexplored. We therefore investigated aspects of the species’ ecology with a focus on seed dispersal in a Nigerian montane forest-grassland mosaic. We compared the results of our investigation with those of other studies on seed dispersal by cercopithecines. At our study site tantalus monkeys frequented both forest edge and grassland daily, spending an average of 6.5% (93.6 minutes) of the day in grassland and the remainder of the time in forest edge. Of the 164 tantalus monkey faecal samples obtained, 95.7% contained intact seeds. Faecal samples collected from the grassland contained significantly more seeds (median = 20) than faecal samples from the forest edge habitat (median = 4), however a greater proportion of the grassland seeds were small-sized (2-5 mm). Given this, an estimated 28.0 ± 10.8 tantalus monkey individuals per km² dispersed 356 and 124 seeds > 2 mm in diameter km⁻² d⁻¹ in the forest edge and grassland habitats, respectively.

Key words: Cercopithecine, forest regeneration, habitat loss, primates, seed dispersal

INTRODUCTION

Primates are an important guild of frugivores in tropical forests (Garber & Lambert 1998; Lambert & Garber 1998), primarily because most disperse large numbers of seeds (Lambert & Garber 1998; Link & Di-Fiore 2006; Kunz & Linsenmair 2008) and in turn influence forest structure (Webb & Peart 2001; Wright *et al.* 2007; Nuñez-Iturri *et al.* 2008).

One prominent group of frugivorous African primates are the cercopithecines, which are characterised by the presence of cheek pouches and typically have long daily ranges and lengthy gut retention times (Kaplin & Lambert 2002; Lambert 2002). Historically, cercopithecines have been considered to be poor seed dispersers because of their tendency toward seed predation and/or seed spitting (Corlett & Lucas 1990; Lambert 1999). However, more recent evidence suggests that they defecate large numbers of viable seeds (Lambert 2001; Kaplin & Lambert 2002; Gross-Camp & Kaplin 2011; Albert *et al.* 2014) and that spitting can be advantageous for seedling recruitment (see Albert *et al.* 2014 for a review, but see Dominy & Duncan 2005).

The tantalus monkey (*Chlorocebus tantalus*) is a medium-sized monkey (females = 4.1 kg, males = 5.5 kg; Figure 1) possessing several traits
indicating that it is likely to be an effective seed disperser with the potential to contribute to the restoration of Afrotropical forests. Its diet comprises approximately 50% fruit (Agmen et al. 2009) with a gut retention time of approximately 30 h (Wallis et al. 2008), allowing the potential for seed dispersal via faeces. The species is semi-terrestrial, spending one-third of its time on the ground and visiting both forest and grassland habitats daily (Kavanagh 1980; Agmen et al. 2009; Grassham 2012), thereby enabling the potential for dispersal of forest seeds into grassland areas. The tantalus monkey is also relatively common with an IUCN rating of ‘least concern’ (Kingdon & Gippoliti 2008; Wallis 2013).

In spite of such characteristics and its widespread distribution throughout Central and West Africa (Kingdon & Gippoliti 2008), much of the seed dispersal ecology of tantalus monkeys remains under-studied (but see Agmen et al. 2009). It is therefore important to learn more of its seed dispersal ecology, especially as the widespread decline in forest primate species is now adversely affecting seed dispersal services and plant recruitment throughout tropical forests (Webb & Peart 2001; Wright et al. 2007; Nuñez-Iturri et al. 2008; Markl et al. 2012; McConkey et al. 2012).

The overall aim of this contribution was to explore the ecology of tantalus monkeys, particularly with respect to their potential to move seed from the forest into degraded landscapes. Because spitting by tantalus monkeys was almost never observed in the grassland (Bawaro, pers. obs.) we decided to concentrate on endozoochory (the dispersal of seeds by animals after passage through the gut) and ask the following questions: 1. How do tantalus monkeys compare with other cercopithecines in their seed dispersal behaviour?; 2. Taking population density into consideration, how do seed dispersal rates compare to those of other cercopithecines?; 3. Do tantalus monkeys spend sufficient time in the grasslands to disperse significant quantities of seed into these degraded habitats?; and 4. what type of plant species are dispersed?

