Background
On a global scale a lack of seed dispersers, rather than more overt physical destruction, may constitute a major threat to the long-term survival of tropical forests. This is because many forests have sufficient protection to prevent them being logged or farmed, but insufficient protection to prevent hunting. Yet almost nothing is known about plant-frugivore (fruit eating bird and animal) interactions, and the consequences of loosing dispersers in African montane forests.

The aims of our research were to:

1. Identify key diurnal frugivores in Ngel Nyaki forest
2. Investigate the effect of fragmentation on diurnal frugivore communities
3. Predict the effect of changes in frugivore composition on seed dispersal of tree species
4. Investigate the role of putty nose monkeys in seed dispersal.

Understanding the role of montane forest frugivores in tree seed dispersal is crucial information for sustainable management of montane forests.

A: The identification of key diurnal frugivores in Ngel Nyaki forest and the effect of forest fragmentation on these communities:

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*Submitted as a paper to Biotropica July 2007
*Presented as a poster at AETFAT 2007 in Cameroon (see NMFP website)

Methods

STUDY AREA. – Ngel Nyaki forest (N07° 14’, E011° 04’) is located between 14500-1500m elevation on the western escarpment of Mambilla Plateau, an area of 3100 km² in the south east corner of Taraba State (Figure 1). The Plateau is now dominated by rolling, overgrazed grassland, at an altitude of 1500-1600m. Only one stand of forest remains on the Plateau, Ngel Nyaki Forest Reserve. The forest lies on the west facing slopes of an old volcano, between 1650m to 1450m elevation, and is
ca 6.6 km² in area. It was gazetted a Local Government Reserve in 1969, but then
the nearby riparian fragments along streams feeding into the Mayo Jigerwal (Fig 1)
were not included in the reserve. Since the early 1980’s the political situation in
Nigeria has meant that patrolling and reserve management of Ngel Nyaki Forest
Reserve has been neglected (although this is beginning to change). Local human
and cattle populations have increased, exacerbated by a new road, which is only
40 mins walk from the forest edge. Hunting has been rife (it is only because of a
lapsing taboo against eating primates that so many of them remain), and the riparian
fragments outside the Reserve have suffered various degrees of degradation, more
severe the closer to the main road and Yelwa village (Fig. 2).

The study was designed to compare woody species composition and frugivore
populations at four sites: within Ngel Nyaki forest, and three small riparian forest
fragments A, B, and C (Fig. 2), suffering from increasing degradation in terms of
species loss and disturbance with increasing distance from Ngel Nyaki forest
and closer proximity to Yelwa village (Fig. 2).

IDENTIFICATION OF KEY DIURNAL FRUGIVORES IN NGEL NYAKI FOREST AND
FRAGMENTS
At each of the four sites 20 focal fruiting trees (a total of 20 tree species) were
identified and watched from 600-1200 and 1500-1800 hrs. Every frugivore visiting the
tree was recorded in both morning and afternoon, giving a total of 180 hours of
observations of focal fruiting trees at each of the four sites (720 hours in total). The
observer used binoculars and a scope and was concealed in the undergrowth in a
position to see as much of the canopy as possible. Observations were carried out

DATA ANALYSIS
In order to illustrate the difference among the four sites in terms of frugivore species
composition, the frugivore data from 20 morning and 20 afternoon observations per
site were reduced to a summary table of the number of times a frugivore species was
observed feeding on a focal tree over those 40 visits. We used detrended
correspondence analysis (DCA) (Hill & Gauch 1980) to analyse species occurrences,
and the results are presented as biplots where both frugivore species and sites are
plotted in ordination space. Simpson’s unbiased diversity index was calculated for
each site. The statistical package (MVSP v3.13, Kovach Computing Services) was
used for both analyses.

