Postdispersal Removal and Germination of Seed Dispersed by *Cercopithecus nictitans* in a West African Montane Forest

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Key Words

Cercopithecus nictitans • Germination • Directed dispersal • Nigerian montane forest • Secondary seed dispersal • Seed predation

Abstract

Factors that determine the effectiveness of primates as seed dispersers include (i) the microsite into which they deposit seed, (ii) secondary removal of seed by other taxa and (iii) the effect of gut passage and/or spitting on subsequent seed germination. This contribution evaluated these factors in the little studied putty-nosed monkey, *Cercopithecus nictitans*, in a Nigerian montane forest. Field experiments showed that *C. nictitans* has greatly increased in its importance as a disperser of medium-sized seed (>5 mm) because other large primates have been hunted to near extinction. *C. nictitans* disperses seed across habitats by spitting and defaecation. Rates of secondary seed removal were high for all seed species irrespective of the presence or absence of *C. nictitans* faecal matter, size or microsite variables. Gut passage enhanced germination relative to hand-cleaned seed, while spitting had either no effect or decreased the germination rate.

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Introduction

It is well established that primates play a key role in seed removal and dispersal in tropical forest trees [Gautier-Hion, 1984; Chapman, 1989; Wrangham et al., 1994; Kaplin and Lambert, 2002; Lambert and Chapman, 2005], where up to 90% of the tree and shrub species produce fleshy fruits adapted for animal dispersal and, as such, provide important primate food resources.

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0015–5713/10/0811–0041\$26.00/0

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In general, in tropical forest ecosystems, as seed size increases there is a predictable decrease in the availability of suitably wide-gaped frugivore species able to ingest and disperse them [Wheelwright, 1985; Chapman et al., 1992; Peres and van Roosmalen, 2002; Gross-Camp et al., 2009]. Furthermore, due to the loss of some primate species through the effects of hunting and deforestation, those that remain have become commensurably more significant as predominant dispersers of medium- (from >5 to ≤ 25 mm) and large-sized (>25 mm) seeds [Wright et al., 2007]. This situation applies to Nigerian montane forests (i.e. $>1,500$ m elevation), where a previously common large-gaped primate, the Nigerian/Cameroon chimpanzee (*Pan troglodytes ellioti*) [Matschie, 1914, cited in Oates et al., 2009], is now rare [Kormos and Bakarr, 2003]. However, the ecological effects of this decline may be partially offset, in some forests, by the compensatory presence of the more resilient, arboreal putty-nosed monkey (*Cercopithecus nictitans*) [Chapman et al., 2004]. Other potential primate dispersers of medium and large fruit in Nigerian Afromontane forests include the olive baboon *Papio anubis*, which Kunz and Linsenmair [2008] have shown to potentially disperse seed of up to 27 mm and the tanzania monkey (*Chlorocebus tantalus tantalus*) which ingests and deposits intact seed of up to 22 mm [Agmen et al., 2009]. However, *P. anubis* is uncommon at the study site discussed in this contribution, and *C. t. tantalus* is associated with the forest edge [Agmen et al., 2009]. In contrast, *C. nictitans* forages throughout Ngel Nyaki forest, as do chimpanzees.

P. troglodytes in montane forest in Uganda disperse seed ranging from 1 mm in length to 27.4 mm [Wrangham et al., 1994]. Associated with this contribution, seeds ranging in size from 1 mm (*Ficus* spp.) to 30 mm in length (*Pouteria altissima*) have been recovered from both *P. t. ellioti* and *C. nictitans* faecal deposits in Ngel Nyaki forest [H.M. Chapman, unpubl. data].