METHODS

Study Site

We conducted our study at in the Ngel Nyaki Forest Reserve situated on the western escarpment of the Mambilla Plateau (7°30’ N, 11°30’ E), Taraba State, Nigeria, within the Cameroon Highlands ecoregion (Olson et al. 2001). This location comprises habitats ranging from intact submontane forest, forest edge, riverine forest fragments and open grassland (Figure 2). It is floristically diverse, being rich in endemic or near-endemic plant species (Chapman & Chapman 2001). The mean annual rainfall is approximately 1800 mm p.a., most of which occurs between mid-April and mid-October (Nigerian Montane Forest Project (NMFP) Weather Data). The forest reserve is subjected to frequent fires and cattle grazing. Of the six primate species present, three (Cercopithecus nictitans (putty nose monkey), Ce. mona (mona monkey), and Colobus guereza occidentalis (black and white colobus monkey) are restricted to the forest, while the other three, Pan troglodytes ellioti (Nigerian/Cameroon chimpanzee), Papio anubis (olive baboon), and tantalus monkey venture into the surrounding grassland areas. Of these latter three, the tantalus monkey is the most commonly observed at Ngel Nyaki (Agmen et al. 2009).

For the purpose of this study, grassland is characterised as the area comprising over-grazed Sporobolus dominated tussock grassland interspersed with very occasional savanna tree species and small streamside forest remnants. Ngel Nyaki forest is confined to the steep slopes of an ancient volcano and much of the 5.2 square km of forest can be considered as edge, which is approximately 200m wide (Aliyu et al. 2014) (Figure 2). Forest edge habitat differs from forest core in as much as there
is evidence of past and/or current cattle presence in the edge and in comprising a high frequency of light demanding, pioneer species such as Bridelia speciosa, Trema orientalis, and Psychotria succulenta relative to core forest. Light demanding forest species such as Albizia gummiifera, Anthonotha noldeae and Polyschius fulva are common in both core and edge. Occasionally shade loving forest core species such as Pouteria altissima are found in forest edge habitat. The forest edge has a relatively open understory with shrubs, herbs and vines including Clausena anisata and Aframomum angustifolium (Chapman et al. 2010). The Sporobolus grassland is burnt annually by the Fulani pastoralists to stimulate new grass growth, but close to Ngel Nyaki forest large areas of this grassland have been fenced off by the Nigerian Montane Forest Project to protect it from burning and grazing in order to encourage forest expansion into areas which historically are likely to have been forested (Barnes & Chapman 2014).

**Data Collection**

**Time spent in each habitat**

We observed three semi-habituated tantalus monkey troops (ranging in size from 16 to 38 individuals) approximately twice a week in the dry season and once a week in the rains along the northern boundary of Ngel Nyaki Forest Reserve from November 2008 until January 2009 and from November 2009 until November 2010 to determine the time spent in the forest, forest edge and grassland habitats.

Upon locating a troop, two of us took scan samples (Altmann 1974) every 10 minutes. Scan sampling was stopped after the troop was out of sight for two consecutive scan samples. Our observations were between 0700 and 1800 hours, during which time we recorded the number of individuals visible in each of the forest and grassland habitats.

Usually the tantalus monkey troops disappeared into the forest undergrowth during the heat of the day and/or at dusk and we never observed monkeys between the hours of 1300 and 1500. After 1500 hours, the troops had to be located again before sampling could resume. In total our study comprises data from a total of 2270 scans amounting to 378.3 hours of observations. We observed troops from a distance of between 20 to 50 m using binoculars to minimise disturbance and potentially altering their behaviour.

**Density**

To estimate the density of tantalus monkeys in the Ngel Nyaki Forest Reserve, we used distance sampling (Buckland et al. 2001) and analysed the data using the software DISTANCE 6.0 release 2 (Thomas et al. 2010). This involved walking along...
six line transects, 800 m apart set perpendicular to the forest edge, providing a combined length of 4.69 km. These transects passed through forest, forest edge and grassland areas and two observers walked quietly at c. 1 – 1.5 km h⁻¹ to avoid disturbing any tantalus monkeys present. This procedure was repeated 18 times between December 2009 and September 2010, with at least one walk a month. The total distance surveyed was 84.5 km. Throughout each transect walk, we made regular pauses to scan the surroundings for tantalus monkeys and thereby minimise the chances of missing a troop in the vicinity. When one or more tantalus monkey individuals were observed, a GPS location was taken from a position on the transect that was perpendicular to the animals’ location. At the same time an estimate was made of the distance to the centre of the troop and the number of individuals was noted along with the date and time of observation. The same observer always made the estimate of distance to the centre of the group to ensure consistency.

