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DIPLOCHORY IN NORTHERN NIGERIA: YOU CAN'T PREDICT DISPERSAL OF SEED BY ITS FRUIT SIZE

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ABSTRACT

Diplochory is well known to contribute to the regeneration of Neotropical forests, particularly in the context of frugivore decline. However, this phenomenon in Old World woodlands is virtually unknown. Here we contribute to our understanding of diplochory in woodland habitats experiencing frugivore loss by investigating for the first time the interaction of habitat and seed type on secondary dispersal by rodents. Moreover, our study combines information on degraded woodland (habitat), organism (Scatterhoarding rodent) and large seeded species dispersed by frugivores. We established seed 'dumps' to simulate frugivore dispersed seed in each of three woodland - habitats Yankari Game Reserve, Kanawa woodland, and Nafada degraded woodland. We quantify how degradation and seed size interact to affect the balance between predation and dispersal. We distinguish between burial and cached seed. Bayesian statistics was used to compare predation rates and proportion of seed i) buried and ii) cached in each habitat, large and small seeded species were used. Infra-red cameras were established 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 species than for the small seeded species. The probability of scatterhoarded 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 Old World 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 small seeded species. Seed burial is more common than caching across all habitats and dispersal is markedly higher in Reserve than disturbed or degraded woodland. Our findings should stimulate a new area of research into Old World plant-animal mutualisms.

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

INTRODUCTION

Tropical woodland are facing a seed dispersal crisis (McConkey *et al.* 2012) as dispersal networks are destroyed through anthropogenic drivers such as habitat degradation, fragmentation and hunting. Such changes affect woodland composition and structure (Peres *et al*. 2003; Nuñez-Iturri & Howe 2007; Wright et al. 2007; Vanthomme, Bellé & Forget 2010) for example, regenerating woodlands tend to have a higher proportion of wind dispersed species than their ancestral populations (Vanthomme, Bellé & Forget 2010). Anderson *et al*. (2011) provide evidence for the decline in native bird species in New Zealand having already led to insufficient seed dispersal and vastly reduced recruitment of native tree species, which the authors suggest could trigger a cascade of extinctions. Until recently such negative effects of years of inadequate dispersal have been masked by the long generation time of woodland tree species (Guimaraes, Galetti & Jordano 2008) but insufficient seed dispersal is now recognised as the major threat to the future of many types of woodland (Schupp 1993; McConkey *et al*. 2012).

Up to 70% of tropical woodland 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 & John Kress 2011). Without animal dispersers many tropical woodland 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 & Beck 2010). Tree species with large fruit are most at risk because they depend on large bodied frugivores for dispersal (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 & 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 & 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 2005). This behaviour will depend on the relative abundance of seed versey scatterhoarder density and the advantage to a seed of being cached verse left on the forest floor (Jorge & Howe 2009).

Despite the potential importance of scatterhoarding to seed dispersal in tropical woodland it has rarely been quantified. While several cases have been described in the Neotropics

(Forget & Milleron 1991; Forget 1992; Forget 1993), only a few investigations cite the probability of seed fate in terms of predation verse caching and/or burying (Feer & Forget 2002; Jorge & 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 & Kruger . 2012).

The overall aim in this study is to determine the extent to which secondary seed dispersal by rodents is affected by habitat degradation. To do this the extent to which seeds deposited by frugivores onto the forest floor are then secondarily moved (i.e. diplochory *sensu*) (Vander Wall & Longland 2004) by rodents to sites with more suitable conditions for germination was investigated (Vander Wall 1990; McConkey & Brockelman 2011). How this behaviour varies with a) seed characteristics and b) habitat in terms of increasing degradation was determined.

One large seeded (> 20 mm in diameter) and one small seeded (<10 mm) tree species with different palatability to rodents were chosen. We investigate the fate of these seeds over three woodland habitats (i.e. from Reserve habitat through woodland slightly degraded to extremely degraded one) was investigated. Ihuma *et al*. (2011), report that forest/woodland 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 was hypothesise that predation rates will be markedly higher in *Detarium microcarpum* (Guill. & Perr.) a large seeded than *Diospyrous mesfiliformis* (Hochst. ex A. DC.) a small seeded species.
2. Consequently, it was hypothesised that caching and burying rates (seed dispersal) combined will be higher for small seeded species.
3. Seed dispersal Network will be less strong in degraded/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 *D. microcarpum* a large seeded species.

MATERIALS AND METHODS

Study Site

Our study site were Yankari Game Reserve (9^o 50’ N and 10^o 30’E) Bauchi, Bauchi State, Kanawa woodland (between 10^o 16’ 30’’ N and 10^o 18’ 32’’ N and 11o 18’ 32’’ E and 11^o 18’ 34’’ E) and Nafada (9^o 31 N, 11’ 3^o E) Gombe State, northeast Nigeria. Yankari Game Reserve is 2,242 km^2 in area, it is the largest area of woodland in Bauchi State (Bauchi Native Authority, 1945). The Reserve lies at 400-600 m elevation.

