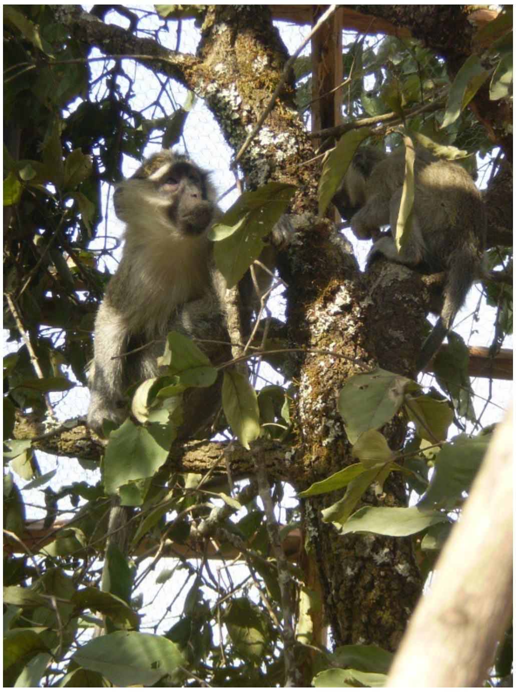
# The role of the tantalus monkey (*Chlorocebus tantalus tantalus*) in forest restoration via seed dispersal in a West African montane forest.



A thesis submitted in partial fulfilment of the requirements for the Degree of Master of Science in Ecology at the University of Canterbury

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2012

# Table of Contents

# List of tables

# List of Figures

# Acknowledgements

I would like to thank my supervisors for their continued support and patience throughout the duration of the field work and subsequent preparation of this thesis. I am immensely appreciative of my senior supervisor, Hazel Chapman, for providing me with the opportunity to carry out the research presented here, with the continued support, encouragement and patience required for its completion. Likewise, my gratitude for the invaluable primatological advice and comments and suggestions provided by my associate supervisor, Britta Kunz, is huge. Without their assistance and guidance this thesis would not have been possible.

I further wish to thank Jason Tylianakis and Elena Moltchanova for their statistical advice and assistance with my data analysis and learning to successfully navigate R, without which I could not have written this thesis.

The Nigerian Montane Forest Project field assistants all deserve a special thank you for all their support and kindness during my stay at the fieldstation. I am especially indebted to Musa Bawaro for his enormous assistance with my data collection. Without his help, this research would have remained uncompleted. I also wish to thank Misa Zubairu for making sure I was well looked after during my time at Ngel Nyaki.

Additionally, I wish to thank the other students and researchers who shared my time at the fieldstation for their company, support and friendship during my stay there. I am further thankful for those in my lab group, Andrew Barnes, Delyse Campbell, Dayo Osinubi, Jane Gosden, Josh Van Vianen, Kristy Udy, Paul Dautton, Babale Aliyu, Danladi Umar and Charles Nsor for their helpful feedback at various times and enlightening and thought provoking discussions.

I am very grateful for the continued love and support of my family and friends during the past two years. There are too many of you to mention here, however, I would like to give special thanks to Anne Grassham, Janice and John Stauffer, Katie Wandell, Barbara Clendon and Tracey Goodrich for their constant encouragement, especially at those times I found this thesis challenging.

# Abstract

Many of the world's tropical forests are under threat, with anthropogenic deforestation and degradation occurring at an alarming rate. Seed dispersal in an important process in forest restoration and regeneration, however seed rain is often low in degraded habitats, hindering reforestation efforts. Up to 90% of tropical fruit are dispersed by vertebrates, animal seed dispersers are incredibly important in maintaining forest health. Additionally, frugivores that disperse seeds into degraded areas may be of great importance in aiding natural reforestation. I therefore, investigated the potential role of the frugivorous monkey, *Chlorocebus tantalus tantalus*, in forest regeneration via seed dispersal. I assessed its patterns of habitat use, the quality and quantity of seed dispersal it provides, the effectiveness of current conservation management actions and the density of *C. t. tantalus* at Ngel Nyaki Forest Reserve. I found *C. t. tantalus* utilised forest, edge and grassland habitats, and dispersed seeds of 28 pioneer and forest edge species into these habitats. Moreover, the number of seeds dispersed per faeces was significantly higher in the grassland than the forest with means of 16.4 +/- 6.1 and 3.4 +/- 0.97 seeds >2 mm in these habitats respectively. Germination of *C. t. tantalus* dispersed seeds was highest in grazed grassland and lowest in grassland protected from grazing and fire, suggesting the current practice of fencing off grassland to protect from cattle grazing may not be sufficient on its own, due to seed-seedling conflict in habitat suitability. These findings combined with an estimated density of 28 +/- 10.8 *C. t. tantalus* individuals km$^{-2}$ suggests *C. t. tantalus* may benefit forest regeneration via its role as a seed disperser, provided appropriate management actions are implemented. This and other

frugivorous species may play similar roles in other locations but such roles need to be investigated in order to implement management actions that ensure their seed dispersal benefits are maximised for forest restoration and regeneration.

# Chapter 1:

# Introduction

## 1.1 Background to seed dispersal and forest regeneration

### *1.1.1 Plant regeneration process*

Forest regeneration is a multi-staged process, comprised of several ecological interactions (Nathan and Muller-Landau 2000; Wang and Smith 2002; Balcomb and Chapman 2003; Wright *et al.* 2007). These include pre-dispersal seed predation, primary and secondary seed dispersal, post-dispersal seed predation and herbivory (Balcomb and Chapman 2003; Wright *et al.* 2007). These interactions influence the spatial template for all subsequent plant regeneration by determining the quantity, location and survival of dispersed seeds and resulting seedlings (Chambers and MacMahon 1994; Wright *et al.* 2007).

Pre-dispersal seed predation is the consumption of either ripe or unripe seeds directly from the food plant, rendering them unviable (Gautier-Hion *et al.* 1993; Wright *et al.* 2007). Such seeds may be destroyed via chewing, digestion or by preventing unripe seeds maturing, for example, through premature removal from the plant (Kunz and Linsenmair 2007). Usually in such instances, the seed itself is the desired food source of the organism consuming them, although fruit pulp may also be consumed (Snow 1981).

Seed dispersal is the movement of seeds away from the parent plant (Wang and Smith 2002). If a seed avoids pre-dispersal predation and becomes dispersed, movement away from the parent may occur via abiotic mechanisms such as wind or water, plant mechanisms such as dehiscent pods that release seeds upon maturity, or by animals (Wang and Smith 2002). The process of seed dispersal itself may constitute several components, namely primary and secondary dispersal.

Primary seed dispersal is the initial movement of the intact seed, directly from the parent plant to another location. Animal seed dispersers may consume whole fruit including the seeds, but only digest the soft parts of the fruit, voiding the seeds intact, either through regurgitation or defecation (Snow 1981; Lambert 1999). The seed may be dropped beneath the parent tree, spat out nearby or swallowed and transported hundreds of metres away (Garber and Lambert 1998). The swallowing of seeds and their subsequent defecation away from the parent is a commonly reported mode of seed dispersal (Corlett and Lucas 1990; Lambert 1999).

Secondary dispersal is the movement of seeds from the initial deposition site of primary dispersal to its final location. The seed may be moved by abiotic means such as wind or water (Vander Wall *et al.* 2005) but often the seed is taken from a faecal clump and cached or buried by animals, where it later may germinate (Forget and Millerton 1991; Forget 1993; Andresen 1999; 2001). Most secondary dispersal only moves seeds short distances, for example, while dung beetles may move seeds up to 5 m horizontally (Estrada and Coates-Estrada 1991), they typically bury seeds within 1 m of the original defecation (Andresen 2001).

Post-dispersal seed predators consume seeds rendering them unviable after they have been dispersed (Gautier-Hion *et al.* 1993). Seed predators however, may also function as a seed disperser for some seeds consumed (Forget and Millerton 1991; Forget 1993; Norconk *et al.* 1998). Scatterhoarders, for example, cache seeds for later consumption but may not recover all seeds cached (Forget and Millerton 1991; Forget 1993; Forget and Cuijpers 2008). In many instances seed predation forms a continuum with seed dispersal, for example, some frugivores function as seed dispersers at a particular time of year but as seed predators at other times (Garber and Lambert 1998; Kunz and Linsenmair 2007), or may become seed predators during periods of food scarcity (Kaplin *et al.* 1998). Additionally, a frugivore may disperse the seeds of one species but prey upon the seeds of another species (Gautier-Hion *et al.* 1985; Kunz and Linsenmair 2008a).

Seedlings developed from seeds which have survived the dispersal process and successfully germinated then become subject to herbivory while they grow to reach maturity (Garber and Lambert 1998). Herbivores consume leafy vegetation, reducing a plant's carbon balance, often resulting in death for plants without sufficient energy stores, such as young seedlings (Wright *et al.* 2007).

Here, I focus on three of these components of the plant recruitment process, namely primary seed dispersal, secondary seed dispersal and seed predation.

### *1.1.2 Importance of seed dispersal*

Seed dispersal by animals can offer a range of benefits to the plants whose seeds they disperse, both at the individual, population and community level. These benefits are not mutually exclusive; a plant may benefit from seed dispersal in one or more ways (Augspurger 1984). At the level of the individual and population three main hypotheses (Janzen-Connell/escape hypothesis, colonisation hypothesis and directed-dispersal hypothesis) exist explaining why movement away from the parent plant is beneficial.

Undispersed seeds typically fall beneath the parent and for many species the probability of survival beneath the parent is low due to density dependant mortality (Augspurger 1984; Chapman and Chapman 1996). Under the Janzen-Connell or escape hypothesis, seeds dispersed away from the parent crown benefit from higher survival probabilities by escaping high levels of density dependant mortality in the form of host specific pathogens and seed predators and intraspecific competition (Augspurger 1984; Harms *et al.* 2000; Howe and Miriti 2000; Wang and Smith 2002).

Under the colonisation hypothesis, dispersal provides seeds with opportunities to colonise new sites in which the species has a competitive advantage (Augspurger 1984; Cain *et al.* 2000; Webb and Peart 2000; Dalling and Hubbell 2002; Babweteera and Brown 2010). A greater dispersal area leads to greater seed survival through the increased probability that a seed will reach a light gap or other site suitable for colonisation (Augspurger 1984).

Non-random dispersal directed at sites favourable for germination and establishment is known as the directed dispersal hypothesis and ensures a large proportion of seeds find themselves in microhabitats suitable for successful germination and establishment than would result from chance (Wenny and Levey 1998; Wenny 2000). It occurs when the disperser preferentially carries seeds directly to sites critical for seedling establishment (Wenny and Levey 1998; Howe and Miriti 2004).

Regardless of which hypothesis is operating, seed dispersal is important in controlling plant population dynamics and community structure. Seed dispersal can serve as a conduit of gene flow with diploid seeds contributing twice as much to the genetic neighbourhood as haploid pollen, when all else is equal (Hamilton 1999; Wang *et al.* 2011). Seed dispersal therefore has impacts on both local genetic structure and maintenance of genetic diversity within and among plant populations (Hamilton 1999; Hardesty *et al.* 2006), by reducing genetic drift and the loss of genetic variation through maintaining larger local genetic neighbourhoods (Ellstrand and Elam 1993)

Additionally, seed dispersal may benefit whole plant communities by promoting species diversity and the formation of diverse local seedling assemblages, which may increase seedling survival through diversity dependent effects (Webb and Peart 2001).

### *1.1.3 Animal mediated seed dispersal*

Vertebrates, including primates, are the main dispersers of 70-90% of woody tropical plants (Willson *et al.* 1989; Corlett 1996; da Silva and Tabarelli 2000; Hardesty and Parker 2002; Stoner *et al.* 2007), making animal mediated seed dispersal both a common and important service in the tropics. Animal mediated seed dispersal is a mutualistic interaction between plants and frugivorous animals where the plant relies upon the frugivore to remove seeds away from the parent plant in a viable condition and the frugivore relies upon the plant as a food source (Howe and Westley 1988; Bascompte and Jordano 2007; Flörchinger *et al.* 2010). Fruit pulp functions as an attractant and reward for animal seed dispersal agents (Corlett and Lucas 1990), although in some instances, a portion of seeds are sacrificed as the attractant and reward in exchange for the dispersal of others (e.g. scatter hoarding rodents) (Forget and Millerton 1991). While a few relatively tight mutualisms between food plants and dispersers do occur (e.g. Temple 1977; Hampe 2003) most seed dispersal mutualisms involve any given plant being dispersed by several to many frugivores and any given frugivore dispersing seeds of multiple plant species (Julliot 1996; Lambert 1999; Jordano and Schupp 2000; Bascompte and Jordano 2007; Kunz and Linsenmair 2008a; Babweteera and Brown 2010). As a result, interactions are usually fairly loose and can involve hundreds of species (Bascompte and Jordano 2007; Julliot 1996; Herrera 1985).

Most primates include at least some fruit and seeds in their diet making them important seed dispersers and pre-dispersal seed predators for many of their food plants (Wrangham *et al.* 1994; Juliott 1996; Lambert and Garber 1998; Kaplin and

Moermond 1998; Link and Di-Fiore 2006; Kunz and Linsenmair 2007). Primates differ in the way they handle fruits (Gautier-Hion *et al.* 1993; Kaplin and Moermond 1998; Lambert 1999; Gross-Camp and Kaplin 2005). Seeds may be either swallowed, spit out/dropped after the removal of the fruit pulp, or chewed (Kaplin and Moermond 1998; Lambert 1999; Kunz and Linsenmair 2007; 2008b). Primates often drop or spit large seeds at or close to the feeding site (Corlett and Lucas 1990; Kaplin and Moermond 1998; Dominy and Duncan 2005; Gross-Camp and Kaplin 2005), as seeds can displace nutritious digesta and significantly increase the weight of the animal if swallowed, representing a cost to the animal (Corlett and Lucas 1990; Lambert 1999). As a result, smaller seeds are more likely to be swallowed and subsequently dispersed some distance away (Corlett and Lucas 1990; Kaplin and Moermond 1998; Dominy and Duncan 2005). Most primates employ a mixture of seed swallowing and seed spitting depending on species, gender, age, habitat, season and fruit species consumed (Corlett and Lucas 1990; Rowell and Mitchell 1991; Kaplin and Moermond 1998; Lambert 1999; Kunz and Linsenmair 2007; 2008b).

There is plenty of evidence to suggest that primates can disperse large numbers of seeds over a wide area (Chapman 1989; Wrangham *et al.* 1994; Poulsen *et al.* 2001; Link and Di-Fiore 2006, Kunz and Linsenmair 2008a) and are important for the recruitment of the species they disperse, influencing the maintenance of forest structure, dynamics, composition and diversity (Chapman and Chapman 1995; Chapman and Onderdonk 1998; Balcomb and Chapman 2003; Marsh and Loiselle 2003; Nuñez-Iturri and Howe 2007). While individual primate species differ in their seed dispersal effectiveness (Chapman 1989; Wrangham *et al.* 1994; Lambert and

Garber 1998; Kaplin and Lambert 2002) as a group, primates make up a large proportion of tropical forest biomass allowing them to consume large quantities of fruit and disperse large quantities of seed (Chapman and Onderdonk 1998; Chapman and Peres 2001).

### ***1.1.4 Effectiveness of seed dispersers***

Plant recruitment, distribution and regeneration in tropical forests depend to a large extent on the effectiveness of their seed dispersers (Cordeiro *et al.* 2009). Disperser effectiveness is the contribution a disperser makes to the future reproduction of a plant (Schupp 1993) and can be considered from either the perspective of the dispersal agent or the dispersed plant, at a range of scales from individuals to communities (Schupp 1993; Jordano and Schupp 2000; Poulsen *et al.* 2001). The effectiveness of an animal as a seed disperser depends on the quantity of seeds dispersed as well as the quality of dispersal (Schupp 1993; Dennis and Westcott 2006). Both these aspects of dispersal determine the final fate of the seed, and therefore, the relative impact dispersers have on the structure and composition of plant communities (Jordano and Schupp 2000; Schupp 1993).

#### *1.1.4.1 <u>Components of quantity</u>*

Successful seed dispersal of animal dispersed plants requires dispersers to move large numbers of seeds (Schupp 1993). As the proportion of seeds produced by a tree that successfully germinate is low, and survive to maturity is even lower (Howe *et al.*

1985; McConkey 2000), it is important for plant communities that dispersers move large numbers of seeds from their food trees. For any given plant species, an effective disperser will remove and disperse a high number of seeds from that species. This is often considered to be a function of the number of visits made by a disperser and the number of seeds dispersed per visit (Schupp 1993; Jordano and Schupp 2000), which in turn are influenced by the abundance of the disperser, its feeding behaviour, and reliability of visitation (Schupp 1993; McConkey 2000, Stevenson 2000; Dennis and Westcott 2006).

Additionally, from a forest wide perspective, an effective disperser will also have a broad diet and consume fruits from many different species, enabling it to disperse large numbers of seeds for a range of plant species (Andresen 2002; Wehncke *et al.* 2003; Dennis and Westcott 2006).

Assessing and monitoring the abundance and density of frugivores is an important part of assessing a frugivore's seed dispersal service as a frugivore may cease to provide effective seed dispersal well before they become rare (McConkey and Drake 2006).

#### *1.1.4.2* *Components of quality*

High quality dispersal will deposit dispersed seeds unharmed in a site suitable for their germination and establishment (Schupp 1993). Dispersal quality has been defined as the distance seeds are moved away from the parent plant combined with the density of conspecifics the seed is dispersed with (Schupp 1993), but is also influenced by the effect of mouth and gut treatment, defecation pattern, predator pressures and probability of establishment in a given location (Schupp 1993; Andresen 1999; Stevenson *et al.* 2002).

It is important dispersers do not decrease the viability of the seeds they handle, otherwise they may function as seed predators rather than seed dispersers (Norconk *et al.* 1998). A blurry line exists between seed dispersal and seed predation as few animals are strictly either. Inevitably, even a highly successful disperser will damage a few seeds while passing out many viable ones (Kaplin and Moermond 1998; Kunz and Linsenmair 2008a). In a similar manner, animals that function primarily as seed predators may disperse the odd seed unharmed (Norconk *et al.* 1998). Clearly the higher the proportion of seeds remaining viable after handling by an animal, the more successful a disperser it will likely be. However, an animal that disperses few viable seeds into sites highly favourable for their germination may have a disproportionate affect upon seedling recruitment than one that disperses many viable seeds into unsuitable microsites (Wenny 2000).

Researchers have reported positive, neutral and negative effects of primate gut passage on seed germination, however, positive effects are most frequent (Julliot 1996; Stevenson *et al.* 2002; Traveset and Verdú 2002; Wehncke and Dalling 2005; Agmen *et al.* 2009; Chaves *et al.* 2011). Gut passage may increase germination rates and/or shorten latency times (Wrangham *et al.* 1994; Stevenson *et al.* 2002; Traveset and Verdú 2002), through the removal of fruit pulp with germination inhibiting properties, scarification of the seed coat and/or the depositing of seeds with fertilising faecal matter (Traveset and Verdú 2002). A negative effect occurs when gut passage either damages the seed sufficiently that it is subsequently unable to germinate or destroys the seed entirely through digestive processes (Corlett and Lucas 1990).

Safe handling and movement away from the parent do not guarantee that a seed will be able to germinate and establish (Balcomb and Chapman 2003). The physical environment at the site of deposition and the likelihood of encountering seed predators and secondary dispersers determine the probabilities for germination and establishment (Wrangham *et al.* 1994; Andresen 2001; Balcomb and Chapman 2003). Post dispersal seed predators and secondary dispersers affect seeds between deposition and establishment, and can be important in determining whether the fitness of the plant has been increased through dispersal by frugivores (Estrada and Coates-Estrada 1991; Levey and Byrne 1993; Chambers and MacMahon 1994; Andresen 1999). It is important to note that the suitability of a microsite is a continuum through space and time of survival probabilities, rather than simply being suitable or unsuitable (Schupp 1993). In addition, what may be a suitable microsite for seed germination may not always be a suitable site or ideal site for seedling growth and survival (Schupp and Frost 1989; Rey and Alcantara 2000).

Seeds that have been buried by secondary seed dispersers often have higher rates of survival than those remaining unburied (Andresen 2001; Andresen and Levey 2004). Burial by secondary dispersal may benefit the seed by reducing its chances of detection by post-dispersal seed predators (Estrada and Coates-Estrada 1991;

Shepherd and Chapman 1998; Andresen 1999). Burial may also benefit seeds by reducing the variability of microclimatic conditions and reducing the seed's risk of desiccation by effectively planting the seed (Vander Wall 1993).

Seed predation can be just as significant a force influencing the structure and composition of the plant community as seed dispersal (Albert *et al.* 2005) as it is the combined effects of dispersal and mortality patterns that determine the spatial pattern of recruits (Hardesty *et al.* 2006). Seed and seedling predation rates may differ among habitats (Burkey 1993; Hammond 1995; Nepstad *et al.* 1996; Chapman and Chapman 1999; Duncan and Duncan 2000;  DeMattia *et al.* 2004; Iob and Vieira 2008; Cole 2009) or with the amount and consistency of faecal matter it is dispersed with (Andresen 2001; Santos-Heredia *et al.* 2010). Additionally, the state of the forest community can have important impacts of rates of seed predation, for example, hunting can remove seed predators reducing rates of predation, or increase their relative abundance to frugivores, increasing relative rates of predation (Wright *et al.* 2000; Peres and Palacios 2007)

The overall success of a given primate seed disperser will depend on how well they meet the whole suite of requirements for successful seed dispersal and will vary among species based on  behavioural, physiological and morphological differences. As long as a primate fulfils each requirement to some level or at some time, then seed dispersal will result.

### 1.1.5 *Seed dispersal in degraded habitats and its role in forest restoration*

Habitat loss and fragmentation are serious threats to biodiversity worldwide but especially in tropical forests (Wieczkowski 2010). Tropical forest ecosystems face a range of threats including deforestation, fragmentation and degradation (Chapman and Lambert 2000; Balcomb and Chapman 2003; Marsh and Loiselle 2003; Dausmann *et al.* 2008; Isabirye-Basuta and Lwanga 2008), resulting from fire, logging, hunting and conversion of forest to agriculture (Balcomb *et al.* 2000; Chapman and Peres 2001; Isabirye-Basuta and Lwanga 2008). This has led to a rate of tropical forest loss worldwide between 1990 and 1995 was 0.7% per annum, with a staggering 12.5 million ha of forest being converted every year (Chapman and Peres 2001). Africa lost 10.5% of its tropical forests in the fifteen years from 1980 to 1995 (Chapman and Peres 2001). These trends are continuing, both in Africa and elsewhere.

These threats not only have direct negative effects on plant populations, the removal of plant populations and fragmentation of forest habitat also affect wildlife populations, for example, 90% of primate species are found in the tropics and depend on these forests for their survival (Chapman and Peres 2001; Chapman *et al.* 2006). The decline in or loss of wildlife populations can in turn affect plant populations (Chapman and Chapman 1995; Nuñez--Iturri and Howe 2007; Peres and Palacios 2007; Nuñez-Iturri *et al.* 2008), through the creation of negative feedback cycles, resulting in not only loss of biodiversity but also of ecosystem processes and services, including seed dispersal (Chapman and Onderdonk 1998).

A strong argument for primate conservation is that trees dependent on primate seed dispersal may experience reduced regeneration with the removal of primates (Chapman and Peres 2001), however the reverse argument for the conservation of primate fruit trees to aid the conservation of primate populations also applies. People are highly reliant on natural resources, and population growth rate is correlated with rate of deforestation in Africa (Harcourt 1995), as land is converted for pasture and agricultural purposes (Zanne and Chapman 2001; Zahawi and Augspurger 2006) and hunting and/or harvesting pressures increase to meet increasing needs for food and fuelwood (Zanne and Chapman 2001). Hunting and forest clearance for agriculture are not new to Africa, with archaeological evidence suggesting such activities have been occurring for more than 2000 years (Chapman *et al.* 2006), however, as the human population booms the impact of these activities on natural ecosystems has dramatically increased. The conservation of existing forest and restoration and regeneration of degraded areas are therefore important, not only from the perspective for the intrinsic value of these forests and their wildlife, but for the services and resources they provide to the human population such as watershed protection and medicinal products (Chapman *et al.* 2004).

Seed dispersal is important for the long term survival of forests (Nuñez-Iturri *et al.* 2008), and as such needs consideration and incorporation into conservation plans. This may be particularly important in fragmented landscapes, with dispersal among fragments vital in preventing loss of evolutionary adaptability and local extinction resulting from reduced genetic heterozygosity caused by genetic isolation (Ellstrand and Elam 1993; Hamilton 1999). Seed dispersal may be essential in restoring areas where the seed bank has been destroyed, either by direct actions such as weeding or burning or simply due to the length of time since the forest was converted (Chapman and Chapman 1999). The colonising benefits of seed dispersal to vacant sites within the local ecological succession are just as important to conservation and the maintenance of forest structure as longer distance seed dispersal is to the colonisation and regeneration of degraded distant sites (Howe and Miriti 2004).

Understanding factors affecting the post dispersal fate of seeds such as the activity of secondary dispersers and post dispersal seed predators are also important in informing conservation decisions, these parts of the regeneration process determine the fitness effect of primary dispersers upon their food plants (Andresen 2002). Due to these interacting steps in forest regeneration, conservation programmes must look at the whole forest and not just flagship species (Marsh and Loiselle 2003).

