



## Factors affecting seed removal by large rodents in a West African woodland

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### Abstract

*Detarium microcarpum* and *Diospyros mespiliformis* are dispersed by herbivores and frugivorous birds, but *D. microcarpum* has large seeds that are potentially attractive to rodents which could act as seed predators and dispersers. Here, we simulate primary dispersal by birds (placing seed on ground), the seeds were secondarily dispersed by scatterhoarding rodents. This adds to our understanding of diplochory in woodland habitats experiencing frugivore loss; by investigating the interaction of habitat and seed type on secondary dispersal by rodents. Moreover our study combines information on two understudied habitat (degraded woodland), a large seed disperser organism (Scatter hoarding rodent). We quantify how degradation and seed size interact to affect the balance between predation and dispersal. We distinguish between burial and cached seed, and measure dispersal distances. We established seed ‘dumps’ to simulate frugivore dispersed seed in each of three woodland- habitats Yankari Game Reserve, Kanawa woodland, and Nafada degraded woodland habitats and used a Bayesian statistics to compare predation rates and proportion of seed i) buried and ii) cached in each habitat with large and small seed species. Infrared cameras were used to identify predators and/or seed dispersers. Seed fate differed markedly among habitats. Seed predation rates were highest in degraded woodland habitats than in Reserve habitat (YGR->NFD)  $P = 0.94$ , however, the probability of being predated was higher for the large seeded than for the small seeded species. The probability of scatter hoarded seed being buried was markedly higher than being cached. Almost all seeds were predated and dispersed by the African pouched rat, *Cricetomys gambianus*. In this study we demonstrate the importance of diplochory in woodlands and quantify the role of scatterhoarding with respect to habitat and seed size in the context of habitat degradation. Seed predation is markedly higher in degraded habitats particularly for large seeded species ( $\Delta DIC=1719$ ). Seed burial is more common than caching across all habitats and dispersal is markedly further in Reserve than disturbed or degraded woodland. Our findings would stimulate a new area of research into woodland plant-animal mutualisms.

**Keywords:** Woodland habitats, rodents, diplochory; seed dispersal, scatterhoarding, conditional mutualisms

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### Introduction

Woodland in Tropical Savannas are facing a seed dispersal crisis (McConkey *et al.*,

2012) as dispersal networks are destroyed through anthropogenic drivers such as habitat degradation, fragmentation and

## Factors affecting seed removal by large rodents in a West African woodland

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hunting. Such changes affect woodland composition and structure (Peres *et al.*, 2003; Nuñez-Iturri and Howe, 2007; Wright *et al.*, 2007; Vanthomme, Bellé and Forget, 2010) for example, regenerating woodlands tend to have a higher proportion of wind dispersed species than their ancestral populations (Vanthomme, Bellé and Forget, 2010). provide evidence for the decline in native bird species in plateau state having already led to insufficient seed dispersal and vastly reduced recruitment of native tree species (Anderson *unpublished data*), which this is likely to trigger a cascade of extinctions. Until recently such negative effects of years of inadequate dispersal have been masked by the long generation time of forest tree species (Guimaraes, Galetti and Jordano, 2008) but insufficient seed dispersal is now recognised as the major threat to the future of many woodlands (Schupp, 1993; McConkey *et al.*, 2012).

Up to 70% of tropical savannah tree species produce fleshy fruits which have evolved for dispersal by animals (Corlett, 2007; McConkey *et al.*, 2012). This dependence of trees with fleshy fruits on animals for dispersal makes them particularly vulnerable to frugivore decline and extinction (Corlett, 2011; Fleming and John Kress, 2011). Without animal dispersers many tropical savanna tree species will lose recruitment to high levels of seed predation and seedling competition under the parent tree (Janzen, 1969; Janzen, 1970; Connell, 1971; Harms *et al.*, 2000; Chapman, Goldson and Beck, 2010). Tree species with large fruit are most at risk because they depend on large bodied frugivores (>1kg) for dispersal (Forget *et al.*, 2007; Schupp, 1993) and the larger bodied frugivores are more vulnerable to the effects of reduced habitat size, habitat degradation and hunting than are small bodied frugivores (Corlett 2007; Wright *et al.*, 2007). However, while predictions about the potential consequences of frugivore loss on seed dispersal are possible, particularly in the case of large seeded tree species (McConkey and Brockelman, 2011), the actual effect of frugivore decline on any given plant species depends on the