Seeds per faecal deposit
We opportunistically collected faeces from across forest edge and grassland, the two habitats in which we recorded tantalus monkeys, between October 2009 until January 2010 and again during April 2010. These intervals coincided with those periods of peak fruiting (NMFP unpublished phenological records) that occurred outside of the rainy season. The avoidance of the wet season was necessary because under such conditions the samples were frequently washed away by the rain and any data that we did collect would have been spurious. While concentrating on dry season data will have inevitably biased our results and altered interpretation somewhat, nevertheless our dry season data provide important information regarding seed dispersal by tantalus monkeys. During the collection intervals, we also recovered faecal samples from the sleeping sites of the three semi-habituated troops. We located these sites by following a troop in the late afternoon until it settled down for the night. The following morning, we searched the ground and undergrowth for faecal deposits which we uplifted with trowels and placed into labelled polythene bags. The samples were relatively easy to locate and identify based on their size and shape. Of the 164 tantalus monkey faecal samples collected, 129 were from the forest edge and 35 from the grassland areas. While we could not be completely certain that all our samples were from tantalus monkeys, we never observed other primate species sharing sleeping sites with them.

Seed removal from the faecal samples in the wet-laboratory was based on the methods of Kunz and Linsenmair (2008). We formed a slurry from each sample that was then sieved through a 2 mm mesh. For comparison with other studies all trapped seeds > 2 mm in diameter were counted and identified where possible; seeds < 2 mm were not considered. Two millimetres has frequently been used in other studies (Wrangham et al. 1994; Kaplin & Moermond 1998; Poulsen et al. 2001) as the point below which seeds were not counted due to difficulties in their removal and counting. We identified seeds > 2 mm to species level when possible using the NMFP reference collection. Seed sizes were obtained from Agmen et al. (2009), Chapman et al. (2010) and Dutton and Chapman (2015). These values were means of n = 20 seeds per species. Seed sizes of species of seeds not included in any of these studies were measured with digital callipers to the nearest mm.

Defecation Rate
In order to estimate the daily quantity of seeds dispersed per monkey, it was necessary to estimate the defecation rate of tantalus monkeys and then multiply this by the mean number of seeds per faecal deposit. As it is usually impractical to obtain accurate data on defecation rates from primates observed in the wild, captive individuals are often used instead (e.g., Poulsone et al. 2001; Lambert 2002). Thus, we used three captive tantalus monkey individuals (one adult male, one adult female and one sub-adult female) to estimate tantalus monkey defecation rates. The captive monkeys were part of a (cancelled) release program (Wallis, pers. comm.) and temporarily housed close to the NMFP field station and were fed a diet of fruits and vegetables (bananas, pineapples, tomatoes, onions, carrots) as well as locally-collected forest fruits of Aframomum angustifolium and Leea guineensis. While this diet did not completely reflect the feral diet, it was seen to provide an adequate estimate of field defecation rates.

Two of us observed the captive subject animals for three consecutive days in November 2010, during which time records were kept of individual defecation events.

Statistical Analyses
Time spent in each habitat
For ease of analysis, we grouped individual scan samples together into six two-hour time periods. We used a binomial generalised linear mixed model
(GLMM) to test for significance differences in the proportion of time spent in the grassland versus forest during each of the two hour time intervals. Date was included as a random factor to account for a possible lack of independence of scans taken on the same day. Additionally, an observational level random factor was included to account for over-dispersion of the data. We used a log-likelihood ratio test (using the ANOVA function in R) to determine the significance of time of day on the proportion of time spent in the grassland.

Density of tantalus monkeys

We used DISTANCE (Thomas et al. 2010) to estimate the density of tantalus monkeys from the observational data collected along the transects. A half-normal detection function with cosine adjustment model (AIC = 103.53) provided an effective strip width of 33.8 m.

Difference in the number of seeds per faecal deposit in each habitat

The number of seeds per faecal deposit were not normally distributed, hence it was necessary to calculate the median and 1st and 3rd quartiles, instead of mean and standard deviation. These values were then used in subsequent calculations. However, we included the corresponding mean and standard deviation values in Table 1 to allow comparison with other studies.

We used only intact seed data and these were analysed using Poisson GLMMs to test for differences in the number of seeds per faecal deposit in the forest edge and grassland habitats. We included month as a random factor to control for variation among months. Data were entered whereby seeds in each faecal deposit constituted one observation. This allowed the model to account for unequal sample sizes among habitats and months. Overdispersion of data for seeds was accommodated by including an additional random factor at the observational level to create a Poisson-lognormal GLMM as suggested by Elston et al. (2001). We determined the significance of a factor using a log-likelihood ratio test.

