

**A Comparison of the Seed  
Dispersal Service Offered by  
Chimpanzees (*Pan troglodytes*)  
and Gorillas (*Gorilla gorilla*).**

**Katherine Bunney**

**Supervisor: William Bond**

**In partial fulfillment of my Botany Honours degree (Ecology).**

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*KD Bunney*

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## **A comparison of the seed dispersal service offered by chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*).**

### **Abstract**

The handful of studies that have investigated chimpanzee and gorilla seed-dispersal identify these primates as important dispersal agents. These studies do not, however, make any measure of the 'quality' of the dispersal service offered by chimpanzees and gorillas. Determining 'quality' requires a measure of the dispersal distance and the microsite to which the seeds are dispersed. In this study, I report the first estimate of seed dispersal curves for chimpanzees and gorillas. Seed dispersal curves were produced by combining ape movement data with gut passage curves from literature. The derived dispersal distances for chimpanzees and gorillas are similar *c.* 7.7 km; this is surprisingly large when compared with other seed dispersal agents. This is likely due to a combination of foraging behaviour and gut physiology. At a species level, chimpanzees (*Pan troglodytes*) were shown to direct dispersal of *Uapaca palidosa* to favourable microsites even though gorillas (*Gorilla gorilla*) were responsible for moving a greater number of seeds. This study presents a novel method for the rapid derivation of dispersal curves and highlights the importance of incorporating species level as well as community level studies to assess the quality of seed dispersal agents. It is my hope that the methods presented here be applied elsewhere so that the role of extant megaherbivores as seed dispersal agents be incorporated into future models that investigate forest dynamics.

### **Introduction**

#### Seed Dispersal

Vertebrates are responsible for dispersing the seeds of the majority of woody plants in tropical forests (Willson *et al.*, 1989 in Sun *et al.*, 1997). The importance of this interaction on plant regeneration and forest population dynamics is well appreciated and has been the focus of extensive study in recent decades (Howe and Smallwood, 1982; Sun *et al.*, 1997). However studies focussing on the effectiveness of dispersal agents are limited (Nathan and Muller-Landau, 2000). The effectiveness of the

dispersal agents is central to understanding the ecological and evolutionary consequences underlying each plant-animal interaction (Murray, 1988; Sun *et al*, 1997) especially since dispersal effectiveness varies considerably from one dispersal agent to another (Schupp, 1993). This report explores the relative effectiveness of seed dispersal by gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) in a tropical lowland forest.

### Great Ape Dispersal

Fruit and insects compose the majority of gorilla and chimpanzee diet even though until recently gorillas were regarded as folivores (Tutin *et al*, 1991; Goodall, 1968; Nishida, 1970). Qualitatively, their diets appear similar, being dominated by an equally diverse array of fruit species (Tutin *et al*, 1991). The handful of studies that have investigated chimpanzee and gorilla seed-dispersal identify these primates as important dispersal agents (Voysey *et al*, 1999; Wrangham *et al*, 1994, Tutin *et al*, 1991). In a generalised comparative study on primate seed dispersal in the Dja Faunal Reserve, Poulsen *et al* (2001) found that the seven resident primate species were responsible for dispersing a larger number of seeds per unit area than did either elephants (Lope Reserve – White *et al*, 1991) or three species of *Ceratogymna* hornbills (Dja Faunal Reserve – Whitney *et al*, 1998). He further highlighted that the two ape species (*Gorilla gorilla* and *Pan troglodytes*) had the lowest population densities of all the primates yet they accounted for over half of the seeds dispersed in the forest (Poulsen *et al*, 2001). They went on to suggest that the large size of gorillas and chimpanzees may strengthen their importance as seed dispersers as there are few vertebrates that can handle large-seeded fruit.

Moreover, in a study on gorillas by Voysey (1999) it was concluded that these vertebrates were highly effective seed dispersers. There it was shown that the quality of gorilla seed dispersal is high because they treat seeds benignly and tend to direct seeds to microsites favourable for their establishment. In a plant-animal interaction study, Tutin *et al* (1991) looked at the interaction between *Cola lizae* (an endemic tree with a limited geographic range) and the lowland gorillas of the Lopé Reserve, Gabon. These gorillas were identified as being the only vertebrate that swallows the seeds of *Cola lizae*, thus being their only potential long distance dispersal agent.

Observations of *Cola* seeds in gorilla faeces demonstrated a very high germination rate, particularly in gorilla nest sites where they are commonly deposited (Tutin *et al.*, 1991).

The results of the above studies establish that gorillas and chimpanzees are important dispersal agents. However as they make no measure of ape long distance dispersal they do not lend themselves to being incorporated into a model. Measures of long distance dispersal have been spurred on so as to explain the rapid range expansion since the last glacial maxima (L.G.M.). Adding dispersal to current models will also allow us to assess the community and ecosystem consequences of contemporary climate change (McLachlan and Clark, 2004). In the case of chimpanzees and gorillas this is of fundamental importance given their 'endangered' status (I.U.C.N., 2003)

### Assessing seed dispersal

Studies of seed dispersal endeavour to understand both process and pattern (Wang and Smith, 2002). There are a few established methods for elucidating seed dispersal patterns. The most common method to date involves documenting variation in seed deposition or density with distance from the source (Willson, 1993, Nathan and Muller-Landau, 2000). The true source and dispersal distances are not known but can be inferred in a variety of ways. However up until now the majority of studies of seed dispersal were conducted in single populations over single seasons and without consideration of the microsite in which the seeds are deposited (Nathan and Muller-Landau, 2000). These studies have unavoidably failed to capture important variation at large spatial and temporal scales (Clark, 1999).

**'It matters who defecates what where' (Janzen, 1986)**

### Dispersal Effectiveness

There are two components to the effectiveness of a dispersal agent: the quantity of seeds dispersed and the quality of dispersal for each seed (Herrera and Jordano, 1981). This study addresses the 'quality' of dispersal by apes; this necessitates

determining both the dispersal distance and the microsite to which the seed is dispersed. These questions are tackled at both the community and species level.

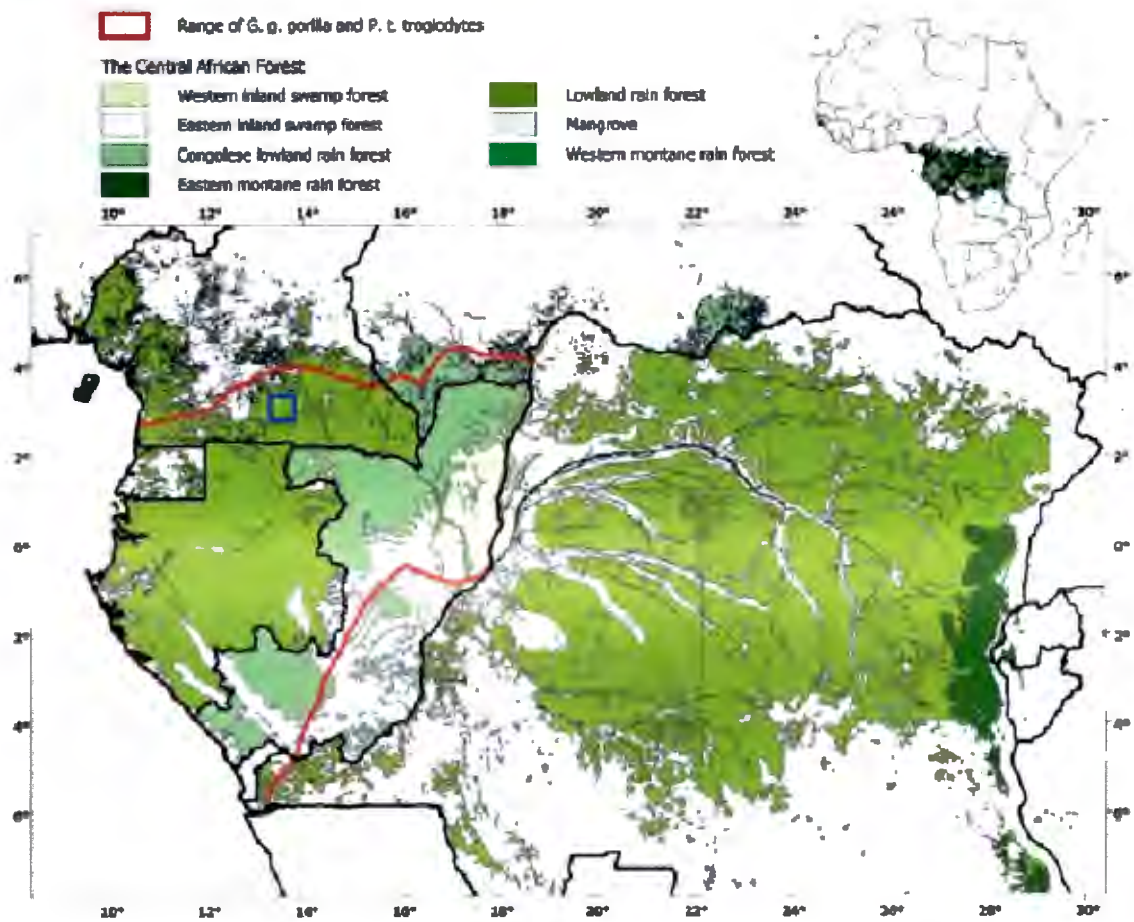
At the community level I addressed three questions. 1) How far do gorillas and chimps disperse seeds? To determine this I integrated movement and gut passage rates, deriving expected seed shadows for both species. 2) Is there a monthly difference in the distance chimpanzees and gorillas travel? This is of interest as if monthly distance travelled is variant then the shape of the dispersal curve will change over time. 3) Does the number of seeds transported away from the parent vary seasonally?