Vertebrate frugivores, in particular primates, play an important role in the regeneration of tropical forest habitats through their roles as seed dispersers (Oliveira and Ferrari 2000) and understanding this role in conservation and restoration projects is highly valuable. Moreover, maximising natural seed dispersal services has the potential to be a cost effective approach to conservation efforts (Wunderle 1997; Duncan and Chapman 1999).

While natural forest regeneration on abandoned agricultural lands can occur in just a few years to decades, often such natural succession is arrested (Zanne and Chapman 2001). Frequently, one of the major barriers to natural forest regeneration in such sites is low rates of seed dispersal (Duncan and Chapman 1999; Cordeiro and Howe 2001; Howe and Miriti 2004).

## 1.2 Study site

### *1.2.1 Cameroon Highlands*

The Cameroon Highlands are a mountainous chain running north-east south-west along the Nigerian/Cameroon border and culminating in the island of Bioko (Bergyl *et al.* 2007). The Cameroon Highlands ecoregion is a biodiversity hotspot (Olson *et al.* 2001) with high rates of endemism among such taxanomic groups as primates, amphibians, birds, insects and vascular plants (Bergl *et al.* 2007, Chapman *et al.* 2004). Nigeria and Cameroon both have high primate species richness (Chapman *et al.* 2006). However, the area is subject to burgeoning human populations, putting increasing pressure on remaining forests (Bergl *et al.* 2007). Nigeria, for example, has the second highest density of people in Africa with an average of 140 people per square kilometre (Bergl *et al.* 2007). In addition, Nigeria has lost 94% of 1987 forest cover, leaving only about 4 million ha remaining (Ikojo 2008 in Saliu *et al.* 2010). Furthermore, many Nigerian's supplement their diet with bushmeat, including primates (Fa *et al.* 2006).

### *1.2.2 Mambilla Plateau*

Situated within the Cameroon Highlands, the few remaining forests on Nigeria's

Mambilla Plateau are home to many Afromontane endemic trees or near endemics while other species are mainly confined to the Nigerian/Cameroon highlands (Chapman *et al.* 2004). With the other montane forests of the Cameroon Highlands, the forests have a high level of diversity including birds, mammals, reptiles and amphibians (Chapman *et al.* 2004). Areas such as this, with a high level of species diversity and endemism deserve high-priority conservation treatment (Fimbel 1994). Additionally, the forests are important for watershed conservation and as sources of food and medicine, and hold potential for ecotourism and outdoor recreation (Chapman *et al.* 2004). However, like the other montane forests in the region, hunting, fire and cattle grazing continue to threaten these montane forest fragments, putting them at risk of further fragmentation and degradation (Bergl *et al.* 2007, Chapman *et al.* 2004). This has led to declines in frugivore numbers, which may lead to reduced recruitment of seedlings, especially of species that require frugivore dispersal (Chapman *et al.* 2004). Surveys conducted in the 1970s and in 2002 found that the wildlife of these forests had dramatically reduced in that time (Chapman *et al.* 2004). Many of the birds with gapes wide enough to disperse large seed are now less common, such as pigeons and turacos, likely leaving the rare chimpanzee as the main disperser of larger seed as the smaller frugivorous primates tend to spit large seeds under the parent, or close by, rather than ingest them for dispersal further afield (Chapman *et al.* 2004). Therefore without successful conservation efforts, it has been suggested these forests risk becoming empty forests in the mid to long term (Chapman *et al.* 2004).

### *1.2.3 Ngel Nyaki Forest Reserve*

Ngel Nyaki Forest Reserve (7º30 N, 11º30E) lies on the western escarpment of the Mambilla Plateau, Taraba State, Nigeria (Chapman *et al.* 2004). Within the 46km$^2$ reserve, 7.2km$^2$ of forest remains in two main fragments – Ngel Nyaki Forest and Danko Forest (Beck and Chapman 2008), surrounded by numerous small riverine forest fragments in a matrix of grassland that has been modified by annual burning and cattle grazing (Chapman *et al.* 2004; Fig 1.1). The 5.3km$^2$ submontane Ngel Nyaki Forest ranges between 1400-1600m elevation. The forest is of a dry type (Akinsoji 1994) with a mean annual rainfall of approximately 1800mm (Nigerian Montane Forest Project (NMFP) Weather Data), most of which falls in a single wet season lasting from mid April to mid October. Mean monthly temperatures do not exceed 30ºC (NMFP Weather Data).

Ngel Nyaki Forest is one of the most floristically diverse in Nigeria, containing many endemic plant species, including several on the IUCN red list (Chapman *et al.* 2004). Despite facing pressures from slash and burn agriculture, cattle trampling and hunting, Ngel Nyaki Forest is still relatively abundant in wildlife (Chapman *et al.*2004). The area has a rich bird fauna and is a Birdlife International Important Bird Area (Fishpool and Evans 2001). Additionally, the reserve is home to six primate species: *Pan troglodytes ellioti*, *Papio anubis*, *Cercopithecus nictitans* cf. subspecies *martini* (J. F. Oates, pers comm.), *Cercopithecus mona*, *Colobus guereza occidentalis* and the subject of my thesis, *Chlorocebus tantalus tantalus* (Chapman *et al.* 2004).

Current conservation efforts at Ngel Nyaki include the controlled 'early burning' of fire breaks around the forest to prevent fires encroaching into the forest and the fencing off areas of grassland close to the Nigerian Montane Forest Project fieldstation protects these areas from cattle grazing to allow forest regeneration (Beck and Chapman 2008). Additionally, the forest is regularly patrolled to deter hunters (NMFP Annual Report)

**Fig. 1.1:** Photo showing a riverine forest fragment extending into grazed grassland at Ngel Nyaki Forest Reserve.

### 1.3 Study Species: *Chlorocebus tantalus tantalus*

*Chlorocebus tantalus tantalus* (Ogilby 1841 in Groves 2001) is a mid size diurnal monkey with an average weight of 3.36kg for females and 4.6kg for males

(Nakagawa 2000a). It forms multi-male, multi-female troops, with troop sizes ranging from 11 to 76 individuals (Kavanagh 1980) and occupies overlapping home ranges of up to 90 ha (Nakagawa 1999).

Despite being widespread across Central Africa (Kingdon and Gippoliti 2008), *C. t. tantalus* remains poorly studied, however it possesses several traits indicating it may be an important seed disperser that with appropriate conservation management could contribute to the regeneration of degraded forests. The omnivorous *C. t. tantalus* spends around 200 minutes per day feeding (Kavanagh 1980; Nakagawa 2000b; Agmen *et al.* 2009). Approximately half its diet consists of fruit and it additionally consumes foliage, flowers, plant sap and insects (Nakagawa 2000b; Agmen *et al.* 2009). As a large portion of its diet consists of fruit, *C. t. tantalus* has the potential to disperse many seeds, and previous research indicates it defecates seeds in a viable state (Agmen *et al.* 2009).

As a semi-terrestrial monkey, *C. t. tantalus* spends one third of both their total and feeding time on the ground (Kavanagh 1980) allowing it the ability to be adaptable in its habitat use. It is often observed frequenting both grassland and forested areas while foraging (Kavanagh 1980; Agmen *et al.* 2009) allowing for the potential of seed dispersal by *C. t. tantalus* to occur between forested and grassland habitats and among forest fragments. *C. t. tantalus* also has a relatively long daily ranging pattern, regularly travelling 1.3 to 2.5 km per day (Nakagawa 1999; Agmen *et al.* 2009) and this combined with a long gut retention time of 30 hours (Wallis *et al.* 2008) provides seeds the opportunity to be deposited far from the parent plant.

Despite being listed as Least Concern by the IUCN (Kingdon and Gippoliti 2008), the dietary flexibility of *C. t. tantalus* also allows them to become agricultural pests. They are known to raid crops leading to active hunting by some farmers (Kavanagh 1980; Warren *et al.* 2007; pers. obs.). Additionally, considerable bushmeat consumption occurs in Nigeria (Fa *et al.* 2006), and as significant primate population declines can occur over relatively short time frames (Isbell *et al.* 1990), *C. t. tantalus* cannot be assumed to be immune to future population decline and a change in conservation status.

## 1.4 Objectives

The overall aim for my research was to investigate and evaluate the potential role of the tantalus monkey in forest regeneration and restoration via their role as seed dispersers. To achieve this, my objectives were to:

- Investigate patterns of habitat use by *C. t. tantalus* in order to determine the range of habitats into which it has potential to disperse seed.
- Investigate components of the quantity and quality of seed dispersal by *C. t. tantalus* among habitats to assess the role of this monkey in the regeneration of forest in degraded areas.
- Investigate the germination success of seeds dispersed by *C. t. tantalus* among habitats to:
    - Determine whether *C. t. tantalus* disperses seeds into habitats suitable for their germination and establishment.
    - Further understand the potential role of *C. t. tantalus* in forest

regeneration.

    - Determine whether current conservation practices at Ngel Nyaki Forest Reserve will allow *C. t. tantalus* to reach its full potential in aiding the plant recruitment process.
- Calculate the density of *C. t. tantalus* at Ngel Nyaki Forest Reserve:
    - For use as a benchmark against which to measure future population trends of *C. t. tantalus*.
    - To allow the estimation of seed dispersal rates by *C. t. tantalus*.

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# Chapter 2:

# Habitat use by the tantalus monkey (*Chlorocebus tantalus tantalus*): implications for forest restoration.

## 2.1 Introduction

Forest loss and degradation is a major issue for conservation throughout the world, particularly in tropical regions, where human populations are high and incomes low (Chapman *et al.* 2006). Over 125000 km$^2$ of tropical forest cover is lost annually, with the highest rates of deforestation occurring in Africa (Chapman and Peres 2001). In Nigeria, for example, approximately 4 million hectares of forest remains, comprising only 6% of the forest cover present in 1987 (Ikojo 2008 in Saliu *et al.* 2010). The conservation of remaining forests and restoration of degraded areas are therefore of great importance to the preservation of forest plant and animal species (Pimm and Raven 2000).

Seed dispersal has the potential to play an important role in restoring altered habitats (Chapman and Chapman 1999), as it is a key process controlling plant population and community dynamics within degraded landscapes (Higgins *et al.* 2003). It is considered the major process behind plant invasion of open habitats during both range extension (Higgins *et al.* 2003; Pearson and Dawson 2005) and ecological succession (Hooper *et al.* 2005; Ronce *et al.* 2005). Natural regeneration in degraded habitats relies upon three factors: 1) primary forest located close to the degraded site, 2) the presence of potential seed dispersing animals and 3) a vegetation structure in the degraded site that is attractive to seed dispersers (Karlowski 2006). However, rates of seed dispersal among habitats in degraded landscapes are often greatly reduced, severely slowing or preventing restoration of such habitats (Chapman and Onderdonk 1998; Cordeiro and Howe 2001; Duncan and Chapman 1999; Higgins *et al.* 2003; Worman and Chapman 2006).

In the tropics, animal mediated seed dispersal is particularly common, with up to 90% of tropical forest plants being dispersed by vertebrates (Willson *et al.* 1989; Corlett 1996; da Silva and Taberelli 2000; Hardesty and Parker 2002; Stoner *et al.* 2007). The role of frugivorous primates as seed dispersers in tropical ecosystems has been widely studied (e.g. Chapman 1989; Corlett and Lucas 1990; Andresen 1999; Wehncke *et al.* 2003; Flörchinger *et al.* 2010), providing evidence suggesting primates can be important in ecosystem maintenance and restoration (Fimbel 1994a; Chapman and Onderdonk 1998; Oliviera and Ferrari 2000; Nuñez-Iturri and Howe 2007; Kunz and Linsenmair 2008). The effectiveness of these dispersers depends to a large extent on where seeds are deposited (Wenny and Levey 1998), therefore, their choice of habitat has a significant influence on the deposition patterns of seeds and seed survival (Schupp 1993).

Degraded landscapes often comprise a range of habitats ranging from remnants of original habitat to heavily altered habitats (Anderson *et al.* 2007), that frugivores may potentially use. The physical environmental characteristics of habitats, such as temperature, food availability and canopy cover, influence frugivore behaviour and their use of habitats (Schupp 1993; Wunderle 1997; Hill 2006). For example, frugivores may choose between forested and open habitats (Cowlishaw 1997; Higgins *et al.* 2003), mature and secondary forest (Fimbel 1994a, b), or along moisture, vegetation and/or human disturbance gradients (Karr and Freemark 1983; Rakotondranary *et al.* 2011; Wang *et al.* 2011). The physical environmental characteristics of habitats also influence probabilities of seed survival, germination and successfully reaching maturity (Schupp and Frost 1989; Howe 1990; Willson and Whelan 1990; Forget 1997). As such, habitat use by dispersers influences the probability seeds are deposited into suitable sites for their germination and establishment (Sorenson 1981; Wenny and Levey 1998; Gross-Camp and Kaplin 2011). Frugivores that utilise a combination of primary forest and degraded habitats, such as abandoned agricultural fields or secondary forest, can significantly contribute to the further succession of that degraded habitat (Wunderle 1997; Karlowski 2006). However, there are few species of seed disperser that make these inter-habitat movements necessary for the colonisation of degraded sites by forest plants (Wunderle 1997).

The frugivorous monkey *Chlorocebus tantalus* (Ogilby 1841 in Groves 2001) is widespread across Central Africa (Kingdon and Gippoliti 2008) and remains poorly studied. This adaptable species often frequents grassland and forested areas while foraging (Kavanagh 1980; Agmen *et al.* 2009) but is generally considered to be absent from continuous forest (Kavanagh 1980). In addition, as it has previously been shown to disperse defecated seeds in a viable state (Agmen *et al.* 2009), understanding its patterns of habitat use will aid in understanding its role as a seed disperser in forest restoration. I therefore investigated patterns of habitat use by the subspecies *C. tantalus tantalus* in order to i) determine the range of habitats into which they may disperse seed and ii) assess, in relation to their habitat use, the potential of *C. t. tantalus* in maintaining forest structure and aiding forest regeneration.

## 2.2 Methods

### *2.2.1 Study site*

Ngel Nyaki Forest Reserve lies on the western escarpment of the Mambilla Plateau, Taraba State, Nigeria (Chapman *et al.* 2004), ranging between 1400-1600 m elevation. The reserve lies within the Cameroon Highlands ecoregion (Olson *et al.* 2001), belonging to a biodiversity hotspot and contains many endemic plant species, including several on the IUCN red list (Chapman *et al.* 2004). The area is also a Birdlife International Important Bird Area (Fishpool and Evans 2001). The reserve experiences a mean annual rainfall of approximately 1800 mm (Nigerian Montane Forest Project (NMFP) Weather Data), most of which falls in a single wet season lasting from mid April to mid October. Mean monthly temperatures do not exceed 30ºC (NMFP Weather Data).

Within the 46 km$^2$ reserve, 7.2 km$^2$ of forest remains in two main fragments – Ngel Nyaki Forest and Danko Forest (Beck and Chapman 2008), surrounded by numerous small riverine forest fragments in a matrix of grassland that has been modified by annual burning and cattle grazing (Chapman *et al.* 2004). In addition to *C. t. tantalus*, *Papio anubis* and *Pan troglodytes ellioti* also enter grassland in the reserve, however these species are rare at Ngel Nyaki. Three further primate species are found within the forest in the reserve, *Cercopithecus nicititans, C. mona* and *Colobus guereza occidentalis* (Chapman *et al.* 2004).

### *2.2.2 Study species*

*Chlorocebus tantalus tantalus* (Ogilby 1841 in Groves 2001) is a mid size monkey with an average weight of 3.36kg for females and 4.6kg for males (Nakagawa 2000a). It forms multi-male, multi-female troops ranging in size from 11 to 76 individuals (Kavanagh 1980). The omnivorous *C. t. tantalus* spends approximately 200 minutes per day feeding (Nakagawa 2000b; Agmen *et al.* 2009). Approximately half its diet consists of fruit and it additionally consumes foliage, flowers, plant sap and insects (Nakagawa 2000b; Agmen *et al.* 2009). This semi-terrestrial monkey spends one third of both its total and feeding time on the ground (Kavanagh 1980).

### *2.2.3 Data collection*

I regularly observed three semi-habituated *C. t. tantalus* troops (A, B and C) from November 2008 through January 2009 and November 2009 through November 2010 to gather information on habitat use. Troops A, B and C differed in size with an average of 21, 30 and 18 individuals respectively. The focal troops had home ranges along the north eastern border of Ngel Nyaki Forest Reserve (Fig 2.1), frequently

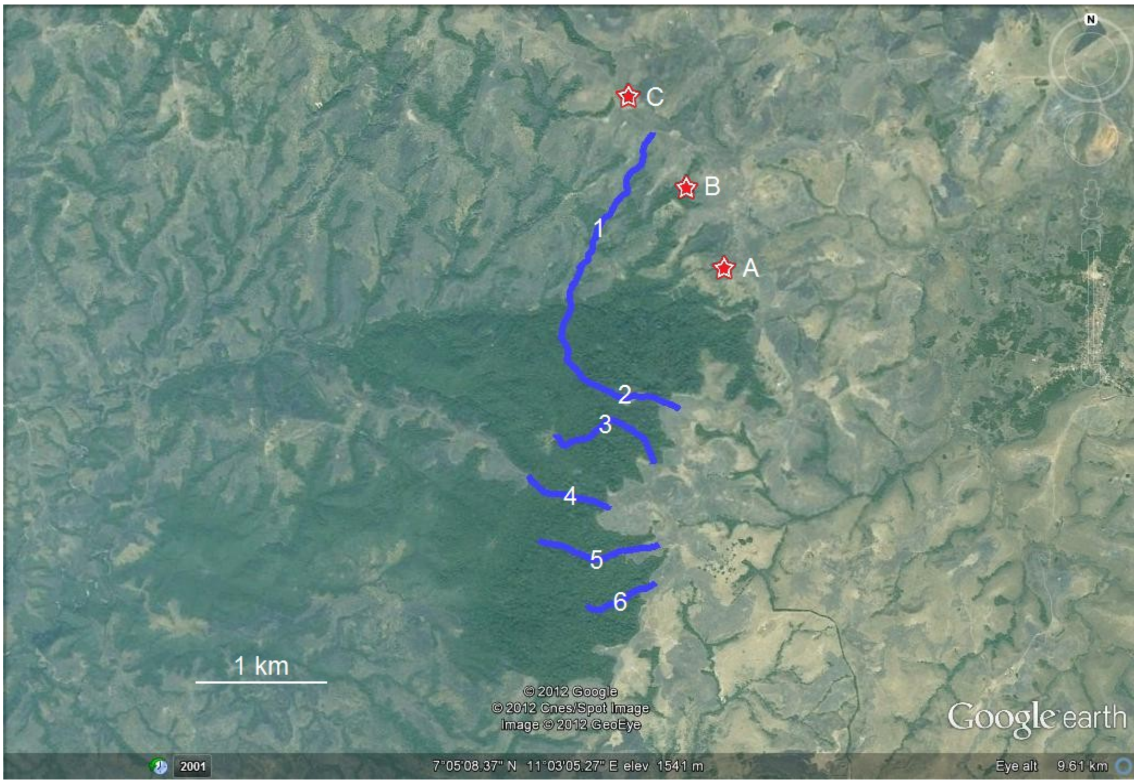

**Fig. 2.1:** The location of transects (lines 1-6) walked and one location where each of the focal *C. t. tantalus* troops (stars A-C) were frequently observed.
*Source:* 'Ngel Nyaki', 7º06'02.03"N and 11º03'26.34"E, **Google Earth**, 29 Jan 2012.

being sighted in both riparian forest fragments, the edge of the main forest and open grassland. The forest in the area occupied by the three focal troops is restricted to forest edge and tongues of riparian forest extending out into the grassland (Fig. 2.1). In many places the forest is only a few metres wide, so for the purpose of this study I defined edge habitat as the area covered by the canopy of the single row of trees forming the forest edge. Forest habitat was defined as the remaining area of trees and grassland as the surrounding grassland with occasional savannah tree species.

On each day of observations, I observed one troop from the time it was located until it either disappeared into the undergrowth in the middle of the day or settled down for the night at a sleeping site. As such, observations were conducted between the hours of 7:00 to 13:00 and 15:00 to 18:00. I took scan samples (Altman 1974) every 10 minutes, recording the number of individual *C. t. tantalus* present in each of three habitats (forest, edge, grassland). I collected data from a total of 2270 scans, providing 378.3 hours of observation. I observed the monkey troops using binoculars at distances of approximately 20 to 50 m to minimise disturbance to the troop and potentially altering their behaviour.

To determine whether *C. t. tantalus* is present in continuous forest at Ngel Nyaki, I used methodology similar to Lwanga (2006). I walked six line transects running perpendicular to the forest edge, traversing grassland through core forest habitats (Fig. 2.1) a total of 18 times between December 2009 and June 2011. Transects ranged in length from 645 m to 1.9 km and had a combined length of 6.3 km, resulting in a total length of 113 km walked during the course of the study. I walked transects as carefully and quietly as possible at approximately 1 to 1.5km per hour to avoid disturbing any *C. t. tantalus* present. Regular pauses to scan the surrounding habitat for the presence of *C. t. tantalus* also helped minimise the chance of missing a troop that was indeed present. When one or more *C. t. tantalus* individuals were observed, I took a GPS location on the transect at a position perpendicular to the monkey(s). I estimated distance from the transect to the centre of the group by eye and recorded the date and time. When I found faeces along the transects I also recorded their GPS location. Faeces were identified as belonging to *C. t. tantalus* based on their size and shape.

### *2.2.4 Statistical Analyses*

Overall visibility of my focal troops was low, therefore habitat use of visible individuals may not accurately reflect actual habitat use of the troop. Additionally, visibility was much greater in the grassland than the forest due to differences in vegetation structure, leading to a visibility bias favouring the grassland. To reduce this visibility bias, I scored data for presence or absence of *C. t. tantalus* in each habitat.

I carried out analyses in R 2.7.1 (R Core Development Team, 2008). I first assigned scans to one of five time periods. These were early morning (7 – 9am; n=789 scans), late morning (9 – 11am; n=1142 scans), midday (11am – 1pm; n=170 scans), late afternoon (3pm – 5pm; n=92 scans) and evening (5pm – 7pm; n=77 scans). As no observations were made between 1 and 3pm, I omitted the early afternoon group (1 – 3pm). To approximate the mean percentage time at least one *C. t. tantalus* individual was present in each habitat during each time period for each troop, I calculated the mean percentage of scans in which at least one individual was present for each habitat, troop and time of day combination (Altman 1974). For a given troop and time period, the cumulative percentages of time spent in each habitat are greater than 100% because often individuals from the troop were present in more than one habitat at a given time.

To assess differences in trends throughout the day by my focal troops in each habitat

I ran a binomial generalised linear mixed model (GLMM) testing the effect of troop, habitat and time of day on the presence of at least one individual in each habitat for each scan.  Date was included as a random factor to control for lack of independence between observations taken on the same day and therefore belonging to the same troop. The model accounts for the differences in sample sizes among time periods, producing larger standard errors for time periods with fewer scans. I used log likelihood ratio tests (using the anova function in R) to compare models with and without each factor as a method of assessing the significance of individual factors included in the generalised linear mixed model.

I used the software Garmin MapSource v6.13.7 to plot the GPS locations of each *C. t. tantalus* troop I sighted and faeces found during transect walks onto a Google Earth image of Ngel Nyaki Forest and its surrounds. I then measured the distance from those locations which fell inside the forest to the closest forest edge, to allow me to determine how far *C. t. tantalus* ventures into forest. To estimate the area of core forest deemed unsuitable *C. t. tantalus* habitat in Ngel Nyaki Forest Reserve, I drew a line around the core forest in both Ngel Nyaki and Kurmin Danko Forests, that was the maximum estimated distance that *C. t. tantalus* enters the forest, from the edge. Area was then estimated using a 200m by 200m grid overlaid on the map.

## 2.3 Results

### *2.3.1 Focal Troops*

The amount of time I observed the presence of at least one *C. t. tantalus* individual differed among habitats ($\chi^2$ = 247.35, df = 30, P<2.2x$10^{-16}$). At least one individual was present in the grassland for an average of 49.6 +/- 1.3% of the day. This was less than the time spent in the forest (60.3 +/-1.3%) but greater than the amount of time spent at the edge (46.5 +/- 1.3%).