Kanawa lies at 350-368 m a.s.l., the size of the woodland is about 41hectares (Gombe Native Authority, 1945) the black soil is good for a rapid growth of tree species. and Nafada (9^o 31 N, 11’ 3^o E), the Reserve lies at 200-300 m elevation and are affected by annual grass burning, cattle grazing and logging. Three obvious differences among the habitats we studied (Yankari Game Reserve, Kanawa and Nafada); from here on referred to as YGR, 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. & Perr) and *Diospyrous mesfiliformis* (Hochst. ex A. DC.) are common in YGR. *Diospyrous mesfiliformis* is common in KNW and NFD degraded woodlands (unpublished data, B. Aliyu).

The mean annual rainfall in YGR, KNW and NFD is approximately 1400 mm, 1200 mm and 1200 mm respectively (Yankari weather station, 2015 and Gombe State metrological rainfall data, 2015). And the mean monthly maximum and minimum temperatures for the wet and dry seasons are 34 and 20^{o}C, and 38 and 26^{o}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 (*Pan troglodytes 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) (Chapman, Olson & Trumm 2004).

Study Species

For our investigation we chose *Detarium microcarpum* a large seeded and *Diospyrous mesfiliformis* a small seeded species with similar flowering and fruiting phenology and primary dispersal agents.

Detarium microcarpum is a small tree that grows up to 15 m in height. It produces yellowish fruit when ripe, with 1 cm of greenish mealy pulp, fibrous and sweet, (indehiscent drupe-like pod) 2.5–4.5 cm in diameter. Seed size is 15–20 mm x 6.5–8.5 mm. *Detarium microcarpum* family Caesalpiniaceae is one of the species which is used in many different ways through all west tropical Africa; it is utilized for its timber, as fuel wood, food source (seeds, leaves and roots) and to treat 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. The bark leaves and roots are widely used because of their diuretic and astringent properties. They are also used against malaria, leprosy and impotence.

Diospyrous mesfiliformis (Ebenaceae) produces fleshy fruit of approximately 3 cm in diameter and contain 4-6 seeds. Seeds, dark brown, bean-shaped shiny and glabrous. x 41 (± 0.71) mm with three or four seeds measuring 28.4 (0.43) mm x 26.5 (± 0.38) mm in length. 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. mesfiliformis* 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. Microcarpum* is soaked and the endocarp is thrown, many fruit were observed sucked by primates, with seeds accumulating on bare ground under parent tree or primates roosts (Chauvet, Feer & Forget 2004; Feer & Forget 2002; Forget 1991).

Ebenaceae and Caesalpiniaceae plant families are a preferred source of fruit in the diet of World primates and thus act as key dispersers for a range of seed size (Fujita & Tuttle, 1991). The tree is widely distributed in dry Savannah areas of Africa, and in Sudan it is found in Darfour, Blue Nile and Kordofan States, where it is locally known as Abu-laili in Sudan, 'dank' in Senegal and 'tamba dala' in Mali. Overall, seeds measuring 1 mm up to 7 mm are ingested and defecated during movement or 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 members this family (Caesalpiniaceae) fruit and seeds were found in the faecal sample and under feeding roosts, of 5 monkeys species. among them the two Olive baboons present in YGR.

Experimental Design

Our experiment included three habitats: i) Extremely degraded woodland in Nafada (NFD), ii) Degraded woodland in Kanawa (KNW) which was within 100 m of the grassland and iii) Yankari Game Reserve (YGR) located in Bauchi. 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 simulating primary dispersal of our key species (frugivores).

Within the grid, each seed was marked with a one meter long white nylon thread following the method of Forget (1990) to aid us in finding them. As the seed coat of *D. mesfiliformis* 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 three (3) and seven (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).

The experiments were repeated two times, on the 27th April 2016 and 7th May 2016 for each species.

Infra-red motion detector cameras (Spy point IR-6) were attached to trees above the plots to determine which rodent genera were predating/dispersing the seeds.

Data Analysis

We were 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 & Hill 2007). Bayesian inference is based on testing hypotheses of probability distributions and is increasingly used in ecology (Ellison 2004), see McCarthy (2007) for an introduction to Bayesian methods in ecology.

We 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) affected fate. We fitted one mixed effect 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) (Table 2). 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 (fig. 2).

We fitted another mixed effect 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 images taken by the infra-red cameras 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 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 in each habitat is presented in Table 1. The probability of any recovered seed being predated, cached, buried or missing after 3 and 7 days, as predicted from the mixed effects logistic multinomial regression model is presented in Figures 1 and 2. As the conclusions drawn from day 3 and day 7 census were very similar, from here on in this paper we discuss the results for day 7 only.