At the species level I selected a single species (*Uapaca palidosa*) that represented a significant food source in the primates' diet. Firstly I looked at the abundance of seeds present in gorilla and chimpanzee faeces over time. I then made the assumption that the distribution of the adult trees would accurately reflect the microsite most suitable for their seedlings establishment. I then asked, which species would be the more effective dispersal agent based on where they commonly drop their faeces.

question all based  
on what was  
available in the  
literature?

## Study site and Methods

### Study site



□ = Study site

**Figure 1.** Position of the study site within the range of chimpanzees, (*Pan troglodytes*) and gorillas (*Gorilla gorilla gorilla*), in Western Equatorial Africa. Adapted from Tutin *et al* (2005).

The study was conducted on the periphery of the Dja Faunal Reserve, in South-east Cameroon (Figure 1). It is officially an unprotected area that is situated in the south-west corner of a logging concession (DeBlauwe, 2004). The study site is approximately 40km<sup>2</sup> and falls in a transition zone between the Atlantic coastal rainforests of Southern Nigeria/South-west Cameroon, and the evergreen forests of Equatorial Guinea/Congo Basin (Letouzey, 1985).

In previous publications (Dupain *et al*, 2004, DeBlauwe, 2003) the vegetation of the study area was divided into seven types, namely near primary forest (NPF), old secondary forest (OSF), secondary forest (SF), young secondary forest (YSF), riverine forest (RF) and *Rapphia*-swamps (RS) (Nguneng and Dupain, 2002).

However in this study, to simplify analysis these vegetation types have been grouped into old forest (NPF and OSF), secondary forest (SF), young secondary forest (YSF) and hydromorphic forest (RF and RS). The climate is characterised by two wet and two dry seasons, with the major and minor rainfall peaks in September and May, respectively. The average annual rainfall at the site is c. 1570 mm (PAP, 2001).

The area has a low human population density. It is characterised by subsistence farming and low market-orientated culture of cocoa and coffee. However despite this, perturbations by humans (former villages until 30 years ago and selective logging until about 25 years ago) and elephants have left a marked impact on the vegetation in the site (Nguneng and Dupain, 2002).

## **Community Level Analysis**

### Movement analysis

To determine the distance that gorillas and chimpanzees cover per unit time, groups were followed daily from September 2004 to January 2005. GPS points and times were taken upon encountering a chimpanzee or gorilla group. The group was then tracked with a following distance of 50-100m. A second GPS and time reading was then taken when the trace was abandoned. Where possible, groups were tracked until they came to their final rest site for the night. The distance measured represents the average straight-line distance travelled in a given period. Approximately four trace days were chosen per month to best represent each species.

### Gut transit times

It is a popular belief that the habituation of gorillas and chimpanzees in non-protected areas results in their increased vulnerability to hunting pressure. For this reason it was decided that field methods such as the 'feeding bout observation' method (Whitney *et al*, 1998; Malmborg and Willson, 1988), for estimating seed passage times were inappropriate. Thus for the purpose of this study gut passage times were sourced from the available literature.



A gut passage time of 31.5 hours for chimpanzees was taken from a study conducted by Lambert (1997) on four chimpanzees in captivity. A gut passage time of 47.3 hours was taken for gorillas from a study (Remis, 2000) which employed Lambert's (1997) method on 6 captive gorillas.

Three measures of gut passage were calculated in these studies – the appearance of the first marker (TT), time of last appearance (TLA) of a marker, and the mean retention time of markers (MRT). The mean retention time was used in this study as it is deemed to be the single best estimate of digesta movement through mammalian gastrointestinal tracts (Remis, 2000). MRT is calculated as follows:

$$t = \frac{\sum_{i=1} m_i t_i}{\sum_{i=1} m_i}$$

where  $m_i$  = the amount of marker excreted at the  $i$ th defecation time  $t_i$  after dosing (Warner, 1981; Lambert, 1997 in Remis, 2000).

Using the gut passage times from literature, the movement analysis conducted in the field could be normalized as follows:

### ***For Chimpanzees***

Average Straight-Line Distance/Gut Passage Time

= Average Straight-Line Distance Travelled/hour x (31.5 hours – 12 hours of inactivity)

### ***For Gorillas***

Average Straight-Line Distance/Gut Passage Time

= Average Straight-Line Distance Travelled/hour x (47.3 hours – 24 hours of inactivity)

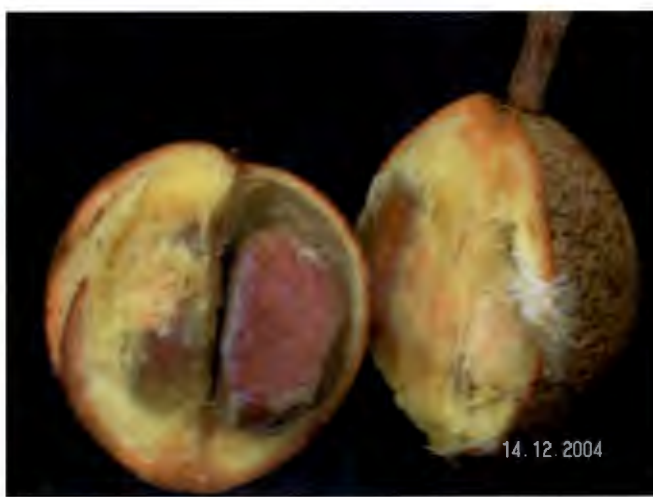
### **Dispersal curve estimation**

Dispersal curves were derived by combining gut passage curves (Figure 3 and 4) with displacement curves (Figure 5 and 6). This method of dispersal curve estimation was

modelled upon a study by Westcott and Graham (2000). It involved substituting the time axis on the gut passage curve with the corresponding distance value. A plot of the proportion of the seeds passed against the distance travelled is produced. The displacement curve was derived from distance measures across all months.

### Composition of diet

Faecal analyses, complemented by behavioural observations, were employed to reveal dietary flux. Faecal samples were collected at nest and feeding sites as well as along primate trails. These were sealed in plastic bags for analysis upon return to the camp. Later, the faeces were weighed and then washed in running water using a 1mm mesh metal sieve. The particulate matter that remained was then analysed macroscopically according to Tutin and Fernandez (1993). Briefly, the proportion (by volume) of seeds in each faecal sample was estimated before seeds were grouped by species and counted. In the case of large-seeded species (> 2 mm) the exact numbers of seeds were counted, while the abundance of small seeds (< 2 mm) was estimated to the nearest hundred seeds given that a single faecal sample could, for example, contain thousands of *Ficus* seeds. Identification of the species to which each group of seeds belonged was determined where possible using the reference collection. Seeds that could not be identified in the field were assigned a code, photographed and then placed in 10% ethanol for identification in the Yaounde Herbarium/ Antwerp Botanical Gardens.



**Figure 2.** The fruit and seeds of *Uapaca palidosa*. The fruit is approximately 3cm in diameter while the seeds are about 0.75 x 1.5 cm.

## Species Level Analysis – A case study of *Uapaca palidosa*

### Distribution of *Uapaca palidosa*

Phenological data on fruit production was collected on the first ten days of each month (September 2004 to January 2005). This involved walking along each of the ten transects (each c.6km in length) and recording the number of fallen fruits. The fruiting parent tree was then located, identified and marked. A distance along the transect measure and vegetation type was assigned to each parent tree. From ~~this~~<sup>these</sup> data it was possible to determine the distribution and fruiting pattern of *Uapaca palidosa*.