Results
A table of focal trees observed in each of the four sites, with their fruit type and size,
is presented in Table 1. A total of 38 diurnal frugivore species were recorded from all
four sites (Table 2), with more species in Ngel Nyaki forest (27) than in any of the
fragments A, B or C (20, 18 and 22 respectively) (Table 3). Simpson’s unbiased
diversity indices, which takes into account both number of species and their
abundance, indicate a small decrease in frugivore diversity with increasing
degradation (Table 3). Differences in frugivore visitors among sites are illustrated on
the DCA biplot (Fig 3). The first axes of the biplot (which ordinates both frugivores
and sites) explained 84.7% of the variation, and axis 1 and 2 together, 90.7%. Ordination of the data separated out species such that the frugivores more frequently
associated with Ngel Nyaki forest lie to the right of axis 1, and those more frequently associated with fragments, towards the left of the axis. Diurnal frugivores only recorded from Ngel Nyaki (Group 1 on the DCA plot) include all of the primate frugivores except for the Cercopithecus aethiops (Tantalus) and several of the wide gaped avian frugivores including the green turaco (Tauraco persa) and the piping hornbill (Bycanistes fistulator). Group 2 is the largest group with 21 species, and comprises frugivores recorded from both Ngel Nyaki and at least one of the fragments, through to species recorded only from the fragments - the farther along to the left of axis 1, the more often was the species recorded in fragments rather than Ngel Nyaki. This group includes C. aethiops, but mostly avian frugivores with gape widths ranging from ca 13mm Tauraco leucolophus, small passerines (Table 2). Species recorded from at least two fragments but not Ngel Nyaki forest were included in the same group because observational data show that all of these frugivores do feed on the edge of Nagel Nyaki, so that it would be contrived to include them in a separate group. Frugivores recorded only from the most degraded fragment C are located on the top left of the diagram. Despite only being recorded from fragment C, it is highly unlikely that they would not feed in the other fragments as well.

Discussion

There is generally a positive correlation between body size (weight) and the maximum size of fruit (seed) eaten by primates (Corlett 1998) and between avian frugivores body weight and gape size (Dunning 1993), which means that large frugivores are most important in dispersing large seed (Wheelwright 1985; Wright et al. 2007), but they also disperse small seed. In Africa primates have been shown to be especially important in the dispersal of large seed (Wrangham et al. 1994; Lambert 1998; Stoner et al. 2007). For example Chimpanzees in Kibale are known to disperse seed up to 2.7cm in diameter (Wrangham et al. 1994), and Cercopithecus species also disperse seed of a range of sizes in Afromontane forests (Dowsett Lemaire 1989; Beeson et al. 1996; Kaplin & Moermond 1998). In Ngel Nyaki forest P. troglodytes vellerosus and Cercopithecus nictans spit, swallow, and disperse intact, viable seed of Pouteria altissima 1.5 cm in diameter, Isolona cf. deightonii 1.5 cm and Santiria trimera up to 1.7cm, as well as small Celtis (<6mm) and tiny Ficus seed (<1mm). Bucerotidae (hornbills) are one of the most important seed dispersers in Afrotropical forests (Whitney et al.1998) as they disperse seed of a wide range of sizes and move a high proportion of seed away from the parent plant (Whitney et al. 1998; Holbrook & Smith 2000). After Bycanistes brevis with a gape width of 40-49mm, Musophagidae (turacos) have gapes of ca. 12-13mm (Dowsett-Lemaire 1988) and Capitonidae (barbets) and Colidae (mousebirds) slightly less, depending on the species.

So - are local frugivore populations sufficient in diversity and abundance to effectively disperse seed within Ngel Nyaki Forest Reserve and among Ngel Nyaki and fragments A, B and C?

Despite the fact that some very large fruited species occur in Ngel Nyaki (eg Tabernaemontana contorta and Carapa grandiflora) (Table 1) there is no evidence of any tree species suffering from lack of dispersers (H. Chapman pers. obs). Fruit of C. grandiflora are commonly found on the ground, but almost always empty of seed and away from conspecific adults. The very similar species Carapa procera is dispersed
by rodents (Forget & Jansen 2007), and unlike some forests (Forget pers. com) there is no evidence of fruit piling up beneath parent trees. Similarly the large fruits of *Tabernaemontana contorta*, and *Voacanga bracteata* appear to be effectively dispersed, probably also by rodents. The large fruit of *Isolona* sp. is broken open by primates and seed swallowed; we have found viable seed in both *P. troglodytes vellerosus* and *C. nicator* dung (unpublished results), and seedlings of *Isolona* sp. are abundant throughout the forest (pers. obs). So despite the fact that large mammalian frugivore diversity is less than it has been historically (eg. Colquhoun (1962) reported a high diversity of wildlife in the forest, including buffalo (*Syncerus caffer*), red river hog (*Potamochoerus porcus*) and abundant bushbuck (*Tragelaphus scriptus*) (cited in Chapman 1993)), and that frugivore abundance has dropped dramatically (eg. the black and white Colobus (*Colobus guereza* (a seed predator) was extremely common in 1978 but is now reduced to a few individuals in the forest, and bushbuck are now rare) (Chapman pers. obs), fruit is still being eaten and seed dispersed. It may be that the wide range of promiscuous frugivores capable of dispersing fruit up to 40mm in diameter are still ensuring dispersal. During this study six frugivore species were observed feeding on *Pouteria altissima* (seed 28mm in diam) and sixteen species on *Polyscias fulva* (4mm in diam).