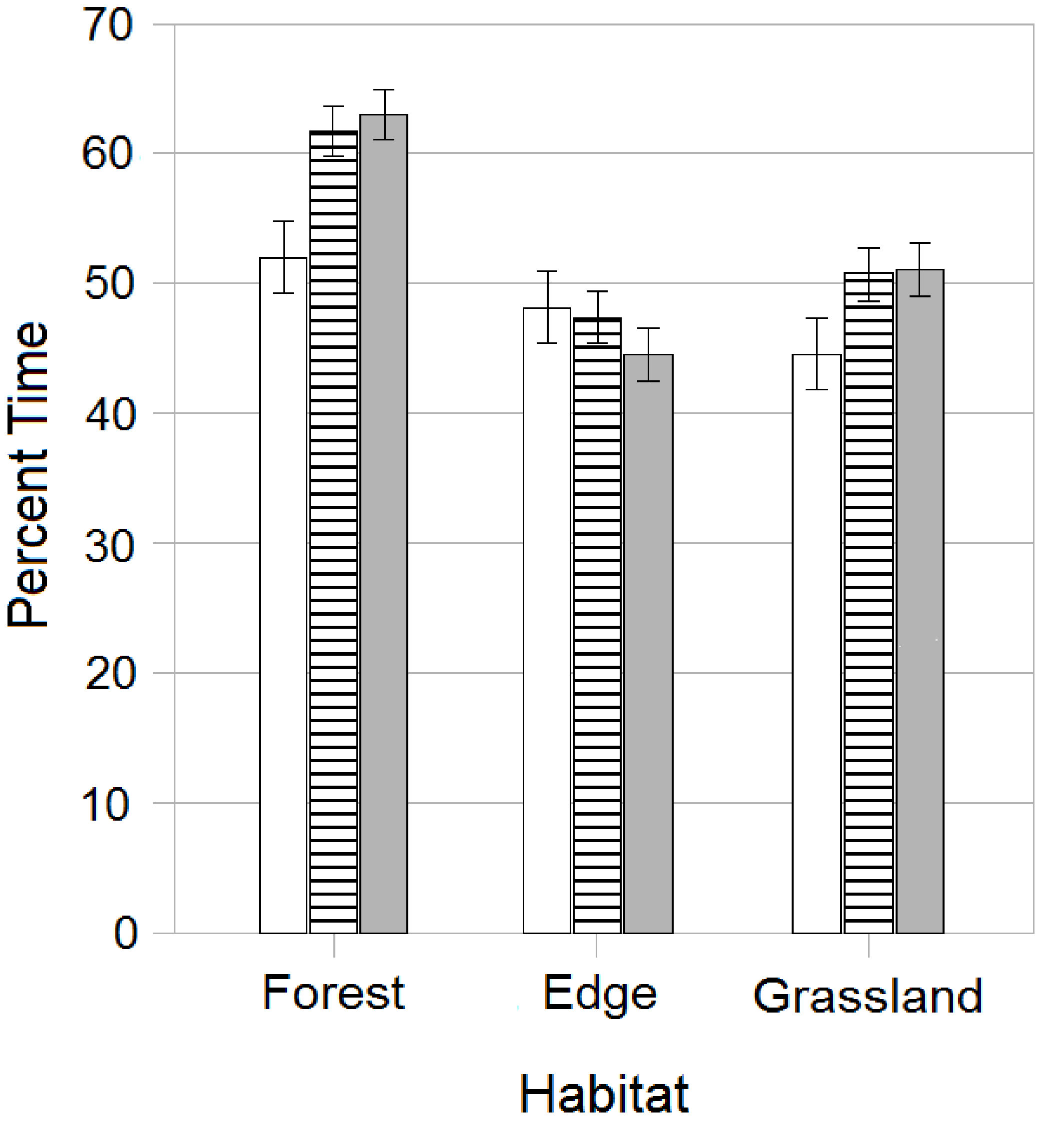

**Fig 2.2:** Estimated percentage of time that at least one individual from each of troops A (white), B (stripes) and C (gray) were present in edge, forest and grassland habitats.

The amount of time at least one individual was present in each habitat differed among troops ($\chi^2$=78.54, df=20, P=6.95x$10^{-9}$, Fig. 2.2). The percentage of time at least one individual was present in the edge and grassland did not differ among troops but troops B and C had at least one individual visible in the forest for longer than troop A.

Time of day also had an effect on the percentage of time at least one individual was present in each habitat ($\chi^2$=140.52, df=24, P<2.2x$10^{-16}$, Fig. 2.3). More time was spent in the forest during late morning than early morning, but neither of these differed from midday and evening time periods. Less time was spent in the forest during the late afternoon than other times of day. Time spent in the edge decreased from early morning to midday, peaked in the late afternoon and dropped again in the evening. Time spent in the grassland was high in the early morning and decreased through late morning to midday. Time spent in the grassland was similar in the late afternoon to midday, but in the evening was similar again to the early morning.

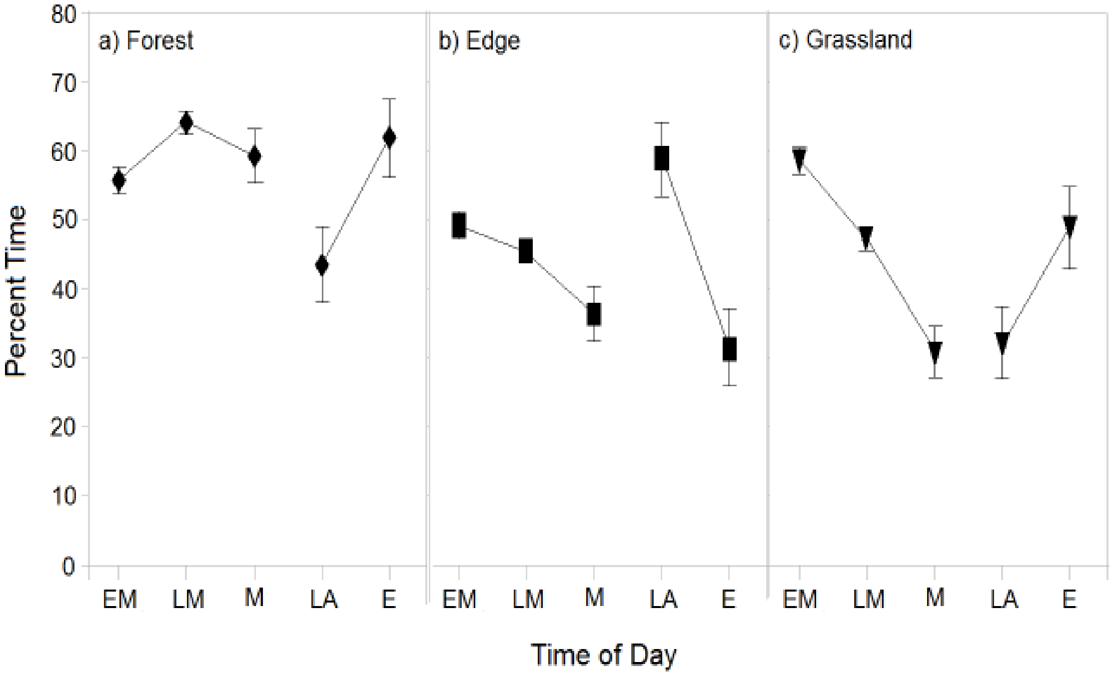

**Fig 2.3:** Average percentage of time at least one individual is present in each of forest (diamonds), edge (squares) and grassland (triangles) habitats throughout the day. Time of day is defined as follows: EM = early morning (7-9am), LM = late morning (9-11am), M= midday

(11am-1pm), LA = late afternoon (3-5pm) and E = evening (5-7pm).

At least one individual was present in the forest and grassland for longer than the edge during the early morning. More time was spent in the forest in the late morning and midday time periods than the edge or grassland. More time was spent in the edge than the forest or grassland in the late afternoon. In the evening more time was spent in the forest and grassland than the edge.

The percentage of time at least one *C. t. tantalus* individual from each troop was present in each habitat also varied throughout the day ($\chi^2$=66.40, df=16, P=4.23x$10^{-8}$, Fig. 2.4). Use of the forest differed between troops in both the early and late morning (Fig. 2.4a,d,g). Troops B and C had at least one individual present for a greater percentage of time than troop A during both early and late morning.

The percentage of time at least one individual was present in the edge only differed between troops in the late afternoon, with troop C spending less time in the edge than troops A and B (Fig. 2.4b,e,h).

Use of the grassland differed between troops both in the late afternoon and evening (Fig. 2.4c,f,i). Troops B and C had at least one individual present for a greater percentage of time than troop A during both late afternoon and evening. There were no differences between troops in the use of any habitats in the middle of the day.

During the early morning, troop A had at least one individual present for more time in the edge than the forest, however the percentage time spent in the grassland did not differ from either the edge or the forest (Fig. 2.4a,b,c). More time was spent in the forest in the late morning than both edge and grassland habitats. At midday, troop A spent more time in the forest than the edge, however neither forest nor edge differed from the percentage time spent in the grassland. Troop A spent more time in the edge in the late afternoon than any other time of day and than any other habitat within the late afternoon. Additionally, more time was spent in the forest than the grassland in the late afternoon. Use of the grassland did not differ between late afternoon and evening, however, more time was spent in the forest than the edge in the evening.

Troop B did not differ in the amount of time spent in each habitat during the early morning, however, more time was spent in the forest in the late morning and midday time periods than in the other habitats (Fig. 2.4d,e,f). In the late afternoon, more time was spent in the edge than the forest or grassland, while in the evening more time was spent in the forest than the edge. The percentage time spent in the grassland in the evening did not however, differ from the edge or forest.

In the early morning, Troop C spent less time in the edge than the forest and grassland, while in the late morning, more time was spent in the forest than edge and grassland habitats (Fig. 2.4g,h,i). At midday, more time was spent in the forest than the edge and grassland, but only marginally so for the edge. The percentage time at least one individual was present in the forest and grassland habitats did not differ during the late afternoon, however, marginally more time was spent in the forest than the edge. Troop C spent more time in the grassland in the evening than the forest or

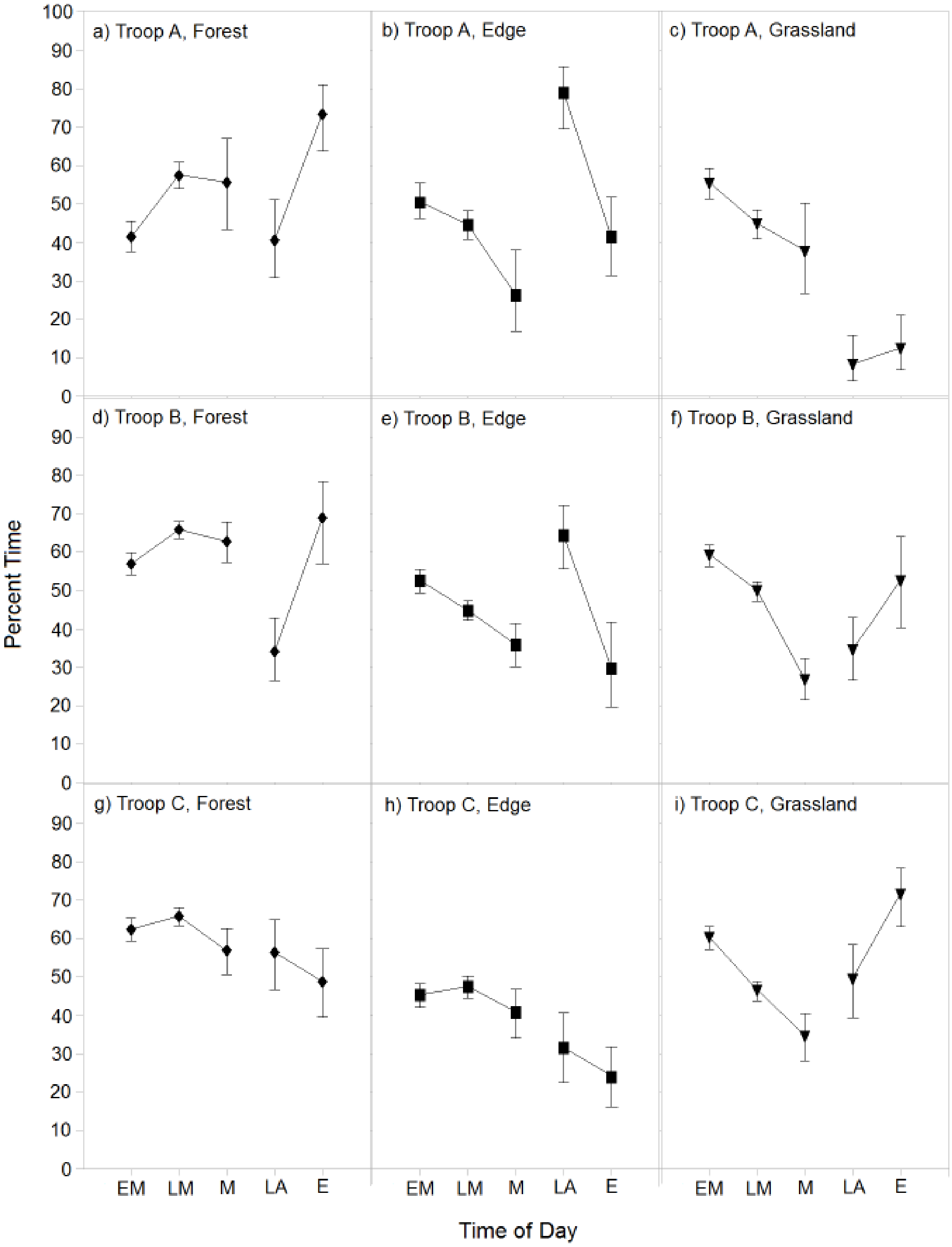

**Fig. 2.4:** Percent time at least one individual from each focal troop is present on average in each of edge, forest and grassland habitats at different times of day. Diamonds, squares and triangles represent forest, edge and grassland habitats respectively. Time of day is defined as follows: EM = early morning (7-9am), LM = late morning (9-11am), M = midday (11am-1pm), LA = late afternoon (3-5pm), E = evening (5-7pm).

edge, while forest was used more than the edge.

### *2.3.2 Transects*

Four of the twelve recorded sightings of *C. t. tantalus* I obtained from transect walks were in grassland, five at the edge of the forest, leaving only three sightings within the forest (Fig. 2.5). Of those sightings within the forest, the sighting furthest from the edge was 90 m into the forest. Of the three faecal samples located along transects, two were in grassland while the third was found 175 m into the forest. To account for the fact that individuals within a troop are usually somewhat spread out, I rounded up and chose 200 m from the nearest forest edge as the definition of the core

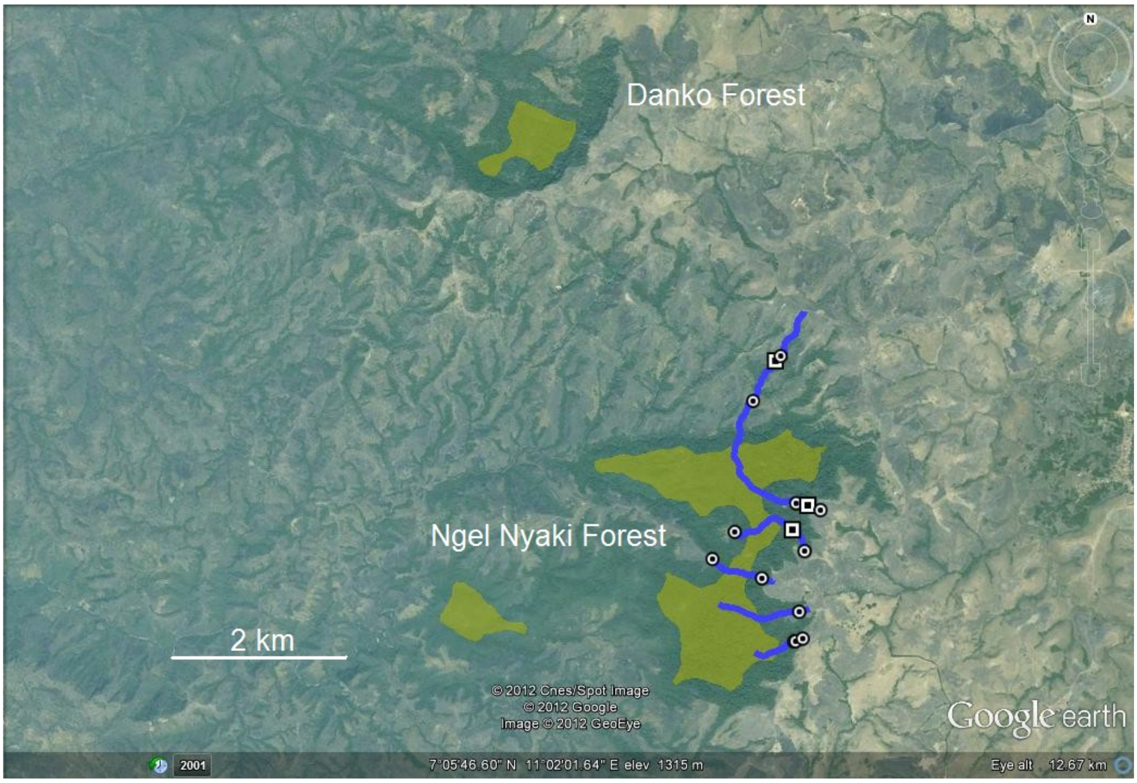

**Fig. 2.5:** Map showing the location of *C. t. tantalus* troops (circles) and faeces (squares) encountered during transect walks within Ngel Nyaki Forest. The shaded areas depict core forest habitat within Danko and Ngel Nyaki Forests where *C. t. tantalus* is absent.
*Source:* 'Ngel Nyaki', 7º05'00.25"N and 11º03'10.48"E, **Google Earth**, 7 February 2012.

forest boundary. I therefore estimated the area of core habitat within Ngel Nyaki Forest Reserve as 3.2 $km^2$.

## 2.4 Discussion

### *2.4.1 Possible behavioural explanations for observed patterns of habitat use*

Each of the three habitats - grassland, edge and forest, visited by my focal troops, were used on a daily basis. On a typical day, use of the grassland peaked early morning and evening, while edge use declined throughout the day, with the exception of a large peak during the late afternoon. Use of the forest was relatively steadier throughout the day, with only minor fluctuations in use. Several potential explanations exist for this pattern of habitat use, including diurnal fluctuations in temperature, activity budget, diet and perceived predation risk.

Temperature changes throughout the day seem the most likely explanation for the observed pattern of grassland use. *C. t. tantalus* may make more use of the grassland habitat in the early morning and evening when temperatures are cooler, spending more time in the forest during the middle and hottest part of the day. During the heat of the day, forest temperatures can be up to 10°C cooler than in the grassland (Harrison 1985). Additionally, I assume during the early afternoon that *C. t. tantalus* is resting within the undergrowth of the forest. I base this assumption upon the difficulty of locating the monkeys during this time (hence the lack of data for this time period) and observations of troops disappearing into the undergrowth of forested habitat around this time of day. Temperature can place a significant constraint upon primate activity budgets, enforcing periods of resting that cannot be used for other activities, especially in open habitats (Dunbar 1992). When possible, primates often seek shade when temperatures are high (e.g. *Papio anubis*, Hill 2006; *Cercopithecus sabaeus*, Harrison 1985) in which to rest or conduct social interactions.

Perceived predation risk is often considered greater in open grassland, preventing some primate species from utilising this habitat (Tutin *et al.* 1997). However, this may not be the case for *C. t. tantalus* in some savannah and open woodland habitats, as areas of grassland often provide more cover at ground level than higher up (Kavanagh 1980). This seems unlikely to be the case for *C. t. tantalus* at Ngel Nyaki however. Heavy grazing and regular burning of the grassland at Ngel Nyaki keeps the amount of available cover relatively low. Reduced ground cover in grasslands can increase visibility and predator detection making such habitats more favourable (Jaffe and Isbell 2009). Individuals of *C. t. tantaus* frequently sit or stand on rocks or termite mounds in the grassland to gain greater elevation over surrounding grassland and exhibit vigilant behaviours (pers. obs.) and a reduced predation risk in this habitat may allow them to utilise it for foraging and travel between fragments. Group size can additionally alter perceived predation risk and may therefore explain differences in habitat use between troops (Hill and Dunbar 1998). Habitat for resting and social interaction behaviours may be selected based on reduced predation risk (Cowlishaw 1997, Hill 2006), meaning that while predation risk in the grassland is low enough for them to use this habitat, it may be lower in the forest undergrowth where they rest during the heat of the day.

Fluctuations in activity budget patterns throughout the day have also been observed for many primate species. Feeding often follows a bimodal pattern, with peaks in the morning and late afternoon, while resting peaks during the middle of the day (e.g. *Cercopithecus mitis doggetti*, Kaplin and Moermond 2000; *Nomascus concolor jingdongensis*, Fan *et al.* 2008; *Alouatta palliata*, Estrada *et al.* 1999). Moreover, time spent feeding by primates often differs among habitats (e.g. *Cercopithecus l'hoesti*, Kaplin and Moermond 2000; *C. ascanius*, Thomas 1991, but see *C. aethiops*, Isbell and Young 1993). At Ngel Nyaki, *C. t. tantalus* is no exception, with 72% of feeding occurring at the forest edge (Agmen *et al.* 2009). In contrast, 20% and 8% of feeding occur within the forest and grassland habitats, respectively (Agmen *et al.* 2009). A bimodal feeding pattern therefore seems likely for *C. t. tantalus* as I would expect more time spent feeding during periods when edge use is relatively high, as in the early morning and late afternoon. It also seems logical that *C. t. tantalus* may want to feed at these times, as they are both after periods of resting and they may require energy intake.

Diet may also play a role in *C. t. tantalus* habitat use. Approximately half their diet consists of fruit, with other important components including insects, leaves and flowers (Agmen *et al.* 2009). Fruits, leaves and flowers are all relatively abundant in the forest and edge explaining why more time spent feeding occurs in these habitats than the grassland. Indeed, the high proportion of time spent feeding in the edge likely reflects the abundance of common *C. t. tantalus* food sources, e.g. *Aframomum angustifolium*, around the forest edge (Agmen *et al.* 2009; Chapter 3).

Despite general trends, each of the focal troops, A, B and C, differed in their patterns of habitat use. Troop A spent more time in the edge during the late afternoon and less time in the grassland during the late afternoon and evening than the other troops. Troop C on the other hand, spent more time in the forest in the early and late morning than either of the other troops. Group size may influence the habitat use of individual troops by affecting their activity budget. Larger troops, for example, may be required to devote more time to social interactions (Dunbar 1992; Dunbar et al. 2009) and spend more time in the relative safety of the forest. On the other hand, larger troops may have longer daily ranging distances (Hill and Dunbar 2002) and therefore may cross more grassland during the day. The differences among troops in this study are not as clear cut however.  For example, the smallest troop, troop A, used forest less during the late morning and midday time periods than the other troops, while troops B and C did not differ significantly. The difference in size between troops A and C is relatively small however, while troop B is much larger. Any influence of group size therefore, is likely to be in combination with other factors, such as the temperature fluctuations, perceived predation risk and dietary requirements already mentioned.

### *2.4.2 Habitat use by* **Chlorocebus tantalus tantalus** *and forest regeneration*

*Chlorocebus tantalus tantalus* was not recorded in the core of the forest, with sightings restricted to within 100m of the edge. However, additional sightings in the forest (A. Barnes, pers. comm.) and faecal evidence were restricted to within 200 m from the edge, suggesting that *C. t. tantalus* at least occasionally ventures this deep into the forest. These findings support the notion that *C. t. tantalus* is absent from core forest habitat and is therefore unlikely to be a major disperser of core forest species. Given the size of Ngel Nyaki Forest Reserve is approximately 46 km$^2$ (Chapman *et al.* 2010) and I estimated an area of 3.2 km$^2$ as unsuitable *C. t. tantalus* habitat, there is approximately 42.8 km$^2$ of suitable *C. t. tantalus* habitat within Ngel Nyaki Forest Reserve.

Many forest seed dispersers are often absent from forest fragments and other altered or degraded habitats (Cordeiro and Howe 2001). Those primate species that do occupy forest fragments typically are species that also occupy forest edge habitats (Onderdonk and Chapman 2000). Edge species are likely to be better adapted to fragment conditions because forest fragments have large edge to area ratios and therefore provide similar environmental conditions (Onderdonk and Chapman 2000). Primates utilising forest fragments (either a single fragment as an entire home range or multiple fragments within a home range) must be highly mobile and have a highly flexible diet to take advantage of reduced and unpredictable food resources (Tutin *et al.* 1997; Onderdonk and Chapman 2000). Additionally, primates with generalist diets are better able to utilise secondary forest habitats than those with more specialist diets (Fimbel 1994a). Such frugivorous primates may be excluded from fragments if they require a consistently diverse diet however, as fragments are often florally impoverished (Onderdonk and Chapman 2000). *C. t. tantalus* possesses traits allowing it to occupy fragmented landscapes including a long daily ranging distance of 1.5 to 2 km and a generalist and opportunistic diet (Kavanagh 1980; Agmen *et al.*

2009).

As *C. t. tantalus* visits fragments as small as a single tree within the grassland matrix (pers. obs.), this highlights their potential importance as seed dispersers in small fragments where other dispersal agents may be rare or absent. Furthermore, fruit production fluctuates among years at Ngel Nyaki (NMFP Phenology data, 2005-2011 unpub.) and may lead to inter-annual variation in habitat use (Herrera and Garcia 2009). Remnant fruit trees in a grassland matrix may be used more by frugivores when fruit availability is low in the forest (Herrera and Garcia 2009). During such years, frugivores, such as *C. t. tantalus*, may therefore spend more time in the grassland matrix, increasing the potential for seed dispersal in this habitat (Herrera and Garcia 2009). As *C. t. tantalus* is common throughout its distribution, it may be particularly important in areas where other seed dispersing primates known to utilise grassland habitats, such as *Papio anubis* and *Pan troglodytes*, are rare, as at Ngel Nyaki.

Seed dispersal is an important factor in the restoration of altered habitats (Chapman and Chapman 1999) and in such habitats it is often limited (Duncan and Chapman 1999; Higgins *et al.* 2003). As such, the ability of potential dispersers to enter and spend time in these habitats is key (Karlowski 2006). I have shown that *C. t. tantalus* spends a significant portion of each day in each of forest, edge and grassland habitats. This combined with its frugivorous diet supports the hypothesis that *C. t. tantalus* has the potential to not only be important in the maintenance of forest structure in areas of existing forest, but also as part of forest restoration efforts in areas of nearby grassland.