interaction of multiple factors (Galetti *et al.*, 2006) because plant-frugivore networks are often nested within wider interaction networks which may build resilience into the system (Gilbert 1980).

The loss of primary frugivores does not necessarily lead to extinction because seed may be secondarily dispersed by abiotic means such as water or gravity, or by scatterhoarding animals (Vander Wall, 1990; Forget, 1996; Vander Wall, Kuhn and Gworek, 2005). Scatterhoarding refers to an animal behaviour whereby seed is collected during periods of abundance and stored for later consumption in scattered caches with just one or a few seed in each (Vander Wall, 1990). In the case of rodents, scatterhoarding can be seen as a conditional mutualism (Bronstein, 1994) in that an animal's behaviour will depend on the environment. When food is scarce they will act as predators but when food is abundant they may store some seed and act as mutualists, such that their contribution to the seed dispersal mutualism varies along a predation-mutualism gradient (Theimer, 2015), depending on the relative abundance of seed vs scatterhoarder density and the advantage to a seed of being cached vs left on the woodland floor (Jorge and Howe, 2009).

Despite the potential importance of scatterhoarding to seed dispersal in tropical savanna it has rarely been quantified. While several cases have been described in the Neotropics (Forget and Milleron, 1991; Forget, 1992; Forget, 1993), only a few investigations cite the probability of seed fate in terms of predation vs caching and/or burying (Feer and Forget 2002; Jorge and Howe 2009). Moreover in Africa scatterhoarding by rodents has only been described in few instances (Nyiramana *et al.*, 2011; Aliyu *et al.*, 2014) and quantification of seed fate by secondary dispersal has rarely been attempted (Midgley, Gallaher and Kruger, 2012).

Our overall aim in this study is to determine the extent to which secondary seed dispersal by rodents is affected by woodland degradation. To do this we investigate the

extent to which seeds deposited by frugivores onto the woodland floor are then secondarily moved (i.e. *diplochory sensu*) (Vander Wall and Longland, 2004) by rodents to sites with more suitable conditions for germination (Vander Wall, 1990). We determine how this behaviour varies with a) seed characteristics and b) habitat in terms of increasing degradation. To this end the interaction among habitat, disperser networks, conditional mutualists and seed species must be addressed (McConkey and Brockelman, 2011).

We have chosen one large seeded (> 20 mm in diameter) and one small seeded (<10 mm) tree species with different palatability to rodents and we investigate the fate of this seeds over three woodland habitats from Reserve habitat through woodland slightly to extremely degraded habitat. Ihuma *et al.* (2011), report that habitat degradation is accompanied by frugivore loss in Africa. (1) To address the question of how seed size may affect seed fate in terms of predation vs dispersal we hypothesise that predation rates will be markedly higher in *Detarium microcarpum* a large seeded than *D. mespiliformis* a small seeded species. (2) Consequently we hypothesise that caching and burying rates (seed dispersal) combined will be higher for small seeded species. (3) Seed dispersal Network will be less strong in disturbed habitats because in such habitats there are fewer fruiting trees and less frugivores than in the Game Reserve woodland, such that rates of seed predation by rodents will increase. This will be most severe in large seeded species.

## Materials and Methods

### Study site

Our study site were Yankari Game Reserve (9° 50' N and 10° 30'E) in Bauchi State, Kanawa woodland (10° 16' 30'' N and 11° 18' 32'' E) and Nafada (11° 22' 23'' N and 11° 16' 17'' E) in Gombe State, northeast Nigeria. Yankari Game Reserve is 2,242 km<sup>2</sup> in area, it is the largest woodland area in Bauchi State. The Reserve lies at 400-600 m elevation at its upper limit the reserve borders directly onto overgrazed grassland.