In spite of the ubiquitous distribution of *Cercopithecus* spp. (guenons) in African forests, there is evidence that different species of guenon behave differently in terms of diet and seed dispersal, and this, in turn, can be affected by forest type [Kaplin and Moermond, 1998; Chapman et al., 2002; Kaplin and Lambert, 2002]. Given the probable increasing importance of the ecological function of *C. nictitans* in Nigerian montane forests, this paper seeks to update prevailing views on the species' ecological role in forest conservation and regeneration. Such answers have been sought by exploring the following: (1) Does *C. nictitans* defaecate in any particular forest habitats as described in this study, for example plots with mature, tall trees versus more degraded forest edge plots? (2) Does the presence of *C. nictitans* faecal matter influence the rate of postdispersal seed removal? (3) What other factors affect postdispersal seed removal? (4) Are there differences in the germination rates of seeds that have been defecated by *C. nictitans*, spat out by *C. nictitans* and hand-cleaned experimentally?

Methods

Study Site

The research was conducted in the 46-km² Ngel Nyaki Forest Reserve (7°30' N, 11°30' E), located on the Mambilla Plateau in Taraba State, Nigeria, at an elevation of approximately 1,550 m. This reserve contains 7.5 km² of contiguous forest which is the largest on the Plateau [Chapman and Chapman, 2001]. The mean annual rainfall of approximately 1,800 mm occurs mainly between mid April and mid October (Nigerian Montane Forest Project [NMFP], rain-

fall data). Mean monthly maximum and minimum temperatures for the wet and dry seasons are 26 and 13°C, and 23 and 16°C, respectively [Chapman and Chapman, 2001].

Ngel Nyaki is one of the most floristically diverse montane forest stands in Nigeria [Dowsett-Lemaire, 1989], and at least 4 endangered tree species are common: *Entandrophragma angolense*, *Lovoa trichilioides*, *Millettia conraui* and *P. altissima*. Resident forest-dwelling primates include the endangered Nigerian chimpanzee (*P. t. ellioti*) [Beck and Chapman, 2008], the locally uncommon mona monkey (*Cercopithecus mona*) and the locally common putty-nosed monkey (*C. nictitans*) [Chapman et al., 2004] which is considered to be the genetically distinct *C. nictitans* subspecies *martini* [J.F. Oates, pers. commun.]. Other species (see above) include *P. anubis* and *C. t. tantalus*. This forest is an IUCN Important Bird Area and is likely a centre of diversity for amphibian and reptilian species [Blackburn, 2009].

C. nictitans Study Group, Forest Habitat and Microhabitat Identification

A focal group of semi-habituated *C. nictitans* (n = approx. 20) was studied for 359 days (from November 2005 to December 2006). Each day one of two designated observers followed the group from 6.00 to 12.00 h and from 16.00 to 18.00 h, and recorded the locations of opportunistically encountered *C. nictitans* faecal deposits. These defaecations varied from semi-intact deposits on the ground to more dispersed evidence found stuck to foliage and containing seeds.

Forest habitats ranged from disturbed areas sporadically grazed by cattle, usually with a herbaceous or grass understorey, to undisturbed forest comprising tall trees (up to 30 m in height), with a dense leaf litter layer and comprising little herbaceous understorey. Within each of these major habitats, microhabitats varied mainly according to herbaceous vegetation cover and its height, as well as slope.

In order to investigate (a) the prevalent forest habitat where *C. nictitans* defaecate (e.g. degraded forest edge vs. established forest) and (b) whether microhabitat variables influence removal rates of dispersed seed, twenty 10 × 10 m randomly selected plots, each centred on a *C. nictitans* faecal deposit, were selected and described. These plots were located across forest habitat types. Within these, 7 environmental variables were measured within each plot using the approach of Gross-Camp and Kaplin [2005]. These variables were chosen to reflect characteristics considered likely to influence (a) *C. nictitans* foraging behaviour and (b) the removal of *C. nictitans* dispersed seeds.