Difference in size of dispersed seed between habitats

The seeds collected from faeces were placed into one of two categories: small (2-5 mm) and medium (5-20 mm), following Wrangham et al. (1994) and Kunz and Linsenmair (2008).

We used a binomial GLMM model to test if the proportion of small seeds collected per deposit found in the forest and grassland habitats differed significantly. Habitat was included as a fixed factor, while month and an observational level factor were included as random factors. A log-likelihood ratio test was used to test the significance of habitat.

Difference in the number of seeds dispersed into forest and grassland

To estimate the seed dispersal rate into each habitat, we used the following equation:

\[ S = D \cdot s \cdot d \cdot t \]

where,

\[ S = \text{rate of seed dispersal by } C. \ tantalus \text{ into a habitat} \]
\[ D = C. \ tantalus \text{ population density} \]
\[ s = \text{median number of seeds released per defecation in the habitat} \]
\[ d = \text{number of defecations per day} \]
\[ t = \text{average proportion of time spent by } C. \ tantalus \text{ in the habitat per day} \]

Table 1. Mean and median values of the number of seeds collected per faeces from Chlorocebus tantalus in forest and grassland habitats. Q1 = first quartile and Q3 = the third quartile.

<table>
<thead>
<tr>
<th>Range</th>
<th>Median Number of Seeds per Faeces</th>
<th>Q1 - Q3</th>
<th>Mean ± SD Number of Seeds per Faeces</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total seeds</td>
<td>0 – 551</td>
<td>5</td>
<td>2 – 23.25</td>
</tr>
<tr>
<td>Forest total seeds</td>
<td>0 – 258</td>
<td>4</td>
<td>1 – 14</td>
</tr>
<tr>
<td>Forest small seeds</td>
<td>0 – 258</td>
<td>2</td>
<td>0 – 8</td>
</tr>
<tr>
<td>Forest medium seeds</td>
<td>0 – 54</td>
<td>0</td>
<td>0 – 2</td>
</tr>
<tr>
<td>Grassland total seeds</td>
<td>0 – 551</td>
<td>20</td>
<td>4 – 64.5</td>
</tr>
<tr>
<td>Grassland small seeds</td>
<td>0 – 551</td>
<td>19</td>
<td>2 – 64</td>
</tr>
<tr>
<td>Grassland medium seeds</td>
<td>0 – 9</td>
<td>0</td>
<td>0 – 1.5</td>
</tr>
</tbody>
</table>
RESULTS

Time in Each Habitat

We found that the tantalus monkeys never ventured more than 100m into the forest, so that they were confined to forest edge habitat. On average, the monkeys spent 6.5% of the day (93.6 minutes) in the grassland habitat, with the remainder of the day spent in the forest edge. Across the two-hourly intervals, tantalus monkey presence in the grassland varied significantly ($\chi^2 = 68.75$, df = 4, $P < 0.0001$) showing peaks in the grassland between 0700 – 0900 hours and 1700 – 2100 hours.