### Microsite targeting

For each faecal sample, the vegetation type in which it was found was recorded.

## Results

### Gut Passage Rates

Gut passage rates were slower in gorillas relative to chimpanzees (Table 1, Figure 3 and 4). The transit time (the appearance of the first marker) was similar but the time of last appearance (TLA) of markers differed by 46 hours (Table 1, Figure 3 and 4). The mean retention time (MRT) was used throughout this study as the measure of gut passage rate (Table 1, Figure 5 – 10). The gut passage curve of chimpanzees (*Pan troglodytes*) is bimodal whereas the gut passage curve of gorillas (*Gorilla gorilla*) has a Poisson distribution (Figure 3 and 4).

**Table 1.** Mean transit times, retention times (S.D.) and time of last appearance (hours) of gorillas and chimpanzees. The number in brackets next to the study animal denotes the sample size.

Study Animal	Transit Time (TT)	Mean Retention Time (MRT)	Time of Last Appearance (TLA)
Chimpanzees (4)	23.2	31.5 (S.D. = 12.1)	63.3
Gorillas (6)	23.0	47.3 (S.D. = 21.32)	109.3

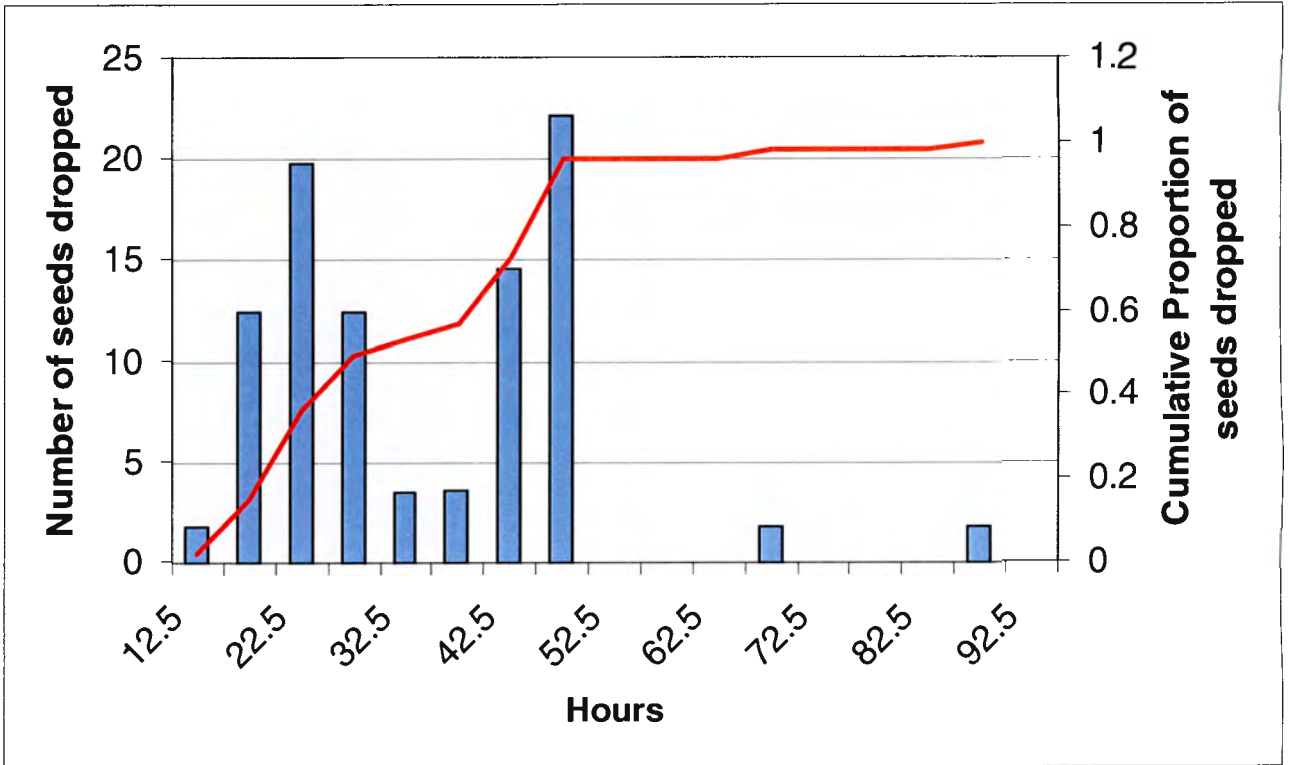


Figure 3. Proposed passage of seeds through the chimpanzee gut (adapted from Lambert, 1997). The red line indicates the cumulative proportion of seeds passed.

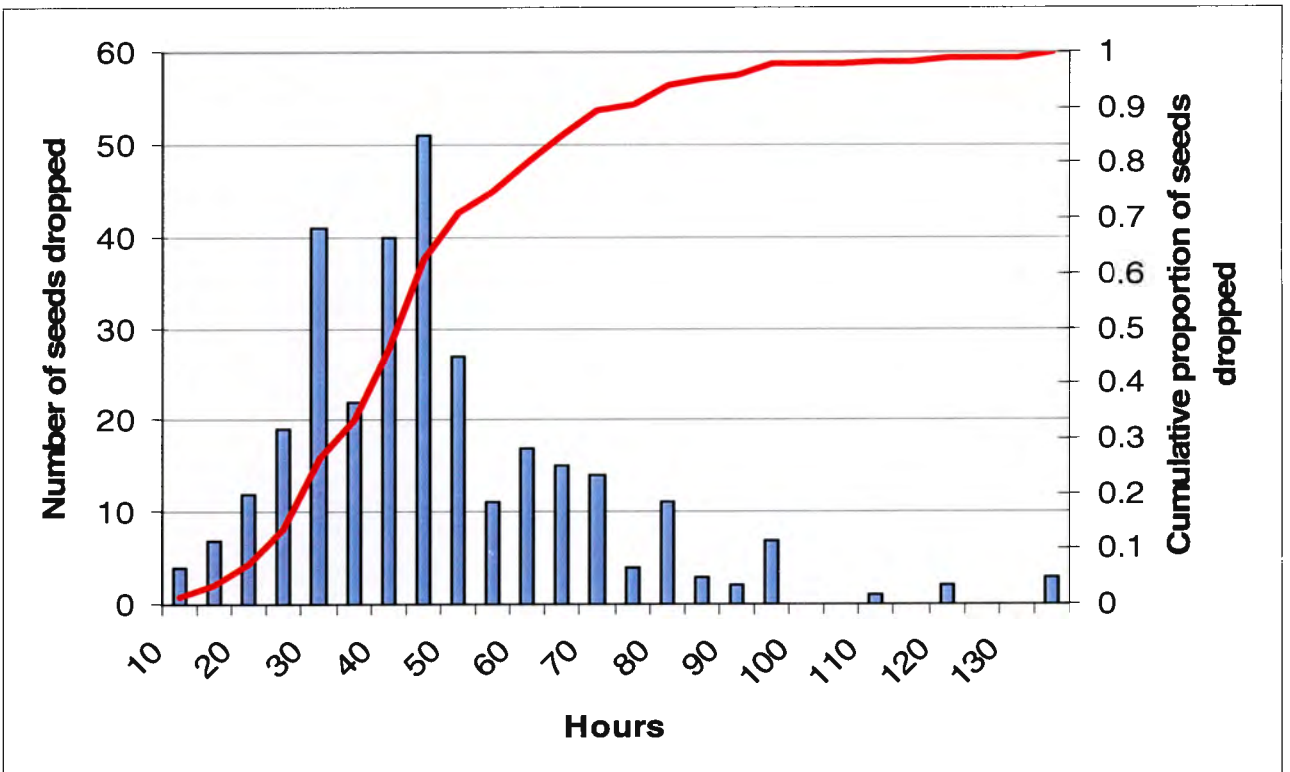
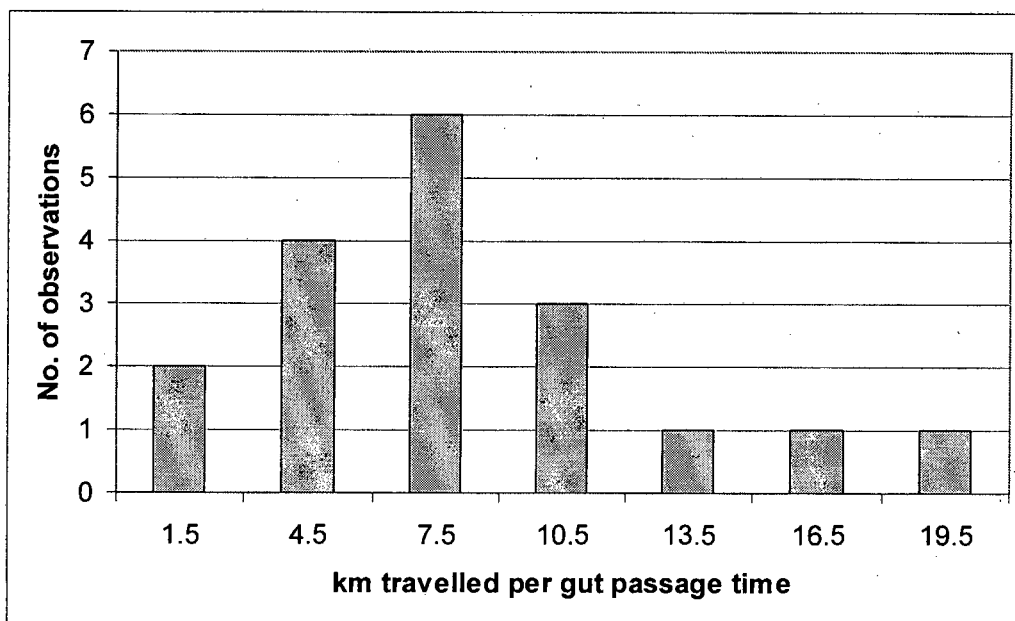