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# Chapter 3

# Patterns of seed dispersal by the tantalus monkey (*Chlorocebus tantalus tantalus*) at Ngel Nyaki Forest Reserve, Nigeria.

## 3.1 Introduction

The proportion of degraded forest is increasing throughout Africa (Chapman *et al.* 2006), with some countries, such as Nigeria having lost 94% of its 1987 forest cover, leaving only approximately 4 million hectares (Ikojo 2008 in Saliu *et al.* 2010). Maintaining the health of remaining intact forest is therefore of great importance in the preservation of forest plant and animal species (Pimm and Raven 2000). Likewise, the restoration of degraded areas is likely crucial to maintain long term viable populations of some species (Fimbel 1994; Jacquemyn *et al.* 2003).

Plant recruitment, distribution and regeneration in tropical forests depend to a large extent on the effectiveness of their seed dispersers (Schupp 1993; Chapman and Chapman 1996; Wenny 2000). Seed dispersal is an essential process underlying forest community structure and dynamics (Hamilton 1999; Harms *et al.* 2000; Peres and Palacios 2007). It underpins local plant population dynamics and plant migration over larger time and spatial scales (Pitelka *et al.* 1997; Higgins *et al.* 2003). In degraded landscapes seed dispersal is the major process behind range extension (Pitelka *et al.* 1997; Higgins *et al.* 2003; Pearson and Dawson 2005) and ecological succession (Hooper *et al*. 2005; Ronce *et al.* 2005), both important aspects of forest restoration. Degraded tropical forest landscapes comprise a variety of habitats ranging from remnants of mature forest to heavily degraded grasslands (Anderson *et al.* 2007). While natural seed dispersal should theoretically play a critical role in the restoration of such habitats (Chapman and Chapman 1999) dispersal rates are such that most forest species are extremely slow to arrive (Duncan and Chapman 1999; Cordeiro and Howe 2001; Higgins *et al.* 2003; Howe and Miriti 2004). Slow dispersal rates are therefore a major obstacle to natural reforestation (Chapman and Onderdonk 1998; Duncan and Chapman 1999; Cordeiro and Howe 2001; Howe and Miriti 2004).

One factor contributing to slow seed dispersal is that only a small proportion of frugivores make the inter-habitat movements required for the colonisation of degraded sites by forest plants (Wunderle 1997). The seed deposition pattern created by a disperser is one component of dispersal quality (Poulsen *et al.* 2001) and is a reflection of its choice of habitat (Wenny and Levey 1998). The structure of surrounding habitat types (matrix) can be important in buffering the effects of forest fragmentation (Ricketts 2001; Murphy and Lovett-Doust 2004; Bender and Fahrig 2005; Prevedello and Vierira 2010). If a seed disperser is able to regularly frequent and utilise the matrix habitat in addition to more intact forest habitats then the potential for dispersers to disperse forest seeds into the matrix habitat exists. In this situation, seed dispersal by animals has the potential to help restore forest plant diversity on degraded sites in a reasonable period of time, thereby helping to defray restoration costs (Wunderle 1997). Consequently, a disperser’s choice of habitat has a significant influence on seed survival (Schupp 1993).

The frugivorous monkey *Chlorocebus tantalus* (Ogilby 1841 in Groves 2001) utilises both forested and grassland habitats on a daily basis (Chapter 2), allowing it the potential to disperse seed from the forest into the grassland matrix as well as among forest fragments. I therefore investigated seed dispersal by *C. t. tantalus* among habitats, along with aspects of quantity and quality in order to assess the role this monkey may play in the regeneration of forest in degraded areas.

## 3.2 Methods

### *3.2.1 Study site*

Ngel Nyaki Forest Reserve lies on the western escarpment of the Mambilla Plateau, Taraba State, Nigeria, ranging in elevation from 1400-1600 m (Chapman *et al.* 2004). Within the 46km$^2$ reserve, 7.2km$^2$ of forest remains in two main fragments – Ngel Nyaki Forest and Danko Forest (Beck and Chapman 2008). The forest is of a dry type (Akinsoji 1994) with a mean annual rainfall of approximately 1800 mm (Nigerian Montane Forest Project Weather Data), most of which falls in a single wet season lasting from mid April to mid October. Mean monthly temperatures do not exceed 30 ºC (Chapman and Chapman 2001).

The reserve lies within the Cameroon Highlands ecoregion (Olson *et al.* 2001), belonging to a biodiversity hotspot and contains many endemic plant species, including several on the IUCN red list (Chapman *et al.* 2004). The area is also a

Birdlife International Important Bird Area (Fishpool and Evans 2001). Six primate species are found at the reserve: *Cercopithecus nictitans* cf. subspecies *martini*, *Cercopithecus mona*, *Colobus guereza occidentalis*, *Papio anubis*, *Pan troglodytes ellioti* and the focus of my study, *Chlorocebus tantalus tantalus* (Chapman *et al.* 2004).

### *3.2.2 Study species*

*Chlorocebus tantalus tantalus (*Ogilby 1841 in Groves 2001) is a mid size monkey with an average weight of 3.36kg for females and 4.6kg for males (Nakagawa 2000a). Troop sizes range from 11 to 76 individuals (Kavanagh 1980). *C. t. tantalus* is an omnivore with a flexible and generalist diet and spends around 200 minutes per day feeding (Kavanagh 1980; Nakagawa 2000b; Agmen *et al.* 2009). Approximately half of its diet consists of fruit, with the rest consisting of foliage, flowers, plant sap and insects (Nakagawa 2000b;  Agmen *et al.* 2009). This semi-terrestrial monkey spends one third of both its total and feeding time on the ground (Kavanagh 1980), venturing into open grassland to move among forest fragments or to forage on a daily basis ( Kavanagh 1980; Agmen *et al.* 2009; Chapter 2). *C. t. tantalus* is locally common within Ngel Nyaki Forest Reserve with an estimated 90 troops comprising 1200 individuals occupying the reserve (Chapter 5).

### *3.2.3 Data collection*

I collected faeces of wild *C. t. tantalus* opportunistically from October 2009 to

January 2010 and in April 2010. During this time, I collected additional faeces from the sleeping sites of three troops with home ranges along the north-eastern edge of Ngel Nyaki Forest. Sleeping sites were located by following a troop in the late afternoon until dusk and noting where the monkeys settled down for the night. The following morning, I visited the sleeping site and searched the ground and undergrowth for faeces. Faeces were identified as coming from *C. t. tantalus* based on size and shape. Faeces were relatively abundant beneath sleeping sites resulting in 110 of the 164 faeces being collected from sleeping sites. Faeces were collected and stored until they could be processed in separate zip lock plastic bags. I only collected a faeces if it appeared intact and recorded the habitat in which it was found. To allow comparison with work on the habitat use of *C. t. tantaus* (Chapter 2), I defined 'edge' as the area covered by the canopy of the single row of trees forming the forest edge, 'forest' as the remaining area of trees and 'grassland' as the surrounding grassland with the occasional savannah tree species. I collected a total of 164 *C. t. tantalus* faeces, including 74 from the forest, 55 from the edge and 35 from the grassland. It is important to note that this reflects the opportunistic nature of the faeces collection rather than the frequency *C. t. tantalus* defecates in each habitat.

Faeces were taken to the field station, where I kept them in a cool shady location for up to three days, until they were processed to remove seeds. Seed removal was based on the methods of Kunz and Linsenmair (2008). I weighed a subset of 26 faeces prior to seed removal to establish an average mass for *C. t. tanalus* faeces. I mixed each faeces with water to form a slurry and sieved it through 2x2 mm mesh. Seeds large enough to be caught in the mesh were counted and identified where possible. I subsequently passed the slurry through a 1x1mm sieve to check for the presence of smaller seeds. These seeds tended to be present in large quantities and I recorded them on a presence/absence basis only. Two millimetres has been used as the cut off below which seeds are only recorded on a presence-absence basis by several researchers previously (e.g. Wrangham *et al.* 1994; Kaplin and Moermond 1998; Poulsen *et al.* 2001), allowing comparison with these studies. I took photographs of the seed species found to aid with identification (Appendix 1). I identified seeds to species level where possible, so that out of 28 seed species collected, 8 were identified to species level and 7 to genus level. Thirteen seed species remained unidentified.

Seed size was not measured while in the field, so to assess whether variations in the number of seeds >2mm dispersed among habitats could be attributable to differences in seed size, I obtained approximate seed sizes for each of the seed species I found from my identification photographs. Three of the identified seed species I found lacked photographs, so I obtained seed size values for these species from Agmen *et al.* (2009) and P. Dutton (pers. comm.). As this yielded less accurate size values than would have been obtained from their measurement in the field, seeds were placed into size categories for analysis. The categories I used were i) small 2-5mm, ii) medium 5-25mm and iii) large >25mm, as used by Chapman *et al.* (2010) to allow comparison among studies at Ngel Nyaki Forest Reserve. However, I collected no seeds larger than 25mm, so the large category was excluded from the analysis.

### *3.2.4 Statistical analyses*

I only used intact seeds in analyses and conducted data analyses using the statistical software program, R v2.14.1 (R Core Development Team 2011).

I used Poisson generalised linear mixed models (GLMMs) to test the effect of habitat on the number of seed species found per faeces and the number of seeds >2mm per faeces. When the effect of habitat was being tested, month was included as a random factor to control for variation among months. Likewise, when month was being tested, habitat was included as a random factor to control for variation among habitats. Habitat and month were not both included as main factors in the same model because I was unable to obtain faecal samples for all habitats in most months. Data was entered with each faeces constituting one observation, allowing the model to account for differences in sample sizes among habitats and months. I dealt with overdispersion of data for seeds >2 mm by including an additional random factor at the observational level to create a Poisson-lognormal GLMM as done by Elston *et al.* (2001). The significance of a factor was determined with a log-likelihood ratio test (using the anova function in R) to compare the same model with the factor of interest included and excluded.

I also analysed the number of seeds per faeces at the species level for seed species >2 mm that were found in at least 5% of faecal samples to test for differences among habitats, using Poisson GLMMs. The effect of month was controlled for in all models by its inclusion as a random factor. Species with overdispersed data were analysed using Poisson-lognormal GLMMs as above. I also analysed the proportion of faeces containing seeds at the species level, as above, using Binomial GLMMs. This allowed the comparison between species with seeds >2 mm and those with <2 mm for which count data was not available.

Finally, I used a Poisson-lognormal GLMM to test if habitat had an effect upon the size of seeds found within faeces collected from that habitat. The number of seeds in each habitat/seed size category combination was included as the response variable, with habitat and seed size as factors. Faeces was included as a random factor to control for individual faeces containing both small and large seeds.

### 3.3 Results

The mean weight of the measured *C. t. tantalus* faeces was 15.5 +/- 4.5g. Of 164 *C. t. tantalus* faeces collected 157 (95.7%) faeces contained intact seeds, and of those 87.9% (138) contained at least one intact seed larger than 2mm. Twenty (12.20%) faeces contained damaged seeds. Faeces containing damaged seeds had a mean of 3.0 +/- 3.37 seed fragments and a maximum of 14 seed fragments. I identified fragments as coming from *Aframomum angustifolium* and *Croton macrostachyus* based on colouration and excluded them from further analyses.

I found a total of 28 species of seed collected from *C. t. tantalus* faeces (Table 3.1), with a mean of 2.85 +/- 1.45 species per faeces (range: 0-8). There was no difference in the number of seed species per faeces among habitats ($\chi^2$=3.69, df=2, P= 0.1578), however, the number of seed species found per faeces did differ among months

**Table 3.1:** Seed species found in *C. t. tantalus* faeces, with species information where available. N/A = Data not available.

| Species[a] | Family[e] | Number of faeces (%) | Total seeds collected | Average seeds/ faeces | Seed size (mm) | Habitat[e] | Life Form[e] |
|---|---|---|---|---|---|---|---|
| *Ficus* spp. | Moraceae | 118 (85.51) | N/A | N/A | 1 | F, E | Tree |
| *Aframomum angustifolium* (Hook.f) K. Schum. | Zingiberaceae | 60 (36.59) | 2244 | 37.4 | 4.5 | E, F | Herb |
| *Croton macrostachyus* Hochst. ex Del. | Euphorbiaceae | 36 (21.95) | 185 | 5.14 | 7 | E, SF | Tree |
| *Leea guineensis* G. Don | Leeaceae | 36 (21.95) | 196 | 5.44 | 4.5 | E, G | Shrub |
| U2 | | 33 (20.12) | 1755 | 53.18 | 4 | | Liana |
| *Maesa lanceolata* Forssk. | Myrsinaceae | 29 (21.01) | N/A | N/A | 1 | E | Tree |
| U24 | | 28 (20.29) | N/A | N/A | 1 | | |
| U1 | | 23 (14.02) | 77 | 3.35 | 3 | | |
| *Psychotria* sp. | Rubiaceae | 20 (12.20) | 27 | 1.35 | 5.5 | | |
| U9 | | 19 (11.59) | 35 | 1.84 | 2.5 | | |
| *Grewia* sp. | Tiliaceae | 10 (6.10) | 47 | 4.7 | 9 | E | Shrub |
| *Rytigynia umbellulata* (Hiern) Robyns | Rubiaceae | 9 (5.49) | 23 | 2.56 | 6 | E | Tree |
| *Harungana madagascariensis* Lam. ex Poir. | Guttiferae | 9 (5.49) | N/A | N/A | 2 | E, SF | Tree |
| U6[b] | | 8 (4.88) | 15 | 1.88 | 10 | | Liana |
| U14 | | 5 (3.05) | 8 | 1.6 | 10 | | |
| U10 | | 3 (1.83) | 6 | 2 | 2.5 | | |
| U12 | | 3 (1.83) | 8 | 2.67 | 2.5 | | |

**Table 3.1** *Continued*

| Species[a] | Family[e] | Number of faeces (%) | Total seeds collected | Average seeds/ faeces | Seed size (mm) | Habitat[e] | Life Form[e] |
|---|---|---|---|---|---|---|---|
| *Landolphia* sp. | Apocynaceae | 3 (1.83) | 9 | 3 | 12[c] | F, E | Liana |
| *Syzygium guineense* (Willd.) DC. | Myrtaceae | 3 (1.83) | 4 | 1.33 | 12[d] | F, S | Tree |
| U5 | | 2 (1.83) | 2 | 1 | 4 | | |
| U16 | | 2 (1.83) | 2 | 1 | 3 | | |
| U21 | | 2 (1.22) | 38 | 19 | 3 | | |
| U7 | | 1 (0.61) | 1 | 1 | 7 | | |
| *Vitex* sp. | Verbenaceae | 1 (0.61) | 1 | 1 | 20 | F, E, S | Tree |
| U18 | | 1 (0.61) | 3 | 3 | 4 | | |
| *Pouteria* sp. | Sapotaceae | 1 (0.61) | 1 | 1 | 19 | F | Tree |
| *Synsepalum* sp. | Sapotaceae | 1 (0.61) | 1 | 1 | 15.5 | | Tree |
| *Bridelia speciosa* Müll. Arg. | Euphorbiaceae | 1 (0.61) | 1 | 1 | 8[c] | E | Tree |

[a] Species authorities from Chapman and Chapman (2001)

[b] Species U6 is the same as Agmen *et al.* (2009) Vine 2.

[c] Seed size taken from Agmen *et al.* (2009) and rounded to nearest 0.5 mm to be of a similar level of accuracy as the sizes estimated from photographs.

[d] As for [c] but seed size obtained from Paul Dutton, pers. comm.

[e] Obtained from Chapman and Chapman (2001). Habitats are as follows: E=edge, SF =secondary forest, G=light gaps, F=forest and S=savannah/grassland.

($\chi^2$=24.40, df=4, P=6.63x10$^{-5}$). Both April and October had significantly fewer species found per faeces than the other months (Fig. 3.1). The number of species found per faeces increased from November through January.

A total of 4748 seeds >2 mm were collected from the 164 tantalus faeces. Numerically *Aframomum angustifolium* was the most abundant seed found, making up almost half (2244) of the seeds collected. The second most abundant seed found was U2 for which a total of 1755 seeds were found. The remaining 22 species with seeds >2 mm were much less abundant ranging from 1 to 196 seeds found (Table 3.1). The number of seeds >2 mm found per faeces ranged from 0 to 551, with a median of 5 (q1=2, q3=22.25, mean+/-SD=28.59+/-65.2).

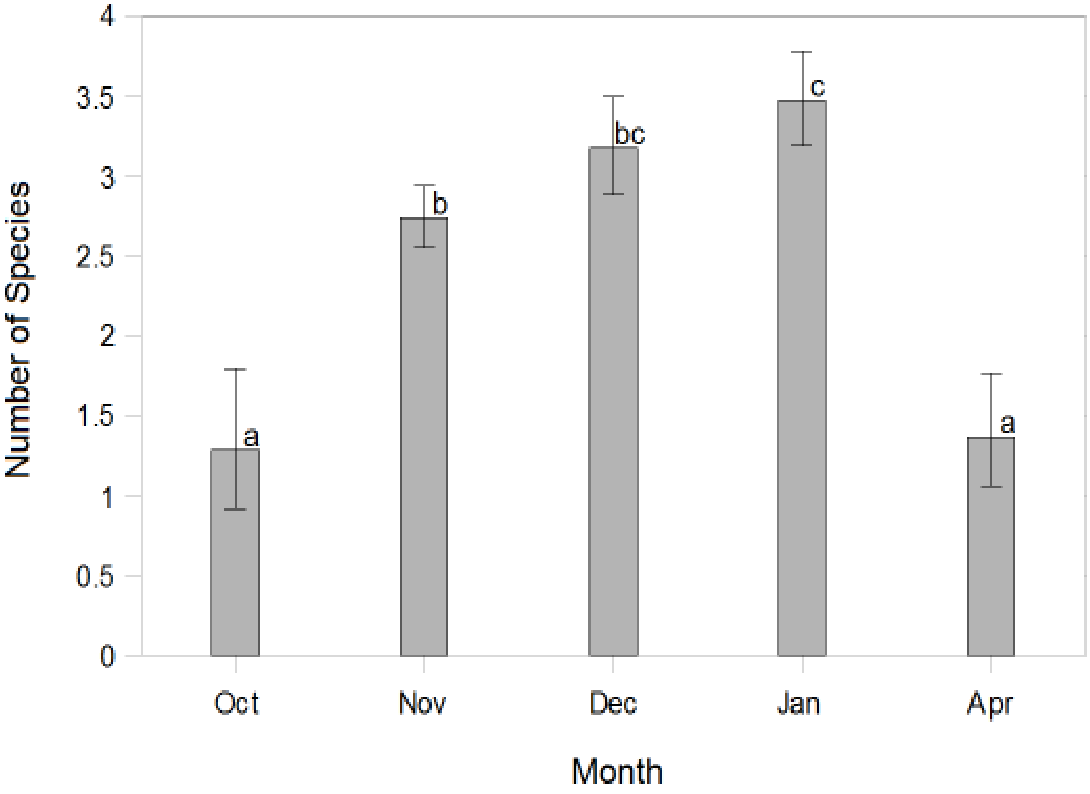

**Fig. 3.1:** Mean +/- SE number of species found per faeces in each month for which faeces were collected. Letters denote significant differences among months.

The number of seeds >2 mm per faeces differed among habitats ($\chi^2$=13.51, df=2, P=0.0012). The model gave estimates of 3.42 +/- 0.97 and 4.67 +/- 1.48 seeds >2 mm per faeces for the forest and edge respectively, however these estimates were not significantly different (z=0.840, P=0.4010). These estimates were however, signifcantly less than the estimate of 16.4 +/- 6.13 for the grassland (Forest: z=3.69, P=0.0002; Edge: z=3.06, P=0.0022; Fig. 3.2). The number of seeds per faeces did not differ among those months for which data were obtained in this study ($\chi^2$=7.93, df=4, P=0.0941).

Of the individual seed species analysed, six species had significantly different numbers of seeds per faeces among habitats (Table 3.2). The proportion of faeces containing a given seed species also differed significantly among habitats for six of the seed species assessed (Table 3.2).  Four of these species were the same as numbers, but two additional species were significantly different in the proportion of faeces containing seeds.

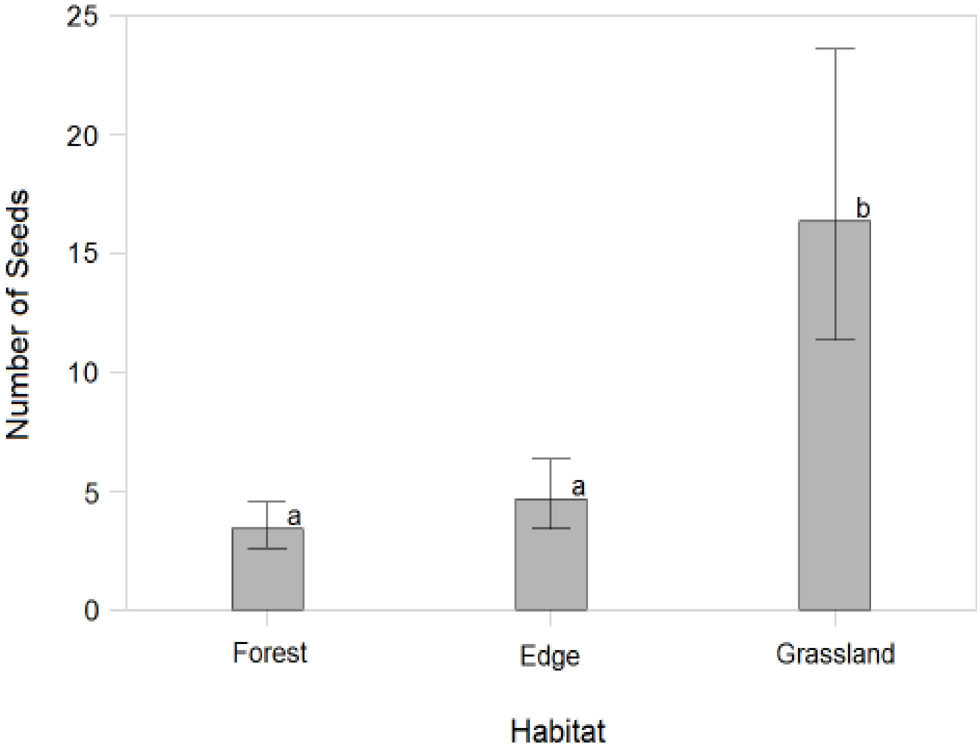

**Fig. 3.2.** Mean +/- SE number of seeds >2 mm found per faeces in each habitat. Letters denote significant difference among habitats.

Fewer faeces containing *Aframomum angustifolium* seeds were found in the forest than either the edge or grassland (Fig. 3.3a). Faeces in the forest also contained less *A. angustifolium* seeds than those in the edge and grassland (Fig. 3.4a).  Fewer faeces in the forest also contained U24 seeds than those in the edge and grassland (Fig. 3.3f), however there was no significant difference in the average number of U24 seeds per faeces among habitats (Table 3.2).

**Table 3.2:** Values for the average number of seeds/faeces and the proportion of faeces containing seeds for seed species commonly collected from *C. t tantalus* faeces and P-values indicating whether these differed significantly among habitats. * denotes a significant difference among habitats when α=0.05.

| Species | Average number seeds/faeces | Number of faeces (% faeces) | Number seeds/faeces among habitats | Proportion faeces among habitats |
|---|---|---|---|---|
| *Ficus* spp. | N/A | 118 (85.51%) | N/A | P=0.6151 |
| *Aframomum angustifolium* | 37.4 | 60 (36.59%) | $P=8.10\times10^{-8}$* | P=0.0002* |
| *Croton macrostachyus* | 5.14 | 36 (21.95%) | P=0.0027* | P=0.0011* |
| *Leea guineensis* | 5.44 | 36 (21.95%) | P=0.0002* | P=0.0001* |
| U2 | 53.18 | 33 (20.12%) | P=0.4525 | P=0.0254* |
| *Maesa lanceolata* | N/A | 29 (21.01%) | N/A | P=0.8837 |
| U24 | N/A | 28 (20.29%) | N/A | P=0.0066* |
| U1 | 3.35 | 23 (14.02%) | P=0.1253 | P=0.213 |
| *Psychotria* sp. | 1.35 | 20 (12.20%) | $P=2.92\times10^{-5}$* | P=0.0005* |
| U9 | 1.84 | 19 (11.59%) | P=0.1727 | P=0.0537 |
| *Grewia* sp. | 4.7 | 10 (6.10%) | P=0.0001* | P=0.1049 |
| *Rytigynia umbellulata* | 2.56 | 9 (5.49%) | P=0.0428* | P=0.2847 |
| *Haurangana madagascariensis* | N/A | 9 (5.49%) | N/A | P=0.8935 |

Significantly more faeces in the forest contained *Croton macrostachyus* and *Psychotria* sp. seeds than faeces from the edge or grassland (Fig. 3.3b, d). Additionally, faeces in the forest contained significantly more *Psychotria* sp. seeds than faeces collected from the edge or grassland (Fig. 3.4d), however, faeces from the forest only contained significantly more *C. macrostachyus* seeds than faeces collected from the edge (Fig. 3.4b).