Table 2. Species of seed collected from 164 Chlorocebus tantalus faeces at Ngel Nyaki Forest Reserve, with basic information.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Total Seeds Collected</th>
<th>Seed Size (mm)</th>
<th>Habitat$^a$</th>
<th>Life Form</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aframomum angustifolium</em> (Hook.f) K. Schum.</td>
<td>Zingiberaceae</td>
<td>2244</td>
<td>4.5</td>
<td>E</td>
<td>Herb</td>
</tr>
<tr>
<td>Species 2</td>
<td></td>
<td>1755</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leea guineensis</em> G. Don</td>
<td>Leeaceae</td>
<td>196</td>
<td>4.5</td>
<td>E, G</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>Croton macrostachyus</em> Hochst ex Del.</td>
<td>Euphorbiaceae</td>
<td>185</td>
<td>7</td>
<td>E, SF</td>
<td>Tree</td>
</tr>
<tr>
<td>Species 1</td>
<td></td>
<td>77</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Grewia</em> sp.</td>
<td>Tiliaceae</td>
<td>47</td>
<td>9</td>
<td>E</td>
<td>Shrub</td>
</tr>
<tr>
<td>Species 21</td>
<td></td>
<td>38</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species 9</td>
<td></td>
<td>35</td>
<td>2.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Psychotria peduncularis</em> (Salisb.) Steyerl</td>
<td>Rubiaceae</td>
<td>27</td>
<td>5.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Psychotria succulenta</em> (Hier) E.M.A. Petit</td>
<td>Rubiaceae</td>
<td>23</td>
<td>6</td>
<td>E</td>
<td>Tree</td>
</tr>
<tr>
<td>Species 6</td>
<td></td>
<td>15</td>
<td>10</td>
<td></td>
<td>Liana</td>
</tr>
<tr>
<td><em>Landolphia</em> sp.</td>
<td>Apocynaceae</td>
<td>9</td>
<td>12</td>
<td>F, E</td>
<td>Liana</td>
</tr>
<tr>
<td>Species 12</td>
<td></td>
<td>8</td>
<td>2.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species 14</td>
<td></td>
<td>8</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species 10</td>
<td></td>
<td>6</td>
<td>2.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Syzygium guineense</em> (Willd.) DC.</td>
<td>Myrtaceae</td>
<td>4</td>
<td>12</td>
<td>F, S</td>
<td>Tree</td>
</tr>
<tr>
<td>Species 18</td>
<td></td>
<td>3</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species 5</td>
<td></td>
<td>2</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species 16</td>
<td></td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species 7</td>
<td></td>
<td>1</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Vitex doniana</em> (Sweet)</td>
<td>Verbenaceae</td>
<td>1</td>
<td>20</td>
<td>F, E, S</td>
<td>Tree</td>
</tr>
<tr>
<td><em>Pouteria altissima</em> (A. Chev.) Baehni</td>
<td>Sapotaceae</td>
<td>1</td>
<td>19</td>
<td>F</td>
<td>Tree</td>
</tr>
<tr>
<td><em>Synsepalum</em> sp.</td>
<td>Sapotaceae</td>
<td>1</td>
<td>15.5</td>
<td></td>
<td>Tree</td>
</tr>
<tr>
<td><em>Bridelia speciosa</em> Müll. Arg.</td>
<td>Euphorbiaceae</td>
<td>1</td>
<td>8</td>
<td>E</td>
<td>Tree</td>
</tr>
</tbody>
</table>

* Abbreviations as follows: E = Forest edge; F = Forest; L = Light gaps; S = Savanna/Grassland; SF = Secondary forest
Distance Analysis
The estimated troop density of tantalus monkeys in this study was $2.1 \pm 0.8$ per km$^2$ and the average troop size was $13.3 \pm 1.8$. The density of tantalus monkey individuals in the area was $28.0 \pm 10.8$ per km$^2$.

Numbers of Seeds
Of the 164 tantalus monkey faecal samples we collected 84.1% contained at least one intact seed > 2 mm. Overall, the number of seeds found per faecal deposit was highly variable, ranging from zero to 551 (Table 1). The median number of seeds per faecal deposit differed significantly between habitats ($\chi^2 = 12.5$, df = 1, $P = 0.0004$) with five times as many seeds in the grassland deposits as in the forest (Table 1).

In total we recovered 4748 seeds and, irrespective of the habitat they were collected from, a high proportion belonged to either the forest herb *Aframomum angustifolium* (47.3%) or an unidentified seed species designated sp. 2 (40%). The remaining 749 seeds comprised an additional 22 species (Table 2).

Size of Dispersed Seed
Tantalus monkeys dispersed seeds up to 20 mm long and 12 mm diameter, with the largest seed being from the forest tree *Pouteria altissima*. Small seeds were more abundant in faeces from both habitats than medium seeds (Table 1), however the relative proportion of small seeds dispersed in grassland faeces was significantly higher than in those from the forest edge ($\chi^2 = 6.64$, df = 1, $P = .010$, Figure 3).

Seed Dispersal Rates
Individual captive tantalus monkeys defecated 3.4 ± 1.5 times per day. The monkey spends an average 6.5% of its day in the grassland and 93.5% in the forest edge. Assuming the defecation rate in each habitat is a function of the amount of time spent in these habitats, a tantalus monkey defecates 0.22 times per day in the grassland and 3.18 times in the forest. An individual tantalus monkey therefore defecates an estimated 4.4 and 12.7 seeds per day in the grassland and forest habitats, respectively.

Using the estimated population density of 28 tantalus monkey individuals per km$^2$, the mean daily defecation rate in the forest and grassland and the median number of seeds dispersed per defecation, we estimate that at Ngel Nyaki tantalus monkeys disperse 356 and 124 seeds km$^{-2}$ d$^{-1}$ for the forest edge and grassland habitats respectively.