Kanawa and Nafada, the Reserve lies at about 200-300 m elevation and are affected by annual grass burning, cattle grazing and logging. Three obvious differences among the habitats we studied (Game Reserve, Kanawa and Nafada); Yankari Game Reserve and degraded woodlands of Kanawa and Nafada, from here on Yankari is referred to as YGR, Kanawa and Nafada as KNW and NFD respectively. Are i) presence/absence of focal tree species and therefore food abundance; ii) density and number of primary seed dispersers and iii) rodents behavior in terms of food satiation. Both *D. microcarpum* (Guill. and Perr.) and *Diospyros mesfiliformis* (Hochst. ex A. DC.) are common tree species in the YGR. However, while *D. mesfiliformis* is also common in KNW and in NFD, *D. microcarpum* is rare (unpublished data, B. Aliyu).

The mean annual rainfall is approximately 1200 mm YGR, 1000 mm in KNW and 800 mm NFD (Yankari and Gombe State, rainfall data) and the mean monthly maximum and minimum temperatures for the wet and dry seasons are 40 and 27 °C; 34 and 20°C, and 38 and 26 °C, respectively. YGR has been identified as a Birdlife International Important Bird area and is home to several primate species including the Red Data Listed subspecies of chimpanzee (*Pantrogodytes ellioti*, the putty-nosed monkey (*Cercopithecus nictitans* Gray), black-and-white colobus (*Colobus guereza occidentalis* de Roch.), mona monkey (*Cercopithecus mona* Schreb.), tantalus monkey (*Chlorocebus tantalus tantalus* Ogilby) and olive baboon (*Papio anubis* Lesson) Elephant (Naziru *et al.*, 2016) (Chapman, Olson & Trumm, 2004).

### Study species

For our investigation we chose one large seeded and one small seeded tree species with similar flowering and fruiting phenology and primary dispersal agents. *Detarium microcarpum* is an emergent tree. The plant belongs to the family Caesalpiniceae; it can grow up to 14 m in height. It produces green fleshy fruits 28.6

## Factors affecting seed removal by large rodents in a West African woodland

( $\pm 0.81$ ) mm long and 22 ( $\pm 0.49$ ) mm in diameter. Seed size is 18 ( $\pm 0.33$ ) mm x 12.3 ( $\pm 0.21$ ) mm. *D. microcarpum* is one of the species which is used in many different ways through all west tropical Africa; it is utilized for timber, as fuelwood, food source (seeds, leaves and roots) and for the treatment of numerous ailments (diarrhoeas, dysenteries, haemorrhoids, leprosy, syphilis etc.), but the species does not appear to be affected from the harvesting level at present. *Detarium microcarpum* is one of the local fruit-bearing species most exploited in Burkina Faso (Maja *et al.*, 1998). The bark, leaves and roots are widely used because of their diuretic and astringent properties. They are also used against malaria, leprosy and impotence (Maja *et al.*, 1998). *Diospyros mespiliformis* belongs to the family Ebenaceae, the plant produces round fleshy fruit of approximately 12 ( $\pm 0.9$ ) mm x 08 ( $\pm 0.71$ ) mm. The fruit bears three or four seeds measuring 10.4 (0.43) mm x 03.5 ( $\pm 0.38$ ) mm. Mature trees can reach up to 10 m in height. Fruiting phenology for both species varies among years but is mostly towards the end of the dry season into the middle of the wet season July to August. Fruit of *D. mespiliformis* is swallowed by primates (including *P. t. ellioti*, *C. nictitans*, *P. anubis* and *C. t. tantalus*) and large gaped birds such as the Cameroon olive pigeon (*Columba sjostedti* Reich.) and the piping hornbill (*Bycanistes fistulator* Cassin) (Ihuma 2011), while the mesocarp of the fruit of *D. mespiliformis* is soaked and the endocarp is thrown, many fruit were observed sucked by frugivores, with seeds accumulating on bare ground under parent or frugivore roosts in Neotropical forests (Chauvet, Feer and Forget, 2004; Feer and Forget, 2002; Forget, 1991).