Figure 4. Proposed passage of seeds through the gorilla gut (adapted from Remis, 2000). The red line indicates the cumulative proportion of seeds passed.

## Movement Analysis

On average chimpanzees moved *c.* 3200m during a day's foraging while gorillas moved *c.* 2600 m. However the average distance moved per gut passage time (mean retention time) is *c.* 7700m for both gorillas and chimpanzees. On average four measures of daily distance travelled were made each month for both chimpanzees and gorillas. Observed distance travelled measures had a normal frequency distribution (Kolmogorov-Smirnoff goodness-of-fit test  $d = 0.1084$ ,  $P > 0.5$  for chimpanzees and for  $d = 0.1728$ ,  $P < n.s.$  gorillas). This movement is thought to be somewhat constrained within home ranges.



**Figure 5. Frequency distribution of distances travelled per gut passage time for chimpanzees (*Pan troglodytes*). The gut passage time for chimpanzees is 31.5 hours (Lambert, 1997).**

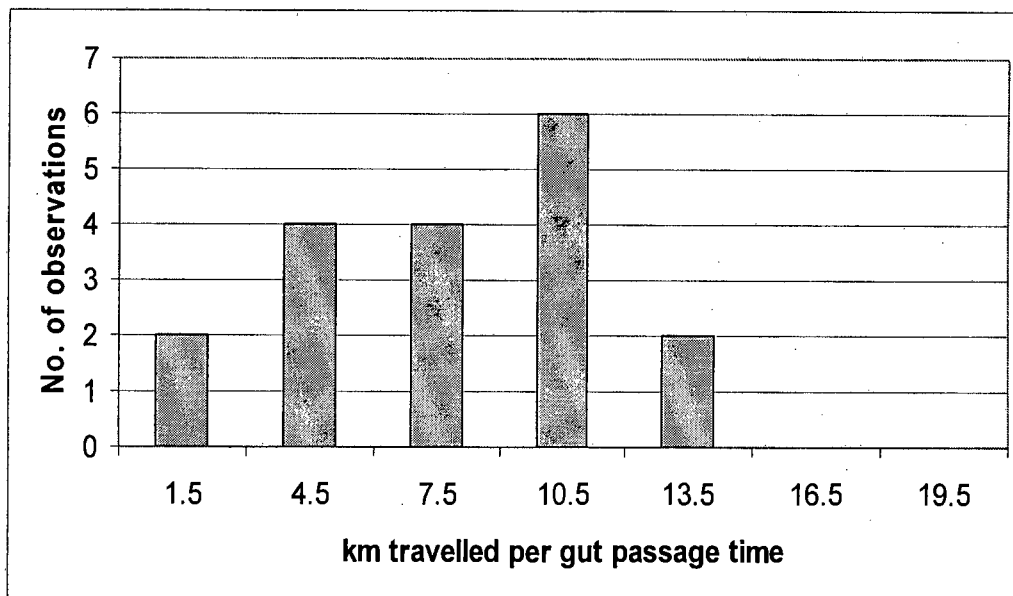


Figure 6. Frequency distribution of distances travelled per gut passage time for gorillas (*Gorilla gorilla*). The gut passage time for gorillas is 47.3 hours (Remis, 2000).

### Dispersal Curves

A seed shadow is a function of the disperser's movement and the gut passage rate (Westcott and Graham, 2000). Figure 7 and 8 represent average expected seed shadows as they are not specific to one plant species. Estimated minimal dispersal distances were 285 m and 487 m for gorillas and chimpanzees respectively.

Maximum estimated dispersal distances showed very little variation; approximately 7700 m for both gorillas and chimpanzees. Mean dispersal estimates were 3994 m (+/- 2265 m SD) for gorillas and 4143 m (+/- 2320 m SD) for chimpanzees (Figure 7 and 8). The minimum dispersal distance recorded for each species was observed during the month of September.

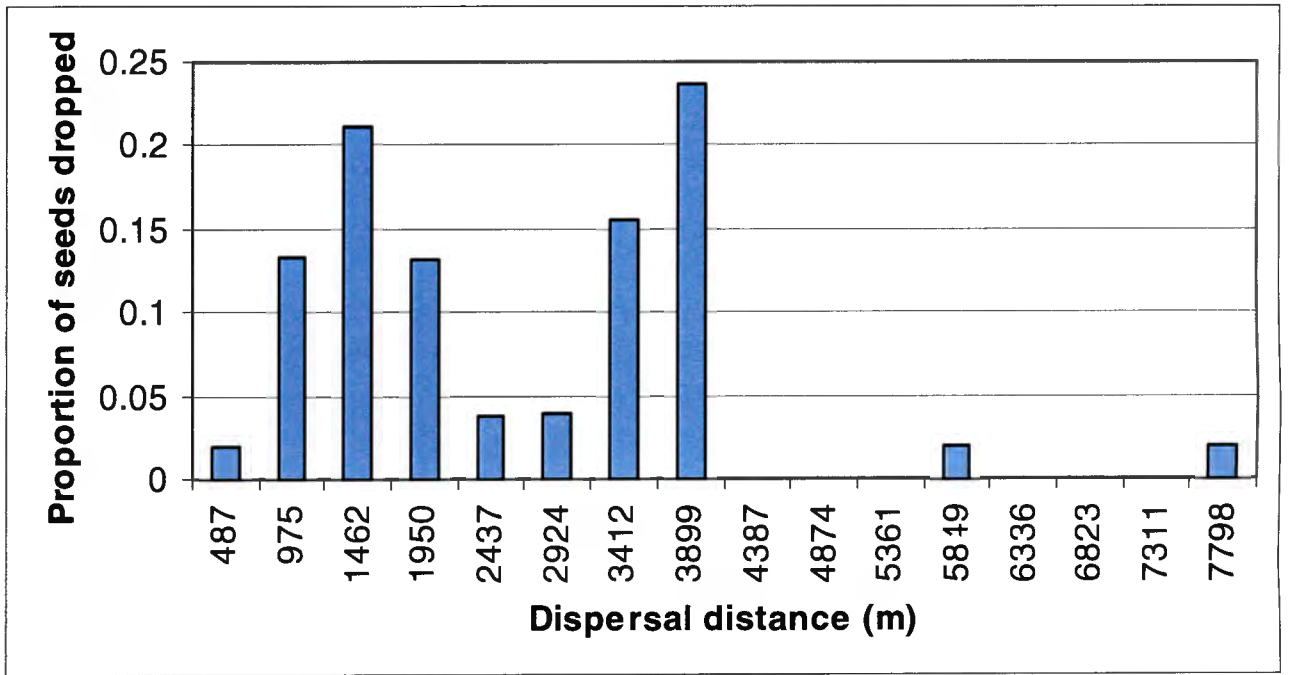


Figure 7: Dispersal curves estimated for seeds consumed by *Pan troglodytes* using the gut passage times from Remis (2000) and distance travelled per gut passage data.