DISCUSSION
Our study highlights that the tantalus monkey is a regular and potentially important disperser of seeds from a number of plant species across forest edge and into grassland areas in the degraded landscape of the study area.

How Does *C. tantalus* Compare with Other Cercopithecines in Their Seed Dispersal Behaviour?
We found that tantalus monkeys at Ngel Nyaki dispersed a median of five seeds and a mean of $29.0 \pm 65.2$ (SD) seeds per faecal deposit, which is considerably more than the reported mean numbers of seeds dispersed by several other *Cercopithecus* spp. such as *Cercopithecus mitis* (blue monkeys) and *Lophocebus albigena albigena* (grey cheeked mangabey) but slightly less than that of *Cercopithecus l'hoesti* (L’Hoest’s monkey) and a mixed group of *Cercopithecus* spp. (Table 3). The tantalus rates were similar to the much larger olive baboon (Table 3). Thus tantalus monkeys also appear to be a quantitatively important disperser of seeds, at least during the dry season when this study was carried out.

Tantalus monkeys dispersed seeds up to 12 x 20 mm in size, which is among the larger sizes reported for most other cercopithecines (Albert et al. 2014) although, as would be expected, this seed size is smaller than what can be dispersed by baboons (Table 3). Some cercopithecines have a very low swallowing size threshold, e.g., *Macaca fascicularis* (crab-eating macaque) and *Ce. ascanius* (red tailed monkey) which typically swallow seeds up to only 4 mm in diameter (Corlett & Lucas 1990; Lambert...
<table>
<thead>
<tr>
<th>Species</th>
<th>N Faecal Samples Analyzed</th>
<th>% Faeces Containing Intact Seeds &gt; 2 mm</th>
<th>Mean Number of Seeds per Faeces (&gt; 2 mm)</th>
<th>Population Density (Individuals per km²)</th>
<th>Population Seed Dispersal Rate (km².d⁻¹)</th>
<th>Max Seed Size (mm)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorocebus tantalus Tantalus monkey</td>
<td>164</td>
<td>87.9</td>
<td>29.0 ± 65.2 (median = 5)</td>
<td>28</td>
<td>Forest: 356 Grassland: 124</td>
<td>20</td>
<td>This study</td>
</tr>
<tr>
<td>Cercopithecus aethiops Green monkey</td>
<td></td>
<td></td>
<td></td>
<td>Up to 96</td>
<td></td>
<td></td>
<td>Isbell et al. 1990</td>
</tr>
<tr>
<td>Cercopithecus ascanius Red tailed monkey</td>
<td></td>
<td></td>
<td></td>
<td>130</td>
<td></td>
<td>4</td>
<td>Lambert 1999</td>
</tr>
<tr>
<td>Cercopithecus spp.</td>
<td>55</td>
<td>51.0</td>
<td>8.58 ± 19.58</td>
<td></td>
<td></td>
<td></td>
<td>Kaplin &amp; Moermond 1998</td>
</tr>
<tr>
<td>Cercopithecus mitis doggetti Doggetti's blue monkey</td>
<td>50</td>
<td>60.0</td>
<td>2.33 ± 1.45</td>
<td>6.8</td>
<td></td>
<td></td>
<td>Kaplin &amp; Moermond 1998</td>
</tr>
<tr>
<td>Cercopithecus l'hoesti L'Hoest's monkey</td>
<td>58</td>
<td>69.0</td>
<td>6.43 ± 8.27</td>
<td>6.8</td>
<td></td>
<td></td>
<td>Kaplin &amp; Moermond 1998</td>
</tr>
<tr>
<td>Cercopithecus nictitans nictitans Putty nosed monkey</td>
<td>402</td>
<td>42.8</td>
<td>1.0 ± 1.9</td>
<td>14.7</td>
<td>73.5</td>
<td></td>
<td>Poulsen et al. 2001</td>
</tr>
<tr>
<td>Cercopithecus mona pogonias Mona monkey</td>
<td>75</td>
<td>54.7</td>
<td>2.1 ± 3.4</td>
<td>24.6</td>
<td>258.3</td>
<td></td>
<td>Poulsen et al. 2001</td>
</tr>
<tr>
<td>Cercopithecus cephus cephus Moustached guenon</td>
<td>83</td>
<td>37.3</td>
<td>1.5 ± 2.9</td>
<td>10.3</td>
<td>77.3</td>
<td></td>
<td>Poulsen et al. 2001</td>
</tr>
<tr>
<td>Lophocebus albigena albigena Grey cheeked Mangabeys</td>
<td>3070</td>
<td>33.7</td>
<td>1.6 ± 26.4</td>
<td>19.7</td>
<td>158.6</td>
<td></td>
<td>Poulsen et al. 2001</td>
</tr>
<tr>
<td>Macaca fuscata Japanese macaque</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13.79 Tsuji et al. 2011</td>
</tr>
<tr>
<td>Mandrillus leucophaeus Drill</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>42 Astaras &amp; Waltert 2010</td>
</tr>
<tr>
<td>Papio anubis Olive baboon</td>
<td>396</td>
<td>28.2 ± 70.5 (median = 7)</td>
<td></td>
<td>129</td>
<td>27</td>
<td></td>
<td>Kunz &amp; Linsenmair 2008</td>
</tr>
</tbody>
</table>
1999). However, some cercopithecines can spit large seeds (e.g., Corlett & Lucas 1990; Lambert 2001; Gross-Camp & Kaplin 2011) which may be an important method of seed dispersal (see Albert et al. 2014 and references within) but is unlikely to result in the transfer of seeds across habitats. Irrespective, talantalus monkeys swallow and disperse via defecation seeds as large as those that other cercopithecines are likely to spit. In terms of moving seeds of tree species into grassland however, seed size is not important; it is the pioneer tree species with small seeds adapted for germination under high light conditions that are most likely to establish.