Table 1: The fate of the recovered seed in each habitat after day 3 and day 7

Habitat	species	Day	Predated	Cached	Buried	Missing	TOTAL
YGR	*Diospyrous*	3	8	24	44	23	99
	Diospyrous	7	8	14	29	17	68
	Detarium	3	18	32	17	17	84
	Detarium	7	22	27	40	28	117
KNW	*Diospyrous*	3	18	15	40	27	100
	Diospyrous	7	16	3	31	25	75
	Detarium	3	43	8	28	17	96
	Detarium	7	39	3	33	44	119
NFD	*Diospyrous*	3	29	18	54	45	146
	Diospyrous	7	21	0	23	13	57
	Detarium	3	60	5	26	31	122
	Detarium	7	36	0	21	27	84
TOTAL			318	149	386	314	1167

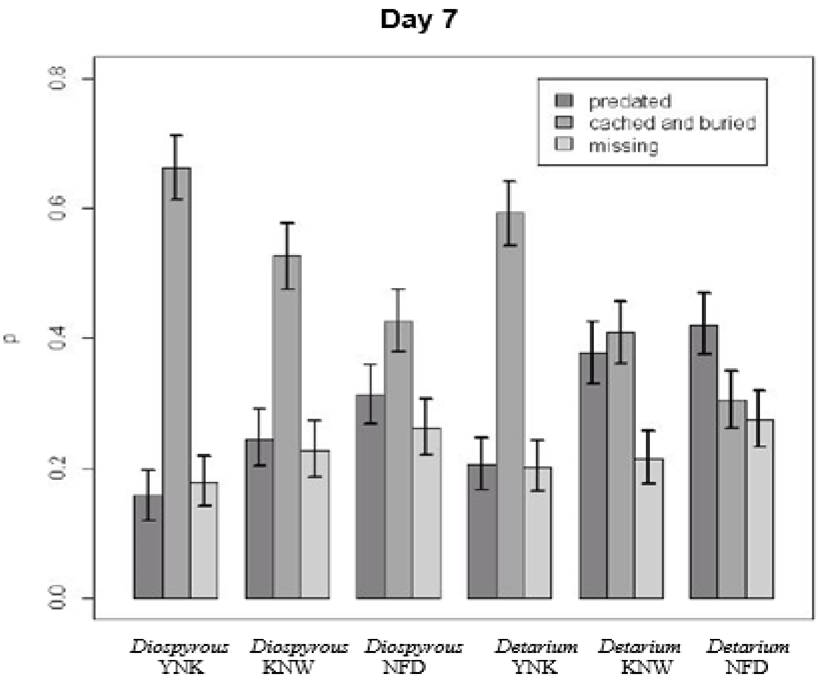

Figure 1: The fates of seeds in the three habtats.

Predation rates

Detarium microcarpum seeds had a higher probability of being predated than *D. mesfiliformis* seeds in all three habitats but especially in the NFD and KNW (ΔDIC=80.3) (Table 2). 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 (ΔDIC=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 *Diospyrous mesfiliformis.*

Table 2. Estimated posterior means and 95% CIs for the probability of being predated by habitat type and species

Species	YGR	KNW	NFD
Diospyrous	0.59 (.54,.64)	0.47 (.42,.51)	0.42 (.37,.47)
Detarium	0.57 (.53,.62)	0.40 (.36,.45)	0.30 (.26,.35)

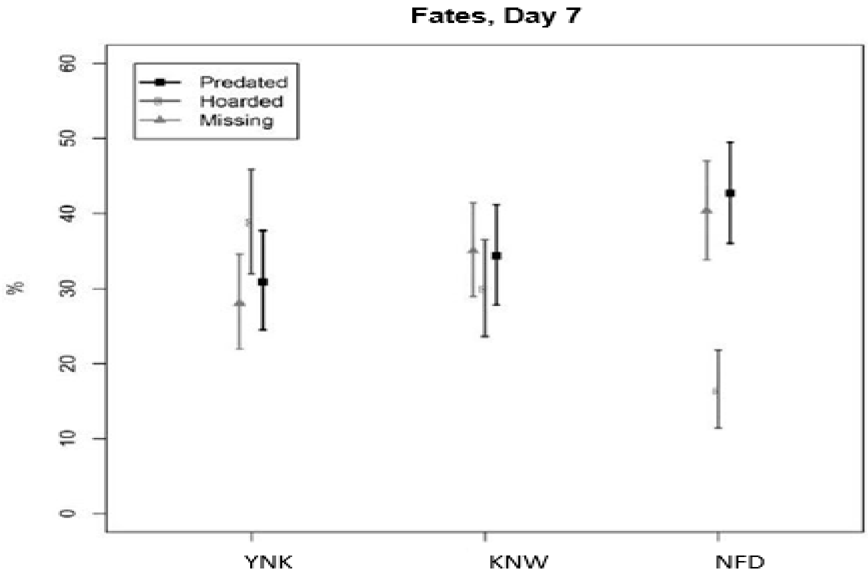

Figure 2: The fates of seeds in the three habitats

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. mesfiliformis* than in *D. microcarpum* across the three habitats (ΔDIC=1719) (Table 1). 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. mesfiliformis* YGR P=0.0439; KNW P<0.0001 and NFD P<0.0001 (Table 1).

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 interplay 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 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 & Forget, 2002). To date research into diplochory in African woodlands has been minimal (Nyiramana *et al*. 2011; Midgley, Gallaher & Kruge 2012; Aliyu *et al*. 2014), yet African woodlands are just as vulnerable as Neotropical forests to degradation. The results of our study strongly supported two of our three original hypotheses i) that irrespective of habitat,