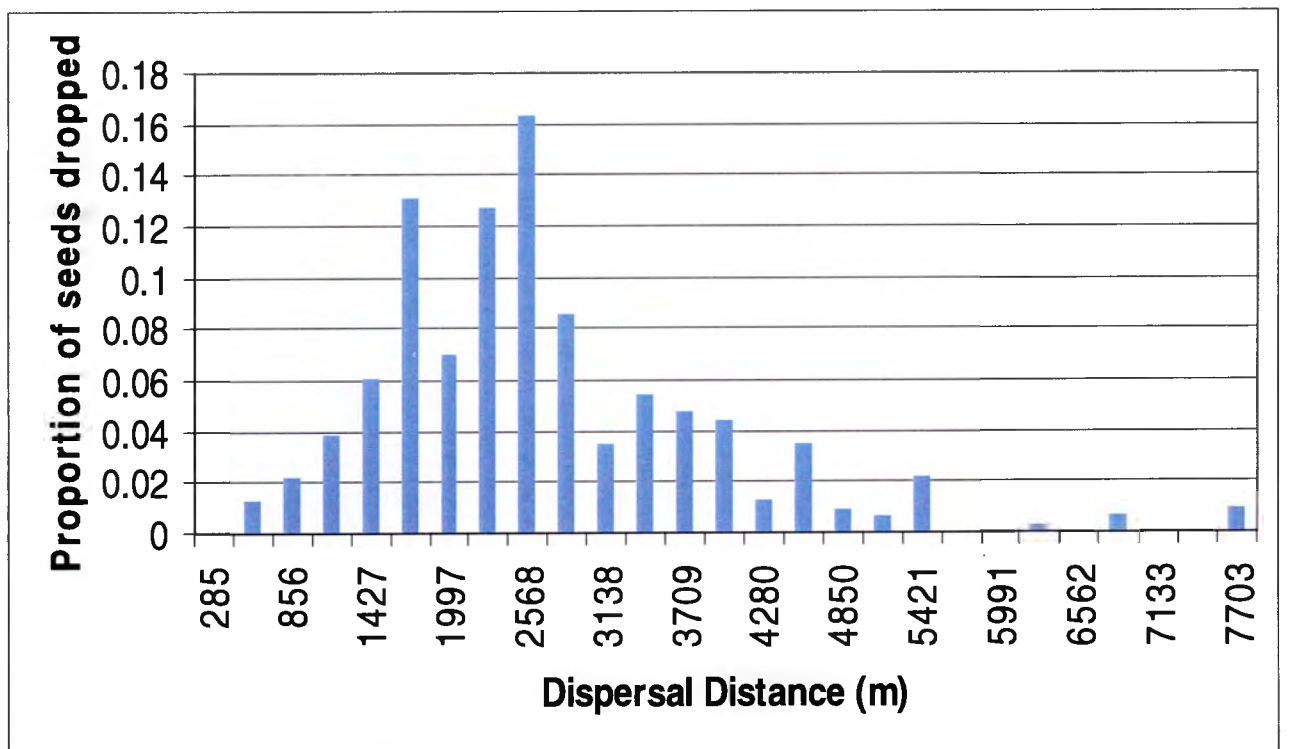
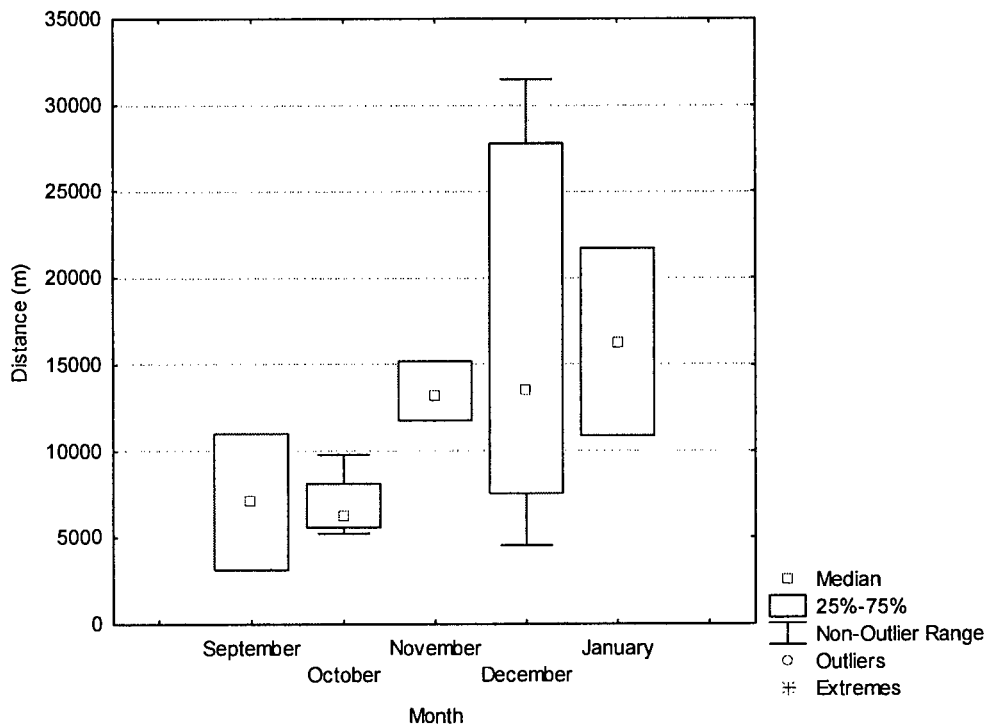


Figure 8: Dispersal curves estimated for seeds consumed by *Gorilla gorilla* using the gut passage times from Remis (2000) and distance travelled per gut passage data.

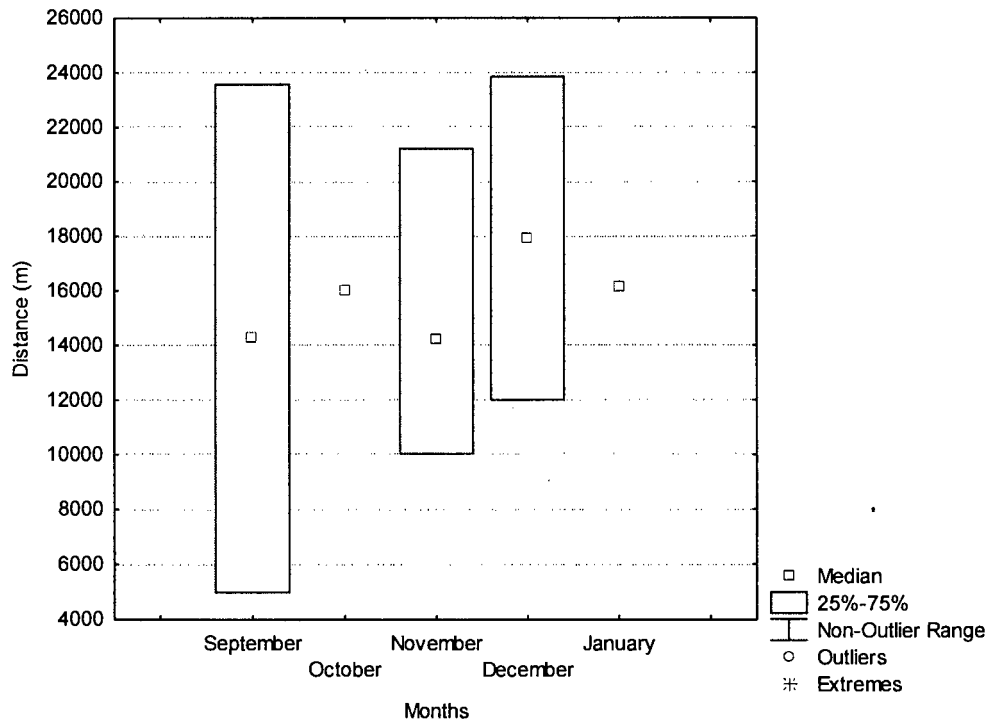
## Seasonal Component to Movement

Chimpanzees demonstrate marked differences in their seasonal movement (Figure 9); they travel further in the dry season (November, December and January) than in the wet season (September and October). Consequently their seed shadow becomes extended during the dry season. In contrast, gorillas do not appear to alter the distance that they travel seasonally (Figure 10).



**Figure 9. Mean distance travelled (+/- quantiles) by *Pan troglodytes* over a five month period. September and October = wet season; November, December and January = dry season.**





**Figure 10. Mean distance travelled (+/- s.d.) by *Gorilla gorilla* over a five month period. September and October = wet season; November, December and January = dry season.**

### Composition of diet

Divergent dietary trends are apparent in Figure 11 and 12. Chimpanzees appear to retain the volume of seeds in their faeces over the five month period (Figure 11). In contrast, gorillas demonstrate a marked decline in the volume of seeds (Figure 12) in their faeces from the wet season (September, October) to the dry season (November, December and January).