There was a large difference in the number and size of seeds per faecal deposit collected from the grassland versus the forest edge. Faeces collected in the forest edge contained fewer seeds than the grassland samples (medians of four and 20, respectively) but a higher proportion of seeds of medium size, whereas the material collected in the grassland areas typically contained more seeds in the small size class. This is likely at least in part to be a reflection of daily foraging patterns. The possibility that faeces may be overlooked by searchers in the forest cannot be dismissed and this may have contributed to the discrepancy in our findings between forest edge and grassland in terms of number of seeds dispersed. However, searches for faecal deposits in the forest edge habitat were painstakingly carried out.

### Variation in Tantalus Monkey Seed Dispersal Rates Compared with Other Cercopithecines

During the transect walks, the small number of talantalus monkey sightings (n = 12) was not ideal for the DISTANCE analytical technique (Buckland et al. 2001). However, in the absence of any other talantalus monkey population density data, the DISTANCE technique was applied in order to provide a reference point for future studies of talantalus monkey populations. Additionally, the measured mean talantalus monkey troop size of 13.3 could have been an underestimate; talantalus monkey troop sizes may vary considerably from 11 to 70 individuals (Kavanagh 1980) with troop sizes of 18 to 40 being most commonly reported (Nakagawa 1999; Agmen et al. 2009). The three semi-habituated talantalus monkey troops used in this study to calculate the amount of time spent in forest edge and grassland habitats ranged between 16 and 38 individuals.

There is sparse reference to talantalus monkey population densities in the literature. However, using the data from Nakagawa’s (1999) Cameroon study, a talantalus monkey population density of 1.7 troops per km² corresponding to 30 individuals per km² can be calculated. While this troop density is less than the 2.1 per km² measured in the Ngel Nyaki Forest Reserve, the overall density of 30 individuals per km² is comparable to the 28 individuals per km² found by Nakagawa (1999). Such density estimates are greater than the reported densities for many other cercopithecine populations (Table 3). However, notable exceptions do occur; higher population densities of red tailed monkeys have been measured at Kibale National Park, Uganda (Lambert 1999) and Ch. pygerythrus (formerly Cercopithecus aethiops, vervet monkey at Amboseli National Park, Kenya (Isbell et al. 1990). These were reported to be 130 per km² and up to 96 per km², respectively (Table 3).

Based on the population data discussed above, talantalus monkeys at Ngel Nyaki moved more than twice as much seed through defecation within the forest edge habitat than into the grassland, dispersing 356 and 124 seeds km⁻² d⁻¹, respectively. The forest edge dispersal rate of swallowed seeds is greater than most other reports for Cercopithecus spp. (Table 3), and is closer to the 369 seeds km⁻² d⁻¹ dispersed by chimpanzees at Kibale National Park, Uganda (Wrangham et al. 1994). Conversely the grassland seed dispersal rate for the talantalus monkeys in our study is in the middle of the range of seed dispersal rates for other Cercopithecus spp. (Table 3) and is similar to the 129 km⁻² d⁻¹ seeds dispersed by the olive baboon in the Comoé National Park, Ivory Coast (Kunz & Linsenmair 2008). The absolute rates of seed dispersal by talantalus monkeys are greater than those reported here as the faeces also contained an unquantified number of seeds < 2 mm, such as Ficus spp. Moreover Lambert (1999, 2011) illustrated how dispersal rates of cercopithecines in Kabale National Park, which included both defecated and spat seeds, were considerably higher than dispersal rates based on defecation rates alone and easily equated to dispersal rates of larger primate taxa such as chimpanzees.