The first 4 variables were taken from twenty 1 × 1 m quadrats randomly placed within each of the 10 × 10 m plots. The measurements made were: (i) the numbers of each herbaceous plant species, (ii) the average height (cm) of the herbaceous vegetation, (iii) the percentage of bare ground and (iv) the leaf litter depth. The latter was measured by ascertaining the number of leaves pierced by a wire probe pushed into the soil [Feeley, 2004]. The remaining 3 variables measured once for each 10 × 10 m plot were: (i) the slope, using a Suunto handheld clinometer, (ii) the presence of mature trees (trees considered able to produce fruit) and (iii) the average tree diameter at breast height (when >10 cm).

To determine whether *C. nictitans* disperses seeds into distinct and preferred habitat types, the same descriptions were repeated for 20 randomly selected plots (10 × 10 m) without faecal deposits. The criteria for selection of these were that they were located over 50 m from any defecation study site and they were the first to be found without any evidence of *C. nictitans* deposits.

A principal component analysis using the MVSP software package version 3.1 [Kovach, 2003] was performed to investigate differences between *C. nictitans* defaecation and non-defaecation habitats following the rationale of Gross-Kamp and Kaplin [2005]. A spatial ordination of the sites was created using the environmental variables (see above) as well as the slope, presence/absence of mature trees and mean diameter at breast height of trees at each site. The data were log e transformed in order to meet better the assumption of normality.

Removal of C. nictitans Distributed Seeds

Five actively fruiting tree species were chosen for an experiment seeking to investigate the removal of seeds dispersed by *C. nictitans*. Each seed species was identified as being a common

Table 1. Seed species and family, seed dimensions and average number of seeds in faecal samples and spits

Species	Family	n	Mean seed size (length × breadth) mm	n	Mean number per faecal sample	n	Mean number per spit
<i>Isolona pleurocarpa</i>	Annonaceae	20	22.3 (2.4) × 12.5 (1.8)	12	3.3 (1.4)	7	3.9 (2.1)
<i>Santiria trimera</i>	Burseraceae	20	24.7 (0.1) × 16.9 (0.04)	24	2 (1.3)	13	11.9 (6.3)
<i>Celtis gomophylla</i>	Cannabaceae	20	3.0 (0.4) × 2.0 (0.3)	20	5 (1.4)	1	5
<i>Parkia filiciodea</i>	Fabaceae	20	22 (1.6) × 9.2 (0.6)	12	2 (1.1)	–	–
<i>Deinbollia pinnata</i>	Sapindaceae	20	7.0 (0.3) × 5.4 (0.2)	16	2 (1.1)	1	5
<i>Rytigynia umbellulata</i>	Rubiaceae	20	4.2 (0.4) × 3.0 (0.1)	18	5 (2.0)	–	–

Figures in parentheses indicate standard deviations.

source of fruit for *C. nictitans* in Ngel Nyaki forest and comprised a range of seed sizes known to occur in *C. nictitans* faecal deposits [unpubl. data]. Species fruit size data in this study were obtained by collecting 20 mature fruits from 5 individual trees comprising each of the chosen species. The fruit length and diameter of each of the 20 seeds per species were measured using digital callipers, and the mean length and diameter calculated. Seed size was measured in a similar way; the fruit was cleaned of pulp and 1 seed from each of the 20 fruits from each tree species was measured (table 1).

Seed Numbers in Each C. nictitans Faecal Deposit

The experiments described below required an estimate of the numbers of seed from each of the tree species found in a typical *C. nictitans* faecal deposit (table 1). This information was acquired by the opportunistic collection of 90 faecal deposits. These samples were taken to the NMFP field laboratory and wet sieved through a 0.5 mm mesh. Seed species within each deposit recovered were identified where possible, using the NMFP seed collection and their numbers per deposit recorded. Spat seed was also opportunistically collected from the forest floor between January and May 2006.