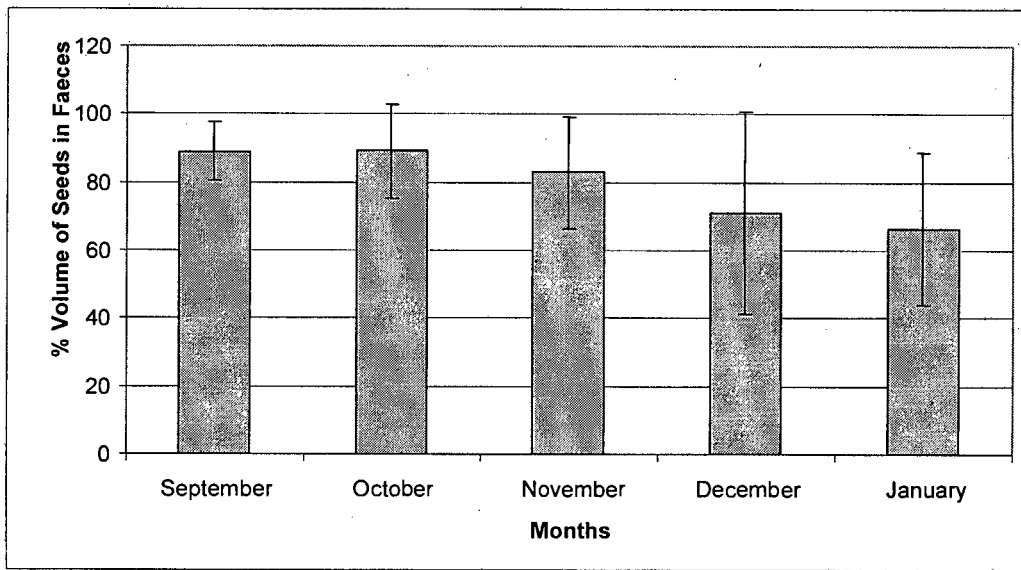


Figure 11. The percentage of seeds (volume) in the faeces of *Pan troglodytes* over a five month period. September and October = wet season; November, December and January = dry season.

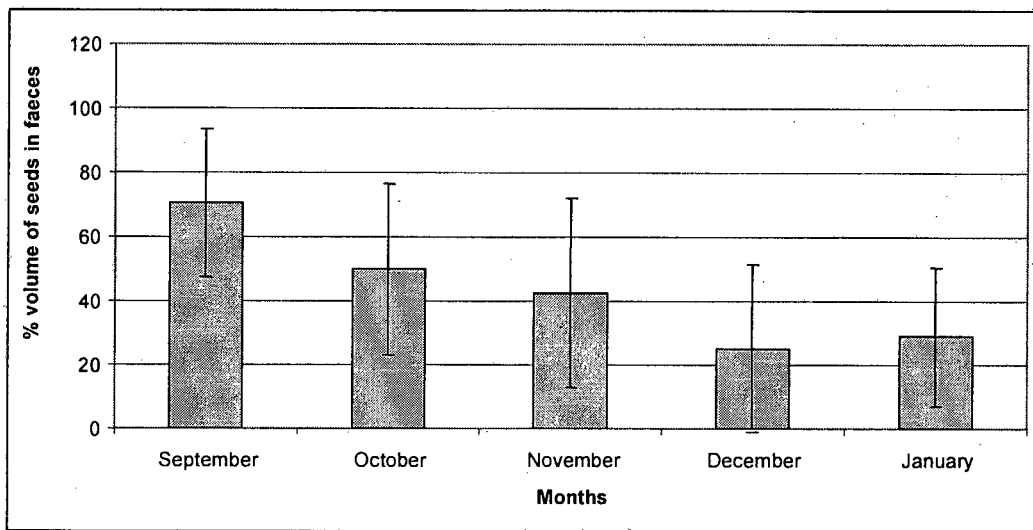


Figure 12. The percentage of seeds (volume) in the faeces of *Gorilla gorilla* over a five month period. September and October = wet season; November, December and January = dry season.

#### Case Study – *Uapaca palidosa*

To answer questions at a species level I selected a species that <sup>working!</sup> likely to depend heavily on apes for their dispersal. *Uapaca palidosa* (Figure 13 - 17) is a likely candidate for the following reasons:

1. It is a highly abundant and conspicuous plant within the study sight

2. It ranks amongst the most predominant fruits within both chimpanzee and gorilla diets.
3. Passage through the gut of apes has been shown to improve germination success of *Uapaca sp.* by 50% (Poulsen *et al.*, 2001).
4. The seeds are sufficiently large to preclude dispersal by small vertebrates.

*Uapaca palidosa* has a particularly long fruiting season, with fruits available from September to January (Figure 13 and 14). Chimpanzees (Figure 13) appear to predominantly feed on *Uapaca palidosa* during the dry season (November – January) whereas gorillas appear to feed on *Uapaca palidosa* throughout the wet and dry season (Figure 14). *Uapaca palidosa* parent trees seem to favour two microsites; old forest and hydromorphic forest (Figure 15).

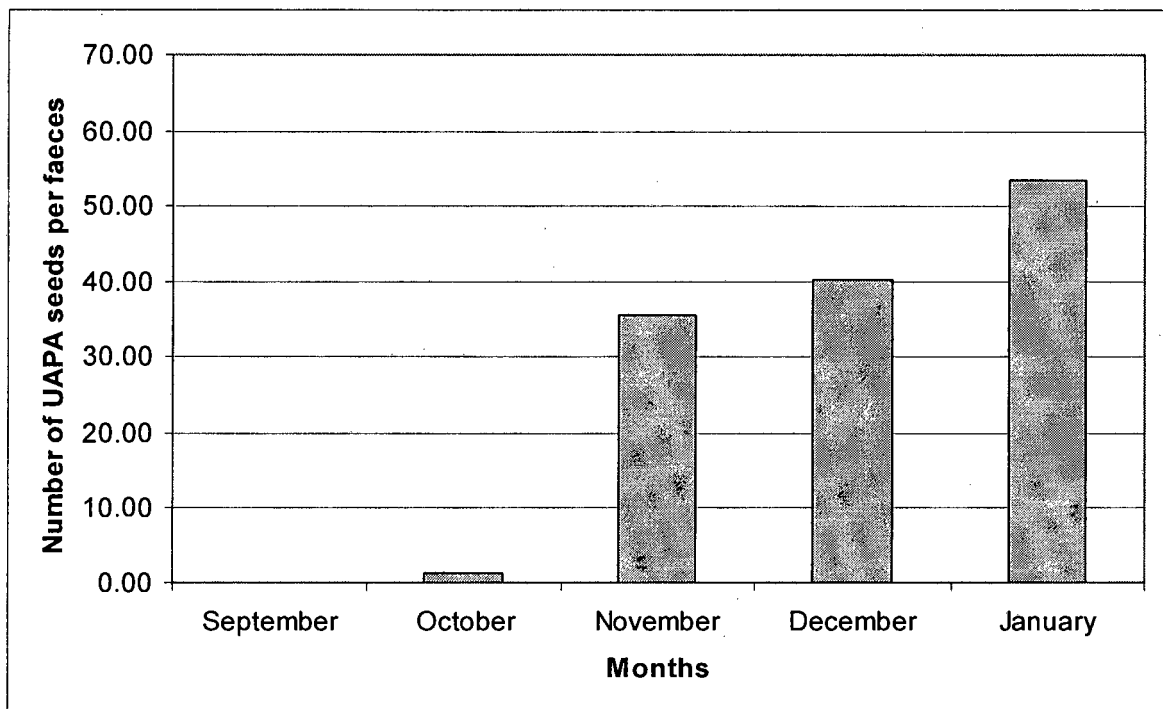


Figure 13. The number of *Uapaca palidosa* seeds per faeces dropped over the five month period by chimpanzees (*Pan troglodytes*).