*Detarium microcarpum* and *Diospyros mespiliformis* plant families are a preferred source of fruit in the diet of frugivores and thus act as key dispersers for a range of seed size (Fujita and Tuttle, 1991). Overall, seeds measuring ca. 1 mm or up to 7 mm are ingested and defaecated during flight, whereas larger seeds are dropped beneath feeding roost once the pulp has been sucked

(Forget *et al.* 2007; Picot *et al.* 2007). In Benin, for instance, Djossa *et al.* (2008) observed that the pulp of *Vittelaria paradoxa* Kotschy (Sapotaceae) fruit and seeds (31 x 23 mm, Length x Width) were found in the faecal sample and under feeding roosts, respectively, of Bat species among them the two *E. gambianus* and *M. pusillus* bat species present in West Africa.

### Experimental design

Our experiment included three habitats: i) extremely degraded woodland NFD, ii) Degraded woodland KNW which was within 100 m of the grassland and iii) YGR located in the woodland. Within each habitat five replicates of a 1x1 m grid of 4 x 5 seeds were set up at least 25 m apart. The grids were set in areas of each habitat in which adult trees of either or both focal species were present, or where seed of these species had been observed to have been primarily dispersed by frugivores. The grid design aimed at stimulating primary dispersal of our key species by frugivores.

Within the grid, each seed was marked with a one meter long thread following the method of Forget (1990) to aid us in finding them. As the seed coat of *D. mespiliformis* was too thin to tolerate glue, the thread on these seeds was attached by drilling a hole through the seed and tying the thread round. This was feasible because the cotyledons are sufficiently robust that they do not break with drilling. In contrast the hard seed coat of *D. microcarpum* shattered when drilled but was hard enough to tolerate glue. To test for any effect of the two treatments, we compared seed removal rates of glued versus drilled seeds at NFD and YGR. No difference in seed removal was observed.

Once set up, the grids were censused after 3 and 7 days for seed fate, which was categorized into four classes: i) immediate consumption (predation); ii) caching under the litter, seeds being hidden below leaves; iii) burying into the ground with seeds being buried into soil; and iv) removed (fate unknown). Predated seeds were identified by having been partially consumed or by the presence of a thread with no seed attached. Removed seeds were searched for within a 5

m radius which was then extended to 10 m if all seeds were not found. When a seed was found buried or cached a knot was made in the end of the thread. All threads from missing or eaten seeds were removed following the method of (Forget, 1996).

Infra-red motion detector cameras (Spypoint IR-6) were attached to trees above the plots to determine which rodent genera were predated/dispersing the seed.

#### Data analysis

We analysed our data on rates of predation vs caching and burying within a Bayesian framework because this approach is superior to classical statistical approaches when it is necessary to fit complex multilevel models (Clark 2005; Gelman and Hill, 2007). Bayesian inference is based on testing hypotheses of probability distributions and is increasingly used in ecology (Ellison, 2004). We were interested in seed fate, that is, the probabilities of seed remaining on the plot, being predated, cached or buried (dispersed) or lost in the different habitats (YGR, KNW and NFD), and how seed species (large vs small) affect seed fate. We fitted one mixed effects logistic multinomial regression model to examine the influence of seed species and habitat on seed fate. Additive random effects were fitted for plot, habitat and replicate variables. The multinomial probabilities of each seed fate were averaged over habitat plot replicate and were reported in terms of posterior means and a 95% credible interval (Bayesian analogue of a 95% confidence interval). The effects of species as well as species habitat interaction were assessed by evaluating deviance information criterion (DIC) for the model with and without the above factors.