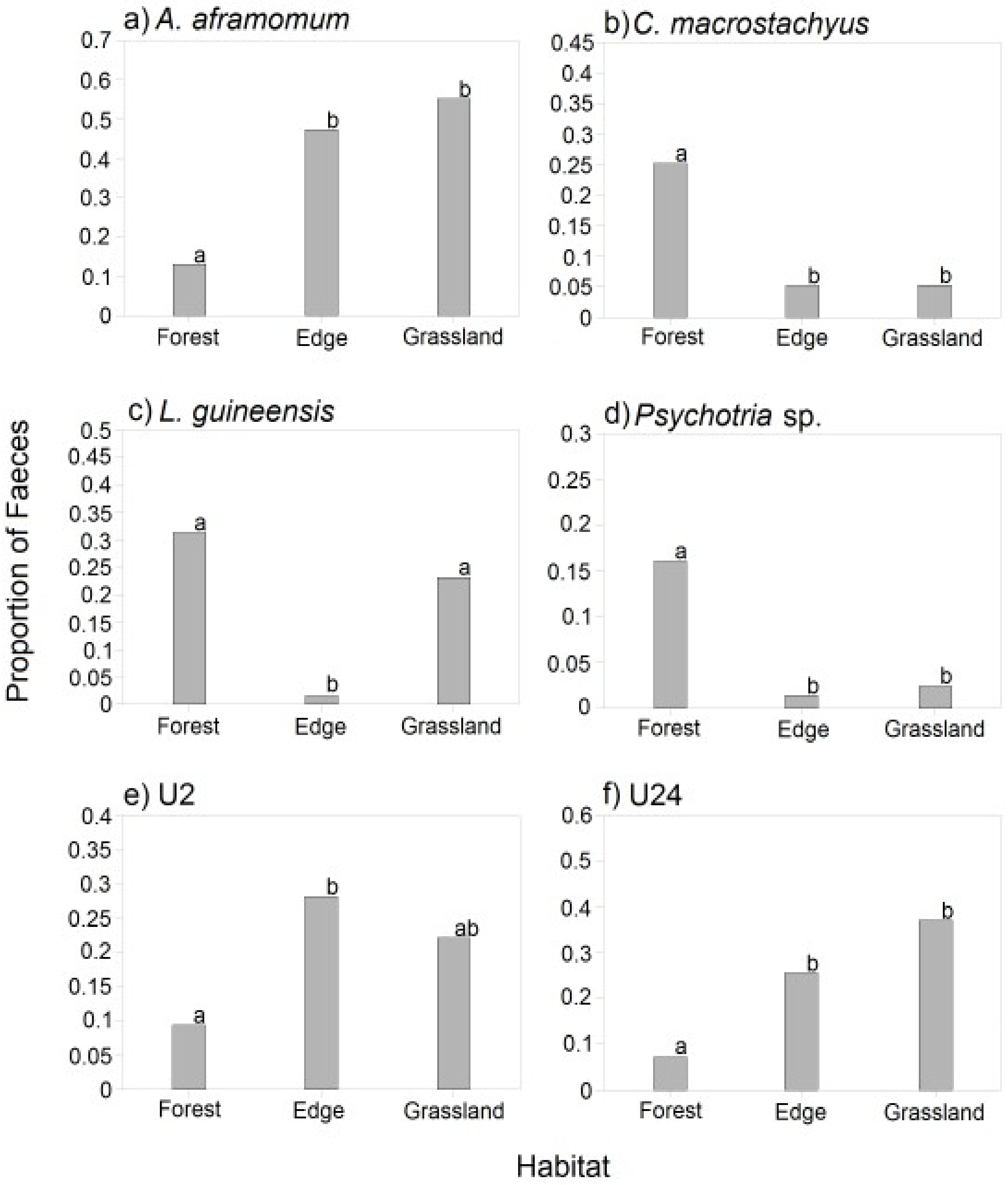

**Fig. 3.3.** Proportion of faeces from each habitat containing a) *Aframomum angustifolium*, b) *Croton macrostachyus*, c) *Leea guineensis*, d) *Psychotria* sp., e) U2 and f) U24 seeds. Letters denote significant differences among habitats.

Fewer faeces in the edge contained *Leea guineensis* seeds than the forest and grassland (Fig. 3c). Faeces in the edge on average also had fewer seeds present than faeces collected from the forest and grassland habitats (Fig. 3.4c).

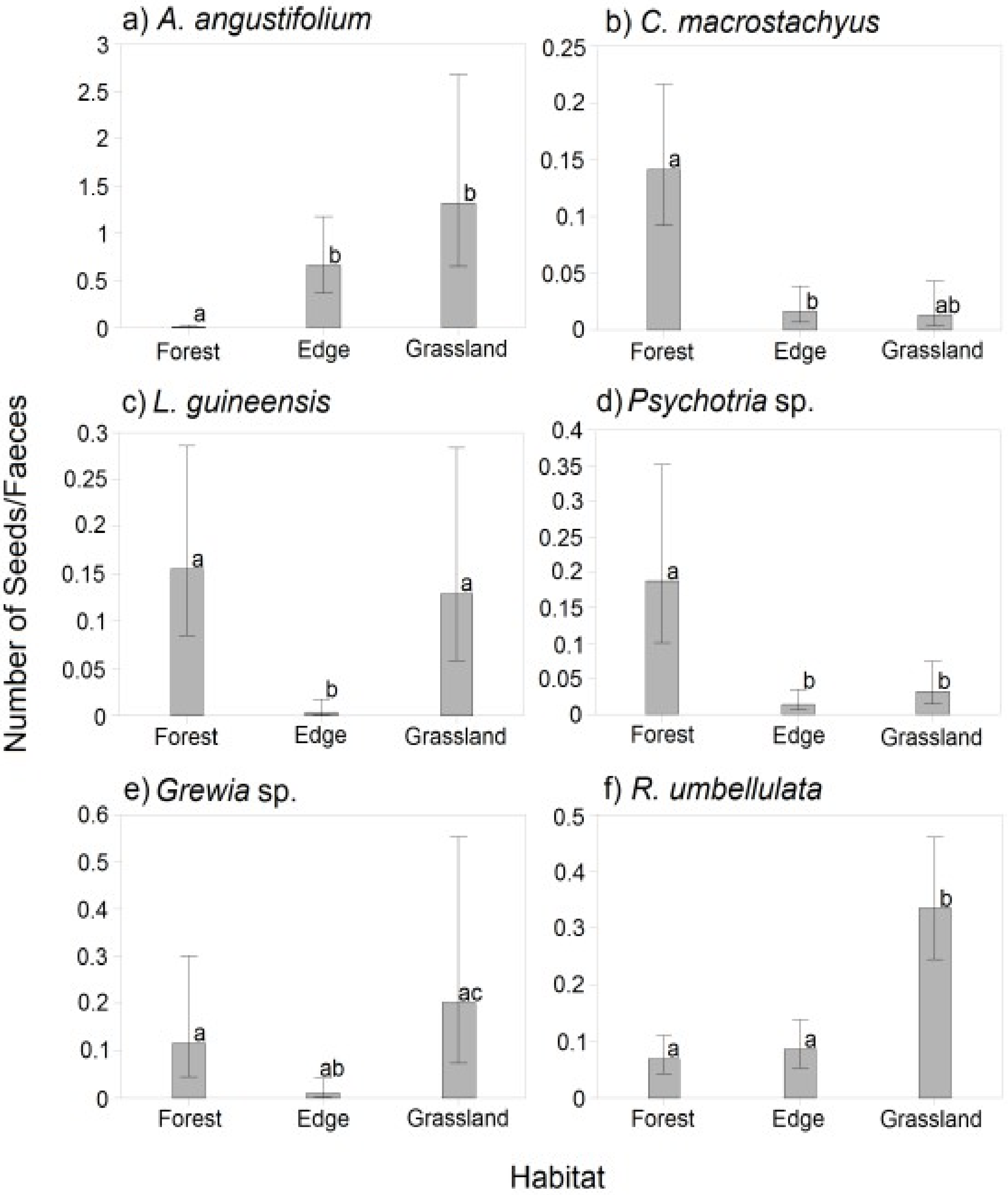

**Fig. 3.4.** The mean (+/- SE) number of seeds belonging to each of a) *Aframomum angustifolium*, b) *Croton macrostachyus*, c) *Leea guineensis*, d) *Psychotria* sp., e) *Grewia* sp. and f) *Rytigynia umbellulata* found per faeces in each habitat. Letters denote significant differences among habitats.

Fewer faeces from the forest contained U2 seeds than those in the edge, but not grassland (Fig. 3.3e). There was no significant difference in the number of U2 seeds per faeces among habitats however (Table 3.2).

There was no significant difference in the proportion of faeces containing *Grewia* sp. and *Rytigynia umbellulata* seeds among habitats, however, both species differed in the average number of seeds per faeces among habitats (Table 3.2). Fewer *Grewia* sp. seeds were found in faeces collected from the edge than grassland (Fig. 3.4e) and more *R. umbellulata* seeds were found per faeces collected from the grassland than other habitats (Fig. 3.4f).

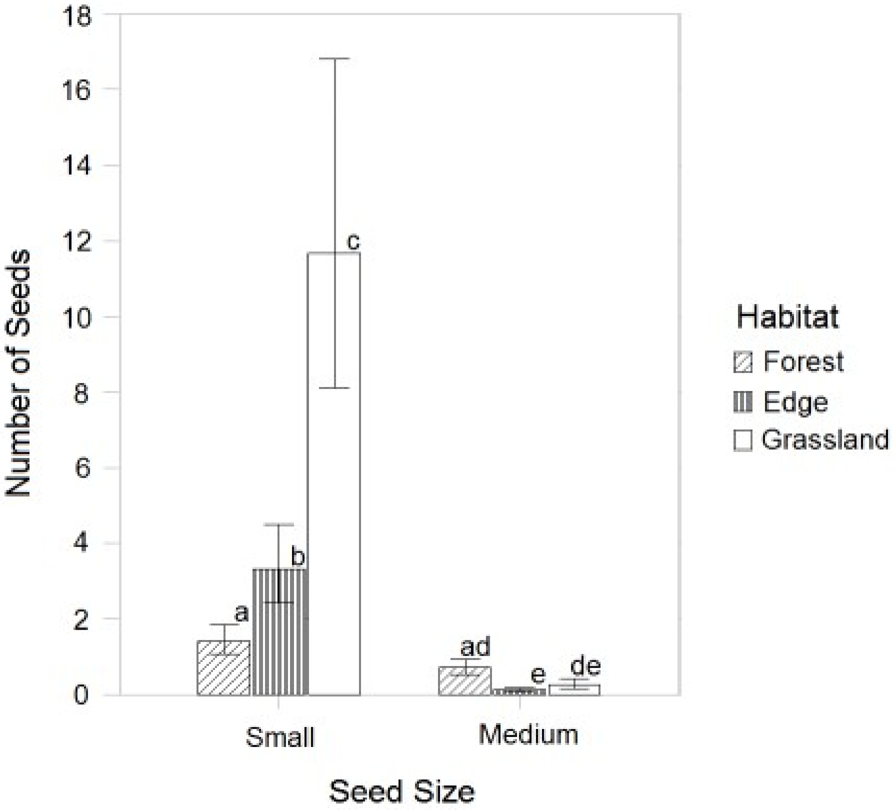

**Fig. 3.5.** Number of seeds >2 mm per faeces in each seed size category for each of forest, edge and grassland habitats. Letters denote significant differences among habitats and between seed sizes.

Only the small and medium seed size categories were used, as *C. t. tantalus* dispersed no seeds larger than 20mm. The size of seeds dispersed in *C. t. tantalus* faeces differed among habitats ($\chi^2$=25.849, df=2, P=2.44x10$^{-6}$). While small seeds were more abundant in all habitats than medium seeds, the number of small seeds dispersed increased from forest to edge to grassland, meanwhile the number of medium seeds dispersed decreased from forest to edge to grassland (Fig. 3.5).

## 3.4 Discussion

### *3.4.1 Dispersal quantity*

Almost ninety six percent of faeces contained seeds, suggesting *C. t. tantalus* disperses seeds regularly and consistently. Primates in general are widely accepted as being important seed dispersal agents and indeed much supporting research exists in the literature (e.g. Wrangham *et al.* 1994; Kaplin and Moermond 1998; Lambert 2001; Poulsen *et al.* 2001; Kunz and Linsenmair 2008). Cercopithecine monkeys have a tendency to spit large numbers of seed beneath or near the parent (Corlett and Lucas 1990; Lambert 1999) and as such have long been considered poor seed dispersers on this basis (Lambert 1999; Dominy and Duncan 2005), however recently it has been observed that seed dispersal via spitting may be more important than previously realised, at least for some species (Lambert 2001; Gross-Camp and Kaplin 2011). Although seed spitting was not assessed in this study, that seeds were regularly found in *C. t. tantalus* faeces suggests that its contribution to seed dispersal via the swallowing and defecation of seeds is also important, regardless of its role as a seed spitter.

Using the overall median of 5 seeds >2 mm per faeces, *C. t. tantalus* disperses slightly more seeds per faeces than some other Cercopithecine monkeys (Poulsen *et al.* 2001). This is a lot less than that of *Papio anubis* in Ivory Coast (Kunz and Linsenmair 2008a) and *Pan troglodytes* in Cameroon (Poulsen *et al.* 2001), however, the estimated number of seeds >2 mm per faeces of 16.4 +/- 6.1 produced by the GLMM for the grassland is somewhat more comparable to these species. Even low numbers of seeds per faeces can be important to seed dispersal, especially if that disperser is abundant. For example, I found rates of *C. t. tantalus* dispersal for seeds >2 mm in  forest and edge habitats, using 4.0 seeds >2 mm per faeces (chapter 5) are comparable to that of other disperser species considered important seed dispersers such as *Papio anubis* (Kunz and Linsemair 2008a) and *Pan troglodytes* (Wrangham *et al.* 1994). Additionally, *C. t. tantalus* disperses considerable but unquantified numbers of seeds <2 mm, such as *Ficus* spp.

The effectiveness of a disperser is not limited only to the population level of a particular plant species, but can also be assessed at the community level with prevalent dispersers dispersing the seeds of many plants in the plant community (Andresen 2002; Wehncke *et al.* 2003; Dennis and Westcott 2006). I obtained 28 seed species from faecal samples in this study, eight of which were also found by Agmen *et al.* (2009). An additional four species reported by Agmen *et al.* (2009) were not found in my faecal samples, bringing the total number of species known to be dispersed by *C. t. tantalus* at Ngel Nyaki to 32.  This is more than some primate species (e.g. *Cercopithecus mona pogonias*, *C. cephus* and *Gorilla gorilla*, Poulsen *et al.* 2001), but is less than that of others (e.g. *Papio anubis*, *Pan troglodytes* and *Lophocebus albigena*, Wrangham *et al.* 1994; Poulsen *et al.* 2001; Kunz and

Linsenmair 2008a).

### *3.4.2 Dispersal quality*

*Aframomum angustifolium* was the most dispersed seed in terms of the number of faeces it was recorded in and the overall number of seeds recorded in this study. The unidentified vine, U2, was not far behind in terms of the overall number of seeds recorded, however the mean number of seeds recorded in faeces in which it was present was higher than that of *A. angustifolium*. *C. t. tantalus* may be especially important dispersal agents for these species. However, *C. t. tantalus* dispersal may still be important for those species for which few seeds were collected such as *Vitex* sp. and *Pouteria* sp., if the subsequent survival of these seeds is disproportionately high.

Another important consideration in investigating a species role in seed dispersal is the amount of seeds it destroys relative to those dispersed intact. Only 12.20% of *C. t. tantalus* faecal samples showed any evidence of damaged seeds. Additionally, most of the damaged seeds appeared to come from *Aframomum angustifolium*, a species for which *C. t. tantalus* also disperses thousands of intact seeds during the same period, suggesting that the small amount of seeds lost to seed predation is unlikely to significantly affect *A. angustifolium* plant populations. However, a lack of seed fragments in faeces is not in itself evidence that *C. t. tantalus* does not act as a seed predator for some species. Seeds consumed intentionally as a food source as opposed to those consumed incidentally with the consumption of fruit pulp, are likely to be broken up and digested, becoming undetectable in faeces.

### *3.4.3 Seed dispersal among habitats*

*C. t. tantalus* is primarily a disperser of edge and pioneer species, rather than mature forest species, however many mature forest species would probably be unable to germinate and establish in grassland (Foster and Janson 1985). As such, seed dispersal by *C. t. tantalus* may still be beneficial for forest restoration efforts, by potentially allowing the formation of secondary forest, which dispersers that never or rarely enter grassland may be able to utilise, and subsequently disperse mature forest species into these areas (Vulinec *et al.* 2006).

Even among edge and pioneer species however, differences in habitat suitability for different seed species exist (Table 3.1). Of the seed species commonly dispersed by *C. t. tantalus,* at least a few seeds are deposited in each habitat, however, none are preferentially dispersed into those recorded as the habitats of those species in Chapman and Chapman (2001). Seeds of *L. guineensis*, *Grewia* sp. and *R. umbellulata* are preferentially dispersed into habitats other than the habitat in which the plant species is reportedly found. For the other species, I found seeds were dispersed equally between two or three of the habitats assessed, including at least one reported by Chapman and Chapman (2001) and at least one habitat where they were not. This suggests that most *C. t. tantalus* dispersed species are deposited into habitats where they have potential to survive, although the potential for some seed wastage to occur through deposition into unsuitable habitats exists.

The long gut retention time of *C. t. tantalus* (30 hours, Wallis *et al.* 2008) is of interest in combination with the habitat use of *C. t. tantalus* and how this relates to the habitat in which defecated seeds are found. *C. t. tantalus* primarily feeds in edge and forest habitats with only 8% of feeding occurring in grassland (Agmen *et al.* 2009), yet the most seeds were found in faeces from the grassland. Moreover, much feeding in the grassland is on non-fruit items such as invertebrates (Agmen *et al.* 2009). This indicates an offset between the feeding site and defecation site, and provides evidence that seeds are being dispersed away from parents, in addition to seeds being dispersed into degraded habitat and therefore, having the potential to be important in the formation of secondary forest. Despite forest faeces containing a relatively low number of seeds, *C. t. tantalus* may additionally be an important contributor to forest seed dispersal, simply through the relative abundance of faeces beneath sleeping sites. *C. t. tantalus* therefore may play an important role in the seedling structure and community composition at such sites. Moreover, as *C. t. tantalus* regularly utilises a range of sleeping sites throughout its home range (Nakagawa 1999), such seed dispersal may be spread, albeit in clusters, throughout the forest.

Additionally, while more seeds were collected from grassland faeces, compared to faeces from the forest, a greater proportion of these seeds were small. Moreover, smaller seeded species are typically earlier successional species, while later successional and mature forest species tend to have larger seeds (Foster and Janson 1985). These differences in seed sizes found among habitats could also help to explain why faeces containing a greater number of seeds were found in the grassland than in the forest. Undigested seeds in the gut may pose a cost by adding considerable weight to the animal and limiting space available for nutritious digesta in the gut (Lambert 1999, Corlett and Lucas 1990). Therefore, there is likely a limit on the volume of seeds an individual monkey can have present in their gut at a given time. A larger number of small seeds can be ingested before this volume is reached than large seeds. Moreover, seed size may influence the gut retention time of frugivores, often with larger seeds being defecated first (Traveset 1998; Levey and Grajal 1991), however instances of faster gut passage rates for small seeds in primates have also been reported (Tsuji *et al.* 2010; Julliot 1996). So in combination with activity budget and habitat use patterns of *C. t. tantalus*, seed size may indirectly influence the habitat that different seeds are deposited into.

The regular and consistent dispersal of seeds belonging to a range of species by *C. t. tantalus*, suggests they are important dispersers of small and medium size seeds and contribute to the maintenance of forest structure at Ngel Nyaki. Moreover, *C. t. tantalus* disperses seed from forest and forest edge habitats into grassland habitat, including some species which have the potential to successfully germinate and establish, providing real potential for the species to contribute to forest conservation by aiding forest regeneration.

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# Chapter 4:

# Habitat suitability of seeds dispersed by *Chlorocebus tantalus tantalus* at Ngel Nyaki Forest Reserve, Nigeria: implications for conservation management.

## 4.1 Introduction

Plant recruitment results from the number and spatial distribution of new individuals that are incorporated into the population (Wakibara 2005). While seed dispersal is a vital component of the plant recruitment process, it does not guarantee recruitment (Nathan and Muller-Landau 2000). The ability of a seed to germinate, establish and survive to reproduction in the location to which it was dispersed is also crucial, as without success in these later stages, seed dispersal is irrelevant (Kaplin and Moermond 1998).

Once dispersed, seeds become subject to a range of abiotic and biotic factors differentially effecting seed and seedling fates among habitats (Augspurger 1983; Schupp and Frost 1989; Lamont *et al.* 1993; Chambers and MacMahon 1994; Jarvis and Moore 2008). Abiotic factors such as amount of litter, light intensity, water and nutrient availability differ among habitats and play an important role in recruitment patterns (Ibañez and Schupp 2001, 2002; Jarvis & Moore 2008). Seed dispersal patterns are not necessarily concordant with sites physically suitable for germination and subsequent seedling growth (Herrera *et al.* 1994; Schupp *et al*. 2002). Additionally, biotic factors including pathogen attack, secondary dispersal and seed and seedling predation differ among habitats further determining that habitat's suitability for germination and growth (Janzen 1982; Augspurger 1983; Schupp and Frost 1989; Andresen 1999, 2001). Primary seed dispersers are therefore only a single component in a complex web of interaction with pathogens, secondary dispersers and seed predators and their influences on seed fate (Estrada and Coates-Estrada 1991; Chambers and MacMahon 1994; Andresen 1999; Nathan and Muller-Landau 2000).

As the spatial distributions and dynamics of plant populations reflect the interactions between seed distributions and subsequent seed and seedling survival (Becker *et al.* 1985; Wright and Howe 1987; Estrada and Coates-Estrada 1991; Nathan and Muller-Landau 2000; Paine and Beck 2007), the net impact of primary dispersers on plant recruitment and fitness cannot be assessed without consideration of post-dispersal seed fate (Estrada and Coates-Estrada 1991; Levey and Byrne 1993; Chambers and MacMahon 1994; Andresen 1999).

Understanding the interplay between primary seed dispersal and post-dispersal seed and seedling fate is important for forest regeneration, particularly in Africa where the proportion of degraded forest is increasing (Chapman and Peres 2001; Chapman *et al.* 2006; Bergl *et al.* 2007). Such forests face many threats including trampling and browsing/grazing of forest plants by cattle (Maisels *et al.* 2000; Chapman *et al.* 2004; Mpanza *et al.* 2009; Wassie *et al.* 2009). Fencing off areas of forest and surrounding edge and grassland areas is a simple method of excluding cattle from forest areas with the aim of preventing trampling and browsing in the forest and protecting the surrounding edge and grassland areas from grazing to allow the natural regeneration of forest species in these areas (Mpanza *et al.* 2009; Wassie *et al.* 2009).

*Chlorocebus tantalus* (Ogilby 1841 in Groves 2001) is an adaptable species, often frequenting both forested and grassland areas while foraging (Kavanagh 1980; Agmen *et al.* 2009; Chapter 2) and is widespread throughout Central Africa (Kingdon and Gippoliti 2008). In addition, recent evidence has found *C. tantalus* to disperse viable seeds to both forest and grassland habitats (Agmen *et al.* 2009; Chapter 3), suggesting that it may be an important species in aiding forest maintenance and regeneration efforts. However the dispersal of seed into such habitats is of no consequence unless it is followed by post-dispersal survival. Here I investigated the germination success of seeds dispersed by the subspecies *C. tantalus tantalus* in four forest and grassland habitats in order to i) determine whether *C. t. tantalus* disperses seeds to habitats suitable for their germination and establishment, ii) to understand the potential role of *C. t. tantalus* in forest regeneration and the maintenance of forest structure, iii) to assess forest regeneration in fenced off areas of forest and surrounding grassland in terms of seed species dispersed by *C. t. tantalus* and iv) to determine whether current conservation actions will allow *C. t. tantalus* to reach its full potential in aiding the plant recruitment process.

## 4.2 Methods

### *4.2.1 Study Site*

Ngel Nyaki Forest Reserve lies on the western escarpment of the Mambilla Plateau, Taraba State, Nigeria (Chapman *et al.* 2004). Within the 46 km$^2$ reserve, the floristically diverse 5.3 km$^2$ Ngel Nyaki Forest ranges between 1400-1600 m elevation with mean monthly temperatures not exceeding 30ºC (Nigerian Montane Forest Project (NMFP) Weather Data). The forest is of a dry type (Akinsoji 1994) with a mean annual rainfall of approximately 1800 mm, most of which falls in a single wet season lasting from mid April to mid October (NMFP Weather Data).

Ngel Nyaki Forest Reserve is of high conservation value, belonging to a biodiversity hotspot within the Cameroon Highlands ecoregion (Olson *et al.* 2001). It contains many endemic plant species, including several on the IUCN red list (Chapman *et al.* 2004). Due to its many restricted range species Ngel Nyaki is listed as a Birdlife International IBA (Important Bird Area) (Fishpool and Evans 2001). Other primates aside from *C. t. tantalus* inhabiting the reserve include *Cercopithecus nicititans* cf. subspecies *martini*, *Cercopithecus. mona*, *Colobus guereza occidentalis*, *Papio anubis* and the rare *Pan troglodytes eliottii* are also present (Chapman *et al.* 2004).

My study area comprised both grazed and non-grazed grassland. It was located towards the northern edge of Ngel Nayki Forest where an area of forest and adjoining grassland has been protected from cattle grazing and fire since 2006.