It has been observed by the authors that after primary dispersal by *C. nictitans*, a significant component of dispersed seed in the forests is then either removed (predation) or moved (secondary dispersal) by other forest-dwelling species. In order to examine the potential influence of *C. nictitans* faecal matter on such secondary removal rates of deposited seeds, experiments were established in 10 of the 20 plots (10 × 10 m) in which *C. nictitans* deposits had been found; the seeds for the experiment were manually extracted from the fruit of the 5 tree species. The plot choice was based on ensuring a representative selection of microhabitats. Each of the 10 plots was divided into quarters, and each quarter was designated as a subplot. The seed removal experiment was conducted in 2 phases. The first was between November 2006 and January 2007 and used 3 seed species (table 1), and the second occurred between March 2007 and May 2007 and used the remaining 2 species (table 1). Each population of the seeds was then divided into 2 groups. One group remained untreated (the control), whereas the other group was rubbed in 1-day-old *C. nictitans* faecal matter (the treatment) in order to test whether *C. nictitans* faecal odour had any influence on seed removal rates. Both the control and treatment seeds from the 5 tree species were then placed as piles in each of the 4 subplots replicated 10 times (= a total of 400 piles). The size of each seed pile was determined by the mean number of seeds of each species recovered from a single *C. nictitans* defaecation (table 1).

The numbers of seeds from each of the 5 species found to have been removed was recorded every morning between 6.30 and 8.00 h and in the evening between 16.00 and 18.00 h for the first 7 days, every morning for 9 days after that, and every second morning for a further 47 days

resulting in a total of 63 days of seed removal data. The decrease in frequency of observations over time was based on an observed decline in seed removal rate as the experiment progressed.

The significance of observed differences in seed removal rates in the controls and faecal treatments were tested using a Wilcoxon Mann Whitney test after 7 and 63 days. All 8 plot environmental variables, and the presence of faecal matter and seed size were incorporated into a quasi-Poisson regression model to investigate any effects on the observed seed removal rates. The least predictive factors were eliminated with automated backward selection, using the minimum value for Akaike's information criterion as the selection statistic.

Germination Experiments

The effect of *C. nictitans* gut passage and seed spitting on seed germination rates of the same 5 tree species was investigated via 3 treatments. These were (i) defaecated seed, unwashed, (ii) hand-cleaned seed and (iii) spat seed, unwashed. Sample sizes comprised 20 seeds per treatment and were sown at a depth of 1 cm into individual plant pots using moist soil collected from the edge of the research forest. These pots were arranged in the NMFP nursery using a randomized block design. They were monitored daily for seedling emergence for 232 days between December 2005 and August 2006. To avoid any confounding genetic influences arising from individual trees, the seeds for each tree species were collected from a number of conspecific trees.

A mean number of days to germination for each species, in relation to treatment, was determined using only seeds that germinated within the experiment's time limits. A binomial generalized linear regression was used to determine any significant treatment effects on the proportion of seeds germinated. All analyses were carried out using the statistical software R, version 2.5.1 [R Development Core Team].

Results

Habitat Influence on C. nictitans Defaecation

The results of the multivariate principal component analysis showed no differences between defaecation and non-defaecation sites; thus, there was no indication of any 'directed dispersal' by *C. nictitans*.

Seed Species Characteristics and Seed Removal Rates

Seed species, mean seed size and average number of seeds per defaecation and spit are presented in table 1.

Seeds from all 5 tree species were removed at high rates. Of the 400 piles of seed placed on the forest floor, 65% of the total seeds had been removed by the first week and 88.5% by the end of the study period (63 days). Eighty one percent of seed removal in the first week occurred between 16.30 and 9.00 h. All of the *Parkia filiciodea* seed had been removed by 8 days after the start of the experiment and by 30 days for *Deinbollia pinnata*. After 60 days (the end of the experiment), 10% of seed remained of *Rytigynia umbellulata*, 5% of *Celtis gomophylla* and 2% of *Santiria trimera*.