In the riparian fragments only three tree species were identified with fruit between 28-40mm diam: *Anthocleista vogelii*, *Garcinia smeathmannii* and *Ficus sur* (Table 1). While ripe *Ficus* and *Anthocleista* fruit can be pecked at and chunks with seed swallowed by small passerine birds, *G. smeathmannii* will depend upon large gaped frugivores for dispersal, and it would seem that the only likely diurnal candidates are *C. aethiops*, and the *Funisciurus* sp, the latter a scatter horderer, which were the only two frugivores observed feeding on this species.

Species with fruit up to 12mm in diameter depend on frugivores with equally wide, or wider, gapes for dispersal, and there are several such species which live in, or visit, the fragments. For example fruit of *Syzygium guineense* subsp *guineense* were fed on, and presumably swallowed, by ten frugivorous species. Small (3 mm) *Maesa lanceolata* fruit were eaten by all frugivores recorded in the fragments. The only species which we have identified from this study as being dispersal limited is *Garcinia smeathmannii*. Another possible candidates is *Symphonia globulifera* (the latter not recorded in this survey but present in fragments). Both species have fruits of > than 14mm in diameter and occur in the fragments. These findings were not unexpected, as large fruited (or seeded) species are more vulnerable to loss of large frugivores than small ones (Bennett & Robinson 2000; Peres 2001; Babweteera *et al.* 2007). However we have not included nocturnal frugivores in our study, such as ungulates, bats and civet cats. These may well contribute to dispersal and ameliorate the consequences of the loss of large diurnal dispersers.

Demonstrating adequate dispersal in ecological and evolutionary terms entails much more than simply demonstrating lack of dispersal limitation. Loss of frugivore diversity is likely to adversely affect patterns of dispersal (Clark *et al.* 2005), which may have negative, (but see (Farwig *et al.* 2006)), consequences on community structure and function. Loss of large frugivores may lead to increased clumping of seed closer to the parent tree, which in turn may lead to loss of fitness through increased seed and seedling mortality (Janzen 1970; Connell 1971), and less gene flow among populations and into new habitats. However seed shadows of seed
dispersed my mammalian (and avian) frugivores vary according to factors such as body size, digestive strategy, ranging behavior and defecation patterns (Stoner et al. 2007). Using a combination of seed traps and DNA-based genotyping of *Prunus mahaleb*, (Jordano et al. 2007) were able to demonstrate that different frugivores were responsible for dispersing seed to different distances away from the parent tree and into different habitats, so that different frugivores made a different contribution towards dispersal and affected the genetic structure of populations in unique ways. In African forests hornbills are able to disperse seed the greatest distances of any frugivore, and rarely deposit seed closer than 500m to the parent tree (Holbrook & Smith 2000). Historically on Mambilla Plateau it is likely that *B. fistulator* would have been much more common, and played a major role in effecting gene flow for a wide range of species among Afrotropical fragments. Chimpanzees would also have moved seed large distances on Mambilla; they have large home ranges, and their propensity for seed swallowing, coupled with extended gut retention times (estimated mean >31 hrs (Lambert 2002) is ideal for long-distance dispersal (Gross-Camp & Kaplin 2005; Wrangham et al. 1994). However today the small Ngel Nayki population of chimpanzee is unlikely to disperse seed outside Ngel Nyaki forest; even the small distance across open grassland to fragment A would be dangerous. Likewise *Cercopithecus nictans* is very rarely found outside Ngel Nyaki forest, so despite the fact that Cercopithecus monkeys have long gut retention times and move across a range of habitats (Kaplin & Lambert 2002); they are unlikely to effect seed dispersal among populations at the moment.