Protection from grazing is maintained by a fence and fire is controlled through the controlled burning of fire breaks, preventing later grassland burns from spreading beyond them. Additionally, the study site fell within the home range of a previously studied *C. t. tantalus* troop (Troop A; Chapter 2) and *C. t. tantalus* has been observed entering all four habitats (forest, edge, grazed grassland and non-grazed grassland) used in this study.

### *4.2.2. Study species*

I used five seed species (Table 4.1) in this study. I chose these species on the basis that they were commonly found in *C. t. tantalus* faeces and had seeds larger than 2 mm, allowing the seeds to be easily obtained from faeces.

**Table 4.1:** Seed species used in germination experiment.

| Species[a] | Family[b] | Seed Size (mm)[c] | Life Form[b] | Habitat[b] |
|---|---|---|---|---|
| *Aframomum angustifolium* (Hook.f) K. Schum. | Zingiberaceae | 4.7x2.5 | Herb | Forest/Forest edge |
| *Leea guineensis* G. Don | Leeaceae | 4.7x3.6 | Shrub | Forest edge, Grassland |
| *Rytigynia umbellulata* (Hiern) Robyns | Rubiaceae | 5.1x2.2 | Tree | Forest edge |
| *Croton macrostachyus* Hochst. ex Del. | Euphorbiaceae | 9x5 | Tree | Forest edge, Secondary forest |
| U2 (unidentified sp.) | | 4 | Liana | |

[a] Species authorities taken from Chapman and Chapman (2001)

[b] Taken from Chapman and Chapman (2001)

[c] Seed size for *C. macrostachyus* is taken from Teketay and Granström (1997) and U2 from Chapter 3, pg. 68. All other seed sizes are taken from Agmen *et al.* (2009).

### *4.2.3 Experimental set up and data collection*

My study site was divided into four habitats – grazed grassland, non-grazed grassland, edge and forest. To allow comparison of results from this study with previous work on the habitat use of *C. t. tantaus* (Chapter 2), I defined ‘edge’ as the area covered by the canopy of the single row of trees forming the forest edge, ‘forest’ as the remaining area of trees and ‘grassland’ as the surrounding grassland with the occasional savannah tree species. I further divided grassland into two habitats for this study – ‘grazed grassland’ that was heavily grazed by cattle and ‘non-grazed grassland’ where, in the absence of cattle the grass was up to 2 m tall. Both grassland habitats were protected from fire by the use of fire breaks during this study.

I set up twelve plots in each of the four habitats (Fig. 4.1). Half of the plots in each habitat were caged to exclude seed removal by secondary dispersers and seed predators, allowing me to assess habitat suitability for germination in the absence of seed removal. Cages were 40x40x40 cm and were constructed from 1x1 mm wire mosquito mesh, preventing access by all potential seed removers except possibly the smallest species of ants. I buried the sides of the cages 5 cm into the ground to prevent seed removers from pushing underneath the mesh, as done by Beckman and Muller-Landau (2007) and Wenny (2000). I left the remaining plots uncaged allowing access to seed removers and the assessment of natural levels of seed survival, germination and seedling establishment in each habitat.

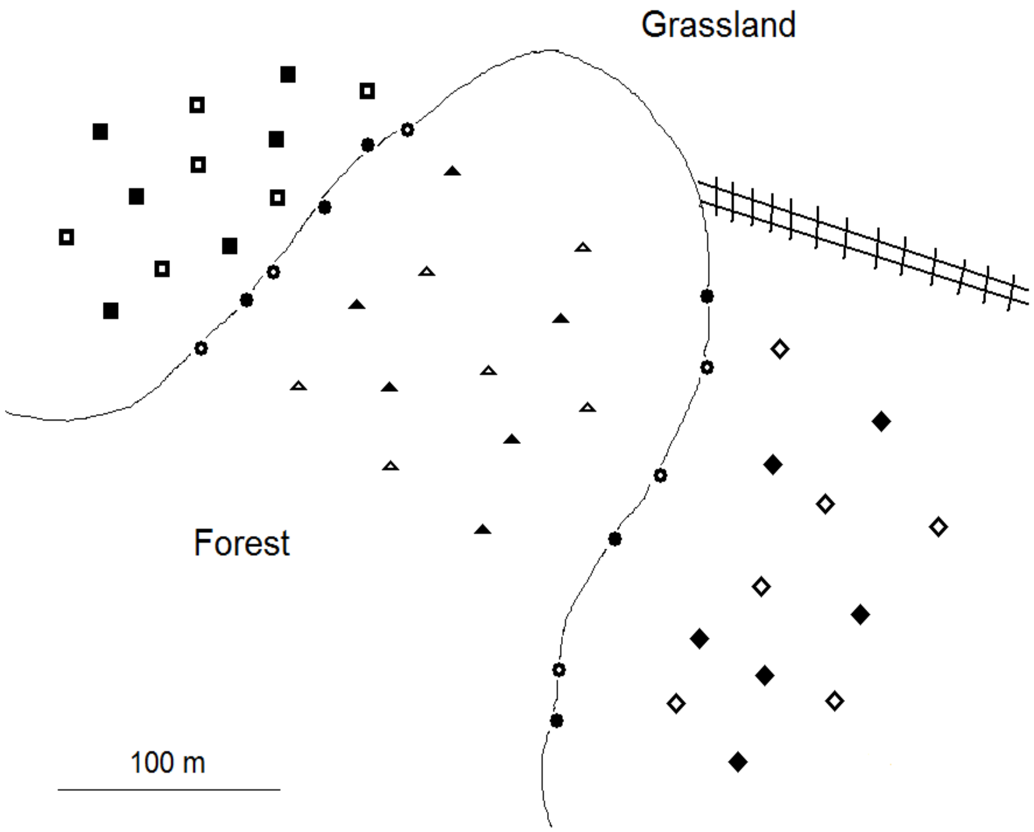

**Fig 4.1:** The layout of the germination experiment at Ngel Nyaki. Squares, circles, triangles and diamonds represent the approximate locations of plots in grazed grassland, edge, forest and non-grazed grassland respectively. Open symbols represent uncaged plots, while closed symbols represent caged plots.

The seeds I used in this experiment were collected from opportunistically located *C. t. tantalus* faeces throughout November and early December 2009. Faeces were identified as belonging to *C. t. tantalus* based on size and shape. I removed seeds from the faeces by mixing each faeces with water and sieving the resultant slurry through a 2x2 mm mesh sieve. I collected additional seeds of *Leea guineensis*, *Croton macrostachyus* and *Rytigynia umbellulata* from ripe fruits and hand cleaned them, as numbers collected from faeces were insufficient. Therefore, approximately only 5% of the seeds used for these species came from *C. t. tantalus* faeces, while 100% of *Aframomum angustifolium* and U2 seeds came from *C. t. tantalus* faeces.

Hand cleaned seeds may have differential germination success compared with those which have passed through the gut of *C. t. tantalus* (Agmen *et al.* 2009). Therefore, where applicable, I mixed the seeds for a given species from both collection methods prior to dividing them among the plots, allowing each plot to receive a random mix of hand cleaned and defecated seeds and ensuring any differences in germination among plots were not due to differences in the seed collection method. Insufficient faecal material was available to add each plot's seeds into a complete faeces. Instead I simply rubbed all seeds with fresh *C. t. tantalus* faeces to provide seeds with the same olfactory cues of those defecated by the *C. t. tantalus* so that they would be as attractive to seed removers as seeds deposited in dung. I gave each of the twelve plots in each habitat a total of 147 seeds (58 *L. guineensis*, 36 *C. macrostachyus*, 21 *R. umbellulata*, 19 *A. angustifolium* and 13 U2) in mid December 2009, giving a total of 1764 seeds in each habitat. I checked plots fortnightly until May when germination was first observed and monthly thereafter until September 2010 for evidence of germination and recorded the number of seedlings of each species. I intended to count the remaining seeds in each plot, but locating seeds among existing vegetation in some plots, e.g. in non-grazed grassland, proved difficult and few seeds remained in other plots two weeks after the experiment began. As such, I was unable to quantify rates of seed removal.

### *4.2.4 Statistical Analyses*

I used Poisson generalised linear models (GLMs) to test for differences in the number of seeds that germinated per plot among habitats and between cage versus uncaged treatment. Where data were overdispersed, I used quasipoisson GLMs instead. I also calculated mortality rates of germinated seedlings but these were not analysed further due to the short duration of my study. I conducted all analyses using the software, R 2.7.1 (R Core Development Team 2008).

## 4.3 Results

I first recorded germination on 9 May 2010; 144 days after seeds were placed in plots and, 70 days after the first rainfall of the rainy season. Eighty six percent of germinating seedlings were recorded at this time, with additional germinating seedlings recorded through to 3 October 2010, when my study ended.

I observed few remaining seeds two weeks after the start of the experiment and recorded no evidence of germination for any species in the uncaged plots throughout the duration of my study. Uncaged plots were therefore omitted from the following analyses. Overall germination rates in caged plots were relatively low (Table 4.2), ranging from 0% for *Croton macrostachyus* and the unidentified species through to 22.02% for *Rytigynia umbelluata*. Therefore, I only considered *L. guineensis*, *Aframomum angustifolium* and *R. umbellulata* germination in caged plots in the following analyses.

A mean of 14.0 +/- 2.56 seeds germinated per caged plot. The total number of seeds that germinated per plot differed among habitats ($F_{(3,20)}$=10.15, P=0.0003, Fig. 4.2a). Similar numbers of seeds germinated in the edge and forest habitats. The number of

**Table 4.2:** Germination rates among habitats for each species.

| | Number of seeds germinated in each habitat (Percentage of germinating seeds in that habitat out of all seeds of that species available). | | | | |
|---|---|---|---|---|---|
| Species | Forest | Edge | Non-grazed Grassland | Grazed Grassland | Total |
| *Leea guineensis* | 33 (9.48%) | 26 (7.47%) | 2 (0.57%) | 119 (34.20%) | 180 (12.93%) |
| *Aframomum angustifolium* | 8 (7.02%) | 9 (7.89%) | 0 (0%) | 29 (25.44%) | 47 (10.31%) |
| *Rytigynia umbellulata* | 56 (44.44%) | 39 (30.95%) | 2 (1.59%) | 14 (11.11%) | 111 (22.02%) |
| *Croton macrostachyus* | 0 (0%) | 0 (0%) | 0 (0%) | 0 (0%) | 0 (0%) |
| Unidentified species | 0 (0%) | 0 (0%) | 0 (0%) | 0 (0%) | 0 (0%) |
| Total | 97 (16.50%) | 74 (12.59%) | 4 (0.68%) | 162 (27.55%) | 337 (14.33%) |

seeds germinating per plot in grazed grassland was not significantly different from the forest, but was more than in the edge. Germination in non-grazed grassland plots was significantly less than all other habitats.

The number of *A. angustifolium* seeds that germinated differed among habitats (df=3, $P=5.81x10^{-8}$, Fig. 4.2b). Significantly more seeds germinated per plot in the grazed grassland than the other habitats, while significantly fewer germinated per plot in the non-grazed grassland than the other habitats.

Germination rates for *L. guineensis* were significantly higher in grazed grassland than all other habitats ($F_{(3,20)=}6.77$, P=0.0025, Fig. 4.2c).

*R. umbellulata* also had differing germination success among habitats ($F_{(3,20)}=9.84$, P=0.0003, Fig. 4.2d). Edge and forest had similar numbers of seeds germinate per

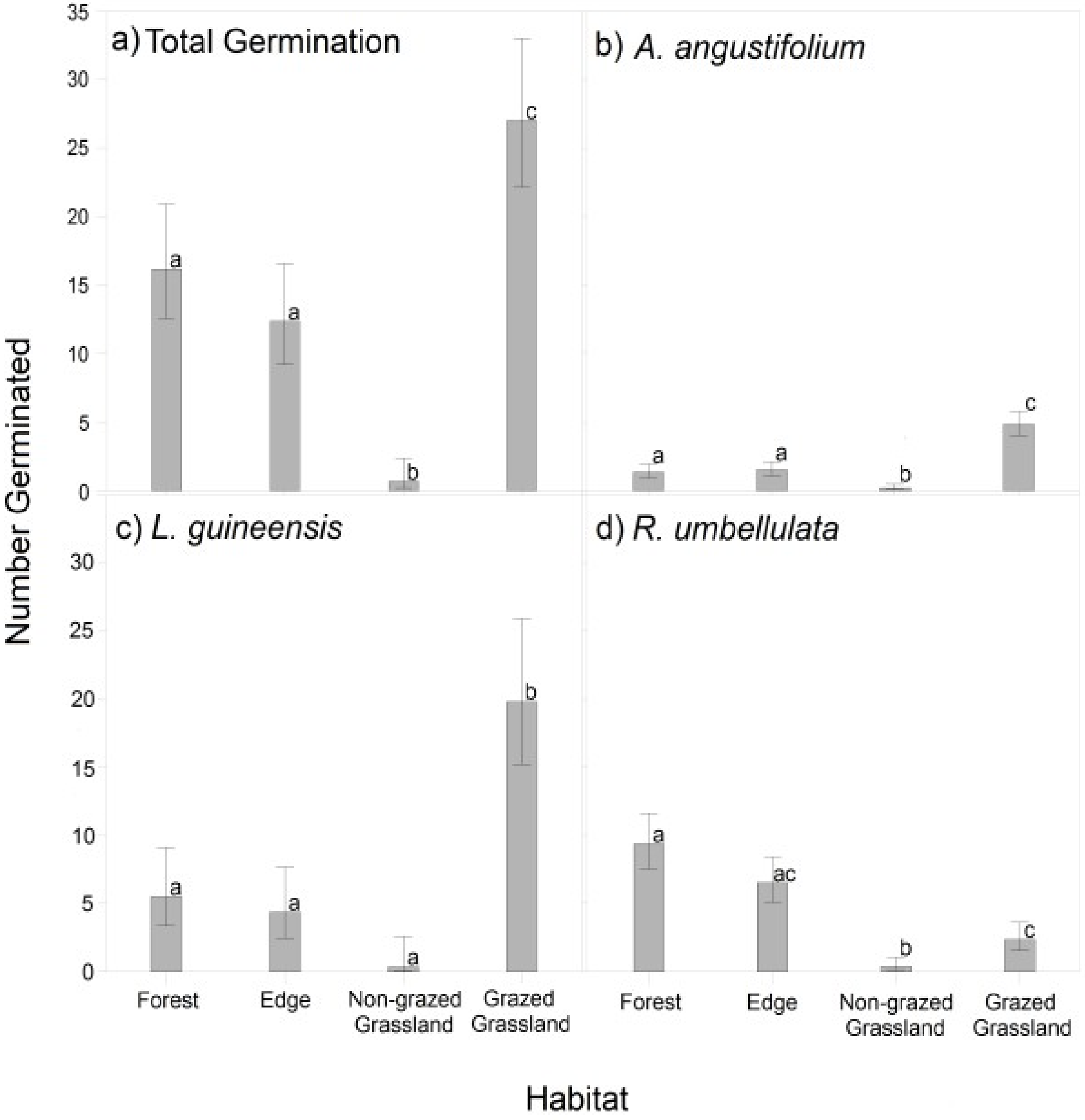

**Fig. 4.2:** Mean +/- SE number of seeds germinating per caged plot in each habitat. Letters denote significant differences among habitats.

plot and likewise with both the grassland habitats. The number of *R. umbellulata* seeds that germinated per non-grazed grassland plot was significantly less than both in the forest and edge. Grazed grassland however, had significantly fewer seeds germinate per plot than the forest, but not the edge.

Of the 306 seedlings that germinated in my study, 89.87% were still alive at the conclusion of the study (Fig. 4.3a). Of the 10.13% of seedlings that died, 87.10% were from the forest (Fig. 4.3b,c) and were the shrubs *R. umbelluata* (55.55%) and *L. guineensis* (44.44%). The remaining 12.90% of deaths were from the monocot herb *A. angustifolium* from both edge and grazed grassland habitats. No seedling mortality was recorded in non-grazed grassland.

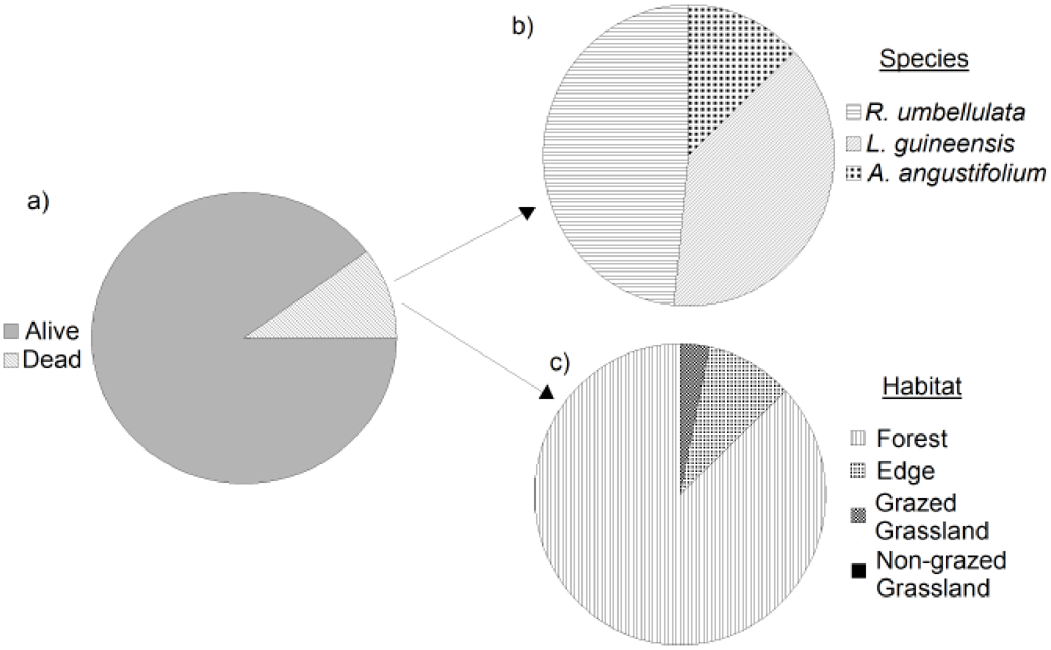

**Fig. 4.3:** a) Proportion of germinated seedlings that had died by the end of the study, b) the proportion of deaths that belonged to each species and c) proportion of deaths in each habitat.

## 4.4 Discussion

### *4.4.1 Seed removal*

My results confirmed that dispersal is only part of the regeneration cycle and that both post dispersal removal and habitat have a significant effect on seed germination (Wenny 2000; Balcomb and Chapman 2003; Wang and Smith 2002). Few seeds remained after two weeks and no germination was recorded in any of the plots where removal was allowed, suggesting removal rates were high across all habitats. High removal rates have previously been recorded at Ngel Nyaki for five seed species dispersed by *Cercopithecus nicititans* (Chapman *et al.* 2010). Known seed removers present at Ngel Nyaki are predominately rodents including *Cricetomys gambianus* and *Atherurus africanus*, however birds, ants and dung beetles have also been observed removing seeds (Chapman *et al.* 2010; Paul Dutton, Pers. Comm.)

Removal rates of up to 100% are not uncommon in the literature, however, rates vary considerably in space and/or time (Chapman 1989; Chapman and Chapman 1996; Blate *et al.* 1998). Such variation is due to many factors such as forest community, amount of faecal material and its consistency, season, habitat and seed characteristics (Chapman 1989; Andresen 1999, 2002; Vander Wall *et al.* 2005; Kunz and Krell 2011; Santos-Heredia *et al.* 2010). Changes in these factors may additionally alter the proportion of removal that is due to secondary dispersal and predation (Andresen 1999; Vander Wall *et al.* 2005).

Seed and seedling predation rates have been reported to be greater in grassland habitats (Nepstad *et al.* 1996; Chapman and Chapman 1999; Duncan and Duncan 2000), although many seeds may still survive, suggesting grassland may be a suitable habitat for germination for at least some species (Duncan and Duncan 2000). Furthermore, forest tree species may suffer disproportionate predation in secondary forest relative to mature forest (Hammond 1995; Cole 2009). In contrast, other work has revealed no differences between secondary and mature forest habitats (DeMattia *et al.* 2004) or higher seed predation rates in forest than grassland (Iob and Vieira 2008). Seed predation may occur along an edge gradient with increasing predation rates in the forest interior relative to the edge (Burkey 1993).

Often removal rates are substituted for rates of seed predation, however, removal on its own is not necessarily a negative for tree recruitment (Andresen 1999; Vander Wall *et al.* 2005; Moore and Swihart 2008). The fate of removed seeds depends upon the identity of the remover. In addition to removal by seed predators, seeds may be removed by secondary dispersers, who take them, usually from faeces, to new locations, where the seeds may be able to germinate and establish (Andresen 1999; Vander Wall *et al.* 2005). Even when the identity of the remover is known, seed fate can be difficult to establish, due to seed predation and secondary dispersal occurring on a continuum for some species of seed remover. For example, scatter hoarding rodents bury excess seeds for consumption later, but may fail to recover some seeds, allowing them to escape predation and successfully germinate and establish (Forget and Millerton 1991; Forget 1993). In addition, Duncan and Duncan (2000) found not all plots visited by rodents exhibited predation in their seed removal study.

Dung beetles are abundant (Barnes 2011) at Ngel Nyaki, and may remove a significant proportion of seeds from *C. t. tantalus* faeces. Although, secondary dispersers such as dung beetles typically only move seeds short distances, any secondarily dispersed seeds could easily have been moved outside the 0.16 $m^2$ plots, and therefore any subsequent germination not recorded. Dung beetles can move seeds up to 20 m horizontally (Kunz and Krell 2011) and 12 cm vertically (Estrada and Coates-Estrada 1991), although horizontal movement is often less than 1.5 m (Andresen 2001; Kunz and Krell 2011). A greater abundance of dung beetles is found in the forest at Ngel Nyaki than in the grassland (Barnes 2011), suggesting a greater capacity for secondary seed dispersal by dung beetles in the forest.

Removal by dung beetles may have been artificially reduced in my study by the lack of faecal material associated with the seeds (Andresen 2001; Andresen and Levey 2004), however, dung beetles may also mistake single, dung ball sized seeds for dung balls and subsequently remove them (Kunz and Krell 2011). Insufficient faecal matter may also have artificially raised predation rates by providing olfactory cues attractive to rodents and other seed predators, but without providing the opportunity for seeds to be hidden in the middle of the faecal pile and/or not providing the opportunity for seeds to escape predation through removal by secondary dispersers (Andresen 2001;  Andresen and Levey 2004).

### *4.4.2 Habitat suitability and implications for conservation management*

Caging the treatments removed any possibility of seed removal and I observed the effect of habitat on germination. The non-grazed grassland exhibited the lowest rate of germination, with only 0.68% seeds germinating. In contrast, overall germination rate was highest in the grazed grassland, where over 27% of seeds germinated. This large difference in germination success between the two grassland habitats may be the result of intense competition from the dense layer of grasses in the non-grazed grassland, which grow up to 2 m tall. Cattle grazing and annual burning keeps grasses outside the fenced off areas at less than approximately 30 cm tall and less dense (pers. obs.). Indeed, intense competition by grasses, ferns and other dense and strongly competitive vegetation have been found to severely limit regeneration processes elsewhere (Chapman and Chapman 1999; Duncan and Chapman 2003; Ortega-Pieck *et al.* 2011). This suggests that simply protecting areas of grassland from grazing and fire in Ngel Nyaki Forest Reserve may not be adequate for regeneration to occur on its own and is further emphasised by all three germinating species having their poorest germination rates in the non-grazed grassland.

There was no difference in germination success between forest and edge habitats for any of the species I assessed. This is not surprising, given that edge effects almost certainly penetrate much further into the forest than my definition of 'edge' as the single outermost row of trees (Ewers and Didham 2008). All forest plots were less than 100 m from the edge, likely not far enough to escape such edge effects.

While it was beyond the scope of my study to investigate the effect of habitat on seedling survival beyond a few months after germination, the suitability of habitats may differ between seeds and seedlings (Schupp and Frost 1989; Rey and Alcantara 2000; Lamont *et al.* 1993). As germinated seedlings were protected from herbivory by the presence of cages, seedling mortality was limited to that caused by unsuitable physical habitat conditions and/or competition among seedlings and/or other vegetation. While overall germination was greatest in the grazed grassland, unprotected seedlings in this habitat face an extremely high risk of mortality through cattle grazing and this habitat may be the poorest in terms of seedling survival over longer time scales. In contrast, the non-grazed grassland had the poorest germination success, but is protected from cattle herbivory and had no recorded mortality during my study, suggesting that the few seeds that germinate may have relatively high rates of survival. While recorded mortality was greatest in the forest, over longer time scales, this initial mortality seems likely to be less than the very high rates of mortality expected for seedlings subjected to cattle grazing in the longer term. However, even with protection from cattle grazing and intense grass competition, other habitat specific environmental conditions may prevent seedling establishment, affecting the suitability of these habitats for seedling establishment. As such, seedling survival will need to be assessed over the long term.

The relatively high rates of germination of *C. t. tantalus* dispersed seed species in grazed grassland suggests *C. t. tantalus* has the potential to be a valuable seed disperser contributing to reforestation of grassland habitats, provided suitable management actions are set in place. The fencing off of areas of forest, edge and grassland to exclude cattle grazing may not on its own be adequate to ensure natural forest regeneration in a reasonable time frame, as suggested by my relatively poor germination rates in the fenced, non-grazed grassland. Further research is clearly needed to identify management approaches that will maximise the benefits of seed dispersal services offered by *C. t. tantalus* in forest regeneration and restoration efforts. Problems that need to be overcome include how to protect seedlings in areas with cattle grazing without removing the benefits offered by cattle grazing and/or how to increase germination in areas protected from cattle grazing.