We fitted another mixed effects logistic multinomial regression model to examine the influence of seed species (large) and habitat (YGR, KNW and NFD) on the response variable dispersal distance. Dispersal distance was multinomially distributed. Additive random effects were fitted for plot, habitat and replicate

variables. As in the previous model the multinomial probabilities were averaged over habitat plot replicate and were reported in terms of posterior means and a 95% credible interval. We used DIC to evaluate whether considering the effects of species as well as species habitat interaction improved the fit of our models.

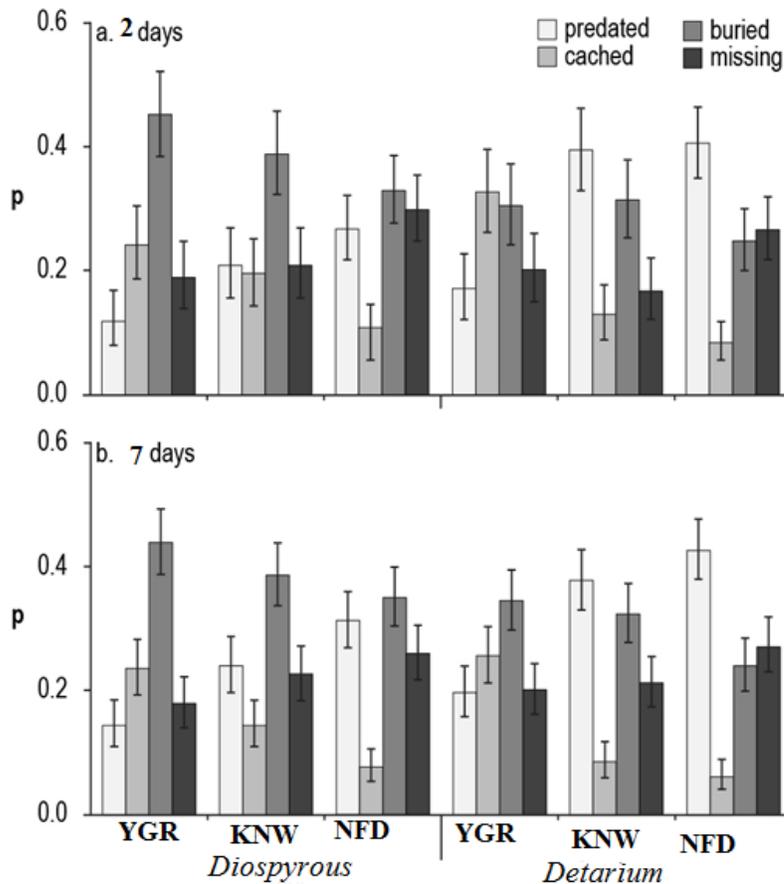
The DIC reflects the goodness-of-fit of a model while penalizing for complexity (Spiegelhalter, 2002). The smaller DIC value corresponds to the better model, and while a difference of 5-10 is suggestive, a difference of >10 indicates that the model with the smaller DIC is clearly statistically better. 100 000 iterations were run for each model, after the first 10 000 were discarded as a burn-in. The convergence was assessed visually. We used the statistical software package WinBUGS (Spiegelhalter *et al.*, 2002) for our analysis.

#### Results

Fifteen of the 16 out of the 17 images taken by the infra-red cameras of animals visiting the plots were of the African pouched rat *Cricetomys gambianus* Waterhouse (Nesomyidae). The other visitor caught by the camera was a porcupine *Atherurus africanus* Gray (Erethizontidae).

Rodents visited all plots regularly, irrespective of habitat. After 7 days, of the total 2,400 seeds deposited and censured across all the three habitats, 1167 (48%) were removed from the plots. Of those removed 853 (73%) were recovered. The actual fate of the recovered seed at day 2 and 7 in each habitat is presented in figure 1a and 1b. The probability of any recovered seed being predated, cached, buried or missing after 2 and 7 days, as predicted from the mixed effects logistic multinomial regression model is presented in Figures 1a and 1b. As the conclusions drawn from day 2 and day 7 census were very similar, from here on in this paper we discuss the results for day 7 only.