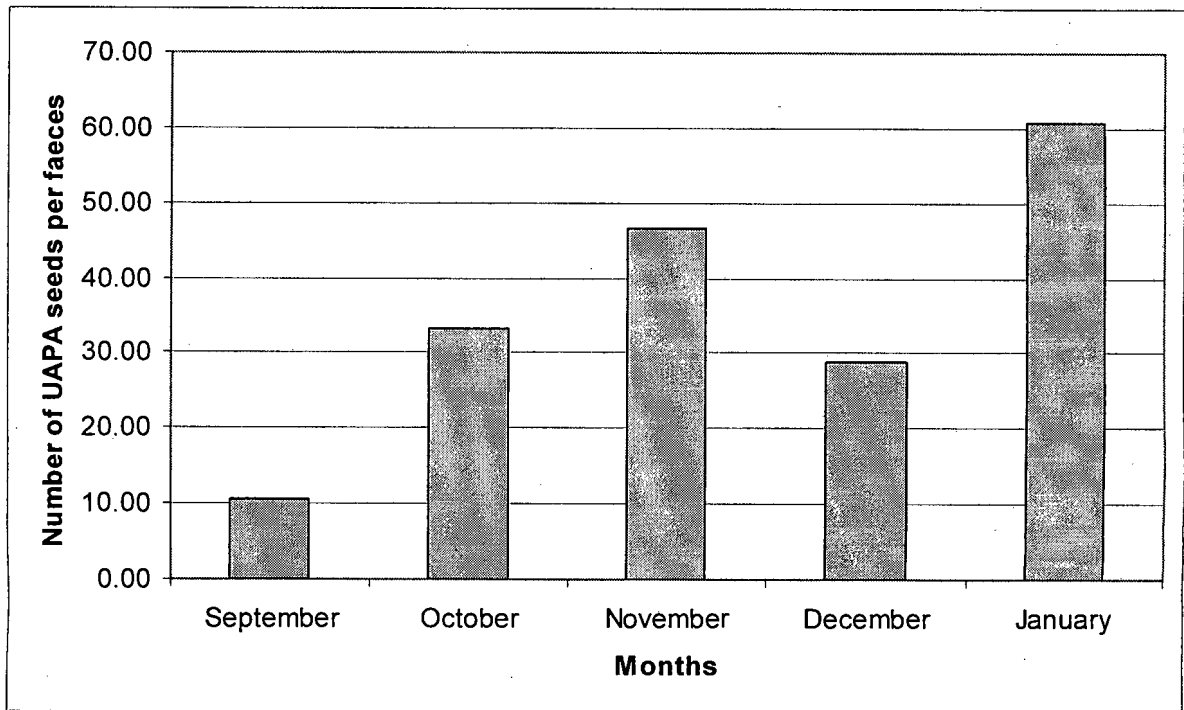


Figure 14. The number of *Uapaca palidosa* (UAPA) seeds per faeces dropped over the five month period by gorillas (*Gorilla gorilla*).

Chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) also appear to favour certain microsites. This is evident in Figure 16 and 17 that depict the proportion of faeces dropped over the various vegetation types. Chimpanzees drop over 30% of their faeces in old forest while gorillas drop over 45% in hydromorphic forest.

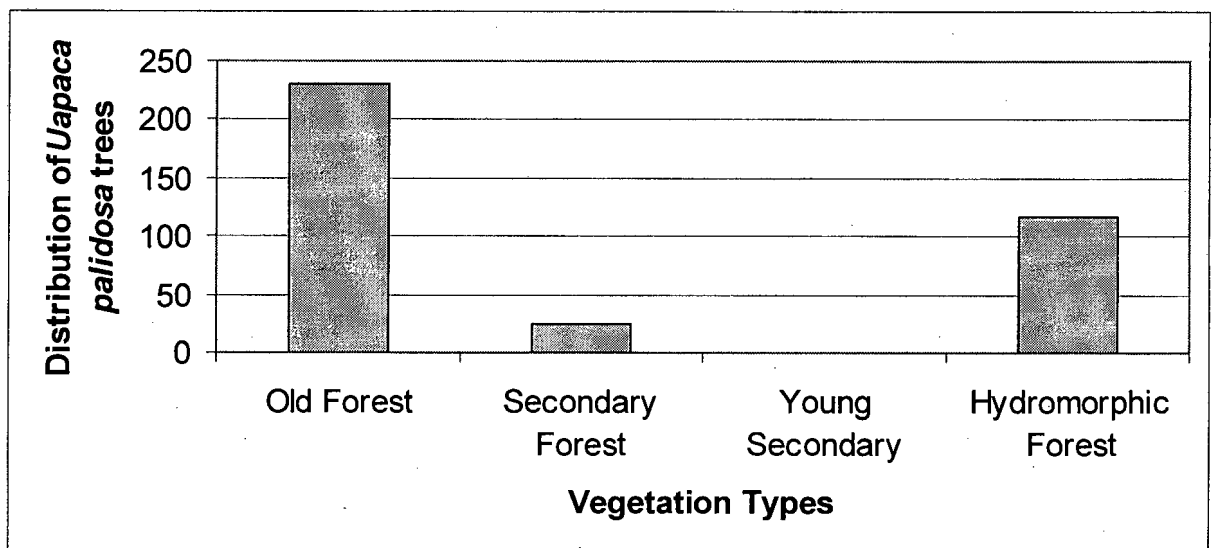


Figure 15. The distribution of the *Uapaca palidosa* parent trees over the four vegetation types. These trees were distributed over 60km of transect.

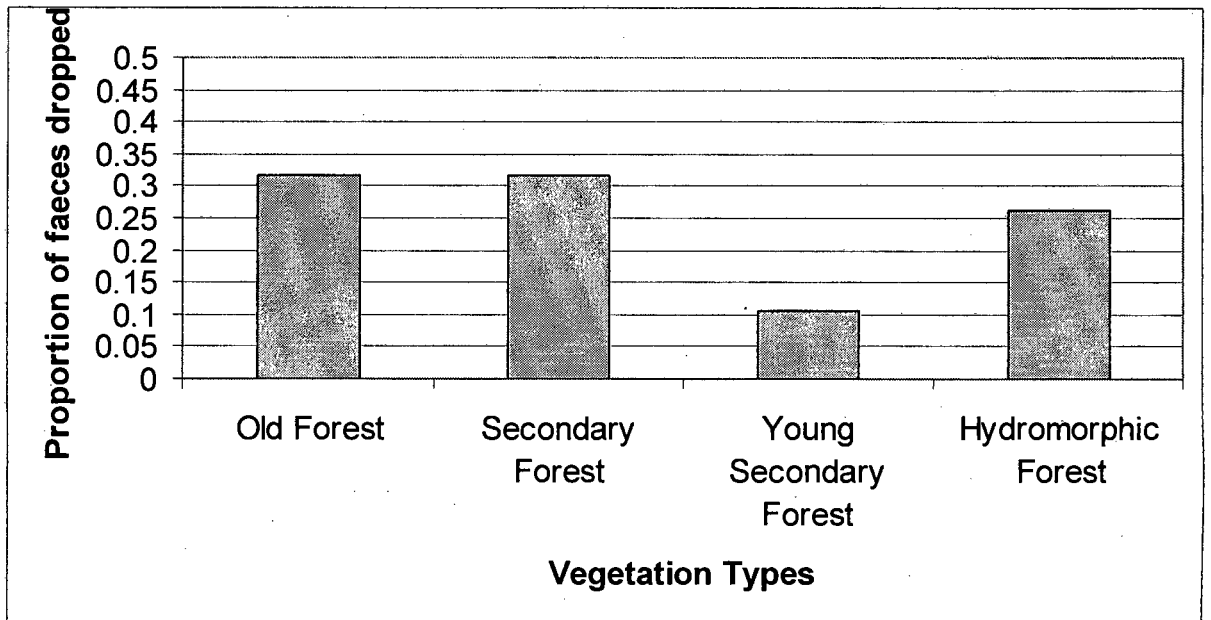


Figure 16. The proportion of faeces dropped by *Pan troglodytes* over the four vegetation types.