It is possible that fragmentation may lead to increased fruit removal in some species; Farwig et al. (2006) found a marginally significant increase in the removal of *Prunus africana* fruit in Afrotropical fragments as compared with continuous forests. However, as already discussed, fruit removal is only one part of the seed dispersal cycle.

If no action is taken to more effectively control hunting within, and to keep cattle out, of Ngel Nyaki and the surrounding riparian fragments, the response of the forest trees (especially in the riparian fragments) to changes in frugivore composition is purely academic. Much more immediate than lack of dispersal or reduced gene flow is the threat of burning, cutting and trampling by cattle. However IF action is taken to control hunting, to fence off areas of forest from cattle grazing, to prevent fires, and to include the riparian fragments within in Ngel Nyaki Reserve as a single conservation unit, there may be a future for these forests and their associated fauna, so that issues of seed dispersal and other ecosystem processes then become important.

Forest restoration of degraded habitats is often dependant on naturally dispersed seeds (Wunderle 1997; Duncan & Chapman 1999). The riparian fragments in our study are already pre-adapted to fragmentation, and comprise trees adapted to disturbance, light and generalist seed dispersers, an advantage for restoration (Aizen & Feinsinger 1994). Several species, especially legumes such as *Albizia gummifera*, are wind dispersed, and many of the pioneers have small, light seeds well adapted for dispersal by a wide range of frugivores, eg. *Trema orientalis* (Richards 1998; Aerts et al. 2007) has shown that pioneers shrubs in Afrotropical fragments in Northern Ethiopia act as nurse crops for *Olea europea* ssp.cuspidata. However the authors stress the need to exclude livestock if there is any hope of forest restoration.
On Mambilla protection of the fragments from grazing and fire is essential. If this is achieved, then it is possible that natural restoration of most tree species could occur.

References


B: The role of *Cercopithecus nictans* (putty nose monkey) in seed dispersal at Ngel Nyaki Forest Reserve.

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The field work for this part of the project was completed in January 2007, and is in the process of being analysed and written up for a PhD thesis (see above).

In summary a group of about 15 *Cercopithecus nictans* at Ngel Nyaki forest were followed for five days a week, eight hours a day (6am-12pm; 4pm-6pm) for 18 months, from January 2005-January 2007. A focal group of Putty-Nosed Monkeys was followed for 8hrs. A day: 6hrs. In the morning from 6:00am – 12 noon, and 2hrs. In the evening from 4pm – 6pm local time. The method used was scan sampling with a fixed time interval; each scan sample was for 15 minutes, beginning on the hour, with an observation period of 5 minutes. Binoculars and a spotting scope were used for observation. During each observation period, the focal group was scanned from left to right on the first scan, then right to left next scan and so on. All feeding behaviour was observed and recorded. Only one activity was recorded for each member of the focal group during each scan period. Individuals were recorded as feeding if they were handling, pulling, biting, ingesting or chewing food. If they were feeding, the plant species and part (eg. leaf, flower or fruit) was recorded. The abundance of plant parts available was recorded using a score of 0 to 5 for each item. Scan sampling was chosen because it gives a representative cross-section of the activity budget (Nakawa, 2000).
This investigation has provided data on which tree species *C. nicitans* feed, and how this varies over the year.

In addition, information on seed species dispersed in *C. nicitans* dung was obtained by collecting seed information from 65 dumps, collected over a year. Within each dump the number of seeds, seed species, and seed size was recorded.

An experiment was then carried out to determine if the germination success of seed from each species was enhanced by passing through a *C. nicitans*; the experiment was designed to compare germination rates of seed that had undergone one of three treatments: 1) not dispersed (fallen below the tree), 2) collected and then spat out by *C. nicitans* and 3) swallowed and passed out by *C. nicitans*.

Information on whether or not *C. nicitans* disperse seed into specific microsites was collected by recording microsite data (a 50 m radius round a dump), from 20 microsites sites where *C. nicitans* dumps were observed, and 20 sites where they were not. Habitat variables of these microsites included ground layer species composition; litter depth; light availability; tree species, height of tallest tree and distance to the nearest conspecific tree (conspecific to the seed species found in the dung).

All this data, as well as additional studies to estimate *C. nicitans* group size and range, are being analysed and written up for publication at the moment.