## Factors affecting seed removal by large rodents in a West African woodland



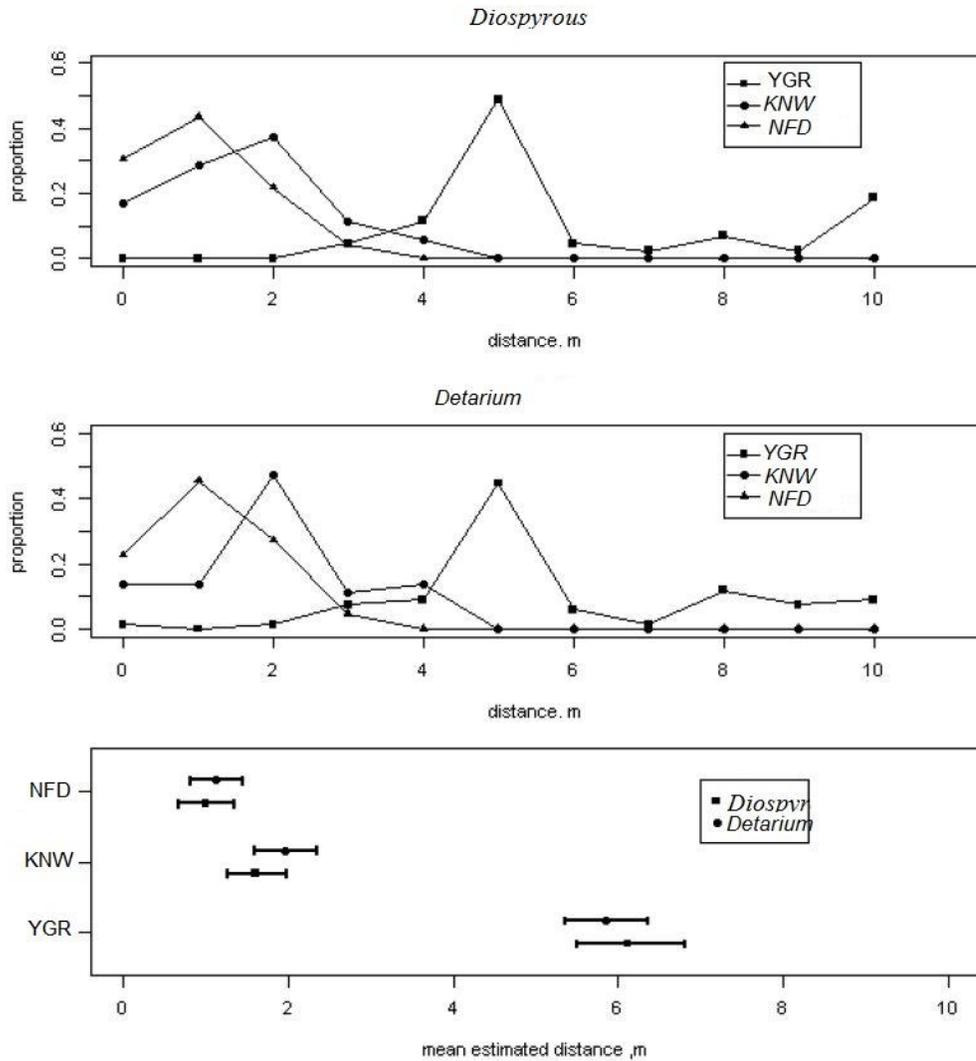
**Figure 1a and 1b: Seed fate for day 2 and day 7 in the three habitats Predation rates**

*Detarium microcarpum* seeds had a higher probability of being predated than *D. mespiliformis* seeds in all three habitats but especially in the NFD and KNW ( $\Delta\text{DIC}=80.3$ ) (Table 1). Predation rates increased with degradation irrespective of species; the probability that predation rates increased with degradation (YGR->KNW->NFD) is 0.94. This probability is comparable to p-values in classical,

statistics. The inclusion of the interaction term species habitat significantly improved our model fit ( $\Delta\text{DIC}=6.9$ ), implying that the effects of habitat on the multinomial distribution of seed fates were different for the two species. In general, the predation rates of *D. microcarpum* increased relatively more with degradation from KNW to NFD than did *D. mespiliformis*.