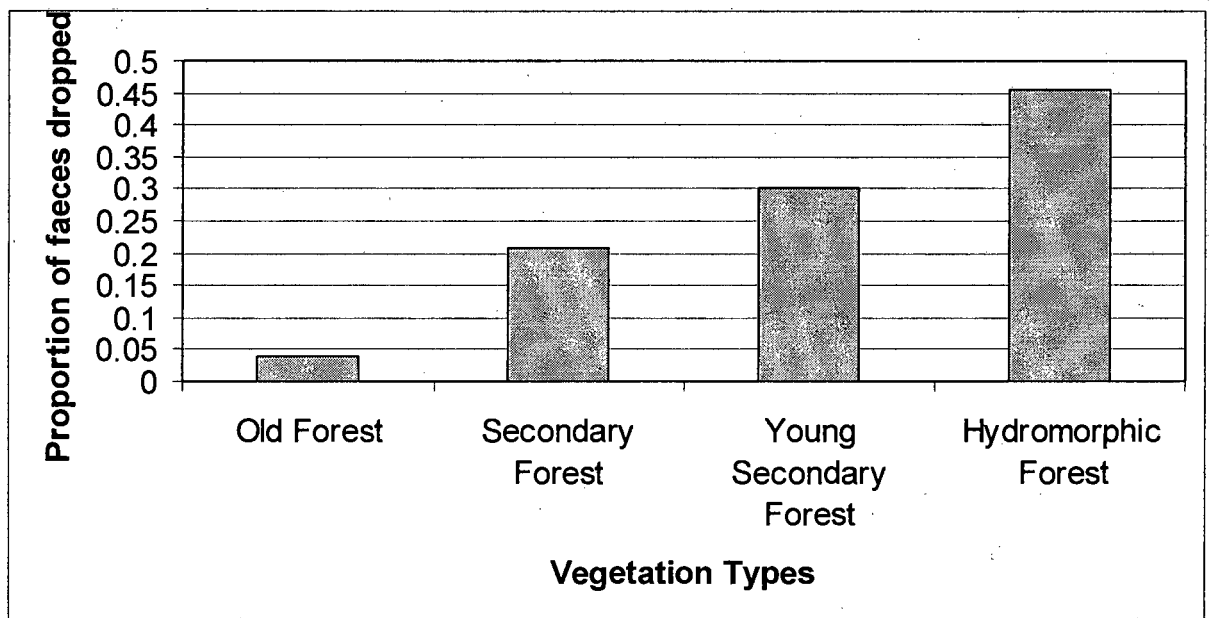


Figure 17. The proportion of faeces dropped by *Gorilla gorilla* over the four vegetation types.

## Discussion

### Seed Shadows

Here I report the first estimate of seed dispersal curves for chimpanzees (Figure 7) and gorillas (Figure 8). In addition, I present a novel method for rapid derivation of

such curves. Traditionally (Murray, 1988; Sun *et al.*, 1997; Janzen *et al.*, 1997; Fragaso, 1997; Westcott and Graham, 2000) seed dispersal curves have been derived from direct tracking of seeds from source to sink. In contrast, seed dispersal curves in this study were produced by combining readily available ape movement data with gut passage curves from literature. As fore mentioned, this paper was modelled on a previous study by Westcott and Graham (2000).

From the dispersal curves (Figure 7 and 8) chimpanzees and gorillas appear to be excellent dispersal agents. The magnitude of their dispersal distances (*c.* 7.7 km for both species) is surprisingly large when one compares them to other seed dispersal agents (Table 2).

**Table 2: Maximum dispersal distances observed for a selection of seed dispersal agents from various biomes.**

<b>Dispersal Agent</b>	<b>Biome</b>	<b>Maximum Dispersal Distance</b>
Hornbills	African Tropical Lowland Forest	6km (Murray, 1988)
Turacos	African Tropical Montane Forest	0.304km (Sun <i>et al.</i> , 1997)
<i>Mionectes oleaginous</i>	Australasian Tropical Forest	1.4km (Westcott and Graham, 2000)
Tapirs	Amazon Rain Forest	2km (Fragaso, 1997)

It is apparent that apes possess the potential to disperse seeds further than the majority of seed dispersal agents investigated to date. This is likely due to a combination of fortuitous foraging behaviour and gut physiology. Indeed, both chimpanzees and gorillas travel large distances in order to meet their dietary requirements and in addition they possess slow gut passage times (relative to other primates) for maximal absorption of nutrients (Lambert, 1997 and Remis, 2000).

Seed shadows are generally considered to be highly leptokurtic, with the majority of the seeds deposited close to their source (Harper, 1977). This is thought to be the

result of most seeds failing to be dispersed and falling beneath the parent tree (Mack, 1995). However, it has also been suggested that even when considered alone, the seed shadows of dispersal agents will be highly leptokurtic (Fleming and Hiethaus, 1981). In contrast, our seed shadows follow a Poisson distribution similar to those produced by a limited number of other seed dispersal agents in African tropical forests (hornbills, Holbrook and Smith, 2000; turacos, Sun *et al.*, 1997). Although my sampling is limited in that it only accounts for the seeds swallowed; it is clear from a number of other studies that both gorillas and chimpanzees swallow the majority of seeds (Poulsen *et al.*, 2001). Hence the dispersal curves produced in this study are close to being an accurate reflection of the actual seed shadow.

The Poisson distribution is significant because it reduces the proportion of seeds being dropped within the 'minimal critical distance' from the parent (Janzen, 1970). Within the 'minimal critical distance', seeds and seedlings experience a disproportionately high mortality rate due to the density-dependent activity of pathogens, seed predators and parasites (Janzen, 1970; Packer and Clay, 2000).

The second notable feature of the seed dispersal curves (Figure 7 and 8) is the extended tail. This feature appears to be common to all dispersal agents (Murray, 1988; Sun *et al.*, 1997; Janzen *et al.*, 1997; Fragaso, 1997; Westcott and Graham, 2000). In keeping with Janzen's distance/density hypothesis, seeds dropped in the tail region are important in spreading the parental genes more widely (Willson, 1989). In fact, it has been suggested that plant traits which affect the behaviour of such a tail could be subject to selection (Willson, 1989).

It is of importance to mention here that the seed dispersal curves of vertebrates are often confounded by secondary dispersal agents (rodents, ants and dung beetles). Thus where the seeds are initially dropped by the primary seed dispersal agent is not always reflective of where they recruit (Wang and Smith, 2002).

### Seasonal Trends

In the shift from the wet (September, October) to the dry season (November to January) there is a marked decline in fruit abundance in the forest (Tutin and

Fernandez, 1993; Remis, 1994; Kuroda *et al*, 1996). Periods of fruit scarcity, consistently result in a divergence of foraging strategy by chimpanzees and gorillas (Tutin *et al*, 1991; Tutin and Fernandez, 1993; Remis, 1994; Kuroda *et al*, 1996). This divergence is apparent in their foraging distance (Figure 9 and 10) and in the proportion of seeds in the faeces (Figure 11 and 12). Chimpanzees show social adjustment, foraging greater distances (Figure 9) in smaller groups in order to retain the proportion of fruit (Figure 11) in their diet (Wrangham, 1977). In contrast, gorillas maintain their large group size, make no adjustment to their foraging distance (Figure 10) and are consequently forced to partly replace fruit (Figure 12) with foliage (Remis, 1994).

### Case Study

The trends discussed above represent a generalized analysis of seed dispersal by chimpanzees and gorillas. They are useful in assessing the potential value of these apes as seed dispersal agents and will certainly add a new dimension to forest spread models. However, as Wang and Smith (2002) stated, 'all seed dispersal is not created equal'. In order to gain insight into the effectiveness of a dispersal agent, one must analyse the quantity and quality of seed dispersal at the species level (Nathan and Muller-Landau, 2000).

The relative effectiveness of chimpanzees and gorillas for the dispersal of *Uapaca palidosa* presents an interesting paradox and is a testament to the hidden complexities of the seed dispersal process. In terms of quantity it is apparent that gorillas consume more *Uapaca palidosa* fruits (Figure 14). Furthermore their consumption of *Uapaca palidosa* fruits is far more consistent, providing a dispersal service over both the wet and dry season. This is in stark contrast to chimpanzees, who only start consuming *Uapaca palidosa* in the dry season when other fruit becomes scarce (Figure 13). This is supported by Wrangham (1977) who identified *Uapaca palidosa* as a 'fall-back fruit' in the diet of chimpanzees.

Given that there is little difference in the dispersal curves of chimpanzees and gorillas (Figure 7 and 8), one might be tempting to assume that Gorillas provide a more effective dispersal service for *Uapaca palidosa*.



However, Nathan and Muller-Landau (2000) point to the importance of considering foraging behaviour in assessing the quality of the dispersal event. In order to account for this, we looked at the distribution of chimpanzee and gorilla faeces dropped over the four vegetation types and related this to the distribution of *Uapaca spp.* in our study site (Figure 15 -17). The disproportionate distribution of chimpanzee dispersed seeds closely fits the distribution of *Uapaca palidosa* trees (overlap in old forest and hydromorphic forest) in the forest identifying them as key dispersal agents. Gorillas, on the other hand move seeds to largely unfavourable sites thus making them poor dispersers of *Uapaca palidosa*.

The use of *Uapaca palidosa* as a case study, allowed us to explore the relative dispersal effectiveness of chimpanzees and gorillas to this particular tree. This study will hopefully promote more of its kind; these will allow us to begin to grasp the role of extant megaherbivores to forest dynamics. Before these apes become ghosts of our past we must endeavour to understand each of their interactions.

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*Here should be alphabetical!*

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