Influence of Faecal Matter, Seed Size and Microsite Variables on Seed Removal Rates

The only significant effect of faecal matter on seed removal rates was found in *R. umbellulata*, where the presence of faecal matter increased seed removal rates by 10% ($W = 475$, $p < 0.01$) and 8% ($W = 435$, $p < 0.001$) after 7 and 63 days, respectively (fig. 1). Seed size had no effect on removal rates, and no single environmental variable was found to have any significant common effect on the removal rates. How-

Fig. 1. The percentage of seeds from faeces, spits and ripe fruit germinating in the germination trials, showing the proportion of *Deinbollia pinnata* (a), *Santiria trimera* (b) and *Isolona pleurocarpa* (c) seeds germinating. ● = Defaecated seeds; ■ = spat seeds; ▲ = seeds hand cleaned of pulp.

ever, in the case of *S. trimera* and *R. umbellulata*, 6 of the variables did explain a small proportion of the variability associated with removal rates. For example, in the case of *S. trimera*, removal rates increased positively with vegetation height ($Z = 8.668$, $p < 0.001$). Conversely, rates were found to be significantly reduced in the presence of mature trees ($Z = -14.016$, $p < 0.001$). In the case of *R. umbellulata*, the seed removal rate was significantly higher under canopy cover ($Z = 9.340$, $p < 0.01$).

Effects of C. nictitans Gut Passage and Spitting on Seed Germination Rates

The effect of gut passage on germination rate was positive for 3 of the trial species, i.e. *S. trimera* (35%, $Z = 4.9$, $p < 0.001$), *D. pinnata* (33%, $Z = 4.8$, $p < 0.001$) and *Isolona pleurocarpa* (65%, $Z = 7.772$, $p < 0.001$; fig. 1). Conversely, in the case of spat seed, the germination rate was either not significantly different to cleaned seed, or, in the case of *S. trimera*, germination was significantly lower (8%, $Z = -0.5$, $p < 0.05$; fig. 1).

Discussion

Primary Dispersal of Viable Seed

This study has confirmed that the ecological function of *C. nictitans* has characteristics in common with that of other guenons [Chapman et al., 2002]. However, this work has also shown that *C. nictitans* is now a particularly efficient disperser of medium-sized seeds by virtue of its relatively wide gape and its relative abundance compared with other primates in the Ngel Nyaki forest. That there was no detected preference for defaecation in the more open, sporadically grazed versus relatively undisturbed forest habitat means that seeds are widely dispersed by *C. nictitans*. Seeds dispersed into the degraded areas of forest have the potential to contribute to forest regeneration [Lambert and Chapman, 2005; Chapman and Russo, 2007]. Moreover, as some such degraded areas of forest at Ngel Nyaki have recently been protected from grazing and burning, there is a realistic opportunity for regeneration.

Gut Passage and Spitting Effects

As the result of gut passage, enhanced germination rates compared to clean seed were observed amongst all 3 of the seeds tested. This finding is interesting as not all primates enhance the germination rate of seed they swallow and defaecate intact [Wrangham et al., 1994; Stephenson et al., 2002]. However, several studies have reported increased germination rates for some species after passage through primate guts [Estrada and Coates-Estrada, 1984; Agmen et al., 2009; Valenta and Fedigan, 2009]. Conversely, spitting was found to offer no improvement in germination rate. In fact, spat seed had reduced germination rates in *S. trimera*. This result does not however discount the possibility in other species that spitting (seed cleaning) could enhance seed survival rates in the field, as reported by Lambert [2001].

Secondary Seed Removal Rates

Seeds from all 5 of the tree species tested in this study underwent high rates of removal, particularly between 16.30 and 9.00 h, and of these, only *R. umbellulata* showed higher rates of removal in the presence of *C. nictitans* faecal matter. Generally, these results support Feer and Forget [2002], who also found that dung presence

had no effect on seed fate. While the *R. umbellulata* result in this study is consistent with other findings where faecal olfactory cues did in fact increase postdispersal seed removal [Chapman, 1989; Shepherd and Chapman, 1998; Andresen, 1999, 2002], it cannot be discounted that this result was more a reflection of the large seed size of *R. umbellulata*, rather than the presence of faecal matter. Nocturnal predators may have been attracted by olfactory cues and found the control seeds because they were relatively close to the seeds exposed to faecal matter. To overcome this problem, a future study should include some plots with only seed exposed to faecal matter and others that are not exposed, as well as some plots with both exposed and unexposed seeds, at the same time controlling for seed numbers.