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# Chapter 5:

# Density of *Chlorocebus tantalus tantalus* at Ngel Nyaki Forest Reserve and their seed dispersal rates.

## 5.1 Introduction

Between 70-90% of tropical forest plants produce fruits adapted to vertebrate seed dispersal (Willson *et al.* 1989; Corlett 1996; da Silva and Tabarelli 2000). These plants depend upon frugivores to disperse their seeds from the parent plant to a location suitable for seed germination and seedling establishment (Howe and Westley 1988; Bascompte and Jordano 2007). As the number of seeds from a given plant that successfully germinate and survive to maturity is low relative to the total amount of seed produced by that plant (Howe *et al.* 1985; Howe and Miriti 2004), it is important for the regeneration of plant communities that dispersers move large numbers of seeds (Schupp 1993; Chapman and Onderdonk 1998). Frugivorous animals are therefore of importance in tropical plant-animal mutualisms and the maintenance of forest structure and health (Levey 1988; Lambert and Garber 1998; Poulsen *et al.* 2002; Beckman and Muller-Landau 2007).

Highly frugivorous animals have the potential to disperse large numbers of seeds (Schupp 1993; Lambert and Garber 1998). For any given plant species, an effective disperser will remove and disperse a high number of seeds to locations suitable for germination, while at a community level an effective disperser will also have a broad diet and disperse seeds of a wide range of species (Andresen 2002; Wehncke *et al.*

2003; Dennis and Westcott 2006).

Primates are an important guild of frugivores in tropical forests (Gautier-Hion *et al.* 1985; Chapman 1989; Wrangham *et al.* 1994; Julliott 1996; Lambert and Garber 1998; Stevenson 2000). Most have frugivorous diets and successfully disperse many seeds (Kunz and Linsenmair 2008; Link and Di-Fiore 2006; Kaplin and Moermond 1998; Lambert and Garber 1998; Juliott 1996; Wrangham *et al.* 1994). That they play an important role in forest structure is well documented (Chapman and Chapman 1995; Chapman and Onderdonk 1998; Marsh and Loiselle 2003; Nuñez-Iturri and Howe 2007). Moreover, primates are social mammals, usually visiting fruit sources in groups, increasing their capacity for large scale seed removal (Dennis and Westcott 2006). Nevertheless, the effectiveness of primate frugivores as seed dispersers varies among primate species, as a result of the quality and quantity of the seed dispersal provided (Schupp 1993). As such group size and group density impacts primate effectiveness as seed dispersers (Schupp 1993; Peres and Palacios 2007).

Many primate species are in decline (Chapman *et al.* 2006), threatening forest plants through the loss or reduction of effective seed dispersal (Webb and Peart 2001; Nuñez-Iturri and Howe 2007; Wright *et al.* 2007). As the effectiveness of seed dispersal may suffer even before a given frugivore becomes rare (McConkey and Drake 2006), the role of primates as seed dispersers may be under more threat than initially apparent. Therefore, obtaining the density and abundance of primate populations is a vital part of monitoring not only their conservation status and the impact of any implemented management actions (Chapman *et al.* 2000; Muoria *et al.* 2003; Plumptre and Cox 2006), but assessing the quantity of seed dispersal offered (Schupp 1993).

*Chlorocebus tantalus* (Ogilby 1841 in Groves 2001) is widely distributed throughout central Africa (Kingdon and Gippoliti 2008) and the subspecies *C. tantalus tantalus* is locally common at Ngel Nyaki Forest Reserve in north-eastern Nigeria. As a frugivorous monkey utilising both forested and grassland habitats (Chapter 2), it disperses a range of seed species into both habitats giving it the potential to be important in forest regeneration (Chapter 3). I therefore calculated i) the abundance and density of *C. t. tantalus* at Ngel Nyaki and ii) used this to estimate seed dispersal rates for the *C. t. tantalus* population in both habitat types at Ngel Nyaki Forest Reserve.

## 5.2 Methods

### *5.2.1 Study site*

Ngel Nyaki Forest Reserve lies on the western escarpment of the Mambilla Plateau, Taraba State, Nigeria (Chapman *et al.* 2004). Within the 46km$^2$ reserve only c7.2km$^2$ of forest remains in two fragments – Ngel Nyaki Forest and Danko Forest (Beck and Chapman 2008). The 5.3km$^2$ submontane Ngel Nyaki Forest ranges between 1400-1600m elevation. Ngel Nyaki Forest is of a dry type (Akinsoji 1994) with a mean annual rainfall of approximately 1800mm (Nigerian Montane Forest Project (NMFP) Weather Data), most of which falls in a single wet season lasting from mid April to mid October. Mean monthly temperatures do not exceed 30ºC (NMFP Weather Data).

The reserve lies within the Cameroon Highlands ecoregion (Olson *et al.* 2001), belongs to a biodiversity hotspot and contains many endemic plant species, including several on the IUCN red list (Chapman *et al.* 2004). The area is also a Birdlife International Important Bird Area (Fishpool and Evans 2001). The five primate species inhabiting the reserve in addition *C. t. tantalus* are: *Cercopithecus nicititans*, *C. mona*, *Colobus guereza occidentalis*, *Papio anubis* and the rare *Pan troglodytes eliottii* (Chapman *et al.* 2004).

### *5.2.2 Study species*

*Chlorocebus tantalus tantalus* is a mid size monkey with an average weight of 3.36kg for females and 4.6kg for males (Nakagawa 2000a). Troop sizes range from 11 to 76 individuals (Kavanagh 1980). *C. t. tantalus* is omnivorous, spending around 200 minutes per day feeding (Nakagawa 2000b; Agmen *et al.* 2009). Approximately half its diet consists of fruit and it additionally consumes foliage, flowers, plant sap and insects (Nakagawa 2000b; Agmen *et al.* 2009). The semi-terrestrial *C. t. tantalus* spends one third of both its total and feeding time on the ground (Kavanagh 1980) and utilises both forest edge and grassland habitats (Chapter 2) into which it disperses the seeds of forest and edge species (Chapter 3).

### *5.2.3 Data collection*

I walked six line transects running perpendicular to the edge of Ngel Nyaki Forest, transversing grassland through core forest habitats (Fig 5.1), as carefully and quietly as possible at approximately 1 to 1.5km per hour to avoid disturbing any *C. t. tantalus* present. Regular pauses to scan the surroundings for *C. t. tantalus* also helped minimise chances of missing a troop that was indeed present. When one or more *C. t. tantalus* individuals were observed, I took a GPS location on the transect perpendicular to the monkey(s). I estimated the perpendicular distance of the centre of the troop from the transect by eye and recorded the number of monkeys observed, along with the date and time of observation.

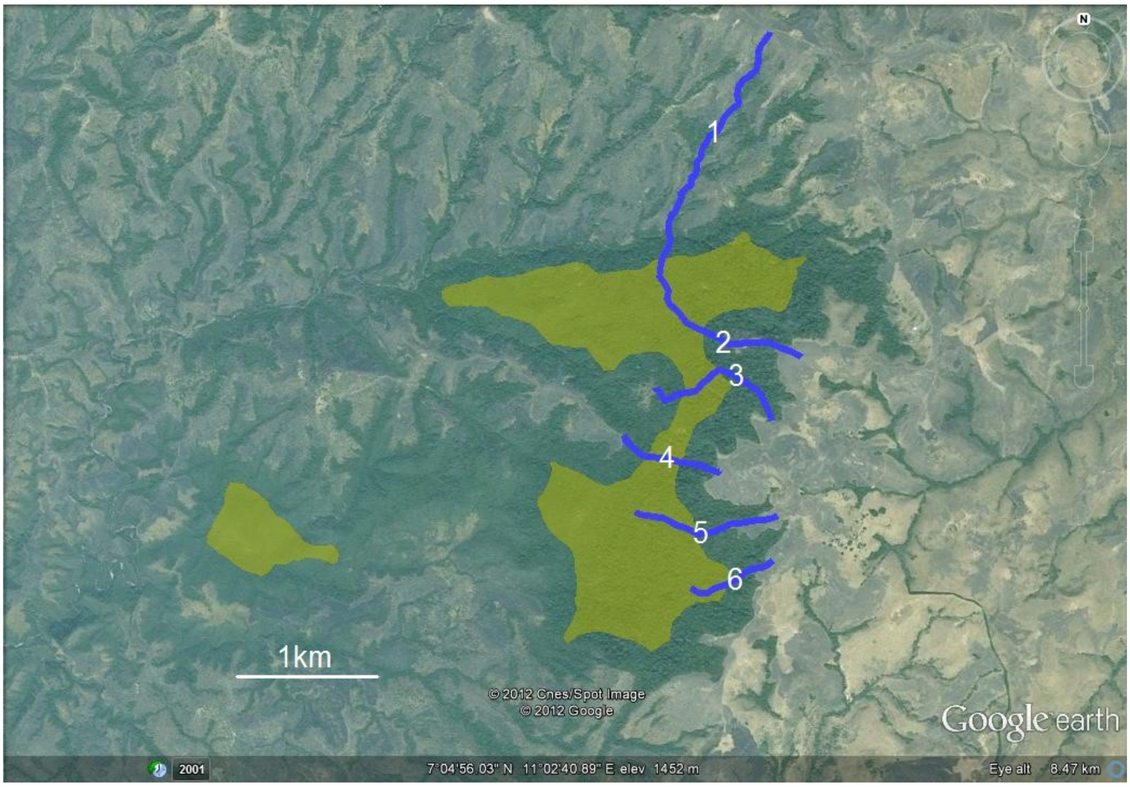

**Fig 5.1:** Map showing the transects (lines, 1-6) walked and their location within the study site at Ngel Nyaki. Core forest habitat where *C. t. tantalus* is absent is shaded and sections of transect passing through this were omitted from analysis.
*Source:* 'Ngel Nyaki', 7º04'53.63"N and 11º03'17.98"E, **Google Earth**, 7 February 2012.

Although transects traversed core forest habitat (more than 200 m to the nearest forest edge), I omitted sections of transect passing through this habitat from analysis as core forest habitat is deemed unsuitable for *C. t. tantalus* at Ngel Nyaki (Chapter 2; Fig. 5.1) and no individuals were sighted there. This resulted in useable transect lengths ranging from 352 m to 1.75 km, providing a combined length of 4.69 km. I walked all transects a total of 18 times between December 2009 and September 2010, with at least one walk being conducted every month, bringing the total distance walked to 84.5 km.

Finally, to estimate the quantity of seeds dispersed per monkey per day, I estimated the defecation rate of *C. t. tantalus*. I made all day observations of three *C. t. tantalus* individuals (one adult male, one adult female and one subadult female) housed at the Nigerian Montane Forest Project fieldstation on three consecutive days in November 2010. The monkeys were fed their usual diet comprising a mixture of fruit and vegetables (banana, pineapple, tomato, onion, carrot) and forest fruits collected from Ngel Nyaki Forest (*Aframomum angustifolium*, *Leea guineensis*). I watched the monkeys for 12 hours from 6am until 6pm. When I observed an individual defecating, I recorded the identity of the individual, date and time of defecation. The monkeys had been hand-raised and were comfortable in the presence of humans. I made observations while sitting quietly outside their enclosure, thus providing minimal disruption to their activities.

### *5.2.4 Data analyses*

I collected these data with the aim of using DISTANCE 6.0 release 2 (Thomas *et al.* 2009) to produce estimates of *C. t. tantalus* density and abundance. DISTANCE is widely used to obtain population estimates of primates and other large vertebrates from line transect sampling (Buckland *et al.* 2010). However, as a minimum sample size of 60 to 80 sightings of the species of interest is recommended in order to produce reliable estimates of density and abundance (Buckland *et al.* 2001) the twelve sightings of *C. t. tantalus* I obtained during the census constitutes a sample size much smaller than recommended. Small sample sizes seem to be particularly common among primate censuses and as such several researchers have used the Kelker method (Kelker 1945 in Buckland *et al.* 2010) as an alternative to DISTANCE (Chapman *et al.* 2000; Ferrari *et al.* 2010). However, there has recently been debate about the suitability of the Kelker method, especially with small sample sizes (Marshall *et al.* 2008; Buckland *et al.* 2010; Ferrari *et al.* 2010). As such I analysed the data using the Kelker method in addition to DISTANCE to allow comparison between the estimates produced.

DISTANCE uses sighting functions to estimate density. A range of models can be fit to the data within the program, and the one with the lowest Akaike's Information Criterion (AIC) score is chosen (Buckland *et al.* 1991), with the program calculating density using the chosen model.

The Kelker method involves first calculating the transect half-width (w) within which it is assumed that all *C. t. tantalus* troops present will be recorded (Chapman *et al.* 2000). I arbitrarily grouped sighting distances into 5 m wide intervals and plotted the frequency of observations within each distance class (Fig 5.2). I used a 50% cut-off to calculate w from the plot, following Chapman *et al.* (2000) such that both $X_{i+1}/X_i \leq 0.5$ and $X_{i+2}/X_i \leq 0.5$, where $X_i$ is the number of sightings in distance class i (Chapman *et. al.* 2000). All sightings at distances greater than w I then discarded, resulting in six remaining observations. I calculated transect area following Ferrari *et al.* (2010) as 2Lw, where L is the total length of transect walked. I then calculated the density of troops as the number of remaining observations divided by transect area and estimated the density of individuals was by multiplying the density of troops by the average troop size. To estimate the number of *C. t. tantalus* troops and individuals, I multiplied density by the estimated area of habitat suitable for *C. t. tantalus* within Ngel Nyaki Forest Reserve (Chapter 2).

I calculated seed dispersal rates by multiplying the average number of seeds >2 mm recorded per faeces from each of forest and grassland habitats, as obtained from (Chapter 3) with mean defecation rate and the estimated density of *C. t. tantalus*. As the average number of seeds faeces$^{-1}$ for forest and edge habitats were not significantly different (Chapter 3), I used the combined average from both habitats to obtain estimates of forest seed dispersal rates.

## 5.3 Results

### *5.3.1 Kelker method*

I calculated a transect half width (w) of 15 m from the plot of frequency of observations at each 5 m distance interval plot according to the Kelker method (Fig. 5.2). This yielded density estimates for *C. t. tantalus* of 2.4 troops km$^{-2}$ and 31.5 individuals km$^{-2}$ . Using the estimated area of suitable *C. t. tantalus* habitat within Ngel Nyaki Forest Reserve (Chapter 2), I estimated a total population size for *C. t. tantalus* of 101.1 troops comprising a total of 1348 individuals at Ngel Nyaki.

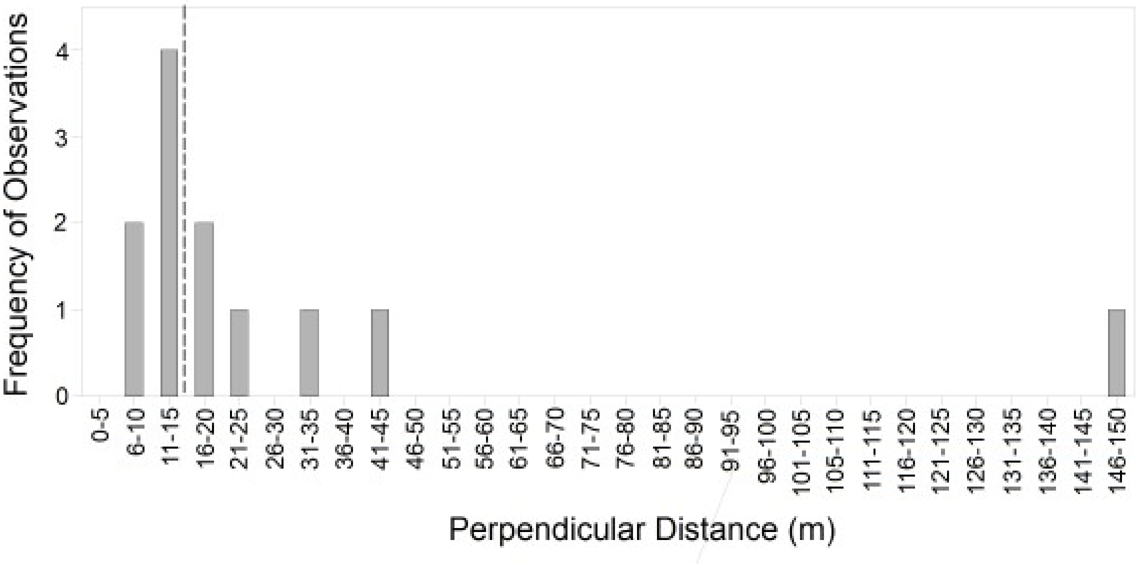

**Fig. 5.2:** Frequency of observations plotted against perpendicular distance from the transect for the 12 observations obtained. The dashed line shows the transect half width as calculated for the Kelker method, above which the observations are discarded.

The captive *C. t. tantalus* I observed produced an average of 3.4 +/- 1.5 defecations each per day. Using this and the means of 16.4 and 4.0 seeds faeces$^{-1}$ I obtained for the grassland and forest previously (Chapter 3), I estimated seed dispersal rates for *C. t. tantalus* of 1754 and 508 seeds >2 mm km$^{-2}$ day$^{-1}$ for grassland and forest habitats, respectively. This equates to approximately 640000 and 185000 seeds dispersed km$^{-2}$ year$^{-1}$ in the grassland and forest, respectively.

**Table 5.1:** Comparison of density and seed dispersal rates derived from the Kelker method and DISTANCE.

| | Kelker Method | DISTANCE |
|---|---|---|
| Effective strip width | 2x15 m = 30 m | 33.8 +/- 6.3 m |
| Density of troops | 2.4 km$^{-2}$ | 2.1 +/- 0.8 km$^{-2}$ |
| Average troop size | 13.3 +/- 1.8 | 13.3 +/- 1.8 |
| Encounter rate | 0.14 troops km$^{-1}$ | 0.14 troops km$^{-1}$ |
| Density of individuals | 31.5 km$^{-2}$ | 28.0 +/- 10.8 km$^{-2}$ |
| Number of troops in reserve | 101.1 | 90.0 |
| No. of individuals in reserve | 1348 | 1201 |
| Seeds dispersed in grassland per km$^2$ per day | 1754 | 1560 |
| Seed dispersed in forest per km$^2$ per day | 508 | 385 |
| Seeds dispersed in grassland per km$^2$ per year | 640000 | 569000 |
| Seeds dispersed in forest per km$^2$ per year | 185000 | 141000 |

### *5.3.2 DISTANCE*

The DISTANCE model which best fit the data was the half normal function with cosine adjustment (AIC = 103.53, Fig. 5.3) and calculated an effective strip width of 33.8m. The density of *C. t. tantalus* estimated by DISTANCE were lower than those estimated via the Kelker method (Table 5.1). Using DISTANCE, I produced estimates of 2.1 +/- 0.8 troops per km$^2$ and 28.0 +/- 10.8 individuals per km$^2$. From this, I estimated a total population size for *C. t. tantalus* within the reserve of 90.0 troops, comprising a total of 1201 individuals. Using *C. t. tantalus* density as estimated by DISTANCE, I estimated 1560 seeds >2 mm per km$^2$ per day are dispersed by *C. t. tantalus* in the grassland and 385 in the forest. This equates to the dispersal of approximately 569000 and 141000 seeds >2 mm km$^{-2}$ year$^{-1}$ in the grassland and forest, respectively.

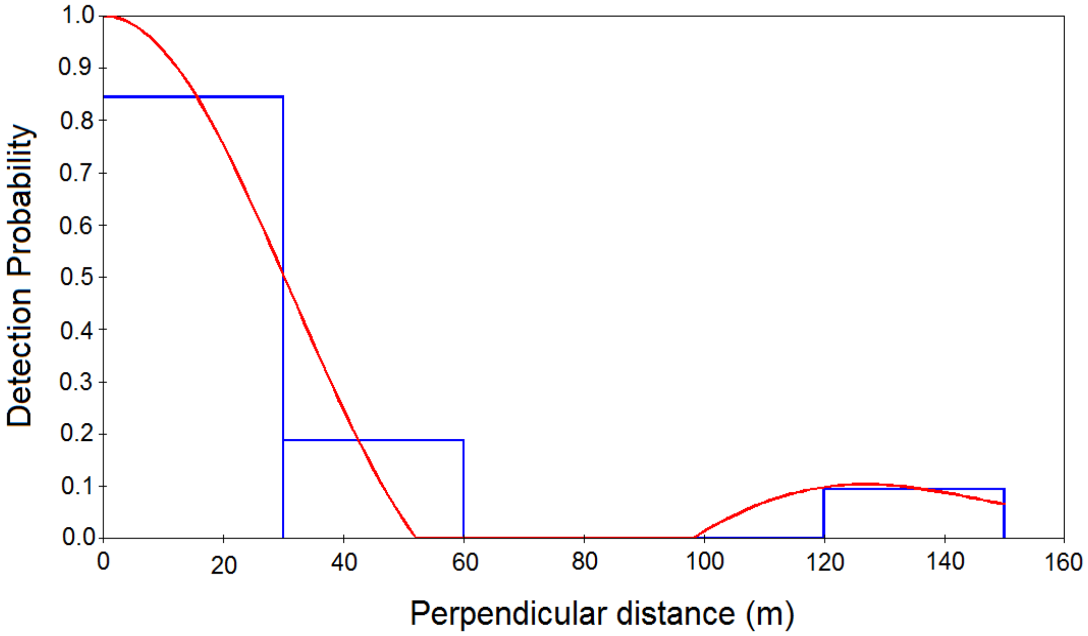

**Fig. 5.3:** Detection probability plot for *C. t. tantalus* at Ngel Nyaki Forest Reserve as derived from DISTANCE 6.0. Histogram showing probability of detecting a *C. t. tantalus* group that is present within each distance class. Line shows the fitted half normal function with cosine adjustment model.

## 5.4 Discussion

### *5.4.1 Comparison of models*

Despite the small sample size obtained, I produced similar estimates of *C. t. tantalus* density using DISTANCE and the Kelker method, that differed by only 3.4 individuals km$^{-2}$. However, even this difference in density of a few individuals km$^{-2}$ leads to substantial differences in seed dispersal estimates for both forest and grassland habitats. This indicates the importance of developing methods for analysing line transect data with small sample sizes to produce accurate density estimates. The difference between the estimates from the two methods also highlight the importance of the contribution that even a few individuals can make to the seed dispersal process and how a decline in the density of a seed disperser can affect the effectiveness of seed dispersal services long before it becomes rare at a given location (McConkey and Drake 2006).

While the mean troop size was the same regardless of the method used, this may be an underestimate (Ferrari *et al.* 2010). The three troops of *C. t. tantalus* I used to investigate patterns of habitat use at Ngel Nyaki all had a greater number of individuals than the mean of 13.3 calculated here (sizes ranged from 18 to 30) (Chapter 2) and it is likely that the troop counts obtained during census walks failed to detect all members of the troop in at least some instances. As the foraging group of *C. t. tantalus* is the same as the social group (Kavanagh 1980), it seems unlikely that the groups where I counted a small number of individuals are smaller foraging units. Additionally, troop sizes ranging from 11 to 70 have previously been recorded for *C. t. tantalus* (Kavanagh 1980), and although the average troop size used here falls within that range, it is at the low end and troop sizes of 18 to 40 seem common (Nakagawa 1999; Agmen *et al.* 2009; pers. obs.).

### *5.4.2 Density of Chorocebus tantalus tantalus and rates of seed dispersal*

To my knowledge, no direct reports of *C. t. tantalus* density appear in the literature, however I obtained a crude estimate by using the home range and troop size data from Nakagawa's (1999) study troop. This gives an approximate dry season density of 23 individuals km$^{-2}$ (1.1 troops km$^{-2}$) and 37 individuals km$^{-2}$ (2.3 troops km$^{-2}$) in the wet season. Averaging across seasons gives a troop density of 1.7 troops km$^{-2}$, less than that obtained for Ngel Nyaki Forest Reserve but an overall density of 30 individuals km$^{-2}$, a value intermediate between the density estimates I obtained from the two different methods. While the estimate for *C. t. tantalus* density derived from Nakagawa (1999) only uses data from one troop, it suggests that the densities of *C. t. tantalus* obtained in this study may be similar to elsewhere. However, densities of up to 96 individuals km$^{-2}$ have been recorded for the closely related species, *Cercopithecus aethiops* (Isbell *et al.* 1990).

My observations of captive *C. t. tantalus* indicated one individual defecates 3.4 +/- 1.5 times day$^{-1}$. This is comparable to defecation rates of four other captive Cercopithecine monkey species in which defecation rates ranged between 3 and 7 times per day (Poulsen *et al.* 2001). Taking the overall median of 5 seeds >2mm per faeces (Chapter 3), *C. t. tantalus* disperses on average 17 intact seeds >2mm per day, far fewer than some important primate seed dispersers, for example, *Papio anubis* (Kunz and Linsenmair 2008) and *Pan troglodytes* (Poulsen *et al.* 2001; Gross-Camp *et al.* 2009).