**Table 1: Estimated posterior means and 95% CIs for the probability of being predated by habitat type and species.**

Species	YGR	KNW	NFD
<i>Diospyros</i>	0.59 (0.54,0.64)	0.47 (0.42,0.51)	0.42 (0.37,0.47)
<i>Detarium</i>	0.57 (0.53,0.62)	0.40 (0.36,0.45)	0.30 (0.26,0.35)



**Figure 2: Distance a seed is moved in the three habitats**

**Caching and burying rates**

Rodents either cached seeds beneath the thick litter that covers the ground early in the rainy season or buried them 1-2 cm deep and covered the site with litter. The probability of seeds being hoarded in this way varied between the two species; it was markedly higher in *D. mespiliformis* than in *D. microcarpum* across all three habitats ( $\Delta DIC=1719$ ). For both seed species in each habitat, burying was more common than caching: *D. microcarpum* YGR  $P= 0.0021$ ; KNW  $P< 0.0001$ ; NFD  $P< 0.0001$ ; *D. mespiliformis* YGR  $P=0.0439$ ; KNW  $P<0.0001$  and NFD  $P<0.0001$  (Figure 1a & 1b).

While we found that there was no significant difference between species in the distance seed was moved before being cached or buried (Figure 2), there was a marked difference in the distance seed was moved among habitats ( $\Delta DIC= 635.27$ ). In the YGR up to 10% of non –predated (remaining) seed was moved up to 10 m from the plot before being buried, with a mean distance of 5.93 m +/- (*D. mespiliformis*) and 5.65 m (*D. microcarpum*) (Figure 2). In contrast in KNW and NFD habitats no buried seed was recovered more than four meters from the plot with mean of 1.59 m and 1.00 (*D. mespiliformis*) and 1.97 m and 1.14 m (fig. 2) (*D. microcarpum*) respectively ( $\Delta DIC=1602$ ).

## Factors affecting seed removal by large rodents in a West African woodland

### Discussion

When plant-frugivore mutualisms are threatened by frugivore decline, the wider interaction networks in which they are embedded may become critical by building resilience into the system (Gilbert, 1980). In this study we have quantified the role of habitat and seed type on rodent behavior in the secondary dispersal of large, frugivore dispersed seeds in a range of woodland habitats suffering increasing levels of degradation. While rodents may hinder regeneration of frugivore-dispersed tree species through predation (De Steven and Putz, 1984), they may, under some circumstances enhance regeneration through scatterhoarding (Forget, 1993). In woodlands which have lost their primary dispersers scatterhoarding may be key to a species survival (Feer and Forget, 2002). To date research into diplochory in African woodlands has been minimal (Nyiramana *et al.*, 2011; Midgley, Gallaher and Kruge, 2012), yet African woodlands are just as vulnerable as Neotropical habitats to degradation. The results of our study strongly supported two of our three original hypotheses i) that irrespective of habitat, predation rates would be higher in the more large *D. microcarpum* than *D. mesfiliformis* and iii) that rodent behaviour would vary according to land use such that rates of seed predation will increase with increasing degradation. In contrast, hypothesis ii) that combined caching and burying rates (seed dispersal) would be higher for *D. mesfiliformis* than for *D. microcarpum* across all three habitats was only weakly supported. The most parsimonious explanation for higher predation of *D. microcarpum* seeds relative to *D. mesfiliformis* and the one we used in developing our first hypothesis was based on comparative studies of Neotropical *Moronobea coccinea* Aubl. (Clusiaceae) (Forget, 1991) and *Chrysophyllum lucentifolium* Cronq. and *Manilkara huberi* (Ducke) A.Chev. (Sapotaceae) (Feer and Forget, 2002; Chauvet, Feer and Forget, 2004). As is the case for *M. coccinea*, the fruit of *D. mesfiliformis* has sour yellow-to-orange latex which in *M. coccinea* has been shown to be relatively unpalatable to rodents. In contrast, Neotropical members of the Sapotaceae family have palatable and nutrient rich cotyledons, a hard seed coat (associated with a rich resource and show