No environmental effects were found to universally affect all seed species. Indeed, where environmental effects were observed, they were only in association with single species and these effects were consistently weak and sporadic. Seed size or interaction between seed size and the measured environmental variables had no effect on removal rate, which is in contrast to the findings of Forget et al. [1998], who found a positive correlation between seed size and removal rate. This may be because the seed sizes used in this experiment were not as large as those used by Forget et al. [1998] and were too small to attract predators/dispersers. However, the combinations of seed predators and probably dispersers were highly efficient and relatively consistent in locating the seed species tested. The observed seed removal rates in this study were comparable to those reported elsewhere [Andresen, 1999], although different from the finding of Chapman [1995], in Kibale National Park where seed removal rates varied significantly among species, such that the probability of disappearance ranged from 10 to 100% after 6 months.

Seed removal cannot be attributed to predation only; removal can also result from secondary dispersal [Forget and Millerton, 1991; Andresen, 1999; Vander Wall et al., 2005]. The relative importance of these two influences has been found to depend on a number of factors including season, habitat, forest community and seed characteristics [Andresen, 1999; Vander Wall et al., 2005]. More specifically, seed burial by dung beetles (Scarabidae) has been found to account for a significant proportion of seed removal from frugivore faecal deposits in tropical forests elsewhere [Estrada and Coates-Estrada, 1991; Andresen, 2002]. Such a mechanism is a possibility in Ngel Nyaki forest where, recently, high densities of dung beetles have been recorded [A. Barnes, pers. commun.]. Moreover, seed removal in Ngel Nyaki may also be attributable to rodents, particularly porcupines. Old World porcupines (Hystriidae) are known to scatter hoard [Vander Wall, 1990], and in this study they were frequent nocturnal visitors to the experimental plots, as evidenced by tooth marks on the metal tags marking the quadrats. This is consistent with the finding of Feer and Forget [2002] from the Neotropics that showed that rodents, by scatter hoarding of seeds, effect secondary dispersal. Such behaviour offers seeds a number of advantages, such as escape from pathogens and predation, decreased interspecific competition and deposition into favourable microsites [Forget, 1990; Forget and Millerton, 1991; Stoner et al., 2007]. In view of the above, the role of rodents in seed dispersal in African forests is worthy of more formal investigation as secondary seed dispersal by rodents in African forests has not been documented to date [Stoner et al., 2007].

Conclusion

In general, this work has shown that *C. nictitans* has the potential to play an important role in the maintenance and restoration of Ngel Nyaki forest and, by extrapolation, other Nigerian montane forests, because they are still common relative to other large primates. This advantage of large-bodied frugivores comes primarily from large seed dispersal via defaecation and gut passage and the provision of opportunity for secondary dispersers to move seed around. This study has advanced the understanding of the ecological role of *C. nictitans* and tests assumptions about the monkey's fruit-frugivore impacts within Afromontane forests. Such findings should contribute to the development of effective strategies essential to the conservation and re-establishment of forest remnants in West African forests.

Acknowledgments

We would like to thank Steve Gawaisha for his data contribution, Musa Bawuro and Matt Walters for field assistance, Dr. Jenny Brown for her guidance with data analyses and 3 anonymous reviewers who made valuable comments on an earlier draft of the manuscript. We are grateful to the Taraba State Forest Service for their invitation and permission to conduct research. Financial Support came from the University of Canterbury in the form of a Summer Scholarship to J.B., the North of England Zoological Society and Nexen Nigeria.

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