However, if the density of a seed disperser is high, then even low levels of seed dispersal at the level of the individual can contribute to effective dispersal by the population. Likewise, frugivore density does not on its own accurately predict the contribution of a given species to the community seed rain (Poulsen *et al.* 2001) as the seed rain is the result of both the seed dispersal rate of the individuals of a given species in combination with the abundance or density. Considering the more conservative seed dispersal rates, derived from the DISTANCE estimate of density, estimated seed dispersal rates for the grassland are four times higher than those for the forest and are much higher than those reported for many primates considered important seed dispersers (Wrangham *et al.* 1994; Poulsen *et al.* 2001; Kunz and Linsenmair 2008). However, even the rates of forest seed dispersal are higher than those reported for some species (e.g. *Papio anubis*, Kunz and Linsenmair 2008) but are comparable to others (e.g. *Pan troglodytes*, Wrangham *et al.* 1994). The grassland seed dispersal rates estimated for *C. t. tantalus* at Ngel Nyaki are greater even than the seed dispersal rates for one forest primate community (Poulsen *et al.* 2001). This strongly suggests that *C. t. tantalus* contributes substantially to the seed rain at Ngel Nyaki, both in forest and grassland habitats.

*C. t. tantalus* is frequently seen within Ngel Nyaki Forest Reserve and is considered locally common. This further increases the importance of their role as seed dispersers as the abundance of other primates potentially capable of dispersing forest seeds into grassland habitats (*Papio anubis* and *Pan troglodytes*) at Ngel Nyaki Forest Reserve are likely to be insufficient to provide effective seed dispersal services (Beck and Chapman 2008; Chapman *et al.* 2010). While *C. t. tantalus* is listed as least concern by the IUCN (Kingdon and Gippoliti 2008), it is known to raid crops leading to active hunting by farmers who consider it a pest (Kavanagh 1980; Warren *et al.* 2007; pers. obs.), so a knowledge of its current abundance may be useful in detecting population declines in the future. Additionally, as considerable bushmeat consumption occurs in Nigeria (Fa *et al.* 2006), and as significant primate population declines can occur over relatively short time frames (Isbell *et al.* 1990), *C. t. tantalus* cannot be assumed to be immune to future population decline and a change in conservation status.

Based on these estimates of population density and seed dispersal, *C. t. tantalus* contributes substantially to the seed rain at Ngel Nyaki, where it is an abundant primate able to disperse seed between habitats (Chapter 3). As at least some species of seed dispersed by *C. t. tantalus* can successfully germinate (Agmen *et al.* 2009, Chapter 4), these levels of seed rain suggest the role of *C. t. tantalus* is of great importance in not only maintaining forest structure in areas of existing forest, but also in the regeneration of forest within Ngel Nyaki Forest Reserve. This role should be investigated and considered elsewhere to develop a greater understanding of how seed dispersal by *C. t. tantalus* may be taken advantage of in forest restoration and conservation schemes.

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# Chapter 6:

# Seed dispersal by *Chlorocebus tantalus tantalus*: potential for forest regeneration

## 6. 1 Effectiveness of the tantalus monkey seed dispersal service and evidence for their role in forest regeneration

Seed dispersal is an important factor in the restoration of altered habitats (Chapman and Chapman 1999) yet in such habitats it is often limited (Duncan and Chapman 1999; Cordeiro and Howe 2001; Higgins *et al.* 2003; Howe and Miriti 2004). Therefore, the ability of potential seed dispersing animals to enter and spend time in these habitats is key (Karlowski 2006). This is especially so as conservation practices that utilise natural processes are more likely to be successful and more cost effective in terms of time and labour (Duncan and Chapman 1999). The results of my study indicate that *Chlorocebus tantalus tantalus* (Ogilby 1841 in Groves 2001) plays an important role in seed dispersal within Ngel Nyaki Forest Reserve, and has the potential to play a useful role in the conservation and forest restoration in the area.

Large bodied forest seed dispersers are often absent from forest fragments and other altered or degraded habitats (Cordeiro and Howe 2001). Typically primates that do occupy forest fragments are species that also occupy forest edge habitats as they are better adapted to forested areas with large edge to area ratios (Onderdonk and Chapman 2000). Moreover, primates with generalist diets are better able to utilise secondary forest habitats than those with more specialist diets (Fimbel 1994).

Primates occupying forest fragments are required to be mobile in addition to having a flexible diet in order to take advantage of reduced and unpredictable food resources (Tutin *et al.* 1997; Onderdonk and Chapman 2000). The frugivorous *Chlorocebus tantalus tantalus* possesses such traits including daily ranging distances of 1.5 to 2 km and having a generalist and opportunistic diet (Kavanagh 1980; Agmen *et al.* 2009), allowing it to occupy fragmented landscapes. The fact that *C. t. tantalus* will visit single trees within the grassland matrix (pers. obs.), highlights their potential importance as seed dispersers in small fragments where other dispersal agents may be rare or absent.

The use of both forested and grassland habitats by *C. t. tantalus* fulfils one of the requirements for reforestation proposed by Karlowski (2006): for a frugivore to be important in restoration efforts, the degraded habitat must be sufficiently suitable and attractive for the frugivorous animal. The patterns of habitat use by *C. t. tantalus* I observed in my study likely reflect behavioural adaptations to daily temperature fluctuations, perceived predation risk, energy/nutritional requirements and troop size (Dunbar 1992; Tutin *et al.* 1997; Hill and Dunbar 1998; Kaplin and Moermond 2000). *C. t. tantalus* spent a substantial proportion of each day in the grassland, with peaks in its use of grassland habitat in the early morning and evening (Chapter 2). Here it forages, primarily on invertebrates, and passes through the grassland when travelling between forest fragments (Agmen *et al.* 2009). For forest regeneration, it is important that frugivores also spend time feeding on fruits in forested habitat, in order for them to be able to disperse this seed into the degraded habitat (Wunderle 1997; Karlowski 2006). While *C. t. tantalus* did not enter core forest habitat in this study, they did however spend a considerable part of their time budget in forested habitats, up to 200 m from the forest edge (Chapter 2). This allowed them the potential to disperse the seeds from forest species into the grassland. The fact that *C. t. tantalus* do not forage within the forest core means that the seeds of forest tree species that are restricted to the forest core are not dispersed by them.

Despite a tendency for Cercopithecine monkeys to spit large quantities of seed beneath or close to the parent (Corlett and Lucas 1990; Lambert 1999), over 95% of the *C. t. tantalus* faecal samples I examined in this study contained seeds. This suggests that they disperse large quantities of seed, potentially up to distances of 2 km from the parent plant (Agmen *et al.* 2009). Moreover, a substantial number of these seeds were larger than 2 mm diameter. I recorded an average defecation rate of 3.4 times day$^{-1}$ for *C. t. tantalus* and a median of 5 seeds larger than 2 mm in size in its faeces, allowing 17 seeds greater than 2 mm to be dispersed on average per individual per day (Chapter 3). At the level of the individual therefore, the number of seeds *C. t. tantalus* disperses is comparable to other Cercopithecine monkeys (Kaplin and Moermond 1998; Poulsen *et al.* 2001) but is less than other important primate seed dispersers including *Papio anubis* (Kunz and Linsenmair 2008) and *Pan troglodytes* (Wrangham *et al.* 1994; Poulsen *et al.* 2001; Gross-Camp *et al.* 2009). Additionally, *C. t. tantalus* disperses seeds from at least 32 plant species (Agmen *et al.* 2009: Chapter 3), which is more than some primate species (e.g *Cercopithecus mona pogonias*, *C. cephus* and *Gorilla gorilla*, Poulsen *et al.* 2001) and less than others (e.g. *Papio anubis*, *Pan troglodytes* and *Lophocebus albigena*, Wrangham *et al.* 1994; Poulsen *et al.* 2001; Kunz and Linsenmair 2008). This suggests *C. t.*

*tantalus* is intermediate in terms of its effectiveness of seed dispersal at a community level.

I found few faeces containing evidence of damaged seeds, suggesting *C. t. tantalus* disperses the vast majority of seeds intact, especially as most of the damaged seeds were *Aframomum angustifolium*, a species for which *C. t. tantalus* also disperses vast amounts of intact seed (Chapter 3). However, a lack of seed fragments in faeces is not in itself evidence that *C. t. tantalus* does not act as a seed predator for some species (Kunz and Linsenmair 2008). The effect of *C. t. tantalus* gut passage has been found to enhance germination rates and shorten latency times for some species, although most species experience a neutral effect (Agmen *et al.* 2009). With little predation and a neutral effect of gut passage, *C. t. tantalus* appears to provide quality seed handling.

I confirmed the potential for seed dispersal between forest, edge and grassland habitats, finding *C. t. tantalus* faeces in all habitat types contained seeds primarily from forest edge plant species. Additionally, faeces I collected from the grassland contained significantly more seeds than those from the forest and edge with an estimated number of seeds >2 mm of 16.4 +/- 6.1, 3.42 +/- 0.97 and 4.67 +/-1.48, respectively (Chapter 3). The greater number of seeds collected from faeces in the grassland may be a result of an offset between gut retention time and pattern of habitat use. Moreover, I collected more medium size and fewer small seeds from faeces in the forest compared to the grassland, perhaps as a result of an interaction between the threshold of seeds able to be carried in the gut at any one time (Lambert

1999) and an influence of seed size on gut passage length (Traveset 1998). As the maximum seed size swallowed by *C. t. tantalus* is 20 mm diameter (Agmen *et al.* 2009, Chapter 3), it is unable to disperse large seed (>25 mm) in their faeces. However, as shade tolerance in seedlings is often associated with increasing seed size (Foster and Janson 1985), medium sized seeds (5-25 mm) dispersed by *C. t. tantalus* are likely to be able to germinate and establish in shaded forest environments. Small seeds (<5 mm) on the other hand, are more likely to be able to germinate and establish in the open grassland than medium sized seeds. By dispersing such pioneer and forest edge species into the grassland, *C. t. tantalus* has the potential to aid forest restoration, assuming the grassland is a suitable habitat for the germination and growth of these seeds. The lack of dispersal of mature core forest species is not necessarily a concern, as many of these species are mature forest species that may not successfully germinate and grow in edge and grassland habitats. The regeneration of secondary forest composed of pioneer and forest edge species may encourage core forest seed dispersal agents facilitating their dispersal at a later date (Tutin *et al.* 1997; Vulinec *et al.* 2006). Additionally, such secondary forest may provide a more suitable environment for the establishment of these seeds.

The quick disappearance of seeds and lack of germination in plots allowing access to seed removers, suggests high seed removal rates across the four habitats I tested at Ngel Nyaki Forest Reserve (Chapter 4). This combined with previous reports of high rates of seed removal at Ngel Nyaki (Chapman *et al.* 2010) indicate that post dispersal seed removal may have a big impact on the fate of dispersed seeds within the reserve. Removal rates of up to 100% are not uncommon in the literature, however, rates vary considerably in space and time (Chapman 1989; Chapman and Chapman 1996; Blate *et al.* 1998). I did not assess the identity of seed removers so some removal may have been the result of secondary seed dispersers, such as dung beetles which are abundant at Ngel Nyaki (Barnes 2011), and as such some seeds may have survived undetected outside of the plots.

When seed removers were excluded, the grazed grassland was the habitat with the greatest levels of germination for two of three species tested, *Aframomum angustifolium* and *Leea guineensis*, showing that for at least some species dispersed by *C. t. tantalus*, grassland is a suitable habitat for germination (Chapter 4). In contrast, I found higher levels of *Rytigynia umbellulata* germination in the forest than the grassland, indicating that seed dispersal by *C. t. tantalus* in the forest is beneficial for other species. Of the two grassland habitats I investigated, grazed and non-grazed, germination rates for all three species were higher in the grazed grassland. This difference between grassland habitats may result from intense competition from the dense layer of grasses in the non-grazed grassland. However, as any seedlings germinating in areas of grazed grassland, face imminent death through cattle herbivory and/or fire, this may be an example of a seed-seedling conflict in habitat suitability (Schupp and Frost 1989; Rey and Alcantara 2000). This suggests that while *C. t. tantalus* disperses seeds into habitats suitable for their germination, the current conservation approach of simply protecting areas of grassland from cattle grazing and fire may be insufficient for timely natural forest regeneration to occur.

Finally, I calculated the density of *C. t. tantalus* at Ngel Nyaki as approximately 2.1

troops km$^{-2}$, which equates to approximately 28 individuals/km$^{-2}$ (Chapter 5). On average *C. t. tantalus* dispersed approximately 4.0 and 16.4 seeds >2 mm per faeces in the forest and grassland respectively, leading to average seed dispersal rates of 385 seeds day$^{-1}$ km$^{-2}$ for the forest habitat and 1560 seeds day$^{-1}$ km$^{-2}$ for the grassland (Chapter 5). The rate of seed dispersal for the forest, while substantially less than for the grassland, is higher than the seed dispersal rates reported for some important seed dispersing primate species (e.g. *Papio anubis*, Kunz and Linsenmair 2008) but is comparable to others (e.g. *Pan troglodytes*, Wrangham *et al.* 1994). The rate of seed dispersal by *C. t. tantalus* into grassland is therefore substantially higher than those of many other primate species which are nevertheless regarded as important seed dispersers (Wrangham *et al.* 1994; Poulsen *et al.* 2001; Kunz and Linsenmair 2008). In fact, *C. t. tantalus* disperses more seed into the grassland at Ngel Nyaki Forest Reserve than the entire primate community described by Poulsen *et al.* (2001) disperses into a forest in Cameroon. This strongly suggests that *C. t. tantalus* contributes substantially to both the total and primate dispersed seed rain at Ngel Nyaki Forest Reserve, both in forest and grassland habitats. However, the complex web of interactions between seed dispersers and the plants they disperse make determining the importance of any single disperser difficult (Wakibara 2005) and it is important to remember that each species in any seed disperser assemblage plays its part, and together contributes to the overall seed dispersal in the forest (Wrangham *et al.* 1994; Lambert 1999; Poulsen *et al.* 2001).

Such large numbers of seed being moved are promising for the potential of natural forest regeneration within Ngel Nyaki Forest Reserve, and highlight the importance of *C. t. tantalus* in this ecosystem. Given an estimated 42.8 km$^2$ of Ngel Nyaki Forest Reserve comprises habitat suitable for *C. t.* tantalus (Chapter 2), I estimated the reserve is home to approximately 1200 *C. t. tantalus* individuals, forming 90 troops (Chapter 5). This highlights the importance of *C. t. tantalus* seed dispersal at Ngel Nyaki even further. The other fruviorous primates, *Papio anubis* and *Pan troglodytes*, known to visit grassland habitats within Ngel Nyaki Forest Reserve are regarded as effective seed dispersers (Wrangham *et al.* 1994; Kunz and Linsenmair 2008). However, as both these species are uncommon or rare at Ngel Nyaki (Beck and Chapman 2008; Chapman *et al.* 2010), they likely disperse relatively few seeds into grassland habitats. Despite this, *C. t. tantalus* is not immune from future population declines from hunting due to its pest status as a crop raider (Warren *et al.* 2007; pers. obs.) and bushmeat demand (Fa *et al.* 2006). As seed dispersal can cease to be effective long before a frugivore becomes rare (McConkey and Drake 2006), these estimates of *C. t. tantalus* abundance at Ngel Nyaki Forest Reserve can serve as a baseline against which to measure future population changes.

I have shown that *C. t. tantalus* spends a significant portion of each day in each of forest, edge and grassland habitats and this, combined with their frugivorous diet and role as seed dispersers, supports the hypothesis that *C. t. tantalus* has the potential to be important in the maintenance of forest structure in areas of existing forest and as part of forest restoration efforts in areas of nearby grassland, assuming appropriate conservation management.

## 6.2 Future conservation directions

The large quantity and relatively high rates of germination of *C. t. tantalus* dispersed seed species in grazed grassland suggests *C. t. tantalus* has the potential to be a valuable seed disperser contributing to reforestation of grassland habitats, provided suitable management actions are set in place. Seed removal rates were high across all habitats however, and what proportion of this is due to secondary dispersal relative to post dispersal predation will be important in implementing appropriate conservation measures. Therefore, I suggest an important component of future research should be to identify seed removers for *C. t. tantalus* faeces and quantify the relative component of predation versus secondary dispersal.

Impedances to forest regeneration in grassland habitats in Ngel Nyaki Forest Reserve depend on management. In grassland protected from cattle grazing and fire, competition from pasture grasses is so intense that germination and establishment of dispersed seed is unlikely. For example, I found only 0.68% of seeds germinated in grassland habitat protected from cattle grazing and fire (Chapter 4). Competition by grasses, ferns and other dense vegetation severely limit regeneration processes elsewhere (Chapman and Chapman 1999; Duncan and Chapman 2003; Ortega-Pieck *et al.* 2011). Therefore, the fencing off of areas of forest edge and grassland to exclude cattle grazing may not, on its own, be adequate to ensure natural forest regeneration in a reasonable time frame. On the other hand, survival of seedlings germinating in the grazed grassland, where germination rates were considerably higher, face imminent death as grazing and/or fire will destroy them within a single growing season.

Further research is clearly needed to indentify management approaches to maximise the benefits of seed dispersal by *C. t. tantalus* in forest regeneration and restoration efforts. Problems that need to be overcome include how to protect seedlings in areas with cattle grazing and/or burning, without removing the benefits offered by cattle grazing and/or how to increase germination rates in areas protected from cattle grazing. Potential management practices successful in the control of competitive vegetation in Europe include the mowing of grasses or other competitive vegetation (e.g. Endels *et al.* 2007; Ammer *et al.* 2011). If this approach is used, I further suggest the marking of seedlings to avoid accidental destruction. Such approaches are likely to be very labour intensive, considering the size of Ngel Nyaki Forest Reserve. Alternatively, there is a possibility that germinating seedlings in grazed areas could be located and protected from grazing by the erection of cattle exclosures. However, grass within such exclosures would also be released from herbivory and may gain a competitive advantage. The development of a suitable combination of both these approaches may be feasible to reduce labour intensiveness and control the competitive ability of the grasses. A different approach involves the planting of a temporary nurse crop which may suppress grasses while forest seedlings establish (Wunderle 1997; Zanne and Chapman 2001), with species such as *Ficus* spp. or *Musa* spp. (Duncan and Chapman 1999; Zanne and Chapman 2001). Seed rain can further be increased beneath the temporary crop by choosing a species attractive to seed dispersers and can either be left with the regenerating forest eventually replacing it, or harvested when regenerating seedlings are of a sufficient size to withstand grass competition and cattle grazing (Zanne and Chapman 2001). While this approach has been suggested for assisting natural reforestation in Africa before (Duncan and Chapman 1999; Zanne and Chapman 2001), thorough investigation is required before implementation, especially if the temporary crop is of an exotic species, to ensure it will not become invasive, will attract suitable seed dispersers and that dispersed seedlings can establish in its understory (Duncan and Chapman 1999; Zanne and Chapman 2001).

While it is clear that *C. t. tantalus* already disperses significant amounts of seed into grassland habitats, one may be able to encourage dispersal to specific locations by the planting of individual or small groups of favoured fruit trees. The presence of remnant trees in grassland areas can act as foci for seed dispersal by attracting forest frugivores into grassland areas (Duncan and Chapman 1999; Zahawi and Augspurger 2006), especially in years with forest-wide fruit shortages (Herrera and Garcia 2009). Recently, an attempt at planting *Ficus* spp. poles as a living fence around Ngel Nyaki Forest Reserve was made, however its success was poor due to its subsequent removal by local Fulani cattle herders (NMFP Annual Report 2010). While not a solid plantation, *Ficus* spp. are attractive to a range of frugivores including birds and primates (Thornton *et al.* 1996; Zanne and Chapman 2001), including *C. t. tantalus*. Some forest frugivores will be unable to utilise this fence as they are unable or unwilling to frequent open habitat in order to reach the new trees. *C. t. tantalus* however, is among those that will be able to reach them, eat of their fruit and disperse seeds within their vicinity. If the living fence alters the habitat conditions of the grassland in the immediate vicinity around it, in such away to limit grass competition then these seeds could germinate and establish, leading to forest regeneration (Wunderle 1997). Subsequently, I suggest the suitability and viability of actions such as this should be considered for Ngel Nyaki Forest Reserve and investigated so that the benefits of *C. t. tantalus* seed dispersal be maximised for conservation.

## 6. 3 Implications for primate frugivores in restoration elsewhere

*C. t. tantalus* contributes substantially to the seed rain at Ngel Nyaki. As at least some species dispersed by *C. t. tantalus* are deposited into habitats where they can successfully germinate (Chapter 4), these levels of seed rain suggest the role of *C. t. tantalus* is of great importance in not only maintaining forest structure in areas of existing forest, but also in the regeneration of forest at Ngel Nyaki. I suggest this role should be investigated and considered elsewhere to develop a greater understanding of how seed dispersal by *C. t. tantalus* and other primates may be taken advantage of in forest restoration and conservation schemes. It is quite probable that *C. t. tantalus* could fill similar roles in forests elsewhere in the Cameroon Highlands and within their African distribution. However, as generalisations about primate behaviour and seed dispersal roles are difficult to make, even within a species (Gautier-Hion *et al.* 1993; Isbell and Young 1993; Kaplin *et al.* 1998), such roles should not be assumed and further research at the location of interest should be undertaken prior to the implementation of conservation actions to ensure appropriate actions are chosen. Alternatively, investigation into such roles may be conducted concurrently with the implementation of conservation actions as a means to assess the effectiveness of the actions implemented and allow them to be appropriately amended if necessary, as I have done at Ngel Nyaki Forest Reserve.

Other primate species that are able to utilise both intact and degraded habitats with potential seed dispersal roles may be considered for locations where *C. t. tantalus* is absent or otherwise unsuitable. Indeed the potential existence of a similar role has been previously mentioned for *Papio anubis* (Kunz and Linsenmair 2008). Species of African primate that are non-dependant on closed forest include *Galago gallarumn*, *G. Moboli*, *G. senegalensis*, *Otolemur crassicaudatus*, *Cercopithecus aethiops*, *Erythrocebus patas*, *Papio anubis*, *P. cynocephalus*, *P. hamadryas*, *P. papio*, *P. tursinus*, *Theropithecus gelada* and *Cercocebus galeritus* (Cowlishaw 1999; Wieczkowski 2010). Furthermore, Kaplin and Lambert (2002) further suggest that *Cercopithecus* monkeys may pass through a range of habitats and are an ideal taxon with which to investigate the role of seed dispersal and forest restoration. These species may fill similar roles in areas where they are present and if so, be able to be utilised in forest restoration and regeneration projects. Their potential suitability needs to be addressed however, in order to implement appropriate conservation actions and maximise their roles. Species which rarely enter grassland but are able to utilise both mature and secondary forest habitats such as *Saguinas midas niger* in South America, may play important related roles in dispersing the seeds of mature forest species into secondary forests (Oliveira and Ferrari 2000), with equally important consequences for forest restoration and regeneration. Additionally, *P. troglodytes* can disperse large numbers of seeds per individual and can range through open grassland, however, population sizes at some locations may be insufficient for such forest restoration (Beck and Chapman 2008). However, the potential for rare species such as *P. troglodytes* and C. *galeritus* (Beck and Chapman 2008; Wieczkowski 2010) to be important to forest restoration may add an additional argument for their conservation.

## 6.4 Conclusions

*Chlorocebus tantalus tantalus* frequents both forest and grassland habitats (Chapter 2). As a relatively frugivorous monkey, *C. t. tantalus* is able to disperse large quantities of seed between these habitats (Chapter 3). *C. t. tantalus* disperses significantly more seeds per faeces into the grassland than into forest habitats, highlighting the potential importance of this species as a source of seed rain into regenerating habitats. This is especially important given that forest regeneration in such habitats is often limited by a lack of seed rain (Cordeiro and Howe 2001; Howe and Miriti 2004). Moreover, for some *C. t. tantalus* dispersed seed species, germination rates are highest in the grassland, suggesting that this monkey disperses seeds into habitats suitable for their germination (Chapter 4). However, as I found the poorest rates of germination in non-grazed grassland, it appears that simply protecting areas of grassland from cattle grazing and fire may not be a sufficient conservation action to allow timely forest regeneration (Chapter 4). This is because of intense competition from grasses. Clearly the role of seed dispersal by *C. t. tantalus* will be of little help to forest regeneration at Ngel Nyaki Forest Reserve unless conservation actions are implemented that allow reasonable numbers of *C. t.*

*tantalus* dispersed seed to germinate and establish. *C. t. tantalus* and other primates may have the potential to provide similar roles in forest conservation elsewhere, although these roles need to be assessed at the given locality where conservation measures are to be put in place, as generalising the behaviour and seed dispersal roles of primates is difficult, even within a species (Gautier-Hion *et al*. 1993, Isbell and Young 1993; Kaplin *et al.* 1998).

## 6.5 References

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# Appendix 1:

# Photographs of seed species collected from Chlorocebus tantalus tantalus faeces at Ngel Nyaki Forest Reserve, Nigeria.

Three seed species (*Landolphia* sp., *Syzygium* sp. and *Bridelia* sp.) were identified by my field assistant and never photographed. Photographs of the remaining 25 seed species are presented here in the order they appear in Table 3.1, based on their frequency of appearance in *Chlorocebus tantalus tantalus* faeces.

*Ficus* spp.

*Aframomum angustifolium*

*Croton macrostachyus*

*Leea guineensis*

*Maesa lanceolata*

U24

U2

U1

*Psychotria* sp.

U9

*Grewia* sp.

*Rytigynia umbellulata*

*Haurangana madagascariensis*

U6

U14

U10

U12

U5

U16

U21

U7

*Vitex* sp.

U18

*Pouteria* sp.

*Synsepalum* sp.