### The Potential for Tantalus Monkeys to Disperse Significant Quantities of Seed into the Degraded Grassland Habitat

In general, the rate of seed dispersal into grassland areas from forest remnants can be slow as few animal dispersers make the required inter-habitat movements (Wunderle 1997; Cordeiro & Howe 2001). However, we have shown that, not only do talantalus monkeys frequent grassland, but they disperse seeds of pioneer, light demanding, early successional species and deep forest species
into grassland habitats, making tantalus monkeys potentially important for forest expansion. While the overall rate of seed dispersal by tantalus monkeys into grassland habitats (at least during the dry season) is less than their rate of seed dispersal within forest edge habitats, the number of seeds the species dispersed into the grassland appears to be disproportionately high, given they spend only 6.5% of their time in the grassland. Additionally, tantalus monkeys at Ngel Nyaki feed primarily on the forest edge (70% of feeding time), with only 8% of feeding occurring in grassland areas where non-fruit items such as invertebrates are consumed (Agmen et al. 2009).

Considering the proportion of seeds from each size class distributed in the forest edge and grassland ecosystems, the disproportionate number of seeds dispersed by tantalus monkeys into grassland in part reflects diurnal foraging patterns. While Wallis et al. (2008) report a gut retention time of 30 ± 2.83 hours for captive tantalus monkeys, defecation rates have been shown to be influenced by diet and activity levels of the individuals (Lambert 2002). In addition, seed size affects gut passage time, with smaller seeds being defecated significantly sooner than larger, heavier seeds (Tsuji et al. 2010). This study and the work of Agmen et al. (2009), suggests that with a slightly shorter gut retention time than estimated by Wallis et al. (2008), faeces deposited in the grassland could be associated with forest edge feeding, which could explain why grassland-deposited faeces contained more seeds. Additionally, seed-size is an influence; a greater number of small seeds than medium seeds can be swallowed before reaching the threshold volume at which too much nutritious gut content becomes displaced by undigestible seeds (Lambert 1999).

Of those seeds dispersed into grassland areas by tantalus monkeys, the vast majority were small-seeded understory herbs/shrubs associated with the forest edge such as Aframomum angustifolium and Leea guineensis. The few medium-sized seeds dispersed into grassland included pioneer species such as Croton macrostachyus and Bridelia speciosa, again associated with the forest edge habitats. In terms of practical conservation value, such observations indicate that, providing the dispersed seeds germinate and are given adequate protection from regular burning and grazing, such dispersal into grassland could support forest regeneration through tantalus monkeys. This and the fact that larger seeds, such as Pouteria sp., associated mainly with forest core were relatively rare in any tantalus monkey faeces, suggests that the conservation contribution made by tantalus monkeys - in conjunction with other species, particularly birds such as pigeons and doves (Roselli 2014) in Afromontane ecosystems, lies in their dispersing of pioneer species into grassland habitats and degraded forest edge habitat.

Within Ngel Nyaki Forest Reserve tantalus monkeys are frequently seen and are additionally important for conservation as the abundance of other primates capable of dispersing seeds of pioneer tree species into grassland habitats (olive baboon and chimpanzee) are generally thought to be insufficient at Ngel Nyaki Forest Reserve to provide effective seed dispersal services (Beck & Chapman 2008, Chapman et al. 2010).

In summary, this contribution provides an important addition to the knowledge of tantalus monkey ecology, particularly in relation to seed dispersal. At the individual level, they disperse at least as many seeds, and in some cases larger seeds, than most other cercopithecine species, and the tantalus population at Ngel Nyaki Forest Reserve disperses a similar number of seeds as some chimpanzee populations elsewhere. Furthermore, tantalus monkeys not only regularly spend time in grassland habitats but also disperses the seeds of pioneer and secondary forest plant species from the forest edge into such habitats, suggesting they may be an important source of seed rain into such degraded habitats. While it is recognised that gaining an understanding of the ecology of rare or threatened species is important, our study also highlights the importance of gaining an ecological understanding of relatively common species that are less affected by anthropogenic habitat modifications.

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