intense post-dispersal seed predation by rodents (Feer and Forget, 2002; Chauvet, Feer and Forget, 2004).

Rodent behaviour is well known to vary both temporally and spatially. For example Feer and Forget (2002), found that rates of seed predation on *Chrysophyllum lucentifolium* were higher in years when fruit was overall more abundant. The proportion of seed predated vs scatterhoarded varies with increasing degradation. While some authors report decreased dispersal with increasing degradation (Asquith *et al.*, 1999; Cordeiro and Howe, 2003; Galetti *et al.*, 2006; Cramer Mesquita and Williamson, 2007a; Cramer *et al.*, 2007b; Wright *et al.*, 2007) our results were concordant with those of Dennis *et al.* (2005), and Jorge and Howe (2009), in that we measured the highest predation rates in the NFD an extremely degraded habitat and the lowest in the YGR a protected and comparatively less degraded habitat, across both species. The reason for this finding may be that NFD support fewer large seeded fruiting trees because of their inability to tolerate exposure effects such as high light intensity, logging, fire encroachment, and low relative humidity relative to habitat like Reserve such as the YGR (Knorr and Gottberger, 2012). In addition, what primary dispersers there are in the NFD do not disperse seeds as far away from the parent tree as they would have being in YGR habitat (Howe and Smallwood, 1982). Together these factors can explain why rodents behaved more as predators than dispersal agents in the NFD and the KNW woodland (Theimer, 2005). In contrast, in the YGR habitat, markedly more seeds were scatterhoarded because the abundance of seed dispersed onto the woodland floor satiates the rodents (Feer and Forget, 2002), leaving excess seed to be scatterhoarded (Forget, 1993).

In addition to more seed being dispersed in the YGR, we found that dispersal quality (Schupp, 1993) was higher in YGR than in the NFD and the KNW. Seed was moved on average five times further in the YGR than in the NFD (fig. 2). Theoretically the farther an individual seed is moved from a parent tree, the higher the likelihood of its survival because it 'escapes' from density dependant intraspecific competition and host specific parasites and predators (Janzen, 1970; Connell, 1971; Terborgh *et al.*, 1993;

Notman Gorchov and Cornejo, 1996; Peres and Baider, 1997).

Our third hypothesis, that caching and burying rates (seed dispersal) combined would be higher for the small *D. mesfiliformis* than for *D. microcarpum* was only weakly supported. It may be that within the context of the whole community other factors came into play which obscures this expected result. For example the density of rodents and/or other fruiting trees may vary among the habitats.

### Conclusion

Overall this study suggests that any resilience built into this system of dispersal networks varies according to habitat and seed type. Unfortunately we found that the breakdown of primary dispersal networks associated with increasing degradation is mirrored by a reduction in secondary dispersal, indicating little resilience in the system to the effects of anthropogenic change. However, the magnitude of increase in predation with degradation varies with species, such that while both *D. mesfiliformis* and *D. microcarpum* are likely to suffer dispersal limitation through predation and reduced primary dispersal in degraded habitats, *D. mesfiliformis* is more likely than *D. microcarpum* to tolerate increasing degradation effects because its seeds are not particularly large with much nutrients to predators; would- be predators become dispersers.

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## Factors affecting seed removal by large rodents in a West African woodland

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